

CONTRIBUTED PAPERS

Importance of habitat heterogeneity in tidal flats to the conservation of migratory shorebirds

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Abstract

Understanding species distribution patterns and what determines them is critical for effective conservation planning and management. In the case of shorebirds migrating along the East Asian–Australasian Flyway (EAAF), the loss of stopover habitat in the Yellow Sea region is thought to be the primary reason for the precipitous population declines. However, the rates of decline vary considerably among species, and it remains unclear how such differences could arise within a group of closely related species using apparently similar habitats at the same locales. We mapped the spatial distributions of foraging shorebirds, as well as biotic (benthic invertebrates consumed by migrating shorebirds) and abiotic (sediment characteristics) environmental factors, at a key stopover site in eastern China. Five of the six sediment characteristics showed significant spatial variation with respect to distance along the shoreline or distance from the seawall in the same tidal flat. The biomasses of four of the six most abundant benthic invertebrates were concentrated in the upper or middle zones of the tidal flat. The distribution patterns of all three focal shorebird species on the tidal flat were best explained jointly by this heterogeneity of sediment characteristics and invertebrate prey. These results suggest that the loss of tidal flats along the Yellow Sea, which is typically concentrated at the upper and middle zones, may not only reduce the overall amount of staging habitat, but also disproportionately affect the most resource-rich portions for the birds. Effective conservation of shorebird staging areas along the EAAF and likely elsewhere must consider the subtle habitat heterogeneity that characterizes these tidal flats, prioritizing the protection of those portions richest in food resources, most frequently used by focal bird species, and most vulnerable to anthropogenic threats.

Article impact statement: Heterogeneity of tidal flats with respect to biotic and abiotic factors must be considered in shorebird conservation planning.

KEYWORDS

benthic invertebrate, East Asian–Australasian Flyway, habitat heterogeneity, migratory shorebird, resource distribution, sediment, staging site

Importancia de la heterogeneidad de hábitat en las llanuras intermareales para la conservación de aves playeras migratorias

Resumen: Entender las pautas de distribución de las especies y los factores que las determinan es fundamental para planificar y gestionar eficazmente su conservación. En el caso de las aves playeras que migran a lo largo de la ruta migratoria Asia Oriental–Australasia (EAAF, en inglés), se cree que la pérdida de puntos de parada en la región del Mar Amarillo es la razón principal de la declinación poblacional precipitada. Sin embargo, las tasas de declinación varían considerablemente entre especies, y sigue sin estar claro cómo pueden

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surgir tales diferencias dentro de un grupo de especies emparentadas que utilizan hábitats aparentemente similares en los mismos lugares. Mapeamos las distribuciones espaciales de las aves playeras forrajeras, así como los factores ambientales bióticos (invertebrados bénticos consumidos por las aves playeras migratorias) y abióticos (características de los sedimentos), en un punto de parada clave en el este de China. Cinco de las seis características de los sedimentos mostraron una variación espacial significativa con respecto a los cambios lineales en la distancia a lo largo de la costa o la distancia desde el malecón en la misma llanura mareal. La biomasa de cuatro de los seis invertebrados bénticos más abundantes se concentró en las zonas superior o media de la llanura mareal. Esta heterogeneidad de las características de los sedimentos y de las presas invertebradas es la que mejor explica los patrones de distribución de las tres especies de aves playeras en la llanura mareal. Estos resultados sugieren que la pérdida de llanuras mareales a lo largo del Mar Amarillo, que suele concentrarse en las zonas superior y media, puede no sólo reducir la cantidad total de hábitat de parada, sino también afectar de manera desproporcionada a las partes más ricas en recursos para las aves. La conservación eficaz de los puntos de parada de las aves playeras a lo largo del EAAF, y probablemente en otros lugares, debe tener en cuenta la sutil heterogeneidad del hábitat que caracteriza a estas llanuras mareales, priorizando la protección de las partes más ricas en recursos alimenticios, más frecuentemente utilizadas por las especies de aves focales y más vulnerables a las amenazas antropogénicas.

Palabras Clave:

ave playera migratoria, distribución de recursos, heterogeneidad de hábitat, invertebrado bentónico, punto de parada, ruta migratoria Asia Oriental-Australasia, sedimento

潮间带滩涂异质性在迁徙 鹬类保护中的重要意义

【摘要】了解物种的分布格局及其决定因素,对于制定有效的栖息地保护和管理规划至关重要。在东亚-澳大利西亚迁飞区,迁徙鹬类的种群数量正在快速下降,其主要原因是作为鹬类迁徙停歇地的黄渤海地区潮间带滩涂面积大幅减少。然而,尽管许多迁徙鹬类亲缘关系密切,并且都利用潮间带滩涂(甚至是同一片滩涂),但是它们的种群数量下降速率却存在巨大差异,而导致这种差异的原因仍然缺乏了解。在这项研究中,我们在渤海沿岸一个重要的鹬类迁徙停歇地进行了调查和取样,分析了鹬类以及相关的生物因子(鹬类的食物,即底栖无脊椎动物)和非生物环境因子(沉积物特征)在潮间带滩涂上的空间分布格局。研究发现,在六种沉积物组分特征中,其中五种都在垂直或平行于海岸线的方向上呈现出显著变化。在潮间带滩涂上数量最多的六种底栖无脊椎动物中,其中四种的生物量主要分布于高潮滩或中潮滩。沉积物特征以及底栖无脊椎动物的异质性分布共同解释了三种目标鹬类在潮间带滩涂上的分布格局。这些研究结果表明,黄渤海区域潮间带滩涂栖息地的丧失,尤其是高潮滩和中潮滩面积的急剧减少,不仅会造成迁徙停歇地的面积下降,更会极大地影响鹬类所依赖的资源最丰富的栖息地斑块。因此,为了更有效地保护东亚-澳大利西亚迁飞区和其他迁飞区的鹬类迁徙停歇地,保护实践中必须将潮间带滩涂栖息地普遍存在的异质性特征考虑在内,优先保护潮间带滩涂中食物资源最丰富,鸟类利用最频繁,以及受人类活动威胁最严重的斑块。

关键词: 底栖无脊椎动物, 东亚-澳大利西亚迁飞区, 栖息地异质性, 迁徙鹬类, 资源分布, 沉积物, 迁徙停歇地

INTRODUCTION

Habitat loss and degradation pose a major threat to global biodiversity (IPBES, 2019). Although the availability of habitat usually determines a species' occurrence across its potential range in a general sense, the species may not use that habitat homogeneously and may even be absent from seemingly suitable patches (Bijleveld et al., 2015; Elsen et al., 2017). This fine-scale varia-

tion in a given species' distribution is often related to variations in the quality of the habitat (Jones, 2001). Consequently, conservation planning that focuses on preserving a given amount or extent of habitat runs the risk of oversimplifying species' habitat requirements or underestimating the impact of habitat loss on target species, thereby rendering habitat conservation practices less effective. In particular, if habitat loss or degradation occurs disproportionately in portions of habitat that are of

higher-than-average quality, the result could be declines in species abundance that are disproportionate to the amount of habitat affected (Montejo-Kovacevich et al., 2022; Mu & Wilcove, 2020; Yin et al., 2021). It is thus important to understand how key biotic (e.g., food, predators) and abiotic (e.g., temperature, topography) factors in a given habitat vary spatially and temporally and how that variation drives overall patterns of habitat quality. Such knowledge enables conservation practitioners to more effectively protect the habitats of species of concern.

Shorebirds undertake some of the longest migrations on Earth, and many of them depend on intertidal habitat at coastal staging sites to refuel and rest during their epic journeys (Buehler & Piersma, 2008). However, due to multiple anthropogenic threats, many shorebird populations around the world have been declining rapidly (Delany et al., 2009; Donaldson et al., 2000; Rosenberg et al., 2019). This is especially true along the East Asian-Australasian Flyway (EAAF). The EAAF is one of the nine major global flyways, and it extends from Siberia and Alaska to Australia and New Zealand. Home to over 200 species of migratory waterbirds totaling over 50 million individuals, the EAAF is an especially vulnerable system, with more than one-quarter of its waterbird populations listed as threatened or near threatened by the International Union for the Conservation of Nature (Mundkur & Langendoen, 2022). Extensive land reclamation of tidal flats, especially along the coast of China and the Korean Peninsula in the Yellow Sea region, has drastically reduced the area of staging habitat for migratory shorebirds (Murray et al., 2014; Murray et al., 2012). However, rates of population decline among the migratory shorebirds of the EAAF exhibit considerable interspecific differences at local and flyway scales, sometimes even showing opposing trends with respect to local population sizes, flyway population sizes, and the area of staging habitats (Studds et al., 2017; Wang et al., 2022; Yang et al., 2011). This suggests the need for a more nuanced understanding of shorebirds' habitat use patterns and the impacts of land reclamation on staging habitat quality at the flyway and local scales.

Fine-scale habitat use patterns of migratory shorebirds, combined with different rates of habitat loss and degradation along the flyway, may underlie many of the contradictory and puzzling trends in rates of decline among shorebirds (Morrisk et al., 2021; Mu & Wilcove, 2020). This is because during a single migration period, shorebirds may not only stage at different sites or even different habitats within the same site (Baker, 1979; Jing et al., 2007; Recher, 1966; Zwarts & Wanink, 1993), but they may also exhibit major interspecific differences with respect to where they forage on the same tidal flat habitat at a given site (Granadeiro et al., 2006; Mu & Wilcove, 2020; Nehls & Tiedemann, 1993). In addition, different parts of the same tidal flat system may face threats that vary in type and intensity, making some areas (and the shorebirds that rely heavily on these areas) more vulnerable than others (Choi et al., 2022; Jackson et al., 2021). Despite well-documented cases of changes and acute declines in benthic invertebrate communities at coastal staging sites in China (Peng et al., 2021; Zhang et al., 2021; Zhang et al., 2019), major gaps remain in the understanding

of how shorebirds and their food resources are distributed on tidal flats along the EAAF (Choi et al., 2014; Jing et al., 2007). Even less is known about how interconnected the two distributions (i.e., shorebirds and their food resources) are (Yates et al., 1993). These knowledge gaps hinder the ability to predict the impacts of habitat loss and degradation on shorebirds, to identify high-quality habitat for protection, and to restore degraded habitats within the scale of practical conservation. Consequently, a more detailed understanding of the distributions of key food resources and migratory shorebirds is urgently needed to guide the effective conservation of these species.

We mapped the distribution of benthic invertebrates and sediment characteristics of a tidal flat at a key shorebird staging site in the Yellow Sea region. We then investigated how these biotic and abiotic environmental factors jointly explain the distribution patterns of foraging shorebirds within this system. Our aim was to provide a much-needed ecological understanding of resource and species distributions so as to guide effective planning for shorebird conservation.

METHODS

We conducted all fieldwork at Nanpu (39.1 N, 118.2 E) in the Yellow Sea region of China (Figure 1a). This internationally important shorebird staging site largely consists of periodically exposed tidal flats and adjacent inland saltpans, where large populations of shorebirds refuel and rest, especially during northward migration (Lei et al., 2018; Yang et al., 2011). Field data on environmental factors and shorebird distributions were collected during April–May 2017, coinciding with the peak of shorebird northward migration at this site. Data collection protocols were approved by the Institutional Animal Care and Use Committee of Princeton University (2025B-15, 2024F-15).

Environmental data

Coastal shorebirds forage almost exclusively on benthic invertebrates on tidal flats, and use a combination of pecking and probing techniques (Van de Kam et al., 2017). As a result, sediment characteristics of tidal flats may affect shorebird habitat selection indirectly by determining the distribution of benthic invertebrates (Yates et al., 1993), and directly through differences in sediment penetrability that affect the energetic costs of probing for food or the risk of physical damage to the bills of probing shorebirds (Finn et al., 2008; Mouritsen & Jensen, 1992; VanDusen et al., 2012). To test and quantify the relative importance of different environmental factors on the distribution of foraging shorebirds, benthic invertebrates (abundance, type, and biomass) and sediment characteristics (particle size and organic content) were collected as biotic and abiotic environmental factors, respectively (Compton et al., 2013; Goss-Custard, Kay, et al., 1977; VanDusen et al., 2012) from 14 to 20 April 2017 along six environmental transects. Four of these transects aligned with shorebird counting transects (see below), and the other two were placed separately from the

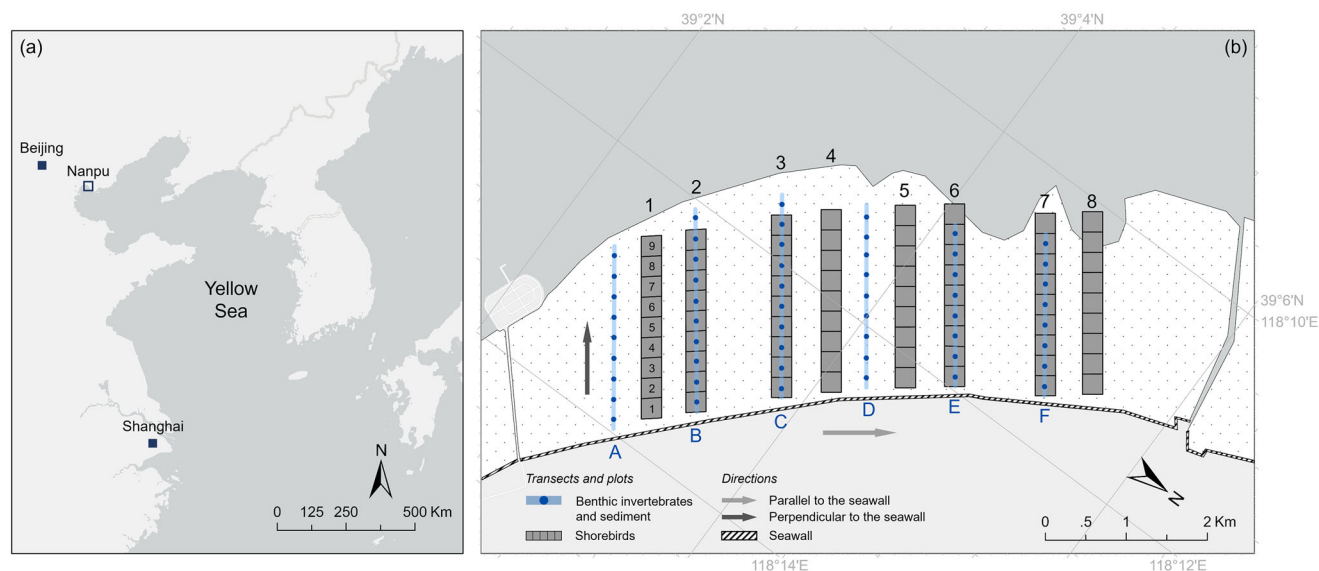


FIGURE 1 (a) Location of the study site, Nanpu, China, in the Yellow Sea region and (b) layout of transects and plots at Nanpu (light gray areas, permanent landmass; gray areas, sea; stippled white area, tidal flat; dark gray squares, shorebird counting transects [1–8, each consisting of nine plots numbered 1–9 from sea wall to low tide line]; blue lines with dots, benthic invertebrate and sediment transects [A–F]).

shorebird counting transects to provide more comprehensive coverage of the entire tidal flat to better capture the variations in environmental factors along the axis running parallel to the seawall (Figure 1b). The distance between adjacent transects was 1 km. Along each environmental transect, 8–10 sampling sites were set 250 m apart, and three benthic core samples (diameter 15.5 cm, depth 20 cm) and one sediment core sample (diameter 2.6 cm, depth 5 cm) were taken at each sampling site.

The top 5 cm of each benthic core sample were processed and treated separately from the bottom 15 cm to take into account potential differences in the relationship between surface- and deep-dwelling benthic invertebrates and shorebird species with different foraging depths as determined by their bill lengths and foraging techniques (van Gils et al., 2009; Yang et al., 2016; Zhang et al., 2019). Each sample was sieved through a 0.5-mm mesh, and the remaining prey items were put immediately into tubes with > 75% ethanol (polychaetes and other soft-bodied prey) or plastic bags (mollusks, crabs, etc.). The sieved samples were then stored at -20°C within 12 h of sample collection.

In the laboratory, invertebrate samples were sieved and washed again through a 0.5-mm mesh and transferred to a white tray. All invertebrates were identified to the lowest identifiable taxonomic category (Appendix S1), measured to the nearest 0.01 mm along their longest dimension, and counted under dissecting microscopes. For a selection of abundant bivalve species, we also calculated their ash-free dry mass (AFDM, g) as a measurement of biomass, based on the relationships discovered in earlier studies conducted at Nanpu and Yalu Estuary, a nearby site in the Yellow Sea region (Yang et al., 2013; Zhang et al., 2019). Owing to the large variations in body length among different polychaete species and individuals, as well as a high proportion of fragmented polychaete individuals

in the samples, we summed the length of polychaete fragments from each sample, and this total length of polychaete segments was used as the measurement of polychaete abundance in each sample.

Sediment core samples were stored in plastic bags and transferred to -20°C within 12 h of collection until processed. In the laboratory, samples were thawed, dried for 72 h at 55°C , and then cooled to room temperature. Following the Wentworth scale (Wentworth, 1922), four meshes with different aperture widths (0.5, 0.25, 0.125, and 0.0625 mm) were used for sequential sieving, and the particles remaining on each mesh were weighed to the nearest 0.1 mg. The composition of sediment in each sample was measured as the proportion of the sediment dry weight within each of the five groups: coarse sand (> 0.5 mm), medium sand (0.25–0.5 mm), fine sand (0.125–0.25 mm), very fine sand (0.0625–0.125 mm), and silt (< 0.0625 mm). Two to three grams of each sediment sample were dried again at 55°C for 24 h and then incinerated at 550°C for at least 6 h; the 3-g mass was chosen to maximize the amount of sediment measured, but still allow complete and thorough ignition during the measurement (Wang et al., 2011). The percentage of organic content was derived as the weight loss after incineration divided by the dry sediment weight before incineration.

Shorebird counts and distribution

To quantify shorebird distribution on the tidal flat, eight 2.25-km transects were set out perpendicular to the seawall covering the entire elevational gradient (Figure 1b). Each shorebird transect was divided into nine plots of 250×250 m in size. The distance between two adjacent transects ranged from 300 to

800 m. Four shorebird transects aligned with the environmental data transects. The other nonoverlapping shorebird transects were placed not to test the relationship between environmental factors and shorebird distribution, but rather to systematically sample the distribution of shorebirds across the entire tidal flat by covering the entire study site as much as possible, especially to provide better resolution of the shorebird distribution along the axis running parallel to the seawall (Figure 1b).

Two to four experienced observers conducted shorebird surveys during daytime from 11 to 18 May 2017, recording the species and numbers of foraging shorebirds in each plot at an average interval of 32 min (SD 22) throughout 1–2 full tidal cycles during spring tides. To avoid disturbing birds, observers stayed at least 100 m away from the boundaries of plots and walked between adjacent transects. The detailed shorebird survey procedures are described in Mu and Wilcove (2020).

We mapped the distribution of three shorebird species, red knots (*Calidris canutus*), sanderlings (*C. alba*), and bar-tailed godwits (*Limosa lapponica*), for which we had enough field survey data and enough information on their major prey items from the literature (Connors et al., 1981; Yang et al., 2013; Zhang et al., 2019) to enable us to determine the relationship between environmental factors and the distribution patterns of foraging birds. Two different metrics were calculated to describe the distribution pattern of these three shorebird species: *low-tide spatial distribution* and *cumulative foraging time*. In most studies, shorebird spatial distribution typically considers the distribution of birds during a specific time, especially the low tide period when all of the tidal flats are exposed and available for birds to use (Finn et al., 2008; Lunardi et al., 2012; Rolet et al., 2015). We calculated the average number of individuals (to the nearest integer) of each species observed foraging in each plot during the 1 h before and 1 h after low tide, to represent the low-tide spatial distribution of each species. However, this particular distribution measurement focuses on a relatively short period during the entire tidal cycle and does not account for the temporal changes in shorebird distribution that result from tidal movement while the birds are foraging on the tidal flats (Gils et al., 2006; Granadeiro et al., 2006). The resulting incomplete coverage or representation of shorebirds' habitat use may lead to biased or erroneous relationships between environmental factors and shorebird distribution.

Accordingly, we also calculated shorebird cumulative foraging time, which simultaneously considers the spatial distribution of shorebirds and the temporal changes in their distribution throughout the entire tidal cycle (Mu & Wilcove, 2020). Cumulative foraging time was calculated as the area under the curve of the abundance of foraging shorebirds plotted against time during the full tidal cycle for each species in each plot (Appendix S2). This measurement takes into account the number of shorebirds foraging in each plot and the duration of time these individuals spend there, so it may be more suitable for investigating the relationship between environmental factors and shorebird distribution because tidal movement considerably affects habitat and food availability (Gils et al., 2006; Mu & Wilcove, 2020; Ribeiro et al., 2004).

Data analyses

With data collected along all six environmental transects, we used linear regressions to analyze the distribution patterns of environmental factors along the two main axes of the tidal flat: parallel (distance from transect A in meters) and perpendicular (distance from the seawall in meters) to the seawall (Figure 1b). The interaction term between the two directions, which represented the approximate direction of the tidal movement at the study site, was also included if it showed a significant effect.

For biotic factors, we used the average value of three benthic core samples collected at each sampling site to test the distribution patterns of six benthic invertebrate taxa. These benthic invertebrates included three important food resources of the three focal shorebird species (Connors et al., 1981; Yang et al., 2013; Zhang et al., 2019): biomass of the bivalve *Potamocorbula laevis* (POLA, the main prey of red knots) in the top 5 cm of the cores, abundance (total length) of all polychaetes (main prey of bar-tailed godwits) in the full 20 cm of the cores, and density of the crustaceans Cumacea plus Amphipoda (CU+AM, main prey of sanderlings) in the top 5 cm of the cores. We included the biomass of POLA in the top 5 cm of the core samples instead of the full 20 cm of the cores because red knots, the main avian consumers of POLA, can probe up to 5 cm into the substrate while foraging. Therefore, the biomass in the top 5 cm of the cores better represents the food resources available to the red knots (Yang et al., 2016). Both CU and AM are surface-dwelling groups; thus, the density in the top 5 cm of the cores would essentially be the same as that in the full 20 cm of the cores. We also tested the distribution patterns of three additional benthic invertebrate taxa that other shorebird species may feed on (Zhang et al., 2019) and for which we gathered sufficient data (i.e., occurring in >10% of the sampling sites): in the full 20 cm of the core samples, biomass of the bivalve *Macra veneriformis* (MAVE) and of the bivalve *Moerella iridescens* (MOIR) and abundance (as total length) of the polychaete *Magelona cincta* (MACI).

For abiotic factors, we tested the distribution pattern of the proportion of five particle size groups and the proportion of organic content. We also tested how strongly correlated the distributions of biotic (i.e., benthic invertebrates) and abiotic (sediment characteristics) environmental factors were with linear regressions; the six benthic invertebrate taxa mentioned above were dependent variables and four out of five sediment particle size groups were independent variables. We excluded the silt group owing to its strong collinearity with very fine sand (linear regression $F_{1,31} = 1189$, $p < 0.01$, $R^2 = 0.975$) and the potential problem of including a set of independent variables that sum to 1 in linear models.

We then modeled the distributions of our three focal shorebird species on the tidal flat in relation to biotic and abiotic environmental factors along the four shorebird transects with matched environment transects (i.e., transects 2/B, 3/C, 6/E, and 7/F) (Figure 1b) with linear (for shorebird cumulative foraging time) and generalized linear (for shorebird low-tide spatial distribution; family negative binomial to account for

overdispersion) models. We also employed (generalized) linear mixed-effects models with random intercepts for each transect to take into account the potential differences in the total number of shorebirds along each transect owing to different proximities to high tide roosts and human disturbance levels. In the mixed-effects models, all fixed-effect independent variables were recentered and rescaled using the respective means and SDs to reduce the potential impact on model performance when variables are on different scales. Specific shorebird species and potential major prey (as biotic factors) included were red knots feeding on POLA (biomass and density), sanderlings feeding on CU+AM (density), and bar-tailed godwits feeding on polychaetes (total length) (Connors et al., 1981; Yang et al., 2013; Zhang et al., 2019).

As for abiotic factors, we included four out of five sediment particle size groups in the distribution models. We excluded the silt group, again, owing to its strong collinearity with very fine sand (linear regression $F_{1,31} = 1189, p < 0.01, R^2 = 0.975$) and the potential problem of including a set of independent variables that sum to 1 in linear models. To identify the set of biotic and abiotic factors that best explains the observed distribution pattern of shorebirds, we conducted model selection with the corrected Akaike information criterion (AIC_c) (Burnham & Anderson, 2002). Data analyses were conducted in R 3.6.3 (R Core Team, 2020) and with package lme4 for the mixed-effects models (Bates et al., 2015). The R package ggplot2 (Wickham, 2016) was used to draw the distribution heat maps.

RESULTS

Spatial heterogeneity of environmental factors

All six benthic invertebrate prey taxa had considerable heterogeneity in their spatial distributions across the tidal flat at Nanpu (Figure 2 & Table 1). The biomass of POLA and the total length of MACI were concentrated around transect F and were higher closer to the seawall. The density of CU+AM increased in the approximate direction of the outgoing tide. The abundance (as total length) of polychaetes showed a pattern similar to but more homogeneous than POLA biomass and MACI total length, although no significant effect of the interaction between the two main axes was found (Table 1). The biomass of MOIR was concentrated toward transect A; higher biomass occurred in the middle to lower tidal flat without a significant linear trend. Likewise, the biomass of MAVE peaked around the middle portion of transect D, and there were no significant linear changes along the two axes despite the spatial heterogeneity in its distribution shown by the heat map (Figure 2f).

Spatial heterogeneity was also apparent in sediment characteristics (Figure 3 & Table 2). The proportion of organic content was highest in the plots close to the seawall but did not change significantly along the axis parallel to the seawall. Two out of five particle size groups (silt and very fine sand) made up >85% (dry weight) of sediment particles on the Nanpu tidal flat and showed significant heterogeneity along directions parallel and perpendicular to the seawall. Silt was present in higher propor-

tions closer to the seawall in transect A, whereas the opposite trend occurred with very fine sand (Figure 3). Fine sand showed a similar pattern to that of very fine sand. Medium sand concentrated toward transect F; proportions were higher closer to the seawall. No significant linear trend was found for coarse sand.

Despite both exhibiting high heterogeneity on the tidal flat, the distributions of benthic invertebrates and sediment characteristics were only moderately correlated; $\leq 30\%$ of the variance in the distribution of benthic invertebrates was explained by sediment characteristics (Appendix S5).

Shorebird distribution relative to environmental factors

Across the Nanpu tidal flat, heat maps of three representative shorebird species showed considerable heterogeneity in spatial distribution patterns with respect to both distribution metrics (i.e., low-tide spatial distribution and cumulative foraging time) (Figure 4). The distribution patterns of red knots were similar with both metrics, indicating that red knots concentrated on the tidal flat close to the seawall (Figure 4a,d). The low-tide spatial distributions of sanderlings and bar-tailed godwits, however, showed high counts of individuals in plots close to the low-tide line (Figure 4b,c). The cumulative foraging time of sanderlings, compared with their low-tide spatial distribution, appeared more evenly distributed across all plots (Figure 4e), whereas that of the bar-tailed godwits was concentrated toward the seawall and transect 8 (Figure 4f).

The models investigating the distributions of foraging shorebirds in relation to environmental factors showed that the two metrics of shorebird distribution yielded similar results for red knots and bar-tailed godwits; both metrics indicated that the distributions of these two species on the tidal flat were best explained by biotic (benthic prey) and abiotic (sediment) environmental factors together (Table 3). Similarly, the low-tide spatial distribution of sanderlings was best explained by the density of potential prey (CU+AM) and the proportion of very fine sand in the sediment. The cumulative foraging time of sanderlings, however, was best predicted by the null model. None of the models with $\Delta AIC < 2$ for sanderling cumulative foraging time included potential prey as an independent variable, likely due to sanderling's rather uniform distribution on the tidal flat (Table 3 & Figure 4e). The (generalized) linear mixed-effects models with random intercept for each transect produced similar results to the results of the above models that did not consider the random effect of different transects (Appendix S6).

Using the best-fit models, we further calculated the relative contribution of biotic and abiotic factors to explaining shorebird distribution patterns. For the low-tide spatial distributions, the biotic factors explained only 2.41% (SD 2.17), 2.86% (3.30), and 30.60% (0.00) of the variance in the distribution of red knots, sanderlings, and bar-tailed godwits, respectively, on average across all candidate models with $\Delta AIC < 2$. Adding the corresponding abiotic factors increased the explained variance to 61.96% (6.47), 25.21% (8.48), and 51.06% (2.83), respectively. In models using cumulative foraging time as the distribution

TABLE 1 Results of linear models describing the distribution of benthic invertebrate prey of shorebirds on the Nanpu tidal flat.^a

Predictor	POLA (5 cm)			MACI (20 cm)			CU+AM (5 cm)		
	est.	SE	p	est.	SE	p	est.	SE	p
Intercept	-1.82×10^{-2}	2.80×10^{-1}	0.949	3.21×10^2	3.56×10^2	0.373	1.70×10^1	1.73×10^1	0.333
Perpendicular to seawall	9.42×10^{-5}	1.97×10^{-4}	0.634	6.81×10^{-3}	2.50×10^{-1}	0.978	-5.21×10^{-3}	1.22×10^{-2}	0.670
Parallel to seawall	3.57×10^{-4}	9.44×10^{-5}	$<0.001^b$	7.49×10^{-1}	1.20×10^{-1}	$<0.001^b$	-7.43×10^{-3}	5.84×10^{-3}	0.209
Perpendicular * parallel to seawall	-2.57×10^{-7}	7.38×10^{-8}	0.001^b	-4.13×10^{-4}	9.37×10^{-5}	$<0.001^b$	1.70×10^{-5}	4.56×10^{-6}	0.001^b
df	3, 49			3, 49			3, 49		
R ²	0.394			0.647			0.482		
est.	Polychaeta (20 cm)			MOIR (20 cm)			MAVE (20 cm)		
	SE	p	est.	SE	p	est.	SE	p	
Intercept	9.87×10^3	1.29×10^3	$<0.001^b$	4.83×10^{-1}	1.26×10^{-1}	$<0.001^b$	9.63	1.25×10^1	0.443
Perpendicular to seawall	-3.20	7.25×10^{-1}	$<0.001^b$	-3.90×10^{-5}	7.13×10^{-5}	0.587	-3.80×10^{-3}	7.03×10^{-3}	0.592
Parallel to seawall	9.98×10^{-1}	2.77×10^{-1}	$<0.001^b$	-9.15×10^{-5}	2.72×10^{-5}	0.001^b	4.32×10^{-3}	2.68×10^{-3}	0.114
Perpendicular * parallel to seawall	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
df	2, 50			2, 50			2, 50		
R ²	0.432			0.185			0.060		

Note: Numbers next to species abbreviations are depths of the benthic samples.

Abbreviations: AM, Amphipoda; CU, Cumacea; est., estimate; MACI, *Magelona chinata*; MAVE, *Macra veruiformis*; MOIR, *Moerella iridescens*; POLA, *Polanorbulina laevis*.

^a Models without interaction terms are shown if the interaction effects were not significant (see Appendix S3 for models with interaction terms). Distribution patterns were tested along two main axes of the tidal flat (i.e., parallel [distance from transect A in meters] and perpendicular [distance from seawall in meters] to the seawall).

^b Statistically significant results at $p < 0.05$.

TABLE 2 Results of linear models describing the distribution of abiotic factors (sediment particle size groups and proportion of organic content) on the Nanpu tidal flat.^a

Predictor	Organic content (%)				Silt (%)				Very fine sand (%)			
	est.	SE	p		est.	SE	p		est.	SE	p	
Intercept	4.79	2.09×10^{-1}	<0.001 ^b		8.32×10	3.33	<0.001 ^b		1.51×10	3.57	0.000 ^b	
Perpendicular to seawall	-1.43×10^{-3}	1.20×10^{-4}	<0.001 ^b		-2.69×10^{-2}	1.91×10^{-3}	<0.001 ^b		2.57×10^{-2}	2.04×10^{-3}	<0.001 ^b	
Parallel to seawall	-2.16×10^{-5}	4.47×10^{-5}	0.631		-2.29×10^{-3}	7.12×10^{-4}	0.002 ^b		1.68×10^{-3}	7.63×10^{-4}	0.033 ^b	
Perpendicular * parallel to seawall	N/A	N/A	N/A		N/A	N/A	N/A		N/A	N/A	N/A	
df	(2, 49)				(2, 49)				(2, 49)			
R ²	0.747				0.803				0.763			
Predictor	Fine sand (%)				Medium sand (%)				Coarse sand (%)			
	est.	SE	p		est.	SE	p		est.	SE	p	
Intercept	1.17	8.99×10^{-1}	0.199		2.47×10^{-1}	1.01×10^{-1}	0.018 ^b		1.81×10^{-1}	9.10×10^{-2}	0.053	
Perpendicular to seawall	1.43×10^{-3}	5.14×10^{-4}	0.008 ^b		-1.68×10^{-5}	7.09×10^{-5}	0.814		-9.47×10^{-5}	5.20×10^{-5}	0.075	
Parallel to seawall	5.68×10^{-4}	1.92×10^{-4}	0.005 ^b		6.65×10^{-5}	3.42×10^{-5}	0.007 ^b		2.28×10^{-5}	1.94×10^{-5}	0.247	
Perpendicular * parallel to seawall	N/A	N/A	N/A		-6.51×10^{-8}	2.69×10^{-8}	0.020 ^b		N/A	N/A	N/A	
df	(2, 49)				(3, 48)				(2, 49)			
R ²	0.224				0.321				0.101			

Abbreviation: est., estimate.
^aModels without interaction terms are shown if the interaction effects were not significant (see Appendix S4 for models with interaction terms). Distribution patterns were tested along two main axes of the tidal flat (i.e., parallel [distance from transect A in meters] and perpendicular [distance from seawall in meters] to the seawall).
^bStatistically significant results at $p < 0.05$.

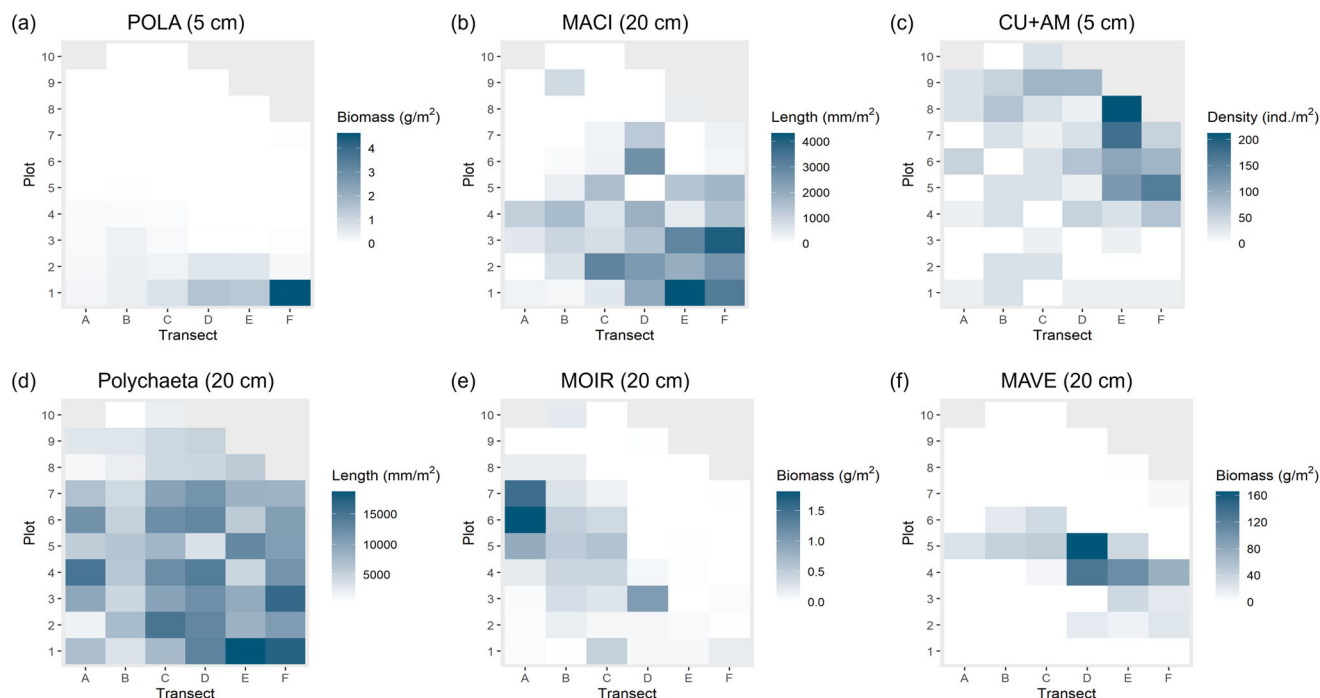


FIGURE 2 In the Nanpu tidal flat, distributions of benthic invertebrate prey of (a) *Potamocorbula laevis* (POLA), (b) *Magelona cincta* (MACI), (c) Cumacea and Amphipoda (CU+AM), (d) all polychaetes, (e) *Moerella iridescens* (MOIR), and (f) *Mactra veneriformis* (MAVE) (x-axes, direction parallel to the seawall; y-axes, direction perpendicular to the seawall [plot 1 closest to the seawall]; numbers in parentheses, depths of the benthic samples).

metric, 60.39% and 37.70% (0.00), respectively, of the variance in the distribution of red knots and bar-tailed godwits were explained by biotic factors. Adding abiotic factors increased the explained variance up to 66.79% and 75.74% (0.74) for red knots and bar-tailed godwits, respectively.

DISCUSSION

Tidal flats may appear to be a homogeneous habitat on which many closely related migratory shorebirds congregate and disperse rhythmically with the tidal cycles. Our results suggest, however, that a single stretch of tidal flat—one that supports hundreds of thousands of migratory shorebirds annually (Lei et al., 2018)—exhibits considerable heterogeneity with respect to biotic (benthic invertebrate prey) and abiotic (sediment characteristics) environmental factors (Figures 2 & 3, Tables 1 & 2). The shorebirds foraging on this tidal flat also exhibited considerable heterogeneity with respect to their distribution patterns, which can be jointly explained by the heterogeneity of these key biotic and abiotic environmental variables. Species-specific food resources and sediment particle sizes were especially strong predictors of shorebird distributions (Table 3).

This spatial heterogeneity in food resources, abiotic environmental variables, and shorebirds reaffirms the idea that tidal flats are indeed a spatially heterogeneous habitat (Choi et al., 2014; Goss-Custard, Jones, et al., 1977; Granadeiro et al., 2006; Mu & Wilcove, 2020) shaped by tidal forces, topography, salinity, and other physical features (Choi et al., 2014; Compton et al., 2013;

Dyer et al., 2000; VanDusen et al., 2012; Wang et al., 2002). Such heterogeneity, however, is rarely considered in plans relating to the protection and restoration of tidal flat habitats. Studies of the loss of tidal flat habitat and its effect on waterbird populations have focused primarily on changes in habitat area (Murray et al., 2014; Studds et al., 2017; Wang et al., 2022), which, without consideration of habitat quality, may greatly underestimate the severity of habitat loss to waterbird populations if portions of tidal flats that are of higher quality and greater importance to shorebirds are disproportionately destroyed, as is often the case in the Yellow Sea region (Choi et al., 2018; Murray et al., 2014).

The upper tidal flats are especially important to foraging shorebirds at major staging sites along the EAAF, potentially a result of the long exposure time and hence greater availability to foraging shorebirds (Mu & Wilcove, 2020). Our results showed that at a major staging site, many benthic invertebrates occur at much higher densities and biomass in areas close to the seawall (Figure 2), suggesting that the importance of the upper tidal zone to foraging shorebirds is likely not just a result of its longer exposure time during each tidal cycle, but also a direct consequence of its higher food density and biomass. These findings also suggest that the loss of upper tidal flats at our study site may result in the largest local population declines in red knot, followed by bar-tailed godwit, and the smallest population declines in sanderling, based on the distributions of birds and their preferred prey items as measured at a fine scale in the intertidal zone (Figures 2 & 4).

Historical losses of tidal flat area in the EAAF have been concentrated in the upper zone (Choi et al., 2018; Murray et al.,

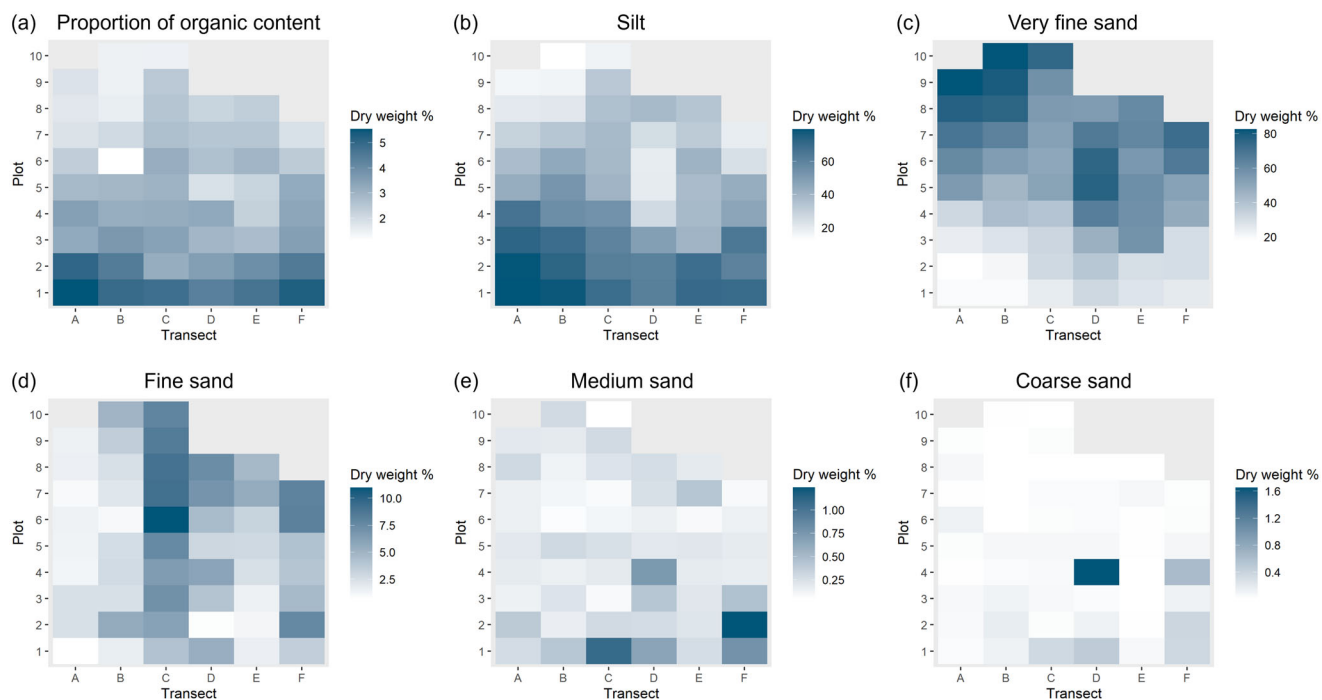


FIGURE 3 Distribution of abiotic factors (sediment particle size groups and proportion of organic content) on the Nanpu tidal flat (x-axes, direction parallel to the seawall; y-axes, direction perpendicular to the seawall [plot 1 closest to the seawall]).

Shorebird low-tide spatial distribution

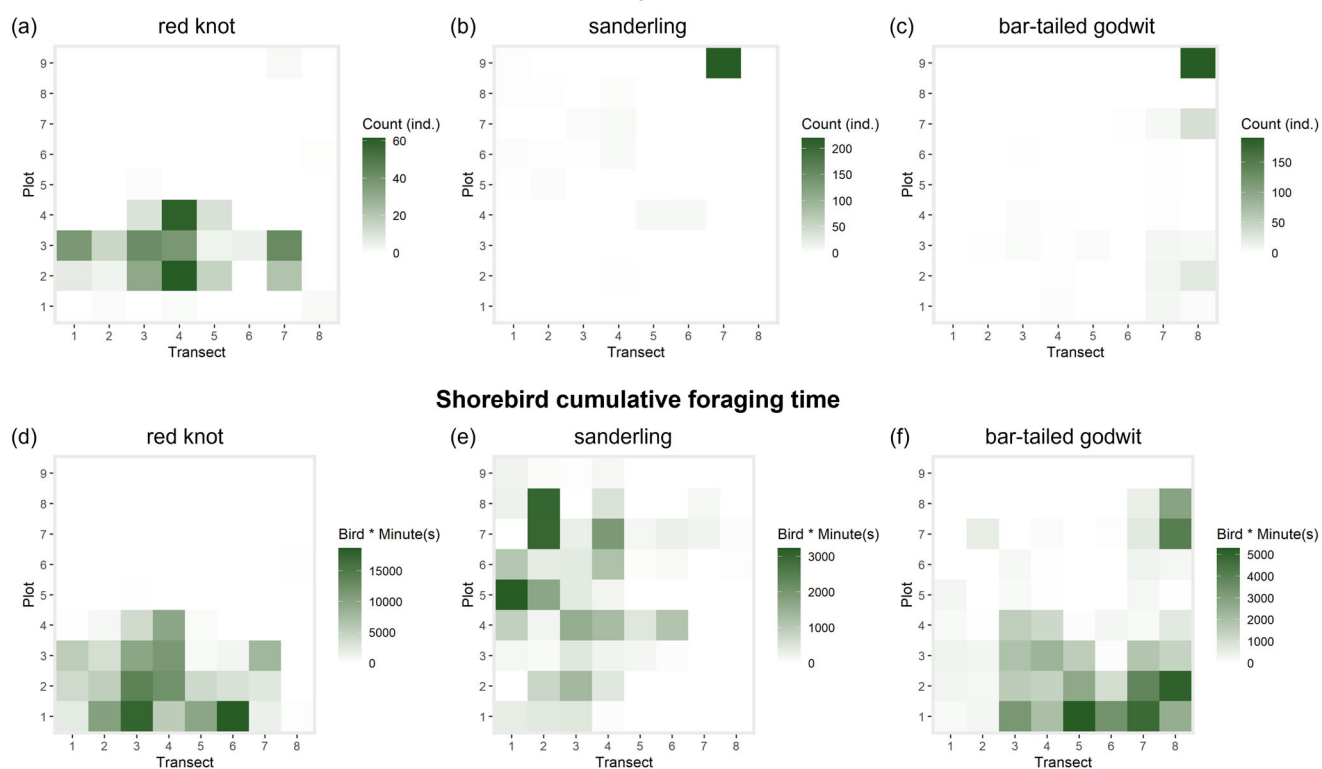


FIGURE 4 Spatial distribution of three shorebirds on the Nanpu tidal flat based on two metrics of shorebird distribution: (a–c) low-tide spatial distribution and (d–f) cumulative foraging time (x-axes, direction parallel to the seawall; y-axes, direction perpendicular to the seawall [plot 1 closest to the seawall]).

TABLE 3 Models that best explain shorebird distribution on the Nanpu tidal flat.

Model	df	AIC _c ^a	ΔAIC ^b
Low-tide spatial distribution ^c			
red knot			
– POLA biomass + very fine sand ^d	4	111.05	–
– POLA biomass + very fine sand + medium sand + coarse sand	6	111.92	0.87
– POLA biomass + very fine sand + coarse sand	5	112.09	1.05
– POLA density + very fine sand	4	112.36	1.32
– POLA density + very fine sand + coarse sand	5	112.48	1.43
– POLA density + POLA biomass + very fine sand + medium sand + coarse sand	7	112.84	1.79
– 1	2	122.25	11.20
sanderling			
– CU+AM density + very fine sand ^d	4	73.49	–
– Coarse sand	3	74.39	0.91
– CU+AM density + coarse sand	4	74.84	1.35
– very fine sand	3	75.39	1.91
– 1	2	76.13	2.65
bar-tailed godwit			
– polychaete length + fine sand ^d	4	97.07	–
– polychaete length + fine sand + coarse sand	5	97.25	0.18
– polychaete length + fine sand + medium sand	5	98.54	1.47
– 1	2	108.11	11.03
Cumulative foraging time ^c			
red knot			
– POLA density + POLA biomass + medium sand ^d	5	616.46	–
– 1	2	643.84	27.38
sanderling			
– 1 ^d	2	522.77	–
– coarse sand	3	523.50	0.73
– very fine sand	3	523.83	1.06
– fine sand	3	524.11	1.34
– medium sand	3	524.13	1.36
bar-tailed godwit			
– polychaete length + medium sand ^d	4	513.89	–
– polychaete length + very fine sand + medium sand	5	514.85	0.96
– polychaete length + fine sand + medium sand	5	515.34	1.44
– 1	5	553.07	39.18

Abbreviations: AM, Amphipoda; CU, Cumacea; POLA, *Potamocorbula laevis*.

^aCorrected AIC values for small sample sizes.

^bDifference in AIC_c between each model and the model with lowest AIC_c (only models with ΔAIC_c < 2 are shown). All models in Appendix S7.

^cModeled with generalized linear models; family negative binomial.

^dModels with lowest AIC_c scores.

^eModeled with linear regressions.

2019), which, combined with the species and site-specific preferences for the upper zone by migrating shorebirds (Mu & Wilcove, 2020), may help explain the interspecific differences in shorebird population declines at local and global scales (Studds et al., 2017; Wang et al., 2022). Apart from coastal development and conversion, which has been the dominant cause of histori-

cal tidal flat loss, most current and emergent threats to tidal flats are also concentrated on the upper tidal flats, including *Spartina* encroachment (Jackson et al., 2021), mangrove afforestation (Choi et al., 2022), and construction of solar panels.

Accordingly, conservation plans for critical staging habitats along the EAAF and elsewhere should consider this

heterogeneity and prioritize the protection (and subsequent management) of those portions of the intertidal zone that are of higher quality and thus more frequently used by focal species, especially where such sites are vulnerable to anthropogenic threats. Exploitation or destruction of tidal flats will not only reduce the amount of habitat but may also render specific shorebird species especially vulnerable. As a result, stakeholders involved with coastal development projects targeting tidal flats should strive to understand the distribution of shorebirds and key environmental factors, as well as the underlying heterogeneity and interannual variation of those factors. Otherwise, the loss of even a small portion of the tidal flats could disproportionately harm shorebirds.

In addition, the heterogeneity of tidal flat environment should be considered in efforts to quantify or monitor staging habitat quality because insufficient or inadequate coverage of the study area via monitoring plots or sampling transects may result in a dangerously incomplete understanding of variation in or changes to habitat quality, leading to biased conclusions. Quantifying the distribution of benthic food resources provides more direct and finer-scale information on the quality and heterogeneity of tidal flat habitats (Bijleveld et al., 2012; Mu et al., 2022), but it is also more labor- and time-intensive and may, therefore, not be feasible in all cases. Given the tight relationship between shorebird distributions and the distributions of important biotic and abiotic environmental variables related to tidal flats, full tidal cycle mapping of shorebird distributions can generate useful inferences on the quality and heterogeneity of tidal flat habitats at a scale that is meaningful for habitat conservation and restoration.

The amount of available foraging area and the availability of benthic invertebrates residing in tidal flats also exhibit temporal heterogeneity over the course of the daily tidal cycle (Ribeiro et al., 2004; VanDusen et al., 2012). This cycle causes changes in shorebird distributions as it progresses. Thus, focusing on the spatial distribution of birds during just a portion of the tidal cycle (e.g., around low tide) may produce an incomplete understanding of the actual relationships between shorebird distributions and various environmental factors. This may be especially the case for shorebird species that are tide followers (e.g., sanderling), defined as species that preferentially forage close to the tidal front (Granadeiro et al., 2006; Mu & Wilcove, 2020). During the low-tide period, it may appear that such species preferably use the lower tidal flat (Figure 4b); however, their cumulative foraging time is divided relatively evenly across the entire tidal flat during the entire tidal cycle (Figure 4c).

For this reason, in comparing models investigating the relationship between the distribution of sanderlings and various environmental factors, our two different distribution metrics (low-tide spatial distribution and cumulative foraging time) led to very different results (Table 3). The low-tide spatial distribution of sanderlings was best explained by the density of their potential prey (CU+AM) and the proportion of very fine sand in the sediment, whereas using cumulative foraging time as the distribution metric suggested that none of the environmental factors explained sanderlings' distribution especially well.

The reason for this is because the cumulative foraging time of sanderlings is almost evenly distributed across the entire tidal flat (Figure 4e), as would be expected for a tide follower (Mu & Wilcove, 2020); thus, it did not show any significant relationship to other factors (Table 3). In comparison, for generalists (i.e., species that feed wherever there are exposed tidal flats, as represented by bar-tailed godwits in this study) and zone specialists (species exhibiting a preference for a certain part of tidal flats, usually the upper tidal zone, as represented by red knots in this study), low-tide spatial distribution and cumulative foraging time did not show drastically different relationships with resource distributions (Table 3).

The models that best explained the distributions of our three focal shorebirds on the Nanpu tidal flat indicated that sediment characteristics, apart from their indirect effect on shorebirds by affecting the distribution of benthic invertebrates (Philippe et al., 2016; VanDusen et al., 2012), may also directly affect the distribution of these birds. The differences in penetrability associated with sediment particle sizes, for example, can influence shorebirds' habitat selection by increasing the energetic costs of probing for food or even by creating a risk of physical damage to the bills of probing shorebirds (Finn et al., 2008; Mouritsen & Jensen, 1992; Ribeiro et al., 2004; VanDusen et al., 2012).

Another difference in model results we observed when using two different distribution metrics relates to the relative contribution of biotic and abiotic factors in the best models. The contribution of biotic factors and the total variance explained by environmental factors were generally higher in models that used cumulative foraging time as the distribution metric, compared with models that used low-tide spatial distributions of shorebirds. This suggests that incorporating temporal changes in distribution metrics may better reveal the relationship between shorebird distributions and environmental factors than focusing solely on the low-tide spatial distributions of these birds. However, due to the small number of comparisons in our study, more work comparing these two metrics of shorebird distribution is needed.

Owing to the paucity of information on shorebirds' diets along the EAAF and at our study site in particular, as well as the limited quality of distributional data for many low-density benthic invertebrates, we analyzed the distribution patterns of only six benthic invertebrate taxa and three shorebird species. The lack of fundamental knowledge about the diets of most shorebirds and their prey distributions may impede a nuanced understanding of their habitat requirements. Yet, such information is necessary to accurately evaluate habitat quality and carrying capacity of staging sites (Mu et al., 2022), as well as to understand the impacts of habitat changes to those sites (Choi et al., 2017). Innovative approaches to sampling benthic species (e.g., for burrowing crabs [Kent & McGuinness, 2006]), more quantitative benthic sampling designs (Behney et al., 2014; Bijleveld et al., 2012), and less labor-intensive and higher throughput shorebird dietary analyses (e.g., stable isotope of tissue samples and metabarcoding of fecal samples [Lei et al., 2021; Pompanon et al., 2012]) need to be developed or more widely applied along the EAAF and elsewhere. Moreover, we

focused on only one site, albeit an extremely important one (Lei et al., 2021). Similar studies are needed at other major staging sites along the flyway to determine the degree of consistency in the distribution patterns of shorebirds and environmental factors across different sites, seasons, and years (Choi et al., 2014; Mu & Wilcove, 2020; Peng et al., 2021).

Given the complexity, heterogeneity, and high dynamism of tidal flat ecosystems, conservation targets should be set so as to protect more than the minimum area of habitat that shorebirds appear to need as revealed by short-term studies. A larger area is needed to accommodate potential shifts and fluctuations in prey availability, foraging ranges, and habitat topography (Chang et al., 2021; Mu et al., 2022; Murray et al., 2019). The heterogeneous distributions of foraging shorebirds and the biotic and abiotic environmental factors that characterize their staging habitat make effective conservation of these birds especially challenging. If staging habitat is highly heterogeneous, then losses of only a small portion can have disproportionately large impacts on overall habitat quality. This possibility may help explain why EAAF shorebirds have declined at a much faster rate than has total tidal flat area (Mu & Wilcove, 2020; Murray et al., 2014; Studds et al., 2017). However, other factors, including hunting and climate change, may also be depressing shorebird populations (Gallo-Cajiao et al., 2020; Kubelka et al., 2018; Lameris et al., 2022).

Nanpu is a critically important site for shorebirds, but in terms of overall structure, it does not appear to differ greatly from other staging sites along the EAAF. Therefore, we would not be surprised if many or even all of the other important shorebird coastal staging sites along the EAAF (Bai et al., 2015; Chan et al., 2019; Peng et al., 2017) exhibit similar heterogeneity on the tidal flats (Choi et al., 2014; Mu & Wilcove, 2020; Peng et al., 2021), especially because tidal movement plays a key and universal role in determining the distribution of sediment, benthic invertebrates, and foraging shorebirds. It is thus critical to accurately map and take into account the heterogeneity of tidal flat habitats when devising coastal development plans (so as to minimize the loss of the high-quality portions of the habitat) and conservation plans (to prioritize the protection or restoration of high-quality habitat) to protect these precipitously declining migratory shorebirds along the EAAF and beyond.

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SUPPORTING INFORMATION

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

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