



Male and female Black-tailed Godwits *Limosa limosa bohaii* show differences in habitat use and daily rhythms during spring staging in China

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Abstract

Sexual dimorphism in body size among shorebirds is typically linked to reproductive roles, yet such differences may also lead to ecological differences during the remainder of the annual cycle. Here, we investigate whether the smaller males and larger females of Bohai Black-tailed Godwits *Limosa limosa bohaii* differ in habitat use and rhythmic behaviours as they refuel in coastal China during northward migration. Based on visual observations, increasing abdominal profiles confirmed their refuelling in the Bohai Bay study area. Using GPS telemetry, we found that males predominantly occurred on coastal mudflats and the adjacent saltworks, whereas females used a wider array of habitats, including freshwater and saline wetlands further inland. In late April and early May, females shifted progressively to these inland habitats. Accelerometry measurements show that on the mudflats, both males and females had the highest intensity of movement around high tide. We interpret this as an expression of their restlessness during the hours they were squeezed into small shoreline areas close to intense human activity. In non-coastal habitats, the two sexes showed similar and pronounced diurnal activity rhythms, with reduced movement intensities in the late-night hours before sunrise. The intensities of movement in inland habitats double those on the mudflats, probably reflecting the high foraging activity required to satisfy food demands because of relatively small arthropod prey in rice fields (Chironomid larvae) and saltworks (brine fly larvae), compared to the larger polychaete prey on mudflats.

Keywords Habitat use · Migration · Refuelling · Sexual size dimorphism · Shorebirds · Stopover · Time-activity budgets · Accelerometer

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Zusammenfassung

Männliche und weibliche Uferschnepfen (*Limosa limosa bohaii*) zeigen während ihrer Frühjahrsrast in China Unterschiede in der Nutzung ihres Lebensraums und in ihren Tagesrhythmen

Der Geschlechtsdimorphismus in der Körpergröße bei Watvögeln hängt in der Regel mit ihren Fortpflanzungsrollen zusammen, doch solche Unterschiede können auch zu ökologischen Unterschieden während des restlichen Jahreszyklus führen. Hier untersuchen wir, ob sich die kleineren Männchen und größeren Weibchen der Bohai-Uferschnepfen (*Limosa limosa bohaii*) in ihrer Lebensraumnutzung und ihrem rhythmischen Verhalten unterscheiden, wenn sie während ihrer Nordwanderung an der chinesischen Küste neue Energie tanken. Basierend auf visuellen Beobachtungen bestätigte das zunehmende Bauchprofil ihre Energieaufnahme im Untersuchungsgebiet der Bohai-Bucht. Mithilfe von GPS-Telemetrie stellten wir fest, dass Männchen vorwiegend an Küstenwatten und den angrenzenden Salinen vorkamen, während Weibchen eine größere Bandbreite an Lebensräumen nutzten, darunter Süßwasser- und Salzwasserfeuchtgebiete weiter im Landesinneren. Ende April und Anfang Mai verlagerten sich die Weibchen zunehmend in diese Lebensräume im Landesinneren. Beschleunigungsmessungen zeigen, dass sowohl Männchen als auch Weibchen auf den Wattflächen bei Flut die höchste Bewegungsintensität aufwiesen. Wir interpretieren dies als Ausdruck ihrer Unruhe während der Stunden, in denen sie in kleine Küstengebiete in der Nähe intensiver menschlicher Aktivitäten gedrängt waren. In nicht-küstennahen Lebensräumen zeigten beide Geschlechter ähnliche und ausgeprägte Tagesaktivitätsrhythmen mit reduzierter Bewegungsintensität in den späten Nachtstunden vor Sonnenaufgang. Die Bewegungsintensität in Binnenlandlebensräumen ist doppelt so hoch wie auf den Wattflächen, was wahrscheinlich auf die hohe Nahrungssuchaktivität zurückzuführen ist, die erforderlich ist, um den Nahrungsbedarf zu decken, da die Beutetiere in Reisfeldern (Chironomidenlarven) und Salinen (Salzfliegenlarven) im Vergleich zu den größeren Polychaeten auf Wattflächen relativ klein sind.

Introduction

Sexual dimorphism in morphology is widespread among animals and is often linked to the differing roles and selection pressures experienced by males and females (Blanckenhorn 2005). These morphological differences, however, extend beyond reproduction, influencing ecological strategies throughout the annual cycle. For instance, sexual size dimorphism may cause males and females to differ in prey selection, foraging strategies, and energetic requirements, leading to sexual differences in spatial distributions (e.g. Alves et al. 2013; Sprogis et al. 2018; Gantcho et al. 2019). Nevertheless, habitat use encompasses more than just spatial elements; it also includes temporal aspects (Helm et al. 2017). Animals make decisions not only about where to forage but also when and for how long. These temporal choices are manifested in rhythmic behaviours, shaped by daily, seasonal, or annual cycles, and synchronised by environmental cues such as light, temperature, and food availability. Thus, a comprehensive examination of sex-specific habitat use should integrate both spatial distributions and temporal rhythms in resource exploitation and habitat selection (e.g. Rijnsdorp et al. 1981; Zwarts et al. 1990; Lok et al. 2024; Henriques et al. 2025).

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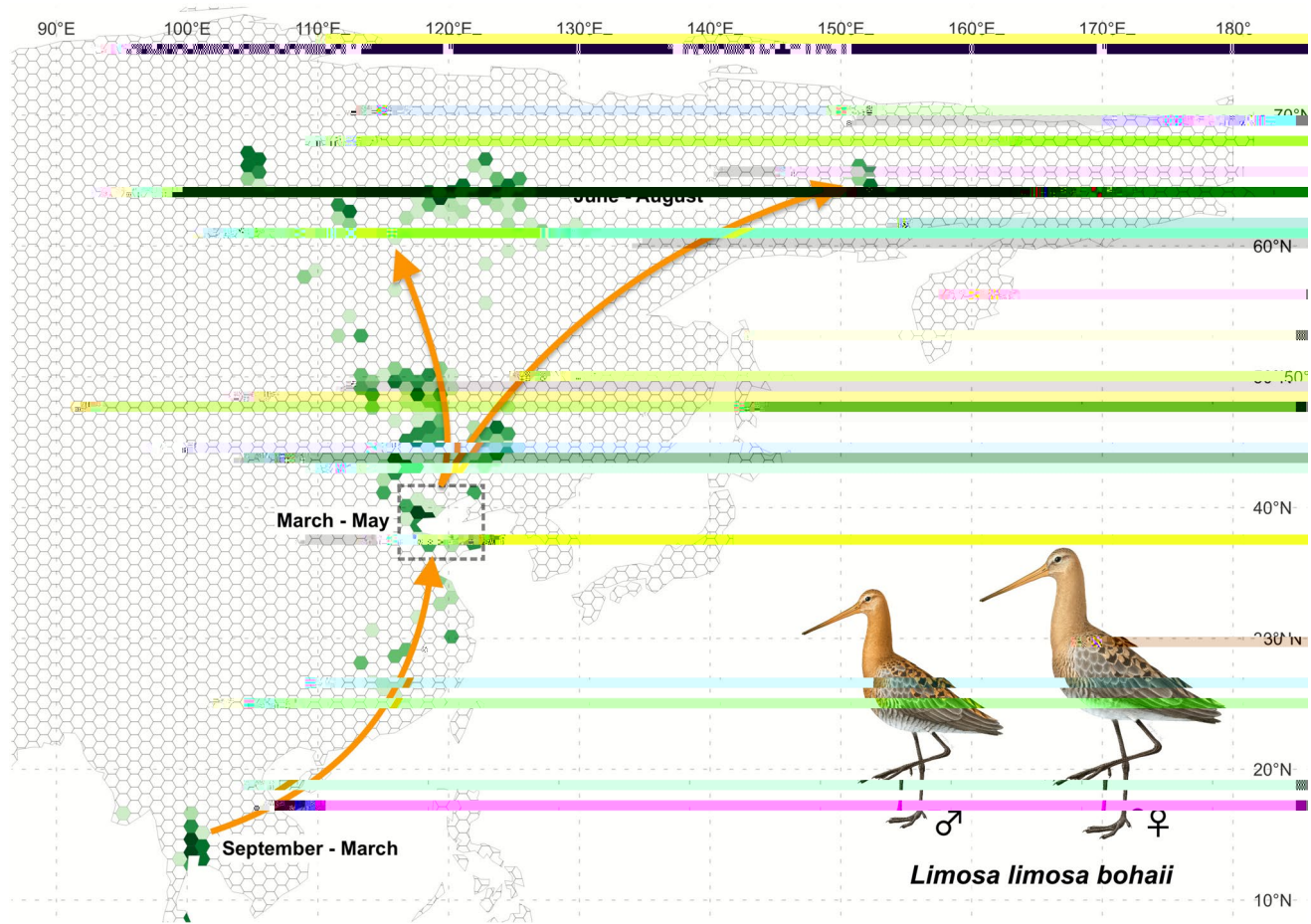


Fig. 1 Spatial distributions and migration corridors of Bohai Black-tailed Godwits during northward migration. Timing of migratory movements follows Zhu et al. (2021b). The dashed rectangle indicates the location of Bohai Bay. Drawings of Bohai Black-tailed Godwits

by Seungha Oh. Hexagonal cells represent GPS telemetry locations collected between January–July, and darker shading indicates higher densities of recorded occurrences

et al. 2021a; Figs. 1 and 2). We combined GPS telemetry data with accelerometer-derived activity measurements. Based on abdominal profile scoring of random individuals (Wiersma and Piersma 1995), we confirmed that godwits were actively refuelling at Bohai Bay, and we then documented the tidal and daily patterns of habitat use at this staging area during northward migration. Specifically, we examine (1) the differences in habitat use between males and females, and (2) how daily and tidal cycles were associated with the activity rhythms of each sex.

Material and methods

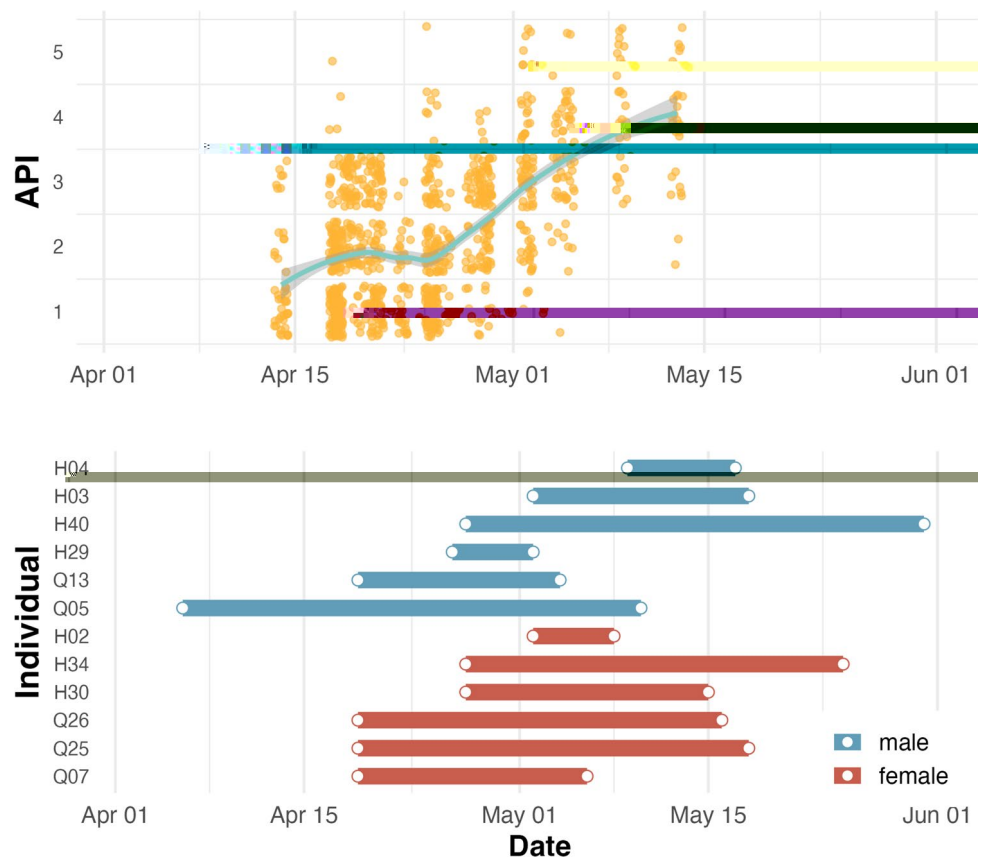
Fieldwork

We conducted the fieldwork in northern Bohai Bay, China (39°N, 118°E; Fig. 1) during the northward migration seasons of 2016–2018 of the *bohail* Black-tailed Godwits

(hereafter, “godwits”). The study area and the methods for catching and transmitter-tagging were described by Zhu et al. (2021b). Godwits typically arrive in Bohai Bay in early April, following mostly direct flights from non-breeding areas in Thailand (Fig. 1; Zhu et al. 2021b). The *bohail* godwits stay until their northward departure throughout May for the migration to the boreal breeding grounds. During this journey, they may make more stops (Fig. 1).

We completed catching and tagging work before the last week of April to ensure that spatial movements and temporal activity were recorded as thoroughly as possible. Godwits were fitted with solar-powered GPS-GSM transmitters (HQPG2009P, 9 g, Hunan Global Messenger Co., Ltd.) using leg-loop harnesses. Including harness and rings, the total mass of attached equipment was ~10 g, representing 2.7–3.1% of body mass. The transmitter had a flexible data collection schedule, ranging from 1 to 6 hours, depending on solar charging. In total, 15 birds were tagged, four of these

Fig. 2 Abdominal Profile Index (API) scores (upper panel; orange dots) with a smoothed trend line (light blue) and its 95% confidence interval (shaded area), and the intervals between capture and departure towards the breeding grounds of male and female (lower panel) Bohai Black-tailed Godwits in northern Bohai Bay



were excluded from analysis because of insufficient data or activity sensor malfunction. The final dataset consisted of 11 tagged individuals ($n_{2016} = 3$, $n_{2017} = 4$, $n_{2018} = 4$), five males and six females, with 869 and 1,243 location fixes in Bohai Bay, respectively, spread relatively evenly among the tagged birds (Table S1).

In the springs of 2017 and 2018, we assessed the abdominal profiles of godwits at primary foraging and roosting sites, not distinguishing males and females. Following Wiersma and Piersma (1995), a score of 1 denoted a bird exhibiting a very lean profile, characterised by a concave abdomen. A score of 3 indicated a slightly convex abdomen, and a score of 5 a bulging abdomen. Intermediate profiles received scores of 2 and 4. Observations were repeated every 1–4 days, resulting in a total of 971 abdominal profile scores. All observations were conducted by a single researcher (B-R Zhu) to avoid inter-observer variation, and readings were taken from ~100–150 m, the closest range that allowed reliable scoring without flushing the birds.

The tracking of individuals

Since no individuals in this study provided repeated tracks in subsequent years, we were only able to use data collected after capture and tag-attachment. We therefore checked for

short-term tagging effects. We compared the intensity of bodily movements (i.e., activity, see below) recorded during the first 72 hours after tagging with activity recorded later (Chan et al., 2016). We performed a linear mixed-effects model, accounting for repeated measurements per individual and adjusting for varying data collection intervals using an offset term. The model revealed a significant increase in activity after the initial 72-hour recovery period (estimate \pm SE = 631.2 ± 97.6 , $t = 6.47$, $p < 0.001$). Therefore, we excluded data collected within the first three days post-tagging from the analyses to ensure our analyses reflect natural behaviour and minimise potential bias from short-term tagging effects.

To visualise the spatial distribution of godwits in northern Bohai Bay without overplotting individual GPS fixes, we generated 1 km buffers around each location point in QGIS 3.4.3 (Fig. 3). These buffers were used exclusively for graphical representation and do not influence the quantitative analysis. To compare the use of intertidal versus inland habitats by the sexes over time, we manually digitised the coastline using satellite imagery in QGIS 3.4.3 and calculated the shortest distance from each GPS fix to this reference line. The reference was drawn along the seaward edge of the intertidal mudflats, and all distances were treated as positive values. These distances were then used as the response variable in a Generalised

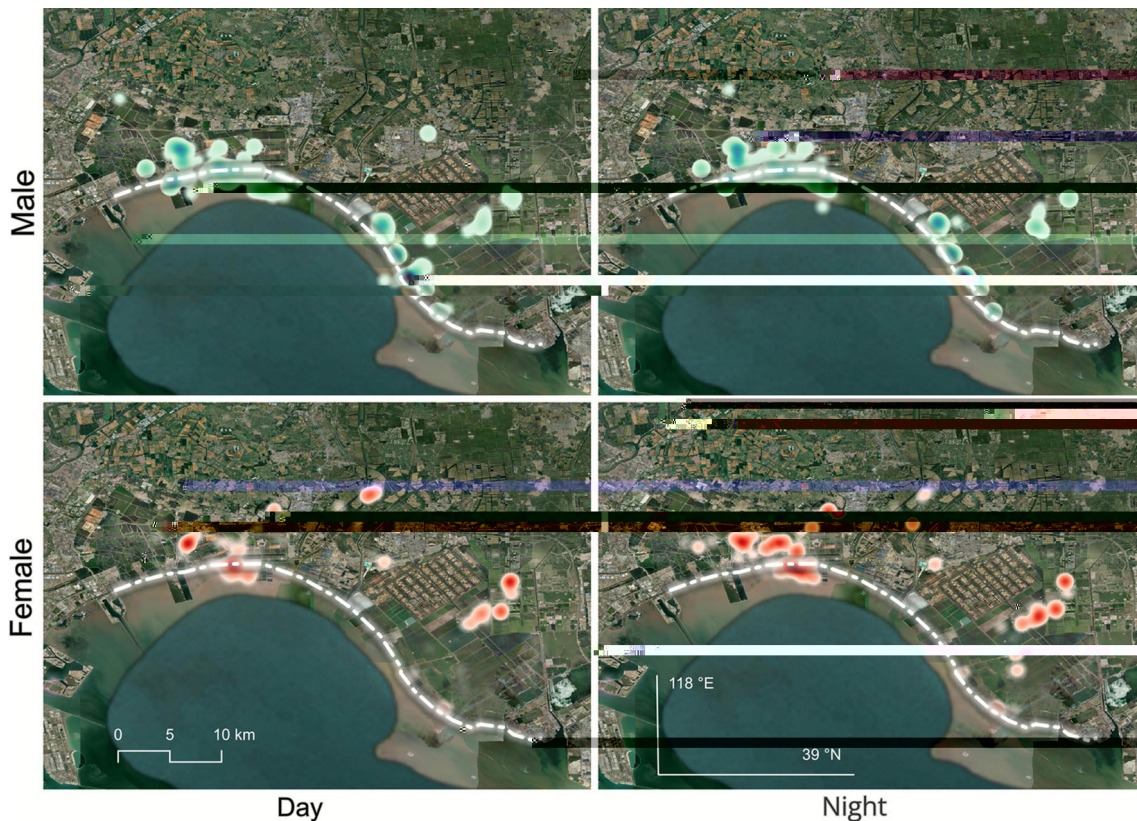


Fig. 3 Sex-specific spatial distribution heatmaps showing daytime and nighttime habitat use by male (upper panels) and female (lower panels) godwits during northward migration in northern Bohai Bay. The intensity of colours indicates the frequency of recorded occur-

rences. The white line represents the coastline, used as a reference for calculating distances of godwit locations from the nearest coastal boundary

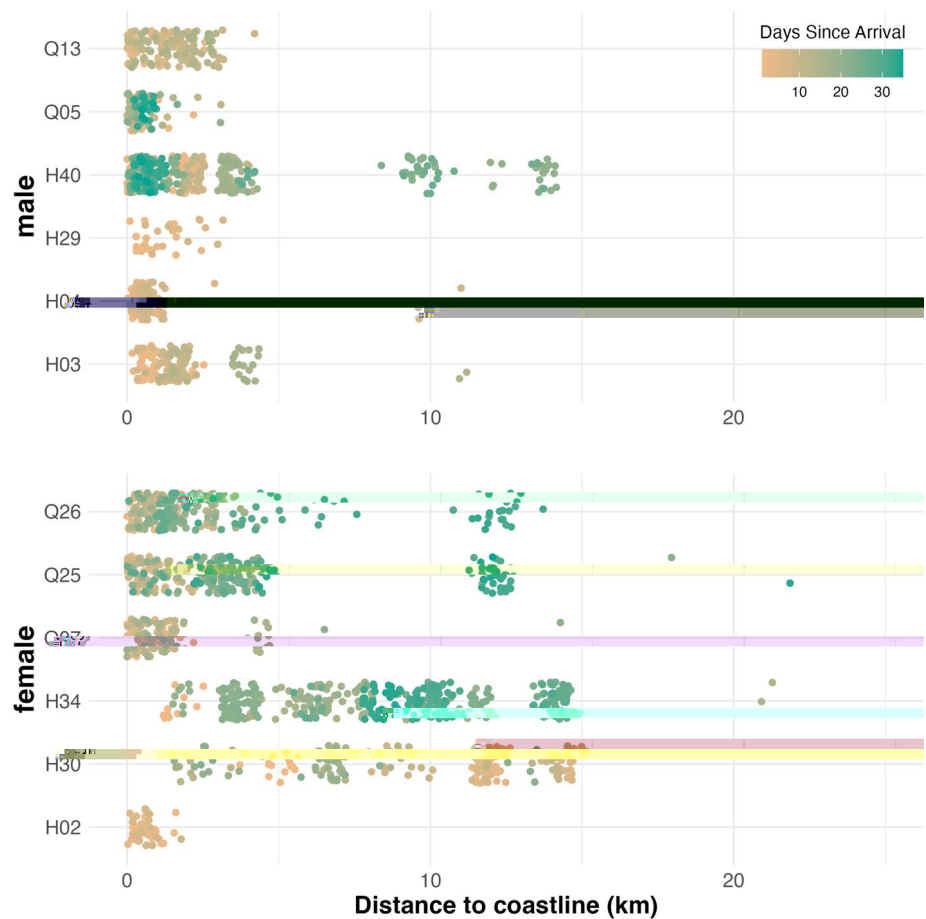
Linear Mixed-Effects Model (GLMM; Bolker et al. 2009) to examine spatial shifts relative to the coast (Figs. 3, 4, S1), with the interaction between sex and day since arrival included as fixed-effect predictors. Individual godwits were treated as a random effect to account for variability. Year of tagging was additionally tested, both as a fixed effect and as a random intercept, but it did not explain significant variation in habitat use and was therefore excluded from the final model ($\Delta AIC = 0$; $\chi^2 = 1.95$, $df = 1$; $p = 0.163$).

Based on field visits and published studies (Lei et al. 2018, 2021), we identified three primary habitat types utilised by godwits in northern Bohai Bay: (1) mudflats, (2) saltworks, and (3) inland wetlands (e.g., flooded rice fields, aquaculture ponds). In northern Bohai Bay, shorebirds typically use inland wetlands (saltworks, flooded rice fields and aquaculture ponds) as high tide or overnight roosts, and they forage on the mudflats (Yang et al. 2011; Lei et al. 2018). To examine if godwits follow a tidal rhythm, we obtained tide tables for Hangu, Tianjin, where godwits highly frequented mudflats. We determined the “hours to the nearest high tide” for each recorded

activity time by calculating the time differences between the recording and the high tides occurring before and after. We chose the smallest time difference as the nearest high tide. Similarly, we computed the “hours to the nearest sunset” by comparing recorded activity times with dusk times and selecting the smaller difference. Dusk times for northern Bohai Bay (39°N, 118°E) were obtained using the R package “suncalc”.

We measured the intensity of bodily movement (“activity”) of each godwit using accelerometer data from GPS tags, following a system previously applied to study activity patterns in Whimbrel (*Numenius phaeopus*; Kuang et al. 2019). The accelerometer recorded data simultaneously along three spatial axes (surge, heave, and sway) at a frequency of 50 Hz. Activity data were stored cumulatively over variable duty cycles ranging from one to six hours, determined by battery charge and environmental conditions. Within each duty cycle, the transmitter added one ‘activity unit’ whenever the sum of the acceleration vectors surpassed 0.15 g. This resulted in intensities of (bodily) movement ranging from 0 to 4095 at the end of the cycle, after which the counter was reset to zero at the start of the next recording

Fig. 4 Sex-specific changes in habitat use over time for Bohai Black-tailed Godwits during northward migration in northern Bohai Bay. Each dot represents a GPS-recorded location fix, coloured by the number of days since arrival



cycle. To account for variations in sampling intervals during data collection, we used the precise duration (in hours) of each duty cycle as an offset term when fitting subsequent statistical models.

Statistical analyses

To analyse godwit activity patterns in northern Bohai Bay, we utilised a Generalised Additive Model (GAM, Hastie and Tibshirani 1987) implemented in the R package “mgcv” (Wood 2017). The model included linear and non-linear predictors to assess the effects of sex, habitat type, and various rhythmic and temporal factors on activity. We specified an interaction between sex and habitat type to examine differences in activity patterns across these groups. Non-linear relationships were modelled using smooth functions. We applied cyclic cubic splines to the predictors representing hours to the nearest sunset and hours to the nearest high tide. We separated smooths for each sex-habitat combination, capturing distinct group-specific patterns. We also included a smooth term for days since arrival with separate smooths for each sex to account for potential temporal differences. Year of tagging was initially tested as a fixed effect, but it did not explain significant variation and was excluded from the final model. We incorporated the interval between consecutive

data collection points as an offset, using a log transformation to account for variations in observation times. Moreover, we included individual godwits as a random effect. The GAM was fitted using a Gaussian distribution, and the Restricted Maximum Likelihood (REML) method was employed to estimate the smoothing parameters. We selected all predictors based on ecological relevance and their known influence on shorebird behaviours, rather than relying on automated model selection methods such as AIC or stepwise selection (Whittingham et al. 2006). This approach aimed to ensure that the effect of each predictor on activity was explicitly examined (Guisan and Zimmermann 2000). Model and residual diagnostics confirmed that the GAM was appropriately specified. We checked for autocorrelation and found no significant issues, indicating that our model fit the data well and provided reliable estimates of the effects of the predictors.

Results

After capture in Bohai Bay, males remained in the staging area for another 18.8 d (range: 6–34 d), whereas females continued staging for an average of 20.8 d (range: 6–29 d) (Fig. 2). No significant differences were found between sexes

in either time between tagging and departure ($\Delta = -2.00 \pm 6.23$ days, $t = -0.32$, $p = 0.75$) or departure date ($\Delta = -1.00 \pm 5.21$ days, $t = -0.19$, $p = 0.85$), indicating no sex differences in overall migration timing. Abdominal profile scores (combined for the sexes) increased significantly over the staging period (Fig. 2; $\Delta = 0.090 \pm 0.004$ SE, $t = 22.26$, $p < 0.001$). This confirmed that godwits were indeed refuelling in the Bohai Bay study area.

Males primarily occupied coastal mudflats and nearby saltworks. (3 = -0.19, $p = 0.19$, $p = 0.19$)

Employing GPS telemetry data with accelerometers, we reveal that whereas the overall timing of migration and staging did not differ between the sexes, there were sex-specific habitat use patterns. Males predominantly occupied coastal mudflats and nearby saltworks, while females utilised a broader range of habitats, including mudflats, saltworks, and inland freshwater wetlands (Fig. 3). Over time, females gradually moved inland, favouring inland saltworks and freshwater wetlands, resulting in significantly different spatial distributions between the sexes (Figs 3 and 4).

In Icelandic Black-tailed Godwits *L. l. islandica*, Alves et al. (2013) argue that larger females are better equipped to exploit higher-quality foraging sites, which provide deeper-buried prey. Males, with their shorter bills, focus on shallower prey. This is in stark contrast with our finding that the larger females utilised inland freshwater wetlands and saltworks characterised by smaller potential prey types such as Chironomid larvae and brine fly larvae, respectively. The larger polychaete prey on the mudflats attracted the smaller males. The fact that females occurred more in areas with smaller prey does not mean that such areas are of lower quality (van Gils et al. 2004). Evaluated as achieved intake rates (Piersma et al. 1995), they may offer richer prey resources than coastal mudflats (Lei et al. 2021).

Physiological adaptations, particularly related to osmoregulation, would add another layer of complexity to the observed sex-specific habitat use patterns. Saline environments may impose significant osmoregulatory stress, affecting energy budgets, body condition, and immune performance in migratory shorebirds (Masero et al. 2017). Salt glands, which facilitate the excretion of excess salt, are known to exhibit phenotypic flexibility, allowing shorebirds to adjust to variable salinity levels (Gutiérrez et al. 2012). The broader habitat use by female godwits, from freshwater wetlands with minimal salinity stress to saltworks with elevated salinity, suggests a strategy to balance osmoregulatory costs with the benefits of accessing potentially more abundant food resources. This diverse habitat selection, facilitated by their larger body size, their possibly greater dominance (see Sirot et al. 2012), and flexible osmoregulatory capacity, likely enables females to maximise energy intake during migration.

The somewhat elevated activity in the mudflat areas around high tide, especially the females (Fig. 5), represents

national and institutional guidelines. Ethical approvals were issued by the Wildlife Protection Division of the Hebei Provincial Forestry Bureau and the Tianjin Binhai New Area Administrative Committee.

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