

Research



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Upper tidal flats are disproportionately important for the conservation of migratory shorebirds

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Migratory animals play vital ecological roles in ecosystems worldwide, yet many species are threatened by human activities. Understanding the detailed patterns of habitat use throughout the migration cycle is critical to developing effective conservation strategies for these species. Migratory shorebirds undertake some of the longest known migrations, but they are also declining precipitously worldwide. To better understand the dynamics of shorebird declines along the East Asian–Australasian Flyway, we quantified the spatiotemporal foraging distribution of 17 migratory shorebirds at two critical stopover sites. We found that shorebirds exhibit substantial interspecific and site-specific differences in their foraging distributions. Notwithstanding these differences, however, the upper tidal flats appear to be especially important to most shorebirds by providing more than 70% of the birds' cumulative foraging time, twofold greater than their proportional area. Because the upper tidal flats are also more prone to coastal development, our findings may help to explain why shorebird populations along the flyway have declined much faster than the overall rate of tidal flat loss. Our work highlights the importance of protecting upper tidal flats to conserve migratory shorebirds and demonstrates the value of a detailed ecological understanding of habitat usage by migratory animals for conservation planning.

1. Introduction

Animal migration is a ubiquitous global phenomenon, and migratory species play vital ecological roles that are crucial for the functioning of ecosystems [1]. Yet, many migratory animals are rapidly declining due to human activities [2]. Pinpointing the causes and magnitude of these declines is challenging, given the need to understand species' habitat requirements at multiple sites, often over very long distances. Moreover, many migrants face multiple threats, which further complicate efforts to conserve them. While identifying the magnitude and causes of declines in migratory animals usually requires large-scale monitoring efforts [3–7], insights from site-level studies that consider explicitly the ecology of individual species and site-specific threats are crucial to develop and implement effective conservation strategies to conserve migratory species [8,9].

Migratory shorebirds undertake some of the longest migrations of any migratory animals [10], but they are also declining precipitously worldwide [4,5], especially in the East Asian–Australasian Flyway (EAAF) [11–13]. Shorebird declines along the EAAF have been largely attributed to the loss of tidal flats, which provide critical stopover habitats, in the Yellow Sea region due to coastal development [14–16]. During the 1950s–1980s, more than half of the tidal flats in the Yellow Sea disappeared ($-3.0\% \text{ yr}^{-1}$); during the 1980s–2000s, the rate of loss slowed down but was still $-1.2\% \text{ yr}^{-1}$ [17,18]. However, many species along the EAAF have experienced much steeper population declines than the rate of habitat loss. Spoon-billed sandpipers (*Calidris pygmaea*) declined at an estimated rate of $26\% \text{ yr}^{-1}$ during 2002–2009 [19]. Five of the

fastest-declining shorebird populations that winter in Australia and New Zealand were all declining at rates ranging between 5.1 and 7.5% yr⁻¹ during the 1990s–2010s [11]. A more in-depth understanding of the nature of shorebird declines along the EAAF may help to conserve not only these species but shorebirds along other flyways as well.

The discrepancy between the rates of habitat loss and population decline remains a puzzle. One part of the explanation possibly lies in the fact that not all stopover sites along the EAAF are of equal value to migrating shorebirds [11]; destroying the key stopover sites could have disproportionately detrimental impacts on migrant populations [16,20]. However, where exactly habitat loss occurs within the tidal flats could also matter greatly. Tidal flats are a spatially heterogeneous habitat due to the elevational gradient and the resulting changes in substrate characteristics and benthic invertebrate communities from the high-tide line to the low-tide line [21–24]. Moreover, because of the tidal cycle, only a portion of the tidal flats can be accessed for most of the day at a given site, making the tidal flats temporally heterogeneous. Most of the previous studies of shorebirds' habitat preferences and foraging distributions along other flyways have been conducted during the low-tide periods when all of the tidal flats are freely accessible (e.g. [23,25,26]), while shorebird population monitoring studies are focused on the high-tide periods when birds are packed into a small area and therefore easier to count [20].

Thus, we lack a complete picture as to how shorebirds use the tidal flats, one that takes into account both the spatial and temporal distributions of foraging shorebirds across the entire tidal cycle, especially during ebbing and flooding tides when only a portion of the tidal flats is available to the birds [26]. This gap in our knowledge may impede our ability to develop sound conservation practices for these birds in terms of identifying areas of higher conservation values within the tidal flats. If the portions of the tidal flats that are most important to shorebirds are also the portions that are disproportionately lost due to development, then treating the tidal flats as a homogeneous habitat and averaging the rate of tidal flat loss across the entire range would underestimate the intensity of the threat from coastal development and its potential impact on shorebird populations.

Here, we quantified the habitat use patterns and preferences exhibited by migratory shorebird communities at two major stopover sites in the Yellow Sea. We conducted field surveys to simultaneously map the spatial and temporal foraging habitat use of shorebirds throughout tidal cycles. We identify the foraging types based on the species' use of tidal flats and compare the consistency of these patterns between sites. We also assess the importance of different portions of the tidal flats based on the cumulative time that different species spent foraging on them. In so doing, we identify the upper tidal flat as probably crucially important for the conservation of migratory shorebirds.

2. Material and methods

(a) Field sites and data collection

We conducted fieldwork at two well-known stopover sites for migratory shorebirds in the Yellow Sea region of China: Rudong (32.5 N, 121.2 E) from September to October, 2016, and Nanpu (39.1 N, 118.2 E) from April to May, 2017 (figure 1), coinciding

with the peak migration at each site. Rudong is an important site for 18 coastal shorebirds, especially during the southward migration [20,27], and Nanpu supports large populations of at least 12 shorebirds during the northward migration [28,29].

We set out survey transects on the tidal flats (figure 1) following the design of an earlier study [30]. The transects ran perpendicular to the tidal fronts and covered the entire elevational gradient from the seawall (approx. the average high-spring-tide line) to the low-tide line. The design and layout of transects differed slightly between the two sites because of local conditions: At Rudong, our two transects ran 4.5 km each and were set out so as to avoid areas of high human disturbance, or with numerous tidal channels, or covered by invasive *Spartina* grass; at Nanpu, four pairs of transects, running 2.25 km each, were set out to increase the coverage of the width of the tidal flat, and the data from each transect pair were analysed together to increase the temporal resolution of data. Along each of these transects, we delineated sets of nine adjacent survey plots, 500 m × 500 m at Rudong and 250 m × 250 m at Nanpu. Each plot was numbered 1 to 9, starting from the plots closest to the seawall, to indicate its relative position along the transects. At various steps of data analysis, we pooled the data from different transects at the same site in order to increase sample size by combining the value or data from plots of the same number. The average distance of each numbered plot to the seawall was calculated for the combined transects, using the distance to the seawall from the midpoint of each plot.

In daylight during the spring tides, two to four experienced observers conducted simultaneous surveys of foraging shorebirds in different plots along a given transect. We chose spring tides because they are the periods when the whole tidal flats are flooded and exposed over the course of a full tidal cycle. Each transect was surveyed for 2 to 4 days to ensure that every plot was counted at different times of the tidal cycle, with the cumulative data representing at least two entire tidal cycles pooled for the analysis. For each transect, observers walked parallel to the transects, staying at least 100 m outside the boundaries of each plot to avoid disturbing the birds, and recorded the species and numbers of foraging shorebirds within a plot at the time. The time spent surveying each plot varied depending on the number of shorebirds in it, and the surveyors started counting the next plot as soon as they finished the previous one. Time of exposure/immersion of each plot was also noted to estimate the speed of tidal front movements.

Shorebirds were identified to species in most cases. However, three pairs of similar-looking shorebirds were grouped together: great knot (*Ca. tenuirostris*) and red knot (*Ca. canutus*, 'knots'; in Rudong only, as conditions permitted us to identify them to species at Nanpu); Eurasian curlew (*Numenius arquata*) and Far Eastern curlew (*N. madagascariensis*, 'curlews', both sites); lesser sand plover (*Charadrius mongolus*) and greater sand plover (*Ch. leschenaultii*, 'sand plovers', both sites). In total, 21 shorebird species (or species groups, referred to as 'species' hereafter) were recorded in 827 plot counts. Species recorded in 10 or fewer plot counts at a site were excluded from the analysis, leaving 13 species at Rudong and 13 species at Nanpu. With the data from different transects combined, the average interval (\pm s.d.) between two counts of the same plot was 15.7 (\pm 17.3) min, indicating a relatively high degree of temporal resolution in the counting data.

For easier interpretation of our analysis and results, we divided transects into three zones, each consisting of three plots, representing the upper (plot 1–3), middle (plot 4–6) and lower (7–9) tidal flats. We recognize that this does not follow the classical delineation of intertidal zones based on the tide levels of different tidal cycles [31]; however, due to the lack of detailed information on the topology of our study sites, we followed previous studies in delineating the zones by dividing each transect into three parts [30,32].

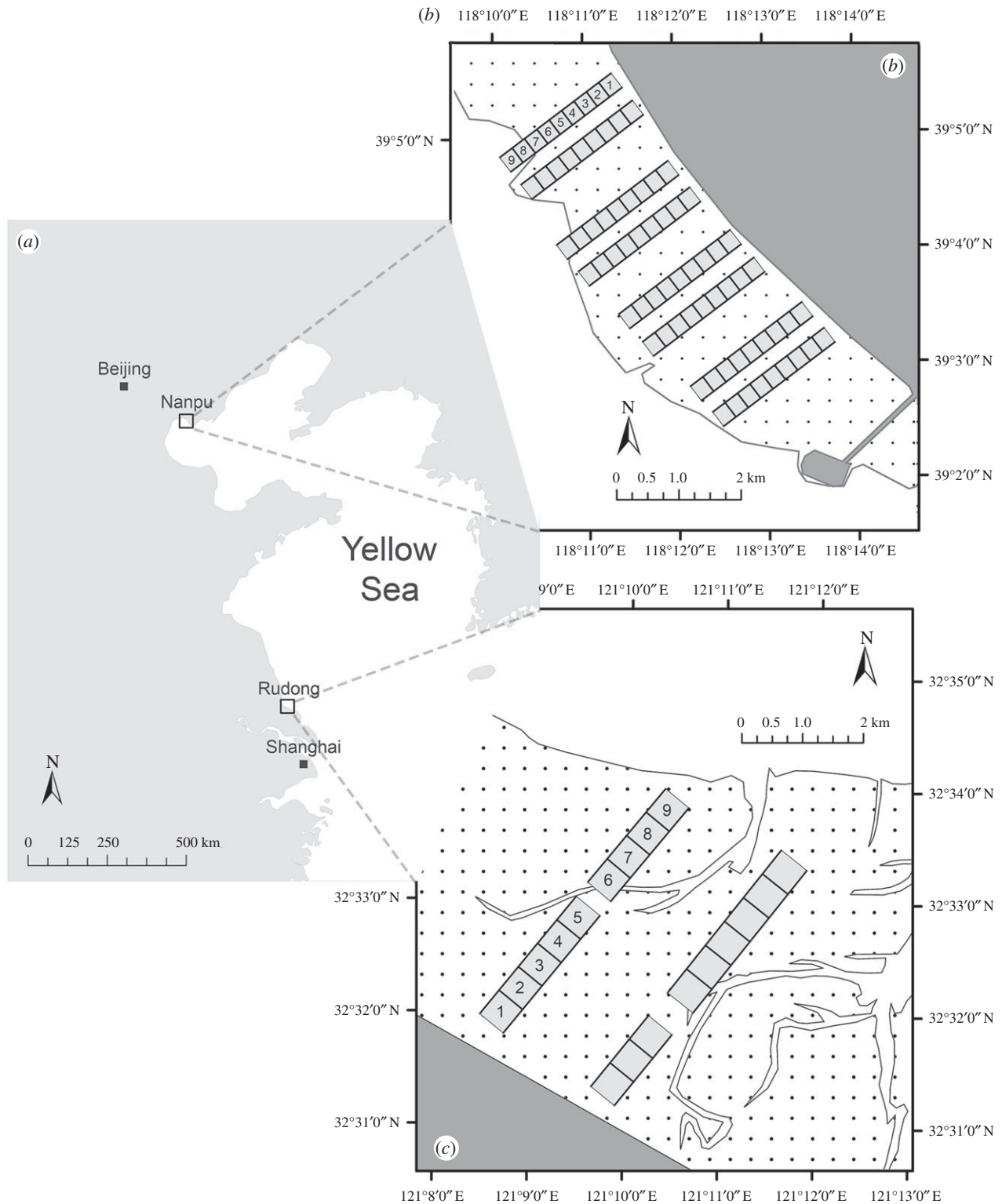


Figure 1. Location of study sites in the Yellow Sea (a) and layout of transects at Nanpu (b) and Rudong (c). At Nanpu (b), each transect contained nine plots of $250\text{ m} \times 250\text{ m}$; adjacent transects constituted a transect pair whose data were combined and analysed together. At Rudong (c), each transect contained nine plots of $500\text{ m} \times 500\text{ m}$. Plots were numbered 1–9 based on their relative position to the seawall. In (b) and (c), dark grey areas represent land above the high-tide line; stippled areas represent tidal flats and light areas represent the sea beyond the low-tide line. Tidal flat data are from [35].

(b) Spatial and temporal distribution of shorebirds

To quantify shorebirds' spatial and temporal distributions, we calculated how the positions of shorebirds' 'abundance centroid' changed with the proportion of tidal flats exposed. A species' 'abundance centroid' is the average position of all the individuals during a specific time, and the proportion of tidal flat exposed is a temporal index showing the relative time during a tidal cycle (figure 2). Because a given species may use tidal flats differently depending on the season and site [26], we analysed the counts of

species that occur at both Rudong and Nanpu separately, and we will refer to them as two different populations hereafter because of the potential site-specific patterns.

Based on our field observations and consistent with previous studies [26,30], we proposed three foraging types for shorebirds using the tidal flats: generalists, zone specialists and tide followers (figure 2). *Generalists* feed whenever and wherever the tidal flats are exposed, thus, on a graph showing the positions of the abundance centroid against the proportion of tidal flat

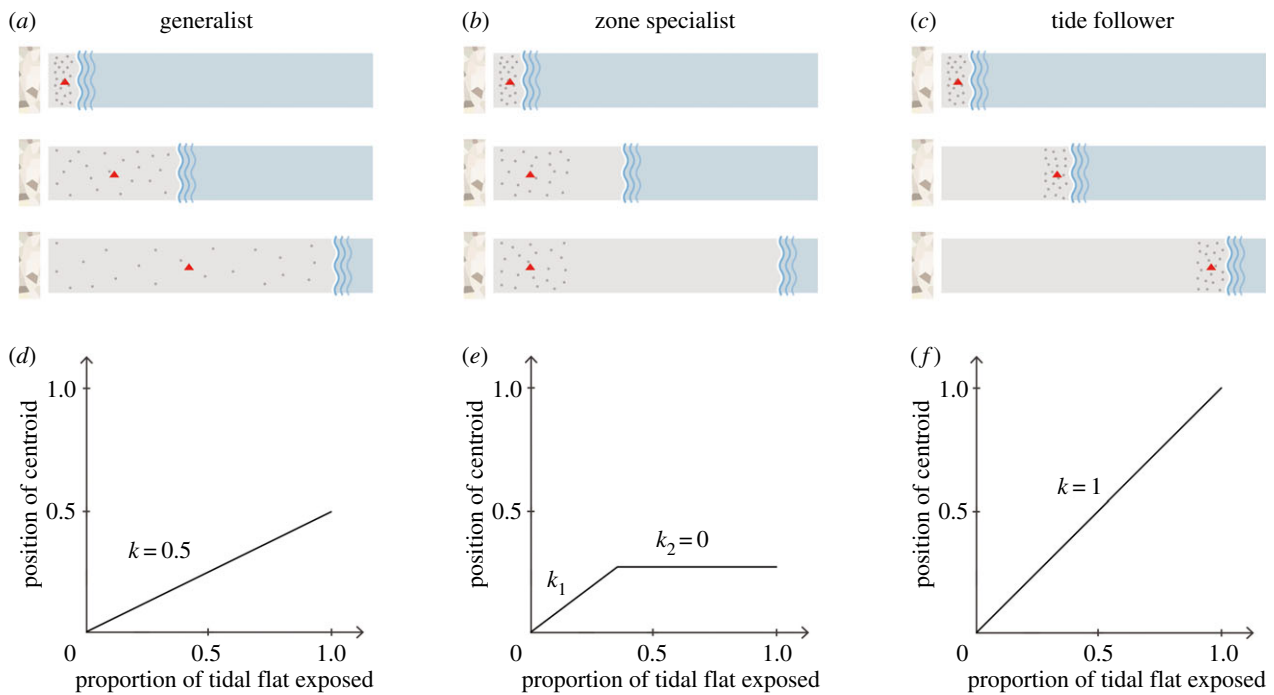


Figure 2. Schematic representation of three foraging types exhibited by shorebirds. Boxes in (a, b, c) represent the same stretch of a tidal flat with the seawall (high-tide line) on the left and the low-tide line on the right, when varying proportions of the tidal flats are exposed, representing high, ebbing/flooding and low tides, from top to bottom. The leftmost blue wavy lines represent the location of the tidal front, with the areas to the right of the lines covered by water. Grey dots represent individual foraging shorebirds, and the red triangles represent the positions of the abundance centroid. (d, e, f) The centroid plots show the relationship between the position of the abundance centroid and the proportion of tidal flats exposed. (Online version in colour.)

exposed ('centroid plot' in short), the slope k will be around 0.5, as the centroid will move towards the middle area when the entire tidal flat is exposed. *Zone specialists* exhibit a strong preference for a particular part of the tidal flats and remain there even when additional area becomes available. On the centroid plot, the line will be segmented: the slope will increase initially (k_1) and then stay unchanged (k_2 , around 0). *Tide followers*, as the name suggests, follow the movement of the tidal front and feed in areas that are freshly exposed or about to be submerged. On the centroid plot, the slope k for tide followers will be around 1.

The abundance centroids were calculated in three steps. First, we transformed the time when each plot was counted into the position of the tidal front based on an average speed of tidal front movements which we measured during the survey separately for ebbing and flooding tides for each transect. When scaled to 0–1, with 0 representing the seawall and 1 representing the end of a transect (approx. the position of high- and low-tide lines, respectively), this relative position of the tidal front is also the proportion of tidal flats exposed. Next, we combined the counts from different transects at the same site and binned the plot counts into eight tidal periods based on the proportion of tidal flat exposed, in intervals of 0.125. The number, eight, was chosen subjectively as a trade-off between the number of time periods and the number of plot counts in each period. For each plot in a given tidal period, we calculated the average number of foraging individuals of each species. Finally, a species' abundance centroid for a given tidal period at a study site was calculated as the weighted average distance to the seawall, using the distance of each plot to the seawall and the average numbers of individuals of the species in the plot during the tidal period. We normalized the abundance centroids to the same scale as the proportion of tidal flat exposed.

To identify the foraging types, we tested the slope k using a linear model starting at (0, 0). We then used the *segmented* function in R Package *segmented* [33] to test how the relationship fits a broken line. We chose the following set of criteria to assign each population to a corresponding foraging type based on the results

of statistical tests: generalists, $0.45 \leq k \leq 0.55$ and $r^2 > 0.90$; zone specialists, $-0.05 \leq k_2 \leq 0.05$, $r^2 > 0.90$; tide followers: $0.9 \leq k \leq 1.0$ and $r^2 > 0.90$. This set of criteria was chosen subjectively, and slightly altering them would not change our results and conclusion substantively. Testing whether the specific slope of the relationship falls in the given ranges was done by either testing whether the residuals of the specific linear model overlapped with 0 (for generalists and tide followers), or by overlapping the 95% CI (± 1.96 SE) of k_2 with the specified range (for zone specialists). Note that these criteria are not mutually exclusive or exhaustive: if a species was assigned to more than one type, we used Bayesian information criterion (BIC) to choose the better fit between the linear and segmented models [34]; if a species was not assigned to any type, we grouped that species as 'not assigned'.

(c) The importance of different tidal flat zones

To quantify the importance of different tidal flat zones as foraging habitat to shorebirds, we calculated the cumulative foraging time in bird*minute(s) for each plot across entire tidal cycles. The cumulative foraging time takes into account both how many birds used the area and how long they spent feeding there, providing a comparable and quantitative measurement of habitat importance for within-site comparisons. Assuming the birds were constantly foraging between successive plot counts, for each plot in a transect, we plotted the changes in the number of foraging individuals for each species against the time during the tidal cycle and calculated the area under the curve, i.e. the cumulative foraging time of the species for the plot.

To determine the importance of different zones of the tidal flats to the overall foraging by shorebirds, we summed the cumulative foraging time for each species across all transects at the same site. This enables us to show the relative importance of each zone and to simulate the instantaneous impacts of coastal development of the tidal flats on shorebird foraging by calculating the loss of foraging time, assuming that the habitat loss progresses from the seawall to

Table 1. Foraging types of shorebirds at Nanpu and Rudong. Each shorebird population was grouped into a foraging type by testing whether the slope of the relationship between the positions of the species' abundance centroid and the proportion of tidal flats exposed falls within the specified range of values. —: Not recorded or with too few observations for analysis.

species	Nanpu	Rudong
grey plover <i>Pluvialis squatarola</i>	zone specialist	generalist
Kentish plover <i>Charadrius alexandrinus</i>	zone specialist	generalist
sand plovers <i>Ch. mongolus</i> and <i>Ch. leschenaultii</i>	—	generalist
curlews <i>Numenius madagascariensis</i> and <i>N. arquata</i>	not assigned	generalist
bar-tailed godwit <i>Limosa lapponica</i>	zone specialist	zone specialist
ruddy turnstone <i>Arenaria interpres</i>	generalist	zone specialist
great knot <i>Calidris tenuirostris</i>	tide follower	—
red knot <i>Ca. canutus</i>	generalist	—
knots <i>Ca. tenuirostris</i> and <i>Ca. canutus</i>	—	not assigned
curlew sandpiper <i>Ca. ferruginea</i>	zone specialist	—
red-necked stint <i>Ca. ruficollis</i>	not assigned	generalist
sanderling <i>Ca. alba</i>	tide follower	—
dunlin <i>Ca. alpina</i>	tide follower	zone specialist
Terek sandpiper <i>Xenus cinereus</i>	zone specialist	zone specialist
grey-tailed tattler <i>Tringa brevipes</i>	—	not assigned
common greenshank <i>T. nebularia</i>	zone specialist	generalist
marsh sandpiper <i>T. stagnatilis</i>	—	zone specialist

the low-tide line, with no rapid population response or reassortment by the benthic invertebrate fauna upon which the shorebirds feed in the remaining undeveloped portions of the tidal zone.

3. Results

(a) Generalists, zone specialists and tide followers

Among the 26 populations recorded, we identified eight generalists, 11 zone specialists, and three tide followers (table 1; figure 3; electronic supplementary material, figure S1). Four populations were not assigned to any type, mostly due to small sample sizes or intermediate patterns. Among the nine species that occur at both Rudong and Nanpu, seven species were assigned a foraging type at both sites, and among them, only two species, the Terek sandpiper (*Xenus*

cinereus) and bar-tailed godwit (*Limosa lapponica*), exhibited the same foraging type at both sites.

(b) Upper tidal flats as critical foraging habitat

For most shorebirds among the 26 populations, the majority of their foraging time was spent in the plots closer to the seawall, shown by the cumulative foraging time along the tidal flats (figure 4; electronic supplementary material, figure S2). This is especially the case among generalists and zone specialists; tide followers predictably divided their foraging time roughly equally across the different plots or zones. For example, the proportions of cumulative foraging time spent by a generalist, the Kentish plover at Rudong, on the upper, middle and lower tidal flats, respectively, were 74.5%, 17.5% and 8.0%; for a zone specialist, the Terek sandpiper at Nanpu, these values were 99.0%, 1.0% and 0% and for a tide follower, the sanderling at Nanpu, they were 17.7%, 46.8% and 35.5%.

We aggregated the cumulative foraging time and plotted the loss of total foraging opportunity that would occur in response to a hypothetical loss of tidal flats that progresses from the seawall outward into the ocean to simulate the instantaneous effect of coastal development (dashed lines in figure 4; electronic supplementary material, figure S2 for individual species; solid lines in figure 5 for all species in a given foraging type). Losing the upper third of the current tidal flats would lead to a reduction in cumulative foraging time of, on average (\pm s.d.), 77.6% (\pm 13.6%) for generalists, 81.0% (\pm 20.9%) for zone specialists, 23.5% (\pm 17.0%) for tide followers, and 75.0% (\pm 32.3%) for species not assigned to any foraging types.

4. Discussion

The conservation of migratory species requires an understanding of both their ecology at a fine spatial scale and the site-specific threats they face. By quantifying the spatial and temporal patterns in shorebird foraging distributions throughout the tidal cycle at two critical stopover sites in the Yellow Sea, we found that 17 migratory shorebirds exhibit substantial interspecific and even site-specific differences in their use of different portions of the tidal flats (table 1; figure 3; electronic supplementary material, figure S1). These populations can be mostly grouped into three foraging types: generalists, zone specialists and tide followers. Notwithstanding these differences in foraging behaviour, however, the upper tidal flat zone provides the majority of the cumulative foraging time of both the generalists and the zone specialists, far greater than the upper tidal zone's proportional area (figures 4 and 5; electronic supplementary material, figure S2). Because coastal development projects typically start near the high-tide line and proceed outward toward the sea [35,36], the upper tidal flats are also more prone to development than are the lower tidal flats, which may help to explain why shorebird populations along the EAAF have declined much faster than the overall rate of stopover habitat loss. Our work highlights the need to conserve as much of the upper tidal flats as possible within important stopover sites in order to protect today's diminished populations of migratory shorebirds. Our study also demonstrates the value of understanding the detailed patterns of habitat usage by migratory species throughout their journeys in order to properly conserve them.

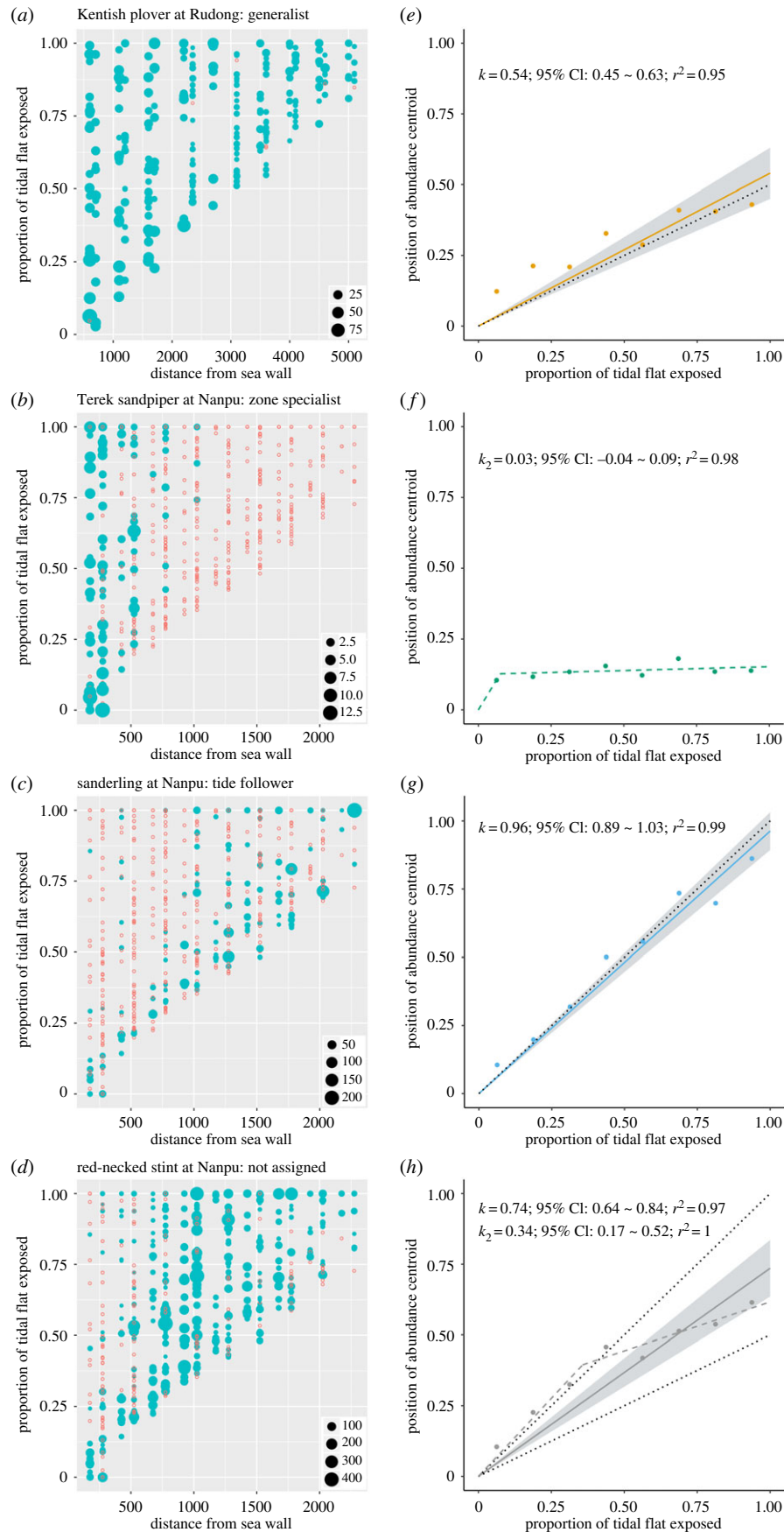


Figure 3. Distribution and centroid plots of four representative shorebird populations. We show here the representative populations of the three foraging types, and one population that was not assigned. In the spatiotemporal distribution plots (a, b, c, d), the number of foraging individuals recorded in a plot count is represented by the size of the solid blue circles, and the red open circles represent counts with 0 individuals. In the centroid plots (e, f, g, h), solid circles represent the positions of abundance centroid calculated for each tidal period along the tidal flats (0: seawall/high-tide line; 1: low-tide line). The solid line is the best-fitting line for the centroids passing through (0, 0), with 95% confidence intervals shown in grey. The dotted reference line has a slope of 0.5 (generalist) or 1 (tide follower). The dashed line represents the predicted broken-line relationship (zone specialists). All analysed populations are in electronic supplementary material, figure S1. (Online version in colour.)

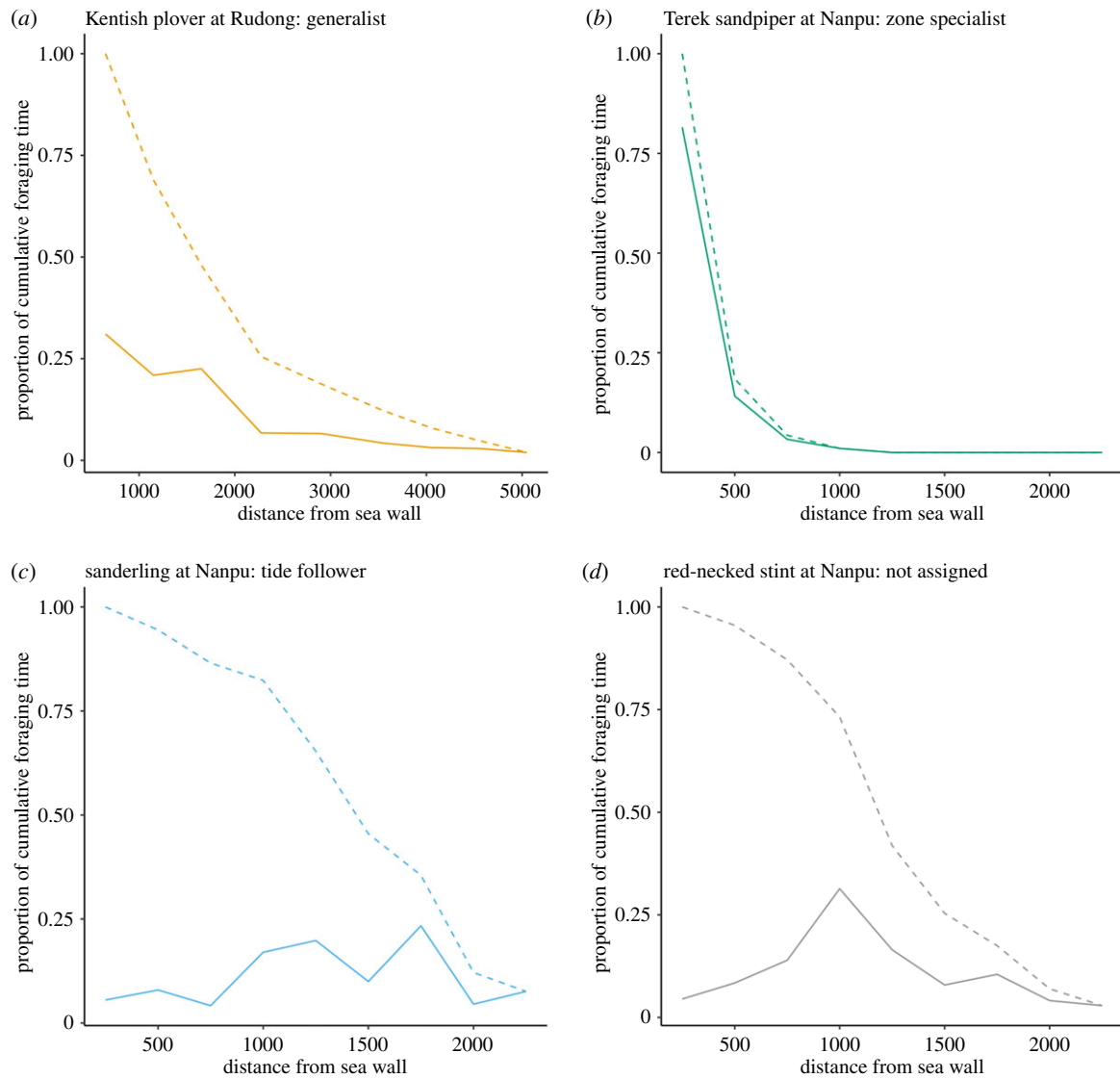


Figure 4. (a–d) Cumulative foraging time along the tidal flat for four representative shorebird populations. The cumulative foraging time of the same species in figure 3 is shown as the proportion of total cumulative foraging time for a given population at a given site with transects summed. Solid lines show the distribution of cumulative foraging time of each plot along the tidal flat. Dashed lines show the reduction in total cumulative foraging time that would result from the hypothetical loss of tidal flats starting from the seawall and progressing seaward. (Online version in colour.)

(a) Differences in the foraging types

By taking into account the temporal changes in habitat availability, we show that most shorebird species at the two stopover sites fall into the three foraging types. Previous studies along other flyways about the foraging distribution of shorebird communities and their relationship with food availability have focused almost entirely on the spatial pattern during low tides [23,25], thereby overlooking the temporal changes in habitat (and thus food) availability and their effect on shorebirds' foraging behaviour during ebbing and flooding tides (see [26,30,37,38] for studies that considered tidal movements). Our analysis also shows that the same species may display different foraging behaviours at different stopover sites (table 1; figure 3). Of the seven species that occurred at and could be assigned to a foraging type at both sites, only two exhibited the same type, suggesting that these foraging behaviours may not be a species-specific behavioural property but, as suggested by earlier studies, may change in response to local environmental conditions [38–41], or differ between sexes or subspecies that constitute the local populations [42,43].

This result, while statistically robust for some species, needs to be validated by further studies. To simultaneously quantify the spatial and temporal aspects of shorebirds' foraging distributions, our statistical tests rely on a single-derived and consolidated property (the position of shorebirds' abundance centroid in relation to the proportion of tidal flats exposed), which limits our ability to identify and account for finer patterns and changes in foraging distributions (e.g. red knot at Nanpu, in electronic supplementary material, figure S1). Our approach is expected to be especially poor at distinguishing between a generalist and a zone specialist, because a zone specialist will gradually turn into a generalist if its preferred foraging zone covers an increasingly large portion of the tidal flats. This was evident in our analysis when we had to rely on BIC to choose the better model describing the distributions of two populations that fell into both the generalist and zone specialist categories. There is clearly a need for more sophisticated statistical methods and more comprehensive field studies focused on the foraging behaviours of shorebirds using tidal flat habitat.

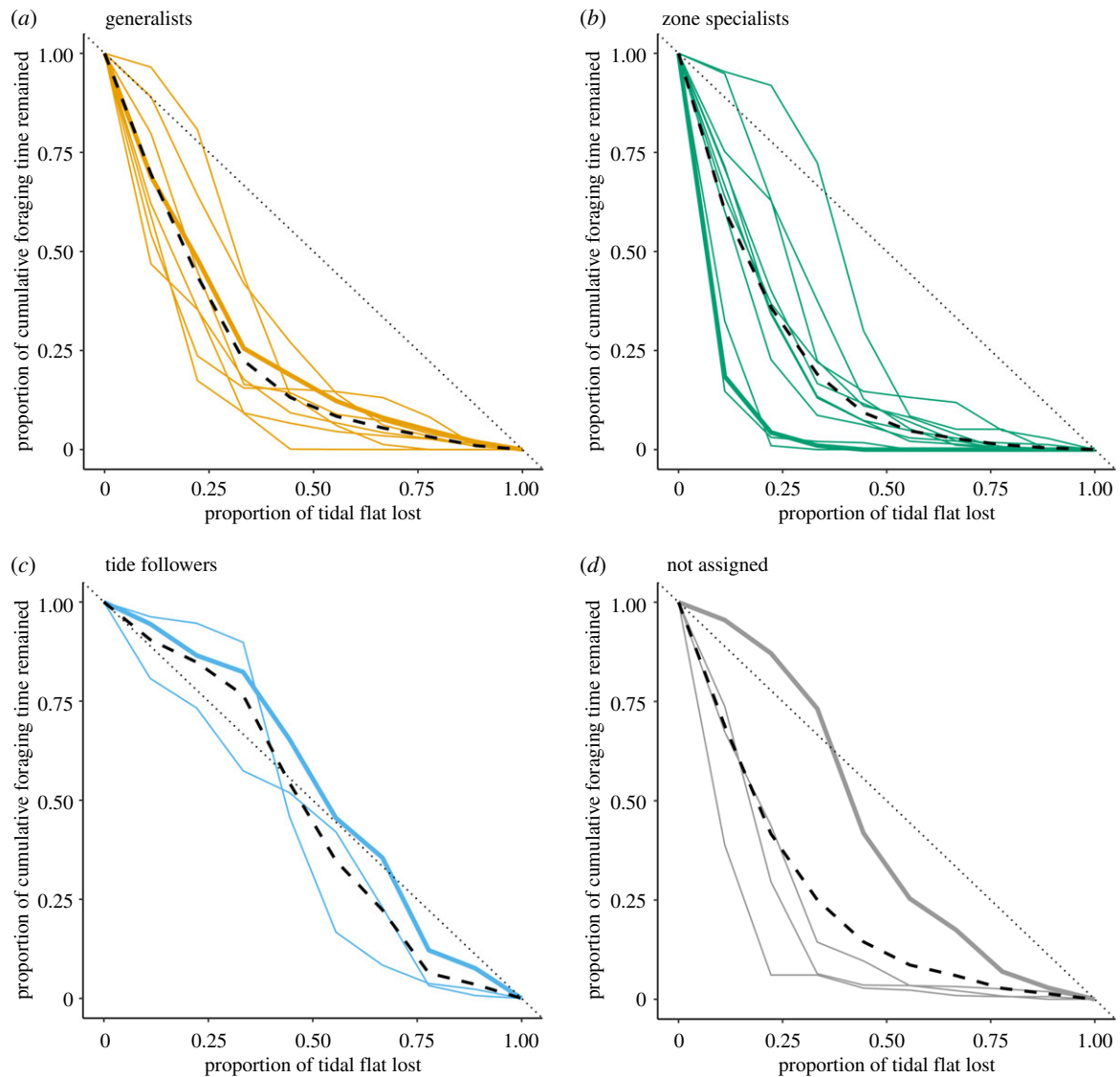


Figure 5. (a–d) The importance of upper tidal flats to shorebirds of each foraging type. Solid lines in each plot show the reduction in total cumulative foraging time assuming habitat loss of the tidal flats starting from the seawall for all populations within the specified foraging type, in which the thicker line is the representative population in figure 4. The black dashed line shows the average proportion of decline of the type, and the dotted line is a reference line showing a proportional reduction when different portions of the tidal flat are of equal importance. (Online version in colour.)

(b) The importance of upper tidal flats

We show that most shorebird populations at the two stopover sites spend disproportionately large amounts of time foraging on the upper tidal flats, particularly the generalists and zone specialists (figure 5), a combined result of the upper zone's longer exposure time and the shorebirds' preference for it. It may seem counterintuitive that the upper tidal flats are almost as important for the generalists ($77.6\% \pm 13.6\%$) as they are for the specialists ($81.0\% \pm 20.9\%$), but this reflects the relatively minor contributions of the middle and lower tidal flats to the cumulative foraging time of the generalists, a consequence of the limited exposure time relative to the upper tidal zone.

Unfortunately, the upper tidal flats are also the part of the habitat that is most prone to coastal development [30,35,36]. Decreases in the amount of available foraging habitat and foraging time could lower shorebirds' survival rates and/or breeding success, directly or via carryover effects [8,44,45]. By simulating progressive seaward development of the tidal flats, we predicted that the loss of upper tidal flats may cause substantial and disproportionately severe reductions

in overall foraging opportunities (figures 4 and 5), assuming the benthic invertebrate species upon which the shorebirds feed do not reassort in a way that partially compensates for the loss of foraging opportunities. Note that our results were generated from surveys conducted only during the spring tides, when the entire tidal flats are covered and then exposed during a tidal cycle, leading to more uniform distributions of foraging time among different zones. During a neap tide, the upper tidal zone would be exposed even longer relative to the lower tidal zone, suggesting that the overall importance of upper tidal flats to the foraging shorebirds could be much higher than we showed in the current study.

We suggest that the disproportionate importance of the upper tidal flats to EAAF shorebirds, combined with their heightened historical and current vulnerability to coastal development, may help to explain the discrepancy between the overall rates of coastal habitat loss ($-1.2\% \text{ yr}^{-1}$ [17]) and the rate of population decline in EAAF shorebirds (up to $-26\% \text{ yr}^{-1}$ in a similar period [11,19]). Thus, analyses based on the average rate of habitat loss may have significantly

underestimated the severity of the threat that coastal development poses to EAAF shorebird populations. However, we could not perform any correlational analysis to confirm this hypothesis, as we lack detailed information on the changes in the total area of the different tidal flat zones in the Yellow Sea region, especially with respect to exactly how much more of the upper tidal flats was lost relative to the lower tidal flats, apart from the fact that most of the development has proceeded from the high-tide line outward to the sea, impacting the upper tidal flats most severely [17,35,36,46].

We recognize that our measure of tidal flat importance looked only at the number of foraging individuals and their foraging time, but not their intake rates. However, other studies have indicated that the higher intake rates often achieved at lower tidal flats are insufficient to compensate for the shorter exposure times [30,47] and that shorebirds select areas where the tidal flats are exposed for longer periods [48].

Another limitation of our study is that our simulation of upper tidal development takes into account only the instantaneous impact of habitat loss and assumes no reassortment of the benthic invertebrate species upon which the birds feed or other changes in local conditions. Coastal development in the long term, however, not only leads to direct habitat loss, but also alters the remaining habitat by changing its hydrodynamic and deposition patterns in ways that can lead to erosion or siltation [35], which, in turn, affect the substrate structure, size, physiochemical conditions and benthic invertebrate faunas of stopover sites [21,49]. A comprehensive and long-term monitoring programme focusing on the changes in both benthic fauna and shorebird distributions is needed to provide a mechanistic understanding on how coastal development affects local shorebirds both instantaneously and in the long term, as well as whether and how fast the tidal flats may recover their sizes and benthic invertebrate fauna.

(c) Conservation recommendations

As the most valuable yet most vulnerable parts of the tidal flat for shorebirds, the upper tidal zones should be the focus of conservation actions within the Yellow Sea region, through a combination of protecting them from further development and improving the quality of existing habitat. The planning of future development projects in this region should entail

careful consideration of any activities that disproportionately affect the upper tidal flats and/or areas providing major foraging opportunities identified by local studies following our approach. For threatened species with very small population sizes (e.g. spoon-billed sandpipers), tracking the movement of individuals throughout the tidal cycle using a combination of direct observations and telemetry may be needed to understand their habitat preferences [9], in addition to our population-level approach.

We encourage researchers to conduct similar studies on the spatiotemporal distribution of foraging shorebirds elsewhere along the EAAF and along other flyways to better understand how shorebird species are using the tidal flats throughout their annual migration and to determine if the upper tidal flats are of disproportionate importance to these birds elsewhere. Development of tidal flats is not limited to the Yellow Sea. A recent study showed extensive losses of tidal flats around the world: more than 15%, or 20 000 km² worldwide between 1984 and 2016 [35]. Such development, combined with sea-level rises triggered by global climate change [50], simultaneously threatens the tidal flats and many of the world's shorebirds. Absent a concerted, international effort to protect the intertidal stopover sites these birds depend upon, the world stands to lose some of its most remarkable long-distance migrants.

Ethics. The field survey protocol was approved by the Institutional Animal Care and Use Committee of Princeton University.

Data accessibility. Data and R code are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.gmsbcc2jb> [51].

Authors' contributions. T.M. perceived and designed the study, collected and analysed the data, and drafted the manuscript. D.S.W. code-signed the study, provided critical input for analysis and extensively revised the manuscript. All authors gave final approval for publication.

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