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Being at the right place at the right time

Leyrer, Jutta

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Chapter 1

General Introduction

Jutta Leyrer

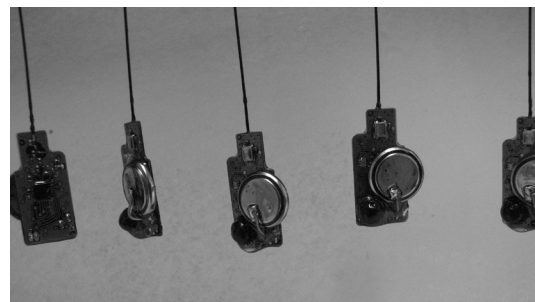


Shorebirds from the High Arctic tundra spend the nonbreeding season thousands of kilometres away, and therefore face an extremely challenging task: They need to arrive in their arctic breeding grounds at the optimal time to take full advantage of the short summer. There is only limited time to raise 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 for-

ging 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.