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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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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 to 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 subspecies (*piersmai*). Based on data from tagging of Red Knots on the terminal non-breeding grounds in northwest Australia with 4.5- 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* subspecies 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 onwards. Southward departures mainly occurred in the last week of July and the first week of August. We documented six non-stop flights of over *c.* 5000 km (with a maximum of 6500 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

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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 subspecies 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.

Keywords: East-Asian Australasian Flyway, migration, population regulation, seasonal timing, shorebirds, staging.

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 metres of bookshelf, but the field has been 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.* 2006, 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.* 1993, 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.* 2005), 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 geographical 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 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 3 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. make 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 Eighty 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, 2019b, Peng *et al.* 2021). 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 the 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, Chan *et al.* 2019b, Lok *et al.* 2019). Red Knots were captured using cannon-nets at the northern beaches of Roebuck Bay, Broome (17°48′58″S, 122°17′60″E) and at Eighty Mile Beach (19°20′24″S, 121°24′36″E), both located in NW Australia (see Table 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 2 years) were selected for tagging. Due to incomplete breeding plumages at the time of year the birds were captured, we were unable to confirm subspecies identity, but we should have been picking mostly *piersmai* as it outnumbers *rogersi* in NW Australia (see Rogers *et al.* 2010, Verhoeven *et al.* 2016). All birds were marked with an Australian Bird and Bat Banding Scheme (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 Platform Terminal Transmitters (PTTs) (Microwave Telemetry, Inc., Columbia, MD, 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 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 of 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). 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 h. 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 because of 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, although some other problems remained. 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 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 and 1; for details on Argos location classes see CLS 2016) were retained, whereas 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 2 h 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°54′N and 42°30′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 was 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., Wareham, UK; see Table 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.* 2016) attached to a leg of the Red Knots. The combined mass of flag and geolocator was *c.* 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, while the other one yielded information for 2 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 in February 2020. Only the former yielded reliable information of the return migration in 2015 (see Table 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 geographical 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 geographical information when compared with 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 the coast of China

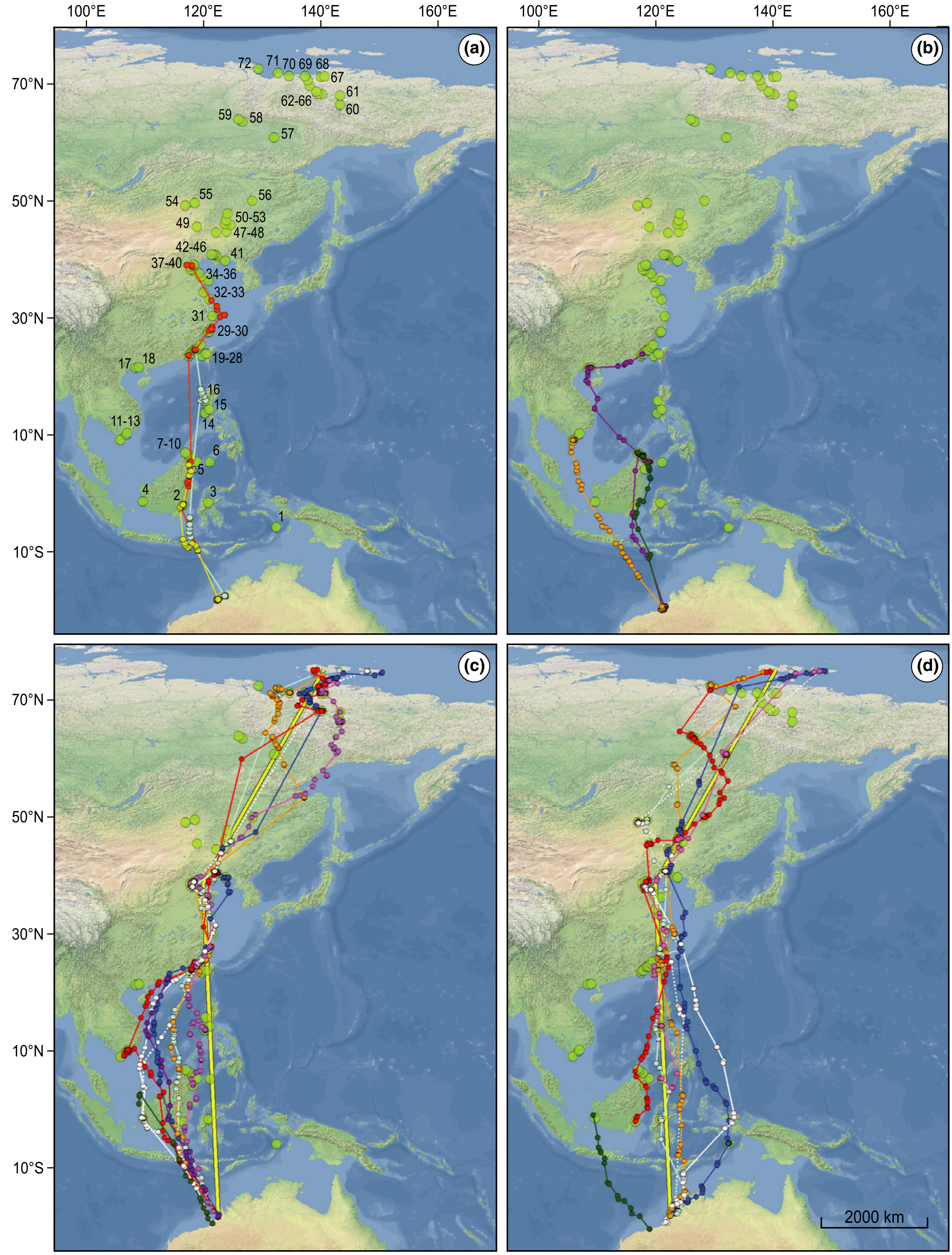
From early April to late May 2018, we sampled the preferred benthic food of Red Knots, *P. laevis* (Yang *et al.* 2013), at 18 intertidal flats along the coast of China known to have shorebirds utilizing them during migration (Chan *et al.* 2019b), extending from Dongliaodao, Guangdong Province, in the far south (20°49′30″N, 110°23′02″E) to Panjin, Liaoning Province, in the far north (40°45′47″N, 121°51′36″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 sample adequately 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°24′27″N, 117°51′06″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 individual's stops are 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. 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. 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 2 weeks on the Kalimantan coast just southwest 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


100°E
120°E
140°E
160°E
70°N
50°N
30°N
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(a)
(b)
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32-33
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29-30
19-28
17
18
16
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14
11-13
7-10
6
5
4
2
3
1
2000 km

Figure 1. A summary of all migratory tracks recorded by PTTs in Red Knots marked in NW Australia between 2011 and 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 migrations combined. All sites are plotted in all four panels, with the numbers in panel (a) corresponding to additional information of the sites in Table S3. These stopping sites were calculated by means of grouping all individual stopping sites (see Methods for definition) within a 10-km radius. The yellow lines in (c) and (d) represent the shortest, great circle, routes between Roebuck Bay in NW Australia and Bohai Bay in the Yellow Sea and between the Yellow Sea and New Siberian Islands. With respect to the birds marked in early 2018, Table 1 presents details on timing, number of stopping sites used, length of non-stop flights and detours. In (c) and (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 1) only migrated as far as westernmost Kalimantan, returning from there to NW Australia. For Red Knot 48953 (in purple; not in Table 1) transmissions stopped during northward migration at the Chinese coast.

northwest of Sandakan. We lost contact on 8 May while the bird was 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. 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. 1c,d). The other six made complete migrations to the New Siberian Islands (Table 1, Fig. 1c,d). In the case of the bird carrying transmitter 48950 (coloured white in Fig. 1c, 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. 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. 1c,d), most Red Knots took a longer route by initially flying north-westwards. 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. 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 6500 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. 1). Once in the Yellow Sea, the birds stopped at one to four different sites (Fig. 1, Table 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, at either the coast of Bohai Bay, Hebei and Tianjin Municipality, or in upper Liaodong Bay, Liaoning (Fig. 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 one to five 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 (38°24′27″N, 117°51′06″E; see Fig. 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 of 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; the other birds made one to three 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 1).

Table 1. Timing, number and duration of stops, and maximum non-stop 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[a]	48950[b]	48950-2[b] yr	48937[c]	48936	48905[d]	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 Mar.	16 Feb.		16 Feb.	16 Feb.	01 Mar.	01 Mar.
Tracking year	2018	2018	2019	2018	2018	2018	2018
From NW Australia to Yellow Sea							
Date of departure from NW Australia	24 Apr.	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 Jun.	8 Jun.	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 Jun.	11 Jun.	7 Jun.	23 Jun.	24 Jun.	2 Jun.	3 Jun.
Date of arrival at New Siberian Islands	8 Jun.	?	12 Jun.	27 Jun.	29 Jun.	8 Jun.	8 Jun.
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 Jul.	30 Jul.	3 Aug.	27 Jul.	30 Jul.
Date of arrival in Yellow Sea	15 Aug.	signal from 10 Aug.	30 Jul.	18 Aug.	16 Aug.	31 Jul.	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 Sep.	3 Sep.	28 Aug.	17 Sep.	21 Sep.	27 Aug.	31 Aug.
Number of detected stops *en route*	3	0	0	1	1	1[e]	3
Date of arrival in NW Australia	–	9 Sep.	3 Sep.	–	26 Oct.[f]	12 Sep.	3 Oct.
Flight lengths							
Longest non-stop 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 non-stop flight during southward migration (km, days)	–	–	6548, 6.6	–	5540, 4.2	4914, 4.9	3352, 2.7

[a] Transmissions stopped during southward migration on 6 November during a stopover at Siasi Island, Sula, Philippines. [b] Did not transmit any locations from its departure from the Yellow Sea to its return there in 2018, but gave a full track in 2019. [c] Transmission stopped on 16 November during southward migration during a stopover in a bay just southwest of Balikpapan, East Kalimantan, Indonesia. [d] 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. [e] Staged in western Taiwan from 28 August to 7 September where it was seen and photographed by C.-Y. Choi. [f] 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. 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 to 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 (*c*. 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 to 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 1, Fig. 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 days in southeast Asia and southern China (5.5 days per site), and 13.8 days in the Yellow Sea (5.4 days per site). Departures from the Yellow Sea occurred between 2 and 23

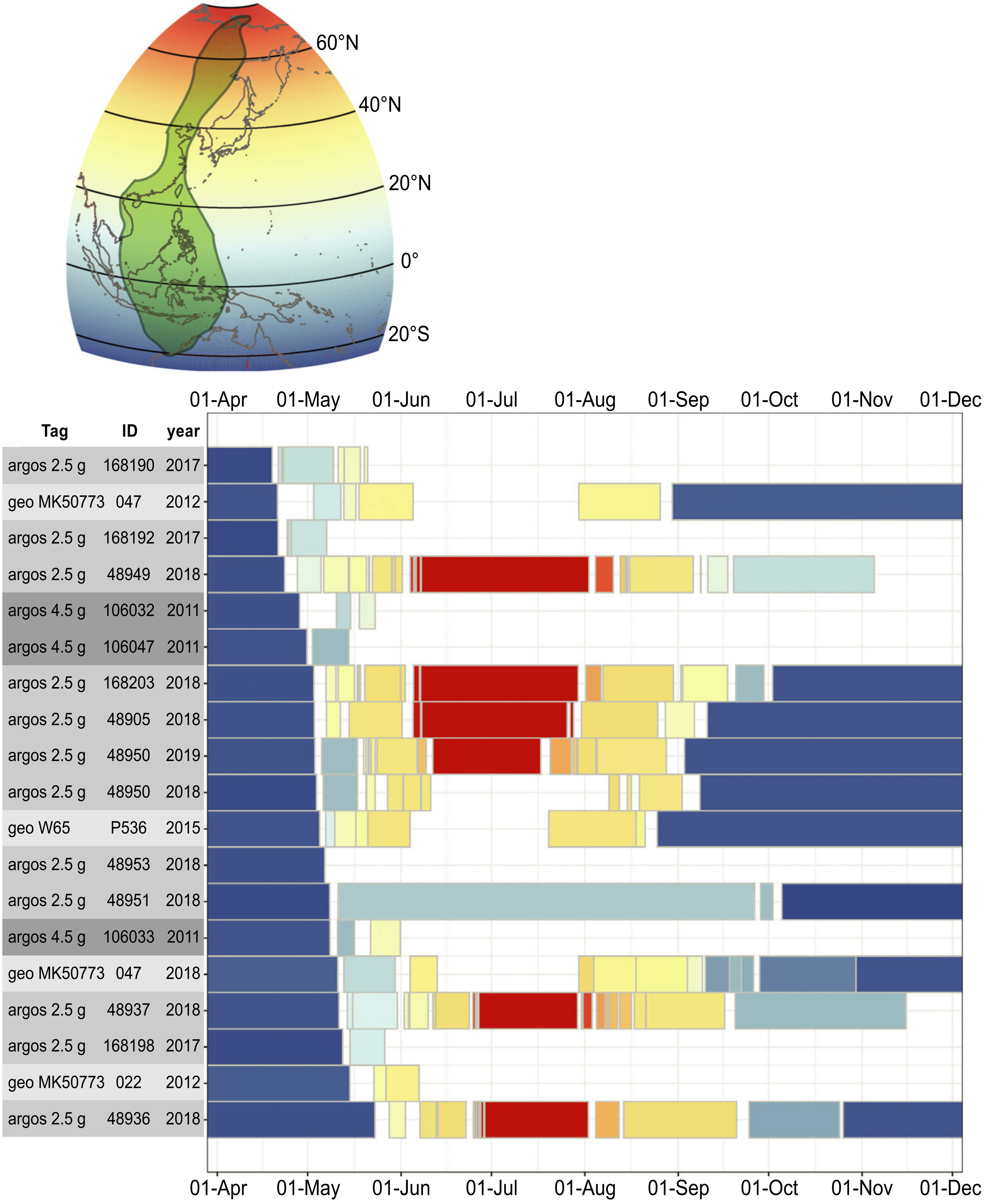

Figure 2. Summary of the timing of migration as indicated by the presence at different latitudinal bands in 19 tracks by 17 Red Knots tagged in NW Australia with three different methods differentiated in grey shades. In 2011 we obtained results from three birds with glued 4.5-g PTTs (dark shade), in 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 to 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 S1. Stationary periods are coloured by the latitude at which they occurred according to the colour-gradient presented in the inset. The tracks are arranged from earliest to latest migratory departure from NW Australia.

June. Arrival on the New Siberian Island tundra breeding grounds occurred during 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 and the latest on 26 October.

All three types of tracking devices yielded the same pattern of timing of Red Knots reaching different latitudes (Fig. 2), with no clear clustering of different devices with respect to either departure or arrival dates. The three geolocator tracks that yielded sufficient information regarding the entire migratory period (047, 022 and P536; Fig. 2) confirmed that staging in the northern Yellow Sea was much longer during southward than 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 macrozoobenthos in spring 2018, we found the bivalve *P. laevis* at 14 sites (Fig. 3, Table S2). Not all the sites where *P. laevis* was found were used by the tracked Red Knots but *P. laevis* was found at all seven sites where they did stop during northward migration (including the longest used sites in Bohai and Liaodong Bays). At the five sites 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.

DISCUSSION

In this study we confirm that Red Knots from their terminal non-breeding grounds in NW Australia stop in the Yellow Sea region of China (especially Bohai and Liaodong Bays) during both northward and southward migration seasons, and 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. 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- and 2.5-g solar PTTs and 1-g geolocators; Fig. 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 5000 km (Conklin *et al.* 2017 used 5000 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 1000 km up the Chinese coast before making the first stop. Their northwestward, rather than northward great circle, bearings during departure from NW Australia are consistent with the visual onshore observations made as early as 1991 by Tulp *et al.* (1994) and Broome Bird Observatory data to 2021 (C. J. Hassell pers. obs.). This suggests that the departure directions in this study are similar to those in 1991, and that the Red Knots, by not stopping at the first suitable coastal site in southern China, were not running out of fuel upon arrival at the Chinese coast. In addition, individuals vary in their use of stops in Southeast Asia and southern China and this has consequences in the 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). This variation in the ways that individuals distribute their fuelling

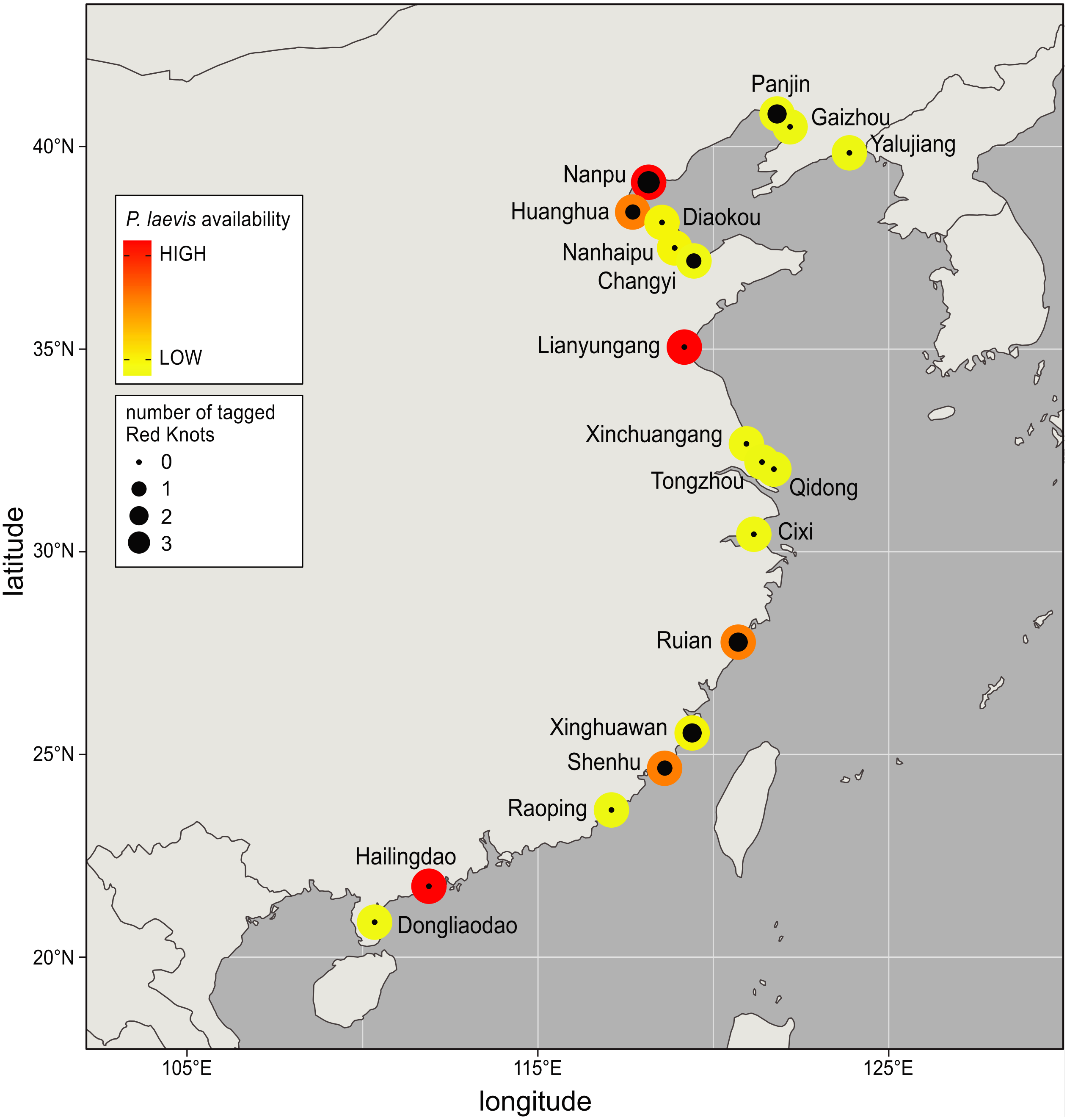

Figure 3. Intertidal sites along the coast of China with information on the availability of *Potamocorbula laevis*. The local availability of *P. laevis* was calculated by multiplying local density with the average size at that site. The exact numerical prey densities and size classes and the number of tagged Red Knot occasions are presented in Table S2.

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. 1; see e.g. Niles *et al.* 2010, Newstead *et al.* 2013, Kok *et al.* 2020 for similar feats in other

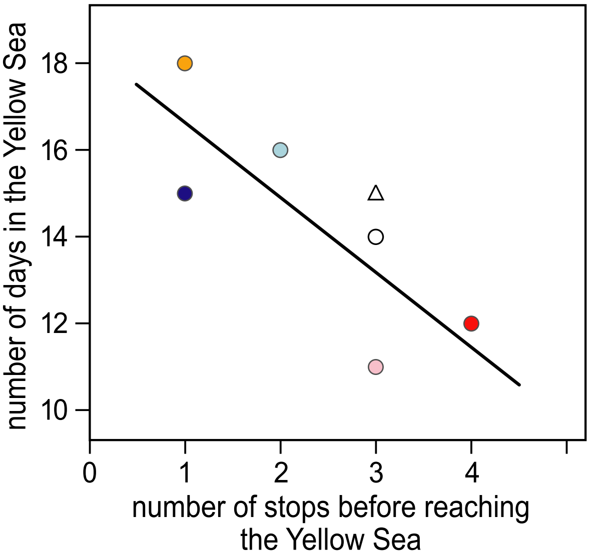

Figure 4. The number of refuelling days spent by six Red Knots in the Yellow Sea during northward migration as a function of the number of stops made previously *en route* from NW Australia to the Yellow Sea. Colours correspond to the colours of the tracks plotted in Figure 1c,d. The negative correlation ($r = -0.92$, $P < 0.01$) is based on the six points from 2018; the repeat point from 2019 is represented by a white triangle (see Table 1 for details).

Red Knot subspecies including the 8100-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. 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, 2019b). During the 3-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* subspecies achieved non-stop flight distances comparable to those by other subspecies during northward migration from NW Australia to the Yellow Sea (Table 1), contrary to the other subspecies, *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 suggested not only 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 compared with *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 S3, corresponding to the graphical listing in Fig. 1a.

This, then, invites the question of whether the recent reductions in the extent of suitable habitat in the Yellow Sea area (Murray *et al.* 2014, Piersma *et al.* 2016) have 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 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 larger two to three decades ago than now, and thus before the time of rapid intertidal losses due to land claims (Ma *et al.* 2014). 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 shellfish aquaculture on mudflats, which in fact could have increased the range and densities of *P. laevis* (Peng *et al.* 2021), and 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 ‘organizational’ changes to organs and body composition (Piersma 1998, Piersma *et al.* 1999, Hua *et al.* 2013) and the predation-related ‘safety’ gains from not having to fly with compromised manoeuvrability (van denHout *et al.* 2010). Equally, even in places where intertidal losses due to land claims have been small, variation such as 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, should a site would be lost to industrialization or other factors.

The ecological reasons for the occurrence of several stops in freshwater habitats during the migrations from the 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, Clemens *et al.* 2016, Piersma *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 places of death (Loonstra *et al.* 2019) will reveal 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.

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AUTHOR CONTRIBUTION

Theunis Piersma: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal);

Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing-original draft (lead); Writing-review & editing (lead). **Eva M. A. Kok:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Writing-original draft (equal); Writing-review & editing (equal). **Chris J. Hassell:** Investigation (equal); Methodology (equal); Project administration (equal); Writing-review & editing (supporting). **He-Bo Peng:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing-original draft (supporting); Writing-review & editing (supporting). **Yvonne I. Verkuil:** Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Writing-review & editing (supporting). **Guangchun Lei:** Funding acquisition (equal); Methodology (equal); Project administration (equal). **Julia Karagicheva:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Writing-review & editing (supporting). **Eldar Rakhimberdiev:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal). **Paul W. Howey:** Investigation (equal); Methodology (equal). **T. Lee Tibbitts:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (equal); Writing-original draft (supporting); Writing-review & editing (supporting). **Ying-Chi Chan:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (supporting).

Data Availability Statement

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 with co-authors T.L.T. or Y.C.C.

REFERENCES

Battley, P.F., Rogers, D.I., van Gils, J.A., Piersma, T., Hassell, C.J., Boyle, A. & Yang, H.-Y. 2005. How do Red Knots *Calidris canutus* leave Northwest Australia in May and reach the breeding grounds in June? Predictions of stopover times, fuelling rates and prey quality in the Yellow Sea. *J. Avian Biol.* **36**: 494–500.

Bijleveld, A.I., MacCurdy, R.B., Chan, Y.-C., Penning, E., Gabrielson, R.M., Cluderay, J., Spaulding, E., Dekinga, A., Holthuijsen, S., ten Horn, J., Brugge, M., van Gils, J.A., Winkler, D.W. & Piersma, T. 2016. Understanding spatial distributions: Negative density dependence in prey causes predators to trade-off prey quantity with quality. *Proc. R. Soc. B* **283**: 20151557.

Bijleveld, A.I., van Gils, J.A., van der Meer, J., Dekinga, A., Kraan, C., van der Veer, H.W. & Piersma, T. 2012. Designing a benthic monitoring programme with multiple conflicting objectives. *Methods Ecol. Evol.* **3**: 526–536.

Bodey, T.W., Cleasby, I.R., Bell, F., Parr, N., Schultz, A., Votier, S.C. & Bearhop, S. 2018. A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. *Methods Ecol. Evol.* **9**: 946–955.

Chan, Y.-C., Brugge, M., Tibbitts, T.L., Dekinga, A., Porter, R., Klaassen, R.H.G. & Piersma, T. 2016. Testing an attachment method for solar-powered tracking devices on a long-distance migrating shorebird. *J. Ornithol.* **157**: 277–287.

Chan, Y.-C., Peng, H.-B., Han, Y.-X., Chung, S.-S.-W., Li, L., Zhang, L. & Piersma, T. 2019a. Conserving unprotected important coastal habitats in the Yellow Sea: Shorebird occurrence, distribution and food resources at Lianyungang. *Global Ecol. Conserv.* **20**: e00724.

Chan, Y.-C., Tibbitts, T.L., Lok, T., Hassell, C.J., Peng, H.-B., Ma, Z., Zhang, Z.W. & Piersma, T. 2019b. Filling knowledge gaps in a threatened shorebird flyway through satellite tracking. *J. Appl. Ecol.* **56**: 2305–2315.

Choi, C.Y., Battley, P.F., Potter, M.A., Ma, Z.J., Melville, D.S. & Sukkaewmanee, P. 2017. How migratory shorebirds selectively exploit prey at a staging site dominated by a single prey species. *Auk* **134**: 76–91.

Clemens, R.S., Rogers, D.I., Hansen, B.D., Gosbell, K., Minton, C.D.T., Straw, P., Bamford, M., Woehler, E.J., Milton, D.A., Weston, M.A., Venables, B., Wellet, D., Hassell, C., Rutherford, B., Onton, K., Herrod, A., Studds, C.E., Choi, C.-Y., Dhanjal-Adams, K.L., Murray, N.J., Skilleter, G.A. & Fuller, R.A. 2016. Continental-scale decreases in shorebird populations in Australia. *Emu* **116**: 119–135.

CLS. 2016. *Argos user's manual*. Available at: http://www.argos-system.org/manual/ (accessed 10 December 2020).

Conklin, J.R., Senner, N.R., Battley, P.F. & Piersma, T. 2017. Extreme migration and the individual quality spectrum. *J. Avian Biol.* **48**: 19–36.

Conklin, J.R., Verkuil, Y.I. & Smith, B.R. 2014. *Prioritizing migratory shorebirds for conservation: Action on the East Asian-Australasian flyway*. Report WWF-Hong Kong. Available at: http://awsassets.wwfhk.panda.org/downloads/wwf_prioritization_finalpdf.pdf (accessed 10 December 2020).

Crossland, A. 2009. Passage of Red Knot *Calidris canutus* through North Sumatra province, Indonesia. *Stilt* **55**: 13–15.

de Fouw, J., van der Heide, T., Oudman, T., Maas, L.R.M., Piersma, T. & van Gils, J.A. 2016. Structurally complex sea grass obstructs the sixth sense of a specialized avian molluscivore. *Anim. Behav.* **115**: 55–67.

Douglas, D.C., Weinzierl, R.C., Davidson, S., Kays, R., Wikelski, M. & Bohrer, G. 2012. Moderating Argos location errors in animal tracking data. *Methods Ecol. Evol.* **3**: 999–1007.

Higgins, P.J. & Davies, S.J.J.F. (eds) 1996. *Handbook of Australian, New Zealand and Antarctic Birds. Volume 3. Snipe to Pigeons*. Melbourne: Oxford University Press.

Hua, N., Piersma, T. & Ma, Z. 2013. Three-phase fuel deposition in a long-distance migrant, the Red Knot (*Calidris canutus piersmai*), before the flight to High Arctic breeding grounds. *PLoS One* **8**: e62551.

Iwamura, T., Possingham, H.P., Chadès, I., Minton, C., Murray, N.J., Rogers, D.I., Treml, E.A. & Fuller, R.A. 2013. Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. *Proc. R. Soc. B* **280**: 20130325.

Kok, E.M.A., Tibbitts, T.L., Douglas, D.C., Howey, P.W., Dekinga, A., Gnep, B. & Piersma, T. 2020. A Red Knot as a black swan: how a single bird shows navigational abilities during repeat crossings of the Greenland Icecap. *J. Avian Biol.* **51**: e02464.

Lindström, Å., Minton, C.D.T. & Bensch, S. 1999. First recovery of a Red Knot *Calidris canutus* involving the breeding population on the New Siberian Islands. *Wader Study Group Bull.* **89**: 33–35.

Lisovski, S., Gosbell, K., Hassell, C. & Minton, C. 2016. Tracking the full annual-cycle of the Great Knot *Calidris tenuirostris*, a long-distance migratory shorebird of the East Asian-Australasian Flyway. *Wader Study* **123**: 177–189.

Lok, T., Hassell, C.J., Piersma, T., Pradel, R. & Gimenez, O. 2019. Accounting for heterogeneity when estimating stopover duration, timing and population size of Red Knots along the Luannan coast of Bohai Bay. *China. Ecol. Evol.* **9**: 6176–6188.

Loonstra, A.H.J., Verhoeven, M.A., Senner, N.R., Both, C. & Piersma, T. 2019. Adverse wind conditions during northward Sahara crossings increase the in-flight mortality of Black-tailed Godwits. *Ecol. Lett.* **22**: 2060–2066.

Ma, Z., Melville, D.S., Liu, J., Chen, Y., Yang, H., Ren, W., Zhang, Z., Piersma, T. & Li, B. 2014. Rethinking China's new great wall. Massive seawall construction in coastal wetlands threatens biodiversity. *Science* **346**: 912–914.

Martin, G.R. & Piersma, T. 2009. Vision and touch in relation to foraging and predator detection: insightful contrast between a plover and a sandpiper. *Proc. R. Soc. B* **276**: 437–445.

Mu, T. & Wilcove, D.S. 2020. Upper tidal flats are disproportionately important for the conservation of migratory shorebirds. *Proc. R. Soc. B* **287**: 20200278.

Murray, N.J., Clemens, R.S., Phinn, S.R., Possingham, H.P. & Fuller, R.A. 2014. Tracking the rapid loss of tidal wetlands in the Yellow Sea. *Front. Ecol. Environm.* **12**: 267–272.

Newstead, D.J., Niles, L.J., Porter, R.R., Dey, A.D., Burger, J. & Fitzsimmons, O.N. 2013. Geolocation reveals mid-continent migratory routes and Texas wintering areas of Red Knots *Calidris canutus rufa*. *Wader Study Group Bull.* **120**: 53–59.

Newton, I. 2008. *The Migration Ecology of Birds*. Amsterdam: Academic Press.

Niles, L.J., Burger, J., Porter, R.R., Dey, A.D., Minton, C.D.T., González, P.M., Baker, A.J., Fox, J.W. & Gordon, C. 2010. First results using light level geolocators to track Red Knots in the Western Hemisphere show rapid and long intercontinental flights and new details of migration pathways. *Wader Study Group Bull.* **117**: 123–130.

Oudman, T., Piersma, T., Ahmedou Salem, M.V., Feis, M.E., Dekinga, A., Holthuijsen, S., ten Horn, J., van Gils, J.A. & Bijleveld, A.I. 2018. Resource landscapes explain contrasting patterns of aggregation and site fidelity by Red Knots at two wintering sites. *Mov. Ecol.* **6**: 24.

Peng, H.-B., Chan, Y.-C., Compton, T.J., Cheng, X.-F., Melville, D.S., Zhang, S.-D., Lei, G., Zhang, Z.-W., Ma, Z. & Piersma, T. 2021. Aquaculture and the homogenization of intertidal communities along the coast of China. *Distrib. Divers.* in press.

Piersma, T. 1987. Hop, skip or jump? Constraints on migration of arctic waders by feeding, fattening, and flight speed. *Limosa* **60**: 185–194.

Piersma, T. 1997. Do global patterns of habitat use and migration strategies co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure? *Oikos* **80**: 623–631.

Piersma, T. 1998. Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of fueling and flight? *J. Avian Biol.* **29**: 511–520.

Piersma, T. 2003. 'Coastal' versus 'inland' shorebird species: interlinked fundamental dichotomies between their life- and demographic histories? *Wader Study Group Bull.* **100**: 5–9.

Piersma, T. 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *J. Ornithol.* **148**(Suppl.): 45–59.

Piersma, T. & Baker, A.J. 2000. Life history characteristics and the conservation of migratory shorebirds. In Gosling, L.M. & Sutherland, W.J. (eds) *Behaviour and Conservation*: 105–124. Cambridge: Cambridge University Press.

Piersma, T. & Davidson, N.C. 1992. The migrations and annual cycles of five subspecies of Knots in perspective. *Wader Study Group Bull.* **64**(Suppl.): 187–197.

Piersma, T., Gudmundsson, G.A. & Lilliendahl, K. 1999. Rapid changes in the size of different functional organ and muscle groups during refueling in a long-distance migrating shorebird. *Physiol. Biochem. Zool.* **72**: 405–415.

Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P.F. & Wiersma, P. 1993. Scale and intensity of intertidal habitat use by Knots *Calidris canutus* in the western Wadden Sea in relation to food, friends and foes. *Neth. J. Sea Res.* **31**: 331–357.

Piersma, T., Lok, T., Chen, Y., Hassell, C.J., Yang, H.-Y., Boyle, A., Slaymaker, M., Chan, Y.-C., Melville, D.S., Zhang, Z.-W. & Ma, Z. 2016. Simultaneous declines in summer survival of three shorebird species signals a flyway at risk. *J. Appl. Ecol.* **53**: 479–490.

Piersma, T., Rogers, D.I., González, P.M., Zwarts, L., Niles, L.J., de Lima Serrano do Nascimento, I., Minton, C.D.T. & Baker, A.J. 2005. Fuel storage rates before northward flights in Red Knots worldwide. In Greenberg, R. & Marra, P.P. (eds) *Birds of Two Worlds: The Ecology and Evolution of Migratory Birds*: 262–274. Baltimore: Johns Hopkins University Press.

Piersma, T., van Aelst, R., Kurk, K., Berkhoudt, H. & Maas, L.R.M. 1998. A new pressure sensory mechanism for prey detection in birds: the use of principles of seabed dynamics? *Proc. R. Soc. Lond. B* **265**: 1377–1383.

Prater, A.J. (with O'Connor, R.J.) 1981. *Estuary Birds of Britain and Ireland*. Calton: Poyser.

Quaintenne, G., van Gils, J.A., Bocher, P., Dekinga, A. & Piersma, T. 2010. Diet selection in a molluscivore shorebird across Western Europe: does it show short- or long-term intake rate-maximization? *J. Anim. Ecol.* **79**: 53–62.

Rakhimberdiev, E., Saveliev, A., Piersma, T. & Karagicheva, J. 2017. FlightR: an R package for reconstructing animal paths from solar geolocation loggers. *Methods Ecol. Evol.* **8**: 1482–1487.

Rakhimberdiev, E., Senner, N.R., Verhoeven, M.A., Winkler, D.W., Bouten, W. & Piersma, T. 2016. Comparing inferences of solar geolocation data against high-precision GPS data: annual movements of a double-tagged Black-tailed Godwit. *J. Avian Biol.* **47**: 589–596.

Rakhimberdiev, E., van den Hout, P.J., Brugge, M., Spaans, B. & Piersma, T. 2015a. Seasonal mortality and sequential density dependence in a migratory bird. *J. Avian Biol.* **46**: 332–341.

Rakhimberdiev, E., Winkler, D.W., Bridge, E., Seavy, N.E., Sheldon, D., Piersma, T. & Saveliev, A. 2015b. A hidden Markov model for reconstructing animal paths from solar geolocation loggers using templates for light intensity. *Mov. Ecol.* **3**: 25.

Rogers, D.I., Scroggie, M.P. & Hassell, C.J. 2020. *Review of Long-term Shorebird Monitoring in north Western Australia*. Arthur Rylah Institute for Environmental Research Technical Report Series No. 313. Heidelberg, Australia.

Rogers, D.I., Yang, H.Y., Hassell, C.J., Boyle, A.N., Rogers, K.G., Chen, B., Zhang, Z.-W. & Piersma, T. 2010. Red Knots (*Calidris canutus piersmai* and *C. c. rogersi*) depend on a small threatened staging area in Bohai Bay, China. *Emu* **110**: 307–315.

Rogers, K., Rogers, A. & Rogers, D. 1990. *Banders Aid, Supplement Number one*. RAOU Report No. 67, Melbourne.

Shamoun-Baranes, J., Leyrer, J., van Loon, E., Bocher, P., Robin, F., Meunier, F. & Piersma, T. 2010. Stochastic atmospheric assistance and the use of emergency staging sites by migrants. *Proc. R. Soc. B* **277**: 1505–1511.

Studds, C.E., Kendall, B.E., Murray, N.J., Wilson, H.B., Rogers, D.I., Clemens, R.S., Gosbell, K., Hassell, C.J., Jessop, R., Melville, D.S., Milton, D.A., Minton, C.D.T., Possingham, H.P., Riegen, A.C., Straw, P., Woehler, E.J. & Fuller, R.A. 2017. Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. *Nat. Comm.* **8**: 14895.

Tomkovich, P.S. 1992. An analysis of the geographical variability in Knots *Calidris canutus* based on museum skins. *Wader Study Group Bull.* **64**(Suppl.): 17–23.

Tomkovich, P.S. 2001. A new subspecies of Red Knot *Calidris canutus* from the New Siberian Islands. *Bull. Br. Ornithol. Club* **121**: 257–263.

Tomkovich, P.S. & Riegen, A. 2000. Mixing of Red Knot populations in Australia: some thoughts. *Stilt* **37**: 25–27.

Tulp, I., McChesney, S. & de Goeij, P. 1994. Migratory departures of waders from north-western Australia: behaviour, timing and possible migration routes. *Ardea* **82**: 201–221.

van de Kam, J., Ens, B.J., Piersma, T. & Zwarts, L. 2004. *Shorebirds. An Illustrated Behavioural Ecology*. Utrecht: KNNV Publishers.

van den Hout, P.J., Mathot, K.J., Maas, L.R.M. & Piersma, T. 2010. Predator escape tactics in birds: linking ecology and aerodynamics. *Behav. Ecol.* **21**: 16–25.

van der Velde, M., Haddrath, O., Verkuil, Y.I., Baker, A.J. & Piersma, T. 2017. New primers for molecular sex identification of waders. *Wader Study* **124**: 147–151.

van Gils, J.A., Battley, P.F., Piersma, T. & Drent, R. 2005. Reinterpretation of gizzard sizes of Red Knots world-wide emphasises overriding importance of prey quality at migratory stopover sites. *Proc. R. Soc. B* **272**: 2609–2618.

van Gils, J.A., Piersma, T., Dekinga, A. & Battley, P.F. 2006. Modelling phenotypic flexibility: an optimality analysis of gizzard size in Red Knots (*Calidris canutus*). *Ardea* **94**: 409–420.

Verhoeven, M.A., van Eerbeek, J., Hassell, C.J. & Piersma, T. 2016. Fuelling and moult in Red Knots before northward departure: a visual evaluation of differences between ages, sexes and subspecies. *Emu* **116**: 158–167.

Warnock, N. 2010. Stopping vs. staging: the difference between a hop and a jump. *J. Avian Biol.* **41**: 621–626.

Warnock, N. & Warnock, S. 1993. Attachment of radiotransmitters to sandpipers: review and methods. *Wader Study Group Bull.* **70**: 28–30.

Yang, H.-Y., Chen, B., Barter, M., Piersma, T., Zhou, C.-F., Li, F.-S. & Zhang, Z.-W. 2011. Impacts of tidal land reclamation in Bohai Bay, China: ongoing losses of critical Yellow Sea waterbird staging and wintering sites. *Bird Conserv. Int.* **21**: 241–259.

Yang, H.-Y., Chen, B., Ma, Z., Hua, N., van Gils, J.A., Zhang, Z.-W. & Piersma, T. 2013. Economic design in a long-distance migrating molluscivore: how fast-fuelling Red Knots in Bohai Bay, China, get away with small gizzards. *J. Exp. Biol.* **216**: 3627–3636.

Yang, H.-Y., Chen, B., Piersma, T., Zhang, Z. & Ding, C. 2016. Molluscs of an intertidal soft-sediment area in China: Does overfishing explain a high density but low diversity community that benefits staging shorebirds? *J. Sea Res.* **109**: 20–28.

Zhang, S.-D., Ma, Z., Choi, C.-Y., Peng, H.-b., Bai, Q.-Q., Liu, W.-L., Tan, K., Melville, D.s., He, P., Chan, Y.-C., Van gils, J.a. & Piersma, T. 2018. Persistent use of a shorebird staging site in the Yellow Sea despite severe declines in food resources implies a lack of alternatives. *Bird Conserv. Int.* **28**: 534–548.

Zhang, S.-D., Ma, Z., Choi, C.-Y., Peng, H.-B., Melville, D.S., Zhao, T.-T., Bai, Q.-Q., Liu, W.-L., Chan, Y.-C., van Gils, J.A. & Piersma, T. 2019a. Morphological and digestive adjustments buffer performance: How staging shorebirds cope with severe food declines. *Ecol. Evol.* **9**: 3868–3878.

Zhang, S.-D., Ma, Z., Feng, C.-C., Melville, D.S., van Gils, J.A. & Piersma, T. 2019b. Individual diet differences in a molluscivore shorebird are associated with the size of body instruments for internal processing rather than for feeding. *J. Avian Biol.* **50**: e02255.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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

Table S2. List of intertidal sites along the coast of China with information on densities of *Potamocorbula laevis* and usage by satellite-tagged Red Knots.

Table S3. Name list of stopping sites used by Red Knots in the East Asian-Australasian Flyway.