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Research

Hidden in plain sight: migration routes of the elusive Anadyr bar-tailed godwit revealed by satellite tracking

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Satellite and GPS tracking technology continues to reveal new migration patterns of birds which enables comparative studies of migration strategies and distributional information useful in conservation. Bar-tailed godwits in the East Asian–Australasian Flyway *Limosa lapponica baueri* and *L. l. menzbieri* are known for their long non-stop flights, however these populations are in steep decline. A third subspecies in this flyway, *L. l. anadyrensis*, breeds in the Anadyr River basin, Chukotka, Russia, and is morphologically distinct from *menzbieri* and *baueri* based on comparison of museum specimens collected from breeding areas. However, the non-breeding distribution, migration route and population size of *anadyrensis* are entirely unknown. Among 24 female bar-tailed godwits tracked in 2015–2018 from northwest Australia, the main non-breeding area for *menzbieri*, two birds migrated further east than the rest to breed in the Anadyr River basin, i.e. they belonged to the *anadyrensis* subspecies. During pre-breeding migration, all birds staged in the Yellow Sea and then flew to the breeding grounds in the eastern Russian Arctic. After breeding, these two birds migrated south-westward to stage in Russia on the Kamchatka Peninsula and on Sakhalin Island *en route* to the Yellow Sea. This contrasts with the other 22 tracked godwits that followed the previously described route of *menzbieri*, i.e. they all migrated northwards to stage in the New Siberian Islands before turning south towards the Yellow Sea, and onwards to northwest Australia. Since the Kamchatka Peninsula was not used by any of the tracked *menzbieri* birds, the 4500 godwits counted in the Khairusova–Belogolovaya estuary in western Kamchatka may well be *anadyrensis*. Comparing migration patterns across the three bar-tailed godwits subspecies, the migration strategy of *anadyrensis* lies between that of *menzbieri* and *baueri*. Future investigations combining migration tracks with genomic data could reveal how differences in migration routines are evolved and maintained.

Keywords: migration, shorebird, telemetry, Yellow Sea, East Asian–Australasian Flyway, *Limosa lapponica anadyrensis*

Introduction

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

A third subspecies in this flyway, *L. l. anadyrensis*, was first proposed by Engelmoer and Roselaar (1998), and later its taxonomic status was reassessed and verified by Tomkovich (2010) who compared morphological characteristics of museum specimens of breeding birds collected from the Anadyr River basin, Chukotka, Russia with *menzbieri* and *baueri* specimens from more westerly (Yakutia-Chaun) and more easterly (Alaska) breeding areas, respectively. Although the Anadyr birds differed significantly from *menzbieri* and *baueri* in several size and plumage characteristics, the ranges of these measurements among subspecies still overlapped, thus, outside of breeding areas, *anadyrensis* cannot be identified with certainty in the hand or by observation in the field. To date, nothing is known about its population size and non-breeding distribution.

Satellite tracking has revealed details of the migration routes of *baueri* and *menzbieri* bar-tailed godwits (Battley et al. 2012). Both use the Yellow Sea as their main staging area during pre-breeding migration (Battley et al. 2012). In post-breeding migration, *baueri* migrates across the Pacific Ocean from Alaska to New Zealand, thousands of kilometers east of their northbound route (Gill et al. 2009). In contrast, post-breeding *menzbieri* first migrate northwards from breeding areas in eastern Russia to stage on the New Siberian Islands before migrating southwards to stage for a second time in the Yellow Sea region (Battley et al. 2012). The double reliance on the Yellow Sea by *menzbieri* has been used to explain their lower annual survival rate (Conklin et al. 2016) and steeper population decline in comparison to *baueri* (Studds et al. 2017). If the *anadyrensis* subspecies uses similar migration routes and staging areas as either *baueri* or *menzbieri*, it likely is experiencing similar pressure from habitat destruction and deterioration at staging sites in the EAAF.

Among the 24 bar-tailed godwits we tracked in this study in 2015–2018 from northwest Australia, the main non-breeding area for *menzbieri* (Wilson et al. 2007), two individuals migrated to the Anadyr River basin to breed indicating that they belonged to the *anadyrensis* subspecies. Here we describe the migration itineraries of these two *anadyrensis* individuals and compare their itineraries with those of *menzbieri* individuals tracked during the same period. We found that during post-breeding migration, only the *anadyrensis* individuals used staging sites on the coast of the Kamchatka Peninsula, which lead us to examine the only concurrent and available shorebird monitoring data from the Kamchatka Peninsula which was at the Khairusova–Belogolovaya estuary. Assuming that the bar-tailed godwits staging on the Kamchatka Peninsula consist of only *anadyrensis*, then counts there would represent a minimum first estimate of the population size of *anadyrensis*. Finally, to gain more insight into the non-breeding distribution of *anadyrensis*, we collate the flyway-wide banding origin and resighting data of the flagged individuals observed at the Khairusova–Belogolovaya estuary.

Methods

Satellite tracking

Bar-tailed godwits were captured by cannon netting at two non-breeding sites in northwest Australia: at the northern beaches of Roebuck Bay (17.98°S, 122.35°E) in October 2014 and 2015 and February 2017 and at the central and northern portions of Eighty Mile Beach (19.40°S, 121.27°E), in February 2017. Individuals were colour-ringed with unique ring combinations (Piersma et al. 2016), aged based on moult characteristics, and sexed based on bill length (female's bills longer than males' by 22 mm on average) and plumage (females have paler plumage, Hassell et al. unpubl.); sexing was later verified by genetic analysis of blood samples. Adult females older than 3 years were selected for tagging because their larger size would likely minimize any tag effects on migration behavior. Solar Argos satellite transmitters of 5 and 9.5 g (Microwave Telemetry, Maryland, USA) were attached to the birds' backs by leg-loop harnesses made with Teflon ribbon. This work was carried out under ABBBS Banding Authority Number 2184 issued by the Department of the Environment of the Australian Government, and Regulation 17 permits SF010074, SF010547 and 01-000057-2 issued by the West Australian Department of Biodiversity, Conservation and Attractions.

Satellite tags were programmed to send signals at intervals of 60–65 s for a duty cycle of 8 h ON and 25 h OFF. These signals were received by the Argos receiving system via satellites (Collecté Localization Satellites, <www.argos-system.org>), from which a bird's position was subsequently estimated using Doppler geolocation. We retained all standard-class Argos locations (i.e. the location classes 3, 2 and 1) and

removed any implausible auxiliary locations (i.e. classes 0, A, B and Z) by applying the Hybrid Douglas filter (Douglas et al. 2012). The filtering parameters were set at 120 km h^{-1} for the maximum sustainable rate of movement and 10 km for the minimum redundant distance. To get a better estimate of the Argos locations based on the error ellipses provided, the data were fitted with a continuous-time random walk state-space model with the 'foieGras' R package (Jonsen et al. 2020). To improve model performance, we filtered out points within 5 min of one another before fitting the model. If standard-class locations occurred within 5 min we retained the point with the higher-accuracy location class; and if auxiliary locations occurred within the 5 min we retained the point closest to a previous and a subsequent location. The following analyses concerning route and timing were conducted with the fitted values from the model.

Both of the *anadyrensis* individuals were tagged in February 2017, one in Roebuck Bay and one at Eighty Mile Beach. Morphological measurements of the two *anadyrensis* individuals (bill length: 106.2 and 109.7 mm; wing: 239 and 243 mm; tarsus: 58.2 and 61.0 mm) are within the range of that of the 22 *menzbieri* (bill: 108.5 ± 4.2 mm, range = 100.0–116.2 mm; wing: 231.2 ± 6.5 mm, 218–243 mm; tarsus: 58.1 ± 2.2 mm, 52.7–62.7 mm). For the *menzbieri* bar-tailed godwits in 2017, no significant difference was found between birds tagged at different wintering locations (Roebuck Bay or Eighty Mile Beach) in timing of departure and arrival at Northwest Australia (departure: $t_9 = -0.214$, $p = 0.835$; arrival: $t_8 = 0.018$, $p = 0.986$). Moreover, no observable difference in migration route and distribution of stopover sites was found between birds tagged at the two locations. Therefore, we did not distinguish tagging locations of birds in the subsequent analyses. As the notable differences in migration behavior between *menzbieri* and *anadyrensis* individuals occurred during the post-breeding period, we included individuals in our analysis that were tracked at least until they reached the Yellow Sea during post-breeding (n = 24).

Stopping sites (including 'staging sites', i.e. sites where migrating birds make long stops, and 'stopover sites' where birds make short stops, Piersma 1987, Warnock 2010), were extracted by first clustering consecutive points where rate of movement was under 5 km h^{-1} and then grouping all clusters within 20 km of each other. Habitat descriptions and elevation of breeding sites were based on satellite imagery and elevational information from Google Earth Pro v7.3 (65.87°N, 174.92°E, eye altitude 121 km, Landsat/Copernicus, accessed on 21 October 2019). For analyses concerning the migration routes, we used only the first migration track of each individual in our analyses because individuals tended to take the same route in successive years (Y.-C. Chan et al. unpubl.). Total migration distances were estimated as the sum of all flight distances (distance of all consecutive points within each flight segment, i.e. from the last point at a site to the first point at the next site) plus distances between first and last point recorded at each site. Since birds were assumed to fly along the shortest great-circle path from one point to the next, the calculated distances are likely to be an underestimation

of the actual distances travelled. One *menzbieri* individual made a U-turn after flying > 1580 km during its first attempt migrating southward from the New Siberian Islands. Since this sort of U-turn was rarely observed in our dataset and our main objective was to compare average migration routes between the two subspecies, the travel distance incurred from the U-turn was excluded from the calculations of the average post-breeding migration distances.

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

Counts and resightings at Khairusova–Belogolovaya estuary

We conducted a total of 84 counts of bar-tailed godwits at the Khairusova–Belogolovaya estuary, western coast of Kamchatka Peninsula (57.1°N, 156.7°E), June–September 2015–2019. Counts were conducted every 3 days at roosts during high or incoming tides when birds moved from their foraging areas to their roost sites. A total of 2–5 observers used 20–60× spotting scopes or 10 × 40 binoculars to survey an area of approximately 45 km². Since birds were passing through the estuary in these months, these numbers represent the minimum number of bar-tailed godwits using the site.

Resighting of colour-flagged birds was also carried out at the Khairusova–Belogolovaya estuary in 2016–2019. The banding location of each resighted flagged bird was then deduced from its flag colour combination. For flagged birds marked individually (i.e. with engraved flags or ancilliary colour rings), flyway-wide resighting records and additional details on banding locations were obtained from the coordinators of the corresponding banding schemes.

Results

Migration route

Pre-breeding migration

The northward route of *anadyrensis* from wintering sites to the Yellow Sea largely overlapped with *menzbieri* individuals, but one *anadyrensis* took a route on the eastern edge of the *menzbieri* route towards the Yellow Sea (Fig. 1A). From
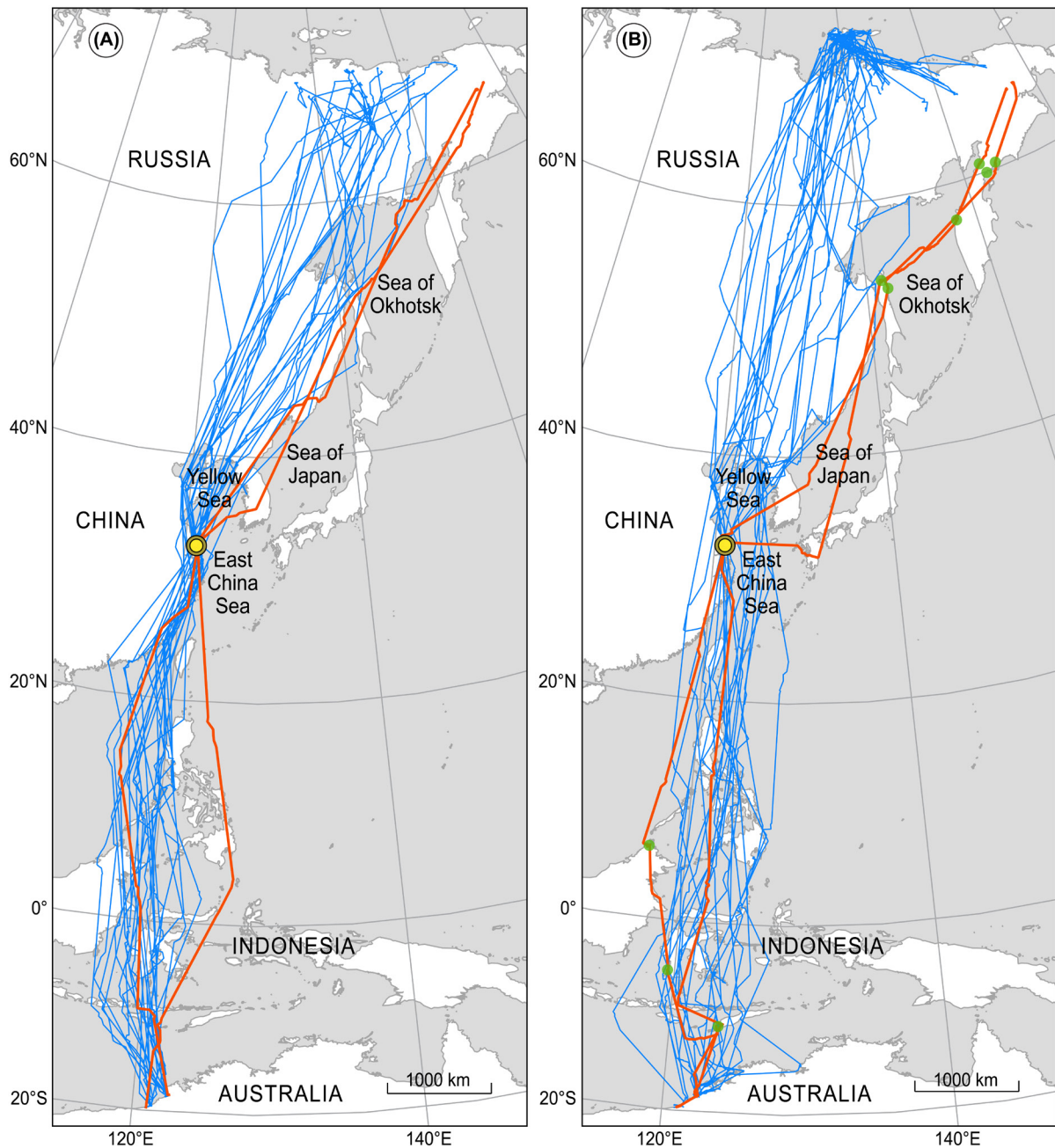
Figure 1. Pre-breeding (A) and post-breeding (B) migration tracks of bar-tailed godwits *Limosa lapponica anadyrensis* (orange, n = 2) and *L. l. menzbieri* (blue, n = 22) in 2015–2018. The satellite tags were deployed in northwest Australia. Yellow dots represent the staging area of *L. l. anadyrensis* in the Yellow Sea at the Dongtai coast in southern Jiangsu, China. Green dots represent the other stopping sites of *L. l. anadyrensis* mentioned in the text.

the Yellow Sea to the breeding grounds, *anadyrensis* took a north-easterly route towards their breeding sites, on the eastern edge of the routes taken by *menzbieri* (Fig. 1A). During the entire pre-breeding migration, *anadyrensis* birds staged along the Dongtai coast of southern Jiangsu Province, China (32.6–33.0°N, 120.9–121.3°E, Fig. 1A) within the Yellow Sea, where one individual mainly occurred at the Tiaozini mudflats next to the mainland, and another at the offshore Gaoni and Dongsha Shoals. This stretch of coastline was also used by 10 of the 22 *menzbieri* individuals. While all the *menzbieri* individuals stopped at the Yellow Sea coast, 19 of the 22 also made stops of more than one day in other regions. Before reaching the Yellow Sea, 15 (68%) stopped along the coasts of Southeast Asia and south China; and after leaving the Yellow Sea, 18 (82%) stopped along the coastline or inland tundra of Russia before arriving at the breeding sites. The overall distances covered by the two *anadyrensis* during pre-breeding migration were 11 247 and 11 255 km, falling
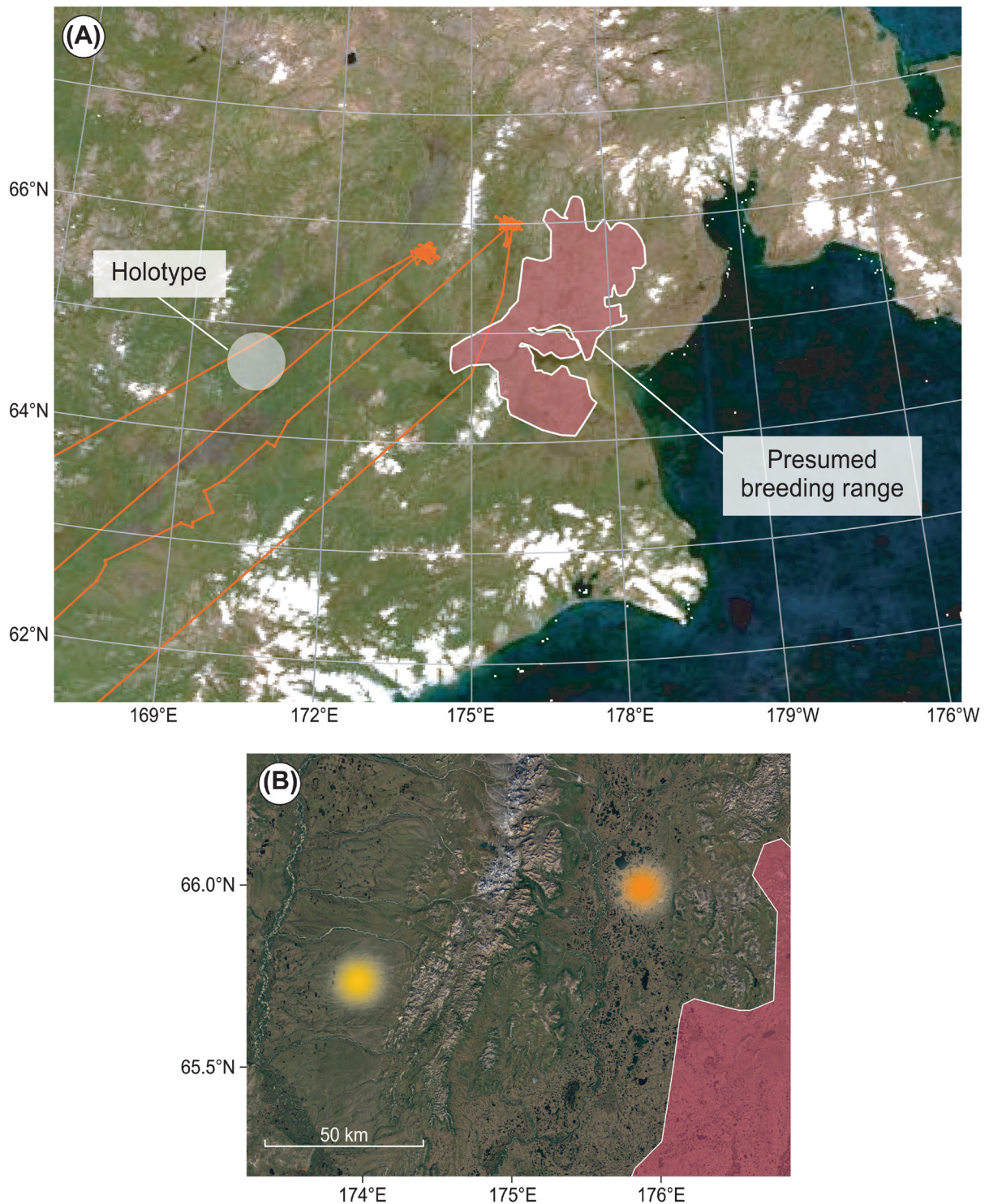
Figure 2. (A) Tracks of the two *Limosa lapponica anadyrensis* satellite-tagged bar-tailed godwits in relation to the presumed breeding range of *anadyrensis* (Lappo et al. 2012), and the approximate location where the holotype was collected near the town of Markovo along the Anadyr River (64.7°N, 170.4°E, Tomkovich 2010). (B) Enlarged map of generalized Argos locations of the two tagged bar-tailed godwits on the Anadyr River lowlands during breeding (24 May–1 August, this study).
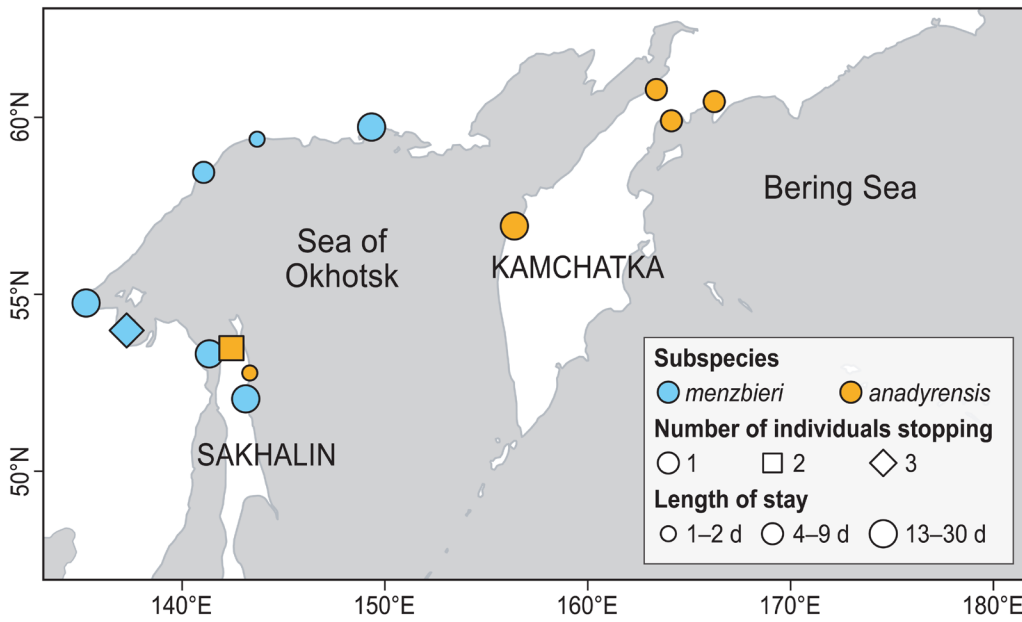
Figure 3. Post-breeding stopping sites at the Sea of Okhotsk and the eastern coast of Kamchatka of tracked bar-tailed godwits (7 *Limosa lapponica menzbieri* and 2 *L. l. anadyrensis* individuals) in 2015–2018.

within the range of 10 179–11 941 km (mean ± SD, 10 972 ± 403 km) of the 22 *menzbieri* individuals.

Breeding

During the breeding season, the two *anadyrensis* individuals stayed in the Anadyr River lowlands, 30–100 km west of the presumed breeding range (Lappo et al. 2012, Fig. 2A) and about 300 km southeast of the closest tracked *menzbieri* in the Chaun Gulf (68.3°N, 172.1°E). One *anadyrensis* individual was on a mountain slope with stream runoffs at an elevation of 155 m, and the other in a wetland in a valley at an elevation of 46 m (Fig. 2B).

Post-breeding migration

After leaving their breeding sites, the two *anadyrensis* individuals migrated south-westward to stage along the coast of the Kamchatka Peninsula and on Sakhalin Island in the Sea of Okhotsk (Fig. 3), and then staged again along the Dongtai coast of the Yellow Sea (Fig. 1B). This contrasts with the 22 *menzbieri*, which after breeding migrated northwards to stage in the New Siberian Islands (76.3°N, 140.4°E), and then travelled south towards the Yellow Sea (Fig. 1, 4). Along the way from the New Siberian Islands to the Yellow Sea, a small proportion of *menzbieri* individuals also stopped in the Sea of Okhotsk (for 2015–2018, 7 out of 22, Fig. 3; for 2017 only,
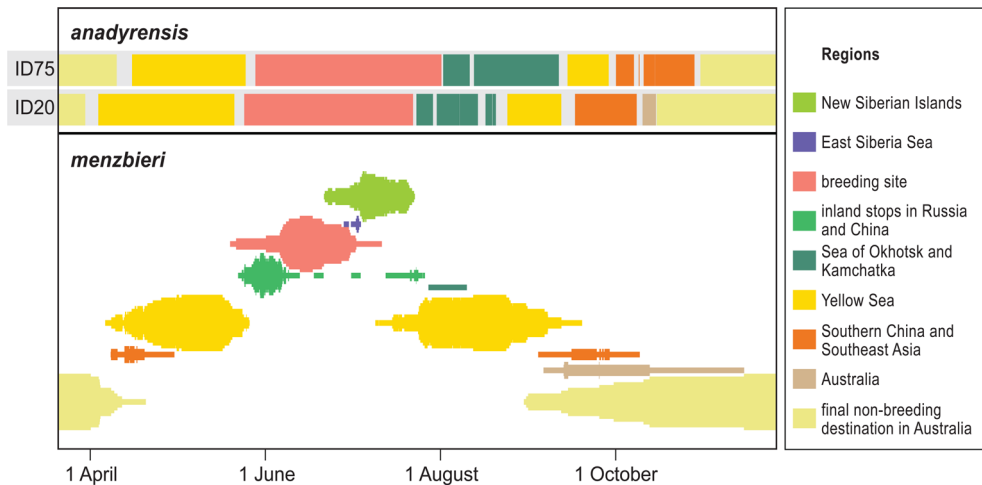

Figure 4. Migration timing of the two *Limosa lapponica anadyrensis* bar-tailed godwits and 10 *L. l. menzbieri* with complete migration tracks in 2017. Different colours indicate time spent stopping at regions along the EAAF. For *menzbieri*, height of box corresponds to the number of individuals. Regions are ordered by latitudes.

1 of the 10, Fig. 4) but on the western shore; there was a clear gradient from west to east in the stopping sites of *menzbieri* and *anadyrensis*, respectively (Fig. 3). Along the Yellow Sea coast, *menzbieri* staged at a range of sites from 32.2°N to 40.9°N.

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

The overall distances travelled during post-breeding migration by *anadyrensis* were 11 710 and 12 367 km which were at the lower end of those by *menzbieri* of 11 569–14 032 km (mean ± SD, 12 443 ± 646 km, n=17). For *anadyrensis*, migration distances of post-breeding migrations were longer than pre-breeding migrations by 455 and 1120 km whereas for *menzbieri* the post-breeding route was considerably longer than the pre-breeding route by 1471 km (95% CI: 1064, 1878, paired t-test: t_{16}=7.67, p < 0.001).

Migration timing

Pre-breeding migration
One of the two *anadyrensis* individuals was the first among the 2017-tracked godwits to depart northwest Australia on 30 March 2017 (the *menzbieri* godwits departed on average on 8 April ± 5.4 days, range=1–20 April, n=11, Fig. 4). Since it did not stop *en route*, it was also the first to reach the Yellow Sea on 3 April. The other *anadyrensis* individual departed on 10 April and also flew nonstop to reach the Yellow Sea on 15 April. The time period that the *anadyrensis* were in the Yellow Sea during pre-breeding migration largely overlapped with that of the *menzbieri*. The two *anadyrensis* godwits departed the Yellow Sea on 21 and 25 May, which was similar in timing to the *menzbieri* birds (22 May ± 3.4 d, 17–26 May, n=11). The total staging durations over the entire pre-breeding migration were similar between *anadyrensis* (40 and 48 d) and *menzbieri* (47.0 ± 5.7 d, n=11). The Yellow Sea is where both subspecies spent the longest time staging (100% of the total staging duration for *anadyrensis* and 73% for *menzbieri*).

Breeding
The two *anadyrensis* individuals arrived on 24 and 28 May at their breeding sites, earlier than that of the *menzbieri* godwits (3 June ± 7.5 d, 19 May–13 June, n=11, Fig. 4) and remained there for 59 and 65 d which was longer than that for *menzbieri* (10–53 d, median=22 d, n=11). Length

of stay at breeding sites likely reflected breeding success. Consequently, the *anadyrensis* birds left their breeding sites (22 July and 1 August) much later than the *menzbieri* (27 June ± 7.0 d).

Post-breeding migration
Over the entire post-breeding migration, the two *anadyrensis* godwits spent 70 and 78 d staging, which fell within the range of the 40–125 d of the *menzbieri* (mean ± SD = 77 ±
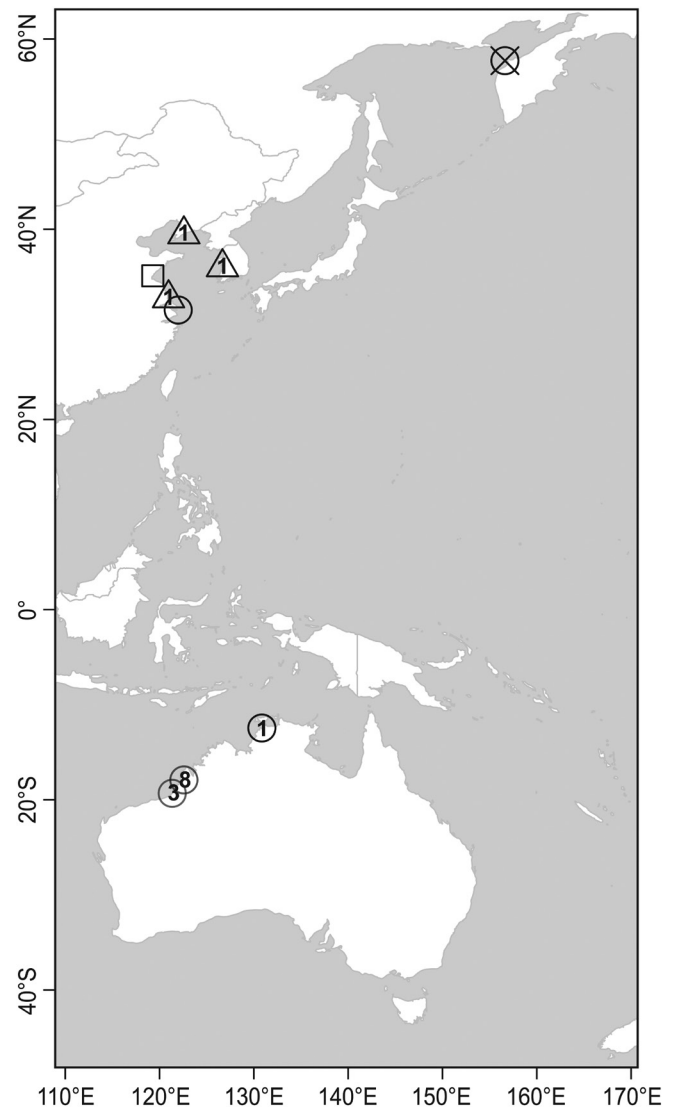

Figure 5. Banding locations (circles) of the bar-tailed godwits that were resighted in July–August 2016–2019 at the Khairusova–Belogolovaya estuary, Kamchatka, Russia (circle with a cross). Numbers in circles indicate number of individuals observed; plain-coloured flags were used at one site in China and thus number of individuals is not known. Triangles represent locations where birds banded in northwest Australia (and seen in the Khairusova–Belogolovaya estuary) were resighted. The square represents the resighting location of an individual banded at the Khairusova–Belogolovaya estuary.

25 d, n = 10, Fig. 4). While the tracked *anadyrensis* individuals divided their time among the Sea of Okhotsk (24 and 39 days), the Yellow Sea (14 and 19 days) and Southeast Asia (21 and 24 days), the *menzbieri* spent the majority of their time in the Yellow Sea (41.6 ± 8.2 d, 30–56 d, 58% of total staging durations, n = 10). The staging periods of *anadyrensis* in the Yellow Sea (24 August–12 September; 14–28 September) were considerably later than that of the *menzbieri* (28 July ± 12.7 d to 3 September ± 8.7 d). When the *anadyrensis* birds reached northwest Australia on 10 and 29 October, all *menzbieri* had already arrived there (mean arrival date = 13 September, range = 30 August–10 October, Fig. 4).

Counts and resightings at Khairusova–Belogolovaya estuary

Bar-tailed godwits were already present at the Khairusova–Belogolovaya estuary when the 2015–2019 post-breeding surveys commenced (the earliest starting date was 25 June 2018, while in some years the surveys were initiated in July). The peak of migration occurred at the beginning of August when > 2500 bar-tailed godwits were recorded; the overall highest count was 4500 bar-tailed godwits on 5 August 2018.

A total of 12 individually-banded bar-tailed godwits were observed at the Khairusova–Belogolovaya estuary in 2016–2019. Eleven of these birds (six females and five males) were banded in northwest Australia (eight in Roebuck Bay and three in Eighty Mile Beach) and one in Darwin, Northern Territory (Fig. 5). Three of these individuals were also resighted at Zhuanghe, Liaoning Province, China (39.5°N, 122.6°E), Dongtai, Jiangsu Province, China (32.8°N, 121.0°E) and Geum Gang estuary, South Korea (36.0°N, 126.7°E). In addition, we recorded bar-tailed godwits on 5 occasions with plain color flags (from which individuals cannot be identified) that had been banded in Chongming Dongtan, China (31.5°N, 121.9°E). Finally, one bird banded at the Khairusova–Belogolovaya estuary was resighted at Xiuzhenhe estuary, Lianyungang, China (35.1°N, 119.3°E).

Discussion

In this contribution, we described the first complete migrations of bar-tailed godwits of the enigmatic *anadyrensis* subspecies. We highlighted the uniqueness of migration patterns of the *anadyrensis* subspecies by contrasting them with that of the *menzbieri* subspecies tagged at the same non-breeding location. During pre-breeding migration, birds of the two subspecies shared similar routes and showed similar migration timing, and both used the Yellow Sea as their main staging area. We found that *anadyrensis* made only one stop in the Yellow Sea during pre-breeding migration from northwest Australia to breeding areas, while some pre-breeding *menzbieri* stopped at sites in Southeast Asia and southern China before staging in the Yellow Sea. Another difference was that the majority of *menzbieri* individuals used inland sites during the migration leg between the Yellow Sea and breeding

grounds while *anadyrensis* travelled non-stop. The function of these inland stops for *menzbieri* are unclear – birds could be fuelling up or waiting for better migratory conditions. Since only two *anadyrensis* individuals were tracked, any differences in migration patterns between the subspecies could also be due to the larger sample size of tagged *menzbieri*. Larger samples would lead to a larger between-individual variability of, for example, reaction to environmental conditions en route. The key difference we documented during post-breeding migration was that *anadyrensis* individuals staged along the coast of the Sea of Okhotsk instead of staging on the New Siberian Islands (found for all *menzbieri* in this study, confirming the findings of Battley et al. 2012). Another difference during post-breeding migration was that *anadyrensis* stopped in the Yellow Sea for a much shorter period than *menzbieri*. This latter difference could arise from the fact that the two *anadyrensis* stayed much longer at their breeding sites than the *menzbieri*, and suggests that the two tracked *anadyrensis* bred successfully while the majority of the tracked *menzbieri* appeared not to have bred successfully. Tracking of more *anadyrensis* individuals with a range of lengths of stay at breeding areas would clarify if the difference in post-breeding staging duration in the Yellow Sea is subspecies-specific.

We found that both of the tracked *anadyrensis* godwits, but none of the *menzbieri* ones, used sites on the Kamchatka Peninsula during post-breeding migration (Fig. 3), which leads us to infer that the bar-tailed godwits staging at the Khairusova–Belogolovaya estuary comprised mainly *anadyrensis*. The absence of *menzbieri* in Kamchatka was also evident in the earlier satellite-tracking study of bar-tailed godwits from the same northwest Australia population (Battley et al. 2012). Flyway-wide resightings of godwits either observed or banded at Khairusova–Belogolovaya provided more detail on the movements of *anadyrensis* and showed that assumed *anadyrensis* used additional migratory stopovers in China and South Korea besides the Dongtai coast in Jiangsu, and that the non-breeding range includes the coast of Northern Territory, Australia (Fig. 5). Less clear is whether birds banded in New Zealand have occurred in Kamchatka; the August 2004 observation of two godwits in Kamchatka with white flags (the New Zealand flag colour, Schuckard et al. 2006) was ambiguous due to flag loss by birds with similar combinations from elsewhere (e.g. black and white flags from Chongming Dongtan, China). However, one godwit banded in New Zealand was reported as shot in Kamchatka in early October (Riegen 1999). Putting together resightings and satellite tracks indicates that the non-breeding range of *anadyrensis* extends from at least northwest Australia to Northern Territory of Australia (Fig. 5), but it remains to be documented whether its range extends to eastern Australia and New Zealand.

The counts at Khairusova–Belogolovaya estuary show that at least 4500 bar-tailed godwits used this staging area during post-breeding migration. The actual number of birds using the estuary was likely higher as some birds could have departed earlier or arrived later than the date this high count was recorded. We deduce that among the 146 000 bar-tailed godwits estimated to occur in northwest Australia (Rogers et al.

2011, Conklin et al. 2014), at least several thousand are *anadyrensis* based on all satellite tracking of godwits to date from northwest Australia where 6.3% (2 of 32 individuals tracked at least until the Yellow Sea during post-breeding) apparently bred in Anadyr (this study and Battley et al 2012). Since *anadyrensis* also likely occur at other non-breeding sites, we suggest that the population of *anadyrensis* is about 10 000 birds

Based on knowledge gained from this study, three aspects of research and monitoring will be particularly informative in designing measures to conserve the *anadyrensis* subspecies and its unique migration route. First, given that *anadyrensis* individuals are indistinguishable by morphometrics and plumage from *menzbieri* that also occur in northwest Australia during non-breeding, identification methods other than satellite tracking are needed to monitor population trends and study stopover ecology. Such methods could include developing genetic markers that distinguish subspecies (Conklin et al. 2022) with the added benefit that these markers could be applied to the archive of bar-tailed godwit blood samples collected by Global Flyway Network in Australia since 2005. Second, we found that bar-tailed godwits staging at the Kamchatka Peninsula during post-breeding migration are likely to be mainly of the *anadyrensis* subspecies. Thus, counts conducted there can be used to monitor population trends, and individually-banding godwits at the Khairusova–Belogolovaya estuary can be a targeted effort to generate an adequate sample size to monitor trends in survival rates with mark-resighting methods (Piersma et al. 2016). Third, during pre-breeding migration, the two tracked *anadyrensis* individuals only staged at the Dongtai coast of Jiangsu, China in the Yellow Sea; they also returned to stage there during post-breeding migration. Although with only two individuals tracked we cannot establish the proportion of *anadyrensis* godwits that staged at Dongtai, the seemingly high site fidelity and long staging durations imply the high importance of this site to *anadyrensis* bar-tailed godwits. Since a high percentage of *menzbieri* also stopped along the Dongtai coast, this area is apparently important for both subspecies of bar-tailed godwits. A portion of this site (part of the offshore Dongsha Shoals) belongs to the recently listed World Heritage site of Yancheng coastline (UNESCO World Heritage Convention 2020), and the reclamation of intertidal flats planned for 2010–2020 on this stretch of coastline (see Piersma et al. 2017 for details) have not occurred. However, the spread of invasive cordgrass *Spartina alterniflora* in the upper tidal flats (Peng et al. 2017), is expected to reduce foraging and roosting opportunities for shorebirds (Mu and Wilcove 2020, Jackson et al. 2021) and represents an ongoing threat. Other potential threats include the erosion of mudflats next to the seawall and windfarms covering large areas of the mudflats (L. Zhang and K. Leung pers. comm.). Further research on how these potential threats at this important staging site affect godwits would be informative for designing conservation measures for *anadyrensis* godwits.

Our results enable a comparison of migration patterns of all the three subspecies of EAAF bar-tailed godwits, an extension of the two-subspecies comparison by Battley et al. (2012). All three subspecies rely strongly on the Yellow Sea during pre-breeding migration (for *anadyrensis* and *menzbieri*, see Results; for *baueri*, Battley et al. 2012). The migration patterns of the three subspecies differ the most during post-breeding migration and reveal three distinct migration strategies as the birds travel the > 10 000 km from the Arctic breeding sites to the Southern Hemisphere non-breeding destinations. After breeding, *anadyrensis* mainly staged on mudflats at coastal estuaries at the Sea of Okhotsk, and in this respect resemble *baueri* who stage on mudflats on the Yukon-Kuskokwim Delta, Alaska, particularly at the Kuskokwim Shoals (Battley et al. 2012). In contrast, *menzbieri* staged on tundra at the New Siberian Islands. *Anadyrensis* stopped in East Asia as did *menzbieri*, while *baueri* bypassed East Asia entirely, flying from Alaska to New Zealand directly across the Pacific Ocean (Battley et al. 2012). In terms of reliance on the Yellow Sea during post-breeding, the subspecies varied on a scale from a high reliance (*menzbieri*), low reliance (*anadyrensis*) to no reliance (*baueri*). This puts *anadyrensis* somewhere in-between the other two subspecies in terms of migration strategy. Reliance on the Yellow Sea is proposed as a major determinant of annual survival and population trends for shorebirds in the EAAF (Conklin et al. 2016, Studds et al. 2017). Based on the migration patterns, we can predict the demographic statistics of *anadyrensis* to fall between those of the other two subspecies. Lastly, the evolution and maintenance of differences in migration routines is extensively studied but many aspects remain to be understood (Piersma 2011). Now that the migration of the three subspecies of bar-tailed godwits in the EAAF has been described, future investigations combining migration tracks with genomic data would reveal how these divergent migratory phenotypes arose.

Author contributions

Ying-Chi Chan: Conceptualization (equal); Data curation (supporting); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **T. Lee Tibbitts**: Conceptualization (supporting); Data curation (lead); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Supervision (equal); Writing – review and editing (equal). **Dmitry Dorofeev**: Data curation (equal); Funding acquisition (equal); Investigation (supporting); Resources (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Chris Hassell**: Data curation (supporting); Project administration (equal); Resources (lead); Writing – review and editing (supporting). **Theunis Piersma**: Conceptualization (equal); Funding acquisition (lead); Project administration (equal); Supervision (equal); Writing – review and editing (equal).

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