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RESEARCH ARTICLE

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Filling knowledge gaps in a threatened shorebird flyway through satellite tracking

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Abstract

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

at the lesser known sites to collect information on bird numbers and habitat characteristics. To recognize and subsequently protect valuable coastal habitats, filling knowledge gaps by integrating bird tracking with ground-based methods should be prioritized.

KEYWORDS
East Asian–Australasian Flyway, great knot, intertidal mudflats, migration, satellite telemetry, Southeast Asia, stopover site, Yellow Sea

1 | INTRODUCTION

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

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

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

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

2 | MATERIALS AND METHODS

2.1 | Study species

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

2.2 | Satellite tracking

In September and October 2014, 2015 and 2016, we deployed 4.5 g solar Platform Terminal Transmitters (PTTs, Microwave Telemetry) on great knots captured with cannon nets at a primary non-breeding site, the northern beaches of Roebuck Bay, Broome, Northwest Australia (17.98°S, 122.31°E). After capture, each bird was measured and individually marked on its tarsi with a unique combination of leg flag and colour bands. Birds were aged based on plumage characteristics (Higgins & Davies, 1996) and adults were selected for satellite tagging. Transmitters were deployed using a body harness (Chan et al., 2016) made of elastic nylon (Elastan, Vaessen Creative), which degrades and breaks, thus releasing the tags after one to two years. The birds were kept indoors and observed for at least 24 hr to ensure acclimatization to the transmitter and harness. We then released the birds at the capture location.

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

2.3 | Spatial analyses

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

To investigate how tagging effort affected the number of sites discovered, we explored the relationship between the accumulated number of sites discovered per region and the number of satellite transmitters deployed. The mean site accumulation curve and its standard deviation were obtained from 1,000 permutations of adding sites in random order, using the function *specaccum* in the "vegan" R package (Oksanen et al., 2018).

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

We analysed migration patterns (i.e. the timing and frequency of site use by tracked birds) at three decreasing spatial scales: regional,

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

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

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

2.4 | Ground surveys

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

3 | RESULTS

Based on the movements of 32 great knots tracked in 2015–2017, we identified a total of 92 stopping sites along the EAAF with 19–25 sites in each of the four regions (Southeast Asia, Southern China, Yellow Sea and Russia; Figures 1 and 2a, all sites are listed in Table S2). Individuals made three to nine stops (mean of 5.6) during northward migration and three to eight stops (mean of 5.0) during southward migration, visiting 1.0–2.5 sites per region. The rate of discovery of new stopping sites decreased with increasing numbers of birds being tracked, but rates of "diminishing returns" varied between regions (Figure 3). The Yellow Sea was the only region where the site accumulation curve reached an asymptote (i.e. fewer than 0.5 sites would have been found there for every new tag added), indicating that most sites have been identified. In contrast, the curve for Southeast Asia hardly levelled off, meaning that most Southeast Asian sites still remain to be discovered.

Southeast Asia was used by 40% of the individuals during northward migration for an average of 11.5 ± 5.7 days (mean ± *SD*), and by 80% of the individuals during southward migration for 19.0 ± 7.4 days (Figure 2). During northward migration, all individuals stopped in Southern China for 9.4 ± 3.5 days, but none were detected there during southward migration (Figure 2). All individuals used the Yellow Sea, stopping there for 33.0 ± 7.7 and 29.1 ± 8.0 days during northward and southward migration, respectively (Figure 2). During

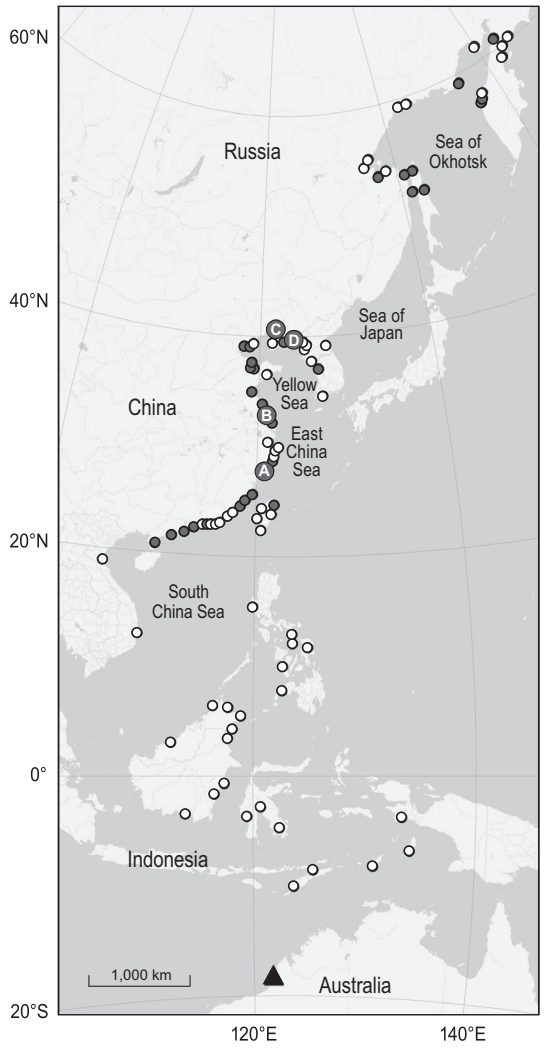

FIGURE 1 Sites along the East Asian–Australasian Flyway used by 32 satellite-tracked great knots during migration in 2015–2017. Filled circles were known important non-breeding sites of at least 1 of the 15 species of coastal obligate shorebirds, while open circles were unknown non-breeding sites for these shorebirds prior to our study. Sites visited by more than one-third of tracked individuals are: A, Wenzhou Bay, B, Yangkou–Dafeng coast, C, Liaohe (Shuangtaizi) Estuary and Inner Gulf of Liaodong and D, Yalu Jiang Estuary. Triangle shows Roebuck Bay, Northwest Australia where the satellite transmitters were deployed

northward migration, 55% of birds stopped for 3.2 ± 2.4 days along the Russian east coast, whereas during southward migration all birds stopped there for much longer (20.6 ± 5.8 days, Figure 2). Passage pattern for each latitudinal interval are shown in Figure 2d and the dates are listed in Table S3.

Latitudinal intervals within regions that were most frequently visited (i.e. by 85%–100% of tracked individuals) were 20.2–26°N within the Southern China region during northward migration, 51.5–56.5°N within the Russia region centred on the Sea of Okhotsk during southward migration and 36.5–41.5°N within the Yellow Sea region, during both migration seasons (Figure 2b). Accordingly, these intervals also contained the sites that were most frequently used (the ones visited by more than one-third of tracked birds are highlighted in Figure 1 and Table S2). At eight sites in Southern China where the tracked great knots stopped, flocks of 34–2,160 great knots per site were counted within the northward migration period during our surveys or reported by local observers (Table 1). The mean count of 729 birds represents 0.25% of the estimated great knot population in 2007 (Wetlands International, 2019).

Overall, only 16 of the 92 sites (17%) had been previously identified as important for great knots, and 34 of the 92 sites (37%) as important for "coastal obligate" shorebirds; the rest (63%) were unknown (Figures 1 and 4, Table S2). In the relatively intensely surveyed Yellow Sea, relatively few sites were unknown (9 of 23; 39%) of which five were in North Korea (Figures 1 and 4). For the other regions, the majority of sites that great knots used were unknown: 53% of the sites in Russia, 56% in Southern China and 100% in Southeast Asia (Figure 4). All 20 individuals with complete migration tracks stopped at one or more unknown sites. The degree of usage, measured by the number of individuals stopping and their stopping duration, did not differ significantly between known and unknown sites in Southern China (U = 53, p = .144; $F_{1,45}$ = 1.52, p = .224; Figure 5). In the Yellow Sea and Russia, more great knots stopped at known sites (U = 25.5, p = .015; U = 23.5, p = .036) and stayed longer ($F_{1,74}$ = 4.03, p = .048; $F_{1,39}$ = 4.29, p = .045; Figure 5).

4 | DISCUSSION

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

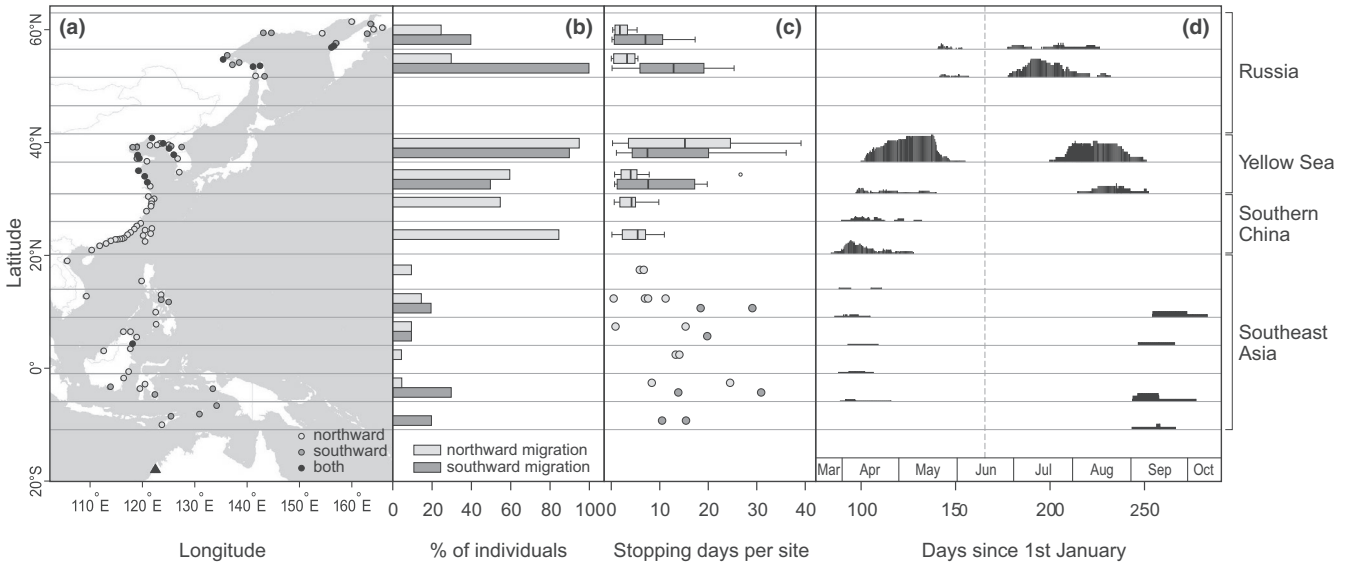

FIGURE 2 Occurrence of satellite-tracked great knots along the East Asian–Australasian Flyway. Horizontal lines indicate boundaries of latitudinal intervals for analyzing bird usage. (a) Sites used by satellite-tracked great knots during northward, southward and both migrations in 2015–2017. Triangle shows the tag deployment location in Northwest Australia. (b) Percentage of individuals stopping and (c) Number of stopping days per site, amalgamated at latitudinal intervals. (d) Temporal occurrence of individuals across the latitudinal intervals, with height corresponding to number of individuals that migrated through a latitudinal interval

We recognize that the increased load and drag from the transmitters (Pennycuick, Fast, Ballerstaedt, & Rattenborg, 2012) may have caused the birds to reduce their non-stop flight distances. External devices are known to handicap birds (Barron et al., 2010; Chan et al., 2016; Hupp et al., 2015). Accordingly, the great knots in this study showed lower survival (0.51, 95% CI: 0.38–0.65) during their first year of carrying a transmitter compared to birds without a transmitter (0.75, 0.64–0.83; Appendix S1). This difference may have been caused by tagged birds being less agile in flight and thus more prone to predation by raptors (Chan et al., 2016). However, estimated breeding success of the satellite-tracked great knots (60% of 20 birds, defined as a stay of more than 34 days at the breeding site would result in eggs hatching, as reported in Lisovski, Gosbell, Hassell, & Minton, 2016) was very similar to that of Arctic-breeding shorebirds (61% of 7,418 nests of 17 taxa, range = 46%–73%, Weiser et al., 2018), and of great knots tracked with leg-flag mounted geolocators from the same non-breeding area in Northwest Australia (50% of eight birds; Lisovski, Gosbell, Hassell, et al., 2016). Moreover, all the eight geolocator-tracked great knots stopped in Southeast Asia and Southern China during northward migration (though the exact locations and durations of these stops could not be determined at the level of detail as of satellite-tracked birds; Lisovski, Gosbell, Hassell, et al., 2016) and arrival dates at the northern Yellow Sea (36.5–41.5°N) during northward migration do not differ between geolocator-tracked birds (19 April ± 9 days, n = 6, excluding a late bird which arrived on 10 June) and satellite-tracked birds (25 April ± 11

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

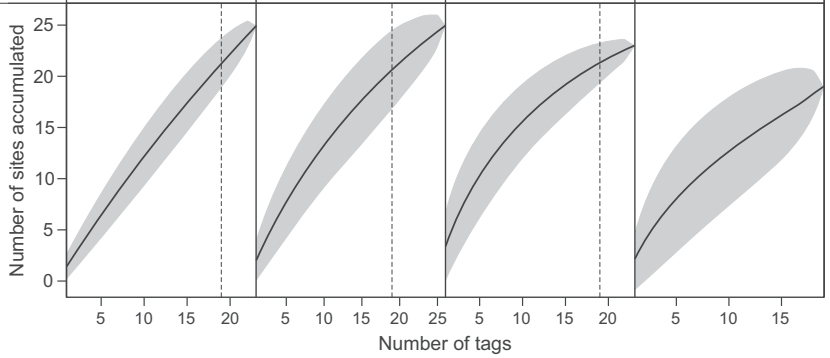

FIGURE 3 Accumulated number of sites discovered per region with increasing number of tracked birds (shaded regions, ±2*SD*). To help comparing between regions, the 19th tag is indicated by a dotted line

days, $n = 19$; Mann–Whitney $U = 38$, $p = .25$; note that none of the six geolocator-tracked birds stopped in the southern Yellow Sea).

Stopping patterns of the geolocator-tracked birds (Lisovski, Gosbell, Hassell, et al., 2016), together with the observations of flocks of great knots in Southern China presented here, indicate to us that the use of Southeast Asia and Southern China cannot simply be regarded as an effect of tagging. Rather, there could be biological explanations for the difference in arrival time to the Yellow Sea between tracked birds and earlier ground observations. The earliest arriving great knots at the Yellow Sea could be from wintering populations other than Northwest Australia (where the geolocator- and satellite-tracked birds were captured). Moreover, migration strategy of great knots could have been changing over the past 20 years, possibly as a response to the destruction and deterioration of Yellow

TABLE 1 Counts at sites visited by satellite-tracked great knots along the Southern China coast from April 2015 to 2017 (the same years as the satellite tracking)

Site	Province/region	Coordinates of centroid	Count date	Count of great knots	Occurrence of tracked birds[a]	Number of tracked birds
Surveys in this study						
Dongli, Leizhou	Guangdong	20.82°N, 110.38°E	8 April, 2016	836	4–11 April, 2015	1
Hailingdao, Yangjiang	Guangdong	21.71°N, 111.93°E	6 April, 2017	192	27–29 March, 2015	2
Dacheng Bay, Chaozhou	Guangdong	23.59°N, 117.14°E	8 April, 2017	34[b]	1–10 April, 30 April–7 May, 2016 and 2017	2[c]
Ruian, Wenzhou Bay	Zhejiang	27.79°N, 120.79°E	10 April, 2017	2,160	31 March–11 May, 2015, 2016 and 2017	9
Linhai, Taizhou	Zhejiang	28.72°N, 121.69°E	14 April, 2017	950	16–22 April, 2015 and 2017	2
Cixi, Hangzhou Bay	Zhejiang	30.38°N, 121.18°E	16 April, 2017	204	7–11 April, 2015 and 2016	3
Other records						
Mai Po, Deep Bay	Hong Kong SAR	22.49°N, 114.02°E	31 March, 2016	278[b]	30 March–7 April, 2016	1
Dadengdao, Xiamen	Fujian	24.55°N, 118.27°E	4 April, 2015	115[b]	31 March–21 April, 2015 and 2016	4

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

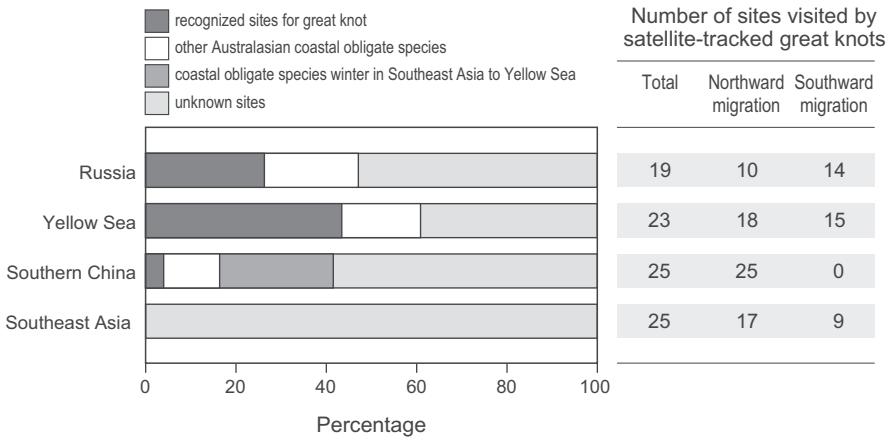

FIGURE 4 Knowledge status of East Asian–Australasian Flyway stopping sites of satellite-tracked great knots. Bars represent percentage of sites that are currently recognized as: important for great knots (i.e. listed in at least one of the published lists of important sites within the flyway; Conklin et al., 2014; Jaensch, 2013; Zhang et al., 2017; East Asian–Australasian Flyway Partnership, 2018a), important for other coastal migratory shorebird species wintering in Australia and/or New Zealand, or important for other coastal obligate shorebird species that winter from Southeast Asia to Yellow Sea (Table S1). "Unknown" sites have not been recognized as important shorebird sites

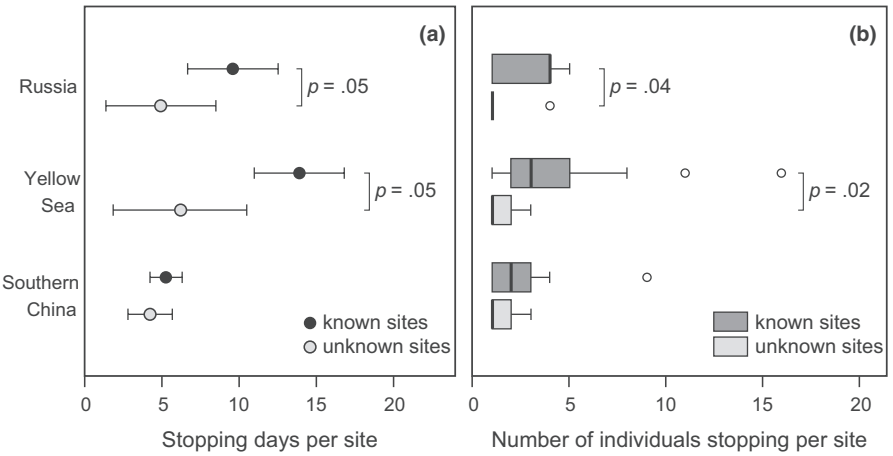

FIGURE 5 (a) Means and 95% Confidence Intervals of stopping duration and (b) boxplots representing number of individuals stopping per known and unknown sites within the regions of Russia, Yellow Sea and Southern China. Significant differences between known and unknown sites within a region are depicted with the corresponding p-values, as determined by a (a) one-way ANOVA or (b) Mann–Whitney–Wilcoxon test

Sea habitats (Murray et al., 2014; Zhang et al., 2018). However, the lack of historical data from Southeast Asia and Southern China prevents further interpretation. Nevertheless, the pattern of great knots stopping in Southern China and Southeast Asia probably represents the current migration behaviour of individuals from the Northwest Australia non-breeding area (where the tagged individuals were caught and where >55% of the flyway population resides; Hansen et al., 2016). The high rates of habitat degradation in these regions from coastal development and hunting (Li & Ounsted, 2007; Martinez & Lewthwaite, 2013; Zöckler et al., 2016) therefore represent potential big threats for this species.

At the site level, we mapped 92 stopping sites used by the tracked great knots (Figure 1, Table S2). Our analysis of the number of sites discovered per tag revealed that, in Southeast Asia, Southern China and Russia, more new sites could have been discovered per region if more birds had been tracked (Figure 3). Therefore, our list of sites should not be viewed as comprehensive, but rather as a sample of great knot stopping sites independent of ground survey efforts. Likewise, our list contains sites that are potentially important for other coastal obligate shorebird species. The general co-occurrence of great knots with these other species may be explained by their shared prey preferences (Choi et al., 2017; Yang et al., 2013) and the fact that productive mudflats contain high densities of benthos and biofilm and the shorebirds that feed on them (Mathot, Piersma, & Elner, 2019).

The conventional thinking that conservation priorities should be placed at sites with high concentrations of birds and where birds stop the longest (the staging sites sensu Warnock, 2010), is in accordance with our finding that the sites used by more than one-third of the tracked individuals were all known (Figure 1). However, the majority of sites that the tracked great knots used were not included in existing conservation listings of important coastal shorebird sites. Notably, every tracked great knot used unknown sites, implying that the bulk of the population faces unknown conditions and threats during part of their migration. Although stops at unknown sites were briefer in general (Figure 5), these brief stops may represent "emergency staging sites" that migrants rely on when encountering poor weather conditions during migration (Shamoun-Baranes et al., 2010). Some stopping sites could also allow migrants to recover from the exhaustion of long non-stop flights (see discussion in Piersma, 2011), for example, to catch up on sleep (e.g. Moore, 2018; Schwilch, Piersma, Holmgren, & Jenni, 2002). Moreover, they may provide alternative habitat if established prime sites become degraded. We suggest that an expansion of conservation efforts beyond protecting the stopping sites with most birds (i.e. the classical "staging sites") could be evaluated as a framework for greater population resiliency.

To assist in prioritizing conservation efforts, we need to start collecting information on bird numbers, habitat characteristics and threats at these lesser known sites. Important waterbird sites have traditionally been discovered through ground surveys. Sites that were unknown before our study likely lacked surveys and observers. Far less knowledge of bird occurrence existed for coastlines outside of the Yellow Sea and Japan, and recent waterbird counts are usually conducted by volunteers at a much smaller scale than citizen science projects in Western Europe and North America (Bai et al., 2015; Chandler et al., 2017). Brief surveys might also miss birds that stop only briefly, which might explain why some sites within the comparatively well-studied Yellow Sea were unknown before our study. Satellite tracking data can help by focusing survey efforts during periods with the greatest chances of encountering birds. Moreover, a major advantage of satellite tracking over geolocation (a method commonly used to track small bird species, see Lisovski, Gosbell, Christie, et al., 2016 for an example to identify important areas for conservation) is that potential roosting and feeding areas within a large area can be located from the relatively higher accuracy locations (error < 2.5 km; Douglas et al., 2012) of satellite-tracked birds (e.g. Chan, Peng, Han, 2019). For example, observers used the spatial and temporal information from our tracking data to narrow down the search area in the extensive Liaohe Estuary and Inner Gulf of Liaodong in the Yellow Sea, and discovered *c*. 60,000 great knots at Gaizhou in 2015 (Melville, Peng, Chan, 2016). Moreover, the spatial and temporal information from our tracking data also enable us to find several sites in Southern China with >0.25% of great knot flyway population during our surveys (Table 1).

Tracking data can help interpret counts from ground surveys. While current conservation listings are based on counts, the proportion of tracked birds using a site provides a complementary measure

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

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

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AUTHORS' CONTRIBUTIONS

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

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.f2g5f49 (Chan, Tibbitts, Lok, 2019).

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SUPPORTING INFORMATION

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

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