



Predicting the non-breeding distributions of the two Asian subspecies of Black-tailed Godwit using morphological information



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ABSTRACT

Until recently, *Limosa limosa melanuroides* was thought to be the only subspecies of Black-tailed Godwit in the East Asian–Australasian Flyway. For this reason, all previous occurrences and counts of Black-tailed Godwits in the flyway have been assigned to *melanuroides*. However, a larger-bodied subspecies, *bohaili*, has recently been discovered in the flyway. As a result, the occurrence of Black-tailed Godwits in the flyway needs to be reconsidered such that the specific distribution of each subspecies becomes known. To this end, we developed a simple discriminant function to assign individuals to subspecies based on their bill and wing length. Cross-validation with individuals known to be *bohaili* or *melanuroides*, based on molecular analysis, showed the developed function to be 97.7% accurate. When applied to measurements of godwits captured at 22 sites across 9 countries in East–Southeast Asia and Australia, we found that *bohaili* and *melanuroides* occurred at most sites and overlapped in their distribution from Kamchatka to Australia. We examined photos from all along the flyway to verify this surprising result, confirming that both subspecies co-occur in most locations. Based on these results, we hypothesise that *bohaili* and *melanuroides* from the west of their breeding ranges mostly migrate over Chinese mainland. Birds of both subspecies from the east of their ranges are expected to migrate along the Pacific Ocean. We encourage ringing groups in East–Southeast Asia and Australia to use this simple method to keep adding knowledge about Black-tailed Godwits in the East Asian–Australasian Flyway.

1. Introduction

Obtaining information on the distribution of different avian

subspecies is often challenging due to subtle differences in morphology, plumage colour or songs (Clayton, 1990; Inouye et al., 2001; Wojczulanis-Jakubas et al., 2011). This can be even more complicated for

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migratory animals that occur at multiple sites throughout the year. Such knowledge on the distribution of subspecies and populations, however, is essential to understand morphological variation, selective pressures, and phylogenetic relationships (Piersma and Baker, 2000; Phillimore and Owens, 2006). When such information is scarce, it also becomes very hard to assess population trends and develop conservation strategies (Chan et al., 2019a; Smith et al., 2020).

This problem is now relevant in the case of Black-tailed Godwits (*Limosa limosa*), a long-distance migratory shorebird, in the East Asian–Australasian Flyway (EAAF), where recently a new and large-bodied subspecies named *bohail* has been discovered (Zhu et al., 2021a). *Bohail* godwits breed in the Russian Far East subarctic region and share the EAAF with *melanuroides* godwits that breed further south in the steppes of Mongolia and Inner Mongolia, China (Zhu et al., 2022). Previously, *melanuroides* was thought to be the only godwit subspecies in this flyway (Zhu et al., 2021a, b). For this reason, all previous occurrences and counts of Black-tailed Godwits in the EAAF were attributed to *melanuroides* alone. As a result, there is a real need to update our knowledge on the distribution of both subspecies in the EAAF to make new population estimates, fill knowledge gaps and design conservation strategies.

In recent years, satellite tracking has become a leading method for obtaining the annual distributions of migratory animals (Zhu et al., 2021b; Kuang et al., 2022). It represents a powerful but expensive method and is often limited to a few individuals from one spot rather than including many birds from multiple locations (Lindberg and Walker, 2007). Our study aims to provide the first information on the non-breeding distributions and potential migratory corridors of both godwit subspecies by using morphological information. Morphological measurements of godwits are available from 22 ringing sites across 9 countries in the EAAF. To analyse this data set, we developed a simple discriminant function that can distinguish between the two subspecies on the basis of the individual's bill and wing length.

Discriminant functions have been widely used in species classification (Genovart et al., 2003; Santiago-Alarcon and Parker, 2007; Izenman, 2013). Gunnarsson et al. (2006) demonstrated that this method can also be used to reliably predict the sex of individual *islandica* godwits. Since the differences between godwit subspecies are more significant than the previously analysed sexual size differences, we expect that a discriminant function will also be able to predict subspecies reliably (Zhu et al., 2020, 2021a). We validated the accuracy of our discriminant function by checking its performance on individuals known to be *bohail* or *melanuroides* through molecular analysis (see Zhu et al., 2021a). Our discriminant function provides an accessible and affordable tool to keep adding knowledge about godwits in the EAAF that will hopefully help design effective conservation strategies, as this flyway continues to face threats from human-caused habitat destruction (Szabo et al., 2016).

2. Methods

2.1. Discriminant function analysis

To develop our discriminant function, we used reference measurements from Black-tailed Godwits (hereafter 'godwits'), for which the subspecies was genetically determined using a genetic marker from mitochondrial DNA (see Zhu et al., 2021a). Godwits have reversed sexual size dimorphism (Engelmoer and Roselaar, 1998; Zhu et al., 2020). Fortunately, our reference dataset for both subspecies contained a near-equal number of males and females which minimises the potential for bias as a result of the existing sexual dimorphism (*bohail*: 21♀ and 24♂; *melanuroides*: 85♀ and 87♂). Samples of *bohail* were collected in Bohai Bay, China (39.2° N, 118.0° E) and *melanuroides* samples in Roebuck Bay, Australia (17.9° S, 122.3° E). To limit the potential for measurement errors, the same team performed ringing and measuring at each site (led by B.-R. Zhu in Bohai Bay and C.J. Hassell in NW Australia).

These reference measurements were checked for normality with a Shapiro-Wilk Test ($p \geq 0.11$), for homogeneity with variance-covariance

matrices ($\chi^2 = 93.979$, $df = 1980$, $p = 1$). The two linear dimensions with the lowest collinearity and variance inflation factor ($VIF = 3.1$) were selected using R-packages "covTestR" and "car", namely bill and wing (the flattened wing chord). Next, we normalised the reference data to minimise the effect on the model caused by the scale or unit of the predictors and randomly split the reference data into a training set (80%) and a testing set (20%; Picard and Berk, 1990). We then obtained the discriminant function by fitting a linear model to the bill and wing lengths in the training set with the function 'lda' from the R-package "MASS".

We cross-validated the performance of the resulting discriminant function by applying it to the testing set. This method is proven to be more precise than re-substitution or sample splitting (Dechaume-Moncharmont et al., 2011). Lastly, to estimate the error rate of the function when discriminating subspecies, we examined the discriminant function using 50 samples (each sample: $n = 217$) that were resampled by bootstrapping from the reference data. The resulting prediction accuracy and 95% confidence interval (CI) are reported (Shimura, 2015).

2.2. Predicting and mapping the non-breeding distributions

To investigate the non-breeding distribution of both subspecies in East-Southeast Asia and Australia, we applied our discriminant function to the ringing data (e.g., biometric measurements, ringing dates, locations and ring numbers) of 994 adults captured at 22 ringing stations in 9 countries (Fig. 1; Appendix Table S1). We set the western border of our data collection area in Thailand (ca. 95° E) for two reasons: (1) this is the westernmost site where both subspecies have been confirmed to occur through molecular methods (Zhu et al., 2016–2018 unpubl. data, 2021a); (2) at sites further west, e.g., in Bangladesh, India and Sri Lanka, there is anecdotal evidence suggesting the occurrence of *L. l. limosa*, which is similar in body size to *bohail* and would therefore influence our non-breeding range predictions (Zhu et al., 2020). We classified each ringing site as a stopping or non-breeding site by the month in which the ringing work was conducted, i.e., spring (April–June), autumn (July–October) and winter (November–March; Fig. 1).

If a bird was expected to belong to the *bohail* subspecies, but the ringing site was not previously known as a *bohail*-site from satellite tracking, i.e., Russia or Australia (see Zhu et al., 2021b). We performed additional checks for the possibility of their occurrence by examining photos of godwits taken in those regions. Godwit photos from Kamchatka, Russia, were collected from the local ringing group, and photos of non-breeding godwits in Australia were collected from eBird (<https://ebird.org/home>) and individual researchers. The godwit photos were assessed by B.-R. Zhu and K.K.-S. Leung who have the most experience with identifying *bohail* in the field. We first shuffled the photos and concealed their locations to reduce potential bias. Then, both examiners verified the photos independently and their results were cross-checked and turned out to be identical. As a result, 75 photos were examined (Fig. 1).

We collected additional information about the presence of Black-tailed Godwits in regions beyond our sampling sites, i.e., the Korean Peninsula, Japan, Taiwan of China, the Philippines and Australia by interviewing bird watchers, photographers and shorebird researchers along the flyway. When the presence of godwits was reported, we also collected and examined photos from these sites. We present the predicted proportion of each subspecies in the ringing stations on a map using Qgis 3.1.6, sightings of godwits from the interviews were also marked out.

3. Results

The discriminant analysis yielded the following function with a cut-off value of 13 (also see Fig. 2):

$$\text{Discriminant coefficient} = -2.1 \times \text{bill} + 0.86 \times \text{wing} + 13$$

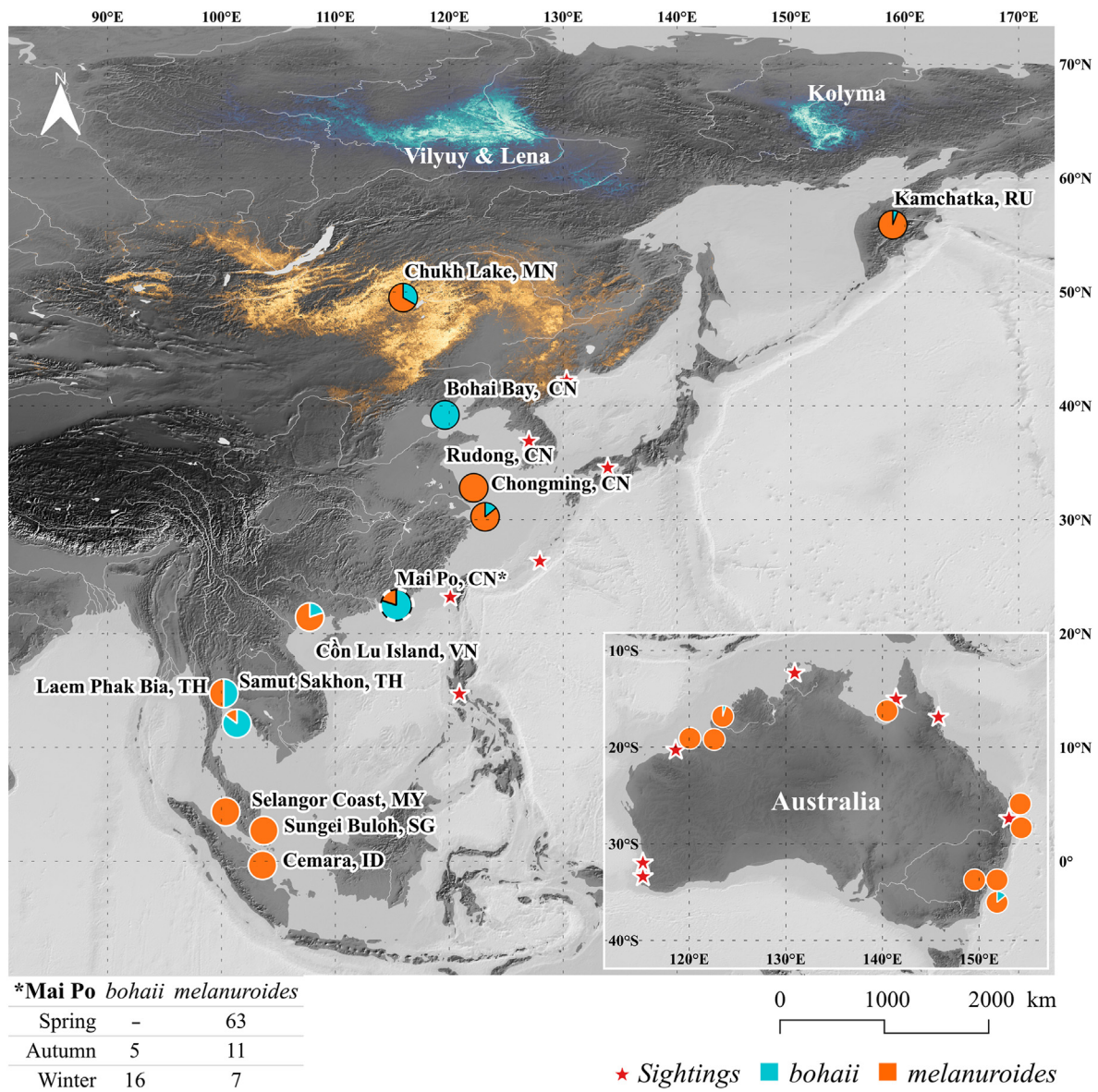


Fig. 1. Predicted non-breeding distributions of *bohaii* and *melanuroides*. Sightings of *bohaii* type godwits confirmed by photos are shown with stars. Stopping sites are marked with black outlines, and non-breeding sites are white. Mai Po Nature Reserve (black and white outline) was the northernmost non-breeding site for both subspecies and also a stopping site for *melanuroides*. The known breeding range of *bohaii* (ca. 61–66° N) is shown in light blue and that of *melanuroides* (ca. 42–52° N) in orange (adapted from Zhu et al., 2022). Ring stations and countries are in bold.

An individual is predicted to be *bohaii* when the discriminant coefficient is less than 0 and *melanuroides* when it is greater than 0. The cross-validation of this function on our testing set ($n = 44$) showed it to be 97.7% accurate in predicting subspecies. The prediction accuracy of the discriminant function on the bootstrapped samples was 97.0% (95% CI: 95.7–98.3%, $n = 2357$) for *bohaii* and 95.5% (95% CI: 95–96.1%, $n = 8493$) for *melanuroides*.

Out of the 22 ringing stations that provided biometric data on godwits, Mai Po Nature Reserve in Hong Kong, China (ca. 22° N) was the northernmost non-breeding site of both subspecies (Fig. 1; Appendix Table S1). The morphological data showed that *bohaii* was captured at nine ringing stations in six countries and that *melanuroides* was captured at all ringing stations (Fig. 1; Appendix Table S1). Moreover, the distribution of the two subspecies overlapped in six countries, i.e., Russia, Mongolia, China, Vietnam, Thailand and Australia (Fig. 1; Appendix Table S1).

The discriminant function identified *bohaii* occurred at sites not previously known from satellite tracking: Kamchatka, Russia, Nudgee Beach,

Australia and Roebuck Bay, Australia (Fig. 1; Appendix Table S1; Zhu et al., 2021b). In Kamchatka, 6% of the measured birds (four in total) were identified as *bohaii*. This was 14% in Nudgee Beach (three birds) and 5% in Roebuck Bay (28 birds). These proportions are higher than the model's average error rate (3%) in discriminating *bohaii* and thus support the presence of *bohaii* at these new locations. To verify this finding, we examined photos of one of the four godwits predicted to be *bohaii* in Kamchatka and both examiners agreed that the individual was *bohaii*. Similarly, we also identified numerous *bohaii* type individuals in photos from near Nudgee Beach and Roebuck Bay (see Appendix Table S2 for details).

Additionally, amongst photos from bird watchers, photographers and researchers, we found *bohaii* type godwits together with *melanuroides* type godwits in Rason (North Korea, N. Moores, pers. comm.), Chungcheongnam-do (South Korea, H-K. Nam, pers. comm.), Okinawa and Hiroshima (Japan, T. Kawasumi pers. comm.), Tainan (China, B. Chen, pers. comm.), Bulacan (the Philippines, I. Dy, pers. comm.) and the Gulf of Carpentaria, Australia (R. Jaensch, pers. comm. Fig. 1).

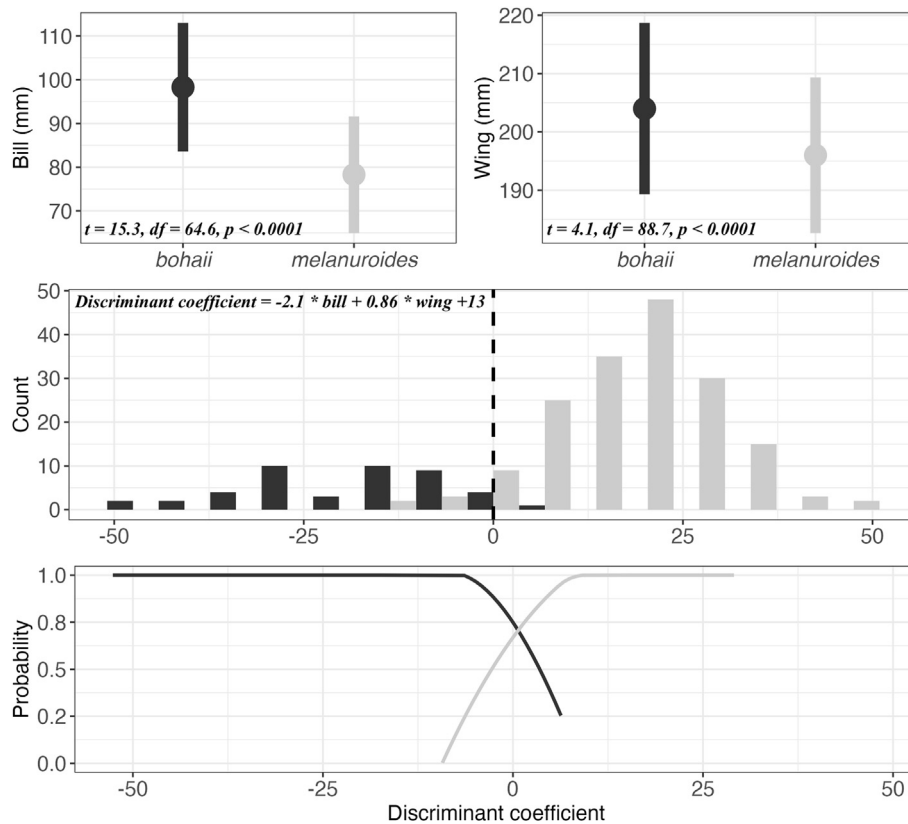


Fig. 2. (A) average bill and wing length (95% CI) of *bohaii* and *melanuroides*. The results of the Student *t*-tests are displayed in the bottom left. (B) subspecies assignment of all individuals from our reference dataset based on the discriminant function (top left; black = *melanuroides*, grey = *bohaii*). The dashed line indicates the cut-off value (13). (C) the probability of correct subspecies prediction at different discriminant coefficients. The sample size for all figures: *bohaii*: 45, *melanuroides*: 172.

4. Discussion

We developed a discriminant function based on the bill and wing length, which was >95% accurate in assigning godwits captured throughout the EAAF to either the *bohaii* or *melanuroides* subspecies. It is worth noting that the difference in body size between the analysed godwit subspecies is greater than the sexual dimorphism within the subspecies (Zhu et al., 2020, 2021a). Therefore, even without considering an individual's sex, the discriminant function was able to assign it to subspecies with high accuracy. We applied this function to godwits captured at 22 sites across 9 countries in East-Southeast Asia and Australia. We found that *bohaii* and *melanuroides* co-occurred in most sampled sites except for the stopping site in Rudong, China and the non-breeding sites in Malaysia, Singapore, and Indonesia, where only *melanuroides* godwits were captured (Fig. 1). The overlap in the distribution of *bohaii* and *melanuroides* extends as far south as Australia. Previously, only the latter was thought to occur here (Fig. 1; van Gils et al., 2020).

The discriminant function revealed that *bohaii* has stopping sites in Chinese mainland and non-breeding sites in Thailand. This is consistent with previous satellite tracking results (Zhu et al., 2021b) and supports the subspecies assignment based on our function. Surprisingly, the discriminant function also uncovered some godwits captured in Kamchatka, Russia and Australia to be *bohaii*. These sites are outside of *bohaii*'s previously known distribution. Still, the number of godwits assigned as *bohaii* in these sites was higher than expected on the basis of the function's error rate. In addition, our examination of photos from these regions also confirmed the occurrence of *bohaii* here. Therefore, we conclude that the actual distribution of *bohaii* is larger than previously identified via tracking (Zhu et al., 2021b). This is further supported by

photos from the Korean peninsula, Taiwan of China and the Philippines, which also include *bohaii* in addition to *melanuroides*. Noteworthy is that photos from the southeastern Gulf of Carpentaria, Australia even indicated that *bohaii* is the dominant non-breeding population there (R. Jaensch, pers. comm.).

Based on these results, we hypothesise that *bohaii* from the west of their breeding range (e.g., the Lena and Vilyuy River basins, see Fig. 1 and Zhu et al., 2022) predominantly migrate over Chinese mainland. In contrast, *bohaii* from the east of their range (e.g., the Kolyma River basin) are expected to predominantly migrate along the Pacific Ocean via the Kamchatka Peninsula, Japan, Korean Peninsula, Taiwan of China and the Philippines to Australia (Fig. 1). We believe that the same is true for *melanuroides*, i.e., an inland corridor is mainly used to reach their western range and an oceanic corridor is used to reach their eastern range (see Fig. 1 and Zhu et al., 2022). This idea is supported by two satellite tagged adult *melanuroides* godwits from the west of their range in Chukh Lake, Mongolia. They migrated from inland China, over the Himalayas, and overwintered on the Indian subcontinent (Bangladesh and Sri Lanka; Tserenbat and Purev-Ochir, 2019–2020, unpubl. data). There is no published information about the eastern breeding locations of *melanuroides* that use the Kamchatka Peninsula as a stopping site. However, they are likely to breed in Chukotka or on islands in the Bering Strait (Lappo et al., 2012). Furthermore, molecularly determined *melanuroides* from Northwest Australia, were sighted in Taiwan, Lianyungang and Kamchatka (Chan et al., 2019b; Hassell et al., 1998–2019 unpubl. data), suggesting an oceanic migratory corridor for the eastern breeding population of this subspecies.

While the geographical and ecological characteristics of the breeding grounds of these two Asian godwits subspecies are considerably different (Zhu et al., 2022), their non-breeding distributions overlap to a large

extent. This pattern is also seen in *islandica* and *limosa* in the East-Atlantic Flyway (Gill et al., 2007). Outside their core breeding grounds in Iceland and the Netherlands, the two subspecies co-occur from the UK to Morocco during the non-breeding season (Lopes et al., 2013; Verhoeven et al., 2021). That said, *islandica* is primarily found in intertidal habitats while *limosa* mostly uses rice fields (Alves et al., 2010). The same might be the case for *bohii* and *melanuroides* in Southeast Asia. For example, in Thailand, tracked *bohii* rarely used saline habitats. In contrast, large groups of *melanuroides* type godwits were recorded on the Samut Prakan coast near Bangkok (Zhu et al., 2016–2018 unpubl. data, 2021b).

We encourage ringing groups in East-Southeast Asia and Australia to use this accessible and effective method to examine their data and contribute to our collective knowledge of Black-tailed Godwits, such as their non-breeding range. However, we caution against using this method when subspecies of similar body sizes co-occur, e.g., in Myanmar, Bangladesh, India and Sri Lanka, where *limosa* and *bohii* may co-exist, we recommend using the genetic markers already developed and applied in four godwit subspecies to assess population structure (Lopes et al., 2013; Zhu et al., 2021b).

Authors' contribution

ZBR designed this study, analysed the data, wrote and reviewed the manuscript; MAV analysed the data and reviewed the manuscript; CJH, KKS, DD, QM, KE, JTC, UT, GPO, DL collected the data in the field and reviewed the manuscript. ZZ, TP reviewed the manuscript. All authors read and approved the final manuscript.

Ethics statement

The local forestry or nature reserve authorities approved the ringing work in Chinese mainland. The Agriculture, Fisheries and Conservation Department of the Government of the Hong Kong SAR approved the ringing work at Mai Po Nature Reserve, China. The Federal Service for Supervision of Natural Resources (Rosprirodnadzor) approved the ringing work in Kamchatka, Russia. The Ministry of Environment and Tourism of Mongolia approved the work in Mongolia. The National Parks Board, Singapore, authorised the ringing work in Singapore. The Department of National Park, Wildlife and Plant Conservation, Ministry of Natural Resource and Environment, approved the ringing work in Thailand. The Australian Federal Government, the Australian Bird and Bat Banding Scheme (ABBBS) approved the ringing work in Australia.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Beach, the traditional lands of the Karajarri and Nyangumarta people. We appreciate the many anonymous photographers for their photos of Black-tailed Godwits in Japan and Australia. CJH would like to thank GFN's major funders for the NWA work, Spinoza Premium of Netherlands Organisation Prize for Scientific Research to Theunis Piersma (2014–2017), WWF Netherlands (2010–2017 and 2019–2021) and MAVA, Fondation pour la nature (2018). This study was funded by the National Natural Science Foundation of China [31830089, 31801985, 32270518].

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.avrs.2022.100069>.

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