



Where to draw the line? Using movement data to inform protected area design and conserve mobile species



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ABSTRACT

Protected areas (PAs) are a cornerstone of modern conservation. For PAs that are established to conserve mobile species, it is important to cover all the key areas regularly used by these species. However, zonation and boundaries of PAs have often been established with limited knowledge of animal movements, leaving the effectiveness of some PAs doubtful. We used radio tracking data to evaluate the extent to which two coastal PAs in mainland China encompassed the full range of habitats used by migratory shorebirds during non-breeding seasons. The core zone (highest restriction on human activities) of the Yalu Jiang Estuary National Nature Reserve (Liaoning) incorporated only $22 \pm 6\%$ ($n = 34$) of the diurnal home range (95% kernel density) of the endangered great knots *Calidris tenuirostris*. In contrast, the core zone of Chongming Dongtan (Shanghai) incorporated $73 \pm 24\%$ ($n = 25$) of the home range of dunlins *Calidris alpina*. During high tide, great knots in Yalu Jiang mostly occurred in the experimental zone (least restriction on human activities) or sometimes outside the PA boundary altogether, where the birds could face substantial threats. By investigating satellite tracking records, consulting published literature, interviewing local experts and mapping habitat composition in different coastal PAs in China, we found that wet artificial supratidal habitats were frequently used by migratory shorebirds but the coverage of these habitats in coastal PAs was low. These PA boundaries and/or zonations should be revised to conserve mobile species more effectively. With the increasing number of tracking studies, analysing the spatial relationships between PAs and the movement ranges of mobile species can increasingly inform the development of a representative, comprehensive PA network.

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1. Introduction

Establishing protected areas (PAs) is a critical step for conserving wildlife and habitats (Gaston et al., 2008; Venter et al., 2014). > 15% of the global terrestrial area (including inland waters) and 4% of global oceans have now been designated, covering > 34 million km² (UNEP-ECMC and IUCN, 2016). Well-managed PAs can deliver important benefits to biodiversity by reducing rates of habitat loss, maintaining species richness and, to some extent, species abundance (Geldmann et al., 2013; Gray et al., 2016). However, the effectiveness of PAs in conserving mobile species is compromised if PAs fail to take the movement patterns of target species into account by not covering all of the key habitats utilised during their stay (Carter et al., 2012; Hull et al., 2011; Thirgood et al., 2004). Therefore, it is important to consider the seasonal, diurnal and/or tidal movement patterns of target species when planning or modifying the location of PAs and making management plans (Allen and Singh, 2016; Fuller et al., 2010). These considerations are particularly important when PAs are small in size (therefore unlikely to cover entire home-range of target species), and when the surrounding habitats beyond PA boundaries are threatened or contain threats to target species.

Here we evaluate the extent to which nature reserves (NRs), a strictly managed form of PA, are protecting migratory shorebird populations in China, a critical non-breeding region in the East Asian–Australasian Flyway (EAAF). This flyway is the home to at least 8 million shorebirds (Bamford et al., 2008). Compared to other flyways, the EAAF holds not only the largest number of shorebird populations (79 populations) but also the highest number of globally threatened or near threatened shorebird species (Stroud et al., 2006). The conservation of these long-distance migratory species requires protection and improved management of their habitats in non-breeding, stopover, staging and breeding grounds (Runge et al., 2014; Szabo et al., 2016). The populations of many shorebird species along the EAAF are declining rapidly, with coastal intertidal habitat loss, degradation, hunting and pollution at their migratory staging sites in East Asia being the likely causes (Melville et al., 2016; Murray et al., 2014; Piersma et al., 2016; Studds et al., 2017; Zhang et al., 2018), and hence their adequate protection in China is crucial (Murray and Fuller, 2015).

Along China's coast, many coastal NRs have been established over the past 20 years to conserve threatened waterbirds (Table S1; Meng et al., 2017; Qiu et al., 2009). However, most of the NRs in China were established opportunistically without a systematic plan to maximise efficiency and represent conservation targets (Qiu et al., 2009; Wu et al., 2011). 'Nature reserves' are just one of the 11 types of PAs in mainland China and the subclass 'national nature reserve' has the highest administrative rank, requiring approval from the State Council of China for establishment and major management decisions (Zhang et al., 2017). China's national nature reserves are divided into three different functional zones, namely the core, buffer and experimental zones, in descending order of management strictness. All human activities are prohibited in the core and buffer zones except permitted research work, while research, education, training and tourism as well as other sustainable use of resources are permitted in the experimental zone (The State Council of the People's Republic of China, 2017). The buffer zone is often used to buffer the core zone from human disturbances. Recent evidence suggests that many threatened waterbird species that occur within these NRs utilise habitats both within and outside NR boundaries, as well as crossing multiple functional zones (Choi et al., 2010; Ma et al., 2009a). A full understanding of habitat use by key waterbird species (the tidal or daily local movements between alternative feeding and roosting locations (Rogers et al., 2006)) is critical for designing and managing PAs (Allen and Singh, 2016). The commitment to expand and rework coastal PAs in China, as reflected partly in World Heritage sites nomination that includes unprotected sites (at the national level (Ma et al., 2019)), creates an opportunity for such an understanding to have immediate influence on the placement of

PA boundaries.

In this study, we aim to determine the extent to which coastal PAs in China protect the full range of habitats used by non-breeding migratory shorebirds at the local site level to inform decision-makers on what should be represented within the PA boundaries. To meet this aim, we (1) analysed telemetry data from 3 case studies to determine the full range of habitats used by the migratory shorebirds at staging and non-breeding sites; (2) summarised the habitat types visited by the birds using published information, expert opinion and satellite tracking data; and (3) analysed the extent to which coastal PAs encompass important habitat types. Together, these will demonstrate the potential conservation benefit of incorporating local movement patterns of target species into PA boundary-setting.

2. Materials and methods

To investigate the ability of PAs to conserve the entire diurnal local movement of migratory shorebirds, we selected two NRs in coastal China that met these criteria: (i) sufficient local movement data for a migratory shorebird species experiencing population decline; (ii) rapid land-use transformation around the NR, and (iii) risk of ongoing land-use or management changes that could affect shorebird habitat within the NR. The three case studies thus focused on great knot *Calidris tenuirostris* at the Dandong Yalu Jiang Estuary Wetland National Nature Reserve (hereafter Yalu Jiang) in two different years (Choi et al., 2015; Ma et al., 2013; Riegen et al., 2014), when food availability underwent a significant change (Zhang et al., 2018), and dunlin *Calidris alpina* at the Chongming Dongtan National Nature Reserve (hereafter Chongming Dongtan) (Andres et al., 2012; Choi et al., 2014; Ma et al., 2009b; Morrison et al., 2006). Both NRs were gazetted to conserve migratory waterbirds (Table S1).

In the EAAF, great knot and dunlin are long-distance migratory species that breed in the high-Arctic tundra, refuel at coastal wetlands in East Asia and spend the non-breeding season in Australia and China, respectively (Conklin et al., 2014; Piersma et al., 1996). Great knot is listed as Endangered under the IUCN Red List and while dunlin is currently listed as Least Concern, population decline has been recorded along the EAAF (Andres et al., 2012; IUCN, 2017; Morrison et al., 2006). Like many other shorebird species, the activity pattern of great knot and dunlin at coastal wetlands is driven mainly by the tidal rhythm, with many birds foraging during low tide on exposed intertidal flats and roosting in artificial supratidal (the coastal zone above high-tide inundation) habitats such as fishponds and saltpans during high tide when the tidal flat is inundated (Choi et al., 2014; Rogers et al., 2006; Jackson et al., 2019).

2.1. Study areas

Yalu Jiang is located in the northern Yellow Sea, China (Liaoning, 39°40'–39°58'N, 123°34'–124°07'E). This NR comprises bare intertidal flats with negligible extent of saltmarsh, some aquaculture ponds, and other artificial infrastructure (Fig. 1c). Human-dominated land uses such as roads, towns and industrial plants occur in the buffer and experimental zones. This NR is considered an internationally important area for migratory shorebirds, supporting > 250,000 shorebirds (Choi et al., 2015; Riegen et al., 2014).

Chongming Dongtan is located in the Yangtze Estuary in eastern China (Shanghai, 31°25'–31°38'N, 121°50'–122°05'E; Fig. 1b). This NR comprises mainly bare intertidal flats and saltmarsh but no artificial supratidal habitats. It supports > 100,000 shorebirds annually, including 5000 or more dunlins and it is an important site for both migrating and wintering shorebirds (Barter, 2002; Choi et al., 2014).

2.2. Radio tracking surveys

We conducted radio tracking surveys (VHF radio transmitters) to

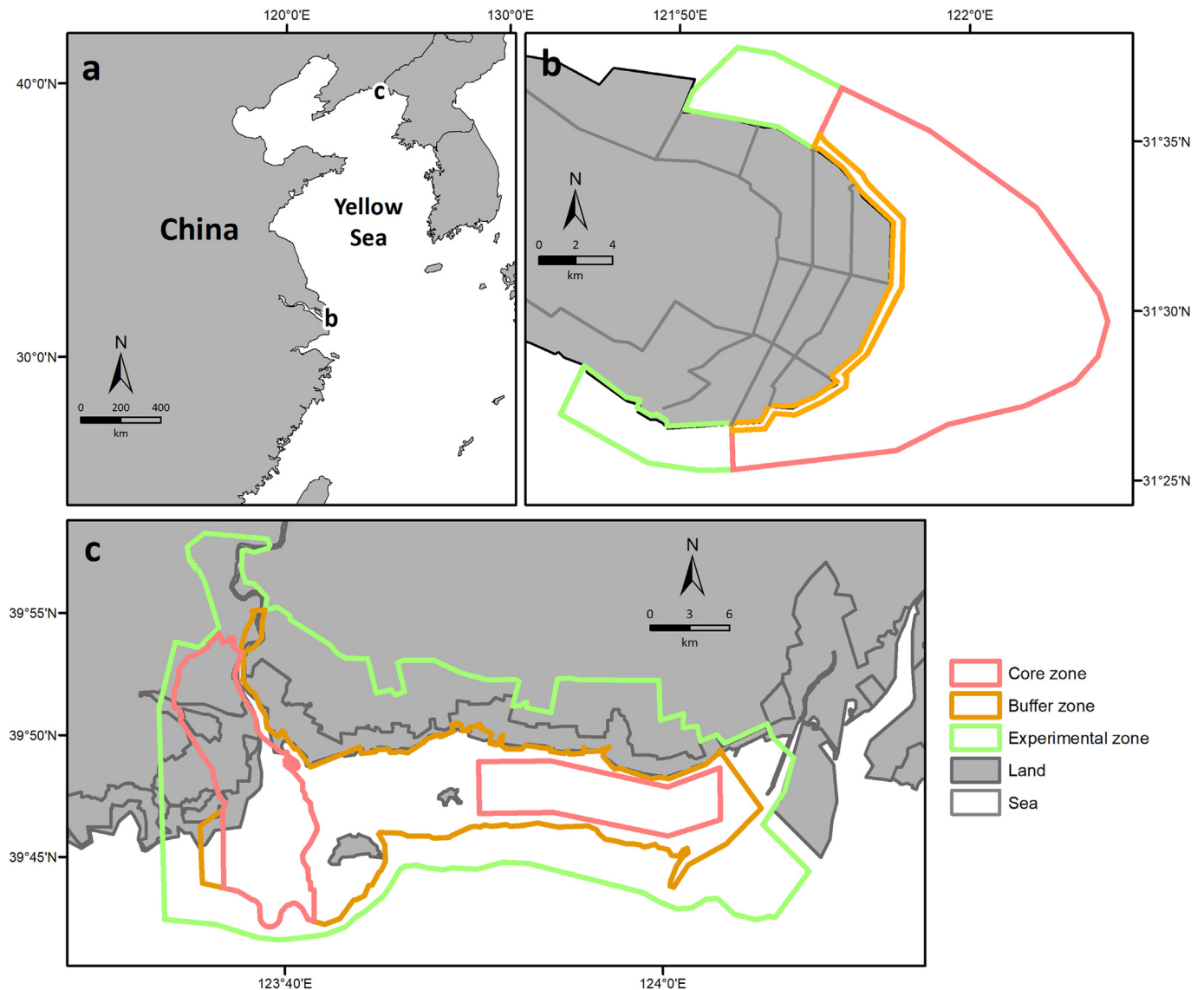


Fig. 1. Location in the Yellow Sea (a) and functional zones of (b) Chongming Dongtan National Nature Reserve and (c) Dandong Yalu Jiang Estuary Wetland National Nature Reserve. Letters in panel (a) indicate the location of (b) Chongming Dongtan and (c) Yalu Jiang. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

monitor the movement and habitat use of 51 dunlins during non-breeding and northward migration stopover from December 2006 to May 2007 in Chongming Dongtan, and 44 great knots that stopped in Yalu Jiang during northward migration from March to May in 2012 ($n = 22$) and 2015 ($n = 22$). We captured the birds using clap nets at both sites and conducted diurnal manual tracking surveys to scan for tagged birds regularly. We followed a similar daily routine in each of the study areas as much as possible (in terms of time and space) to minimize any biases in our surveys. Detailed methods can be found in [Ma et al. \(2013\)](#) and [Choi et al. \(2014\)](#).

2.3. Data analysis

2.3.1. Overlap between shorebird ranges and reserve boundaries

We modelled home range as a fixed kernel density estimator (KDE; 95% and 50% probability contours; [Seaman and Powell, 1996](#)). R package `adehabitatHR` ([Calenge, 2006, 2011](#)) was used to estimate home range (as the 95% KDE) and core range (50% KDE), and the kernel smoothing parameter was optimized by visual inspection, with $h = 1000$ determined to be the most suitable to show the their home

range and core range ([Silverman, 1986](#); [Wand and Jones, 1995](#)). Due to different amounts of sampling effort in the tracking dataset, we selected individuals of great knot with at least 30 fixes and dunlin with at least 18 fixes for home and core range analysis. The home range of dunlin was also estimated using 95% minimum convex polygon (using smaller number of location fixes but larger number of tagged birds), which is less sensitive than KDE to small number of location fixes, to see if different estimation methods would yield different results. Any consecutive location fixes within a 30 min time interval were excluded ([Haig et al., 2002](#)). To estimate the extent to which NRs encompass the home (core) range of shorebirds, we calculated the area of overlap between the home (core) range of each individual and the NR zonation in QGIS and these were pooled together in each case study and reported as mean \pm SD unless mentioned otherwise.

2.3.2. Distribution and habitat use of shorebirds during high and low tides

To determine the habitat use of each of the tracked great knot and dunlin, we classified each of our study areas into the following habitat types: (i) tidal flats and shallow sea on the seaward side of the seawall, (ii) wet artificial supratidal habitats, which are wet areas (e.g.,

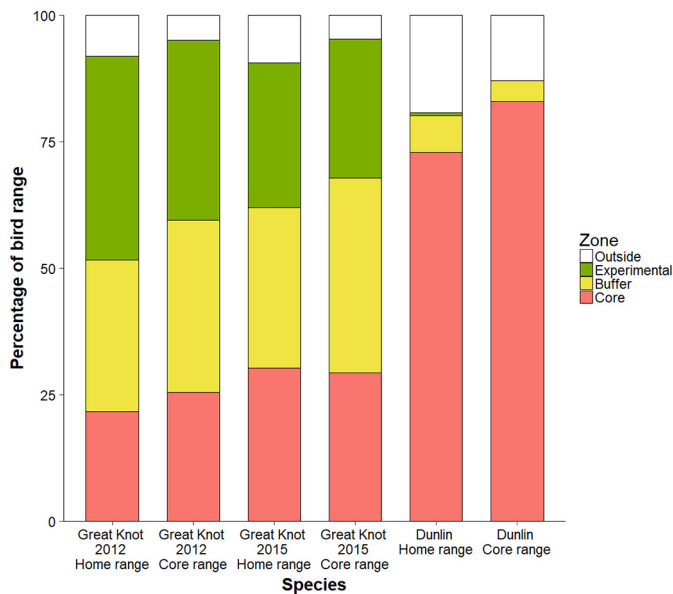


Fig. 2. Functional zone composition in the home range and core range of great knots ($n = 20$ for 2012; $n = 14$ for 2015) and dunlins ($n = 12$). Home range: 95% fixed kernel density estimator; Core range: 50% fixed kernel density estimator.

aquaculture ponds) and recently claimed but undeveloped land on the landward side of the seawall, and (iii) dry artificial supratidal habitats, which are predominantly agricultural areas (e.g., farmland including rice paddies) on the landward side of the seawall (Choi et al., 2018). The boundary for the baseline of habitat composition was set by plotting the minimum convex polygon using all the location fixes from all tagged-individuals in each case study. To estimate the habitat use and proportional cover of each of the three habitat classes, we used (i) Landsat images acquired during the tracking period, (ii) maps of the normalized difference water index (McFeeters, 1996), and (iii) visual verification. We calculated the proportion of location fixes recorded in these habitats during three different tidal ranges (0–33%, 34–66 and 67–100% of the maximum tide height). The tidal level for each location fix was obtained from the local tide table (National Marine Data and Information Service, 2006, 2011, 2014). Finally, we compared the proportions of different habitat availability (using the methods described in this paragraph) with the actual usage of the 95% Bailey confidence intervals to examine preference for different habitats (Cherry, 1996).

Pearson's correlation test was conducted to investigate the relationship between the size of individual home range and the proportion of unprotected area within the home range. Contingency table analysis was used to compare the coverage of functional zones in 2012 and 2015 at Yalu Jiang because food availability collapsed in the region after 2012 (Zhang et al., 2018) and the boundary of different functional zones in the NR was adjusted in 2013 (Ma et al., 2019), both of which might lead to different extent of protection of the ranges of the birds. If there was no significant difference in their home-ranges between years, data were pooled to understand the home range and habitat use of great knots in relation to tidal stages. We used $p < 0.05$ as the significance level for all statistical tests which were conducted in R 3.3.1 for Mac (R Core Team, 2018).

To understand the extent to which findings from two species and two PAs are applicable to other shorebird species in other locations along the coast of China, we also investigated habitat use more generally and examined the extent to which different habitats are protected in different PAs. This was achieved by investigating satellite tracking records, consulting published literature, interviewing local experts and mapping habitat composition in different coastal PAs in China.

2.3.3. Habitat use of migratory shorebirds along the coast of mainland China

We developed a country-wide analysis of habitat use by migratory shorebirds based on a separate satellite telemetry dataset, published literature and opinions from experts involved in shorebird monitoring through the China Coastal Waterbird Census. We confined our search to the important waterbird sites that have been surveyed regularly (Bai et al., 2015) or coastal national NRs that are important to migratory shorebirds in mainland China (Conklin et al., 2014). The telemetry dataset consisted of satellite tracking records of bar-tailed godwits, grey plovers *Pluvialis squatarola*, and Nordmann's greenshanks *Tringa guttifer*. Published literature included both Chinese and English publications that report the habitat use of shorebirds. Local experts were consulted about the habitat types used by shorebirds and whether the high tide reaches the seawall in the survey areas. The latter allows us to determine the potential importance of different artificial supratidal habitats because shorebirds often use such habitat when the intertidal flat is inundated.

2.3.4. Habitat composition in different functional zones and different coastal PAs

To understand whether the important shorebird habitats identified in our study are included within the NR boundary for other coastal NRs in China, we estimated habitat composition in the 12 coastal national NRs (Conklin et al., 2014). We classified each NR into the three habitat types (intertidal flats and shallow sea; wet artificial supratidal habitats; dry artificial supratidal habitats), using recently acquired Landsat images (2016–2017). In one rare occasion, the Jiuduansha Wetland Nature Reserve, which is located on an alluvial island with natural supratidal habitat, we treated such habitat as intertidal flats and shallow sea just for this part of the analysis.

3. Results

3.1. Bird movements in relation to protected area boundaries

Although $> 90\%$ of the home range and core range of great knot were inside the NR (Tables S4; $n = 20$ in 2012 and 14 in 2015), the proportion of ranges that fell within the core zone was low. The overlap between each functional zone in the reserve and the ranges of great knots was similar in 2012 and 2015 (proportion of home ranges: $\chi^2 = 3.11$, $df = 3$, $p = 0.38$; core ranges: $\chi^2 = 1.92$, $df = 3$, $p = 0.59$), with less than a quarter of the home range ($22 \pm 6\%$) and core range ($22 \pm 11\%$) occurring inside the core zone of the reserve (Figs. 2 and S1, Tables S3 and S4). A similar pattern was found in the distribution of individual location fixes (Table S2). The percentage of home ranges that were unprotected decreased significantly with increased size of their total home ranges (Fig. 3), and great knots with larger home range had a smaller percentage of their ranges laid outside the NR (great knot combined: $p = 0.03$, $r = -0.38$).

In dunlins ($n = 12$), about three-quarters of the home range and core range were inside the core zone ($73 \pm 21\%$ and $83 \pm 33\%$ respectively) and $> 80\%$ of the home range and core range were found within the reserve (Figs. 4 and S3, Tables S3 and S4). The use of a different home range estimation method (95% minimum convex polygon) with fewer location fixes per dunlin but larger overall sample size ($n = 25$) yielded similar results (Table S5). In contrast to great knots, dunlins with larger home ranges tended to have a larger percentage of their range outside the NR, but the correlation is not significant ($p = 0.33$, $r = 0.3$).

3.2. Distribution and habitat use of shorebirds in different tidal stages

3.2.1. Yalu Jiang

Great knots in Yalu Jiang mostly occurred on the tidal flats in the core and buffer zones during low tide, but in wet artificial supratidal

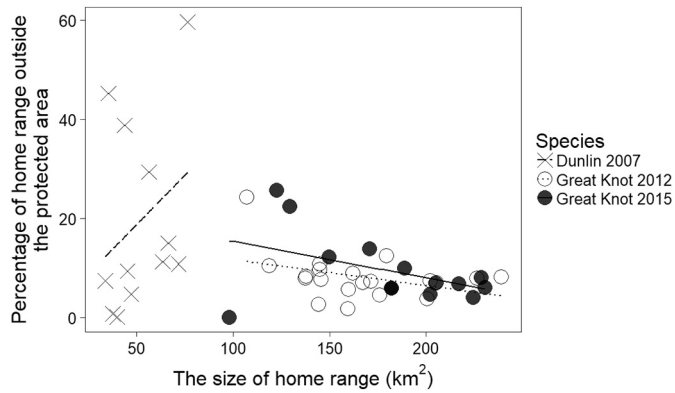


Fig. 3. The correlation between individual home range size and the percentage of home range outside the PA. The data were obtained from radio-tagged dunlins in Chongming Dongtan ($n = 12$), and great knots in Yalu Jiang in 2012 ($n = 20$) and 2015 ($n = 14$).

habitat in the experimental zone or outside the NR during high tide. During the high tide period, only $8 \pm 12\%$ (range: 0–59) of location fixes were in the core zone of the reserve and most of the high tide location fixes occurred in the experimental zone ($66 \pm 16\%$, range: 17–93), followed by the buffer zone ($17 \pm 15\%$, range: 0–83) and outside of the reserve ($9 \pm 9\%$, range: 0–30; Fig. S4, Table S6). These were in sharp contrast to low the tide period, when $44 \pm 21\%$ (range: 0–80) of location fixes occurred in the core zone and $51 \pm 22\%$ (range: 18–100%) in the buffer zone. Only a small percentage of location fixes ($5 \pm 7\%$, range: 0–25) were detected in the experimental zone and none outside of the reserve during low tide (Fig. S4, Table S6).

Across the full tidal range, the proportion of location fixes within the reserve dropped as the tidal range moved from 60% to 100% of the tidal range (i.e. from intermediate tidal height to the highest tidal height), indicating that birds were increasingly moving beyond the reserve boundary as the higher tide forced them off the tidal flats (Fig. 4). Similarly, about 50% of location fixes were found within the core zone during lower tidal ranges and this dropped to only 10% during upper tidal ranges (Fig. 4).

Great knots used tidal flats substantially more than artificial supratidal habitats (Table 1). > 80% of the location fixes for great knot

was found on the tidal flats while < 20% were consistently found on artificial supratidal habitats on the landward side of the seawall (Table S7). Habitat use was substantially different between high and low tides. During the lower third of tidal range, almost all location fixes were located on the tidal flats. The percentage of location fixes recorded in the wet artificial supratidal habitats were markedly higher during the upper tidal range ($37 \pm 8\%$ in 2012 and $24 \pm 12\%$ in 2015) than lower tidal range ($1 \pm 2\%$ in 2012 and $1 \pm 1\%$ in 2015) and the percentage of location fixes in wet artificial supratidal habitat increased with height of high tide (Table S7, Figs. 4 and S5).

3.2.2. Chongming Dongtan

Unlike the great knot, the distribution of dunlins in different functional zones in Chongming Dongtan was similar between high and low tides (Fig. S4, Table S6). Dunlins used tidal flats substantially more, and dry artificial supratidal habitats substantially less than expected considering their availability (Table 1). Their usage of wet artificial supratidal habitat was proportional to availability during both upper and lower tidal ranges (Table S7, Figs. 4, S5).

3.3. Habitat use of migratory shorebirds along the coast of mainland China

The country-wide analysis of habitat use by migratory shorebirds reinforced the results from local-scale tracking studies. Shorebirds use tidal flats as well as artificial supratidal habitats on the landward side of the seawall (Table S8). The use of wet artificial supratidal habitats (e.g. aquaculture pond) was reported in all of the 18 sites where such habitat was present, including 13 NRs. The use of dry supratidal habitats (e.g. farmland), in contrast, was reported in only 10 out of 18 sites (Fig. 5, Table S8). The tide was reported to inundate the entire tidal flat during high tide in eight out of ten areas where information was available, indicating that shorebirds in these areas would have no option but to move to artificial supratidal habitats during high tide.

3.4. Habitat composition in different functional zones and different coastal PAs

Of the 12 coastal NRs analysed, an average of $74 \pm 20\%$ of the area comprised intertidal and shallow sea habitat while $20 \pm 18\%$ area was dry artificial supratidal habitats and $7 \pm 6\%$ area was wet artificial

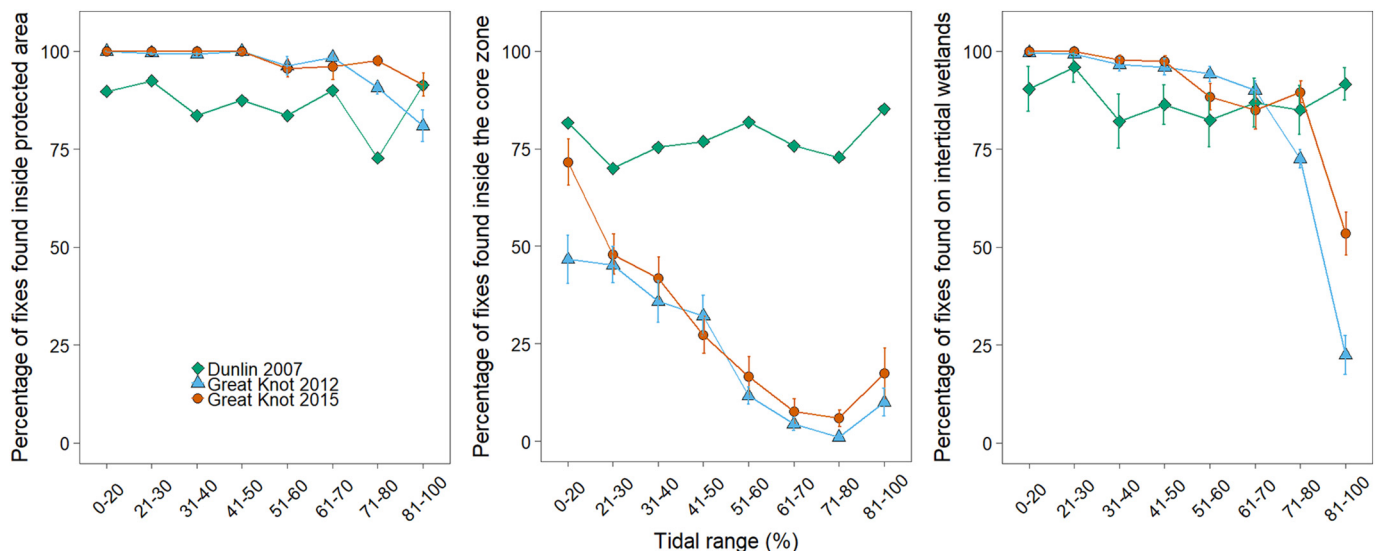


Fig. 4. The change in distribution of location fixes (mean \pm S.E. of percentage) with tidal ranges (0% as the lowest tide level and 100% as the highest) inside and outside of the reserves (left panel); inside and outside of core zone in a reserve (middle panel); on intertidal wetlands and artificial supratidal habitats (right panel). No standard error was given in dunlins in the first two panels as location fixes from all individual dunlins were pooled due to the small number of location fixes per individual.

Table 1

Habitat availability (estimated from all the habitats within the detected location fixes), actual habitat use and Bailey's 95% confidence intervals for percentage of use by radio-tagged birds. Habitat type with an availability less than that in the Bailey's 95% confidence interval of use indicated that such habitat type was used more than expected (i.e. preferred), and vice versa. Habitat type with % available that falls into the range of Bailey's 95% confidence interval indicated that such habitat type was used in proportion to its availability. The results on Dunlin were adopted from the same dataset used in an earlier study (Choi et al., 2014). TF denotes tidal flats; WASH denotes wet artificial supratidal habitat; DASH denotes dry artificial supratidal habitat.

	Dunlin 2007			Great knot 2012			Great knot 2015		
	TF	WASH	DASH	TF	WASH	DASH	TF	WASH	DASH
Habitat available (%)	67	15	18	60	25	15	65	19	16
Habitat use (%)	84	16	0	83	16	0.01	88	12	0
Bailey's 95% confidence interval for % of usage	(82–85)	(15–18)	(0.04–0.12)	(81–85)	(14–18)	(0–0.01)	(86–90)	(10–14)	(0.09–0.41)

supratidal habitats (Fig. S6, Table S9). Dry and wet artificial supratidal habitats combined were found mostly in the experimental zone (mean = 58%, range 0–100%). Only 20% (range 0–100%) of these habitats, on average, was located inside the core zone and the remaining 22% (range 0–65%) in the buffer zone of NRs.

4. Discussion

This study demonstrates how movement data of mobile species could be used to inform and improve protected area zoning and boundary placement. We found that migratory shorebirds frequently move outside of the core zone of a PA or outside PAs during their migration stopover or boreal winter along the coast of mainland China. Wet artificial supratidal habitats inside and outside of the NRs are frequently used by shorebirds, especially during high tide when tidal flats are inundated. Despite the importance of wet artificial supratidal habitats for shorebirds, such habitats are under-represented and often are weakly protected in coastal PAs in China.

4.1. Protection efficacy of zoning in two coastal PAs

With appropriate management effort, PAs can provide refuge for wildlife including endangered species (Ma et al., 2009a) by conserving important habitats and protecting wildlife from anthropogenic activities (Geldmann et al., 2013; Gray et al., 2016). The latter has become one of the major concerns in conservation worldwide (Jones et al., 2018) and in mainland China in particular, due to the increasing human population and rapid economic development around PAs (Xu et al., 2016a; Xu et al., 2016b). Our study shows that migratory shorebirds often move between different functional zones within a PA, as well as beyond the PA boundary. In Yalu Jiang, over 90% of the home and core ranges of great knots were within the reserve boundary while > 80% of the home and core ranges of dunlins were within the reserve boundary in Chongming Dongtan. However, less than a quarter of home ranges of great knots fell into the core zone, with the rest lying outside the core zone where wet artificial supratidal habitats are bounded with roads and human settlements. Given the generally higher amount of human disturbance in the buffer and experimental zones than the core zone (Hull et al., 2011; Xu et al., 2016b), the great knots were likely to be exposed to more frequent disturbance from birdwatchers, photographers and fishermen when the birds move outside the core zone of the reserve to roost during high tide (Li et al., 2017; Wang et al., 2011). With only a quarter of great knots' range having strict control on human activities, the zoning scheme of Yalu Jiang does not align as well as it might with the movement patterns of the birds. A further expansion of the core zone to include key habitats could improve the protection extent, as reflected by the increased proportion of great knots' range that fell into the core zone in 2015 (Table S4). On the other hand, the core zone in Chongming Dongtan had good coverage of the ranges of dunlins (about 80%), but this still leaves almost one-fifth of the home range of dunlins beyond the NR boundary.

In addition to species-specific local movement ecology and site-

specific characteristics, unequal sampling effort in terms of both the total number of location fixes used and the number different number of location fixes collected at different tidal stages could have contributed to the differences in home range behaviour between case studies and to potential biases during certain tidal stages. However, the use of different number of location fixes to estimate ranges yield fairly consistent results on the extent to which NR protects the full range used by shorebirds (great knot: Table S4; dunlin: Table S5). Thus, our results do reflect the extent to which these birds are protected in the NRs. Moreover, a comparison of the frequency distribution of hourly tidal height records during field days and the location fixes used for home range analysis indicated that our sampling effort generally matched the natural tidal states, with at most only a small bias towards high tide for the dunlin case study (Fig. S7). The exclusion of location fixes taken within 30 min in our analysis will have lowered potential bias towards certain tidal states.

4.2. Protection level during high and low tides

Our results revealed that NRs offer differing levels of protection depending on the tide height. Great knots at Yalu Jiang rely on wet artificial supratidal habitats outside the core zone or the NR as tide height increases, indicating a heavy reliance on wet supratidal and less protected habitats when intertidal habitats are unavailable. In contrast, dunlins in Chongming Dongtan used wet artificial supratidal habitats more consistently throughout the tidal cycle, perhaps due to suitable conditions in aquaculture ponds and its generalist habitat use compared to the more coastal wetland specialist like great knots (Choi et al., 2014; Piersma et al., 1996). Still, our findings that a small percentage of the ranges and location fixes were located in wet artificial supratidal habitats outside the reserve, indicate that birds move beyond the PA boundary during any part of the tidal cycle. Previous work has shown that birds use wet artificial supratidal habitats for both foraging and roosting (Choi et al., 2014; Green et al., 2015; Jackson et al., 2019; Masero and Perez-Hurtado, 2001) and birds can suffer intensive human disturbance when they move outside of a core zone or beyond a PA boundary (Choi et al., 2015; He et al., 2016; Melville et al., 2016; Smart and Gill, 2003; Xu et al., 2016a). There is no guarantee that the current land use on artificial supratidal habitats outside of the reserve will remain suitable as shorebird habitat over time. The latter may arise when wet artificial supratidal habitats are abandoned and become densely vegetated, or different practices are used and deepen the water level.

These results suggest that having a relatively large and continuous core zone covering tidal flats in a PA (as in Chongming Dongtan, and Yalu Jiang 2015), while including wet artificial supratidal habitats (as in Yalu Jiang) are important when delineating the boundary and composition of PAs for shorebirds.

4.3. Management of coastal protected areas in mainland China

Our country-wide analysis of habitat use by migratory shorebirds reinforced the results from local-scale tracking studies. Despite the

potential differences in behaviour, dietary and habitat preferences among species, we found that shorebirds use both tidal flats on the seaward side of the seawall and wet and dry artificial supratidal habitats on the landward side of the seawall in most of the 21 sites along Chinese coast (Fig. S6, Table S8). In many of these coastal areas, the tide inundates the entire tidal flat during high tide, indicating that shorebirds in these areas would need to seek roosting habitats on the landward side of the seawall (Choi et al., 2014; He et al., 2016), or stay airborne throughout the high tide, which could be costly given the additional amount of energy required (Rogers et al., 2006). The movement between tidal flats and wet artificial supratidal habitats, and potential problems of PA design revealed from our radio tracking work, is therefore likely to be applicable to other shorebird species and other coastal sites where no natural supratidal habitats remain.

Rapid loss of natural supratidal habitats for shorebirds has occurred widely along coastal areas in East Asia, mainly due to land-claim (Murray et al., 2014; Yang et al., 2011; Yim et al., 2018). This highlights the increasing importance of artificial supratidal habitat in shorebird conservation (Jackson et al., 2019). However, with > 80% of such habitats within coastal PAs in China being located outside the core zone (Table S9), shorebirds are generally exposed to more regular disturbances from fishermen, livestock and traffic when they use artificial supratidal habitat (Barter, 2002; He et al., 2016; Melville et al., 2016). Without safe, undisturbed and adequate artificial supratidal habitats, shorebirds may not use the coastal areas as the increased energy expenses mean the site is no longer profitable (Rogers et al., 2006). Moreover, these habitats are often overlooked during the zoning process when PAs are established. As a result, many of the coastal PAs in mainland China only include a very small fraction of wet artificial supratidal habitats in the core zone (Figs. S8; Table S9). This lack of protection and high potential of disturbance risk during high tide may put shorebirds at risk when using these PAs in China (Melville et al., 2016; Xu et al., 2016a). These results suggest that wet artificial supratidal habitats are systemically vulnerable to human disturbances and potential land-use changes. It also highlights the very limited amount of wet artificial supratidal habitats currently included in PAs.

5. Conclusion

China's coastal wetlands provide critical stopover and non-breeding habitats for migratory shorebirds along the flyway. The commitment of the Chinese government to expand and rework coastal PAs (The State Council of the People's Republic of China, 2015, 2018) is encouraging but as our study showed, coastal PAs need to include wet artificial supratidal habitats within the NR to provide adequate protection for shorebirds. The daily movements and seasonal migration pattern of many shorebird species could mean management of wet artificial supratidal habitats are mostly needed during high tide, allowing for management actions that are dynamic in space and time (Runge et al., 2014). These offer opportunities for managers and decision-makers to improve current conditions by working more closely with local stakeholders including fishermen, using innovative approaches such as sequential aquaculture harvesting and reverse auctioning system to create wetland habitats for migratory birds (Jackson et al., 2019; Reynolds et al., 2018). However, such local interaction and engagement remain rare in China (Miller-Rushing et al., 2017; Zhang et al., 2017), leaving a critical gap to be bridged by stakeholders such as NGOs.

Our results showed that even with the establishment of PAs specifically targeted at a particular bird group, target species can frequently move in and out of a PA or its core protected zone. This is particularly the case for migratory shorebirds that utilise various habitats in their home range depending on the stage of the tide. Protected area management strategies should be flexible, adaptive and regularly revised using improved information (Bull et al., 2013; Singh and Milner-Gulland, 2011). In the case of migratory shorebirds in China, it may be necessary to enter into cooperative arrangements with supratidal land

managers within the vicinity of the reserve to ensure that shorebirds are adequately protected throughout the tidal cycle. With the increasing number of tracking studies on animals, it is important that the movement data collected are shared with stakeholders so the movement pattern of target species can be taken into account during conservation planning or reserve boundary realignment (McGowan et al., 2017).

Data accessibility

Data is available from the Dryad Digital Repository <http://dx.doi.org/10.17632/44mg6skx4w.1> [to be archived should paper be accepted].

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.03.025>.

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