Journal of Ornithology
https://doi.org/10.1007/s10336-025-02355-4

ORIGINAL ARTICLE

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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Received: 5 June 2025 / Revised: 2 December 2025 / Accepted: 17 December 2025

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

Communicated by C. Barbraud.

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Published online: 19 January 2026

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; Gantchoff 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).

Studies on habitat use and rhythmic behaviours naturally require intense and continuous observation efforts (Giotto et al. 2013; Wang et al. 2014). While telemetry technologies have largely addressed this challenge for the larger-bodied bird species (Godvik et al. 2009; El-Hacen et al. 2013), tracking small-bodied species, particularly the large array of migratory birds, remained difficult (Bridge et al. 2011). Documenting their distribution and behaviours with GPS transmitters equipped with accelerometers is challenging due to limitations in device weight, battery life and data resolution (Frair et al. 2010; Tomkiewicz et al. 2010). However, recent advancements in ultra-light, energy-efficient tracking devices have made the first such studies possible (e.g. Bäckman et al. 2017; Dominoni et al. 2017; Kuang et al. 2019; Loonstra et al. 2023).

In migratory shorebirds, studies of the ways by which males and females meet their distinct ecological and energetic demands throughout the year are relatively new (Catry et al. 2012; Duijns et al. 2014). A crucial but less-studied factor influencing habitat use is the role of rhythmic behaviours, regular patterns of activity shaped by daily or tidal cycles (Daan and Koene 1981; Zwarts et al. 1990). Such rhythmic behaviours enable shorebirds to synchronise their activities with environmental opportunity (Bulla et al. 2017; Basso et al. 2023). As the females of Black-tailed Godwits *Limosa limosa* are larger than the males (Zhu et al. 2020), we expect them to have greater energetic demands and different foraging skills too. Consequently, male and female godwits are likely to exhibit different habitat preferences, and these differences may also shape their daily activity rhythms through variation in energetic demand and prey availability.

Here we studied the recently disclosed Bohai subspecies of the Black-tailed Godwit *L. l. bohaii* (Zhu et al. 2021a). As one of the four subspecies in Eurasia, the relatively small population breeds in the taiga forest zone of the Russian Far East (Fig. 1; Degtyarev et al. 2021; Zhu et al. 2022). Bohai Bay in China is a critical staging site for these birds, where they spend approximately 40 days each spring, utilising the coastal mudflats and adjacent inland habitats to refuel (Zhu

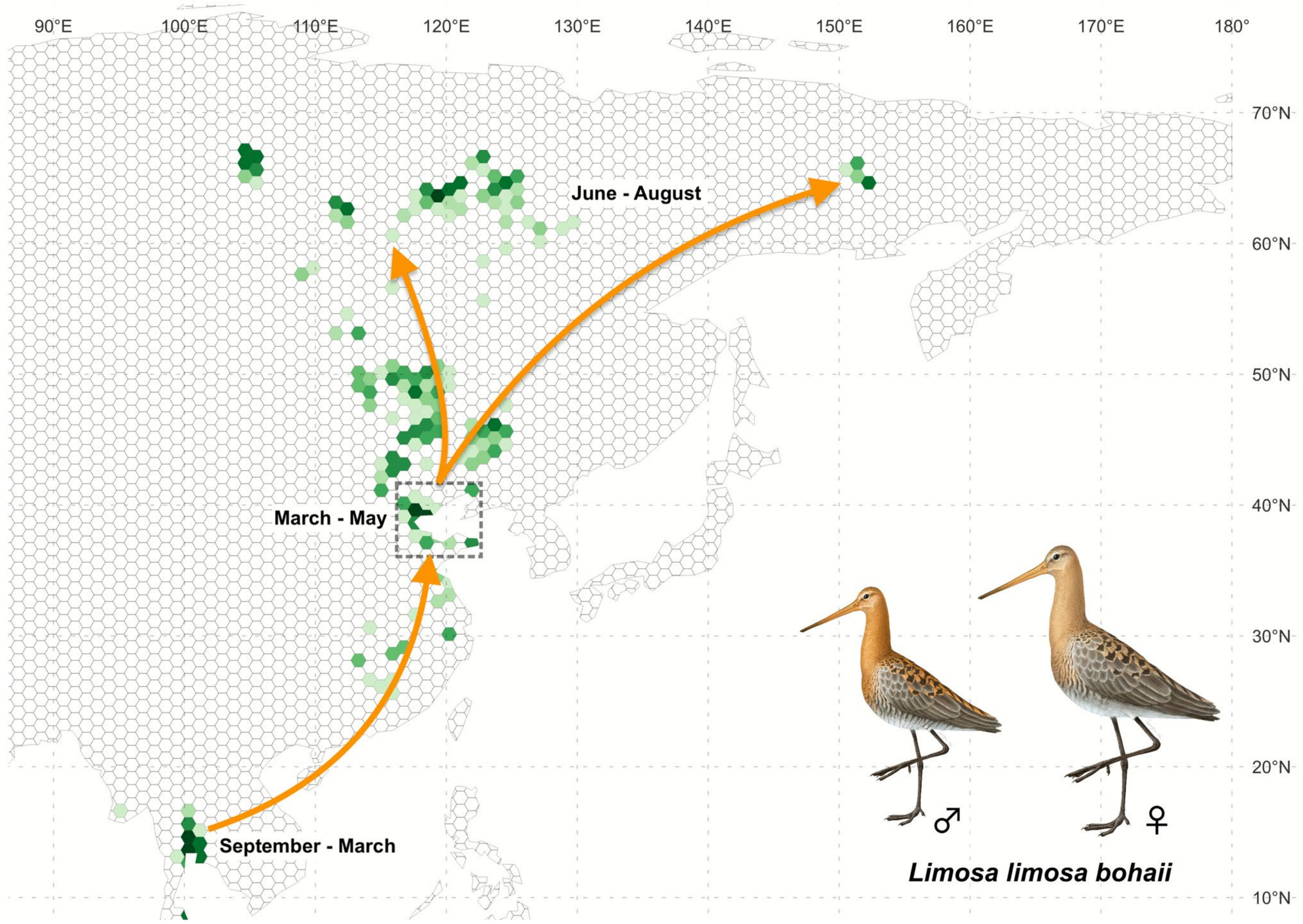

Fig. 1 Spatial distributions and migration corridors of Bohai Black-tailed Godwits during northward migration. Timing of migratory movements follows Zhu et al. (2021b). The dashed rectangle indicates the location of Bohai Bay. Drawings of Bohai Black-tailed Godwits by Seungha Oh. Hexagonal cells represent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

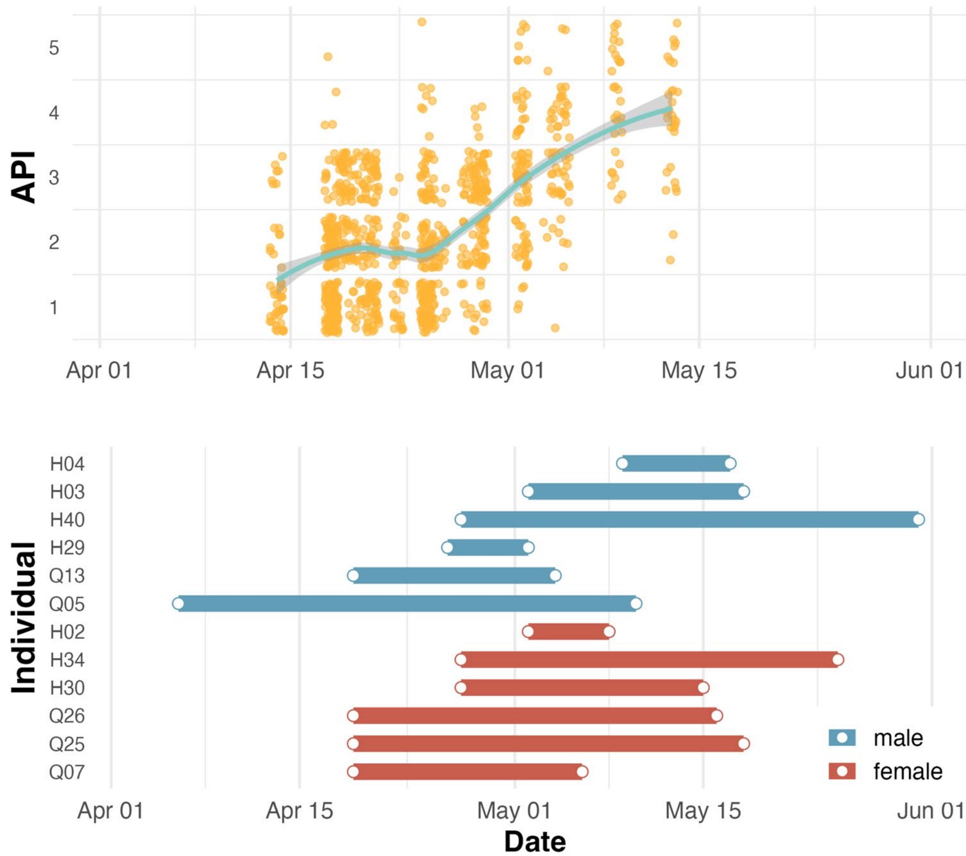

Fig. 2 Abdominal Profile Index (API) scores (upper panel; orange dots) with a smoothed trend line (light blue) and its 95% confidence interval (shaded area), and the intervals between capture and departure towards the breeding grounds of male and female (lower panel) Bohai Black-tailed Godwits in northern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

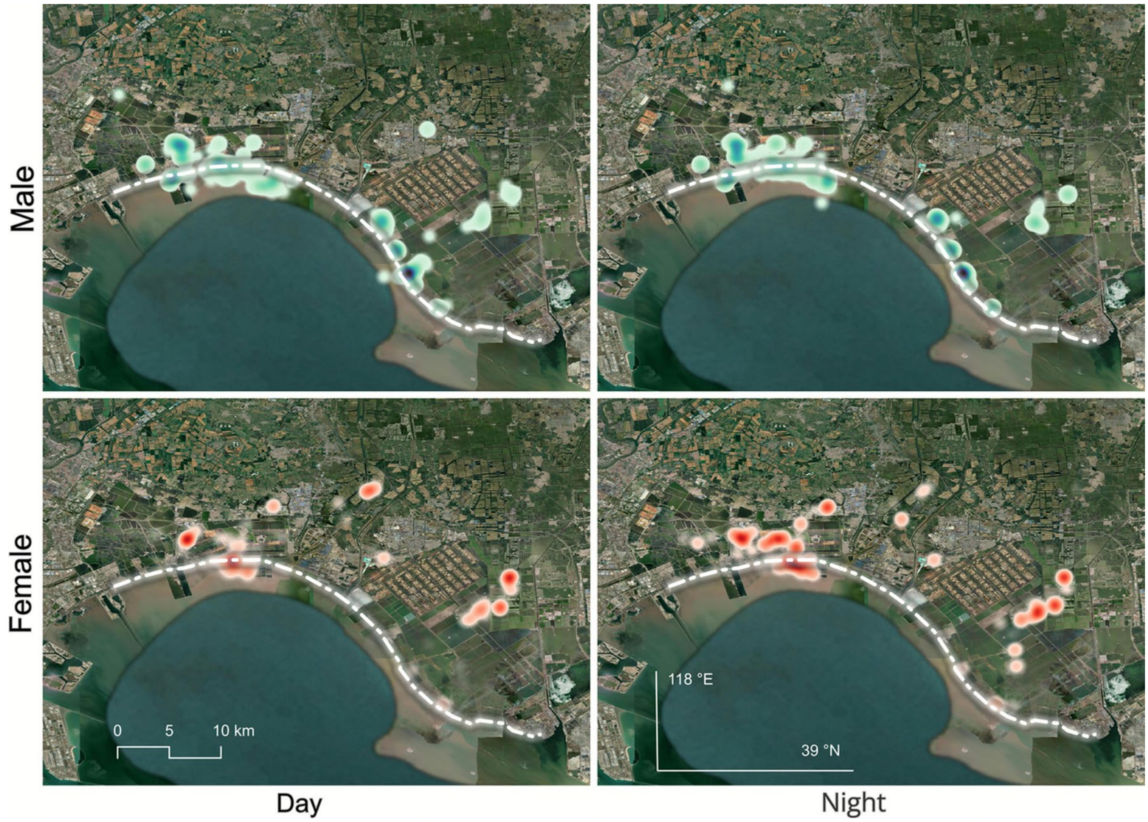

Fig. 3 Sex-specific spatial distribution heatmaps showing daytime and nighttime habitat use by male (upper panels) and female (lower panels) godwits during northward migration in northern Bohai Bay. The intensity of colours indicates the frequency of recorded occurrences. The white line represents the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

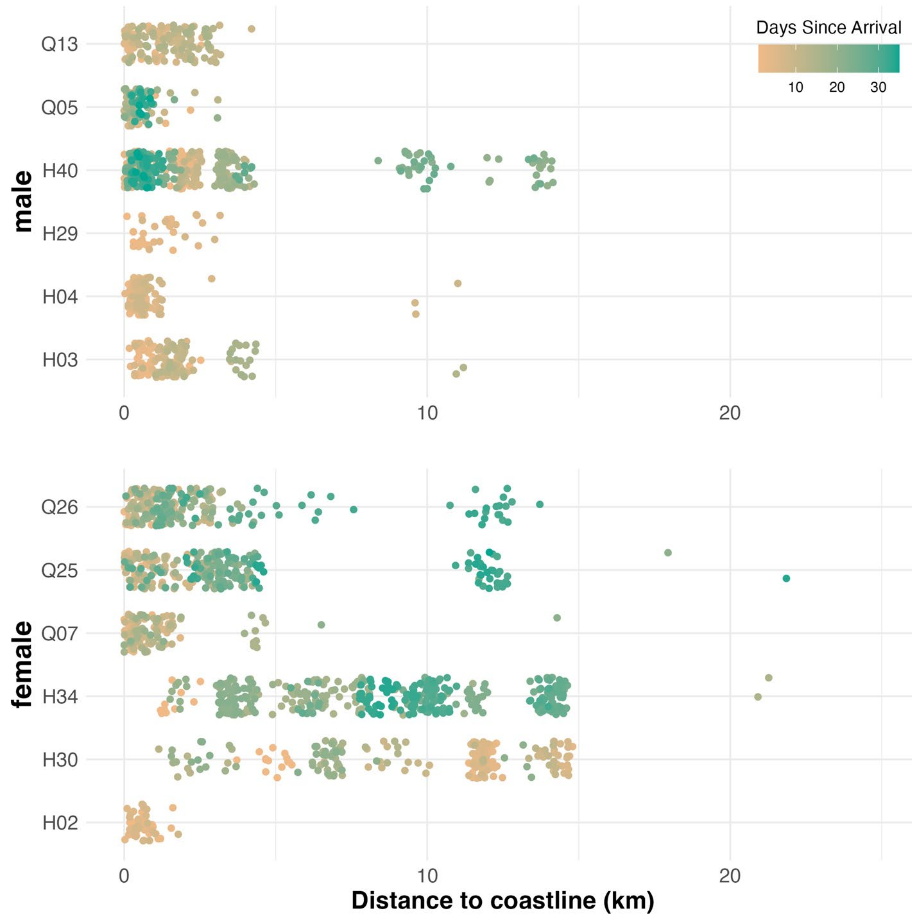

Fig. 4 Sex-specific changes in habitat use over time for Bohai Black-tailed Godwits during northward migration in northern Bohai Bay. Each dot represents a GPS-recorded location fix, coloured by the number of days since arrival

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 (β =–2.00 ± 6.23 days, t = −0.32, p = 0.75) or departure date (β =–1.00 ± 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; β = 0.090 ± 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, whereas females utilised a broader range of habitats, including coastal mudflats, saltworks, and inland freshwater wetlands (Fig. 4). Over time, females progressively moved inland from the coastal mudflats (Fig. 4; z = 5.743, p < 0.001), increasingly frequenting saltworks and freshwater wetlands. These shifts in habitat use resulted in distinct distributions of the sexes during the staging period (Fig. 4, χ^2 = 34.64, df = 2, p < 0.001).

Godwits exhibited distinct rhythmic behaviour influenced by tidal and diurnal cycles. On mudflats, female activity varied with the tide and peaked around high tide (Fig. 5; F = 0.916, edf = 2.287, p = 0.002), while male activity remained more constant across the tidal cycle (Fig. 5; F = 0.000, edf = 0.006, p = 0.601), but showing the highest values just before high tide. In inland habitats, both sexes followed diurnal rhythms, with activity decreasing towards sunset and rising again afterwards (Fig. 5; : F = 2.371, edf = 7.287, p < 0.001, : F = 4.668, edf = 4.230, p < 0.001). Overall, the model explained 43.3% of the deviance (adjusted R^2 = 0.411, Table S2).

Discussion

This study aimed to investigate sex-specific habitat use and rhythmic behaviours in Bohai Black-tailed Godwits during northward migration in northern Bohai Bay, China.

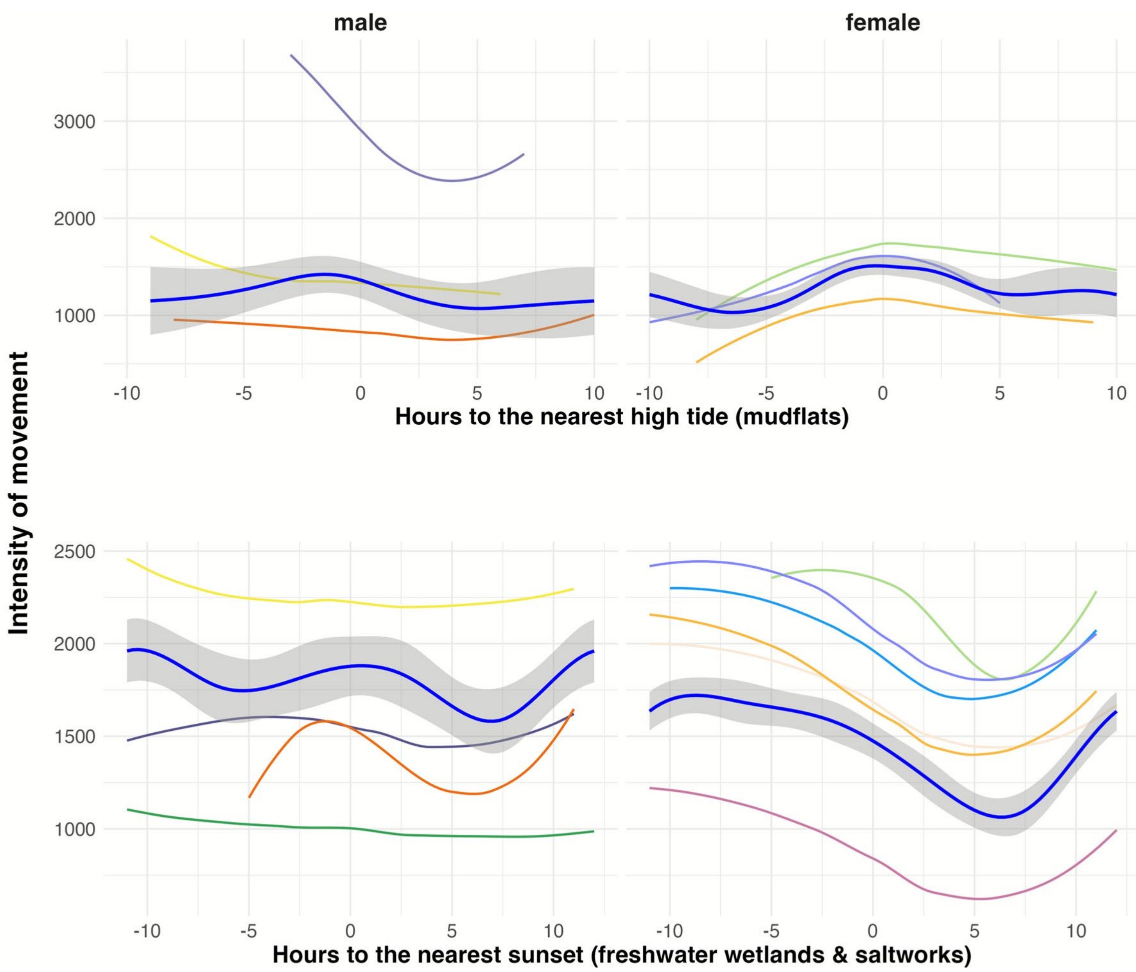

Fig. 5 Sex-specific activity patterns of Bohai Black-tailed Godwits in relation to environmental cycles in northern Bohai Bay. The thin coloured lines show smoothed activity patterns for individual birds, while the thick blue line shows the population-level smooth with its 95% confidence interval (shaded). Plots are shown relative to hours from the nearest high tide (top row, mudflats) and hours from the nearest sunset (bottom row, freshwater wetlands and saltworks)

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 an intriguing departure from the common observation that shorebirds are naturally most active during low tide (Zwarts et al. 1990; van de Kam et al. 2004). We suggest that the restlessness, rather than rest, around high tide may arise from their confinement to smaller shoreline areas, which are very close to intense human activity, including roads and other built-up human infrastructure (see Domínguez and Vidal 2007). In inland wetlands, movement intensity temporarily decreased towards sunset in both sexes (Fig. 5). This may suggest a response to the decreased availability of chironomid larvae (in rice fields; B-R Zhu, unpub. data) and brine fly larvae (in saltworks; Lei et al. 2021) during the coldest part of the day. Notably, the significantly higher intensity of movement observed within inland habitats compared to the mudflats supports the idea that the prey eaten in rice fields and salt ponds are smaller than the polychaete prey found in the mudflats (Hebo Peng, pers. comm.).

Our findings highlight the importance of integrating chronobiological insights into ecological studies of migratory shorebirds to understand behavioural strategies. The distinct patterns of activity and habitat use revealed here suggest that differences in body size and energetic demands between the sexes influence how godwits use space and time during migration. This underscores that in sexually dimorphic species, ecological analyses should not treat *the species* as a single homogeneous unit. Instead, males and females may represent functionally distinct ecological entities with differing constraints and strategies. Recognising such intra-species variation is essential, particularly in increasingly human-altered landscapes where habitat diversity is limited. Protecting a mosaic of wetland types, including coastal mudflats, saltworks, and freshwater habitats, will be key to supporting the full range of ecological requirements across both sexes.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10336-025-02355-4.

Acknowledgements This research was funded by the Natural Science Foundation of China [31830089, 31801985], the National Geographic 'Air and Water Conservation' Fund [GEFC-02-16], SEE Foundation, the Netherlands Organisation for Scientific Research (NWO) with contributions from Hunan Global Messenger Technology, WWF-Netherlands and the Spinoza Premium 2014 of NWO Netherlands Organisation for Scientific Research to TP to keep going the research of Global Flyway Network along the East-Asian Australasian Flyway. We also thank Oso Z. Sánchez for his invaluable companionship, encouragement, and support throughout the writing of this manuscript.

Funding Natural Science Foundation of China,31830089,Zhengwang Zhang, 31801985,Zhengwang Zhang,National Geographic 'Air and Water Conservation' Fund, GEFC-02-16,Bing-Run Zhu, SEE Foundation,Netherlands Organisation for Scientific Research, Spinoza Premium 2014.

Data Availability All tracking data generated during this study are archived in the Movebank data repository (https://www.movebank.org/). The dataset is available upon reasonable request from the corresponding data owner, Bing-Run Zhu (drewbingrun@outlook.com).

Declarations

Conflict of interest The authors declare that they have no competing financial or non-financial interests that are directly or indirectly related to the work submitted for publication.

Ethical approval All fieldwork procedures, including the capture, handling, and tagging of birds, were conducted in accordance with relevant 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.

References

Alves JA, Gunnarsson TG, Potts PM, Sutherland WJ, Gill JA (2013) Sex-biases in distribution and resource use at different spatial scales in a migratory shorebird. Ecol Evol 3:1079–1090

Bäckman J, Andersson A, Pedersen L, Sjöberg S, Tøttrup AP, Alerstam T (2017) Actogram analysis of free-flying migratory birds: new perspectives based on acceleration logging. J Comp Physiol A 203:543–564

Basso E, Horstmann J, Rakhimberdiev E, Abad-Gómez JM, Masero JA, Gutiérrez JS, Valenzuela J, Ruiz J, Navedo JG (2023) GPS tracking analyses reveal finely-tuned shorebird space use and movement patterns throughout the non-breeding season in high-latitude austral intertidal areas. Mov Ecol 11:55

Blanckenhorn WU (2005) Behavioral causes and consequences of sexual size dimorphism. Ethology 111:977–1016

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Bridge ES, Thorup K, Bowlin MS, Chilson PB, Diehl RH, Fléron RW, Hartl P, Kays R, Kelly JF, Robinson WD, Wikelski M (2011) Technology on the move: recent and forthcoming innovations for tracking migratory birds. Bioscience 61:689–698

Bulla M, Oudman T, Bijleveld AI, Piersma T, Kyriacou CP (2017) Marine biorhythms: bridging chronobiology and ecology. Philosoph Trans Royal Soc B Biol Sci 372:20160253

Catry T, Alves JA, Gill JA, Gunnarsson TG, Granadeiro JP (2012) Sex promotes spatial and dietary segregation in a migratory shorebird during the non-breeding season. PLoS One 7:e33811

Chan YC, Brugge M, Tibbitts TL, Dekinga A, Porter R, Klaassen RH, Piersma T (2016) Testing an attachment method for solar-powered tracking devices on a long-distance migrating shorebird. J Ornithol 157:277–287

Daan S, Koene P (1981) On the timing of foraging flights by Oystercatchers, *Haematopus ostralegus*, on tidal mudflats. Neth J Sea Res 15:1–22

Degtyarev VG, Egorov NN, Afanasiev MA (2021) Vilyuy population of the Black-tailed Godwit (*Limosa limosa melanuroides*, Charadriiformes, Scolopacidae). Biol Bull 48:1061–1066

Domínguez J, Vidal M (2007) Vigilance behaviour of preening Black-tailed Godwit *Limosa limosa* in roosting flocks. Ardeola 54:227–235

Dominoni DM, Åkesson S, Klaassen R, Spoelstra K, Bulla M (2017) Methods in field chronobiology. Philosoph Trans Royal Soc B Biol Sci 372:20160247

Duijns S, van Gils JA, Spaans B, ten Horn J, Brugge M, Piersma T (2014) Sex-specific winter distribution in a sexually dimorphic shorebird is explained by resource partitioning. Ecol Evol 4:4009–4018

El-Hacen EHM, Overdijk O, Lok T, Olff H, Piersma T (2013) Home range, habitat selection, and foraging rhythm in Mauritanian Spoonbills (*Platalea leucorodia balsaci*): a satellite tracking study. Waterbirds 36:277–286

Frair JL, Fieberg J, Hebblewhite M, Cagnacci F, DeCesare NJ, Pedrotti L (2010) Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosoph Trans Royal Soc B 365:2187–2200

Gantchoff M, Conlee L, Belant J (2019) Conservation implications of sex-specific landscape suitability for a large generalist carnivore. Divers Distrib 25:1488–1496

Giotto N, Picot D, Maublanc ML, Gerard JF (2013) Effects of seasonal heat on the activity rhythm, habitat use, and space use of the Beira Antelope in southern Djibouti. J Arid Environ 89:5–12

Godvik IMR, Loe LE, Vik JO, Veiberg V, Langvatn R, Mysterud A (2009) Temporal scales, trade-offs, and functional responses in red deer habitat selection. Ecology 90:699–710

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Modell 135:147–186

Gutiérrez JS, Dietz MW, Masero JA, Gill RE Jr, Dekinga A, Battley PF, Sánchez-Guzmán JM, Piersma T (2012) Functional ecology of saltglands in shorebirds: flexible responses to variable environmental conditions. Funct Ecol 26:236–244

Hastie T, Tibshirani R (1987) Generalized additive models: some applications. J Am Stat Assoc 82:371–386

Helm B, Visser ME, Schwartz W, Kronfeld-Schor N, Gerkema M, Piersma T, Bloch G (2017) Two sides of a coin: ecological and chronobiological perspectives of timing in the wild. Philosoph Trans Royal Soc B Biol Sci 372:20160246

Henriques M, Piersma T, Vansteelant WMG, de Goeij P, Lok T (2025) A time and a place for everything: Eurasian Spoonbills divide spring and summer activities across different areas in the eastern Dutch Wadden Sea. Ardea 113:3–20

Kuang F, Wu W, Ke W, Ma Q, Chen W, Feng X, Zhang Z, Ma Z (2019) Habitat use by migrating whimbrels (*Numenius phaeopus*) as determined by bio-tracking at a stopover site in the Yellow Sea. J Ornithol 160:1109–1119

Lei W, Masero JA, Piersma T, Zhu B, Yang HY, Zhang Z (2018) Alternative habitat: the importance of the Nanpu Saltpans for migratory waterbirds in the Chinese Yellow Sea. Bird Conserv Int 28:549–566

Lei W, Masero JA, Dingle C, Liu Y, Chai Z, Zhu B, Peng H, Zhang Z, Piersma T (2021) The value of coastal saltpans for migratory shorebirds: conservation insights from a stable isotope approach based on feeding guild and body size. Anim Conserv 24:1071–1083

Lok T, van der Geest M, de Goeij P, Rakhimberdiev E, Piersma T (2024) Sex-specific nest attendance rhythm and foraging habitat use in a colony-breeding waterbird. Behav Ecol 35:arae020

Loonstra AJ, Verhoeven MA, Both C, Piersma T (2023) Translocation of shorebird siblings shows intraspecific variation in migration routines to arise after fledging. Curr Biol 33:2535–2540

Masero JA, Abad-Gómez JM, Gutiérrez JS, Santiago-Quesada F, Senner NR, Sánchez-Guzmán JM, Piersma T, Schroeder J, Amat JA, Villegas A (2017) Wetland salinity induces sex-dependent carry-over effects on the individual performance of a long-distance migrant. Sci Rep 7:6867

Piersma T, van Gils J, de Goeij P, van der Meer J (1995) Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. J Animal Ecol 64:493–504

Rijnsdorp A, Daan S, Dijkstra C (1981) Hunting in the kestrel, *Falco tinnunculus*, and the adaptive significance of daily habits. Oecologia 50:391–406

Sirot E, Maes P, Gélinaud G (2012) Movements and conflicts in a flock of foraging black-tailed godwits (*Limosa limosa*): the influence of feeding rates on behavioural decisions. Ethology 118:127–134

Sprogis KR, Christiansen F, Raudino HC, Kobryn HT, Wells RS, Bejder L (2018) Sex-specific differences in the seasonal habitat use of a coastal dolphin population. Biodivers Conserv 27:3637–3656

Tomkiewicz SM, Fuller MR, Kie JG, Bates KK (2010) Global positioning system and associated technologies in animal behaviour and ecological research. Philosoph Trans Royal Soc B Biol Sci 365:2163–2176

van de Kam J, Ens BJ, Piersma T, Zwarts L (2004) Shorebirds: an illustrated behavioural ecology. KNNV Publishers, Utrecht

van Gils JA, Edelaar P, Escudero GB, Piersma T (2004) Carrying capacity models should not use fixed prey density thresholds: a plea for using more tools of behavioural ecology. Oikos 104:197–204

Wang Z, Akamatsu T, Wang K, Wang D (2014) The diel rhythms of biosonar behavior in the Yangtze Finless Porpoise (*Neophocaena asiaeorientalis asiaeorientalis*) in the port of the Yangtze River: the correlation between prey availability and boat traffic. PLoS One 9:e97907

Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP (2006) Why do we still use stepwise modelling in ecology and behaviour? J Anim Ecol 75:1182–1189

Wiersma P, Piersma T (1995) Scoring abdominal profiles to characterize migratory cohorts of shorebirds: an example with Red Knots. J Field Ornithol 66:88–98

Wood SN (2017) Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton

Yang HY, Chen B, Barter M, Piersma T, Zhou CF, Li FS, Zhang ZW (2011) Impacts of tidal land reclamation in Bohai Bay, China: ongoing losses of critical Yellow Sea waterbird staging and wintering sites. Bird Conserv Int 21:241–259

Zhu BR, Hassell CJ, Verkuil YI, Gunnarson TG, Hooijmeijer JC, Zhang Z, Piersma T (2020) Size, shape and sex differences in three subspecies of Black-tailed Godwits *Limosa limosa*. Bird Study 67:45–52

Zhu BR, Verkuil YI, Conklin JR, Yang A, Lei W, Alves JA, Hassell CJ, Dorofeev D, Zhang Z, Piersma T (2021) Discovery of a morphologically and genetically distinct population of Black-tailed Godwits in the East Asian-Australasian Flyway. Ibis 163:448–462

Zhu BR, Verhoeven MA, Loonstra AJ, Sanchez-Aguilar L, Hassell CJ, Leung KK, Lei W, Zhang Z, Piersma T (2021) Identification of breeding grounds and annual routines of the newly discovered *bohaii* subspecies of Black-tailed Godwits. Emu 121:292–302

Zhu BR, Verhoeven MA, Velasco N, Sanchez-Aguilar L, Zhang Z, Piersma T (2022) Current breeding distributions and predicted range shifts under climate change in two subspecies of Black-tailed Godwits in Asia. Glob Change Biol 28:5416–5426

Zwarts L, Blomert AM, Hupkes R (1990) Increase of feeding time in waders preparing for spring migration from the Banc d'Arguin, Mauritania. Ardea 55:237–256