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RESEARCH ARTICLE

Evaluating staging habitat quality to advance the conservation of a declining migratory shorebird, Red Knot *Calidris canutus*

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Abstract

1. Identifying where and when population 'bottlenecks' occur is critical to the conservation of migratory species, many of which are declining precipitously worldwide. Especially challenging is the evaluation of changes to staging sites. These sites are indispensable links in the migratory cycle but are typically used only briefly.

2. We devised a field-based approach to assess the quality and carrying capacity of a critical staging site in Nanpu, China, for the declining, migratory Red Knot (*Calidris canutus rogersi* & *C. c. piersmai*) during northward migration. The Nanpu tidal flat supports 50,000–100,000 Red Knots annually, and while there, the knots feed almost exclusively on the bivalve *Potamocorbula laevis*. We simultaneously monitored changes in the abundance of Red Knots and bivalves across this entire staging site in spring 2018.

3. After taking into account potential competition with other shorebird species, we estimated that the Nanpu tidal flat was capable of supporting approximately 1.46–1.70 times the observed level of Red Knot usage of this site, and therefore is operating below, but close to, carrying capacity with respect to food resources for Red Knots. This result suggests that any further habitat loss or degradation at this site could harm the Red Knot population along the entire East Asian-Australasian Flyway.

4. *Synthesis and applications*. Quantitative monitoring and evaluation of habitat quality of staging sites are essential to successfully conserve declining migratory species. In particular, researchers and conservation practitioners should incorporate both population size and staging duration to more accurately assess the importance of different sites and to quantify how changes in staging habitat quality may translate into changes in the population sizes of migratory species at both local and global scales.

1 | INTRODUCTION

Migratory species are crucial for the functioning of ecosystems (Bauer & Hoye, 2014), yet their populations worldwide are declining precipitously due to anthropogenic threats (Wilcove & Wikelski, 2008). To conserve migratory species, it is imperative to identify where and when population 'bottlenecks' occur—that is, to know which sites and life stages are exerting a significant impact on the overall population growth (Crouse et al., 1987; Liu et al., 2022; McGowan et al., 2011). This task is challenging, due to the many sites and habitats migratory animals utilize annually, the myriad threats they face and the scarcity of information on migratory connectivity (Webster et al., 2002). Especially challenging is evaluating the threats or changes to staging sites. The loss or degradation of staging sites has been linked directly to local and global population declines (McGowan et al., 2011; Moores et al., 2016; Piersma et al., 2016); yet, it remains particularly challenging to answer the seemingly simple question, 'how much staging habitat does a migratory species need?' (Kraan et al., 2009).

Coastal shorebirds represent an excellent group for exploring questions related to staging sites, because, in many species, a large fraction of the population crowds into a discrete number of sites, illustrating a migration pattern consisting of two distinct phases: prolonged staging periods and long-distance migratory flights. Moreover, coastal shorebird populations are declining precipitously worldwide (Delany et al., 2009; Rosenberg et al., 2019; Studds et al., 2017). Along the East Asian–Australasian Flyway (EAAF), shorebird declines have been largely attributed to the loss of critical staging habitats, especially Yellow Sea tidal flats, due to coastal development (Piersma et al., 2016; Studds et al., 2017). This raises the important issue of how much of the remaining intertidal habitat needs to be protected to stabilize current populations or, ideally, sustain larger populations of EAAF shorebirds if other threats can be abated (Yang et al., 2011).

Here, we devise a field-based approach to assess the quality and carrying capacity of Nanpu tidal flat, one of the most important staging sites for Red Knots (*Calidris canutus piersmai* and *C. c. rogersi*) migrating along the EAAF, by simultaneously monitoring changes in food abundance and numbers of foraging birds across the entire site. The EAAF Red Knot population has decreased at an average rate of -4.4% year^{-1} over the past three decades (Studds et al., 2017) driven primarily by the loss of staging habitat (Piersma et al., 2016; Yang et al., 2011). During northward migration, at least 45% and likely close to 100% of the EAAF Red Knots funnel into Bohai Bay, primarily to the Nanpu tidal flat and adjacent areas (Lok et al., 2019; Piersma et al., 2021; Rogers et al., 2010; Tomkovich et al., 2013).

Previous research at Nanpu by Yang et al. (2013) found that Red Knots feed almost exclusively on a small bivalve, *Potamocorbula laevis*, which constituted 92.7% (in ash-free dry mass, AFDM) of the knots' diet reconstructed from faecal samples. *P. laevis* is mostly sedentary and does not reproduce during the northward migration

period of Red Knots (Yang et al., 2013). Continuous monitoring of land cover, Red Knots and benthic invertebrates at Nanpu showed no major changes to the intertidal habitat, its bird community (including Red Knots), the foraging behaviour of Red Knots or the benthic invertebrate community from 2013 to 2018, the year when we conducted fieldwork (Yang et al., 2016; Lok et al., 2019; H. Peng, unpubl. data). Thus, there is no evidence to suggest that the importance of *P. laevis* or Nanpu to Red Knots has changed. Accordingly, the Nanpu tidal flat offers a rare opportunity to observe most or all of the flyway population of a declining migratory shorebird at a single critical staging site where its diet is largely restricted to a single food resource that can be measured readily. This is similar to the situation of Red Knots (*C. c. rufa*) staging in Delaware Bay, United States, which rely on the eggs of Atlantic Horseshoe Crabs *Limulus polyphemus* (Baker et al., 2004; McGowan et al., 2011).

We first sample the distribution of food resources on the Nanpu tidal flat. Combining data on food resources with bird monitoring data, we ascertain whether changes in food distribution and abundance during the main staging period of Red Knots arise mainly from foraging by Red Knots. We then estimate the carrying capacity of this critical staging area for Red Knots. Our approach is particularly useful in the absence of information on functional response (a key component of depletion models that are often used to estimate carrying capacities; Sutherland & Anderson, 1993), or giving-up densities (GUDs, the prey density below which birds will stop foraging at a given spot; van Gils et al., 2004).

2 | MATERIALS AND METHODS

2.1 | Study site

Fieldwork was conducted primarily on the Nanpu tidal flat in Bohai Bay, China (39.1 N, 118.2 E) from April to June 2018 (Figure 1). Although the two subspecies of Red Knot of the EAAF differ slightly in their migration schedule and staging duration, they overlap extensively in their seasonal use of this staging site and exhibit identical foraging behaviour (Piersma et al., 2021; Tomkovich et al., 2013); accordingly, we did not distinguish between them in our fieldwork, which encompassed the northward migration period of both subspecies. The fieldwork protocol (2024F-18) was approved by the Institutional Animal Care and Use Committee of Princeton University, and no local permit was required.

2.2 | Mapping the distribution of food resources

To measure the distribution and abundance of food resources for Red Knots, we collected data on benthic invertebrates from two sets
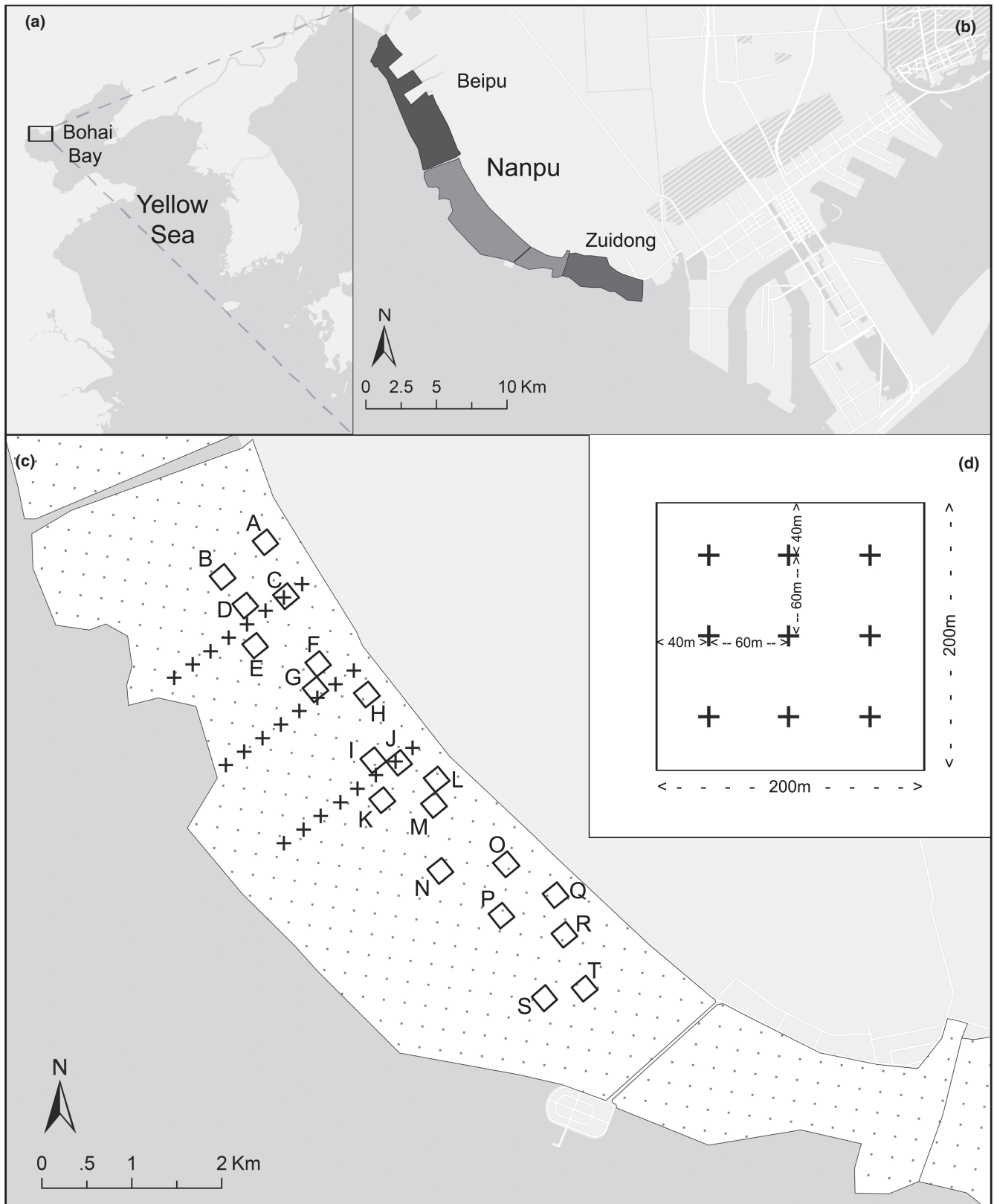
FIGURE 1 Study site and the layout of sampling plots and transects on the Nanpu tidal flat. (a) Location of Nanpu in Bohai Bay. (b) The tidal flats at Nanpu (study site), Beipu and Zuidong constitute the area commonly referred to as the Luannan coast (Rogers et al., 2010). (c) The layout of sampling plots [letter-marked squares, with the layout of benthic sampling points in each plot shown in (d)] and transects on the Nanpu tidal flat. Crosses in (c–d) denote the location or arrangement of benthic sampling points. In all figures, lighter grey areas represent land, grey represents sea or other water body, and darker grey areas in (b) or stippled areas in (c) represent tidal flats.

of sampling points on the tidal flat. First, we randomly selected 20 plots of 200 m x 200 m in size within 1 km from the seawall (squares in Figure 1c), the main area where knots forage (Mu & Wilcove, 2020; Yang et al., 2016). In each plot, we systematically selected nine sampling points in a 3 ×3 array, 60 m apart from each other and 40 m away from the plot boundary (Figure 1d). To cover the entire elevational gradient of the tidal flat, we also set up three transects running perpendicular to the seawall, with 8 sampling points, 250 m apart, along each transect (Figure 1c). This gave us a total of 204 benthic sampling points arrayed in plots (20 plots × 9 points each) and transects (3 transects × 8 points each) across the tidal flat.

We conducted two rounds of benthic sampling, coinciding with the beginning and end of the Red Knot staging period (Figure 2). The first round took place on May 1–2 (transects) and 2–5 (plots), and the second round took place on May 24, 30 (transects) and 24–27 (plots). One benthic core sample (5 cm deep, 15.5 cm in diameter) was taken at each sampling point during each round of sampling, where 5 cm represents the maximum depth that foraging knots can reach (Yang et al., 2013). Core samples were sieved through a 0.5-mm mesh in the field and prey species remaining on the mesh were placed immediately into 75% ethanol (polychaetes and other soft-bodied items) or plastic bags (molluscs, crabs, etc.), and then stored at −20°C. Because bivalves constitute almost the entirety of the Red Knots' diet at Nanpu (Yang et al., 2013), only bivalve species were further processed in the laboratory. Each individual bivalve was identified to species. Shell length of all bivalves collected from plot sampling points plus a randomly selected subsample of individuals from each transect sampling point were measured to the nearest 0.01 mm under a dissecting microscope.

Since *P. laevis* constitutes 92.7% of the Red Knot's diet (Yang et al., 2013) and >94% of all bivalve individuals sampled at this study site, we used the abundance of *P. laevis* with a shell length <8 mm (>99.99% of all *P. laevis* sampled) to represent the potential food resources for Red Knots. To obtain the biomass of food available to the knots, we transformed the shell lengths of *P. laevis* into ash-free dry

mass (AFDM, g), using the allometric relationship derived by Yang et al. (2013). To map the spatial distribution of *P. laevis*, we spatially interpolated the density (log-transformed) and AFDM of *P. laevis* with kriging (Cressie, 1993) using package FIELDS (Nychka et al., 2017) in R (v. 3.6, R Core Team).

2.3 | Verifying the impacts of Red Knot foraging on *P. laevis* abundance

A key yet infrequently tested assumption in estimating carrying capacity is that the consumption of prey by the focal species is the main driver of observed reductions in prey abundance (Bijleveld et al., 2015). While the diet of Red Knots at Nanpu has been well studied (Yang et al., 2013), comparable data do not exist for most other shorebird species there. Based on observed foraging behaviours and distribution patterns of shorebird species at Nanpu, we identified Curlew Sandpiper (*C. ferruginea*) as the only likely shorebird species competing with Red Knots. Similar to Red Knots, the EAAF Curlew Sandpiper population has been declining at ~7.5% annually (Studds et al., 2017). Nanpu is also the most important staging site for Curlew Sandpipers along the EAAF and regularly holds >10%, and up to 69% of the species' total flyway population during northward migration (Lei et al., 2018; Yang et al., 2011). Curlew Sandpipers utilize both saltpans and tidal flat for foraging at Nanpu (Lei et al., 2021). While on the tidal flat, Curlew Sandpipers usually forage with or near Red Knots in the upper zone (Mu & Wilcove, 2020) and consume *P. laevis* at least occasionally (Lei et al., 2021; W. Lei, unpubl. data), but the contribution of this bivalve to Curlew Sandpipers' diet is unknown. Curlew Sandpipers at Nanpu peak approximately 2 weeks ahead of Red Knots, but there is a period of overlap when the two species co-occur in sizeable numbers (Figure 2). To estimate the degree to which Curlew Sandpipers could have competed with Red Knots and contributed to the changes in *P. laevis* abundance, we monitored the abundance of Curlew Sandpipers in the study area once every
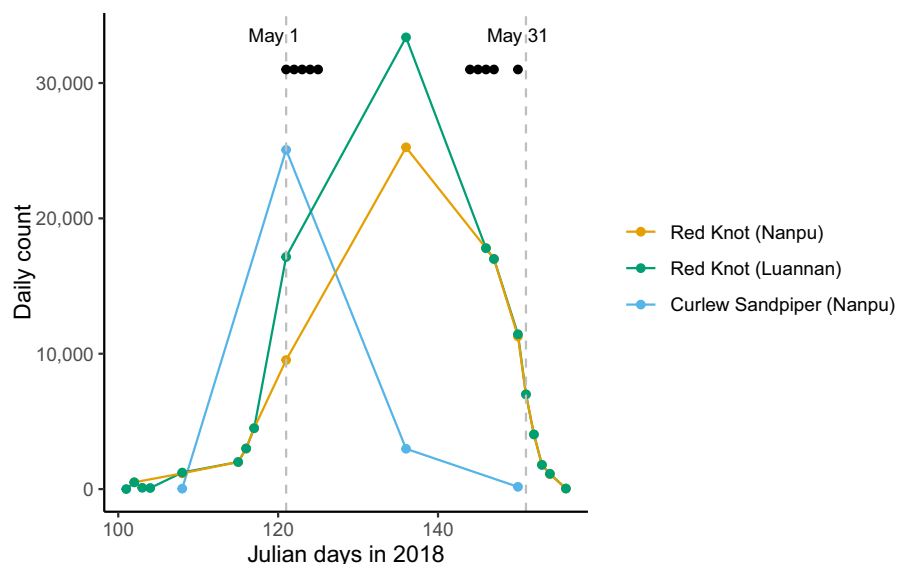

FIGURE 2 Numbers of Red Knots at Nanpu and Luannan (the larger staging area that includes Nanpu; see Figure 1), compared to Curlew Sandpiper numbers at Nanpu. Coloured dots represent bird count data. Black dots denote the days of benthic sampling.

2 weeks, and assumed varying levels of *P. laevis* intake by them, ranging from 0 (no take of *P. laevis*) to 1 (taking *P. laevis* at the same rate as do Red Knot individuals, see Table S1). We define this relative rate of *P. laevis* consumption by Curlew Sandpipers as the 'impact factor' in the following analyses.

We compared the decline in *P. laevis* abundance and the total cumulative foraging time of Red Knots between the two rounds of benthic sampling in the 20 sampling plots, and estimated the intake rate of individual Red Knot consuming *P. laevis*, while taking into account the potential competition from Curlew Sandpipers. If changes in *P. laevis* abundance in the sampling plots are proportional to the total cumulative foraging time of Red Knots recorded within the plots, and the estimated intake rate of Red Knot is comparable to that estimated from an earlier study (90 ± 24 bivalve individuals min^{-1}) that focused on the same study system but used a different approach (Yang et al., 2013), we would then conclude that the observed changes in *P. laevis* abundance were primarily due to depredation by Red Knots (and potentially Curlew Sandpipers) rather than natural death or movement of *P. laevis*.

Specifically, to estimate the total cumulative foraging time of Red Knots, we monitored the number of foraging Red Knots in each plot at an average interval of 28 ± 33 min (mean ± *SD*) during daytime tidal cycles. We first calculated the cumulative foraging time of Red Knots for each plot during each monitored tidal cycle, in bird-minute(s), by plotting the numbers of foraging knots against the time during the tidal cycle. The area under this curve is the cumulative foraging time of Red Knots, which provides a quantitative measurement of Red Knots' foraging intensity compared to using just the peak or average numbers of foraging individuals. We then multiplied the cumulative foraging time of the daytime tidal cycle by 2 to get the daily cumulative foraging time; we did this because there are two tidal cycles per 24-hr day, and Red Knots forage by probing, which allows them to feed with equal intensity during both day and night (Piersma et al., 1998; van Gils & Piersma, 1999). As we did not measure the daily cumulative foraging time during all of the days between the two rounds of benthic sampling, the total cumulative foraging time of Red Knots in each plot was calculated by multiplying the average daily cumulative foraging time (from the days with measurements) by the total number of days between two rounds of benthic sampling.

To evaluate the potential effect of Curlew Sandpipers on changes in *P. laevis* abundance and on our estimation of the intake rate of Red Knot consuming *P. laevis*, we first estimated the total cumulative foraging time of Curlew Sandpipers on *P. laevis* in each plot by multiplying the total cumulative foraging time of Red Knots in each plot by the average ratio of Curlew Sandpiper bird-days to Red Knot bird-days across the entire tidal flat (see below), and multiplying again by the impact factor (0–1; see above). We used this approach because we only counted the Curlew Sandpipers every 2 weeks across the entire tidal flat and did not monitor this species daily in each plot as we did for Red Knots. We then summed up the total cumulative foraging time of Curlew Sandpipers and Red Knots as the adjusted total cumulative foraging time of both species combined, and estimated the intake rate of Red Knot consuming *P. laevis* using linear regression. Detailed steps for these calculations are included in Supporting Information.

2.4 | Estimating the current carrying capacity

Due to the large variation in the available daily foraging time (i.e. duration of exposure time) across the tidal flat, we could not estimate the average daily *P. laevis* consumption rate using the instantaneous intake rate estimated above. Instead, we estimated the carrying capacity of Nanpu (i.e. the maximum number of bird-days that Nanpu may support) by estimating the average daily *P. laevis* consumption rate from the relationship between the observed level of Red Knot usage and the decline of *P. laevis* abundance accessible to Red Knots across the entire tidal flat. The observed level of Red Knot usage, also in bird-days, was estimated by counting the total number of Red Knots using the entire tidal flat throughout the staging period and then calculating the area under the curve of Red Knot numbers against the date in Julian days (Figure 2). The bird-day value for Curlew Sandpiper was derived using the same method.

To estimate the abundance of *P. laevis* accessible to Red Knots, we approximated the giving-up density (GUD) of Red Knots consuming *P. laevis* by finding the lowest *P. laevis* density at sampling points (5th percentile) that have experienced at least a moderate level of Red Knot foraging (showing a decline of >1,000 *P. laevis* individuals m^{-2}) during the second round of benthic sampling. The sensitivity of GUD estimates to the arbitrary selection criteria used above is shown in Table S2. We used GUD here as an operational threshold because it is unrealistic to assume that birds could take all the bivalves in a given area of mud (van Gils et al., 2004). Because the Red Knots may not have fully depleted *P. laevis* in the area with the lowest observed *P. laevis* density during the second round of benthic sampling, the GUD estimate we derived was probably overestimated. To account for the uncertainty around GUD estimates and our analyses based on the GUD, we also conducted a sensitivity analysis to demonstrate how the variation in GUD estimates might affect the carrying capacity estimates for Red Knots (Table S3).

Taking the GUD into consideration, we then calculated the decline in the abundance of accessible *P. laevis* (i.e. the portion above the estimated GUD) between the two rounds of benthic sampling. Assuming a constant daily *P. laevis* consumption rate by Red Knots throughout the staging period and taking into account the potential effect of Curlew Sandpipers, we estimated the maximum bird-days that could be supported by the food resources at the beginning of the staging period, that is, the carrying capacity of the Nanpu tidal flat for Red Knots. Detailed steps for these calculations are included in Supporting Information.

3 | RESULTS

The bivalve *P. laevis*, the main prey of Red Knots at Nanpu, is concentrated on the upper portion of the tidal flat, achieving a

density of >50,000 individuals m^{-2} at the beginning of the Red Knot staging period (Figure 3a). After 3 weeks, the density declined drastically, with areas of higher initial density showing a larger proportional decline (linear regression $F_{1,18} = 38.07$; $p < 0.01$; Figure S1), leading to a more homogenized distribution with lower peaks (Figure 3b). The biomass (AFDM) of *P. laevis* showed a similar but smaller reduction (Figure 3c,d), likely resulting from the natural growth in size of *P. laevis* individuals between the two sampling periods (Figure S2).

It is worth noting that the tidal flat very close to the seawall still held relatively high densities of *P. laevis* towards the end of the staging period (Figure 3b,d). Although we found evidence suggesting that Red Knots spent less time foraging close to the seawall, proximity to the seawall did not lead to statistically detectable decreases in the decline of *P. laevis* abundance, after controlling for the effect of *P. laevis* initial density (Table 1).

The decline of *P. laevis* abundance in sampling plots was proportional to the total cumulative foraging time of Red Knots, and the slope suggested that Red Knots fed on *P. laevis* at an estimated intake rate of 206 ± 48 individual bivalves min^{-1} ($F_{1,18} = 18.69$; $p < 0.01$; $r^2 = 0.509$; Figure 4). This intake rate estimate would be lower, down to as few as 148 ± 34 individual bivalves min^{-1}, after correcting for the potential foraging by Curlew Sandpipers (Table S1).

Between the two rounds of benthic sampling, the total abundance of *P. laevis* decreased by 45.5% across all sampling plots. With a giving-up density (GUD) of 2,750 *P. laevis* individuals m^{-2} estimated for Red Knots (Figure S3; Table S2), the decline in the abundance of accessible *P. laevis* was 54.3% across all sampling plots, and on average 49.0% ± 21.9% for individual sampling plots (Table S3), which, unlike the decline in total *P. laevis* abundance (Figure S1), did not correlate with the initial *P. laevis* density (linear regression $F_{1,16} = 3.335$; $p = 0.087$; Figure S4). This decline in *P. laevis* abundance during
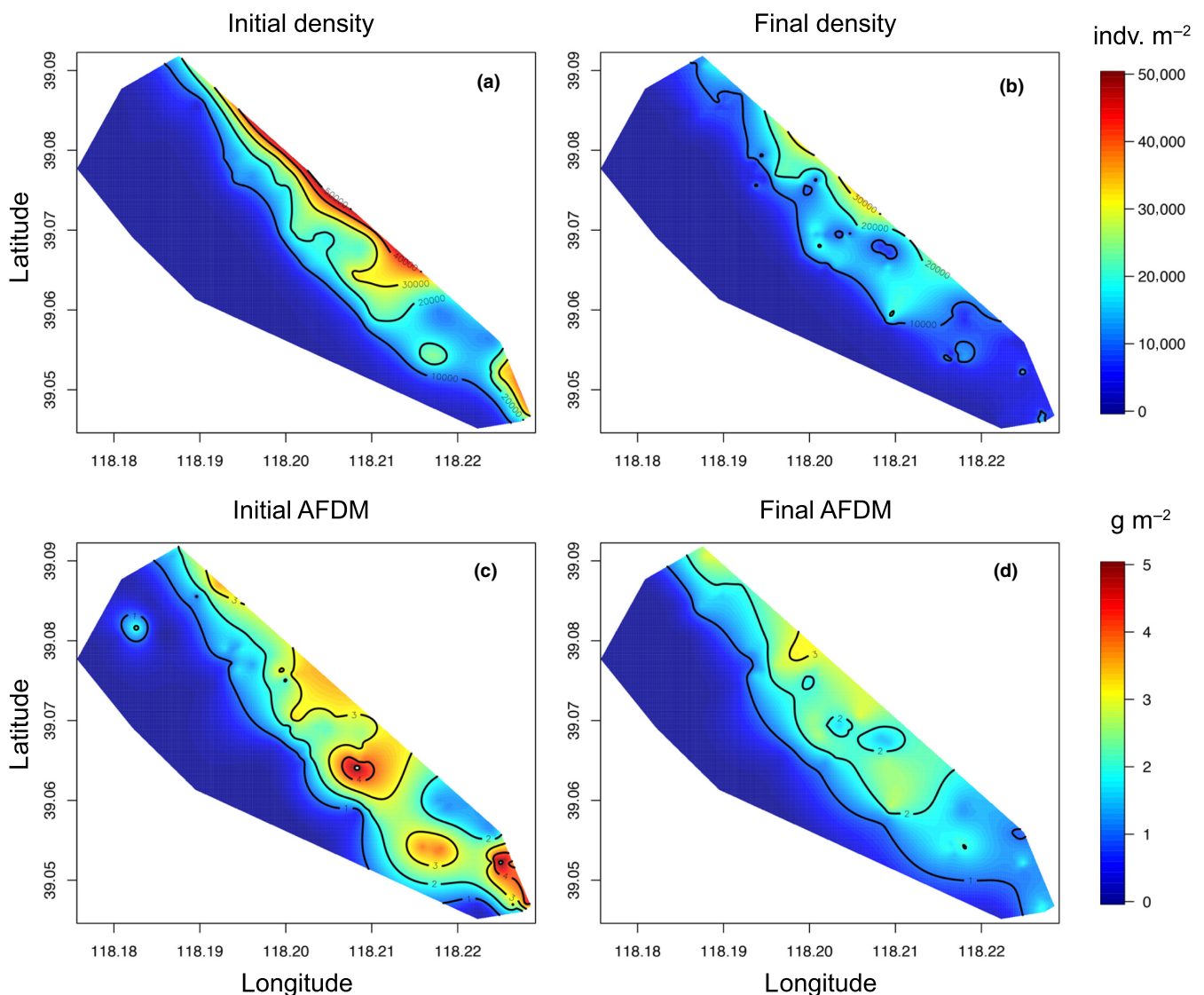

FIGURE 3 Distribution and changes in the density (a, b) and biomass (c, d) of *Potamocorbula laevis* at Nanpu during the first (a, c) and second rounds (b, d) of benthic sampling.

TABLE 1 Model selection results about the effect of proximity to the seawall on Red Knot foraging and *Potamocorbula laevis* density

Full model: Total cumulative foraging time ~ distance to seawall + initial *P. laevis* density + decline in *P. laevis* density + proportion of decline in *P. laevis* density			
Top 6 models	*df*	AIC$_C$	△AIC
Foraging time ~ distance + initial density[a]	4	571.97	—
Foraging time ~ initial density	3	572.64	0.68
Foraging time ~ decline in density	3	573.22	1.25
Foraging time ~ initial density + decline in density	4	574.93	2.97
Foraging time ~ distance + initial density + decline in density[a]	5	575.33	3.37
Foraging time ~ distance + decline in density[a]	4	575.36	3.39
Full model: Proportion of decline in *P. laevis* density ~ distance to seawall + initial *P. laevis* density + total cumulative foraging time			
Top 4 models	*df*	AIC$_C$	△AIC
Proportion of decline ~ initial density	3	−7.17	—
Proportion of decline ~ distance + initial density[b]	4	−6.76	0.42
Proportion of decline ~ initial density + foraging time	4	−4.17	3.01
Proportion of decline ~ distance + initial density + foraging time[b]	5	−3.24	3.93

[a]The coefficients estimated for 'distance to seawall' were all positive, indicating that Red Knots showed reduced foraging intensity close to the seawall.

[b]The coefficients estimated for 'distance to seawall' were all negative, indicating that the *P. laevis* density showed greater decline in plots closer to the seawall, and the effect of seawall was opposite from what we would expect if Red Knots showed reduced foraging intensity close to the seawall.

the study period supported an estimated 4.40×10^5 bird-days of Red Knots staging at Nanpu (Figure 2). Extrapolating to the entire staging period, the maximum bird-days of Red Knots that could be supported by *P. laevis* at the beginning of the northward migration season in 2018 was estimated at 8.88×10^5 bird-days, or 1.46× the level of the actual observed Red Knot usage on the Nanpu tidal flat in 2018 (6.06×10^5 bird-days, Figure 2).

If Curlew Sandpipers deprecate *P. laevis* at the same rate as do Red Knots, the estimated carrying capacity of Nanpu tidal flat for supporting Red Knots could reach 1.03×10^6 bird-days (Table S1). This increase in the carrying capacity estimate of Red Knots, when Curlew Sandpipers are taken into account, is due to the lower estimated daily *P. laevis* consumption rate by Red Knots, resulting from a larger number of individual shorebirds (with the addition of Curlew Sandpipers) contributing to the observed decline in *P. laevis* abundance, which, in turn, leads to a higher estimated number of Red Knot bird-days that can be supported by the bivalves that remain in the tidal flat at the end of the staging period.
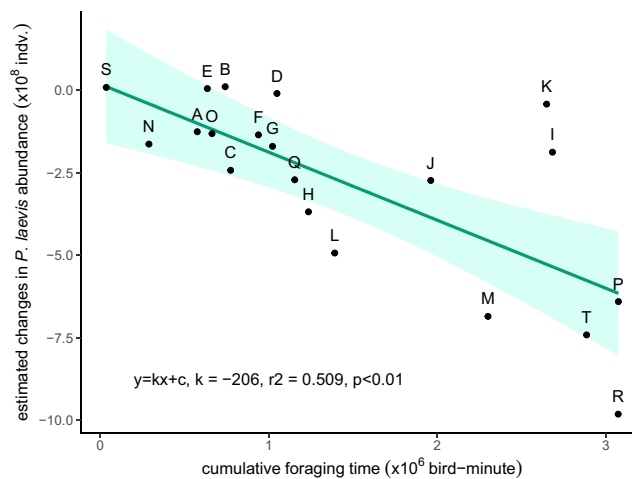

FIGURE 4 The relationship between the decline in *Potamocorbula laevis* abundance and the total cumulative foraging time in sampling plots, and the estimated intake rate of Red Knots consuming *P. laevis* based on linear regression.

4 | DISCUSSION

Staging sites are indispensable links in the annual movement cycles of migratory species, and an understanding of the location, usage, quality and carrying capacity of these sites is crucial for the conservation of migratory species (McGowan et al., 2011; Moores et al., 2016; Piersma et al., 2016). However, these temporarily used sites are probably the least understood aspect of the habitat requirements of migratory species, especially with respect to quality and carrying capacity. In spring 2018, we tested a field-based approach to quantify the habitat quality and to estimate the current carrying capacity for Red Knots at Nanpu in Bohai Bay, China, one of the most important staging sites for this species along the EAAF (Piersma et al., 2021; Rogers et al., 2010). We estimated that, in 2018, Nanpu tidal flat was capable of supporting roughly 1.46–1.70 times the actual level of Red Knot usage, operating below but close to its carrying capacity with respect to food availability. Because our data reflect only a single year at this critically important site, we recognize that this conclusion is only tentative and awaits confirmation with additional years of data. Fortunately, our approach can be applied readily over multiple years, yielding long-term data on the carrying capacities of this or other staging sites for Red Knots.

4.1 | Evaluation of staging habitat quality

Verifying that foraging by the focal species is the main driver of the reduction in food resources is a key (yet infrequently taken) step in estimating carrying capacity (Bijleveld et al., 2015), whether with model-based (Sutherland & Anderson, 1993) or field-based approaches. We identified Curlew Sandpipers as the only likely competitors of Red Knots for *P. laevis* at Nanpu during our study period, based on the abundance and distribution patterns of all shorebird

species on the tidal flat (Mu & Wilcove, 2020). Nonetheless, because detailed information on the diet of Curlew Sandpipers in Bohai Bay is incomplete, we assumed varying levels of Curlew Sandpiper's relative *P. laevis* intake rate (the 'impact factor'), to quantify the potential impact of Curlew Sandpipers on *P. laevis* abundance and, therefore, carrying capacity estimates for Red Knots.

Our estimated intake rate of *P. laevis* by individual Red Knots (206 ± 48 bivalves min^{-1}) is similar to the rate derived in an earlier study in Nanpu: Yang et al. (2013) estimated an intake rate of 90 ± 24 individuals min^{-1} for Red Knots consuming *P. laevis*, based on data collected during northward migration on defecation intervals, sizes of *P. laevis* found in Red Knot droppings, and the relationship between *P. laevis* shell fragments found in droppings and Red Knots' actual *P. laevis* consumption through a digestion experiment using individual birds captured at Nanpu. The overlapping 95% confidence intervals between Yang et al.'s (2013) estimate of intake rate and our own, combined with an intercept close to zero suggesting a proportional relationship between the intensity of Red Knot foraging and the reduction in food abundance (Figure 4), indicated that Red Knot foraging is the principle contributor to the reduction in *P. laevis* abundance we observed. In their estimate, Yang et al. (2013) used a larger average *P. laevis* shell length (3 mm) than we did (2.18 ± 0.49 mm and 2.65 ± 0.51 mm, Figure S2), which we believe most likely reflects a difference in the resolution of measurements between the two studies rather than a true biological difference. Adjusting the average shell length used by Yang et al. (2013) to the smaller value we observed, or taking into account the potential impact of Curlew Sandpiper on *P. laevis* abundance (Table S1), further narrows the gap between the two estimates of intake rates.

Food density and distribution are not the only habitat attributes that affect carrying capacity. We also tested for the potential effects of predation danger and human disturbance on carrying capacity estimates (van Gils et al., 2004), as indicated by proximity to the seawall, on Red Knot foraging and *P. laevis* density (Table 1). In the absence of a significant statistical effect of the distance to the seawall on the reduction of *P. laevis* densities, we cannot conclude whether the high *P. laevis* densities close to the seawall during the second round of benthic sampling (Figure 3b) were solely the result of high initial *P. laevis* densities (Figure 3a), or whether Red Knots avoided foraging in areas close to obstructions as a predator or disturbance avoidance strategy (Piersma et al., 1993).

In recent years, the Luannan coast as a whole (encompassing our study area, Nanpu, where most Red Knots stage, and the adjacent Beipu and Zuidong tidal flats, Figure 1b) has supported 50,000–100,000 Red Knots each spring, with an average staging duration of 5–9 days between May 10 and 30 (Lok et al., 2019). This translates into an average of 4.5–5.0×10^5 bird-days, similar to the 5.0×10^5 bird-days we estimated for Luannan in 2018 during the same period (with most individuals staging in Nanpu, Figure 2). In addition, given that *P. laevis* densities on the Nanpu tidal flat have been relatively stable in recent years, and 2018 did not appear to be an unusually good or bad year for this bivalve (Yang et al., 2016, H. Peng, unpubl. data), we are cautiously confident that our conclusions apply beyond

the single year of our study. However, both identifying and continuously monitoring the full set of key staging sites along the EAAF are needed to understand how the relative changes in carrying capacity and actual bird usage at each site may alter Red Knots' migration strategies, migratory routes and flyway populations (Piersma et al., 2021), using this and other approaches.

4.2 | Applications to conservation

Our results lead to several recommendations for the conservation of EAAF Red Knots and of migratory birds in general. First, had our calculations indicated that Nanpu was operating at or above its carrying capacity for Red Knots, it would suggest that this major staging site is potentially acting as a population bottleneck that is driving the ongoing decline of EAAF Red Knots (Piersma et al., 2016). Fortunately, that does not seem to be the case. Nonetheless, because our results indicate the site is operating close to carrying capacity, it is possible that some Red Knots may have already been displaced to other staging sites of lower quality (Ntiamoa-Baidu et al., 2014), thus cautioning against any further conversion or development of Nanpu tidal flat. To quantify how migratory species have been and will be threatened by habitat loss and degradation, it is imperative to establish more nuanced and mechanistic relationships between changes in habitat quality and migrant population sizes at both local and global scales (Liu et al., 2022).

Second, the spatial heterogeneity of the Red Knot's food resources reaffirms the idea that tidal flats constitute a heterogeneous habitat; thus, the loss of high-quality sections may result in disproportionately large declines in overall habitat quality (Mu & Wilcove, 2020). The subtle heterogeneity of the Nanpu tidal flat, with different shorebird species foraging in different zones of the tidal flat (Mu & Wilcove, 2020), and with densities of a key prey species varying markedly within and between intertidal zones (Figure 3), underscores the importance of considering the quality, and not just the quantity, of tidal flats as shorebird staging habitat (Zhang et al., 2018). Research and long-term monitoring are needed to understand how prey distribution and heterogeneity may be affected by land-use change or sea-level rise to inform more effective habitat conservation and restoration decisions.

Third, a measurement of bird-days, which incorporates both the number of birds present at a staging site and the cumulative time they spend there, provides a more accurate representation of how migratory species actually use a site and therefore the site's relative importance, than does the much more widely used metric, the maximum peak count of birds (Figure 2). Moreover, the bird-day measurement is less sensitive to differences in the migration schedules of each population, whereas factors including staging duration, intraspecific variation in migration timing and survey frequency greatly affect peak count numbers and, consequently, assessments of site importance based on peak counts (Frederiksen et al., 2001; Lok et al., 2019). To facilitate more informative evaluation and comparison of the importance of staging sites to migratory species, population monitoring and surveys need to be conducted frequently across

the entire migration season, and should include metrics that incorporate staging duration (e.g. bird-days).

Furthermore, designation of sites as either Wetlands of International Importance (Ramsar Sites) or as Important Bird and Biodiversity Areas includes a criterion based on supporting ≥1% of the population of a species or subspecies (BirdLife International, 2021; Ramsar Convention Secretariat, 2021). This criterion is usually evaluated using peak counts and does not consider staging duration. We suggest that additional key sites for migratory birds might be identified if the designations include measurements that take staging duration into consideration, because peak counts usually underestimate the total number of birds using a particular site (Frederiksen et al., 2001; Lok et al., 2019).

Finally, we were able to evaluate Nanpu's carrying capacity for Red Knots because the diet, foraging behaviour, staging duration and habitat use of Red Knots have been thoroughly studied at this site (Lok et al., 2019; Mu & Wilcove, 2020; Piersma et al., 1998; Yang et al., 2013). Such information, however, is typically lacking or incomplete for most migratory species, including many shorebird species and sites along the much-threatened EAAF (Choi et al., 2017; Lei et al., 2021; Zhang et al., 2018). Estimating the long-term carrying capacity of a site would further require detailed information on the productivity, recruitment and growth of prey species, as well as how these parameters are affected by both biotic and abiotic factors (Yang et al., 2016; Zhang et al., 2018). This lack of knowledge greatly hampers the development and evaluation of conservation efforts for these species. Whether staging sites are operating above or below carrying capacities will greatly affect how migrant populations respond to habitat loss or degradation, and inform us on how the remaining sites must be protected to secure current populations or even reverse ongoing declines (Liu et al., 2022; Yang et al., 2011; Zhang et al., 2018). While obtaining similar estimates of carrying capacities for other migratory species at other sites will be more challenging than was the case for Red Knots at Nanpu, it is increasingly important to do so as populations of migratory species around the world continue to decline (Wilcove & Wikelski, 2008).

AUTHORS' CONTRIBUTIONS

T.M. and D.W. conceived the study and designed the methodology; T.M., S.C., H.-B.P., C.H. and A.B. collected the data with support from Z.Z.; T.M. and S.C. analysed the data with input from H.-B.P. and T.P.; T.M. and D.W. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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