BEING AT THE RIGHT TIME AT THE RIGHT PLACE

interpreting the annual life cycle of Afro-Siberian red knots

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BEING AT THE RIGHT TIME AT THE RIGHT PLACE

interpreting the annual life cycle of Afro-Siberian red knots

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Chapter 1

General Introduction

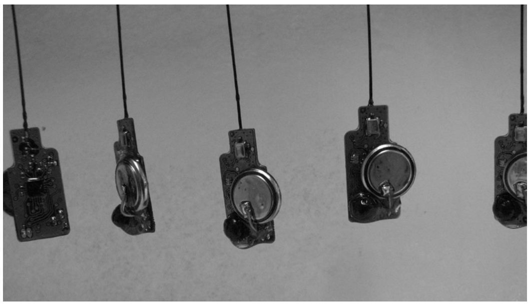
Jutta Leyrer

Shorebirds from the High Arctic tundra spend the nonbreeding season thousands of kilometres away, and therefore face an extremely challenging task: They need to arrive in their arctic breeding grounds at the optimal time to take full advantage of the short summer. There is only limited time to raise chicks before food supplies decline again and breeding conditions (e.g. the onset of snowmelt) can be quite variable from year to year (Drent et al. 2003, Tulp 2007). After the breeding season, adults need to be able to accomplish their return migration and juveniles their first southward migration to the wintering grounds. Subsequently, often right after the return to the wintering grounds, preparations for northward migration to the arctic have to be scheduled accurately for an optimal spring arrival. In the case of Afro-Siberian red knots *Calidris c. canutus*, the wintering grounds are in West Africa, thousands of kilometres and months away from their Siberian breeding grounds.

Studies in passerines and shorebirds have shown that individuals that spend the nonbreeding period in habitats of high quality also occupy breeding habitats of high quality, and have a higher breeding success (Marra et al. 1998, Gill et al. 2001, Gunnarsson et al. 2005a, 2005b, Studds & Marra 2005). There is thus evidence that habitats used by migratory birds throughout the year are linked (Webster et al. 2002) and that events that birds encounter in one habitat/one season have an influence on what may happen in subsequent habitats/seasons (Norris 2005, Harrison et al. 2010). These so-called ‘carry-over effects’ affect the trajectory between seasons, e.g. between wintering and breeding, but also have knock-on effects that may carry over in subsequent years. For example, successfully reproducing geese were constrained by their accompanying less efficiently foraging young in choosing high quality foraging habitat in the subsequent winter, whereas unsuccessful geese did not face that problem (Inger et al. 2010).

When an invention does not work (yet) – and established methods (still) work best

The breeding grounds in the circumpolar High Arctic are vast and difficult to access, which makes studies of the breeding ecology of arctic-breeding birds a challenge. Collecting detailed data on the breeding biology of red knots is rather difficult, because they breed in the very High Arctic and in low densities (Piersma & Davidson 1992, van de Kam et al. 2004, Piersma et al. 2005). Also, shorebirds do not spend the nonbreeding season in family groups as geese do, therefore estimates of (individual) breeding success in the nonbreeding areas cannot be obtained. The key goal of this project initially was to develop and apply a novel generation of archival geolocator tags (GAT) in close cooperation with the Laboratory of Ornithology, Cornell University, Ithaca, USA. The new GATs would be equipped with a transmission unit to enable remote downloads of the data. This would render both the recapture (basically impossible in my study system), and the manual removal of the tag for data reading, unnecessary.



With data on the whereabouts of the red knots away from the Banc d'Arguin we would have been able to merge data on the timing of migration with subsequent survival and an index of breeding success (gauged by looking at the timing of departure from the arctic, as unsuccessful males will leave the arctic earlier than successful breeders (Tomkovich & Soloviev 1996)). Exciting research happens when (technological) frontiers are pushed, but developing new cutting-edge technology is not always straightforward and immediately successful, and the technical difficulties encountered during this project, have not allowed me to achieve success yet with the GATs.

A well-established low-tech and lower-cost method to follow individuals is to mark them with an individually recognisable combination of colour rings that can be read from a distance using binoculars or telescopes. Because colour rings stay with an individual for many years if not for as long as it lives, they not only allow us to study individual spacing behaviour at a site but also enable us to calculate return rates and ultimately survival estimates. The way individual birds adjust their spatial relationships to conspecifics, competitors, predators, food and other features of their environment represents predictable responses to ecological and evolutionary processes (Myers 1984). To continuously follow colour-ringed migrants throughout the year is not possible, especially when working with intercontinental migrants like red knots that prefer to stay well away from human populations whenever possible. Yet, we were in the lucky position to work on a highly site-faithful study population at Banc d'Arguin which allowed us to follow a single population during the year for several years in a row. Using mark-resighting data collected for more than one thousand individually marked red knots at Banc d'Arguin during the past eight years allowed us to shed some light into individual spacing behaviour and site use during the wintering period and resulting fitness costs. Furthermore, we could begin to unlock the black box of survival differences between seasons. Benefitting from expeditions to Banc d'Arguin prior and after the migration and breeding seasons, originally planned to apply GATs and retrieve the data, we could collect resighting data of colour-ringed red knots of a single population at different times in the year and thus split annual survival estimates into the different seasons.

Setting the scene – migration in a nutshell

In seasonal environments, migration can be a fitness-maximizing strategy (Fretwell 1972, Alerstam 1990). Migratory animals have to trade-off benefits from moving to a more favourable environment and the costs of leaving a familiar place. For example birds that migrate into arctic environments during the northern summer will benefit from a rich food abundance and long days to successfully raise their offspring (Schekkerman et al. 2003). Likewise, leaving the High Arctic during the nonbreeding season birds will find more favourable climatic and foraging conditions further south and will therefore maximize the probability to survive the winter. Long-distance migration allows arctic-breeding birds to exploit resources during times of high productivity and over large geographic areas within the annual cycle (Alerstam 1990). Yet, to successfully master such migrations, the birds require suitable habitats along the way in order to fuel up, i.e. to harness the energy subsequently spent in flight. Migration is time-consuming and dangerous, and it also consumes a great deal of energy.

North- and southward migration is estimated to comprise up to 50% of the annual energy budget (Drent & Piersma 1990), with the majority of energy and time spent on the ground foraging for fuel deposition (Hedenström & Alerstam 1997, Lindström 2005). Foraging rates determine fuelling rates, and therefore greatly influence the speed of migration (Hedenström & Alerstam 1997, Piersma et al. 2005). Especially during northward migration and in the arctic, where summers are short and birds that arrive late may not be able to reproduce successfully (Drent et al. 2003), the timing of arrival in the breeding grounds is crucial.

The study system

The red knot is a true long-distance migrant and has fascinated many amateur and professional biologists around the globe for decades. It is therefore one of the best studied migrants. The red knot is a relatively small shorebird species but is capable of performing non-stop flights of several thousand kilometres (Piersma & Davidson 1992, Piersma 1994, Piersma et al. 2005). One of the six recognised subspecies (Tomkovich 1992, 2001), the Afro-Siberian red knot *C. c. canutus*, breeds in central Siberia on the Taimyr Peninsula (Tomkovich & Soloviev 1996) and spends the wintering season along the West African coast, with ca. 75% of the population wintering at Banc d'Arguin, Mauritania (Piersma et al. 1992, Davidson & Piersma 2009). The majority of these birds perform their northward migration from the Banc d'Arguin in two long-distance flights of more than 4,000 km each, via the major staging site in the European Wadden Sea. During the second half of May to early June most of the Afro-Siberian red knots replenish their energy reserves in Schleswig-Holstein, Germany, part of the Wadden Sea (Prokosch 1988, Piersma et al. 1992), though some regularly stop over in the Vendée area, French Atlantic coast (Piersma et al. 1992) as well. From late May until the first days of June flocks of hundreds of red knots can be observed leaving the Wadden Sea in north-easterly directions, arriving in their Siberian breeding grounds on the Taimyr Peninsula starting on 10 June (Tomkovich & Soloviev 1996).

Females leave the arctic breeding areas first, soon after the clutch has hatched, leaving the males behind to raise the chicks. Males will leave as soon as the chicks have become independent, leaving the chicks alone for their first journey south (Tomkovich & Soloviev 1996). When the clutch has been depredated males may leave earlier. While females have been observed fuelling in the Dutch Wadden Sea in late July and early August for their migration further south (Nebel et al. 2000), males are not known to stop anywhere during southward migration. The first adult red knots arrive at Banc d'Arguin as early as mid-August (own unpubl. data).

Outside the breeding areas, red knots are obligate visitors of marine intertidal soft-sediment environments, where they forage and fuel on shellfish. They find their buried prey with special sensory organs in their bill tips (Piersma et al. 1998), and upon encounters they swallow the prey whole, crushing them with their muscular gizzard. Because not only the digestible flesh but also the indigestible shell (bulk material) is ingested, red knots are digestively constrained (they have to get rid of the bulk material from time to time before they can continue foraging), and fuelling rates are thus not only dependent on prey encounter rates but mainly on the quality of the shelled prey, i.e. the thinner the shell, the better (van Gils et al. 2005c). The gizzard is flexible though, and can be adjusted to meet the requirements, but only to a certain degree, because building up and maintaining muscles is costly. Additionally, there is evidence that migratory birds minimize the organs they do not use for locomotion during flight (i.e. gizzard and other digestive organs). These organs have to be rebuilt after arrival at a fuelling site prior to fuelling (Piersma & Gill 1998, Battley et al. 2000).

Timing of migration and carry-over effects

Migrants attempt to schedule their migration such that they arrive in their breeding areas at the optimal time, when the peak of food availability matches the chick-rearing period (Both & Visser 2001, Schekkerman et al. 2003, Both et al. 2010). Long-distance migrants generally use chains of fuelling sites at which they accumulate the stores needed for the next leg of their migration. Closer to the breeding grounds, these necessary stores may include not only the energy for flight but also the nutrients needed for the production of the first egg and for survival during the first days after arrival in the breeding grounds when climate conditions may not allow foraging (e.g. snow and ice cover in the arctic) (Klaassen et al. 2001, Morrison et al. 2007). Hence, the conditions that migrants face during fuelling influence survival upon arrival at the breeding grounds and potentially breeding success. Furthermore, successful reproduction can sometimes be influenced strongly by the wintering areas, as the quality of the winter habitat often decides whether the birds will end up in a high or a low quality breeding site (Marra et al. 1998, Norris et al. 2004, Gunnarsson et al. 2005a, 2005b). In **Chapters 2 and 3** I report on our studies of spacing behaviour and site choice in wintering red knots at Banc d'Arguin, and I discuss our results in the light of foraging habitat quality and survival consequences.

Red knots leave the Banc d'Arguin in the beginning of May and are thus one of the last shorebird species to start migrating north from this area (Piersma et al. 1990a). Meteorological conditions, such as wind, often trigger the onset of migration (Schaub et al. 2004, Shamoun-Baranes et al. 2006, Gill et al. 2009) and overall wind conditions en route may have a great impact on flight, migratory route, and timing (Liechti 2006). Yet, from their take-off site, red knots at Banc d'Arguin have no means of judging wind conditions further along their flight path (Piersma et al. 1990a, Piersma & van de Sant 1992). In **Chapters 4 and 5** we evaluate the influence of wind on migration speed from West Africa to the key stopover site, the Schleswig-Holstein Wadden Sea and discuss potential costs and benefits of using an intermediate staging site on the French Atlantic coast when wind conditions en route are unfavourable.

The Wadden Sea, in Schleswig-Holstein, Germany, is the key staging area of Afro-Siberian red knots during northward migration (Prokosch 1988, Piersma et al. 1992). Especially during northward migration, when energy stores have to be built up in a short time, red knots should favour foraging sites offering high quality prey in order to keep the gizzard as small as possible (Piersma et al. 2003a, van Gils et al. 2003, 2005c), and in **Chapter 6** we describe the large-scale distribution of macrozoobenthos communities in the Schleswig-Holstein Wadden Sea.

Observing the departure of large flocks of birds for migration is an impressive spectacle, which so far has been described to happen in the evening hours just before sunset, even in species that have a tidal rather than a diurnal rhythm (Piersma et al. 1990b). In **Chapter 7** we describe a departure event that took place at 'odd hours', during the morning. We discuss the significance of this observation in relation to timing of migration and consider whether morning departures could be a potential strategy to avoid predation pressure.

In **Chapter 8** we discuss the distribution of mortality throughout the year, by considering how survival probabilities might vary between different stages of the annual cycle. Although migration has been regarded as an energetically demanding (Drent & Piersma 1990) and even dangerous (Newton 2007) period, other events such as breeding or moult may entail survival costs as well. With our observations, we also challenge the notion that tropical marine non-breeding habitats provide benign environments for long-distance migrants such as the red knot.

In **Chapter 9** I discuss the timing of fuelling and fuelling rates in northward migrating red knots, and introduce a conceptual framework for how the new findings of this thesis together with existing knowledge might be implemented in an annual routine model.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Chapter 2

Small home ranges and high site fidelity in red knots (*Calidris c. canutus*) wintering on the Banc d'Arguin, Mauritania

Jutta Leyrer, Bernard Spaans, Mohamed Camara & Theunis Piersma

Abstract

Using automated and manual radio-telemetry and resightings of individual colour-ringed birds, we assessed the daily use of space of red knots *Calidris canutus canutus* at a tropical wintering area along the Sahara coast, the Banc d'Arguin in Mauritania. Confirming earlier suggestions, we found that birds were very faithful to their roosts and that the daily foraging range was small; in the course of several winter months birds used an area only of 2 – 16 km^2 of intertidal area. We found no differences between their movements in daylight and at night. Additionally, individuals seem to return to exactly the same locations in subsequent winters. This pattern is very different from red knots wintering in the temperate Wadden Sea. Here they readily change roost sites and easily cover areas of about 800 km^2 in the course of weeks, but just as in Mauritania, no differences between day and night are apparent. In northern Patagonia and north-western Australia red knots have range sizes closer to those on the Banc d'Arguin, but here they do show differences in space use between day and night. Ecological explanations for these contrasting patterns require further comparative data based on in-depth studies on the predictability of the food base and the presence of diurnal and nocturnal predators.

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Introduction

The way individual birds adjust their spatial relationships to conspecifics, competitors, predators, food and other features of their environment is fundamental to an animal's ecology. Spacing behaviour comprises a broad class of behavioural variability across spatial scales as small as individual distances within a flock, to the global scales embodied by annual migrations (Myers 1984). Shorebirds are a particularly interesting group of birds on which to study space use as they are highly visible in the open habitats that they usually live in. Myers (1984) started to develop a comparative approach to spacing behaviour in nonbreeding shorebirds. He stated that spacing behaviour represents predictable responses to ecological and evolutionary processes. Traditionally, studies on spacing behaviour have focused on individuals at the local level, showing how behavioural traits such as territoriality, flocking behaviour, aggressiveness, and roost dispersion are adjusted to foraging opportunities, levels of raptorial predation, and other environmental conditions (c.f. Myers et al. 1979, Piersma et al. 1993b, Cresswell 1994, Whitfield 2003, Bednekoff & Lima 2004).

This study is inspired by Myers' (1984) comparative approach aimed at an evolutionary understanding of inter- and intraspecific variation of time- and space-use in nonbreeding shorebirds. In this paper we limit ourselves to a study of contrasting space use patterns in a single species, the red knot *Calidris canutus*. Red knots are a suitable study species, as they always occur in coastal habitats, almost always use bivalves as their staple food, yet winter at a wide range of latitudes on all continents except Antarctica (Piersma & Davidson 1992, Piersma et al. 2005). Additionally, although separate flyways are inhabited by morphologically distinct subspecies, their genetic variability suggests that these subspecies are very closely related and have a very recent, post-Pleistocene, origin (Baker et al. 1994, Buehler & Baker 2005, Buehler et al. 2006). This would mean that comparisons between subspecies and flyways are not hampered by deeply rooted genetic differences.

Extensive earlier work in the Dutch Wadden Sea and preliminary colour-ringing studies on the Banc d'Arguin, Mauritania, two major wintering sites on the East Atlantic Flyway, have provided evidence that spacing behaviour of red knots during the non-breeding season shows considerable differences between the two sites (Piersma et al. 1993b; figure 2.1). Home ranges of red knots in the temperate Wadden Sea cover an area of around 800 km² in several weeks (van Gils & Piersma 1999, van Gils et al. 2000, 2005b), whereas home ranges of red knots wintering on the tropical Banc d'Arguin were suspected to be as small as 10 – 15 km² (Piersma et al. 1993b). Interestingly, there are also strong differences in the fuelling rates of birds during northward migration, with red knots in tropical areas, including the Banc d'Arguin, consistently fuelling at lower rates than birds further south or north (Piersma et al. 2005). All these differences suggest the importance of specific ecological conditions in otherwise quite similar coastal intertidal areas shaping the movements and performance of shorebirds in space and time. Using telemetry and colour-ringing we here document home range size and site fidelity within and among years of red knots on the Banc d'Arguin, Mauritania.

Methods

Study site

Twenty birds were captured at night with mist nets at two main roost sites near Iwik, Banc d'Arguin, Mauritania, West Africa, on 17 December 2003 (see figure 2.2a). Four of them (#1-#4) were caught at a high tide roost in the north-western part of Baie d'Aouatif (19°54'N 16°17'W), whereas 16 individuals (#5-#20) were caught at the high tide roost at Abelgh Eiznaya (19°54'N 16°19'W). All birds were released at the beach in the southwest of the Baie d'Aouatif but returned to their original roost site at the latest two days after the catch (figure 2.3). For the analyses, the timing of the tides at Iwik were calculated on the basis of predicted times for high and low tide for Dakar, Senegal (Admiralty Tide Tables (ATT), Vol. 2 Europe (excl. UK and Ireland), Mediterranean Sea and Atlantic Ocean), with both high and low tide on average five hours later in Iwik than in Dakar (Smit *et al.* 1989, Wolff & Smit 1990). Day and night were separated by morning and evening civil twilight, and time of civil twilight was calculated after Burnett (1999).

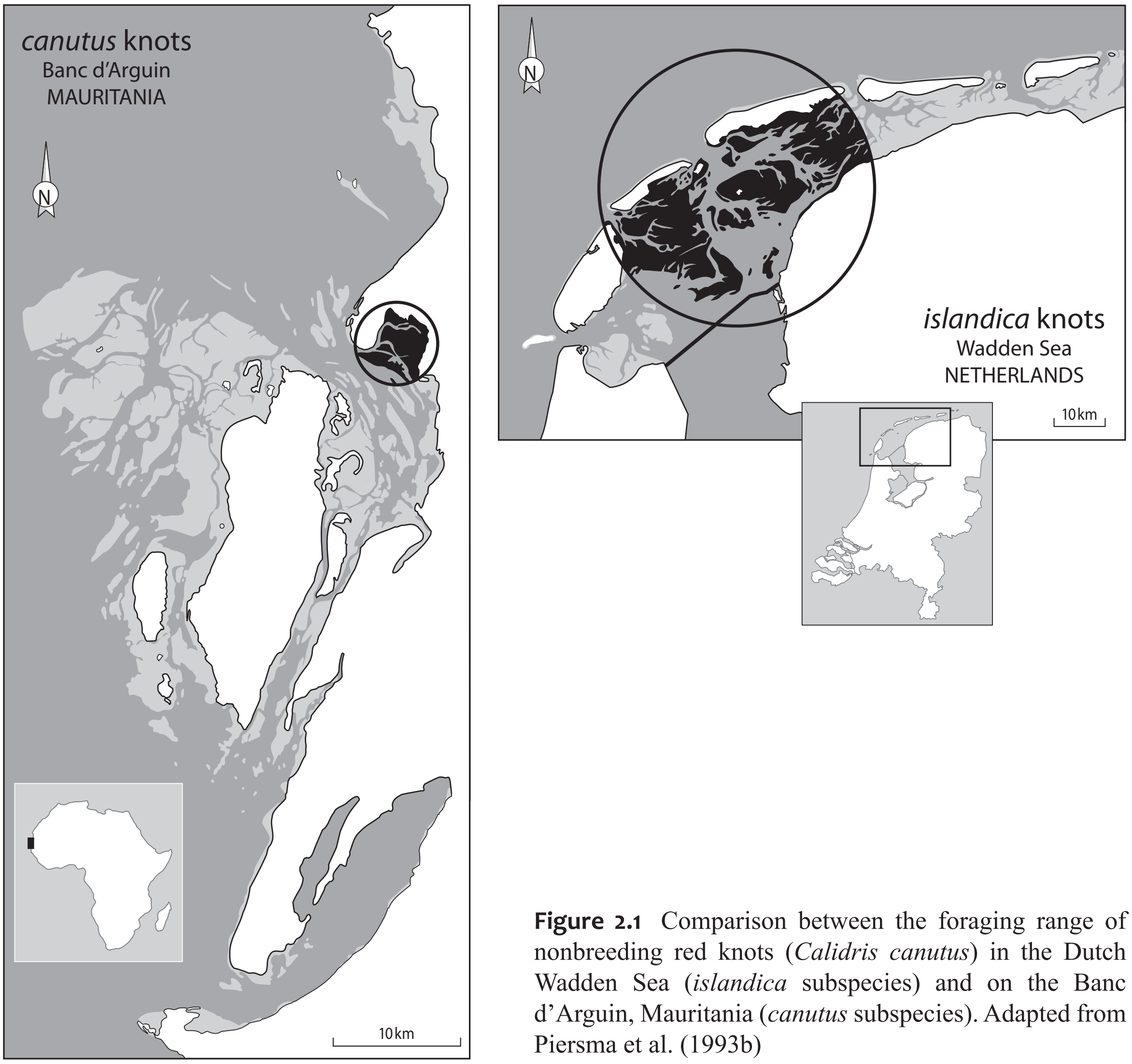

Figure 2.1 Comparison between the foraging range of nonbreeding red knots (*Calidris canutus*) in the Dutch Wadden Sea (*islandica* subspecies) and on the Banc d'Arguin, Mauritania (*canutus* subspecies). Adapted from Piersma et al. (1993b)

Biometric data and radio-telemetry

All birds were ringed with a metal ring from the Dutch ringing scheme and an individual combination of four colour-rings and a red leg flag (see Piersma & Spaans 2004). Birds were aged according to Prater et al. (1977), distinguishing hatch-year old birds (1^{st} calendar year or cy), born the year before (2^{nd} cy) and older birds (adults). Standard biometric data were collected. Additionally, a drop of blood was collected from the brachial vein and stored in 95% ethanol. Using a standard molecular assay verified for red knots (Baker et al. 1999), we determined sex of all transmittered birds. Using superglue, small 1.8 g transmitters (BD2; 173 Mhz, guaranteed lifetime of 6 weeks; Holohil Systems Ltd., Carp, Ontario, Canada) were attached to trimmed back feathers and the underlying skin (Warnock & Warnock 1993, Nebel et al. 2000). Radio signals were collected by two 24h operating automated radio tracking stations (ARTS), supplemented by regular checks with mobile antennae and receivers. The ARTS (Telemetrics, Arnhem, The Netherlands; see Green et al. 2002, Battley et al. 2004) were erected at Abelgh Eiznaya and Baie d'Aouatif (figure 2.2a) and were operating constantly from 18 to 27 and 28 December 2003, respectively. Each bird was scanned every 6.6 min. This receiver set-up recorded signals within a 1-km radius (van Gils et al. 2000, 2005b, Battley et al. 2004).

During the time that the automatic stations were operating signals were received from 14 individuals. For day and night time calculations only days with full 24h recordings were included. Tide related patterns of roost use were calculated by dividing all signals received by the ARTS per hour by all signals that could possibly be received from the three (Baie d'Aouatif) and 11 (Abelgh Eiznaya) tagged individuals at Baie d'Aouatif and Abelgh Eiznaya, respectively, in the given hour.

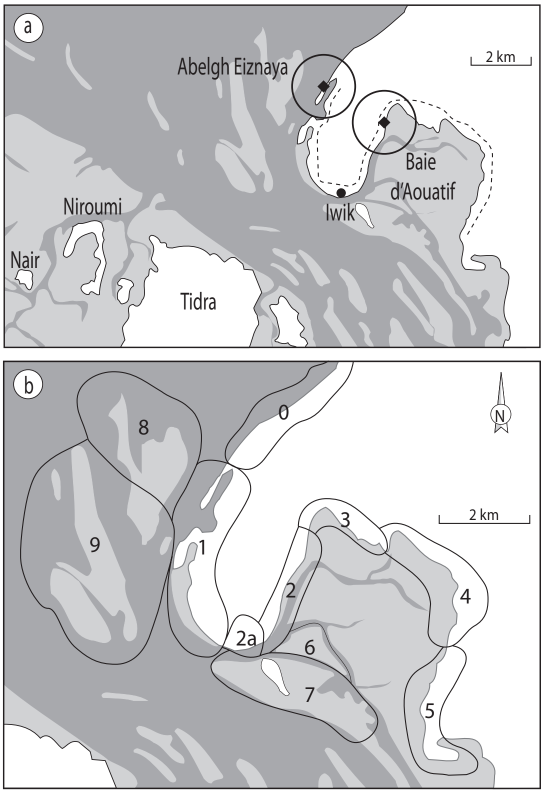

Figure 2.2 a Map of the study area in the north of the Parc National du Banc d'Arguin, Mauritania. Squares indicate the position of the two automatic radio tracking stations (ARTS) at the main high tide roosts at Abelgh Eiznaya and Baie d'Aouatif. Signals could be received by the ARTS within a range of a 1-km radius (circles). The dotted line indicates the area scanned regularly with portable receivers from December 2003 to April 2004. **b** Close-up of the intertidal areas around the village of Iwik (number 2a) in which previously colour-ringed individual red knots were intensively searched for in December 2004. Areas in *light grey* represent mudflats, areas in *dark grey* show water.

Parallel to the automated recordings, scans were made with portable receivers (IC – R10, ICOM) connected to a three-element Yagi antenna. From 18 to 28 December 2003 all individuals were scanned daily along the beaches surrounding Baie d'Aouatif and Abelgh Eiznaya (figure 2.2a). On 27 and 28 December a sailing trip was made to the islands of Niroumi and Nair to check for the transmittered birds (figure 2.2a). There, we regularly checked during different times of the day and all phases of the tide, but no signals were received. Additional scans using portable receivers were made in the periods 11-16 January, 27-30 January, 13-15 February, 17 March, 27 March and 20 April, all in 2004. There were no discrepancies between the automatic receiving stations and the portable receivers. In total we received signals from 17 birds until the last successful check on 15 February 2004 (figure 2.5). Thus, only three radio-tagged birds were 'lost'. Two individuals, one from each catching site, both of which were first year males with rather low body masses at capture, probably left the area and were never observed subsequent to the day of their release. The third individual that went missing was an adult female from Abelgh Eiznaya that was released after several days of nursing for leg cramp (see Rogers et al. 2004); her signals were only received for two subsequent days. However, this bird was seen back in the following year when it eventually returned to the area.

Calculating site fidelity by analysing resightings of individually colour-marked birds

During December 2004 intensive ring reading was carried out at nine different areas inside the study area around Iwik (figure 2.2b). With the help of a telescope (magnification 20x – 60x) we identified individual red knots by their colour-ring combination which could be read up to a distance of about 300m. Close to the high tide roosts flocks were scanned either when they had just left the roost or when they were about to come back. Then high numbers of birds are concentrated on a comparatively small area, yet the individuals are widespread enough to be able to check most of the birds' legs. During low tide we followed the birds to their foraging areas, either by boat or on foot. Red knots are easy to observe on their foraging grounds as it is possible to approach a flock quite close without disturbing them. Site fidelity was analysed by calculating the probability of which either an Abelgh Eiznaya or a Baie d'Aouatif ringed bird was to be seen in one of the nine areas observed. For all calculations only red knots ringed at the Banc d'Arguin before 2004 were taken into account. In Baie d'Aouatif 31 and 9 individuals and at Abelgh Eiznaya 224 and 197 red knots were ringed in 2002 and 2003, respectively. Of these ringed birds 70% were expected to be alive and return the following winters (estimated adult survival of the *canutus* knots is 0.7, B. Spaans and T. Piersma, unpubl. data). This results in a total of 21 Baie d'Aouatif captured individuals and 248 birds captured at Abelgh Eiznaya to be expected to be present in the study area in early December 2004, assuming that all birds are site faithful. Note that of the initially 20 radio-tagged birds three individuals were seen again in December 2004. Supposing an annual adult survival of 0.7 and a resighting probability of 0.4 [calculated with MARK (White & Burnham 1999), B. Spaans and T. Piersma, unpubl. data], the observation of three individuals may be a bit less than the expected five or six individuals, but does not differ significantly. And additionally, in April and May 2005 another three of these formerly radio-tagged birds were seen back in the area (B. Spaans, unpubl. data).

Results

The 17 focal birds included one 1st cy female, one 2nd cy female and two 2nd cy males, and four female and nine male adults. The mean body mass of the three focal transmitter birds from Baie d'Aouatif was 121 g (±11 SD), mean body mass of the 14 focal transmitter birds from Abelgh Eiznaya was 125 g ± 7 g (no difference between the two sites: Mann-Whitney-U-Test $p > 0.05$; $Z = -0.51$, $n = 17$). All individuals had full winter plumage and wing moult was fully completed. The three birds (two 2nd cy and one adult) of Baie d'Aouatif were all males. At Abelgh Eiznaya, there were six females (one 1st cy, one 2nd cy, four adults) and eight males (one 2nd cy, seven adults).

All but one of the 14 birds that were monitored constantly by the ARTS remained faithful to the roost site where they were caught (figure 2.3). The one exception (#19, a 2nd cy male caught at Abelgh Eiznaya) switched roosts twice between Abelgh Eiznaya and Baie d'Aouatif. After its return to Abelgh Eiznaya four days after catching, its signal was received two days later at Baie d'Aouatif for two days before it eventually returned to Abelgh Eiznaya. Results from the hand-held scans in January and February revealed further switching between the two sites as the bird was detected at Abelgh Eiznaya in mid January and back in Baie d'Aouatif in late January. At the last successful scan in mid February it was back at Abelgh Eiznaya. Most birds showed no changes in the use of roosts between day and night in either Baie d'Aouatif or Abelgh Eiznaya Eiznaya, except for two birds. One 2nd cy female (#5) used the roost at Abelgh Eiznaya more during the daylight than at the night-time high tides (Wilcoxon-Test $p < 0.05$, $Z = -2.52$, n = 8) and a 1st cy female (#6) used to roost more at Abelgh Eiznaya at night than during daytime high tides (Wilcoxon-Test $p < 0.05$, $Z = -2.52$, n = 8). We did not discover where these individuals were when out of reach of the ARTS at the roosts.

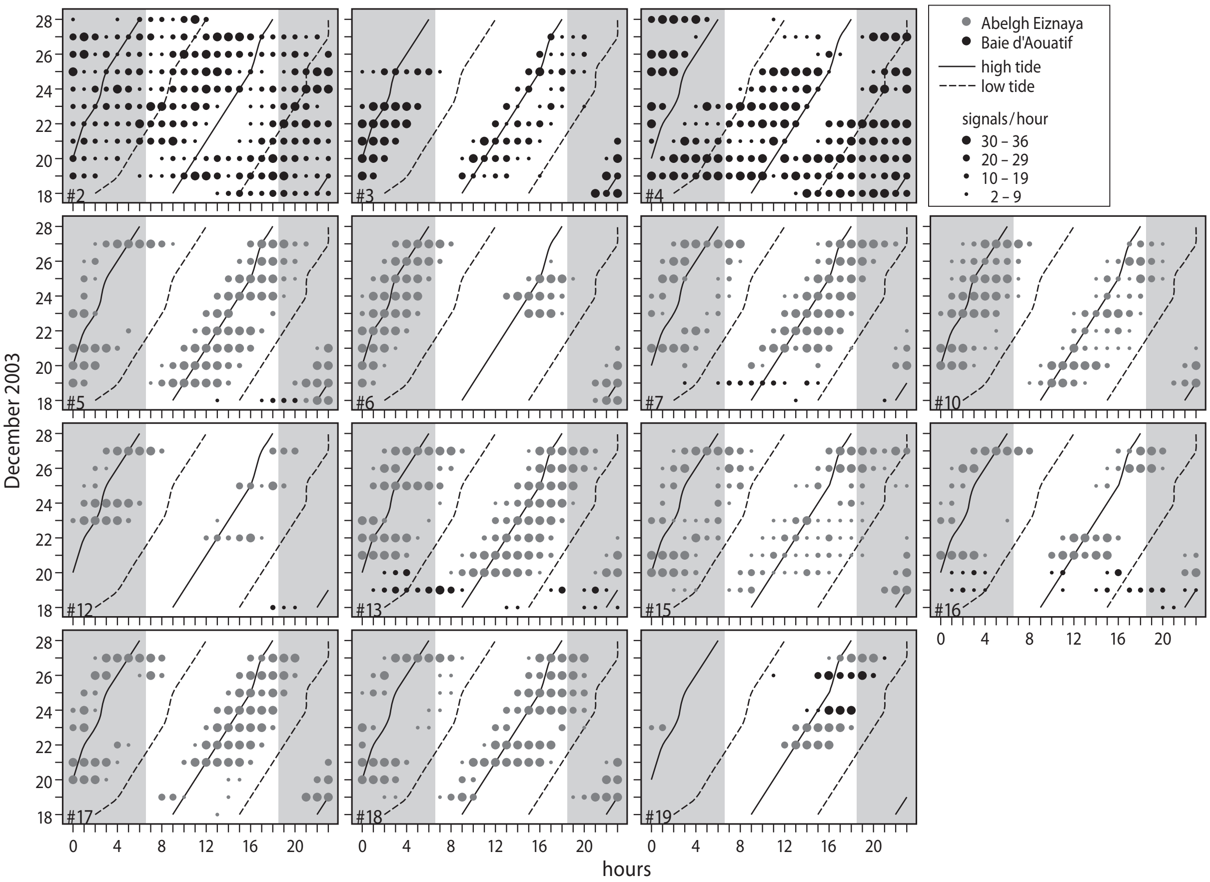

Figure 2.3 Signals received from red knots at the Banc d'Arguin from the automatic radio tracking stations in December 2003 at the two high tide roosts at Baie d'Aouatif and Abelgh Eiznaya. The dot size gives the number of signals received per hour. Knot #2, #3, and #4 were caught at Baie d'Aouatif, all others at Abelgh Eiznaya.

All 17 focal birds were detected during manual radio scans up to 15 February 2004 (figure 2.5) at their normal locations. This is already a few weeks longer than the guaranteed transmitter lifetime of six weeks. It is quite likely that birds remained in the area much longer.

In December 2004 a total of 119 individuals colour-ringed locally in late 2002 and 2003 were observed in different parts of the study area (see figure 2.2b). Of the 102 colour-ringed individuals that were seen at Abelgh Eiznaya and the adjacent mudflats (areas 1, 8, and 9 in figure 2.2b), two were originally caught and ringed at Baie d'Aouatif and 100 at Abelgh Eiznaya, representing respectively 10% (2 out of 21) and 40% (100 out of 248) of the birds ringed at the respective roost. Thus, at Abelgh Eiznaya the resighting probability of a bird caught at the Abelgh Eiznaya roost was four times higher than the probability of seeing a bird caught at Baie d'Aouatif. In the areas along the western and northern fringes of Baie d'Aouatif (areas 2, 2a, 3, and 4) the observed fraction of birds both caught at Abelgh Eiznaya and Baie d'Aouatif was about the same, with 5% of the birds originally captured at Baie d'Aouatif (1 of 21) and also 5% from Abelgh Eiznaya (13 of 248). In the Baie d'Aouatif (areas 6 and 7) the fraction of birds resighted was ten times higher for Baie d'Aouatif birds (2 of 21, = 10%) than for Abelgh Eiznaya birds (2 of 248, = 1%). As most of the resightings of individually marked birds were made close to their original catching site both in the course of one winter and between years, this suggests that red knots wintering on the Banc d'Arguin tend to return to the familiar roosts and feeding areas that they have been faithful to in previous years.

Radio-tagged red knots at Baie d'Aouatif could be detected throughout the tidal cycle, suggesting that the birds remained within a 1-km radius of the ARTS during high and low tide (figure 2.4). We thus calculated that red knots roosting at Baie d'Aouatif use an intertidal area of 1.6 km², as only half of the area inside the listening array consisted of mudflats (figure 2.2a). At Abelgh Eiznaya the birds intensively used the area inside the listening array of the ARTS during the outgoing tide, but left the 1-km radius one hour after low tide, to return to the area only one hour before high tide (figure 2.4). Although these birds left the Abelgh Eiznaya coastline, they apparently did not go as far as the mudflats surrounding the islands of Niroumi, Nair, and Northern Tidra, up to 9 - 11 km away (figure 2.2a). The observations of colour-ringed individuals in December 2004, confirmed that red knots roosting at Abelgh Eiznaya foraged on mudflats west of the roost (minimum distance to coast approx. 700 m), just outside the receiving area of the ARTS at the roost (figure 2.2b). We derived that these birds use a home range covering approximately 16 km^2 (comprising areas 1, 8, and 9, figure 2.2b).

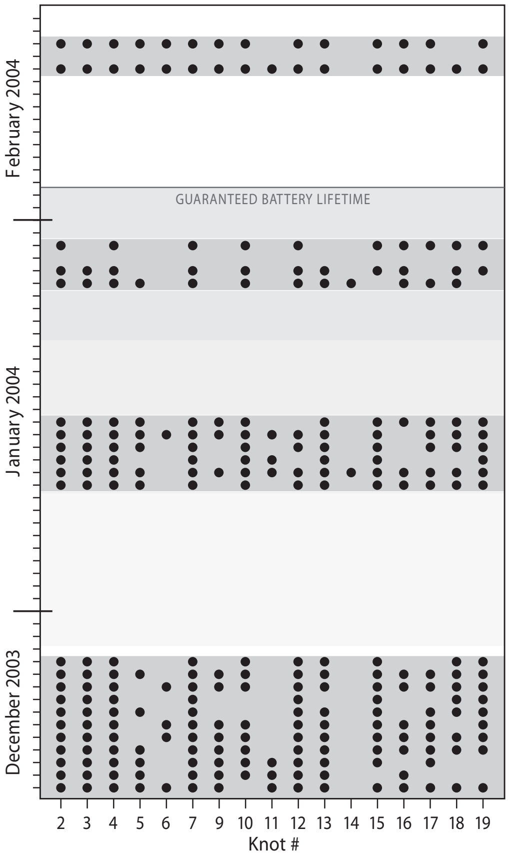

Figure 2.4 Days when signals of radio-tagged red knots were received during checks with portable receivers at the study site near Iwik, Banc d'Arguin, from December 2003 to February 2004. *Dark grey shaded areas* shwo periods when scan were made, *light grey areas* show the guaranteed transmitter lifetime. For area scanned see figure 2.2a.

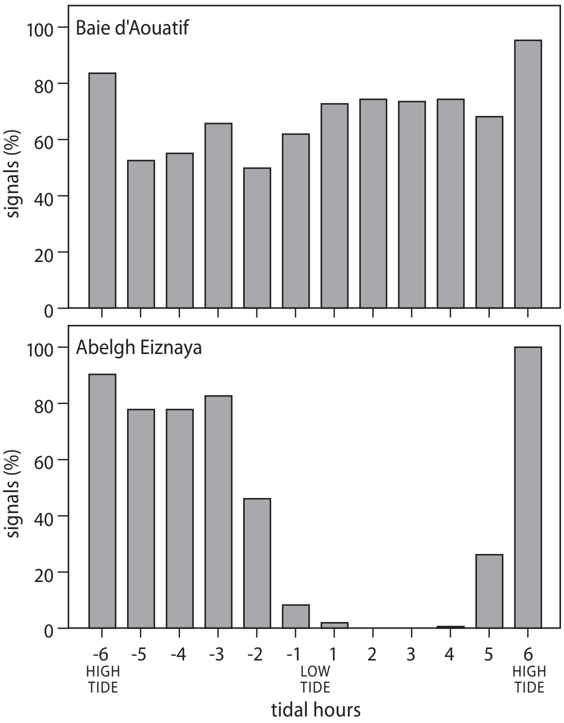

Figure 2.5 Percentages of signals received during the tidal cycle at Baie d'Aouatif (*upper graph*) and Abelgh Eiznaya (*lower graph*) as received by the given automatic radio tracking station. Percentages were calculated by dividing all signals received by the ARTS per hour by all signals that could possibly be received from the 13 (Baie d'Aouatif) and 11 (Abelgh Eiznaya) tagged individuals at Baie d'Aouatif and Ablegh Eiznaya, respectively, in the given hour.

Discussion

Red knots of the nominate *canutus* subspecies wintering at the Banc d'Arguin show a high degree of site fidelity within and between years. Moreover, as the regular detection of the birds in the area over a period of more than two months suggests, this high degree of site fidelity is sustained throughout the whole winter. In contrast to this, *islandica* red knots wintering in temperate British estuaries have shown no or only very little site fidelity between years or within wintering seasons (Symonds et al. 1984, Rehfisch et al. 2003).

The size of the area used by red knots wintering at the tropical Banc d'Arguin was 16 km² or less, much smaller than the home ranges of wintering red knots elsewhere in the world (table 2.1). For example, red knots of the *islandica* subspecies wintering in temperate areas like the Wadden Sea covered an area as large as 800 km² in the course of some weeks (Piersma et al. 1993b, van Gils & Piersma 1999, van Gils et al. 2000, 2005b). At other temperate European wintering areas in British estuaries such as Morecambe Bay (Prater 1972) and the Firth of Forth (Symonds et al. 1984), individual *islandica* red knots also roam over areas of several tens of square kilometres in the course of the winter (see also Rehfisch et al. 2003). Furthermore, they even move quite often between estuaries (Evans 1981, 1984), extending the area used to several hundreds of kilometres. The *rufa* subspecies wintering in the southern hemisphere in temperate Patagonia, Argentina, likewise covers areas of 100 – 200 km² (Sitters et al. 2001). Consequently, both temperate wintering subspecies cover areas up to 50 times larger than the wintering red knots at the tropical Banc d'Arguin. Home ranges of the *piersmai* subspecies at tropical Roebuck Bay, north-west Australia, are as large as 20 km² (Rogers et al. 2006), which is in the same order of magnitude, although still slightly larger than at the Banc d'Arguin. Our comparison thus confirms the idea that home ranges of temperate wintering red knots are much larger than of those wintering in the tropics (Piersma et al. 1993b).

One of the main factors influencing habitat use by shorebirds is the availability of their prey (van de Kam et al. 2004). For shorebirds wintering in the Wadden Sea the food supply may be characterized as unpredictable. Erratic large drops in temperature make benthic food either unavailable to birds, therefore causing them to leave the site in search of warmer areas (e.g. the British estuaries; Evans 1976). Contrarily, benthic food may suddenly be highly available at some spots when e.g. after periods of frost moribund shellfish with gaping valves provide a rich food resource (Zwarts & Wanink 1993). In other years, prey harvestable by red knots may be highly variable due to unpredictable spat fall (Zwarts et al. 1992, Beukema et al. 1993). Consequently, temperate wintering birds have to keep track with ever changing feeding conditions (Evans et al. 1980, Evans 1981). Tropical wetlands lack climatic extremes such as cold spells,

Table 2.1 A worldwide comparison of home ranges and differences in the use of foraging areas and roost sites between day and night in wintering red knots.

Study area	Subspecies	Time of year	Approx. home range	Day/Night differences		Source
				foraging area	roost site	
Banc d'Arguin *Mauritania*	*canutus*	Nov. - Dec. March	2-16 km²	no	no	this study Piersma et al. 1993b
Roebuck Bay *Australia*	*piersmai*	Feb. - April	20 km²	no	yes	Rogers et al. 2006
Patagonia *Argentina*	*rufa*	March - April	100 - 200 km²	yes	yes?	Sitters et al. 2001
Wadden Sea *The Netherlands*	*islandica*	Sep. - Oct.	> 800 km²	no	no	van Gils & Piersma 1999

and no cyclones occur off the West African coast. Moreover, they appear to lack the seasonal synchronization of the reproductive cycle of the invertebrate prey (Wolff 1991, Piersma et al. 1993a, Dittmann 2002, de Goeij et al. 2003). Thus, prey lives close to the surface, and without peaked seasonal occurrences, provides more or less constant feeding conditions throughout the year (Piersma 1982, Piersma et al. 1993b). Additionally, in contrast to temperate wintering *islandica* knots *canutus* knots lack a mass peak (Piersma 1994) and have lower BMRs in winter (Piersma et al. 1996). We propose that this allows birds to confine themselves to very well-known small areas. This even seems to be the case during the period of fuelling for northward migration (P.J. van den Hout & L. van Kooten, pers. comm.), a season when feeding time is stretched to the maximum at Banc d´Arguin (Zwarts et al. 1990b), but rates of mass increase are relatively low (Piersma et al. 2005).

In our comparison of winter spacing behaviour at different wintering sites we came across differences in diurnal and nocturnal habitat choice at some sites. Such differences are often reported in shorebird studies (Mouritsen 1994, Burton & Armitage 2005) and are frequently related to differences in predation risk as the birds are exposed to a different group of predators at night than during the day. Rogers et al. (2006) showed that roosting behaviour of wintering red knots in north-west Australia differed considerably between day and night because of an increased predation risk at the favourite daytime roosts during the night. To decrease predation risk, the birds appeared to accept the extra costs of time and energy expenditure by choosing roost sites further away from the feeding habitats. In wintering red knots in Patagonia, Argentina, predator avoidance has been suggested to lead to the complete avoidance of profitable foraging sites at night (Sitters et al. 2001). These two examples suggest that sites may be so dangerous that increased costs of commuting between foraging areas and roost sites and even the avoidance of good feeding sites may be accepted (Cresswell 1994, Hilton et al. 1999, van Gils et al. 2000). If the lack of differences between the day and night time use of roosts and feeding areas is anything to go by, red knots wintering on the Banc d'Arguin did not seem to encounter differences in predation pressure on the roosts between day and night. Note that daytime predation by raptors is well documented (Bijlsma 1990), just as in the Wadden Sea (van Gils & Piersma 1999, van Gils et al. 2000, 2005b). However, from our results, we cannot exclude small scale differences in feeding site choice between day and night.

In conclusion, we suggest that the combination of food predictability and the absence of day/night differences in predation pressure both at high tide roosts and at foraging areas, allow *canutus* red knots wintering at the Banc d'Arguin to have very small and predictable home ranges compared with red knots wintering in other areas. True to Myers' (1984) research agenda we must now assemble further comparative data based on in-depth studies on the predictability of the food base and the presence of diurnal and nocturnal predators to fully exploit the comparative potential provided by red knots world-wide.

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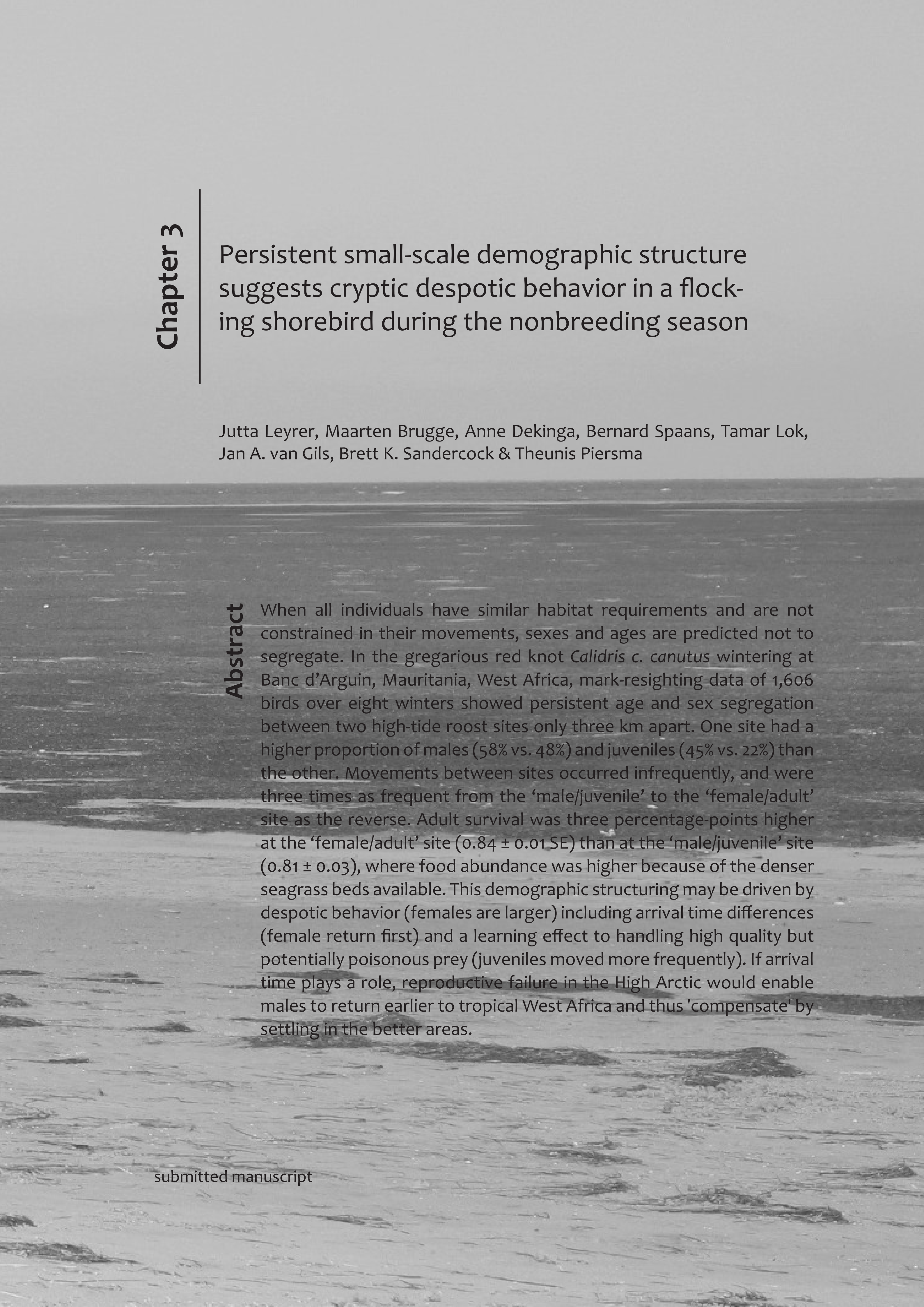


Chapter 3

Persistent small-scale demographic structure suggests cryptic despotic behavior in a flocking shorebird during the nonbreeding season

Jutta Leyrer, Maarten Brugge, Anne Dekinga, Bernard Spaans, Tamar Lok, Jan A. van Gils, Brett K. Sandercock & Theunis Piersma

Abstract

When all individuals have similar habitat requirements and are not constrained in their movements, sexes and ages are predicted not to segregate. In the gregarious red knot *Calidris c. canutus* wintering at Banc d'Arguin, Mauritania, West Africa, mark-resighting data of 1,606 birds over eight winters showed persistent age and sex segregation between two high-tide roost sites only three km apart. One site had a higher proportion of males (58% vs. 48%) and juveniles (45% vs. 22%) than the other. Movements between sites occurred infrequently, and were three times as frequent from the 'male/juvenile' to the 'female/adult' site as the reverse. Adult survival was three percentage-points higher at the 'female/adult' site (0.84 ± 0.01 SE) than at the 'male/juvenile' site (0.81 ± 0.03), where food abundance was higher because of the denser seagrass beds available. This demographic structuring may be driven by despotic behavior (females are larger) including arrival time differences (female return first) and a learning effect to handling high quality but potentially poisonous prey (juveniles moved more frequently). If arrival time plays a role, reproductive failure in the High Arctic would enable males to return earlier to tropical West Africa and thus 'compensate' by settling in the better areas.

submitted manuscript

Introduction

Selecting a good area to live is crucial to all animals, as individuals that occupy sites with greater foraging success and lower predation danger would have higher survival and higher reproductive success, i.e. achieve higher fitness (Fretwell & Lucas 1969). This is no less true for seasonally migrating animals that show drastic shifts in habitat, with the caveat that what happens in one place could well affect what is possible in another (Harrison et al. 2010). Documenting and understanding such so-called 'carry-over' mechanisms is crucial when attempting to determine in which areas and during which time of the year a population is bottlenecked (Runge & Marra 2005, Buehler & Piersma 2008).

The null model for site occupancy by individual animals attempting to maximize fitness is the ideal-free distribution (IFD; (Fretwell & Lucas 1969, Fretwell 1972). The predictions of the IFD for equal competitors are that no individual can improve fitness by changing between areas. Assumptions of the ideal-free distribution are two-fold: animals know where to settle (in habitats where fitness rewards are highest, i.e. the animals are 'ideal') and individuals are not constrained in their movements (e.g. by despotic behavior or travel costs, i.e. the animals are 'free') (Fretwell & Lucas 1969, Fretwell 1972). When some animals are more equal than others, i.e. not 'free' but still 'ideal', they would converge to the ideal-despotic distribution (Fretwell 1972).

Shorebirds tend to occupy open wetland habitats especially during the nonbreeding season. They are a profitable group in which to study spacing and social behavior in relation to food availability, predation pressure, traveling costs, and competition (Myers 1984, van de Kam et al. 2004). Whereas in some species some individuals may show clearly despotic behavior such as defending feeding territories (Turpie 1995, Johnson et al. 2001), in other species interference is either absent, or cryptic, and such species tend live in flocks (Myers et al. 1979, Myers 1980). A good example of a densely flocking species with apparently low interference costs is the long-distance migrating red knot *Calidris canutus* (van Gils & Piersma 2004). During the nonbreeding season they forage socially in intertidal habitats and form flocks of up to several thousand individuals (Piersma et al. 1993b, Folmer et al. 2010). Based on interpreted distribution patterns over a variety of spatial and temporal scales, red knots have been shown to behave as if they are both ideal and free (across all western European coastal wetlands over a whole winter when costs of moving were low in relation to distance traveled; Quaintenne et al. 2011), or ideal but not free (across a single wetland site over a week when costs of moving were relatively high; van Gils et al. 2006b).

Red knots breed circumpolar on the High Arctic tundra. Outside the breeding season they are found at coastal sites offering extensive mollusk-rich intertidal habitats in both the northern and southern hemisphere (Piersma et al. 2005, Piersma 2007). Although females are slightly larger than males, the differences are so small that red knots appear monomorphic and require molecular sexing (Dick et al. 1976, Baker et al. 1999). Unlike more dimorphic sandpiper species such as western sandpipers *Calidris mauri* (Fernández & Lank 2006), in red knots sexes and ages are not known to feed on different prey, nor to favor different habitats.

Here we report sex- and age-related differences in site use by red knots *C. c. canutus* at a tropical West African wintering site, the Banc d'Arguin, Mauritania. Using mark-resighting data and multi-state models, we estimate rates of movements between areas and area-specific survival rates. This leads us to propose that even in gregarious species as red knots subtle intraspecific competition may exclude particular classes of individuals from sites where food is most abundant and survival is highest.

Methods

Study area, catching and marking methods

The study site at Iwik Peninsula is a small section of Banc d'Arguin, the main nonbreeding grounds of the canutus subspecies (Piersma et al. 1992). During the 8-year study, catching and resighting efforts were conducted during 3-week expeditions in November/December of 2002 – 2009. Using mist-nets, red knots were captured at two high-tide roosts: Abelgh Eiznaya (19°54'N, 16°19'W) and Baie d'Aouatif (19°54'N, 16°17'W) around new moon spring-tides. In this study we include data from 1,606 birds individually marked with unique combinations of color-bands (see Appendix 3.A). Of these, 1,292 different individuals were resighted after release yielding a total of 1,544 observations (for details on observation efforts see Appendix 3.A).

Biometric and demographic parameters

Red knots were aged according to Prater et al. (1977), distinguishing hatch-year birds (juveniles, 3-6 months) from older birds (adults, > 12 months). We recorded bill (culmen) length (calipers; ± 0.1 mm), wing length (ruler; ± 1 mm), and tarsus length (calipers; ± 0.1 mm). Body mass was measured within four hours of capture (electronic scales; ± 1 g). A blood sample of 5-20 µl was collected from the brachial vein and stored in 96% ethanol for molecular sexing (Baker et al. 1999, Appendix 3.A).

We used binomial logistic regression to test for differences in sex (females:males) or age (juveniles:adult) ratios between the two sites, using site as a factor.

We used linear regression models with sex, age and site (as factors) as explanatory variables to assess potential differences in structural body size or body mass. As body mass can vary as a consequence of individual variation in size or in nutritional stores (van der Meer &Piersma 1994), wing, tarsus and bill length measurements were analyzed in a Principal Component Analysis (PCA). PC1 explained 58% of the variation on structural body size. The residuals of a linear regression model of body mass against PC1 were used to compare differences in body stores between the two sites (ß ± SE: 5.04 ± 0.16, $t = 31.83$, $p < 0.001$; n = 1,606). We selected the most parsimonious model by stepwise deleting higher interaction and other non-significant terms. We used R 2.10.1 statistical software (R Development Core Team 2008).

Capture and resighting data were combined to create encounter histories for estimating demographic parameters with multi-state models (Arnason 1973, Nichols & Kendall 1995). Multistate models offer site-specific estimates of annual apparent survival Φ (phi), and movement among sites (transition) Ψ (psi), corrected for site-specific encounter rates p. Detections of red knots in the encounter histories were coded by site (A=Abelgh Eiznaya, B=Baie d'Aouatif, 0=not seen), and the site-specific transition parameters ($\Psi^{A\text{-}B}$, $\Psi^{B\text{-}A}$) described the probabilities of movement for individuals switching between the two sites. Because multi-state models have a large number of parameters, we made three a priori assumptions to reduce parameter number and increase parameter precision. Observation effort differed among years and sites, and we included these factors but not sex or age in modeling p (see Appendix 3.A). We were less interested in annual variation within our relatively short time series, and Φ and Ψ were modeled as constant over time, but we tested for differences between sexes, age classes and sites (Appendix 3.A). Earlier analyses of a data subset of the study population indicated that a time-since-marking (tsm) effect explained most of the variation in annual survival (Chapter 8), and we included tsm effects to control for transients or handling effects on Φ (Sandercock 2006). The probability of movement Ψ is conditional upon survival, and we tested age differences only for Φ. For more decision rules see Appendix 3.A.

The global model for testing the goodness of fit was $\Phi_{tsm+sex+age+site}\ \Psi_{sex+site+age}\ p_{site+time}$, using the median-ĉ (c-hat) test implemented in the MARK software (White & Burnham 1999). The estimated ĉ was 1.03 ± 0.00 SE, and ĉ was adjusted accordingly. Model selection was based on Akaike's Information Criterion corrected for small sample size (AICc). The candidate model set consisted of all plausible combinations of parameterizations for Φ, Ψ and *p* (Appendix 3.B, table 3.B1). All models were constructed using design matrices and the logit link function in Program MARK (ver. 6.0,White & Burnham 1999). We used the model averaging function in MARK to calculate survival, transition and resighting probability and present parameter estimates as $\hat{\theta}$ ±1SE.

Results

Catches of red knots at the Baie d'Aouatif high-tide roost included more males (58 ± 2% S.E.) and more juveniles (45 ± 8%) than the roost at Abelgh Eiznaya (males: 48 ± 3%, ß ± SE: -0.41 ± 0.11, z = -3.58, p = < 0.001; juveniles: 22 ± 6%, ß ± SE: -0.74 ± 0.12, z = -6.21, p = <0.001: both n = 8 winters, figure 3.1)

Overall, females were distinctly larger than males (for details see table 3.1, Appendix 3.C table 3.C1). Females had larger bills (t = -29.19, p < 0.001) and tarsi (t = -9.77, p < 0.001) than males. Adult females had longer wings than adults males and juvenile females and males, adult males had longer wings than juveniles females and males, and juvenile females had longer wings than juvenile males (t = -2.2, p = 0.028). Females were heavier than males (t = -11.9, p < 0.001), both in adults and juveniles (t = 7.7, p < 0.001). Between site differences additional to differences between the sexes were found in bill and tarsus length, with red knots having longer bills (t = 3.13, p = 0.002) and longer tarsi (t = 2.02, p = 0.04) at Abelgh Eiznaya than at Baie d'Aouatif.

Table 3.1 Wing [mm], bill [mm], tarsus length [mm] and body mass [g] (average ± s.d.) of wintering red knots were tested in linear regression models for effects of sex, age and/or catching location (site) Abelgh Eiznaya and Baie d'Aouatif. Each letter indicates significant different groupings (p < 0.01, for all relevant parameters see table 3.C1). n = sample size for Abelgh Eiznaya (A) and Baie d'Aouatif (B) respectively. Regressions on body mass were tested on size corrected body mass.

		adults		juvenile	
		female (n: A = 454; B = 86)	male (n: A = 355; B = 111)	female (n: A = 135; B = 72)	male (n: A = 164; B = 98)
wing [mm]	Abelgh Eiznaya	174 ± 4^a	169 ± 4^b	167 ± 4^c	163 ± 3^d
	Baie d'Aouatif	174 ± 4^a	169 ± 4^b	167 ± 3^c	163 ± 3^d
bill [mm]	Abelgh Eiznaya	36.2 ± 1.73^a	34.5 ± 1.62^c	36.4 ± 1.65^a	34.2 ± 1.41^c
	Baie d'Aouatif	36.0 ± 1.72^b	34.4 ± 1.75^d	35.9 ± 1.65^b	33.9 ± 1.62^d
tarsus [mm]	Abelgh Eiznaya	33.0 ± 1.36^a	32.5 ± 1.20^c	33.0 ± 1.17^a	32.3 ± 1.05^c
	Baie d'Aouatif	33.0 ± 1.30^b	32.0 ± 1.30^d	33.0 ± 1.16^b	32.3 ± 1.21^d
body mass [g]	Abelgh Eiznaya	131 ± 8^a	120 ± 8^b	125 ± 8^c	113 ± 9^d
	Baie d'Aouatif	130 ± 7^a	119 ± 7^b	124 ± 10^c	112 ± 9^d

F statistics: wing: $F_{3,1471}$=525.2, r^2=0.52, p<0.001; bill: $F_{2,1472}$=236.9, r^2=0.24, p<0.001;
tarsus: $F_{2,1472}$=51.9, r^2=0.06, p<0.001; body mass: $F_{2,1472}$=109.7, r^2=0.13, p<0.001

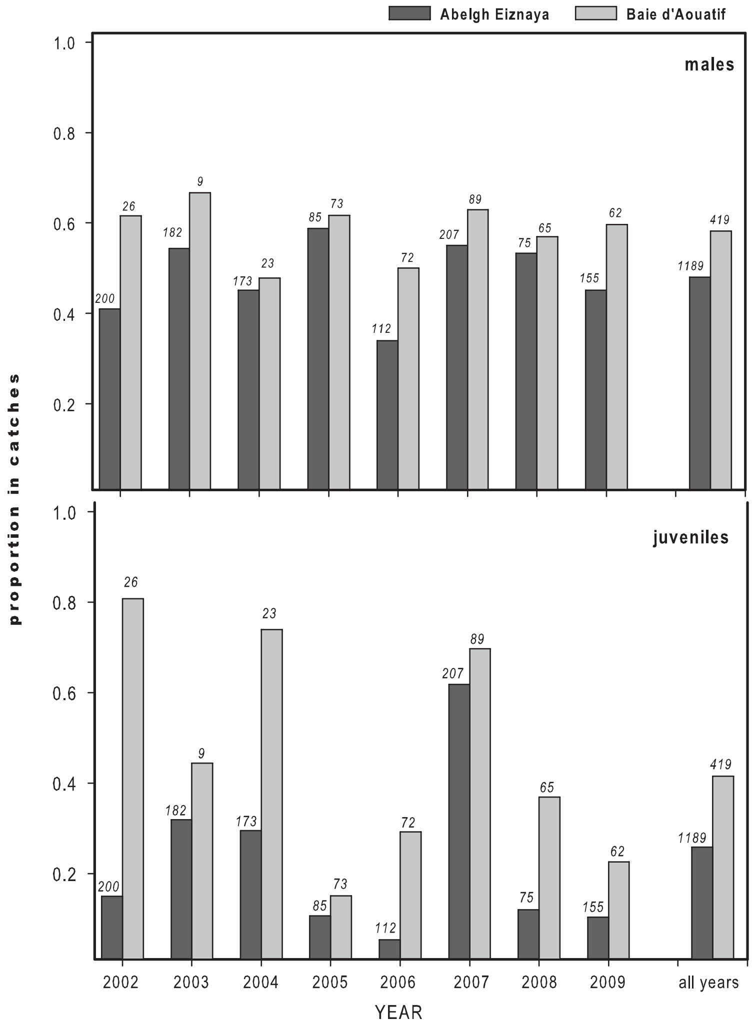


Figure 3.1 Proportions of males and juveniles among captures at Baie d'Aouatif and Abelgh Eiznaya, November-December 2002 to 2009. Numbers in italics indicate the numbers of red knots examined.

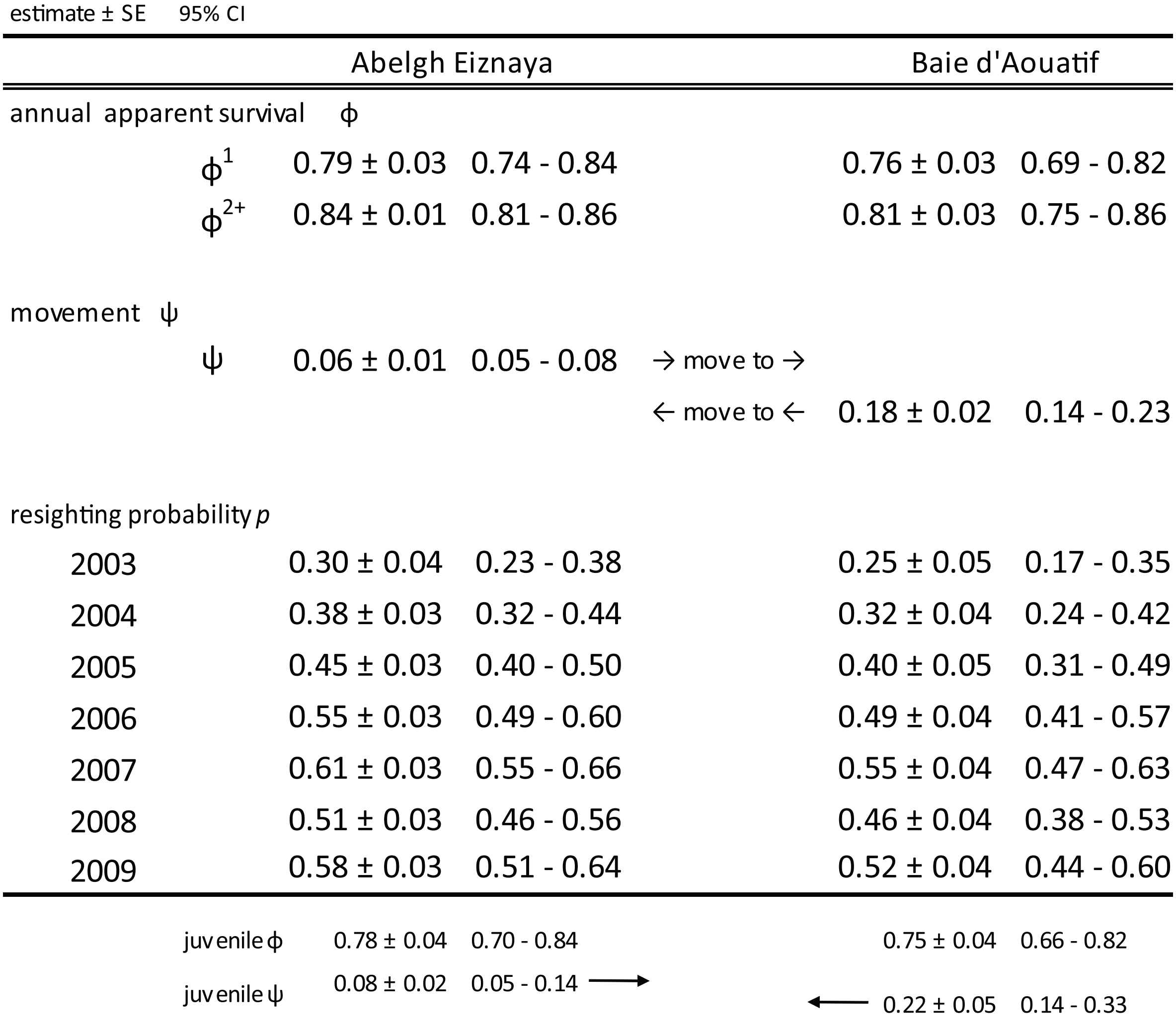
Table 3.2 The most parsimonious multi-state models (ΔQAICc < 2) estimated apparent annual survival Φ and movement probability ψ depending on time-since-marking (tsm), age-class (age: adult/juvenile), sex (male/female) and site (Abelgh Eiznaya/Baie d'Aouatif) for red knots at Iwik Peninsula, Banc d'Arguin, Mauritania, West Africa, in winters 2002 – 2009. Resighting probability *p* was exclusively modeled depending on site and time (year). For a list of all tested models see Appendix 3.B, table 3.B1.

Model	NP	QDeviance	QAICc	Δ QAICc	QAICc weigh
$\phi_{tsm+site}\ \psi_{age+site}\ p_{site+time}$	14	1553.59	6568.48	0	0.098
$\phi_{tsm+age+site}\ \psi_{age+site}\ p_{site+time}$	15	1552.38	6569.29	0.81	0.065
$\phi_{tsm+site}\ \psi_{site}\ p_{site+time}$	13	1556.47	6569.34	0.86	0.064
$\phi_{tsm}\ \psi_{age+site}\ p_{site+time}$	13	1556.52	6569.38	0.90	0.062
$\phi_{tsm+age}\ \psi_{age+site}\ p_{site+time}$	14	1554.92	6569.81	1.32	0.050
$\phi_{tsm+site}\ \psi_{age+sex+site}\ p_{site+time}$	15	1553.17	6570.09	1.60	0.044
$\phi_{tsm+age+site}\ \psi_{site}\ p_{site+time}$	14	1555.25	6570.14	1.66	0.043
$\phi_{tsm}\ \psi_{site}\ p_{site+time}$	12	1559.34	6570.19	1.71	0.042
$\phi_{site}\ \psi_{age+site}\ p_{site+time}$	13	1557.33	6570.20	1.71	0.041
$\phi_{tsm+site}\ \psi_{age+site}\ p_{site+time}$	15	1553.59	6570.51	2.02	0.036

Model statistics include: number of parameters (NP), Deviance, Akaike's information criterion corrected for small sample size (QAICc), ΔQAICc, and QAICc weight. The goodness of fit was tested for the biologically most significant full model $\Phi_{tsm+age+sex+site}\ \psi_{age+sex+site}\ p_{site+time}$ and $\hat{c}$ was adjusted to 1.03 ± 0.00.

The probability of encounter *p* increased among years at both sites (table 3.2). Nine models differed in ΔAICc < 2, describing variations in Φ as a function of tsm, site and/or age and variations in ψ as a function of site, age and/or sex (table 3.2; for a list of all tested models see Appendix 3.B, table B1). At both sites, adult survival was lower in the first year after marking than subsequent years, and survival was lower at Abelgh Eiznaya ($\Phi^1 = 0.79 \pm 0.03$ (95% CI $= 0.74 – 0.84$); $\Phi^{2+} = 0.84 \pm 0.01$ ($0.81 – 0.86$), table 3.3) than at Baie d'Aouatif ($\Phi^1 = 0.76 \pm 0.03$ ($0.69 – 0.82$); $\Phi^{2+} = 0.81 \pm 0.03$ ($0.75 – 0.86$)). The probability of switching sites was low overall, but directional movements of adults were less frequent from Abelgh Eiznaya to Baie d'Aouatif ($\psi^{A\rightarrow B} = 0.06 \pm 0.01$ ($0.05 – 0.08$)) than in the opposite direction ($\psi^{B\rightarrow A} = 0.18 \pm 0.02$ ($0.15 – 0.23$)). Juvenile survival was slightly lower than adult survival and movements were more frequent, showing the same directionality as adults (table 3.3).

Table 3.3 Model estimates of annual apparent survival (Φ), movement (ψ) and resighting probability (p), standard errors (SE), and 95% confidence intervals (CI) for eight years of measuring red knots at their tropical wintering area Banc d'Arguin, Mauritania, West Africa. 2002 - 2009. Results shown are for the top-supported model only (table 3.2). Apparent annual survival Φ showed a time-since-marking effect and differed slightly between sites. Φ^1 denotes apparent survival in the first year after marking, Φ^{2+} denotes apparent survival in subsequent years. Movement ψ was preferential from Baie d'Aouatif to Abelgh Eiznaya. Resighting probability p differed among years and between sites. Other models within ΔAICc units <2 differed in one parameter only and did not explain further variation significantly better.



estimate ± SE 95% CI

		Abelgh Eiznaya			Baie d'Aouatif	
annual apparent survival ϕ						
	ϕ^1	0.79 ± 0.03	0.74 - 0.84		0.76 ± 0.03	0.69 - 0.82
	ϕ^{2+}	0.84 ± 0.01	0.81 - 0.86		0.81 ± 0.03	0.75 - 0.86
movement ψ						
	ψ	0.06 ± 0.01	0.05 - 0.08	→ move to →		
				← move to ←	0.18 ± 0.02	0.14 - 0.23
resighting probability *p*						
2003		0.30 ± 0.04	0.23 - 0.38		0.25 ± 0.05	0.17 - 0.35
2004		0.38 ± 0.03	0.32 - 0.44		0.32 ± 0.04	0.24 - 0.42
2005		0.45 ± 0.03	0.40 - 0.50		0.40 ± 0.05	0.31 - 0.49
2006		0.55 ± 0.03	0.49 - 0.60		0.49 ± 0.04	0.41 - 0.57
2007		0.61 ± 0.03	0.55 - 0.66		0.55 ± 0.04	0.47 - 0.63
2008		0.51 ± 0.03	0.46 - 0.56		0.46 ± 0.04	0.38 - 0.53
2009		0.58 ± 0.03	0.51 - 0.64		0.52 ± 0.04	0.44 - 0.60
	juvenile ϕ	0.78 ± 0.04	0.70 - 0.84		0.75 ± 0.04	0.66 - 0.82
	juvenile ψ	0.08 ± 0.02	0.05 - 0.14	⟶		
				⟵	0.22 ± 0.05	0.14 - 0.33

Discussion

We documented consistent sex and age segregation between the two sites in all eight years of study. As previously documented (Dick et al. 1976, Tomkovich & Soloviev 1996), structural body size and body mass mostly differed between the different sex/age categories, but despite being statistically significant, the absolute differences were small and variance was high, hence the need of molecular methods to reliably sex red knots (Dick et al. 1976, Baker et al. 1999). Yet, the older (more experienced) age-class (adults) and the generally larger sex (females) formed the majority at Abelgh Eiznaya, where individuals also had the longer bills and tarsi even when accounting for sex. Confirming a previous study showing high site-faithfulness within a winter season (Leyrer et al. 2006), there was little interchange between the high tide roosts of Abelgh Eiznaya and Baie d'Aouatif, despite the two being only three km apart. Red knots routinely migrate some 20,000 km each year and the lack of movements between the two sites suggests that individual red knots somehow were restrained from moving freely. Those individuals that did move switched from the male/juvenile dominated (Baie d'Aouatif) to the female/adult dominated (Abelgh Eiznaya) site, to where birds also had a higher annual survival.

The following suggests that the main reason why Abelgh Eiznaya provided higher survival is that it offered better foraging conditions. The intertidal flats at Banc d'Arguin include two main types of foraging habitat: seagrass meadows (predominantly *Zostera noltii*) alternate with bare sandy flats (Wolff & Smit 1990). red knots preferentially feed on dense muddy seagrass (Altenburg et al. 1982), a habitat that harbors higher densities of mollusk prey (Honkoop et al. 2008) and offers higher intake rates (J.A. van Gils, unpubl. data) than the sandy area flats. Landsat satellite images for the years of our study showed that the foraging areas of Abelgh Eiznaya (an assessment made based on Leyrer et al. 2006) provided denser seagrass coverage than the foraging areas in the Baie d'Aouatif (figure 3.2, Appendix 3.D) and thus better foraging opportunities. In contrast to strongly dimorphic migratory shorebirds such as the western sandpipers (Fernández & Lank 2006), red knots have never been shown to segregate among habitats with respect to external morphological traits. Instead, only gizzard size explained differential foraging distributions (van Gils et al. 2005b). Eating hard-shelled mollusks that need to be crushed and processed internally, gizzard size constrains the rate of food intake. Thus, the interaction between prey quality and gizzard size is a central determinant in foraging patch choice (van Gils et al. 2005b). Gizzard size is a plastic trait (Dekinga et al. 2001), and growth and maintenance of a large gizzard takes time and energy (reviewed in van Gils et al. 2007). Consistent with the idea that individual red knots that move from Baie d'Aouatif to Abelgh Eiznaya will do better, at least in terms of foraging, the gizzards of red knots roosting at Abelgh Eiznaya in April 2007 – 2009 (measured by ultrasonography; Dietz et al. 1999) were slightly smaller (8.79 g ± 2.86; n = 9) than at Baie d'Aouatif (10.45 g ± 3.44; n = 77; t-test: $t = 1.607$, df = 10.907, $p = 0.1366$). In addition, Abelgh Eiznaya may be safer, as observations on foraging red knots indicate a lower predation risk (M. van der Geest, J.A. van Gils unpubl. obs.).

Under the IFD we would not have expected survival differences between areas. The predominant movement to the better quality area between winters suggests though that the red knots were well aware of the quality differences. In the following we present three non-mutually exclusive hypotheses potentially explaining the observed movement patterns. In the first place, the difference between the two roost sites could reflect a buffer effect (Kluyver & Tinbergen 1953, Brown 1969, Gill et al. 2001). Since the larger (females) and older birds occurred mostly at the site with the higher survival, we suggest that some type of despotism maintains the sex- and age-related structuring. As females are not only slightly larger, but also return first from the High Arctic

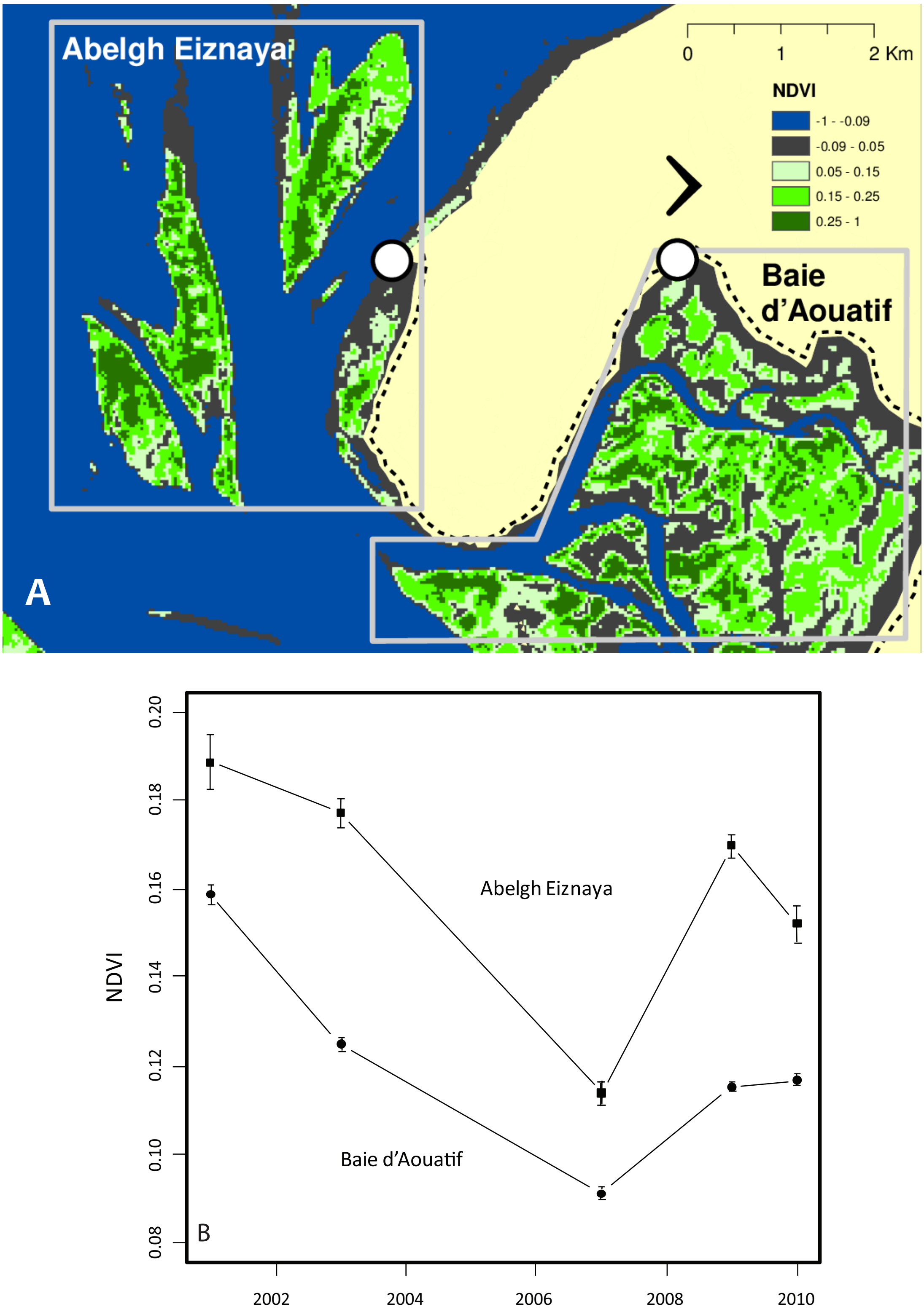


Figure 3.2 A The distribution of seagrass beds in the intertidal foraging area of red knots at Banc d'Arguin, Mauritania, shown as variances in 'Normalized Differences Vegetation Indices' NDVI intensities obtained from five suitable Landsat images (Appendix 3.D, J.A. van Gils, unpubl data). Yellow areas show mainland, blue areas show water, grey areas show bare intertidal mudflats, and green colors indicate various NDVI intensities (see legend). Grey-bordered blocks indicate intertidal foraging areas connected to the respective high tide roosts. **B** NDVI values (mean ± SE) plotted over time for both foraging areas. NDVI values for the foraging areas were higher for Abelgh Eiznaya (Student's $t = 6.2$, df = 4, $p < 0.005$), indicating that Abelgh Eiznaya offered better foraging conditions than Baie d'Aouatif.

breeding to the wintering grounds (Piersma et al. 1992, Tomkovich & Soloviev 1996, Nebel et al. 2000), the order of arrival could also play a key role in site occupancy. As the Afro-Siberian red knot population shows a declining trend (Davidson & Piersma 2009), we may have observed a net movement to the better site as slots become available. If this would be the case, we would expect a net movement towards Baie d'Aouatif as the population increases again.

A second hypothesis is based on recent observations that the preferred prey (*Loripes* ssp.) has high sulfur concentrations and thus could be poisonous prey (J.A. van Gils, unpubl. data). Adult red knots seem to be more resilient in dealing with high sulfur loads (T. Oudman, J.A. van Gils unpubl. obs.), which would support our observations that it was mainly adults that were found at the *Loripes* site Abelgh Eiznaya. We thus expect that red knots would move from Baie d'Aouatif to Abelgh Eiznaya in the course of their life, and this is indeed what seems to happen: juvenile red knots show an even higher likelihood to move there in the first year of their life than (later as) adults.

The third hypothesis is based solely on the timing of arrival back at Banc d'Arguin and the assumption that arrival time determines the resource holding potential of returning red knots. Successfully reproducing males attend their offspring for almost three weeks after females have left the High Arctic (Tomkovich & Soloviev 1996), even though females are physiologically perfectly capable to give this care if experimentally forced to do so (Pierce et al. 2010). One reason could be that females profit from arriving early in the nonbreeding grounds. On their way south, female *canutus* red knots, but not males, appear to stage in the Wadden Sea for a 2-3 week period (Nebel et al. 2000). Instead, *canutus* males may routinely accomplish a 9,000 km nonstop southward migration yet, still arrive later than the females. In years when breeding is unsuccessful (see Meissner 2005), males may be able to catch up and arrive with the females. This might enable some of them to make a move to a better wintering site, thus partially 'compensating' for reproductive failure. With the miniaturization of new tracking devices (e.g. Conklin et al. 2010), assessments of such trade-offs in individual life-histories of long-distance migrants will become within reach.

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Appendices

Appendix 3.A Sexing, marking and observation efforts and resighting probabilities

Red knots captured in 2002 – 2006 were sexed with primers P2/P8 (Griffiths et al. 1998) verified for red knots by Baker et al. (1999). To avoid sexing errors due to potential length polymorphisms in the Z-intron of the CHD gene (Casey et al. 2009, Schroeder et al. 2010), primers 2602F/2669R (Fridolfsson &Ellegren 1999; modified for shorebirds by O. Haddrath, unpubl. data) were used from 2007 onwards.

For survival and movement analysis, 1,292 red knots were caught between 2002 and 2008 at the two neighboring high-tide roosts less than 3km apart at Banc d'Arguin, Mauritania, West Africa. The birds were individually marked with a numbered metal band of the Dutch ringing scheme ('Vogeltrekstation Arnhem') and a unique combination of four color-bands and a leg flag (Piersma & Spaans 2004). More red knots were caught at the Abelgh Eiznaya high tide roost (982 individuals) than at the Baie d'Aouatif high tide roost (310 individuals) (table 3.A1). These birds were followed in subsequent winters 2003 – 2009. Juvenile red knots were considered as juveniles during their first year of life, and were treated as adults as they returned in subsequent years.

Table 3.A1 Numbers of newly ringed red knots at the two study sites Abelgh Eiznaya and Baie d'Aouatif each year (bold numbers in first diagonal). In lines: total number of individuals re-sighted each year of the respective cohort. In brackets number of individuals that have been re-sighted at the other site in that year. Italic numbers: percentages of total numbers seen back per cohort and year.

Abelgh Eiznaya		individuals (moved)						
YEAR	2002	2003	2004	2005	2006	2007	2008	2009
newly ringed	**177**	41 (2)	45 (-)	51 (5)	51 (3)	44 (4)	22 (1)	23 (1)
%		*23*	*25*	*29*	*29*	*25*	*12*	*13*
		171	57 (10)	66 (3)	63 (12)	59 (6)	42 (4)	25 (4)
			33	*39*	*37*	*35*	*25*	*15*
			162	62 (4)	55 (3)	55 (3)	38 (-)	37 (3)
				38	*34*	*34*	*23*	*23*
				83	34 (4)	39 (5)	24 (2)	16 (-)
					41	*47*	*29*	*19*
					112	52 (8)	37 (3)	42 (8)
						46	*33*	*38*
						202	68 (6)	75 (14)
							34	*37*
							75	30 (7)
								40

Baie d'Aouatif		individuals (moved)						
YEAR	2002	2003	2004	2005	2006	2007	2008	2009
newly ringed	**21**	5 (1)	2 (1)	2 (1)	4 (-)	1 (-)	2 (1)	—
%		*24*	*10*	*10*	*19*	*5*	*10*	*0*
		5	2 (1)	—	1 (-)	—	—	—
			40	*0*	*20*	*0*	*0*	*0*
			20	7 (4)	8 (2)	7 (5)	6 (5)	3 (2)
				35	*40*	*35*	*30*	*15*
				68	26 (4)	25 (7)	16 (7)	19 (4)
					38	*37*	*24*	*28*
					49	20 (4)	21 (3)	17 (4)
						41	*43*	*35*
						83	32 (6)	28 (6)
							39	*34*
							64	37 (3)
								58

The high tide roost that the birds were caught at was assigned as ‘their’ high tide roost. Observations made at ‘the other’ site were recorded as movement. More than 50% of the resighted individuals were seen more than one time and/or by more than one observer per year. Individuals that were not recorded for four consecutive years and then resighted for only one time were excluded from the analysis as potentially wrong readings. In the 73 (out of 1,544) cases when an individual was seen at both sites within one year, the site with the higher number of observations was selected and recorded as 'site of observation'. A few individuals that were seen within one year at both sites once only were excluded from the analysis. Of these excluded birds only three individuals were resighted at 'the other' site in subsequent years.

About 30 – 40% of the marked individuals of a cohort were resighted annually. Especially in later study years, sometimes more than 40% of a cohort were resighted. Occasionally, especially in the earlier study years, less than 30% were resighted (table 3.A1). The increase in observed individuals each year was mainly due to having more individuals marked in the population, but also due to improvements in resighting probabilities.

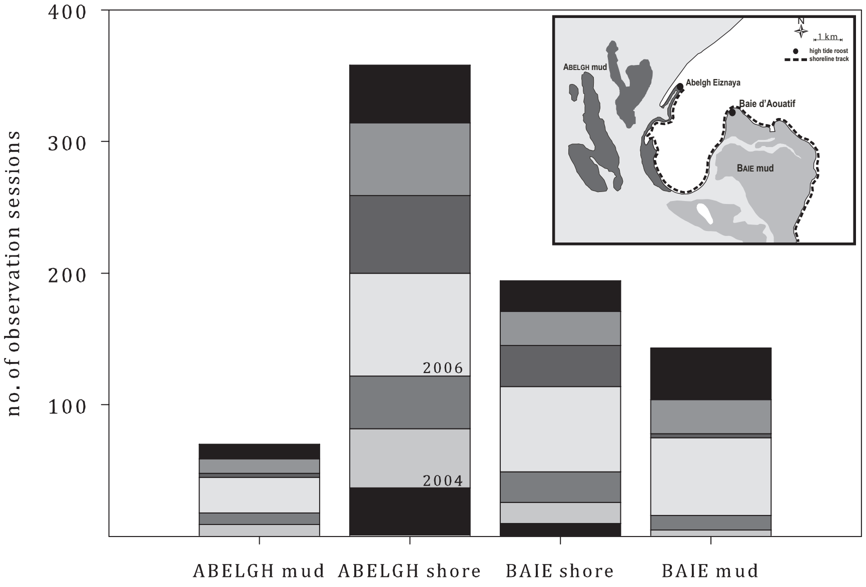

Figure 3.A1 Number of observation sessions per year and area. Abelgh Eiznaya is presented in dark grey, Baie d’Aouatif is presented in lighter grey, other grey shades indicate non-visited mudflats and water. Observations at mudflats away from shore in both areas started in 2004. An observation session is defined as the time (1 – 3 hrs) a single observer spent in an area.

Observations took place within three-week expeditions in November/December 2003 – 2009. On average, ten experienced color-band readers scanned the total study area along the shoreline track every day (figure 3.A1). From 2004 onwards, all inter-tidal mudflats not or hardly accessible from shore were visited by boat as often as weather and tidal conditions allowed. From 2007 onwards the use of snow rackets allowed much better walking on the soft mudflats and the observation radius could be improved once more.

Because numbers marked at the Baie d’Aouatif high tide roost were low in the beginning, Φ and ψ were not modeled as a function of differences in annual conditions. Yet, resighting probability *p* was modeled as a function of time, as logistic improvements suggested resighting effort to differ between years. The habitat used by red knots at Banc d’Arguin is mainly open mudflats and beaches without vegetation. Apart from apparently selecting different high tide roosts and foraging areas, behavior did not differ between the sex and age classes with foraging on the mudflats during low tide and assembling at the high tide roosts during high tide. There was no reason to expect *p* to differ between sex or age, consequently *p* was not modeled as a function of different behavior in sex or age classes within a site.

Appendix 3.B Multi-state candidate models

Table 3.B1 List of all candidate multi-state models tested to estimate demographic parameters for red knots at two nonbreeding sites at Iwik Peninsula, Banc d'Arguin, Mauritania, in winter 2002 – 2009. Annual apparent survival Φ, movement probability ψ and resighting probability *p* were modeled as functions of time-since-marking (tsm), age (adult/juvenile), sex (male/female), site (Abelgh Eiznaya/Baie d'Aouatif), time (year) and constant. Model statistics include: number of parameters (NP), QDeviance, Akaike's information criterion corrected for small sample size (QAICc) (noted at bottom of table for the best model), ΔQAICc, and QAICc weight. The full model (indicated with *) used to test the goodness of fit was built on some a priori assumptions based on existing knowledge about the study system, described in detail in the material and methods paragraph and in Appendix 3.A. Goodness of fit was tested using the median ĉ-test implemented in the MARK software, ĉ was adjusted to 1.03 ± 0.00. The most parsimonious models (ΔQAICc < 2) are shaded in grey.

Model	NP	QDeviance	Δ QAICc	QAICc weights
$\phi_{tsm+age+sex+site}\ \psi_{age+sex+site}\ p_{site+time}$*	17	1551.95	4.43	0.01
$\phi_{tsm+age+site}\ \psi_{age+sex+site}\ p_{site+time}$	16	1551.95	2.41	0.03
$\phi_{tsm+age+sex+site}\ \psi_{age+site}\ p_{site+time}$	16	1552.38	2.84	0.02
$\phi_{tsm+sex+site}\ \psi_{age+sex+site}\ p_{site+time}$	16	1553.17	3.63	0.02
$\phi_{tsm+age+sex}\ \psi_{age+sex+site}\ p_{site+time}$	16	1554.46	4.92	0.01
$\phi_{tsm+age+sex+site}\ \psi_{sex+site}\ p_{site+time}$	16	1554.88	5.34	0.01
$\phi_{tsm+age+sex+site}\ \psi_{age+sex}\ p_{site+time}$	16	1590.16	40.62	0
$\phi_{tsm+age+site}\ \psi_{age+site}\ p_{site+time}$	15	1552.38	0.81	0.07
$\phi_{tsm+site}\ \psi_{age+sex+site}\ p_{site+time}$	15	1553.17	1.60	0.04
$\phi_{tsm+site}\ \psi_{age+site}\ p_{site+time}$	15	1553.59	2.02	0.04
$\phi_{tsm+age}\ \psi_{age+sex+site}\ p_{site+time}$	15	1554.48	2.91	0.02
$\phi_{tsm+age+site}\ \psi_{sex+site}\ p_{site+time}$	15	1554.88	3.31	0.02
$\phi_{tsm+age+sex}\ \psi_{age+site}\ p_{site+time}$	15	1554.90	3.33	0.02
$\phi_{tsm+age+sex+site}\ \psi_{site}\ p_{site+time}$	15	1555.25	3.68	0.02
$\phi_{tsm+sex}\ \psi_{age+sex+site}\ p_{site+time}$	15	1556.04	4.47	0.01
$\phi_{tsm+sex+site}\ \psi_{sex+site}\ p_{site+time}$	15	1556.11	4.54	0.01
$\phi_{tsm+age+sex}\ \psi_{sex+site}\ p_{site+time}$	15	1557.35	5.78	0.01
$\phi_{tsm+age+site}\ \psi_{age+sex}\ p_{site+time}$	15	1590.16	38.59	0
$\phi_{tsm+age+sex+site}\ \psi_{age}\ p_{site+time}$	15	1590.18	38.61	0
$\phi_{tsm+sex+site}\ \psi_{age+sex}\ p_{site+time}$	15	1590.96	39.40	0
$\phi_{tsm+age+sex}\ \psi_{age+sex}\ p_{site+time}$	15	1591.06	39.49	0
$\phi_{tsm+age+sex+site}\ \psi_{sex}\ p_{site+time}$	15	1596.62	45.05	0
$\phi_{tsm+site}\ \psi_{age+site}\ p_{site+time}$	14	1553.59	0	0.10
$\phi_{tsm+age}\ \psi_{age+site}\ p_{site+time}$	14	1554.92	1.32	0.05
$\phi_{tsm+age+site}\ \psi_{site}\ p_{site+time}$	14	1555.25	1.66	0.04
$\phi_{tsm}\ \psi_{age+sex+site}\ p_{site+time}$	14	1556.08	2.49	0.03
$\phi_{tsm+site}\ \psi_{sex+site}\ p_{site+time}$	14	1556.11	2.52	0.03
$\phi_{tsm+sex+site}\ \psi_{site}\ p_{site+time}$	14	1556.47	2.88	0.02
$\phi_{tsm+sex}\ \psi_{age+site}\ p_{site+time}$	14	1556.47	2.88	0.02
$\phi_{site}\ \psi_{age+sex+site}\ p_{site+time}$	14	1556.91	3.32	0.02
$\phi_{tsm+age}\ \psi_{sex+site}\ p_{site+time}$	14	1557.36	3.77	0.01
$\phi_{tsm+age+sex}\ \psi_{site}\ p_{site+time}$	14	1557.73	4.14	0.01
$\phi_{tsm+sex}\ \psi_{sex+site}\ p_{site+time}$	14	1558.93	5.33	0.01
$\phi_{tsm+age+sex}\ \psi_{age}\ p_{site+time}$	14	1590.18	36.59	0
$\phi_{tsm+site}\ \psi_{age+sex}\ p_{site+time}$	14	1590.97	37.38	0

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Model	NP	QDeviance	Δ QAICc	QAICc weights
$\phi_{\text{tsm+sex+site}}\ \psi_{\text{age}}\ p_{\text{site+time}}$	14	1590.98	37.39	0
$\phi_{\text{tsm+age}}\ \psi_{\text{age+sex}}\ p_{\text{site+time}}$	14	1591.08	37.48	0
$\phi_{\text{tsm+age+sex}}\ \psi_{\text{age}}\ p_{\text{site+time}}$	14	1591.09	37.50	0
$\phi_{\text{tsm+sex}}\ \psi_{\text{age+sex}}\ p_{\text{site+time}}$	14	1592.04	38.45	0
$\phi_{\text{tsm+age+site}}\ \psi_{\text{sex}}\ p_{\text{site+time}}$	14	1596.63	43.03	0
$\phi_{\text{tsm+age+sex+site}}\ \psi_{\text{const.}}\ p_{\text{site+time}}$	14	1596.63	43.03	0
$\phi_{\text{tsm+age+sex}}\ \psi_{\text{sex}}\ p_{\text{site+time}}$	14	1597.31	43.71	0
$\phi_{\text{tsm+sex+site}}\ \psi_{\text{sex}}\ p_{\text{site+time}}$	14	1597.65	44.06	0
$\phi_{\text{tsm+site}}\ \psi_{\text{site}}\ p_{\text{site+time}}$	13	1556.47	0.86	0.06
$\phi_{\text{tsm}}\ \psi_{\text{age+site}}\ p_{\text{site+time}}$	13	1556.52	0.90	0.06
$\phi_{\text{site}}\ \psi_{\text{age+site}}\ p_{\text{site+time}}$	13	1557.33	1.71	0.04
$\phi_{\text{tsm+age}}\ \psi_{\text{site}}\ p_{\text{site+time}}$	13	1557.75	2.13	0.03
$\phi_{\text{tsm}}\ \psi_{\text{sex+site}}\ p_{\text{site+time}}$	13	1558.97	3.35	0.02
$\phi_{\text{tsm+sex}}\ \psi_{\text{site}}\ p_{\text{site+time}}$	13	1559.30	3.69	0.02
$\phi_{\text{site}}\ \psi_{\text{sex+site}}\ p_{\text{site+time}}$	13	1559.87	4.26	0.01
$\phi_{\text{site}}\ \psi_{\text{age+sex}}\ p_{\text{site+time}}$	13	1586.57	30.96	0
$\phi_{\text{tsm+site}}\ \psi_{\text{age}}\ p_{\text{site+time}}$	13	1590.99	35.37	0
$\phi_{\text{tsm+age}}\ \psi_{\text{age}}\ p_{\text{site+time}}$	13	1591.10	35.49	0
$\phi_{\text{tsm+sex}}\ \psi_{\text{age}}\ p_{\text{site+time}}$	13	1592.07	36.45	0
$\phi_{\text{tsm}}\ \psi_{\text{age+sex}}\ p_{\text{site+time}}$	13	1592.08	36.46	0
$\phi_{\text{tsm+age+site}}\ \psi_{\text{const.}}\ p_{\text{site+time}}$	13	1596.63	41.01	0
$\phi_{\text{tsm+age+sex}}\ \psi_{\text{const.}}\ p_{\text{site+time}}$	13	1597.32	41.70	0
$\phi_{\text{tsm+age}}\ \psi_{\text{sex}}\ p_{\text{site+time}}$	13	1597.32	41.70	0
$\phi_{\text{tsm+sex+site}}\ \psi_{\text{const.}}\ p_{\text{site+time}}$	13	1597.66	42.04	0
$\phi_{\text{tsm+site}}\ \psi_{\text{sex}}\ p_{\text{site+time}}$	13	1597.66	42.05	0
$\phi_{\text{tsm+sex}}\ \psi_{\text{sex}}\ p_{\text{site+time}}$	13	1598.50	42.88	0
$\phi_{\text{tsm}}\ \psi_{\text{site}}\ p_{\text{site+time}}$	12	1559.34	1.71	0.04
$\phi_{\text{site}}\ \psi_{\text{site}}\ p_{\text{site+time}}$	12	1560.23	2.60	0.03
$\phi_{\text{tsm}}\ \psi_{\text{age}}\ p_{\text{site+time}}$	12	1592.10	34.46	0
$\phi_{\text{site}}\ \psi_{\text{age}}\ p_{\text{site+time}}$	12	1592.86	35.22	0
$\phi_{\text{tsm+age}}\ \psi_{\text{const.}}\ p_{\text{site+time}}$	12	1597.33	39.69	0
$\phi_{\text{tsm+site}}\ \psi_{\text{const.}}\ p_{\text{site+time}}$	12	1597.67	40.03	0
$\phi_{\text{tsm+sex}}\ \psi_{\text{const.}}\ p_{\text{site+time}}$	12	1598.51	40.87	0
$\phi_{\text{tsm}}\ \psi_{\text{sex}}\ p_{\text{site+time}}$	12	1598.53	40.90	0
$\phi_{\text{site}}\ \psi_{\text{sex}}\ p_{\text{site+time}}$	12	1599.70	42.06	0
$\phi_{\text{tsm}}\ \psi_{\text{const.}}\ p_{\text{site+time}}$	11	1598.54	38.88	0
$\phi_{\text{site}}\ \psi_{\text{const.}}\ p_{\text{site+time}}$	11	1599.71	40.05	0
$\phi_{\text{const.}}\ \psi_{\text{const.}}\ p_{\text{site+time}}$	10	1601.03	39.35	0

QAICc = 6568.48

Appendix 3.C Differences in body size and body mass of red knots **Calidris canutus canutus** *in their wintering area Banc d'Arguin, Mauritania, West Africa, in winters 2002 - 2009*

Table 3.C1 Summary tables of linear regression models, non-significant (interaction) terms were dropped and models rerun

		Estimate	Std. Error	t-value	p-value
wing[1]	intercept	167.18	0.27	625.88	<0.001
	sex	-3.97	0.36	-11.1	< 0.001
	age	7	0.21	22.29	< 0.001
	sex:age	-0.95	0.43	-2.2	0.028
bill[2]	intercept	35.95	0.1	360.96	<0.001
	sex	-1.84	0.09	-21.19	<0.001
	site	0.31	0.10	3.13	0.002
tarsus[3]	intercept	32.86	0.07	440.07	<0.001
	sex	-0.63	0.06	-9.77	<0.001
	site	0.15	0.08	2.02	0.04
body mass[4]	intercept	0.09	0.41	0.21	0.8
	age	3.23	0.42	7.7	<0.001
	sex	-4.64	0.39	-11.9	<0.001

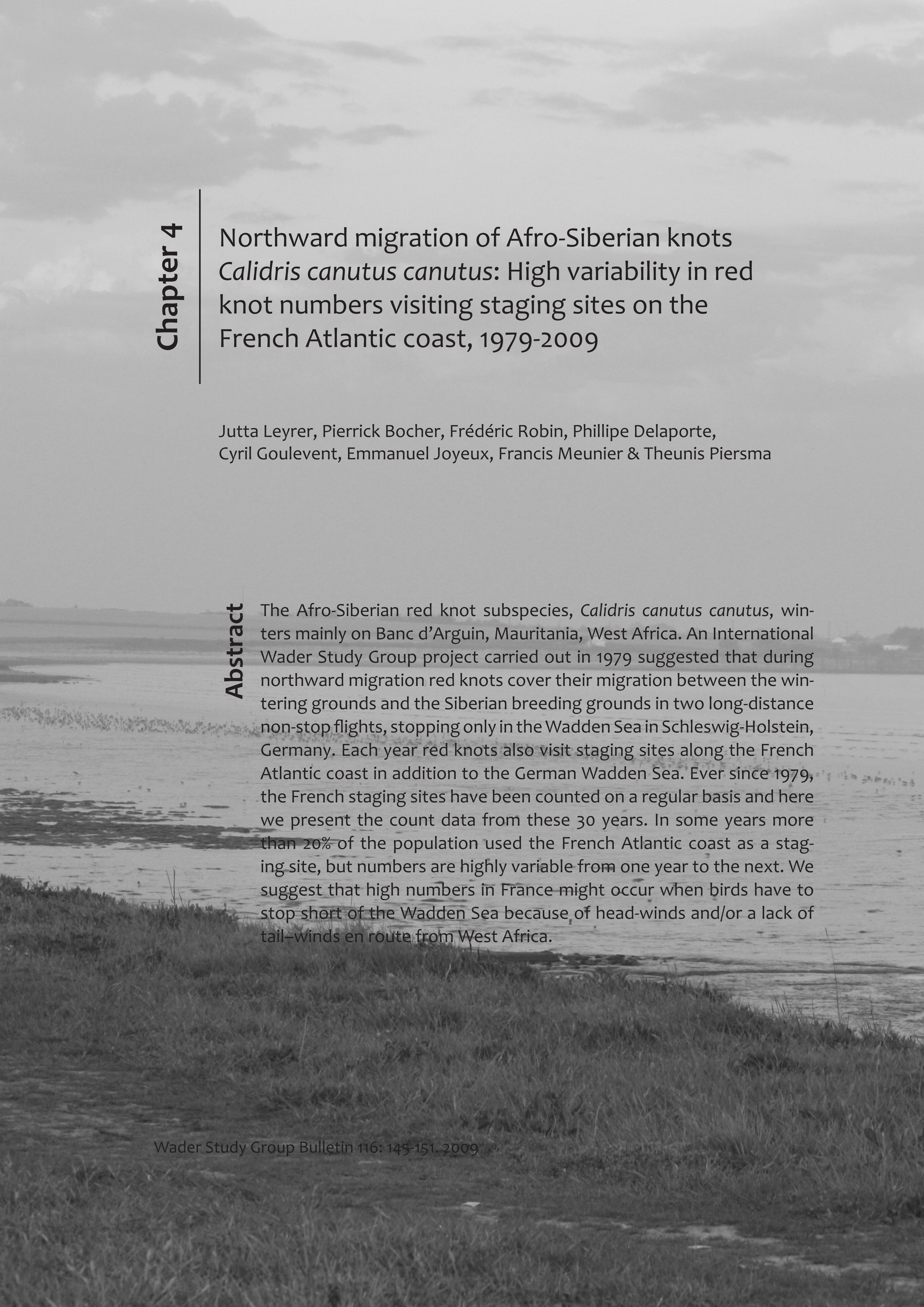
The parameter estimates for sex are given for males in relation to females, for age: adults in relation to juveniles, for site: Abelgh Eiznaya in relation to Baie d'Aouatif.

[1] $F_{3, 1471}=525.2$, $r^2=0.52$, $p < 0.001$; [2] $F_{2, 1472}=236.9$, $r^2=0.24$, $p < 0.001$
[3] $F_{2, 1472} = 51.9$, $r^2=0.06$, $p < 0.001$; [4] $F_{2, 1472}=109.7$, $r^2=0.13$, $p < 0.001$

Appendix 3.D Assessing differences in foraging conditions by means of satellite images

The extent and abundance of intertidal seagrass beds can be accurately assessed using satellite imagery, especially by calculating so called 'Normalized Difference Vegetation Indices' (NDVI; Ferguson & Korfmacher 1997, Mumby et al. 1997). Over the entire study period we found five suitable Landsat images (18 Dec 2001, 22 Jan 2003, 9 Jan 2007, 11 Sep 2009, and 17 Jan 2010; freely downloadable at http://landsat.usgs.gov), from which NDVI values were calculated for both sites (on the basis of pixels of 30 by 30 m). To make the images comparable, we applied so-called 'radiometric calibration' (Chander et al. 2009), using the image from 17 Jan 2010 as a reference.

opposite site:
Aerial photographs of Abelgh Eiznaya and the outer mudflats west of Iwik Peninsula. Photographs taken by EnHaut! Kite Aerial Photography.



Chapter 4

Northward migration of Afro-Siberian knots *Calidris canutus canutus*: High variability in red knot numbers visiting staging sites on the French Atlantic coast, 1979-2009

Jutta Leyrer, Pierrick Bocher, Frédéric Robin, Phillipe Delaporte,
Cyril Goulevent, Emmanuel Joyeux, Francis Meunier & Theunis Piersma

Abstract

The Afro-Siberian red knot subspecies, *Calidris canutus canutus*, winters mainly on Banc d'Arguin, Mauritania, West Africa. An International Wader Study Group project carried out in 1979 suggested that during northward migration red knots cover their migration between the wintering grounds and the Siberian breeding grounds in two long-distance non-stop flights, stopping only in the Wadden Sea in Schleswig-Holstein, Germany. Each year red knots also visit staging sites along the French Atlantic coast in addition to the German Wadden Sea. Ever since 1979, the French staging sites have been counted on a regular basis and here we present the count data from these 30 years. In some years more than 20% of the population used the French Atlantic coast as a staging site, but numbers are highly variable from one year to the next. We suggest that high numbers in France might occur when birds have to stop short of the Wadden Sea because of head-winds and/or a lack of tail–winds en route from West Africa.

Wader Study Group Bulletin 116: 145-151. 2009

Introduction

Afro-Siberian red knots *Calidris canutus canutus* breed in central Siberia and mainly winter along the West African coast, where ca. 75% of the population is concentrated on the Banc d'Arguin, Mauritania (Piersma et al. 1992, Stroud et al. 2004). The majority of these birds perform their northward migration from the Banc d'Arguin in two long-distance flights of more than 4,000 km each via the major staging area within the East Atlantic flyway, the European Wadden Sea (figure 4.1, Piersma et al. 1992). During the second half of May until early June, Afro-Siberian red knots refuel in the Schleswig-Holstein, German, part of the Wadden Sea before they leave for the last leg of their migration, arriving at their breeding grounds on Taymyr Peninsula just before mid June (Prokosch 1988, Piersma et al. 1992, Piersma et al. 1994).

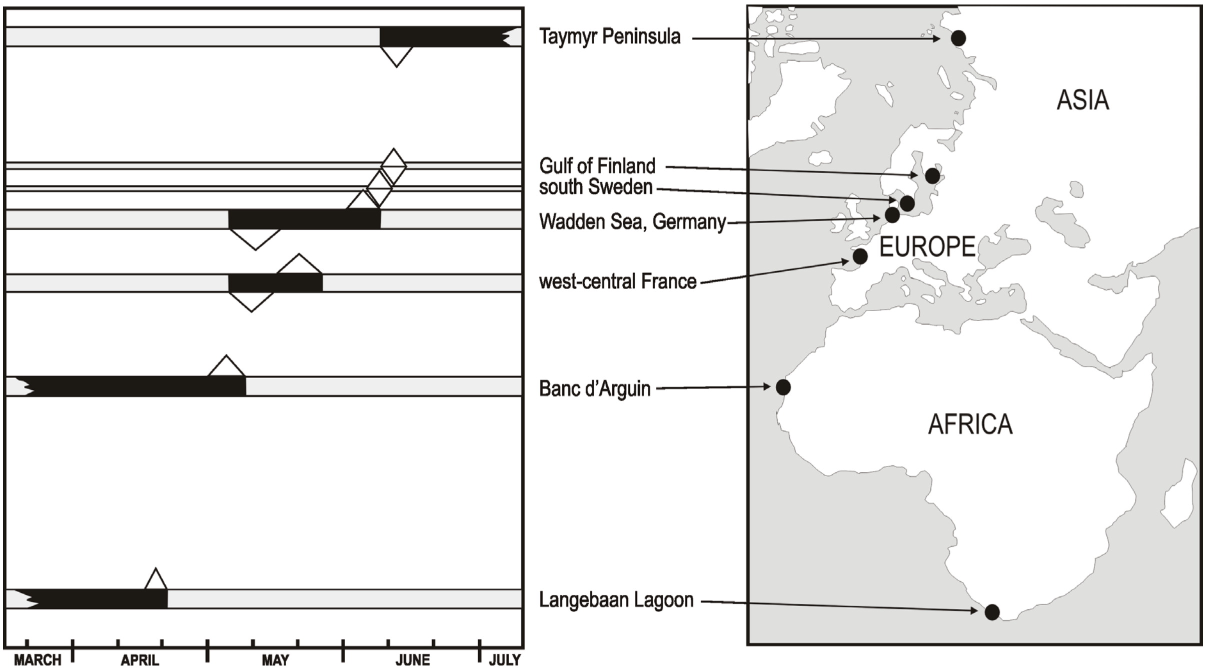


Figure 4.1 The Afro-Siberian red knots *Calidris canutus canutus* that migrate from wintering grounds in South and West Africa to breeding grounds in High Arctic Siberia along the coasts of Africa and Europe have a tight schedule. Black bars indicate staging/fuelling periods, upward pointing triangles departure periods, downward pointing triangles arrival periods. Triangles with no blocks indicate passing birds only (graph from Piersma et al. 1992).

In addition to the Schleswig-Holstein Wadden Sea, a highly variable number of red knots use intertidal areas in the Vendée and Charente-Maritime area of the central Atlantic coast of France on their northward journey (Piersma et al. 1992, van de Kam et al. 2004). It has been assumed that the majority of red knots visiting the French staging sites are in need of an additional stopover because they have run out of fuel and cannot make it to their main staging area in the Wadden Sea in one long flight. It has been suggested that fuel shortage in some of the birds was due to unfavourable winds during the flight from West-Africa leading to a faster depletion of stores (van de Kam et al. 2004). These assumptions are based on detailed studies on the northward migration of Afro-Siberian red knots during the 1980s (Dick et al. 1987, Piersma 1987, Piersma et al. 1992, van de Kam et al. 2004). In the meantime, we have collected more count data on the spring passage of Afro-Siberian red knots on the French Atlantic coast.

Red knots are the most numerous wader species in the area in May (Bredin & Doumeret 1986) and the French staging sites present the most important staging sites between the African wintering grounds and the main staging sites in the Schleswig-Holstein Wadden Sea (Piersma et al. 1992). As part of an International Wader Study Group project, regular counts were initiated in the early 1980s. Here, for the first time, we present a detailed account of all spring counts collected over 30 years.

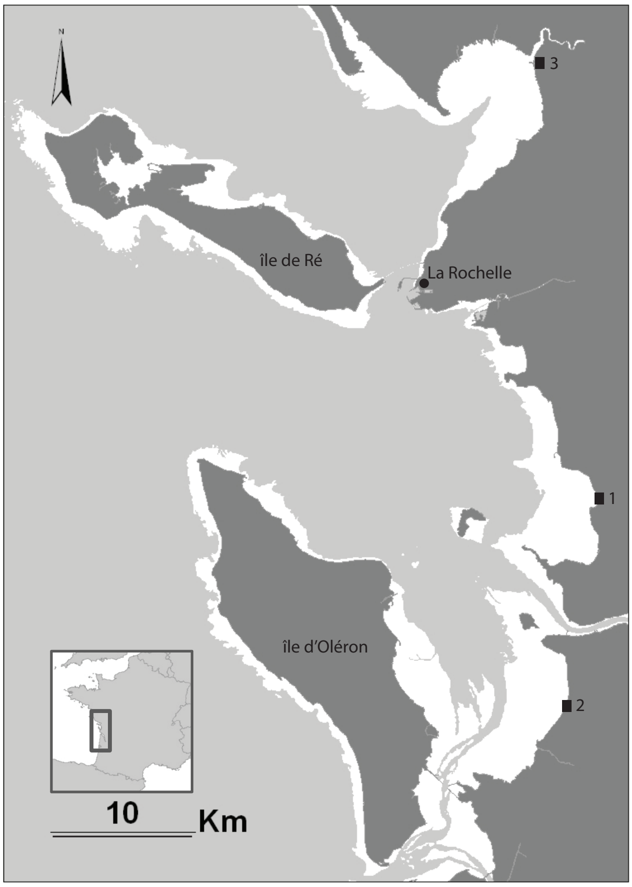


Figure 4.2 Red knot counting sites along the central Atlantic coast of France. There are two main high tide roosts in the southern area: Yves Bay (1) and Marennes-Oléron Bay (2). In Aiguillon Bay (3), birds have been counted on the mudflats (white areas) during incoming and/or outgoing tide.

Methods

In ten of the 30 years 1979-2009, counts were carried out at most known high tide roosts in the South Vendée and Charente-Maritime districts ('Pertuis Charentais'), France. The main areas covered were: Aiguillon Bay (46°16'29"N, 1°09’50”W), Yves Bay (46°02'17"N, 1°05'09"W) and Marennes-Oléron Bay (45°53'29"N, 1°05'59"W) (figure 4.2). The frequency of count-days and the high tide roosts covered varied in some years (details in table 4.1). In Yves Bay and Marennes-Oléron Bay, counts were carried out at the roosts around high tide. In Aiguillon Bay the high tide roost sites are scattered and not always accessible, thus birds were counted on the mudflats when the tide was incoming or outgoing.

In figures 4.3 and 4.4, we present the numbers of red knots counted for the Yves & Marennes-Oléron Bay and the Aiguillon Bay area, respectively. Because in some years only part of the sites were counted or counts were not made on a single day which might have led to birds being missed or double-counted (see table 4.1, figure 4.3), we have estimated the total red knot population staging in the area by linear interpolation of the counted numbers. Assuming a linear daily increase or decrease of birds visiting the sites we calculated the total sum of 'bird days' for each year (table 4.1). 'Bird days' can be used to express the numbers of birds visiting a site; e.g. 20 bird days is either 20 birds visiting a site for one day or one bird visiting a site for 20 days.

To assess the variability of counts between years encountered at the French staging sites in spring, we looked for other data sets where counts were made in the same time period in a comparable number of years in well-defined areas. We calculated the coefficient of variation (CV) as: standard deviation / mean of maximum numbers counted. One comparable dataset for a red knot staging site is for Porsangerfjord, Norway, in the flyway of the *islandica* subspecies. Data were taken from (Strann 1992, Wilson &Strann 2005, Wilson et al. 2006, 2007, 2008). Within this series of count data for nine years between 1985 and 2008 there seemed to be one odd year (1989) when a substantially higher number of red knots visited the area for reasons that were not further elaborated. We calculated CV with and without 1989. Another dataset came from wintering *canutus* red knots on Banc d'Arguin that was collected during regular expeditions in November and December between 2002 and 2008 (T. Piersma, B. Spaans & M. Brugge unpubl. data; for locations see Leyrer et al. (2006)). Note that we did not use count data from the Wadden Sea: the high variation in red knot numbers in the counts is very likely to reflect their large home ranges (Piersma et al. 1993b, van Gils & Piersma 1999) and the potentially resulting variable use of different high tide roost sites, rather than real variation in numbers visiting the whole Wadden Sea.

Results

The numbers of red knots staging in the study area varied considerably between years (figures 4.3 and 4.4, table 4.1). In Yves & Marennes-Oléron Bay, maximum numbers were as high as 12,000 in 1979, 10,850 in 1985, and 10,656 in 2006 and as low as 3,442 in 1986 and 4,149 in 1988. Numbers using Aiguillon Bay were much higher than at Yves & Marennes-Oléron Bay, but showed comparable fluctuations with maxima as high as 24,120 in 1985, 35,965 in 2005, 28,976 in 2006 and 26,126 in 2008 and as low as 13,000 in 1986, 14,173 in 2007 and 12,944 in 2009.

The French staging sites showed a considerably higher variation in annual usage (CV = 0. 49 at Yves & Marennes-Oléron Bay and CV = 0.38 at Aiguillon Bay) than both the Norwegian staging site (CV = 0.27 with 1989 and CV = 0.15 without 1989) and the wintering site in Mauritania (CV = 0.15) (figure 4.5).

Discussion

Data collected during 2000-2009 give no reason to re-assess the view (expressed, for example, by (Piersma et al. 1992, van de Kam et al. 2004) that numbers of Afro-Siberian red knots visiting the French Atlantic coast during northward migration vary considerably from year to year in all areas counted. Many more knots use Aiguillon Bay than Yves & Marennes-Oléron Bay, despite the fact that Aiguillon Bay has a smaller surface area.

Red knots of the same *canutus* subspecies, and probably of the same population, are highly site-faithful in their Mauritanian wintering areas (Leyrer et al. 2006) and numbers wintering in a given area do not differ much between years (figure 4.5). Also, numbers at Porsangerfjord in Norway, which is the last staging site before reaching the Arctic breeding grounds for *islandica* red knots using the route via Norway (Davidson &Wilson 1992), have been stable between years.

The Afro-Siberian red knot population has recently been estimated at approximately 400,000 individuals (Delany et al. 2009, Spaans et al. 2011). If numbers of first-year birds (based on proportions from winter catches at Banc d'Arguin, T. Piersma et al. unpubl. data) that are thought to spend their first summer in their wintering areas are deducted, the migrating population is

Table 4.1 Counts of red knots staging on the central Atlantic coast of France: number of counts at each site, period over which counts made, maximum count, and bird-days (calculated by interpolating counts for days when no counts took place and summing the daily values).
* interpolated bird days for the whole Yves & Marennes-Oléron Bay area.

Year	Site	No. of counts	Period	Max. count	Bird-days
1979	Yves & Marennes-Oléron Bays	6	8–24 May	12,000	75,500
	Aiguillon Bay	6	8–24 May	25,000	220,000
1985	Yves & Marennes-Oléron Bays	7	25 Apr–5 Jun	3,998	143,369
	Aiguillon Bay	6	23 Apr–27 May	24,120	450,000
1986	Yves & Marennes-Oléron Bays	11	25 Apr–20 May	3,442	34,490
	Aiguillon Bay	5	23 Apr–24 May	13,000	253,813
1987	Yves & Marennes-Oléron Bays	8	28 Apr–27 May	6,014	89,303
1988	Yves & Marennes-Oléron Bays	10	2–30 May	4,149	67,981
2005	Yves & Marennes-Oléron Bays	14	20 Apr–25 May	7,700	53,680
	Aiguillon Bay	14	20 Apr–25 May	35,965	251,293
2006	Yves & Marennes-Oléron Bays	14	24 Apr–24 May	10,656	83,342
	Aiguillon Bay	13	24 Apr–22 May	28,976	213,307
2007	Yves Bay	12	27 Apr–23 May	1,900	59,717*
	Marennes-Oléron Bay	8	22 Apr–17 May	2,800	
	Aiguillon Bay	5	8–17 May	14,173	77,406
2008	Yves Bay	7	25 Apr–19 May	1,100	41,223*
	Moëze Nature Reserve	11	18 Apr–19 May	2,600	
	Oléron Island	6	18 Apr–19 May	530	
	Aiguillon Bay	3	6–19 May	26,126	205,545
2009	Yves Bay	14	21 Apr–19 May	6,000	
	Marennes-Oléron Bay	8	21 Apr–29 May	3,500	55,007*
	Aiguillon Bay	2	6–11 May	12,944	71,022

roughly 250,000 individuals. Thus, it is probable that in some years >20% of the total migrating population uses the French staging sites during their northward journey, but in other years far less. However, the reason for this year-to-year variation has not been conclusively determined.

In 2005 and 2006, studies of food abundance were carried out throughout our study area. The staging sites seem to provide food in both sufficient quantity and quality and there were no indications of high variation in food availability between years (F. Robin et al. in prep.). It therefore appears unlikely that, by their variable use of the French stopover sites, red knots have been responding to variation in food availability. Moreover red knots leaving Mauritania for a non-stop flight to their main staging site in the German Wadden Sea are unlikely to have any indication about the food situation in France unless they make a landfall there. We therefore suggest that food abundance does not determine the numbers of red knots staging on the Atlantic coast of France.

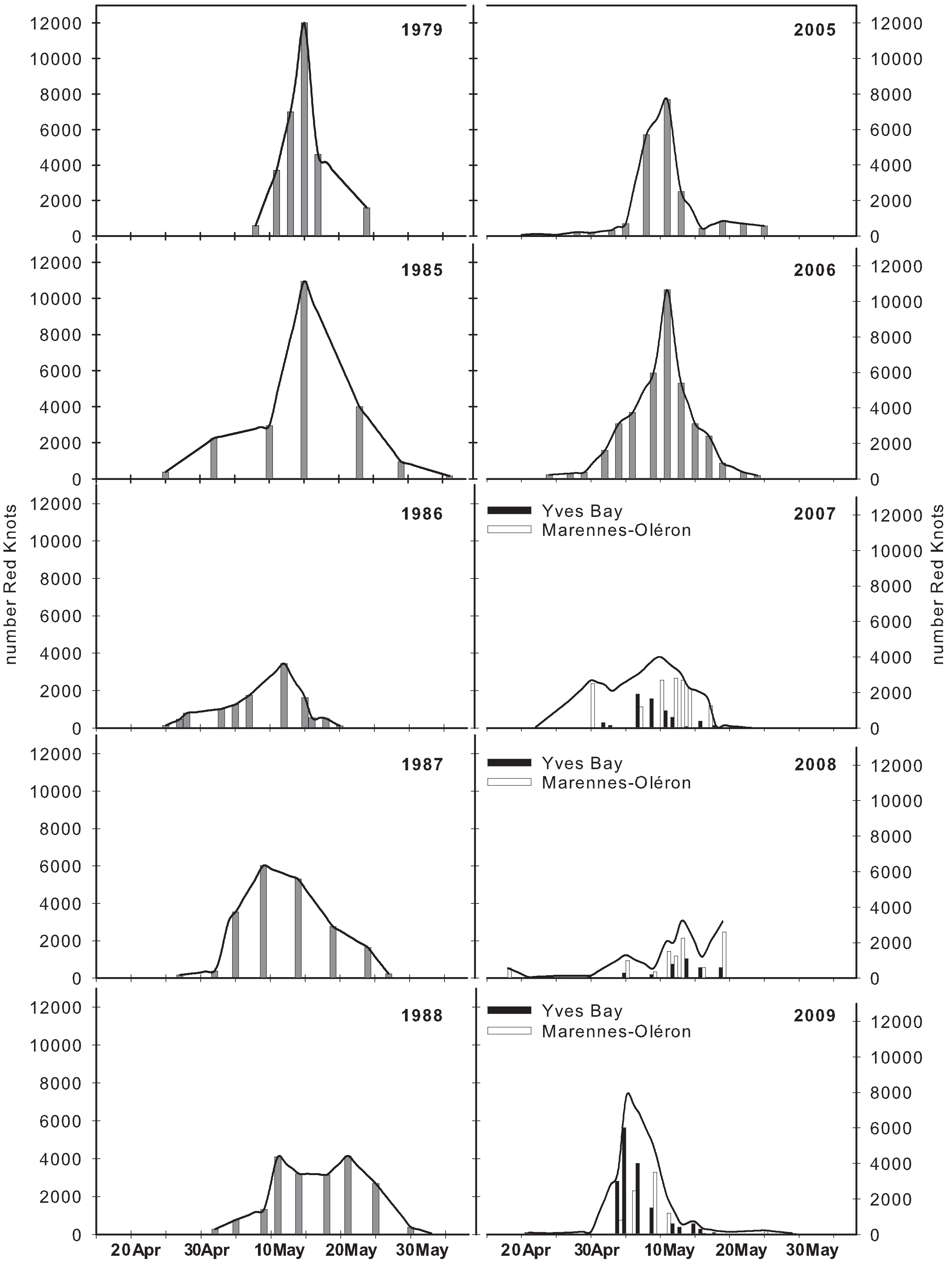


Figure 4.3 Numbers of red knots counted (bars) and estimated (lines) in different years in Yves Bay and Marennes-Oléron Bay, France.

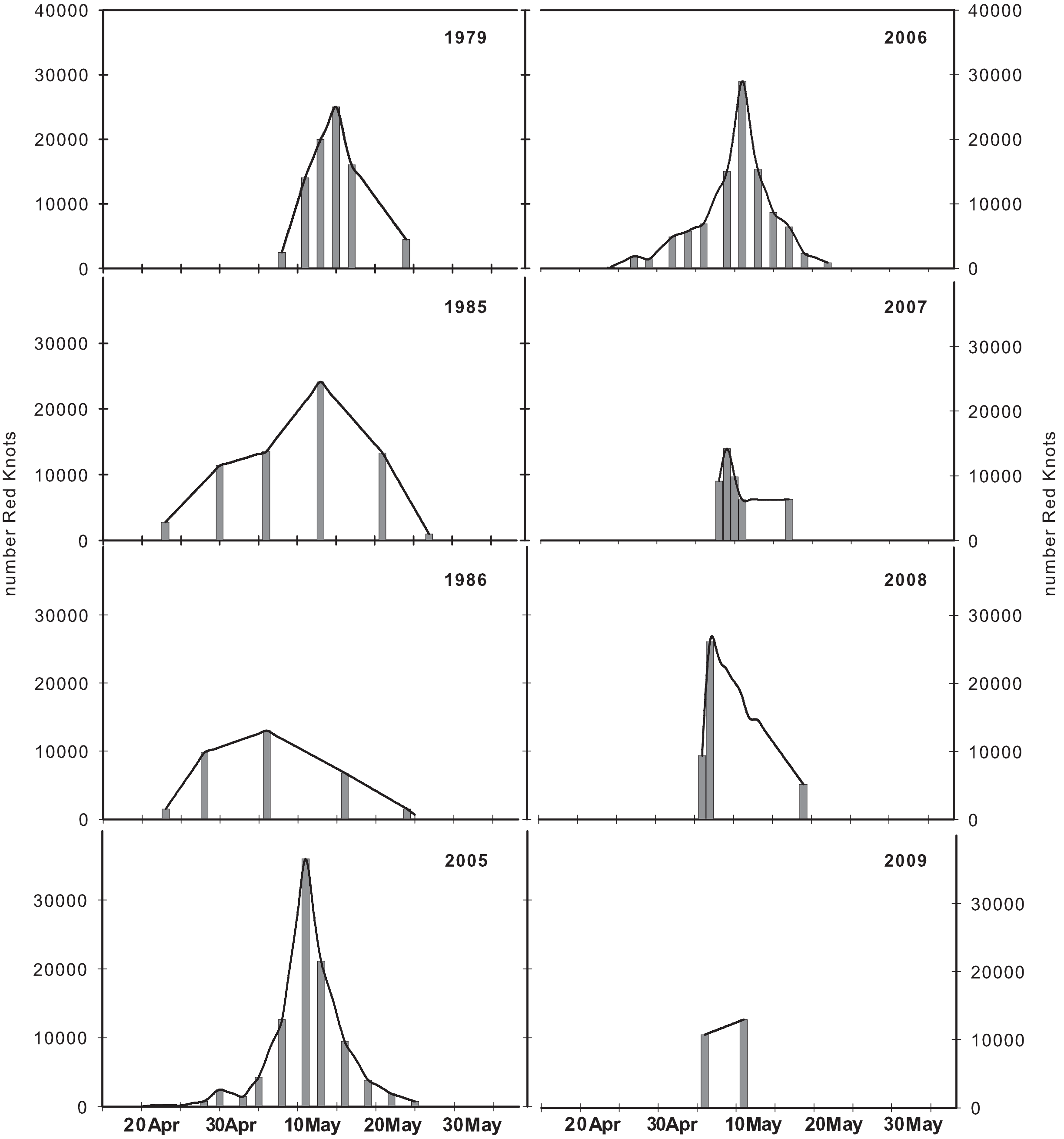


Figure 4.4 Numbers of red knots counted (bars) and estimated (lines) in different years in Aiguillon Bay, France.

Fuelling conditions in spring prior to northward migration at the Banc d'Arguin have been studied in the late 1970s (Altenburg et al. 1982), the mid 1980s (Wolff & Smit 1990, Zwarts et al. 1990a) and in 2007 (van Gils et al. 2009b). Over that time, food and fuelling conditions do not seem to have deteriorated yet the local wintering population of knots has declined by 50%, resulting in a lower bird density compared with a stable density (van Gils et al. 2009b). Therefore it seems that fuelling conditions at the wintering site are not a key factor determining the use of the French staging sites. During northward migration, Afro-Siberian red knots presumably prefer to jump in long-distance flights with only a few stops between wintering and breeding grounds (Dick et al. 1987, Piersma 1987, Piersma et al. 1992). The use of each staging site carries costs, as the birds need to spend time to settle down and find food and, especially in

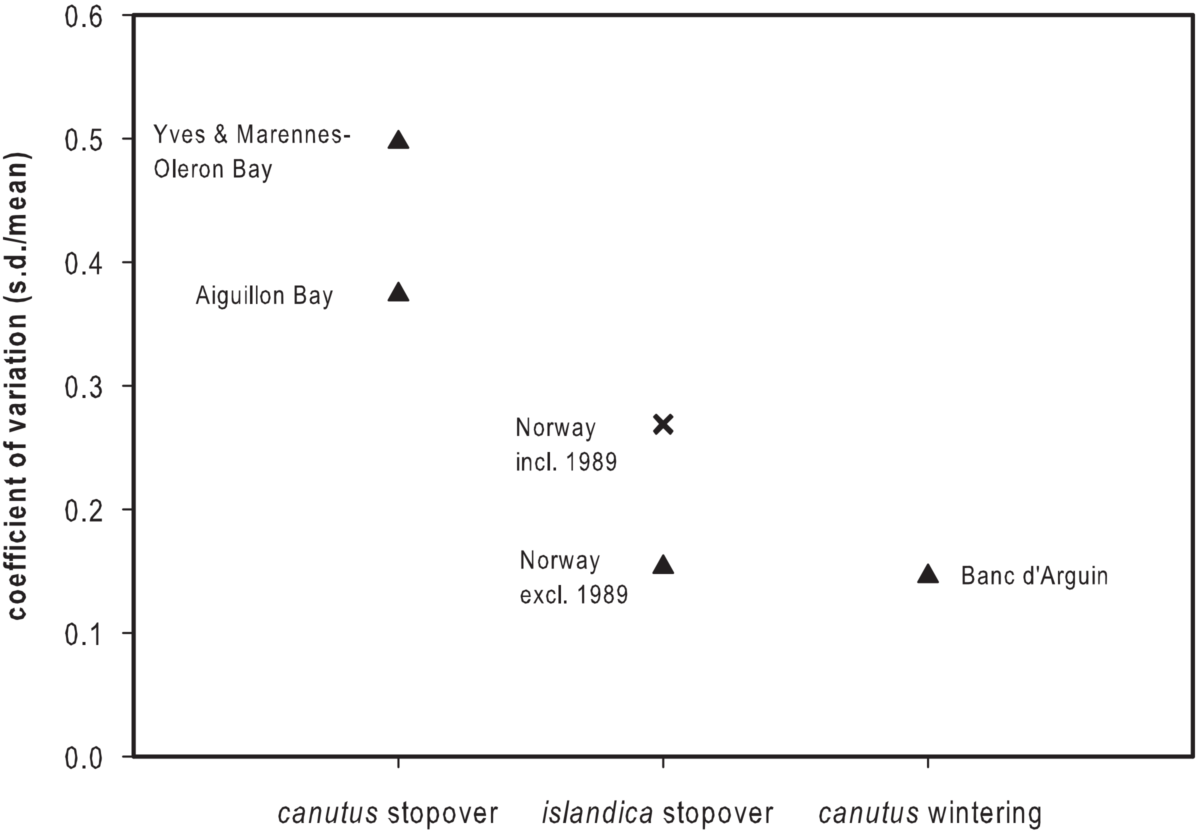


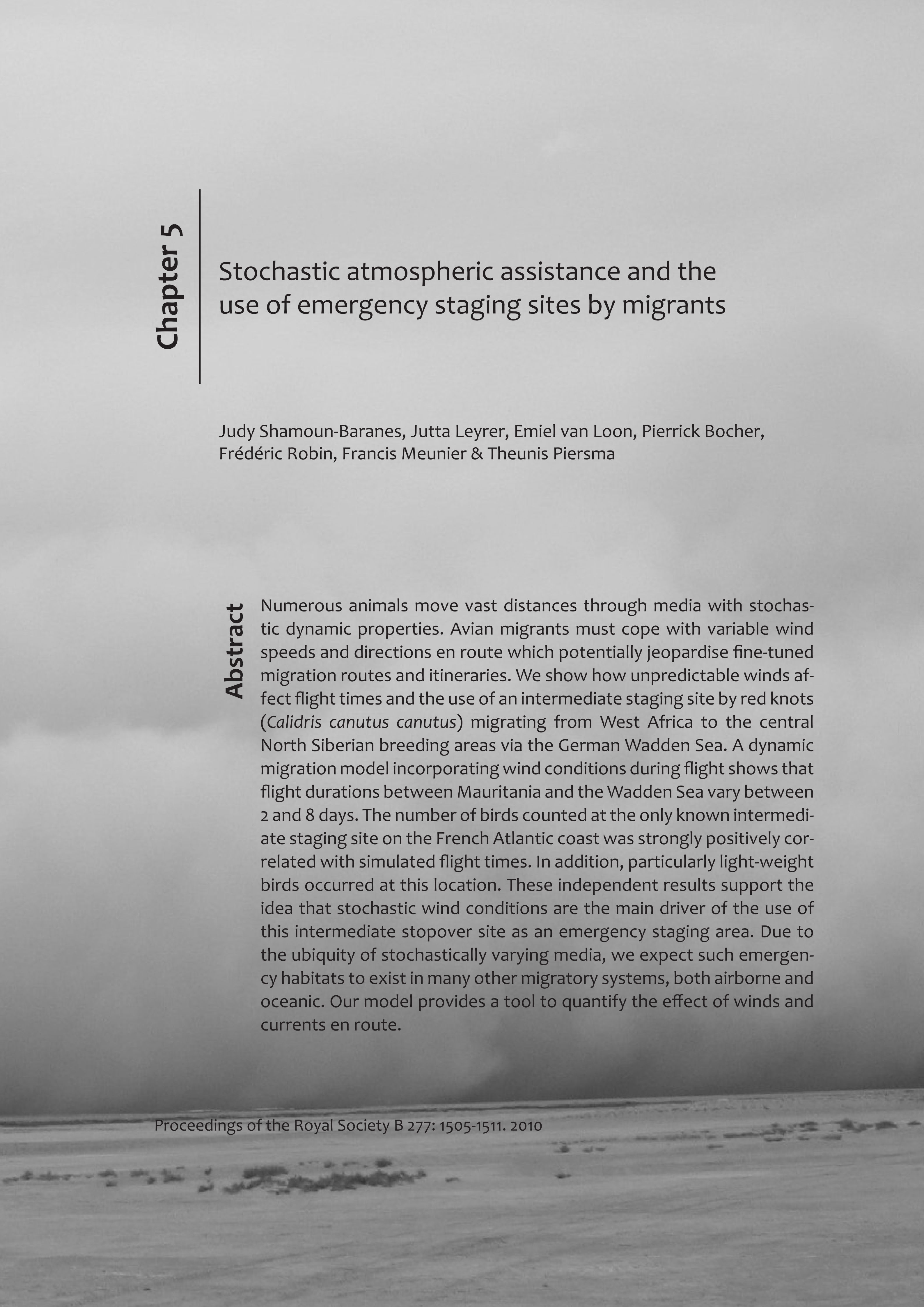
Figure 4.5 Staging sites along the French Atlantic coast show high year-to-year variation in numbers of red knots during spring migration compared to other sites. Coefficient of Variation = standard deviation / mean for various spring staging sites (Yves & Marennes-Oléron Bays and Aiguillon Bay in France, and Porsangerfjord in Norway) and a wintering site (Iwik Peninsula, Banc d'Arguin, Mauritania). Data included are maximum numbers for all spring staging sites, and total winter counts for Banc d'Arguin. Data for Norway were taken from Strann (1992), Wilson & Strann (2005) and Wilson et al. (2006, 2007, 2008). In the Norway data, 1989 seemed to have been an odd year and thus we present two coefficients (with and without 1989). Data for Banc d'Arguin are from T. Piersma (unpubl. data).

the case of red knots, adjust their body structure from flying (large flight muscles, small digestive system) to fuelling (enlarging the digestive system) (e.g. Piersma et al. 1993c, Piersma 1998). Thus they incur both time and energy costs. Additionally, birds on the ground generally face a higher predation risk than during flight (e.g. Gill et al. 2009). Thus, including an extra stopover on their way from Banc d'Arguin to their main staging area in the Wadden Sea does not seem to be advantageous. Yet, in some years, large proportions of the population (>20%) visit the French Atlantic coast in spring.

Red knots departing from Banc d'Arguin have body masses of <180 g (Piersma et al. 1992), which is hardly enough for a 4,500 km journey without wind assistance (Piersma & Jukema 1990). It is therefore quite likely that in some years they will not be able to reach the Wadden Sea in one non-stop flight relying on energy stores alone. Several studies have highlighted the importance of tailwinds in supporting such long-distance flights, but no study has shown that departure intensity from Banc d'Arguin is correlated with favourable tailwinds because in this area such winds are rare at ground level (e.g. Piersma et al. 1990a, Piersma & van de Sant 1992, van de Kam et al. 2004). Indeed, red knots departing from Mauritania are not able to time their take-off to benefit from favourable wind conditions since winds are unpredictable and change-able between years, and also between days (Shamoun-Baranes et al. 2010). Thus, red knots that encounter headwinds will spend more energy during flight and run out of fuel before they arrive at their destination. So it seems that red knots use the French Atlantic coast sites as an emergency stopover, which is visited only when wind conditions are unfavourable (Shamoun-Baranes et al. 2010). The stochastic nature of winds may well explain the high year-to-year variation in the occurrence of knots in this area.

Acknowledgements

We thank Denis Bredin and Alain Doumeret who co-initiated the first counts in the 1980s in co-operation with International Wader Study Group red knot project co-ordinated by William J.A. Dick. We say a big thank you to all the managers and technicians working in the nature reserves. From the nature reserves in Aiguillon Bay ONCF Office national de la chasse et de la faune sauvage and LPO Ligue pour la Protection des Oiseaux Frédéric Corre and Sylvain Haie and all counters: Jaques Marquis, Aurélie Batailleau, Vivien Varoquaux, Marion Boursier, Grégoire Laugier, Phillipe Prieto, Philippe Pineau, and Valérie Huet. From the LPO nature reserve Marais d'Yves: Marie Laure Cayatte, Jean Paul Pillion and Karine Vennel and all counters: Alban Belin, Vincent Delecour, Fabrice Lasserre, Guillaume Roquier, Jérome Fernandez, Rodolphe Delbeque, Benoît Lunven, Guillaume Ogereau, Cécile Detroit, Amélie Fauvel, Mélissa Gallais, Karsten Schmale, Romain Cavier, Nicolas Chaslard, Adeline Pichard, Hélène Hamon, Sylvie Lebhourhis and Elodie Reveillac. From the LPO nature reserve Moëze-Oléron: Jérôme Gauthier, Julien Gonin, Pierre Rousseau and counters: Xavier Reyberat and Guillaume Rethore. We thank Judy Shamoun-Baranes and Silke Nebel for helpful comments on earlier versions of the manuscript.



Chapter 5

Stochastic atmospheric assistance and the use of emergency staging sites by migrants

Judy Shamoun-Baranes, Jutta Leyrer, Emiel van Loon, Pierrick Bocher, Frédéric Robin, Francis Meunier & Theunis Piersma

Abstract

Numerous animals move vast distances through media with stochastic dynamic properties. Avian migrants must cope with variable wind speeds and directions en route which potentially jeopardise fine-tuned migration routes and itineraries. We show how unpredictable winds affect flight times and the use of an intermediate staging site by red knots (*Calidris canutus canutus*) migrating from West Africa to the central North Siberian breeding areas via the German Wadden Sea. A dynamic migration model incorporating wind conditions during flight shows that flight durations between Mauritania and the Wadden Sea vary between 2 and 8 days. The number of birds counted at the only known intermediate staging site on the French Atlantic coast was strongly positively correlated with simulated flight times. In addition, particularly light-weight birds occurred at this location. These independent results support the idea that stochastic wind conditions are the main driver of the use of this intermediate stopover site as an emergency staging area. Due to the ubiquity of stochastically varying media, we expect such emergency habitats to exist in many other migratory systems, both airborne and oceanic. Our model provides a tool to quantify the effect of winds and currents en route.

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Introduction

Migratory animals spend different parts of their lives in widely separated and ecologically distinct locations. Their migratory movements can be very long, energetically costly, and often take place in stochastically dynamic conditions (Dingle 1996, Liechti 2006, Chapman et al. 2008, Gill et al. 2009, Sale & Luschi 2009). As a consequence, animals must store enough fuel to travel, they need to stop in suitable habitats to refuel or rest, and they may need to make use of environmental assistance (e.g. wind or currents) in order to migrate successfully. In birds, migration can comprise up to 50% of the annual energy budget (Drent & Piersma 1990). As wind speeds are within the same order of magnitude as bird flight speeds, wind can have a strong impact on the cost and speed of migration (Liechti & Bruderer 1998, Shamoun Baranes et al. 2003).

A well studied example of a long-distance migrant is the red knot (*Calidris canutus*). The Afro-Siberian nominate subspecies *C.c. canutus* migrates north in two non-stop flights of approximately 4,400 km each from the Mauritanian wintering grounds via the German Wadden Sea (figure 5.1a) to the Siberian breeding grounds in only four weeks (Piersma et al. 1992, van de Kam et al. 2004). Although, red knots and other wader species worldwide routinely make such long non-stop flights (Pennycuick & Battley 2003, van de Kam et al. 2004, Piersma et al. 2005, Gill et al. 2009), individuals may deplete energy stores before reaching their final destination due to unfavourable wind conditions during flight (Piersma & van de Sant 1992, van de Kam et al. 2004). Mauritania is within the trade wind zone where headwinds prevail during spring migration. Previous studies failed to find correlations between surface winds and departure intensity (Piersma et al. 1990a, Piersma & van de Sant 1992); therefore, red knots embarking from Mauritania cannot optimize departure dates on the basis of surface winds. In addition, red knots depart from Mauritania with such low body mass (Dick et al. 1987, Piersma et al. 1992) that a successful migration from Mauritania to the Wadden Sea seems unlikely without wind support.

Annually, highly variable numbers of red knots use stopover sites at the French Atlantic coastal wetlands. In some years over 50,000 individuals use these sites, which is about 25% of the migratory population, whereas in other years these sites are skipped (Stroud et al. 2004, van de Kam et al. 2004, Leyrer et al. 2009a). Due to the specialized diet of red knots, suitable refuelling sites are discretely distributed along the migratory route (Piersma 2007); thus, red knots must fly relatively large distances non-stop with sufficient energy stores before reaching the next suitable refuelling site. However, increasing energy stores increases transport costs and reduces flight manoeuvrability (Kvist et al. 2001, van den Hout et al. 2010), whereas, increasing stopover frequency or duration increases migration time (Newton 2008).

Migration theory predicts that birds minimizing time during migration should store enough fuel in advance and save time by skipping sites with low or unpredictable food supply (Alerstam & Hedenström 1998). Thus birds trying to minimize the total amount of time spent on migration would benefit from storing extra fuel at high quality stopover sites and bypassing sites with lower food quality or quantity. Evidence for skipping has been put forward by a few theoretical and empirical studies (Gudmundsson et al. 1991, Weber et al. 1994, Beekman et al. 2002). These studies focus on the importance of food quality or availability and not the potential influence of wind on stopover site selection.

Wind conditions can strongly influence the cost and speed of migration (Liechti & Bruderer 1998, Shamoun Baranes et al. 2003) as well as stopover duration and take-off decisions (Åkesson & Hedenström 2000, Weber & Hedenström 2000, Åkesson et al. 2002b, Schaub et al. 2004).

Here we propose that irregular site use is an emergency stopover strategy of birds running out of fuel when winds are unfavourable during flight. We introduce the concept that staging site use is a function of stochastic wind conditions. Using a dynamic model, we studied the impact of winds en route at different flight altitudes, migratory start dates and years on flight times. Under increasingly unfavourable wind conditions en route, resulting in longer flight times, we expect that more birds would use the emergency staging site in France. To test this we compared modelled flight times to observed site use on the French Atlantic coast (figure 5.1a).

Methods

Spring migration of red knots *C. c. canutus* from their main wintering area on Banc d'Arguin, Mauritania (19°53'N 16°17'W), to their staging area in the German Wadden Sea (54°01'N 8°48'E) (figure 5.1a) was simulated based on current knowledge of the migration system of this subspecies (Piersma et al. 1990a, 1992, Piersma 2007). The model framework provides a way to simultaneously explore the impact of daily, annual and altitudinal wind variability on flight time along a pre-defined migration route.

Model description

A dynamic model was designed to simulate red knot spring migration using a deterministic one dimensional ODE (ordinary differential equations)-model, implemented by a fixed 6 h time-step forward integration scheme. Six hourly u and v wind components with a 2.5° x 2.5° spatial resolution were extracted for four standard pressure levels (1000mb, 925mb, 850mb, 700mb; corresponding to 111m, 766m, 1457m and 3012m above mean sea level respectively at standard atmospheric conditions (Anonymus 1976) from the NCEP-NCAR reanalysis dataset (Kalnay et al. 1996). In this model, birds moved along a great circle trajectory between the wintering and main stopover site. Air speed of the birds was kept constant (16 ms^{-1}; Noer 1979, Gudmundsson 1994, Kvist et al. 2001); therefore flight time can be considered an indirect measure of flight cost by calculating mechanical power output based on aerodynamic theory (Pennycuick 2008). Ground speed was calculated at each time-step based on wind speed and direction, track heading and air speed (Shamoun-Baranes et al. 2007) at that time and location. Resulting flight times are a direct measure of wind assistance; lower flight times reflect stronger wind assistance. Winds along the flight trajectory were calculated via linear interpolation of the u and v wind components. If wind prohibited forward movement along the trajectory the bird stopped flying until the next time-step. The simulation was run for consecutive migratory start dates (1 May-10 May) with migration starting at 18:00 UTC, at four different pressure levels, for the years 1979-2007. The start dates were selected based on field observations of take-off in Mauritania and arrival in France (Dick et al. 1987, Piersma et al. 1992, 2005). Red knots are considered to predominantly depart for migration in the early evening (Piersma et al. 1990a, but see Leyrer et al. 2009b). Corresponding to the weather data time steps, the model is run in 6 hour time steps thus 18:00 UTC is the most suitable simulation start time. Each of the above simulations was run for a constant pressure level. In addition, we explored an optimal altitude simulation where the pressure level with the highest resultant ground speed at each time step was selected. However, results for the optimal altitude runs did not provide further insight and therefore detailed results are not presented here (see electronic supplementary material for the MATLAB simulation code).

Flight times were calculated along the entire trajectory per migratory start date, pressure

Figure 5.1 (opposite page upper graph) Simulated spring knot migration along the great circle route (a straight line in the chosen map projection) from Banc d'Arguin, Mauritania (circled 1), through their potential staging site along the French Atlantic Coast (circled 2) to their main stopover in the German Wadden Sea (circled 3). **a** Flight trajectories for 1985 (left) and 1986 (right), with May 5 as the starting date. Each segment marks a 6 h time interval. **b** The probability density functions of cumulative flight time up to different latitudes (i) up tp 54° N, (ii) up to 45° N, (iii) up to 36° N and (iv) up to 27° N, over all years (1979 – 2007) and all starting dates (May 1 – May 10) per pressure level.

level and year, resulting in 1,160 simulations (10 days, 29 years, 4 pressure levels). The effects of year (n = 29), start date (n = 10) and pressure level (n = 4) were investigated by using non-parametric replacements for one-way and two-way analysis of variance, the Kruskal-Wallis and Friedman tests (Gibbons & Chakraborti 2003) respectively. In our analysis non-parametric tests are preferred over the normal analysis of variance due to the skewed distribution of flight times, especially within pressure level. Results are reported as significant for p-value < 0.05.

Red knot counts

Red knots were counted during northward migration at known staging sites at the French Atlantic coastal wetlands during several years between 1979 and 2007 (Leyrer et al. 2009a). Counted numbers were linearly interpolated over the main stopover period (25 April-25 May) for each year and bird-days were calculated from the daily interpolation results (Leyrer et al. 2009a). We expect that in years where winds experienced en route are more unfavourable, and hence flight times are longer, more birds will stop in France. The French stopover site is approximately 1000 km from the German Wadden Sea, a distance which can be covered in windless conditions in less than 24 hours (4 simulation time steps). We assume that a bird's decision to stop in France is based on the wind experienced so far and an expectation for what would be experienced further along the trajectory. To test if future wind conditions en route can be predicted over France, we calculated the Pearson correlation per pressure level between simulated ground speeds over France and simulated ground speeds further along the trajectory (up to 6 time steps), ground speeds being a proxy for wind conditions. The results are provided as auto-correlograms.

Finally, to test the relation between staging site usage in France and wind conditions experienced en route, we fitted a linear regression model to the number of birds staging in France (the dependent variable) as a function of the simulated flight time for the entire trajectory, averaged over all the possible departure dates (the independent variable). A separate model was fitted for each pressure level. We calculated the Pearson correlation coefficient to measure the degree of linear association between simulated flight duration and observed bird-days at the French staging site. We provide results for models with significant correlations ($p < 0.05$) only.

Figure 5.2 (opposite page upper graph) Flight times per simulation and mean flight times in relation to observations. **a** The checkerboard plots show simulated number of flight days per pressure level. Each grid cell represents a separate simulation. The plots in the margins highlight the mean and range of flight time by grouping the simulations per year (above) and per start date (left). The circles in the plots in the top margin represent observations in France. **b** Observations (circles) and their corresponding years and linear regression (black line) for number of bird days and the respective mean flight time per pressure level (n = 8). Grey lines represent 95% confidence boundaries.

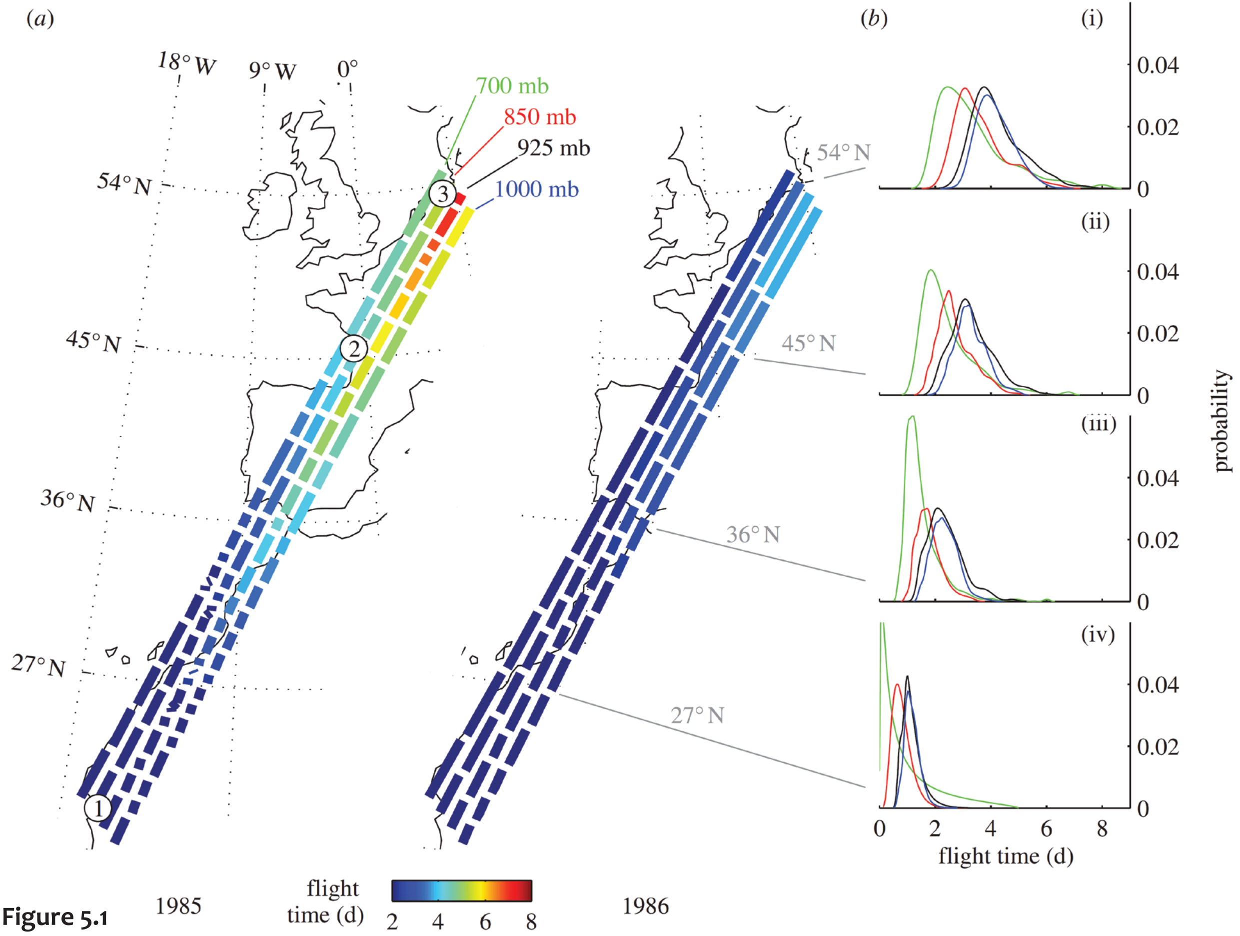

Figure 5.1

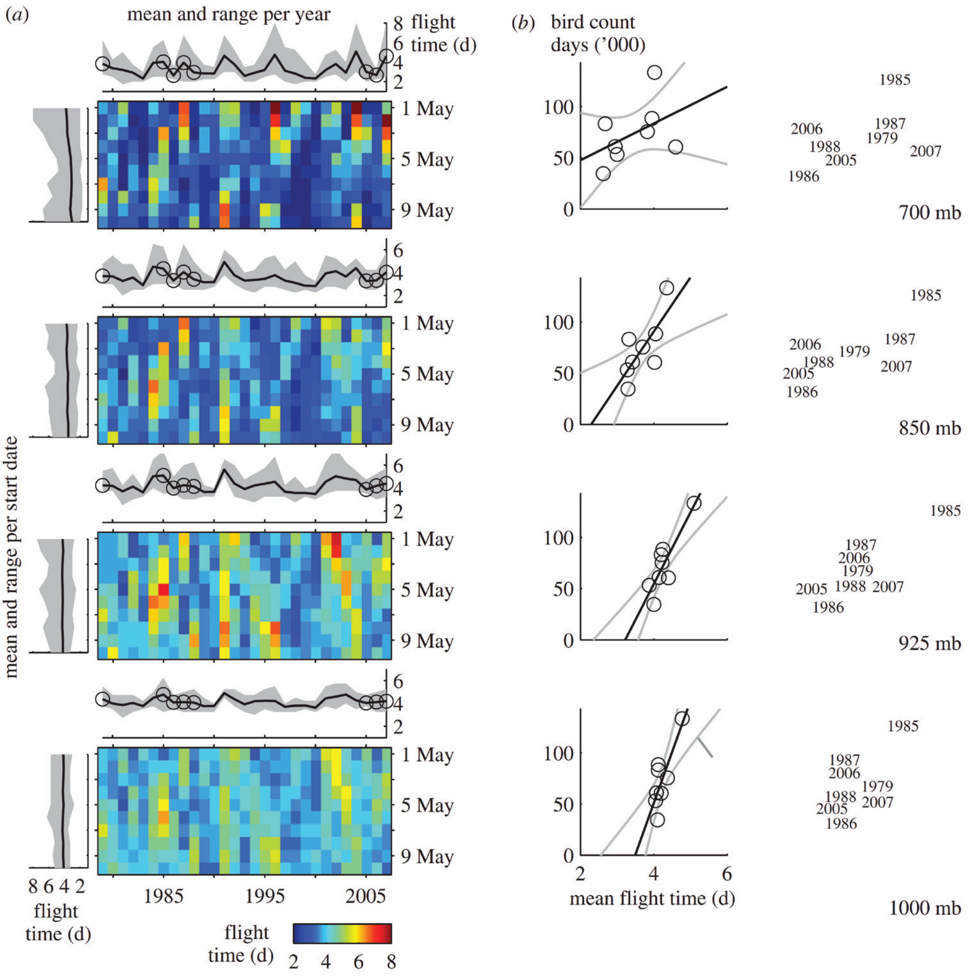

Figure 5.2

Results

Simulated flight times from Mauritania to the Wadden Sea ranged from 2 to 8 days in total with the mode at 3.9 days at the 1000 mb pressure level (111 m above mean sea level at standard atmospheric conditions, Anonymous 1976), 3.8 days at 925mb (766m a.m.s.l.), 3.1 days at 850mb (1457m a.m.s.l) and 2.5 days at 700mb (3012m a.m.s.l.) (figure 5.1b). Along the migration route, the probability distribution functions of cumulative flight times at each pressure level were positively skewed and the variance was highest for the 700mb trajectories, especially at the southerly latitudes (figure 5.1b). With strong wind assistance, birds could complete the trajectory within 2 days or less of non-stop flight, flying at ground speeds of approximately 32 ms^{-1}. The mean and median flight times for all pressure levels and start dates were 3.8 and 3.5 days respectively.

Measured annual, daily and altitudinal variability in wind strongly affected calculated flight times (figure 5.2a). The distribution of flight times varied significantly between years (Kruksal-Wallis, $H_{28} = 258.9$, $p < 0.001$), without a clear inter-annual pattern. 'Good years', years with very short mean flight times, were characterized by low variability in flight times for different start dates and pressure levels (e.g. 1983, 1986, 1990, 2000 and 2006, figure 5.2a) whereas 'bad years' (long mean flight times) were characterized by high variability in flight times. Thus, in ‘good years’ flight times were short regardless of start date and pressure level, whereas in 'bad years' flight times could vary significantly depending on start date and pressure level. The distribution of flight times did not differ significantly between start dates (Kruksal-Wallis, $H_9 = 5.4$, $p = 0.80$) but varied significantly between pressure levels (Kruksal-Wallis, $H_3 = 226.5$, $p < 0.001$). Wind speed generally increased with altitude. With supporting winds, flight times at 700 mb tended to be shorter than at other pressure levels. However, on occasions with very strong opposing winds, flight times at high altitudes were disproportionately longer than at other pressure levels (figures 5.1, 5.2a), on some occasions taking 4 days longer than the flight time at another pressure level (e.g. start date 1 May 2004). When testing the significant factors (pressure level and year) in a two-way model, both factors were also significant (Friedman, pressure level when correcting for year: $\chi^2_3 = 290.6$, $p < 0.001$; year when correcting for pressure level: $\chi^2_{28} = 344.9$, $p < 0.001$).

To explore the hypothesis of a wind driven stopover site use at the French Atlantic coast we analyzed the linear relation between simulated flight times for the entire trajectory and observed bird numbers on French Atlantic coastal intertidal mudflats. The yearly numbers of bird-days in France were positively and significantly correlated with mean flight times along the trajectory at the 1000mb pressure level ($r^2 = 0.67$, $p = 0.013$, $y = 99.9x-348.7$), the 925mb pressure level ($r^2 = 0.76$, $p = 0.005$, $y = 70.0x-225.5$) and the 850mb pressure level ($r^2 = 0.55$, $p = 0.035$, $y = 53.1x - 121.7$) (figure 5.2b).

In our model we implicitly assume that a bird’s decision to use an emergency stopover site is based on the winds already experienced en route as well as those expected in the near future time steps further along the trajectory. Ground speeds over France (a proxy for wind conditions) are positively linearly correlated ($p < 0.05$) with ground speeds three to five 6-hour simulation steps further along the trajectory (depending on the pressure level, figure 5.3). Thus wind conditions in France are highly auto-correlated in space and time with conditions further along the route, sometimes up to 30 hours in advance.

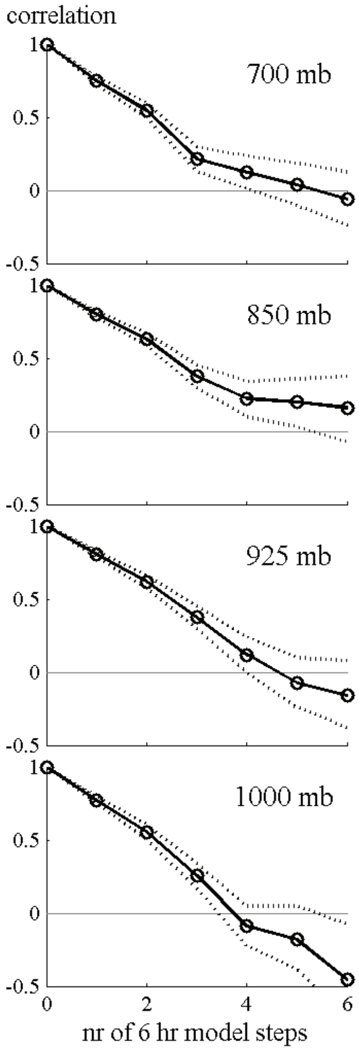

Figure 5.3 Auto- correlograms presenting the Pearson correlation coefficients (y-axis) of simulated ground speeds at the French stopover site (location 2, figure 5.1a) and ground speeds simulated at consecutive 6-hour time steps per pressure level. The x-axis represents the number of forward 6-hour time steps. Dotted lines represent the upper and lower 95 percentile. When the lower 95th percentile crosses 0 on the y-axis, the correlations are no longer significant ($p > 0.05$).

Discussion

We showed that in years with little wind assistance, resulting in longer flight times and hence increased energy expenditure, many more red knots used the French stopover sites than in years with supporting winds en route. Thus, in years with limited wind assistance, the birds make an additional refuelling stop before arriving in the German Wadden Sea. Red knots staging in France were much lighter than any of the birds subsequently found in Germany (Dick et al. 1987, Piersma et al. 1992, van de Kam et al. 2004), providing evidence that they had run out of energy stores and suggesting that they use the French inter-tidal areas as an emergency staging site. In systems, like in the Afro-Siberian red knot system, where birds are unable to predict winds en route based on conditions at the onset of migration (Piersma et al. 1990a), they can either deposit extra fuel stores or make strategic use of emergency stopover sites, here provided by the Central French Atlantic coastal wetlands.

Optimal migration theory predicts that birds minimizing migration duration would benefit from skipping sites with lower or unpredictable food supplies; variability in food supply between years or stopover sites could thus explain the skipping seen in some species (Gudmundsson et al. 1991, Weber et al. 1994, Alerstam &Hedenström 1998, Beekman et al. 2002, Bauer et al. 2008). Currently there is no evidence showing that the quality of resources in the French stopover site are lower or more variable than at the wintering site in Mauritania or the primary stopover site in the Wadden Sea (Leyrer et al. unpublished). We believe that our results strongly supports the hypothesis that wind experienced en route, perhaps in combination with the average level of energy stores achieved at the onset of migration, determine the erratic use of intermediate and emergency stopover sites. The emergency stopover strategy is a facultative response to changing environmental conditions and can be seen as an example of an 'emergency life history stage', which can be described as rapid behavioural and physiological responses to short term unpredictable events (Wingfield 2003).

Although mean as well as median flight times were shorter at the 700 mb pressure level, there were occasions where strong opposing winds resulted in the longest flight times (8 days). Counts of red knots in France were most strongly correlated with flight times at the 925 mb pressure level. Our findings suggest that flight at lower flight altitudes, might be more reliable (including smaller chances to be blown off course) than flying at higher altitudes. Our results also show that wind conditions (assessed by comparing ground speeds) in France are highly auto-correlated in space and time up to 18 hrs in advance and further along the trajectory. This suggests that as birds approach an emergency stopover site such as the French Atlantic coastal wetlands, they can decide whether or not to use that site based on their current energetic state and their short-term future expectation of wind conditions and energetic expenditure along the trajectory. Spatial explicit simulation modelling facilitates the exploration of such relationships (e.g. Erni et al. 2005, Vrugt et al. 2007) and would enable researchers to study the extent of such spatio-temporal auto-correlations along an entire trajectory or trajectory segments in contrast to considering only temporal autocorrelation of wind conditions on stopover decisions (e.g. Weber & Hedenström 2000).

Given the ubiquity of stochastically varying media (air and water), due for example to wind and currents, we expect such emergency habitats to exist in many other systems, both airborne and oceanic migration systems. For example, in marine animals emergency site use due to ocean currents might be reflected in variable visits to foraging areas following the breeding season, such as in adult green turtles Chelonia mydas which cannot forage while crossing the open-ocean to reach coastal foraging sites (Godley et al. 2002). In the well-studied model system of the red knot, the existence of emergency habitats is observable; however, in other migratory systems (e.g. passerine or insect migration) they may remain unidentified due to the high variability in their use. Detecting such emergency staging areas in oceanic environments will prove to be exceptionally challenging due to the difficulty in observing marine animal movements (Godley et al. 2002, Luschi et al. 2003, Rutz & Hays 2009, Sale & Luschi 2009). This has serious implications for conservation measures. Migrating animals depend on the integrity of multiple stopover sites, whose importance is not always readily seen. If we are to protect migratory species and the migration phenomenon, pro-active conservation measures are needed to protect species while they are still abundant (Wilcove & Wikelski 2008) by identifying and protecting habitats along migration routes, even when they are not consistently designated as migratory hotspots. Our model can easily be applied to other migratory systems to quantify the impact of wind on flight times along a migration trajectory and help identify cases where emergency stopover sites might be crucial for migratory success. Similarly, our modelling approach could be applied to marine systems, when currents affect migration as well as foraging movements of marine species (McCleave 1993, Luschi et al. 2003, Brooks et al. 2009, Sale & Luschi 2009) provided current data are available. We believe that the comparison of simulation models integrating dynamic environmental conditions with field measurements (Shamoun-Baranes et al. 2006, Bauer et al. 2008, Felicísimo et al. 2008) and the concurrent improvement of bio-logging technologies (Cooke et al. 2004, Wikelski et al. 2006, Rutz & Hays 2009) will greatly enhance migration research (Bauer et al. 2009).

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Electronic Supplementary Material - The following supplementary material is available for this article:
Shamounbaranes_sourcecode.zip, Matlab simulation model source code

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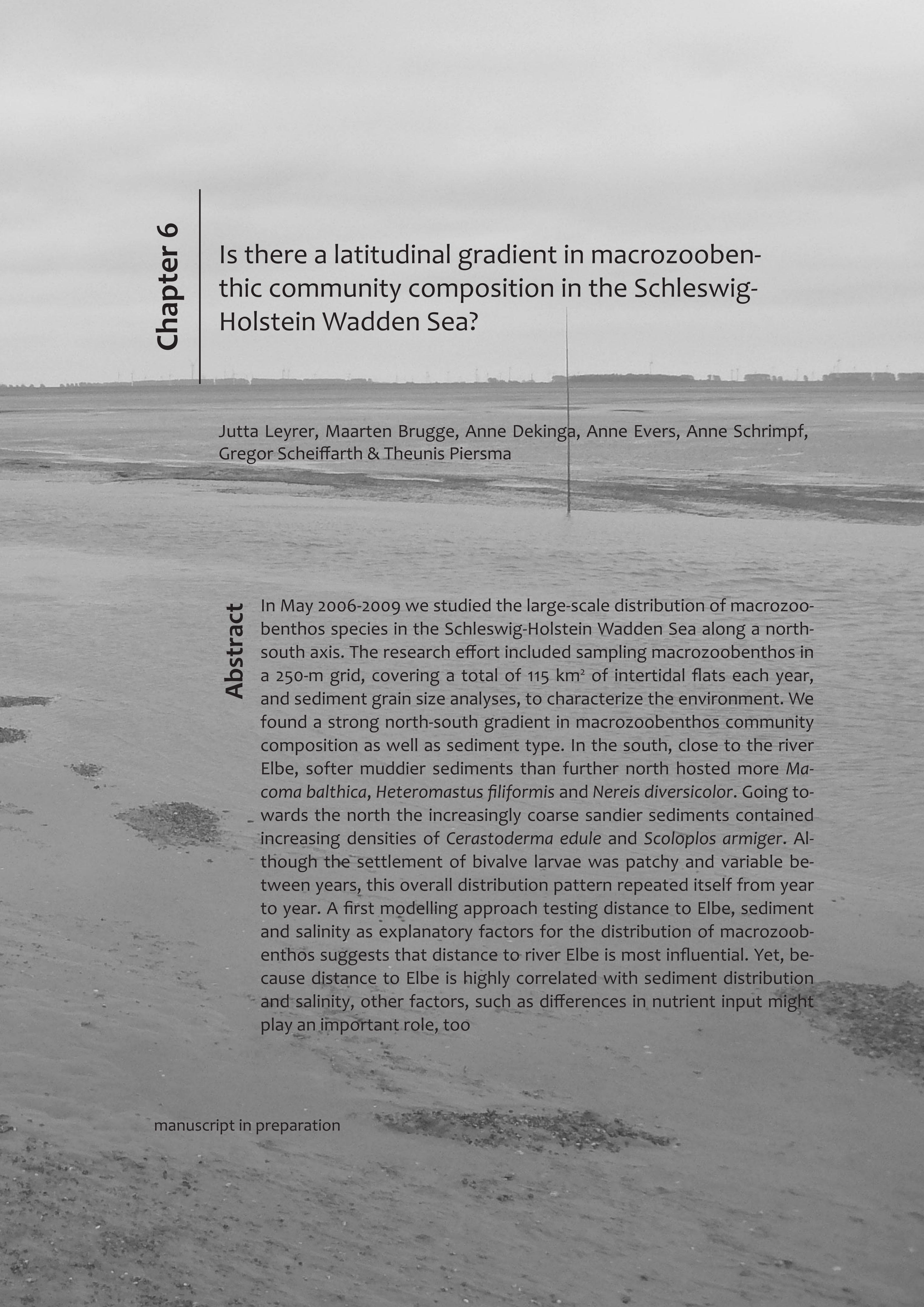

Chapter 6

Is there a latitudinal gradient in macrozoobenthic community composition in the Schleswig-Holstein Wadden Sea?

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Gregor Scheiffarth & Theunis Piersma

Abstract

In May 2006-2009 we studied the large-scale distribution of macrozoobenthos species in the Schleswig-Holstein Wadden Sea along a north-south axis. The research effort included sampling macrozoobenthos in a 250-m grid, covering a total of 115 km^2 of intertidal flats each year, and sediment grain size analyses, to characterize the environment. We found a strong north-south gradient in macrozoobenthos community composition as well as sediment type. In the south, close to the river Elbe, softer muddier sediments than further north hosted more *Macoma balthica*, *Heteromastus filiformis* and *Nereis diversicolor*. Going towards the north the increasingly coarse sandier sediments contained increasing densities of *Cerastoderma edule* and *Scoloplos armiger*. Although the settlement of bivalve larvae was patchy and variable between years, this overall distribution pattern repeated itself from year to year. A first modelling approach testing distance to Elbe, sediment and salinity as explanatory factors for the distribution of macrozoobenthos suggests that distance to river Elbe is most influential. Yet, because distance to Elbe is highly correlated with sediment distribution and salinity, other factors, such as differences in nutrient input might play an important role, too

manuscript in preparation

Introduction

Intertidal marine soft-sediments (mudflats) form dynamic environments and are very productive (Beukema 1976, Reise 1985). While it is relatively straightforward to describe species abundance in exposed marine habitat types such as rocky shores and at coral reefs, to quantify the patchy distribution of the cryptic fauna of marine soft-sediments an extended sampling effort is needed (Kraan et al. 2009a, 2010a, van Gils et al. 2009a). The European Wadden Sea resembles one of the largest intertidal soft-sediment system globally (van de Kam et al. 2004, Lotze et al. 2005), harbouring particularly large shellfish populations (Piersma et al. 1993a) that build the food base for numerous predators such as birds or fish (Reise 1985). The distribution of macrozoobenthos species strongly influences the distribution of their predators (Goss-Custard et al. 1991).

Benthic communities of the intertidal have been thoroughly studied (Beukema 1976, Reise 1985, Beukema et al. 1993, Piersma & Beukema 1993, Gätje & Reise 1998, Beusekom & Reise 2008, Reise & Beusekom 2008), These former studies have shown that sediment characteristics, mainly grain size distributions, are highly correlated with species assemblages (Thrush 1991, Thrush et al. 2003, Bocher et al. 2007, Compton et al. 2009, Kraan et al. 2010a). Sediments, in turn, are influenced by a combination of physical (e.g. hydrodynamic) and biological (e.g. bioturbation) processes. Natural hydrodynamics in intertidal soft-sediment habitats are regulated by tidal currents and river streams and sediments range from muddy (with high proportions of silt and clay) to coarse sands. Further abiotic factors influencing macrozoobenthos distribution are salinity and time of inundation (Ysebaert et al. 2002, Kraan et al. 2010a). Yet, it has also been shown that benthic organisms themselves influence (even create) their environment (bioturbation) (Reise 1985, 2002, Volkenborn & Reise 2007, Bouma et al. 2009, Olff et al. 2009, Reise et al. 2009, Eriksson et al. 2010), which implies that sediment characteristics determine species distributions and vice versa organisms can alter and thus determine sediment characteristics.

The European Wadden Sea plays a central role as a major fuelling site in the annual cycle of many High Arctic breeding waders (or shorebirds) and geese within the East Atlantic flyway. Some species also spend the nonbreeding season in the Wadden Sea, other migrate as far south as South Africa (Exo 1994, van de Kam et al. 2004, Reneerkens et al. 2005). Long-term studies on predator prey interactions and the fuelling ecology of migratory waders in the Dutch Wadden Sea have shown that sediment structures of the intertidal mudflats are easily destroyed by human activities such as bottom-dredging fisheries (e.g. industrial cockle fisheries, Piersma & Koolhaas 1997, Piersma et al. 2001, van Gils et al. 2006a). These activities not only reduced the populations of the target species (e.g. cockles *Cerastoderma edule*), but also of non-target species (e.g. Baltic tellin *Macoma balthica*) that share the same environment (Kraan et al. 2007, Kraan et al. 2011). This decimation of the target and non-target shellfish species had worrysome negative downstream effects on the population size of a migratory wader species, red knots *Calidris canutus* that highly depend on Macoma as a staple prey (van Gils et al. 2006a, Kraan et al. 2009b, 2010c).

Contrary to the situation in the Dutch Wadden Sea, large-scale bottom-dredging fisheries have never taken place in the Schleswig-Holstein Wadden Sea. This part of the Wadden Sea may have relatively non-disturbed sediment-benthos relationships in comparison with the Dutch Wadden Sea. In this study, we focus on the eastern part of the German Wadden Sea, i.e. the Schleswig-Holstein Wadden Sea, which represents the most important fuelling area during northward migration for several wader species (Prokosch 1988, Scheiffarth et al. 2002, van de

Kam et al. 2004). We describe the large-scale correlation of macrozoobenthos organisms (measured abundances and biomass) and sediments (measured median grain size), in conjunction with other potentially structuring environmental factors such as salinity (inferred from literature data) and distance from the river Elbe mouth. This study presents the first multi-year large-scale mapping of the macrozoobenthos distributions in the Schleswig-Holstein Wadden Sea and provides an underpinning of future studies on food web functioning, predator-prey interactions and fuelling ecology of migratory waders.

Methods

Study area and methods

The Schleswig-Holstein Wadden Sea has a north-south orientation with the open North Sea to its west, contrary to the southern and western Wadden Sea (i.e. Niedersachsen Wadden Sea, Germany, and the Dutch Wadden Sea, respectively). The tidal wave runs through the area from south to north. The estuary of the river Elbe defines the southern border of the Schleswig-Holstein Wadden Sea. The river Elbe is a highly frequented shipping route and thus highly maintained. The other larger freshwater river that enters the Schleswig-Holstein Wadden Sea is the river Eider (figure 6.1), which natural flow is partly regulated since the building of the Eiderdamm sluice.

In May and early June 2006-2009 we collected benthic samples at various sites in the Schleswig-Holstein Wadden Sea national park, Germany (figure 6.1; spanning from 53°55'N to 54°35'N and from 08°28'E to 08°55'E). We sampled over a grid with fixed stations at 250 m intervals. The stations were located using hand-held Global Positioning System receivers (GPS, Garmin 60). Sampling was done either by foot (during low tide) or by rubber boat (during high tide). At each station, a sediment core (1/56 m^2) was taken down to a depth of 20cm. The sediment cores were sieved over a 1mm mesh. Only bivalves were taken and stored at - 20°C for subsequent analysis in the laboratory (see van Gils et al. 2006b). All other species encountered in the sieve were identified, counted and released on site. In the laboratory, the length of each bivalve (the longest distance) was measured to the nearest 0.1mm. We removed the soft flesh parts from the shell and dried the flesh to constant mass for three days in a ventilated oven at 55 – 60°C. The dried flesh was subsequently incinerated at 550°C for five hours to determine ash-free dry mass (AFDM), using an electronic balance (± 0.001 g). When bivalves were broken due to the sampling method and we could not separate flesh from shell to determine biomass, we recalculated biomass using regressions coefficients established on the relationship between biomass (AFDM) and body size (shell length) (table 6.1). We focused on the five most abundant species: the two bivalves *Macoma balthica* (Macoma) and *Cerastoderma edule* (Cerastoderma) and the three polychaetes *Heteromastus filiformis* (Heteromastus), *Nereis diversicolor* (Nereis) and *Scoloplos armiger* (Scoloplos).

At the same time, we collected sediment samples within each km^2 at points within the general sampling scheme. We used a core of 50mm diameter and sampled to a depth of 5 – 7 cm. Sediment grain size was analysed using a particle size analyser (LS Coulter Counter) (Bocher et al. 2007, Compton et al. 2009). Median grain size is correlated with the silt content and has been proven to be a good parameter to examine animal-sediment relationships (Rosenberg 1995, Eriksson et al. 2010, Evrard et al. 2010).

The sampling sites were spread across the north-south axis of the Schleswig-Holstein Wadden Sea with the mudflats around Japsand as the northernmost and the mudflats bordering the river Elbe (Nordergründe) as the southernmost sites (figure 6.1). Across years we sampled 751, 765, 795, and 592 stations, respectively. Not all sites were sampled in each year. From north to south we sampled: mudflats adjacent to Japsand (in 2006 only), mudflats east of Norderoog (2006), mudflats between Pellworm and Süderoog (2006–2009), at Westerhever (2007), at Blauortsand (2007–2008), in Meldorfer Bucht (2007–2009), at Mittelplate (2006–2009), at Franzosensand (2006–2009) and at Nordergründe (2006–2009).

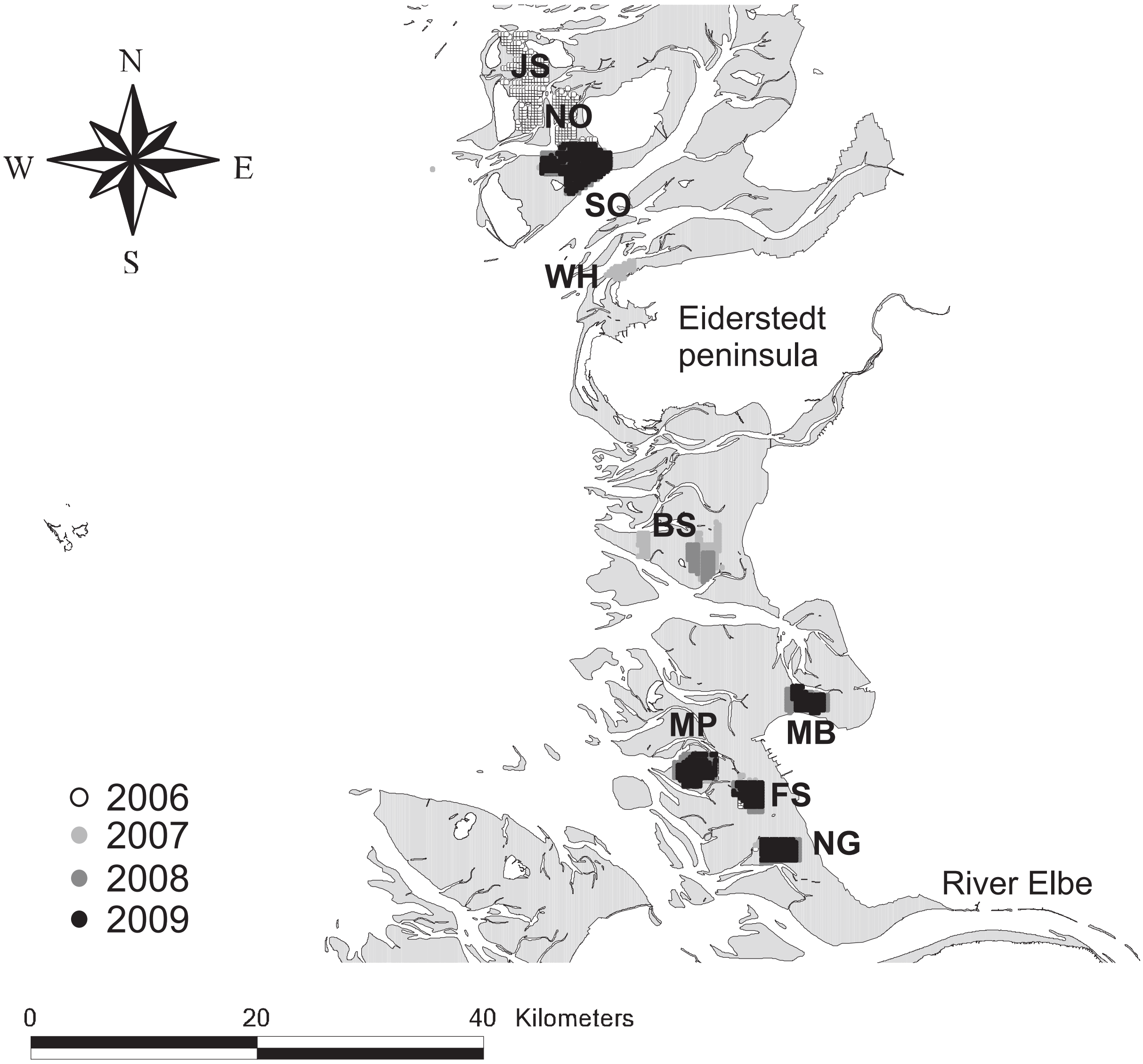


Figure 6.1 Map of the Schleswig-Holstein Wadden Sea, Germany showing the sampling areas in 2006 – 2009. Note that most areas were sampled in subsequent years and grey colours are thus overlaid. JS = Japsand, NO = Norderoog, SO = Süderoog, WH = Westerhever, BS = Blauortsand, MB = Meldorfer Bucht, MP = Mittelplate, FS = Franzosensand, NG = Nordergründe.

We tested the influence of three abiotic factors on the distribution of the macrozoobenthos community: sediment (measured median grain size MGS), salinity (inferred from Landesamt für den Nationalpark Schleswig-Hosteinisches Wattenmeer 1998), and distance to the river Elbe mouth (measured in google earth). We ran a principle component analysis on similarities in benthos community structures among the sampled sites to reduce the number of parameters to be included into the model. PC1 explained 69% of the variation and was subsequently included into a linear regression model with MGS, salinity and distance to Elbe as the explanatory variables. Statistical analysis was done in the software R (version 2.8.1. for MAC OS, R Development Core Team 2008).

Results

Average median grain size was smallest in the southern areas adjacent to the river Elbe (figure 6.2), with the finest sediments at Nordergründe (average median grain size 105 ± 15 (sd) µm). Sediments became coarser towards the north, with the coarsest sediments at Japsand (175 ± 32 µm). There were two exceptions to this pattern: Meldorfer Bucht (100 ± 25 µm) and Westerhever (194 ± 39 µm).

With respect to the two common bivalves, Macoma was more abundant in the more southern, muddier areas whereas Cerastoderma was more abundant in the northerly, sandier areas (figure 6.3a, table 6.2). There was a general decline in abundance but not in biomass among years (figure 6.3, table 6.2). The polychaete species Nereis and Heteromastus were more abundant at the muddier southern sites whereas the distribution of Scoloplos showed a similar pattern as Cerastoderma by being more abundant at the northerly sites. Annual variation was high in most sites and no obvious decreasing or increasing patterns could be observed (figure 6.4). PC1 and PC2 together explained 89% of the variation in the macrozoobenthos community structure across the sites sampled. Distance to river Elbe mouth was the factor that explained most of the macrozoobenthos community variation observed (table 6.3).

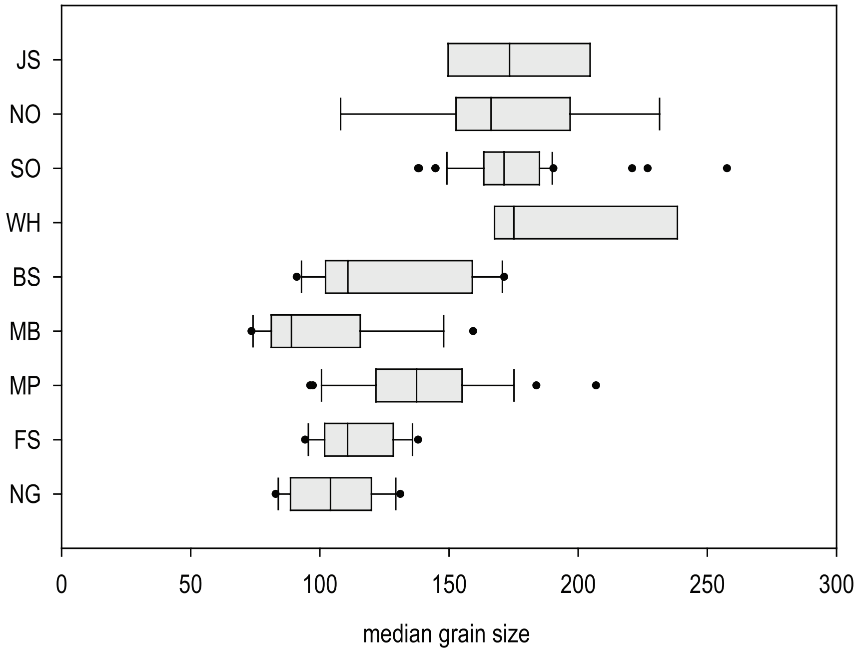


Figure 6.2 Median grain size distribution of sediments in the Schleswig-Holstein Wadden Sea between 2006 and 2009. For locations and name abbreviations see legend Figure 1. For sampling effort see Study area and methods paragraph. Shown are boxplots with median, 10th, 25th, 75th and 90th percentiles.

Table 6.1 Relationship between biomass (AFDM of the flesh) and body size (shell length). We used double logarithmic sales (ln(AFDM) against ln(length)). The regressions were calculated for the two main mollusc species and all measured individuals were pooled across all years and sites. n gives the sample size, range gives the ranges of shell lengths found and included.

species	intercept	slope	r^2	n	range
Macoma balthica	-10.688	2.71	0.8553	2203	1 - 26 mm
Cerastoderma edule	-10.5	2.62	0.9005	3805	3 - 37 mm

Table 6.2 Mean (and maximum) abundance of the most common found benthic macrofauna (ind. per m^2) at the sampled areas in 2006 to 2009. Empty cells = no sampling has been done in that year.

	Macoma				Cerastoderma							
	2006	2007	2008	2009	2006	2007	2008	2009	2006	2007	2008	2009
Japsand	55 (504)				366 (3,472)							
Norderoog	55 (504)				409 (3,304)							
Suederoog	33(336)	16 (224)	11 (112)	15 (224)	190 (2,968)	94 (1,288)	101 (1,848)	45 (840)				
Westerhever		53 (336)				101 (896)						
Blauortsand		73 (392)	57 (336)			143 (3,696)	139 (1,848)					
Mittelplate	50 (280)	51 (336)	19 (224)	63 (448)	11 (224)	44 (1,288)	7 (224)	45 (392)				
Meldorf		149 (2,016)	58 (336)	28 (224)		76 (448)	79 (616)	88 (504)				
Franzosensand	122 (504)	101 (392)	58 (224)	58 (504)	22 (168)	56 (1,008)	12 (168)	27 (224)				
Nordergruende	227 (952)	151 (560)	49 (336)	43 (392)	23 (1,008)	0	3 (224)	0				
	Nereis				Scoloplos				Heteromastus			
Japsand	6 (112)				112 (1,344)				8 (280)			
Norderoog	11 (280)				197 (2,352)				5 (280)			
Suederoog	7 (336)	9 (168)	5 (112)	20 (392)	144 (1,008)	104 (1,120)	182 (2,632)	98 (672)	6 (224)	8 (168)	15 (336)	15 (504)
Westerhever		36 (224)				187 (1,512)				44 (560)		
Blauortsand		25 (336)	31 (280)			20 (784)	43 (952)			83 (1,400)	27 (448)	
Meldorf		111 (6161)	217 (784)	292 (1,624)		35 (336)	1 (56)	3 (112)		330 (1,400)	113 (1,008)	90 (504)
Mittelplate	62 (448)	49 (280)	61 (280)	140 (616)	80 (1,120)	35 (280)	76 (560)	49 (504)	584 (5,600)	99 (1,120)	33 (280)	144 (1,28
Franzosensand	130 (392)	127 (560)	95 (448)	160 (504)	27 (392)	14 (280)	6 (168)	2 (112)	630 (2,408)	210 (840)	55 (616)	241 (896)
Nordergruende	294 (672)	253 (1,512)	92 (728)	85 (448)	85 (2,352)	0	1 (112)	0	353 (1,120)	171 (1,288)	119 (1,624)	107 (448)

The length class distributions of the two bivalve species Macoma and Cerastoderma showed that different length classes were present in all areas in all years (figure 6.5 and 6.6). In Macoma the highest proportions of small individuals (<8mm, juveniles, Zwarts & Wanink 1993) was found across the whole study area in both 2006 and 2007 (Meldorfer Bucht) (figure 6.5). At Süderoog, Macoma mostly only grew larger (and older) in the course of the study years, whereas in the more southern areas smaller (younger) individuals were regularly found beside larger (older) individuals in subsequent years. In Cerastoderma, small individuals (< 12mm, juveniles, Zwarts & Wanink 1993) were found in 2006 at all sampled sites except Nodergründe (figure 6.6); the proportion of small individuals was larger at Japsand, Norderoog and Süderoog than at Mittelplate and Franzosensand. In the following years, the proportion of small individuals was low or non-existent in all sites, and the size distribution shifted towards larger (older) animals.

Table 6.3 GLM with PC1 as independent variable. PC1 from a PCA on macrozoobenthos community structure in the Schleswig-Holstein Wadden Sea was tested against three abiotic variables: sediment (median grain size [µm]), salinity [‰] and distance to Elbe mouth [km]. * = $p < 0.05$.

	estimate	SE	t-value	p -value
sediment	-0.701	1.532	-0.458	0.67
salinity	-4.306	19.102	-0.225	0.83
distance	7.347	2.481	2.961	0.03*

Discussion

The mudflats sampled in the Schleswig-Holstein Wadden Sea were sandy mudflats, which is in accordance with a map published in the late 1990s showing an interpolated sediment distribution of the entire Schleswig-Holstein Wadden Sea (Landesamt für den Nationalpark Schleswig-Hosteinisches Wattenmeer 1998). The distribution pattern we found suggests that there is a general south to north gradient, away from the river Elbe, with "muddier" flats closer to the river estuary and increasingly "sandier" flats further away, i.e. further north. As one of two exceptions, mudflats at Meldorfer Bucht had relatively finer sediments. The Meldorfer Bucht mudflats lie at the end of a bay adjacent to mainland salt marshes and dikes. At this site tidal currents have less energy and thus finer sediments can settle, hence parts of the area were former embankment fields for land reclamation. The other exception was Westerhever, where the mudflats though similar close to the mainland and former land reclamation areas, were influenced by an adjacent major tidal stream forming a high-energy environment where commonly coarser sediments are found.

The distributions of the polychaete species Scoloplos, Heteromastus and Nereis seemed to have followed earlier described patterns. Scoloplos, strongly favoured sandier habitats as described earlier (Dörjes et al. 1986). Heteromastus, a subsurface deposit feeder favouring muddy anaerobic sediments showed a strong correlation to muddier sites. In the late 1970s and early 1980s Heteromastus has been observed to become a dominant species in sandy sediments in the western (Dutch) and southern parts of the Wadden Sea (Cadee 1979, Dörjes et al. 1986). It appears that this was not the case in the Schleswig-Holstein Wadden Sea. The generalist polychaete Nereis showed a preference for the muddier sites. Nereis has been described as a species that occurs in divers sediments, and also in stressed environments (Scaps 2002) like e.g. the vicinity of the Elbe river with its freshwater influence might present.

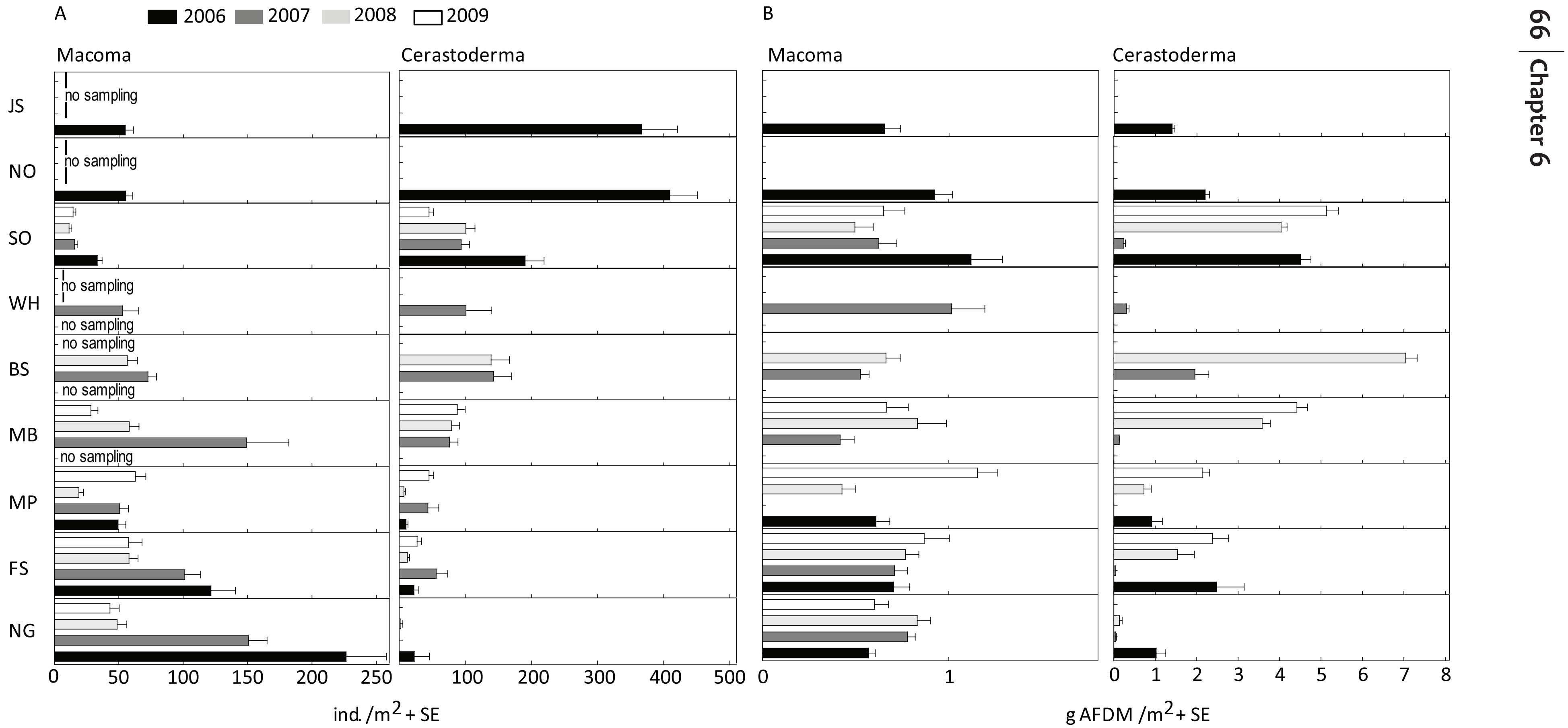


Figure 6.3 **A** Mean densities (ind./m^2 + SE) and **B** mean biomass (gAFDM/m^2) of *Macoma balthica* and *Cerastoderma edule* at different areas in the Schleswig-Holstein Wadden Sea in May/June 2006 – 2009. For locations and name abbreviations see legend figure 6.1.

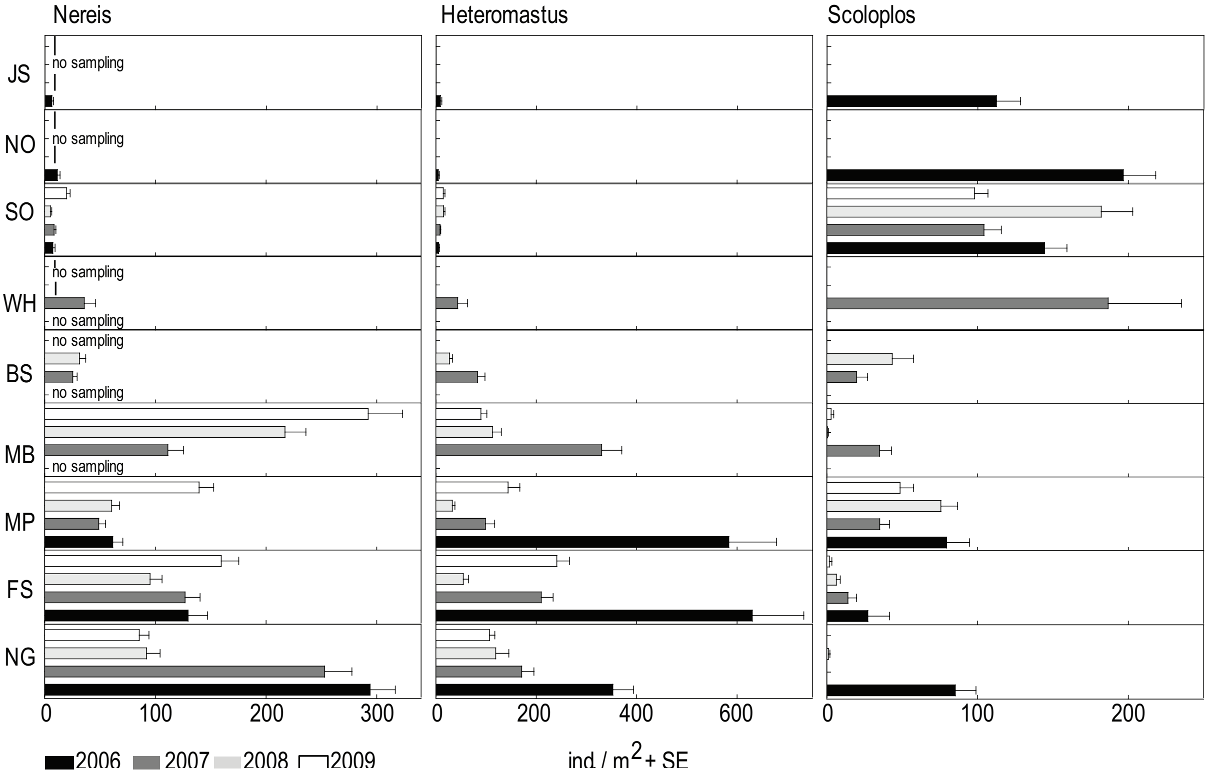


Figure 6.4 Mean densities (ind./m^2 + SE) of *Nereis diversicolor, Heteromastus filiformis* and *Scoloplos armiger* at different areas in the Schleswig-Holstein Wadden Sea in May/June 2006 – 2009. For locations and name abbreviations see legend figure 6.1.

We found the highest densities of the two bivalve species Macoma and Cerastoderma in 2006. The length distributions of both species, showing high proportions of small individuals in that year, suggest that 2005 was a good year with high reproduction for both Macoma and Cerastoderma. For Cerastoderma this pattern was also found in an area south of the river Elbe (G. Scheiffarth, unpublished observation). Cerastoderma generally tended to settle in more northern and sandier habitats, whereas Macoma settled in more southern and muddier habitats. That Cerastoderma prefers sandier and Macoma prefers muddier habitats has been described earlier as a common feature (Compton et al. 2008) and is in contrast to recent observations in the Dutch part of the Wadden Sea where Cerastoderma has settled increasingly in relatively muddier sediment (Compton et al. 2009, Kraan et al. 2010a). In 2007, a new Macoma cohort settled in Meldorfer Bucht, but also at Süderoog, Franzosensand and Nordergründe, though in smaller proportions. This indicates that (1) settlement of new cohorts occurs at different sites in different years, and (2) settlement, and thus reproduction, does not occur in the same intensity each year. In the following years, we did not observe any new settlement of very small individuals in Cerastoderma and for Macoma a new cohort was found only in 2009 at Franzosensand. In general, individuals grew larger over the years. This is likely to explain why the decrease in bivalve numbers was not followed by a decrease in biomass over the years. As a general conclusion on the basis of our observed length distributions over the years, we got the impression that, though some settlement seemed to take place regularly at all sites in both species (but might have not been detected by our sampling scheme in an appropriate way), some years, like 2006 (or 2007 for Meldorfer Bucht) are much better than other years. For such massive and large scale differences in settlement, overall regulating factors like a cold winter must be responsible.

With the river Elbe bringing in large amounts of freshwater, salinity could also influence

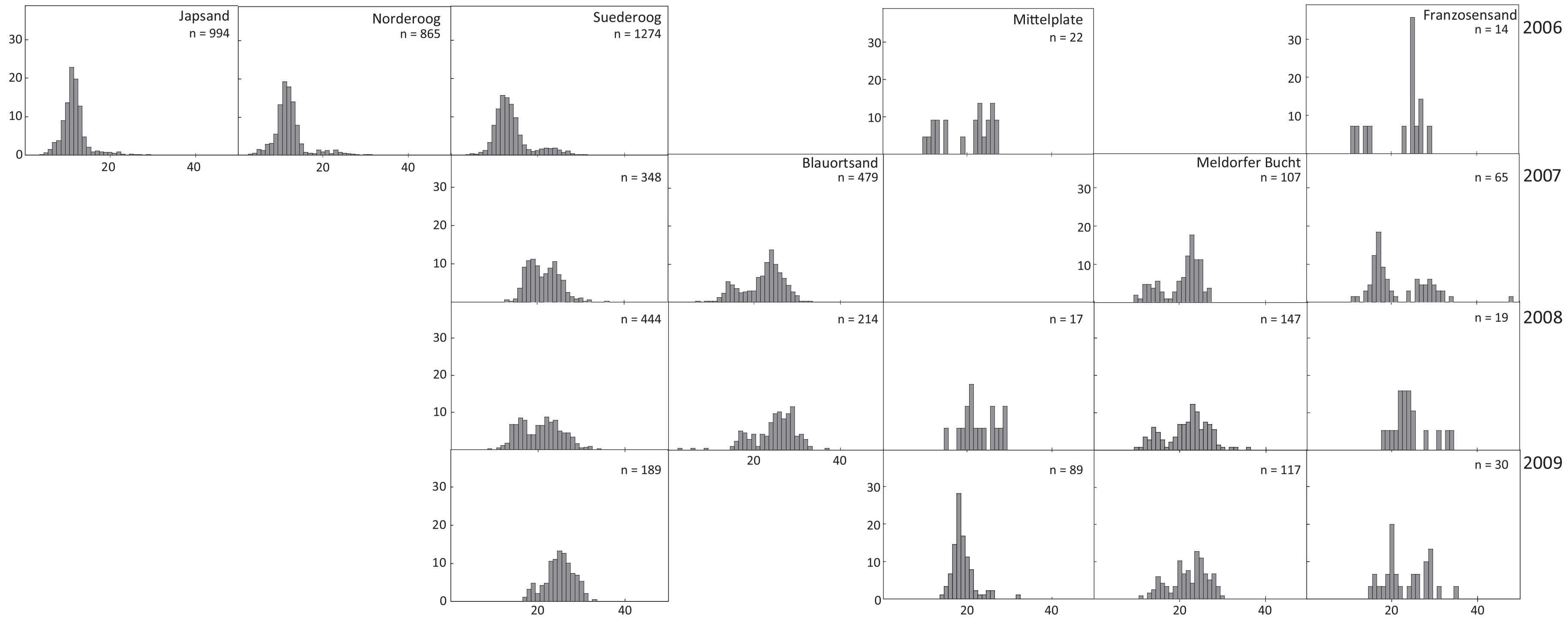


Figure 6.5 Length class distribution of *Macoma balthica*.

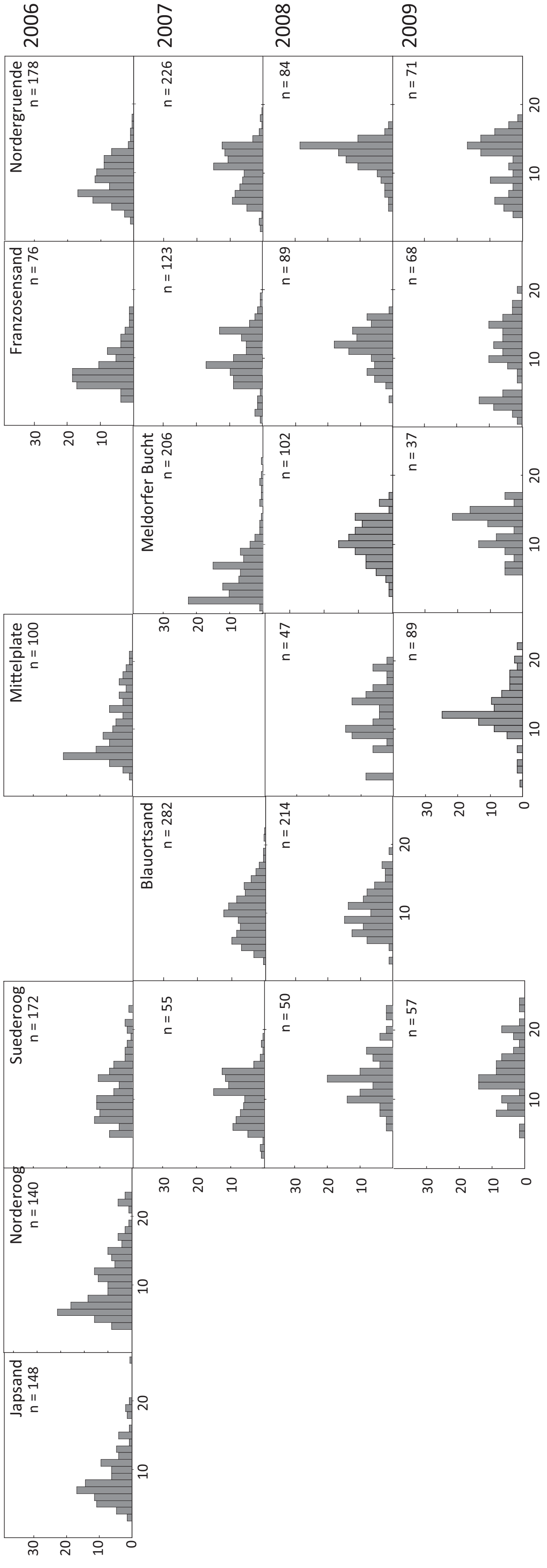
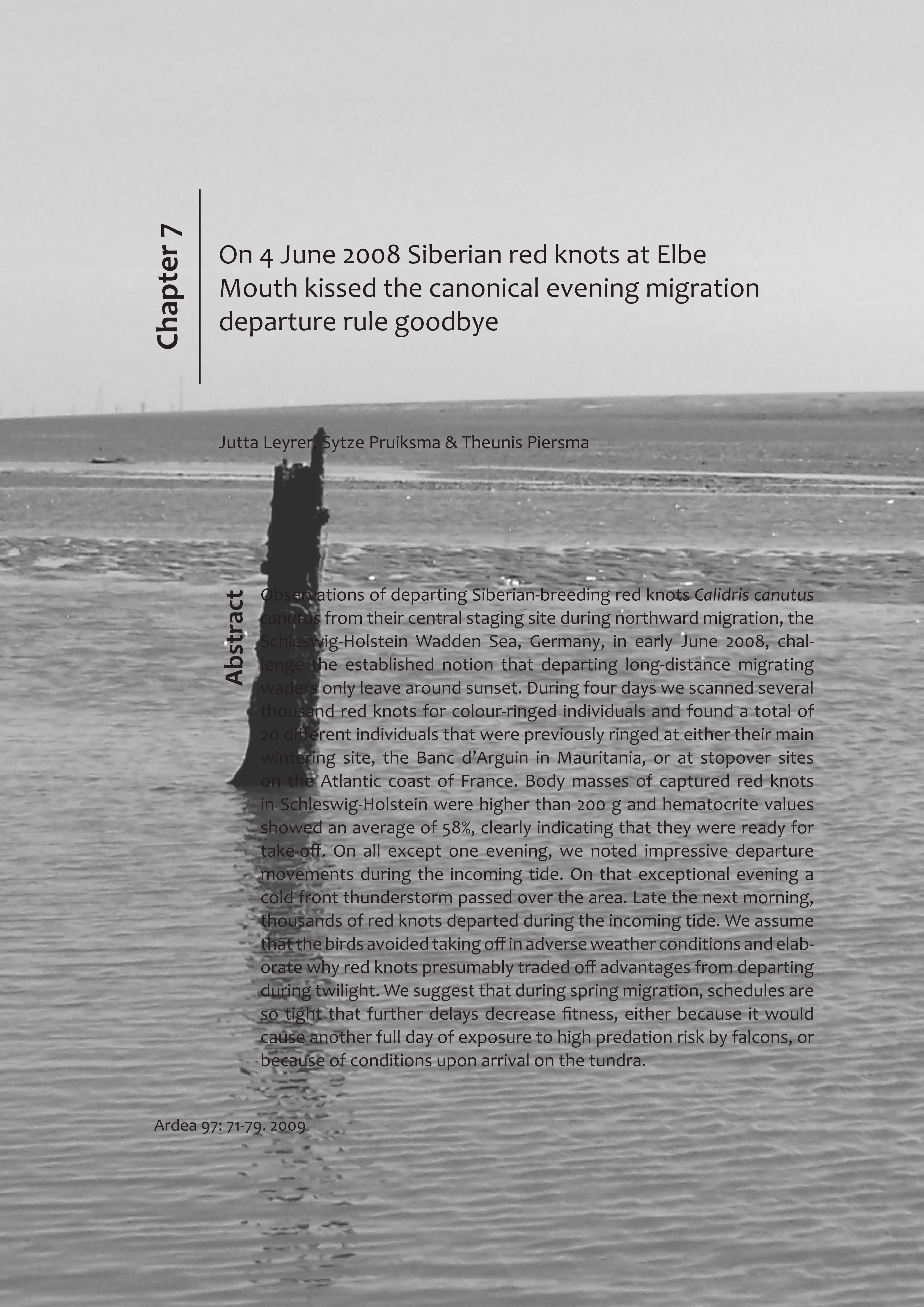


Figure 6.6 Length class distribution of *Cerastoderma edule*.

species distributions and abundances. Salinity in summer increases from 21‰ at Nordergründe to 30‰ at Japsand (Landesamt für den Nationalpark Schleswig-Hosteinisches Wattenmeer 1998). Yet, when tested in a single regression model, distance to river Elbe mouth rather than sediment and salinity had the strongest influence on the observed variance in macrozoobenthos communities. This result might be misleading though, as all three factors are highly correlated and the strong relationship between distance to Elbe mouth and benthos communities might have other (additional) reasons. The Wadden Sea area north of Eiderstedt Peninsula (Westerhever sampling site) forms a separate tidal basin (Reise & Gätje 1997) and nutrients mainly coming from the adjacent open North Sea. The Wadden Sea area south of Eiderstedt Peninsula instead is characterized by the freshwater (and nutrient) discharges deriving from the Elbe river (Tillmann et al. 2000). Thus, future analyses should include potential differences in nutrient supplies into their models as well as measure velocity of water flux, duration of inundation, but also biological interactions (bioturbation) and use statistical powerful methods such as spatially explicit generalized estimating equations (GEE) (Kraan et al. 2010a) to break apart the different determinants of species-environment relationships in the Schleswig-Holstein Wadden Sea. In general though, our observations support earlier studies in that different macrozoobenthos species prefer different sediment types (Bocher et al. 2007, Compton et al. 2009, Kraan et al. 2010a). Yet, comparing the Dutch and the Schleswig-Holstein Wadden Sea, we have found differences in sediment preferences in cockles where they have settled in muddier sediments over the recent years (Compton et al. 2009, Kraan et al. 2010a). A striking difference between the Dutch and the Schleswig-Holstein Wadden Sea is that in Schleswig-Holstein no large-scale bottom dredging fishery, e.g. the industrial cockle fishery, has occurred. Cockles in Schleswig-Holstein, i.e. in the same ecosystem, settle in their apparently preferred sandy habitat (Compton et al. 2009) and having to settle in a potentially suboptimal habitat might have consequences in e.g. food finding or a higher predation pressure. The distribution changes in the Dutch Wadden Sea might thus have negative consequences for the cockles and this observation could be just another example of the long-lasting and potentially detrimental effects of the now banned cockle fishery (van Gils et al. 2006a, Kraan et al. 2009b, 2011).

We have presented the first large-scale multi-year documentation of abundances and distribution patters of five numerous macrozoobenthos species in the Schleswig-Holstein Wadden Sea. Because of their central role in marine food webs, changes in the benthos communities might have large-scale consequences for both higher consumers (predators) and producers at the lower end of such a food web (Olff et al. 2009). Because benthos organisms also create their own environment (e.g. mussel *Mytilus edulis* banks), disturbances at benthos scale are very likely to have consequences for the abiotic environment, such as the velocity of water streams and thus the sinking behaviour of sediment particles and eventually sediment distributions (Eriksson et al. 2010). Migratory waders that depend on the benthic resources for their migrations have been highly affected by changes in their food supply (van Gils et al. 2006a, Kraan et al. 2010b). Yet, changes in population size of these migrants might have even further reaching consequence, i.e. for ecosystems far away, e.g. the Banc d'Arguin in West Africa, a major nonbreeding site within the East Atlantic flyway and closely connected with the Wadden Sea by means of migration (van Gils et al. 2009b). The Wadden Sea represents a key site within the East Atlantic flyway for migratory birds and a major breeding site for marine mammals (seals *Phoca vitulina*) and fish. Studying the biological and ecological processes in macrozoobenthos communities as the linchpin within the marine food web will help to increase our knowledge about the Wadden Sea ecosystem but also closely connected ecosystems such as the open sea (fish, mammals, seabirds), high arctic tundra areas and tropical intertidal mudflats (migratory birds).

Acknowledgements
This sampling program would have not been possible without the help of numerous enthusiastic people. Our first thanks go to the crew of the RV Navicula, K. van der Star, T. van der Vis and H. de Vries, with C. van Heerwarden, F. Wiering and J. Betsema. Over the course of four years we had the help of 23 dedicated volunteers helping, some in multiple years. S. Engelhard analyzed large parts of the 2008 benthos samples in the lab. In Schleswig-Holstein, we had a warm welcome and great support from the Nationalparkverwaltung Schleswig-Holsteinisches Wattenmeer, Tönning, in particular from Bernd Hälterlein and Britta Diederichs. Klaus Günther, Schutzstation Wattenmeer, readily shared his knowledge with us.



Chapter 7

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

Jutta Leyrer, Sytze Pruiksma & Theunis Piersma

Abstract

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.

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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. 2002b, 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 1989, 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 (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,b). 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. 2006b). 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, figure 7.1), 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).

Methods

Between the evening of 31 May 2008 (from around 21:00 hrs) until the afternoon of 5 June 2008 (around 14:00 hrs) 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, figure 7.1). Observations were made continuously from the mudflats and from aboard the RV Navicula. In the course of the observation period evening high tides shifted from 22:22 hrs (31 May) to 2:14 hrs (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. They were digitally cleaned and images were produced using RavenLite 1.0 Build 9 Update 10, by Cornell Lab of Ornithology Bioacoustics Research Program.

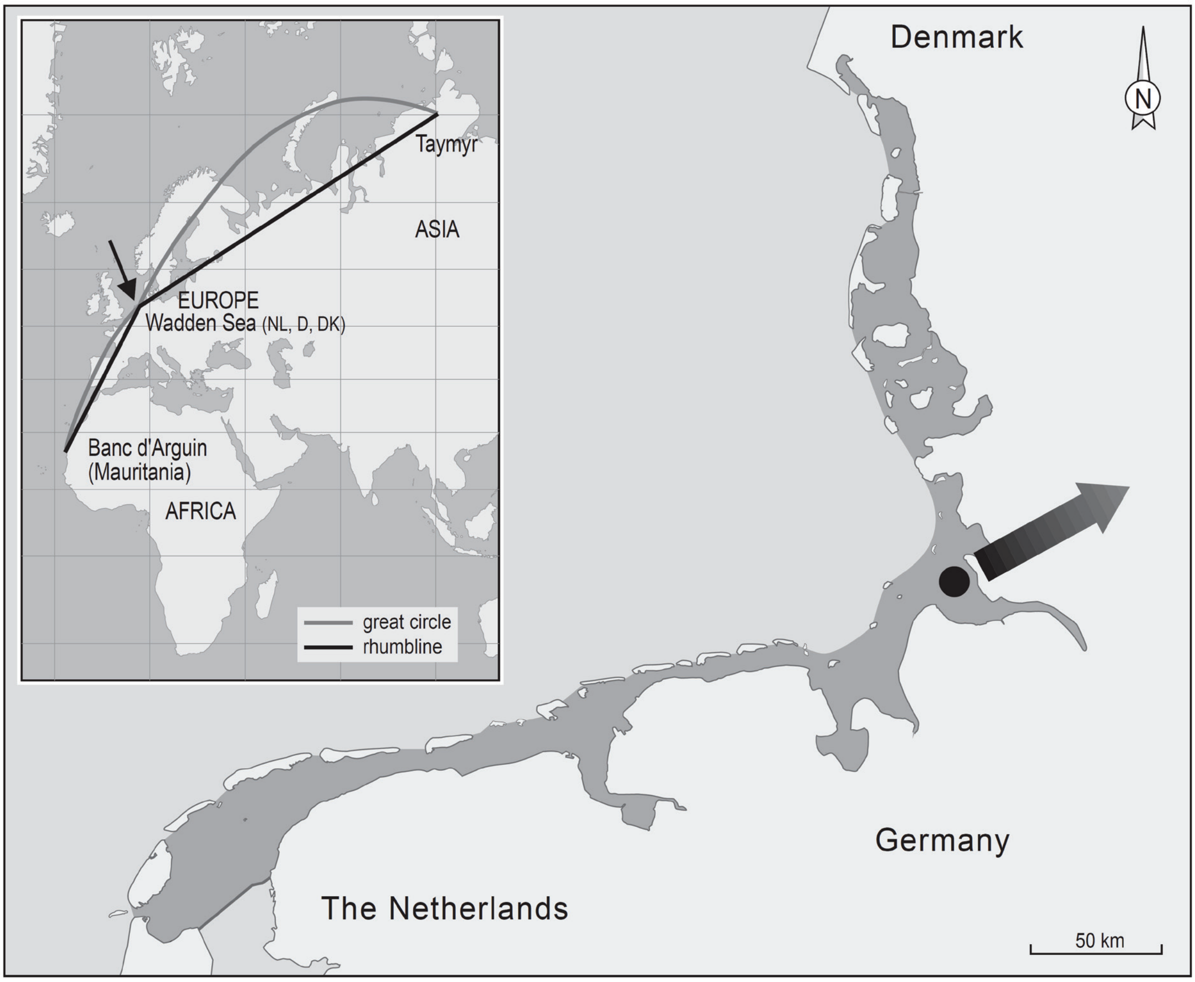

Figure 7.1 The Eastern part of the Dutch-German-Danish Wadden Sea (dark grey shaded area) represents the central stopover area for northward migrating Afro-Siberian red knots. The black dot locates the Nordergründe mudflats, Dithmarschen, Schleswig-Holstein, Germany, north of the Elbe river estuary. 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 black arrow is indicating the study area.

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-Cianelli et al. 2002) as well as for subsequent molecular sexing (Baker et al. 1999). For Hct measures, 25µl were filled into heparinized micro-hematocrite capillary tubes. The tubes were centrifuged at 10,000 x 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-Cianelli 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, 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 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 (figure 7.2).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 21:00 hrs and 21:20 hrs, 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 20:33 hrs and 21:00 hrs. 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 a south-westerly direction crossed the south-eastern shore of the North Sea (the Wadden Sea coast of Lower Saxony and Southern Schleswig-Holstein, Germany) on the early evening of 3 June (figure 7.3). Around 19:00 hrs 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 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 hrs we observed 10,000s of red knots, but also ringed plovers, and, to a lesser extent, dunlins *C. 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 re calculated 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 approx. 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.

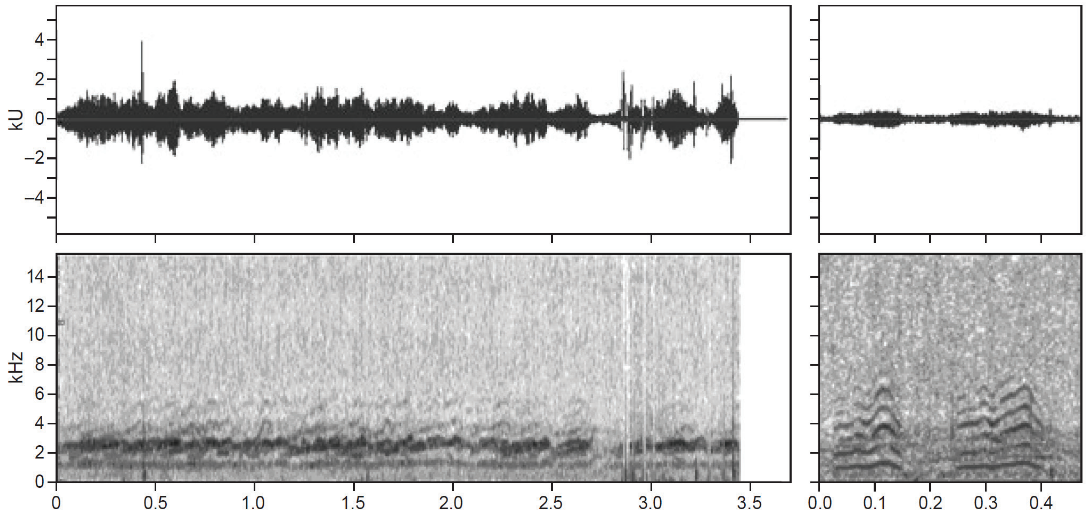

Figure 7.2 Waveform and spectrogram of departure calls of a red knot flock of 160 individuals departing from Nordergründe on 2 June 2008 at 21:05 h in an east-north-easterly direction. Left panel shows calls of several red knots in a flock, right panel shows two single calls of a red knot departing separate and ca. 10 s after the main flock.

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 figure 7.1). 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 figure 7.3, 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 3,800 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 3,000 red knots and found a total of 13 colour-ringed individuals (all different from the day before). Twelve red knots were 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).

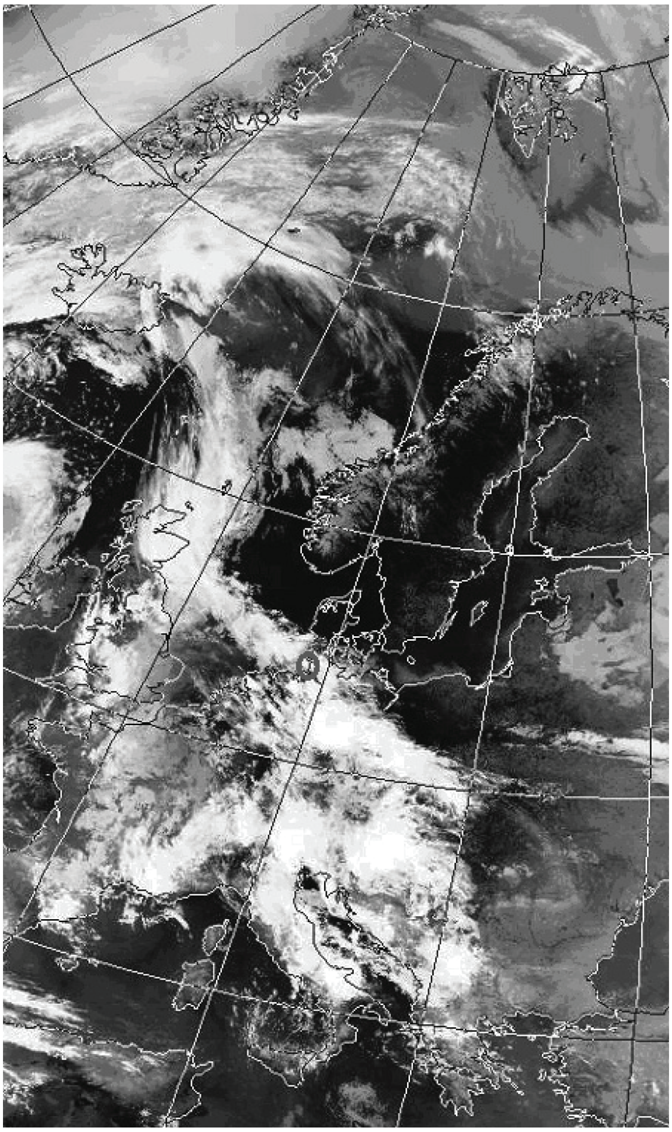

Figure 7.3 Satellite image of the low pressure system passing the Southern North Sea coast on the evening of 03 June 2008. The study area is marked with a circle. The image was made by satellite NOAA-17 at 20:28 hrs and shows AVHRR channel 4. Advanced Very High Resolution Radiometer (AVHRR) instruments measure the reflectance of the earth in various band width; channel 4 is sampling in the infrared window and 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/).

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 1,000 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 (s.d. 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 (figure 7.2). '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, 1994). Red knots setting off from this central staging site by the end of May/beginning of June, presumably fly ca. 5,000 km non-stop directly to their Siberian breeding grounds on the Taymyr 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-Cianelli et al. (2002) showed that in bar-tailed godwits *Limosa lapponica*, Hct values of more than 50% clearly indicated migratory readiness. Wintering knots on the Banc d'Arguin, Mauritania, in December usually show Hct values well below 50% (J. Leyrer et al. unpubl. data). Hence, the high body weight and the high (>54%) Hct 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 approx. 400,000 individuals (Wetlands International 2006, Spaans et al. 2011). Subtracting first years 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, like 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. 2002a, Cochran et al. 2004, Muheim et al. 2006, 2007). Yet, Cochran et al. (2004) suggest that a cali bration 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 don't 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 thousand 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, 2007, 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., see photo below). 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.

Acknowledgments

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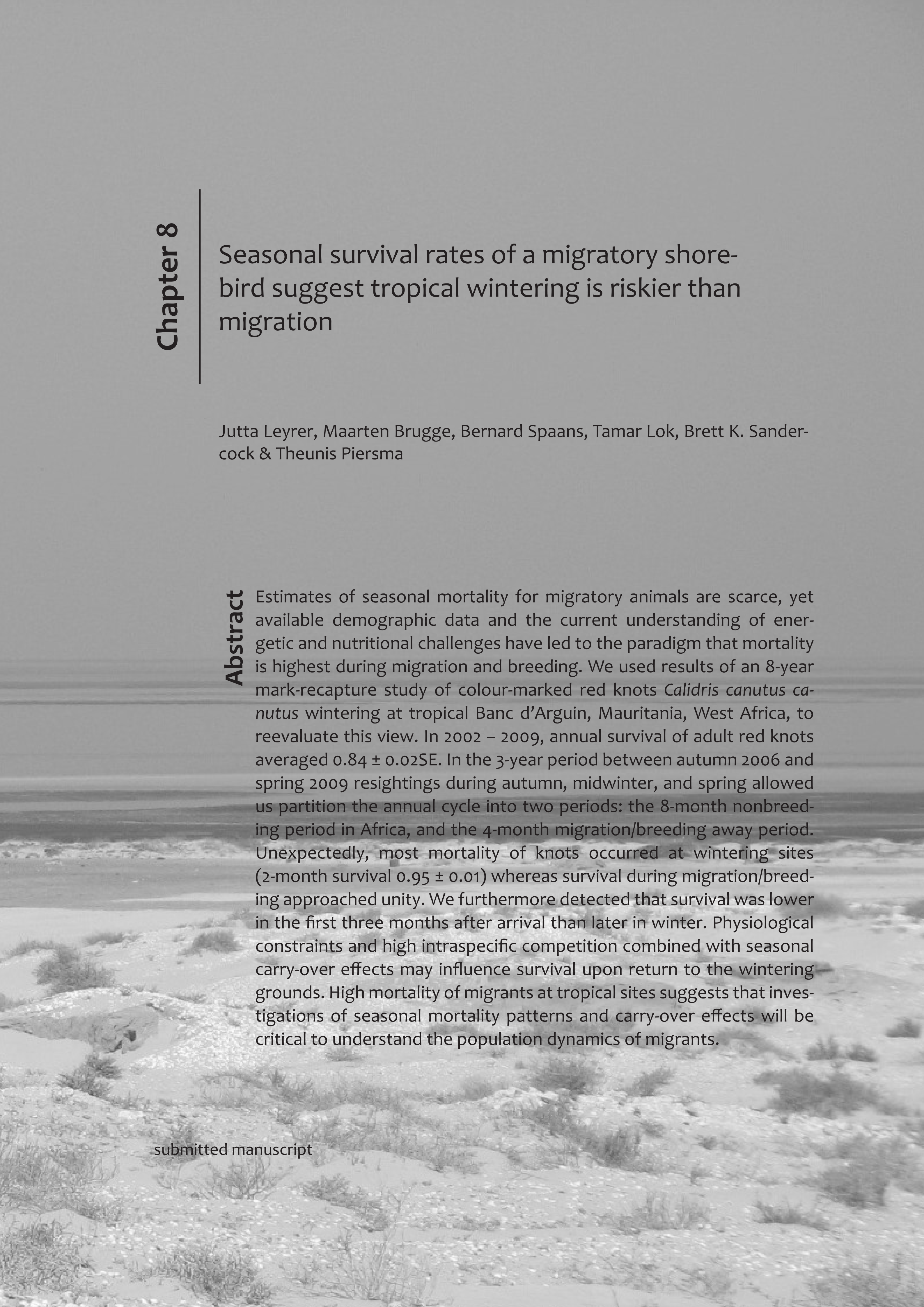
Prey collected by peregrines breeding on the island of Trischen (Schleswig-Holstein Wadden Sea, Germany), found on 9 June 2008. In total, 22 red knots, 3 dunlins, 5 woodcocks, 1 ruddy turnstone, 1 sanderling, 1 feral pigeon, 1 water rail, and 2 common starlings were found in this stack. The red knots appeared to have been killed about 2-3 weeks before being found, and most birds were in breeding plumage and were largely left uneaten. The colour-ringed individuals was caught in France on 6 May the same year. Photo by M. Dorsch.



Chapter 8

Seasonal survival rates of a migratory shorebird suggest tropical wintering is riskier than migration

Jutta Leyrer, Maarten Brugge, Bernard Spaans, Tamar Lok, Brett K. Sandercock & Theunis Piersma

Abstract

Estimates of seasonal mortality for migratory animals are scarce, yet available demographic data and the current understanding of energetic and nutritional challenges have led to the paradigm that mortality is highest during migration and breeding. We used results of an 8-year mark-recapture study of colour-marked red knots *Calidris canutus canutus* wintering at tropical Banc d'Arguin, Mauritania, West Africa, to reevaluate this view. In 2002 – 2009, annual survival of adult red knots averaged 0.84 ± 0.02SE. In the 3-year period between autumn 2006 and spring 2009 resightings during autumn, midwinter, and spring allowed us partition the annual cycle into two periods: the 8-month nonbreeding period in Africa, and the 4-month migration/breeding away period. Unexpectedly, most mortality of knots occurred at wintering sites (2-month survival 0.95 ± 0.01) whereas survival during migration/breeding approached unity. We furthermore detected that survival was lower in the first three months after arrival than later in winter. Physiological constraints and high intraspecific competition combined with seasonal carry-over effects may influence survival upon return to the wintering grounds. High mortality of migrants at tropical sites suggests that investigations of seasonal mortality patterns and carry-over effects will be critical to understand the population dynamics of migrants.

submitted manuscript

Introduction

During the annual cycle, latitudinal migrants pass through complex series of life-history stages that include breeding, migratory movements, moult (in birds), and a nonbreeding period (Murton & Westwood 1977, Newton 1998, Barta et al. 2008, McNamara & Houston 2008). All these events entail potential energetic and survival costs, and to maximize fitness migrants should optimize the seasonal timing of the various stages (Ens et al. 1994, Sandberg & Moore 1996, Alerstam & Hedenström 1998, Greenberg & Marra 2004, Wingfield 2008). Migrants need to arrive in good body condition and when environmental conditions are suitable. Timing of arrival on the breeding grounds is thought to be of crucial importance to maximize reproductive output (Ens et al. 1994, McNamara et al. 1998, Drent et al. 2003, McNamara & Houston 2008). Depending on their migration pattern, migrants may visit one or several staging sites en route to replenish energy stores needed for migration (Piersma 1987). Staging sites are often situated strategically along the migration route and offer conditions that allow migrants to accumulate sufficient fuel loads according to their schedule (van de Kam et al. 2004, Piersma et al. 2005, Colwell 2010). Yet, migrants have to trade-off fuelling rates against other selection pressures such as predation risk (Alerstam & Lindström 1990, Ydenberg et al. 2002), which could create time and survival costs. Generally, migration is regarded as a demanding period when time, energetic, nutritional and other potential bottlenecks coincide (Drent & Piersma 1990, Buehler & Piersma 2008). As a consequence, periods of active migration are considered critical, particularly when climatic conditions are inclement or wind directions are unfavourable (Alerstam 1990, Newton 2007, Shamoun-Baranes et al. 2010).

A fundamental question in the study of population dynamics of migrants is whether the act of migration indeed is risky, and whether higher mortality ('survival costs') would be balanced by a compensatory low mortality on the non-breeding grounds. With the advancement in analytical tools there is an increasing body of knowledge about annual survival rates in migratory species (Sandercock & Jaramillo 2002, Baker et al. 2004, Faaborg et al. 2010) and a number of studies have succeeded in breaking down annual survival into seasonal components, showing that the period of active migration indeed entails higher mortality (Madsen et al. 2002, Hupp et al. 2008, Robinson et al. 2009, but see Gauthier et al. 2001). Yet, these publications mainly examined hunting effects and only two other studies analysed seasonal survival in nongame species. One, followed a single population of geese in the North Atlantic region, documenting that the period of lowest survival within the year was between spring and autumn (Clausen et al. 2001). An earlier study inferred seasonal survival in a Nearctic-Neotropical passerine migrant by studying annual survival in separate nonbreeding and breeding populations with an unknown degree of connectedness and found that 85% of the annual mortality occurred during migration (Sillett & Holmes 2002).

Studying seasonal survival is challenging, as individuals must be monitored at different times of year. Shorebirds (or waders) are a good group for such studies because many species occupy open habitats year round where they are relatively easy to observe (van de Kam et al. 2004). The red knot *Calidris canutus* is a long-distance migrant. Outside the breeding season, red knots are obligate marine birds, depending on intertidal soft-sediment habitats (Piersma 2007). The nominate subspecies *C. c. canutus* (hereafter *canutus*) breeds in north-central Siberia and spends an 8-month nonbreeding period in West African coastal wetlands. *Canutus* knots are concentrated mainly at the two largest West African intertidal areas, Banc d'Arguin, Mauritania (75% of the population) and the Bijagós Archipelago, Guinea-Bissau (Piersma et al. 1992, Davidson & Piersma 2009) and spend their 2-month breeding period in the tundra of the

Taimyr Peninsula (Tomkovich & Soloviev 1996). Excluding predeparture fuelling periods, but including refuelling en route, northward and southward migration each take about one month. The 9,000 km distance between the nonbreeding and breeding grounds is completed by two long-distance non-stop flights with stopovers in the German and Dutch Wadden Sea (figure 8.1). If prevailing winds are unsuitable during northward migration, up to 20% of the population use an additional stopover area along the Atlantic coast of France (Piersma et al. 1992, Leyrer et al. 2009a, Shamoun-Baranes et al. 2010).

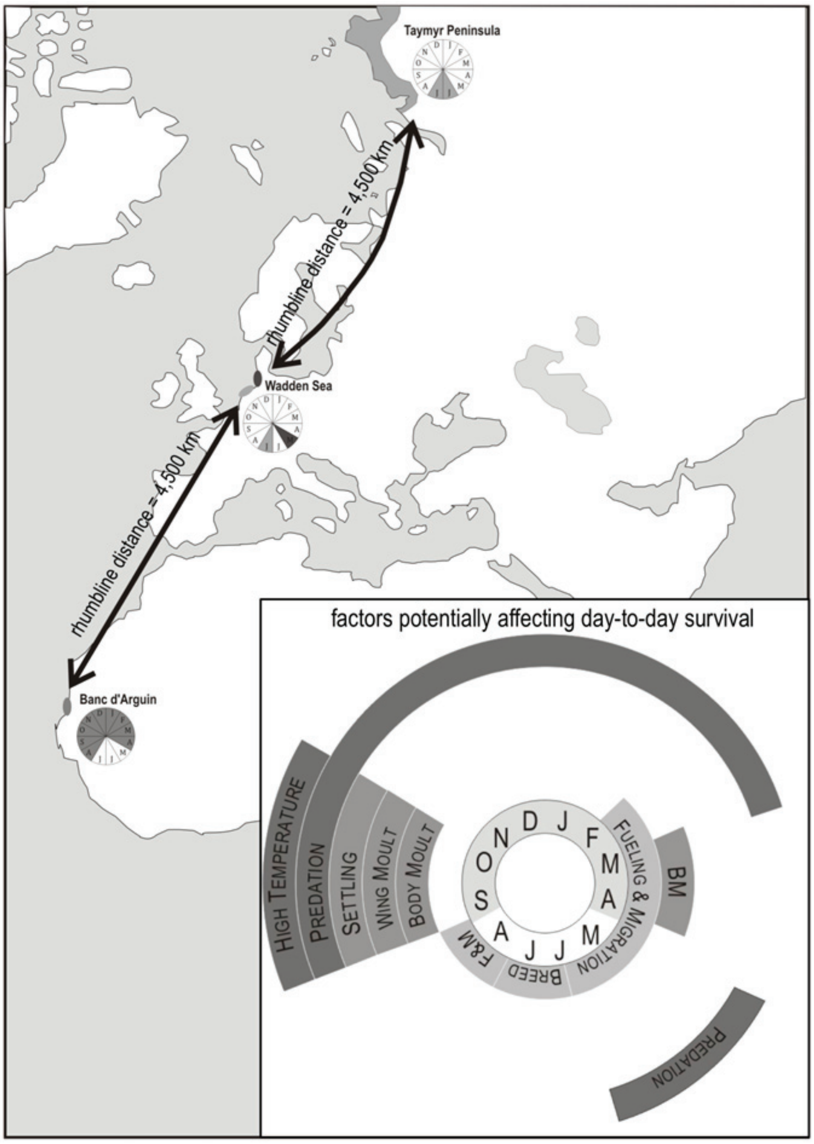


Figure 8.1 Migratory cycle of Afro-Siberian red knots (*C.c. canutus*) covering western Europe, central northern Asia and West Africa. The canutus subspecies spends an 8-month wintering period in West Africa, a 2-month breeding period in Siberia, with 1-month periods of north- and southward migration, with a majority stopping only in the Wadden Sea.
Inset Intrinsic (body and wing moult, and establishing a winter home range = settling) and extrinsic factors (predation, high temperatures) thought to affect seasonal survival of Afro-Siberian red knots as explained in the Discussion. The stationary part of the non-breeding period (wintering) is shaded in light grey.

We conducted an 8-year study in a non-breeding population of *canutus* knots at Banc d'Arguin, Mauritania. We marked, and collected resightings of colour-ringed individuals each midwinter period between 2002 and 2009 to estimate annual apparent survival. We expanded our efforts in Mauritania to include resightings during spring and late summer/early autumn between autumn 2006 and spring 2009. This additional work allowed us to decompose the annual survival rates into two periods: the 8-month nonbreeding period in Africa, and the 4-month migration/breeding period in the northern hemisphere. Below we use mark-recapture results to reevaluate the prevailing view that long-distance migratory movements are necessarily associated with mortality. We demonstrate that mortality can be relatively higher during the stationary nonbreeding period, and may even account for most of the variation in annual survival in a migratory bird.

Methods

Study area and marking methods

Red knots were captured and observed at their main wintering area, the Banc d'Arguin Mauritania, West Africa (Piersma et al. 1992). Our main study site was the high-tide roost of Abelgh Eiznaya on the western shores of Iwik Peninsula (19°54'N 16°17'W, figure 2 in Leyrer et al. 2006). Using mist-nets, we captured red knots at spring high tides and dark nights during new moon lunar phases between mid-November and late December of 2002 – 2008. At first capture, each red knot was individually marked with a metal ring of the Dutch ringing scheme ('Vogeltrekstation Arnhem') and a unique combination of four colour-rings and a plain leg flag (Piersma & Spaans 2004). Birds were aged by plumage characteristics to two age-classes according to Prater et al. (Prater et al. 1977), distinguishing hatch-year birds (juveniles <12 months) and older birds (>12 months). A drop of blood was collected from the brachial vein and stored in 96% ethanol for subsequent molecular sexing. We only included sexed individuals in our analysis. Red knots captured during 2002-2006 were sexed with primers P2/P8 (Griffiths et al. 1998; verified for red knots by Baker et al. 1999). To avoid potential sexing errors due to length polymorphisms in the Z-introns of the CHD-gene (Casey et al. 2009, Schroeder et al. 2010), red knots captured from 2007 - 2009 were sexed with primers 2602F/2669R (Fridolfsson & Ellegren 1999; modified for shorebirds by O. Haddrath). A comparison between the two methods showed that the previous method resulted in an error rate of about 5%, with a bias towards having males incorrectly sexed as females. Sex was not a determining factor in this analysis (see below) and our error was relatively small so we did not correct for miss-sexed individuals.

Sample sizes and observations of red knots

Annual and seasonal apparent survival were estimated using capture-resighting data from colour-ringed red knots caught at the Abelgh Eiznaya high-tide roost, but observed throughout the entire ca. 35 km^2 study area at Iwik Peninsula (figure 2 in Leyrer et al. 2006). A total of 1,007 birds were individually marked during the seven winters of 2002 – 2008. To estimate annual survival, we recaptured and resighted birds in the winters 2003 – 2009 during annual three-week expeditions in November/December. To estimate seasonal survival, we considered observations of marked birds from additional expeditions at the start and end of each non-breeding season during a 3-year period: early August – late September 2006, mid – late April 2007, mid-August – early September 2007, late March – mid-April 2008, late August – mid-September 2008, mid – late April 2009. Red knots marked before winter 2006 and not seen during the second study period were not included in the analysis, and estimates of seasonal survival were based on a reduced sample size of 809 birds.

Observation effort was greatest during the winter expeditions and lower but comparable between late summer and spring (table 8.1). Late summer/early autumn expeditions were timed to coincide with the red knots' return period from the breeding grounds (Piersma et al. 1992), but an unknown number of red knots might not yet have returned when we concluded our observations in late September. Observations in spring were made well before the red knots left the area for northward migration (Piersma et al. 1990a). Counts in our study area in late summer 2006 showed that red knot numbers increased from ca. 7,500 in mid August to ca. 14,000 in late August. Maximum counts of nonbreeding birds in the study area in midwinter averaged 18,000 red knots (T. Piersma, J. Leyrer, unpubl. data).

Data analysis

Apparent survival (Φ) and recapture probabilities (p) were estimated from live encounter data based on captures and resightings using Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992) for annual intervals with equal time steps and seasonal periods with unequal time steps. To improve the precision of the estimates, some a priori assumptions were made to reduce the number of parameters that had to be estimated. Analyses were conducted with program MARK (Version 6.0, White & Burnham 1999).

An initial analysis of annual survival using the full 8-year dataset showed that models including time-dependent variation among years in survival Φ had high delta-AIC scores and low Akaike weights, and that sparse data led to problems with estimations of Φ and p. We were less interested in annual variation in Φ for this study, and opted to exclude time as a factor for Φ, but not for p. Field efforts were greater in later years and resighting skills improved in the course of this study due to observer training and better local field knowledge, therefore, resighting probability p was modelled with variation among years, but not between age or sex. Habitats used by red knots at Banc d'Arguin included open mudflats and beaches without vegetation. We had no evidence that space use differed between sex and age classes as all birds foraged on mudflats during low tide and assembled at communal roosts at high tide. We modelled apparent survival as a function of three factors: age at capture (juveniles vs. adults), sex (male vs. female), and an effect of time-since-marking (tsm) (Sandercock 2006). Time-since-marking was included to test whether newly marked individuals differed in apparent survival during their first year (Φ^{1}) compared with subsequent years (Φ^{2+}). Apparent survival might be lower after first capture if we either had an unknown proportion of transient birds in our study population or a number of individuals experienced a higher mortality immediately after catching due to capture and handling stress. We also occasionally found carcasses of newly marked birds that had been killed by feral cats after release, potentially as a consequence of being captured and handled, and these were excluded from the analyses. The time-since-marking effect was included for each age-class (juveniles and adults). Juvenile red knots become adults at the end of their second calendar year, and low survival could be due to either age or tsm effects, or both. Goodness of fit to the encounter histories was tested for our global starting model $\Phi^{1}_{age+sex}\,\Phi^{2+}_{sex}\;p_{year}$ with the median-$\hat{c}$ test implemented in MARK, and $\hat{c}$ was adjusted with the estimated $\hat{c} = 1.01 \pm 0.00$ SE.

Our time series to model variation in seasonal apparent survival Φ included three years and we thus excluded year as a factor. Due to differences in observation effort, resighting probability p was modelled with season-dependence among expeditions in late spring (April), late summer/early autumn (August/September), and winter (December) (table 8.1), but because the time series was short, annual differences were not included. We set unequal time steps to estimate 2-month rates of apparent survival and tested two different scenarios: (1) dividing the year into three seasons: a 5-month winter (December – April), a 4-month migration+breeding (May – August), and a 3-month autumn (September – November), and (2) dividing the year into two seasons: an 8-month stationary non-breeding season (September – April) vs. a 4-month migration+breeding season (May – August). Migratory behaviour of juveniles differed from adults as they apparently did not depart on northward migration and remained in the non-breeding areas during the boreal summer. We thus included age-class as a factor for Φ in our seasonal models and juveniles were treated differently in estimating Φ until the winter preceding their first northward migration (in their 3rd calendar year). A time-since-marking effect on survival was tested for newly ringed individuals during the season following the marking event (December – April). Individuals marked before December 2006 were included by treating the first encounter within the study period (summer 2006 until spring 2009) as a 'marking event', but because they had already returned to the area, we excluded a tsm-effect for those individuals. We pooled sexes in the seasonal models as, making use of knowledge gained from our annual models we did not expect them to differ. Goodness of fit to the encounter histories was tested using the median-ĉ test in MARK for the starting model $\Phi^1{}_{\text{age}}\ \Phi^{2+}{}_{\text{age+3 seasons}}\ p_{\text{3 seasons}}$, and ĉ was adjusted with the estimated ĉ = 1.54 ± 0.01 SE.

If seasonal survival estimates approached unity, we performed three types of sensitivity analyses to determine whether the parameter estimates were at unity because survival was indeed close to the boundary or because sparse data precluded the estimation of this parameter. We used the sin link function (instead of the more generally applicable logit link function) as it performs better when estimating parameters near the boundaries of zero and one. We also fit reduced models to compare estimated survival values, and assessed convergence of the models using the alternate optimization capability based on simulated annealing in MARK which is more likely to find the global instead of a local maximum (Cooch & White 2010). Last, we fit the best model using a Bayesian procedure, the Markov chain Monte Carlo (MCMC) estimation implemented in MARK and compared the mean, median and mode of the MCMC estimates with the parameters of the same model fitted with maximum-likelihood procedures.

Table 8.1 Number of observation sessions in the study area at Iwik peninsula, Banc d'Arguin, Mauritania in different seasons between 2003 and 2009. Each observation session covers a single period of time (1 - 3 hrs) spent by one observer in a subarea within the study area (for subareas, see Leyrer et al. 2006).

	2003	2004	2005	2006	2007	2008	2009
winter	47	75	83	229	96	118	117
spring					37	11	16
autumn				92	22	17	

Results

Annual survival

The minimum AICc model describing annual apparent survival included an effect of time-since-marking on apparent survival (table 8.2). Annual estimates of apparent survival in 2002 – 2009 were 0.79 ± 0.02 SE (95%CI = 0.74 – 0.82) in the interval after first marking (Φ^1) and 0.84 ± 0.02 (0.82 – 0.87) in subsequent years (Φ^{2+}) (table 8.3). Adding sex and age as parameters led to an increase in delta-AICc and thus were of no explanatory value (table 8.2). However, juveniles tended to have lower annual apparent survival of 0.76 ± 0.04 (0.68 – 0.83).

Seasonal survival

Two models describing seasonal apparent survival were equally parsimonious, and both included a time-since-marking effect and seasonal differences in survival between the stationary wintering periods at Banc d'Arguin and the migration+breeding period away from Banc d'Arguin (table 8.4). Consistent with the annual models, the best supported seasonal model estimated Φ^{1} to be lower (0.85 ± 0.02; 0.81 – 0.89) than in subsequent winters ($\Phi^{2+} = 0.95 \pm 0.01$; 0.93 – 0.97; both 2-month survival, table 8.5). Unexpectedly, 2-month survival was at unity during the migration+breeding season (1.00 ± 0.00; 1.00 – 1.00). The 'second best' model also estimated 2-month survival during the migration+breeding season with 1.00 ± 0.00 (1.00 – 1.00), but suggested 2-month winter Φ^{2+} to be lower during the autumn season September – November (0.92 ± 0.03, 0.85 – 0.96) than 2-month winter Φ^{2+} during the midwinter season December – April (0.98 ± 0.03; 0.83 – 0.99), 2-month Φ^{1} of the second model was 0.86 ± 0.02 (0.82 – 0.90) (table 8.5).

Table 8.2 Model selection results for estimation of annual apparent survival (Φ) and resighting probability (*p*) for red knots *C. c. canutus* at Banc d'Arguin, Mauritania, 2002-2009.

Model	NP	Deviance	AICc	ΔAICc	AICc weight
[1] $\Phi^{1}_{const.}\ \Phi^{2+}_{const.}\ p_{year}$	9	715.56	4830.37	0	0.35
[2] $\Phi^{1}_{age}\ \Phi^{2+}_{const.}\ p_{year}$	10	715.00	4831.83	1.46	0.17
[3] $\Phi^{1}_{sex}\ \Phi^{2+}_{sex}\ p_{year}$	10	715.30	4832.13	1.76	0.14
[4] $\Phi_{age}\ p_{year}$	9	717.88	4832.69	2.32	0.11
[5] $\Phi_{const.}\ p_{year}$	8	720.36	4833.15	2.79	0.09
*[6] $\Phi^{1}_{age+sex}\ \Phi^{2+}_{sex}\ p_{year}$	11	714.69	4833.54	3.18	0.07
[7] $\Phi_{age+sex}\ p_{year}$	10	717.55	4834.37	4.01	0.05
[8] $\Phi_{sex}\ p_{year}$	9	720.13	4834.94	4.57	0.04

Φ^{1} = apparent survival in first year after marking, Φ^{2+} = apparent survival in subsequent years, *p* = recapture (resighting) probability. Parameters included in models were sex (male/female), age (juvenile (1st year)/adult (from 2nd year onwards) and time (year), const. = intercept only. Given are number of estimable parameters (NP), Deviance, Akaike's information criterion values corrected for small sample size (AICc), ΔAICc, and AICc weight. * The goodness of fit (GOF) was tested for model [6] and ĉ was adjusted to 1.01. The sex effect was modelled to have the same additive effect on Φ^{1} and Φ^{2+} and therefore involved only one parameter.

Table 8.3 Annual estimates of apparent survival (Φ) and resighting probabilities (*p*) with standard errors and 95% confidence intervals of adult canutus red knots at a nonbreeding site in Banc d'Arguin, Mauritania, West Africa, in 2003 – 2009.

	estimate ± SE	95% CI
Φ^{1}	0.79 ± 0.02	0.74 - 0.82
Φ^{2+}	0.84 ± 0.02	0.82 - 0.87
resighting probabilities *p*		
2003	0.25 ± 0.04	0.18 - 0.30
2004	0.38 ± 0.03	0.32 - 0.44
2005	0.49 ± 0.02	0.44 - 0.54
2006	0.55 ± 0.03	0.49 - 0.60
2007	0.65 ± 0.03	0.60 - 0.70
2008	0.64 ± 0.03	0.59 - 0.69
2009	0.55 ± 0.03	0.49 - 0.60

Φ^{1} = annual apparent survival in first year after marking
Φ^{2+} = adult annual apparent survival in subsequent years

We further tested the sensitivity of the estimates of φmigration+breeding (1.0 ± 0.00) by fitting reduced models with a constant resighting probability, yet estimates were unchanged from the value of 1.0 for Φ. Using the alternate optimization capability did not change our estimates. Last, comparisons of the mean, median and mode of the MCMC estimation showed that 2-month Φ during the migration+breeding seasons remained high (mean ± s.d. 0.994 ± 0.007; median 0.997; mode 1.00), all other estimates for Φ^{1} and Φ^{2+} differed in the 3rd decimal place only. Our sensitivity analyses gave us confidence that MARK had correctly estimated the parameter, though slightly biased towards the boundary of 1. Furthermore, both resighting probabilities (*p*) and survival (Φ) were estimated with high precision (small CI for p and small CV≤ 0.03 for Φ), Φ should be unbiased.

Table 8.4 Model selection for seasonal estimates of apparent survival (Φ) and recapture probability (*p*) for *canutus* red knots wintering at Banc d'Arguin, Mauritania.

Model	NP	QDeviance	QAICc	ΔQAICc	QAICc weight
[1] Φ^{1} $\Phi^{2+}_{\text{2 seasons}}$ $p_{\text{3 seasons}}$	6	285.07	2300.16	0	0.51
[2] Φ^{1} $\Phi^{2+}_{\text{3 seasons}}$ $p_{\text{3 seasons}}$	7	283.41	2300.52	0.36	0.42
* [3] Φ^{1}_{age} $\Phi^{2+}_{\text{age + 3 seasons}}$ $p_{\text{3 seasons}}$	8	285.92	2305.04	4.89	0.04
[4] Φ^{1}_{age} $\Phi^{2+}_{\text{age + 2 seasons}}$ $p_{\text{3 seasons}}$	7	288.90	2306.01	5.85	0.03
[5] Φ_{age} $p_{\text{3 seasons}}$	5	308.85	2321.92	21.76	0
[6] Φ_{const} $p_{\text{3 seasons}}$	4	311.51	2322.57	22.41	0

Φ^{1} = apparent survival in first winter after marking (comprises December – April), Φ^{2+} = apparent survival in subsequent seasons/years: 2 seasons = year divided in 2 seasons (stationary nonbreeding and migration+breeding), 3 seasons = year divided into 3 seasons (winter, migration+breeding, autumn), age = juvenile/adult. Juvenile red knots were treated as adults from the winter preceding the first migration+breeding season onwards. Given are number of estimable parameters (NP), QDeviance, Akaike's information criterion values corrected for small sample size (QAICc), ΔQAICc and QAICcweight. * The goodness of fit (GOF) was tested for model [3], $\hat{c}$ was adjusted to 1.54. The age effect was modelled to have the same additive effect on Φ^{1} and Φ^{2+} and therefore involved only one parameter.

Discussion

We report, for the first time, estimates of both annual and seasonal survival for a single population of a hemispheric migrant, in this case the red knot. Between 2002 and 2009, annual survival, controlled for a time-since-marking effect, for individuals spending the nonbreeding season at Banc d'Arguin was 0.84 ± 0.02. This estimate is relatively high for such a small-bodied shorebird species (Sandercock 2003) and indicates that red knots generally show strong site fidelity to nonbreeding sites and have high survival rates (Brochard et al. 2002, Baker et al. 2004, Leyrer et al. 2006, Spaans et al. 2011). A combination of factors could have contributed to the five percentage-points difference in survival between the first year after marking and later years (Sandercock & Jaramillo 2002). For one, catching and handling effects could have played a role. When held during catching and marking activities, particularly red knots (and other shorebird species) caught in tropical environments are susceptible to develop capture myopathy (Rogers et al. 2004), which can be fatal or make individuals prone to predation after release. Time-since-marking effects could also have been due to the capture of transient birds during mid winter. The nonbreeding distribution of *canutus* knots extends further south to other sites in equatorial Africa (e.g. Archipélago dos Bijagos, Guinea-Bissau, Piersma et al. 1992), and a subset of marked birds may have permanently emigrated from our study population. Annual survival tended to be even slightly lower among juveniles and the age effect could be explained by lower survival among inexperienced birds (Sandercock 2003).

Unexpectedly, we found that the period of highest seasonal mortality within the annual cycle occurred at tropical wintering grounds in the months after completion of a 9,000 km migration back from the High Arctic breeding grounds. Most theoretical treatments of migration assume that mortality costs are highest during the migration and breeding periods, the times that birds face major time, nutritional, energetic, and predation challenges (Buehler & Piersma 2008), and adverse weather events can severely affect migrating animals working at their physiological limits (Alerstam 1990, Newton 2007, Shamoun-Baranes et al. 2010). In contrast, also to earlier empirical studies (Clausen et al. 2001, Sillett & Holmes 2002), our analyses found lower survival during the stationary wintering period than during the migration+breeding season. Particularly during migration, habitat specialists like red knots depend on high quality staging sites in intertidal areas (van Gils et al. 2005a). Marine soft sediments are threatened ecosystems worldwide (Baker et al. 2004, van Gils et al. 2006a, Rogers et al. 2010), and losses or degradation of these habitats have been shown to have a negative impact on the survival of migrating birds (Baker et al. 2004, van Gils et al. 2006a, Kraan et al. 2010b). However, no major disturbances were observed during our study period at the key staging sites of the Afro-Siberian red knot population along the Atlantic coast or in the Wadden Sea (unpubl. obs.).

We further observed that mortality was highest during the first three months after red knots arrived back in the West African wintering grounds in autumn and early winter, at a time when impacts of multiple stress factors may coincide (figure 8.1). Of these factors, predation by raptors, primarily lanner *Falco biarmicus* and barbary falcons *F. pelegrinoides*, is unlikely to play a direct role because predation at Banc d'Arguin accounts for a mere 0.8% of adult annual mortality (van den Hout et al. 2008). Furthermore, benthic food availability has increased in recent years (van Gils et al. 2009b) and mortality of nonbreeding red knots cannot be explained by degradation of foraging conditions during our study either. Without neglecting the potential role of delayed costs of migration (Harrison et al. 2010), we will now argue that high early winter mortality may reflect a combination of pressures acting on the birds caused by the physiological stress of climatic conditions during a time of relatively high intraspecific competition during settlement (figure 8.1, Chapter 3).

When red knots return to nonbreeding habitats in a tropical environment, moulting of flight and body feathers starts immediately, at a time when ambient temperatures are at seasonal maxima (average August temperature at Banc d'Arguin 31°C (Wolff & Smit 1990), daily maximum temperatures are regularly in the high 40s °C, and humidity is high (unpubl. obs.)). Moult is a physiologically challenging process and generates heat (Lindström et al. 1993, Klaassen 1995, Portugal et al. 2007, Cyr et al. 2008, Vézina et al. 2009). Under prevailing climatic conditions, moulting red knots could be constrained by their capacity to dissipate heat, at a risk of hyperthermia. Hyperthermia can be more problematic than hypothermia and even mild hyperthermia can have long-term negative effects on organismal performance (Speakman & Krol 2010). In addition, during moult birds appear to down-regulate costly immune functions (Buehler et al. 2008). Red knots thus face a series of potential internal and external stressors upon arrival after a 18,000 km return migration (figure 8.1) and an energetically challenging breeding season in the High Arctic (Piersma et al. 2003b), hence carry-over effects may well contribute to the observed higher winter mortality (Harrison et al. 2010).

Our data for Afro-Siberian red knots show the season with highest mortality is early winter in West Africa and not migration or breeding. We propose that physiological challenges in combination with intraspecific competition after arrival on the wintering grounds, possibly amplified by carry-over effects of the stresses endured during the foregoing migration and breeding seasons (Harrison et al. 2010), create periods of high selection pressure. Comparative studies of seasonal mortality patterns are limited yet, and further studies of other subspecies of red knots and migratory birds with wintering grounds in different climatic regions and different annual routines will help testing this idea and thus help explaining the microevolution of migratory behaviour (Piersma 2007, 2011). If the combination of stresses would be particular to this population, our study would articulate again that the devil is in the details. Although this would reduce the generality of the present results, it would not diminish its value in helping to prioritize the conservation resources devoted to this declining shorebird migrant.

Acknowledgments

We thank the Parc National du Banc d'Arguin (PNBA) in Nouakchott for permission to work in the national park and for all invaluable help during all phases of many expeditions. Our colleagues at the Biological Station Iwik always made us feel welcome and helped in many ways during our stays. International and volunteer members of the Mauritania expeditions 2002 – 2009 helped to catch and resight colour-ringed Red Knots: N. Abayie, M. Avloitt, P. Battley, H. Blijleven, P. de Boer, D. Buehler, M. Bulte, A. Dekinga, J. Dierschke, J. van Dijk, A. Evers, P. de Goeij, K. Grond, K. Günther, J. Guilherme, H.O.M. El Hacen, G.T. Hallgrimson, L. Hofstee, J. Hooijmeijer, H. Horn, J. ten Horn, P. van den Hout, J. van de Kam, C. Kelly, C. Ketzenberg, E. Koomson, L. van Kooten, C. Kraan, J. Lewis, B. Loos, L. Mendes, Y. Ntiamoa-Baidu, K. Oosterbeek, P. Potts, S. Pruiksma, A. Purgue, J. Reneerkens, F. Robin, G. Scheiffarth, J. Smart, M. Smart, N. Spaans, I. Tieleman, B. Thorrison, S. Waasdorp, and R. Ward. Valuable comments on the manuscript were provided by G. Aarts, J. A. Gill, P. J. van den Hout, Y. I. Verkuil, the editor and two anonymous reviewers. J. van Dijk once received expeditionary support from the Dutch Ministry of Agriculture, Nature and Food Quality (LNV). JL was financed by a PhD grant from the MAVA Foundation, Switzerland, to TP. Field expeditions were financed by the Royal NIOZ, and grants from the Schure-Beijerinck-Popping Fonds to JL in 2008 and 2009, and the Prins Bernhard Cultuurfondsprijs voor Natuurbehoud to TP in 2004.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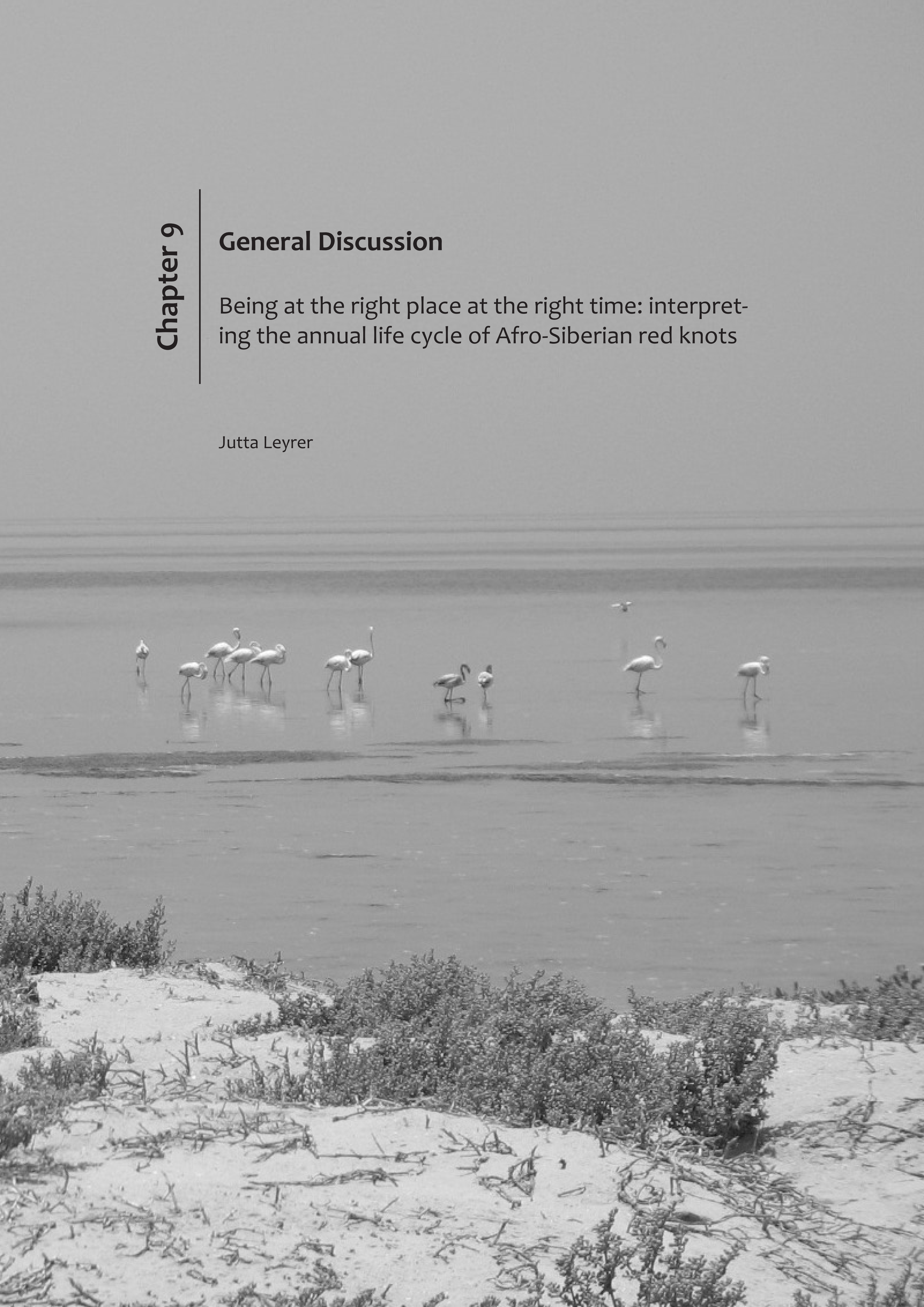
Chapter 9

General Discussion

Being at the right place at the right time: interpreting the annual life cycle of Afro-Siberian red knots

Jutta Leyrer



In this thesis I presented evidence of various potential selection pressures acting on survival and reproduction of Afro-Siberian red knots during the winter and migration seasons. Perhaps the most surprising finding was that seasonal mortality in our Afro-Siberian red knot study population was highest in the first months after return to the Mauritanian wintering grounds, at least in 2006-2009 (Chapter 8). This was contrary to what we would have expected and to what had been described earlier for a few other long-distance migrants, that mortality would be highest during the migration seasons (Sillett & Holmes 2002, Clausen et al. 2006), or towards the end of the wintering period, when food resources are depleted. This has led us to wonder whether what happens during the wintering period on Banc d'Arguin – where we observed persistent and small-scale population structuring with respect to sex and age across areas that may differ in quality (food and predation risk) (Chapter 3) – might present a bottleneck within the annual cycle in Afro-Siberian red knots. For example, individuals occupying the better habitat might have better starting positions into the subsequent northward migration, but settling in the better habitat would require an early arrival in good condition at Banc d'Arguin, to be the first to occupy a good site and to be able to defend that site against conspecifics. If such a winter arrival timing advantage indeed exists, then the wintering period might be the as important for population regulation (through survival) as arrival on the breeding grounds (through reproduction). For now, however, we can only suggest that carry-over effects from the previous migration and breeding period may contribute to mortality in winter.

Annual routine models (McNamara et al. 1998, Houston & McNamara 1999, McNamara & Houston 2008) are a good tool to investigate whether Afro-Siberian red knots are constrained in arriving early and in good condition at their wintering ground and whether this could have carry-on effects on subsequent northward migration and their arrival in the breeding grounds. In this final chapter, I will summarize the various findings of this thesis and discuss the many unknowns that still exist in such a relatively well-studied species. I will outline how in the future, my findings, and those of previous workers/studies, can be implemented in a fully-fledged, mathematically explicit, annual routine model.

Before proceeding, I should make a short comment on the use of terms such as 'wintering' and 'nonbreeding' sites. Many migratory bird species spend the majority of their nonbreeding period in the tropics or the southern hemisphere, where either seasons such as 'summer' and 'winter' do not exist or appear in opposite directions to the seasons in the northern hemisphere. The term 'nonbreeding grounds' is a more and more commonly used surrogate for 'wintering grounds'. Yet, as this term includes all sites visited outside the breeding grounds, it complicates the differentiation between staging sites (e.g. Wadden Sea), and wintering sites (e.g. Banc d'Arguin) where red knots spend most of their time during the nonbreeding season. As red knots are born in the Arctic during the northern summer and are thus birds of the northern hemisphere, I decided to use the term 'wintering' when referring to the period that Afro-Siberian red knots spend on Banc d'Arguin.

Annual Routine Models

Animals that live in seasonal environments follow annual routines: they schedule activities such as breeding, migration and moult in predictable ways over the year (Gwinner 1990, Gwinner & Helm 2003). A major challenge in the mathematical modelling of annual cycles has been to define a 'starting' or 'end point' of such cycles, as the present and future are linked in both directions (Houston & McNamara 1999). The best strategy to choose now will depend on future expectations, but future state will also depend on current actions, and evidently the current state may depend on past actions. The common approach taken (Houston & McNamara 1999) is to determine the terminal reward function, i.e. reproductive value of an organism as a function of body state and timing at a key "terminal" stage. In long-distance migrants such as red knots, arrival date and body condition upon arrival in the breeding grounds are likely to directly influence reproductive performance. This is why I chose the terminal stage in the annual cycle as the return to the breeding grounds, working backwards from there in the dynamic programming.

There are both physiological and ecological state variables that affect the behaviour of (migrating) animals (Houston & McNamara 1999, McNamara & Houston 2008). State variables are any factors that can affect an individual's fitness. These include the internal (physiological) levels of energy and nutrient stores, but also the phenotypic flexibility to adjust e.g. gizzard size or flight muscles according to the external circumstances encountered (Battley et al. 2000, Piersma & Gill 1998, van Gils et al. 2005a). Such external circumstances are variables like food abundance, weather, the number of competitors, the position in a dominance hierarchy or predation pressure. All factors together define the quality of the site used (McNamara & Houston 2008). In the following I will introduce potentially important state variables, discuss their possible influence on the birds' behaviour, and develop a conceptual framework that can be used to model annual routines in Afro-Siberian red knots.

The annual cycle of Afro-Siberian red knots

Distribution range, migration routes and timing

The various wintering, breeding and fuelling sites visited by Afro-Siberian red knots are presented in figure 9.1. As far as we know Afro-Siberian red knots breed exclusively in the Siberian tundra on Taimyr Peninsula (Piersma et al. 1992, Tomkovich & Soloviev 1996). Within the Afro-Siberian red knots, the best studied population winters at Banc d'Arguin, Mauritania (Piersma et al. 1992, van de Kam et al. 2004). Previous studies have documented the northward migration route of these birds to their Siberian breeding grounds via the coasts of the French Atlantic and the Schleswig-Holstein (SH) Wadden Sea, Germany (Piersma et al. 1987, Prokosch 1988, Piersma et al. 1992). During southward migration, they visit the Dutch Wadden Sea on their way back to Mauritania (Nebel et al. 2000, Kraan et al. 2010b). How red knots wintering in South Africa and Guinea-Bissau migrate to and from the breeding grounds has not yet been documented.

Winter distribution - The described winter range of Afro-Siberian red knots stretches along the west coast of Africa (figure 9.1) with the majority of the population (75%) wintering at Banc d'Arguin, Mauritania, and another significant proportion wintering in the Bijágós Archipelago in Guinea-Bissau (Piersma et al. 1992). A few hundred canutus red knots spend the winter in Morocco (Davidson & Piersma 2009). The South African wintering population was reported to consist of 10,000 birds in the 1970s but has since declined to almost zero (Davidson & Piersma 2009). Summers et al. (in prep.) point out that Afro-Siberian red knots first appeared in larger numbers in South Africa, additional 6,000 km further away from the breeding grounds, in the 1970s, when the West-African winter population was approximately double the size of today. Red knots that migrated further to South Africa for the first time largely did so as juvenile birds, but kept returning as adults in subsequent years (Summers et al. in prep.). This suggests that these individuals may have been competed out of the major wintering grounds in West Africa. The overall decline of the Afro-Siberian red knot population over the last decades has

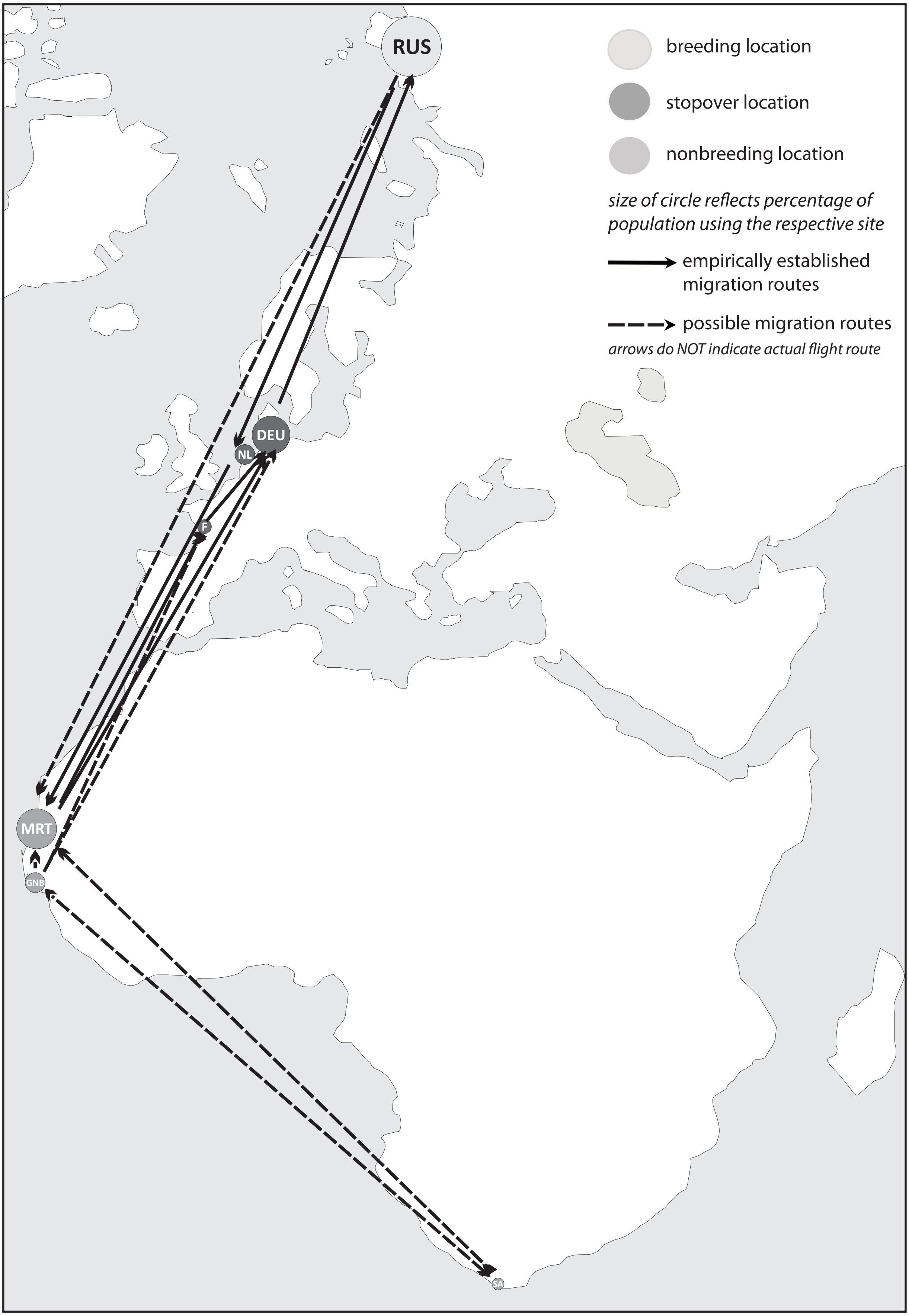


Figure 9.1 Migration routes and key sites used by adult Afro-Siberian red knots during the annual cycle: Outside the breeding season, intertidal soft sediment habitats are used exclusively. Juvenile migration is not indicated.

been associated with strongest declines in South Africa (Davidson & Piersma 2009) which is consistent with the idea that the South African wintering grounds acted as a buffer (Gill et al. 2001; Summers et al. in prep.).

Distribution during northward migration – Because of the lack of knowledge on timing and migration routes taken by red knots wintering in South Africa, Guinea-Bissau and Morocco, I will base the following paragraphs on the Mauritanian population. Afro-Siberian red knots wintering at Banc d'Arguin have been shown to leave later than most other arctic-breeding shorebirds, in early May (Piersma et al. 1990). It has been suggested that they make a non-stop flight of 4,500km to the SH Wadden Sea, where they arrive in mid-May (Prokosch 1988, Piersma et al. 1992, van de Kam et al. 2004). The observations made during this project support and strengthen the earlier observations of annually varying numbers visiting the French Atlantic coast on migration from Mauritania to the SH Wadden Sea (Piersma et al. 1992, van de Kam et al. 2004; Chapter 4). Furthermore, they show that the French Atlantic coast indeed functions as an emergency staging site. Red knots appear to only use France when unpredictable wind conditions en route make a direct non-stop flight to the SH Wadden Sea impossible (birds arriving in France are very lean, ca. 100 g, P. Bocher, F. Robin, unpubl. data; Chapter 5). It is assumed that the whole population of Afro-Siberian red knots stages in the SH Wadden Sea during late May, where the birds spend about three weeks to double their body weight (Prokosch 1988, Piersma et al. 1992, but see below). They leave for their Siberian breeding grounds in the first week of June (Piersma et al. 1991, Piersma et al. 1992; Chapter 7), and arrive at the Siberian grounds around 10 June (Tomkovich & Soloviev 1996).

Distribution during southward migration - By the end of July the first Siberian red knots, mainly adult females that leave the breeding grounds first after the clutch has hatched (Tomkovich and Soloviev 1996), migrate south via the Dutch Wadden Sea (Nebel et al. 2000), arriving at Banc d'Arguin from mid-August onward (own unpubl. obs.). Successful males leave the breeding grounds after the juveniles have fledged and unsuccessful males have been reported to leave shortly after the clutch has been lost (Tomkovich & Soloviev 1996). During southward migration, adult males have not yet been observed regularly in any substantial numbers anywhere on staging areas along the flyway, and it could thus be, that they fly non-stop to Africa. Juvenile red knots have been observed to migrate south last, visiting various fuelling sites along the entire coast in the Baltic (together with small numbers of adults (Meissner 2005, Meissner & Kamont 2005), the Wadden Sea (Nebel et al. 2000, Piersma & Spaans 2004, Spaans et al. 2009), estuaries in the UK (T. Piersma, B. Spaans unpubl. recapture data) and along the French West coast (P. Bocher pers. comm.). The majority of adult red knots has returned to the Mauritanian wintering grounds areas by mid-September, but juvenile red knots do not begin to arrive before October (J. Leyrer, P.J. van den Hout, unpublished observations).

External and internal variables influence the scheduling of activities over the annual cycle

Figure 9.2 graphically summarizes the ways that activities such as moult, migration and breeding are scheduled in the course of a year. External factors such as predation, ambient temperature and settling costs, are also shown as they may affect the performance of an individual and might ultimately influence date and state of arrival in the breeding grounds. Table 9.1 summarizes a general annual schedule, migration distances and a list of external and internal variables influencing this schedule. Table 9.2 provides an exhaustive compilation of facts and inferences from previous empirical and modelling studies, as well as new data collected within the broader framework of this study. The information in these tables highlights remaining gaps in our knowledge, which motivated much of the discussion in the following paragraphs. In a follow-up outside this thesis, these data, together with the questions that remain, will be framed in a mathematical annual routine model to help identify constraints and trade-offs within the annual cycle of Afro-Siberian red knots and to help direct future research.

The importance of arrival timing on the breeding grounds - Arrival date and body condition upon arrival on the breeding grounds are likely to have a direct influence on reproductive performance but also on survival. Ice and snow cover upon arrival vary from year to year (Tulp 2007) and determine whether food is available upon arrival or whether red knots must rely

Table 9.1 External and internal variable influencing survival and reproduction during the annual cycle in Afro-Siberian red knots migrating from their West African nonbreeding grounds (Banc d'Arguin) to their Siberian breeding grounds (Taimyr) via key staging sites in the Wadden Sea and France. The grey arrow connecting Taimyr and the Banc d'Arguin represents a possible, not yet empirically shown migration route.

month	site	distance between sites [km]	status	external/environmental variable	internal/physiological variable
June	Taimyr	5,000	transformation migration ➔ breeding	time of arrival weather conditions availability of mate/territory	body stores for initial survival and body transformation
July			breeding	predators	
August	Taimyr	5,000 9,500	transformation breeding ➔ migration	food availability predators	body transformation gizzard?
	Wadden Sea	4,500	fuelling	food availability predators	gizzard
	Banc d'Arguin		moulting		
	Banc d'Arguin		moulting		
September			moulting	competition among conspecifics ambient temperature predtors	gizzard moult salt stress immuno-competence
October			moulting		
November			moulting		
December			non-breeding		
January			non-breeding		
February			fuelling	food availability predators	gizzard
March			fuelling / moulting	food availability predators heat stress	gizzard moult
April	Banc d'Arguin	3,000 4,500	fuelling / moulting		
May	France	1,500	fuelling	food availability predators wind	gizzard
	Wadden Sea	5,000	fuelling		

on their body stores brought from the previous staging site (Morrison et al. 2007). Initiating a clutch has to be timed in such a way that the chicks hatch when food availability peaks (Schekkerman et al. 2003). Thus, there are costs involved in arriving lean and arriving late (Ens et al. 1994, Drent et al. 2003, Morrison 2006; figure 9.2).

Fuelling for migration at the wintering ground – when something works that shouldn't - Although red knots do not transport nutrient stores for egg production into the arctic (Klaassen et al. 2001), they still rely on stores brought from the ultimate staging site to survive upon arrival in case foraging is impossible and to perform extensive morphological changes from a migratory to a reproductive phenotype (Morrison 2006, Morrison et al. 2007). From studies showing detrimental effects of deteriorating fuelling conditions at a key staging site on survival in the closely related rufa subspecies (Baker et al. 2004), we infer that the possibility to accumulate sufficient stores at the final staging site in the SH Wadden Sea will affect both adult survival and reproductive success.

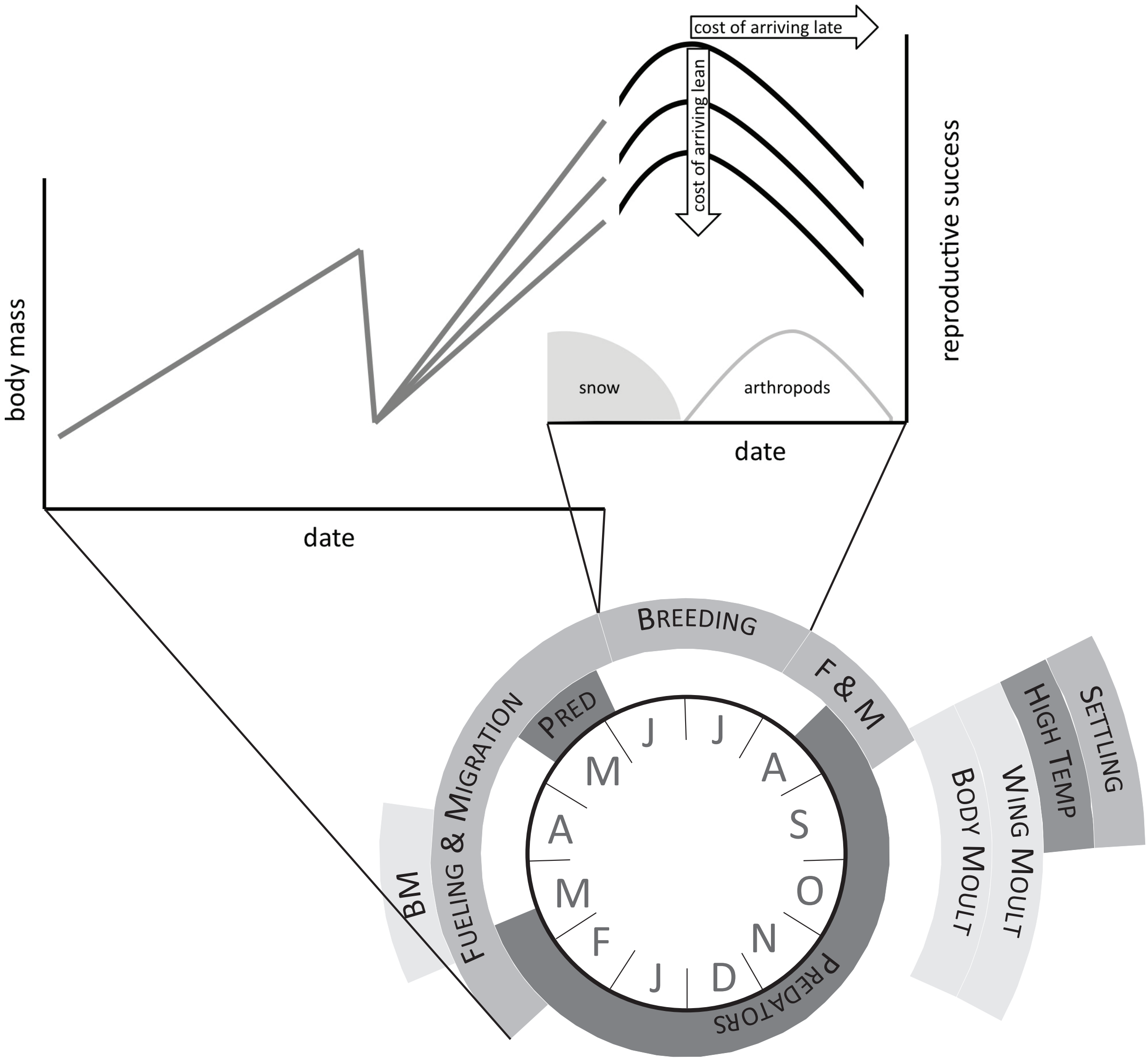


Figure 9.2 Environmental factors (dark grey), organismal activities (light grey), and events where external and internal variables are closely linked (medium grey) affect day-to-day survival in Afro-Siberian red knots during the annual cycle. The goal is to arrive at the breeding grounds at the optimal time to initiate a clutch for chicks to hatch when food abundances peak. Red knots should also arrive in an optimal condition to survive an initial period when snow and ice make food unavailable. Fuelling rates prior and during migration affect the time and state of arrival in the breeding grounds. Figure modified from Ens et al. (1994).

Table 9.2 Known, new and still unknown facts and factors that influence the annual routine of breeding, migration, wintering and moult in Afro-Siberian red knots

location	state	what has been known	this thesis	still unknown	reference
Taimyr	arrival	arrival date: 10 June			Piersma et al. 1992 Tomkovich & Soloviev 2006
		arrival mass is crucial for survival and body transformation			Morrison 2006 Morrison et al. 2007
	breeding	initiation of clutch to match peak in food availability during chick rearing			Schekkerman et al. 2003 Tulp 2007
		predation pressure during breeding is correlated with lemming cycle			Summers et al. 1998
	post-breeding			fuelling conditions	
en route	migration			wind conditions	
		females migrate earliest and stagin in NL Wadden Sea			Tomkovich & Soloviev 2006 Nebel et al. 2000
		successful males migrate latest, unsuccessful males migrate as soon as clutch is lost			Tomkovich & Soloviev 2006
		juveniles migrate latest and in short hops staging along coastline			Meissner 2005 Meissner & Kamont 2995
		staging sites along Baltic coast potential emergency habitats for adult red knots			Meissner 2005 Meissner & Kamont 2995
				do males migrate directly to Mauritania?	
NL Wadden Sea	fuelling	mostly (only?!) females stage in NL Wadden Sea		where do males stage during southward migration?	Nebel et al. 2000
		fuelling conditions have deteriorated in the past decades			Kraan et al. 2010
				fueling rates	
				gizzard size and repertoire and resources to adjust gizzard size	
				predation pressure during fuelling	
en route	migration			wind conditions	

Table 9.2 continued

location	state	what has been known	this thesis	still unknown	reference
Banc d'Aguin	arrival		early arrival potentially crucial for occupying high quality site (Ch. 3)		
			hidden interspecific competition (Ch. 3)		
	moult	moult: ealry September until November	ambient temperature potentially detrimental during moult (Ch. 8)		Piersma et al. 1992
	wintering	predation not influencing winter mortality			van den Hout et al. 2008
		predation pressure influences site use behaviour			van den Hout 2010
	fuelling	fuel from early March to early May (60 days)			Zwarts et al. 1990 Piersma et al. 2005
		departure date: early May			Piersma et al. 1990 Piersma et al. 1992
			small-scale differences in intake rates influence site choice (Ch. 3)		
		mass gain: 0.7g per day		site specific fuelling rate - individual variance	Piersma et al. 2005
		prey quality: 0.9 ± 0.07 kJ/g DM shell mass			van Gils et al. 2005
		gizzard size: 10g	gizzard size: 10 - 12g (unpubl. data)		van Gils et al. 2005
		departure mass: 180g			Zwarts et al. 1990 Piersma et al. 1992
				predation pressure influencing fuelling rates	
				heat stress during fuelling	
en route	migration		wind conditions upon departure non predictable (Ch. 5)	behaviroual repertoire to change flight altitude to find better wind conditions	
			travel time: 2 - 9 days (Ch. 5)		

Table 9.2 continued

location	state	what has been known	this thesis	still unknown	reference
France	fuelling		peak of red knot numbers around 11 May (P. Bocher, F. Robin, unpubl data)		
			variable proportions use France annually (Ch. 4)		
		potentially wind driven staging site usage patterns	usage of French staging site is wind driven (Ch. 5)		van de Kam et al. 204
			mass gain: 2.5g per day (P. Bocher, F. Robin, unpubl data)		
			fuel mainly on Macoma (P. Bocher, F. Robin, unpubl data)		
			prey quality: 3.6 ± 0.14 kJ/g DM shell (P. Bocher, F. Robin, unpubl data)		
			gizzard size: 6g	repertoire and resources to adjust gizzard size	
				length of fuelling period	
				minimum departure mass and date to reach the SH Wadden Sea	
				predation pressure	
SH Wadden Sea	fuelling	fuel from late May to early June (26 days)			Prokosch 1988 Piersma et al. 2005
		mass gain: 3g per day	mass gain: 3.4g per day (unpubl. data)		Piersma et al. 2005
		arrival mass: 130g departure mass: 190g	departure mass <200g (unpubl. data)		Piersma et al. 1992
			site use potentially goverend by prey availability (unpubl. obs.)	individual site use	
			fuel mainly on Macoma (unpubl. data)		
		prey quality: 3.74 ± 0.03 kJ/g DM shell	prey quality: 8.79 ± 1.18 kJ/g DM shell (2006-09)		van Gils et al. 2005
			annually variable prey availability	behavioural repertoire to track prey	
		gizzard size: 8g	gizzard size: 8g	repertoire and resources to adjust gizzard size	van Gils et al. 2005
en route	migration		departure timing potentially influenced by high predation pressure (Ch. 7)	predation pressure during fuelling	
		wind conditions probably not unfavourable		wind conditions	Piersma & van de Sant 1992
				fuelling opportunities en route (emergency habitats)	

In late May 2008 and early June 2009 we were able to catch Afro-Siberian red knots only days before they departed for their breeding grounds and could confirm that departure weights were 200g and more (Prokosch 1988, Piersma et al. 1992; table 9.2, figure 9.3). Our observations on fuelling red knots in the SH Wadden Sea during the study period have shown that they gain mass at about 3.4g per day, a slightly higher gain than has been reported earlier (Piersma et al. 2005; table 9.2). Yet, given the year-to-year variability we found in food availability during this time of the year (Chapter 7), mass gains may well be variable, too. However, assuming that birds arrive in the SH Wadden Sea by mid-May with an average arrival weight of 130g (Piersma et al. 1992) and a fuelling period of about three weeks, red knots can reach 200g and more upon departure (figure 3). A small catch of presumably Afro-Siberian red knots in the SH Wadden Sea in mid May 2007 suggests that (some?) red knots arrive either with substantially more weight, or arrive much earlier than mid May (figure 9.3). As we still haven't been able to empirically document flight duration for non-stop flights from Banc d'Arguin to the SH Wadden Sea, we can only roughly estimate energy expenditure during flight. Energy costs measured during experimental wind tunnel flights indicate that red knots consume about 1g of their body weight per hour of flight (Kvist et al. 2001). Average flight speed is assumed to be about 60km/h (Gudmundsson 1994, Kvist et al. 2001) which would result in a 3-day nonstop flight, and a 70g body mass loss. As departure weights from Banc d'Arguin appear to be around 180g (Piersma et al. 1992), red knots evidently would arrive at masses of less than 130g in the SH Wadden Sea. Yet, they might still be able to reach the 200g goal or more by early June (figure 9.3).

Published fuelling estimates for the Banc d'Arguin show that red knots fuel for about 60 days, and mass gain is around 0.7g per day (Piersma et al. 1992, 2005). Average body mass during winter is around 120g (Chapter 3), thus for red knots to reach 180g by early May, either fuelling rates should be higher or the fuelling period should be longer (figure 9.3). However, body weights measured at Banc d'Arguin in April 2008-09 suggest that mass gain rates are not higher (figure 9.3) and it appears that, indeed, red knots may have a very difficult time reaching a departure mass of 180g by early May. Clearly, here we are missing something! It seems implausible that red knots would set off for migration with insufficient energy stores, especially when they face unpredictable wind conditions during flight (Chapter 5). Although the French Atlantic coast does present emergency stopover habitat when winds en route are unfavourable, budgeting an additional (emergency) stopover in France does not seem to be a promising strategy to make up for insufficient stores in the first place (figure 9.3). Moreover, red knots caught in early and mid-May at the French stopover sites are relatively light (100g and less), supporting again the notion that the French sites primarily act as emergency sites. Even with an extremely brief stop (3 days, P. Bocher, F. Robin, unpubl. data) and a fuelling rate as high as in the SH Wadden Sea (about 2.5g per day; P. Bocher, F. Robin, unpubl. data), a French stopover gets in the way of their migration itinerary (figure 9.2 & 9.3). On the other hand, we have also observed a substantial number of red knots that were (much) heavier and (much) later than predicted at the French staging sites, and we also have indications that red knots arrive earlier or heavier in the SH Wadden Sea than previously assumed (figure 9.3). Realizing that a significant part of the population seems to behave differently from what we expected, we have to admit that we have no idea how these individuals plan their migration. Do they perhaps leave the wintering grounds earlier or arrive in SH (or at the breeding grounds) later? Are they capable of actively sampling different altitudes in order to find the best winds for their flight and thus save time and energy while travelling? Perhaps flight costs are cheaper than previously assumed? To study these questions, we would need to follow individual birds during their flight using data-loggers or transmitters to collect data on timing and flight altitudes. But we also would need to verify energetic costs during (long-distance) flight using experimental set-ups in wind tunnels. Unfortunately, our attempt to develop and deploy altitude-recording light-sensors has failed (see Chapter 1). Yet, the rapid development in the field of data-logger and satellite-transmitter technology and recently operational new generation wind tunnels will enable us to tackle these questions in the very near future.

Fuelling for migration at the spring staging grounds - As puzzling as the situation during the first leg of northward migration from Mauritania to the SH Wadden Sea appears, it seems that by the time red knots depart from the SH Wadden Sea to their Siberian breeding grounds, they have been able to store sufficient energy stores to master their final leg. We have substantial empirical evidence that average fuelling rates might be sufficient (table 9.2), yet we also have indications that food availability in the SH Wadden Sea is rather variable among years (Chapter 6)

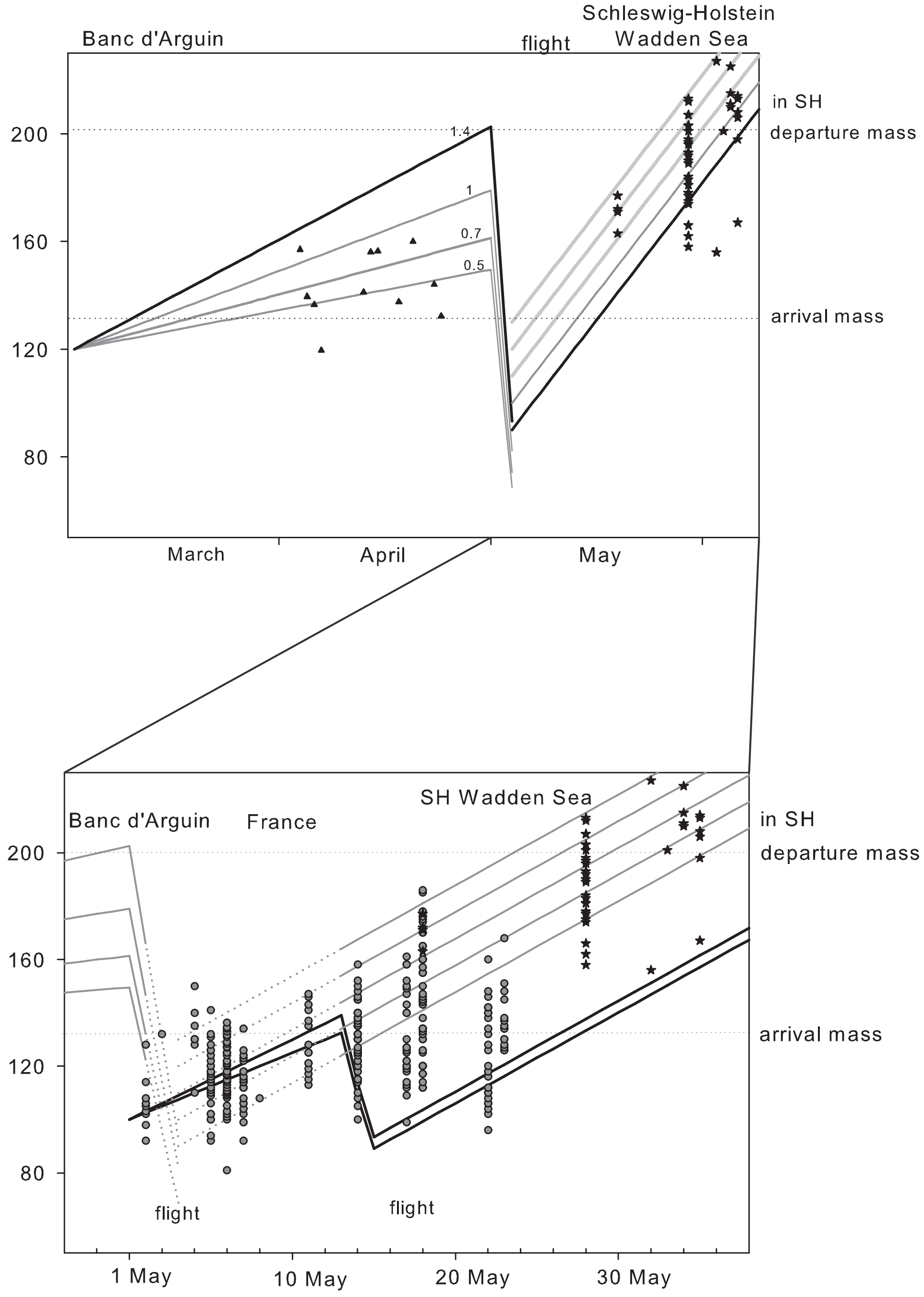


Figure 9.3 **Upper graph:** Red knots start fuelling two months before they depart for northward migration. Mass gain was modelled with different fuelling rates (numbers above lines [g/day]), according to the literature, mass gain is 0.7g/day (Piersma et al. 2005). During flight, mass loss is approximately 1g/hr flight (Kvist et al. 2001). They potentially cover the flight to the SH Wadden Sea nonstop in as fast as 2 – 3 days (Shamoun-Baranes et al. 2010) and arrive with 130g in mid May (Prokosch 1988). In the SH Wadden Sea, red knots gain on average 3.4 g/day (own unpubl. data). Departure mass from the Wadden Sea is approximately 200g in early June. Even with the highest departure mass in Mauritania, they would not be able to reach a departure mass of 200g by early June (black lines). Triangle = measured body mass of individual red knots caught in April 2007 – 2009, stars = measured body mass of individual red knots caught in the Schleswig-Holstein Wadden Sea in 2007-2009. **Lower graph**: Red knots that additionally stop in France arrive with around 100g beginning of May, peak numbers are observed around 10 May (P. Bocher, F. Robin, unpubl. data). They stay for approximately 2 – 4 days and gain 2.5g per day (P. Bocher, F. Robin, unpubl. data). Mass gain is modelled additionally with 3.4g mass gain per day. The flight between France and the SH Wadden Sea is estimated to take 1 – 2 days. Red knots fuelling in France would not be able to reach the required departure mass by early June, either (black lines). Grey dots = measured body mass of individual red knots caught in the French stopover sites in 2006 – 2008.

and as of yet we have no knowledge how this would affect fuelling conditions in red knots. Afro-Siberian red knots appear to arrive in the SH Wadden Sea after a 4,500 km nonstop flight directly from the West African wintering grounds, and during such long flights digestive organs will be reduced so that they need to be rebuilt upon arrival at the next staging site (Piersma & Gill 1998, Battley et al. 2000, Battley & Piersma 2005). Our data on gizzard sizes, noninvasively measured using ultrasound (Dietz et al. 1999) in both the Mauritanian wintering grounds and during refuelling in the Schleswig-Holstein Wadden Sea, confirm that the smallest gizzards occur just after the flights from West Africa, both after arrival on the French Atlantic sites and in the Wadden Sea (figure 9.4). Our measured gizzard sizes of about 10g fresh mass in early April and 12g in late April (Mauritania) and 5-8g in May (France, Germany) tally with predictions based on knowledge of energy demand and prey quality at the different sites (van Gils et al. 2005a). Enlarging their gizzards even slightly might allow fuelling red knots to increase their fuelling rates and/or exploit a larger area of suitable foraging habitats and thus cope with changing food availability (van Gils et al. 2006). Although we did observe foraging red knots during all four years in the SH Wadden Sea, our observation base/data set unfortunately is yet too small to infer site choice and the use of different foraging areas in the course of a tidal cycle. We know from radio-telemetry studies in the Dutch Wadden Sea that red knots roam an area of hundreds of kilometres during the course of some days (van Gils & Piersma 1999, van Gils et al. 2005b) and we might expect the same for red knots fuelling in the SH Wadden Sea. But since the mudflats are huge, we would need state-of-the-art radio-telemetry technology to follow individuals to accurately determine foraging patch choice. Once we know individual tracks on the mudflats, we will be able to sample food availability in more targeted ways and eventually will get more accurate estimates of individual fuelling rates.

The decision of where to forage and the resulting rate of mass gain is also influenced by the presence of predators (Stephens and Krebs 1986, Alerstam and Lindström 1990). Very often, the choice is whether to forage at a high quality but potentially dangerous spot or to go for more safety but potentially at the cost of less rapid mass gain (e.g. Lindström 1990, Cresswell 1994, Ydenberg et al. 2002, Duijns et al. 2009). In general, predation risk is likely to increase with increasing fuel stores as greater body mass leads to a decrease in manoeuvrability and thus reduced escape performance (Dietz et al. 2007). In recent years, there has been a population expansion of peregrine falcons Falco peregrinus in the SH Wadden Sea (Busche et al. 1998), and it is possible that these peregrines profit from the presence of northward migrating very fat shorebirds (van den Hout 2009). As a consequence, fuelling red knots in the SH Wadden Sea may have to trade off between high quality foraging sites and safety. It is very likely that red knots react to this increased predation danger by altering their behaviour. For example, on one occasion we observed an unusual daytime departure in Afro-Siberian red knots (Chapter 7), which we interpreted as the birds preferring to leave at a suboptimal time of day rather than wait and be exposed to hunting peregrines for another full day.

On the wintering grounds – competition with conspecifics – As discussed in previous paragraphs, achieving a departure weight of 180g (or even more) at Banc d'Arguin appears impossible on the basis of what we know about average fuelling rates and average mass gain in Afro-Siberian red knots. In general, food abundance at Banc d'Arguin seems to be comparable to, or even higher than, in the Wadden Sea (Piersma et al. 1993, van Gils et al. 2009). Yet, densities of feeding shorebirds are higher at Banc d'Arguin (Zwarts et al. 1990a, van Gils et al. 2009), which could lead to inter- and intraspecific competition among foragers. Indeed, during the eight years of our study at Banc d'Arguin between 2002 and 2009 we observed a persistent small-scale population structuring, with individuals being highly site faithful to 'their' high-tide roost and adjacent foraging area, both within and between winters (Chapters 2 & 3).

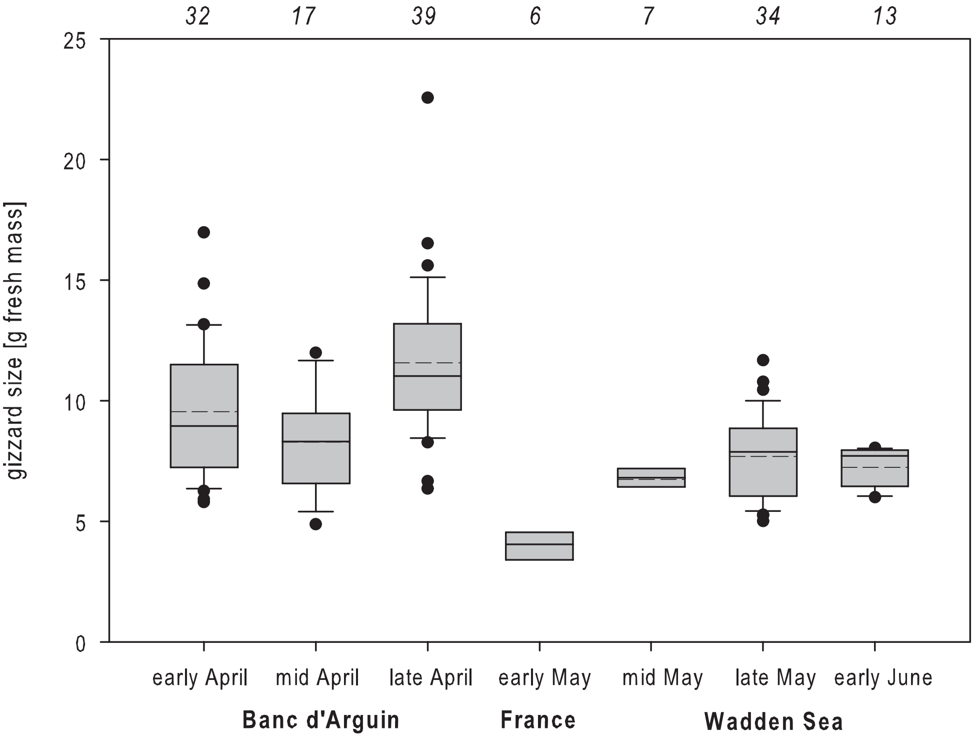


Figure 9.4 Gizzard sizes in g fresh mass of Afro-Siberian red knots, measured using ultrasonography during different fuelling phases: in their main non-breeding area Banc d'Arguin, Mauritania, and the key staging area, the Wadden Sea, Germany. Data from France are from dead Afro-Siberian red knots. Shown are median (solid line), average (dashed line), 25th and 75th percentiles (boxes) and the 9th and 91th percentile. Italic numbers above boxes give sample size n.

Our observations were made at two adjacent sites, with noticeable differences in the quality of their foraging habitat. At Banc d'Arguin, we can roughly distinguish 'seagrass mudflats', with higher quality prey and higher intake rates, from 'bare sand' habitats with lower intake rates and lower quality prey. In our study sites, relatively more larger-bodied females (relative to smaller males) and more adults (relative to juveniles) were found at the higher quality site than at the lower quality site only three kilometres away. The observed site-specific differences in size and age (adult birds are more experienced?) suggest that despotic behaviour maintains this segregation. When we caught red knots in April during fuelling, birds at the higher quality site had maintained slightly smaller gizzards than at the lower quality site (Chapter 3). Last but not least, red knots from the higher quality site seem to have had a slightly higher annual survival (Chapter 3). In which way these differences translate into differences during fuelling or northward migration remains to be studied. Perhaps individuals from the better quality site have higher departure masses, and thus higher energy reserves for coping with difficulties during migration?

How to establish a good winter foraging range? – As our observations on directed movements between the two sites have shown, it appears to be highly achievable to change from the lower quality site to settle in the higher quality habitat (Chapter 3). It is thus interesting to discuss potential strategies how individuals might gain this access to a better foraging area. That mainly relatively larger females and adults occupy the better sites suggests that some sort of cryptic despotic behaviour maintains the observed segregation between sexes and ages (Chapter 3). Yet, females and adults are not only relatively larger (and more experienced?), they also potentially arrive relatively early back at Banc d'Arguin. As described previously, females leave the arctic breeding grounds before males and juveniles and migrate back to West Africa via a stopover in the Dutch Wadden Sea. They would probably be the first sex/age class to arrive first at Banc d'Arguin and thus have the first choice when establishing a winter feeding range (first come, first served?). That successful males would come much later and consequently would need to settle in poorer habitats would indicate the presence of a high but delayed cost of reproduction (Inger et al. 2010).

However, one could also imagine that (successful) males developed ways to advance their arrival and be able to settle for the winter in better habitats. In the absence of observations of substantial numbers of Afro-Siberian males anywhere along the flyway during southward migration, we have started to think that they might migrate non-stop from Siberia to Banc d'Arguin. By doing so, they might win time and thus might arrive around the same time as females. Observations in the closely related islandica subspecies have shown that southward migrating males routinely skip Iceland, a major staging site during northward migration for both sexes and also used by females on their way south (Dietz et al. 2010). If canutus males also routinely fly back to the wintering grounds nonstop, then this would lay the basis of a rather spectacular hypothesis. Could unsuccessfully reproducing males who leave earlier (Tomkovich & Soloviev 1996) be able to advance their return substantially by migrating non-stop? If yes, by doing so they could upgrade themselves to better habitats with the potential downstream effect of being more successful in the future. Using the stable isotope approach of Dietz et al. (2010) in combination with the application of data-loggers or logging transmitters, we could test this idea in the future.

Possible costs of an early arrival on the wintering grounds? – It is likely that individuals that occupy a better wintering habitat might have a better starting position for the subsequent northward migration (Gunnarsson et al. 2006). This puts the timing and condition of arrival in the wintering areas into a central position within the year. Upon arrival in the wintering grounds, red knots not only have to establish themselves on a good habitat, they also have to cope with changes in diet and water demands during a time of the year when it is particularly hot and when a complete feather moult needs to be carried out. This period also coincides with the highest mortality observed during the annual cycle (Chapter 8). Whether this enhanced mortality is due to intraspecific competition during settling, high physiological stress or a carry-over effect from a potentially extremely time-stressed southward migration, or all three, arises as an interesting question.

Conservation of red knots in the Schleswig-Holstein Wadden Sea

Between 2006 and 2009 we studied Afro-Siberian red knots in their key staging area during northward migration, the Schleswig-Holstein Wadden Sea. The mudflats in the Wadden Sea are spacious, and we were lucky to work from a flat-bottom research vessel, the RV Navicula (figure 5), Royal NIOZ, Texel, NL, which enabled us to be constantly right in the middle of where things happen – or so we thought. What we learned though was, that although Afro-Siberian red knots primarily use the southern part of the Schleswig-Holstein Wadden Sea (Dithmarschen), which narrowed our working area down considerably from more than 2,000 km^2 (in cluding islands) to less than 300 km^2, we still did not seem to find all the red knots that ought to be there at that time of the year.

A recent population estimate puts the size of the Afro-Siberian red knot population at about 418,000 individuals (Spaans et al. 2011). If we deduct the number of first year birds (based on proportions from winter catches at Banc d'Arguin, T. Piersma, unpublished data) that are thought to remain in Mauritania during their first summer, the migrating population should still be 300,000 individuals. These birds should all visit the Schleswig-Holstein Wadden Sea during May to refuel for their onward journey (Prokosch 1988, Piersma et al. 1992). We did not encounter that many red knots during any of the four consecutive springs that we spent there on the mudflats, scanning every corner of the area. The largest group of red knots we came across was 40,000 individuals in early June in 2008, when we observed departing flocks in front of the Dieksander Koog coastline. Adding up all red knots we encountered during our regular horizon scanning from our elevated observation platform on board the RV Navicula during the incoming and outgoing tides never sum up to more than 100,000 individuals. Even the fortnightly high-tide counts fall way short of the expected 300,000 birds (Blew et al. 2005, Nationalparkverwaltung Schleswig-Holstein, unpublished data) and flying over the whole area of the German Wadden Sea by plane once during high tide did not reveal any unknown high-tide roosts either. Thus, we still have no idea where even the majority of the Afro-Siberian red knots are during May: all we can say is that they are not where we thought they are.

The fact that we don't know where they are is disturbing. There seem to be only two alternatives available: alternative staging areas and higher turnover rates. If the birds are using alternative staging sites, it is very hard to imagine where they are, as the entire coast of Europe is searched every spring for concentrations of waders. It is also possible that the knots are cycling through SH flats faster than we expect, and that SH thus supports many more birds than the peak census results suggest. But if they are doing so, they must be managing to re-constitute their guts from their reduced migratory state (Piersma & Gill 1998, Battley et al. 2000) faster and/or they are achieving higher rates of re-fueling than previously observed (e.g. Piersma et al. 2005, this thesis). None of these seem like particularly likely scenarios (see tables 9.1 and 9.3).

Afro-Siberian red knots migrate in one of the best studied flyways along one of the best known migration routes in the world, yet we have no idea where the majority of the population fuels during northward migration. If we are to protect this species, as shorebird scientists and with support of the conservation community, we need to implement projects that at least come up with answers to the above mentioned questions. Detailed observations on known individuals will be necessary to answer questions about staging area residence times and fuelling rates. Although colour-marking may answer some of these questions, innovations in tracking technology seem to have the best prospects of yielding detailed answers in the future.

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SUMMARY

This thesis describes the possible selection pressures acting on survival and, indirectly, on reproduction of Afro-Siberian red knots *Calidris canutus canutus* while wintering and migrating. Afro-Siberian red knots are long-distance migrants. They travel between the West African wintering areas and the High Arctic Siberian breeding grounds in two non-stop flights of 4000-5000 kilometres each during spring and autumn. The Schleswig-Holstein Wadden Sea, Germany, is the key staging area during northward migration: it is assumed that the entire population fuels there during the second half of May. To maximize reproductive success, red knots have to time their arrival on the tundra such that food peaks when growing chicks need it most. However, the timing of arrival in the Siberian Arctic may be constrained by events along the way or in West-African wintering areas, thousands of kilometres and months away.

About 75% of the Afro-Siberian red knot population winters on tropical Banc d'Arguin, Mauritania, where most of the field studies were carried out. The red knots wintering in this tropical environment showed high site fidelity and small home ranges (Chapter 2), in contrast to red knots that winter in temperate areas in both the northern and the southern hemisphere. At Banc d'Arguin red knots could avoid browsing larger areas and thus save on flight costs, because both weather and foraging conditions are more predictable than e.g. in the northern temperate Wadden Sea. This remarkable small-scale habitat use was not the only contrast I detected between red knots wintering on the Banc d’Arguin, and red knots wintering in other parts of their distribution range. Independently from where they spend the non-breeding period, red knots have been described as a gregarious, flock-feeding species with no obvious hierarchical structuring. Yet, during our study period, we observed a persistent small-scale demographic structuring at Banc d'Arguin, with the larger sex and age-classes (females and adults) occupying better quality foraging sites (Chapter 3). Individuals that settled in these better foraging sites also experienced a slightly higher annual survival. Further research will reveal which mechanisms govern and sustain this unexpected structuring. Using new tracking tools to follow individuals throughout the year is needed to indentify whether the differences in habitat quality translate e.g. into individual differences in timing during northward migration and breeding success.

At the end of the winter, many red knots depart from Banc d’Arguin with seemingly insufficient fuel stores to reach the German Wadden Sea non-stop, and so the birds depend on favourable wind conditions en route. However, tail winds happens to be an unpredictable 'resource'. Red knots get away with this because of a safety net in the form of (emergency) staging habitats in western France. The French intertidal areas provide a back up in years when tailwinds are rare (Chapters 4 & 5). While the French staging sites enable red knots to survive their journey (in some years more than 20% of the population make use of these sites), we still have to assess the knock-on consequences of such an additional stopover, e.g. causing delays in migration which could negatively affect the subsequent breeding season.

The main staging area during northward migration is the Schleswig-Holstein Wadden Sea where the intertidal mudflats need to provide adequate fuelling conditions to prepare for the ultimate flight north. Earlier studies described that Afro-Siberian red knots were mainly concentrated in the more southern areas along the coast of Dithmarschen, Germany, just north the river Elbe mouth. These areas offered relatively high densities of the Baltic Tellin *Macoma balthica*, the favourite prey of fuelling red knots. Though, we observed that food availability in these areas varied largely from year to year between 2006 and 2009 and was lower in the later

years (Chapter 6). Yet, longer time-series with a higher spatial resolution would be needed to assess whether food availability generally is declining. Recruitment processes may enclose cycles longer than four years, or settlement of both bivalves and worms may happen over a larger area than we could sample during this project. We also have found evidence that peregrine falcons *Falco peregrinus* that breed in the vicinity of the mudflats may affect the area used by red knots. Red knots potentially have to trade off foraging needs with safety, especially when they get close to departure and body stores make them less manoeuvrable when being attacked. This increased predation risk might have been an influential factor leading thousands of red knots to depart "ahead of schedule": Shorebirds generally depart in the evening hours. If weather conditions do not allow so, as on the evening of 3 June 2008, one would expect the birds to postpone departure to the following evening. Yet, in the morning hours of 4 June 2008, thousands of red knots and other shorebird species advanced their departed, presumably in an attempt to avoid being predated (Chapter 7).

After the breeding season the red knots return to the Banc d'Arguin. If the quality of the wintering habitat affects subsequent northward migration and breeding success, we would expect strategies that ensure that one settles at a good site. Red knots show a differential arrival at the Banc d'Arguin, with adult females returning first, followed by adult males, and juveniles arrive last. Given that in our study area at Banc d'Arguin adults and females occupy the better areas (Chapter 3), and given that they are also the first returnees, arrival timing in the wintering grounds might determine where birds settle. If timing of arrival on the wintering grounds determines winter habitat quality interesting cross-seasonal interactions may arise. Females are known to make one stopover during southward migration, but later migrating males have been notably absent at staging sites in autumn and we therefore suggest that they may advance their arrival on Banc d'Arguin by making a single non-stop journey from Siberia to Banc d'Arguin (Chapter 3). Upon arrival in the wintering grounds red knots not only have to establish themselves on a good home range, they also have to cope with changes in diet and water demands during a time of the year when it is particularly hot and when the complete feather moult is carried out. We demonstrate that, unlike earlier claims for intercontinental migrants, this is also the time of the year when most mortality takes place, and not during migration (Chapter 8). Whether this is due to intraspecific competition during settling, physiological stress or whether carry-over effects from the previous migration and breeding period remains subject to scrutiny.

Published sources identify the Schleswig-Holstein Wadden Sea as key fuelling site for northward migrating Afro-Siberian red knots. Even more so, we could confirm earlier observations that Afro-Siberian red knots tend to concentrate on the more southern parts just north of the river Elbe mouth, along the Dithmarschen coast. A rough calculation suggests that about 300,000 individuals should be seen in the Schleswig-Holstein Wadden Sea during May, yet neither could we see that many red knots, nor are they registered during the regular fortnightly high-tide counts carried out by volunteers, that cover all important sites along the German Wadden Sea coast. The fact that we don't know where the Afro-Siberian red knots are, is disturbing as conservation measures depend on the knowledge of the whereabouts of this protected species. Yet, it also reveals that our knowledge is still relatively poor and we still cannot answer some basic biological and ecological questions: maybe individual Afro-Siberian red knots have different migration strategies, and thus use different (additional?) staging sites, and/or spend a shorter time in the Wadden Sea? As in many other shorebirds species, Afro-Siberian red knot numbers are declining. If we are to protect this species, we need to implement projects that help answering these questions. Finding out where they are and where they go would be a good start.

SAMENVATTING - Beschouwingen van het jaarcylclus van een kanoetstrandloper

Het netwerk van trekbanen (flyways) van kanoetstrandlopers *Calidris canutus* (verder 'kanoeten') omspant de gehele wereld. Deze wereldwijde trekbanen zijn de jaarlijkse migraties van zes verschillende kanoeten ondersoorten. Dit proefschrift onderzoekt in de Afro-Siberische ondersoort (de nominaat) *Calidris canutus canutus* de mogelijke selectiedrukken op overleving en voortplanting gedurende de trek en in het overwinteringsgebied. De Afro-Siberische kanoeten zijn exemplarische langeafstandstrekkers; zij reizen elk jaar heen en weer tussen overwinteringsgebieden in West Afrika en broedgebieden in de hoog-Arctische toendra's van Siberië. Zowel in het voorjaar als in het najaar wordt deze reis afgelegd in twee etappes van elk 4000-5000 km lengte. Onderweg moet er bijgetankt worden en in het voorjaar is de Duitse Waddenzee bij Schleswig-Holstein daarbij de belangrijkste pleisterplaats. Verondersteld wordt dat hier in het voorjaar, in de tweede helft van mei, de gehele *canutus* populatie een tussenstop maakt om op te vetten. Begin juni vliegen deze kanoeten door naar de broedgebieden. Om hun broedsucces te optimaliseren moeten kanoeten hun aankomst op de toendra zo plannen dat de beschikbaarheid van lokaal voedsel op zijn hoogtepunt is wanneer de kuikens de grootste voedselbehoefte hebben.

De winter op de Banc d'Arguin

Ongeveer 75% van de Afro-Siberische kanoeten overwintert op de Bank d'Arguin in tropisch Noordwest Afrika. De meeste gegevens voor dit proefschrift werden daar verzameld tussen 2006 en 2009. De kanoeten die overwinteren op deze tropisch hete wadplaten waren bijzonder plaatstrouw en hadden een beperkte actieradius (Hoofdstuk 2), in tegenstelling tot kanoeten die overwinteren in de gematigde streken van zowel het Zuidelijke en Noordelijke halfrond. De kanoeten hoefden geen grote gebieden af te speuren naar voedsel, omdat weer- en voedselcondities voorspelbaar zijn op de Banc d'Arguin, in tegenstelling tot bijvoorbeeld de Waddenzee in de winter, en daarmee bespaarden ze ook op vliegkosten van en naar de rustplaatsen. De kleine actieradius was niet het enige verschil tussen kanoeten op de Banc d'Arguin en kanoeten in andere delen van het verspreidingsgebied. Buiten het broedseizoen komen kanoeten meestal voor in grote groepen zonder duidelijke hiërarchische structuur. In de Banc d'Arguin echter vertoonden de kanoeten leeftijd- en geslachtsgebonden verschillen in ruimtegebruik: de grotere vogels (vooral vrouwtjes en volwassenen dieren) bezetten consequent de kwalitatief betere foerageergebieden (Hoofdstuk 3). Individuen die de betere foerageerplekken wisten te bezetten hadden ook een hogere overlevingskans. Verder onderzoek is nodig om de mechanismen te ontrafelen waardoor deze ruimtelijke structurering wordt veroorzaakt en waardoor die stand blijft. Met instrumenten waarmee individuele kanoeten gedurende het hele jaar gevolgd kunnen worden (zoals miniatuur satellietzenders), zouden we in de toekomst moeten kunnen vaststellen of verschillen in habitatkwaliteit in de winter leiden tot verschillen in het moment van vertrek in het voorjaar en tot een verschillend broedsucces in het hoge noorden. We zouden dan ook kunnen onderzoeken of individuen met toenemende leeftijd en ervaring kunnen stijgen op de sociale ladder en zo toegang krijgen tot de betere habitats op de Banc d'Arguin.

De vlucht naar het noorden

Aan het eind van de winter verlaten de kanoeten de Banc d'Arguin en gaan op weg naar het noorden. Veel Afro-Siberische kanoeten hadden onvoldoende lichaamreserves om de Duitse Waddenzee onder alle omstandigheden in één enkele vlucht te bereiken. Kanoeten gokken er klaarblijkelijk op, dat de luchtstromingen onderweg gunstig zijn (rugwinden), maar dat bleek soms tegen te vallen. Gelukkig bleek er een vangnet te bestaan in de vorm van (kleine) gebieden met droogvallende wadplaten in het westen van Frankrijk, waar in geval van nood een tussenstop gemaakt kon worden. In jaren met tegenwind werden deze pleisterplaatsen inderdaad gebruikt en in sommige jaren maakte meer dan 20% van de kanoeten een tussenstop in Frankrijk (Hoofdstuk 3 en 4). Dankzij deze getijdebieden konden kanoeten hun reis dus ook onder ongunstige omstandigheden volbrengen, maar we weten niet wat de uiteindelijke kosten zijn van het maken van zo'n extra tussenstop. De vertraging zou bijvoorbeeld kunnen leiden tot een verlate aankomst op de noordelijke toendra's. Door een late aankomst zouden deze kanoeten de piek in voedselbeschikbaarheid in de broedgebieden kunnen mislopen, met negatieve gevolgen voor het broedresultaat.

De belangrijkste pleisterplaats in het voorjaar, de Waddenzee van Schleswig-Holstein, zou kanoeten voldoende voedsel moeten bieden om de laatste etappe van hun jaarlijkse trekweg in één keer te voltooien. Eerdere studies hebben laten zien dat Afro-Siberische kanoeten vooral foerageren in het zuidelijke deel bij Dithmarschen, juist ten noorden van de monding van de rivier de Elbe. De wadplaten in dit gebied bevatten hoge dichtheden nonnetjes *Macoma balthica*, een favoriete prooi van kanoeten. Mijn onderzoek tussen 2006 and 2009 liet echter wel zien, dat de voedselbeschikbaarheid hier van jaar tot jaar sterk verschilde en vooral dat de dichtheden lager waren in de latere jaren. Het kan zijn dat er meer dan vier jaren verstrijkt tussen opeenvolgende massale broedval. Dit zou betekenen dat de voedselvoorraad misschien niet afneemt, maar dat we de opkomst van een nieuwe generatie schelpdieren hebben gemist. Om na te gaan of de voedselbeschikbaarheid in het algemeen afneemt, is een langere tijdserie nodig en een grootschaliger bemonsteringsprogramma. Slechtvalken *Falco peregrinus* die in de buurt van de wadplaten broedden, hadden een duidelijke invloed op de ruimtelijke verspreiding en het gedrag van de kanoeten in het gebied. Kanoeten moeten de risico's van het zich blootstellen aan predatie afwegen tegen hun voedselbehoefte. Dit probleem speelt vooral vlak voordat de vogels wegtrekken. Kanoeten moeten dan snel opvetten en zullen geneigd zijn voor de meest voedselrijke gebieden te kiezen. Omdat de kanoeten door het opslaan van vet zwaar worden, zijn ze minder wendbaar en een gemakkelijkere prooi voor de valken. In jaren met veel predatoren kunnen kanoeten die al flink vet en daardoor minder wendbaar geworden zijn, het gebied soms verlaten voordat ze er eigenlijk helemaal klaar voor zijn. Kanoeten vertrekken vaak aan het eind van dag, bij zonsondergang. Als de weersomstandigheden wegtrek niet toestaan, dan wordt het vertrek meestal tot de volgende avond uitgesteld. Zo niet in 2008, een jaar met een ogenschijnlijk hoge predatie door slechtvalken. Het weer verhinderde de kanoeten 's avonds op 3 juni 2008 te vertrekken, maar tegen verwachting in vertrokken de kanoeten, en met hen andere soorten steltlopers, de volgende ochtend vroeg. Vermoedelijk waren de risico's, de kans op predatie door Slechtvalken, te groot om nog een hele dag langer te blijven (Hoofdstuk 7).

Terug in de Banc d'Arguin

Na het broedseizoen keren de kanoeten weer terug op de Banc d'Arguin. Als de kwaliteit van het overwinteringsgebied een effect heeft op de komende voorjaarstrek (en misschien zelfs op het broedsucces in het volgende seizoen), dan verwachten we dat ze steeds zullen proberen om de beste plekken op de Banc d'Arguin te bezetten. De aankomst van de kanoeten in het begin van de winter is weinig gesynchroniseerd. Volwassen vrouwtjes arriveren eerst, gevolgd door volwassen mannetjes en pas later komen de jonge vogels aan. Vroeg gearriveerde kanoeten (wijfjes, volwassen dieren) wisten steeds de meest voedselrijke en ogenschijnlijk minst gevaarlijke plekken te bezetten. Als het moment van aankomst in de overwinteringsgebieden bepalend is voor de toegang tot kwalitatief goede gebieden, dan zouden de kaarten al vroeg in de winter geschud kunnen zijn voor wat betreft de kansen op een goed broedsucces in het volgende seizoen (beste overwinteringsplekken, voldoende reserves voor snelle trek naar Schlweswig-Holstein, tijdige aankomst in de broedgebieden). Tekenend is dat tijdens de najaarstrek in het Europese Waddengebied wel Afro-Siberische vrouwtjes worden waargenomen, maar dat mannetjes niet worden gezien. Zij maken deze tussenstop waarschijnlijk niet, ter compensatie van hun latere vertrek uit de broedgebieden (mannetjes nemen de jongenzorg voor hun rekening, vrouwtjes kunnen eerder weg). Door non-stop van Siberië naar de Banc d'Arguin te vliegen kunnen de mannen de competitie met de vrouwtjes voor goede plekken in de overwinteringsgebieden met beter gevolg aangaan.

Na aankomst in de overwinteringsgebieden moeten kanoeten niet alleen een goede foerageerplek bemachtigen, zij ondergaan ook flinke lichamelijke aanpassingen. Zo moet hun waterhuishouding worden aangepast aan het (hete) klimaat en hun spijsverteringsorganen moeten geschikt worden om het beschikbare voedsel (voornamelijk schelpdieren) te kunnen verwerken. Ze maken in de Banc d'Arguin ook een complete rui door (zowel slagpennen als lichaamsveren). Het is daarom niet per sé verwonderlijk dat er juist in de winter onder Afro-Siberische kanoeten veel sterfte optreedt (Hoofdstuk 8). Toch is dit opmerkelijk, omdat bij veel andere langeafstandstrekkers de meeste sterfte gedurende de trek plaatsvindt. Of deze hoge wintersterfte het gevolg is van intensieve competitie tijdens de vestiging in het overwinteringsgebied, van (hitte)stress, van de trek die zojuist voltooid werd, of van de inspanningen in het voorafgaande broedseizoen, blijft vooralsnog onduidelijk.

Problemen in de Waddenzee?

Eerdere studies hebben aangetoond dat de Waddenzee van Schleswig-Holstein een belangrijke rol speelt als centrale pleisterplaats tijdens de voorjaarstrek van Afro-Siberische kanoeten. Afro-Siberische kanoeten concentreren zich in het zuidelijke deel langs de kust van Dithmarschen. Uitgaande van een overwinterende populatie van ongeveer 400.000 kanoeten, die niet allemaal een reis naar de broedgebieden ondernemen, zouden er in mei in Schleswig-Holstein naar schatting minstens zo'n 300.000 vogels een tussenstop moeten maken. Helaas werd een dergelijk aantal kanoeten bij Dithmarschen nooit aangetroffen, maar ze werden ook niet gevonden tijdens de tweewekelijkse hoogwatervluchtplaatstellingen in de gehele (Duitse) regio. Dit was een onplezierige verrassing. Waar zijn al die kanoeten? Het is verontrustend dat we niet weten waar ze zijn, omdat het nemen van eventuele beschermingsmaatregelen afhangt van voldoende kennis over de verspreiding van beschermde soort.

Translated by Yvonne Verkuil & Kees Camphuysen

ZUSAMMENFASSUNG-Betrachtungen des Jahreszyklus des AFRO-Sibirischen Knutts

Knutts *Calidris canutus* sind *global player*, deren Zugwege (flyways) die ganze Welt umspannen. Weltweit sind sechs verschiedenen Unterarten des Knutts beschrieben, die alle in hocharktischen Tundragebiten brüten, und außerhalb der Brutsaison in Wattengebiete entlang der Küsten zu finden ist. Im Rahmen diese Doktorarbeit wurde am Beispiel der Afro-Sibirische Unterart *Calidris canutus canutus* untersucht, welchem potentiellen Selektionsdruck die Knutts während des Zugs sowie zeitens des Aufenthalts in den Überwinterungsgebieten ausgesetzt sind. Afro-Sibirische Knutts sind typische Langstreckenzieher; sie wandern jedes Jahr zwischen ihren Überwinterungsgebieten in Westafrika und den Brutgebieten in den hocharktischen Tundragebieten Sibiriens hin und her. Weg- und Heimzug im Frührjahr und Herbst werden jeweils in zwei Etappen á 4000 – 5000km ausgeführt. Zwischendurch müssen die verbrauchten Energievorräte aufgefüllt werden, und in diesem Zusammenhang stellt das Schleswig-Holsteinische Wattenmeer das wichtigste Rastgebiet während des Frühjahrszugs dar. Es wird angenommen, dass zu dieser Zeit, in der zweiten Maihälfte, die gesamte canutus population im Schleswig-Holsteinischen Wattenmeer rastet. Anfang Juni wandern die Knutts weiter in ihre Brutgebiete. Um ihre Chancen auf eine erfolgreiche Brut zu vergrößern, müssen sie dabei ihre Ankunft in den Brutgebieten so planen, daß die Küken in der Zeit aufwachsen, in der das lokale Nahrungsangebot in der Tundra am größten ist.

Der Winter auf der Banc d'Arguin

Ungefähr 75% der Afro-Sibirischen Knuttpopulation überwintert auf der Banc d'Arguin, im tropischen Nordwestafrika. Der Großteil der Daten dieser Doktorarbeit wurde dort in den Jahren 2006 – 2009 gesammelt. Im Gegensatz zu Knutts, die in gemäßigten Zonen der Nord- und Südhalbkugel überwintern, zeichneten sich die in den tropischen Wattengebiet der Bacn d'Arguin überwinternden Knutts durch eine hohe Ortstreue und einen vergleichsweise kleinen Aktionsradius aus (Kapitel 2). Sie nutzen den Umstand, daß Nahrung- und Wetter vergleichsweise berechenbar sind, und können so, im Vergleich mit z.B. im Wattenmeer überwinternden Knutts, erhöhte Flugkosten zwischen Nahrungs- und Hochwasserrastgebieten einsparen. Dieser vergleichsweise kleine Aktionsradius war jedoch nicht das einzige, was die Afro-Sibirischen Knutts von ihren Artgenossen in anderen Überwinterungsgebieten unterschied. Außerhalb der Brutsaison treten Knutts meist in großen Gruppen ohne erkennbare Hierarchiestrukturen auf. Auf der Banc d'Arguin jedoch zeigen sich deutliche Unterschiede in der Habitatnutzung zwischen Alt- und Jungvögel, sowie zwischen Weibchen und Männchen: die größeren Individuen (im allgemeinen Weibchen und Altvögel) waren durchweg in qualitativ hochwertigeren Nahrungsgebieten zu beobachten (Kapitel 3). Diese Individuen, die in besseren Nahrungsgebieten zu finden waren, hatten zudem höhere Überlebenschancen. Ob sich, als Folge dieser Unterschiede in der Qualität der Nahrungsgebiete, Knutts in unterschiedlichem Maß für den Zug in die Brugebiete vorbereiten können und ob dies Auswirkungen auf den Bruterfolg im hohen Norden hat, wird Gegenstand folgender Untersuchungen sein. Hierfür müsste es jedoch möglich sein, dass wir individuellen Knutts über den gesamten Zeitraum folgen können. Die sich schnell entwickelnde Technologie im Bereich der Satellitensender lässt uns hoffen, daß dies sehr bald möglich sein wurd. Dann sollte es im folgenden Schritt auch möglich sein zu untersuchen, ob Knutts mit zunehmendem Alter und Erfahrung sozial aufsteigen können, und sich somit in den besseren Nahrungsgebieten ansiedeln können.

Der Frühjahrszug

Zu Beginn des Frühjahrs verlassen die Knutts die Banc d'Agruin und machen sich auf den Weg nach Norden. Es scheint, daß, im allgemeinen, die Afro-Sibirischen Knutts auf der Banc d'Arguin nicht genügend Energievorräte einspeichern, um das Wattenmeer ohne die Unterstützung durch Rückenwinde erreichen können. Tatsächlich scheinen die Knutts den Erfolg ihrer erste Etappe ins Schleswig-Holsteinische Wattenmeer davon abhängig zu machen, dass die Winde günstig wehen – eine Strategie, die bisweilen nicht aufgeht. Glücklicherweise jedoch scheinen (kleinere) Wattengebiete entlang der französichen Westküste im Notfall als Rastgebiete zur Verfügung zu stehen. Dort werden in Jahren, in denen der Direktflug durch Gegenwinde erschwert wird oder gar unmöglich ist, gehäuft Knutts beobachtet. In manchen Jahren finden sich sogar mehr als 20% der Afro-Sibirischen Knutt Population in den französischen Wattengebieten ein (Kapitel 3 und 4). Die Rastgebiete entlang der Atlantikküste ermöglichen es also den Knutts auch unter widrigen Umständen ihren Zug nach Norden durchzuführen. Noch wissen wir jedoch nicht, welche Kosten ein solcher Extra-Zwischenstop mit sich bringt. Es könnte z.B. zu einer verspäteten Ankunft im Wattenmeer kommen, die sich weiterziehen könnte und letzlich zu einer verspäteten Ankunft in den Brutgebieten führen könnte. Als Folge könnten die Knutts dann den Gipfel des lokalen Nahrungsangebots in der Tundra verpassen, was wiederum negative Auswirkungen auf das Kükenwachstum und somit den Bruterfolg haben könnte.

Der wichtigste Rastplatz im Frühjahr ist das Schleswig-Holsteinische Wattenmeer. Hier sind die Knutts darauf angewiesen, daß sie genügend Nahrung finden, um die nötigen Energievorräte für die abschließende Etappe in die Brutgebiete speichern zu können. Frühere Untersuchungen haben gezeigt, daß die Afro-Sibirischen Knutts hauptsächlich im südlichen Schleswig-Holsteinischen Wattenmeer, nördlich der Elbemündung vor der Dithmarscher Küste, zu beobachten sind. Wäherend unserer Untersuchungen fielen die Wattflächen in dieser Gegend durch vergleichsweise hohe Bestandsdichten der Baltischen Plattmuschel (Rote Bohne) *Macoma balthica*, der bevorzugten Nahrung der Knutts, auf. Weiterhin jedoch kam zu Tage, daß das Nahrungsangebot, das den Knutts zur Verfügung stand, von Jahr zu Jahr unterschiedlich ausfiel, und daß die Bestandsdichten zwischen 2006 und 2009 abnahmen. Ob es sich hierbei um "echte", großflächige Bestandsabnahmen handelt, ist zu diesem Zeitpunkt nicht einschätzbar. Es ist gut möglich, daß mehr als vier Jahre zwischen dem Auftreten bedeutender Brutfall-Vorkommen liegen, und wir somit ("lediglich") die Ansiedlung einer neuen Generation Muscheln verpasst haben. Entsprechend ist ein langfristiges und großflächiges Monitoringprogramm erforderlich, um realistische Einschätzungen zur Entwicklung der Nahrungsvorkommen für Knutts im Schleswig-Holsteinische Wattenmeer zu erhalten. Neben dem Nahrungsvorkommen bestimmt auch der Prädationsdruck, welche Gebiete von den Knutts genutzt und welche besser gemieden werden sollten. Wanderfalken *Falco peregrinus*, die auf den Inseln und Außensänden im Bereich des Dithmarscher Wattenmeers brüten, beeinflussten merkbar das Verhalten der Knutts. Während der Rast im Wattenmeer müssen die Knutts stets zwischen dem "Sich-der-Gefahr-der Prädation-Aussetzen" und der Notwendigkeit, Nahrungsvorräte anzulegen, abwägen. Dieses Dilemma wird vor allem dann deutlich, wenn sich der Abzug nähert. Dann nämlich sind die Knutts besonders dick und schwer und weniger beweglich, was ein großer Nachteil ist, wenn Wendigkeit beim Ausweichen von Wanderfalkenangriffen gefragt ist. So kann es sein, daß in Jahren, in denen besonders hoher Prädationsdruck herrscht, der Abzug der Knutts früher als geplant statt findet. Der Abzug aus dem Wattenmeer findet normalerweise in den Abendstunden, rund Sonnenuntergang, statt. Wenn das Wetter dann einen Strich durch die Rechnung macht, sollte der Abzug erwartungsgemäß auf den folgenden Abend verschoben werden. Jedoch nicht im Frühjahr 2008, ein Jahr in dem der Prädationsdruck vergleichsweise hoch erschien. Ein durchziehendes Tiefdruckgebiet verhinderte den Abzug der Knutts am Abend des 3. Juni 2008, anstatt jedoch, wie erwartet, am folgenden Abend abzuziehen, beobachteten wir wie zehntausende Knutts, zusammen mit anderen Watvögeln, bereits am folgenden Morgen abzogen. Wir nehmen an, daß sie bestrebt waren, dem erhöhten Risiko, einem Wanderfalken zum Opfer zu fallen wenn sie noch einen Tag länger blieben, aus dem Weg zu gehen.

Zurück auf der Banc d'Arguin

Nach der Brutsaison kehren die Knutts wieder zurück zur Banc d'Arguin. Wenn wir davon ausgehen, daß die Qualität des Nahrungsgebiets im Winter Auswirkungen auf den folgenden Frühjahrszug hat (und eventuell sogar auf den Bruterfolg im folgenden Jahr), dann würden wir erwarten, dass die Knutts alles daran setzen, die besten Nahrungsgebiete zu besiedeln. Die Ankunft im Überwinterungsgebiet ist nicht synchronisiert: Als erstes kommen die erwachsenen Weibchen zurück, gefolgt von den erwachsenen Männchen, die Jungvögel kommen zuletzt. Die früh ankommenden Knutts (Weibchen, Altvögel) wurden im Winter stets in den besseren Nahrungsgebieten (die wahrscheinlich auch sicherer sind) beobachtet. Sollte tatsächlich die Ankunftszeit im Wintergebiet darüber entscheidend sein, welches Nahrungsgebiet besiedelt werden kann, dann würden die Würfel für den Erfolg/Nichterfolg in der folgenden Brutsaison bereits früh im Winter fallen (gute Nahrungsgebiete im Winter, genügend Nahrungsvorräte für einen frühzeitigen Zug ins Schleswig-Holsteinische Wattenmeer, pünktliche Ankunft im Brutgebiet). Auffällig ist, daß während des Herbstzugs zwar Afro-Sibirische Weibchen, aber keine Männchen im Wattenmeer beobachtet werden. Es scheint immer wahrscheinlicher, daß die Männchen im Herbst keine Rast im Wattenmeer machen. Ob sie in anderen Wattgebieten entlang des Zugwegs rasten ist nicht bekannt. Allerdings ist es wahrscheinlich, daß, wenn sie es täten, dies bekannt wäre. Denkbar wäre demnach, daß sie direkt aus den Brut- in die Wintergebiete fliegen – um zu Kompensieren, daß sie später aus den Brutgebieten abziehen, da sie alleinig für die Aufzucht der Jungen zuständig sind. Ein solcher non-stop Flug wäre theoretisch möglich, und würde sie damit in die Lage versetzen, zeitgleich – oder nur wenig später – in den Überwinterungsgebieten anzukommen, um mit den Weibchen um die besten Nahrungsgebiete zu konkurrieren zu können.

Nach der Ankunft im Überwinterungsgebiet müssen die Knutts sich nicht nur gute Nahrungsgebiete sichern, sie durchlaufen auch verschiedene köperliche Veränderungen. Das heiße und trockene Klima der Banc d'Arguin stellt großere Herausforderungen an ihren Wasserhaushalt, und auch der Verdauungstrakt muß umgestellt werden, so daß die hauptsächlich aus Muscheln bestehende Nahrung verdaut werden kann. Zusätzlich wird direkt nach Ankunft das komplette Federkleid gemausert. Es scheint daher nicht allzu überraschend, daß in dieser ersten Phase des Winters auch die Sterblichkeit am höchsten ist (Kapitel 8). Dennoch ist dies bemerkenswert, da bei vielen Langstreckenziehern der Zug mit einer erhöhten Sterblichkeit in Verbindung gebracht wird. Ob die hier beobachtete erhöhte Sterblichkeit eine Folge des Konkurrenzkampfes um die guten Nahrungsgebiete ist, ob das heiße Klima oder der soeben abgeschlossene Zug eine Rolle spielen, oder ob sich hier die Anstrengungen der vorangegangenen Brutsaison erkennbar machen muß zu diesem Zeitpunkt noch offen bleiben.

Probleme im Wattenmeer?

Es ist aus früheren Untersuchungen bekannt, daß das Schleswig-Holsteinische Wattenmeer eine wichtige Rolle als zentraler Rastplatz während des Frühjahrszugs der Afro-Sibirischen Knutts einnimmt. Sie sind hier vor allem im südlichen Bereich entlang der Dithmarscher Küste zu beobachten. Die Afro-Sibirische Knutt Population umfaßt ungefähr 400.000 Knutts. Da Knutts in ihrem ersten Lebensjahr in ihren Überwinterungsgebieten bleiben, sollte sich der tatsächlich ziehende Anteil auf ungefähr 300.000 Knutts belaufen, die alle in der zweiten Maihälfte das Schleswig-Holsteinische Wattenmeer besuchen sollten. Allerdings konnten wir diese Anzahl während unserer vier Jahre dauernden Untersuchungen nie beobachten. Auch die während der 14tägig stattfindenden Hochwasserrastplatz-Zählungen beobachteten Knutt-Ansammlungen unterschreiten diese Zahl weit. Im Laufe dieses Projekts mußten wir demnach feststellen, daß sich die theoretisch zu erwartenden und die wirklich beobachteten Anzahlen unerklärlicherweise widersprechen. Zurück bleibt die Frage, wo sich die "fehlenden" Knutts befinden? Es ist bedenklich und beunruhigend, daß wir die Antwort auf diese Frage nicht kennen, hängen doch die Entwicklung und der Erfolg von Schutzmaßnahmen davon ab, daß wir wissen, wo sich die Tiere befinden.

RÉSUMÉ - Méditer sur le cycle annuel du Bécasseau maubèche Afro-Sibérien

Les Bécasseaux maubèches Afro-Sibérien *Calidris canutus canutus* migrent sur de très grandes distances. Selon la littérature, au printemps et à l'automne, en seulement deux sauts de 4,000-5,000 kilomètres, ils rallient les sites d'hivernage de l'ouest africain aux sites de reproduction des hautes latitudes de Sibérie Arctique. Le Schleswig-Holstein, partie allemande de la mer de Wadden, est le principale site de halte migratoire à mi-chemin sur leur route prénuptiale. Ce site accueille l'ensemble de la population au cours de la deuxième moitié du mois de mai. Afin de maximiser son succès reproducteur, le Bécasseau maubèche doit programmer son arrivée dans la toundra de façon à ce que le pic de nourriture concorde au mieux avec la période de croissance des poussins. Toutefois, cette date d'arrivée dans l'Arctique sibérien peut être affecté par des événements ayant eu lieu plusieurs milliers de kilomètres et quelques mois auparavant sur les sites d'hivernage d'Afrique occidentale ou encore le long du chemin.

Environ 75% de la population de Bécasseaux maubèches Afro-Sibérien hiverne sur le Banc d'Arguin en Mauritanie, site où la plupart des études sur le terrain de ce projet a été effectuée. Contrairement aux Bécasseaux maubèches hivernant dans les régions tempérées des hémisphères nord ou sud, ceux hivernant sur les tropiques utilisent des zones d'hivernage très restreints avec une forte fidélité (chapitre 2). Il semble que les conditions d'alimentation et climatique soient plus prédictibles sur le Banc d'Arguin, et les Bécasseaux maubèches peuvent ainsi économiser sur les coûts résultant des vols sur de grandes distances, contrairement aux individus hivernant par exemple en mer de Wadden. Indépendamment de l'endroit où ils passent la période de non-reproduction, les bécasseaux maubèches ont été décrits comme une espèce grégaire, se nourrissant en groupe sans structuration hiérarchique évidente. Pourtant, au cours de cette étude, nous avons pu établir que pendant l'hiver, il existe des structurations démographiques traduites par une occupation des sites de meilleure qualité alimentaire par les oiseaux de grandes tailles (les femelles et les adultes)(chapitre 3). Les individus qui s'installent dans ces sites de forte qualité alimentaire présentent également une survie annuelle légèrement supérieure. Des recherches plus poussées révéleront quels mécanismes gouvernent et permettent de maintenir cette structuration inattendue. L'utilisation de nouveaux outils de suivi des individus au long de l'année est nécessaire pour identifier si les différences de qualité d'habitat s'expriment, par exemple, de façon individuelle sur le calendrier de la migration prénuptiales et donc sur le succès de reproduction. Et selon, des stratégies pourraient évoluer, permettant ainsi aux individus de gravir les échelons pour parvenir aux meilleurs habitats (voir ci-dessous).

En général, il semble que de nombreux Bécasseaux maubèches présentent des réserves énergétiques insuffisantes au départ du Banc d'Arguin pour atteindre en un seul bond la partie allemande de la mer de Wadden. Ceci induit une dépendance de ces oiseaux à l'assistance de vents favorables au cours de leur vol migratoire. Cependant, ces derniers peuvent être imprévisibles. Néanmoins, quand les vents portant son faible certaine année, les Bécasseaux maubèches peuvent s'en sortir grâce à un filet de sécurité sous la forme de "site de secours" que sont les sites de la côte ouest Française (Chapitres 4 & 5). Bien que les sites français permettent aux bécasseaux de survivre à leur voyage (certaines années, plus de 20% de la population utilise la France), il reste à évaluer les conséquences d'une telle escale supplémentaire, par exemple, sur le retard occasionné sur le reste de la migration pouvant nuire à la saison de reproduction.

Les zones de halte migratoire du Schleswig-Holstein en Mer de Wadden, semblent offrir des conditions adéquates d'alimentation. Comme les études antérieures l'ont décrit, les Bécasseaux maubèches Afro-sibérien sont principalement cantonnés dans les régions le plus au sud, le long de la côte de Dithmarschen en l'Allemagne, juste au nord de l'embouchure du fleuve Elbe. Ces zones mettent à disposition des densités relativement importante de la telline baltique *Macoma balthica*, reconnue proie favorite du Bécasseau maubèche.

Cependant, nous avons observé que la disponibilité alimentaire dans ces zones a fortement varié d'une année sur l'autre entre 2006 et 2009 et semble diminuer dans le temps (chapitre 6). Maintenant, une série temporelle plus importante avec une résolution spatiale plus élevée serait nécessaire pour confirmer cette tendance à savoir, si globalement les disponibilités alimentaires sont en baisse. Il se pourrait bien que les processus des cycles de recrutement soient supérieurs à la durée de l'étude ou que l'organisation des populations de deux bivalves et des vers se passe sur une surface plus importante, non considérées ici par la stratégie d'échantillonnage de ce projet. Nous avons aussi trouvé des preuves que le faucon pèlerin *Falco peregrinus* se reproduisant au voisinage des vasières, peut interagir sur la sélection du secteur par le bécasseau. En effet, ces derniers pourraient faire des compromis entre les besoins de s'alimenter en toute sécurité, surtout à l'approche du départ du fait de leur poids important, ou, comme cela l'a déjà été décrit, devenir moins manœuvrable en cas d'attaque. Cela pourrait être un facteur influençant au départ prématuré de milliers de bécasseaux : Il a été fréquemment observé que indépendamment des marées, les limicoles diurnes partent généralement en fin de journée. Si les conditions météorologiques ne permettent pas de le faire, comme le soir du 3 Juin 2008, on aurait pu s'attendre à ce que les oiseaux reportent leur départ à la soirée suivante. Malgré cela, des milliers de bécasseaux maubèches et d'autres espèces de limicoles ont avancé leur départ au matin, ce qui nous pensons, correspond à une stratégie pour éviter d'être prédaté (chapitre 7).

Si la qualité de l'habitat d'hivernage affecte la prochaine migration prénuptiale et le succès de reproduction, nous nous attendons à des stratégies qui garantissent que les premiers arrivés s'installent sur les meilleurs sites. Les Bécasseaux maubèches montrent un modèle de migration diffèrent lors de la migration postnuptiale, avec un retour des femelles adultes en premier, précédées des mâles puis des juvéniles en dernier. Étant donné que dans notre zone d'étude du Banc d'Arguin les premiers arrivants (adultes et femelles) occupent les meilleurs secteurs, la date d'arrivée d'un individu sur la zone d'hivernage pourrait déterminer sur quel type d'habitat ce dernier va s'installer. Si le calendrier d'arrivée sur les lieux d'hivernage détermine la qualité des habitats d'hivernage, d'intéressantes interactions saisonnières pourraient être rencontrées: effectivement, alors que les femelles sont connues pour faire une escale pendant la migration postnuptiale, les mâles, migrant plus tardivement, sont les grands absents de ces escales ce qui laisse suggérer qu'ils peuvent avancer leur date arrivée sur le banc d'Arguin en faisant un saut unique de la Sibérie au Banc d'Arguin. À son arrivée sur l'aire d'hivernage, les Bécasseaux maubèches doivent non seulement s'établir sur le meilleur habitat mais aussi faire face aux contraintes liées à l'alimentation (proies et eau) à une période de l'année où il fait particulièrement chaud et où ils doivent terminer leur mue. Nous démontrons que, contrairement aux précédentes observations faites sur les migrateurs intercontinentaux, c'est aussi l'époque de l'année où il y a un fort taux de mortalité, et non, lors de la migration (chapitre 8). Que ce soit en raison de la compétition interspécifique au cours de l'installation, d'un stress physiologique, d'un report des effets de la migration postnuptiale ou de la période de reproduction, ces questions restent en suspens.

La littérature présente le Schleswig-Holstein comme un site clé pour la reconstruction des réserves énergétiques au cours de la migration prénuptiale du Bécasseau maubèche Afro-Sibérien. De plus, nous avons pu confirmer les observations antérieures que les Bécasseaux maubèches Afro-Sibérien ont tendance à se concentrer sur les parties les plus au sud, juste au nord de la bouche Elbe, le long de la côte de Dithmarschen. Il semble donc surprenant que personne n'ai été en mesure jusqu'à présent de compter tous les Bécasseaux maubèches - et nous avons fait pas exception à la règle. Un calcul approximatif indique qu'environ 300,000 individus devraient être observés en mai sur la mer de Wadden du Schleswig-Holstein, cependant nous n'avons pu observer autant d'oiseaux, ils n'ont pas non plus été enregistrés au cours comptages bimensuels à marée haute couvrant tous les sites importants. Le fait que nous ne savons pas où ils sont exactement est inquiétant car les mesures de conservation dépendent de la connaissance de la localisation des espèces protégées. De plus, il se révèle aussi que nos connaissances sur certaines questions biologiques et écologiques de base sont encore relativement pauvres: il est possible que les bécasseaux aient des stratégies migratoires individuelles, et ainsi utiliseraient différents (supplémentaires?) sites de halte migratoire, et/ou passeraient moins de temps en mer de Wadden? Comme dans de nombreuses espèces d'oiseaux limicoles, les Bécasseaux maubèches Afro-Sibérien sont en déclin. Si nous voulons protéger cette espèce, nous avons besoin pour mettre en œuvre des projets qui aident à répondre à ces questions. Trouver où ils sont et où ils vont serait un bon début.

Translated by Frédéric Robin

ملخص

تناقش هذه الأطروحة ضغط الانتخاب الطبيعي المحتمل, مباشرا علي البقاء ولا مباشرا علي تكاثر طائر الطيطوى الإفريقي-السيبيري Calidris canutus أثناء فترات التشتية والهجرة .

الطيطوى الإفريقي – السيبيري مهاجر عابر للمسافات الطويلة. تهاجر ما بين مناطق التشتية في إفريقيا الغربية و مناطق التكاثر في المناطق القطبية في سيبيريا في رحلتين لا توقف فيهما و لمسافة تناهز 4000-5000كلم في كل من رحلة الربيع و الخريف .

تعتبر منطقة ساخسويج –هولستين من بحر الوادن في ألمانيا إحدى أهم مناطق التوقف أثناء الهجرة الشمالية : حيث يقدر أن كامل هذه المجموعة تتوقف هنالك للتزويد بالطاقة في النصف الثاني من مايو.

من أجل نجاح أمثل لعملية التكاثر فإن على هذه الطيور أن تصادف أوقات وصولها إلى التندرا مع أوقات وفرة الطعام عند ما تكون صغارها في أمس الحاجة إليه. على كل حال ، فإن توقيت الوصول إلي سيبيريا القطبية يمكن أن تعرقلها عدة ظواهر على طول طريق الهجرة أو في مناطق التشتية في غرب إفريقيا بعيد آلاف الكيلوميترات.

إن حوالي 70% من مجموعات الطيطوى الإفريقي – السيبيرية تقضى فترة الشتاء في منطقة حوض آرغين في موريتانيا, تلك المنطقة التي أجرينا فيها معظم الدراسات الميدانية.

لقد أظهر طائر الطيطوي المشتي في هذه البيئة المدارية وفاءا لنفس المناطق و صغرا لمناطق الانتشار (فصل 2), بخلاف الطيطوي المشتي في المناطق المتوسطية في كل من النصف الشمالي و الجنوبي من الكرة الأرضية.

يتحاشى الطائرالطيطوى في حوض آرغين استعمال مناطق واسعة الشيء الذي يقلل من مخاطر الطيران و كذالك بسبب أن التنبؤ بالظروف المناخية و ظروف التغذية في هذه المنطقة أسهل من المناطق المعتدلة من بحر الوادن على سبيل المثال. إن هذا الإستغلال المثير للاهتمام للمؤئل على السلم الصغير لم يكن المفارقة الوحيدة التي اكتشفناها بين الطيطوى المشتي في حوض آرغين و الطيطوي المشتي في مناطق توزيعها الأخرى في العالم. بمعزل عن الأماكن التي تتكاثر فيها فإن الطائر الطيطوى يوصف بأنه طائر اجتماعي حيث أنها تتغذي في جماعات و ينعدم فيها أي تركيب اجتماعي جلي.

خلال فترة هذه الدراسة تمت ملاحظة وجود تركيب ديموغرافي على المقاييس الصغيرة في حوض آرغين, حيث أن الطيور الكبيرة الحجم (الإناث و البالغين) يشغلون أماكن التغذية المثلي (فصل 3). لقد لاحظنا أيضا أن الأفراد التي تستقر في هذه الأماكن الجيدة لها نسب بقاء سنوي أعلى من الآخرين. مزيد من البحث سوف يكشف الميكانيكية التي أدت و حافظت على هذه التركيبة الغير متوقعة.

إن هناك حاجة ماسة الاستعمال تقنيات جديدة كأنظمة للتعقب من أجل رصد تحركات الأفراد طوال العام من أجل تحديد ما إذا كان هذا التباين في جودة أماكن التغذية سوف ينعكس على توقيت الوصول خلال الهجرة الشمالية لمختلفة الأفراد على سبيل المثال و كذالك على مدى نجاح عملية التكاثر.

في نهاية الشتاء يغادر العديد من طيور الطيطوى حوض آرغين مع أن الظاهر أن مخزون الدهون لديهم لا يكفي لإكمال الرحلة إلي بحر الوادن في رحلة واحدة دون توقف ولذلك فإن هذه الطيور تعتمد علي الرياح الملائمة أثناء الطيران لإنجاز رحلتها وعلى كل حال فإن الرياح الخلفية مصدر يصعب التنبؤ به.

فـقوتلا قطانم نم ةكبشب ةناعتسإلا اب اهتلحر ىوطيطلا رويط لمكت فـورظلا هذه يف
. اسنرف برغ يف (ةيرارطضإلا)

تاونسلا يف ىوطيطلاروويطل طايتحاو معد قطانم ةيسنرفـلا ةلحضلا هايملا تاحطسم ربتعت
.(5و 4 لصف) ةيفـلخلا حايرلا اهيف لقت يتلا

ضعب يف(نامأب اهتالحر لامكإ يلع ىوطيطلا رئاط دعاست هذه ةيسنرفـلا فـقوتلا قطانم نأ عم
تاعبتت سردن نأ انيلع امازل يقبيو,)قطانملا هذه لغتست ةعومجملا نم20% نمرثكأ نإف نينسلا
ابلس رثأي دق يذلا ءيشلا لوصولا يف رخأتلا نع مجني دق ام لثم ةيفاضإلا تافقوتلا هذه
. رثاكتلا ةيلمع يلع

يتلاو ةيلامشلا ةرجهلا ءانثأ فـقوتلا قطانم مهأ يدحإ نداولا رحب يف نتسول وه –جيوسلس .
ةيلامشلا ةلحرلا هذهل ةمزاللا ةقاطلاب دوزتلل ةمئالملا فـورظلا ةلحضلا ةينيطلا اهتاحطسم نمؤت
. ةينضملا

قطانملا يف اساسأ زكرتت يريبسلا يقيرفإلا ىوطيطلا نأ يلوألا تاساردلا ترهظأ دقل
. بلألا رهن بصم لامش, اينامليأ يف نشرامتيد لحاس لثم ةيبونجلا

ربتعت يتلاو Macoma balthica فادصأ نم ايبسن ةيلاع تافاثك يلع تلمتشا قطانملا هذه
.ىوطيطلا رئاط دنع ةقاطلاب دوزتلل يلثم ةسيرف

دقو 2009 و 2006 نيب ام يرخأ يلإ ةنس نم فلتخت قطانملا هذه يف ءاذغلا ةرفو نأ اندجو دقل
يف ءاذغلا ةرتفو تناكاذإ ام ةفرعملو .(6 لصفلا) ةريخألا تاونسلا يف هترتفو تصقن
.ربكأ يفارغج زيح يلعو دملأا ةليوط ةساردب مايقلا مزلي هنإف مومعلا يلع مئاد صقانت

نإ تارود ةايح رثاكتو لايجألا دق يدعتت عبرألا تاونس كلذكو نإف رامعتسا فادصألا و نيدلا
. ثحبلااذه لالخ هنم تانيعي ذخأ اننكمي امم ربكأ ينالكم زيح يلع ثدحي دق

دقل اندجو ايضا نأ روقصلا Falco peregrinus يتلا رثاكتت يف قطانملا ةرواجملا تاحطسملل
. ىوطيطلا رئاط فرط نم ةلغتسملا قطانملا هذه يلع رثؤت دق ةلحضلا

قبست يتلا تارتفلا يف ةصاخ, ةمالسلاو ءاذغلا يلإ ةجاحلا نيب نزاوي نأ هيلع ىوطيطلا
يلع اهتاردق نم صقني امم, هتايوتسم يلعأ لصو دق نوهدلا نم هنوزخم نوكي نيحو ةرداغملا ةرتف
. تمجوه ام اذإ ةروانملا

:ناوألا لبق ةرداغملا يلإ ىوطيطلا فالآب يدؤي ارثؤم الماع نوكي دق هذه سارتفإلاب رطخلا ةدايز
ءاسم يف ثدح امك ةيوجلا فورظلا حمست مل اذإ .ءاسملا تاعاس يف رداغت ام ةداع ةيئطاشلا رويطلا
.يلاوملا ءاسملا يلإ ةرداغملا لجأت فوس رويطلا هذه نأ أبنتي نأ نكمي دحاولا نإف, 2008 ويني 3
ةدع ةقفر ىوطيطلا رويط نم فالآ رداغ 2008 ويني 4 ل قفاوملا يلاوملا مويلا ةحيبص يف
وه امنإ كلذ نأ نظلا بلغأو, يدايتعإلا رداغملا تقو كلذب نيمدقم ةيئطاشلا رويطلا نم يرخأ عاونأ
.(7 لصف) ةسيرف عقت نأ يدافتل

دعب ءاضقنإ ةرتف جوازتلا عجري رئاط ىوطيطلا يلإ ضوح نيغرآ ,اذإكانت ةدوج لئوم هيتشتلا
دمتعت نأ اهنم عقوتن اننإف خيرفتلا ةيلمع حاجنو ةقحالل ةيلامشلا تارجهلا يلع رثؤي
. ةيلاعلا ةدوجلا تاذ قطانملا يف ناطتسإلا لجأ نم تايجيتارتسا

طائر الطيطوى أظهر تباينا في أوقات الوصول لحوض آرغين, حيث أن الإناث البالغة تصل أولا متبوعة بالذكور البالغة ومن ثم تصل الطيور اليافعة أخيرا. لقد توصلنا من خلال هذه الدراسة إلي أن البالغين والإناث يستوطنون أفضل الأماكن (فصل 3). كما توصلنا إلي أنهم أول المغادرين حيث أن أوقات الرجوع إلي مناطق التشتيه قد تحدد أين تستقر الطيور .

إذا كانت أوقات الوصول إلي مناطق التشتيه تحدد إختيارالموائل المثلي فإن من المحتمل أن يحدث تداخل للتأثيرات عبر الفصول. من المعروف أن الإناث يتوقفن مرة واحدة أثناء الهجرة الجنوبية بينما لوحظ غياب الذكور التي تهاجر بعد ذلك من أماكن التوقف في فصل الخريف مما يدعونا للإقتراح بأنهم ربما يعجلون الوصول لحوض آرغين من خلال القيام برحلة واحدة لا يتوقفون فيها من سيبيريا إلي حوض آرغين (فصل 3).

عند الوصول لمناطق التشتيه فإنه ليس علي طائر الطيطوى أن يجد لنفسه حيز جغرافي جيد فحسب, بل عليهم أيضا أن يتعاملوا مع تغير النظام الغذائي ووفرة الماء خلال فترة من العام تتميز خاصة بارتفاع درجات الحرارة وفي فترة تبدل الطيور فيها الريش .

لقد أثبتنا أنه علي خلاف ما كان يعتقد علي مستوي الطيور المهاجرة العابرة للقارات, فإن أعلي نسبة للوفيات تحدث خلال هذه الفترة من السنة وليس أثناء الهجرة كما كان يعتقد (فصل 8).

سواء كان هذا نتيجة المنافسة أثناء التوطن, أوالضغط الفسيولوجي أو كان بسبب تأثيرات تراكمية ناتجة عن الهجرات السابقة وعمليات التكاثر فإنها تبقي موضوعا خصبا ومهما للبحث.

لقد صنفت البحوث السابقه سخلسويس—هولستن في بحر الوادن علي أنه أهم منطقة للتزود بالطاقة أثناء الهجرة الشمالية لطيور الطيطوى الإفريقية السيبيرية. وزيادة علي ذلك فإنه يمكننا تأكيد هذه المشاهدات الأولي والقاضية بأن طائر الطيطوى يميل إلي التواجد بكثرة في الأجزاء الجنوبية من هذه المنطقة والواقعة شمال مصب نهر الألب وعلي طول ساحل "ديتمارشن".

بناء علي تقديرات دقيقة فإنه من المتوقع مشاهدة حوالي 300000 طائر دريحة في سلسويج - هولستن خلال شهر مايو. في هذه الأثناء فإننا لم نشاهد هذا العدد وحتي أن عمليات التعداد الدورية التي يقوم بها متطوعون أثناء مد البحر لم تسجل هذا العدد المتوقع, عمليات التعداد هذه تغطي كل المواقع المهمة علي طول ساحل الوادن في ألمانيا .

إن حقيقة أننا لا ندري أين يختفي طائر الطيطوي مزعجة لأن عمليات المحافظة الفعالة تعتمد علي معرفة أماكن تحركات النوع المحمي.

ولقد تبين أيضا أن معرفتنا لازالت محدودة نسبيا وما زلنا غير قادرين علي الإجابة علي بعض الأسئلة البيولوجية والإكولوجية الأساسية: ربما أن أفراد الطيطوي الإفريقية السيبيرية لديهم استراتيجيات مختلفة للهجرة, وبالتالي يستخدمون مناطق مختلفة (إضافية؟) للراحة والتزود بالطاقة, و /أو يقضون وقتا أقل في بحر الوادن؟.

كما هو الحال في العديد من أنواع الطيور الشاطئية فإن اعداد الطيطوي في تناقص.

إذا أردنا حماية هذا النوع, فإنه علينا القيام بمشاريع للمساعدة علي الإجابة علي هذه التساؤلات. إن إيجاد أين يتواجدون أو أين يذهبون يمكن ان يشكل بداية جيدة.

Translated by Hacen El Hacen

Резюме

В данной работе описаны возможные последствия давления естественного отбора на выживание и, косвенно, на размножение афро-сибирской популяции исландского песочника *Calidris canutus canutus*. Эти птицы – дальние мигранты. Весной и осенью они преодолевают расстояние между зимовками в западной Африке и местами размножения в арктической Сибири за два броска по 4-5 тысяч км каждый. Прибрежные отмели Шлезвиг-Гольштейна (Германия) являются ключевыми местами остановки этих птиц во время их миграции на север – считается, что вся популяция кормится там во второй половине мая. Для повышения успеха размножения, исландским песочникам необходимо подгадать сроки прибытия в тундру так, чтобы пик пищевых ресурсов приходился на то время, когда они больше всего необходимы растущим птенцам. В то же время, на сроки прибытия в арктическую Сибирь могут влиять события, происходившие за тысячи километров и много месяцев до того, на пути или даже на зимовках в западной Африке.

Около 75% афро-сибирской популяции исландского песочника зимует в тропическом Банк д'Арген, Мавритания, где проводилась большая часть полевых исследований. Исландский песочник, зимующий в этой тропической среде, демонстрирует высокую верность территории и малый ее размер (Глава 2), в отличие от исландского песочника, зимующего в умеренных широтах северного и южного полушарий. В Банк д'Арген исландским песочникам нет необходимости исследовать большие территории, т.к. погода и условия кормежки более предсказуемы, чем например на умеренных северных прибрежных отмелях, что позволяет им экономить энергетические затраты на полет. Кроме необычного использования малых территорий, мы обнаружили и другие отличия между исландскими песочниками, зимующими в Банк д'Арген и зимующими в других частях ареала. Независимо от того, где они находились вне периода размножения, исландские песочники описываются в литературе как стайные виды, кормящиеся в группах без видимой иерархии. Тем не менее, в период наших исследований мы наблюдали постоянную маломасштабную демографическую структурированность групп в Банк д'Арген, когда более крупные птицы (самки и взрослые) оккупировали кормовые территории более высокого качества (Глава 3). Особи, завладевшие этими более качественными участками, также демонстрировали несколько пониженную годовую смертность. Дальнейшие исследования должны выявить механизмы регуляции и поддержания этой необычной структурированности. Изучение перемещения особей в течение года с использованием новых инструментов отслеживания перемещений необходимо для выявления возможного влияния различий в качестве сред обитания на индивидуальные различия сроков весенней миграции и на успех размножения.

В конце зимы многие исландские песочники покидают Банк д'Арген с запасами жира, заведомо недостаточными для безостановочного перелета до немецких прибрежных отмелей Северного моря, и таким образом, птицы зависят от благоприятного ветра en route. Однако, попутный ветер является непредсказуемым «ресурсом». Исландские песочники справляются с этим благодаря наличию (аварийных) мест остановок в западной Франции. Французские приливно-отливные зоны играют роль резервных в годы редкого попутного ветра (Главы 4-5). Поскольку французские места миграционных остановок позволяют исландским песочникам пережить путешествие (в некоторые годы до 20% популяции используют эти места), нам следует принимать во внимание косвенные последствия этих дополнительных остановок, такие как более поздняя миграция, которая может отрицательно сказываться на последующем сезоне размножения.

Главная территория миграционной остановки исландского песочника на пути на север – прибрежные отмели Шлезвиг-Гольштейна, где ватты приливно-отливной зоны предоставляют подходящие пищевые резервы для заключительного перелета на север. Более ранние исследования указывали на то, что афро-сибирская популяция исландского песочника в основном концентрируется в более южных частях ареала вдоль побережья Дитмаршен, Германия, к северу от устья р. Эльба. Эти участки особенно отличаются высокой плотностью обитания двустворчатого моллюска макомы *Macoma balthica*, излюбленой пищи исландского песочника во время набора жира. Тем не менее, мы наблюдали большие ежегодные вариации в обилии пищи на этих территориях между 2006 и 2009 годами, которое снижалось в более поздние годы (Глава 6). Однако, чтобы выяснить, уменьшаются ли пищевые ресурсы в действительности, необходимы более продолжительные исследования на более обширных территориях. Процесс смены поколений моллюсков может включать циклы дольше 4х лет, и распространение двустворчатых моллюсков и червей может варьировать на участках, не охваченных данным исследованием. Мы также получили доказательства того, что наличие сокола сапсана *Falco peregrinus*, который размножается неподалеку от прибрежных отмелей, может влиять на использование территории исландскими песочниками. Исландским песочникам потенциально приходится выбирать между потребностями в питании и безопасностью, особенно ближе к отлету, когда накопленные жировые резервы делают их менее маневренными в случае атаки. Эта возрастающая угроза хищников является, возможно, одним из факторов, заставляющих тысячи песочников сниматься с места раньше срока. Обычно кулики стартуют в вечерние часы. Если погодные условия в это время неблагоприятны, как например вечером 3 июня 2008 года, можно ожидать откладывания старта на следующий вечер. Тем не менее, в часы мониторинга 4 июня 2008, тысячи исландских песочников и других куликов «досрочно» стартовали, предположительно с целью избежать хищников (Глава 7).

После сезона размножения исландские песочники возвращаются в Банк д’Арген. Если качество территорий зимовок влияет на последующую весеннюю миграцию и на сезон размножения, можно ожидать появление стратегий, направленных на избирательное занятие особями лучших территорий на зимовках. В Банк д’Арген исландские песочники прибывают не одновременно, первыми возвращаются взрослые самки, затем взрослые самцы, и последними молодые птицы. Учитывая, что в районе наших исследований в Банк д’Арген самки и взрослые особи занимали лучшие территории (Глава 3), и принимая во внимание их более раннее прибытие, мы можем сделать вывод, что сроки прибытия на зимовки могут влиять на выбор территорий. Если время прибытия на зимовки определяет качество занимаемой территории, возникают интересные межсезонные взаимосвязи. Известно, что самки совершают одну остановку при миграции на юг, но самцы, мигрируя позже, отсутствуют на месте миграционной остановки осенью, и поэтому мы предполагаем, что они ускоряют свое прибытие в Банк д’Арген засчет безостановочного перелета из Сибири (Глава 3). По прибытии на места зимовок, исландским песочникам необходимо не только закрепить за собой хорошую территорию, им также приходится приспосабливаться к изменениям потребностей в корме и воде в течение периода года, когда особенно жарко и протекает полная смена оперения. В отличие от более ранних работ по внутриконтинентальным мигрантам, мы демонстрируем, что основная смертность приходится именно на этот период, а не на время миграции (Глава 8). Является ли это результатом внутривидовой конкуренции во время становления территорий, физиологического стресса, или последствий миграции и сезона размножения, еще предстоит выяснить.

В литературе, прибрежные отмели Ваттового моря Шлезвиг-Гольштейна описаны как ключевой пункт миграционной остановки во время весенней миграции исландского песочника. Нам удалось подтвердить наблюдения, что афро-сибирская популяция исландского песочника в основном концентрируется в более южной части, к северу от устья Эльбы, вдоль побережья Дитмаршена. По примерным оценкам, около 300 тысяч особей может наблюдаться в Ваттовом море Шлезвиг-Гольштейна в течение мая. Однако, мы не видели такого количества песочников, и их не регистрировали во время регулярных ночных приливных подсчетов волонтеры, проверявшие все важные территории в на побережье Ваттова моря в Шлезвиг-Гольштейне. Тот факт, что мы не знаем, где находятся афро-сибирская популяция исландского песочника, не позволяет принимать меры по охране этого вида птиц, т.к. для принятия мер по охране необходимо знать место нахождения охраняемого вида. Это также показывает, что наши знания об этом виде все еще относительно малы, и мы не можем ответить на основные биологические и экологические вопросы. Возможно, отдельные особи афро-сибирской популяции исландского песочника обладают различными миграционными стратегиями, и поэтому используют различные (дополнительные?) места остановок, и/или проводят более короткое время в Ваттовом море. Размер афро-сибирской популяции исландского песочника уменьшается, что происходит и со многими другими видами куликов. Чтобы сохранить этот вид, необходимо реализовывать проекты, которые помогут ответить на основные вопросы вопросы. Для начала, надо понять где эти птицы, и куда они летят.

Translated by Olga Dolnik


NAVICULA
HI
NAVICULA
TEXEL
SECTEUR NORD

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The years at NIOZ on Texel have been made "feel like home" by many people. Within my research group my buddies Anne Dekinga, Maarten Brugge and Bernard Spaans have been the "heart and soul" of diverse activities in the field, both in Mauritania and in the German Wadden Sea: preparing expeditions to both study sites, being in the field and collecting data, and processing the samples back in the lab would not have been possible without their help and would have been way less fun! Anne and Maarten: I'll never forget the time when we planned and prepared our first cannon net catches at Banc d'Arguin! Heel erg bedankt voor de goede tijd!

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