STRUGGLES ASHORE

Migration Ecology of Threatened Shorebirds in the East Asian–Australasian Flyway

Ying-Chi Chan

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I have witnessed flocks of tens of thousands of shorebirds swirling around and above me, surrounded by their calls and the sounds of flapping wings. No words can describe their beauty. Ironically, the backdrop of this fascinating act of nature was an ugly landscape: oil rigs, tall chimneys of huge factories, the occasional loud trucks driving along the seawall, layers of fishing nets zigzagging the mudflat, all within a yellow blanket of smog.

This is a scene not unfamiliar to shorebird watchers and researchers in East Asia. It is a microcosm of our current world: humans continuously conquering and destroying the space for nature, and, as we begin to realize, also the space for us. This thesis is on the scientific investigation on shorebird migrants that are struggling to survive in the East Asian–Australasian Flyway (EAAF), where the human-wildlife conflict is probably the most serious among all bird flyways in the world.

The threatened shorebird flyway

'Flyway' is the term used to describe an established geographic region where populations of migratory waterbirds migrate within annually (Boere & Stroud 2006). The EAAF extends from the Arctic region of the Russian Far East and Alaska to Australia and New Zealand, and includes eastern Asia and parts of south Asia (Bamford et al. 2008). Being the most species-rich flyway among the nine flyways in the world, the status of the EAAF is also the worst, with the highest proportion of waterbird populations in decline (Wetlands International 2010).

The EAAF is used regularly by at least 52 species of migratory shorebirds, with six species having more than one recognized subspecies within the flyway, giving a total of 63 migratory shorebird populations (Bamford et al. 2008, Conklin et al. 2014). For most populations (60%) the trends are unknown, and of the remaining 25 populations with known trends, 24 are in decline and only one (Black-winged Stilt *Himantopus himantopus*) is increasing (Conklin et al. 2014). If the current trend continues, 20 populations of 17 species are approaching extinction in the near future (Conklin et al. 2014).

The Yellow Sea as a key staging area for shorebirds

Coastal wetlands are key habitats to many shorebird species during migration and the non-breeding season. During annual migration between their wintering area and breeding areas, shorebirds concentrate at staging sites to fuel their migratory flights, and importance of these sites is usually based on numbers of birds. Shorebird surveys were conducted along the South Korean coast since 1993, and by Mark Barter and others along the Chinese coast of the Yellow Sea in the 1990s. In 2002, Mark Barter published 'Shorebirds of the Yellow Sea: Importance, threats and conservation status', summarizing results from these surveys. This significant publication established the Yellow Sea (31–42°N, 117–127°E, Fig. 1.1) as the most important staging area for migratory shorebirds in the EAAF, supporting at least 2,000,000 shorebirds during northward migration (Barter 2002).

A deeper understanding of how the Yellow Sea supports such huge numbers of shorebirds came from studies of shorebird prey in the intertidal flats. Systematic sampling of macrobenthos were initated at two important staging sites in China, the Luannan Coast of Tangshan in north Bohai Bay (39.1°N, 118.3°E, Fig. 1.1B) by a team led by Nicky Hong-Yan Yang (Yang et al. 2016), and the Chinese side of the Yalu Jiang Estuary (39.8°N, 124.0°E, Fig. 1.1B) led by Jimmy Chi-Yeung Choi (Choi et al. 2014).

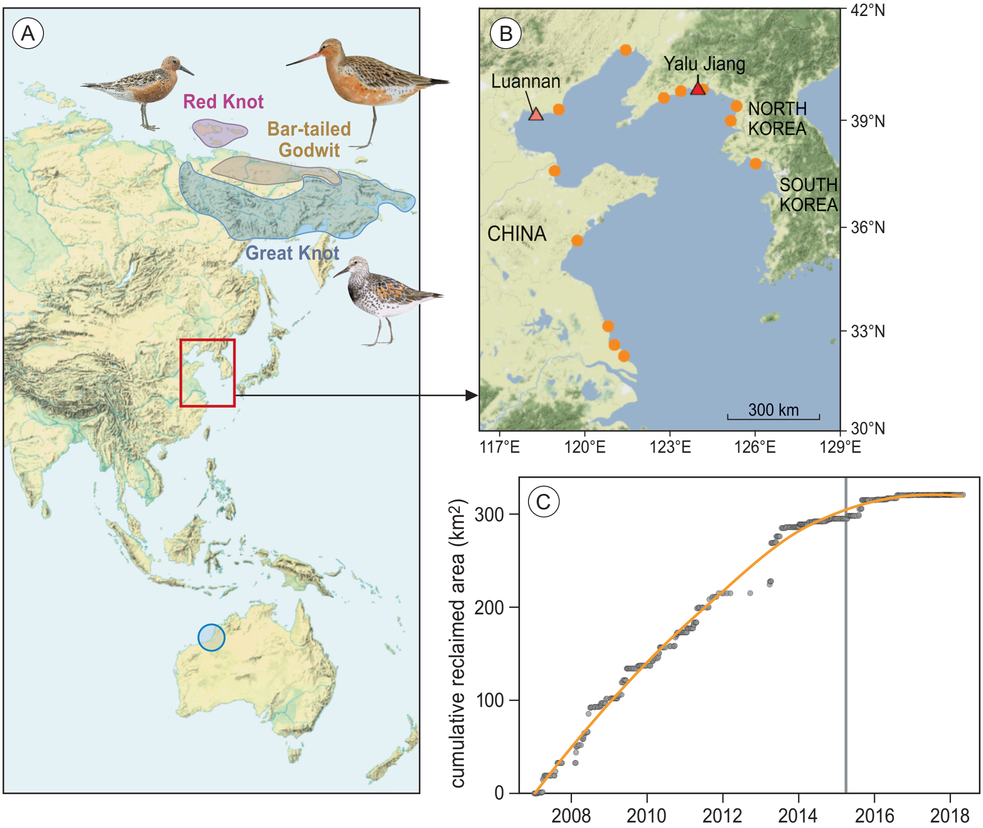

Figure 1.1. (**A**) The breeding areas in the Russian Arctic (blue-grey bordered) and the staging areas along the Yellow Sea coast (red rectangle) of the Red Knot, Great Knot and Bar-tailed Godwit populations from the non-breeding grounds in Northwest Australia (blue circle). (**B**) Some of the key shorebird staging sites along the Yellow Sea coast: Luannan, Tangshan, Hebei Province, and the Yalu Jiang Estuary, Liaoning Province, and orange dots indicate 12 staging sites extracted from locations of 11 Bar-tailed Godwits tracked by satellite transmitters in 2008 from Roebuck Bay, Northwest Australia (18°S, 122°E; details are described in Battley et al. 2012). (**C**) Land reclamation trend from January 2007 to June 2018 in areas within 10-km of the centroids of the 12 Bar-tailed Godwit staging sites, based on an analysis of Landsat and Sentinel satellite images. Vertical line indicates April 2015, when the first batch of Great Knots and Bar-tailed Godwits being tracked within this thesis project migrated north.

Both teams found high densities of *Potamorcobula laevis*, and established this bivalve as the main prey of Red Knots (*Calidris canutus*), Great Knots (*C. tenuirostris*) and Bar-tailed Godwits (*Limosa lapponica*) fuelling up in these sites (Yang et al. 2013, Choi et al. 2017).

Human threats to shorebirds: multiple pathways to declines

Habitat loss is identified as the main threat to shorebirds in the EAAF, and by far the most studied. Many shorebird species forage mainly on natural tidal flats outside of the breeding season, and loss of this habitat type has been rigorously assessed by remote sensing methods. An analysis of satellite imagery by Murray et al. (2014) found that 28% of tidal flats in the Yellow Sea existing in the 1980s have been lost by the late 2000s (at a rate of –1.2%/yr), and reference to historical maps suggested that up to 65% have been lost since the 1950s. The main cause of this loss is **land reclamation** for agriculture, aquaculture, and urban and industrial development (Ma et al. 2014, Melville et al. 2016a); mudflat erosion has also played a role (Chen et al. 2019). A more recent study focussed on the Chinese Yellow Sea coastline found that, from 1984 to 2015, mudflat area has decreased by 49% from 4,992 to 2,547 km^2 (Chen et al. 2019).

Another key threat reducing habitat availability to shorebirds in the EAAF is the **invasion of the exotic smooth cordgrass *Spartina alterniflora***. This tall plant (sometimes >2 m) grows in dense patches that cover tidal flats and prevent shorebirds from foraging. Cordgrass was intentionally introduced to the Jiangsu coast, China, in 1979 to promote marsh accretion to ‘create land’ (An et al. 2007). Liu et al. (2018) found that in 2015, *S. alterniflora* was found along the coastline of 9 out of the 10 coastal provinces of China, from 20.9 to 39.2°N from Guangxi to Hebei Provinces, with a total area of approximately 550 km^2 . The northernmost Liaoning is currently the only cordgrass-free province in China, probably due to its cold winters which inhibit cordgrass growth. However, under climate warming *S. alterniflora* is predicted to eventually spread into Liaoning (Liu et al. 2018). The spread of *S. alterniflora* in upper-intertidal and supratidal areas also reduces habitats suitable for shorebirds to roost, as shorebirds avoid roosting close to tall vegetation, likely because it impedes their ability to notice predators approaching (Melville et al. 2016a).

Land claims and cordgrass invasion not only reduce the area of tidal flats, but also their availability for foraging shorebirds because the upper tidal flats, which are exposed the earliest after high-tide, are the first to be enclosed by seawall or colonized by cordgrass. With shorter exposure times of mudflats, birds will be more time-constrained in foraging and might not be able to fuel at a rate efficiently enough to be prepared for migration (Mu and Wilcove 2020).

Artificial supratidal habitats associated with agriculture, aquaculture and salt production, especially in the form of shallow-water ponds, are widely used as high-tide roosts for shorebirds, and also as foraging habitats for some species (Li et al. 2013, Lei et al. 2018, Jackson et al. 2019, 2020). However, the availability of these habitats is reduced when they are converted to dry land for oil fields and industries, and also by certain type of aquaculture (e.g. sea cucumber farming) and saltpond management practices which maintain a deep level of water (Melville et al. 2016a, Lei et al. 2018, Jackson et al. 2020).

Hunting (includes shooting, trapping and poisoning of birds, both legally and illegally) are documented in all parts of the flyway, from the breeding grounds in Russia and Alaska, the areas where shorebirds stopped for fuelling in East Asia, to non-breeding grounds in Southeast Asia, Australia and New Zealand (Gallo-Cajiao et al. 2020). However, at the scale of the flyway, there is no coordinated monitoring on this issue and data are mostly anecdotal (Gallo-Cajiao et al. 2020), therefore its extent and impact on shorebird populations cannot be quantified. To date, shorebirds are still widely harvested for subsistence in many Southeast Asian countries such as Myanmar, Indonesia and Vietnam (Li and Ounsted 2007, Zöckler et al. 2010). In China, hunting seemed to have become less prevalent in the last decade. In the late 1990s, shorebird hunting using a clap net was common around Shanghai, China (Barter et al. 1997a, Ma et al. 1998, Battley 2012). However, during surveys in March–May 2013 and 2014 along the entire Yellow Sea coastline of China, only a few mist-nets were recorded in use (Melville et al. 2016a). Mist-netting of shorebirds occurs more often along the coast of the southern Chinese provinces of Guangdong and Guangxi; species caught included the Critically Endangered Spoon-billed Sandpiper (Martinez and Lewthwaite 2013). Harvesting birds using poison has been widely practiced in China for centuries (Melville et al. 2016a). Although large waterfowl like geese, swans and cranes are the main targets, substantial numbers of shorebirds are also poisoned (MaMing et al. 2012). Shorebirds being trapped in fishing nets and traps on tidal flats were observed at many sites along the Chinese coast during surveys in 2015–2018 (Box A of this thesis), and reported at the southern Jiangsu Coast (Peng et al. 2017) and the Chinese side of the Yalu Jiang Estuary (Zhang et al. 2019a).

Prey community in intertidal flats

Shorebirds stop at staging sites to fuel, and the amount of food available, a function of both the extent of *area* and the *density* of prey, determines how many shorebirds a site can sustain. While trends of changes in area of tidal flats have been extensively measured, we know relatively little about the well-being of the prey populations in the EAAF. Shou-Dong Zhang et al. (2018) reported the year-to-year trends in the macrozoobenthos community, the food of shorebirds, in the mudflats of the Chinese side of the Yalu Jiang Estuary, a major staging site of this flyway, especially for Great Knots and Bar-tailed Godwits (Choi et al. 2015). The authors took benthic samples along transects every spring from 2011 to 2016. They found that the biomass of the bivalve *P. laevis*, which accounted for 94% of the total biomass of macrozoobenthos, decreased by 99.9%

from 2011–2016, with the sharpest decrease occurring from 2012 to 2013 and *P. laevis* densities remained low ever since (sampling was conducted annually till spring 2021; S.-D. Zhang unpublished data). Whether the disappearance of *P. laevis* is caused by change in the hydrology after the reclamation of tidal flats for construction of the Dandong Port in 2009 adjacent to the site, by run-off and discharge of agrochemicals from sea cucumber farms along the shoreline, or by other factors, remained a mystery. Nevertheless, the collapse of prey stocks left 'barren' mudflats that lowered the intake rates of Great Knots by 85% (Zhang et al. 2019a) and has likely affected their migration success.

The situation in Yalu Jiang highlights the importance of understanding how human activities are affecting prey communities on intertidal flats. Some factors that require attention and further studies include: (1) water pollution from sources such as pesticides used in aquaculture and untreated industrial wastewater, which could potentially negatively affect prey populations and taxa in lower trophic levels (Liu et al. 2008, Melville et al. 2016a, Xie et al. 2017); and (2) the harvesting and cultivating shellfish and polychaetes as food or feed for aquaculture widely occurring on the tidal flats of China, Vietnam and North and South Korea, which probably have a large effect on prey densities and community compositions (Yang et al. 2016, Peng et al. 2021).

Motivation for this study

At the start of my PhD project, it became increasingly clear that the main 'problem' for shorebirds in the EAAF was mudflat loss due to land reclamation, although mechanistic links of this loss to shorebird declines were still lacking. The challenge is that most threats are localized phenomena, e.g. with land reclamation, there are places with very fast rates of reclamation alongside places that remain relatively untouched, and birds can move from the former to the latter. Moreover, impacts can manifest at later stages of the bird's annual cycle through carry-over effects. Therefore, the tracking of individual birds throughout their annual cycle was deemed essential to understanding the impact of land reclamation on shorebirds. In other words, only by putting the threats we observed on the ground in the perspective of the itinerary of a migrating bird can we understand the relevance of the threats and properly assess their impacts on shorebird populations as well as target any conservation efforts. The advent of small solar-powered satellite transmitters made my PhD project possible.

Land reclamation in the Yellow Sea slowed down considerably since we started tracking migrations of Great Knots and Bar-tailed Godwits in 2015 (Fig. 1.1C), but it does not mean that these migratory shorebirds were not threatened anymore. During the project other problems have emerged, most notably the collapse of the bivalve stock at Yalu Jiang Estuary mentioned above (Zhang et al. 2018). It became apparent that rapid actions are key in the conservation of these threatened migratory shorebirds, therefore I decided to first focus on exploring the ways that the spatial-temporal information from satellite tracking can provide an evidence base for monitoring, management, and conservation of shorebirds in this flyway. To understand the impact of human-induced environmental changes on shorebird populations, we first need to understand how birds are responding and adjusting. Therefore, my second aim was to understand what determines their capacity to cope with habitat loss and deterioration by movement. These aims resulted in a thesis containing both applied and fundamental research on migratory shorebirds in the EAAF.

Study system

This study focuses on the Northwest Australian populations of three long-distance migratory shorebird species: Bar-tailed Godwits (*L. l. menzbieri*), Great Knots and Red Knots (*C. c. piersmai*, Fig. 1.1A). They migrate annually to breeding areas in the eastern Russian Arctic and depend on the Yellow Sea as the main staging area for fuelling during both northward and southward migration (Barter 2002, Battley et al. 2012, Hua et al. 2013, Yang et al. 2013, Conklin et al. 2014, Choi et al. 2015, Lisovski et al. 2016a). All three species forage mostly on intertidal flats: the Great Knots and Red Knots are shellfish specialists (Yang et al. 2013, Choi et al. 2017) while Bar-tailed Godwits in the EAAF have a broad diet and consume both shellfish and polychaetes (Choi et al. 2017).

The EAAF populations of these species are in strong decline (Conklin et al. 2014, Studds et al. 2017). On the IUCN red list which assesses the extinction risk at the species level, the Bar-tailed Godwit and Red Knot, which have global distributions, are listed as 'Near Threatened'; the Great Knot, which is endemic to the EAAF, is listed as 'Endangered' (IUCN 2017). Likewise, under the Environment Protection and Biodiversity Conservation Act 1999 of the Australian government, the *menzbieri* subspecies of Bar-tailed Godwit and the Great Knot are listed as 'Critically Endangered', and the Red Knot as 'Endangered' (Australian Government 2019).

Since 2006, under the umbrella of Global Flyway Network our research group has been monitoring the demographics of these study populations. We have found that the survival rates of the three species during the migration and breeding seasons dropped significantly since 2011 (Piersma et al. 2016). We argued that the declines in adult survival were caused by events happening during migration rather than in the breeding areas; and the rapid habitat destruction in the Yellow Sea is probably a major cause of decline. The idea that threats in the Yellow Sea had a major impact on migratory shorebird populations is also supported by a study evaluating the importance of several factors in predicting population trends of 10 EAAF migratory shorebird taxa spending non-breeding season in Australia and New Zealand, in which Yellow Sea dependence was found to be the single most important predictor of population trend variation (Studds et al. 2017). Difference in Yellow Sea dependence was also suggested as a possible explanation to the less drastic decline in adult survival of Bar-tailed Godwits of New Zealand, which belong to the subspecies *baueri* that breeds in Alaska, in comparison to *menzbieri* from Northwest Australia (survival rates declined from 0.88–0.94 in

2006–2010 to 0.83 in *baueri* and 0.71 in *menzbieri* in 2011–2012; Conklin et al. 2016), since *baueri* passes through the Yellow Sea only once per year on northward migration, rather than twice as the *menzbieri* does (Battley et al. 2012).

Thesis outline

The key methodology employed in my thesis is the global tracking of individual shorebirds by solar-powered Argos satellite transmitters, and tracking entire migration journeys requires long-term external attachment of transmitters. For long-legged shorebird species like the Bar-tailed Godwit, transmitters can be attached by leg-loop harnesses. However, this type of harness quickly slips off the legs of more compact species such as the Knots as they have no external 'knee'. In ***Chapter 2***, utilizing captivity trials and a field test, we develop a full-body harness suitable for knot-like shorebirds that is able to accommodate the dramatic body size changes the birds experience before and after their long migratory flights.

The start of any scientific inquiry into nature requires first a careful observation of nature. Only with a detailed description of patterns, may we start to ask meaningful questions on processes (Travis 2020), and to direct appropriate conservation actions and management practices. Part II comprises two chapters describing bird migration patterns discovered from our tracking efforts. ***Chapter 3*** describes a surprising discovery: two Bar-tailed Godwits tagged in Northwest Australia turned out to belong to the elusive and little studied *anadyrensis* subspecies, from which we make a first description of the migration route and timing of *anadyrensis* godwits and compare their itineraries with those of *menzbieri* godwits tracked during the same period. In ***Chapter 4*** we describe how the Red Knot subspecies *piersmai*, previously thought to be a 'long-jump' migrant, in fact made a number of short stops ('skipping') during northward migration.

Since galvanizing conservation actions is an urgent matter in the EAAF, Part III comprises several cases of applying satellite tracking of shorebirds in coastal conservation. ***Chapter 5*** explores the value of the new knowledge obtained from tracking compared to past knowledge of key sites that had been mostly based on ground observations. Using the tracking data of the Great Knot, an indicator species for shorebirds dependent on coastal wetlands, we showed that satellite tracking have uncovered many potentially important sites that were unknown before our study, thus highlighting regions and sites which lack conservation recognition. ***Box A*** describes expeditions utilising the almost 'real-time' distributional information obtained from satellite tracking, in which we 'followed' the satellite-tracked Great Knots and Bar-tailed Godwits along the Chinese coastline. To gain a deeper understanding of factors affecting shorebird's fuelling at stopping sites, benthic sampling, foraging observations and bird counts were conducted in spring 2015–2018 at 18 sites visited by the tracked birds. Here we highlight some key findings on distribution of main prey species and bird numbers.

Following the migrations of satellite-tracked birds, in early May 2015 together with fellow expedition team members I visited Lianyungang, Jiangsu Province, China for the first time. There we witnessed tens of thousands of shorebirds on mudflats alongside lots of human disturbances and reclamation activities. To galvanize conservation efforts in this unprotected area, in ***Chapter 6*** we summarise all available data on shorebird numbers, distribution, food resources and threats in Lianyungang. ***Box B*** was a response to a planned large-scale reclamation on the Tiaozini mudflats and Dongsha shoals in southern Jiangsu Province, China. Our satellite tracking data showed that this site is used by a large proportion of tracked Bar-tailed Godwits for staging during northward and southward migration and also how the birds distributed within this area, which served as one of the key lines of evidence against the planned reclamation in the area. Another Yellow Sea site that requires urgent conservation attention is Tongzhou Bay, Jiangsu Province, China, where large areas of mudflats are being dredged or reclaimed to build a big port. ***Box C*** summarizes the findings of my collaboration with hydraulic engineers on this issue, where we applied satellite tracking data of shorebirds in ecological impact assessment of port construction and in port design following the 'Building with Nature' approach.

Unlike hunting, which directly kills birds, threats leading to habitat loss and prey declines affect birds in non-lethal ways, and birds might be able to mitigate the impacts to a certain extent, e.g. by moving to suitable sites nearby. The propensity to move might be negatively linked to site fidelity which is the tendency to return to a site. In ***Chapter 7*** we characterize site fidelity in two distinct phases of the non-breeding period (wintering and migration) for Great Knots and Bar-tailed Godwits, using both satellite tracking data and resighting data, and discuss how site fidelity differences between these species could affect their movement responses to local threats. In general, the costs of moving as a way to cope with environmental changes, depended on information on suitable alternative sites, which animals could acquire by exploring new environments. Strategies related to information use and movements in new situations have been found to be rather fixed within an individual across situations, and to be correlated with personality differences (e.g. in the tendency to explore) measured under standardized laboratory environments. In ***Chapter 8***, we investigate how exploratory tendencies of Great Knots might underlie differences between individuals in their spatial responses to the collapse in prey stock at Yalu Jiang (Zhang et al. 2018), and in the timing of breeding and in breeding success. In ***Chapter 9***, based on some of our findings I discuss ways that shorebirds could cope with habitat deteriorations, from small to large spatial scales, i.e. from the single site to the flyway; and then expand to the scale of the life history of a migratory shorebird.

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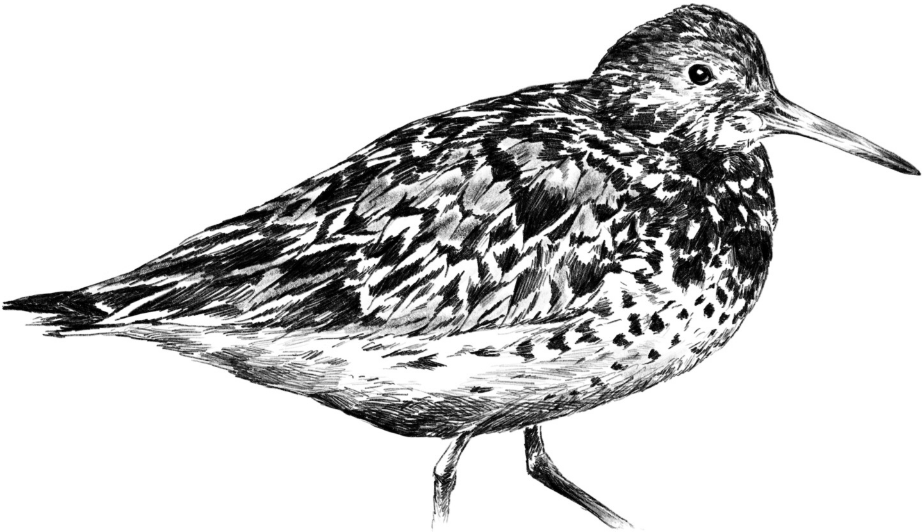
PART I

Methodological development



CHAPTER 2

Testing an attachment method for solar-powered tracking devices on a long-distance migrating shorebird

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Abstract

Small solar-powered satellite transmitters and GPS data loggers enable continuous, multi-year, and global tracking of birds. What is lacking, however, are reliable methods to attach these tracking devices to small migratory birds so that (1) flight performance is not impacted and (2) tags are retained during periods of substantial mass change associated with long-distance migration. We developed a full-body harness to attach tags to Red Knots (*Calidris canutus*), a medium-sized shorebird (average mass 124 g) that undertakes long-distance migrations. First, we deployed dummy tags on captive birds and monitored them over a complete migratory fattening cycle (February–July 2013) during which time they gained and lost 31–110 g and underwent a pre-alternate moult of body feathers. Using each individual's previous year fattening and moult data in captivity as controls, we compared individual mass and moult differences between years between the tagged and reference groups, and concluded that the attachment did not impact mass and moult cycles. However, some birds shed feathers under the tags and under the polyester harness line commonly used in avian harnesses. Feather shedding was alleviated by switching to smoothed-bottom tags and monofilament harness lines. To field-trial this design, we deployed 5-g satellite transmitters on ten Red Knots released on 3 October 2013 in the Dutch Wadden Sea. Bird movements and tag performance appeared normal. However, nine tags stopped transmitting 11–170 days post-release which was earlier than expected. We attribute this to bird mortality rather than failure of the attachments or transmitters and suggest that the extra weight and drag caused by the tag and its feather-blocking shield increased the chance of depredation by the locally common Peregrine Falcons (*Falco peregrinus*). Our results demonstrate that species- and place-specific contexts can strongly determine tagging success. While captive trials are an important first step in developing an attachment method, field trials are essential to fully assess attachment designs.

Introduction

In the past decade, satellite telemetry and GPS (Global Positioning System) tracking studies have revolutionized our understanding of local movements, dispersal and migration patterns (Tomkiewicz et al. 2010, Bridge et al. 2011a). Satellite transmitters, also called platform transmitter terminals (PTTs), send signals at interval of 60–65 s during pre-programmed transmitting periods. The Argos receiving system (CLS, Collecte Localization Satellites, http://www.argos-system.org) collects the signals via satellite, and a bird's position is subsequently calculated. GPS tags receive signals from a network of GPS satellites and store the position data within the device. Depending on tag design, tag retrieval, remote downloading, or data transmission via satellites are required to download the data (for reviews, see Bridge et al. 2011, Klaassen et al. 2014). Both satellite and GPS technologies enable animal tracking at a global scale. Solar-powered (i.e. rechargeable) satellite transmitters are now as small as 5 g (Microwave Telemetry), while solar-powered GPS data loggers are as small as 6 g (UvA-BiTS http://www.uva-bits.nl; Bouten et al. 2013), enabling multi-year tracking of small bird species.

Tracking devices can be implanted or externally attached (see Hooijmeijer et al. 2014), but, for solar-harvesting devices, external attachment is necessary. For external devices, the design components that facilitate charging (e.g. feather shields, elevating platforms) are important considerations. Since the early days of VHF radio tagging, various external attachment techniques have been developed. For shorebirds, gluing the radio tag onto the bird's back (Warnock and Warnock 1993) has been a preferred and very successful method. For example, 1.3- to 1.8-g glue-mounted radio tags have been used to successfully track movements of Red Knots (*Calidris canutus*) in both the Dutch Wadden Sea (van Gils and Piersma 1999, Nebel et al. 2000, van Gils et al. 2005a, 2006a, Spaans et al. 2009) and in northwest Australia (Battley et al. 2005, Rogers et al. 2006a). Gluing is a relatively simple process that can be completed at the banding site, and birds will shed the tag at or before the next moult. However, glue-mounted tags weighing more than 2.0 g are likely to be shed prematurely, within a few weeks after deployment, especially in hot and humid conditions (Y.C.C., T.P., T.L.T., C. Hassell, personal observations). Since most studies using satellite transmitters and GPS tags seek to track local movements and migration over a few months or years, developing methods for long-term attachment is necessary. Leg-loop harnesses (described in Rappole and Tipton 1991) have been applied in some long-legged shorebird species (Sanzenbacher et al. 2000, Watts et al. 2008, Page et al. 2014), but this harness design is unsuitable for more compact species such as the Red Knot. This is because Red Knots have no external 'knee', so a leg-loop harness slips off the legs within seconds after deployment, no matter whether the harness is made of fixed or elastic materials (T.P. and R.P., personal observations). An alternative is a full-body harness consisting a neck and a body loop, first described by Brander (1968). This design has been used for attaching satellite and GPS tags on several bird taxa, such as raptors (e.g. Fuller et al. 1998, Hake et al. 2001, Klaassen et al. 2010), waterfowl (e.g. Roshier and Asmus 2009), gulls (e.g. Shamoun-

Baranes et al. 2011, Klaassen et al. 2012) and Crab Plovers *Dromas ardeola* (R. Bom, personal communication).

An important issue confronting attachment in many long-distance migrants relates to their dramatic changes in body mass before and after migratory flights. For example, the body mass of Red Knots increases up to 190 % before making long-distance migratory flights (Piersma et al. 1995, 2005), resulting in a marked change in circumference. For small migratory bird species that cannot wear a leg-loop harness, no harness designs have been developed to cope with these regular, substantial changes in bird size. A potential solution is fitting a full-body harness with dimensions larger than the maximum size the bird could attain; such a harness would need to fit loosely but securely when a bird is not at its peak mass. We set out to investigate the effects of full-body harnesses on Red Knots in captivity and subsequently in a field setting, in preparation for a world-wide tracking study of the migratory behaviour of this species (see Piersma 2007 for context).

We used an iterative refinement approach involving two captive trials. Our first captive trial lasted for 4 months in spring and tested the effect of this attachment design on bird behaviour, body mass and moult cycles. The individual Red Knots we instrumented show seasonal cycles in mass and moult, with a mass peak in May to June (Piersma et al. 1995). Since their mass and moult cycles are highly repeatable between years (J. Karagicheva, M.B., T.P., unpublished data), we were able to compare an individual's weekly body mass and plumage score between years in both tagged and untagged birds to assess effects of tag attachment.

During the first trial, we observed problems of irritation associated with wearing the harness. We examined the possible causes of these problems and came up with further refinements of the attachment technique, and then conducted a second trial to test our improved design on a subset of the captive birds. On the basis of improved results from the second trial, we deployed 5-g solar-powered satellite transmitters on ten free-ranging Red Knots to test field performance of our attachment method.

Methods

Testing the effect of the attachment on mass and moult cycles

STUDY ANIMALS AND HOUSING

The Red Knots used in the captive trials were caught in the Dutch Wadden Sea between 1994 and 2004, and since then have been held in captivity at the NIOZ Royal Netherlands Institute for Sea Research on Texel, the Netherlands. The birds are housed in aviaries of approximately 4 m × 2 m and 2.5 m high, in groups of 6–7 birds per aviary. During the harness trials, birds were fed ad libitum with protein-rich trout pellets (Produits Trouw, Vervins, France). Each aviary contained a tray with running fresh water for the birds to bathe and drink, and a patch of mudflat with running saltwater where the birds could probe the sediment.

ATTACHMENT DESIGN AND DEPLOYMENT

Using a 3D printer, we produced Acrylonitrile Butadiene Styrene (ABS) dummy tags of 24 × 14 × 8 mm, weighing 3.5 g each, in the same shape of the 5-g satellite transmitters manufactured by Microwave Telemetry that we intended to use in the field. We glued a 3-mm layer of neoprene to the underside of the dummy tags to give them a higher profile in anticipation that the real tags would need this extra height to prevent feathers from covering the solar panels (as observed in Cohen et al. 2007). Our first harness was made of inelastic braided polyester line (1.5 mm wide; Kivikangas Oy, Finland) that has been used successfully in many tagging studies of raptors (R.H.G.K., personal observations). It consisted of a neck loop and a body loop that went underneath the wings and in front of the legs (Fig. 2.1). We first constructed the neck loop that measured 55–65 mm when stretched by a calliper placed within the loop, and then attached this loop to the front end of the tag. Then, the neck loop was put over the bird's head and neck. The tag sat on the bird's back and was held in place while the body loop was constructed, for which we slid the two lines underneath the wings, passed them through the mounting loops at the tag's rear end, and tied them to the tag. In our first deployment session, to ensure the body loop was not too tight, we placed a finger between the tag and the back of the bird when tightening the 'rear knot' (see Fig. 2.1). However, we found that it was difficult to tell the actual size of the body loops when tightening it on the bird, therefore in later sessions, we drew a mark on each of the harness lines at 120 mm from the 'breast

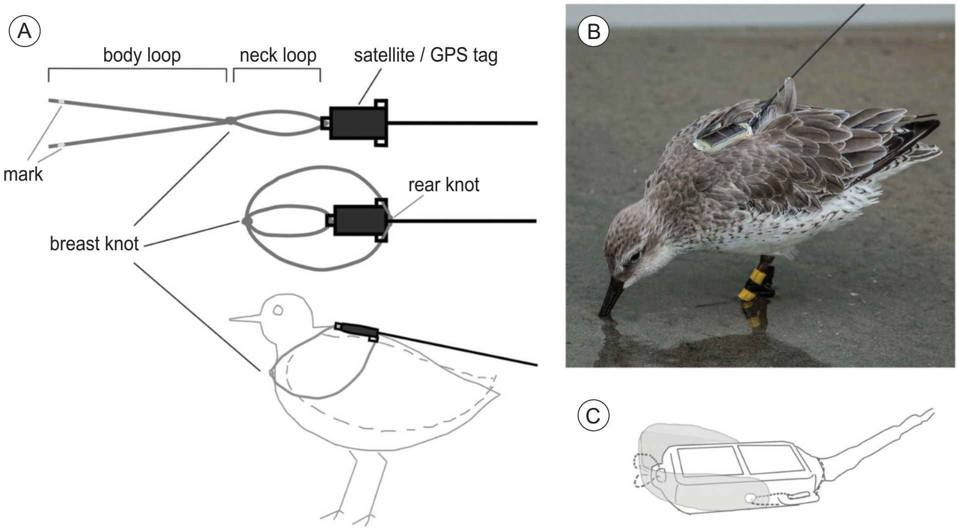

Figure 2.1. (**A**) The loose neck-body loop harness attached to Red Knots (*Calidris canutus*). Top the harness before deployment, where a mark at 120 mm from the breast knot is drawn on each side of the line forming the body loop. *Middle* dorsal view of the harness after deployment. *Bottom* the position of the harness on a Red Knot. (**B**) A Red Knot with a 5-g solar satellite transmitter deployed. (**C**) A small transparent plastic shield (in grey in the diagram for illustration purposes) was tied to the transmitter to prevent feathers from covering the solar panels.

knot’ (Fig. 2.1), and tightened the rear knot at 15–25 mm (to create variation in body loop widths) away from the marks. The exact size of the body loop was measured after removing the harness at the end of the trial. We deployed the dummy tags with harnesses on 1 Red Knot on 5 November 2012 during a pilot trial, and on 22 Red Knots between 25 February 2013 and 7 March 2013. At deployment, the dummy tag with harness weighed about 3 % of the body mass of the birds.

MONITORING BIRD’S RESPONSE TO THE ATTACHMENT

Bird response was assessed by observing their behaviour through the one-way aviary window at least 3 times a day for the first 72 h after tagging; afterwards, they were checked daily and weighed weekly. We noted if abnormal behaviours (e.g. excessive preening, movements to remove the tag and harness) occurred. From late April onwards, we observed that a few birds had shed feathers beneath the tag and on the breast especially around the area of the ‘breast knot’, to the extent that the skin had become bare. Subsequently, during weekly handling, we closely examined birds for skin irritations and scored the degree of feather shedding under the tag and on the breast under the harness lines (quantified by a score from 0, no feather shedding, to 3, large area of bare skin similar in size to the surface area of the tag). As feather shedding could have been related to constant rubbing of harness/dummy tag on the feathers, we hypothesised that the tighter the harness, the more feathers the bird would shed. Using Poisson regression, we tested whether (1) the maximum body mass, (2) the length of the neck loop and (3) the length of the body loop predicted the degree of feather shedding (quantified by a score from 0, no feather shedding, to 3). Statistical analysis was conducted in R v.3.01 (R Core Team 2013).

Six birds that were clearly irritated by the harness lines in the first few weeks after deployment were relieved of their harnesses by 1 April. Together with five birds that never wore harnesses, they served as the reference group (n = 11 birds) in analyses of timing and magnitude of mass and moult changes in the birds that wore harnesses for 4 months until the end of the trial on 8 July 2013 (n = 13).

BODY MASS CYCLE

To determine if the harness attachment prevented birds from following normal fattening patterns, we calculated the between-year differences in mass by week of individuals between 2012 and 2013, from the start of April (week 14), which was the onset of mass increase, until the end of the trial on 8 July (week 27). This weekly mass difference was then compared between the reference group and the harness group by two-way ANOVA.

MOULT CYCLE

During the weekly handling, we scored the amount of breeding plumage (from 1, complete winter plumage, to 7, complete breeding plumage using methods described in Piersma et al. 2008). The plumage score could differ by one score point between observers scoring the same bird, or within observers scoring the same bird again on the following day; therefore, a difference of one point would not indicate plumage differences. To assess whether between-year differences in the timing of plumage gains were different between the reference group and harness group, we visually examined each individual's plot of plumage score against time.

Testing alternative attachment materials

In an attempt to alleviate the feather shedding and skin irritation problems observed in the first trial, we produced a new batch of ABS dummy tags. To prevent feather shedding underneath the tag, we did not glue neoprene on the underside surface of the tag; instead, we smoothed the surface by wiping it with a solvent (Tangit PVC-U/C/ABS Cleaner). Two other types of harness lines were tested: (1) multifilament Dacron (Micron) fly line backing (0.5 mm diameter; Cortland, USA) and (2) monofilament nylon fishing line (0.5 mm diameter; Albatros, Netherlands). For the nylon harness, we wrapped a heat-shrink tubing around the 'breast knot' (Fig. 2.1) so that it was less irritable to the bird, and prevented the 'breast knot' from loosening.

We applied these attachment designs to birds that had their harnesses removed during the spring trial due to irritation. Birds were checked by watching their behaviour through the one-way aviary window at least three times a day for the first 72 h after tagging; afterwards, they were checked daily and weighed weekly. During the weekly handling, we checked for any feather shedding beneath the tag and the harness lines.

Initially, we applied the monofilament nylon harness to two birds on 4 July 2013, and then on 24 July we equipped one bird with the monofilament nylon harness and three with the Dacron harness. Three more birds were equipped with monofilament nylon harness on 30 July, two of which had worn the Dacron harness but had it removed (see "Results"). From 30 July onwards, six birds in total were wearing the monofilament nylon harness, and this second trial ended on 18 September 2013.

Field test

Five second calendar year and five adult Red Knots (*C. c. islandica*) were caught in Richel (53.3°N, 5.1°E) on 6 September 2013 and transported about 40 km to the NIOZ aviary facilities. The housing conditions were the same as described in "Study animals and housing". By housing the new birds with birds that have been kept in captivity for years, the new birds learnt to feed on trout pellets within 2 days, and were fed ad libitum.

We deployed satellite transmitters (5.0 g solar PTT; Microwave Telemetry) on these 10 birds on 27 September 2013, using a harness constructed with monofilament nylon line as described above. We tied a small transparent plastic shield with a height of 7–8 mm around the front of the transmitter (Fig. 2.1C) to block feathers from covering the solar panels. The tag with shield and attachment weighed c. 3.1–4.0 % of body mass at release. After deployment, we kept the birds for 7 days in the aviaries so they could acclimate to the harness and tag, and we could monitor their condition.

We released the birds on 3 October 2013 at mudflats at De Schorren, Texel (53.1°N, 4.9°E), 25 km from the capture site. We chose this location over the capture location because it is easily reached by car from the NIOZ aviaries, thus minimizing stress caused by transportation; moreover, a Red Knot's wintering home range is much wider than 25 km (Piersma et al. 1993a, van Gils and Piersma 1999, Spaans et al. 2009) and birds released at De Schorren in the past were subsequently resighted at Richel and locations further away (NIOZ resighting database).

Transmitters were programmed to operate on a duty cycle of 10 h on and 48 h off and data were collected via the Argos data collection system. Received data were converted to locations which were classified according to accuracy (CLS 2015); generally four or more messages received during a satellite overpass resulted in a 'standard' location with an estimated radius of error, whereas fewer messages, or overpasses low on the horizon, resulted in an 'auxiliary' location without an estimate of accuracy. The transmitters also measured battery voltage.

We evaluated the field performance of our attachment method by assessing the duration of tag retention (as determined by length of satellite contact with the tags) and its effect on tracked bird movements as compared to what is known of typical movements of Red Knots in the Wadden Sea (van Gils and Piersma 1999, van Gils et al. 2006a). We also assessed patterns of battery voltage and the ratio of standard to auxiliary locations, since these variables reflect how well a tag is positioned on a bird, i.e. how well it is receiving sunlight and how well the antenna is oriented. Regular field observations were also conducted in a section of the Wadden Sea for an unrelated mark-resighting project, in which the tagged Knots were searched for and recorded.

Results

Testing the effect of the attachment on mass and moult cycles

HARNESS EFFECTS

When captive birds gained weight, harnesses became tighter and the tags moved upwards along the back. However, with the exception of one bird, a small gap always remained between the bird's back and the tag even when birds were at their maximum masses. For the exception, the neck loop circumference was 132 mm (widest of all birds) and body loop was 145 mm; the harness was so tight that we had to remove it before the end of the trial. A different bird repeatedly put one foot into the body loop which was 189 mm; however, it was behaving normally otherwise so we did not remove the harness.

In the course of the experiment, but mainly early on, the harnesses were removed from ten birds which were clearly irritated by the inelastic braided polyester line and/or the tag. These individuals either got their bills stuck in the harness multiple times as a result of intense preening around the harness (seven birds); or the harness became very tight during fattening up in May (one bird); or many feathers were shed beneath the tag and on the breast (two birds). For the remaining 13 birds, their harnesses were completely covered by feathers within a few days as the birds preened the harness lines down towards their skin. These birds went through the cycle of fattening up and slimming down from April to June without obvious problems and were the ‘harness group’ in the analysis of the body mass and moult cycles.

FEATHER SHEDDING

The amount of feathers shed in the 13 birds in the harness group varied between individuals, and even within individuals; some individuals shed feathers on the back but none on the breast, or vice versa. In mid-June, new feathers started to grow on the bare parts, and by mid-July, all bare parts were covered by new feathers. We did not find any associations between the lengths of the neck and body loops, or the maximum body mass, with the degree of feather shedding at the back or the breast (all $P > 0.1$).

BODY MASS CYCLE

Body masses of all captive birds increased from early April onward and peaked in mid- to late May (Fig. 2.2A). The pattern was similar in both years, but in 2013 the decline in masses occurred earlier than in 2012; thus, the mass differences ($\text{mass}_{2013} - \text{mass}_{2012}$) in weeks 26 and 27 were significantly more negative than in other weeks ($t_{\text{week26}} = -4.725$, $t_{\text{week27}} = -6.405$, both $P < 0.001$; Fig. 2.2B). The individual mass differences were the same between the harness group and reference group for all weeks (ANOVA, $F = 1.7885$, $P = 0.1822$; Fig. 2.2B).

MOULT CYCLE

Starting in March, plumage scores increased and reached a plateau in early May; birds then kept their breeding plumage until the end of the experiment. No differences in plumage progression were detected in the majority ($n = 22$) of the birds (Fig. 2.3). However, for one bird, the increase in plumage score was faster in 2013 than in 2012, and for a second bird, the maximum plumage reached was higher in 2013 than in 2012 (birds 427 and 609 in Fig. 2.3). Both birds belonged to the harness group.

Testing alternative attachment materials

Within the first 24 h of wearing the Dacron harness, all three birds had their bills stuck multiple times and we had to remove the harnesses. Three of the six birds wearing the monofilament nylon harness also stuck their bills in the harness: for one bird this occurred once, and for another bird twice, both within the first 24 h; for a third bird, this was observed once at 53 h after deployment. We did not detect this behaviour again for the remaining 7–10 weeks of the trial. All six birds spent almost no time preening around the monofilament harness, in contrast to the intense preening exhibited when they were wearing harnesses made of the multifilament braided polyester or Dacron. When the trial ended, the birds had almost completed their contour feather and wing moult, and none of these birds showed any feather shedding on their backs or breasts.

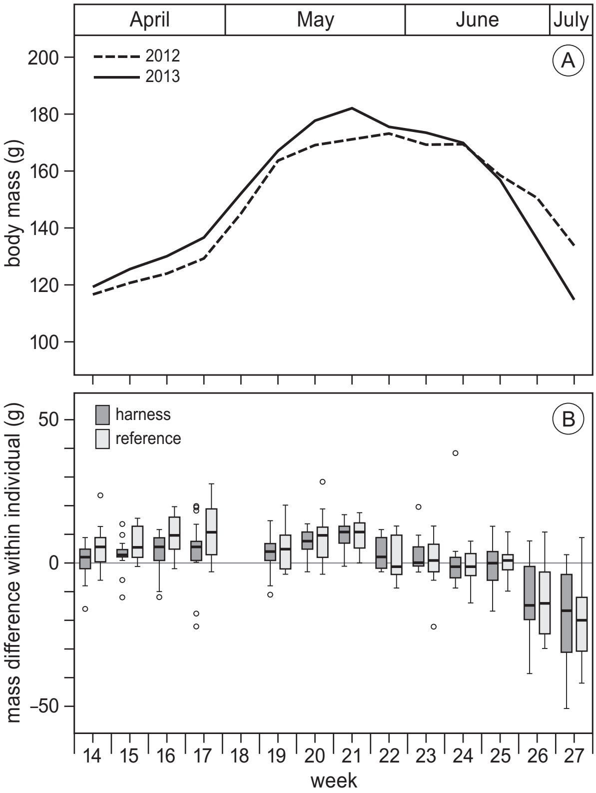

Figure 2.2. (**A**) Body masses of captive Red Knots carrying dummy tags in 2013 from week 14 (2 April 2012; 1 April 2013) to 27 (2 July 2012; 1 July 2013). (**B**) The weekly within-individual mass difference (mass_{2013} - mass_{2012}) of the harness group (*dark grey*) and the reference group (*light grey*).

Field test

During their 1 week in captivity, none of the 10 field-trial birds stuck their bills into the harness. Of the 10 tags, we lost contact with 2 in the first month: the last signals were obtained 9 and 19 days after release. From December onwards, we lost contact with more tags (Fig. 2.4), and by mid-March we were only receiving continuous data from one tag (which is still transmitting from a live bird as of July 2015). Median retention time for the nine tags was 65 days. A few signals were received from three tags at certain times afterwards, but no locations were generated, therefore it is doubtful whether these signals came from tags on live birds; they also could have been parity errors. Battery voltage and number of locations per duty cycle dropped from October through December and then increased gradually from January onwards (Fig. 2.4), while the percentage of 'standard quality' locations (Argos location classes 3, 2 and 1) received per duty cycle ranged from 23 to 37 %. On average, we received 2.8 standard quality locations per duty cycle of 10 h.

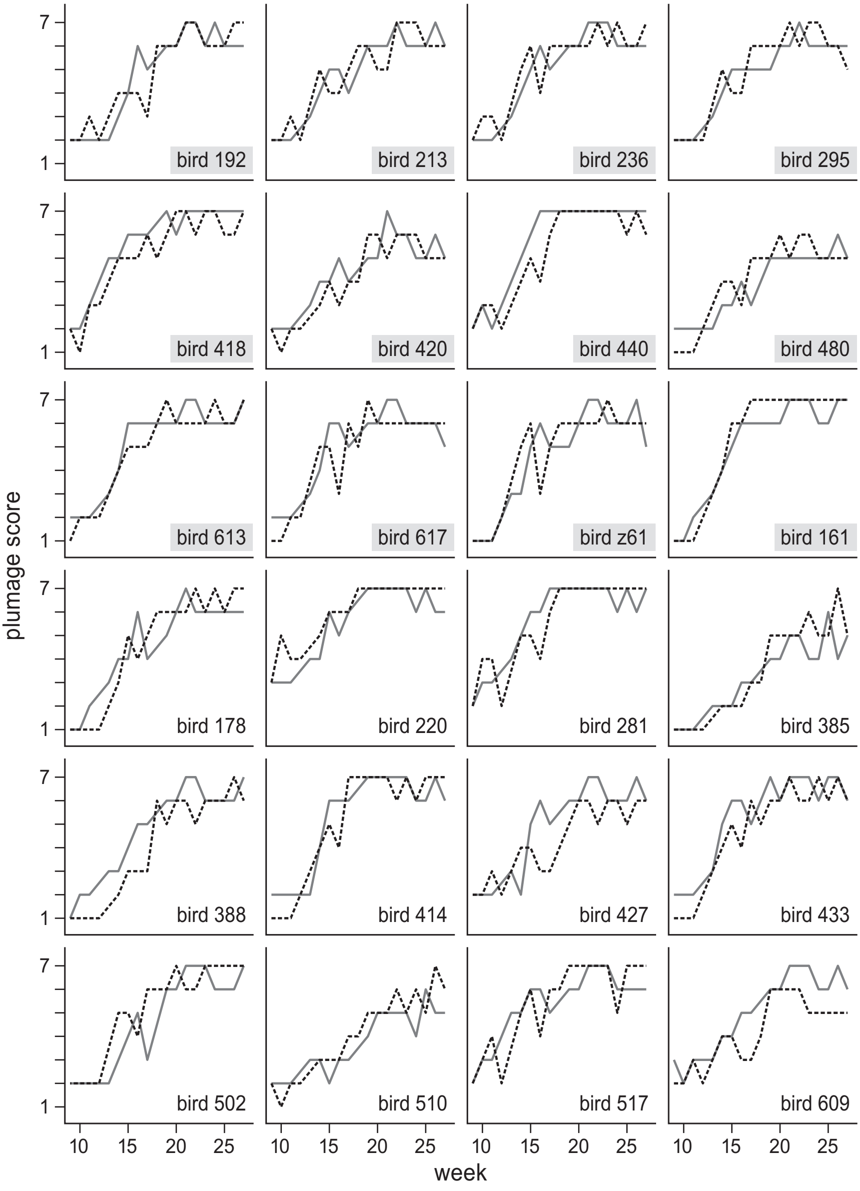

Figure 2.3. Plots of individual plumage scores in 2012 (*dotted line*) and 2013 (*grey line*) by week. Bird IDs belonged to the reference group are enclosed in shaded rectangles.

Two birds moved more than 300 km from the release site shortly after release: one bird travelled over 300 km to mudflats around the islands Föhr and Sylt (54.7°N, 8.6°E) in northern Germany within 2 days of release, and another bird flew 340 km to the Wash (52.9°N, 0.1°E) in England within 9 days. Most other birds remained in the Wadden Sea within 150 km of the release site. As the area where the tagged Red Knots occurred is large and mostly difficult to access (e.g. Piersma et al. 1993a), we had only two field observations of tagged birds, and in both cases the bird had normal appearance and behaviour.

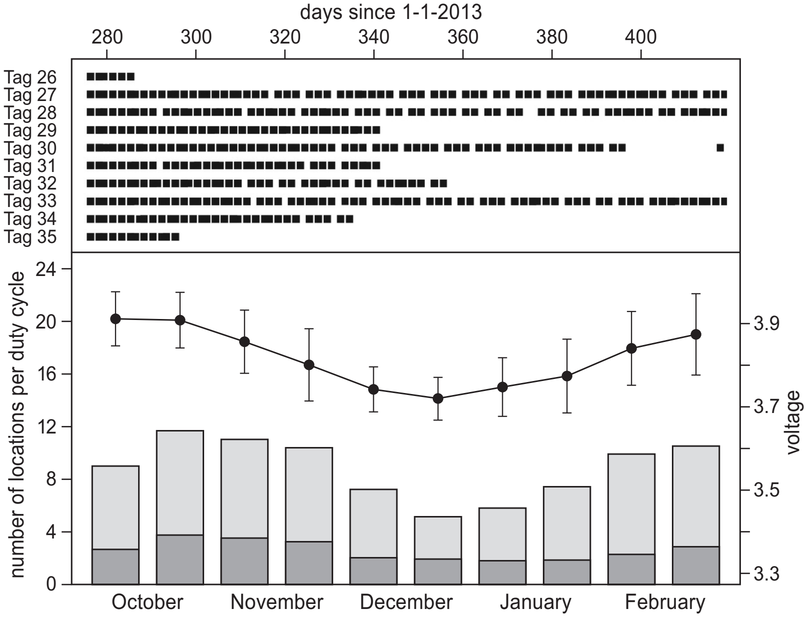

Figure 2.4. (*Upper graph*) signals received from each tag per duty cycle, (*middle line*) mean battery voltage within the first 2 h of a duty cycle and (*lower bars*) number of standard (*dark grey*) and all locations (*whole bars*) per duty cycle per half-month (first half, 1–15, second half, 16 onwards), from satellite-tagged Red Knots released on 3 October 2013 at De Schorren, Texel (53.1°N, 4.9°E) in the Wadden Sea.

Discussion

Through our first and second captive trials, we developed a method of attaching small solar-powered tags onto Red Knots that showed more potential for successful field application than any other method had shown previously. Provided that the harness was constructed large enough, it could accommodate the seasonal changes in body size of Red Knots. By using suitable harness line material, any skin irritation to the birds was minimal. We first discuss several aspects in attachment methodology that we learnt from our captive trials. Then, based on the field test results, we discuss how attachment design, tag properties, and the specific ‘environment’ that the birds experience jointly determine the success of a field application.

Harness construction

Before actual deployments using our harness, trials with captive birds are necessary to determine the appropriate size for each (sub-) species. Although wider loops will prevent the harness from getting too tight when a bird fattens, a neck loop that is too wide will not lie on the bird's shoulder and might fall sideways, possibly affecting wing movement. If the body loop is too wide, there is a risk of the bird putting its foot into the loop; moreover, the tag will be lower on the bird's back away from the centre of gravity. Thus, we determined that the suitable harness size for *islandica* Red Knots is a neck loop of 100–110 mm in circumference, and a body loop of 160–170 mm. Visible marks at equal distances from where the 'rear knot' is tied (in this case, about 120 mm from the 'breast knot') are very useful for checking whether the two sides of the body loop are symmetrical during deployment (Fig. 2.1). Symmetry of the loops will ensure that the tag sits on the central axis of the bird and that the weight load is balanced. As birds preened the harness so that it is trapped by feathers, the harness position on the body was stabilised and the harness sat close to the skin; therefore, there is very little risk of the harnesses getting tangled with vegetation.

Materials

We reasoned that the feather shedding we observed was caused by the multifilament polyester lines and the neoprene layer constantly rubbing against the tiny barbs and hooks and bases of feathers which are connected to nerves. This resulted in irritation to birds (as manifested in increased preening) and wearing of the feathers. Our second trial tackled this particular problem by testing materials that would minimize irritation. Monofilament nylon line had a smooth surface and did not appear to rub against feathers as much as multi-threaded Dacron and polyester lines. We found it to be the least irritating among the three materials we tested. Although tubular Teflon Ribbon is the most commonly used material for harnesses (e.g. Klaassen et al. 2012, Kesler et al. 2014, Page et al. 2014), we did not test this material because of its extra weight and thickness (thinnest available Teflon thread is 3.5 mm width, weighing 1.0 g per 40 cm, whereas the nylon line weighs 0.1 g per 40 cm).

In many satellite/GPS tag deployments, a layer of neoprene is attached to the underside of the tag (T.L.T., K. Camphuysen, personal communication), to (1) insulate the tag from the bird's back; (2) raise the height of the tag so that the solar panels are not covered by feathers; and (3) act as a 'padding' so that the bird feels more comfortable. However, our first trials showed that this material irritated birds. K. Camphuysen (personal communication) also observed that Herring Gulls *Larus argentatus* constantly pecked and eventually removed the neoprene. While neoprene could still be useful for tags attached by gluing onto the skin, a smooth surface seems more suitable for tags attached with our harness design for Red Knots.

Deployment protocol

The chance of birds trapping their bills in the harness was related to the type of harness material used, as some materials were more irritating to birds than others. This response was very individualistic—some individuals preened furiously around the harnesses which provided many more opportunities for the bill to become trapped. Even for the nylon monofilament lines, the least irritating material, the chance of getting stuck was high during the first 24 h of wearing the harness (2 of 6 birds). This problem still persisted when using a flexible material such as an elastic nylon line and silicon-rubber line (Y.C.C. et al., unpublished data). Based on these observations, we strongly recommend keeping birds in captivity for at least 24 h prior to release so that they can acclimate to the harness and tag in a safe environment. Then, those individuals that do not appear suitable for satellite tagging, i.e. those that are stressed or repeatedly putting their bills into the harness, can be identified and their tags removed. It follows that tagging should not be done for species that could become too stressed in captivity, or when this observation period is not possible, e.g. the breeding season when birds need to care for young. As keeping birds in captivity requires a lot of effort and can be carried out adequately only by experienced bird handlers, some researchers might opt to skip this procedure; however, we feel that in such cases they would be introducing an avoidable source of mortality by including some 'unsuitable' birds. Although the risks get smaller with time, it is still possible that birds will get stuck after the first 24 h, so we further recommend a longer assessment period (e.g. 7 days for our field trial) in those situations where the infrastructure is suitable for keeping birds and the tagged species can be maintained in good condition. Finally, keeping extra birds in captivity along with the tagged birds helps distinguish tag-induced behaviours from captivity-induced behaviours, thus helping to focus the assessment.

Field performance

Initially, the full-body harness appeared to have minimal negative effects on free-ranging Red Knots as all birds moved between tidal basins of the Wadden Sea, and two birds performed long-distance flights within the first 2 weeks in the wild. These latter movements were much longer than the typical daily flights between roosting and foraging areas performed by Red Knots in the region (van Gils and Piersma 1999, van Gils et al. 2006a) and would require considerable energy expenditure.

The voltage levels of the transmitters closely tracked the winter decrease/spring increase in day length and sun angle, indicating that the tags were positioned well and that feathers were not interfering with charging. The ample number of total and standard class Argos locations also indicated that the antennas were positioned well. Overall, the percentage of standard class locations (31 % of locations were standard class) was sufficient to describe wintering movements of Red Knots in good detail even though it was lower than the published figures of 55 % in Marbled Godwits (*Limosa fedoa*) with 9.5-g tags (Olson et al. 2014) and 58 % in Long-billed Curlews (*Numenius americanus*) with 18-g tags (Page et al. 2014).

We lost contact with nine of the ten transmitters 10 days to 5 months after releasing the birds into the wild. We considered insufficient battery charging as an unlikely cause, since we did not receive signals from the lost tags when battery charge began increasing in the functioning tags in spring. We doubt that birds could have escaped their harnesses, since none ever slipped a harness during the 4-month captive trial and the harnesses were unlikely to break. Although malfunctioning of a small percentage of transmitters has been observed in some studies (R.H.G.K., Y.C.C., T.L.T., C. Hassell, unpublished data), it is unlikely that all nine of the missing transmitters failed. Transmitter failure is usually confirmed by resighting a live bird wearing a non-transmitting device, but the low resighting rate of 0.26 year^{-1} of colour-marked Red Knots in the Dutch Wadden Sea (Rakhimberdiev et al. 2015a) precluded us from using resightings to assess transmitter failure. If the birds died and their transmitters were subsequently 'lost' in sea, mud or vegetation, their survival rate would have been lower than the wild population's average survival rate of 0.81 year^{-1} calculated from mark-resighting data of colour-ringed individuals from 1999 to 2013 (Rakhimberdiev et al. 2015a). A likely explanation of the high mortality rate of our tagged birds is that they experienced high predation. In the Wadden Sea, predators like Peregrine Falcon are common in winter (van den Hout 2010, p. 59). The tactic knots use to escape predation by falcons is persistent coordinated aerial escape flight manoeuvres performed by the whole flock (van den Hout et al. 2010). Even if the extra load and drag from the 5-g transmitter is relatively small, any slight handicap in maneuverability experienced by a tagged bird could have led to a higher probability of them being singled out of the flock into a one-to-one chase with a raptor and being killed.

When determining the suitability of tags, much emphasis is placed on tag mass (e.g. the 5 % rule in Kenward 2001), whereas tag size and associated drag are often not considered (Barron et al. 2010). As turning maneuverability is determined by weight and drag (van den Hout et al. 2010), a tag's effects on these aspects need to be considered such that agility is not significantly hampered. Although the feather-blocking shield likely contributed to the overall good performance of the transmitters, the shield rises an extra 3–4 mm above the tag which significantly increases the drag coefficient (Pennycuick et al. 2012). Consequently, we do not recommend using the shield when tagging Red Knots or other species where flocks are attacked at high rates by aerial predators and individuals must successfully evade them (van den Hout et al. 2010). Experiments to examine the effects on aerodynamics of different tag sizes, shapes, and varying antenna length and angle would greatly aid future tag design. These experiments would also help researchers balance the risk of negative effects on survival caused by the increased drag of tags or feather-blocking shields against benefits of data collection during months or situations with low solar radiation.

In our study, deleterious effects of the tagging, beyond what could be tested in captivity, appeared to be determined by species and environmental factors in the wild, including the presence of certain species of predators. The loss of so many of the tagged birds in the field, after using what we thought was a suitable tag attachment method, points to the need for further refinement of our methods for Red Knots. Given that the harness worked well in the captive trials, and if the missing birds were indeed predated, the reduced agility caused by a large tag was limiting the success of the field applications. If this is indeed the case, our harness design may currently be suitable for attaching 5-g satellite transmitters to larger shorebird species with Red Knot-like body structure, or for studies of Red Knot-sized shorebirds in areas with few aerial predators.

Acknowledgments

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PART II

Migration patterns

CHAPTER 3

Hidden in plain sight: migration routes of the elusive Anadyr Bar-tailed Godwit *Limosa lapponica anadyrensis* revealed by satellite tracking

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Abstract

In the East Asian–Australasian Flyway, the Bar-tailed Godwit populations *Limosa lapponica menzbieri* and *L. l. baueri* are declining, threatened by the rapid degradation of their staging sites along the Yellow Sea coastline of China, North Korea and South Korea. A third subspecies in this flyway, *L. l. anadyrensis*, which breeds in the Anadyr River basin, Chukotka, Russia, is morphologically distinct from *menzbieri* and *baueri* based on comparison of museum specimens collected from breeding areas. However, their non-breeding distribution, migration route and population size are entirely unknown. In 2015–2018 we tracked the migrations of 24 female Bar-tailed Godwits from Northwest Australia, the main non-breeding area for *menzbieri*. During pre-breeding migration, all birds staged in the Yellow Sea and then flew to the breeding grounds in the eastern Russian Arctic. Two birds migrated further east than the rest to breed in the Anadyr River basin. After breeding, they migrated southwestward to stage in Russia on the Kamchatka Peninsula and on Sahkalin Island *en route* to the Yellow Sea. This contrasts with the other 22 tracked godwits, that followed the post-breeding migration route of *menzbieri* described previously, i.e. they all migrated northwards to stage in the New Siberian Islands before turning south towards the Yellow Sea, and onwards to Northwest Australia; the Kamchatka Peninsula was not used by any of the tracked *menzbieri* birds. For this reason, the 4,500 Bar-tailed Godwits counted in the Khairusova-Belogolovaya estuary in western Kamchatka in August 2018 may well be *anadyrensis*. The counts there provide a minimum estimate of the *anadyrensis* population size. The Dongtai coast in southern Jiangsu Province, China, being the only staging area they used within the Yellow Sea in both pre- and post-breeding migration, calls for adequate protection and management of godwit habitats there.

Introduction

Tracking of individual birds by small tags directly maps their migration routes and often reveals new routes and areas unknown to ground observers (Bridge et al. 2011, Chan et al. 2019b). Especially for declining populations, information on migration routes and key staging areas are critical for their conservation (Piersma & Baker 2000). In the East Asian–Australasian Flyway (EAAF), the extensive degradation of shorebird staging sites in the Yellow Sea (Murray et al. 2015) –most notably the rapid loss of intertidal habitats (Murray et al. 2014), threatens the populations of many shorebird species (Melville et al. 2016a, Piersma et al. 2016, Studds et al. 2017). One of them is the Bar-tailed Godwit (*Limosa lapponica*). The *baueri* subspecies, which breeds in Alaska and spends the non-breeding season mainly in New Zealand (Battley et al. 2012), is listed as ‘At risk – Declining ’ under the New Zealand government (Robertson et al. 2016), and as ‘Vulnerable’ under the Environment Protection and Biodiversity Conservation Act 1999 of the Australian government (Australian Government 2019). The *menzbieri* subspecies, which breeds in the Arctic zone of eastern Russia (northern Yakutia and the Chaun Gulf, northwest Chukotka) and spends the nonbreeding season mainly in Australia (Wilson et al. 2007, Battley et al. 2012), is listed as ‘Critically Endangered’ (Australian Government 2019).

A third subspecies in this flyway, *L. l. anadyrensis*, is described by Tomkovich (2010) who compared morphological characteristics of museum specimens of breeding birds collected from the Anadyr River basin, Chukotka, Russia with *menzbieri* and *baueri* specimens from more westerly (Yakutia-Chaun) and more easterly (Alaska) breeding areas respectively. Although the Anadyr birds differ significantly from *menzbieri* and *baueri* in several size and plumage characteristics, the ranges of these characteristics still overlap with *menzbieri* and *baueri*. Therefore, outside of the breeding areas, *anadyrensis* cannot be identified with certainty neither in the hand nor by observation in the field. To date, nothing is known about its population size and non-breeding distribution.

Satellite tracking has revealed details of the migration routes of the *baueri* and *menzbieri* Bar-tailed Godwits (Battley et al. 2012). Both use the Yellow Sea as their main staging areas during pre-breeding migration (Battley et al. 2012). In post-breeding migration, *baueri* migrates across the Pacific Ocean from Alaska to New Zealand, and this trans-oceanic flight is the longest known non-stop migratory flight of any shorebird (Gill et al. 2009). In contrast, post-breeding *menzbieri* first migrate northwards from breeding areas in eastern Russia to stage on the New Siberian Islands (76.3°N, 140.4°E) before migrating southwards to stage in the Yellow Sea (Battley et al. 2012). The double reliance on the Yellow Sea of *menzbieri* than *baueri* has been used to explain their lower annual survival (Conklin et al. 2016) and steeper population decline (Studds et al. 2017). If the *anadyrensis* subspecies uses similar migration routes and staging areas as the *baueri* and *menzbieri*, it might be under similar threats from habitat destruction and deterioration of staging sites in the EAAF.

Among the 24 Bar-tailed Godwits we tracked in this study in 2015–2018 from

Northwest Australia, the main non-breeding area for *menzbieri* (Wilson et al. 2007), two individuals migrated to the Anadyr River basin to breed, i.e. they belonged to the *anadyrensis* subspecies. Here we describe the migration itineraries of these two *anadyrensis* individuals, and compare their itineraries with those of *menzbieri* individuals tracked during the same period. We found that during post-breeding migration, only the *anadyrensis* individuals used staging sites on the coast of the Kamchatka Peninsula, which lead us to examine the only concurrent and available shorebird monitoring data in Kamchatka Peninsula which was at the Khairusova-Belogolovaya estuary. Assuming that the Bar-tailed Godwits staging on the Kamchatka Peninsula consist of only *anadyrensis*, counts there would represent a minimum estimate of the *anadyrensis* population size. Finally, to provide more insight on the non-breeding distribution of *anadyrensis*, we collate the banding and flyway-wide resighting data of the flagged individuals being seen at the Khairusova-Belogolovaya estuary.

Methods

Satellite tracking

Bar-tailed godwits were captured by cannon netting at two non-breeding sites in Northwest Australia: the northern beaches of Roebuck Bay (17.98°S, 122.35°E) and at Eighty Mile Beach (19.40°S, 121.27°E), in October 2014 and 2015 (at Roebuck Bay), and February 2017 (at both sites). Individuals were colour-ringed with unique ring combinations (Piersma et al. 2016), aged based on moult characteristics, and sexed based on bill length and plumage (the sexing was later verified by genetic analysis of blood samples). Adult females older than 3 years were selected for tagging. Solar Argos satellite transmitters of 5 g and 9.5 g (Microwave Telemetry, Maryland, USA) were attached to the birds' backs by leg-loop harnesses made with Teflon ribbon. Satellite tags were programmed to send signals at interval of 60–65 s for a duty cycle of 8 h ON and 25 h OFF. These signals were received by the Argos receiving system via satellites (Collecte Localization Satellites, www.argos-system.org), from which a bird's position was subsequently calculated. We kept all standard Argos locations (i.e. the location classes 3, 2, and 1) and removed implausible auxiliary locations (i.e. classes 0, A, B and Z) by applying the Hybrid Douglas filter (Douglas et al. 2012). The filtering parameters were set at 120 km/h for the maximum sustainable rate of movement and 10 km for the minimum redundant distance. To get a better estimate of the Argos locations based on the error ellipses provided, the data were fitted with a continuous-time random walk state-space model with the 'foieGras' R package (Jonsen et al. 2020). To improve model performance, before fitting the model we filtered out points within 5 mins of one another. For standard locations we retained the point with higher-accuracy location class; and if all points within the 5 mins were auxiliary locations, we retained the point closest to a previous and a subsequent location. The following analyses concerning route and timing were conducted with the fitted values from the model.

Both *anadyrensis* individuals were tagged in February 2017, one in Roebuck Bay and one at Eighty Mile Beach. For the *menzbieri* Bar-tailed Godwits in 2017, no significant difference was found between birds tagged at different wintering locations (Roebuck Bay or Eighty Mile Beach) in timing of departure and arrival at Northwest Australia (departure: $t_9 = -0.214$, $P = 0.835$; arrival: $t_8 = 0.018$, $P = 0.986$). Moreover, no observable difference in migration route and distribution of stopover sites was found between birds tagged at the two locations. Therefore, we did not distinguish tagging locations of birds in the following analyses. As the notable differences in migration behavior between *menzbieri* and *anadyrensis* individuals occurred during the post-breeding period, we included individuals in our analysis that were tracked at least until they reached the Yellow Sea during post-breeding ($n = 24$).

For analyses concerning the migration routes, since individuals tend to take the same route in successive years (Y.-C. Chan et al. unpubl. data), we used only the first migration track of each individual in our analyses. Stopping sites were extracted by first clustering consecutive points of under 5 km/h and then grouping all clusters within 20 km of each other. Total migration distances were estimated as the sum of all flight distances (distance of all consecutive points within each flight segment, i.e. from the last point of a site to the first point of the next site) plus distances between first and last point recorded in each site. Since birds were assumed to fly along the shortest great-circle path from one point to the next, the calculated distances are likely to be an underestimation of the actual distances flown. One *menzbieri* individual made a U-turn after flying > 1,580 km during its first attempt migrating southward from the New Siberian Islands. Since this sort of U-turn is rarely observed, the travel distance incurred from the U-turn was excluded from the calculations of post-breeding migration distances.

Since the two *anadyrensis* birds were tracked first in 2017, to prevent potential confounding inter-annual differences, migration timing of these two birds are compared with only that of *menzbieri* birds tracked in 2017 ($n = 11$ for pre-breeding and $n = 10$ for post-breeding migration). Arrival time at each site was estimated by extrapolation following Chan et al. (2019b), using speed of the flight before the site, or in the case of no such data, using median flight speed of all flights recorded within similar latitudes (in intervals of 10°). Departure times were estimated in the same way. All arrival and departure times from a region (e.g. the Yellow Sea) were defined as the time arriving (departing) the first site within the region. The staging duration in a region was the sum of stopping duration at all the sites within the region, excluding time used to fly between these sites.

Counts and resightings at Khairusova-Belogolovaya estuary

We conducted a total of 84 counts of Bar-tailed Godwits at the Khairusova-Belogolovaya estuary, western coast of Kamchatka peninsula (57.1°N, 156.7°E), June–September 2015–2019. Counts were conducted every 3 days, at roosts during high tides or during incoming tides when birds moved from their foraging areas to their roosts. A total of 2–5 observers used 20–60x spotting scopes and 10x40 binoculars to survey an area of approximately 45 km^2. Since birds are passing through the estuary in these months, the numbers represent the minimum number of Bar-tailed Godwits using the site.

Resighting of flagged birds was also carried out at the Khairusova-Belogolovaya estuary in 2016–2019, and these resighting data allow us to gain more insight into the non-breeding distribution of *anadyrensis* godwits. The banding location of each resighted bird was deduced from its flag colour combination. For birds marked individually by engraved flags or colour ring combinations, flyway-wide resighting records and additional details on banding locations were obtained from the banding coordinator of the corresponding banding schemes.

Results

Migration route

Pre-breeding migration

The northward route of *anadyrensis* from wintering sites to the Yellow Sea largely overlapped with *menzbieri* individuals, but one *anadyrensis* took a route more easterly than the rest towards the Yellow Sea (Fig. 3.1A). From the Yellow Sea to the breeding grounds, *anadyrensis* took a north-easterly route towards their breeding sites, on the eastern edge of the routes taken by *menzbieri* (Fig. 3.1A). During the entire pre-breeding migration, *anadyrensis* birds staged at the Dongtai coast of southern Jiangsu Province, China (32.6–33.0°N, 120.9–121.3°E, Fig. 3.1A) within the Yellow Sea, where one individual mainly occurred at the Tiaozini mudflats next to the mainland, and another at the offshore Gaoni and Dongsha Shoals. This stretch of coastline was also used by 10 of the 22 *menzbieri* individuals. While all the *menzbieri* individuals stopped at the Yellow Sea coast, 19 of the 22 also made stops of more than one day in other regions. Before reaching the Yellow Sea, 15 (68%) stopped along the coasts of Southeast Asia and South China; and after leaving the Yellow Sea, 18 (82%) stopped along the coastline or inland tundra of Russia before arriving at the breeding sites. The overall distances covered by the two *anadyrensis* during pre-breeding migration were 11,247 and 11,255 km, falling within the range of 10,179-11,941 km (mean ± SD, 10,972 ± 403 km) of the 22 *menzbieri* individuals.

Breeding

During breeding season, the two *anadyrensis* individuals stayed in the Anadyr River lowlands, 30–100 km west of the presumed breeding range (Lappo et al. 2012, Fig. 3.2A) and about 300 km southeast of the Chuan Gulf (68.3°N, 172.1°E), the nearest breeding area of *menzbieri* where two other tracked individuals stayed. One *anadyrensis* individual was on a mountain slope with stream runoffs at an elevation of 155 m, and the other in a wetland in a valley at an elevation of 46 m (Fig. 3.2B).

POST-BREEDING MIGRATION

After leaving their breeding sites, the two *anadyrensis* individuals migrated south-westward to stage at the coast of the Kamchatka peninsula and on Sahkalin Island in the Sea of Okhotsk (Fig. 3.3), and then staged again at the Dongtai coast of the Yellow Sea. This contrasts with the other 22 *menzbieri*, which after breeding migrated northwards to stage in the New Siberian Islands, and then travelled south towards the Yellow Sea (Fig. 3.1

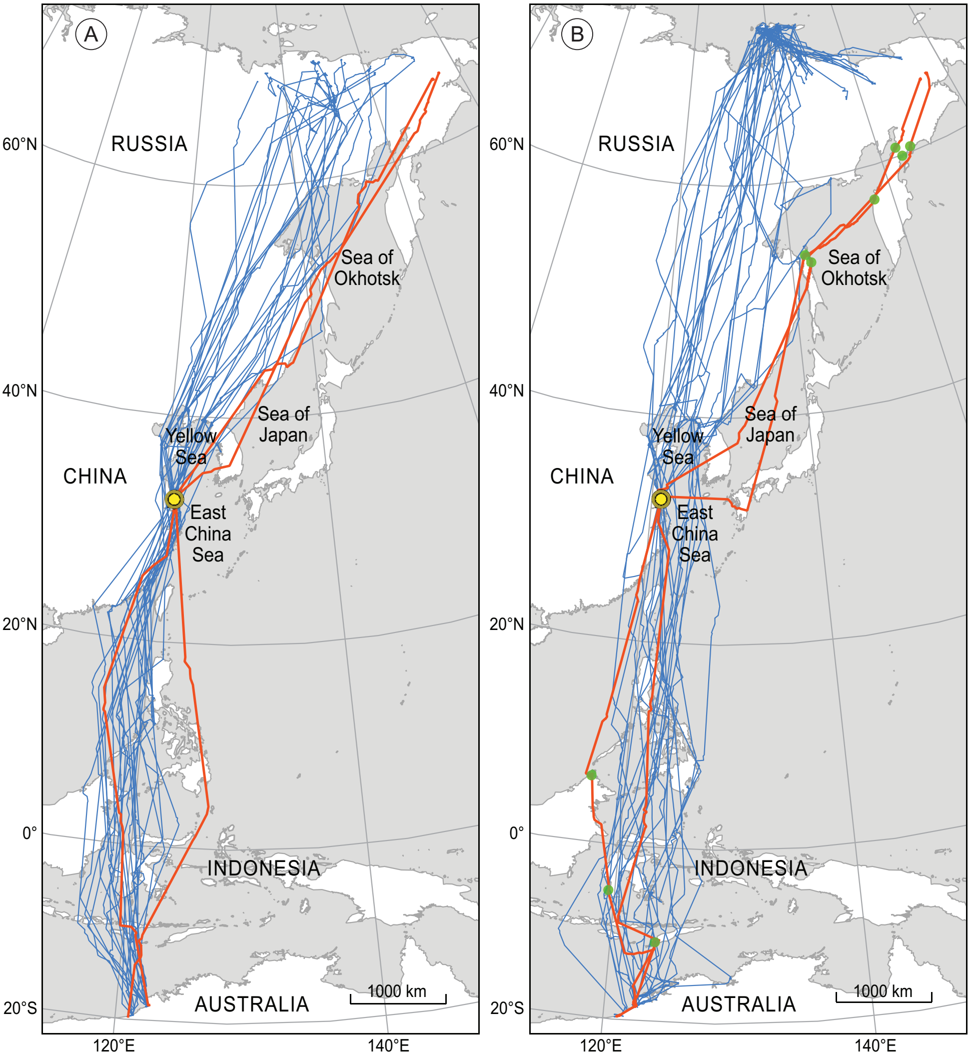

Figure 3.1. Pre-breeding (**A**) and post-breeding (**B**) migration tracks of Bar-tailed Godwits *Limosa lapponica anadyrensis* (orange, *n* = 2) and L. l. menzbieri (blue, *n* = 22) in 2015–2018. The satellite tags were deployed in Northwest Australia. Yellow dots represent the staging area of *L. l. anadyrensis* in the Yellow Sea, the Dongtai coast in southern Jiangsu, China. Green dots represent other stopping sites of *L. l. anadyrensis*.

and 3.4). Along the way from the New Siberian Islands to the Yellow Sea, a small proportion of *menzbieri* individuals also stopped at the western part of the Sea of Okhotsk (for 2015–2018, 7 out of 22, Fig. 3.3; for 2017 only, 1 of the 10, Fig. 3.4). In the Sea of Okhotsk, there was a clear gradient of west to east of stopovers of *menzbieri* and *anadyrensis* (Fig. 3.3). Along the Yellow Sea coast, *menzbieri* staged in a range of sites from 32.2°N to 40.9°N.

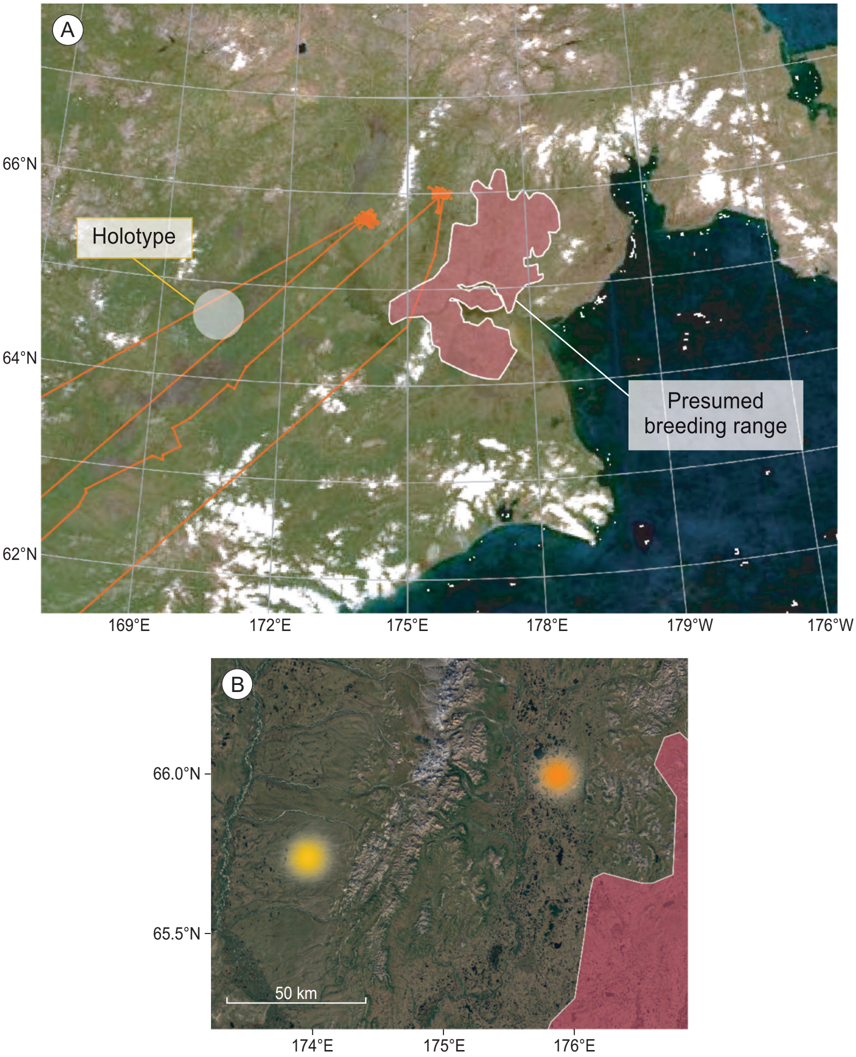

Figure 3.2. (**A**) Tracks of the two *Limosa lapponica anadyrensis* Bar-tailed Godwits in relation to the presumed breeding range of *anadyrensis* (Lappo et al. 2012), and the approximate location where the holotype was collected, around Markovo, the middle Anadyr River (64.7°N, 170.4°E, Tomkovich 2010). (**B**) Enlarged map of locations of the two Bar-tailed Godwits present on the Anadyr River lowlands during breeding (from this study).

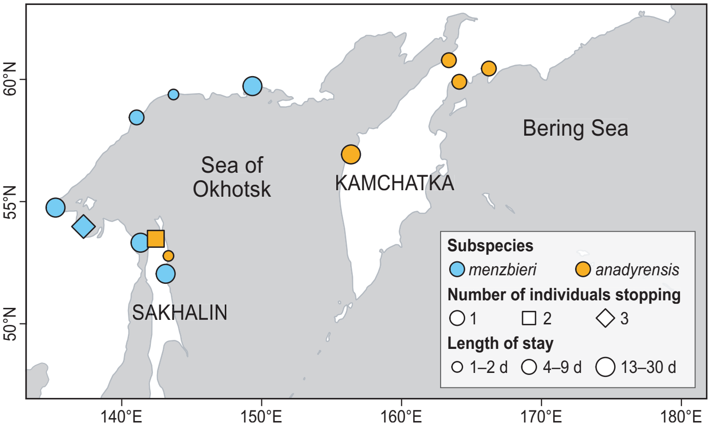

Figure 3.3. Post-breeding stopping sites at the Sea of Okhotsk and the eastern coast of Kamchatka of tracked Bar-tailed Godwits (7 *Limosa lapponica menzbieri* and 2 *L. l. anadyrensis* individuals) in 2015–2018.

After staging in the Yellow Sea, the two *anadyrensis* staged on the coast near Kupang, Timor island, Indonesia (10.2°S, 123.6°E) and then flew directly to Northwest Australia. The individual that had spent the previous non-breeding season on Eighty Mile Beach stopped briefly for 4 days in Roebuck Bay before continuing 190 km southwest to return to Eighty Mile Beach. Individual *menzbieri* varied in stopping strategies: 10 flew directly from the Yellow Sea to the coast of Australia, while seven stopped *en route* on the coasts of southern China ($n = 1$) and Southeast Asia ($n = 6$). Like the one *anadyrensis*, 10 of the 17 individuals first stopped north and east of their final non-breeding destination, along the coast of Australia's Northern Territory or the Kimberley region of Northwest Australia.

The overall distances covered during post-breeding migration by *anadyrensis* were 11,710 and 12,367 km; at the lower end of the distances of 11,569–14,032 km (mean ± *SD*, 12,443 ± 646 km, $n = 17$) by the *menzbieri* individuals. For *anadyrensis*, the migration distances of post-breeding migrations were longer than pre-breeding migrations by 455 and 1,120 km; for *menzbieri* the post-breeding route was considerably longer than the pre-breeding route by 1,471 km (95% CI: 1064, 1878, paired *t*-test: $t_{1\ 6} = 7.67$, $P < 0.001$).

Migration timing

PRE-BREEDING MIGRATION

One of the two *anadyrensis* individuals was the first among the 2017-tracked godwits to depart Northwest Australia on 30 March 2017 (the *menzbieri* godwits departed on average on 8 April ± 5.4 days, $n = 11$, Fig. 3.4). Since it did not stop *en route*, it was also the first to reach the Yellow Sea on 3 April. The other *anadyrensis* individual departed on 10 April and also flew nonstop to reach the Yellow Sea on 15 April. The time period that the *anadyrensis* were in the Yellow Sea during pre-breeding migration largely overlapped with that of *menzbieri*. The two *anadyrensis* godwits departed the Yellow Sea on 21 and 25 May, which is similar in timing to the *menzbieri* birds (22 May ± 3.4 d, $n = 11$).

The total staging durations over the entire pre-breeding migration are similar between *anadyrensis* (40 and 48 d) and *menzbieri* (47.0 ± 5.7 d, *n* = 11). The Yellow Sea is where both subspecies spent the longest time staging (100% of the total staging duration for *anadyrensis* and 73% for *menzbieri*).

BREEDING

The two *anadyrensis* individuals arrived on 24 and 28 May at their breeding sites, earlier than that of the *menzbieri* godwits (3 June ± 7.5 d, *n* = 11, Fig. 3.4). They remained at their breeding sites for 59 and 65 d which was longer than that for *menzbieri* (10–53 d, median = 22 d, *n* = 11). Consequently, the *anadyrensis* birds left their breeding sites (22 July and 1 August) much later than that of the *menzbieri* (27 June ± 7.0 d).

POST-BREEDING MIGRATION

Over the entire post-breeding migration, the two *anadyrensis* spent 70 and 78 d staging, which falls within the range of the 40–125 d of the *menzbieri* (mean ± *SD* = 77 ± 25 d, *n* = 10, Fig. 3.4). While the *anadyrensis* godwits divided their time among the Sea of Okhotsk (24 and 39 days), the Yellow Sea (14 and 19 days) and Southeast Asia (21 and 24 days), the *menzbieri* godwits spent the majority of their time in the Yellow Sea (41.6 ± 8.2 d, 58% of total staging durations, *n* = 10). The staging periods of *anadyrensis* individuals in the Yellow Sea (24 August to 12 September; 14 to 28 September) were considerably later than that of the tracked *menzbieri* individuals (28 July ± 12.7 d to 3 September ± 8.7 d). When they reached Northwest Australia on 10 and 29 October, all *menzbieri* godwits had already arrived there (mean arrival date = 13 September, range = 30 August–10 October, Fig. 3.4).

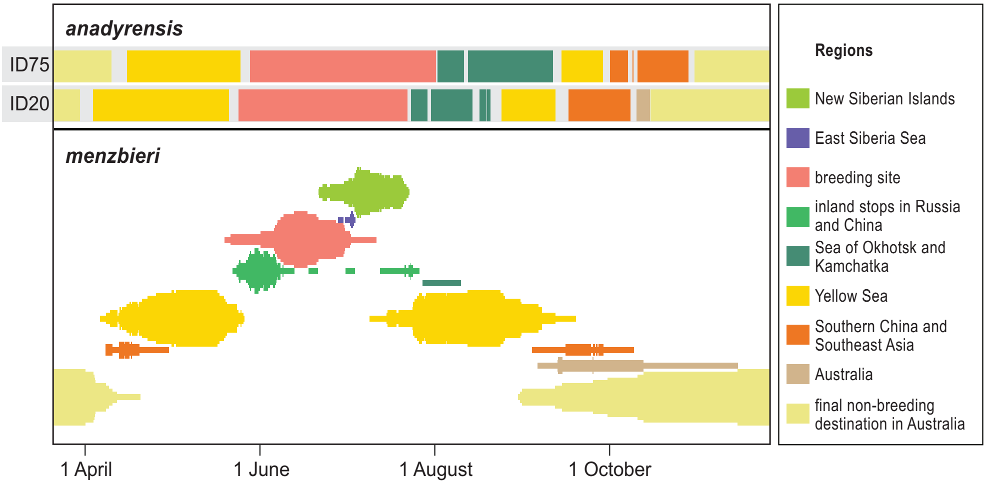

Figure 3.4. Migration timing of the two *Limosa lapponica anadyrensis* Bar-tailed Godwits in 2017, and that of *L. l. menzbieri* (*n* = 10 of which the complete migration was tracked) in 2017. Colour show the time spent stopping at regions along the EAAF. For menzbieri, height of box corresponds to the number of individuals. Regions are ordered by latitudes.

Counts and resightings at Khairusova-Belogolovaya estuary

In 2015–2019, Bar-tailed Godwits were already present at the Khairusova-Belogolovaya estuary when the surveys commenced (the earliest starting date being 25 June 2018, while in some years the surveys only started in July). The peak of migration occurred at the beginning of August, with more than 2,500 Bar-tailed Godwits recorded in all years. The highest count was 4,500 Bar-tailed Godwits on 5 August 2018. Counts remained higher than 1,000 until the end of the survey period, the latest being 7 September in 2015.

A total of 12 individually-banded Bar-tailed Godwits were observed at the Khairusova-Belogolovaya estuary in 2016–2019. Eleven of these birds (six females and five males) were banded in Northwest Australia (eight in Roebuck Bay and three in Eighty Mile Beach) and one in Darwin, Northern Territory (Fig. 3.5). Three of these individuals were also resighted at Zhuanghe, Liaoning Province, China (39.5°N, 122.6°E), Dongtai,

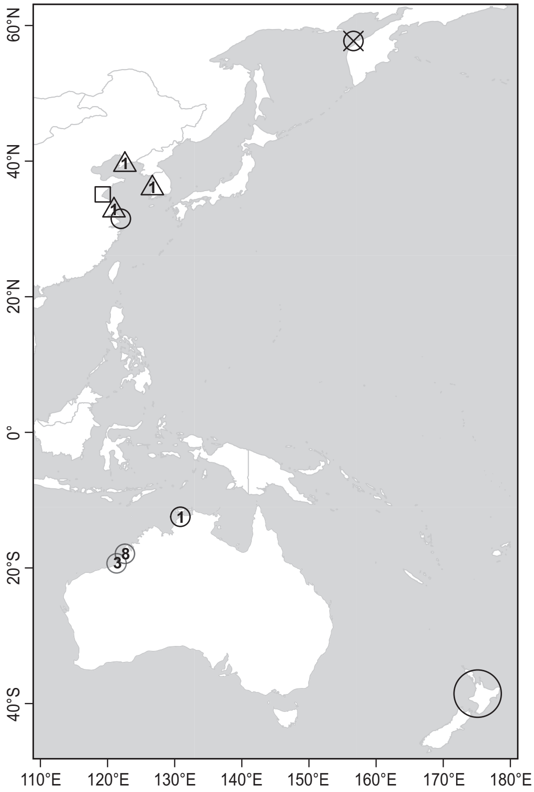

Figure 3.5. Banding locations (circles) of the Bar-tailed Godwits that were resighted in July-August 2016–2019 at the Khairusova-Belogolovaya estuary, Kamchatka, Russia (circle with a cross). Numbers in circles indicate number of individuals observed; plain-coloured flags were used at one site in China and at New Zealand and thus number of individuals is not known. Triangles represent other locations where those birds banded in Northwest Australia were resighted. Square represents the resighting location of an individual banded at the Khairusova-Belogolovaya estuary.

Jiangsu Province, China (32.8°N, 121.0°E) and Geum Gang estuary, South Korea (36.0°N, 126.7°E). Moreover, we recorded Bar-tailed Godwits with plain color flags (from which individuals cannot be identified) that had been banded in New Zealand and Chongming Dongtan, China (31.5°N, 121.9°E). In addition, one bird banded at the Khairusova-Belogolovaya estuary was seen at Xiuzhenhe estuary, Lianyungang, China (35.1°N, 119.3°E) on 20 August 2020.

Discussion

In this contribution, we have described the first complete migrations of Bar-tailed Godwits of the enigmatic *anadyrensis* subspecies. We highlighted the uniqueness of migration patterns of the *anadyrensis* subspecies by contrasting them with that of the *menzbieri* subspecies tagged at the same non-breeding location. During pre-breeding migration, birds of the two subspecies shared similar routes and showed similar migration timing, and both used the Yellow Sea as the main staging area. One key difference is that *anadyrensis* made only one stop in the Yellow Sea in the entire migration from Northwest Australia to the breeding area, while for *menzbieri*, some stopped at sites in Southeast Asia and southern China before reaching the Yellow Sea, and the majority of *menzbieri* individuals used inland sites during the migration leg between the Yellow Sea and breeding grounds. The function of these inland stops for *menzbieri* is unclear – it could be for fuelling up, or for waiting for better weather conditions or snowmelt (so that breeding habitats become available). After breeding, the *anadyrensis* individuals staged in the Sea of Okhotsk for 3.5 and 5.5 weeks, instead of staging on the New Siberian Islands (found for all *menzbieri* in this study, confirming the findings of Battley et al. 2012). Another key difference during post-breeding migration was that *anadyrensis* stopped in the Yellow Sea for a much shorter period than *menzbieri*. However, we could not tell if this difference is subspecies-specific or just a result of the much longer stay at the breeding sites of the two *anadyrensis*.

Our results enable a comparison of migration patterns of all the three subspecies of EAAF Bar-tailed Godwits, an extension of the two-species comparison by Battley et al. (2012). All three subspecies rely strongly on the Yellow Sea during pre-breeding migration (for *anadyrensis* and *menzbieri*, see Results; for *baueri*, see Battley et al. 2012). The migration patterns of the three subspecies differ the most during post-breeding migration. In migrating the >10,000 km from the Arctic breeding sites to the southern hemisphere non-breeding destinations, the three subspecies clearly use different strategies. After breeding, *anadyrensis* mainly staged at coastal estuaries (at the Sea of Okhotsk), and in this respect resembles *baueri* (Yukon-Kuskokwim Delta and Kuskokwim Shoals in Alaska, Battley et al. 2012). It is very different from *menzbieri*, which staged on the tundra at the New Siberian Islands. *Anadyrensis* used stopovers in East Asia as did *menzbieri*, while *baueri* bypassed East Asia entirely, flying from Alaska to New Zealand directly crossing the Pacific Ocean (Battley et al. 2012). In terms of reliance on the Yellow

Sea, they vary on a scale from a high reliance (*menzbieri*), little reliance (*anadyrensis*) to no reliance (*baueri*). This puts *anadyrensis* somewhere between the other two subspecies in terms of migration strategy. Since reliance on the Yellow Sea is a major determinant of annual survival and population trends for shorebirds in the EAAF (Conklin et al. 2016, Studds et al. 2017), we expect the demographic statistics of *anadyrensis* to also fall between those of the other two subspecies.

Since we found that only *anadyrensis*, but no *menzbieri*, used sites in the Kamchatka peninsula during post-breeding migration (Fig. 3.3), we can infer that the Bar-tailed Godwits staging at the Khairusova-Belogolovaya estuary comprised only *anadyrensis*. Flyway-wide resighting data of godwits being seen and banded there give further insight on the migration paths and non-breeding distribution of *anadyrensis*. The resighting data show that, in the Yellow Sea, *anadyrensis* also used other sites in China and South Korea beside the Dongtai coast in Jiangsu (Fig. 3.5). Recent (this study) and past records of godwits of New Zealand origin being seen in southwest Kamchatka (Riegen 1999, Schuckard et al. 2006) show that New Zealand is a non-breeding destination of *anadyrensis*. Putting together the resightings and satellite tracking data, non-breeding destinations of *anadyrensis* include Northwest Australia, Northern Territory of Australia, and New Zealand (Fig. 3.5).

The counts at Khairusova-Belogolovaya estuary show that at least 4,500 Bar-tailed Godwits used this staging area during post-breeding migration. The actual number of birds using the Khairusova-Belogolovaya estuary may be higher, as some birds could have departed earlier or arrived later than the date in which this count was conducted. Also, this site is just one of the few that *anadyrensis* used during post-breeding migration around the Sea of Okhotsk (Fig. 3.3). Moreover, given that 2 out of the 24 satellite-tracked birds from Northwest Australia (8.3%) are *anadyrensis*, we can deduce that among the 146,000 Bar-tailed Godwits counted in Northwest Australia (Rogers et al. 2011, Conklin et al. 2014), at least several thousands are *anadyrensis*. Since *anadyrensis* also occurs in other non-breeding destinations, we suggest that the population of *anadyrensis* would be around 10,000 birds.

Further research and monitoring on the *anadyrensis* population would galvanize the conservation of this subspecies and its unique migration route. Our study has provided knowledge to achieve that. First, we established that a small proportion of *anadyrensis* Bar-tailed Godwits (2 out of 24 in this case) spent their non-breeding season in northwest Australia. Since *anadyrensis* is indistinguishable from the other two subspecies neither in the hand nor by observation in the field, in addition to satellite tracking, the population trends and stopover ecology of *anadyrensis* could be monitored by developing genetic markers to distinguish the two subspecies and assaying the existing blood samples of marked individuals accumulated by Global Flyway Network. Second, we found that Bar-tailed Godwits staging at the Kamchatka Peninsula during post-breeding migration are likely to be mainly of the *anadyrensis* subspecies. Counts conducted there can be used to monitor the population, and banding of Godwits at the Khairusova-Belogolovaya estuary can be a targeted effort of generating an adequate sample size of individually-marked birds for monitoring survival rates by mark-resighting methods (Piersma et al. 2016). Third, during pre-breeding migration, the two tracked *anadyrensis* individuals only staged at the Dongtai coast of Jiangsu, China in the Yellow Sea. And, they returned to stage there during post-breeding migration. Although with only two individuals we cannot establish the proportion of *anadyrensis* godwits that staged there, the seemingly high site fidelity and long staging durations imply the high importance of the Dongtai coast to *anadyrensis* Bar-tailed Godwits. A portion of this site (part of the offshore Dongsha Shoals) belongs to the recently listed World Heritage site of Yancheng coastline (UNESCO World Heritage Convention 2020), and the reclamation of intertidal flats planned for 2010–2020 on this stretch of coastline (see Piersma et al. 2017 for details) have not occurred. However, the spread of invasive cordgrass (*Spartina alterniflora*) in the upper tidal flats (Peng et al. 2017), which would reduce foraging and roosting opportunities for shorebirds (Mu & Wilcove 2020, Jackson et al. 2021), is an ongoing threat. Other potential threats include the erosion of mudflats next to the seawall and large areas of windfarms being built on the mudflats (L. Zhang & K. Leung pers. comm.). Since the Dongtai coast is apparently important for *anadyrensis* Bar-tailed Godwits, and a high percentage of *menzbieri* also stopped there, it warrants adequate management of shorebird habitats to safeguard the viability of both subspecies.

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CHAPTER 4

When a typical jumper skips: itineraries and staging habitats used by Red Knots *Calidris canutus piersmai* migrating between northwest Australia and the New Siberian Islands

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Abstract

The ecological reasons for variation in avian migration, with some populations migrating across thousands of kilometres between breeding and non-breeding areas with one or few refuelling stops, in contrast with others that stop more often, remain to be pinned down. Red Knots *Calidris canutus* are a textbook example of a shorebird species that makes long migrations with only a few stops. Recognizing that such behaviours are not necessarily species-specific but determined by ecological context, we here provide a description of the migrations of a relatively recently described sub-species (*piersmai*). Based on data from tagging of Red Knots on the terminal non-breeding grounds in northwest Australia with 4.5 g and 2.5 g solar-powered Platform Terminal Transmitters (PTTs) and 1.0 g geolocators, we obtained information on 19 route-records of 17 individuals, resulting in seven complete return migrations. We confirm published evidence that Red Knots of the *piersmai* sub-species migrate from NW Australia and breed on the New Siberian Islands in the Russian Arctic and that they stage along the coasts of southeastern Asia, especially in the northern Yellow Sea in China. Red Knots arrived on the tundra breeding grounds from 8 June onward. Southward departures mainly occurred in the last week of July and the first week of August. We documented six non-stop flights of over ca. 5,000 km (with a maximum of 6,500 km, lasting 6.6 days). Nevertheless, rather than staging at a single location for multiple weeks halfway during migration, *piersmai*-knots made several stops of up to a week. This was especially evident during northward migration, when birds often stopped along the way in southeast Asia and 'hugged' the coast of China, thus flying an additional 1000–1500 km compared with the shortest possible (great circle route) flights between NW Australia and the Yellow Sea. The birds staged longest in areas in northern China, along the shores of Bohai Bay and upper Liaodong Bay, where the bivalve *Potamocorbula laevis*, known as a particularly suitable food for Red Knots, was present. The use of multiple food-rich stopping sites during northward migration by *piersmai* is atypical among sub-species of Red Knots. Although *piersmai* apparently has the benefit of multiple suitable stopping areas along the flyway, it is a subspecies in decline and their mortality away from the NW Australian non-breeding grounds has been elevated.

Introduction

There are good biological reasons for some birds to breed in one part of the planet and spend the rest of the year in another. The published research for these reasons now occupies a few meters of bookshelf, but the field was ably summarized by Newton (2008). For example, long-distance migratory shorebirds that breed during the northern summer in the Arctic combine their reproductive activities on the tundra with long periods at soft-sediment seashores during the northern winter (or austral summer), the terminal non-breeding (or 'wintering') areas being found as far south as the Sub-Antarctic (see generalizations in Piersma 1997, 2003, van de Kam et al. 2004, Conklin et al. 2017).

Coastal shorebirds show a range of feeding specializations (Prater 1981). Among them, the Red Knots *Calidris canutus* possess a sensory system for the remote detection of hard objects in wet soft sediments (Piersma et al. 1998, de Fouw et al. 2016). Red Knots make a living by probing for hard-shelled prey (usually bivalves) in intertidal soft-sediment flats (e.g. van Gils et al. 2006b, Quaintenne et al. 2010), which is combined with visual hunting for surface-living arthropods on the tundra (Martin & Piersma 2009). Away from the tundra breeding grounds, using sensory attributes and prey types tolerant to foraging in dense flocks, they are highly social and often occur in large flocks (Piersma et al. 1993a, Bijleveld et al. 2016, Oudman et al. 2018); this is also part of a strategy to avoid depredation by falcons (van den Hout et al. 2010). As suitable feeding habitats are rare and widely dispersed across the globe (e.g. van Gils et al. 2005b), the long migratory flights of Red Knots (Piersma & Davidson 1992, Piersma et al. 2005, Shamoun-Baranes et al. 2010) may be considered a consequence of their ecological specialization.

Despite extensive knowledge of geographic variation and migratory connectivity of Red Knot populations worldwide (Piersma & Davison 1992, Tomkovich 1992), a new subspecies of Red Knot was described as recently as 2001 (*C. c. piersmai*, Tomkovich 2001). Evidence for their migration route included five re-sightings between November 1995 and September 1996 in NW Australia of a single Red Knot that was individually colour-marked on 10 July 1994 at the Faddeyevski Island, New Siberian Islands group, Russia (Lindström et al. 1999). Also, biometric data and plumage observations of Red Knots in Roebuck Bay, NW Australia (e.g. Verhoeven et al. 2016), were all consistent with the idea that many *piersmai* spend the austral summer in NW Australia. Some appear to migrate as far south as New Zealand (Tomkovich & Riegen 2000, Rogers et al. 2010).

The observation that Red Knots departed on northward migration from NW Australia late into May, led Battley et al. (2005) to predict: (1) the use of high-quality shellfish food at potential staging areas along the Yellow Sea, (2) a window of about three weeks of potential fuelling time in Asia, and (3) arrivals on the New Siberian Island breeding grounds in early June. The prediction of high food quality and abundance in the Yellow Sea was confirmed by Yang et al. (2013, 2016) for Red Knots staging in Luannan County, Hebei Province, Bohai Sea (see also Rogers et al. 2010, Yang et al. 2011, Hua et al. 2013, and see yearly field reports at http://globalflywaynetwork.com.au/bohai-bay/reports-and-papers/). However, a capture-resight analysis of individually marked Red Knots showed that large numbers stage at this site for just 5–9 days (Lok et al. 2019), implying that there are other stopping sites *en route*. Does this mean that, in contrast to what Red Knots have been shown to do elsewhere in the world (Piersma et al. 2005, Piersma 2007), in the East Asian-Australasian Flyway they do not necessarily 'long-jump', i.e. making a single refuelling stop during the migration from wintering to breeding areas (Piersma 1987)? Do they make multiple stops as in the 'skipper' strategy, and if so, where are the additional stopping areas located? Can such areas be characterized in terms of food availability?

To answer these questions, we applied an approach that combined tracking of individual red knots during migration with *in situ* sampling of benthic prey at potential stopping sites. In 2011-2019 we tracked the migratory routines of knots caught at Roebuck Bay and 80 Mile Beach, NW Australia using three different tracking devices. Complementary to the 2018 tracking effort, in March-May 2018 we conducted surveys at several potential stopping sites for shorebirds and sampled macro-benthic bird food along the coast of China (Chan et al. 2019a,b, Peng et al. in press). Here we provide a detailed description of the seasonal migration of Red Knots from NW Australia, assessing the timing of migration, the lengths of non-stop flights, the locations and numbers of stopping sites used, as well as examining the possible food resources at these coastal stopping sites during northward and southward migration. With the knowledge that a small bivalve *Potamocorbula laevis* is the key high-quality prey of Red Knots at a staging area in China (Yang et al. 2013), we focused on comparing densities of *P. laevis* between sites that the tracked Red Knots did and did not visit along the Chinese coast.

Methods

Satellite tracking

This study is part of an international collaborative long-term effort by Global Flyway Network and associated institutions to study the demography and migration ecology of several representative shorebird species along the East Asian-Australasian Flyway (e.g. Rogers et al. 2010, Piersma et al. 2016, Lok et al. 2019, Chan et al. 2019b). Red Knots were captured using cannon-nets at the northern beaches of Roebuck Bay, Broome (17.98°S, 122.30°E) and at Eighty-Mile Beach (19.34°S, 121.41°E), both located in NW Australia (see Table 4.S1 for an overview of all tracking efforts included in this study). After capture, birds were measured and weighed, and a small blood sample was taken for molecular sexing (van der Velde et al. 2017). Birds were aged based on plumage characteristics (see Rogers et al. 1990, Higgins & Davies 1996 for guidance) and adults (birds older than two years) were selected for tagging. Due to incomplete breeding plumages at the time of year the birds were captured, we were unable to confirm sub-species identity (i.e. we should have been picking mostly *piersmai*, which outnumbers *rogersi* in NW Australia; see Rogers et al. 2010, Verhoeven et al. 2016). All birds were marked with an ABBBS metal band and a unique colour band combination allowing individual identification in the field. The tagging work was carried out under Regulation 17 permits SF 010074, SF010547 and 01-000057-2 issued by the West Australian Department of Biodiversity, Conservation and Attractions.

In April 2011 we deployed 4.5 g solar-powered PTTs (Microwave Telemetry, USA) on 30 Red Knots by gluing the transmitters onto the back of the birds with superglue (Warnock & Warnock 1993). Despite using methods that were previously successfully used in temperate climates on the same species, on the basis of field observations of colour-ringed birds that were seen without tags, we conclude that most birds shed their PTTs before migration. Here we report on the migratory movements of the remaining three birds (see Table 4.S1 for an overview). We faced a similar problem in March 2012 when we tagged another 15 birds using the same method, with all transmitters technically failing before northward migration started. Consequently, the individuals tagged in 2012 were excluded from the analyses presented here. The 4.5 g PTTs were on a duty cycle 10 h on for transmitting and 48 h off.

Before the start of migration in 2017 we tagged 21 Red Knots ($n = 2$ in October 2016 and $n = 19$ in February-March 2017), and in February-March 2018 we tagged 18 Red Knots, with 2.5 g solar-powered Argos 3 PTTs (Microwave Telemetry, USA). The 2.5 g PTTs were deployed using a body harness (Chan et al. 2016) made of nylon coated stainless steel jewellery wire (provided by Microwave Telemetry; in 2017) or 1 mm thick Flyneema (a smoothly covered fishing line with a strong Dyneema ® core; de Lijnenspecialist, Amsterdam, The Netherlands; in 2018). After transmitter deployment, to allow them to acclimatize to the transmitter and harness, the birds were kept in cages indoors and observed for a few hours up to 48 hours. We then released them on the beach near their capture sites. All but three of the deployed PTTs stopped before departure from NW Australia in 2017 due to what we think was loss of the PTTs due to corrosion and breakage of the harness. Here we report on movements of the remaining three Red Knots for which we collected data on migration in 2017. This problem of harness breakage was resolved when 18 PTTs were deployed in February-March 2018. Two of these PTTs never transmitted locations, eight provided locations from the area of release but stopped transmitting before departure (four of these birds were later resighted in NW Australia or China), one transmitter stopped transmitting at the Chinese coast during northward migration and one operated too intermittently for a complete reconstruction of the carrier's itinerary. Analyses presented in this paper are based on the migrations of six birds captured and tracked in 2018, one of which gave us a repeat track in 2019 (Table 4.S1).

The 2.5 g PTTs were not on a duty cycle, but rather transmitted whenever sufficiently charged. All PTTs (when on) transmitted signals every 60 s to the Argos satellite system. When signals from the PTTs were received by a satellite, the perceived Doppler shift in signal frequency of successive transmissions was used to estimate the position of the transmitter (CLS 2016). We used the hybrid filter option of the Douglas-Argos Filter set for a high rate of speed (130 kph) and a relaxed minimum redundant distance (10 km) suitable for summarizing long-distance flights (Douglas et al. 2012). During filtering, all standard-quality locations (i.e. location classes 3, 2, 1; for details on Argos location classes see CLS 2016) were retained while low-quality locations (i.e., location classes A, 0, B, and Z) were retained only if they passed filter thresholds.

Following Chan et al. (2019b), we refer to the places where birds during migration spent time on the ground as 'stopping sites', with no distinction between 'stopover sites' and 'staging sites (see Warnock 2010 for definitions). To identify potential migratory stops, we first assigned a status of stationary (groundspeed <5 km/h) or moving (>5 km/h) to each filtered location after each bird departed its terminal non-breeding site (Roebuck Bay or Eighty Mile Beach). We then defined stops as a cluster of at least three stationary locations within 20 km of each other, with the first and last recorded locations at the stopover being at least two hours apart.

Using speed of movement, departure times from a stopping site were extrapolated over the intervening travel distance between the last location at a stop and the next location. Extrapolation used the speed from the last location at the stop to the next non-stationary (in-flight point), or the median of flight points of all flights recorded in the same latitudinal interval and migration direction, whichever was faster. If there was no recorded location in-flight, the migratory flight was assumed to have occurred over the interval between the last point of a stop and the first point of the next stop. Arrival times were extrapolated in the same way over the interval between the first recorded location of a stop and the previous location (in-flight or not). Arrival times in the Yellow Sea area (between latitudes 30.9 and 42.5 °N) and at the New Siberian Islands were defined as the estimated times of arrival at the first stop within these respective regions. Duration of time at stopping sites were calculated as the time between the estimated arrival and departure times. Movements between detected stops were assumed to be carried out non-stop. Flight distances were calculated by summing up intervening distances between locations along the flight.

Geolocation

We deployed a total of 129 geolocators ($n = 36$, Intigeo-W65; Migrate Technology Ltd, Cambridge, UK) in March 2012 and February and June-July 2015 ($n = 93$, mk50773; Biotrack, Lotek Wireless inc. see Table 4.S1 for an overview). Geolocators were attached to a Darvic PVC leg-flag using Kevlar thread reinforced with Araldite resin cement (after Lisovski et al. 2016a) attached to a leg of the Red Knots. Combined mass of flag and geolocator was ca. 1 g.

Of the 36 geolocators attached in early 2012, two were retrieved in November 2013, one of these only contained reliable migratory information for 2012, the other one yielded information for two years of tracking (for 2012 and 2013). Another tag was retrieved in February 2015 but did not contain reliable information. Of the 93 geolocators attached in February 2015, one was retrieved in September 2015 and another one was retrieved in February 2020. Only the former yielded reliable information of the return migration in 2015 (See Table 4.S1 for an overview).

We analysed data with the template fit approach (Rakhimberdiev et al. 2015b) in the R package *FlightR* (Rakhimberdiev et al. 2017). For calibration, we used average coordinates of individual re-sightings during their non-breeding season in NW Australia (from early-September to mid-April). The stops were defined by the probability cut off value of 0.1. The geolocation tracks were consistent with the geographic description of tracks obtained by the PTTs, However, due to the coarse nature of the geolocation data, the representations of geolocation tracks added no novel geographic information when compared to the tracks obtained by the PTTs and are therefore not presented in this study (Rakhimberdiev et al. 2015b, 2016). Due to the constant daylight conditions at the high Arctic breeding grounds of the Red Knots, solar geolocation is unsuitable to position the birds in these areas. Therefore, we only present the migration timing and latitudes of geolocator-tagged birds until a latitude of 42°N, i.e. the northern boundary of the Yellow Sea.

Benthic food sources along coast of China

From early April to late May 2018, we sampled the preferred benthic food of Red Knots, *P. laevis* (Yang et al. 2013), at 18 intertidal flats along the coast of China known to have shorebirds utilizing them during migration (Chan et al. 2019b), extending from Dongliaodao, Guangdong Province, in the far south (20.825°N, 110.384°E) to Panjin, Liaoning Province, in the far north (40.763°N, 121.860°E; see Peng et al. 2021 for further details). At each site, we sampled macro-zoobenthos across gridlines (after Bijleveld et al. 2012). Depending on the local geography, sampling stations were elected to be 50, 125, 250 or 500 m apart to adequately sample the area from the coast to the low water line. A total of 838 sampling stations were visited by foot. At each station, one sediment core with a surface area of 0.019 m^2 was taken to a depth of 20 cm and washed over a 0.5 mm sieve. The sieved samples were frozen and stored before analysis in the laboratory where shellfish were identified to the species level, counted and their maximum shell length measured. In the site Huanghua (38.346°N, 117.746°E), the soft mud made grid sampling by foot impossible. However, it is an important area for commercial harvesting of *P. laevis*, so observations (visual, touching mud surface) were made to estimate the density-level of *P. laevis* there. We examined whether a benthic sampling site was visited by any tracked Red Knot during the northward migration of 2018. A site is defined as visited by a tracked individual when the average coordinates of the individuals' stop is within 10 km of the centre point of a benthic sampling area.

Results

Geography of the migrations

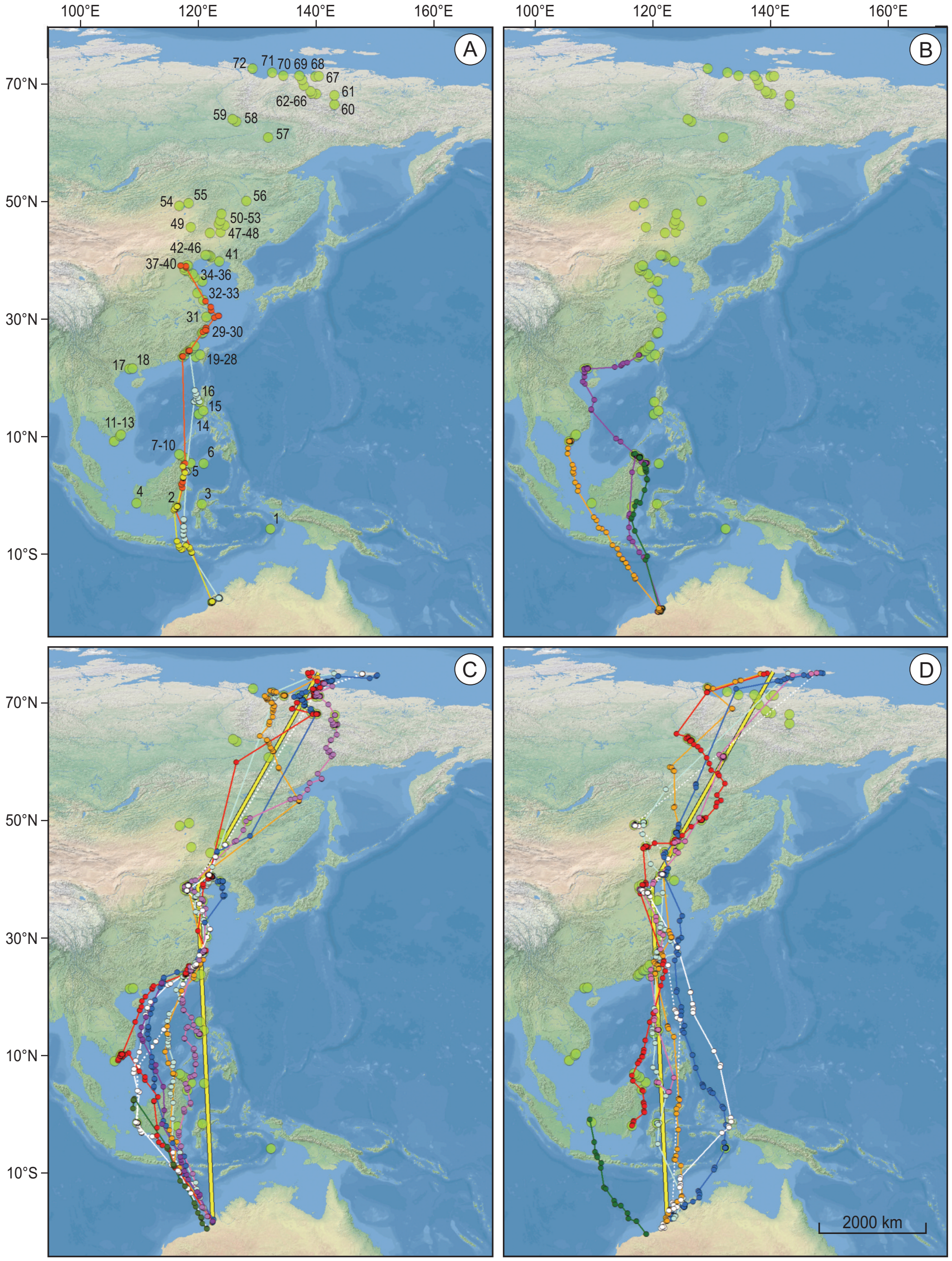
Of the three Red Knots departing from NW Australia in 2011 (Fig. 4.1A), one was last recorded during its first stop in northeast Kalimantan, Indonesia. A second Red Knot also made a stop there and then continued to the Chinese coast, making a landfall on the coast of Fujian province. It then tracked the coastline of China to arrive in Bohai Bay, after which we lost contact. The third Red Knot of 2011, like the previous two, also travelled north across Makassar Strait, i.e. keeping to the east of Kalimantan, made a stop in the Philippines and an onward flight to the Fujian coast, at which point we lost contact.

Of the three Red Knots which we tracked in 2017 (Fig. 4.1B), one bird took a rather north-westerly course on a non-stop flight to the southern coast of Vietnam. After 10 days, while the bird was still at this site, we lost contact. A second bird migrated north over eastern Kalimantan, turning southeast at the northern tip for a stop of two weeks on the Kalimantan coast just southeast of the city of Sandakan, Malaysia (5°50’N, 118°07’E). It then continued migration to make landfall on the western-most coast of China close to the border with Vietnam. It continued east by tracking the Chinese coastline until we lost contact, probably in flight across south Fujian on 21 May. The third bird travelled north across Makassar Strait, i.e. keeping to the east of Kalimantan, and also made a turn when it reached the northern tip of Kalimantan, and then stopped on the coast northwest of Sandakan. We lost contact on 8 May with the bird still at this site.

Of the eight PTTs deployed in 2018 that returned migratory movements, transmission of one PTT stopped during northward migration at the Chinese coast (the bird indicated in purple in Fig. 4.1C). Another bird migrated only as far as western Kalimantan to return to NW Australia from there after the northern summer (the bird indicated in green in Fig. 4.1C & D). The other six made complete migrations to the New Siberian Islands (Table 4.1, Fig. 4.1C & D). In the case of bird carrying transmitter 48950 (coloured white in Fig. 4.1 C & D), in 2018 no signals were received after it left the Yellow Sea on northward migration until August; however, a complete track was obtained during the second season of migration in 2019.

As suggested by the tracks in Fig. 4.1, during the first leg of the northward migration after leaving NW Australia, rather than following the shortest northward flight route (i.e. a route close to a great circle route across Sulawesi to the Yellow Sea as illustrated by the yellow line in Fig. 4.1 C & D), most Red Knots took a longer route by initially flying north-westwards. Then, the birds reached the coast of China between Guangdong and Fujian, rather than in the Shanghai area where they would have arrived if they had flown from NW Australia to the Yellow Sea along a great circle route (Fig. 4.1C). Most birds continued to the Yellow Sea by closely tracking the coastline. This flight behaviour added 1000–1500 km to a great circle distance of 6,500 km between NW Australia and northern Bohai Bay in the Yellow Sea.

All tracks obtained from Red Knots carrying PTTs confirm that during the first leg of migration to the Yellow Sea, Red Knots made one to four stops (Fig. 4.1). Once in the


100°E
120°E
140°E
160°E
70°N
50°N
30°N
10°N
10°S
A
B
C
D
72
71
70
69
68
67
61
62-66
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50-53
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47-48
42-46
41
37-40
34-36
32-33
31
29-30
19-28
17
18
16
15
14
11-13
7-10
6
5
4
2
3
1
2000 km

Yellow Sea, the birds stopped at 1–4 different sites (Fig. 4.1, Table 4.1). During northward migration, the last coastal stopping sites before the trans-continental flight towards the New Siberian Islands were in the northern part of the Yellow Sea, in either the coast of Bohai Bay, Hebei and Tianjin Municipality, or in upper Liaodong Bay, Liaoning (Fig. 4.1). The stops in 2018 of two tagged Red Knots in Luannan County in northern Bohai Bay, China, were confirmed with on-the-ground observations of the colour-ringed birds.

Flying from the Yellow Sea to the New Siberian Islands, all six birds tracked in 2018-2019 made 1–5 stops at inland sites or on the coastal tundra just before crossing the Laptev Strait. On the way back to the Yellow Sea the birds also stopped at continental sites (n = 1–6), and one stopped in the Lena River Estuary (72.57°N, 129.22°E; see Fig. 4.1D). Thus, during the migrations across the thinly populated areas of northern China, Mongolia and eastern Russia, most tracked Red Knots spent some days at freshwater lakes and riverbanks. Birds often used lowland lake systems, but some stops were made at water bodies at altitudes up to 1100 m in mountainous terrain.

During migration from the Yellow Sea to NW Australia, only bird 48950 (Table 1) made a single non-stop flight in both years during which it was tracked, while the other birds made 1–3 stops in Taiwan, the Philippines, Malaysia and/or Indonesia during southward migration. Four of the six satellite-tagged Red Knots of the 2018 cohort demonstrated the ability to non-stop fly distances of approximately 5000 km or more (with a maximum of 6500 km, a continuous 6.6 days of flight; Table 4.1).

Figure 4.1. A summary of all migratory tracks recorded by PTTs in Red Knots marked in NW Australia between 2011-2019. Tracks of the partial northward migrations from NW Australia of three individual Red Knots which were tracked with 4.5 g PTTs in 2011 (**A**); and of three Red Knots tracked with 2.5 g PTTs in 2017 (**B**). The lower two panels present the tracks of the northward migration (**C**) and the southward migration (**D**) of eight individual Red Knots tracked from NW Australia with 2.5 g PTTs in early 2018. Small dots indicate the filtered Argos locations used. The larger green dots represent all red knot stopping sites observed in all years, during northward and southward migration combined. All sites are plotted in all four panels with the numbers in panel 1 corresponding to additional information of the sites in ESM Table 4.S3. These stopping sites were calculated by means of grouping all individual stopping sites (see methods for definition) within a 10 km radius, subsequently mean latitude and longitude of these sites were used for plotting and reported in Table 4.S3. The yellow lines in C & D represent the shortest, great circle, routes between Roebuck Bay in NW Australia and Bohai Bay in Yellow Sea and between Yellow Sea and New Siberian Islands. With respect to the birds marked in early 2018, Table 4.1 presents details on timing, number of stopping sites used, length of nonstop flights and detours. In panel C & D the 'white' individual (48950) was tracked in both 2018 and 2019, as indicated by full and dashed lines, respectively. Otherwise the colours depict the tracks of 48949 in pink, 48937 in red, 48936 in blue, 48905 in orange and 168203 in light blue. Red Knot 48951 (in green; not in Table 4.1) only migrated as far as westernmost Kalimantan, to return from there to NW Australia. For Red Knot 48953 (in purple; not in Table 4.1) transmissions stopped during northward migration at the Chinese coast.

Table 4.1. Timing, number and duration of stops, and maximum nonstop flight lengths of six Red Knots tracked away from NW Australia during February 2018 – December 2019, the tracks are ordered by sex and departure date. For the methods to delineate stops, see text. '–' = missing part of itinerary.

Sattag number	48949[1]	48950[2]	48950-2nd yr	48937[3]	48936	48905[4]	168203
Colour combination of leg bands	Y6LYRB	Y6RBBY	Y6RBBY	Y6RBLL	Y6RYYR	Y6LLBR	Y6LRLB
Sex	M	M	M	M	M	F	F
Release location	Roebuck B	80MB		80MB	80MB	Roebuck B	Roebuck B
Release date	01 March	16 Feb.		16 Feb.	16 Feb.	01 March	01 March
Tracking year	2018	2018	2019	2018	2018	2018	2018
From NW Australia to Yellow Sea							
Date of departure from NW Australia	24 April	4 May	4 May	12 May	24 May	4 May	4 May
Number of stops en route	3	3	3	4	1	1	2
Date of arrival in Yellow Sea	22 May	28 May	23 May	12 June	8 June	15 May	18 May
Number of stops in Yellow Sea	4	3	2	2	2	1	4
Number of days in Yellow Sea	11	14	15	12	15	18	16
From Yellow Sea to New Siberian Islands							
Date of departure from Yellow Sea	2 June	11 June	7 June	23 June	24 June	2 June	3 June
Date of arrival at New Siberian Islands	8 June	?	12 June	27 June	29 June	8 June	8 June
Number of days at New Siberian Islands	54	?	36	33	35	49	53
From New Siberian Islands to Yellow Sea							
Date of departure	3 Aug.	?	18 July	30 July	3 Aug.	27 July	30 July
Date of arrival in Yellow Sea	15 Aug.	signal from 10 Aug.	30 July	18 Aug.	16 Aug.	31 July	8 Aug.
Number of stops in Yellow Sea	2	3	2	2	1	1	1
Number of days in Yellow Sea	22	≥24	29	29	37	25	23
From Yellow Sea to NW Australia							
Date of departure from Yellow Sea	6 Sept.	3 Sept.	28 Aug.	17 Sept.	21 Sept.	27 Aug.	31 Aug.
Number of detected stops en route	3	0	0	1	1	15	3
Date of arrival in NW Australia	–	9 Sept.	3 Sept.	–	26 Oct.6	12 Sept.	3 Oct.
Flight lengths							
Longest nonstop flight during northward migration (km, **days**)	4345, **4.1**	–	3449, **2.2**	3862, **2.6**	5462, **4.9**	5597, **4.0**	4958, **4.0**
Longest nonstop flight during southward migration (km, **days**)	–	–	6548, **6.6**	–	5540, **4.2**	4914, **4.9**	3352, **2.7**

[1] transmissions stopped during southward migration on 6 November during a stopover at Siasi Island, Sula, Philippines.

[2] did not transmit any locations from its departure from the Yellow Sea to its return there in 2018, but gave a nice full track in 2019.

[3] transmission stopped on 16 November during southward migration during a stopover in a bay just southwest of Balikpapan, East Kalimantan, Indonesia.

[4] gave a full track in 2018 [summarized here], and made a return migration to the New Siberian Islands again in 2019, but with poor coverage.

[5] staged in western Taiwan from 28 August to 7 September where it was seen and photographed by C.-Y. Choi.

[6] the bird arrived in northern Australia on 26 October and in Roebuck Bay on 17 November.

Timing of the migrations

In 2011 the four Red Knots departed from NW Australia between 30 April and 9 May (Fig. 4.2). In 2017 the three Red Knots departed from NW Australia between 21 April and 13 May. The geolocator tracks obtained from 2012 ($n = 2$) indicate that one bird departed from NW Australia in the last week of April and returned at NW Australia in the last week of August (047-2012). The other bird equipped with a geolocator in 2012 (022), departed from NW Australia in mid May 2012. Its southward migration is unclear. The geolocator track obtained from the migratory season in 2013 ($n = 1$) also came from 047 (047-2013). It then departed from NW Australia slightly later than the previous year (ca. 10 May) and it returned to NW Australia again in the last week of October. The geolocator obtained for the migratory season in 2015 ($n = 1$, P536) showed departure from NW Australia in the first week of May and a return at NW Australia around 20 August.

During seven migrations of six PTT-tagged Red Knots tracked in 2018 – 2019, birds departed from NW Australia between 24 April and 24 May (of which no fewer than four departed on 4 May, see Table 4.1, Fig. 4.2) and reached the breeding grounds on the New Siberian Islands between 8 and 29 June. During northward migration Red Knots stayed on average 12.9 d in southeast Asian and southern China (5.5 d per site), and 13.8 d in the Yellow Sea (5.4 d per site). Departures from the Yellow Sea occurred between 2 and 23 June. Arrival on the New Siberian Island tundra breeding grounds occurred 8–29 June. Three of the four early arriving birds (individuals which also left NW Australia relatively early, i.e. before 4 May) stayed long enough on the New Siberian Islands for a successful breeding season (54, 49 and 53 days, respectively).

The first Red Knots departed from the New Siberian Islands on southward migration on 18 July (recorded in 2019) and between 27 July and 3 August in 2018. Arriving back in the Yellow Sea between 30 July and 18 August, Red Knots then staged here for a period twice as long as during their northward migration (22–37 days, average = 27.7 days). Departure from the Yellow Sea occurred between 27 August and 21 September. The earliest return to NW Australia occurred on 3 September, the latest on 26 October.

All three types of tracking devices yielded the same pattern of timing of Red Knots reaching different latitudes (Fig. 4.2), with no clear clustering of different devices with respect to either departure or arrival dates. The three geolocators tracks that yielded sufficient information regarding the entire migratory period (047, 022 and P536, Fig. 4.2) confirmed that staging in the northern Yellow Sea was much longer during southward than during northward migration.

China coast: use of stopping sites in relation to benthic food

Among the 19 shorebird stopping sites along the coastline of China where we surveyed macro-zoobenthos in spring 2018, we found the bivalve *P. laevis* at 14 sites (Fig. 4.3, Table 4.S2). Not all the sites where *P. laevis* was found were used by the tracked Red Knots, but at all seven sites where they did stop during northward migration (including the longest used sites in Bohai and Liaodong Bays), *P. laevis* was found. In the five sites

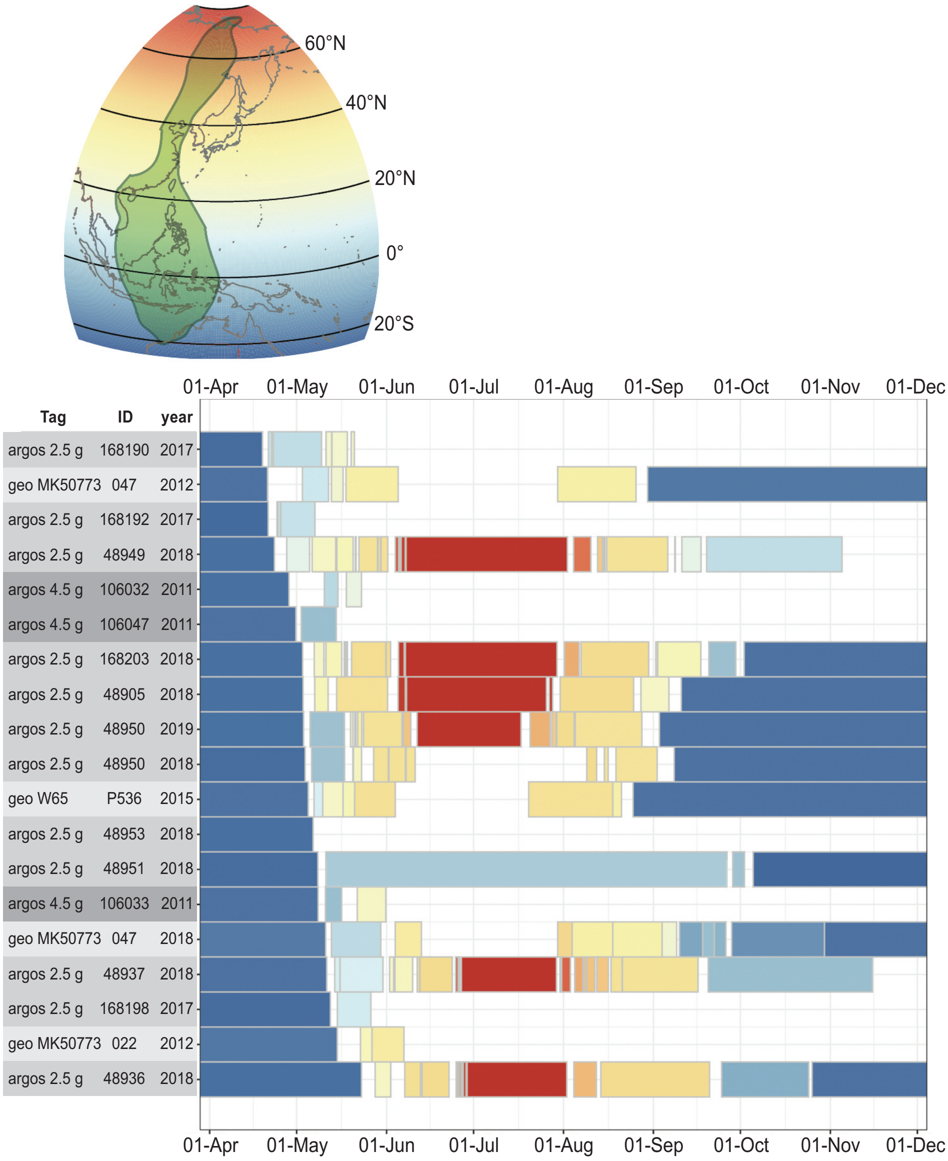

Figure 4.2. Summary of the timing of migration as indicated by the presence at different latitudinal bands in 19 tracks by 17 Red Knots tagged in NW Australia with three different methods differentiated in grey shades. In 2011 we obtained results from three birds with glued 4.5 g PTTs (dark shade), in 2017 and 2018 we obtained results from 12 birds with harness-attached 2.5 g PTTs (one individual tracked during two migrations; light shade), and from 2012–2015 we obtained results from three birds with leg band-attached geolocators (one individual was tracked during two migrations; no shade). Details are presented in Table 4.S1. Stationary periods are coloured by the latitude at which they occurred accordingly to the colour-gradient presented in the inset. The tracks have been arranged from earliest to latest migratory departure from NW Australia.

for which we have benthos data but where tagged Red Knots did not make stops, no *P. laevis* were found. All *P. laevis* encountered were living in the top 5 cm of the sediment and were much smaller than 21 mm, i.e. perfectly harvestable by Red Knots.

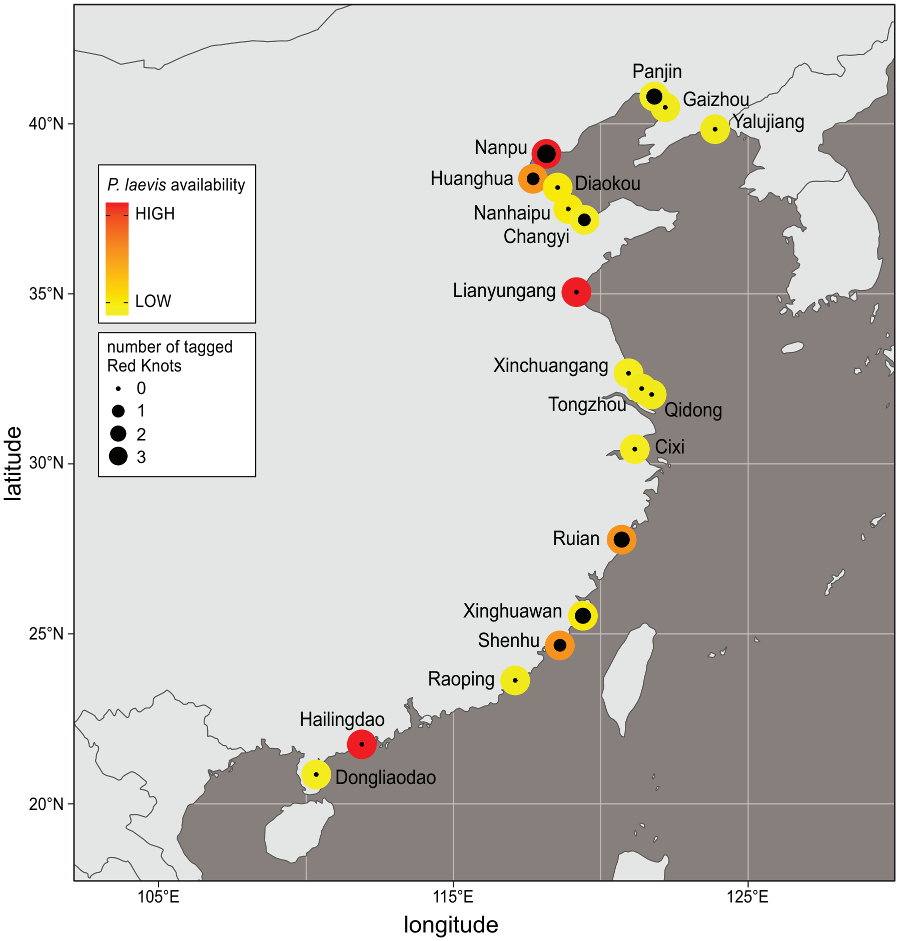

Figure 4.3. Intertidal sites along the coast of China with information on the availability of *Potamocorbula laevis*. The local availability of *P. laevis* was calculated by multiplying local density with the average size at that site. The exact numerical prey densities and size classes and the number of tagged Red Knot occasions are presented in Table 4.S2.

Discussion

In this study we confirm that Red Knots from their terminal non-breeding grounds in NW Australia (1) stop in the Yellow Sea region of China (especially Bohai and Liaodong Bays) during both northward and southward migration seasons, and (2) breed on the New Siberian Islands in Russia and arrive there in June. The fact that all individuals with records during the breeding season were on the New Siberian Islands, and an absence of clear outliers in the timing of migration patterns (Fig. 4.2), suggests that most, and probably all, the tagged Red Knots indeed belonged to the *piersmai* subspecies (Tomkovich 2001). In fact, the data are consistent with earlier inferences on the occurrence and distribution of *piersmai* (Tomkovich 2001, Battley et al. 2005, Rogers et al. 2010), except that the birds were making more stops than anticipated, especially during northward migration.

Although carrying a tag may come with timing delays or foreshortened flight ranges (Bodey et al. 2018), the similarity of the timing of migratory flights and the occurrence of multiple stops during northward migration by Red Knots carrying different tracking devices (4.5 g and 2.5 g solar PTTs and 1 g geolocators; Fig. 4.2) indicate that the stopping behaviour along the migratory trajectories is not an effect of incremental impediments from the tracking devices. Although the smallest devices could have an impact, carrying the devices did not prevent the Red Knots from making non-stop flights of 5,000 km (Conklin et al. 2017 used 5,000 km as a threshold for 'long-jump' migratory flights).

Birds did not make stops ‘at their earliest convenience’ (i.e. stopping at the first possible site in southern China), but rather flew up to 1,000 km up the Chinese coast before making the first stop. Their northwestward, rather than northward great circle, bearings during departure from NW Australia is consistent with the visual onshore observations made as early as 1991 by Tulp et al. (1994) and BBO data to 2021 (C.J. Hassell pers. obs.). This suggests (a) that the departure directions in this study are similar to the ones in 1991, and (b) that the Red Knots, by not stopping at the first suitable coastal site in southern China, were not running out of fuel upon arrival on the Chinese coast. In addition, individuals vary in their use of stops in Southeast Asia and southern China, and this has consequences in subsequent leg of the migration, i.e. the individuals which made more stops *en route* to the Yellow Sea stopped for fewer days in the Yellow Sea (recorded for six birds; Fig. 4.4). This variation in the ways that individuals distribute their fuelling over multiple areas would be an avenue for future investigation.

In view of the general capacity of Red Knots to migrate across large swaths of inhospitable terrain (as they do during the flights across the Asian landmass to and from the New Siberian Islands, Fig. 4.1; and see e.g. Niles et al. 2010, Newstead et al. 2013, Kok et al. 2020 for similar feats in other Red Knot sub-species including the 8,100 km non-stop flight reported at https://whsrn.org/uncovering-the-mysteries-of-red-knot-movements-on-the-gulf-coast/), the Chinese coastline is probably ‘traced’ for good navigational or ecological reasons, including the possibility that they take advantage of favourable winds (Tulp et al. 1994). Northward stops occurred at sites where our sampling of the intertidal feeding areas showed the presence of *P. laevis* (Fig. 4.3), a strongly preferred and high-quality prey type for Red Knots (Yang et al. 2013, 2016) and the similarly molluscivorous and closely related Great Knot *Calidris tenuirostris* (Choi et al. 2017, Zhang et al. 2019a,b). During the three-week southward staging bouts in the Yellow Sea, the Red Knots, using the same areas as on northward migration, most likely again fuelled up on a diet of *P. laevis*.

Although *piersmai* sub-species achieved non-stop flight distances comparable to those by other subspecies during northward migration from NW Australia to the Yellow Sea (Table 4.1), contrary to the other sub-species, *piersmai* behaved as 'skippers' rather than 'long-jumpers' (Piersma 1987). This pattern of making several short stops signals the presence of multiple suitable staging habitats along the east Asian coastline from Vietnam to the northern Yellow Sea. That this may have been going on for quite some time is not only suggested by the migratory departures from Roebuck Bay of shorebirds including Red Knots to the northwest (Tulp et al. 1994), but also by Crossland's (2009) observations of the presence of Red Knots in Sumatra in late March to mid-April 1997. Although these birds occur further west and earlier in the year than *piersmai* from NW Australia, these findings indicate that quite a number of sites are potentially suitable for staging *piersmai*. To help governments and conservation bodies to take appropriate steps towards their protection, we have listed all sites in Table 4.S3, corresponding to the graphical listing in Fig. 4.1A.

This, then, invites the question whether the recent reductions in the extent of suitable habitat in the Yellow Sea area (Murray et al. 2014, Piersma et al. 2016) contributed to the current pattern of stopping at multiple sites. Reductions in the extent of suitable intertidal habitat in northern Bohai Bay appear to have led to a concentration of staging Red

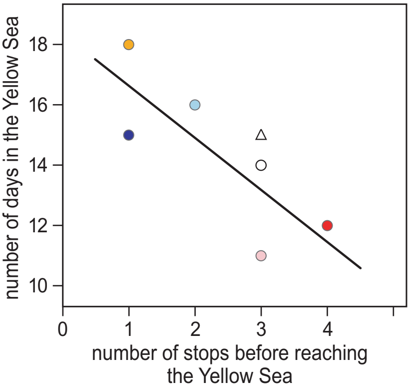

Figure 4.4. The number of refuelling days spent by six Red Knots in the Yellow Sea during northward migration as a function of the number of stops made previously, *en route* between NW Australia and the Yellow Sea. Colours correspond to the colours of the tracks plotted in Fig. 4.1, C & D. The negative correlation ($r = -0.92$, $P < 0.01$) is based on the six points from 2018; the repeat point from 2019 is represented by means of a white triangle (see Table 4.1 for details).

Knots at the Luannan coast (Yang et al. 2011). Land claims for industry, port and city development and aquaculture tend to start from the much-used upper parts of intertidal soft sediment systems, a pattern which would have augmented the reduction of the extent of suitable feeding area for Red Knots along the coast of China (Mu & Wilcove 2020). This suggests that the extent of suitable intertidal habitat for Red Knots was much bigger two to three decades ago than now, before the time of rapid intertidal losses due to land claims (Ma et al. 2014), and Red Knots could have been 'hopping' along even more coastal sites back then. To complicate matters further, the suitability of the remaining Chinese coastal wetlands will be affected by (1) shellfish aquaculture on mudflats, which in fact could have increased the range and densities of *P. laevis* (Peng et al. 2021) and (2) the offshore fishery pressure on the epibenthic predators of small bivalves, such as shrimps and crabs. High fishing pressures may lead to a lack of epibenthic predation, which facilitate the late-winter settlement of *P. laevis* (Yang et al. 2016).

One of the benefits of making several shorter migratory flights, rather than a single long one, would be the cost reduction that comes from flying with, on average, smaller fat stores (Piersma 1987), the lack of need for major 'organisational' changes to organs and body composition (Piersma et al. 1999, Piersma 1998, Hua et al. 2013), and the predation-related 'safety' gains from not having to fly with compromised manoeuvrability (van den Hout et al. 2010). Equally, even in places where intertidal losses due to land claims have been small, variation including reductions in food abundance may still occur (Zhang et al. 2018, 2019a). Thus, the use, at least by *piersmai*, of a succession of several suitable sites should make them less susceptible to resource degradation (Piersma & Baker 2000, Iwamura et al. 2013), and includes the possible benefit that, by visiting multiple sites, Red Knots collect information on the quality of staging areas during migrations. This allows them, in subsequent migrations, to know where probable food resources are, if a site would be lost to industrialisation or other factors.

The ecological reasons for the occurrence of several stops in freshwater habitats during the migrations from Yellow Sea to New Siberian Island and back are not at all clear. On the way north, Red Knots often stopped on the Laptev Strait coast before crossing to the New Siberian Islands, perhaps to await suitable weather conditions before arrival on the tundra. However, some of the birds only made such onshore stops several weeks after conditions on the New Siberian Islands would have become suitable. Many of the Red Knots also used freshwater wetlands during their southward continental crossing. Do these Red Knots capitalize on unknown seasonal peaks in unknown freshwater invertebrates?

Conservation prospect

Even though from 2004 to 2017 there was no significant change in the numbers of Red Knots in NW Australia (Rogers et al. 2020), the East Asian-Australasian Flyway populations of the *piersmai* and *rogersi* subspecies have been in decline for more than a decade (Conklin et al. 2014, Piersma et al. 2016, Clemens et al. 2016, Studds et al. 2017). For a better understanding of the precise causes of such declines in the most threatened shorebird flyway in the world, the present description of migratory pathways and stopping sites of *piersmai*, which still has a population in the tens of thousands, opens up a system amenable to scientific study. We suggest that a combination of studies on local resources and staging, the use of tags to track individual birds lifelong, and analyses of times and place of death (Loonstra et al. 2019), will tell the potential ecological reasons leading up to further declines or recovery (Rakhimberdiev et al. 2015a). In this way we remain vigilant in the hope that this contributes to science-based conservation outcomes which extend beyond the world of Red Knots.

Acknowledgments

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Data availability

The data on locations used by Red Knots and benthic abundance are presented in the text material and Supporting Information. The tracking data used in this study are accessible on Movebank (movebank.org, study name 'Red Knot Piersma Northwest Australia') after consultation of co-author TLT or YCC.

Supporting Information

Table 4.S1. Overview of tracking attempts included in this study.

First migration year	Type of tag	Model	Number of tags	Number of birds presented in this study	Number of birds analyzed in Table 4.1	Tag number
2011	PTT	4.5g solar-powered	30	3	0	106032,106033, 106047
2012	PTT	4.5g solar-powered	15	0	0	
2012	geolocator	1g mk50773	36	2 (+1)	0	047 (2012&2013), 022 (2012)
2015	geolocator	1g Intigeo-w65	93	1	0	P536 (2015)
2017	PTT	2.5 g solar-powered	21	3	0	168190,168192, 168198
2018	PTT	2.5 g solar-powered	18	8 (+1)	6 (+1)	48951, 48953, 48949,168203, 48905, 48950 (2018&2019), 48937,48936
Totals			213	18 (+2)	6 (+1)	

Number in brackets = number of birds being tracked for a second year

Table 4.S2. List of intertidal sites along the coast of China with information on the average densities of a high quality food of Red Knots, the bivalve *Potamocorbula laevis*, and usage by satellite-tagged Red Knots during northward migration in 2018.

Site (site name & province)	Latitude (°N)	Longitude (°E)	Number of sampling cores	*Potamocorbula laevis*		Number of tagged Red Knot occasions
				Density (ind/m^2)	Size and range (mm)	
1. Huanghua, Hebei Province	38.346	117.746		>1000*	small	1
2. Hailingdao, Guangdong Province	21.711	111.936	47	4369	7.6 (0.9-15.4)	0
3. Nanpu, Hebei Province	39.077	118.196	40	3467	2.4 (1.1-5.7)	3
4. Lianyungang, Jiangsu Province	35.013	119.212	72	2020	3.1 (1.1-20.9)	0
5. Shenhu, Fujian Province	24.624	118.658	29	1447	3.0 (0.8-6.0)	1
6. Ruian, Zhejiang Province	27.733	120.755	13	818	2.1 (1.0-3.8)	2
7. Nanhaipu, Shandong Province	37.459	118.942	34	427	2.2 (1.1-12.0)	0
8. Xinghuawan, Fujian Province	25.490	119.441	16	255	2.4 (1.3-4.3)	2
9. Diaokou, Shandong Province	38.089	118.578	35	217	2.5 (1.6-3.9)	0
10. Dongliaodao, Guangdong Province	20.825	110.384	76	17	3.4 (1.9-6.7)	0
11. Cixi, Zhejiang Province	30.396	121.194	27	7	1.9 (1.7-2.2)	0
12. Panjin, Liaoning Province	40.763	121.860	46	5	3.6 (2.7-4.7)	2
13. Changyi, Shandong Province	37.138	119.489	34	3	2.8 (1.8-3.6)	1
14. Xinchuangang, Jiangsu Province	32.627	120.989	58	1	2.6	0
15. Gaizhou, Liaoning Province	40.449	122.232	42	0	0	0
16. Yalujiang, Liaoning Province	39.804	123.926	104	0	0	0
17. Tongzhou, Jiangsu Province	32.177	121.430	12	0	0	0
18. Qidong, Jiangsu Province	32.003	121.775	64	0	0	0
19. Raoping, Guangdong Province	23.593	117.142	36	0	0	0

*estimated based on visual observations, not sampled systematically.

Table 4.S3. List of stopping sites used by Red Knots in the East Asian-Australasian Flyway, matching the numbered sites in Fig. 4.1A. Note that some of the sites in China were sampled for benthos, matching the numbers in Table 4.S2.

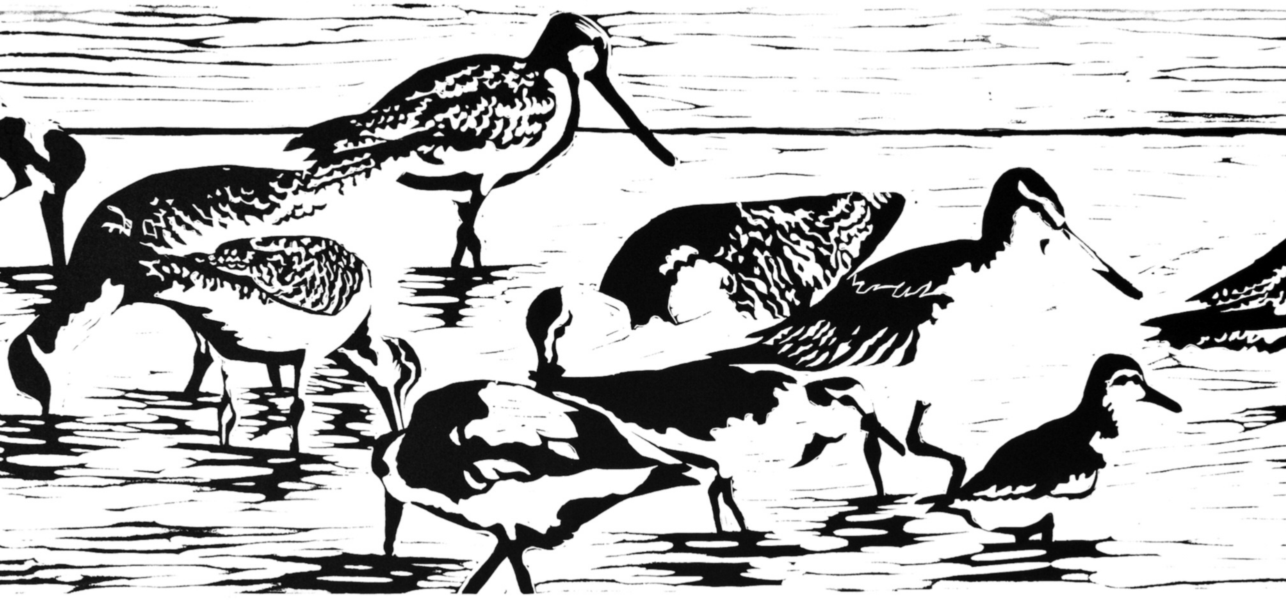
Site Number	Latitude (°N)	Longitude (°E)	Local Name	Region/Province	Country	Number in Table 4.S2
1	-5.6079	132.2746	Pulau Walir	Tayando Islands, Maluku	Indonesia	
2	-1.8093	116.4158	Paser Regency	East Kalimantan	Indonesia	
3	-1.3889	120.6562	Ratolene, Poso Regency	Central Sulawesi	Indonesia	
4	-1.2487	109.5723	Satai, North Kayong Regency	West Kalimantan	Indonesia	
5	4.2671	118.0449	Tawau	Sabah	Malaysia	
6	5.4992	120.9320	Siasi Island	Sulu Province	Philippines	
7	5.5568	118.7397	Kulamba, Kinabatangan	Sabah	Malaysia	
8	6.4968	117.6695	Terusan, Beluran District	Sabah	Malaysia	
9	6.8261	117.1018	Pitas District	Sabah	Malaysia	
10	7.0823	116.7740	Kudat	Sabah	Malaysia	
11	9.2282	105.8032	Bac Liêu, Mekong Delta	Bac Liêu Province	Vietnam	
12	10.1507	106.7702	Bên Tre, Mekong Delta	Bên Tre Province	Vietnam	
13	10.3599	106.8964	Cần Giờ, Mekong Delta	Ho Chi Minh City	Vietnam	
14	13.8472	120.1143	Lubang Island	Occidental Mindoro Province	Philippines	
15	14.4586	120.8636	City of Cavite	Cavite Province	Philippines	
16	16.0064	120.1893	Lingayen Gulf	Province of Pangasinan	Philippines	
17	21.5287	108.3199	Fangchenggang	Guangxi	China	
18	21.6065	108.8567	Qinzhou	Guangxi	China	
19	23.5913	117.3606	Dacheng & Zhao'an Bay	Guangdong & Fujian	China	
20	23.6023	119.5913	Penghu Islands	Taiwan	China	
21	23.8864	117.5780	Dongshan Bay	Fujian	China	
22	23.9989	117.7908	Futou Bay	Fujian	China	
23	24.0050	120.3638	Hanbao, Changhua county	Taiwan	China	
24	24.5872	118.3324	Dadengdao, Xiamen	Fujian	China	
25	24.5878	118.4332	Weitou Bay	Fujian	China	
26	24.6743	118.6668	Shenhu	Fujian	China	5
27	25.0683	119.1237	Meizhou	Fujian	China	
28	25.4853	119.4300	Xinghuawan	Fujian	China	8
29	27.5821	120.6120	Aojiang Estuary	Zhejiang	China	
30	27.7517	120.7711	Ruian, Wenzhou Bay	Zhejiang	China	6
31	30.3498	121.3765	Hangzhou Bay	Zhejiang	China	11
32	33.2310	120.8330	Dafeng Port	Jiangsu	China	
33	34.4665	119.8553	Guanhe Estuary	Jiangsu	China	
34	36.4520	120.7320	Aoshan Bay	Shandong	China	
35	37.1188	119.4583	Changyi	Shandong	China	13
36	37.6737	119.0723	Yellow River Delta	Shandong	China	7
37	38.1933	117.9884	Binzhou	Shandong	China	
38	38.3630	117.7328	Huanghua	Hebei	China	1
39	38.8672	117.6425	Tanggu	Tianjin	China	
40	39.1116	118.2262	Nanpu	Hebei	China	3
41	39.7864	123.5935	Yalu Jiang	Liaoning	China	16
42	40.5807	122.1661	Yingkou	Liaoning	China	
43	40.7862	121.9388	Dawa, Panjin	Liaoning	China	12
44	40.8348	121.7016	Liaohe Estuary	Liaoning	China	
45	40.8575	121.4740	Dalinghe Estuary	Liaoning	China	

Table 4.S3. Continued.

Site Number	Latitude (°N)	Longitude (°E)	Local Name	Region/Province	Country	Number in Table 4.S2
46	40.8782	121.2342	Xiaolinghe Estuary	Liaoning	China	
47	44.6404	121.9874	Kerchin	Inner Mongolia	China	
48	44.8231	123.8092	Tongyu	Jilin	China	
49	45.6080	118.7197	Ulagai River	Inner Mongolia	China	
50	45.9613	124.4727	Daqing	Heilongjiang	China	
51	46.1504	123.5090	Baicheng	Jilin	China	
52	46.7623	123.7240	Tailai	Heilongjiang	China	
53	47.8789	123.9394	Gannan	Heilongjiang	China	
54	49.2265	116.7886	Hulun Town	Inner Mongolia	China	
55	49.6606	118.3812	Hulun Buir Prairie	Inner Mongolia	China	
56	50.0546	128.2014	Pridorozhnoe	Tambovskiy District, Amur region	Russia	
57	60.8466	131.8651	Amginskiy District	Sakha Republic (Yakutia)	Russia	
58	63.5791	126.4241	Lake Kobyay-Kyuyele	Kobyayskiy District, Sakha Republic (Yakutia)	Russia	
59	63.9300	125.8707	Vylyuy River	Kobyayskiy District, Sakha Republic (Yakutia)	Russia	
60	66.4286	143.1368	Indigirka River	Momskiy national District, Sakha Republic (Yakutia)	Russia	
61	68.0066	143.1092	Selennyakh River	Abyyskiy District, Sakha Republic (Yakutia)	Russia	
62	68.2328	140.0530	Chersky mountain range, between the Artyk-Yuryuyete and Sakyakan Rivers	Ust-Yanskiy District, Sakha Republic (Yakutia)	Russia	
63	68.3553	139.2987	Tributary of the Selennyakh River	Ust-Yanskiy District, Sakha Republic (Yakutia)	Russia	
64	68.7195	139.0192	Tributary of the Khayyrdakh River, a tributary of the Selennyakh River	Ust-Yanskiy District, Sakha Republic (Yakutia)	Russia	
65	69.6657	137.9161	Chersky mountain range, headstream of the Ulyugyuye River	Ust-Yanskiy District, Sakha Republic (Yakutia)	Russia	
66	70.6410	137.6125	small lake close to Khoto-Kyuyele Lake and the larger Ukyulyakh Lake	Ust-Yanskiy District, Sakha Republic (Yakutia)	Russia	
67	71.2155	139.8875	Between Syalakh-Tyobyulege River and Kytalyktach-Elgene Lake	Ust-Yanskiy District, Sakha Republic (Yakutia)	Russia	
68	71.2394	140.4733	Kha-Kyuyele Lake	Ust-Yanskiy District, Sakha Republic (Yakutia)	Russia	
69	71.3321	137.1813	Tumus-Khargy-Kyuyel Lake	Ust-Yanskiy District, Sakha Republic (Yakutia)	Russia	
70	71.3656	134.4715	Yanskiy Bay	Ust-Yanskiy District, Sakha Republic (Yakutia)	Russia	
71	71.8443	132.544	Cape Buorg-Khaya (between Yanskiy and Buorg-Khaya Bay)	Ust-Yanskiy District, Sakha Republic (Yakutia)	Russia	
72	72.5728	129.2243	Delta of the Lena River	Bulunskiy District, Sakha Republic (Yakutia)	Russia	

PART III

Applications for conservation



CHAPTER 5

Filling knowledge gaps in a threatened shorebird flyway through satellite tracking

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Abstract

1. Satellite-based technologies that track individual animal movements enable the mapping of their spatial and temporal patterns of occurrence. This is particularly useful in poorly studied or remote regions where there is a need for the rapid gathering of relevant ecological knowledge to inform management actions. One such region is East Asia, where many intertidal habitats are being degraded at unprecedented rates and shorebird populations relying on these habitats show rapid declines.
2. We examine the utility of satellite tracking to accelerate the identification of coastal sites of conservation importance in the East Asian-Australasian Flyway. In 2015–2017, we used solar-powered satellite transmitters to track the migration of 32 great knots (*Calidris tenuirostris*), an 'Endangered' shorebird species widely distributed in the Flyway and fully dependent on intertidal habitats for foraging during the non-breeding season.
3. From the great knot tracks, a total of 92 stopping sites along the Flyway were identified. Surprisingly, 63% of these sites were not known as important shorebird sites before our study; in fact, every one of the tracked individuals used sites that were previously unrecognized.
4. Site knowledge from on-ground studies in the Flyway is most complete for the Yellow Sea and generally lacking for Southeast Asia, Southern China, and Eastern Russia.
5. *Synthesis and applications*. Satellite tracking highlighted coastal habitats that are potentially important for shorebirds but lack ecological information and conservation recognition, such as those in Southern China and Southeast Asia. At the same time, the distributional data of tracked individuals can direct on-ground surveys at the lesser-known sites to collect information on bird numbers and habitat characteristics. To recognize and subsequently protect valuable coastal habitats, filling knowledge gaps by integrating bird tracking with ground-based methods should be prioritized.

Introduction

New tracking and biologging technologies are increasingly used to gather ecological data to inform conservation and resource management decisions (Wall et al. 2014, Wilson et al. 2015, Fraser et al. 2018). Global tracking technologies, such as Argos satellite- and GPS-telemetry, enable the tracking of individual animals during their entire migrations (Kays et al. 2015). The annual distributions of migrants, as well as the extent of their local foraging areas and roosts, which were conventionally mapped from human observations made on the ground, can now be mapped from tracking data (Battley et al. 2012, Bijleveld et al. 2016). Such information can be used by conservation practitioners to inform management actions, e.g. to design spatially and temporally representative monitoring schemes and to delineate site boundaries of protected areas (Choi et al. 2019). This approach is particularly useful in parts of the world that lack basic data on species distributions and habitat use, where rapid gathering of such information remains a conservation priority.

Here we examine how satellite tracking can provide comprehensive distributional data to inform conservation policy in poorly-studied coastal ecosystems, some of which are highly threatened. Intertidal habitats along the shores of East and Southeast Asia contain rich biodiversity and provide unique ecosystem services and livelihoods to many people (MacKinnon et al. 2012, Ma et al. 2014). Additionally, they are used by millions of migratory shorebirds in the East Asian-Australasian Flyway (EAAF) for refuelling and resting during their long annual journeys between northern breeding areas and southern coastal non-breeding areas (MacKinnon et al. 2012). However, these intertidal habitats are currently threatened by human activities such as habitat change, over-fishing, pollution, biological invasions and rising sea levels (Millennium Ecosystem Assessment 2005). Along the Yellow Sea shores, a key staging area for shorebirds in the EAAF (Barter 2002, Choi et al. 2009, Hua et al. 2013, Ma et al. 2013a), the extent of intertidal wetlands has been reduced drastically by infrastructure development and aquaculture (Murray et al. 2014, Piersma et al. 2016). Moreover, these coastal habitats are often severely polluted and increasingly overgrown with alien cordgrass Spartina spp. (Melville et al. 2016a), and in some areas the macrobenthic community has collapsed (Zhang et al. 2018). Migratory shorebirds relying on the Yellow Sea shores currently exhibit reduced annual survival rates (Piersma et al. 2016), with populations that rely on the Yellow Sea the most showing the fastest declines (Studds et al. 2017).

As shorebirds during the non-breeding season tend to concentrate at discrete areas of intertidal habitat with rich food resources, a common approach to conserve them has been to identify important areas, which can then lead to proper threat assessments and appropriate management measures (Boere & Piersma 2012). Traditionally, the identification of important wetlands, including intertidal areas, and the subsequent establishment of international agreements for their protection such as the Ramsar Convention, has been based on bird counts and general observations of bird concentrations by naturalists and citizen scientists (Smart 1976). Long-term count data and citizen science data are much less common in East Asia than in the developed nations of Europe and North America (Chandler et al. 2017). Satellite tracking of species that are representative of the taxa and the habitats of concern can quickly overcome this knowledge deficit by generating species distributions independent of survey efforts. However, in most cases only a small percentage of individuals within the population is tracked, and the tags might cause the animals to alter their behaviour (Barron et al. 2010). Therefore, it is important to assess whether the distributions of tracked individuals are representative of the target populations.

To accelerate the identification of intertidal sites of conservation importance in the EAAF, we tracked the migration of great knots (*Calidris tenuirostris*), a shorebird species that is fully dependent on intertidal habitats for foraging during the non-breeding season (Tulp & de Goeij 1994, Conklin et al. 2014). We summarize the migration patterns of great knots by mapping the distribution of their stopping sites and describing their migration timing. Furthermore, we evaluate the utility of satellite tracking as a tool to fill gaps in conservation knowledge by: (1) examining if the distribution of the tracked individuals represents that of the population, through ground surveys for great knots at sites with few or no survey data; (2) assessing whether the number of stopping sites found is limited by our sample size; and (3) measuring knowledge gain through a tally of sites newly discovered from tracking (i.e., those that were not regarded as important coastal shorebird habitats in the EAAF before our study).

Materials and methods

Study species

Great knots are distributed widely across the EAAF (BirdLife International 2016). More than 90% of the population spend the non-breeding season in Australia (Hansen et al. 2016) and they migrate annually to breed in Eastern Russia at latitudes greater than 61°50’N on upland (>300 m a.s.l.) mountain tundra (Tomkovich 1997). They can carry the lightest (4.5 g) satellite transmitters available at the time of study, which comprise 3% of their average lean mass (mean of 151 g, SD 20, measured in this study). They are listed as globally ‘Endangered’ on the IUCN Red List, reflecting a sharp population decline attributed to the loss and degradation of sites that they rely on during migration (BirdLife International 2016, Moores et al. 2016).

Satellite tracking

In September and October 2014, 2015 and 2016, we deployed 4.5 g solar Platform Terminal Transmitters (PTTs, Microwave Telemetry, USA) on great knots captured with cannon nets at a primary non-breeding site, the northern beaches of Roebuck Bay, Broome, Northwest Australia (17.98°S, 122.31°E). After capture, each bird was measured and individually marked on its tarsi with a unique combination of leg flag and colour bands. Birds were aged based on plumage characteristics (Higgins & Davies

1996) and adults were selected for satellite tagging. Transmitters were deployed using a body harness (Chan et al. 2016) made of elastic nylon (Elastan, Vaessen Creative, The Netherlands), which degrades and breaks, thus releasing the tags after one to two years. The birds were kept indoors and observed for at least 24 h to ensure acclimatization to the transmitter and harness. We then released the birds at the capture location.

PTTs were programmed to operate on a duty cycle of 8 h of transmission and 25 h off. On average, six locations (3 SD) were received from the Argos system (Collecte Localization Satellites, CLS) per tag in each transmission period. Tags that stopped transmitting were considered to indicate a broken harness, a malfunctioning tag, or the death of the bird. This work was carried out under Regulation 17 permits SF 010074, SF010547 and 01-000057-2 issued by the West Australian Department of Biodiversity, Conservation and Attractions.

Spatial analyses

We filtered the Argos locations to retain all standard locations (i.e., the location classes 3, 2, and 1) and applied the Hybrid Douglas filter (Douglas et al. 2012) to remove any implausible auxiliary locations (i.e., the location classes 0, A, B and Z, for details of how locations classes were assigned, see CLS 2016) by setting filtering parameters at 120 km/h for the maximum sustainable rate of movement and 10 km for minimum-redundant-distance. We then classified the filtered locations as either 'flight' or 'stationary'. 'Flight' included all locations >50 km away from the shoreline (shapefile downloaded from https://www.ngdc.noaa.gov/mgg/shorelines/gshhs.html), and/or birds moving in one direction at more than 20 km/h. The remaining locations were considered 'stationary' and were then grouped into distinct sites by region using hierarchical clustering analysis with function *NbClust* in the 'NbClust' R package (Charrad et al. 2014). We used the 'Complete' aggregation method (Sørensen 1948), and the silhouette index to determine the optimal number of clusters, which maximized distances between sites and minimized distance between locations belonging to a site (Charrad et al. 2014). When tracked birds moved between two adjacent sites more than once during a stopping event ($n = 6$ instances), we merged the two sites into one based on our definition of a site as a cluster of habitats that an individual bird moves through for foraging and roosting (this definition is equivalent to a 'shorebird area' in Clemens et al. 2010). The resulting sites were 16.1 km long based on the median for 60 sites with 10 or more standard locations per site; size of the sites was determined to be the 95% quantile of pairwise distances of all standard locations belonging to the site.

To investigate how tagging effort affected the number of sites discovered, we explored the relationship between the accumulated number of sites discovered per region and the number of satellite transmitters deployed. The mean site accumulation curve and its standard deviation were obtained from 1000 permutations of adding sites in random order, using function specaccum in the 'vegan' R package (Oksanen et al. 2018).

We calculated the stopping duration of individuals as the difference between their estimated arrival and departure times at a site. Although sites where migrating birds make long stops are sometimes called 'staging sites' and those where birds make short stops are called 'stopover sites' (Piersma 1987, Warnock 2010), we found that a site could potentially host some individuals making short stops and some staying for weeks. Therefore, we refer to all sites that birds stopped for more than two hours as 'stopping sites'. To calculate arrival times, we identified the first 'stationary' point at a site. If the previous point was classified as 'flight', the arrival time was estimated by extrapolating the average speed of a non-stop flight over the intervening great circle route between the first 'stationary' point and the previous 'flight' point. We estimated the average speed of non-stop flight to be 56.8 km/h (*SD* 8.1) based on all non-stop flights recorded within a duty cycle that were composed of standard class locations only ($n = 11$ segments, 10 birds). Furthermore, if the previous point was a 'stationary' point at a previous site, we assumed that the flight from the previous site to the subsequent one occurred midway of the time interval between the two. We estimated departure times in the same way. For sites with only one data point, or with stopping durations shorter than 2 h, we could not be certain whether they represented a bird stopping or flying over, therefore, these sites were excluded in our analyses of stopping sites.

We analysed migration patterns (i.e., the timing and frequency of site use by tracked birds) at three decreasing spatial scales: regional, latitudinal, and site-based. All stopping sites fell into four geographical regions (Figs. 5.1 & 5.2A): (1) Southeast Asia (11°S–20.2°N), (2) Southern China (20.2–30.9°N, comprising the coastline from the southern tip of China's mainland to the southern boundary of the Yangtze Estuary in Shanghai), (3) Yellow Sea (30.9–41.5°N, including one site on the coast of the Sea of Japan within these latitudes) and (4) Russia (41.5–63°N, the Pacific coast north of the Yellow Sea to the northern edge of the Sea of Okhotsk). At a finer scale, we divided the study area into 14 nearly equal latitudinal intervals. Width of intervals varied slightly (4.9–6.5°), so regions and latitudinal intervals shared the same overall north and south boundaries, and the entirety of a site would fall within a single interval. The percentage of individuals stopping in each region and latitudinal interval was calculated from all complete northward ($n = 20$) and southward ($n = 10$) migration tracks. For the documentation of arrival and departure times and stopping durations, we excluded individuals that did not arrive at the 'next' region. At the site level, to determine sites that were the most popular, we calculated the percentage of tracked birds using a site out of the total number of birds stopping in that region during that migration season.

To assess the current state of knowledge on the existence and location of stopping sites used by the tracked great knots, we compared our findings to the four existing lists of sites important for the 15 EAAF shorebird species that depend entirely on coastal habitats during the non-breeding season (i.e., 'coastal obligate species' defined in Conklin et al. 2014; see Table 5.S1). The four lists are: Zhang et al. (2017; the most up-to-date listing of sites in China that fulfil the Ramsar Criterion 6 of regularly supporting more than 1% of a population), Conklin et al. (2014), Jaensch (2013) , and the EAAF Partnership Flyway Site Network (East Asian-Australasian Flyway Partnership 2018a); the latter three include sites in the flyway that record a count of ≥0.25% of a population, a criterion for identifying stopping sites used by the Asia-Pacific Migratory Waterbird Conservation Strategy (East Asian-Australasian Flyway Partnership 2018b). For 10 of the 15 'coastal obligate' species, the majority of the population is found in Australia and/or New Zealand during the non-breeding season, whereas the remaining five species occur mainly between Southeast Asia and the Yellow Sea (Table 5.S1), and we summarized lists accordingly. For sites that were previously recognized only as wintering sites for coastal obligate species, the fact that our tracked great knots stopped there suggested these sites could also be important to shorebirds during migration seasons as well.

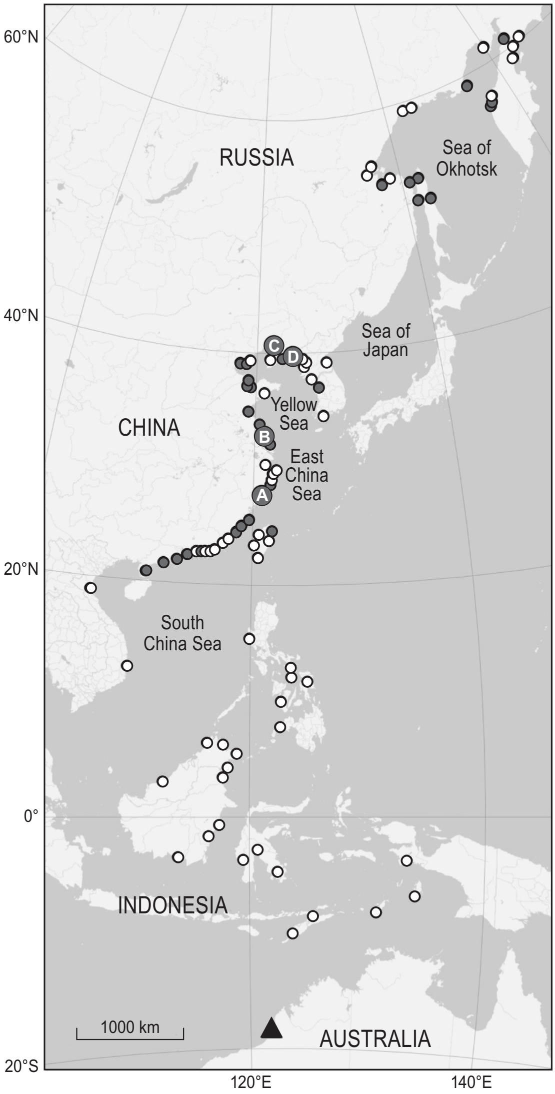

Figure 5.1. Sites along the East Asian-Australasian Flyway used by 32 satellite-tracked great knots during migration in 2015–2017. Filled circles were known important non-breeding sites of at least one of the 15 species of coastal obligate shorebirds, while open circles were unknown non-breeding sites for these shorebirds prior to our study. Sites visited by more than one-third of tracked individuals are: A, Wenzhou Bay, B, Yangkou-Dafeng coast, C, Liaohe (Shuangtaizi) Estuary and Inner Gulf of Liaodong, and D, Yalu Jiang Estuary. Triangle shows Roebuck Bay, Northwest Australia where the satellite transmitters were deployed.

We defined a site's boundary as either an area within a 10-km radius circle of its central coordinates (also used in Hansen et al. 2016) or, if the listed site was an Important Bird Area (IBA), we used the available IBA boundary (data accessed March 2018 from http://datazone.birdlife.org/site/requestgis). We then determined if tracked birds stopped at these listed sites by determining if any stationary points belonging to a tracked bird site fell within the boundaries of listed sites; if they did, we classified this site as 'known'. All other sites were classified as 'unknown'. While some unknown sites have never been documented, others have been surveyed previously but bird counts fell below 0.25% of the flyway population which is the threshold for listing on three of the lists above. For other unknown sites, counts were reported but without exact species counts and/or exact locations. We investigated whether unknown sites are less intensely used by shorebirds, which could make them less likely to be discovered during brief bird surveys. Within each region, we compared intensity of use by great knots between known and unknown sites based on their stopping duration (by a one-way ANOVA) and number of stopping individuals (by a Mann-Whitney-Wilcoxon test).

Ground surveys

To confirm the occurrence of great knots in the region of Southern China which was previously thought to be unimportant to the species (see Discussion), during 8–16 April 2016 and 2017 we travelled to and counted great knots at six stopping sites identified in nearly real-time from the tracking data. As roosts were difficult to locate, we counted great knots on the mudflats during outgoing, low, or incoming tides. For 1–3 days, counts were conducted by one to three observers with 20–60× spotting scopes surveying approximately 0.4–14.2 km^2 of mudflat per site. The surveys were limited by time and accessibility and covered only a fraction of the site identified from tracking, so numbers represent the minimum number of great knots present. In addition, birdwatchers recorded tracked individuals in counted flocks for two other locations in Southern China.

Results

Based on the movements of 32 great knots tracked in 2015–2017, we identified a total of 92 stopping sites along the EAAF with 19–25 sites in each of the four regions (Southeast Asia, Southern China, Yellow Sea and Russia; Figs. 5.1 and 5.2, all sites are listed in Table 5.S2). Individuals made 3–9 stops (mean of 5.6) during northward migration and 3–8 stops (mean of 5.0) during southward migration, visiting 1.0–2.5 sites per region. The rate of discovery of new stopping sites decreased with increasing numbers of birds being tracked, but rates of 'diminishing returns' varied between regions (Fig. 5.3). The Yellow Sea was the only region where the site accumulation curve reached an asymptote (i.e. fewer than 0.5 sites would have been found there for every new tag added), indicating that most sites have been identified. In contrast, the curve for Southeast Asia hardly levelled off, meaning that most Southeast Asian sites still remain to be discovered.

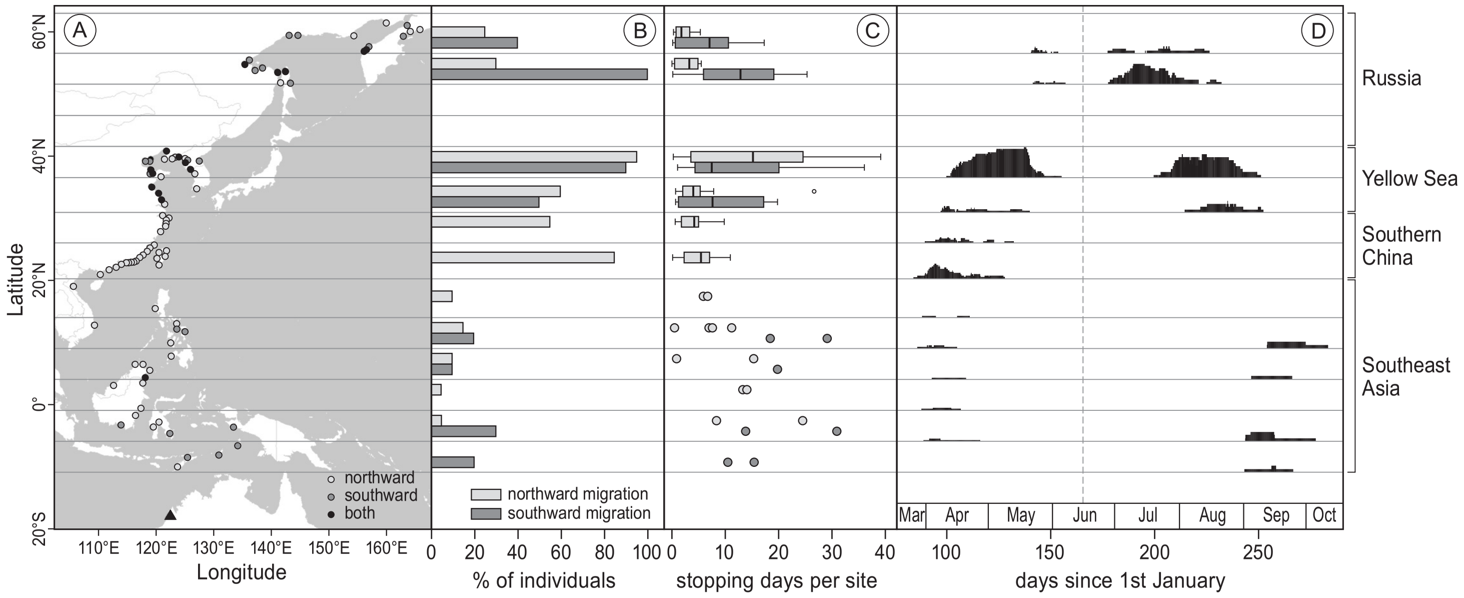

Figure 5.2. Occurrence of satellite-tracked great knots along the East Asian-Australasian Flyway. Horizontal lines indicate boundaries of latitudinal intervals for analysing bird usage. (**A**) Sites used by satellite-tracked great knots during northward, southward and both migrations in 2015–2017. Triangle shows the tag deployment location in Northwest Australia. (**B**) Percentage of individuals stopping and (**C**) Number of stopping days per site, amalgamated at latitudinal intervals. (**D**) Temporal occurrence of individuals across the latitudinal intervals, with height corresponding to number of individuals that migrated through a latitudinal interval.

Southeast Asia was used by 40% of the individuals during northward migration for an average of 11.5 ± 5.7 days (mean ± *SD*), and by 80% of the individuals during southward migration for 19.0 ± 7.4 days (Fig. 5.2). During northward migration, all individuals stopped in Southern China for 9.4 ± 3.5 days, but none were detected there during southward migration (Fig. 5.2). All individuals used the Yellow Sea, stopping there for 33.0 ± 7.7 and 29.1 ± 8.0 days during northward and southward migration, respectively (Fig. 5.2). During northward migration, 55% of birds stopped for 3.2 ± 2.4 days along the Russian east coast, whereas during southward migration all birds stopped there for much longer (20.6 ± 5.8 days, Fig. 5.2). Passage pattern for each latitudinal interval are shown in Fig. 5.2D and the dates are listed in Table 5.S3.

Latitudinal intervals within regions that were most frequently visited (i.e. by 85%–100% of tracked individuals) were 20.2–26°N within the Southern China region during northward migration, 51.5–56.5°N within the Russia region centred on the Sea of Okhotsk during southward migration, and 36.5–41.5°N within the Yellow Sea region, during both migration seasons (Fig. 5.2B). Accordingly, these intervals also contained the sites that were most frequently used (the ones visited by more than one-third of tracked birds are highlighted in Fig. 5.1 and Table 5.S2). At eight sites in Southern China where the tracked great knots stopped, flocks of 34–2,160 great knots per site were counted within the northward migration period during our surveys or reported by local observers (Table 5.1). The mean count of 729 birds represents 0.25% of the estimated great knot population in 2007 (Wetlands International 2019).

	Southeast Asia	Southern China	Yellow Sea	Russia
number of tagged birds (*n*)	23	26	23	19
number of sites added at the:				
2nd tag	1.3	1.7	2.3	1.8
19th tag	0.9	0.7	0.5	0.7
*n*th tag	0.9	0.6	0.4	0.7

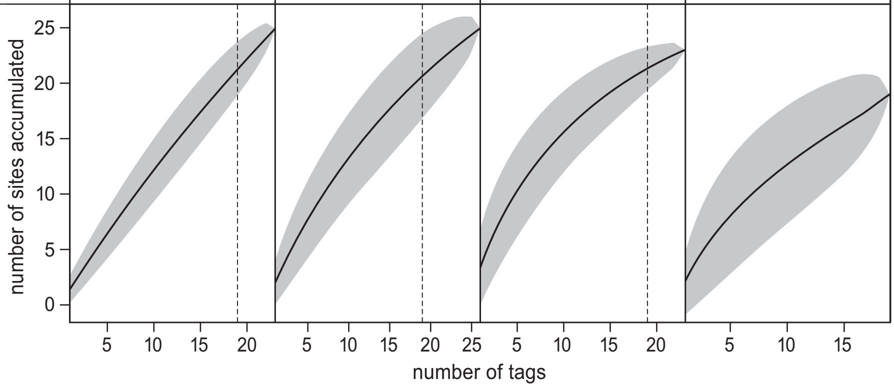

Figure 5.3. Accumulated number of sites discovered per region with increasing number of tracked birds (shaded regions, ±2*SD*). To help comparing between regions, the 19th tag is indicated by a dotted line.

Overall, only 16 of the 92 sites (17%) had been previously identified as important for great knots, and 34 of the 92 sites (37%) as important for ‘coastal obligate’ shorebirds; the rest (63%) were unknown (Figs. 5.1 & 5.4, Table 5.S2). In the relatively intensely surveyed Yellow Sea, relatively few sites were unknown (9 of 23; 39%) of which 5 were in North Korea (Figs. 5.1 & 5.4). For the other regions, the majority of sites that great knots used were unknown: 53% of the sites in Russia, 56% in Southern China and 100% in Southeast Asia (Fig. 5.4). All 20 individuals with complete migration tracks stopped at one or more unknown sites. The degree of usage, measured by the number of individuals stopping and their stopping duration, did not differ significantly between known and unknown sites in Southern China ($U = 53$, $P = 0.144$; $F_{1,4\,5} = 1.52$, $P = 0.224$; Fig. 5.5). In the Yellow Sea and Russia, more great knots stopped at known sites ($U = 25.5$, $P = 0.015$; $U = 23.5$, $P = 0.036$) and stayed longer ($F_{1,74} = 4.03$, $P = 0.048$; $F_{1,39} = 4.29$, $P = 0.045$; Fig. 5.5).

Table 5.1. Counts at sites visited by satellite-tracked great knots along the Southern China coast from April 2015–2017 (the same years as the satellite tracking).

Site	Province/ Region	Coordinates of centroid	Count date	Count of great knots	Occurrence of tracked birds[a]	Number of tracked birds
Surveys in this study:						
Dongli, Leizhou	Guangdong	20.82°N, 110.38°E	8 April, 2016	836	4–11 April, 2015	1
Hailingdao, Yangjiang	Guangdong	21.71°N, 111.93°E	6 April, 2017	192	27–29 March, 2015	2
Dacheng Bay, Chaozhou	Guangdong	23.59°N, 117.14°E	8 April, 2017	34[b]	1–10 April, 30 April–7 May, 2016 & 2017	2[c]
Ruian, Wenzhou Bay	Zhejiang	27.79°N, 120.79°E	10 April, 2017	2160	31 March –11 May, 2015, 2016 & 2017	9
Linhai, Taizhou	Zhejiang	28.72°N, 121.69°E	14 April, 2017	950	16–22 April, 2015 & 2017	2
Cixi, Hangzhou Bay	Zhejiang	30.38°N, 121.18°E	16 April, 2017	204	7–11 April, 2015 & 2016	3
Other records:						
Mai Po, Deep Bay	Hong Kong SAR	22.49°N, 114.02°E	31 March, 2016	278[b]	30 March – 7 April, 2016	1
Dadengdao, Xiamen	Fujian	24.55°N, 118.27°E	4 April, 2015	115[b]	31 March – 21 April, 2015 & 2016	4

[a] Stopping dates of only the birds that reached their next destination are summarised.
[b] A tracked bird was observed within the flock.
[c] Two individuals occurred there, including one individual that visited the site twice, in both 2016 and 2017.

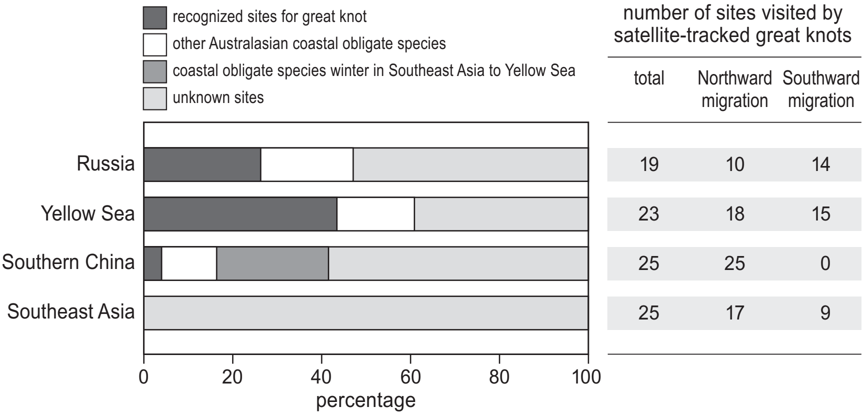

Figure 5.4. Knowledge status of East-Asian-Australasian Flyway stopping sites of satellite-tracked great knots. Bars represent percentage of sites that are currently recognized as: important for great knots (i.e., listed in at least one of the published lists of important sites within the flyway; Jaensch 2013, Conklin et al. 2014; Zhang et al. 2017; East Asian-Australasian Flyway Partnership 2018a), important for other coastal migratory shorebird species wintering in Australia and/or New Zealand, or important for other coastal obligate shorebird species that winter from Southeast Asia to Yellow Sea (Table 5.S1). 'Unknown' sites have not been recognized as important shorebird sites.

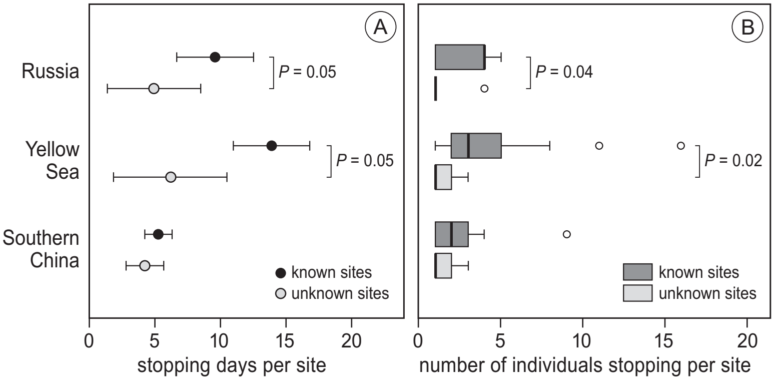

Figure 5.5. (**A**) Means and 95% Confidence Intervals of stopping duration and (**B**) boxplots representing number of individuals stopping per known and unknown sites within the regions of Russia, Yellow Sea and Southern China. Significant differences between known and unknown sites within a region are depicted with the corresponding p-values, as determined by a (A) one-way ANOVA or (B) Mann-Whitney-Wilcoxon test.

Discussion

From the satellite tracking data, we can extract information on bird use during migration ranging from the scale of the whole flyway down to individual sites. At the flyway scale, our results confirmed the importance of the Yellow Sea for relatively long refuelling periods by great knots during both northward and southward migrations (Barter 2002, Ma et al. 2013a, Riegen et al. 2014, Choi et al. 2015). Our results also confirmed the pattern of brief stops during northward migration and long stops during southward migration along the coast of the Sea of Okhotsk, Russia (50–63°N; Tomkovich 1997). However, during northward migration, none of our tracked birds flew the >5,500 km non-stop from Australia to the southern Yellow Sea as proposed by Battley et al. (2000) based on ground observations. Rather, most tracked birds flew a shorter leg of 4,500–5,400 km from northwest Australia to the Southern China coast and stopped there before continuing north towards the Yellow Sea. Moreover, tracked birds arrived at the Yellow Sea (Table 5.S3) later than what was reported from earlier on-ground observations: Battley et al. (2000) reported the first great knots being captured at Chongming Dongtan (31.5°N, 121.9°E) on 31 March in 1998, and Ma et al. (2013a) on 26 March 2012; Choi et al. (2015) reported a mean arrival date of 6–7 April at the Yalu Jiang Estuary (39.8°N, 123.9°E) derived from counts in 2010–2012, and radio-tracked great knots being tagged at Chongming Dongtan arrived there during 28 March–28 April 2012 (Ma et al. 2013a).

We recognize that the increased load and drag from the transmitters (Pennycuick et al. 2012) may have caused the birds to reduce their non-stop flight distances. External devices are known to handicap birds (Barron et al. 2010, Hupp et al. 2015, Chan et al. 2016). Accordingly, the great knots in this study showed lower survival (0.51, 95% CI: 0.38–0.65) during their first year of carrying a transmitter compared to birds without a transmitter (0.75, 0.64–0.83; Appendix 5.S1). This difference may have been caused by tagged birds being less agile in flight and thus more prone to predation by raptors (Chan et al. 2016). However, estimated breeding success of the satellite-tracked great knots (56% of 16 birds, defined as a stay of more than 34 days at the breeding site would result in eggs hatching, as reported in Lisovski et al. 2016a) was very similar to that of Arctic-breeding shorebirds (61% of 7418 nests of 17 taxa, range = 46–73%, Weiser et al. 2018), and of great knots tracked with leg-flag mounted geolocators from the same non-breeding area in Northwest Australia (50% of eight birds; Lisovski et al. 2016a). Moreover, all the eight geolocator-tracked great knots stopped in Southeast Asia and Southern China during northward migration (though the exact locations and durations of these stops could not be determined at the level of detail as of satellite-tracked birds; Lisovski et al. 2016a) and arrival dates at the northern Yellow Sea (36.5-41.5°N) during northward migration do not differ between geolocator-tracked birds (19 April ± 9 days, n = 6, excluding a late bird which arrived on 10 June) and satellite-tracked birds (25 April ± 11 days, n =19; Mann-Whitney U = 38, P = 0.25; note that none of the six geolocator-tracked birds stopped in the southern Yellow Sea).

Stopping patterns of the geolocator-tracked birds (Lisovski et al. 2016a), together with the observations of flocks of great knots in Southern China presented here, indicate to us that the use of Southeast Asia and Southern China cannot simply be regarded as an effect of tagging. Rather, there could be biological explanations for the difference in arrival time to the Yellow Sea between tracked birds and earlier ground observations. The earliest arriving great knots at the Yellow Sea could be from wintering populations other than Northwest Australia (where the geolocator- and satellite-tracked birds were captured). Moreover, migration strategy of great knots could have been changing over the past 20 years, possibly as a response to the destruction and deterioration of Yellow Sea habitats (Murray et al. 2014, Zhang et al. 2018). However, the lack of historical data from Southeast Asia and Southern China prevents further interpretation. Nevertheless, the pattern of great knots stopping in Southern China and Southeast Asia probably represents the current migration behaviour of individuals from the Northwest Australia nonbreeding area (where the tagged individuals were caught and where >55% of the flyway population resides; Hansen et al. 2016). The high rates of habitat degradation in these regions from coastal development and hunting (Li & Ounsted 2007, Martinez & Lewthwaite 2013, Zöckler et al. 2016) therefore represent potential big threats for this species.

At the site level, we mapped 92 stopping sites used by the tracked great knots (Fig. 5.1, Table 5.S2). Our analysis of the number of sites discovered per tag revealed that, in Southeast Asia, Southern China and Russia, more new sites could have been discovered per region if more birds had been tracked (Fig. 5.3). Therefore, our list of sites should not be viewed as comprehensive, but rather as a sample of great knot stopping sites independent of ground survey efforts. Likewise, our list contains sites that are potentially important for other coastal obligate shorebird species. The general co-occurrence of great knots with these other species may be explained by their shared prey preferences (Yang et al. 2013, Choi et al. 2017) and the fact that productive mudflats contain high densities of benthos and biofilm and the shorebirds that feed on them (Mathot et al. 2019).

The conventional thinking that conservation priorities should be placed at sites with high concentrations of birds and where birds stop the longest (the staging sites sensu Warnock 2010), is in accordance with our finding that the sites used by more than one-third of the tracked individuals were all known (Fig. 5.1). However, the majority of sites that the tracked great knots used were not included in existing conservation listings of important coastal shorebird sites. Notably, every tracked great knot used unknown sites, implying that the bulk of the population faces unknown conditions and threats during part of their migration. Although stops at unknown sites were briefer in general (Fig. 5.5), these brief stops may represent 'emergency staging sites' that migrants rely on when encountering poor weather conditions during migration (Shamoun-Baranes et al. 2010). Some stopping sites could also allow migrants to recover from the exhaustion of long non-stop flights (see discussion in Piersma 2011), e.g. to catch up on sleep (e.g. Schwilch et al. 2002, Moore 2018). Moreover, they may provide alternative habitat if established prime sites become degraded. We suggest that an expansion of conservation efforts beyond protecting the stopping sites with most birds (i.e. the classical 'staging sites') could be evaluated as a framework for greater population resiliency.

To assist in prioritizing conservation efforts, we need to start collecting information on bird numbers, habitat characteristics and threats at these lesser-known sites. Important waterbird sites have traditionally been discovered through ground surveys. Sites that were unknown before our study likely lacked surveys and observers. Far less knowledge of bird occurrence existed for coastlines outside of the Yellow Sea and Japan, and recent waterbird counts are usually conducted by volunteers at a much smaller scale than citizen science projects in Western Europe and North America (Bai et al. 2015, Chandler et al. 2017). Brief surveys might also miss birds that stop only briefly, which might explain why some sites within the comparatively well-studied Yellow Sea were unknown before our study. Satellite tracking data can help by focusing survey efforts during periods with the greatest chances of encountering birds. Moreover, a major advantage of satellite tracking over geolocation (a method commonly used to track small bird species, see Lisovski et al. 2016b for an example to identify important areas for conservation) is that potential roosting and feeding areas within a large area can be located from the relatively higher-accuracy locations (error < 2.5 km; Douglas et al. 2012) of satellite-tracked birds (e.g. Chan et al. 2019a). For example, observers used the spatial and temporal information from our tracking data to narrow down the search area in the extensive Liaohe Estuary and Inner Gulf of Liaodong in the Yellow Sea, and discovered c. 60,000 great knots at Gaizhou in 2015 (Melville et al. 2016b). Moreover, the spatial and temporal information from our tracking data also enable us to find several sites in Southern China with >0.25% of great knot flyway population during our surveys (Table 5.1).

Tracking data can help interpret counts from ground surveys. While current conservation listings are based on counts, the proportion of tracked birds using a site provides a complementary measure of numerical significance. For example, the 33% of tracked birds that stopped at Wenzhou Bay in China suggested that this site's importance to great knots was greater than what was evident from count-based assessments. Stopping duration of individuals can also be used to correct regular counts to determine the number of birds using a site. For example, in Deep Bay, Hong Kong, the number of great knots stopping there was estimated to be 1.8–2.7 times the maximum count if corrected for turnover rate (Appendix 5.S2). This improved estimation of stopping population size can make a difference in whether sites meet the criteria for listing as Ramsar sites, IBAs or EAAF Partnership Flyway Sites.

Here we have shown that satellite tracking has shed much-needed light on the use of intertidal habitats in poorly-known regions such as Southern China and Southeast Asia by migrating shorebirds. Ultimately, to monitor the ecological effects of rapid destruction and future restoration of intertidal habitats along this flyway, real-time data on spatial and temporal changes in distributions are necessary. These data can be collected by tracking the migration of individual shorebirds or other groups of birds that depend on intertidal habitats. Such information can be fed into a comprehensive monitoring scheme integrating regular counting, on-the-ground threat monitoring, and benthic community sampling. We hope that our study will catalyse the momentum for scientists and conservationists to work together to bridge the knowledge gap for effective conservation in rapidly changing regions.

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Authors' contributions

Y.-C.C. and T.P. designed the study. Y.-C.C., C.J.H. and T.L.T. collected the satellite tracking data, supported by T.P. Y.-C.C. and H.-B.P. collected the count data with support from T.P., Z.M. and Z.Z. Y.-C.C. analysed the tracking and count data with the help of T.L.T. and T.L. C.J.H. and T.P. organized the mark-and-resight programme and T.L. conducted the survival analysis. Y.-C.C. wrote the manuscript with the help of all the authors. All authors gave final approval for publication.

Data availability

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.f2g5f49
(Chan et al. 2019c).

Supporting Information

Table 5.S1. Migratory shorebird species that are coastal obligates in the East Asian-Australasian Flyway (EAAF; after Conklin et al. 2014, Table 5.1) and their global conservation status in the IUCN Red List.

	Common name	Scientific name	IUCN[a]
Species spending the non-breeding season primarily in Australia and/or New Zealand:			
1	Bar-tailed godwit	*Limosa lapponica*	NT
2	Whimbrel	*Numenius phaeopus*	LC
3	Far eastern curlew	*Numenius madagascariensis*	EN
4	Terek sandpiper	*Xenus cinereus*	LC
5	Grey-tailed tattler	*Tringa brevipes*	NT
6	Ruddy turnstone	*Arenaria interpres*	LC
7	Great knot	*Calidris tenuirostris*	EN
8	Red knot	*Calidris canutus*	NT
9	Sanderling	*Calidris alba*	LC
10	Grey plover	*Pluvialis squatarola*	LC
Species spending the non-breeding season primarily from Southeast Asia to the Yellow Sea:			
11	Spotted greenshank (also known as Nordmann's greenshank)	*Tringa guttifer*	EN
12	Asian dowitcher	*Limnodromus semipalmatus*	NT
13	Dunlin	*Calidris alpina*[b]	LC
14	Spoon-billed sandpiper	*Calidris* (*Eurynorhynchus*) *pygmeus*	CR
15	Eurasian oystercatcher	*Haematopus ostralegus osculans*	NT

[a] LC - Least Concern, NT – Near Threatened , VU – Vulnerable, EN – Endangered, CR – Critically Endangered, as listed in IUCN (2017).

[b] Among the four *C. alpina* subspecies occurring in the EAAF, only *C. a. arcticola* is listed as a 'coastal obligate'. Since subspecies cannot be distinguished in field observations, counts reported are of unknown subspecies, and site of importance for *C. alpina* are defined by counts ≥0.25% of the total population of all four *C. alpina* EAAF subspecies.

Table 5.S2. Locations and bird occurrence of the 92 sites where satellite-tracked great knots stopped in 2015–2017.

Site #	Site Name	Province/State/Region	Country/ Territory	Latitude	Longitude	Knowledge Status^{a}	Number of tracked great knots stopping		Length of stay (days)^{b}	
							North-ward	South-ward	North-ward	South-ward
1	Oebelo	East Nusa Tenggara	Indonesia	-10.063	123.737	UN	1^{c}			
2	Tibar	Liquica	Timor-Leste	-8.564	125.490	UN		1		
3	Namtabung	Maluku	Indonesia	-8.177	130.930	UN		1		10.4
4	Dosimar	Palau Trangan	Indonesia	-6.730	134.207	UN		1		15.4
5	Matandasa	Southeast Sulawesi	Indonesia	-4.719	122.419	UN		1		13.8
6	Buruway	West Papua	Indonesia	-3.712	133.478	UN		1		31
7	Pinrang	South Sulawesi	Indonesia	-3.680	119.475	UN	2		8.4	
8	Bahaur	Central Kalimantan	Indonesia	-3.416	113.897	UN		1		13.8
9	Pongko	South Sulawesi	Indonesia	-2.823	120.713	UN	1			
10	Sebakoeng	East Kalimantan	Indonesia	-1.636	116.514	UN	3		24.4	
11	Samarinda City	East Kalimantan	Indonesia	-0.685	117.416	UN	3		14	
12	Tarakan City	North Kalimantan	Indonesia	3.431	117.709	UN	1		13.3	
13	Mukah	Sarawak	Malaysia	3.033	112.602	UN	1			
14	Tawau	Sabah	Malaysia	4.277	118.128	UN	1	1	15.4	19.8
15	Sandakan	Sabah	Malaysia	5.463	118.887	UN	1			
16	Kampong Kaniogan	Sabah	Malaysia	6.244	117.725	UN	1^{c}			
17	Kota Belud	Sabah	Malaysia	6.393	116.333	UN	1^{c}			
18	Sibuguey Bay	Zamboanga Sibugay	Philippines	7.770	122.638	UN	1		0.9	
19	Ilog	Negros Occidental	Philippines	10.001	122.707	UN	2		0.5–11.2	
20	Maqueda Bay	Samar	Philippines	11.711	125.025	UN		1		18.5
21	Borongan, Asid Gulf	Masbate	Philippines	12.083	123.616	UN		1		29.2
22	Vịnh Vân Phong	Khánh Hòa	Vietnam	12.732	109.284	UN	1		7	
23	Donsol	Sorsogon	Philippines	12.915	123.584	UN	1		7.5	
24	Palauig Bay	Zambales	Philippines	15.419	119.898	UN	1		6.7	
25	Vịnh Dien Chau	Nghe An	Vietnam	18.978	105.619	UN	1		5.9	
26	Dongli, Leizhou	Guangdong	China	20.838	110.355	CO	1		6.9	
27	Hailingdao, Yangjiang	Guangdong	China	21.677	111.903	CO	2		2.1	

Table 5.S2. Continued.

Site #	Site Name	Province/State/Region	Country/ Territory	Latitude	Longitude	Knowledge Status[a]	Number of tracked great knots stopping		Length of stay (days)[b]	
							North-ward	South-ward	North-ward	South-ward
28	Jiangmen	Guangdong	China	22.039	113.085	CO	3		2.1–6.3	
29	Deep Bay (inc. Mai Po and Futian NR)	Hong Kong SAR & Guangdong	China	22.491	113.993	CO	1		8	
30	Jiadong	Pingtung	Taiwan	22.408	120.545	UN	1		8.7	
31	Huidong	Guangdong	China	22.807	114.829	UN	1		2.5	
32	Haifeng	Guangdong	China	22.824	115.254	CO	1		11	
33	Lufeng	Guangdong	China	22.858	115.631	UN	2		1.4–5.4	
34	Jiazi	Guangdong	China	22.875	116.090	UN	1		2.5	
35	Haimenwand	Guangdong	China	23.041	116.509	UN	1		2	
36	Dongshi	Chaiyi	Taiwan	23.456	120.151	UN	1		6.8	
37	Dacheng Bay and Zhao’an Bay	Guangdong and Fujian	China	23.630	117.247	UN	2		7–7.2	
38	Shoufeng	Hualien	Taiwan	23.877	121.572	UN	1		1.4	
39	Zhangpu	Fujian	China	24.000	117.744	UN	3		0.1–9.3	
40	Da'an	Taipei	Taiwan	24.381	120.578	UN	1		4.3	
41	Xiamen and Jinjiang Coast (inc. Dadengdao)	Fujian	China	24.618	118.486	CO	4		5.5–10.6	
42	Lanyang River Mouth	Yilan	Taiwan	24.711	121.839	CO	1		1.7	
43	Quangang	Fujian	China	25.151	118.962	CO	1		6.6	
44	South Fuzhou coastline	Fujian	China	25.673	119.666	CO	3		2.8–7.4	
45	**Wenzhou Bay**	**Zhejiang**	**China**	**27.822**	**120.834**	**CO**	**9**		**2.3–8.5**	
46	Linhai, Taizhou	Zhejiang	China	28.731	121.654	GK	2		0.7–5.6	
47	Gaotangdao	Zhejiang	China	29.117	121.751	UN	1		9.8	
48	Xiangshan Harbour	Zhejiang	China	29.645	121.855	UN	1		1.2	
49	Zhoushan	Zhejiang	China	29.980	122.227	UN	1		0.6	
50	Hangzhou Bay	Zhejiang	China	30.437	121.143	UN	3		1.1–3.9	
51	Tongzhou	Jiangsu	China	32.201	121.510	GK	4		1.1–5.3	
52	**Yangkou-Dafeng coast**	**Jiangsu**	**China**	**32.920**	**120.949**	**GK**	**5**	**5**	**0.7–5.2**	**0.7–13.5**

Table 5.S2. Continued.

							Number of tracked great knots stopping		Length of stay (days)[b]	
Site #	**Site Name**	**Province/State/Region**	**Country/ Territory**	**Latitude**	**Longitude**	**Knowledge Status[a]**	North-ward	South-ward	North-ward	South-ward
53	Sheyang	Jiangsu	China	33.899	120.457	CO	2	1	2–2.9	1.8
54	Boseong	Jeollanam-do	South Korea	34.615	127.092	UN	1		5.8	
55	Lianyungang and Lanshan	Jiangsu and Shandong	China	34.988	119.241	GK	2	3	7.8–26.6	17.2–19.8
56	Jimo	Shandong	China	36.611	120.899	UN	1		4.4	
57	Hwaseong	Gyeonggi-do	South Korea	37.068	126.722	GK	1		25.9	
58	Yonan	South Hwanghae	North Korea	37.796	125.964	UN	2	1	0.5–14.2	
59	Changyi	Shandong	China	37.132	119.422	CO	1	2	1.1	3.6–20.4
60	Hanting	Shandong	China	37.206	119.021	CO		1		7.5
61	Yellow River Delta	Shandong	China	37.690	119.132	GK	3	2	3.7–23.4	32.3
62	Wonsan	Kangwon	North Korea	39.194	127.661	UN		1		
63	Onchon	South Pyongan	North Korea	38.923	125.155	UN	1	1	14.4	
64	Pyongwon	South Pyongan	North Korea	39.291	125.413	UN		1		5.8
65	Kwaksan	South Pyongan	North Korea	39.566	125.054	UN	1		0.7	
66	Luannan and Fengnan Coast (inc. Nanpu)	Liaoning	China	39.140	118.155	GK		2		19.7
67	Daqinghekou	Liaoning	China	39.105	118.840	GK		2		1.6
68	Luanhekou	Liaoning	China	39.394	119.228	UN	1	1	14.6	1.1
69	Wafangdian[d]	Liaoning	China	39.502	121.459	UN	1		0.3	
70	**Liaohe (Shuangtaizi) Estuary and Inner Gulf of Liaodong**	**Liaoning**	**China**	**40.736**	**121.828**	**GK**	**15**	**9**	**3.2–37.6**	**2.2–36.1**
71	Dazheng, Zhuanghe	Liaoning	China	39.570	122.874	CO	1		0.6	
72	Qingduizi, Zhuanghe	Liaoning	China	39.759	123.336	GK	2		0.7	
73	**Yalu Jiang Estuary**	**Liaoning**	**China**	**39.814**	**123.967**	**GK**	**9**	**3**	**2.4–39.1**	**5.3–9.2**
74	Tyk Bay	Sakhalin Island	Russia	51.756	141.676	CO	1		0.5	
75	Nabilsky Bay	Sakhalin Island	Russia	51.663	143.341	CO		1		4.8
76	Schastya Bay	Khabarovsk	Russia	53.402	141.137	GK	1	4	1.8	6.5–25.3

Table 5.S2. Continued.

Site #	Site Name	Province/State/Region	Country/ Territory	Latitude	Longitude	Knowledge Status[a]	Number of tracked great knots stopping		Length of stay (days)[b]	
							North- ward	South- ward	North- ward	South- ward
77	Baykal Bay and Okha Coast	Sakhalin Island	Russia	53.549	142.446	CO	1	4	4.9	5.3–21.2
78	South of Ulbanskiy Bay, Turguskiy Bay and Konstantina Bay	Khabarovsk	Russia	53.763	137.214	GK		4		9.7–15.5
79	Nikolaya Bay	Khabarovsk	Russia	54.116	138.499	UN		1		0.3
80	Uda River Estuary	Khabarovsk	Russia	54.749	135.295	UN	3	3	0.1–5.5	5.2–19.8
81	Medyay River Estuary	Khabarovsk	Russia	55.434	136.195	UN		1		0.2
82	Moroshechnaya Estuary	Kamchatka	Russia	56.822	156.196	GK	3	2	2.7–5.4	10.9
83	Khayruzova-Belogolovaya Estuary	Kamchatka	Russia	57.085	156.628	GK	1	4	0.9	0.2–17.3
84	Utkholok River estuary	Kamchatka	Russia	57.524	157.085	UN		1		0.6
85	Karaga Bay and Ossora Bay	Kamchatka	Russia	59.199	163.023	UN		1		0.6
86	Uala Bay and Anapka Bay	Kamchatka	Russia	59.968	164.157	UN	1		2.2	
87	Okhotsk Town	Khabarovsk	Russia	59.373	144.664	UN		1		7.1
88	Inya	Khabarovsk	Russia	59.347	143.174	UN		1		5.9
89	Babushkina Bay	Magadan	Russia	59.238	154.423	CO	1		0.3	
90	Korfa Bay	Kamchatka	Russia	60.312	165.889	UN	1		0.7	
91	Rekkiniky Bay	Kamchatka	Russia	60.914	163.682	GK		1		10.6
92	Impoveyem Bay	Magadan	Russia	61.292	160.028	UN	1		1.4	

Sites visited by more than one-third of the tracked individuals within regions are depicted in bold. Centroid coordinates are displayed. [a] Knowledge Status: GK = known as key site for great knots, CO = known as key shorebird site for at least one coastal obligate species other than the great knot, UN = unknown as a shorebird site.

[b] We exclude from the length of stay calculation the individuals that were not tracked to the ‘next’ region, therefore this column is left blank for some sites.

[c] Sites visited by tracked individuals that aborted northward migration and went back to Australia after stopping in Southeast Asia. [d] Sites with limited location data (number of locations per site = 4); the centroid coordinates may not represent the exact site location.

Table 5.S3. Passage dates of satellite-tracked great knots in the East Asian-Australasian Flyway grouped by latitudinal intervals.

Latitudinal interval	**Passage dates**			
	Northward migration		Southward migration	
	All individuals	80% of individuals*	All individuals	80% of individuals*
56.5–63°N	21 May–3 Jun	22 May–1 Jun	27 Jun–14 Aug	1 Jul–10 Aug
51.5–56.5°N	22 May–6 Jun	23 May–4 Jun	27 Jun–20 Aug	5 Jul–3 Aug
36.5–41.5°N	10 Apr–4 Jun	20 Apr–19 May	19 Jul–8 Sep	30 Jul–28 Aug
30.9–36.5°N	7 Apr–20 May	10 Apr–15 May	3 Aug–9 Sep	10 Aug–3 Sep
26–30.9°N	31 Mar–12 May	5 Apr–2 May		
20.2–26°N	25 Mar–8 May	2 Apr –29 Apr		
14–20.2°N	30 Mar–21 Apr	31 Mar–20 Apr		
9–14°N	27 Mar–15 Apr	30 Mar–13 Apr	11 Sep–10 Oct	13 Sep–5 Oct
4–9°N	3 Apr–19 Apr	5 Apr–18Apr	3 Sep–23 Sep	5 Sep–21 Sep
1°S–4°N	29 Mar–17 Apr	1 Apr–14 Apr		
6–1°S	30 Mar–26 Apr	2 Apr–23 Apr	1 Sep–4 Oct	4 Sep–28 Sep
11–6°S			31 Aug–24 Sep	3 Sep–21 Sep

*Time period when 80% of individuals occurred, centred at the median date

Appendix S1

Survival of great knots with and without satellite transmitters

We compared the survival in the year after capture of adult great knots with transmitters ('tagged') with that of adult birds caught in the same periods that did not receive a transmitter ('untagged'). We only selected birds of age 3+ (i.e. 'in its third year of life or older'). This resulted in a sample size of 15, 26 and 26 tagged great knots and 17, 78 and 46 untagged great knots in September to October 2014, 2015 and 2016. We selected birds captured in Roebuck Bay, and used resightings in subsequent boreal winter years (2015–2018) in Roebuck Bay, where July 2015–June 2016 is referred to as winter year 2015. Consequently, our models estimated apparent (or local) survival, which is the product of true survival and the probability that birds do not permanently emigrate from Roebuck Bay. We tested for but did not find evidence for lack-of-fit of the data to the CJS-model, using program U-Care (Choquet et al. 2009). In all models, survival was estimated separately for the first year after capture and later years. We considered models where survival in the first year after capture did or did not differ between birds with or without a transmitter. Due to the limited number of years, we assumed survival to be the same in different years. For resighting probability, we considered models with and without annual variation in resighting probabilities.

In the most parsimonious model (Table A), untagged birds had higher survival (0.75 (95% CI: 0.64–0.83)) than tagged birds (0.52, 0.38–0.65) in the first year after capture. Survival in subsequent years was estimated at 0.76 (0.64–0.84) for all birds. This model did not include yearly variation in resighting probability. Overall, resighting probability was very high (0.85 (0.75–0.92)).

Table A. Model selection results.

Model	K	Deviance	ΔAICc	Weight
$\phi_{a1*g+a>1*g}\ p_t$	8	35.05	0.00	0.36
$\phi_{a1*g+a>1*g}\ p_c$	6	39.85	0.60	0.27
$\phi_{a1*g+a>1}\ p_t$	7	38.74	1.58	0.16
$\boldsymbol{\phi_{a1*g+a>1}\ p_c}$	5	43.00	1.67	0.16
$\phi_{a1+a>1}\ p_t$	5	46.04	4.71	0.03
$\phi_{a1+a>1}\ p_c$	3	51.14	5.69	0.02

a1 = first year after catching, a2+ = subsequent years, g = group (tagged versus non-tagged birds) and t = year.
The most parsimonious model is depicted in bold.

Data availability

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.f2g5f49 (Chan et al. 2019c).

Appendix S2

Estimation of the size of the great knot stopping population at Deep Bay, Hong Kong, from regular counts with information on individual stopping duration

The stopping duration estimated from the tracking data can be used to calculate the total number of birds using one site, as the sum of daily counts divided by staging duration. We applied this approach to counts collected in the Mai Po Marshes Nature Reserve in Deep Bay, Hong Kong, Southern China (22.49°N, 114.02°E) from 2015–2017 (Hong Kong Bird Watching Society unpublished data) as among the 92 stopping sites we identified from the tracking, this is the only site with frequent regular counts. Synchronised shorebird counts were conducted every three days in various high-tide roosts within the Reserve as part of a long-term monitoring program. For days without counts, we used a weighted mean of the real counts before and after the date concerned. To estimate the number of great knots using this site, we divided the sum of daily counts in Mai Po (averaged over the three years) by the stopping durations. We used the stopping durations of tracked great knots at all sites within 20.2–26°N (mean = 5.16 days, n = 20, range = 0.12–10.96 days). Mean and 95% confidence interval of the population size estimate was obtained by resampling the stopping durations 1000 times.

We estimated that 459 (95% CI: 387–558) great knots used this site. This is 2.2 (1.8–2.7) times the mean peak count of 210 birds in 2015–2017 (Hong Kong Bird Watching Society unpublished data).

BOX **A**

Bird-guided explorations of the Chinese coast: survey sites used by satellite-tracked shorebirds

Ying-Chi Chan & He-Bo Peng

In 2014 when we first deployed satellite transmitters onto Great Knots (*Calidris tenuirostris*) and Bar-tailed Godwits (*Limosa lapponica menzbieri*) in Roebuck Bay, Northwest Australia, several facts were known: (1) The study species, as well as many migratory shorebirds in the East Asian–Australasian Flyway (EAAF), were in steep decline (Conklin et al. 2014); (2) since 2011, survival rates of these two species and the Red Knot (*C. canutus piersmai*) have dropped significantly (Piersma et al. 2016; monitoring of survival rates by mark-resight methods since 2006); (3) the intertidal mudflats in the Yellow Sea which these shorebird populations (and many other shorebirds in the EAAF) depend on for fuelling up during migration (Barter 2002, Conklin et al. 2014) were under rapid loss due to land reclamation (Murray et al. 2014). Meanwhile, habitat destruction might not be the only pressing issue for migratory shorebirds using the Yellow Sea. Monitoring of benthic food resources for shorebirds at Yalu Jiang Estuary, an important Yellow Sea staging site, conducted yearly by Fudan University since 2011 (Choi et al. 2014) revealed a sharp decline in the main shorebird prey, the bivalve *Potamocorbula laevis* since 2013; the very high density in 2011 (708.06 ind/m^2) have declined by >99% in 2016 (Zhang et al. 2018).

While a threat like land reclamation can be assessed remotely from satellite images, as well as bird's migratory patterns by tracking with satellite tags, factors that are key to shorebird's fuelling at staging sites, most notably food availability, can only be assessed on-ground by sampling. Before 2015, systematic benthic sampling was conducted annually in only two Yellow Sea sites along the Chinese coast: at Luannan coast in Hebei Province in 2008–2014 by Hong-Yan Yang of Beijing Normal University (Yang et al. 2016) and at Yalu Jiang Estuary National Nature Reserve in Liaoning Province by Fudan University since 2011 (Choi et al. 2014, Zhang et al. 2018). From the Argos satellite transmitters deployed we can receive data of birds' locations in almost 'real-time', which makes it possible for us to 'follow' the satellite-tracked individuals on-ground. Utilizing this advantage, in 2015, the first year that we tracked the migration of the satellite-tagged individuals, we conducted an expedition during northward migration (April and May) surveying sites along the Chinese coast used by the tagged birds (Table A.1, Fig. A.1). The main focus was to collect data on the foraging ecology of the two focal species, Bar-tailed Godwits and Great Knots. At each site, grid sampling of benthic organisms was conducted to assess food availability, droppings were collected to understand prey choice, and foraging behaviour of individual birds was filmed to estimate food intake rates. Birds were counted, individual birds marked with leg bands were recorded, and threats to the habitats were also noted.

'Following' the tagged birds on-ground was logistically challenging since most sites were new to us: once the tracking data indicated that a tagged bird stopped at a site, we had to arrange transport to get to the site, find ways to access the mudflat, find the big flocks to count and make observations, find a place to sleep and store our samples, etc., all to be done before the birds departing the site to migrate further north. Even though we only managed to collect bird and benthos data at five out of the eight places we visited (Table A.1), key discoveries have resulted from our first year of surveys in 2015: first, the discovery of Gaizhou, Liaoning Province, as a key site for Great Knots with over 60,000 individuals counted (Melville et al. 2016b); second, a very high count of

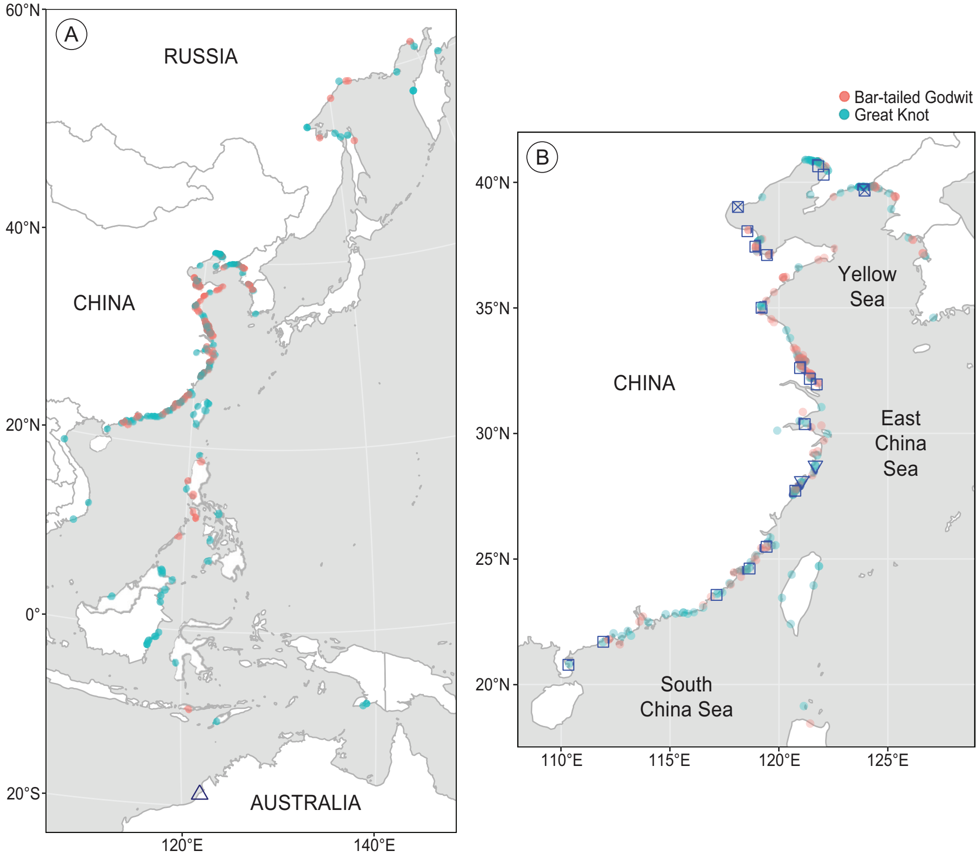


Figure A.1. (**A**). Coastal stopping sites of satellite-tracked Bar-tailed Godwits and Great Knots during northward migration in 2015–2018. (**B**) Surveyed sites along the Chinese coastline in 2015–2018 (see Table A.1 for details). Squares denote sites where benthic sampling, foraging observations and counts were conducted; triangles are sites that only counts were conducted. Squares with a cross indicate Luannan coast and Yalu Jiang Estuary that were already surveyed annually prior to 2015.

>100,000 shorebirds of multiple species was recorded at Lianyungang, Jiangsu Province, and benthic sampling revealed the mudflats there contain high densities of *Potamocorbula laevis* (Chan et al. 2019a), a key prey for shorebirds (Yang et al. 2013, Choi et al. 2017). These discoveries were greatly facilitated by the relatively higher-accuracy locations (error <2.5 km; Douglas et al. 2012) of Argos satellite tags, from which we could locate roosting and feeding areas that birds congregated, therefore narrow down our search within a large area.

One surprising discovery from the satellite tracks of Great Knots in 2015 (the first time ever that this species was tracked) was that, many Great Knots were stopping in southern China coast (Fig. A.1); this region was not regarded as important for Great Knots before our tracking study. To understand the function of these southern China sites, in 2016 we started to also survey in southern China in early to mid-April (Table A.1). As Great Knots only stopped for 9.4 ± 3.5 d in southern China (Chan et al. 2019b),

Table A.1. Surveyed sites along the Chinese coast in April and May 2015–2018.

Site name and Province	**Latitude** (°N)	**Longitude** (°E)	**Benthic sampling and counts conducted**				**Survey dates in 2018**
			2015	2016	2017	2018	
Panjin, Liaoning Province	40.76	121.86		x	x	x	26–27 April
Gaizhou, Liaoning Province	40.45	122.23	x	x	x	x	24–25 April
Yalujiang, Liaoning Province*	39.80	123.93	x	x	x	x	16–29 April
Luannan, Hebei Province#	39.08	118.20	x	x	x	x	23–30 May
Diaokou, Shandong Province	38.09	118.58		x	x	x	13–14 May
Nanhaipu, Shandong Province	37.46	118.94				x	16–18 May
Changyi, Shandong Province	37.14	119.49		x	x	x	11–12 May
Lianyungang, Jiangsu Province	35.01	119.21	x	x	x	x	4–8 May
Xinchuangang, Jiangsu Province	32.63	120.99		x	x	x	20–22 April
Tongzhou, Jiangsu Province	32.18	121.43	x	x	x	x	19 April
Qidong, Jiangsu Province	32.00	121.78		x	x	x	17–18 April
Cixi, Zhejiang Province	30.40	121.19			x	x	13–15 April
Linhai, Zhejiang Province	28.73	121.67			Counts only		13–14 April 2017
Yueqing, Zhejiang Province	28.11	121.04				Counts only	13 April
Ruian, Zhejiang Province	27.73	120.76			x	x	12 April
Xinghuawan and Fuqingwan, Fujian Province	25.49	119.44				x	10–11 April
Shenhu, Fujian Province	24.62	118.66				x	9–10 April
Raoping, Guangdong Province	23.59	117.14		x	x	x	7–8 April
Hailingdao, Guangdong Province	21.71	111.94			x	x	5–6 April
Dongliaodao, Guangdong Province	20.83	110.38		x	x	x	2–4 April

*Benthic surveys are conducted annually by Fudan University since 2011. Counts are organized by Mr. Qingquan Bai, China Coastal Waterbird Census.

#Counts were conducted together by Beijing Normal University and Global Flyway Network.

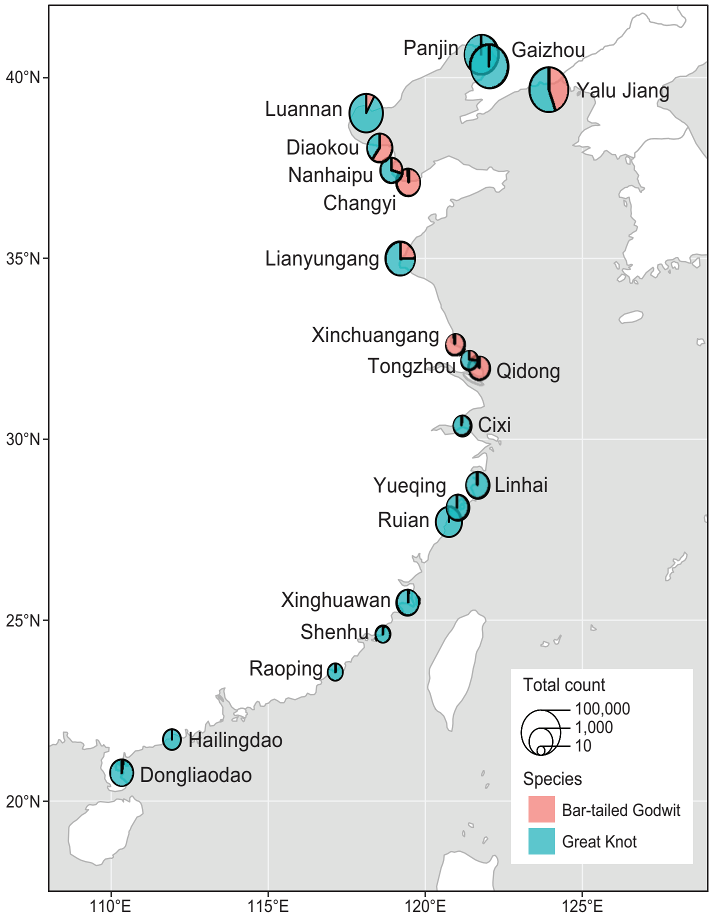


Figure A.2. Maximum counts of Great Knots and Bar-tailed Godwits at surveyed sites along the coast of China in spring 2015–2018. Counts at Yalu Jiang are extracted from Zhang et al. (2018).

the time window when our target species were present (so that we could do foraging observations) was as short as only about a week at some sites. This made it necessary for fieldwork to be conducted at a fast pace! As we gained experience, we could cover more sites every year. In 2018, benthic sampling, foraging observations and bird counts were conducted in 18 sites along the Chinese coast (at 17 sites by our team and at Yalu Jiang by Fudan University), and we additionally conducted bird counts at two southern China sites (Table A.1). We continued the monitoring of these sites in 2019, 2020 and 2021, in expeditions led by He-Bo Peng in the lab of Prof. Guangchun Lei of Beijing Forestry University.

A summary of the counts of Bar-tailed Godwits and Great Knots in 2015–2018 revealed smaller bird numbers in the southern China sites (in magnitudes of 100s–1,000s) compared to the Yellow Sea sites, and largest numbers (>10,000) occurred at the northernmost sites (Luannan coast, Panjin and Gaizhou at Liaohe Estuary, and Yalu Jiang Estuary; Fig. A.2). The low number of Great Knots in southern China can partly be explained by the fast turnover rate that more birds could have used the site than the peak count (Chan et al. 2019b). Also, since we only surveyed each site for about 2 days, we might not have encountered the peak numbers. Despite these circumstances, we have identified five sites (Dongliaodao, Xinghuawan and Fuqingwan, Ruian, Yueqing and Linhai) with >0.25% of Great Knot's world populations. Our counts have complimented existing citizen science count programmes, such as the China Coastal Waterbird Census (Bai et al. 2015), by surveying lesser-known and non-monitored sites.

We have collected a wealth of data on foraging ecology of shorebirds at these sites. Benthic sampling in 2018 revealed that the most abundant species being *P. laevis* (>57%), followed by *Sinonovacula constricta* (9%) and *Moerella iridescens* (6%). All these species are soft-shelled bivalves which are high quality food for shorebirds, especially for the Great Knot which is a mollusc-specialist (Choi et al. 2017, Zhang et al. 2019a). However, the distribution of these species was not even along the coast. Densities of these common prey species, as well as the total density of all mollusc species, were relatively low in the northernmost sites – the Yalu Jiang Estuary and Liaohe Estuary (including Panjin and Gaizhou), compared to other sites we sampled. Nevertheless, we counted the highest numbers of Great Knots there amongst all sites (Fig. A.2). These sites were also visited by more than one-third of the satellite-tracked Great Knots, some of which stayed there for more than a month before departing the Yellow Sea to their breeding grounds (see Chan et al. 2019b for details). Since all these findings indicate the importance of these northern Yellow Sea sites for Great Knots to fuel up during northward migration, the mismatch between bird numbers and densities of high-quality prey is worrying. In contrast, sites in southern China contained high densities of high-quality bivalve prey (Fig. A.3), which allowed rapid fuelling for Great Knots arriving from a long flight from the wintering site in Northwest Australia.

During our expeditions we witnessed lots of human activities at intertidal areas that could negatively impact shorebirds and their benthic prey. Direct intervention on the benthic fauna community includes manual and machinery harvesting of shellfish and polychaetes, as well as activities surrounding the farming of commercial species on mudflats, such as collecting young shellfish for seeding in other mudflats and spraying pesticides to kill competing species (Fig. A.4). All these activities also generated disturbance to foraging shorebirds. Moreover, certain practices directly kill shorebirds, including the use of fine-meshed nets to 'protect' small razor clams (*S. constricta*) from being eaten by shorebirds, and nets for catching fish and shrimps (Fig. A.4). The impact of intertidal and supratidal windfarms on shorebirds is not known, but shorebirds might collide with wind turbines especially at night and in foggy weather. Wind turbines might also deter shorebirds to forage or roost close by (Fig. A.4).

Guided by the satellite-tracked birds, we have developed a ground monitoring programme spanning >20 latitudinal degrees and thousands of kilometres along the Chinese coastline. This unique dataset enables investigations on how populations of

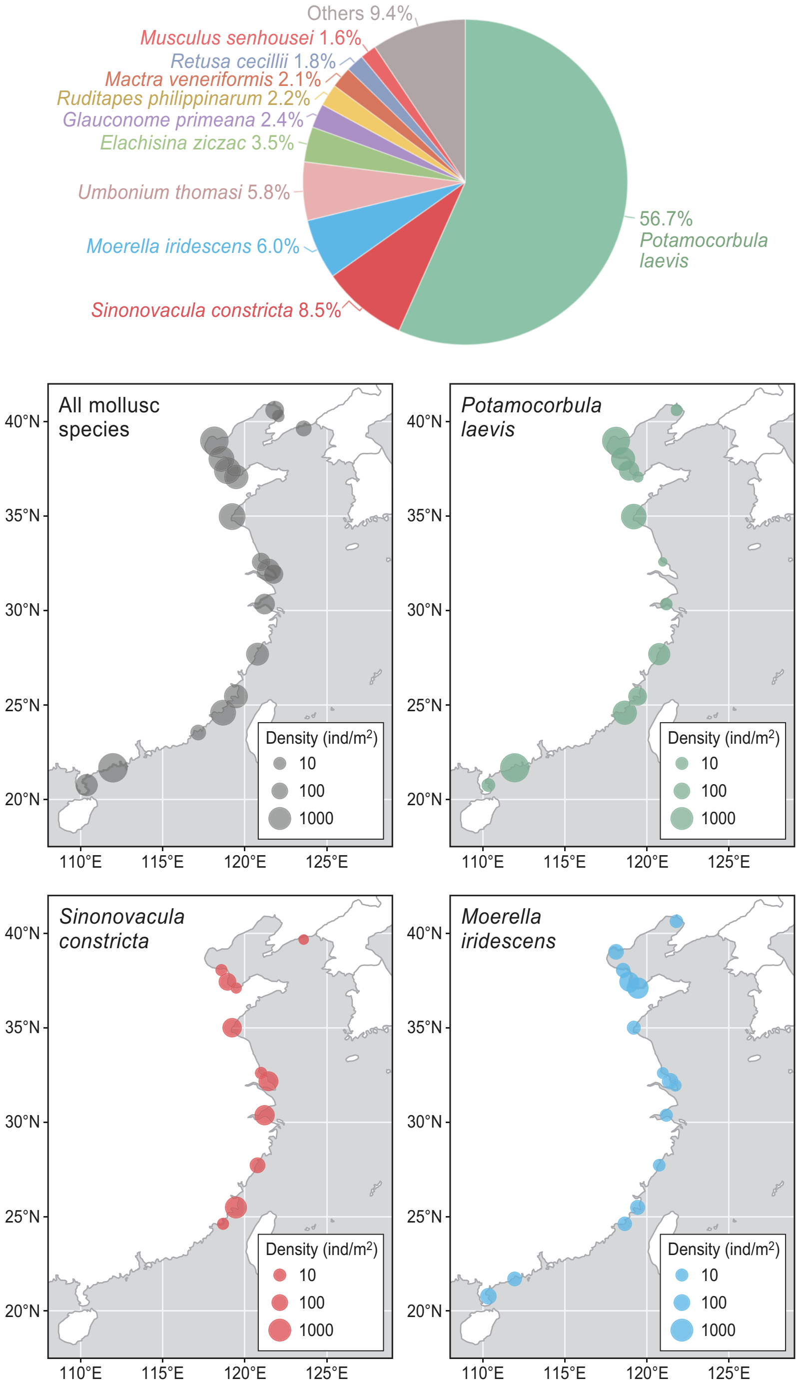


Figure A.3. Overall species composition and distribution of molluscs at 18 sites along the coast of China in April and May 2018.

Manual harvesting of shellfish (left) and polychaetes (right) occurred in most southern China and Jiangsu Province sites that we surveyed. The harvests were very labour-intensive, often involved hundreds of fishermen on mudflats, creating frequent disturbance to shorebirds foraging nearby.

Machinery harvesting of shellfish was common in Bohai Bay (left), which disturbed the top layer of the mudflat (right).

Young *Meretrix* clams (2–3 cm) were harvested at Rudong, Jiangsu Province and transported to mudflats in southern China for farming.

At Tongzhou, Jiangsu Province, fishermen sprayed triazophos solution onto the mudflat to kill polychaetes that were believed to kill the razor clams that the fishermen seeded.

(left) At Yueqing, Zhejiang Province, dense layers of fine-meshed nets were set up on mudflats to trap shorebirds attempting to prey onto the small razor clams seeded on the mudflats. (right) Fishing nets, often already abandoned, killed shorebirds being trapped.

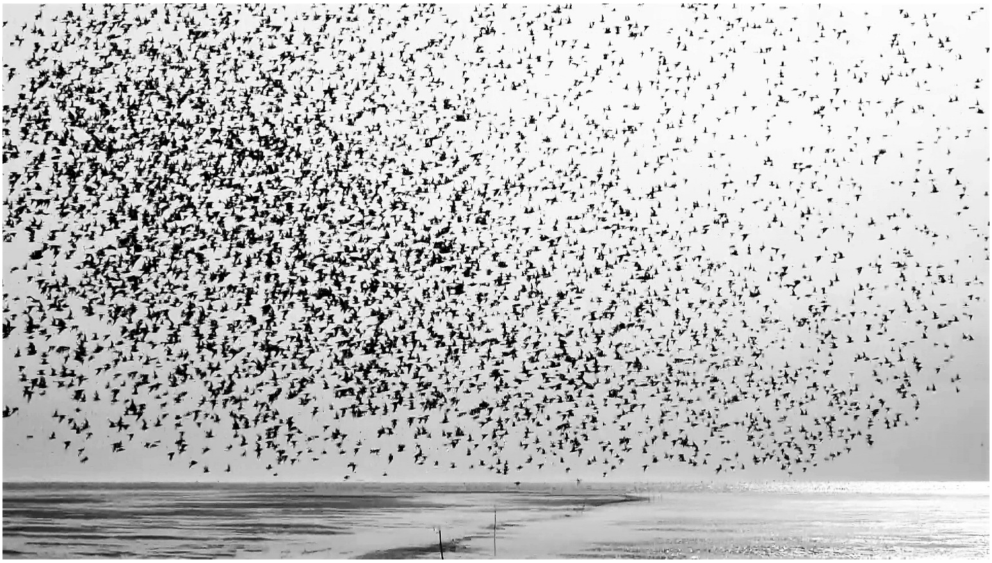
Intertidal windfarms and fishing nets at Rudong, Jiangsu Province.

Figure A.4. Examples of threats to shorebirds recorded at sites along the Chinese coast in April and May 2015–2018.

threatened shorebirds react to environmental changes based on details on foraging ecology. In-depth analysis on the benthic fauna and foraging ecology of shorebirds along these Chinese sites, with a focus on effects of aquaculture practices (led by He-Bo Peng), are in progress. All the data collected on-ground are critical to achieve conservation and effective management of the key shorebird sites (see Chan et al. 2019a for further elaborations). The continuation of this yearly monitoring programme would be of great value to detect threats or environmental deterioration that emerge in the future and the corresponding responses of shorebirds, and also hopefully to document future recoveries of shorebirds in this region. We hope our experience stimulates the initiation of similar endeavours of ground surveys guided by information from satellite tracking to be conducted at sites in Southeast Asia (Fig. A.1) and other parts of the world.

Acknowledgements

We thank all the dedicated volunteers who participated in the China expeditions in 2015–2018, as well as the volunteers who helped with processing of benthic samples, video recordings and data entry. We thank Prof. Zhijun Ma who provided laboratory space and resources for analysing the benthic samples. The purchase of satellite transmitters was supported by the MAVA Foundation, Switzerland and the NWO Spinoza Premium awarded to Theunis Piersma in 2014. The ground surveys in 2016 and 2017 were funded by a KNAW China Exchange Programme grant awarded to Theunis Piersma in collaboration with Prof. Zhijun Ma of Fudan University. Research funds of Zhijun Ma’s lab provides additional support for the fieldwork in China in 2015–2018.



Great Knot flock at Gaizhou, Liaoning Province, China on 9th May 2015.

CHAPTER 6

Conserving unprotected important coastal habitats in the Yellow Sea: Shorebird occurrence, distribution and food resources at Lianyungang

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Abstract

The Yellow Sea coastline in East Asia, an important staging area for migratory shorebirds in the East Asian–Australasian Flyway (EAAF), is rapidly deteriorating. Conserving the declining shorebird populations that rely on the Yellow Sea requires habitat protection and management based on sound ecological knowledge, especially on the seasonal occurrence of shorebirds, their daily movements and their food resources. However, in this region such ecological data are scarce, and expertise to collect them are less-established. Here we gather and assimilate such information for the coastal wetlands at Lianyungang on the Chinese Yellow Sea coast, an understudied and unprotected area where we found 27% of intertidal soft sediment habitats have been destroyed in 2003–2018 by reclamation. In 2008–2018, 43 shorebird species were recorded along this coastline, including 12 globally threatened or 'Near Threatened' species. In terms of number of shorebird species exceeding 1% of the EAAF population, with 22 species meeting this criterion, Lianyungang ranks highest among the >300 shorebird sites in East Asia. The benthic mollusc community of the intertidal flats were dominated by small soft-shelled bivalve species at very high densities, including 9,399 individuals/m^2 of *Potamocorbula laevis*, which are high-quality food for shorebirds to refuel during migration. Satellite tracked bar-tailed god-wits (*Limosa lapponica*) and great knots (*Calidris tenuirostris*) stopped at Lianyungang for 5–30 days during northward and southward migration. The tidal movements of satellite-tagged birds indicated high-tide roosts and low-tide foraging areas, some of which are inaccessible on-ground. These movements can also be used to evaluate whether roosts and foraging areas are close enough to each other, and direct where to create new roost sites. Potential measures to increase the capacity of Lianyungang to support shorebirds include reducing human disturbances, creating roosts at undeveloped parts of the reclaimed land, and removing recently-built sea dikes to restore intertidal flats.

Introduction

The conservation of migratory shorebirds in the East Asian-Australasian Flyway (EAAF) has progressed in the past decades through field research that collected baseline information primarily on bird numbers (Barter 2002, Bai et al. 2015). This has resulted in the discovery and recognition of major staging sites, many of which are in the Yellow Sea (Conklin et al. 2014). However, many coastal sites along the EAAF are undergoing extensive habitat loss and degradation (Murray et al. 2014, 2015, Melville et al. 2016, Piersma et al. 2016). Habitat loss in the Yellow Sea is suggested to be the main driver of declines in adult survival for shorebird populations migrating annually along the EAAF (Piersma et al. 2016), resulting in decreasing bird numbers, especially for those populations that rely the most on the coastal staging areas along the Yellow Sea (Studds et al. 2017).

In the recent years, the governments in the Yellow Sea region have recognised the ecological value of their coastlines and are committing to protect them (Melville 2018). In 2017, the Chinese government included 14 coastal sites in the Yellow Sea in a tentative nomination as UNESCO World Heritage (UNESCO 2017) and released new policies regarding wetland protection and restoration, including the suspension and reconsideration of commercial reclamation at intertidal areas (Melville 2018, Zhao 2018). The design of effective protection and restoration measures needs to be based on solid ecological knowledge at the local scale, such as shorebird's habitat use and prey availability. Such knowledge is inadequate in many countries in East and Southeast Asia (Hua et al. 2015), the likely reason being the shorter history of science-based site management (Lee & Khim 2017) and limited citizen science capacities (e.g. only one in about 65000 people in China are birdwatchers in 2010, Ma et al. 2013b).

To exemplify how the gathering and assimilation of local ecological knowledge may facilitate ecosystem- and bird-friendly management, and to directly fill a key knowledge gap for conservation of the Yellow Sea region, we present the information needed for managing one of the proposed World Heritage sites in the Yellow Sea that is particularly understudied and unprotected, the Lianyungang Coast (34.5–35.2°N, 119.1–119.7°E) in northern Jiangsu Province, China. We first establish the site's importance for shorebirds based on counts conducted in 2008–2018. We also assess the site's importance by the staging duration of satellite-tagged shorebirds. To identify the shorebird habitats along the Lianyungang Coast that require protection and management, we describe how shorebirds use current coastal habitats from our on-the-ground observations and from local movements of the satellite-tagged individuals. Since land reclamation has reduced the area of intertidal flats in the Yellow Sea substantially (Murray et al. 2014), we describe coastal habitat changes along the Lianyungang Coast by measuring rate of coastal reclamation and mapping current status of the reclaimed coastal land from satellite images. We also assess the quality of the intertidal feeding habitat by estimating densities of benthic shellfish, the staple food of many shorebird species (Tulp & de Goeij 1994, Yang et al. 2013, Choi et al. 2017, Zhang et al. 2019a).

Material and methods

Study area and background

Our study area comprises the entire 162 km coastline of Lianyungang City, Jiangsu Province, China (34.5–35.2°N, 119.1–119.7°E), in the southern Yellow Sea. The salt ponds along this coastline were listed as an IBA in 2009 (BirdLife International 2018a) and were proposed as a tentative World Heritage site in 2017 (UNESCO 2017). The proposal was based on the over 18,000 shorebirds detected in the salt ponds on a single survey in 2004 (Barter & Xu 2004). Salt production in Lianyungang has a history of over 1,100 years, but declined after the discovery of nearby salt mines in the 1980s. The over 500 km^2 of salt ponds were steadily converted to aquaculture and industrial uses and are almost non-existent today (Xie & Gao 2011; pers. obs.). Currently, most of the coastline is enclosed by man-made seawalls with aquaculture ponds on the landward side and intertidal flats and rocky coast on the seaward side. During the 2004 survey of the northern portion of these intertidal flats, over 15,000 shorebirds were counted (Barter & Xu 2004).

Bird surveys

To describe the number of birds using this coastline, we summarised citizen science count data of the Chinese Coastal Waterbird Census (Bai et al. 2015). These counts were conducted between February 2008 and May 2018 at eight areas along the coast (Fig. 6.1), covering all the main shorebird habitats (for details see Table 6.A.1). For all shorebirds, we present the maximum numbers and whether the numbers have exceeded 1% of the EAAF population estimates (Conklin et al. 2014), and conservation status (i.e., Near Threatened, Vulnerable, Endangered, Critically Endangered; IUCN, 2017). We also present the maximum counts of waterbird species of other families with numbers that had exceeded 1% of the EAAF population (Wetlands International 2019) and/or listed as 'Near Threatened' or above in the IUCN Red List (IUCN 2017). Physical habitat characteristics were noted during some count sessions in spring 2015–2018 (Table 6.A.1).

Satellite tracking

We characterize bird movements from the tracking data of six great knots and six bar-tailed godwits (maximum counts of these two species at Lianyungang exceed 1% of their EAAF population, Table 6.1) which staged at the Lianyungang Coast during 2015–2018. Solar Platform Terminal Transmitters (PTTs, Microwave Telemetry, USA) of 4.5 and 9.5 g were deployed onto great knots and bar-tailed godwits, in September and October 2014, 2015 and 2016, and February 2017, at the northern beaches of Roebuck Bay, Broome, Northwest Australia (17.98˚S, 122.31˚E). PTTs were programmed to operate on a duty cycle of 8 h on and 25 h off. Positions were received from Argos (Collecte Localization Satellites, CLS 2015). The work was carried out under Regulation 17 permits SF 010074, SF010547 and 01-000057-2 issued by the West Australian Department of Biodiversity, Conservation and Attractions.

For migration timing analysis, we kept all standard Argos locations (i.e. the location classes 3, 2, and 1) and removed implausible auxiliary locations (i.e. classes 0, A, B and Z) by applying the Hybrid Douglas filter (Douglas et al., 2012). The filtering parameters were set at 120 km/h for the maximum sustainable rate of movement and 10 km for the minimum redundant distance. To calculate arrival and departure times to Lianyungang of each bird, the first point with speed <20 km/h within the site boundary was defined as the first point recorded when the individual stopped at Lianyungang, the same for the last point. Arrival times were estimated by extrapolating the average speed of a non-stop flight over the intervening distance between the first stopping point and the previous in-flight point i.e. bird was moving at >20 km/h or was >50 km away from the shoreline. If the previous point was a stop, we assumed that the flight from the previous site occurred at the mid-point of the time interval between the two. We estimated departure times in the same way. Staging duration is the difference between estimated arrival and departure times. Given that the Yellow Sea is the main staging area for both species during northward and southward migrations (Battley et al. 2012, Chan et al. 2019b), to assess whether Lianyungang is a major refuelling site for an individual's migration, we expressed staging duration at Lianyungang as a percentage of an individual's total staging duration within the Yellow Sea (calculated in the same way as described above; the Yellow Sea is defined as locations between the latitudes 30.9 and 41.5°N).

For the analysis of local distributions and movement, we only used standard locations, as the auxiliary locations have an error radius that is too large for the size of our study area (Douglas et al., 2012). These standard locations were classified as being collected at low or high tide using water level predictions from the China Seas Regional model of the Oregon State University Tidal Prediction Software (http://volkov.oce.orst.edu/tides/otps.html; Egbert & Erofeeva 2002). Since some tracking data points were on land where there were no water level predictions, for each tracking point, we extracted the predicted water level at its nearest point along a transect at sea, 500 m away from and parallel to the coastline. A point is assigned as ‘high tide’ if the predicted water level is higher than 0.5 m, which is the 60% quantile of a sample of predicted water levels (every 10 min for a month) along this transect, or is assigned as ‘low tide’ if the water level is lower than 0.5 m (the 40% quantile).

We visualized high- and low-tide locations in heatmaps based on Kernel Density Estimation, using the ‘Heatmap’ plugin in QGIS 2.18.11 (QGIS Development Team 2019). The radius of each point was two times the published 68% percentile error radius (Douglas et al. 2012) and weighed by the inverse of this radius, and therefore each point is designated as the same ‘heat’, but is more concentrated (for class 3 locations) or spread out (for the less precise class 2 and 1 locations). We used locations at least 1 h apart from one another. If there were more than 1 locations within the hour, we chose the point with highest accuracy, or the earliest point in the case of ties. To describe daily movements, we calculated distances between pairs of points of the same individual within a high-tide, within a low-tide, and between consecutive high- and low-tide, using points that were more than 1 h apart.

Table 6.1. Maximum counts of shorebird species along the Lianyungang Coast in 2008–2018, sorted by English common name. Species with counts exceeding 1% of the EAAF population are in bold. IUCN Red List status in parentheses (NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered). [m] indicates species observed to occur on intertidal mudflats.

Species	**1% of EAAF Population**	**Maximum count, date and location**					
		Northward Migration (March–June)		Southward Migration (July–November)		Wintering Period (December–February)	
Asian Dowitcher (NT) [m] *Limnodromus semipalmatus*	230	**7000**	12 May 2018 Xingzhuanghe-Qingkouhe	**1000**	17 Jul 2017 Xingzhuanghe-Qingkouhe		
Bar-tailed Godwit (NT) [m] *Limosa lapponica*	2790	**4702**	14 Apr 2013 Xingzhuanghe-Qingkouhe	2700	25 Jul 2015 Linhonghe	8	19 Feb 2017 Xingzhuanghe-Qingkouhe
Black-tailed Godwit (NT) [m] *Limosa limosa*	1390	**19810**	5 May 2018 Xingzhuanghe-Qingkouhe	**4423**	7 Aug 2012 Linhonghe & Liezikou		
Black-winged Stilt *Himantopus himantopus*	250–1000	88	Jun 2010 Linhonghe	350	25 Jul 2015 Linhonghe	6	11 Jan 2015 Xingzhuanghe-Qingkouhe
Broad-billed Sandpiper [m] *Calidris falcinellus*	250	**720**	5 May 2018 Xingzhuanghe-Qingkouhe	105	12 Sep 2015 Xingzhuanghe-Qingkouhe		
Common Greenshank [m] *Tringa nebularia*	1000	600	May 2008 Linhonghe	694	7 Aug 2012 Linhonghe	8	15 Jan 2011 Liezikou
Common Redshank [m] *Tringa totanus*	1000	500	May 2008 Linhonghe	241	7 Aug 2012 Linhonghe	130	Dec 2008 Linhonghe
Common Sandpiper *Actitis hypoleucos*	500	3	9 May 2011 Linhonghe	10	Jul 2008 Linhonghe		
Common Snipe *Gallinago gallinago*	1000–10000	5	1 Apr 2014 Xingzhuanghe-Qingkouhe	3	Oct 2010 Liezikou	1	Dec 2008 Linhonghe
Curlew Sandpiper (NT) [m] *Calidris ferruginea*	1350	**2500**	16 May 2014 Xingzhuanghe-Qingkouhe	12	25 Jul 2015 Linhonghe	8	27 Jan 2018 Xingzhuanghe-Qingkouhe
Dunlin [m] *Calidris alpina*	6500	**14000**	May 2008 Linhonghe	**8000**	22 Oct 2017 Linhonghe	**7500**	13 Dec 2015 Xingzhuanghe-Qingkouhe
Far Eastern Curlew (EN) [m] *Numenius madagascariensis*	320	300	16 Apr 2017 Xingzhuanghe-Qingkouhe	**543**	23 Oct 2016 Xingzhuanghe-Qingkouhe	30	27-Jan 2018 Xingzhuanghe-Qingkouhe
Eurasian Curlew (NT) [m] *Numenius arquata*	1000	**1110**	18 Mar 2017 Xingzhuanghe-Qingkouhe	825	25 Nov 2017 Xingzhuanghe-Qingkouhe	**2400**	11 Jan 2015 Xingzhuanghe-Qingkouhe
Eurasian Oystercatcher (NT) *Haematopus ostralegus*	110	**406**	16 Mar 2013 Xingzhuanghe-Qingkouhe	70	10 Nov 2013 Xingzhuanghe-Qingkouhe	**3130**	11 Jan 2015 Xingzhuanghe-Qingkouhe
Great Knot (EN) [m] *Calidris tenuirostris*	2900	**4520**	8 May 2018 Xiuzhenhe	**2968**	8 Aug 2012 Xingzhuanghe-Qingkouhe	350	27 Jan 2018 Xingzhuanghe-Qingkouhe

Table 6.1. Continued.

Species	1% of EAAF Population	Maximum count, date and location					
		Northward Migration (March–June)		Southward Migration (July–November)		Wintering Period (December–February)	
Greater Sand Plover *Charadrius leschenaultii*	790	270	1 May 2016 Mutaohe	130	Oct 2010 Liezikou	6	27 Jan 2018 Xingzhuanghe-Qingkouhe
Green Sandpiper *Tringa ochropus*	250–1000	6	8 May 2018 Mutaohe	4	Oct 2010 Linhonghe	4	12 Feb 2012 Huaguoshan Reservoir
Grey Plover [m] *Pluvialis squatarola*	1040	**8870**	16 Mar 2013 Xingzhuanghe-Qingkouhe	**3500**	19 Aug 2015 Xingzhuanghe-Qingkouhe	**3000**	20 Feb 2018 Xingzhuanghe-Qingkouhe
Grey-headed Lapwing *Vanellus cinereus*	250–1000	6	12-Mar 2011 Liezikou	8	Oct 2010 Linhonghe		
Grey-tailed Tattler (NT) [m] *Tringa brevipes*	440	25	9 May 2011 Liezikou	25	Aug 2010 Liezikou		
Kentish Plover *Charadrius alexandrinus*	1000	**2000**	Mar 2010 Linhonghe	**2500**	14 Oct 2012 Linhonghe	100	Feb 2008 Linhonghe
Lesser Sand Plover [m] *Charadrius mongolus*	385[a]	**750**	12 May 2013 Xingzhuanghe-Qingkouhe	**1425**	19 Aug 2016 Linhonghe	60	27 Feb 2018 Xingzhuanghe-Qingkouhe
Little Ringed Plover *Charadrius dubius*	250	10	16 Apr 2017 Xingzhuanghe-Qingkouhe	60	26 Jul 2011 Linhonghe		
Little Stint *Calidris minuta*	NA	1	10 Apr 2014 Linhonghe	1	8 Sep 2012 Liezikou		
Long-billed Dowitcher *Limnodromus scolopaceus*	NA	3	15 Apr 2011 Linhonghe				
Long-toed Stint *Calidris subminuta*	250	4	9 May 2011 Linhonghe	**600**	21 Jul 2012 Liezikou		
Marsh Sandpiper [m] *Tringa stagnatilis*	1000–10000	4150	18 Apr 2015 Xingzhuanghe-Qingkouhe	600	Sep 2010 Linhonghe	145	27 Jan 2018 Xingzhuanghe-Qingkouhe
Nordmann's Greenshank (EN) *Tringa guttifer*	12	77	12 May 2018 Xingzhuanghe-Qingkouhe	**40**	11 Oct 2015 Xingzhuanghe-Qingkouhe		
Oriental Pratincole *Glareola maldivarum*	28000	6	9 May 2011 Linhonghe	1	Oct 2010 Liezikou		
Pacific Golden Plover [m] *Pluvialis fulva*	1000	240	22 Apr 2014 Xingzhuanghe-Qingkouhe	4	15 Oct 2011 Linhonghe	1	14 Dec 2011 Linhonghe
Pied Avocet [m] *Recurvirostra avosetta*	1000	**7000**	3 Apr 2016 Xingzhuanghe-Qingkouhe	**11000**	18 Oct 2014 Xingzhuanghe-Qingkouhe	**7000**	13 Jan 2012 Linhonghe

Table 6.1. Continued.

Species	1% of EAAF Population	Maximum count, date and location					
		Northward Migration (March–June)		Southward Migration (July–November)		Wintering Period (December–February)	
Red Knot [m] *Calidris canutus*	990	**4010**	1 and 2 May 2017 Xingzhuanghe-Qingkouhe & Xiuzhenhe	300	12 Aug 2009 Liezikou	35	27 Jan 2018 Xingzhuanghe-Qingkouhe
Red-necked Phalarope *Phalaropus lobatus*	1000–10000			4	10 Sep 2017 Xingzhuanghe-Qingkouhe		
Red-necked Stint (NT) [m] *Calidris ruficollis*	3150	**4900**	18 Apr 2015 Xingzhuanghe-Qingkouhe	**6837**	8 Aug 2012 Liezikou	250	27 Jan 2018 Xingzhuanghe-Qingkouhe
Ruddy Turnstone [m] *Arenaria interpres*	285	85	5 May 2018 Xingzhuanghe-Qingkouhe	90	12 Aug 2009 Liezikou		
Ruff *Calidris pugnax*	NA	8	16 Apr 2011 Linhonghe	6	10 Sep 2017 Xingzhuanghe-Qingkouhe		
Sanderling *Calidris alba*	220	**232**	May 2010 Liezikou	200	Nov 2010 Liezikou	25	14 Feb 2011 Haitou
Sharp-tailed Sandpiper [m] *Calidris acuminata*	1600	**8000**	May 2008 Linhonghe	**3000**	19 Aug 2015 Xingzhuanghe-Qingkouhe	80	27 Jan 2018 Xingzhuanghe-Qingkouhe
Spoon-billed Sandpiper (CR) *Calidris pygmaea*	6[b]	1	22 Apr 2014 Xingzhuanghe-Qingkouhe	2	16 Sep 2016 Linhonghe		
Spotted Redshank [m] *Tringa erythropus*	250	**406**	16 Apr 2011 Linhonghe & Liezikou	**250**	26 Jul 2011 Linhonghe	48	17 Dec 2011 Liezikou
Terek Sandpiper [m] *Xenus cinereus*	500	**650**	16 Jun 2012 Linhonghe	180	10 Sep 2017 Xingzhuanghe-Qingkouhe		
Whimbrel [m] *Numenius phaeopus*	550	40	13 Jun 2009 Linhonghe	87	12 Aug 2009 Liezikou	1	27 Jan 2018 Xingzhuanghe-Qingkouhe
Wood Sandpiper *Tringa glareola*	1000	100	May 2008 Linhonghe	12	8 Sep 2012 Liezikou		

[a] For Lesser Sand Plover, the 1% threshold is derived from the population estimates of the two populations using the Yellow Sea coast (*C. m. mongolus* and *C. m. stegmanni*).
[b] For Spoon-billed Sandpiper, the 1% threshold is derived from Clark et al. (2018).

Mapping changes in intertidal area

Coastal reclamations were mapped from satellite images from January 2003 to June 2018. Landsat and Sentinel-2 images of 30 m resolution were visualized in Google Earth Engine (GEE; Gorelick et al. 2017). Of the 154 satellite images acquired, we analysed 80 (52%) that had 90% of the coastline visible and not covered by clouds. Coastal reclamations usually started with enclosing an intertidal or subtidal area with seawalls, and then gradually pumped water out and filled sand in. We defined an area as 'reclaimed' when it was completely enclosed by new seawalls visualized at the scale of 1:5000. Satellite images were displayed in false colours, and reclaimed areas were manually mapped on GEE. Mudflat area was estimated from the Murray Global Intertidal Change Dataset (Murray et al. 2019). Beside natural tidal flats, this dataset include other systems with intertidal dynamics, such as rocky shores, aquaculture ponds with frequent wet-dry periods, and tidal flats undergoing reclamation. We manually excluded all these other intertidal systems to obtain the area of natural tidal flats. The rate of reclamation was calculated from 3 separate periods, the break points determined by fitting a piece-

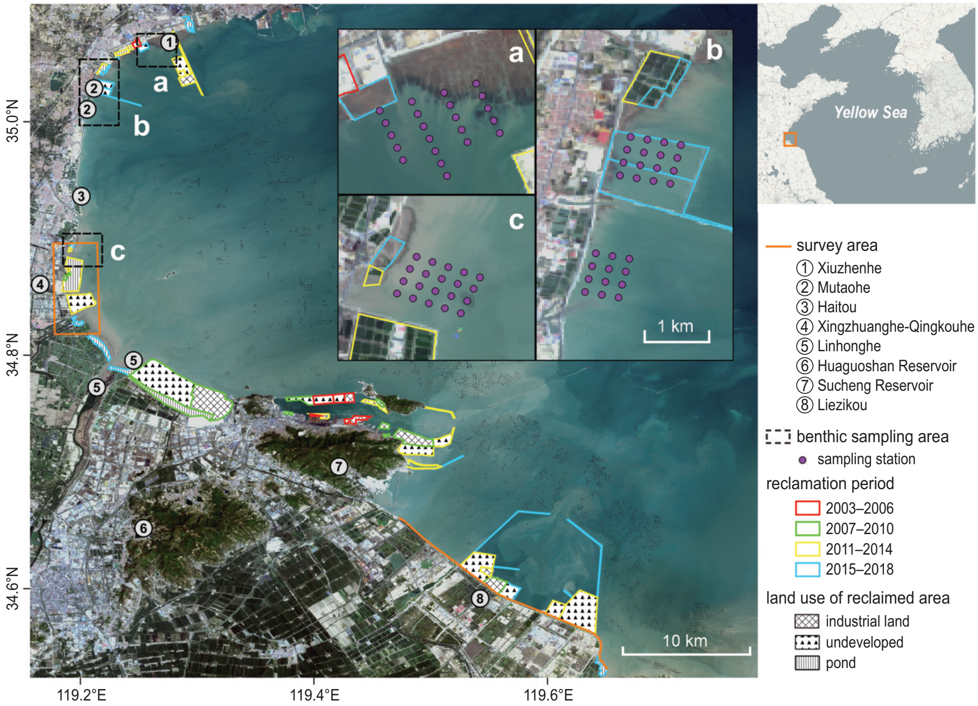

Figure 6.1. Map of the Lianyungang Coast showing the eight bird survey areas and 70 benthic sampling stations at (a) Xiuzhenhe (b) Mutaohe and (c) Xingzhuanghe. Reclaimed areas are depicted on the map with respective year range (coloured outlines) and the type of land use (shaded). The background Sentinel-2 (ESA) image is from June 2018. In the map of the Yellow Sea (upper-right), the Lianyungang Coast is shown as an orange square.

wise regression onto the area-date relationship with R package 'segmented' (Muggeo 2008). Land use of the reclaimed areas (as of June 2018) were classified into aquaculture ponds, industrial land or undeveloped land (for details see Table 6.A.2).

Benthic survey

Sampling grids covered the main intertidal mudflats used by foraging shorebirds at Xiuzhenhe, Mutaohe and Xingzhuanghe (Fig. 6.1). Sampling stations were evenly distributed 250 or 500 m apart depending on the local situation (Fig. 6.1; for methodological rationale, see Bijleveld et al. 2012). During the spring migration period of the birds, a total of 41 stations were visited from 5 to 7 May 2015, 70 stations from 28 April to 1 May 2016, and 60 stations from 28 April to 2 May 2017. At each station, a sediment core with a surface area of 0.019 m^2 was taken to a depth of 20 cm and washed over a 0.5 mm sieve. The sieved sample was then stored frozen prior to analysis. In the laboratory, molluscs were counted, identified and measured to the species level using a dissecting microscope, and high-density species were subsampled by a Motodo Splitter.

Results

Overall, 43 shorebird species were recorded in the surveys, including 12 globally threatened or 'Near Threatened' species (Table 6.1). For 22 species, their numbers have exceeded the 1% of the EAAF population; for 4 out of the 22 species, which are the Asian Dowitcher (*Limnodromus semipalmatus*), Black-tailed Godwit (*Limosa limosa*), Eurasian Oystercatcher (*Haematopus ostralegus*) and Pied Avocet (*Recurvirostra avosetta*), their numbers have exceeded 10% of the EAAF population. The highest total number recorded was the over 100,000 shorebirds at the Qingkouhe mudflats (area 4 in Fig. 6.1) on 5 May 2015. Moreover, 80 species of other waterbird families were recorded in the surveys, in which 13 were globally threatened or 'Near Threatened', and 7 had numbers exceeded the 1% of the EAAF population (Table 6.A.3). Notably, the single count of 63 Dalmatian Pelican (*Pelecanus crispus*) in winter 2012 had exceeded the East Asian population estimate of 50 individuals (Wetlands International 2019).

During both northward and southward migration, the Lianyungang Coast was used by satellite-tracked great knots and bar-tailed godwits, either as a short stop of 5-8 days, or for the long-staging individuals, their time in Lianyungang (18–30 days) was 59–100% of their staging period in the Yellow Sea. In April and May, one great knot stopped for 8 days (representing 22% of its time spent in the Yellow Sea) and two for 27 (100%) and 28 days (84%), respectively. Also, two bar-tailed godwits stopped for 5 days (*SD* ± 0.3; 18–20%), and three for a long period of 29 days (*SD* ± 1.5; 76–100%). During southward migration, three tracked great knots stopped for 18 days (*SD* ± 1.4; 59–100%) in August to September, and one bar-tailed godwit stopped for 8 days (14%).

We have observed 24 species of shorebirds foraging on the intertidal mudflats from Qingkouhe to Xiuzhenhe (Table 6.1). During high-tide, shorebirds roosted in mixed-

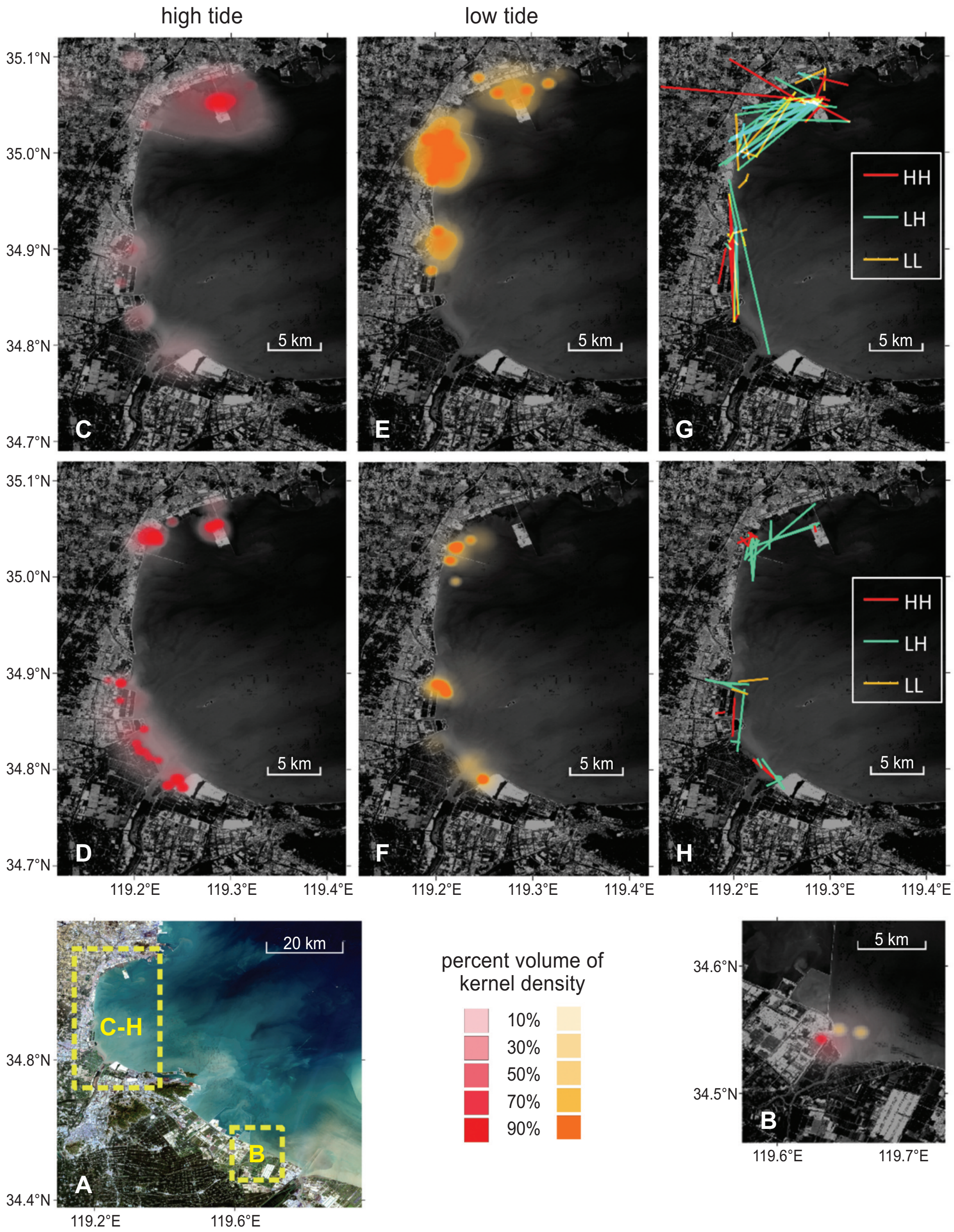

Figure 6.2. (**A**) Areas of occurrence (yellow rectangles) of satellite-tracked great knots and bar-tailed godwits at Ganyu (**C-H**) and Liezikou (**B**) along the Lianyungang Coast. (**B**) High tide (red) and low tide (orange) Kernel densities of locations of an individual bar-tailed godwit at Liezikou. Kernel densities of locations during high tide and low tide for great knots (**C**, **E**) and bar-tailed godwits (**D**, **F**) at Ganyu. Movements within or between tides as depicted by lines connecting pairs of points (within a high tide-HH, between consecutive high and low tides-LH and within a low tide-LL) of the same individual for great knots (**G**) and bar-tailed godwits (**H**).

species flocks in aquaculture ponds or undeveloped land with little vegetation and patches of very shallow water, and sometimes on open bunds of ponds (Fig. 6.A.1). Satellite tracking can collect distributional data even at locations that were not accessible during our surveys. During high tide, the tracked great knots mostly roosted at a piece of undeveloped reclaimed land at Xiuzhenhe, while roosts of bar-tailed godwits were scattered along the coastline (Fig. 6.2). At low-tide, tagged individuals of both species occurred on the Mutaohe and Xingzhuanghe mudflats, but only the great knots occurred on the Xiuzhenhe mudflats, and only the bar-tailed godwits occurred on the Linhonghe mudflats (Fig. 6.2). One godwit stayed at the southern tip of Liezikou but only for 5 days (Fig. 6.2B). Bar-tailed godwits moved shorter distances than great knots, both within and between high and low tides (Fig. 6.2G & 2H; Table 6.2).

The intertidal flats were muddy at most areas, especially at estuaries of Linhonghe, Qingkouhe and Xingzhuanghe, while sandy at Mutaohe (Fig. 6.1). The exotic Smooth Cordgrass (*Spartina alterniflora*) have invaded mudflats next to seawalls, and at Linhonghe extended outwards for around 500 m, and at Xiuzhenhe for around 1 km. From 2003 to 2018 a total of 71.4 km^2 of land was claimed along the Lianyungang coastline, in which 39 km^2 was converted from intertidal flats. Although 10 km^2 of new intertidal flats was formed during this period, overall there is still a net loss of 27% of intertidal flats. More than half of this new land (40.4 km^2) remained undeveloped as of June 2018. Of the land that was developed, 60.3% (18.7 km^2) were used for industrial purposes and the rest (12.3 km^2) for aquaculture ponds (Fig. 6.1). From January 2003, the rate of land claim was low (0.7 km^2/year), but since October 2007 it increased more than fourfold (8.3 km^2/year), before slowing down from February 2015 to June 2018 (2.5 km^2/year; for details see Fig. 6.A.2).

A total of 25 species of molluscs were recorded in the benthic surveys (Table 6.3). The Xingzhuanghe and Mutaohe mudflats were dominated by *Potamocorbula laevis*, while Xiuzhenhe was dominated by *Musculus senhousia*. Although the community composition was rather different between the three areas, the most abundant species (*P. laevis*, *M. senhousia*, *Ruditapes philippinarum*, *Sinonovacula constricta* and *Retusa cecillii*) were all small (averaged 3.5–9.9 mm), rather soft-shelled, bivalves. These species comprised >98% of the molluscs in each area (Table 6.3).

Table 6.2. Average distances travelled within and between tidal cycles by individual bar-tailed godwits (*n* = 6) and great knots (*n* = 6) at Lianyungang based on satellite-tracked locations.

	Distance travelled (km ± *SD*)	
Tide type	**Bar-tailed godwits**	**Great knots**
High	1.52 ± 1.20, *n* = 17	3.84 ± 4.55, *n* = 25
Low	1.94 ± 0.63, *n* = 3	2.76 ± 2.79, *n* = 14
Between consecutive high and low	3.07 ± 2.22, *n* = 29	6.45 ± 4.36, *n* = 33

n = number of pairs of points

Table 6.3. Mean density (MD), percentage (Perc) and shell length of mollusc species at Xingzhuanghe, Mutaohe and Xiuzhenhe of the Lianyungang Coast.

Species	**Xingzhuanghe**		**Mutaohe**		**Xiuzhenhe**		**Overall**	**Shell Length**		
(sorted by abundance)	MD (ind/m^2)	Perc (%)	MD (ind/m^2)	Perc (%)	MD (ind/m^2)	Perc (%)	**MD** (ind/m^2)	Mean (mm ± *SD*)	Range (mm)	Number of individuals measured
Potamocorbula laevis	21724.1	99.56	6471.2	87.52	0	0.00	9398.5	4.80 ± 2.69	1.03–27.77	4831
Musculus senhousia (*Arcuatula senhousia*)	14.4	0.07	390.8	5.28	1897.5	81.69	767.6	3.52 ± 2.53	1.10–19.71	569
Ruditapes philippinarum	12.8	0.06	462.8	6.26	65.9	2.84	180.5	4.31 ± 4.71	1.40–39.33	409
Sinonovacula constricta	6.3	0.03	14.1	0.19	259.8	11.19	93.4	9.87 ± 2.61	3.50–17.60	230
Retusa cecillii	0.9	0.00	0.7	0.01	60.8	2.62	20.8	4.73 ± 1.83	2.52–15.70	48
Umbonium thomasi	30.5	0.14	7.8	0.11	0.0	0.00	12.8	7.26 ± 3.16	1.67–14.81	54
Mactra veneriformis	2.8	0.01	16.3	0.22	3.9	0.17	7.6	24.24 ± 10.19	1.71–41.86	40
Moerella iridescens	9.9	0.05	4.2	0.06	5.2	0.22	6.4	7.54 ± 3.67	2.30–18.81	21
Nassarius festiva	1.8	0.01	4.9	0.07	5.2	0.22	4.0	9.72 ± 3.57	3.41–13.00	13
Salinator fragilis	0.0	0.00	0.0	0.00	10.3	0.45	3.4	2.08 ± 0.61	1.27–3.04	8
Cyclina sinensis	0.0	0.00	0.6	0.01	9.0	0.39	3.2	4.34 ± 4.00	2.11–14.55	9
Meretrix pethechialis	0.0	0.00	9.2	0.12	0.0	0.00	3.1	9.01 ± 4.85	3.20–19.60	22
Theora lata	7.2	0.03	0.7	0.01	0.0	0.00	2.6	6.40 ± 3.40	3.36–13.91	9
Bullacta exarate (*B. caurina*)	1.0	0.00	1.4	0.02	3.9	0.17	2.1	6.78 ± 2.30	3.95–10.88	6
Solen gouldi (*S. strictus*)	0.9	0.00	1.4	0.02	1.3	0.06	1.2	17.56 ± 8.20	10.23–28.69	4
Stenothyra glabra	2.7	0.01	-	-	-	-	0.9	2.96 ± 0.26	2.70–3.22	3
Meretrix meretrix	1.8	0.01	0.7	0.01	-	-	0.8	12.90 ± 17.98	1.70–33.64	3
Scapharca subcrenata (*Anadara kagoshimensis*)	0.9	0.00	1.4	0.02	-	-	0.8	4.24 ± 2.85	2.01–7.45	3
Endopleura lubrica	1.8	0.01	-	-	-	-	0.6	8.91 ± 1.63	7.75–10.16	2
Nassarius semiplicatus	-	-	1.4	0.02	-	-	0.5	2.64 ± 0.11	2.56–2.72	2
Nassarius variciferus	-	-	1.4	0.02	-	-	0.5	15.41 ± 2.57	13.59–17.23	2
Cerithidea sinensis	-	-	0.7	0.01	-	-	0.2	14.47	-	1
Mitrella bella (*M. albuginosa*)	-	-	0.7	0.01	-	-	0.2	11.48	-	1
Neverita didyma	-	-	0.7	0.01	-	-	0.2	5.49	-	1
Punctacteon yamamurae	-	-	0.7	0.01	-	-	0.2	5.84	-	1
Total	21819.8	100	7394.0	100	2322.8	100	10512.2	-	-	6292

Discussion

The high numbers of shorebirds recorded over the past decade indicate that the coastal wetlands at Lianyungang are important for shorebirds, especially during migration. Particularly, we found that Lianyungang supported over 1% of the flyway populations of 22 shorebird species. This 1% criterion is commonly used by global inventories such as the Important Bird and Biodiversity Areas (IBAs) to assess site importance (BirdLife International 2018b), and Lianyungang ranked highest among the >300 shorebird sites in East Asia with this metric being reported (Jaensch 2013, Conklin et al. 2014, Bai et al. 2015). The occurrence of threatened waterbirds of other families, as well as the long staging duration recorded in most of the satellite-tracked individuals, boosted the importance of the site. Clearly these coastal wetlands fulfilled criteria for inclusion as an IBA and as a Ramsar site (BirdLife International 2018b, Ramsar Convention Secretariat 2018).

Although reclamation has taken away more than one-fourth of the intertidal habitats along the Lianyungang Coast (see Results and Fig. 6.1), the remaining intertidal flats are still productive; particularly, the exceptionally high densities of small soft-shelled bivalves are high-quality food for benthivorous shorebirds to refuel during their migration (Yang et al. 2013, Choi et al. 2017, Zhang et al. 2019a). Compared with two other major shorebird staging sites in the Yellow Sea where benthic surveys have been conducted in spring, the mollusc densities at Lianyungang were much higher than in Yalu Jiang estuary (Zhang et al. 2018), and of similar densities as Luannan County, northern Bohai Bay (Yang et al. 2016).

While supporting a large number of shorebirds with high densities of food, the intertidal flats along the Lianyungang Coast are entirely unprotected. Immediate conservation actions are necessary to protect them from future reclamation projects, especially the core foraging areas which can be delineated from the satellite tracking data (Fig. 6.2). Another cause of loss of intertidal flats is the expansion of the invasive cordgrass (*S. alterniflora*). These cordgrass trap sediments and cause intertidal areas to become supratidal and lose their ecological value (Wan et al. 2009). Even worse, these supratidal habitats could be lost eventually through reclamation, as they are not considered as ‘marine’ and reclamation can still proceed under the new coastal reclamation policy of China (Zhao 2018). Limiting the growth and spread of invasive cordgrass is essential to prevent further loss of intertidal flats. Moreover, it is worth to consider restoring intertidal flats by removing cordgrass at intertidal areas where it has a high coverage (Frid et al. 1999) and removing sea dikes at areas recently being enclosed but remained undeveloped (Fig. 6.1), e.g. where the new seawalls were built around some of our benthic sampling stations at Mutaohe (in blue outline in Fig. 6.1b). Additionally, human disturbances to shorebird flocks on the mudflats should be reduced, especially those caused by fishermen and their vehicles while harvesting seafood such as shellfish, crabs, fishes and worms on the mudflats (causing flocks flying up every few mins, pers. obs.).

The spatial coupling of suitable supratidal high-tide roosts with the existing intertidal foraging areas is an important aspect for managing the area for shorebirds. If there are no suitable roosts nearby and/or roosts are disturbed too frequently, foraging areas may become underused or abandoned because the energetic costs of commuting and/or alarm flights outweigh the energy gain from foraging (Rogers et al. 2006b). In addition to the high-tide roosts known from ground observations, satellite tracking has highlighted an important roost at the newly reclaimed 'island' at the port development area of Xiuzhenhe that is not publicly accessible (Fig. 6.1). This roost was intensely used by tracked great knots, and to a lesser degree by bar-tailed godwits (Fig. 6.2). Whether the current set of roosts are within the distance tolerated by great knots and bar-tailed godwits to commute daily can be evaluated by the travel distances between and within tides (Table 6.2) measured in this study. For example, a simple exercise will be to assess if suitable roosts exist within a 3 km radius (Table 6.2) of potential foraging area of bar-tailed godwits. If necessary, roosts can be created within this radius, either by restricting human disturbances at locations that already have the suitable biophysical features (having little or no vegetation, an open view and wet substrate; Burton et al. 1996, Zharikov & Milton 2009; Fig. 6.A1), or creating such habitats on the many pieces of undeveloped land along the coast (Fig. 6.1).

Gaps remained in our knowledge on Lianyungang Coast as our study is limited by manpower and resources; e.g. our surveys along this 162 km coastline were mostly conducted by one person (Y.X.H.) on a voluntary basis, and the number of birds using this site is likely to be considerably higher. Since the benthic sampling stations were reached by foot, sampling could not be done at the mudflats with extremely soft sediment. Nevertheless, by putting together the results from the counts, benthic surveys, satellite tracking and satellite imagery analysis, we have established the site's importance and proposed a set of site management actions. Given the fast pace of destruction and degradation of coastal habitats in Lianyungang, regular and continuous monitoring of bird numbers, movements, their food densities and habitat status is necessary. This combined issue of fast degradation and lack of related ecological knowledge is widespread in many sites in the EAAF and developing countries around the world (Lee & Khim 2017). We hope that our study stimulates the gathering of ecological knowledge and science-based management, and the funding and facilitating of such practices from both the government and non-governmental organisations, at the many ecological important sites that are understudied (BirdLife International 2017).

Acknowledgements

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Appendix A

Supplementary data

Table 6.A.1. Number of survey days per month in each of the eight survey areas.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1. Xiuzhenhe (35.06°N, 119.27°E)												
2016				1*	1*					1		
2017					1*							
2018					1*							
2. Mutaohe (35.02°N, 119.21°E)												
2015					1*							
2016				2*	1*							
2017					1*							
2018					1*							
3. Haitou (34.94°N, 119.20°E)												
2011		1										
2016					1				1			
2017										1		
4. Xingzhuanghe-Qingkouhe (34.86°N, 119.19°E)												
2012								1				
2013	1	1		1	1	1	1		1	1	1	1
2014	1		1	2	1		1	1	1	1	1	1
2015	1		1	1	1*		1		1	1	1	1
2016		1	1	4#	1	1		1	1	1	1	1
2017	1	1	1	2	1*	1	1	1	1	1	1	1
2018	1	1	1	1	3*							
5. Linhonghe (34.79°N, 119.25°E)												
2008	1	1	1		1		1	1	1	1	1	1
2009	1	1	1	1		1	1	1		1	1	
2010	1		1	1	1	1		1	1	1	1	1
2011	1	1	1	1	1	1	1	1		1	1	1
2012	1	1	1		1	1	1	1	1	1	1	1
2013			1	1								
2014				2						1	1	1
2015	1					1	1	1	1	1	2	1
2016		1	1			1		1	1	1		
2017								1		1		1
6. Huaguoshan Reservoir (34.65°N, 119.25°E)												
2011		1										
2012		1	1									
7. Sucheng Reservoir (34.70°N, 119.42°E)												
2009				1								
8. Liezikou (34.59°N, 119.55°E)												
2009	1		1	1			1	1	1			
2010	1	1		1	1	1		1	1	1	1	1
2011	1	1	1	1	1	1	1	1		1	1	1
2012	1	1	1	1	1	1	1	1	1			1
2013	1	1		1								
2014				2			1					

*Surveys with habitat characteristics noted.
#Habitat characteristics were noted only during surveys on 28 and 29 Apr 2016.

Table 6.A.2. Characteristics for classifying land use of reclaimed areas.

	Type of land use		
	Industrial	**Ponds**	**Undeveloped**
Sediment deposits	Present	Absent	Present or Absent
Water	Absent	Present	Present
Infrastructures	Present	Absent	Absent
Distinct characteristics in false colour images	Brown with small patches of pink (indicating vegetation)	Cyan Blue in chequered pattern	Mixture of brown and cyan blue
Example			

Table 6.A.3. Maximum counts of waterbirds species at Lianyungang Coast in 2008–2018, that have an IUCN Red List status of 'Near Threatened' (NT), 'Vulnerable' (VU) or 'Endangered' (EN), or the numbers exceeded 1% of the EAAF population (in bold).

Species (sorted by English common name)	**1% of EAAF Population**[#]	**Maximum number recorded in 2008–2018**	**Count date and location**
Black-faced Spoonbill (EN) *Platalea minor*	20	3	17 Jul 2017 Xingzhuanghe-Qingkouhe
Caspian Tern *Hydroprogne caspia*	250	**300**	14 Nov 2015 Linhonghe
Chinese Egret (VU) *Egretta eulophotes*	35	31	8 Aug 2012 Liezikou
Common Pochard (VU) *Aythya ferina*	3000	96	16 Feb 2016 Xingzhuanghe-Qingkouhe
Common Shelduck *Tadorna tadorna*	1200	**1920**	24 Dec 2017 Xingzhuanghe-Qingkouhe
Dalmatian Pelican (NT) *Pelecanus crispus*	1	**63**	11 Nov 2012 Linhonghe
Falcated Duck (NT) *Mareca falcata*	830	**6000**	15 Jan 2011 Liezikou
Ferruginous Duck (NT) *Aythya nyroca*	1000	4	1 Jan 2015 Linhonghe
Long-billed Murrelet (NT) *Brachyramphus perdix*	NA	2	12 Mar 2011 Linhonghe
Oriental Stork (EN) *Ciconia boyciana*	30	9	12 May 2013 Xingzhuanghe-Qingkouhe
Red-crowned Crane (EN) *Grus japonensis*	4	**25**	9 Mar 2012 Linhonghe
Relict Gull (VU) *Larus relictus*	120	**250**	16 Feb 2016 Linhonghe
Saunders's Gull (VU) *Saundersilarus saundersi*	85	**310**	7 Dec 2016 Xingzhuanghe-Qingkouhe
Streaked Shearwater (NT) *Calonectris leucomelas*	NA	2	1 Oct 2010 Liezikou
Swan Goose (VU) *Anser cygnoid*	680	29	14 Oct 2012 Linhonghe

[#] Estimates from Wetlands International (2019). NA=EAAF population estimate is not available.

Figure 6.A.1. High-tide roosts of shorebirds at Lianyungang Coast, at (**A**, **B**) ponds with shallow water and (**C**) bunds of ponds. Photo credits: Y.C. Chan (A), Y.X. Han (B) and Ziyou Yang (C).

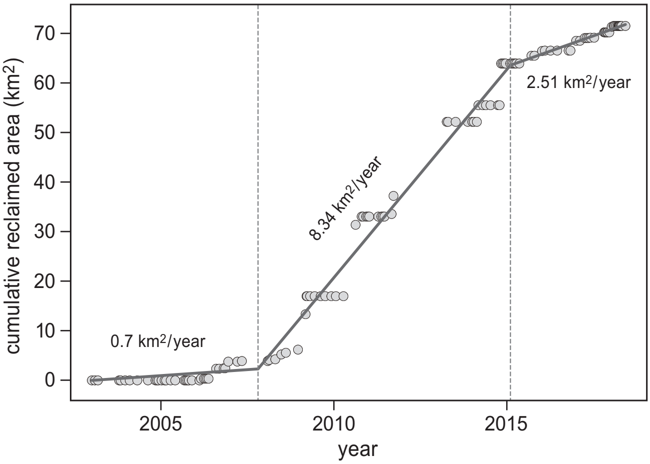
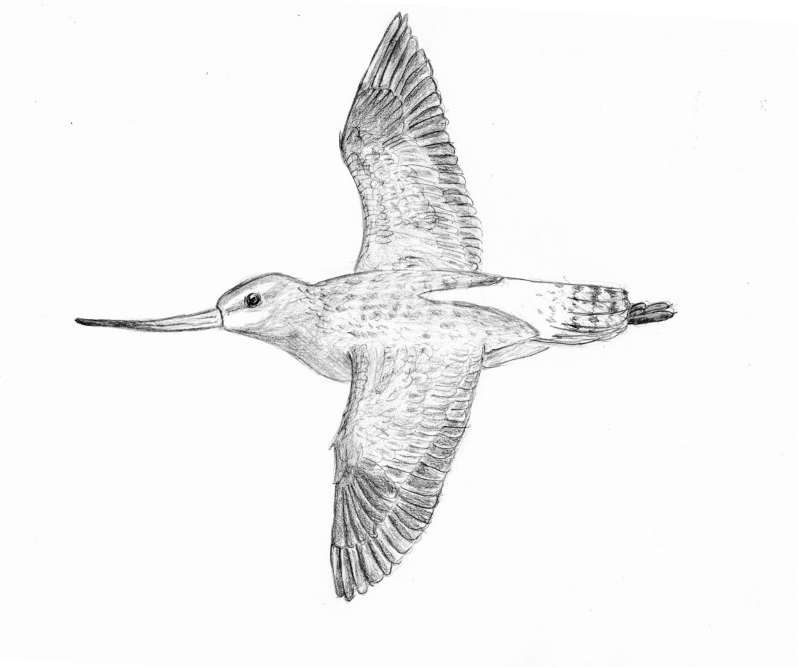


Figure 6.A.2. The trend of reclamation of coastal wetlands at Lianyungang Coast in 2003–2018. Reclamation rates are calculated in three periods, separated on 18 Oct 2007 and 10 Feb 2015.



BOX **B**

Loss of habitat leads to loss of birds: reflections on the Jiangsu, China, coastal development plans

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Wader Study (2017) 124: 93–98

Prompted by the realization that parts of the coast of southern Jiangsu Province, China, are under threat of reclamation, we here summarize evidence that loss of intertidal habitats around the Yellow Sea and at other parts along the Chinese and Korean coasts has already led to severe population declines of migratory shorebirds, including multiple endangered species. All the evidence currently at hand suggest that the plans to reclaim (develop) additional intertidal habitat in this region poses a substantial threat to the remaining shorebird populations. We recommend that new Environmental Impact Assessments are warranted before further reductions in the extent of mudflats take place.

Mudflats take time and effort to appreciate. Watching shorebirds of various shapes and sizes across the mudflats at low tide, birds that gather in impressive flocks when driven towards the boundaries of land and sea at high tide, helps people to acquire that appreciation (van de Kam et al. 2016). Yet, when they are seen wheeling in the airspace above coastal mudflats as they try to evade a hunting falcon, or when in some seasons they forage scattered thinly across vast mudflats, but are absent at other times of year, it is easy to get the impression that the loss of these mudflats would be inconsequential to the birds, as they are continuously on the move. Many people seem to believe that shorebirds using a particular site can simply move on to another if that site is developed, that they always have other places to go.

However, more than half a century of extensive dedicated research on the regulation of migrating shorebird populations around the world (see summaries in Swennen 1976, Pitelka 1979, Evans et al. 1984, van de Kam et al. 2004 and citations below) has shown quite the opposite. Although hard to research, several landscape-scale experiments and before-and-after studies of the consequences of habitat loss have shown that coastal mudflats are filled to capacity (e.g. Burton et al. 2006, Kraan et al. 2009, Duriez et al. 2012). Hence, there is strong scientific evidence that shorebird populations are limited by the space and quality of particular coastal non-breeding areas; moreover, spatial limitation may even extend to the aggregate of all staging areas in an entire flyway (Piersma et al. 2016). Therefore, the loss of mudflats anywhere in a flyway will usually lead to a loss of the flyway's capacity to support shorebirds (Iwamura et al. 2013). So, generally the birds cannot simply 'go someplace else' without negative survival consequences for them or for the birds already present there (Rakhimberdiev et al. 2015a, Piersma et al. 2016).

Perhaps this should not come as a surprise. Breeding over extensive northern tundra and taiga habitat (Lappo et al. 2012), the shorebirds populating the coastal habitats around the world during the migration and winter seasons squeeze into narrow coastal areas that are 2–3 orders of magnitude smaller than the breeding areas. Not only are wetlands generally uncommon, and coastal wetlands in particular rare and small in extent (exacerbated by modern man's requirement for hard developed coastlines worldwide), the extent of wetland area is estimated to have reduced by 87% since the year 1700 (Davidson 2014). The long-term consequences for migrating shorebird populations, for which known causes of changes in population size are found mainly outside their remote Arctic breeding areas (Meltofte 2013), can only be guessed, as comprehensive counts of their numbers on the coastal non-breeding grounds began no earlier than the 1960s (e.g. Smit & Wolff 1980, Prater 1981, Veitch & Habraken 1999).

The recognition that migrating shorebirds, and indeed other waterbirds, represent an internationally shared resource that is worth conserving, has led to several international agreements and appellations (e.g. Boere et al. 2006). This includes coastal areas being designated as Ramsar sites, Important Bird Areas, Man and Biosphere Reserves, World Heritage Sites, and Important Flyway Sites by the East Asian-Australasian Flyway Partnership. Some of these accolades offer various levels of legal protection under national and international frameworks (Boere & Piersma 2012). In view of the fact that the coastal intertidal areas of east Asia, particularly those in China and around the rest of the Yellow Sea, currently represent the largest global concern for safeguarding migrating shorebirds (e.g. Barter 2002, van de Kam et al. 2010, MacKinnon et al. 2012, Conklin et al. 2014, Ma et al. 2014, Xia et al. 2017; Fig. B.1), it is heartening to see that the Government of China has taken steps towards formally protecting some of its key coastal areas as World Heritage Sites (*http://whc.unesco.org/en/tentativelists/6189/*). Nevertheless, many areas are still listed for reclamation. This *Forum* contribution was prompted by the realization that some of the intertidal habitats along the coastline of Jiangsu Province, including the offshore Dongsha Shoals (see Fig. B.2), are still scheduled to be reclaimed. And, from the shorebirds' perspective, reclamation equals destruction. We believe that these areas are likely to be hugely important from an ecological perspective. Let us explain.

Figure B.1. Schematic impression of the Yellow Sea as the main 'hub' in the East Asian–Australasian Flyway. (Prepared and provided by BirdLife International).

Over the last decade, studies using ringing recoveries of all shorebird species (e.g. Iwamura et al. 2013), and the tagging of several species with satellite transmitters and geolocators (e.g. Gill et al. 2009, Minton et al. 2011, Battley et al. 2012, Lisovski et al. 2016a, b), have established the key roles of the Yellow Sea and more southerly Chinese coastal areas as shorebird refuelling areas during both northward and southward migration (Fig. B.1). In addition, a series of recent analyses of shorebird count data has demonstrated overwhelmingly that the species that rely to the greatest extent on the Yellow Sea have shown the steepest population declines (Amano et al. 2010, Wilson et al. 2011, Clemens et al. 2016, Studds et al. 2017), suggesting that the cause is the shrinking coastal habitats of the Yellow Sea.

In addition, detailed demographic studies of the Red Knots *Calidris canutus*, Great Knots *Calidris tenuirostris* and Bar-tailed Godwits *Limosa lapponica* that spend the non-breeding season in Australia (Piersma et al. 2016) and of Bar-tailed Godwits from New Zealand (Conklin et al. 2016), show these three species have each experienced similar declines in survival during the period of the year when they migrate to the Arctic and

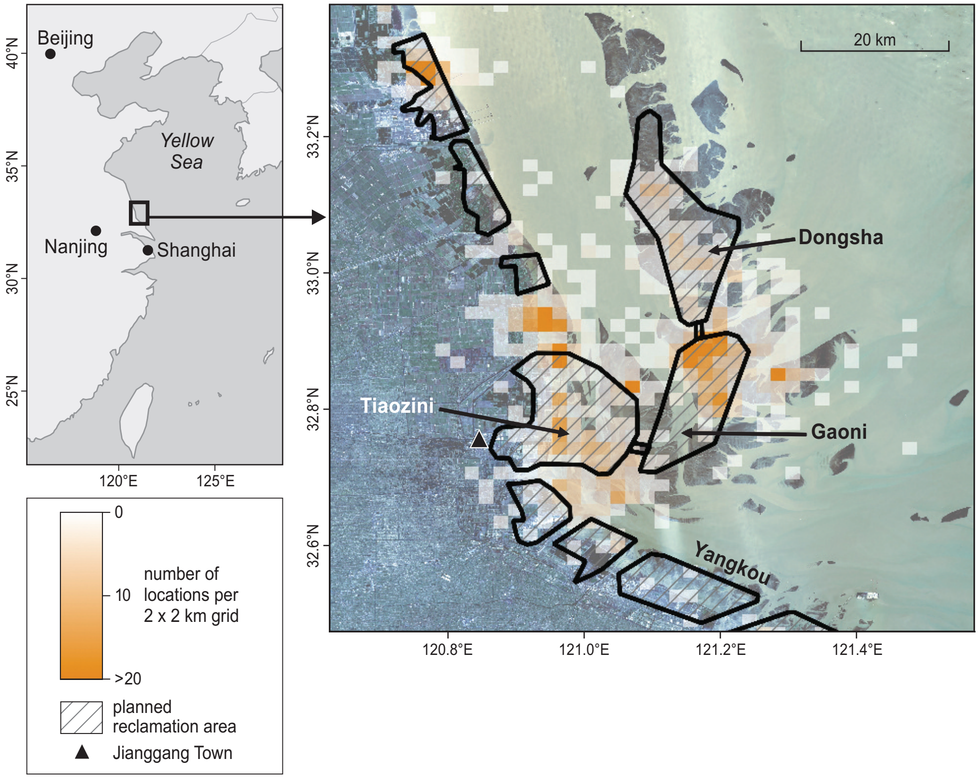

Figure B.2. Situation of the southern Jiangsu Province Tiaozini-Dongsha Shoals tidal flats north of Rudong (left) and the reclamation plans in this area for 2010–2020 (according to Zhang et al. 2011, the intertidal areas indicated in grey) combined with the density distribution of 15 staging, satellite-tagged female Bar-tailed Godwits in May 2015–July 2017 (right). White to orange coloured squares represent the number of locations of godwits in a 2 × 2 km area, obtained from Argos satellite tracking. A lack of grid squares indicates a lack of satellite locations, but of course does not mean that such areas were not visited by shorebirds. (Based on Y.-C. Chan, T.L. Tibbitts, T. Piersma et al. in prep.)

return. This ‘coincidence’ can only be explained by their shared use of the Yellow Sea intertidal zones during the critical refuelling phases. Although they use quite different parts of the Yellow Sea coastline, the fact that they are so similarly affected is consistent with coastal wetlands being lost rapidly along all the coasts of China and the Koreas (Yang et al. 2011, Ma et al. 2014, Murray et al. 2014, 2015, Wang et al. 2014, Piersma et al. 2016). Note that the mortality of these birds does not have to occur on the Asian staging sites; it could take effect as delayed, downstream carryovers from inadequate refuelling in the Yellow Sea (Baker et al. 2004, Senner et al. 2015): undernourished birds being unable to survive the migrations to and from their Arctic breeding grounds.

One of the geomorphologically amazing (Chen et al. 2017), globally unique, yet ecologically very poorly studied coastal areas in China, is the complex of intertidal habitats along the Dafeng-Dongtai-Rudong coastline in southern Jiangsu Province, a complex that includes the Tiaozini mudflats along the mainland coast and the offshore Dongsha Shoals (32.4–33.4°N, 120.7–121.5°E; Kang et al. 2017, Xiong et al. 2017, see Fig. B.2). Peng et al. (2017) summarized the importance of the intertidal areas along the mainland coast for migrating shorebirds and found this area to be the most important in the world during both north- and southward migration for Spoon-billed Sandpipers *Calidris pygmaea* (a 'Critically Endangered' species according to both the IUCN Red List of Threatened Species, Version 2017-1, *www.iucnredlist.org*, and China's Red List, Jiang et al. 2016) and Spotted (or Nordmann's) Greenshanks *Tringa guttifer* ('Endangered').

Work carried out in September–October 2016 by T. Mu and D.S. Wilcove on the spatial and temporal distribution of different shorebird species feeding on the mudflat of the Yangkou foreshore at Rudong, showed that species with different feeding modes (i.e. generalists, zone specialists, and tide followers) have different vulnerabilities to environmental change (Fig. B.3). Along this segment of the mainland coast, the upper intertidal zone provided disproportionally the largest feeding opportunities to most species (Fig. B.3), yet it is also the area most vulnerable to land reclamation (Zhang et al. 2004). In fact, over the last decade, during the first phase of the coastal development programme in Jiangsu Province, 6,750 ha of the upper shore habitat at Tiaozini was

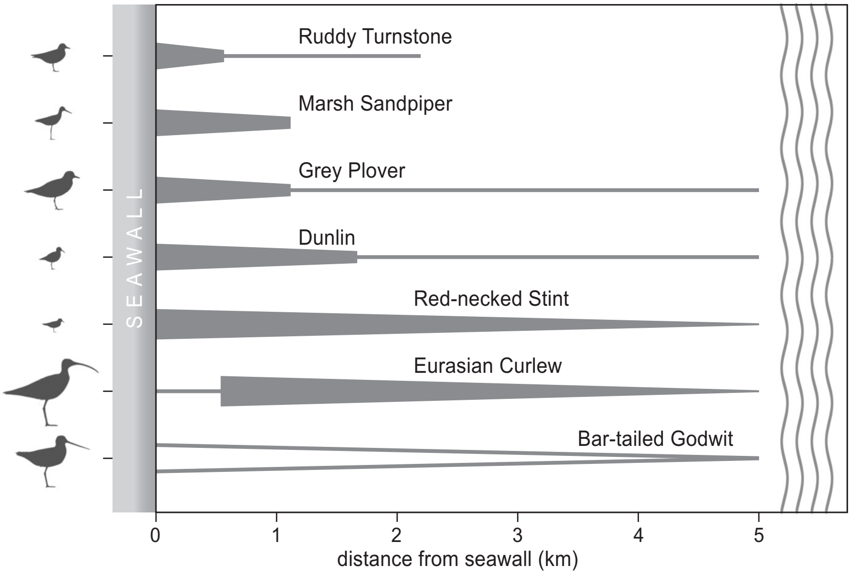

Figure B.3. A schematic view of the feeding shorebird distribution on the Yangkou intertidal muddy foreshore. Between high tide mark (bounded by sea wall in this area) and low tide line, species like Ruddy Turnstones *Arenaria interpres* and Dunlins *Calidris alpina* usually feed intensively in the upper zone ('zone specialists'), Red-necked Stints *Calidris ruficollis* and Eurasian Curlews *Numenius arquata* spread out across the whole stretch of mudflat ('zone generalists'), while Bar-tailed Godwits Limosa lapponica are usually seen feeding close to the water line ('tide-followers'). The thickness of the lines represents the relative accumulated number of feeding birds in the course of the tidal cycles. (Based on T. Mu & D.S. Wilcove in prep.)

converted before the consequences for migrating shorebirds and other forms of biodiversity could be assessed. The infrastructural works are likely to have negatively impacted shorebirds, including Spoon-billed Sandpipers and Spotted Greenshanks.

The importance of the offshore Dongsha Shoals to shorebirds remained largely unknown until satellite-tracking work by Global Flyway Network in 2014–2017. This work showed that the Tiaozini mudflats and Dongsha Shoals were used by no fewer than 15 of 35 (43%) tagged female Bar-tailed Godwits of the *menzbieri* population for several weeks during both northward and southward migration (Fig. B.2). Based on a total population of about 146,000 birds (Wetlands International 2017), and assuming that the tagged birds are representative of this population, the Dongsha Shoals would provide critical staging habitat for at least 0.43*146,000 ≈ 63,000 northward migrating Bar-tailed Godwits. This large number does not include the equally numerous, and equally declining, *baueri* population, which stages in this area during northward migration (Battley et al. 2012, Conklin et al. 2016). Rather alarmingly, 52% of locations of tagged Bar-tailed Godwits using the Dafeng-Dongtai-Rudong coastline fell within the proposed reclamation areas (Fig. B.2). Note that there are additional reports of a satellite-tracked Spotted Greenshank (tagged in Thailand; Yu & Gale 2017, pers. comm.) and Grey Plovers *Pluvialis squatarola* (tagged in South Australia; *http://www.vwsg.org.au/GP2016-news.html*, M. Christie pers. comm.) using the Dongsha Shoals. This area is clearly crucial habitat for many species of shorebirds.

Consequently, there is a lot to be lost if the reclamation plans of the Jiangsu Government are carried out as currently planned (Zhang et al. 2011). The world will lose one of its most ecologically important intertidal zones. Also, the loss of this area will harm populations of multiple rare species of shorebirds, some of which are already close to extinction.

All available evidence shows that the migrant shorebirds of the East Asian-Australasian Flyway need every hectare that remains of their East Asian intertidal staging areas during north- and southbound migration. Further land claims will threaten their long-term prospects. Clearly, before going ahead with any further reductions in the extent of the Tiaozini mudflats and the Dongsha Shoals, new and thorough Environmental Impact Assessments are warranted.

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BOX C

Incorporating shorebird movement information into ecological impact assessment and 'Building with Nature' port design

The economic development of the People's Republic of China has created an increasing demand for usable land, resulting in large-scale land reclamations along the coastal zone (Ma et al. 2014, Tian et al. 2016). However, the Chinese coastline, especially the intertidal mudflats within the Yellow Sea, also provide vital ecosystem services and support numerous wildlife species, including endangered migratory shorebirds within the East Asian–Australasian Flyway (Barter 2002, Yang et al. 2011, Choi et al. 2015, Peng et al. 2017, Chan et al. 2019b). A salient case is Tongzhou Bay at the southern part of the Jiangsu Province, characterized by large intertidal mudflats and deep tidal channels

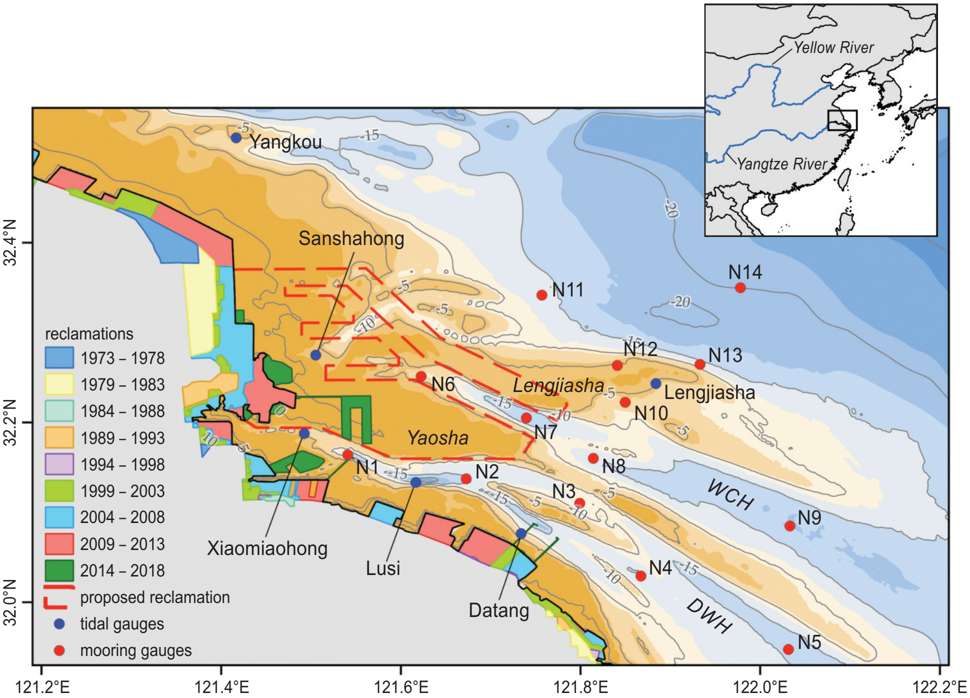


Figure C.1. An overview of shoals and channels at Tongzhou Bay, southern Jiangsu Province, China (units of elevation in m). Past reclamation activities and the proposed Tongzhou Bay port for 2019–2035 (red dashed line) are mapped out. M-stations (blue) are water level gauges and N-stations (red) measured current velocity and direction and sediment concentration. Modified from Muller et al. (2020b).

with past land reclamations along the coastline for agri-aquaculture and industrial uses, and the construction of a deep-sea port was being proposed (Fig. C.1). Here I summarise (for non-engineers) two published articles in the field of hydraulic engineering on Tongzhou Bay that I contributed to, in which satellite tracking data of shorebirds are applied in ecological impact assessment of port construction (Muller et al. 2020a) and in port design following the ‘Building with Nature’ approach (Muller et al. 2020b).

Ecological impact of land reclamation

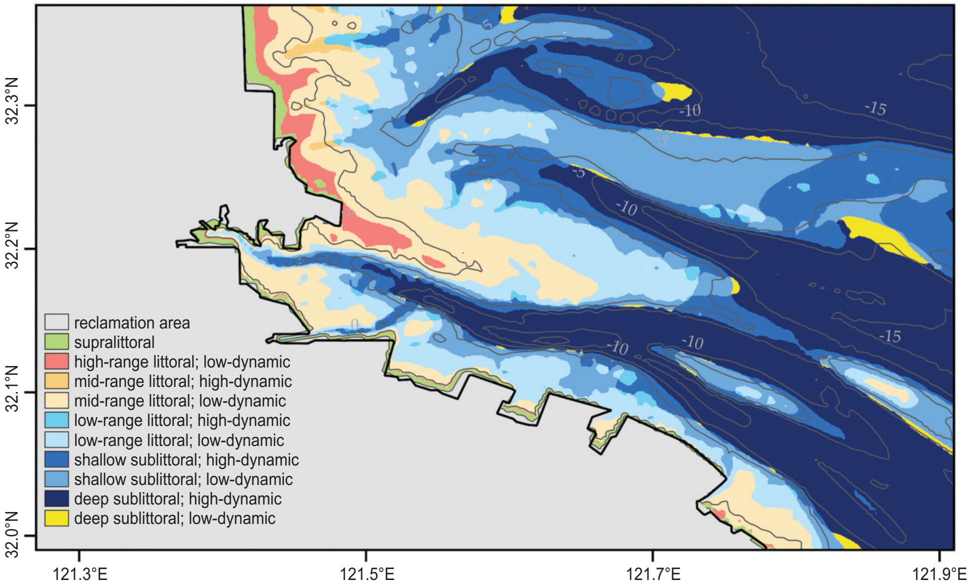
To assess the ecological impact of the land reclamation associated with the port construction (Fig. C.1), Muller et al. (2020a) developed an ecotope map for Tongzhou Bay, where ecotopes were classified based on the salinity, substrate, water depth, flow velocity, and dryfall period (i.e., the period when the mudflats are not inundated during a tidal cycle). Since field data of these parameters were available at only a few locations in the bay (Fig. C.1), a hydrodynamic numerical model for the Tongzhou Bay was developed based on a large-scale model for the entire Jiangsu coast (Su 2016, Yao 2016) to generate the high-resolution spatial hydrodynamic data needed for ecotope mapping. The model was validated quantitatively with measurements from monitoring locations within Tongzhou Bay (Fig. C.1). The model output was subsequently converted into an ecotope map for Tongzhou Bay, with class bounds (Fig. C.2) following the ZES.1 method developed for saline open water ecosystems in the Netherlands (Bouma et al. 2005).

The ecotope map was verified using distributional data of two threatened migratory shorebird species, the Bar-tailed Godwit (*Limosa lapponica menzbieri*) and Great Knot (*Calidris tenuirostris*), within Tongzhou Bay from April 2015 to September 2017. These data were collected by satellite tracking of individual birds from their non-breeding site in Northwest Australia. The ecotope map was overlaid with the 90% home ranges of the two shorebird species. Both species mainly occurred in the mid-range (30–40%) and low-range (18–19%) littoral zones, indicating the importance of these ecotopes to these shorebird populations.

To assess the ecological impact of the current (2014–2018, 35.9 km^2) and the proposed reclamations (2019–2035, 126 km^2), the reclamation areas were overlaid on the ecotope map and the percentage loss of each ecotope was calculated. The combined current and proposed reclamations would lead to loss of high-range (42%), mid-range (48%), and low-range (38%) littoral zones (low and high hydrodynamic conditions combined). This corresponds to 44%–45% loss of the mid-range and low-range littoral zones, which are important ecotopes for the two species.

Building for Nature – preserving bird habitat in port design

The loss of key habitats due to land reclamation projects is prevalent along the Chinese coast, and a more integrated coastal development strategy is needed to maintain ecological values. A design process incorporating both socio-economic and natural perspectives called ‘Building with Nature’ has been adopted in coastal infrastructure projects worldwide over the last decade (de Vriend et al. 2015). Muller et al. (2020b)



Feature	Sub feature (feature bounds)			Ecotope color scheme	
Hydrodynamics				High (>0.8 m/s)	Low (<0.8 m/s)
Depth (I)	Supralittoral (>MHWN)				🟩
	Littoral (MLWS - MHWN)	Dryfall period	High-range (>60% of tidal cycle)	🟥	🟥
			Mid-range (25–60% of tidal cycle)	🟧	🟨
			Low-range (<25% of tidal cycle)	🟦	🟦
	Sublittoral (<MLWS)	Depth (II)	Shallow (<MLWS-5m)	🟦	🟦
			Deep (>MLWS-5m)	🟦	🟦

Figure C.2. Ecotope map of Tongzhou Bay with feature classes and bounds. From Muller et al. (2020b).

demonstrated how the ‘Building with Nature’ concept can be used to design land reclamations in Tongzhou Bay more sustainably.

Traditional port design mostly focuses on primary objectives, e.g., the accessibility for vessels and connection with the hinterland. The impact on nature and ecosystems is considered by creating an inventory of the risks involved and remedying by compensatory actions. With the realization that port developments will also affect morphodynamic processes and therefore can potentially influence the environment positively, the ‘Building with Nature’ design process identifies opportunities to cooperate and collaborate with natural processes, rather than seek to control them (de Vriend et al. 2015). Following the ‘Building with Nature’ process, the following criteria were established: the port design should (1) provide a well-exploitable area for port development (e.g., close to natural channels and over shallow easy-reclaimable shoals), (2) simultaneously maintain crucial wetland habitat which provides vital ecosystem services and (3) enhance natural accumulation of these habitats to fully support the wetland ecosystem.

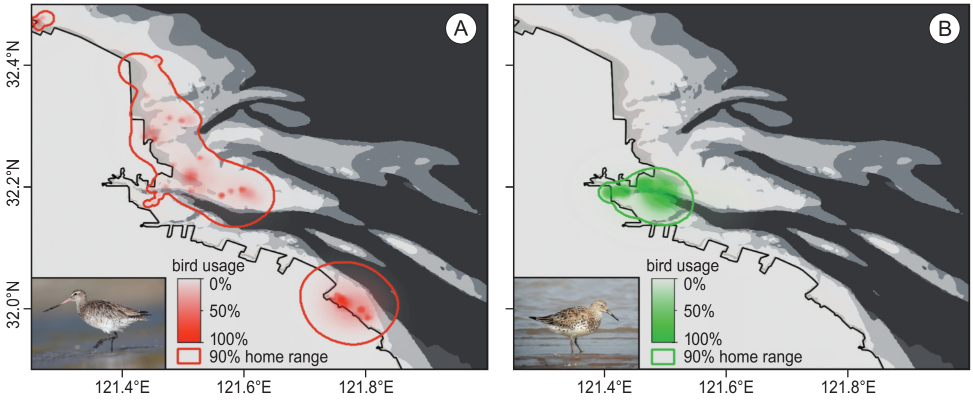


Figure C.3. Kernel density home ranges of the (**A**) Bar-tailed Godwit and (**B**) Great Knot in Tongzhou Bay, generated from satellite-tracking data. From Muller et al. (2020b).

To predict how alternative port designs could affect morphological process, the hydrodynamic model in Muller et al (2020a) was extended with a morphodynamic module that predicted sediment transport patterns. This enabled simulation of how ecotopes changed through time in the study area. To determine ecotopes important for the Bar-tailed Godwit and Great Knot, habitat use was analysed in two spatial scales from satellite-tracking data obtained within the study area from April 2015 to May 2018. First, to show the areas where these species generally occurred within the entire study area, the 90% Kernel density contours, representing the home range of the species, were calculated and overlaid onto the ecotope classifications (Fig. C.3). Bar-tailed godwits and Great Knots occurred mostly in the mid-range low dynamic littoral zone, with 30% and 35% of their 90% home range areas overlapping with this ecotope type (Fig. C.3). Second, to show ecotopes that were more intensely-used within the 90% home range, we calculated, of the total "heat" (i.e., the sum of Kernel density in each output raster cell) within the 90% home range, the percentage that falls in each ecotope. Put together, Bar-tailed Godwit occurred mostly in the mid-range low dynamic littoral zone and selected for it (38% heat vs. 30% area). While 22% of their 90% home range overlap with the reclaimed zone, it was selected against with only 19% of the heat falls within that ecotope. The low-range low-dynamic littoral zone was used in proportion to its area (14%), and godwits also showed a slight preference for the high-range low-dynamic ecotope (7% heat vs. 6% area). For Great Knots, besides the mid-range ecotope, they showed a preference for low-range (17% heat vs. 15% area) and shallow-subtidal range ecotopes (26% heat vs. 20% area).

Based on the resulting knowledge on sediment transport patterns in the bay and high-ecological value ecotopes, three alternative port configurations were designed by modifying the shape, extent and use of offshore terminals of the original port design. Using the hydrodynamic-morphodynamic model, the changes in siltation patterns and ecotope distribution under four scenarios (the three alternative designs and the refer-

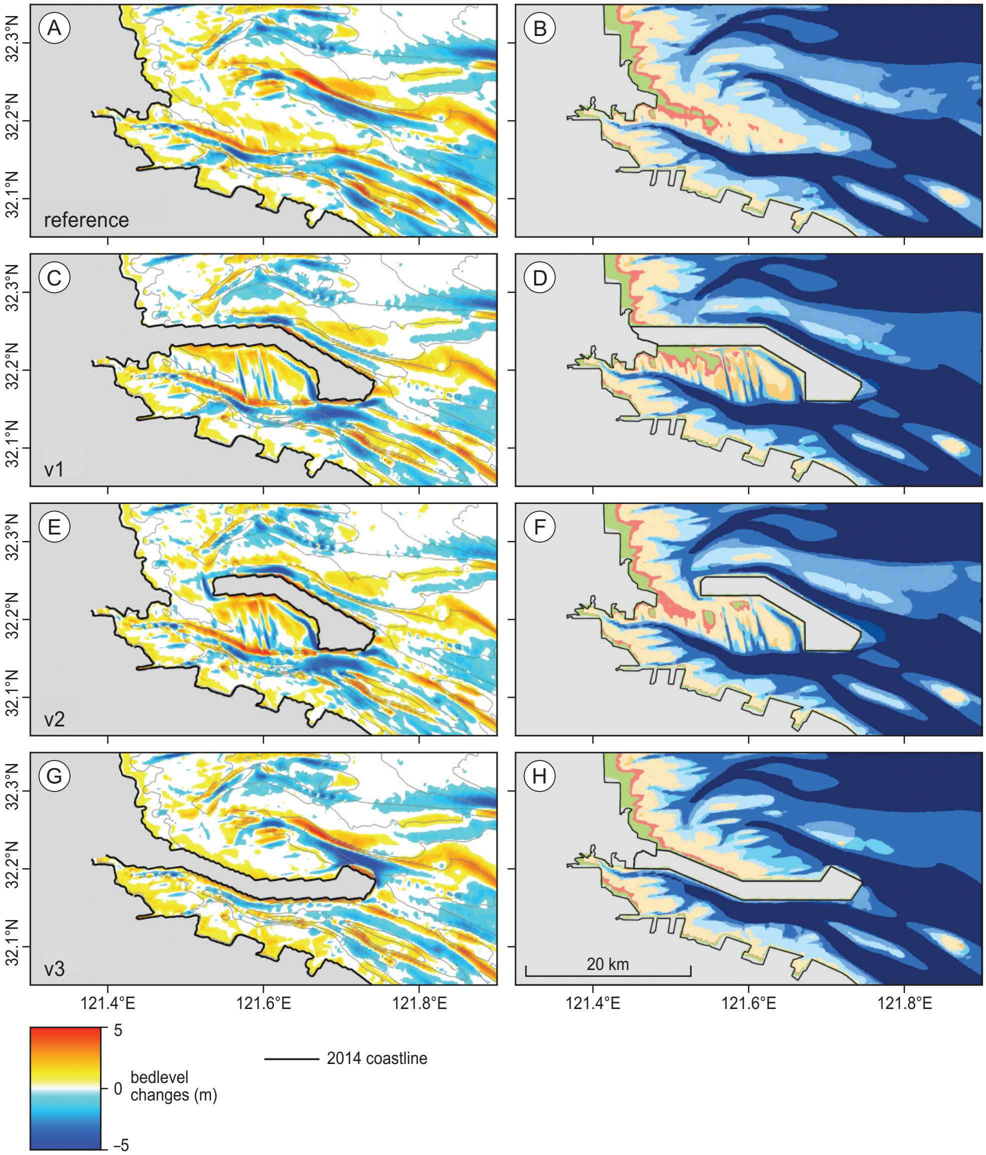


Figure C.4. Left: Total siltation after 20 years of morphological development for the reference case (without further reclamations, **A**) and port configuration v1 (**C**), v2 (**E**) and v3 (**G**). Right: Ecotope distribution after 20 years of development for the reference case (**B**) and configuration v1(**D**), v2 (**F**) and v3 (**H**).

ence case where no reclamation takes place) were simulated for 20 years since 2012 (Fig. C.4). The alternatives and the reference case were compared against each other based on their influence on the natural growth of the shorebird-preferred ecotopes (Fig. C.5).

This work demonstrates the potential of combining hydro-morphodynamical modelling, ecotope mapping and bird spatial distributional data in engineering sustainable solutions for coastal infrastructure development. These 'Building with Nature' solutions, while allowing port development, promote the natural growth of valuable habitats. Rather than the originally-planned reclamation of the entire Yaosha shoal which would result in substantial loss of high-value ecotopes, other port configurations that involve partial reclamation of the shoal will reduce the loss (and in some cases promote the growth) of valuable ecotopes, especially when accounting for morphological feedbacks. For instance, partially reclaiming the south side of the shoal (v3) will lead to a reduction in currents and transport fluxes, while partial reclamation of the north side (v1 and v2) will strengthen siltation rates. This approach can be expanded to more species of birds with different ecological requirements, and even other taxa of lower trophic levels. Future work can aim at a more-refined characterization of habitat preference of species by hydrodynamic parameters, allowing direct calculation of how much preferable habitat of a species is lost/gained for a land reclamation design.

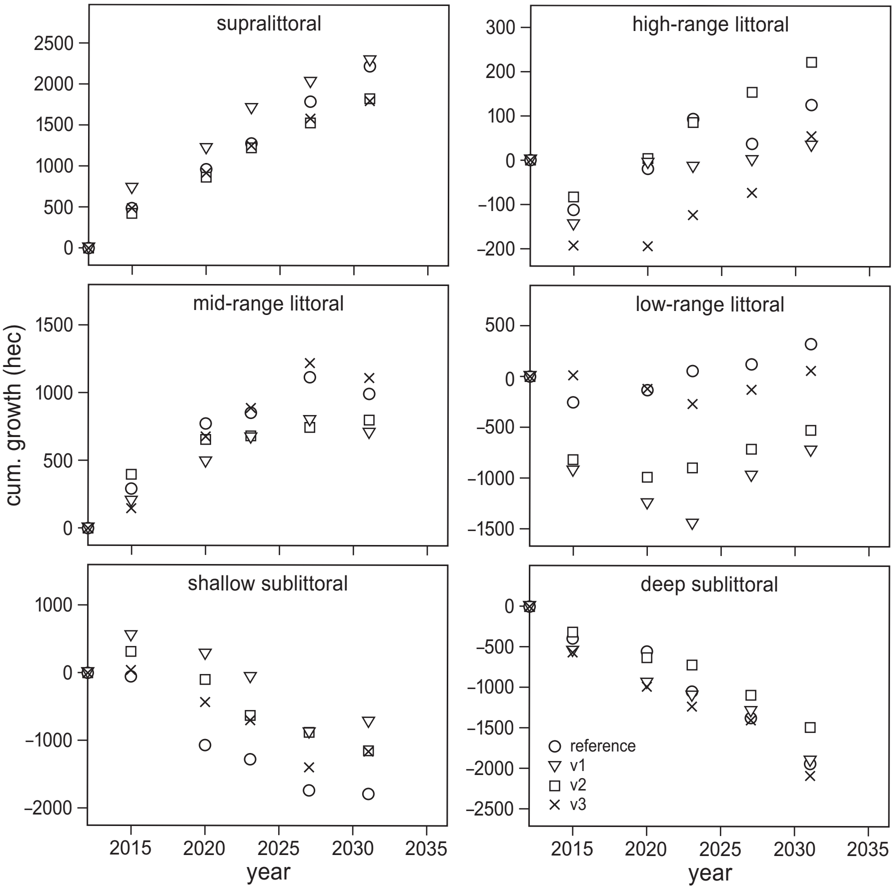


Figure C.5. Net cumulative ecotope growth from 2012–2032 for port configurations v1, v2, v3 and the reference case of no reclamation taking place.

PART IV

Coping with habitat loss and deterioration

CHAPTER 7

Site fidelity of two shorebird species in an imperiled flyway

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Chris J. Hassell & Theunis Piersma

Abstract

Site fidelity, the tendency to return to a previously visited site, is commonly observed in migratory birds. This behavior would be advantageous if birds returning to the same site benefit from their previous knowledge about local resources. However, when habitat quality reduces over time, birds with lower site fidelity might benefit from their higher tendency to switch to better habitats. As a first step towards an understanding of the influence of site fidelity on how animals cope with habitat deterioration, here we describe site fidelity variation in two species of migratory shorebirds (Bar-tailed Godwits *Limosa lapponica menzbieri* and Great Knots *Calidris tenuirostris*). Both species are impacted by the rapid loss and deterioration of intertidal habitats in the Yellow Sea where they fuel up during their annual long-distance migration. Using satellite tracking and mark-resighting data, we measured site fidelity in the wintering (austral summer) and migration periods, during which the species live and co-occur in Northwest Australia and the Yellow Sea, respectively. Although site fidelity was generally high in both species with the majority of individuals using only one site during winter and revisiting the same sites during migration, Great Knots did exhibit lower site fidelity than Bar-tailed Godwits across places and seasons. While there were major habitat deterioration events that had particularly strong impact on the Great Knots during our study period, the fact that they had the same rate of decline in population size and individual survival as the less affected Bar-tailed Godwits suggests that the lower site fidelity in Great Knots might have helped them to cope. Future studies on movement patterns and consequences under different environmental conditions of individuals with different degrees of site fidelity could help understanding how species could cope with, and recover from, local habitat deteriorations.

Introduction

The year-to-year return of migratory birds has long been a source of wonder for humans (Birkhead et al. 2014). Since the start of marking birds individually using metal rings (Berthold 2001), ornithologists discovered that not only the same bird species, but often the same individuals returned to the same place year after year (Piper 2011). Ornithologists have used the terms site fidelity, faithfulness, or philopatry for this tendency to return to a previously visited site. Many bird species show fidelity to their breeding sites, and for migratory birds site fidelity to stopover and wintering sites is also common (Ketterson & Nolan 1990, Cantos & Tellería 1994, Broderick et al. 2007, Schmaltz et al. 2015, Blackburn & Cresswell 2016).

Site fidelity is advantageous in circumstances where animals can benefit from previous knowledge on the distribution of food resources and predation danger; over time, site-faithful individuals may attain dominance over the best and safest local resources (Greenwood & Harvey 1982, Hoover 2003, Piper 2011, Winger et al. 2019). This is beneficial if the environment is stable and predictable. Moreover, in highly variable and unpredictable environments, site fidelity can be advantageous for long-lived species if the benefits of familiarity lead to a higher lifetime fitness, even if this strategy does not consistently lead to favorable outcomes in all years (Switzer 1993, Bradshaw et al. 2004).

Habitat loss and deterioration, which is a major threat to migratory populations (Kirby et al. 2008), can result in a persistent decrease in local habitat quality over a long timescale. In this case, strong site fidelity can be maladaptive (Warner 1990, Cooch et al. 1993). Lower site fidelity strategies might be favored if it promotes the propensity to switch habitats once they deteriorate, and also if it promotes the collection of information on alternative habitats which reduces the risks associated with switching. Therefore, site fidelity strategies may influence how animals adapt to habitat deterioration. As a first step to understand this relationship, it is necessary to describe site fidelity variation of natural populations using deteriorating habitats, and how this variation carries across environments of different degrees of habitat deterioration and different parts of the annual cycle.

Here we explore interspecific variation in site fidelity in two shorebird species, Bar-tailed Godwit *Limosa lapponica menzbieri* and Great Knot *Calidris tenuirostris*. During their annual migration from Northwest Australia to breeding areas in the East Russian Arctic, both species rely on coastal wetlands of the Yellow Sea (Battley et al., 2012; Chan et al., 2019b; Chapter 3, this thesis; Fig. 7.1A and B) which were undergoing rapid habitat loss and deterioration (Murray et al. 2014, 2015, Melville et al. 2016a). Both species showed declines in survival rates and numbers (Piersma et al. 2016, Studds et al. 2017). We compare site fidelity between the two species in two periods of the non-breeding season when they co-occur at the same coastal wetlands at the same time: (1) during winter (the austral summer), when these species are at their final non-breeding destination in Northwest Australia and (2) during migration at the main staging area (i.e. used for the longest), at the coast of the Yellow Sea (Battley et al., 2012; Chan et al., 2019b; Chapter 3, this thesis; Fig. 7.1A and B).

Site fidelity of birds is usually inferred from recapturing or resighting marked individuals (e.g. Hestbeck et al. 1991, Rehfisch et al. 1996, Lok et al. 2011), but inference is limited by the inability to assign a cause for unobserved birds, which could be due to movement of birds to unsurveyed sites (true site infidelity), or mortality or logistical constraints that not all birds present at a certain location could be observed. This limitation can be overcome with technologies that allow tracking of bird movements with global coverage, e.g. an Argos satellite tag or GPS tag. As a step towards a multi-species comparison of site fidelity in different environments using all available data types, we investigate our question with two types of data, tracked itineraries of satellite-tagged individuals and resightings of marked individuals, and examine how data types could affect the patterns inferred.

Methods

Bird marking and resighting

Individual marking of the study species was conducted at Roebuck Bay (18.11°S, 122.27°E) and Eighty Mile Beach, Northwest Australia (19.40°S, 121.27°E), two major non-breeding sites in the East Asian–Australasian Flyway for these species (Rogers et al. 2011), each year in 2005–2019, from February to March, and from June to December. The birds were captured with cannon nets, measured and marked with unique combinations of colour-bands and a flag on their tarsi (see Piersma et al. 2016). First-year (juvenile) and older (adult) birds (i.e. in their 3rd calendar year or older) were distinguished based on plumage characteristics and moult scores.

On the northern shores of Roebuck Bay, throughout the wintering period (August to mid-April), 2007–2020, observations of banded birds (i.e. resightings) were conducted by trained observers using 20–60x zoom telescopes, several times a week during the 4-hour daytime high-tide period. Most observations (~90%) were conducted at high-tide roost sites at the northern beaches. The available shoreline for birds to roost is about 9 km long and consists of sandy beaches interspersed with small rocky areas and roost choice is affected by tide height, disturbance and microclimate (Rogers et al. 2006). About 10% of the time, observations were done during in-coming tides while birds were feeding on the mudflats and being pushed towards the shore by the tide bringing them close enough for observers on shore to read their colour-bands.

Dedicated resighting work was also conducted every April for 3 days, 2010–2017 on a 65 km section in the northern part of the 220 km long Eighty Mile Beach (mid-point = 19.4°S, 121.3°E, 190 km southwest of Roebuck Bay). In addition, each year incidental observations were obtained during population count surveys (6 days/yr. November and December 2006–2017 and 3 days/yr. 2018–2019) and bird catching expeditions (10 to 11 days/yr. in November/December 2007–2010 and February 2011–2020).

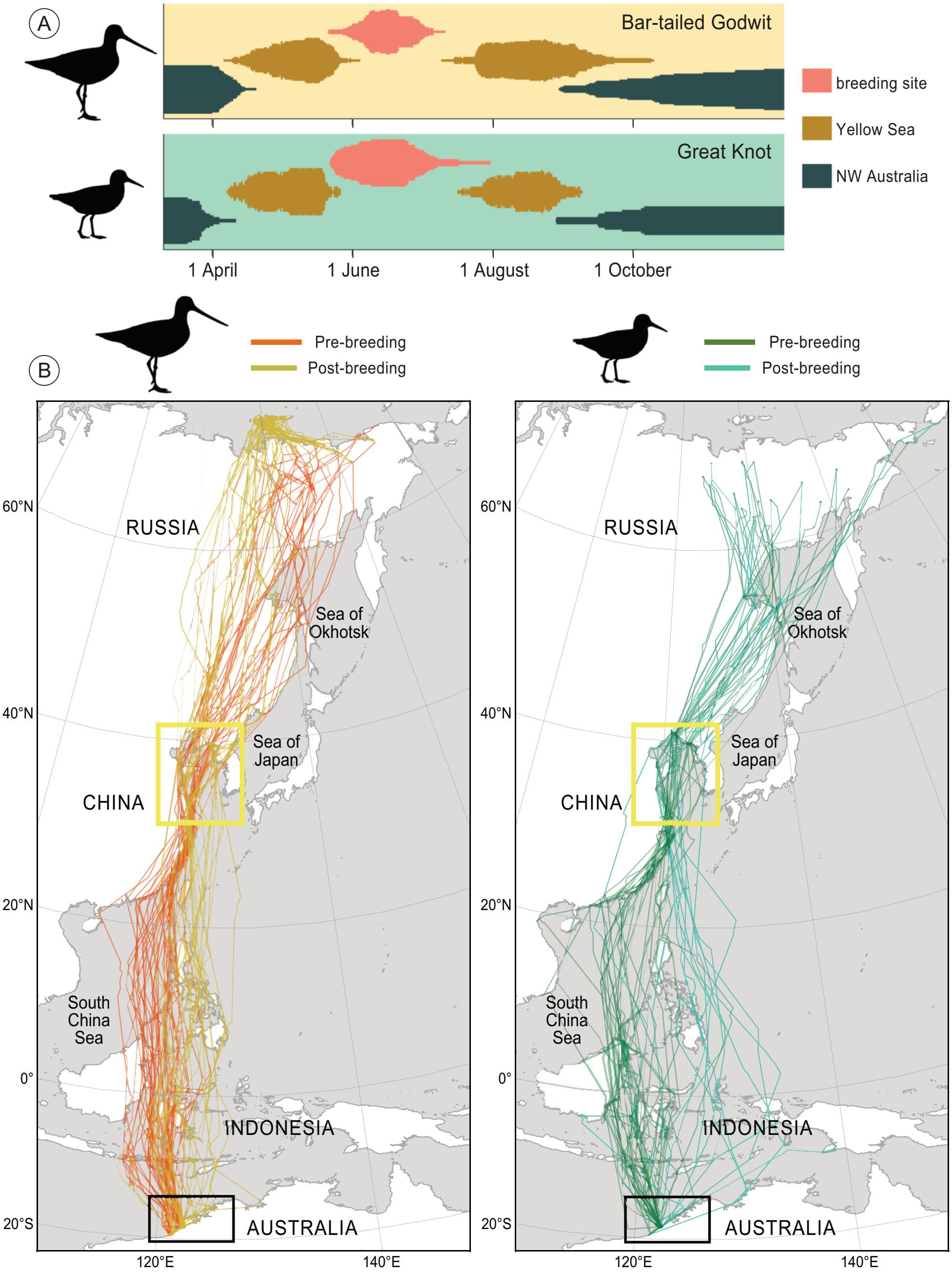

Figure 7.1. (**A**) Occurrence in non-breeding site (Northwest Australia), staging area (Yellow Sea) and breeding areas for satellite-tagged Bar-tailed Godwits and Great Knots in 2015–2017. Height of box corresponds to the number of individuals. (**B**) Migration tracks of satellite-tagged Bar-tailed Godwits (left) and Great Knots (right) in 2015–2017. Black rectangle indicates Northwest Australia and yellow rectangle indicates the Yellow Sea study area.

In the Yellow Sea, at Luannan Coast, Bohai Bay (39.1°N, 118.2°E), a key staging site of Great Knots (Lei et al. 2018), we conducted yearly intensive resighting work of banded birds during the northward migration period (mid-April to early-June), 2010–2020 (Lok et al. 2019). In the Yalu Jiang Estuary National Nature Reserve, Liaoning, China (39.8°N, 123.9°E), a key staging site of both species (Choi et al. 2015), in 2010–2020, mid-March to mid-May, surveys were conducted by Fudan University and Miranda Trust. At 18 shorebird sites along the Chinese coast, surveys were conducted during the spring migration season (April to June) in 2015–2017, with 2–3 field days in each site (Box A of this thesis). At other sites along the flyway, surveys were conducted occasionally or not targeted at observing banded individuals, nevertheless observers reported sightings of banded birds to the banding organization. We compiled these observations into our resighting history of each bird from which we analyzed site fidelity.

Satellite transmitter deployments

In September and October 2014–2016, we deployed 4.5 g and 9.5 g solar Platform Terminal Transmitters (PTTs, Microwave Telemetry, USA) onto a subset of the Great Knots and Bar-tailed Godwits banded in Roebuck Bay, respectively, to track their movements. PTTs were programmed to operate on a duty cycle of 8 hours of transmission and 25 hours off. Tags were attached to Bar-tailed Godwits with a Teflon leg-loop harness (Sanzenbacher et al. 2000), and onto Great Knots using a body harness (Chan et al., 2016) made of elastic nylon (Elastan, Vaessen Creative, The Netherlands). We then released the birds at their capture locations. The work was carried out under Regulation 17 permits SF 010074, SF010547 and 01-000057-2 issued by The West Australian Department of Biodiversity, Conservation and Attractions.

Measures of site fidelity based on tracking data

For all tracking data collected, we kept all standard Argos locations (i.e. the location classes 3, 2, and 1) and removed implausible auxiliary locations (i.e. classes 0, A, B and Z) by applying the Hybrid Douglas filter (Douglas et al. 2012). The filtering parameters were set at 120 km/h for the maximum sustainable rate of movement and 10 km for the minimum redundant distance. We further accounted for spatial error in the Argos telemetry by fitting the tracking data with a continuous-time random walk state-space model with the ‘fit_ssm’ function in the ‘foiegras’ R package (Jonsen et al. 2020). The state-space model incorporated the error ellipse information of the Kalman filter-based Argos locations, and the fitted locations from the model were used in the analysis of identifying migration stops and timing.

We measured fidelity to a ‘site’, which was defined as a cluster of habitats that an individual bird uses daily for foraging and roosting (Clemens et al. 2010). Site fidelity within the wintering period was measured for 41 Great Knots and 24 Bar-tailed Godwits that were tracked from their release date (in September to November) to one week before the first departure date of a tracked conspecific (first departure date: 22 March for

Great Knots, 4 April for Bar-tailed Godwits). We calculated the proportion of birds that remained at a single site during this wintering period and described movements to any other sites. Site fidelity across wintering periods was also estimated for the 10 Great Knots and 9 Bar-tailed Godwits with complete migration tracks to and from the breeding grounds. For these individuals, we present the proportion of birds that returned to Roebuck Bay and describe the movements of those that overwintered at other sites.

Seasonal site fidelity to migratory stopover sites in the Yellow Sea was measured from the first migration track recorded for each tracked individual. As per design, the elastic nylon harness material on Great Knots degrades and breaks within a year of deployment which did not allow for calculation of between-year fidelity of Great Knots to migration sites. Therefore, to characterize seasonal site fidelity for a comparison between species, we determined whether birds re-visited the same northward migration site during the subsequent southward migration in their first tracked migration. We employed the following procedures to identify stopover sites: locations within the Yellow Sea with ground speed less than 5 km/h was identified as 'stationary'. Stopovers were defined as a cluster of at least 3 stationary locations within 50 km of each other, with the first and last recorded locations at the stopover being at least 2 hours apart. Departure times were extrapolated over the intervening travel distance between the last location at a stop and the next location, arrival times were calculated in the same way. A site was defined as re-visited across seasons when a southward site's centroid was within 50 km of a northward site's centroid for a particular bird. The threshold distance of 50 km was determined based on the precision of the reported locations of the band resightings, so that metrics calculated from the satellite tracking data are comparable to that from the resighting data.

In addition to reporting site fidelity as the proportion of birds that re-visited sites across seasons, we also present the degree of site fidelity at the individual level, measured as the proportion of time birds spent at a re-visited site relative to their total length of stay in the Yellow Sea during southward migration. We compare these proportions between the two species by fractional regression. To show the frequency of movements within sites in the Yellow Sea, we present the number of Yellow Sea sites used per individual during northward and southward migration. We compare this metric to the same one from the resighting data, to provide an understanding of the magnitude of any issues resulting from non-observed movements when analyzing resighting data.

Measures of site fidelity based on resighting data

We measured site fidelity during the wintering period from resighting data of marked adult birds captured in June to December in Roebuck Bay, and excluded the individuals carrying a satellite transmitter as their movements are already in the analysis described above. For site fidelity within the wintering period, we analyzed individuals with two or more sightings from 1 November until a week before the first departure of the tracked birds; this resulted in a sample of 641 Bar-tailed Godwits and 775 Great Knots from which we then calculated the number of sites that each individual was sighted. We grouped individuals with >=2 sightings for multiple years into one datapoint to avoid pseudo-replication. Individuals observed in >= 2 sites reflected a move between sites within the wintering period. If an individual was observed at only a single site, it was considered to have stayed there for the entire wintering period, moved to an un-surveyed site, or moved to a surveyed site but not observed there. The nature of the data did not allow us to distinguish between these scenarios.

We then compared the proportions of individuals observed at 1 or 2 sites between the two species by a Fisher's Exact test. The above analysis pertained to within-winter movement between the resighting sites of Roebuck Bay and Eighty Mile Beach. However, a small proportion of individuals were also observed by researchers/bird-watchers at other sites in the flyway during winter. We further examined the sighting history of these few individuals to understand these rare long-distance movements.

To measure site fidelity during the migration period in the Yellow Sea, we expanded our dataset to include birds marked at other sites in Australia because, to realistically assess site fidelity, our sample size of birds marked with unique colour-bands in Northwest Australia was too small (only 34 Bar-tailed Godwits and 135 Great Knots seen two or more times in the Yellow Sea within 2008–2017). Therefore, we included resighting data from birds marked (with a flag engraved with a unique letter-number code) by the Australian Wader Studies Group (AWSG) at four other sites throughout Australia, and the resighting data was collected by the field efforts described above, and collated by the AWSG. The final dataset comprises resightings in the Yellow Sea from 2008 to 2017 of 173 Bar-tailed Godwits marked in Northwest Australia and Victoria, and 513 Great Knots marked in Northwest Australia, Queensland, Northern Territory and Victoria.

Movements within sites in the Yellow Sea within a migration season were described by the number of sites where an individual was resighted. We calculated this metric only for individuals that were resighted >=2 times in a migration season and only for northward migration, because sample sizes were too low during southward migration (only 4 Bar-tailed Godwits and 6 Great Knots were resighted >=2 times). We highlight how the imperfect nature of resighting data affects the results when we compare this metric with the satellite tracking data.

We characterize seasonal site fidelity derived from resighting data the same way as for the satellite-tracking data, i.e. whether birds re-visited the same northward migration site during the subsequent southward migration. We calculated the proportion of individuals seen at the same Yellow Sea stopping site during both northward and southward migration. We characterize between-year site fidelity during northward migration by calculating the proportion of individuals seen at the same Yellow Sea site in >=2 northward migrations. We compare these proportions between the two species by Fisher's exact tests. All data analyses were performed in R version 3.6.2 (R Core Team 2019). We used $P < 0.05$ to establish statistical significance.

Results

Site fidelity in the wintering period

In the wintering period, none of the 24 satellite-tracked Bar-tailed Godwits moved out of Roebuck Bay, while seven out of 41 (17%) Great Knots moved in and out of Roebuck Bay (Fig. 7.2A, Table 7.1). Within-winter patterns of movement for Great Knots were quite varied. Two birds moved to Willie Creek about 20 km north of Roebuck Bay and one of the two returned briefly to Roebuck Bay. One bird moved south to Bidyadanga (80 km) for less than one day and returned to Roebuck Bay. Of those that moved to Eighty Mile Beach (ca. 170–320 km south), two stayed there and one went back-and-forth twice before finally returning to Roebuck Bay in early March. One bird moved north to Northern Territory (ca. 920 km north) and stayed there until 23 May when the tag ceased reporting. Four out of these seven Great Knots departed from Roebuck Bay during northward migration, but none were tracked for a complete return migration. Among the 34 Great Knots that we detected only in Roebuck Bay during the wintering period, 10 reached the breeding grounds and were tracked until October, in which eight returned to NWA and two overwintered in the Northern Territory, Australia (Fig. 7.2A, Table 7.1). Among the 24 Bar-tailed Godwits, nine reached the breeding grounds and all returned to Roebuck Bay (Table 7.1).

The resighting data showed that in both study species, most individuals (>90%) were resighted at only one site during a wintering period. A small percentage were resighted

Table 7.1. Site fidelity during the wintering period for Bar-tailed Godwits and Great Knots, as measured from satellite tracking and resighting data.

	Bar-tailed Godwit	Great Knot	
Satellite-tracking data			
Individuals stayed at one site during entire wintering period	100% (n = 24)	83% (n = 41)	P = 0.04*
Individuals returned to same winter site after migration	100% (n = 9)	80% (n = 10)	P = 0.47
Resighting data			
Proportion of individuals resighted at n sites within a wintering period			
1 site	97.3% (624 birds)	93.8% (727 birds)	
- only Roebuck Bay	617 birds	690 birds	
- only Eighty Mile Beach	7 birds	36 birds	
- only Darwin	0	1 bird	
2 sites (Roebuck Bay and Eighty Mile Beach)	2.7% (17 birds)	6.2% (48 birds)	P = 0.001*

*P < 0.05
Differences between the two species were tested by Fisher's exact tests

at two sites, namely Roebuck Bay and Eighty Mile Beach, implying that individuals moved between the two sites during the wintering period. A higher proportion of Great Knots than Bar-tailed Godwits were resighted within a wintering period at the two sites

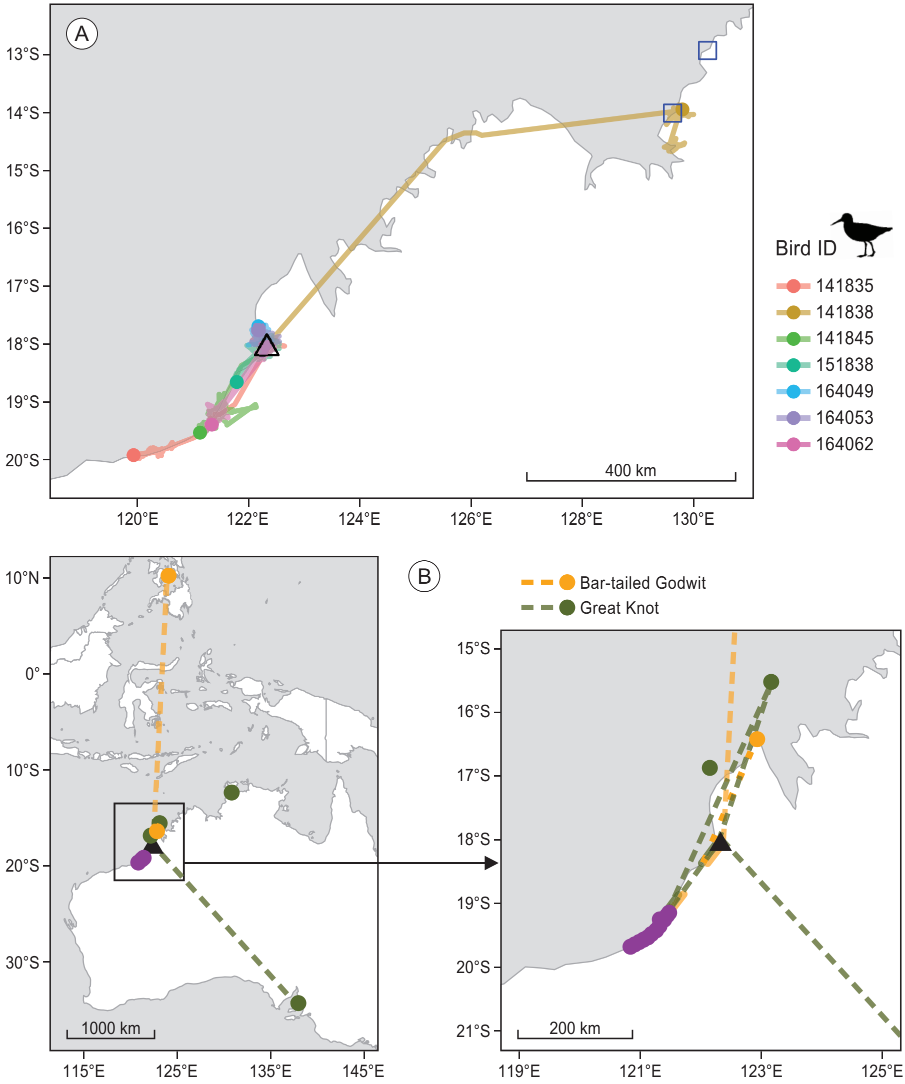

Figure 7.2. (**A**) Movements of satellite-tracked Great Knots out of Roebuck Bay during the wintering period in Northwest Australia, 2014–2017. The triangle denotes Roebuck Bay. Squares denote wintering sites of two individuals that did not return to Roebuck Bay after a complete migration to the breeding grounds. (**B**) Resighting locations of individually marked Great Knots (green) and Bar-tailed Godwits (orange) banded in Roebuck Bay. Triangle denotes Roebuck Bay and purple polygon denotes Eighty Mile Beach. Dotted line connects sites where the same individual was resighted across years. Figure to the right is a zoomed-in version of the area enclosed in the square.

(6.2% vs 2.7%, Fisher's exact test, *P* = 0.001, Table 7.1). Four Great Knots and two Bar-tailed Godwits were resighted outside of Roebuck Bay and Eighty Mile Beach during the wintering period (Fig. 7.2B).

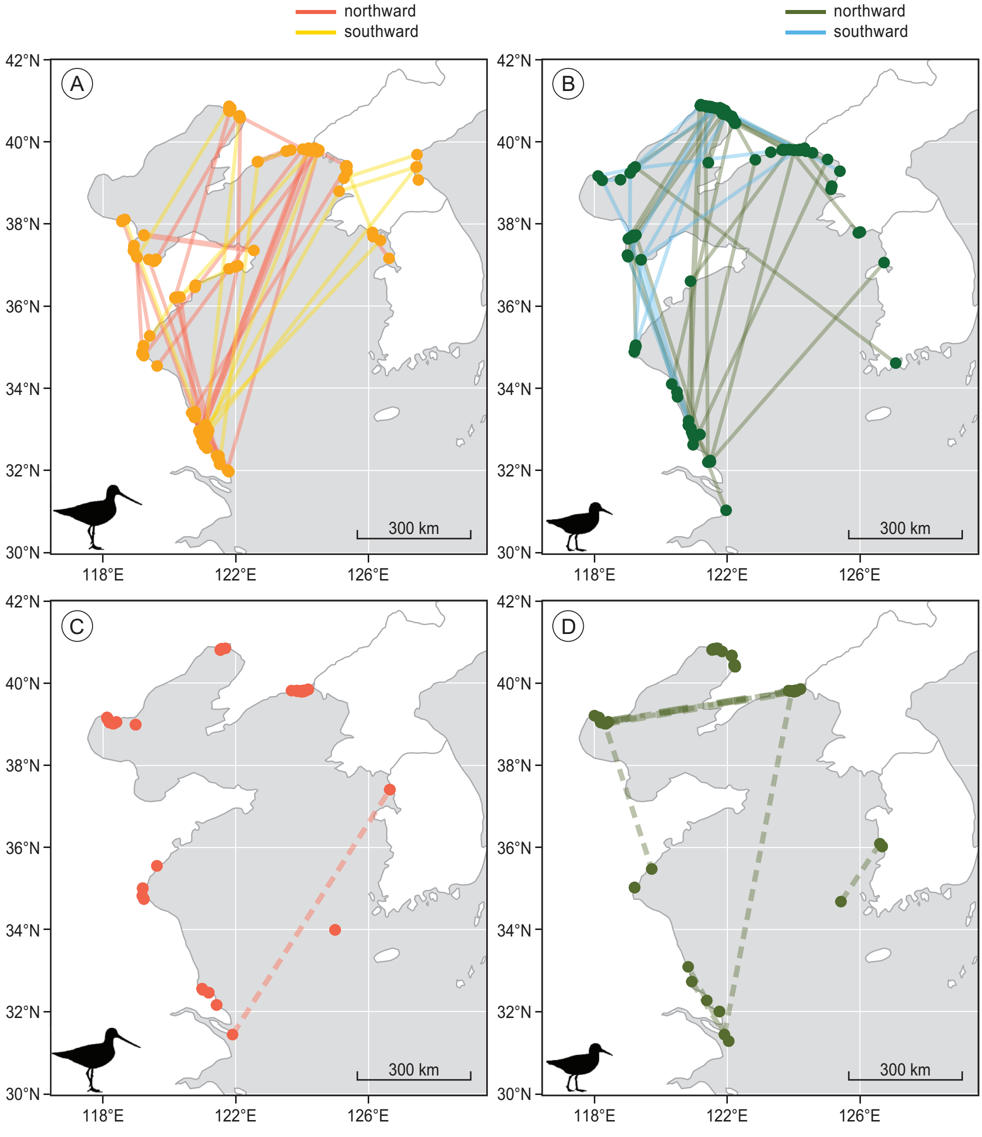

Figure 7.3. Movements among sites within the Yellow Sea used by satellite-tagged (**A**) Bar-tailed Godwits and (**B**) Great Knots in 2015–2017. Solid lines connect sites visited by an individual within the same northward or southward migration season. Sites within the Yellow Sea where individually marked (**C**) Bar-tailed Godwits and (**D**) Great Knots were resighted during northward migration in 2008–2017. Dashed lines connect sites visited by an individual within the same migration season.

Seasonal site fidelity during migration

Our tracking data showed a clear temporal overlap of the two species in the Yellow Sea (Fig. 7.1A). Satellite-tracked Bar-tailed Godwits used fewer Yellow Sea sites than Great Knots (median = 2 sites vs. 3 sites) during both northward and southward migration (Table 7.2, Fig. 7.3A and B). Sixteen of the 20 (80%) tracked Bar-tailed Godwits, and 8 of the 12 (67%) tracked Great Knots, re-visited the same site(s) during southward migration as used during northward migration. Also, Bar-tailed Godwits stayed proportionally longer at the re-visited sites than Great Knots (92% vs 19%, fractional regression, *P* = 0.01, Table 7.2, Fig. 7.4).

From the resighting data, within the northward migration season most individuals (>=98% for both species) were observed at only one of the Yellow Sea sites (Table 7.2, Fig. 7.3C and D). The percentage of individuals seen at two or more sites was not significantly different between Bar-tailed Godwits and Great Knots within a season (0.8% vs. 2.4%, Fisher's exact test, *P* = 0.45). Pulling all the years together, among individuals being resighted in both northward and southward migration, 10 out of 11 Bar-tailed

Table 7.2. Site fidelity of Bar-tailed Godwits and Great Knots in the Yellow Sea during the migration period, as measured from satellite tracking data and resighting data.

	Bar-tailed Godwit	Great Knot	
Satellite tracking data			
Median number of sites used per individual:			
- Northward	2 (range: 1–3)	3 (range: 1–4)	
- Southward	2 (range: 1–3)	2.5 (range: 1–4)	
Proportion of individuals visiting the same sites during northward and southward migration	80% (*n* = 20)	67% (*n* = 12)	*P* = 0.43
Proportion of time spent in the repeatedly visited sites (of total staging duration in southward migration)	Median = 92%	Median = 19%	$P = 0.01^{*}$
Resighting data			
Proportion of individuals resighted at *n* Yellow Sea site(s) within a northward migration			
- 1 site	99.2% (132 birds)	97.7% (333 birds)	
- 2 sites	0.8% (1 bird)	2.1% (7 birds)	*P* = 0.45
- 3 sites	0	0.3% (1 bird)	
Proportion of individuals resighted at the same Yellow Sea site during both northward and southward migration	90.9% (*n* = 11)	63.6% (*n* = 11)	*P* = 0.31
Proportion of individuals resighted at the same Yellow Sea site in >=2 northward migrations	98.0% (*n* = 102)	89.5% (*n* = 267)	$P = 0.005^{*}$

$^{*}P < 0.05$

Differences between the two species in proportions of individuals were tested by Fisher's exact tests. The difference in proportion of time spent in the repeatedly visited sites was tested by fractional regression.

Godwits and 7 out of 11 Great Knots were seen at the same northward stopping site during southward migration. Across years, more Bar-tailed Godwit individuals were seen at the same northward migration Yellow Sea stopping sites (98.0%) than Great Knots (89.5%; Fisher's exact test, $P = 0.005$).

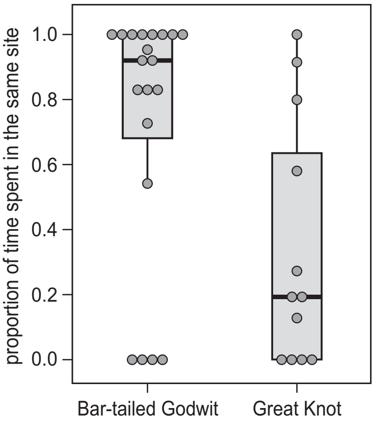

Figure 7.4. Proportion of time spent at the same sites during northward and southward migration (of total staging duration in southward migration) for satellite-tracked Bar-tailed Godwits ($n = 20$) and Great Knots ($n = 12$) in 2015–2017.

Discussion

Our findings based on both satellite tracking and resighting data revealed high site fidelity in both study species, with the majority of individuals using only one site during winter and returning to the same stopping sites during migration. However, the pattern of Bar-tailed Godwits being more site faithful than Great Knots holds across seasons and places. In the wintering period, both data types showed that Bar-tailed Godwits are significantly more site faithful than Great Knots and less likely to move between sites. During migration, seasonal site fidelity (the proportion of individuals visiting the same sites during northward and southward migration) did not differ significantly between the two species in both data types, although in absolute terms the proportion of site faithful Great Knots are lower than that of the Bar-tailed Godwits. However, the degree of site fidelity, measured by the proportion of time spent at the repeatedly visited sites, was significantly higher for Bar-tailed Godwits than Great Knots. This same pattern holds for the fidelity across northward migrations measured from the resighting data.

These results are consistent with those in a study conducted across the entire country of New Zealand (Battley et al. 2011) and at Moray Basin, Scotland (Rehfisch et al. 2003), that the Bar-tailed Godwits were more site faithful than Red Knots (*Calidris canutus*, a sister species of the Great Knot). The consistency in this pattern across time and places suggest that site fidelity is species-specific. However, our data do not allow an investigation of whether it is an individual-specific trait (i.e. if certain individuals are consistently more faithful both in the Yellow Sea and at Northwest Australia), because there is no between-individual variation in site fidelity among Bar-tailed Godwits (all birds are faithful in Northwest Australia), and for Great Knots, the individuals that were not site faithful in Northwest Australia were not tracked pass the Yellow Sea in southward migration (therefore no data on seasonal site fidelity in the Yellow Sea for those individuals).

While the mark-resighting data and satellite tracking data both showed that Bar-tailed Godwits are the more site-faithful species, mark-resighting data alone underestimated the proportion of individuals that moved between sites during winter (Table 7.1) and the number of sites birds used in the Yellow Sea (Table 7.2), e.g. during the northward migration, satellite tracking data showed individual Great Knots used three sites in the Yellow Sea, and Bar-tailed Godwit used two, while the mark-resighting data indicated that most individuals only used one site. This is likely an outcome of the fact that, constrained by logistics, many sites visited by the birds are unsurveyed or only sporadically surveyed (as illustrated for Great Knots in Chan et al. 2019b); and at the surveyed sites, ground observers could have missed some flocks or some marked individuals within a dense flock. Although tracking individual birds with PTTs or GPS tags do have limitations, e.g. the handicap of carrying a tag altered migration patterns in some cases (reviewed in Lameris & Kleyheeg 2017), they do provide a more representative measure of site use and fidelity than mark-resighting data. However, since mark-resighting data is still the most prevalent data set for most shorebird species in the EAAF and elsewhere, it can be harnessed for multi-species comparisons of site fidelity with the caveat that results should be interpreted as a relative measure of site fidelity.

Site fidelity and response to habitat loss and deterioration

During our study period, shorebird habitats in Northwest Australia remained stable, whereas habitats in the Yellow Sea underwent significant loss and deterioration (Murray et al. 2014, 2015, Melville et al. 2016a, Chen et al. 2019). While the lower site faithfulness of Great Knots suggests that they are more likely to respond to local habitat perturbations by moving to alternative sites than Bar-tailed Godwits, the rates of decline in adult survival (2006–2012) and in population size (1993–2012) did not differ between the two species (Piersma et al. 2016, Studds et al. 2017). This may reflect that that there are limits to coping by moving away. First, energetic costs and risk associated with moving could offset the survival benefits of moving. Survival costs of moving was showed in a study by Burton et al. (2006), who found that after a sudden loss of wintering habitat, displaced Redshanks *Tringa totanus* experienced lower body condition and higher mortality compared to birds that were already in the recipient site. Second, the amount of suitable habitat remaining in the Yellow Sea could be limiting the number of birds that it can support.

Further, two major events of habitat deterioration that happened just before and during our study period may have impacted Great Knots more heavily than Bar-tailed Godwits. First, in April 2006, ~290 km^2 of tidal flats was impounded by the closure of the 33 km-seawall at Saemangeum (35.8°N, 126.6°E) in South Korea. This area supported 20–30% of the world population of Great Knots during both northward and southward migration in the late 1990s to early 2000s (Barter 2002). Given that ~100,000 Great Knots disappeared from Saemangeum and the adjacent Geum Estuary and no substantial increase in Great Knot numbers was observed at other staging sites in the Yellow Sea, most of these disappeared birds likely died (Moores et al. 2016). Second, at the Yalu Jiang Estuary of the Yellow Sea, one of the main staging sites for Bar-tailed Godwits and Great Knots (Choi et al. 2015), yearly monitoring of the macrobenthic community in 2011–2016 showed that the population of *Potamocorbula laevis*, a main bivalve prey of shorebirds, had drastically declined starting in 2013; the very high density in 2011 (708.06 ind/m^2) had declined by >99% in 2016 (Zhang et al. 2018). This drastic change likely profoundly impacted the Great Knot, a mollusk specialist, and less so the Bar-tailed Godwit which also feeds on polychaetes (Choi et al. 2017). The fact that the two species showed very similar rates of decline in survival and population size suggests that the higher propensity of Great Knots to move to new sites might have helped to soften the impact of these events.

This leads to the question of whether the individual Great Knots that survived these two habitat deterioration events are the birds with the tendency for lower site fidelity. If so, this could contribute to the site fidelity patterns that we measured at the population level. And, if site fidelity has a heritable component, events selecting for low site fidelity individuals would lead to a decrease in site fidelity level over generations. Of particular interest would be the situation of habitat gains rather than losses: if some Yellow Sea habitats are being restored in the future, would less site faithful individuals be faster at discovering restored sites, and would populations with a higher proportion of low-site fidelity individuals recover more rapidly? To answer such questions, movement patterns of individuals with different degrees of site fidelity could be studied in relation to their survival and recruitment, and interesting differences between species and different environmental contexts may be revealed.

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CHAPTER 8

More explorative individuals of a long-distance migrant shorebird respond more quickly to collapse in prey stock and have higher breeding success

Ying-Chi Chan, T. Lee Tibbitts, Chris J. Hassell & Theunis Piersma

Abstract

Movement and information use strategies are identified as key factors influencing the ability of animals to adapt to human-induced global changes. These strategies are found to correlate with personality traits measured under standardized laboratory environments. Here we examine how personality differences might underlie differences between individuals in coping with ongoing rapid environmental changes in Great Knots (*Calidris tenuirostris*), an endangered long-distance migratory shorebird threatened by loss and degradation of their main coastal refuelling sites halfway between their Northwest Australian nonbreeding area and their eastern Russian mountain tundra breeding grounds. Although the number of sites visited during migration did not correlate with individual exploratory tendencies, birds that were more explorative visited proportionally more new sites during southward migration. At a main staging site where the prey stock of the birds had collapsed, explorative individuals moved on to other staging sites sooner. Explorative individuals, compared with non-explorative individuals, arrived earlier on breeding sites and tended to stay longer there, the latter suggesting successful reproduction. We propose that explorative individuals are better at acquiring environmental information, enabling them to respond faster to environmental changes e.g. sudden food declines. Moving to alternative sites enables them to fuel up faster, and thus arrive earlier on breeding sites which, in turn, helps them to breed successfully. Accordingly, variation in exploratory tendencies within a population could be key to adaptive capacity to rapid human-induced environmental changes in long-distance migratory shorebirds. Survival costs associated with being explorative would constrain their ability to cope.

Introduction

The ability to respond to novel and changing environmental conditions by genetic adaptation, phenotypic plasticity, or range shifts, is critical to the persistence of all organisms, especially in the current world where they are exposed to human-induced global changes (Gienapp et al. 2008). For mobile animals, movement is a core response mechanism enabling individuals to exploit new habitats, from which population patterns in the form of range shifts can eventually emerge. In face of the worldwide declines in many migratory animals (Harris et al. 2009, Vickery et al. 2014, Clemens et al. 2016, Rosenberg et al. 2019), understanding the limits of movement responses to environmental changes will enable a deeper understanding of the causes of decline and allow predictions of the fate of populations under a changing environment.

Movement responses are limited by physical constraints, such as the energetic costs to move long distances; by time constraints, since movements must still fit in the annual cycle of events like breeding, migration and moulting; and by cognitive constraints, such as the animal’s ability to acquire and interpret information about resources in the environment. With relevant information, an animal can move *strategically*, reaching the most profitable habitats with the lowest energetic and time costs of moving (Winkler et al. 2014). For a migratory animal, this can lead to fitness consequences directly (via an increase in survival) and indirectly by carry-over effects to later seasons, e.g. using higher quality non-breeding habitat can lead to higher reproductive success during the breeding season (Marra et al. 1998, Harrison et al. 2011, Senner et al. 2015).

Individuals may vary in the effort they put into gathering information and in the types of information gathered: they can collect information on the environment themselves (‘personal information’) or do it by observing the behaviour of others (‘social information’; Danchin et al. 2004). Individuals can also use environmental information differently by attributing different values to personal and social information and to past and more-recent information when making decisions. Since the information use strategy that maximizes an animal's success varies between situations, optimality theory predicts that animals should be flexible and be able to attribute different values to personal and social information depending on circumstances (Rendell et al. 2011). However, a growing body of evidence suggests that animals have rather fixed information use strategies, e.g. some individuals are consistently more likely to use social than personal information (Beauchamp 2001, Kurvers et al. 2010, Trompf & Brown 2014, Bijleveld et al. 2015). Studies of linkage between information use strategies and animal personality, i.e. repeatable individual behavioural differences (Smit & van Oers 2019), reveal that information use strategies could be linked functionally to other traits which reduces the scope of flexibility.

One personality trait particularly relevant to information use is the tendency to explore. Individual-level variations in this behavioural trait have been studied in natural populations of a variety of taxa (e.g. Cummins & Walsh 1976, Perals et al. 2017, for a review see Bell, Hankison & Laskowski 2009). Exploratory tendency is measured in a controlled laboratory setting that fits the particular ecological traits of the study species and usually involves introducing focal individuals to a novel space or object and measuring speed of approaching the novel object and movement within the novel space (Carter et al. 2013). Laboratory-measured exploratory traits have been shown to correlate with exploratory behaviours in the wild at small spatial scales, e.g. in bullheads (*Cottus perifretum*) exploring a novel stretch of stream (Kobler et al. 2009), and in the likeliness of Blue Tits (*Cyanistes caeruleus*) finding new feeders in their resident forests (Herborn et al. 2010). On the relationship between personality and response to environmental change, one study on Great Tits (*Parus major*) manipulated food availability by emptying feeding stations (van Overveld & Matthysen 2010). The more exploratory a Great Tit, the more rapidly it switched to foraging areas further away in response to the food removal. The home ranges remain the same before and after the food removal and do not relate to the birds' personalities. Thus, the observed quick responses appeared to be caused by the larger amount of environmental information that the birds had already acquired before the food removal. In summary, explorative individuals might be better at adapting to rapid environmental change, by a mechanism of a faster response facilitated by a larger amount of environmental information having already been acquired, which could be due to a higher propensity to go into novel environments to collect new information. Following this logic, exploratory personality could be driving species adaptation to the current human-induced environmental changes, such as climate change and habitat destruction. However, given the challenges of following individual animals with measured exploratory tendencies in the wild, no studies have examined this reasoning with empirical data so far.

Here we investigate the influence of exploratory tendency on individuals' responses to a rapid environmental change in a wild species with a declining population. Our study species is the Great Knot (*Calidris tenuirostris*), a long-distance migratory shorebird, which migrates annually along the East Asian–Australasian Flyway from Northwest Australia to the Eastern Russian Arctic and back (Tomkovich 1997, Chan et al. 2019b). It is listed as globally 'Endangered' on the IUCN Red List (IUCN 2017) with low adult survival (Piersma et al. 2016) and continuous population decline (Studds et al. 2017) linked to the loss and degradation of their main fuelling sites along the Yellow Sea coast. By satellite-tracking individuals with measured exploratory tendencies, we first examine whether the most explorative individuals visit the most stopping sites during migration and, during southward migration if they are more likely to visit 'new' sites (i.e. sites not visited during northward migration). Second, we investigate whether more explorative individuals respond faster to environmental changes by capitalizing on a 'natural' experiment – the sharp decline of the most abundant high-quality shorebird prey (the bivalve *Potamocorbula laevis*) at a main staging site of Great Knots (the Chinese side of the Yalu Jiang estuary, Zhang et al. 2018). We hypothesize that among individuals that stage at the Yalu Jiang estuary, the more explorative birds will switch to alternative sites more quickly, enabled by their knowledge on alternative habitats. We further assess if being more explorative leads to better migratory performance by quantifying arrival dates to the breeding grounds, and whether that may lead to fitness advantages in terms of breeding success.

Materials and Methods

Bird capture

In September and October 2014, 2015 and 2016, we captured Great Knots with cannon nets at their primary non-breeding site, the northern beaches of Roebuck Bay, Northwest Australia (17.98°S, 122.31°E). After capture, each bird was measured and individually marked on their tarsi with a unique combination of leg flag and colour-bands. Birds were aged based on plumage characteristics and 20–30 adults were selected per year to be transported to an indoor aviary.

Testing exploratory tendency

In the aviary, birds were housed in groups of 4–5 in cages made with mesh nets (thus all the birds could see each other in the aviary) with *ad libitum* food (mealworms). The birds were acclimatized for at least 24 hours before being tested for exploratory behaviour. Following the 7 × 7 m experimental arena described in Bijleveld et al. (2014), we designed a exploration trial tent of 3 × 3 m, filled with a layer of water of about 12 cm. Four plastic trays of wet sand (with its surface at the same level as the surrounding water) were placed in the tent for the birds to explore (Fig. 8.1). To motivate the birds to

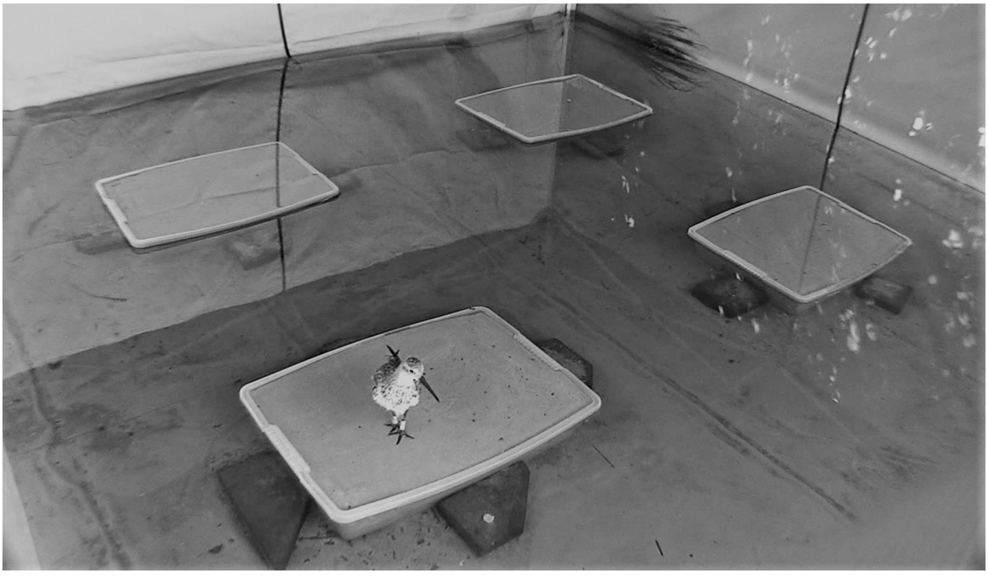

Figure 8.1. Inside view of the 3 × 3 m tent for measuring exploratory tendency in Great Knots (*Calidris tenuirostris*). The tent is filled with a layer of water of about 12 cm, with four plastic trays of wet sand for the bird to explore.

search for food during the trials and to induce standard hunger levels, each focal bird was transported to a waiting cage without food two hours before the start of the trial. The trial lasted 30 mins from the moment that the tent door was closed and the bird had landed on a patch. Trials were conducted between 5:30–9:30 and 15:30–17:30, avoiding the hottest time of the day.

All trials were recorded on video and later analysed with the BORIS software (Friard & Gamba 2016), allowing accurate estimation of time budgets. We recorded the following behaviours: 'searching for food' (include walking and probing), 'standing', 'preening', 'flying', 'swimming' and 'bathing'. We also recorded when the bird was on which patch (i.e., which tray). We quantified exploration by the fraction of total time spent in searching behaviour while on a patch, a metric first used by Bijleveld et al. (2014) as a measure of exploratory tendency. Prior to the current study, we tested our tent set-up in an aviary and experimental facility on Texel, the Netherlands in 2013 using Red Knots (*C. canutus*, a sister species of Great Knots). We tested the same individuals in both the 7 × 7 m arena used in Bijleveld et al. (2014) and in the 3 × 3 m tent, and exploratory tendency between both settings were strongly correlated ($r_{19} = 0.642$, $P = 0.001$). We also found high repeatability between 1st and 2nd trials ($R = 0.798$, $SE = 0.069$, $CI = [0.655, 0.94]$, $P = 0.001$, $n = 28$).

Satellite tracking

After the trial, we fitted a 4.5 g solar Platform Terminal Transmitter (PTTs, Microwave Telemetry, USA) to each of the Great Knots. These tags were the lightest satellite transmitters available at the time of the study. The transmitter comprised 3% of a Great Knot's average lean mass (mean of 151 g, *SD* 20, measured in this study). Transmitters were deployed using a body harness (Chan et al. 2016) made of elastic nylon (Elastan, Vaessen Creative, The Netherlands), which degrades and breaks, thus releasing the tags after one to two years. In some cases the tag was shed earlier, which is evident from several individuals marked with leg-band of colour combinations being resighted after the tag ceased transmitting with the tag not seen on the bird. We then kept the birds for at least 24 hours to allow acclimation to the transmitter and harness before releasing them into the wild at the capture location.

PTTs were programmed to operate on a duty cycle of 8 hours of transmission and 25 hours off. On average, six locations (3 *SD*) were received from the Argos system (Collecte Localization Satellites, CLS) per tag in each transmission period. Tags that stopped transmitting were considered to indicate a broken harness, a malfunctioning tag, or the death of the bird. This work was carried out under Regulation 17 permits SF 010074, SF010547 and 01-000057-2 issued by the West Australian Department of Biodiversity, Conservation and Attractions.

Data analyses

We filtered the Argos locations to retain all standard locations (i.e., the location classes 3, 2, and 1) and applied the Hybrid Douglas filter (Douglas et al. 2012) to remove any implausible auxiliary locations (i.e., the location classes 0, A, B and Z, for details of how locations classes were assigned, see CLS 2016) by setting filtering parameters at 120 km/h for the maximum sustainable rate of movement and 10 km for minimum redundant distance. We further accounted for spatial error in the Argos telemetry by fitting the tracking data with a continuous-time random walk state-space model with the 'fit_ssm' function in the 'foiegras' R package (Jonsen et al. 2020). The state-space model incorporated the error ellipse information of the Kalman filter-based Argos locations, and the fitted locations from the model were used in the analysis of identifying migration stops and timing.

To identify stopover sites, we first identified locations with ground speed less than 5 km/h as 'stationary'. Stopovers were defined as a cluster of at least 3 stationary locations within 20 km of each other, with the first and last recorded locations at the stopover being at least 2 hours apart. Departure times were extrapolated over the intervening travel distance between the last location at a stop and the next location, arrival times were calculated in the same way. Breeding site was defined as the site within the breeding range where the individual stayed the longest. The spatial behaviour during migration was quantified by the number of stops with a length of stay of longer than one day and the proportion of 'new' stops during southward migration (i.e. not visited during northward migration). General linear models with normal errors were used to test for the relationships between these spatial behaviours (log-transformed) and the fraction of time spent searching in the tent ('exploration score' hereafter); sex was included as a fixed effect in the model.

At the Yalu Jiang Estuarine Wetland National Nature Reserve (39.8°N, 123.9°E, located on the Chinese side of the Yalu Jiang estuary on the China-North Korea border; Yalu Jiang NNR hereafter), the population of the bivalve *P. laevis*, a high-quality prey of Great Knots (Choi et al. 2017), has sharply declined in 2013 and continued declining in subsequent years; the very high density in 2011 (708.06 ind/m^2, accounting for 94% of the total biomass of macrozoobenthos at the site) have declined by >99% in 2016 (Zhang et al. 2018). To examine individual responses to the sharp decline in *P. laevis*, we selected the individuals which arrived there in mid-April and extracted the date when they moved to other sites in the Yellow Sea. We also quantified departure date from the Yellow Sea and arrival date at their breeding site. We tested the relationship between these phenological measurements and the exploration score by general linear models.

For all tracked individuals, we quantified their arrival dates at their breeding site. We tested the relationship between arrival dates and exploration scores by general linear models. We used the duration of stay at the breeding site as a proxy for hatching success based on the findings of Lisovski et al. (2016a) and Tomkovich (1996). They found that females take 8–12 d from arrival to egg-laying and the incubation period is 23 d, thus we assume that a stay of ≥34 d meant the birds successfully hatched a clutch. In Great Knots, females leave the brood at the time of hatching and males accompany the chicks for another 24–30 days (Tomkovich 1995). Clearly, the relationships between duration of stay at a breeding site and exploration score have to be examined separately for each sex, but since only 3 males arrived at breeding sites, we could only test this relationship in females. To further understand the linkage between arrival date, breeding site location, and breeding success, we obtained the elevation of all breeding sites from the Global Multi-resolution Terrain Elevation Data 2010 using GoogleEarthEngine. We analysed percent snow cover at breeding sites at a scale of 500 m resolution from MOD09A1.006 Terra Surface Reflectance 8-Day Global 500m dataset (Vermote 2015), where we derived Normalized Difference Snow Index (NDSI; ranges from –1 to 1, the land surface is snow free when NDSI ≤ 0, Riggs & Hall 2016). To obtain the first snow free date at each breeding site, we extrapolated the NDSI values (every 8 days) to obtain the date when it reached 0, i.e. no snow was present. All statistical analyses were performed in R v 3.6.2 (R Core Team 2019) with significance level set at $P < 0.1$.

Results

The satellite-tracked Great Knots stopped at 5.6 ± 1.5 sites during northward migration ($n = 21$ birds with the entire northward migration tracked) and at 5.3 ± 1.8 sites during southward migration ($n = 10$; Fig. 8.2). There was no relationship between the number of stopping sites used and exploration score ($P > 0.1$, Fig. 8.2A & B). However, the more explorative birds visited a higher proportion of 'new' sites (those that were not visited during northward migration) during southward migration ($F_{2,7} = 3.897$, $P = 0.07$; Fig. 8.2C). Among the seven Great Knots that reached Yalu Jiang NNR in 11–22 April 2015–2016, the more explorative individuals left Yalu Jiang NNR earlier than the less explorative ones ($F_{1,5} = 71.3$, $P < 0.001$) and 6 of the birds moved to other staging sites in the Yellow Sea; the least explorative bird did not move to any other staging site (Fig. 8.3). All individuals departed from the Yellow Sea on 19–20 May and reached their breeding sites on average on 25 May (range: 23–27) except the least explorative individual which departed the Yellow Sea on 25 May and reached its breeding site on 2 June (Fig. 8.3).

Among the 21 birds that were tracked till their breeding sites, females arrived on their breeding sites between 21 May and 8 June ($n = 18$), and males between 23 and 27 May ($n = 3$; Fig. 8.4). There was a trend of more explorative individuals reaching their breeding sites earlier than less explorative individuals ($F_{1,19} = 3.366$, $P = 0.082$, Fig. 8.4). The more explorative a female, the longer it stayed at their breeding site ($F_{1,13} = 4.897$, $P = 0.045$). Breeding sites were at altitudes of 117–1816 m (mean = 918 m) and become snow-free between 9 May – 20 June (mean = 1 June). There was no relationship between exploratory tendencies and the breeding site's elevation or phenology (snow-free date) (all $P > 0.1$). Most birds (18 out of 21) arrived 8.2 ± 5.2 days before the first snow-free date at the breeding site. For birds that appeared to successfully hatch a nest, arrival times were predicted by snow-free dates at the breeding sites ($F_{1,8} = 4.704$, $P = 0.062$).

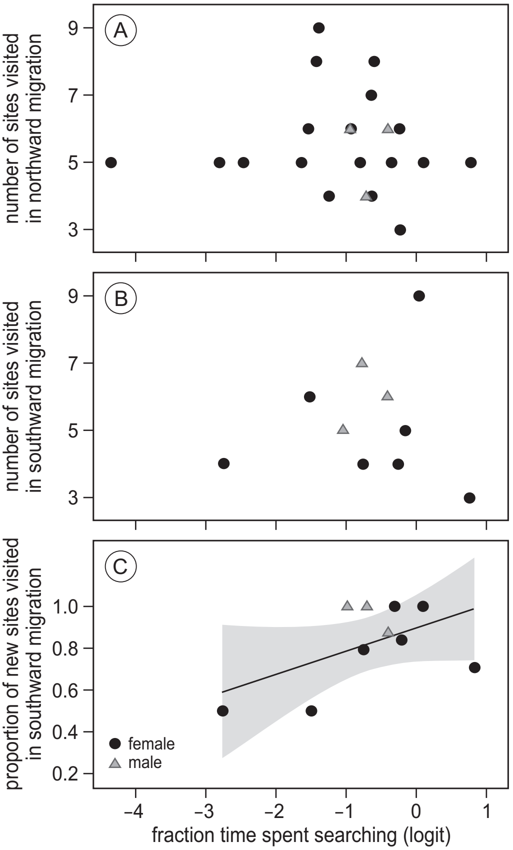

Figure 8.2. The number of stops during (**A**) northward and (**B**) southward migration, and the (**C**) proportion of new sites visited during southward migration (i.e. not visited during northward migration) of Great Knots tracked from a Northwest Australia non-breeding site to eastern Russia breeding sites in 2015–2018.

Discussion

We show that the exploratory tendencies of Great Knots measured in the laboratory is related to the speed of response to a collapse of prey stock at a migratory staging site in 2015 and 2016. Our results of the more explorative birds leaving the site earlier is consistent with the findings of van Overveld & Matthysen (2010) on a small-scale spatial response of Great Tits to a manipulation of reduced food availability. To our knowledge, our study is the first to show this phenomenon on a large spatial scale where a major migratory staging site was experiencing sudden dramatic reduction in food availability.

The quick response to prey collapse of more explorative individuals may be facilitated by the larger amount of environmental information they have acquired by visiting

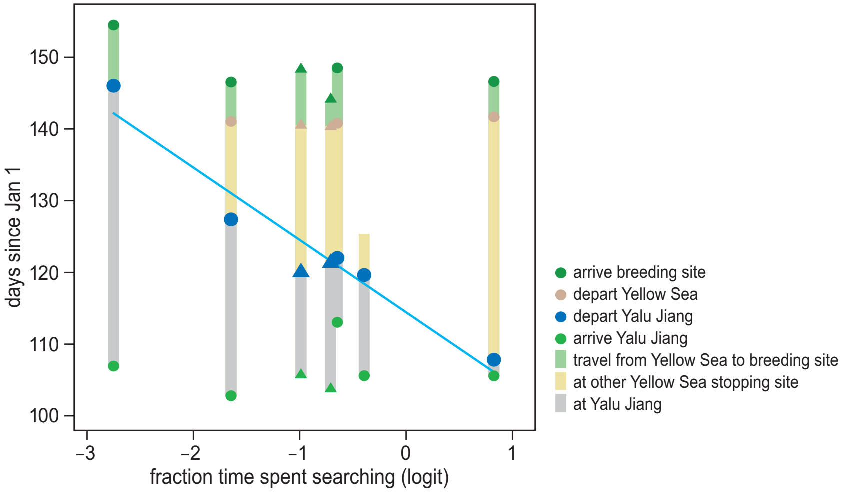

Figure 8.3. The timing of events during northward migration for seven satellite tracked Great Knots that reached Yalu Jiang Estuarine Wetland National Nature Reserve in early to mid-April 2015–2016, plotted against exploration score, i.e. fraction of time spent searching in the tent (see text). Blue line shows the significant negative relationship between departure date from Yalu Jiang and the fraction of time spent searching.

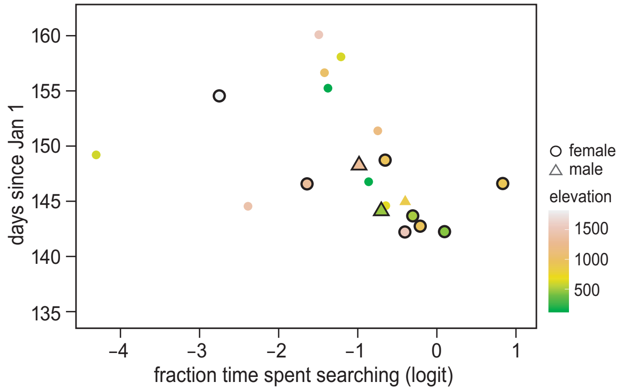

Figure 8.4. Arrival dates at breeding sites and exploration scores of 21 satellite-tracked Great Knots. Symbols with thick borders indicate individuals that apparently hatched eggs (i.e., they stayed at breeding sites for ≥34 d, see text).

sites. We tested the relationship between information acquisition and exploratory tendency by assuming that visiting more sites during migration would represent the gathering of more environmental information. However, we did not find a relationship between exploratory tendency and number of stops during northward and southward migration. We did find that explorative individuals visited relatively more ‘new’ sites during southward migration. This indicates that during southward migration, more explorative individuals tend to forgo the benefits of familiarity which comes with using the same sites as during northward migration, and instead visit sites that they have less information about. The number of sites visited in a single migration might not be indicative of the tendency to gather information, as it could be affected by environmental conditions encountered en route. For example, an unfavourable situation could prompt an individual to move to another site, which might increase the number of sites visited. Information on sites will be accumulated not just during a single migration, but will accumulate over several years. Therefore, only by tracking individuals over multiple years can we properly test the relationship between the number of stops made (as a proxy for amount of environmental information) and exploratory tendency.

Being explorative seemed to be advantageous during the years we conducted our study, as we found that more explorative females stayed relatively longer which suggested they successfully hatched a nest. Our small sample size of three males does not allow testing whether explorative males would attain higher breeding success. We also found that more explorative individuals arrived earlier at breeding sites. There are known benefits of earlier arrival that lead to higher breeding success, such as a higher chance to acquire a higher quality mate and a better territory as shown in previous studies of other bird species (e.g. Lozano et al. 1996, Smith & Moore 2005). Moreover, birds need to arrive in-time to catch the seasonal food peaks at their breeding sites; arriving too late and missing the food peak could negatively impact the growth of chicks and fledging success. We did find that the Great Knots that bred successfully matched their arrival time with the phenology (snow-free date) of their breeding sites. For long-distance migratory shorebirds like the Great Knot, one factor that constrain how early they can arrive at the breeding site is how fast they can fuel up at the stops during their migration. Our results indicate two potential mechanisms of more exploratory individuals to achieve a faster fuelling rate: one being moving more quickly from a site of poor quality, and the other being having more information on alternative stopping sites and their habitat quality.

If exploratory behaviour is heritable in Great Knots like it is in great tits where heritability has been measured (Dingemanse et al. 2002), a higher breeding success of explorative birds could lead to more explorative individuals within the population, which might be better suited to deal with the habitat deterioration at the intertidal areas in the Yellow Sea where they stop for fuelling during migration (Murray et al. 2015, Melville et al. 2016a). Moreover, exploratory tendencies are related to dispersal characteristics in some species (Dingemanse et al. 2003, Cote et al. 2010); therefore a selection for exploration would also lead to more dispersive individuals that are more likely to discover and occupy new breeding and non-breeding habitats, and rely less on the Yellow Sea during migration. As more explorative individuals are able to arrive at the breeding sites earlier, a general increase in the exploratory tendency in the population would also prepare Great Knots to keep up with possible advancements in breeding ground phenology caused by global climate warming which is currently affecting many species (Parmesan & Yohe 2003, Visser & Both 2005).

However, the direction of selection on exploratory tendency also depends on survival costs. For the tracked Great Knots in this study, survival could not be estimated from tag lifespan since the tag was often shed when the harness degraded. Previous studies revealed that the relationship between explorative behaviour and survival depends on the environment and life stage. It has been shown that explorative individuals have survival costs during the juvenile phase in European rabbits *Oryctolagus cuniculus* (Rödel et al. 2015), while other studies showed balancing selection or disruptive selection on exploratory behaviour, dependent on the environmental regime (Dingemanse et al. 2004, Adriaenssens & Johnsson 2013, Bergeron et al. 2013, Le Galliard et al. 2013). For long-distance migratory shorebirds like the Great Knots, their 'long-jump' migration strategy of stopping at only a few sites for fuelling and flying non-stop between them (Piersma 1987) has probably evolved in environments where there are stable and predictable seasonal resources far apart in space, and to reduce risks associated with stopping, e.g. exposure to hunters, predators and pathogens (Gill et al. 2009, Conklin et al. 2017). Nowadays, habitat degradation in the staging sites and global climate change have made resources less stable. Moreover, explorative individuals might be subject to greater risks of exposure to hunters, predators and pathogens when making more and unfamiliar stops during migration. In this study, we have showed that the variation in exploratory tendency provides a way for Great Knots and other long-distance migratory birds to maintain adaptive capacity to sudden environmental changes. Investigations on the costs associated with being explorative would be a next step towards predictions of the responses of these bird populations to negative environmental changes.

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CHAPTER 9

General Discussion

On the ways that migratory birds cope with a deteriorating flyway

Ying-Chi Chan

A central theme in ecology is the study of effects on organisms of human-induced rapid environmental change such as habitat destruction, exotic species and climate change (Vitousek et al. 1997, Thomas et al. 2004, Leprieur et al. 2008, Butchart et al. 2010). As the phenotype is the biological unit that interacts with the environment, many studies (including Chapters 8 of this thesis) have focused on the various aspects of how individuals cope, physiologically and behaviourally, with environmental change (Piersma & van Gils 2011). The hope is that by studying the mechanistic intricacies of coping at the individual level we can better understand any changes in overall population numbers.

An additional idea is that the 'coping capacity' of a species determines its vulnerability to human-induced challenges. Coping capacity can be conceived by identifying the different ways of coping when an organism is challenged by a real-life problem (what are the cards up its sleeves) and how fast the coping mechanisms manifest (the speed of playing these cards). This thesis focuses on the long-distance migratory shorebirds that are already engaged in the hard work of moving across hemispheres, relying on a limited array of specific habitats (mostly intertidal flats) for their migration, and flying thousands of kilometres non-stop between them. As evident from the declining survival and population size of these birds (Piersma et al. 2016, Studds et al. 2017), the rapid deterioration of the birds' habitats in the East Asian–Australasian Flyway (EAAF) have pushed them to the 'edge'. This is an unfortunate situation, but it also gives us a unique opportunity to observe how migratory shorebirds play their cards. Based on what we have observed so far, I discuss the coping mechanisms of the birds, from small to large spatial scales, i.e. from the single site to the flyway; and then expand to the scale of the life history of a migratory shorebird.

Coping by moving, or not?

The study of how animals are impacted by, and are adjusting to, the rapid, human-induced changes to the planet is, in essence, a study of the two-way interaction between organisms and their environment. But what exactly is the environment of an organism? The *relevant* environment is what is interacting with the organism, physically and socially. One particular subset of coping mechanisms is moving away, e.g. displacing to an alternative site. This could be interpreted as an animal actively changing the environment that it experiences. Therefore, we can separate coping mechanisms into two categories: (1) those that do not involve movement but rather staying and changing physiology, foraging behaviour, diet, etc.; and (2) those that involve moving to other places.

An illustrative case of the former is the response of shorebirds to a sharp decline in 2013 and continuing decline in the years after of the soft-shelled bivalve *Potamocorbula laevis*, the main prey for shorebirds staging on the Chinese side of the Yalu Jiang estuary on the China-North Korea border (Choi et al. 2017, Zhang et al. 2018). As a result, Great Knots shifted to feed on harder-shelled molluscs such as the gastropod *Umbonium thomasi* (Zhang et al. 2019a). This shift was accompanied by an increase in size of the bird's gizzard, the digestive organ used to crush hard shells; a larger gizzard exerts a stronger breakforce and thus enables faster processing of bulky prey (van Gils et al. 2006b). To excrete shell fragments that are very hard to break (e.g. the columella of *U. thomasi*), Great Knots also adjusted the pathway of excretion from the normal pathway of defecation to rely mainly on regurgitation. In response Bar-tailed Godwits switched from foraging on *P. laevis* to forage mainly on polychaetes (S.D. Zhang, H.B. Peng and Y.C. Chan, pers. obs.); this diet switch makes sense since the densities of polychaetes at Yalu Jiang was similar throughout the years before and after the collapse of *P. laevis* (Zhang et al. 2018). Bar-tailed godwit is known as a worm-feeder in other parts of the world (Duijns et al. 2013) and also selected for polychaetes in Yalu Jiang before the prey collapse (Choi et al. 2017). With their long bills of approx. 80–110 mm, Bar-tailed Godwits are more 'equipped' than the shorter-billed (~40 mm) Great Knots to catch large polychaetes which usually occur deep in the sediment. The diet changes of Bar-tailed Godwits appeared to bear a lower cost than that made by Great Knots.

The alternative way for birds to cope with prey collapse is by switching to other sites, and there is evidence that Great Knots present on the Chinese side of the Yalu Jiang Estuary in 2015–2016 moved to other, nearby staging sites (Melville et al. 2016b, Ke et al. 2019), including our satellite-tracked Great Knots (Chapter 8). We were not able to study if Bar-tailed Godwits moved to alternative sites, as none of our tracked Godwits visited the Chinese side of the Yalu Jiang Estuary. Therefore, we turned to study a behavioural trait closely related to the propensity to switch sites - site fidelity. In Chapter 7 we showed that Bar-tailed Godwits were more site faithful than Great Knots in both their non-breeding area in Northwest Australia and at migratory stops in the Yellow Sea. Our descriptive study did not investigate the processes behind this difference between the two species; however, the stronger site faithfulness of Bar-tailed Godwits suggested that they benefit more than Great Knots by returning to the same places (and incur a higher cost of not doing so). From our two-species comparison, the species more 'equipped' to cope locally (Bar-tailed Godwit) seemed to be less equipped to cope by moving to other sites. A similar reasoning could also explain the within-species differences in the responses of Great Knots with different exploratory tendencies (Chapter 8): less-explorative individuals might be more equipped to cope locally by the ways described in Zhang et al. (2019a), while explorative birds might incur lower costs of moving to other sites, perhaps because they have more information on alternative sites.

The difference in how knots and godwits cope with the sudden decline in food at Yalu Jiang highlights the importance of studying trade-offs to understand the limits of coping. Trade-offs are embodied in all phenotypically plastic organisms; a 'Darwinian demon' that can adjust continuously to fluctuating environments does not exist (Via & Lande 1985). Trade-offs can be seen as an allocation problem for organisms to invest the limited resources such as time and energy; investments in one direction would prevent investments in another direction. Costs in ways of coping locally, such as growing a big gizzard (van Gils et al. 2003b), are better studied than coping by moving. Future research in quantifying the costs of sampling the environment in terms of risks, time and energy and missed opportunities in foraging would help to understand why species or individuals differ in the degree of coping by moving.

Coping on a flyway scale by altering where to go

For migratory animals which use different habitats at different times of the year, coping can be achieved by adjusting migratory behaviours, i.e. where to go and how long to stay at each place. While advancement in migratory timing of birds in relation to a warming climate has been widely documented (Gordo 2007, Horton et al. 2020), adjustments in migratory behaviour to other human-induced rapid changes have been less explored.

From long jumpers to hoppers

Traditionally, all three study species, the Great Knot, Red Knot and Bar-tailed Godwit, were known as 'long jumpers' (Tulp et al. 1994), i.e. with a migration strategy of accumulate large fuel stores to make long non-stop flights (often of thousands of kilometres) from one site to the next (Piersma 1987), and they flew non-stop for >5,400 km from Northwest Australia to the Yellow Sea (Barter et al. 1997b, Battley et al. 2000). The fact that we documented birds stopping in Southeast Asia and southern China before reaching the Yellow Sea during northward migration for all these species (Chapter 3, 4 and 5) raised the question of whether our findings showed that the old ideas were generally mistaken for the EAAF populations, or whether shorebirds responded to the large-scale habitat destruction and deterioration in the Yellow Sea region by relying more on other regions of the flyway for refuelling. Out of the three species, only Bar-tailed Godwits had been tracked before our studies started; in 2008 Battley et al. (2012) tracked 11 Bar-tailed Godwits flying directly from Northwest Australia to the Yellow Sea, i.e. consistent with the idea that stopping in Southeast Asia and southern China is a recent phenomenon. In the 2008 study, however, satellite tags were implanted, while the solar-powered tags used in our current study were externally attached. Since externally attached tags might influence aerodynamics (Pennycuick et al. 2012, Vandenabeele et al. 2014) and could affect migratory flights (Lameris et al. 2018), we were unable to eliminate the possibility that the stopping behaviour we documented was induced by the presence of an external tag.

Although we cannot tell for sure whether the three study species stopped more frequently in southern China and Southeast Asia than before, we can compare the consequences of flying directly to the Yellow Sea with stopping in more southern regions by quantifying the amount of fat stores remain after a migratory flight. Migratory shorebirds need some remaining fat stores upon arrival at a stop to repair muscle tissues and rebuild organs, since organs such as the intestine are shrunk down before migratory flight (Piersma et al. 1993b, Piersma & Gill 1998) or catabolized during flight (Battley et al. 2000), and muscle tissues are also damaged during flight (Guglielmo et al. 2001).

Pennycuick and Battley (2003) reported fat mass measured from Great Knots caught in the southern Yellow Sea (10.7 g), presumably just after their arrival from Northwest Australia by a direct flight of 5,420 km. Fat stores of 10.7 g could only support a Great Knot's energy expenditure for about one day, therefore high densities of high-quality prey must be available at the stop after the long flight to prevent starvation. However, food conditions might be less and less favourable in the years when the tidal flats in southern Yellow Sea were undergoing rapid loss, especially along the southern Jiangsu and Shanghai coast of China in 1985–2015 (Chen et al. 2019) and Saemanguem in South Korea in 1991–2006 (Moores et al. 2016). At the diminishing tidal flats, Great Knots were likely facing increased competition for food, and coping strategies, such as moving to alternative sites and increasing gizzard size to increase intake rates, take energy and time when foraging opportunities are reduced. The more deteriorated the Yellow Sea became, the riskier flying directly to the Yellow Sea and arriving with low fat stores was for a Great Knot.

To calculate how much fat stores remain after a flight from Northwest Australia to Southeast Asia and southern China, I simulated how body and fat mass of a Great Knot decrease during migratory flight from Northwest Australia based on a flight model by Pennycuick (2008; Fig. 9.1). The simulation results corroborate with measurements of Great Knots caught in the southern Yellow Sea, although the measured fat mass (10.7 g) was slightly lower than the prediction (20 g), perhaps reflecting events not considered in the model, e.g. wind conditions *en route* could have either aided or slowed the birds (Shamoun-Baranes et al. 2017). Our satellite-tracked Great Knots made direct flights of 1,630–5,253 km (median 4,607 km) from Northwest Australia before first landing at

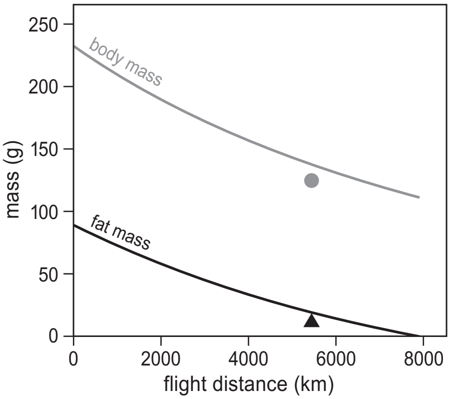

Figure 9.1. Simulated changes in body and fat mass of an average Great Knot during flight, as a function of distance travelled from the site of departure, generated from the Flight program (v 1.25; Pennycuick 2008). Initial values of body and fat mass (at flight distance = 0) are measured from Great Knots caught in Broome, Northwest Australia in 1998, presumably just before their departure for northward migration (Pennycuick and Battley 2003). Circle and triangle denote measured body and fat mass of Great Knots caught at Chongming Island, south Yellow Sea in 1998, presumably when they had just arrived from their non-breeding site in Australia (Pennycuick and Battley 2003).

Southeast Asia or southern China. According to the flight model, a Great Knot landing at southern China after a flight of 4,607 km would still have 28 g of fat stores, and, given the high densities of high-quality food at sites in southern China (see Fig. A3 in Box A of this thesis), Great Knots that stop at southern China might be better prepared for the deteriorating conditions ahead in the Yellow Sea. Ironically, hunting is a key threat to shorebirds in southern China and Southeast Asia (Li & Ounsted 2007, Zöckler et al. 2010, Martinez & Lewthwaite 2013), and the long non-stop flights to the Yellow Sea might have evolved to avoid that in the first place.

If stopping in Southeast Asia and southern China during northward migration is a response to conditions expected in the Yellow Sea, that would require birds to 'remember' the poor conditions in the Yellow Sea last year. Whether birds have this cognitive ability is unknown, however the strong site fidelity of these migratory shorebirds suggest that they do 'remember' places. Also, 'memory' can be stored in internal states such as body conditions (Higginson et al. 2018) and then carry-over to the next spring; a simple mechanism would be birds having poorer body conditions not being able to fly directly to Yellow Sea and having to stop on the way. If stopping in Southeast Asia and southern China increases the chance of survival, natural selection would also lead to an increase in birds migrating with such strategies.

Short-stopping: wintering in Southeast Asia

Another possible way of coping to deteriorating conditions in the Yellow Sea would be by shortening the migration route, known as 'short-stopping' (Elmberg et al. 2014). This phenomenon has been documented in many waterfowl and is suggested to be a response to climate warming as conditions ameliorate at northern sites along migratory routes (Lehikoinen et al. 2013, Podhrázský et al. 2017, Pavón-Jordán et al. 2019, Nuijten et al. 2020). While the majority of Great Knots and Bar-tailed Godwits spend the non-breeding season in Australia, small numbers also winter in Southeast Asia. Since 2000, several hundreds of Great Knots and Bar-tailed Godwits have been counted at various sites in Sumatra, Indonesia (Iqbal et al. 2010, 2012, Putra et al. 2015, 2017) and, in 2004–2006, thousands were present in Thailand and Malaysia (Li & Ounsted 2007). Wintering in Southeast Asia might be more prevalent now than before in Great Knots as is evident in counts at north-central Selangor coast, West Malaysia, where numbers showed a remarkable 7-fold increase from about 500 in 2007–2008 to >3,500 in 2011–2012. Also, in the Inner Gulf of Thailand, numbers increased from ca.1,000 in 2010–2011 to >6,000 in 2013–2014 (Round & Bakewell 2015).

Some of the birds that winter in Southeast Asia might have ended up there because they were unable to fuel sufficiently in the Yellow Sea to power a direct flight to Australia, and they subsequently 'decided' to stay for the winter. Some might be inexperienced juveniles in their first migration, however the juvenile/adult ratio in Thailand is similar to that of Northwest Australia (Eiamampai et al. 2014).

Alternatively, birds might actively disperse to the Southeast Asian wintering sites. This behaviour was recorded for one satellite-tracked Great Knot, which flew to a site at the southern coast of West Papua, Indonesia (–8.2°N, 138.9°E) in November, stayed for the winter and departed for northward migration from there (Fig. 9.2). By doing so, it ended up 660 km closer to its Yellow Sea staging site at Lianyungang, China (Fig. 9.2). To reach the same Yellow Sea staging site, birds that winter further north, such as in the Inner Gulf of Thailand, need to migrate only half of the distance compared to those from Northeast Australia (Fig. 9.2). Birds wintering further north might also benefit from a less time-constrained annual cycle. This particular West Papua Great Knot departed on 10 April, later than most individuals from Northwest Australia (31 March ± 7 d, *n* = 39), but subsequently the migration was similarly scheduled to the rest. To understand whether wintering in Southeast Asia is advantageous, we need to compare between birds wintering in Southeast Asia and those in Northwest Australia their winter body conditions, fuelling rates during spring before migration, migration routes and timing, and ultimately their fitness (survival and breeding success). A difference in fitness would suggest selection played a role in the increase in proportions of Great Knots wintering in Southeast Asia.

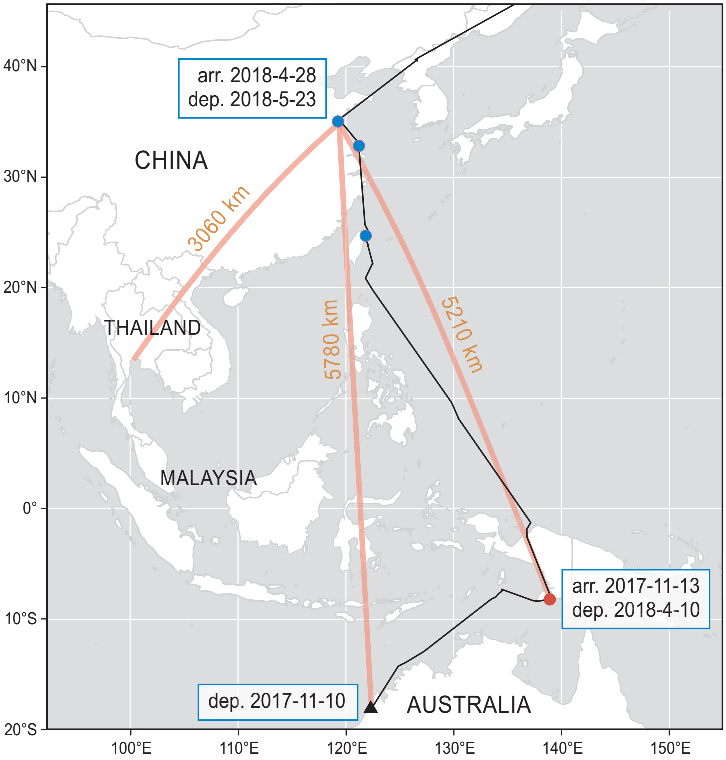

Figure 9.2. Movement track of a Great Knot (black line) tagged in Roebuck Bay, Northwest Australia (triangle), to west Papua, Indonesia, and northward towards the Yellow Sea. Coloured dots denote stops. Pink lines represent great circle paths from three wintering sites (Inner Gulf of Thailand, south coast of West Papua, and Roebuck Bay) to a Yellow Sea staging site at Lianyungang, Jiangsu, China.

To migrate or not? Trade-offs between survival and reproduction

Many long-distance migratory shorebirds, including the three study species of this thesis, are often classified as ‘obligate migrants’. Their annual long-distance migration and the timely preparations such as fattening and moulting schedules are assumed to be ‘hard-wired’ (Berthold 2001). However, there are observations that not all individuals migrate every year. The phenomenon for birds breeding in the northern hemisphere remaining in non-breeding areas during the boreal winter/austral summer is termed ‘oversummering’ (McNeil et al. 1994). Oversummering of young birds, i.e. that juveniles defer migration and remain in the non-breeding area for one or more boreal summers, occurs in many species of migratory shorebirds (e.g. McNeil et al. 1994, Summers et al. 1995, Navedo and Ruiz 2020, Tavera et al. 2020). There is increasing evidence that oversummering also occurs in adults that likely have prior breeding experience (Martínez-Curci et al. 2015).

For the Bar-tailed Godwit and Great Knot populations in Northwest Australia, based on active moult and plumage state, we can distinguish between birds in their 1st, 2nd or 3rd year of life. Here we consider birds tagged when 3 years or older which we thought would embark on their migration, as it is known that birds typically do not migrate during their first and second boreal summers/austral winters. Among the satellite-tracked adult (3 years or older) Great Knots in their first year being tracked, seven (18%) did not migrate and one attempted but turned back after flying ca. 1,300 km. These adult birds could include 3rd year birds that defer migration for another year. One individual migrated in the first year that it was tracked, did not migrate in the second year and migrated again in the third year, showing that oversummering could also occur for birds that have bred before. For the adult *menzbieri* Bar-tailed Godwits, two (5%) did not migrate in their first year being tracked, one in its second year, and two in their third year. One individual never migrated and oversummered for the three years that it was tracked.

Oversummering might be a form of intermittent breeding, which is exhibited in many long-lived birds and generally reflects unfavourable environmental conditions (Cubaynes et al. 2011, Öst et al. 2018). These studies suggested that skipping reproduction could be an adaptive strategy of birds to face the life history trade-off of current and future reproduction given the environmental constraints (Cubaynes et al. 2011). Following this reasoning, oversummering could reflect the survival-reproduction trade-off of birds facing higher reproductive costs induced by the deterioration of refuelling habitats in the Yellow Sea.

Since migration to the breeding grounds is a means to achieve reproduction, key factors determining costs of reproduction would be mortality risk during the migration journey, and the non-lethal negative effects of migration and breeding that carry-over to other seasons (e.g. Daan et al. 1996). The habitat destruction and deterioration in the Yellow Sea has likely caused the reduced survival rates measured during the migration and breeding periods for the three study species (Piersma et al. 2016). Oversummering birds can avoid mortality during the migration journey, and also use that time to dissipate any negative reversible state effects incurred from previous migration and/or breeding events (Senner et al. 2015).

On the mechanism leading to the decision not to migrate, Martínez-Curci et al. (2020) showed that oversummering Red Knots at Punta Rasa, Argentina had low fat loads and incomplete alternate plumages; however, their health was not compromised in terms of weakened immune system, high loads of blood parasites or high stress levels. Therefore, poor health status alone could not explain oversummering. The decision not to migrate was likely made during or even before the pre-migratory preparatory period. By stopping to invest in alternate plumage and fat deposition, the birds conserve energy and reduce predation risk.

Here I use a simple conceptual model to represent the outcomes of a bird's decision to migrate or not that is based on its body condition (fat store level) during the period of preparation for migration, once its body condition is reasonably predictive of the likelihood of successful reproduction and survival in the upcoming migration (Fig. 9.3). A bird should decide to migrate only when migration confers higher fitness (lifetime reproductive success) than oversummering. At the baseline situation (green line in Fig. 9.3), the green dot in Fig. 9.3 represents the minimum threshold of fat stores at the timepoint when decision to continue preparing for migration is made; a bird with fat stores lower than the threshold should stop preparing for migration and eventually oversummer.

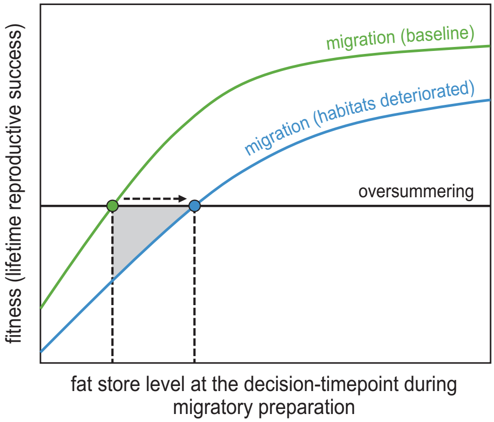

Figure 9.3. Conceptual model on the decision of a bird to continue to prepare for migration or not, based on the expected fitness of eventually migrating (green line) or oversummering (black line) given its fat store level at that decision-timepoint. When habitats at migratory stops deteriorated, expected fitness of migration would be lowered (blue line). A bird should prepare for migration only when that confers higher fitness (lifetime reproductive success) than oversummering, i.e. when it has more fat stores than the green dot in the baseline situation, and more than the blue dot in the situation that habitats deteriorated. Shaded area represents the loss in fitness in birds that still follows the strategy in the baseline situation while habitats in migratory stops have been deteriorated.

When habitat at migratory stops deteriorated, the expected lifetime reproductive success of a decision to migrate would be lowered (blue line in Fig. 9.3). This is because of the smaller chance of surviving the migration journey; also, birds might be delayed and arrive later at the breeding grounds, and with poorer body condition they will have lower chances of breeding success. Negative effects could also carry-over to future seasons. In this scenario, a bird with more fat stores than the blue dot in Fig. 9.3 would achieve higher expected fitness if it continues to prepare for migration, and those with less fat stores than the blue dot should maximize fitness by choosing to oversummer.

However, birds cannot anticipate the conditions of the habitats they will encounter during migration while they are still at the non-breeding (wintering) site. If they make the decision of migrating or not based on the baseline situation (green line) while habitats at migratory stops have already deteriorated, birds with intermediate fat levels would not be following the best strategy and would lose fitness (Fig. 9.3, shaded area). How effective oversummering is as a coping tactic depends on how quickly birds can adjust their strategy to the new situation. Since birds are evolved to deal with environmental fluctuations, they can possibly predict future food availability at migratory stops to a certain extent based on knowledge on past food availability (possible stored by physiological state variables) and an assumption of correlation of food availability between years (McNamara & Houston 2008).

Tracking birds throughout their lifetime could possibly show survival-reproduction trade-offs at the individual level. However, our tracking dataset does not allow this calculation, as we cannot extract the moment of death from the tags; some individuals were resighted after the tag stopped reporting, indicating either the tag was malfunctioned or had been shed. Another consideration is that the assumed negative correlation between survival and reproduction (the trade-off) might be masked by differences in individual quality, as high-quality individuals can acquire more resources and survive and reproduce better, which would result in a positive between-individual relationship between survival and reproduction (van Noordwijk & de Jong 1986).

Mitigation: coping with fitness costs

I have discussed the many ways that migratory shorebirds could cope with destruction and deterioration of staging habitats, and mechanisms of coping that can be achieved by both behavioural and physiological flexibility of individuals. While we are beginning to discover the incredible ways that migrants do cope (e.g. Zhang et al. 2019a), we should beware that the degree and speed of environmental changes in the EAAF seems to be beyond the range that migrants can adjust their behaviour and physiology in a way that still maintains fitness. The coping strategies could be adaptive in the sense that they result in the highest fitness given the circumstances, however the overall fitness is still lowered and will manifest itself into population declines in later years if the environment has not improved or is getting worse.

Coping with fitness costs could be behind the patterns observed in shorebird numbers at sites in the EAAF where tidal flats are lost by land reclamation. One prominent case is the closure of the 33 km-seawall which impounded ~290 km^2 of tidal flats at Saemangeum (35°50′N, 126°45′E) in South Korea in April 2006. Before the closure of seawall, Saemangeum was identified to be the most important shorebird staging site in the Yellow Sea during northward migration, supporting >240,000 shorebirds in 1997–2001 (Barter 2002), including 20–30% of the world population of Great Knots during both northward and southward migration (Barter 2002, Moores et al. 2016). In 2007, Great Knot numbers at Saemangeum decreased by 63%, and only a very small number was counted from 2011 onwards (Moores et al. 2016). Numbers at adjacent sites (Geum Estuary) increased by 20,000 in mid-April 2007, but went down again in May 2007 to similar numbers as in 2006 (Moores et al. 2016). Therefore, some Saemangeum birds appeared to have moved to other staging sites that were likely at full capacity already. As there were no reports of substantial increase in Great Knot numbers at other Yellow Sea sites, Moores et al. (2016) deduced that the ~100,000 Great Knots disappeared from Saemangeum and adjacent Geum Estuary was caused by mortality of birds. This suggests that despite all the ways that migrants can cope, ultimately the amount of habitat in the Yellow Sea is a key constraint (Piersma et al. 2017) and that the destruction of mudflats at Saemangeum has reduced the overall carrying capacity of the Yellow Sea.

However, the birds that died might not all belong to those that staged at Saemangeum before the closure of the seawall. In Chapter 8 we showed that individual Great Knots differ in their speed of responding to sudden environmental change by moving away from a site with very low prey stock, and this speed is related to a lab-measured personality trait, their exploration tendency. The mortality event caused by the Saemangeum reclamation could have selected for explorative individuals that moved away: these would have been the survivors. The explorative individuals would have a behavioural syndrome that would make them invest in information acquisition more than non-explorative individuals would. These birds would be the most likely to discover alternative stopping sites, even in regions outside of the Yellow Sea. This shows how an event at one site in the Yellow Sea could potentially lead to an increase in frequencies of birds employing certain ways of coping via trait correlations within individuals, and increasing the adaptive capacity of the species as a whole.

Flying forward: what is the future for the long-distance migrants in the EAAF?

In terms of predicting population trends, the many behavioural and physiological adjustments of birds play an important role in determining how much birds can mitigate impacts from sudden events such as land reclamations and declines in prey stock, and how much time it takes for the non-lethal effects to reflect in demographic parameters in terms of lowered survival and reproduction rates of the population. The observations we made in this flyway provide insights into the ‘coping space’ of birds to adjust to human-induced local and global environmental changes.

Future studies can focus on understanding why individuals differ in their ways to cope, e.g. by moving to alternative site or staying-put, by migrating or oversummering. Are these decisions correlated, e.g. are birds that move to alternative sites also more likely to migrate? We need more research on the mechanistic underpinnings of these decisions and their correlations (if any). Feedback loops are probably important in the maintenance of these alternative strategies, as individuals with more environmental information would be more likely to move to other sites since they have lower costs associated with moving, and by visiting more sites they gather more environmental information; an opposite negative loop would apply to individuals with less environmental information and staying-put. Birds of different internal states such as residual reproductive value would face life history trade-offs differently (Houston & McNamara 1999), e.g. individuals with large residual reproductive value should choose ‘safer’ options than individuals with small residual reproductive value in order not to jeopardize survival and future reproduction. Lastly, while this discussion focuses on spatial responses of migratory birds to environmental changes, we should bear in mind that these birds have a tight annual cycle with mechanisms evolved to time their events to the seasons (Åkesson et al. 2017). Future research can understand if/how timing mechanisms constrain potential responses in large spatial scales, such as switching wintering areas and forgoing migration.

Although as scientists we are trained to observe and understand nature, we are also humans whose actions have profoundly influenced nature. We should continuously support and explore how to put current knowledge into conservation actions. More and more shorebird tracking studies are conducted in the EAAF, and we are beginning to untap the potential of these investigations to contribute to conservation. In Chapter 5 we used tracking data of the Great Knot to highlight sites and regions that are potentially important to the birds but lacked ecological information and conservation recognition. A logical next step is to do a similar analysis with tracking data of multiple species to identify key sites along the whole flyway; combining tracks of multiple species can also show how a particular site supports migratory birds and help in the design of management practices that could improve habitat conditions on-site, or even create new habitats for shorebirds (an expansion of Chapter 6, Box B and Box C). Conservation plans need to recognize the dynamic nature of migration patterns, that new stopover and wintering areas can be adopted. Therefore, a future avenue is to expand the use of tracking data from identifying current routes and sites to anticipating future routes and site use (Reynolds et al. 2017), based on an increased understanding of the environmental characteristics suitable for migratory shorebirds and the flexibility of migrants to move to new areas (Chapter 7) and use alternative habitats such as saltponds (Lei et al. 2018).

Land reclamation in China has slowed down considerably since in January 2018 when China released new policies that restricted reclamations along the coast (Melville 2018), and put forward to nominations of Yellow Sea sites as World Heritage (UNESCO World Heritage Convention 2020). Part of this positive news is that a portion of the southern Jiangsu Coast, a key area for many migratory shorebirds such as Bar-tailed Godwits (Box B) and spoon-billed sandpipers (Peng et al. 2017), has been included in the Yancheng site, a World Heritage site since 2019, and that reclamations have largely stopped. However, other threats to shorebirds are on-going (see Chapter 1) and their prevalence and impact, unlike the case with habitat loss by land reclamation and spread of cordgrass, cannot be measured by remote sensing methods. Therefore, ground surveys are essential to collect more information on threats and changes in shorebird numbers and their prey, and satellite tracking can guide these surveys in multiple ways (e.g. Chapter 5 and 6, Box A, Melville et al. 2016b). **Concurrent effort in global tracking of birds and on-ground surveys** (Box A) is key to monitoring and conservation of shorebirds and coastal wetlands in the flyway.

Ultimately, the future of these migratory shorebirds depends on the actions by you and me.

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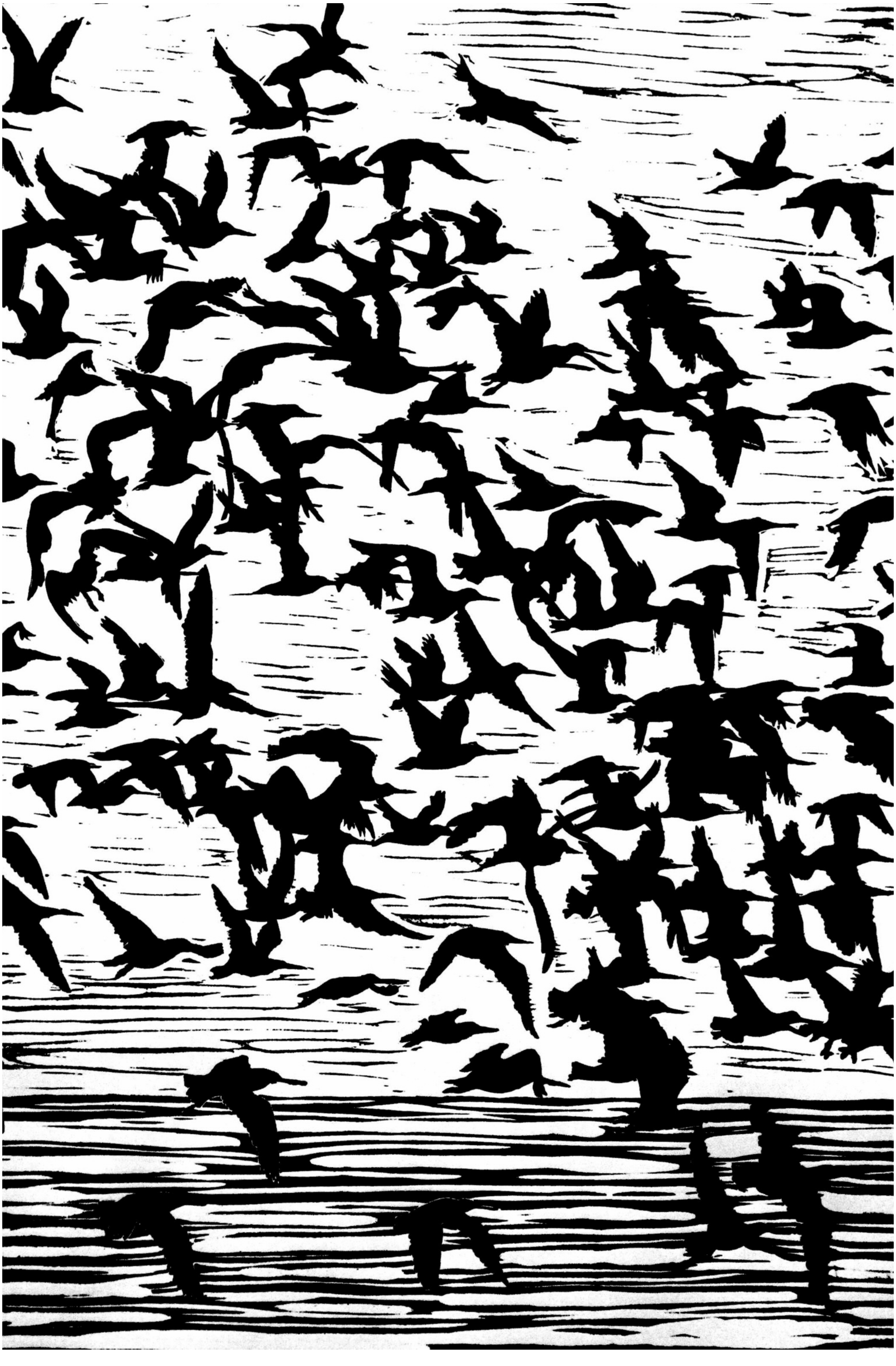


Summary

The **East Asian–Australasian Flyway** (EAAF) is one of the most species-rich flyways in the world, and is used regularly by at least 52 species of migratory shorebirds. Every year, millions of shorebirds migrate along this flyway from non-breeding areas in Southeast Asia and Australasia to breeding areas in the northern hemisphere as far north as the high Arctic. During their journeys, they stop to refuel on rich mudflats along the East Asian shores which have high densities of prey. In the early 2000s, the Yellow Sea was identified as the main area where the EAAF shorebirds fuel up ('stage') during migration.

However, the East Asian shores are becoming more and more hostile for the shorebirds and the birds are facing a number of threats such as loss of mudflats caused by land reclamation, collapse in prey stocks and unregulated hunting. Among the 25 EAAF shorebird populations with known trends, all except one are in decline. This raises a number of questions that are central to this thesis: How are shorebirds responding and coping with these rapid changes in their habitats? And, how can studying their migration ecology galvanize actions to conserve shorebirds in this flyway?

Habitat loss and prey declines often do not kill birds directly, but do reduce the fuelling rates of migratory shorebirds which need to fuel up in a rather short time. Impacts can manifest at a later time when a bird is already in another part of the world, e.g. birds using heavily-impacted sites might have to stop longer to fuel up and thus arrive late at the breeding grounds potentially missing the peak in food abundance there. Also, birds could cope by moving from heavily-impacted places to those that are relatively untouched. To understand these patterns of how the birds respond, we need to collect information throughout entire migratory journeys. This became possible at the beginning of this PhD project when solar-powered satellite transmitters were made small enough to attach to medium-sized shorebirds thus allowing us to track individual birds across the globe at high temporal resolution for multiple years. This study focuses on the Northwest Australian populations of three species in decline: The Great Knot, Red Knot and Bar-tailed Godwit. Every year these birds migrate to their breeding areas in the east Russian Arctic, stopping at mudflats in East Asia during their journeys.

Developing a harness for attaching satellite transmitters to the Knots

Tracking entire migration journeys requires long-term external attachment of transmitters. For Bar-tailed Godwit, transmitters can be attached successfully with leg-loop harnesses. However, this type of harness quickly slips off the legs of more compact species such as the Knots as they have no external 'knee'. Before we started tracking shorebirds in the EAAF, we first needed to develop a harness for Knots that could accommodate the dramatic changes in body size of the birds before and after their long migratory flights. At the Royal Netherlands Institute for Sea Research (NIOZ) on Texel, we developed a full-body harness that fit captive Red Knots without harming them. We then tested the design with a field test in the nearby Wadden Sea.

Discovering migration patterns

Among the three study species, only the Bar-tailed Godwit had been tracked with satellite tags before our study in 2007–2008; thus our study provided the first migration tracks of the Red Knot and the Great Knot (Chapter 4 and 5). While traditionally the two Knot species are regarded as 'long jumpers' in terms of migration strategy (making long non-stop flights, often of thousands of kilometres, between stops during migration), we found they were more like 'skippers' during northward migration. Instead of flying directly to the Yellow Sea, they stopped at sites in Southeast Asia and southern China, many of which contain high-quality prey such as the bivalve *Potamocorbula laevis* (Chapter 4, Box A).

We were also able to describe the migration of the third subspecies of Bar-tailed Godwits in the EAAF, as two of the godwits tagged in Northwest Australia (who we originally identified as the more numerous *menzbieri* at the banding site) turned out to belong to the *anadyrensis* subspecies that breeds in the Anadyr River basin in Russia (Chapter 3). As *anadyrensis* cannot be distinguished from the other EAAF Godwits (*baueri* and *menzbieri*) based on size and plumage alone, their non-breeding distribution and migration routes had gone undetected prior to our study. We found two key differences in migration itineraries between the tagged *menzbieri* and *anadyrensis* and both occurred during the post-breeding migration period. First, from the breeding areas, *menzbieri* migrated northwards to stage in the New Siberian Islands, Russia, while *anadyrensis* migrated southwestward to stage along the coast in the Sea of Okhotsk, Russia. Second, although both subspecies proceeded to migrate southward to the Yellow Sea, *menzbieri* used the Yellow Sea as their main southbound staging area, whereas *anadyrensis* stopped there for a much shorter time and continued on to stage at the Indonesian side of Timor Island. We also found that the two *anadyrensis* birds used the Kamchatka Peninsula on the east side of the Sea of Okhotsk during post-breeding migration while *menzbieri* used the west side of the Sea, therefore counts conducted at Kamchatka would be one way to monitor the *anadyrensis* population.

How can we use the knowledge gained from tracking shorebirds in nature conservation?

Satellite tracking has revealed new migration routes and stopping areas of shorebirds in the EAAF. We explore the value of the new knowledge obtained from tracking compared to past knowledge of key shorebird sites that had been mostly based on ground observations (Chapter 5). Among the 92 sites used by the tracked Great Knots during their migration, surprisingly, 63% were not known as important shorebird sites before our study. While the majority of sites in the Yellow Sea region were known before our study, most sites in Southeast Asia, southern China and Eastern Russia were new. We highlighted coastal habitats in these other regions that are potentially important for shorebirds but lack ecological information and conservation recognition. Further, the distributional data of tracked individuals can help plan on-ground surveys at lesser-known sites, which we did in 2015–2018 along the Chinese coast. We conducted field work at 18 sites visited by the tracked Great Knots and Bar-tailed Godwits to collect information on bird numbers, bird diet and intake rates, and density and composition of prey populations (Box A). We found that the northernmost sites in the Yellow Sea (Liaohe estuary and the Yalu Jiang estuary) had the highest bird numbers yet contained relatively low densities of high-quality prey compared to sites further south.

Local movements of shorebirds at stopping sites extracted from our tracking data were used to guide conservation actions at three Yellow Sea sites in the Jiangsu Province of China in need of protection. First, at Lianyungang in north Jiangsu (Chapter 6), from analysing satellite images we found that 27% of mudflats had been lost by land reclamation in 2003–2018. We assess the site's importance for shorebirds by putting together the results of a decade of counting efforts. One criterion to assess a site's importance is if the site contains >1% of a species' entire flyway population. Lianyungang had the most species (22) meeting this criterion among the >300 shorebird sites in East Asia. We conducted three years of benthic sampling at Lianyungang and showed that the intertidal flats were dominated by small, soft-shelled bivalve species (including *P. laevis*) which are high-quality food for shorebirds. The duration of stay of satellite-tracked Great Knots and Bar-tailed Godwits revealed that some birds used the site as a short stopover and others for month-long staging. Tidal movements of the tracked birds showed locations of high-tide roosts and low-tide foraging areas that should be protected and managed.

Second, a large-scale reclamation was planned at the Dafeng-Dongtai-Rudong coast in south Jiangsu (Box B). This site was the only place where the tracked *anadyrensis* Bar-tailed Godwits stopped in the Yellow Sea, and was also used by almost half of the tracked *menzbieri* (Chapter 3). The spatial-temporal distribution of the tracked Bar-tailed Godwits served as one of the key pieces of information to urge the reconsideration of the planned reclamation in light of the area's ecological importance. Part of this site was eventually included as World Heritage site, and to date the planned reclamation has not occurred.

Third, at Tongzhou Bay in south Jiangsu, large areas of mudflats are being dredged or reclaimed for port construction (Box C). To assess the ecological impact of current and future reclamation projects, in collaboration with hydraulic engineers, distributions of satellite-tagged shorebirds were used to detect the 'ecotopes' with the bay (derived from a hydrodynamic model) that were most important for shorebirds. This allowed the loss of shorebird habitat to be quantified. In a follow-up study, the 'building with nature' concept was applied in port design. By developing a hydrodynamic model to simulate sediment transport in the bay, alternative port configurations were assessed (and compared to the null situation that no port is built) on the degree to which the existing high-value ‘ecotopes’ for shorebirds could be preserved and their natural growth be promoted by increasing siltation.

How do shorebirds cope with habitat loss and deterioration?

Consider the situation that shorebirds arrive at their staging sites and discover that mudflats are gone due to land reclamation, or that prey densities have plummeted. Other than staying-put and expanding their diet or prolonging the time spent in foraging, the birds could also cope by moving to other places. However, many species of shorebirds are known for their strong site fidelity, that is the tendency to visit the same sites year after year. In theory, this tendency can deter them from leaving a site when habitat deteriorates. Using both satellite tracking data and resighting data of banded individuals, we showed that site fidelity was lower in Great Knots than in Bar-tailed Godwits (Chapter 7). This difference was found in the non-breeding sites in Northwest Australia and also at the migratory stopover sites in the Yellow Sea. The less-site faithful Great Knots also showed more variation among individuals in site fidelity than the Godwits.

We investigated what determines individual variation in ‘coping by moving’ by focusing on a personality trait: the tendency to explore (Chapter 8). This trait was measured by a standardized trial before releasing the tracked Great Knots into the wild. Since more explorative birds are known to put more effort into acquiring information, they likely have more information about the locations and habitat conditions of alternative sites. This site knowledge would lower the risks and energetic and time costs of moving. We found that the individual Great Knots that were more explorative in the trials responded quicker to the collapse in prey stock at their main staging site by moving to other sites earlier than less explorative individuals. Moreover, they arrived on the breeding grounds earlier and bred more successfully.

Lastly, are these migrants coping with the deteriorations in the Yellow Sea in other ways (Chapter 9)? Is it currently more advantageous to first stop in Southeast Asia and southern China and then continue to fly to the Yellow Sea, instead of a direct flight from Northwest Australia to the Yellow Sea? And an increasing number of Great Knots are wintering in Southeast Asia. Do these birds do better than their Northwest Australia counterparts? Also, some tracked birds skipped migration. Is that a better strategy than migrating every year? To answer all these questions will require additional tracking of the migration journeys of these populations and also measuring aspects of their habitats such as food availability, their fuelling rates, survival and breeding success. I hope that this thesis will inspire future studies on how birds are dealing with the human-induced environmental problems in the world. This will eventually lead to better predictions on how these problems lead to declines in bird populations. And, by understanding how the birds are dealing, we can perhaps become better at dealing with the mess that humans created.

Samenvatting

De **Oost Aziatische-Australaziatische (OAA) trekroute** wordt gebruikt door ten minste 52 kustvogelsoorten en is daarmee is één van de meest soortenrijke routes ter wereld. Elk jaar migreren miljoenen vogels langs deze route van de overwintersgebieden in Zuidoost-Azië en Australazië naar de broedgebieden op het noordelijk halfrond tot in het noordpoolgebied. Hun reis onderbreken ze om bij te tanken op wadplaten met een hoge prooidichtheid langs de Oost-Aziatische kusten. In het begin van deze eeuw werd de Gele Zee gezien als het belangrijkste gebied om de trek te onderbreken.

De Oost-Aziatische kustgebieden worden daarvoor echter steeds minder geschikt als gevolg van bijvoorbeeld het verlies van wadplaten door landwinning, een sterke afname van prooibestanden en ongereguleerde jacht. Van de 25 kustvogelpopulaties waarvan de omvang bekend is en die van deze trekroute gebruik maken nemen er maar liefst 24 af. Dit roept een aantal vragen op, die centraal staan in dit proefschrift: Hoe gaan de vogels om met deze snelle veranderingen in hun leefgebied? En hoe kan het bestuderen van hun migratie-ecologie helpen om deze trekroutes te behouden?

Het verlies van voedselgebieden of een afname van de dichtheid aan prooidieren hoeft niet direct te leiden tot sterfte van vogels, maar wel tot een verminderde energie-opname van dieren die tijdens de trek onder een enorme tijdsdruk staan. De gevolgen daarvan kunnen zich op een later tijdstip manifesteren, wanneer de vogels zich al weer in een ander deel van de wereld bevinden. Het kan ook zo zijn dat vogels hun trek gedurende een langere periode moeten onderbreken, om genoeg voedsel op te kunnen nemen, waardoor zij (te) laat aankomen op de broedplaatsenen een piek in het voorkomen van voedsel daar mislopen. Mogelijk moeten trekvogels traditionele, maar nu zwaar verarmde plaatsen opgeven en naar alternatieven uitkijken. Om te begrijpen wat er mogelijk is en hoe de vogels reageren, moeten we informatie verzamelen over het volledige migratietraject. Dit werd mogelijk doordat er kleine satellietzenders beschikbaar kwamen, die geschikt zijn om toegepast te worden op middelgrote kustvogels. Deze zenders werken op zonne-energie, waardoor we de vogels overal, continu en gedurende meerdere jaren kunnen volgen. Deze studie richtte zich op de Noordwest-Australische populaties van drie afnemende soorten: de grote kanoet, de (rode) kanoet en de rosse grutto. Elk jaar trekken deze vogels naar hun broedgebieden in het Oost-Russische Noordpoolgebied en onderbreken ze hun reis op wadplaten in Oost-Azië.

Ontwikkeling van een harnas om satellietzenders aan kanoeten te bevestigen

Om de trekwegen helemaal te kunnen volgen, moeten de zenders lang meegaan en gekozen werd voor instrumenten die buiten op het lichaam van de vogels werden aangebracht. Bij rosse grutto werden de zenders bevestigd door middel van lussen om de poten. Deze manier van aanbrengen is ongeschikt voor de kleinere kanoeten, omdat zij geen externe ‘knie’ hebben, waardoor de lussen afglijden. Voordat we begonnen met het volgen van kustvogels in de OAA trekroute, moesten we daarom eerst een geschikt tuigje voor kanoeten ontwikkelen, waarmee weook nog eens de extreme veranderingen in lichaamsgrootte voor en na hun lange trekvluchten kon opvangen. Bij het Koninklijk Nederlands Instituut voor Onderzoek der Zee (NIOZ) op Texel hebben we een tuigje ontwikkeld en (in gevangenschap) getest, dat de kanoeten past en ze niet beschadigd. Vervolgens werd het ontwerp in het vrije veld getest en geschikt bevonden.

Migratiepatronen ontdekken

Van de drie soorten die we wilden bestuderen was alleen de rosse grutto wel eens gevolgd met satellietzenders (2007-2008); zo leverde onze studie de eerste complete routes op van de kanoet en de grote kanoet (hoofdstuk 4 en 5). Terwijl deze twee soorten traditioneel in de gradatie ‘hink-stap-sprong’ worden beschouwd als '(ver-)springers' wat betreft migratiestrategie (lange non-stop vluchten, vaak over duizenden kilometers, tussen trekonderbrekingen in), ontdekten we dat ze meer als 'hinkers' beschouwd moesten worden. In plaats van rechtstreeks naar de Gele Zee te vliegen, stopten ze al eerder op locaties in Zuidoost-Azië en Zuid-China, waar voedsel van hoge kwaliteit voorkomt, zoals de tweekleppige *Potamocorbula laevis* (hoofdstuk 4, kader A).

We waren ook in staat om de trekbewegingen van de derde ondersoort van rosse grutto's in de OAA trekroute te beschrijven, aangezien twee van de in Noordwest-Australië gezenderde grutto's (die we oorspronkelijk identificeerden als de talrijkere *menzbieri* op de vangstlocatie) bleken te behoren tot de *anadyrensis*-ondersoort die broedt in het stroomgebied van de Anadyr in Rusland (hoofdstuk 3). Omdat *anadyrensis* niet op basis van grootte en verenkleed kan worden onderscheiden van de andere OAA trekroute-grutto's (*baueri* en *menzbieri*), waren hun verspreiding buiten het broedgebied en migratieroutes onopgemerkt gebleven vóór onze studie. We vonden twee belangrijke verschillen in migratieroutes tussen de gezenderde *menzbieri* en *anadyrensis* en beide traden op tijdens de migratieperiode na het broeden. Ten eerste trok *menzbieri* vanuit de broedgebieden naar het noorden om een tussenstop te maken op de Nieuw-Siberische eilanden (Rusland), terwijl *anadyrensis* naar het zuidwesten migreerde om langs de kust in de Zee van Okhotsk, Rusland, bij te tanken. Ten tweede, hoewel beide ondersoorten verder naar het zuiden trokken naar de Gele Zee, gebruikte *menzbieri* de Gele Zee als hun belangrijkste pleisterplaats in zuidelijke richting, terwijl *anadyrensis* daar maar heel even stopte om meteen weer door te gaan naar de Indonesische kant van het eiland Timor. We ontdekten ook dat de twee *anadyrensis*-vogels het schiereiland Kamtsjatka aan de oostkant van de Zee van Okhotsk gebruikten, terwijl *menzbieri* langs de westkant van die zee trok. Tellingen uitgevoerd in Kamtsjatka zouden daarom misschien een geschikte manier zijn om ontwikkelingen in de populatie van *anadyrensis* te volgen.

Hoe kan kennis verkregen door het volgen van kustvogels met satellietvolgsystemen gebruikt worden bij natuurbehoud?

Moderne satellietvolgsystemen hebben zowel nieuwe routes als pleisterplaatsen van kustvogels langs de OAA trekroute aan het licht gebracht. Om de betekenis daarvan te beoordelen, hebben we de nieuwe informatie vergeleken met wat er bekend was van de aantallen vogels op de 92 pleisterplaatsen die werden gebruikt door de gezenderde grote kanoeten. We beschouwen deze vogel als een indicatorsoort voor kustvogels langs de trekroute die afhankelijk zijn van wetlands aan de kust (hoofdstuk 5). Maar liefst 63% van deze pleisterplaatsen waren voordat we ons onderzoek uitvoerden onbekend als belangrijke kustvogellocaties. Terwijl we weinig nieuwe plekken vonden rond de Gele Zee, kwamen er tal van locaties naar voren die belangrijk waren in Zuidoost-Azië, Zuid-China en Oost-Rusland. Het bleek dus dat kustgebieden in deze regio's heel belangrijk kunnen zijn voor kustvogels, terwijl adequate ecologische informatie, maar ook erkenning voor natuurbehoud in deze gebieden ontbreekt. De nieuwe verspreidingsgegevens van de gezenderde individuen kunnen helpen bij het plannen van aanvullend onderzoek in minder bekende locaties, zoals we dat in 2015–2018 langs de Chinese kust hebben gedaan. Wij hebben veldwerk verricht op 18 locaties, die werden bezocht door de gezenderde grote kanoeten en rosse grutto's, om informatie te verzamelen over vogelaantallen, dieet, samenstelling van prooipopulaties, voedselaanbod en de snelheid van voedselopname (kader A). We ontdekten dat de noordelijkste gebieden in de Gele Zee (Liaohe estuarium en het Yalu Jiang estuarium) de hoogste aantallen wadvogels herbergden, maar relatief lage dichtheden aan geschikte prooien in vergelijking met zuidelijker gelegen gebieden.

Lokale vliegbewegingen op de pleisterplaatsen, zoals we die uit onze volggegevens konden afleiden, zijn gebruikt bij natuurbeschermingsacties in drie gebieden in de Gele Zee in de provincie Jiangsu in China die dringend aandacht vereisten voor natuurbehoud.

Bij Lianyungang in het noorden van Jiangsu (hoofdstuk 6), ontdekten we door het analyseren van de satellietbeelden dat 27% van de wadplaten verloren was gegaan door landaanwinning in de periode tussen 2003 en 2018. We hebben het belang van deze locatie voor kustvogels vastgesteld door de resultaten van een decennium aan telinspanningen samen te nemen. Voor 22 kustvogelsoorten was de populatie in Lianyungang groter dan 1% van de gehele populatie langs de OAA trekroute, wat deze pleisterplaats de belangrijkste maakt van >300 kustvogellocaties in Oost-Azië. We hebben drie jaar benthos bemonsterd in Lianyungang en daarbij aangetoond dat de getijdenplaten vol zaten met kleine tweekleppigen met zachte schelpjes (waaronder *P. laevis*) die als hoogwaardig voedsel voor kustvogels mogen worden beschouwd. Ook bleek dat dit gebied door grote kanoeten en rosse grutto's zowel voor korte als lange tussenstops werd gebruikt. Voedselvluchten van de gevolgde dieren die het getijritme volgden brachten de precieze locaties van hoogwatervluchtplaatsen aan het licht, maar ook waar er nu daadwerkelijk gefoerageerd werd en daarmee welke gebieden bijzondere bescherming verdienden.

Aan de kust van Dafeng-Dongai-Rudong in het zuiden van Jiangsu was een grootschalige drooglegging gepland (kader B), uitgerekend op de enige plaats die de gezenderde *anadyrensis* Rosse Grutto's gebruikten in de Gele Zee. Deze locatie wordt ook nog eens gebruikt door bijna de helft van alle gezenderde *menzbieri* (hoofdstuk 3). De informatie die we kregen door rosse grutto's met zenders te volgen bleek uiteindelijk cruciaal om de geplande drooglegging voorlopig te voorkomen en dit gebied werd uiteindelijk ook opgenomen als werelderfgoed.

Bij Tongzhou Bay in het zuiden van Jiangsu worden grote delen van het slik uitgebaggerd of juist drooggelegd voor de aanleg van havens (kader C). Om de ecologische impact van huidige en toekomstige landaanwinningsprojecten te beoordelen, werden verspreidingspatronen van kustvogels met satellietzenders gebruikt om de 'ecotopen' (gedefinieerd door hydrologische omstandigheden) te detecteren die van de grootste betekenis zijn voor kustvogels. Hierdoor kon het verlies aan leefgebied van kustvogels worden gekwantificeerd. In een vervolgstudie is het concept 'bouwen met de natuur' toegepast in havenontwerp. Met hydrologische simulaties van sedimenttransport in de baai werden alternatieve havenconfiguraties beoordeeld (en vergeleken met de nulsituatie dat er geen haven wordt aangelegd). Hierbij onderzochten we of de bestaande hoogwaardige 'ecotopen' voor kustvogels kunnen worden behouden, of dat hun natuurlijke groei kan worden bevorderd door kunstmatige aanslibbing.

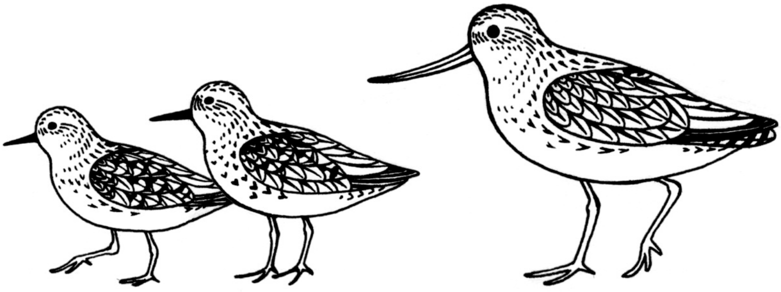
Hoe gaan kustvogels om met verlies en achteruitgang van hun leefgebied?

Wanneer kustvogels bij hun traditionele pleisterplaats aankomen en daar ontdekken dat er wadplaten verloren zijn gegaan, of dat de voedseldichtheid sterk is afgenomen, blijven er nog een aantal mogelijkheden over. Blijven en minder kieskeurig zijn wat betreft hun voedselkeuze of meer tijd aan foeregeren is een mogelijkheid, maar vertrekken naar een andere plek is een andere optie. Veel soorten kustvogels leggen echter een sterke plaatstrouw aan de dag, die ze kan weerhouden om te vertrekken, zelfs wanneer de omstandigheden ongunstig zijn geworden.

Dankzij onze satellietzenders, maar ook door vogels met kleurringen te volgen, konden we aantonen dat grote kanoeten minder plaatstrouw zijn dan rosse grutto's. Dit verschil viel op in het overwinteringsgebied in Noordwest-Australië, maar ook in de Gele Zee (hoofdstuk 7). De kanoeten verschilden ook onderling sterker in hun mate van plaatstrouw dan individuele rosse grutto's. We onderzocht wat de individuele variatie in plaatstrouw bepaalt, waarbij we ons concentreerden op een individueel verschillende neiging tot meer of minder exploratiegedrag (hoofdstuk 8). Het is bekend dat explorerende vogels meer energie steken in het verzamelen van informatie, en daarbij beschikken ze mogelijk ook over meer informatie over alternatieve plekken. De kosten om te verplaatsen zijn dan lager. Voordat we de gezenderde grote kanoeten in het wild loslieten, hebben we eerst experimenteel hun neiging tot exploreren gemeten. We ontdekten dat meer exploratieve grote kanoeten sneller reageerden op de ineenstorting van het prooibestand op hun belangrijkste pleisterplaats door naar andere plekken te verhuizen dan minder exploratieve individuen, waardoor ze eerder in hun broedgebieden aankwamen en een grotere kans hadden om jongen groot te brengen.

Ten slotte, zouden deze trekvogels op andere manieren kunnen omgaan met de verslechterende omstandigheden op hun pleisterplaatsen in de Gele Zee (hoofdstuk 9)? Is het inderdaad voordeliger om eerst de trek in in Zuidoost-Azië en Zuid-China te onderbreken, om daarna naar de Gele Zee door te vliegente bereiken tijdens de noordwaartse trek in plaats van een rechtstreekse vlucht vanuit Noordwest-Australië naar de Gele Zee? En een toenemend aantal grote kanoeten overwintert in Zuidoost-Azië. Doen deze vogels het beter dan hun soortgenoten in Noordwest-Australië? Het bleek dat sommige gezenderde vogels de trek zelfs helemaal oversloegen; is dat een betere strategie dan elk jaar trekken en broeden?

Om al deze vragen te beantwoorden, moeten we de trekroutes van deze vogels blijven volgen en de kwaliteit van hun leefgebieden blijven meten, waaronder de beschikbaarheid van voedsel en de resulterende energiereserves, de overleving en het broedsucces van de vogels die deze gebieden gebruiken. Ik hoop dat dit proefschrift toekomstige studies zal inspireren over hoe vogels omgaan met de door de mens veroorzaakte achteruitgang van leefgebieden in de wereld. Dit zal uiteindelijk leiden tot betere voorspellingen over hoe deze problemen leiden tot de achteruitgang van trekvogels. En door te begrijpen hoe de vogels hiermee omgaan, kunnen we misschien beter worden in het omgaan met de rotzooi die de mens heeft gecreëerd.



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My first taste of shorebird research was a Master's research project with Allert Bijleveld. On my second day as a student in NIOZ I was dropped off in the middle of a wavy sea and lived five weeks on an uninhabited tiny island with three other Dutchies. During the fieldwork I was deeply influenced by Allert's dedication and persistence in the field; nothing is impossible after long days of following Knot flocks around, walking 20 kms on the mudflats carrying heavy equipment including a tripod designed for people twice my size – heavy they were, they might be the reason I wasn't blown away by the strong wind. I particularly enjoyed the walks on the beach around Griend during which Emma shared her knowledge and love for the birds and wildlife in the Wadden Sea. The attention to details and critical thinking of Allert also shaped my attitudes in doing science.

After the experience in the Wadden Sea I was eager to study shorebirds in other parts of the world. I gladly took the opportunity that Theunis offered to join the satellite tracking fieldwork in Roebuck Bay, Australia in 2012. Under the 40-degree hot sun I met Chris Hassell and Lee Tibbitts, the two key people in my PhD project. Amidst the rather nerve-wrecking cannon-netting sessions, Lee was there, being the expert in satellite tagging of shorebirds, getting the work done, keeping a good spirit and making sure everyone is alright. From there on I looked up to Lee as a scientist and as a person. Chris has taught me a great deal about shorebirds and the Australian wildlife during the months that I followed him around Roebuck Bay almost daily to read colour rings of shorebirds. We also went ring-reading for a few days in Eighty Mile Beach, and then we followed the Broome Red Knots to Nanpu, Bohai Bay, China. Ady, Matt and Chris introduced me to Nanpu and from them I learnt about the many shorebirds in this amazing site and how to read as many rings as possible. At the field site I lived with Nicky Yang, one of the first people studying shorebirds in Bohai Bay. She infected me with her enthusiasm and positivity, and shared her experience of conducting fieldwork in China. Nanpu was a combination of extremes: there were huge flocks of all species of shorebirds in almost full breeding plumage that were stunningly beautiful, while the landscape was very industrial and without any consideration on aesthetics. During my month-long stay there, my curiosity and interest in shorebirds developed into a deeper sense of concern, which is a source of motivation to this day to research about the shorebirds in East Asia.

Before I could start tracking birds in the East Asian–Australasian Flyway, a harness had to be developed and tested for attaching tags onto Knots; also, I needed to come up with a field set-up to measure exploratory tendency of knots in Australia. I would like to thank Anne and Maarten who took care of the birds, helped with tagging Knots with (dummy) satellite trackers, thought along with the design and built the set-up. I also thank Jorge, who was working in the aviaries in the same period, for his help, company and sharing his knowledge on shorebirds. From working with them I gained a lot of experience in handling birds and keeping them in captivity, which prepared me well to the task of keeping birds in captivity in Australia.

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