



Intraseasonal movements between staging sites by migrating great knots: Longer distances to alternatives decrease the probability of such moves

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ABSTRACT

Distance is a key constraint for animals in moving between suitable habitats, but is this also the case in staging long-distance migrating shorebirds that habitually cover thousands of kilometers during migrations? We conducted multi-year field observations, benthic prey sampling and satellite tracking, to compare how endangered great knots *Calidris tenuirostris* respond to the food shortage at two similarly functioning staging sites (Gaizhou and Beijingzi) in the northern Yellow Sea, China. Food availability declined by >95 % at both sites across the study period, with the intake rates of great knots declining by 87 %. However, whereas the number of great knots declined by 91 % at Gaizhou, only a 29 % decrease was seen at Beijingzi. Satellite tracking showed that during the time when food was poor in Gaizhou, tagged great knots crossed 20 km to suitable alternative high-quality sites where food was not scarce. From Beijingzi, tagged great knots flew at least 124 km to find a good alternative. We show that longer distances to alternative sites decreased the probability of a bird leaving. Thus, habitat degradation in staging sites induced great knots to move to alternative sites, but only if such alternatives were relatively close. As staging habitats become more isolated, the negative effects of habitat degradation will be more serious due to a distance constraint on exploratory movements. This emphasizes the importance of maintaining networks of nearby high-quality refueling sites for migratory birds to provide buffers in seasons when local food conditions are lean.

1. Introduction

Human activities have caused rapid environmental changes (Foley

et al., 2005) and altered the habitats of animals globally (Vitousek et al., 1997; Newbold et al., 2016). Long-distance migratory birds only succeed during their seasonal travels if the staging areas where they refuel have

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enough food on offer (Piersma and Jukema, 1990; Warnock, 2010; Rakhimberdiev et al., 2018). Although some species may benefit from human-made habitats (e.g., Lei et al., 2021), many of them suffer when natural habitats are converted to artificial habitats (Piersma et al., 2016; Studds et al., 2017; Johnson et al., 2017; Wang et al., 2021). The coastal intertidal mudflats of the Yellow Sea provide key staging areas for shorebirds along the East Asian-Australasian Flyway (EAAF) (Bai et al., 2015; Choi et al., 2016; Zhang et al., 2018). Land claims and intense exploitation of intertidal mudflats have caused a rapid loss in the extent and ecological integrity of mudflats over the last 60 years (Murray et al., 2014, 2015; Melville et al., 2016a; Choi et al., 2018). This is associated with reduced survival of shorebirds (Piersma et al., 2016), resulting in population declines, especially if highly reliant on these disappearing habitats (Studds et al., 2017).

Individual migratory birds can try to cope with habitat loss and degradation, e.g., by extending the length of stay at staging areas during periods of food shortage (Rakhimberdiev et al., 2018; Ke et al., 2019; Conklin et al., 2021), advancing the timing of their migration to extend the overall refueling time (Robson and Barriocanal, 2011), and even by altering migration trajectories to track large-scale changes in habitat suitability (Dolman and Sutherland, 1995; Verkuil et al., 2012). Birds may also cope with local adversity by moving to alternative sites (Betini et al., 2015; Yang et al., 2011), or by adjustments in foraging routines and digestive processes (Zhang et al., 2019).

Continuing habitat loss and degradation, however, mean that

remaining suitable habitats become more isolated, and migratory birds become more concentrated at the remaining sites (Yang et al., 2011). For example, in the Nanpu, Luannan coast, Bohai Bay, China the abundance of red knots *Calidris canutus* increased following the destruction of the adjacent intertidal mudflats due to land claim (Yang et al., 2011). If habitats are isolated from each other, then finding alternatives will inevitably become more difficult. Nevertheless, for birds that easily make nonstop migratory flights of thousands of kilometers, flight distances which appear inconsequential for annual survival (Conklin et al., 2017), the need to move by 10s or 100 s of km between suitable sites would seem a rather small challenge – an argument that developers often make when converting intertidal mudflats to other land-use.

Surprisingly then, the abundance of great knots *Calidris tenuirostris* remained relatively stable at the Yalu Estuary, Liaoning Province, China, a key refueling area for great knots in the Yellow Sea (Fig. 1), in the earlier years after their preferred food declined dramatically (Zhang et al., 2018). This suggests that most of them somehow choose not to move to potential alternative refueling areas at distances of ~100 km (Fig. 1, Chan et al., 2019, Zhang et al., 2018, 2019). It appears that something similar may have happened at the Saemangeum estuary in South Korea, which was far from the two most important alternative areas in the northern Yellow Sea (500 km to Yalu Estuary, 650 km to Upper Liaodong Bay, Fig. 1). Saemangeum supported >80,000 great knots in 2006, but the global population decreased by tens of thousands in the years following the destruction of the intertidal flats when the

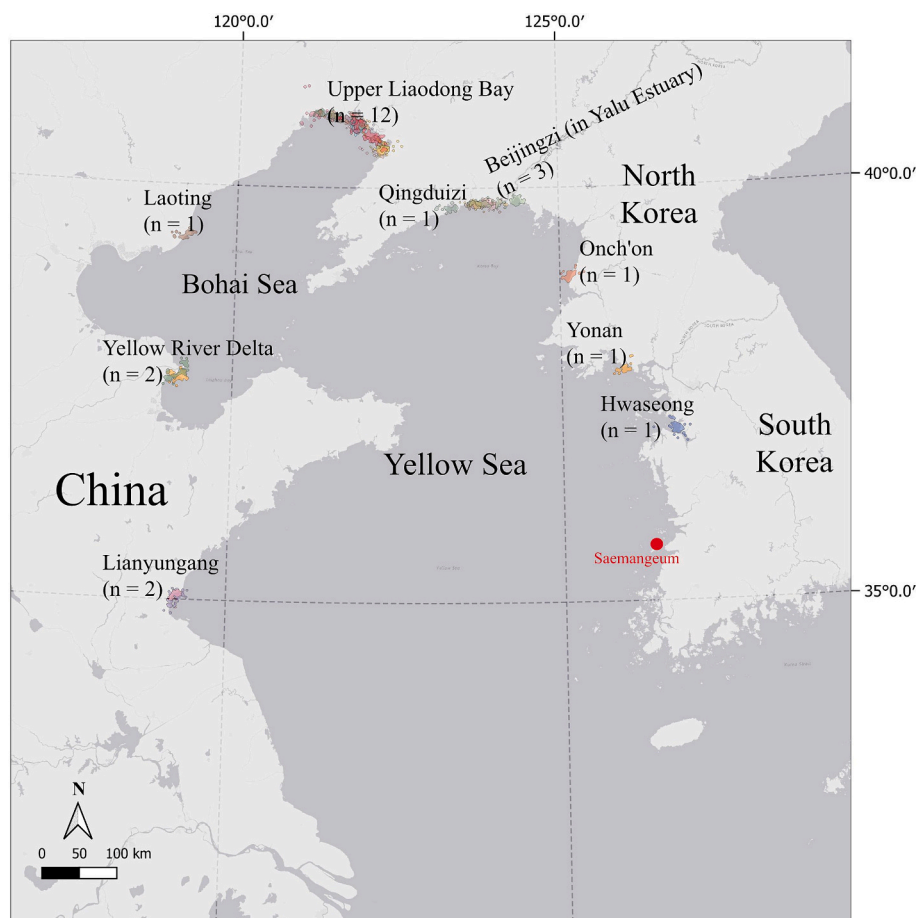


Fig. 1. The distribution of key staging areas of tracked great knots in the Yellow Sea (Chan et al., 2019). The coloured polygons show the home ranges of great knots at their key staging sites (or meta-sites, a combination of high-quality neighbouring sites) in the Yellow Sea, each colour at each site (or meta-sites) representing an individual (see Materials and Methods). Saemangeum in South Korea was the most important staging site for great knots in the Yellow Sea prior to its destruction following the closure of the seawall in 2006 (Moore et al., 2016). The numerical values under the name of each staging (meta-) site (e.g. $n = 12$ in Upper Liaodong Bay), represents the numbers of birds that used the (meta-) site before migrating to the breeding grounds. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

seawall was closed in April 2006 with only a few birds apparently moving to other areas (Moore et al., 2016). Does distance to alternative staging sites affect the probability of moving in response to food shortage during a time of the year when the birds are time-constrained (Rakhimberdiev et al., 2018)?

Along with advances in tracking technology, our understanding of the site use by migratory birds is increasing (e.g. Chan et al., 2019). There is always the issue of what defines a site. Several studies have suggested that the previously chosen boundaries of important bird sites do not fully encompass the full range of habitats (Clemens et al., 2014; Choi et al., 2019). Especially for contiguous, high-quality habitats, site delineations based on incomplete knowledge would be less effective in conserving threatened migratory birds. Often birds also use parts of what are defined as ‘neighbouring’ sites (Clemens et al., 2014). Hence, combinations of neighbouring sites (which we will call ‘meta-sites’) may improve the realistic capture of space use.

In this study, we tested the idea that when encountering local food shortages during staging, birds only moved away in search of alternative sites if such alternatives were relatively close by. To do so we (1) compared counts of great knots from sites and years with different food abundances at two staging sites in the Yellow Sea; (2) monitored how the abundance and intake rates of great knots changed when food

densities changed; and (3) examined the probability that satellite-tagged birds would move away from a particular site under conditions of food scarcity.

2. Materials and methods

2.1. Study species

Great knots occur mainly in the East Asian-Australasian Flyway (BirdLife International, 2022). They breed on mountainous tundra in northeast Russia, and spend the non-breeding season mainly in north-west Australia (Tomkovich, 1997; Choi et al., 2016). During migration, great knots depend on coastal wetlands in the Yellow Sea for refueling both during their northward and southward journeys (Chan et al., 2019, Choi et al., 2016, Ma et al., 2013, Fig. 1a). During northward migration they stage for up to two months in the Yellow Sea, some individuals double their body mass before departing to Arctic breeding grounds (Ma et al., 2013; Peng et al., 2015).

Because they are a specialized molluscivore relying on intertidal mudflats during their non-breeding period (Tulp and de Goeij, 1994; Choi et al., 2016), food availability can be quantified on the basis of the density of shallow-living, and comparatively soft-shelled, molluscs on

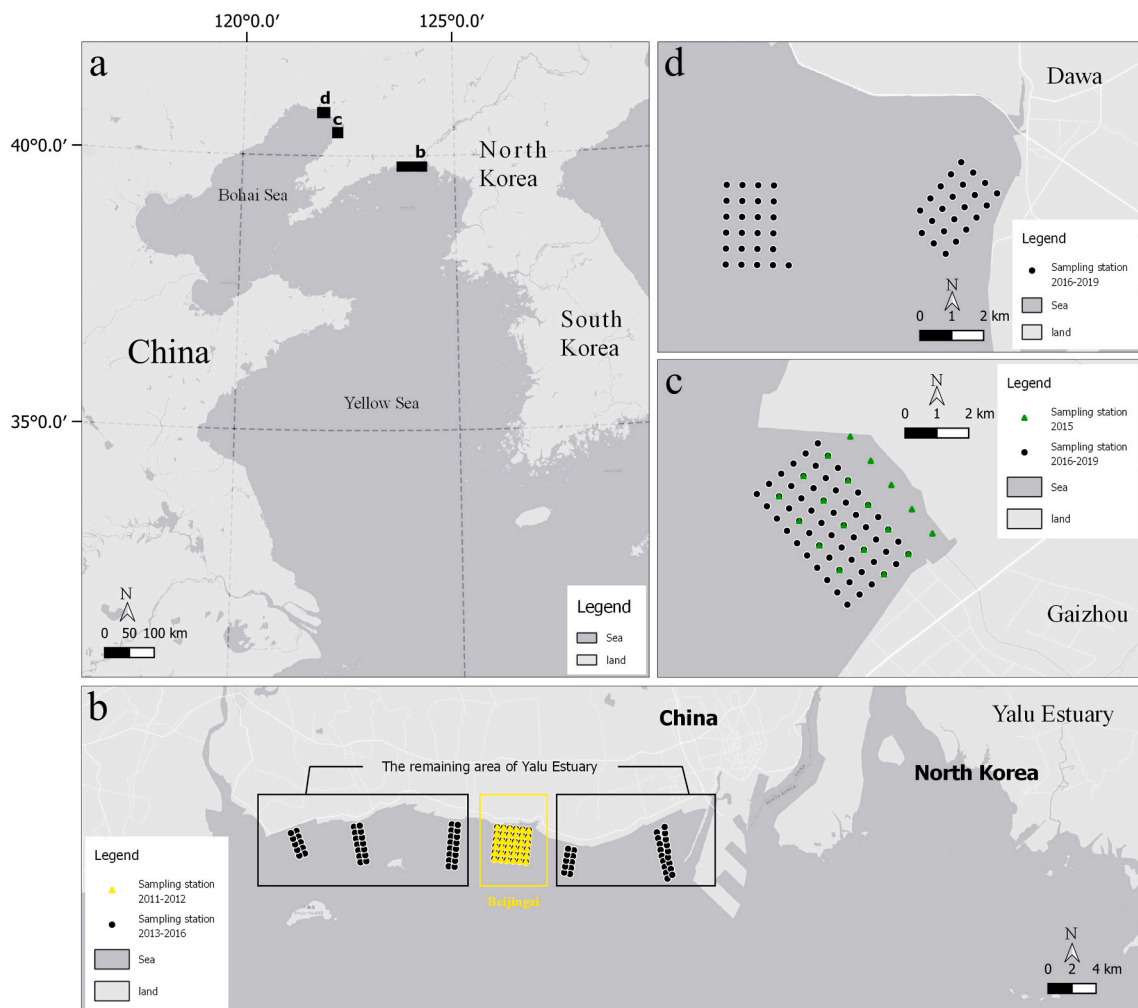


Fig. 2. Locations of the sampling sites and distribution of sampling stations for molluscs in our study areas. (a) Locations of Beijingzi site of the Yalu Estuary meta-site, the remaining area of the Yalu Estuary, Gaizhou and Dawa sites of the Upper Liaodong Bay meta-site in the Yellow Sea. (b) Sampling station for benthos in the Yalu Estuary meta-site: yellow triangles show the stations of Beijingzi site from 2011 to 2016 (inclusive), black dots show the sampling station of the remaining area of the Yalu Estuary meta-site from 2013, 2015, 2016. (c) Sampling stations for benthos at the Gaizhou site of Upper Liaodong Bay; green triangles show the stations of 2015, and black dots show the stations from 2016 to 2019 (inclusive). (d) Sampling stations for benthos at the Dawa site in Upper Liaodong Bay from 2016 to 2019 (inclusive). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the intertidal flats (Zhang et al., 2019). The variation in the abundance of molluscs at staging sites will influence rates of energy accumulation of great knots (Choi et al., 2016; Zhang et al., 2019). Along with habitat loss and degradation in the Yellow Sea, great knots showed a population decline (Studds et al., 2017) and were uplisted to 'Endangered' in the IUCN Red List in 2015 by BirdLife International (2016).

2.2. Study areas (sites and meta-sites)

This study was carried out in two meta-sites in the northern Yellow Sea, China: (1) Yalu Estuary (spanning 100 km of coastline with the intertidal flats being on average ~5 km wide, our study was conducted at Yalu Estuary National Nature Reserve (hereafter Yalu Estuary, 39°40'–39°58'N, 123°34'–124°07'E), which is located at the western side of Yalu Jiang Estuary); (2) Upper Liaodong Bay (spanning 120 km of coastline and six km-wide intertidal flats, with some large intertidal shoals 8 km offshore, 40°24'–40°52'N, 121°08'–122°17'E) (Fig. 2a). These are the two most important staging meta-sites for great knots in the EAAF (Fig. 1; Chan et al., 2019). The monitoring of shorebirds and macrobenthos are parts of our national scale monitoring effort along the Chinese coast (Choi et al., 2020; Peng et al., 2021). The Yalu Estuary meta-site, located at China's boundary with North Korea (Fig. 2b, Choi et al., 2015; Zhang et al., 2018), supported as many as 75,000 great knots refueling during northward migration (17.6 % of the global population), and was divided into >15 study sites in previous studies (Choi et al., 2015). Upper Liaodong Bay meta-site, located in the northeast of the Bohai Sea, consists of several study sites: Jinzhou, Panjin, Dawa, Yingkou and Gaizhou (Bai et al., 2015; Hua et al., 2015; Melville et al., 2016b).

In the Yalu Estuary meta-site, we mainly conducted monitoring of shorebirds and macrobenthos at the staging site Beijingzi in the central area of the National Nature Reserve – the main foraging area of great knots (Choi et al., 2019). The stopover ecology of shorebirds at Beijingzi has been studied since 2011. We also monitored the macrobenthos in the remaining area of Yalu Estuary meta-site in some of the study years (see below), which was occasionally used by great knots for foraging and as (pre)roost sites (the term pre-roost site indicates the upper intertidal flats last covered by the incoming tide where shorebirds concentrated before flying to landside roosts, Choi et al., 2015).

In Upper Liaodong Bay meta-site, most studies on shorebirds and macrobenthos were conducted at the staging site Gaizhou (Fig. 2c), where 60,000 great knots were discovered foraging during northward migration in 2015 by means of satellite tracking (Melville et al., 2016b; Chan et al., 2019). We also surveyed macrobenthos in Dawa, which also supports thousands of foraging great knots. All these sites are important for staging great knots (Bai et al., 2015; Melville et al., 2016b; Choi et al., 2020).

Because the food declines happened in different years at the two study sites Beijingzi and Gaizhou, the years that we monitored bird numbers and macrobenthos density are slightly different (Table 1). Satellite tracking of the movements of great knots was conducted during northward migrations from 2015 to 2017 when there was a scarcity of food at both sites. This allowed us to explore the responses of individual great knots to local food shortages.

Table 1

Overview of specifics of sampling efforts and periods at each study (meta-) site.

Meta-site	Study site	Benthos	Bird		
		Abundance	Abundance	Intake rate	Tracking
Yalu Estuary	Beijingzi	2011–2016	2011–2016	2011, 2012, 2016	2015–2017
	The remaining	2013–2016	NA	NA	
Upper Liaodong Bay	Gaizhou	2015–2019	2015–2019	2015–2019	NA
	Dawa	2016–2019	NA	NA	

2.3. Bird counts

Great knots started to arrive in the Yellow Sea from non-breeding areas in northwest Australia and southeast Asia from early April onwards. We counted bird numbers in early May when the peak numbers of great knots occurred at both Yalu Estuary and Upper Liaodong Bay (Ma et al., 2013; Peng et al., 2015; Chan et al., 2019). Because great knots depart from their last staging sites in the north Yellow Sea within a period of 1–2 weeks in mid-May (Ma et al., 2013; Peng et al., 2015; Chan et al., 2019), the peak number counted in early May will approximate the total number of great knots staging at Beijingzi and Gaizhou.

At Beijingzi site, great knots foraged over a large area (mudflat spanning 7 km coastline and 4 km width) (Choi et al., 2019). As it is difficult to count birds during low tide when they are widely dispersed, we counted them when concentrated at (pre)roost sites during high tide. Based on satellite-tracking (this study, see below) and radio-tracking studies (Choi et al., 2019), great knots foraging at Beijingzi fly to roosts dispersed along the whole coast of Yalu Estuary when the main foraging area is covered by water. From 2011 to 2016, we counted the birds at 16 fixed (pre-) roost areas during spring high tide in early May (detailed information in Zhang et al., 2018). Because satellite tracking and field observations (Riegen et al., 2018) showed that most great knots at Yalu Estuary meta-site stayed on the Chinese side, especially during high tide, rather than moving to the North Korean part of the Yalu Jiang Estuary, our bird counts should reflect the (relative) abundance of great knots utilizing Beijingzi site.

At Gaizhou site, great knots feed in a small area (mudflat spanning 2 km coastline and 2 km width), and satellite tracking (this study) showed great knots to be faithful to this foraging area. We thus made counts in the foraging area during low tide in early May from 2015 to 2019 inclusive.

2.4. Food availability and intake rate

At Beijingzi site, we sampled molluscs in May from 2011 to 2016 inclusive to assess food availability for great knots (Choi et al., 2016; Zhang et al., 2019). Six sampling transects were set across the intertidal flats with a total of 36 sampling stations spaced 500 m apart (Fig. 2b). To explore the food available to great knots in sites nearby Beijingzi, we also surveyed the macrobenthos in the remaining areas of the Yalu Estuary meta-site, in May 2013, 2015 and 2016, using 10 transects with 68 sampling stations spaced 500 m apart, the distance between each transect being from 500 m to 10 km, to ensure at least two transects in each 10 km of the coast (see Zhang et al., 2018 for earlier analyses of the benthos data).

At Gaizhou site, 65 sampling stations were sampled in May from 2015 to 2019 inclusive. Among these, 20 stations 500 m apart (Fig. 2c) were sampled in 2015, and 60 stations 250 m apart (Fig. 2c) were sampled in 2016–2019. There was no significant difference in the mollusc density between the stations sampled in 2015 and those stations added in 2016–2019 (Table S1). To explore the food availability of great knots in the nearby alternative sites, we also sampled macrobenthos in Dawa site, Upper Liaodong Bay meta-site, which is 45 km from Gaizhou site. Eight transects with 48 sampling stations (500 m apart) were sampled in May from 2016 to 2019 inclusive (Fig. 2d).

At each station, one core sample (diameter 15.5 cm, 20 cm in depth)

was collected and then washed through a 0.5 mm sieve (Peng et al., 2021). All samples were kept frozen until identification and measurement in the laboratory. We only included molluscs and one brachiopod species *Lingula anatina* (which has a similar morphological and functional role as a bivalve, expressed as “mollusc” hereafter) in our analysis because molluscs comprised >99 % of the diet of great knots at Yalu Estuary meta-site (Choi et al., 2016). All molluscs were identified to species and size (the longest measurement) measured (to 0.01 mm) (see Zhang et al., 2019).

To measure intake rates during low tide, focal great knots were chosen randomly from a flock of foraging birds and then watched for 5 min with a 20–60× zoom-telescope. Before the start of each 5-min observation bout, the date, time, and location were noted. At Beijingzi site, during each observation bout, activities such as pecks, probes, items swallowed and interference with other individuals were recorded on digital voice recorders (2011 and 2012), while we used digital video cameras to record all behaviours in 2016. Foraging observations were conducted from early April to early May of each year of 2011, 2012 and 2016, but not 2013–2015. The digital sound files were transcribed using JWatcher 1.0 (Blumstein et al., 2006), which allowed us to quantify the time a bird spent on different activities. We used BORIS software (Friard and Gamba, 2016) to transcribe behaviours on video. At Gaizhou site, all the recordings were conducted by digital video cameras from late April to early May in 2015–2019, and processed in BORIS. Because food selection was easily observed from the videos, we identified ingested prey to species level, except for the few times that great knots ate polychaete worms (<0.1 % of total prey biomass ingested).

Intake rates of great knots at Beijingzi site were obtained from Zhang et al. (2019). By using the composition of the prey size from dropping analysis (described in Zhang et al., 2019) and video analysis, and the regression of size-species ash-free dry mass (AFDM), based on the species and numbers of prey taken by great knots, and the relationship of size-species AFDM, we calculated AFDM intake rate per unit time (see Zhang et al., 2019 for details). At Gaizhou site, we assessed the size of food by using the mean size of each species at this site (Zhang et al., 2019). The species and numbers of prey taken by great knots were obtained from the foraging videos, then using the relationship of size-species AFDM, we calculated the intake rate for each year. For each mollusc species at both Beijingzi and Gaizhou sites, the size – AFDM relationship was obtained from the data in Zhang et al. (2019).

Least squares linear regressions were used to test the correlation between peak numbers of great knots and food density, and intake rate of great knots and food density at both Beijingzi and Gaizhou sites. Because the distribution of macrobenthos on an intertidal mudflat is not uniform (Compton et al., 2013), there will be some hotspots with very high densities and some areas with very low densities. The peak number and the intake rate of great knots cannot be linked to the specific food density of a sampling station, so we used the average food density for the corresponding year for the least squares linear regressions. We log-transformed the density before regression because of the large range of macrobenthos densities. The significance level was set at 0.05.

2.5. Satellite tracking

From September to October in 2014, 2015, and 2016, we deployed 4.5 g solar Platform Terminal Transmitters (PTTs, Microwave Telemetry) onto 63 adult great knots at Roebuck Bay, Broome, in Northwest Australia. PTTs were attached with a body harness (Chan et al., 2016) made of elastic nylon. This work was carried out under Regulation 17 permits SF 010074, SF 010547 and 01-000057-2 issued by the West Australian Department of Biodiversity, Conservation and Attractions.

PTTs were programme with a duty cycle of 8h on and 25 h off. On average, 6 locations were received per 8-hour transmission. The tags that ceased transmission could be resulted from tag loss, as the harness made of elastic nylon degraded after 1-2 years. Other causes include the death of the bird or tag malfunctioning.

2.6. Movement between staging sites

We used the Douglas-filtered tracking locations (Douglas et al., 2012) as reported by Chan et al. (2019), where all standard locations (estimated error radius <1500 m i.e., location classes 3, 2 and 1) were retained, and all implausible auxiliary locations (i.e., location classes 0, A, B and Z) were removed. Only “stationary” locations were used in the spatial analyses in this study, therefore, all locations >50 km away from the shoreline, and/or birds moving in one direction at >20 km/h were excluded (Chan et al., 2019). Since Argos PTTs do not record the ground speed, we calculated the speed based on the interval between two consecutive fixes. A fix was considered as a stationary location if the speed was <20 km/h. Those places where a tracked great knot stopped for >72 h were regarded as staging sites, where birds feed for refueling rather than only for rest and maintenance activities (Warnock, 2010).

We checked the locations of tracked birds to determine the use of “site” and the movement of individuals between “sites”. Since the habitat use of great knots is not distinctly site-specific, birds rarely utilize only one of the sites. This raises the question of whether traditional “site” definitions effectively covered the habitat utilization of great knots. We calculated the home range of each great knot at its key staging meta-sites in the Yellow Sea to determine their local habitat utilization, and to assess the rationalization of the defined sites in representing the habitat use. Home range was assessed as a fixed kernel density estimator (KDE; 95 % probability contours; Seaman and Powell, 1996). R package adehabitatHR (Calenge, 2011) was used, and the kernel smoothing parameter was optimized by visual inspection, with those location fixes well beyond (2 km away) the lowest waterline and the shoreline were excluded, with $h = 1000$ determined to be the most suitable to show their home range size.

All great knots tracked to the latitudes of the Yellow Sea ($n = 27$) utilized the Yellow Sea for refueling during northward migration, however we lost the signal from two of these birds before late May (the time that they would be expected to leave the Yellow Sea to their breeding grounds) and one stayed in the Yellow Sea until mid-June when migratory great knots should be on their breeding grounds (note that in the absence of competitors, its movements should be little affected by food and will be different from that of individuals in April and May). These three birds were excluded from our analysis. We defined an area that supports tagged great knot(s) as the last staging area in the Yellow Sea as a ‘key’ staging area, because it is usually where the most pre-migratory fueling takes place, and thus has the potential to impact on migration (Warnock, 2010; Ma et al., 2013). Nine key staging meta-sites were identified (Fig. 1). Given the tag attachment harness often broke after one year, or individuals may give up migrating north in some years, we only have tracks for one spring for all tagged birds, so although some birds tagged in 2016 still survived in 2018, we only have data for one spring migration. All birds were tagged at the same site in Northwest Australia, therefore the tagging site should not influence the choice of staging site in the Yellow sea. The tracking data we analyzed in the study were collected from 2015 to 2017. In our analysis of where great knots went during food shortage at Gaizhou, two birds that staged at Gaizhou in 2015 was excluded because the food was abundant in Gaizhou site that year (Fig. S2).

To explore the responses of great knots to food shortage at the two most important staging sites (Beijingzi and Gaizhou), we tracked the change in the number of birds (bird count data), intake rate (observation data), and food availability (benthos data) at these two sites and summarized the movements (tracking data) between key staging sites, after tagged great knots left the Beijingzi and Gaizhou respectively when food was scarce. Since individuals utilized different sites in Upper Liaodong Bay and Yalu Estuary meta-sites at different tide heights (e.g. individuals foraging at Gaizhou site may roost at Yingkou site during high tide when mudflats were submerged), only when great knots left Gaizhou or Beijingzi and never returned to the site to forage (locations recorded within 3 h before and after low tide), were they considered as individuals that

left Gaizhou or Beijingzi. Only the first landing site after great knots left Beijingzi and Gaizhou was used to explore the distance moved to an alternative site to respond to the food shortage. The distance moved by individuals switching staging sites is the straight-line distance between the geometric centre of the original study site and the centre of the alternative site. Note that within the Yalu Estuary meta-site only the Beijingzi site had abundant food (Zhang et al., 2018 and 2019), so tracked great knots had no reason to shift location within the Yalu Estuary meta-site.

3. Results

3.1. Food availability

At the Beijingzi study site in the Yalu Estuary meta-site, 13 mollusc species were recorded. The highest density of available prey was in 2011 (Table S2, Fig. 3a). From 2011 to 2016, the densities declined by >95 % (lowest in 2013, Table S2, Fig. 3a). Sampling in the remaining area of the Yalu Estuary in 2013, 2015 and 2016 showed that mollusc densities in these areas were as low as those at Beijingzi (Table S2, Fig. 3d).

At Gaizhou site in the Upper Liaodong Bay meta-site, 17 mollusc species were recorded. The mollusc density was highest in 2015; from 2015 to 2018 the mollusc density decreased by >99 % (Table S2, Fig. 3h), but recovered a little in 2019 (Table S2, Fig. 3a). At Dawa, by contrast, 12 mollusc species were recorded. The total mollusc density varied greatly from 2016 to 2019, with a marked peak in 2017 (Table S2, Fig. 3h).

3.2. Bird abundance and food intake rates

At Beijingzi site the northward migration peak number of great knots ranged from 27,960 to 74,900, with the highest abundance being recorded in 2013 and the lowest abundance in 2014 (Table S2, Fig. 3c).

The most dramatic change was found in the number of birds, which declined 29 % from 42,357 (2011) to 29,938 (2016), but there was no clear linear trend (Table S2, Fig. 3c). At the Beijingzi site the overall average intake rate of great knots was highest in 2011 and lowest in 2016 (Table S2, Fig. 3b). At Gaizhou site, from 2015 to 2019 the northward migration peak numbers of great knots declined, and showed the greatest change between 2015 (60,000 birds) and 2018 (5120 birds), a decline of 91 % (Table S2, Fig. 3g). The intake rate was highest in 2015, and lowest in 2018 (Table S2, Fig. 3f), a decline by 87 %.

3.3. Individual changes in the use of key staging sites

In both the Yalu Estuary and Upper Liaodong Bay meta-sites we monitored macrobenthos, intake rates and bird numbers. From 2016 to 2017, seven satellite-tracked great knots (in different years) utilized the Yalu Estuary meta-site (Fig. S3). Their mean home range size was $350 \pm 100 \text{ km}^2$ ($n = 7$), and all these seven birds utilized (foraged at) Beijingzi site; four of them (57 %) left Beijingzi but did not move to elsewhere within the Yalu Estuary meta-site, instead they moved to other remote alternative staging sites (or meta-sites) in Upper Liaodong Bay, North Korea (not in the Yalu Estuary) or South Korea (Fig. 4a). Among the individuals that left Beijingzi site, one moved 50 km west, but subsequently it stopped sending signals. The average distance moved by the other three individuals was $179 \pm 74 \text{ km}$ (range from 124 to 264 km, $n = 3$) (Fig. 4).

In contrast, 12 tagged great knots (in different years) staged in the whole Upper Liaodong Bay meta-site from 2015 to 2017 (the one bird remaining at Upper Liaodong Bay in June was excluded from the analysis), the mean home range size was $299 \pm 143 \text{ km}^2$ ($n = 12$), no significant difference from home range in the Yalu Estuary meta-site ($t = -0.9$, $df = 16.5$, $p = 0.37$). Among these, three birds only utilized one of the five sites, six birds used two sites, two birds used three of the sites, and one bird used all of the five sites in Upper Liaodong Bay (Table S3,

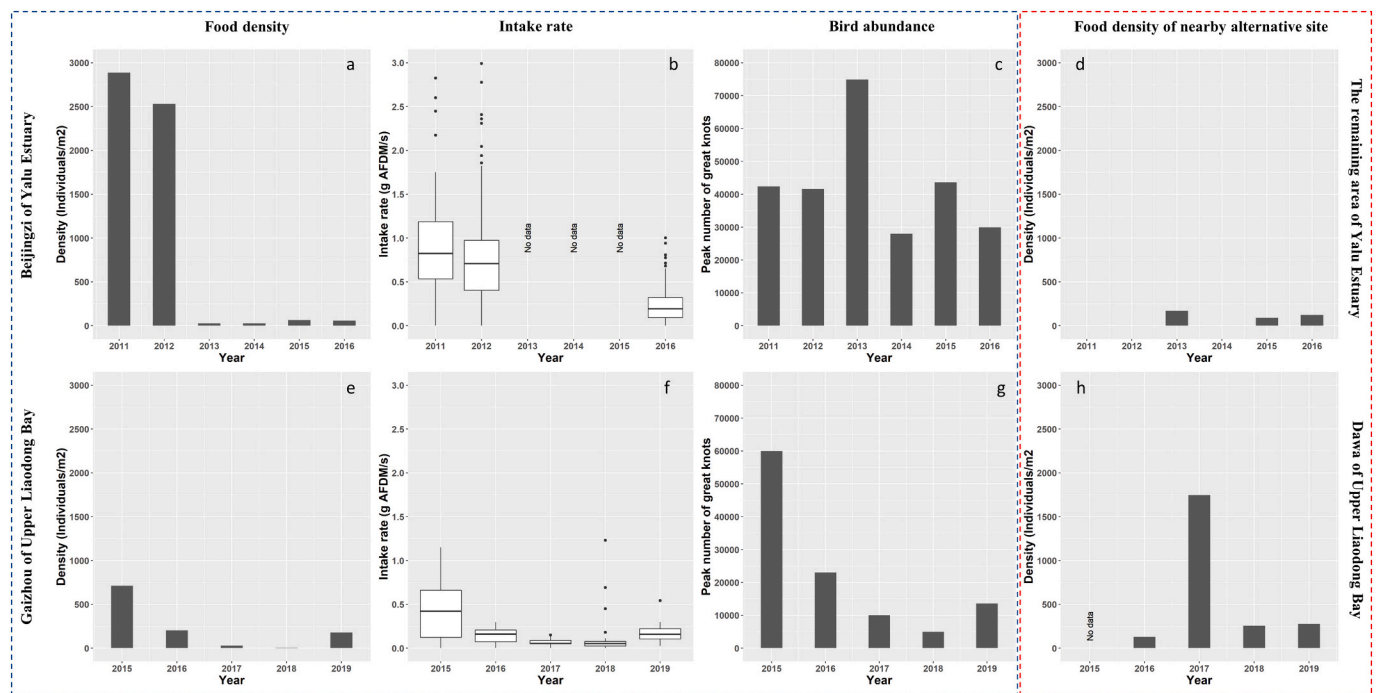


Fig. 3. Responses of bird abundance and intake rate of great knots to the variation of food density at Beijingzi and Gaizhou sites. a-c) Food density, intake rate and bird abundance of great knots from 2011 to 2016 at Beijingzi site, Yalu Estuary meta-site; d) Food density from 2011 to 2016 in the remaining area of the Yalu Estuary; e-g) Food density, intake rate and bird abundance of great knots from 2015 to 2019 at Gaizhou site, Upper Liaodong Bay meta-site. h) Food density from 2015 to 2019 at Dawa site, Upper Liaodong Bay meta-site. Only Bivalvia, Gastropoda and Brachiopoda were included as potential food items. For Beijingzi site, the data are shown from 2011 to 2016 (inclusive); in the remaining area of the Yalu Estuary meta-site, the data are shown for 2013, 2015 and 2016. For Gaizhou site, the data are shown from 2015 to 2019 (inclusive); for Dawa site, the data are shown from 2016 to 2019 (inclusive).

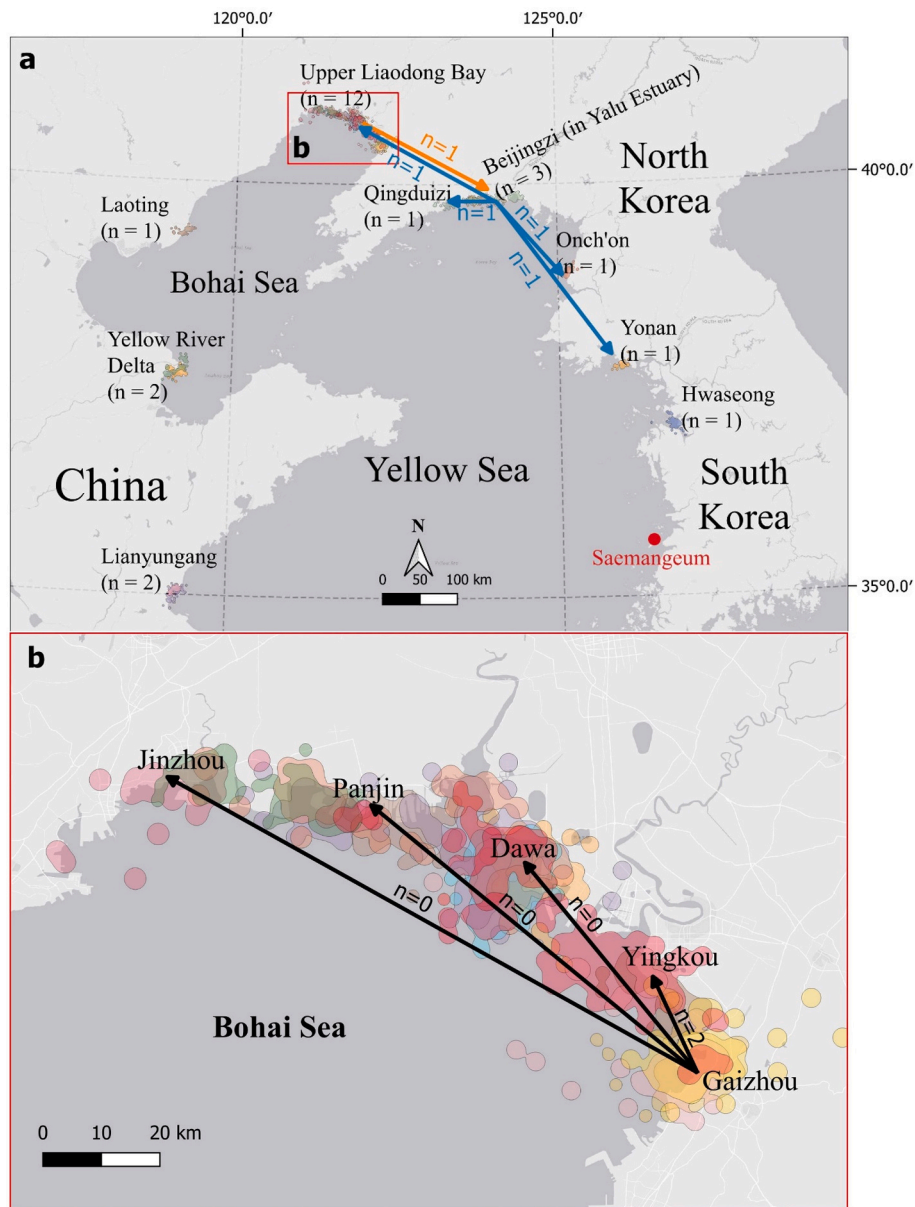


Fig. 4. Movements of great knots between the key staging areas in the northern Yellow Sea. Colour patches show the home range of each individual great knot at their key staging site (or meta-site, a combination of high-quality neighbouring sites). a) The changing of staging meta-sites of great knots after they refueled at the Yalu Estuary and Upper Liaodong Bay. The blue arrows show the directions of great knots which left the Yalu Estuary meta-site to another (meta-) sites; the orange arrow shows the direction of a great knot which left Upper Liaodong Bay to another (meta-)sites. b) The plot shows the first alternative site great knots depart to within the Upper Liaodong Bay meta-site. Black arrows show the direction of site changes, and the number of tracked birds was showed along with arrows, $n = 0$ means no tracking birds moved from Gaizhou site to that site. The numerical values under the name of each staging (meta-) sites (e.g. $n = 12$ in Upper Liaodong Bay), represent the numbers of birds that used the (meta-) site before migrating to the breeding grounds. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. S2). Only 1 of 12 individuals left Upper Liaodong Bay to Yalu Estuary meta-sites and stayed there until migration to the breeding ground (Fig. 4a). Four tracked great knots utilized Gaizhou site (in different years). Three of them were present in 2016 and 2017 when food availability was low; two were present in 2015 when food availability was high, they were excluded from the following analysis. Of these three tracked birds, after staging for 21 ± 2 days (range from 19 to 22, $n = 3$), two of them (67 %) moved 20 ± 0 km to the alternative site Yingkou (still within Upper Liaodong Bay); the third bird remained at Gaizhou site, using it as the last staging site before onward migration.

3.4. How great knots responded to the food decline in their staging sites

At Beijingzi site, when food density declined >95 %, the intake rate of great knots significantly decreased by 87 % (mollusc density was log-transformed, $r^2 = 0.19$, $F = 93.4$, $p < 0.001$), but the abundances of great knot only declined 29 % ($r^2 = 0.01$, $F = 0.02$, $p = 0.90$). During the staging time in the Yellow Sea, four of seven (57 %) tracked individuals left Beijingzi site; none of these departed birds moved to a nearby site within Yalu Estuary meta-site, where food availability was also low (Table S2, Fig. 3d). All birds that departed moved to other sites at least 120 km away (Table 2).

In Gaizhou site, when food density declined >99 %, the intake rate of great knots significantly declined 87 % ($r^2 = 0.17$, $F = 42.15$, $p < 0.001$).

Table 2

Overview of changes in food abundance, intake rate, bird abundance and numbers of tracked birds at each study (meta-) site. “↓” showed the proportion of decline.

Items	Beijingzi	Gaizhou
Food abundance at site	95 %↓	99 %↓
Food intake rate	87 %↓	87 %↓
Food abundance around site (in meta-site)	Low	High
Bird abundance at site	29 %↓	91 %↓
Tracked birds		
Departed from site	57 % (4 of 7 birds)	67 % (2 of 3 birds)
Distance to the closest alternative site used	124 km	20 km
Mean home range size in meta-site	350 km ²	299 km ²
Left study site but stayed within meta-site	0	100 %
Left meta-site	Yalu Estuary	Upper Liaodong Bay
	57 % (of 7 birds)	8.3 % (of 12 birds)

In contrast to Beijingzi site, the number of great knots declined by 91 % ($r^2 = 0.97$, $F = 147.2$, $p = 0.001$).

4. Discussion

Migratory birds may adaptively respond to food changes at staging sites (or meta-sites) by adjusting their length of stay at any one site, by shifting between sites or by adjusting their diet and their digestive apparatus (Robson and Barriocanal, 2011; Verkuil et al., 2012; Rakhimberdiev et al., 2018; Zhang et al., 2019). Because they have to cope with changes in several different areas along the migration route, changes in a single site are likely to have cross-seasonal effects along the entire migration route (Piersma, 1987; Saura et al., 2014; Senner et al., 2015; Xu et al., 2020). Our study showed that the decline of food resources resulted in a significant reduction in the intake rate of great knots at both Beijingzi and Gaizhou. However, the abundance of great knots decreased as mollusc density decreased at Gaizhou, but not at Beijingzi. We also monitored the food density at sites near Gaizhou and Beijingzi, and some alternative sites that the tracked birds moved to. This comparison showed that the difference in numerical and movement response between great knots at Gaizhou and Beijingzi may be explained by the distance to alternative high-quality sites. At Gaizhou, birds only had to fly 20 km to find alternative food-rich sites (within the Upper Liaodong Bay meta-site) and they did. However, at Beijingzi there were no food-rich alternative sites within the Yalu Estuary meta-site, so the tracked birds flew at least 124 km to find an alternative site (concluded in Table 2 and Fig. S1).

The monitoring of food resources in both the Yalu Estuary and Upper Liaodong Bay meta-sites showed that the whole Yalu Estuary meta-site was lacking food, but geographic variability in year-to-year food abundance within the Upper Liaodong Bay meta-site meant that great knots relying on Gaizhou site could find alternative food close by (only six of 12 tracked great knots utilized Dawa site although food was always good in this site, and three of these six individuals only utilized the Dawa site briefly, suggesting that the food at other unsurveyed sites in Upper Liaodong Bay may be good as well). Indeed, 92 % of the tracked great knots staging in Upper Liaodong Bay kept using multiple close sites during local food shortages. In contrast, when food was scarce at all alternative sites within the Yalu Estuary meta-site, only 43 % of tracked great knots refueling at this meta-site were not alter staging site. The potential searching range which increased with the distance between alternative high-quality sites (for unfamiliar environments, it is unlikely that birds can fly directly to alternative sites where food is available, they need to search the entire area), resulting in distance limits the shift of staging sites for great knots when food declined, most of the great

knots in Beijingzi site choose not to move to the alternative sites, with Onch'on in North Korea being the closest alternative at 124 km distance.

4.1. Is 124 km too far for great knots to move in response to food shortages?

Shorebirds are champions of long-distance, nonstop flights, the record being set by Bar-tailed Godwits *Limosa lapponica baueri* crossing the Pacific from Alaska to New Zealand in ca 12,000 km nonstop flights (Gill Jr. et al., 2009; Battley et al., 2012). Some great knots make flights of >5000 km or more from Northwest Australia to the Yellow Sea (Battley et al., 2000; Chan et al., 2019). In view of these enormous migration distances, if birds have perfect information on the availability and distribution of alternative foraging sites, flying 124 km would be an easy task.

However, the selection of migration routes and habitats of migrants is mainly based on knowledge, which may be acquired from conspecifics or accumulated through previous migrations (Doligez et al., 2002; Danchin et al., 2004; Németh and Moore, 2007; Newton, 2007). A bird's familiarity with habitats and routes will reduce energy expenditure and risks during exploratory trips (Doligez et al., 2002; Bijleveld et al., 2010), this may be the reason why there were still many great knots using Beijingzi and Gaizhou after food availability declined by 87 %. In fact, at Beijingzi the numbers were even a little higher in the food-scarce years of 2015 than in the food-rich years of 2011 and 2012. Furthermore, the number of great knots in 2013, when food was scarce, was double that of previous years (2011 and 2012) when food was abundant. This was most likely because of the information sharing among birds. In 2012, the main food of the great knot in Beijingzi site, *Potamocorbula laevis*, was distributed on the surface of the sediment rather than within the substrate in 2012, and shells were open, allowing birds to feed directly on the meat rather than swallow shellfish whole (Zhang et al., 2018). This made it easier to feed and reduced the energy costs of cracking shells in the birds gizzard. This may have led the great knots to mistakenly believe that local food had become abundant and extremely palatable, and this message was passed on to other individuals, resulting in lots of great knots using Beijingzi in 2013. However, the experience and knowledge that a shorebird previously gained may no longer be usable due to the rapid habitat loss and degradation of intertidal flats in the Yellow Sea (Murray et al., 2014). It is unlikely that birds hold much information on the quality of distant and unfamiliar staging sites.

Experienced adult great knots encountering food scarcity may now be facing the same problems of lack of knowledge as those migrating for the first time, although shared information may reduce some of the extra energy required for searching by filtering useful information (Bijleveld et al., 2010). However time appears too short for great knots to build up sufficient information about potential alternative sites at the individual level, especially considering the constraints imposed by refueling and the pressure to reach the tundra breeding grounds (Drent et al., 2003; van Gils et al., 2016; Rakhimberdiev et al., 2018). Therefore, compared to 20 km, 124 km will make more great knots remain rather than leave in response to food shortages. The fact that alternative sites used by great knots were much closer for the Gaizhou birds than those at Beijingzi would explain why more great knots left Gaizhou site than Beijingzi site.

4.2. Spatially comprehensive surveys to assess the changing quality of habitats

Bird counts play an important role as the criterion to judge site quality for waterbirds (e.g. BirdLife International, 2006). However, our study and that of Zhang et al. (2018) demonstrate that relying solely on surveys of bird numbers can be misleading when it comes to assessing the quality of habitat. In fact, stable numbers may still mask food problems, thereby leading to lags in the implementation of remedial conservation management and protective actions. Therefore, to ensure

adequate knowledge to underpin the protection of bird habitats, simply using bird counts, which are relatively easy to undertake, may be inadequate. Ideally, we need a combination of information on numbers, distributions, but also food availability (Tucker et al., 2022), while satellite tracking will give us spatially unbiased information on the way that birds respond to the documented changes (this study).

4.3. The application: protecting meta-sites rather than single sites

A 'site' is usually defined as an area where an organism lives (IUCN, 2016). Migratory birds move between breeding and non-breeding areas with different environments and climates, with stopping sites in between (e.g., Verhoeven et al., 2021). Typically, we define a site based on the aggregation of birds and the connectedness of habitats, e.g., by the activities of the birds (Clemens et al., 2014). A site is usually separated from other sites by natural barriers such as rivers or man-made structures.

The site concept has served us well in bird conservation, as we were better able to develop effective conservation measures and effective recovery measures within a defined area (IUCN, 2016). However, with the development of individual tracking techniques, it was found that birds not only moved within a defined area (Choi et al., 2019), but there are large variations between individuals in how they use a site, with most individuals utilizing only part of a given site (Choi et al., 2019). Birds also often frequently move between closely neighbouring sites. When local feeding conditions decline and birds have to move away (van Gils et al., 2006; Kraan et al., 2009), the use of nearby alternatives may prevent declines in survival (Bijleveld et al., 2014; Bowgen et al., 2022). Also in the present study, great knots could choose among different staging sites within the Upper Liaodong Bay meta-site for refueling before they flew to the alpine tundra breeding grounds. Although seven of thirteen tracked great knots utilized only one site within Upper Liaodong Bay, the other six individuals were supported by more than one single site for refueling and roosting (Fig. 4b).

The present findings on great knots emphasize the importance of the 'spatial grain' across which high-quality staging habitats are distributed. To better represent these necessary continuums of habitats, based on the traditional sites we recognized, we propose 'meta-sites' to represent these functionally complementary neighbouring sites. 'Meta-sites' are series of neighbouring sites that have complementary functions for a species or populations. Due to the rapid habitat loss and degradation in the Yellow Sea (Melville et al., 2016a; Piersma et al., 2016; Studds et al., 2017), timely conservation measures are imperative. A 'meta-site', e.g. the Upper Liaodong Bay, supported refueling great knots better, since problems at one site in the system could be partially mitigated by birds moving to other high-quality alternative sites close by. However, when high-quality alternative sites are too far away from sites that are destroyed or lose their food supply (as at Saemangeum and the Yalu Estuary, respectively) birds are likely to suffer constraints on feeding, fuel deposition and subsequently potentially lower survival rates (Zhang et al., 2021).

Author statement

The work is all original research carried out by the authors. All authors agree with the contents of the manuscript and its submission to Biological Conservation. No part of the research has been published in any form elsewhere. The manuscript is not being considered for publication elsewhere while it is being considered for publication in this journal. Any research in the paper not carried out by the authors is fully acknowledged in the manuscript. All sources of funding are acknowledged in the manuscript, and authors have declared any direct financial benefits that could result from publication. All appropriate ethics and other approvals were obtained for the research.

CRedit authorship contribution statement

He-Bo Peng: Writing – original draft, Visualization, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ying-Chi Chan:** Writing – review & editing, Investigation, Data curation. **Yingrong Huang:** Investigation, Data curation. **Chi-Yeung Choi:** Writing – review & editing, Investigation. **Shou-Dong Zhang:** Investigation. **Sicheng Ren:** Investigation. **Chris J. Hassell:** Investigation. **Zhenchang Zhu:** Writing – review & editing, Funding acquisition. **David S. Melville:** Writing – review & editing, Investigation. **Zhijun Ma:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Guangchun Lei:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Theunis Piersma:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

Data availability

Satellite tracking of great knots: data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.f2g5f49> (Chan, Tibbitts, Lok, 2019). Other data can be found in Supplementary Materials.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110547>.

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