Li, Donglai, Zhang, Jing, Liu, Yu, Lloyd, Huw, Pagani-Núñez, Emilio and Zhang, Zhengwang (2020) Differences in dietary specialization, habitat use and susceptibility to human disturbance influence feeding rates and resource partitioning between two migratory Numenius curlew species. Estuarine, Coastal and Shelf Science, 245. p. 106990. ISSN 0272-7714

DOI: https://doi.org/10.1016/j.ecss.2020.106990

Publisher: Elsevier BV

Version: Accepted Version

Differences in dietary specialization, habitat use and susceptibility to human disturbance influence feeding rates and resource partitioning between two migratory *Numenius* curlew species

Donglai Li[a,*], Jing Zhang[a], Yu Liu[b], Huw Lloyd[c], Emilio Pagani-Núñez[d], Zhengwang Zhang[b]

[a] *Provincial Key Laboratory of Animal Resource and Epidemic Disease Prevention, College of Life Sciences, Liaoning University, Shenyang 110036, PR China*
[b] *Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing 100875, PR China*
[c] *Ecology and Environment Research Centre, Department of Natural Sciences, Manchester Metropolitan University, Chester Street, Manchester, M1 5GD United Kingdom*
[d] *Department of Health and Environmental Sciences, Xi'an Jiaotong-Liverpool University, Suzhou, 215123, PR China*

ARTICLE INFO

Keywords:
Diet specialization
Migration
Foraging ecology
Mixed models
Coastal wetlands
Numenius species

ABSTRACT

Migratory shorebirds select stopover sites to fuel their migration across heterogeneous coastal landscapes with abundant prey resources. Quantifying the degree of dietary specialization between closely-related species and how they partition resources across different coastal habitat types during both spring and autumn migration could identify some interesting possibilities for conservation management given the extent of anthropogenic habitat degradation at critical stopover sites. Here we used a comparative approach to examine diet specialization and feeding rates of two migratory *Numenius* curlew species, Far Eastern Curlew *Numenius madagascariensis* and Eurasian Curlew *N. arquata* populations, at an important stopover site in the Yellow Sea, China, and to assess the influence of habitat type, presence of human disturbance (activities related to aquaculture and oil production), and migratory season on their feeding behavior. Far Eastern Curlews were more dependent on tidal crabs and exhibited less dietary flexibility than its closely-related congener. Feeding rates on crabs by Far Eastern Curlews were not significantly different between mudflat and *Suaeda salsa* saltmarsh habitat but were negatively influenced by human disturbance and were higher during spring migration. In contrast, these effects were not apparent for Eurasian Curlew which fed predominantly on ragworms in saltmarsh habitat. The differences in prey type and feeding rates between adjacent habitats and migration seasons could explain how these two congeners fit syntopically along coastal wetland resource gradients. The extensive utilization of *S. salsa* habitat by both species suggests that saltmarshes represent an important feeding habitat for these species and that further conservation efforts aimed at reducing human disturbance would benefit both species and may lead to improved feeding rates for Far Eastern Curlews.

1. Introduction

Diet specialization is widespread among closely-related migrant shorebird species (van de Kam et al., 2004) enabling them to partition niche space and fit syntopically along resource gradients (Mathot et al., 2007; Piersma et al., 1994; Tsipoura and Burger, 1999; Tulp et al., 1994). Many migratory shorebirds depend on abundant food-rich stopover sites across coastal landscapes to fuel their migration (Horn et al., 2020; Martins et al., 2013; Piersma, 1987). Within these highly heterogeneous coastal environments, tidal mudflats and adjacent saltmarshes represent some of the most important foraging habitats due to the richness and abundance of macrozoobenthic prey resources (Burger et al., 1997; Enners et al., 2019; Jing et al., 2007; Li et al., 2014). Shorebird population viability depends on their ability to exploit these habitat-dependent food resources during climatically variable migration seasons (breeding vs. non-breeding). However, such critical food resources can be impacted by extensive anthropogenic habitat loss and degradation, especially along the East Asian–Australasian Flyway (Choi et al., 2017; Gallo-Cajiao et al., 2019; Melville et al., 2016; Studds et al., 2017). Thus, there is a need for more detailed studies that examine the degree of dietary specialization by shorebird species at critical stopover sites to help assess the impacts of these anthropogenic threats on foraging migratory shorebird populations to improve future coastal wetland conservation and management strategies.

---

* Corresponding author.
E-mail address: lidonglai@lnu.edu.cn (D. Li).

https://doi.org/10.1016/j.ecss.2020.106990
Received 10 April 2020; Received in revised form 27 July 2020; Accepted 31 July 2020

Long-distance migratory shorebirds experience extreme feeding time-constraints (Atkinson et al., 2007). Thus, they tend to select stopover-sites where their preferred prey types are abundant, for which they have tactile specialized behaviors that permit the highest feeding rates (Choi et al., 2017; Yang et al., 2013). In contrast, short-distance migrant species that use multiple stopovers sites should exhibit a more generalist diet and greater plasticity in their foraging behavior linked to variation in habitat-dependent prey density and availability (Piersma, 2007). Furthermore, variation in shorebird foraging behavior caused by human disturbance (Fitzpatrick, 1998; Stillman and Goss-Custard, 2002; Yasué, 2005) or the presence of competitors in the form of conspecifics or congenerics (Duijns and Piersma, 2014; Fernández and Lank, 2008), can reduce feeding rates below what is required for a species to sustain minimum energy intake requirements (Burger and Gochfeld, 1991; Thomas et al., 2003).

The Far Eastern Curlew *Numenius madagascariensis* and Eurasian Curlew *N. arquata* are two large congeneric migrant shorebird species that feed on deep burrowing prey in the soft sediments of saltmarshes and inter-tidal mudflats (Lambert, 1992; Navedo and Masero, 2008; Piersma, 1985). The Far Eastern Curlew is found in the East Asian–Australasian Flyway (EAAF) and migrates over much greater distances than its congener (12,000 km vs 5000 km; BirdLife International, 2020) with which it shares the same flyway (Driscoll and Ueta, 2003; Zhao et al., 2017). Populations of Far Eastern Curlew mainly breed in northeastern Asia (from northeastern China to eastern Russia) and spend the non-breeding season in Australia and New Zealand, whereas Eurasian Curlew mainly breed in central and eastern Russia (Gerasimov et al., 1997; Zheng, 2017), and wintering in southern China and other countries in South Asia (BirdLife International, 2020). The global population of both species has declined in the last two decades (Pearce-higgins et al., 2017); however, the Far Eastern Curlew population has declined more rapidly, and the species is now considered globally threatened and listed as Endangered by the IUCN Red List (BirdLife International, 2020). Quantifying the degree of dietary specialization and plasticity in foraging behavior between these two closely related species in relation to different stopover habitats and levels of human disturbance, could shed light on how these two species partition niche space during migration and may indicate possible factors driving the rapid population decline of Far Eastern Curlew.

Here, we use data obtained from digital video-recordings to quantify the foraging behavior of these two sympatric curlew species to assess differences in diet and feeding rates in adjacent *Suaeda salsa* saltmarsh and inter-tidal mudflat stopover habitats at the Liaohekou National Nature Reserve, northeastern China, during their spring and autumn migration stopover periods. We use these data to examine the hypothesis that these two species exhibit divergent feeding rates in adjacent *S. salsa* saltmarsh and inter-tidal mudflat, and to assess the influence of human disturbance (associated to aquaculture practices and oil production) and seasonality on congeneric foraging behavior. Since previous research has shown that curlew bill length is correlated to prey specialization (e.g. Dann, 2005), we predict that the longer-billed Far Eastern Curlew should be more specialized on deep burrowing prey (i.e. crabs) than its congener. Since the Far Eastern Curlew may have higher energy demands to fuel their longer-distance migration and be more time-constrained in their use of stopover sites, we also hypothesized that this species would exhibit less foraging behavior plasticity than the shorter-billed Eurasian Curlew.

2. Materials and methods

2.1. Study site

The study was conducted in the Liaohekou National Nature Reserve (121°50.5′E, 40°33.5′N), situated on the north of the Yellow Sea, in Liaoning Province, China, during 2017–2019. This reserve represents some of the last remnant areas of inter-tidal mudflat and *Suaeda salsa* dominated saltmarsh habitat on both sides of the river mouth, which serve as critical stopover habitats for migratory shorebirds along the East Asian-Australasian Flyway (Bai et al., 2015). Almost all coastal wetland habitat outside the reserve has been reclaimed for aquaculture production or other anthropogenic land uses. About 700-1000 Far Eastern Curlews (corresponding to approximately 2.2–3.1% of the global population) and 1250–1500 Eurasian Curlews (corresponding to approximately 1.25–1.5% of the global flyway population) stopover at the reserve for nearly 2–3 months in total during their northward and southward migrations (Bai et al., 2015) where they typically forage amongst flocks of other shorebirds or as solitary individuals. Previous studies and our own unpublished observations confirm that *S. salsa* saltmarshes and inter-tidal mudflats are regularly utilized by both species during stopover periods (Huang, 2019; Piersma, 1985).

We selected two adjacent areas of saltmarsh (Fig. 1A) and intertidal mudflats (Fig. 1B) for the study. The saltmarsh is dominated by *S. salsa* grass averaging 15–30 cm in height, and situated in the supra-tidal zone, with the adjacent intertidal mudflat area largely devoid of any coastal wetland vegetation. There were eight oil wells (Fig. 1B) within the study site, which were connected by two 3-m wide unpaved roads (Fig. 1B). Tidal regimes in this region are typically a mixture of irregular semi-diurnal tide with amplitude of 1.4–4.4 m (Zhang et al., 2016), with the saltmarsh habitat inundated with tides >3.46 m in height and tidal mudflats inundated with flood tides > 2.5 m.

2.2. Density of crabs and ragworm burrows

We sampled the density of burrows of two main curlew prey types - crabs and ragworms - in May and September 2019, since studies have shown that burrow density is a reliable indicator of crab and ragworm availability (e.g. Zharikov and Skilleter, 2004). The crab community was dominated by two species - *Helice tientsinensis* and *Macrophthalmus japonicas*, whilst *Nereis multignatha* was the dominant ragworm species (Zhang et al., 2016). In May, 16 sampling points were established in both the saltmarsh and mudflat habitats with an additional ten sampling points established in the saltmarsh and seven sampling points in mudflats, in September. For each sample point, we positioned three 0.5 m × 0.5 m quadrats randomly distributed within a 10 m radius of the sample point. The number of crab and ragworm burrows were counted and averaged to represent the density per sample point (per/0.25 m^2).

2.3. Curlew foraging observations and human disturbance assessment

We used digital video-recordings to quantify the foraging behavior of both curlew species at either saltmarsh (Fig. 1C) or intertidal mudflat (Fig. 1D) during the northward (March–May) and southward (August–October) migration period. Data recording was conducted only on days of suitable weather, i.e. with no heavy rain, snow or strong wind. All recordings were made from semi-concealed vantage points on human-made structures such as drilling platforms or dykes, to reduce the risk of the observers influencing curlew foraging behavior. Each vantage point was separated by distances of 50–250 m. On arrival at each point we waited for several minutes to reduce any potential disturbance of the birds caused by observers moving between points. Following this, we randomly selected one foraging individual of either species and began recording its behavior using a NIKON P900S digital camera for 10 min or until the focal individual moved away from the observer’s view. During each focal period, we recorded the following variables: time of day, foraging habitat, absolute time to low tide, total number of individual curlews, number of other bird species within 10 m of the focal individual, the presence/absence of water within 5 m radius of the focal individual, and presence/absence of human disturbance within 50 m of the focal individual. Human disturbance included either clam-harvesting activities by fishmen, tourism or oil field production operations (e.g. road traffic; Li et al., 2017). At the end of each recording period, we moved onto the next vantage point and repeated the survey

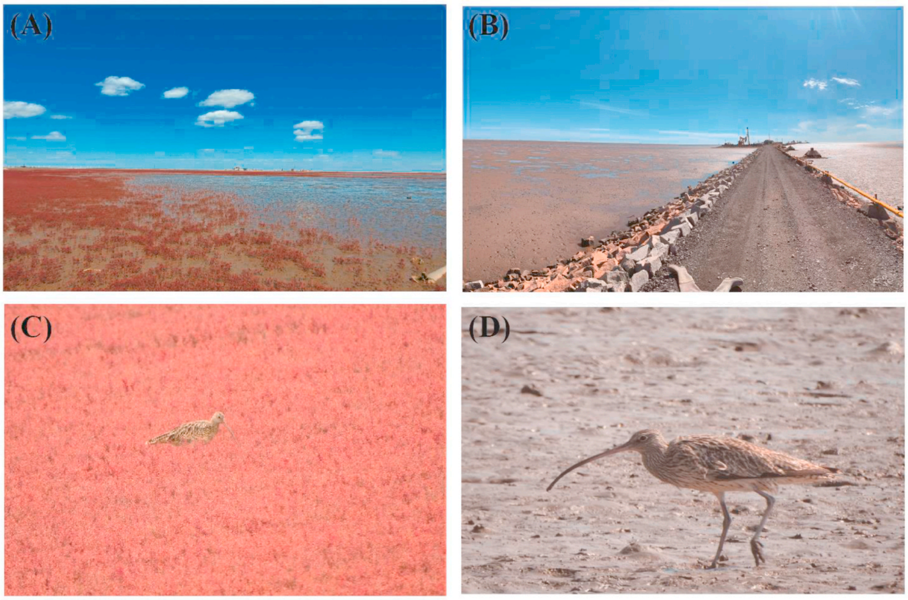

Fig. 1. Showing typical *S. salsa* saltmarsh (A) and intertidal mudflat habitats (B) of the study site and Far Eastern Curlews foraging in both habitats (C and D).

protocol. Although individual curlews were not color-marked, we concluded that these distances and time periods represented the best compromise between recording adequate sample sizes whilst minimizing the risk of pseudo-replication.

2.4. *Digital video analysis*

Feeding data were transcribed from video recordings by watching each video at half- normal speed using Baofeng player (v.5.0). We only considered video samples that were >5 min duration. From each of these recordings, we noted the number and type of each prey consumed by both curlew species. We categorized prey type as crabs, ragworms or ‘other unidentified preys’ because they were difficult to distinguish between different species of crabs or ragworms whilst some prey items were too small to enable accurate identification. We used the percentages of each prey type consumed to represent the diet composition of each curlew species and used the numbers of crabs and ragworms consumed per time unit as the ‘feeding rate’ since it was not possible to measure prey size from the video recordings.

2.5. *Statistical analyses*

All statistical analyses were conducted using R 3.6.0 (CRAN, http://cran.r-project.org). Independent sample t-tests were used to compare the density of crab and ragworm burrows between habitat types (saltmarsh vs. and mudflats) and migration seasons (spring vs. autumn). We used Chi-square tests to compare differences in the percentage of crabs and ragworms foraged by both curlew species between different habitat types and migration seasons.

We used zero-inflated negative binomial (ZNB) mixed models with the *glmmTMB* package (version 0.2.3; Magnusson et al., 2019) to examine the influence of habitat type, human disturbance and migration season on the number of crabs and ragworms fed by both curlew species in each observational bout. These two-component mixed models perform well with count data containing excess zeros and overdispersion of non-zero values (Brooks et al., 2017). The first component is the conditional negative binomial model that examines the influence of factors on the response variable, whilst the second binary component, termed the zero-inflated model, describes the probability of observing an extra zero (i.e., structural zero) that is not generated by the conditional model (Brooks et al., 2017; Lambert, 1992). Prior to ZNB model construction, all continuous predicting variables were z-score transformed, with the number of other bird species log-transformed prior to z-score transformation to achieve better model fit. Variance inflation factor (VIF) and Pearson’s correlation coefficients revealed no collinearity between all variables included in the models (VIF = <1.62 (Zuur et al., 2010); Pearson’s correlation coefficients $r^2 < 0.45$).

For the crab dataset, we fitted ZNB mixed models using the count of crabs foraged by both curlew species at each recording as the response variable, with curlew species (Far Eastern Curlew vs. Eurasian Curlew), habitat type (saltmarsh vs. mudflat), migration season (spring vs. autumn), human disturbance (yes vs. no), water cover (yes vs. no), time of day (morning: 8–11 a.m.; noon: 11–14 p.m.; afternoon: 14–17 p.m.), observation distance, flock size of curlews, number of other bird species within 10 m radius of focal individual, and tidal time (the absolute time to the low tidal of each observation) included as explanatory variables. Year was included as a random effect, and observation time for each sample was used as the offset. Due to a relatively low percentage of zeros (31.9%) for the response value in the crab dataset, we used the *nbinom1* (link = “log”) as the family function (overdispersion parameter for the most parsimonious model = 0.473). Results were the same whether the zero-inflated component was included (Table S1) or not or under model averaging operation when computing AICc for the two alternative models (ΔAICc<2; Symonds and Moussalli, 2011) (Table S2, S3).

Only 2.9% (n = 173) of ragworm count data for Far Eastern Curlews were non-zero values. Consequently, we were only able to use a ZNB mixed model for the Eurasian Curlew ragworm dataset to examine the influence of habitat type, human disturbance and migration season on ragworm feeding rates for this species. All fixed and random factors were the same as for the previous crab dataset model, with the exception of “curlew species”. Due to a greater proportion of zero counts (>50%) in the ragworm data, we used the *nbinom2* (link = “log”) as the family function (overdispersion parameter for the best model = 1.55). The model was fitted with both conditional and zero inflated components with a single zero-inflation parameter applied to all observations (ziformula~1).

For model selection of the above crab and ragworm datasets, we first developed the null model (including only the intercept) followed by alternative candidate models using only one explanatory variable from the conditional model component. Only explanatory variables with $P < 0.5$ were retained for inclusion in subsequent models, and all possible combinations for selected fixed factors and their two-way interaction terms were fitted in the conditional model as model sets. During model building, we used Akaike's Information Criteria corrected for small sample sizes (AICc, Burnham & Anderson, 2002) to select between all competing models. Goodness-of fit was examined by checking residual plots generated using a simulation-based approach with the package *DHARMa* (Hartig, 2019) in R. We tested for significance of fixed terms using Wald chi-square tests, with statistical significate P value set as <0.05. The significances of parameters were also illustrated using profiled confidence intervals. Values are presented as mean ± SE except where indicated.

3. Results

3.1. Differences in density of crab and ragworm burrows

There was a significantly higher density of crab burrows in the *S. salsa* saltmarsh habitat compared to the adjacent mudflat in autumn ($t = 3.56$, $df = 15$, $P = 0.003$) but not in spring (Fig. 2A). The density of crab burrows in saltmarsh was also significantly higher in autumn than spring, but not in mudflat habitat (Fig. 2A). There was a higher density of ragworm burrows in spring than in autumn in both habitats (saltmarsh: $t = 6.204$, $df = 23$, $P < 0.001$; mudflat: $t = 18.820$, $df = 21$, $P < 0.001$) but there were no significant habitat differences in both seasons ($Ps \geq 0.075$; Fig. 2B).

3.2. Differences in diet of curlew species

In total, we collected 298 video recordings (mean duration ± SD: 9.72 ± 1.02 min) representing 173 and 125 recordings of Far Eastern and Eurasian Curlew respectively. Crab species were accounted for 80.6% of the total Far Eastern Curlew consumed prey and there were no significant differences in the frequency of crab prey consumed by this species between the different habitat types (Chi-square test: $\chi^2 = 1{,}299$, $df = 1$, $P = 0.254$) and seasons ($\chi^2 = 0.265$, $df = 1$, $P = 0.607$). Feeding on crabs by Eurasian Curlew showed significant differences between migration seasons and habitat types ($Ps < 0.001$ for all variables) with crabs constituting 76.7% of all prey foraged from mudflat habitat during the spring, compared with less than 5% of prey in saltmarsh habitat during the same season (Table S4). Eurasian Curlew foraged more on ragworm prey (74.4% of total number of prey items) in *S. salsa* saltmarsh, whereas ragworms represented a much smaller percentage of prey in mudflat habitat (10%) and during the autumn migration (<15%). Overall, Eurasian Curlew foraged more on ragworms (44%) than the Far Eastern Curlew (1.8%) (Table S4).

3.3. - Factors influencing feeding rate on crabs by two curlew species

The most parsimonious model showed that there were significantly higher feeding rates on crabs by Far Eastern Curlews than Eurasian Curlews and significantly higher feeding rates on crabs in mudflat habitat than in *S. salsa* saltmarsh (Table 1). Additionally, there were significant interactions between curlew species and habitat type (Wald Chi square test: $\chi^2 = 13.960$, $df = 2$, $P < 0.001$) and between curlew species and presence/absence of human disturbance ($\chi^2 = 6.616$, $df = 2$, $P = 0.037$) with a near significant interaction between curlew species and migration season ($\chi^2 = 5.364$, $df = 2$, $P = 0.068$). Feeding rate on crabs by Far Eastern Curlew did not differ between the two habitats, but there was a significantly lower feeding rate on crabs for Eurasian Curlew in the saltmarsh compared to the mudflat. Moreover, crab feeding rates in both habitats were significantly lower for Eurasian Curlew than for Far Eastern Curlew (Table 1; Fig. 3A). There were significant differences

Table 1
Estimated regression parameters, standard errors, profile confidence intervals (2.5% PCL and 97.5% PCL), z-values and P values for the most parsimonious ZNB generalized linear model used in this study, modelling the effects of habitat, season and human disturbance on the feeding rate on tidal crabs by two curlew species. A positive estimate (β) in the conditional model represents a higher feeding rate. The referenced categories for the fixed factors of curlew species, habitat type, migration season and human disturbance were "Eurasian Curlew", "mudflat", "autumn" and "no", respectively. Far Eastern Curlew and Eurasian Curlew were abbreviated as FEC and EC respectively. Bold text represents significance at 0.05 level.

Conditional model:	Estimate (β)	Std. Error	2.5% PCL	97.5% PCL	z value	*P*
(Intercept)	−1.93	0.24	−2.40	−1.46	−8.05	**<0.001**
habitat (saltmarsh)	−1.30	0.27	−1.82	−0.78	−4.88	**<0.001**
species (FEC)	0.46	0.21	0.04	0.88	2.16	**0.03**
Tidal	0.20	0.06	0.09	0.31	3.62	**<0.001**
species (FEC): habitat (saltmarsh)	1.10	0.29	0.52	1.67	3.74	**<0.001**
species (EC): disturbance (yes)	−0.04	0.28	−0.59	0.50	−0.15	0.88
species (FEC): disturbance (yes)	−0.41	0.16	−0.73	−0.10	−2.57	**0.01**
species (EC): season (spring)	0.19	0.24	−0.28	0.65	0.79	0.43
species (FEC): season (spring)	0.36	0.15	0.05	0.66	2.30	**0.02**

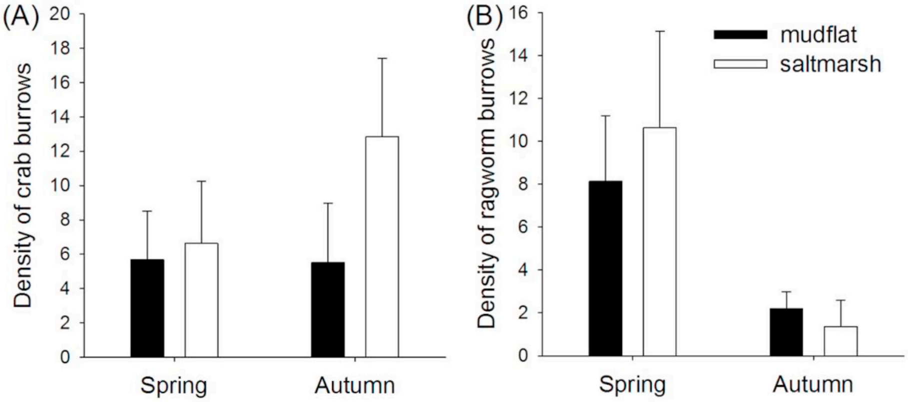

Fig. 2. Difference in the density (number of burrows/0.25 m^2) of crab (A) and ragworm (B) burrows between habitats and migration seasons. Data showed are mean ± SD.

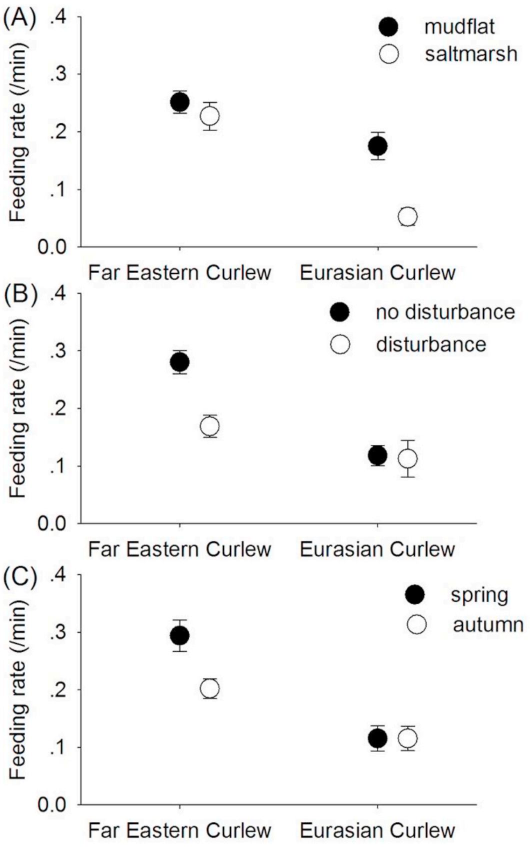

Fig. 3. Difference in the feeding rate on crabs (mean ± SE) by Far Eastern Curlew and Eurasian Curlew in different habitat types (A), in the presence/absence of human disturbance (B), and during both migration seasons (C), in Liaohekou National Nature Reserve, China during 2017–2019.

in the feeding rate responses to human disturbance between both curlew species. Human disturbance had a significant negative effect on the Far Eastern Curlew feeding but no evident effect for the Eurasian Curlew (Table 1; Fig. 3B). Far Eastern Curlews also had significantly higher crab feeding rate in the spring compared to autumn while there was no seasonal difference for Eurasian Curlews (Table 1; Fig. 3C). Feeding rates on crabs also significantly increased with the tidal time (the absolute time to the low tidal of each observation) (Table 1). No other factors, including flock size of curlews, exhibited any significant influence on feeding rates for either species.

3.4. - Factors influencing Eurasian Curlew feeding rate on ragworms

As for the feeding rate on ragworms, the most parsimonious model showed that there were no significant effects of habitat, season (Table 2) and human disturbance (z = 0.467, P = 0.670) in the case of Eurasian Curlews. However, there were seasonal differences between the two habitats; ragworm feeding rates in *S. salsa* saltmarsh habitat were significantly higher in spring than in autumn (z = 7.194, $P < 0.001$), while this effect was not apparent in mudflat habitat (z = 1.191, $P =$ 0.634; Fig. 4A). No significant habitat-related effects of the presence of human disturbance on the feeding rate on ragworms were found (Fig. 4B; Table 2). In addition, the most parsimonious model also indicated that the feeding rate was positively related to flock size of other bird species and negatively related to observation distance (Table 2).

4. Discussion

This work represents the first comparative study on the foraging ecology of Far Eastern Curlew and Eurasian Curlew populations at an important migration stopover site in the Yellow Sea, China. We found that Far Eastern Curlews were more dependent on tidal crabs as food resources (80%), more likely to feed on crabs during their spring migration stopover season (Fig. 3C) and, overall, exhibited less dietary flexibility in relation to foraging habitat type and migratory season (Table S4), than its closely-related congener the Eurasian Curlew. We found no differences in crab feeding rates for Far Eastern Curlews between mudflat and saltmarsh habitats, yet crab feeding rates were negatively influenced by human disturbance (Fig. 3). In contrast, Eurasian Curlews were less likely to feed on crabs in *S. salsa* saltmarsh habitat, feed more on ragworms (44%), exhibited no significant seasonal differences in crab feeding rates, and crab feeding rates were less influenced by human disturbance. Eurasian Curlews, however, did exhibit higher ragworm feeding rates during the spring migration stopover season and in saltmarsh habitat.

The differences in prey types and feeding rates between adjacent habitats and successive migration stopover seasons could explain how these two closely related curlew species fit syntopically along the coastal wetland resource gradient. Several studies have found that crabs are the main prey types of curlew species (e.g. Barker and Vestjens, 1989; Tulp and de Goeij, 1994). Populations of Eurasian Curlews in the East Atlantic Flyway have quite a generalist diet (e.g. Navedo and Masero, 2008), although the common littoral crab *Carcinus maenas* is the most common prey type in intertidal mudflats (e.g. Navedo and Masero, 2007). A recent paper found that wintering Eurasian Curlews in northern Spain switched to preferentially feed on earthworms (Oligochaeta) in coastal pastures (Navedo et al., 2020). Far Eastern Curlew populations wintering in Australia and New Zealand exhibit a high degree of dietary specialization, feeding almost exclusively on soldier crab *Mictyris longicarpus*, sentinel crab *Macrophthalmus crassipes* and ghost-shrimp *Trypaea australiensis* (e.g. Zharikov and Skilleter, 2004, 2003), and populations that stopover in South Korea are known to prefer *Macrophthalmus* and other *Ocypodid* crabs (e.g. Piersma, 1985). Furthermore, Dann (2014) found significant changes in the proportion of different

Table 2
Estimated regression parameters, standard errors, profile confidence intervals (2.5% PCL and 97.5% PCL), z-values and *P* values for the most parsimonious ZNB mixed model assessing the influence of habitat type, migration season and presence/absence of human disturbance on ragworm feeding rates by Eurasian Curlew. The referenced categories for each fixed factor were same to Table 1. Bold text represents significance at 0.05 level.

Conditional model:	Estimate (β)	Std. Error	2.5% PCL	97.5% PCL	z value	*P*
(Intercept)	−4.23	0.54	−5.29	−3.16	−7.77	**<0.001**
habitat (saltmarsh)	−1.29	1.16	−3.56	0.98	−1.11	0.27
season (spring)	0.55	0.60	−0.62	1.72	0.92	0.36
other bird species	0.57	0.19	0.19	0.95	2.96	**<0.001**
Distance	−0.39	0.15	−0.68	−0.09	−2.59	**0.01**
habitat (saltmarsh): season (spring)	4.85	1.17	2.56	7.13	4.15	**<0.001**
habitat (mudflat): disturbance (yes)	0.28	0.66	−1.01	1.57	0.43	0.67
habitat (saltmarsh): disturbance (yes)	0.22	0.48	−0.73	1.16	0.45	0.65
Zero-inflated model:						
(Intercept)	−19.71	7488.42	−14696.74	14657.32	0.00	1.00

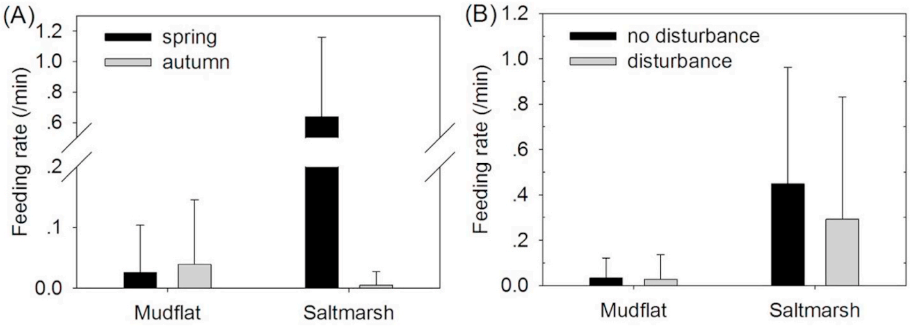

Fig. 4. Differences in feeding rates (mean ± SD) on ragworms by Eurasian Curlew in the two habitat types during different migration seasons (A) and in the presence/absence of human disturbance (B) in Liaohekou National Nature Reserve, China during 2017–2019.

crab species in Far Eastern Curlew diet during two non-breeding periods. Although crab prey quality, represented as the total energy content per gross weight (g) of crabs, is lower than that of ragworms, the energy intake per prey item is believed to be much higher (Casto et al., 2008; Li et al., 2014; Zwarts and Esselink, 1989). Thus, crab specialization by Far Eastern Curlews at our study site could be, in part, related to the longer migration distance of Far Eastern Curlews and the need to maximize their intake rate by pursuing short-term energy payoffs during limited windows of opportunity.

We found no significant habitat-specific differences in feeding rates on crabs by Far Eastern Curlew between *S. salsa* saltmarsh and adjacent mudflats (Fig. 3A). Previous research has shown that foraging habitat selection by wintering populations was positively correlated with prey density and was negatively influenced by a measure of substrate resistance (Finn et al., 2007), and that prey choice can be determined by both the profitability of prey items and the frequency with which they can be captured (Zharikov and Skilleter, 2004). Other studies have suggested associations between the relative bill lengths of *Numenius* curlew species (including sexual dimorphism) and selection of foraging habitat during the non-breeding season (e.g. Barter, 1990; Cramp and Simmonds, 1983). Consequently, the longer bill of the Far Eastern Curlew may be a factor in it preferencing soft sediment burrowing prey where it can probe to greater depths (Dann, 2005; Finn et al., 2007; Finn, 2010). Whether crab abundance across different habitat types at Liaohekou National Nature Reserve is influenced by factors such as sediment organic matter merits further investigation.

Human disturbance had a significant influence on crab feeding rates by Far Eastern Curlews (Fig. 3B; Table 1) but not for Eurasian Curlews, suggesting that the former may be more susceptible to human disturbance than its congener. This susceptibility to human disturbance by Far Eastern Curlews has also been suggested for the wintering populations on the Moreton Bay, south-eastern Queensland, where the choice of foraging sites was positively correlated with the width of the tidal flat (Congdon and Catterall, 1994). Thus, a greater susceptibility to human disturbance during stopover periods possibly contributes to the species' decline. Further conservation actions for this endangered species should therefore focus on efforts to reduce various forms of human activities in proximity to their main feeding grounds during the migratory stopover stage. However, human disturbance in the form of traditional shellfish harvesting does not affect the abundance and distribution of Eurasian Curlews foraging in intertidal mudflats along the East Atlantic Flyway (e.g. Navedo and Masero, 2007). We acknowledge that our purely observational dataset might have some limitations on the overall interpretation of the human disturbance effects because some birds may be flushed by the disturbance event before we were able to record the foraging behavior. The use of foraging observations is one of the most commonly used protocols to examine the effect of human activity on wildlife behavior (e.g. Yasué, 2005; Navedo and Masero, 2008; Li et al., 2017) and ideally, further field experiments examining the flight initiation distance (FID) of two curlew species could help to fully understand their susceptibility to human disturbance.

Furthermore, relatively high feeding rates on ragworms by Eurasian Curlews reported in this study during the spring migration stopover may have been influenced by recent conservation efforts to restock ragworm populations in the *S. salsa* saltmarsh habitat (efforts intended to benefit Saunders's Gull *Chroicocephalus saundersi* nestling-feeding during the breeding season, Li Yuxiang pers. Com.). Further research is needed to determine whether differences in feeding rates, use of habitat types and the degree of dietary specialization are typical for other populations of both species.

Unlike other shorebird species that typically forage in large monotypic or mixed species flocks, we found that both curlew species foraged in small loosely associated flocks or just as solitary individuals (Ens et al., 1990; Navedo and Masero, 2007; Zharikov and Skilleter, 2004), which could explain why curlew flock size had no significant influence on feeding rates. Also, we did not find any significant effect of time of day on feeding rates. However, we only recorded the foraging behavior in daylight hours, thus a limitation of the study was not knowing what birds did during the night (Enners et al., 2020). Yet, feeding rates on crabs were significantly influenced by tidal cycles, with increased feeding rates in longer low tide periods. Prolonged high tides are known to have a significant negative effect on the abundance of foraging Eurasian Curlews (e.g. Navedo and Masero, 2007) and other shorebird species (e.g. Fonseca et al., 2017). The positive relationship between feeding rate on ragworms by Eurasian Curlews and the number of individuals of other shorebird species may be a result of the fact that the Eurasian Curlews were more likely to feed in mixed species flocks in spatially aggregated prey-rich foraging sites (Navedo and Masero, 2007).

Here, we have shown the value of comparative ecological and behavioral studies of phylogenetically-closely related species to identify the factors that enable congeners at different ends of the threatened species conservation spectrum to fit syntopically along a resource gradient. The differential resource use, habitat use and feeding rates between these two congeners raises some interesting possibilities for conservation management, and along with data on the densities of both curlew species and their prey, provide interesting clues as to the rapidity of the Far Eastern Curlew's population decline that merit further investigation at other stop over sites along the East Asia-Australasian Flyway.

Author contributions

D.L. and Z.Z. conceived the idea and designed the study, D.L. and J.Z. conducted fieldwork and digital video analysis, D.L. and Y.L. performed statistical analyses and draft writing, H.L., E.P. and Z.Z. provided further assistance on statistical analyses and language improvement. All authors approved the final version of the article.

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.

Acknowledgements

This work was supported by National Natural Science Foundation of China (Nos 31672316 and 31911540468 to D.L.; 31572288 to Z.Z.) and Natural Science Foundation of Liaoning Province, China (2019-MS-154 to D.L). This study was permitted by the Liaohekou Nature Reserve Management Bureau (issued by Yuxiang Li), and the experiments complied with the current laws of China, where the study was performed. We would like to thank Ziqiang Huang, Yu Bai, Hang Zhang, Yanyan Liu for their assistance with data collection in the field. We also thank Richard Fuller, University of Queensland, and one anonymous reviewer for their constructive comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2020.106990.

References

Stillman, R.A., Goss-Custard, J.D., 2002. Seasonal changes in the response of oystercatchers Haematopus ostralegus to human disturbance. J. Avian Biol. 33, 358–365. https://doi.org/10.1034/j.1600-048X.2002.02925.x.

Atkinson, P.W., Baker, A.J., Bennett, K.A., Clark, N.A., Clark, J.A., Cole, K.B., Dekinga, A., Dey, A., Gillings, S., González, P.M., Kalasz, K., Minton, C.D.T., Newton, J., Niles, L.J., Piersma, T., Robinson, R.A., Sitters, H.P., 2007. Rates of mass gain and energy deposition in red knot on their final spring staging site is both time- and condition-dependent. J. Appl. Ecol. 44, 885–895. https://doi.org/10.1111/j.1365-2664.2007.01308.x.

Bai, Q., Chen, J., Chen, Z., Dong, G., Dong, J., Dong, W., Fu, V.W.K., Han, Y., Lu, G., Li, J., Liu, Y., Lin, Z., Meng, D., Martinez, J., Ni, G., Shan, K., Sun, R., Tian, S., Wang, F., Xu, Z., Yu, Y. tung, Yang, J., Yang, Z., Zhang, L., Zhang, M., Zeng, X., 2015. Identification of coastal wetlands of international importance for waterbirds: a review of China Coastal Waterbird Surveys 2005-2013. Avian Res 6, 12. https://doi.org/10.1186/s40657-015-0021-2.

Barker, R.D., Vestjens, W.J.M., 1989. The Food of Australian Birds, 1. Non-passerines. CSIRO Division of Wildlife and Ecology, Canberra.

Barter, M., 1990. Morphometrics of the eastern curlew *Numenius madagascariensis*. Stilt 16, 36–42.

BirdLife International, 2020. IUCN Red List for Birds. Downloaded from. https://www.birdlife.org.on.07/03/2020.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. Rom. Jahrb. 9, 378–400. https://doi.org/10.32614/rj-2017-066.

Burger, J., Gochfeld, M., 1991. Human activity influence and diurnal and Nocturnal foraging of sanderlings (*Calidris alba*). Condor 93, 259–265. https://doi.org/10.2307/1368941.

Burger, J., Niles, L., Clark, K.E., 1997. Importance of beach, mudflat and marsh habitats to migrant shorebirds on Delaware Bay. Biol. Conserv. 79, 283–292.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretical Approach, second ed. Springer, New York.

Casto, M., Masero, J.A., Megina, C., Amat, J.A., Perez-hurtado, A., 2008. Energy macronutrient assimilation efficiencies of snowy plover(*Charadrius alesandrinus*) feeding on the ploychaete ragworm nereis diversicolor. Auk 125, 368–373. https://doi.org/10.1525/auk.2008.060144.

Choi, C.Y., Battley, P.F., Potter, M.A., Ma, Z., Melville, D.S., Sukkaewmanee, P., 2017. How migratory shorebirds selectively exploit prey at a staging site dominated by a single prey species. Auk 134, 76–91. https://doi.org/10.1642/AUK-16-58.1.

Congdon, B.C., Catterall, C.P., 1994. Factors influencing the eastern curlew's distribution and choise of foraging sites among tidal flats of Moreton Bay, South eastern Queensland. Wildl. Res. 21, 507–518. https://doi.org/10.1071/WR9940507.

Cramp, S., Simmons, K.E.L., 1983. The Birds of the Western Palearctic, vol. 3. Clarendon Press, Oxford.

Dann, P., 2005. Is bill length in curlews Numenius associated with foraging habitats and diet in non-breeding grounds. Wader Study Group Bull. 106, 60–61.

Driscoll, P.V., Ueta, M., 2003. The migration route and behaviour of Eastern Curlews *Numenius madagascariensis*. Ibis 144, E119–E130. https://doi.org/10.1046/j.1474-919x.2002.00081.x.

Duijns, S., Piersma, T., 2014. Interference competition in a sexually dimorphic shorebird: prey behaviour explains intraspecific competition. Anim. Behav. 92, 195–201. https://doi.org/10.1016/j.anbehav.2014.04.007.

Enners, L., Chagas, A.L.J., Ismar-Rebitz, S.M.H., Schwemmer, P., Garthe, S., 2019. Foraging patterns and diet composition of breeding Pied avocets (*Recurvirostra avosetta*) in the German Wadden Sea. Estuar. Coast Shelf Sci. 229, 106399 https://doi.org/10.1016/j.ecss.2019.106399.

Enners, L., Guse, N., Schwemmer, P., Chagas, A.L.J., Christian, C., Voigt, C.C., Garthe, S., 2020. Foraging ecology and diet of Eurasian spoonbills (Platalea leucorodia) in the German Wadden Sea. Estuar. Coast Shelf Sci. 233, 106539 https://doi.org/10.1016/j.ecss.2019.106539.

Ens, B.J., Esselink, P., Zwarts, L., 1990. Kleptoparasitism as a problem of prey choice: a study on mudflat-feeding curlews, *Numenius arquata*. Anim. Behav. 39, 219–230. https://doi.org/10.1016/S0003-3472(05)80866-8.

Fernández, G., Lank, D.B., 2008. Foraging behaviour of non-breeding Western Sandpipers *Calidris mauri* as a function of sex, habitat and flocking. Ibis 150, 518–526. https://doi.org/10.1111/j.1474-919X.2008.00812.x.

Finn, P.G., 2010. Habitat Selection, Foraging Ecology and Conservation of Eastern Curlews on Their Non-breeding Grounds. Griffith University (PhD Thesis).

Finn, P.G., Catterall, C.P., Driscoll, P.V., 2007. Determinants of preferred intertidal feeding habitat for Eastern Curlew: a study at two spatial scales. Austral Ecol. 32, 131–144. https://doi.org/10.1111/j.1442-9993.2006.01658.x.

Fitzpatrick, S., 1998. Effects of recreational disturbance on the foraging behaviour of waders on a rocky beach. Hous. Theor. Soc. 45, 157–171. https://doi.org/10.1080/00063659809461088.

Fonseca, J., Basso, E., Serrano, D., Navedo, J.G., 2017. Effects of tidal cycles on shorebird distribution and foraging behaviour in a coastal tropical wetland: insights for carrying capacity assessment. Estuar. Coast Shelf Sci. 198, 279–287. https://doi.org/10.1016/j.ecss.2017.09.016.

Gallo-Cajiao, E., Morrison, T.H., Fidelman, P., Kark, S., Fuller, R.A., 2019. Global environmental governance for conserving migratory shorebirds in the Asia-Pacific. Reg. Environ. Change 19, 1113–1129. https://doi.org/10.1007/s10113-019-01461-3.

Gerasimov, Y.N., Artukhin, Y.B., Gerasimov, N.N., 1997. The eastern curlew *Numenius madagascariensis* in Kamchatka, Russia. Stilt 30, 14–15.

Hartig, F., 2019. DHARMa: Residual Diagnostics for Hierarchical (Multi-level/mixed) Regression Models. R package, version 0.2.4. http://florianhartig.github.io/DHARMa/.

Horn, S., Schwemmer, P., Mercker, M., Enners, L., Asmus, R., Garthe, S., Asmus, H., 2020. Species composition of foraging birds in association with benthic fauna in four intertidal habitats of the Wadden Sea. Estuar. Coast Shelf Sci. 233, 106537 https://doi.org/10.1016/j.ecss.2019.106537.

Huang, Z., 2019. The Habitat Use of Migrant Shorebirds in *Suaeda Salsa* Salt Marshes and the Ntertidal Flats in Liaohe River Delta. Liaoning University (Master dissertation).

Jing, K., Ma, Z., Li, B., Li, J., Chen, J., 2007. Foraging strategies involved in habitat use of shorebirds at the intertidal area of Chongming Dongtan, China. Ecol. Res. 22, 559–570. https://doi.org/10.1007/s11284-006-0302-7.

Lambert, D., 1992. Zero-inflated Poisson regression, with an application to defects in manufacturing. Technometrics 34, 1–14. https://doi.org/10.1080/00401706.1992.10485228.

Li, D., Ding, Y., Yuan, Y., Lloyd, H., Zhang, Z., 2014. Female tidal mudflat crabs represent a critical food resource for migratory Red-crowned Cranes in the Yellow River Delta, China. Bird. Conserv. Int. 24, 416–428. https://doi.org/10.1017/S0959270913000555.

Li, D., Liu, Y., Sun, X., Lloyd, H., Zhu, S., Zhang, S., Wan, D., Zhang, Z., 2017. Habitat-dependent changes in vigilance behaviour of Red-crowned Crane influenced by wildlife tourism. Sci. Rep. 7, 1–11. https://doi.org/10.1038/s41598-017-16907-z.

Martins, R.C., Catry, T., Santos, C.D., Palmeirim, J.M., Granadeiro, J.P., 2013. Seasonal variations in the diet and foraging behaviour of dunlins *Calidris alpina* in a south European estuary: improved feeding conditions for northward migrants. PloS One 8 (12), e81174. https://doi.org/10.1371/journal.pone.0081174.

Mathot, K.J., Smith, B.D., Elner, R.W., 2007. Latitudinal clines in food distribution correlate with differential migration in the western sandpiper. Ecology 88, 781–791. https://doi.org/10.1890/06-1225.

Melville, D.S., Chen, Y., Ma, Z., 2016. Shorebirds along the Yellow Sea coast of China face an uncertain future - a review of threats. Emu 116, 100–110. https://doi.org/10.1071/MU15045.

Navedo, J.G., Masero, J.A., 2007. Measuring potential negative effects of traditional harvesting practices on waterbirds: a case study with migrating curlews. Anim. Conserv. 10, 88–94. https://doi.org/10.1111/j.1469-1795.2006.00076.x.

Navedo, J.G., Masero, J.A., 2008. Effects of traditional clam harvesting on the foraging ecology of migrating curlews (*Numenius arquata*). J. Exp. Mar. Biol. Ecol. 355, 59–65. https://doi.org/10.1016/j.jembe.2007.11.016.

Navedo, J.G., Gutiérrez, J.S., Salmón, P., Arranz, D., Novo, M., Díaz-Cosín, D.J., Herrera, A.G., Masero, J.A., 2020. Food supply, prey selection and estimated consumption of wintering Eurasian Curlews feeding on earthworms at coastal pastures. Ardea 107, 263–274. https://doi.org/10.5253/arde.v107i3.a10.

Pearce-higgins, J.W., Brown, D.J., Douglas, D.J.T., Alves, J.A., Bocher, P., Buchanan, G. M., Clay, R.O.B.P., Conklin, J., Dann, P., Elts, J., Friis, C., Fuller, R.A., Gill, J.A., Gosbell, K.E.N., Johnson, J.A., Marquez-ferrando, R., Masero, J.A., David, S., Millington, S., Minton, C., Mundkur, T., Nol, E., Pehlak, H., 2017. A global threats overview for Numeniini populations: synthesising expert knowledge for a group of 2 declining migratory birds. Bird. Conserv. Int. 27, 6–34. https://doi.org/10.1017/S0959270916000678.

Piersma, T., 1985. Eastern curlews *Numenius madagascariensis* feeding on Macrophthalrnus and other ocypodid crabs in the Nakdong estuary, South Korea. Emu 86, 155–160. https://doi.org/10.1071/MU9860155.

Piersma, T., 1987. Hop, skip or jump? Contraints on migration of arctic waders by feeding, fattening and flight speed. Limosa 60, 185–194.

Piersma, T., 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. J. Ornithol. 148 (Suppl. 1), S45–S59. https://doi.org/10.1007/s10336-007-0240-3.

Piersma, T., Verkuil, Y., Tulp, I., 1994. Resources for long-distance migration of knots *Calidris canutus islandica* and *C. c. canutus*: how broad is the temporal exploitation window of benthic prey in the Western and Eastern Wadden Sea? Oikos 71, 393–407. https://doi.org/10.2307/3545827.

Studds, C.E., Kendall, B.E., Murray, N.J., Wilson, H.B., Rogers, D.I., Clemens, R.S., Gosbell, K., Hassell, C.J., Jessop, R., Melville, D.S., Milton, D.A., Minton, C.D.T., Possingham, H.P., Riegen, A.C., Straw, P., Woehler, E.J., Fuller, R.A., 2017. Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. Nat. Commun. 8, 14895. https://doi.org/10.1038/ncomms14895.

Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav. Ecol. Sociobiol. 65, 13–21. https://doi.org/10.1007/s00265-010-1037-6.

Thomas, K., Kvitek, R.G., Bretz, C., 2003. Effects of human activity on the foraging behavior of sanderlings *Calidris alba*. Biol. Conserv. 109, 67–71.

Tsipoura, N., Burger, J., 1999. Shorebird diet during spring migration stopover on Delaware Bay. Condor 101, 635–644. https://doi.org/10.2307/1370193.

Tulp, I., de Goeij, P., Tsipoura, N., Burger, J., Piersma, T., Verkuil, Y., Tulp, I., Mathot, K. J., Smith, B.D., Elner, R.W., 1994. Latitudinal clines in food distribution correlate with differential migration in the Western Sandpiper. Ecology 71, 781–791. https://doi.org/10.2307/3545827.

Van de Kam, Ens, B.J., Piersma, T., Zwarts, L., 2004. Shorebirds. An Illustrated Behavioural Ecology. KNNV Publishers, Utrecht. Page: 188-204.

Yang, H.Y., Chen, B., Ma, Z. -j., Hua, N., van Gils, J.A., Zhang, Z.-W., Piersma, T., 2013. Economic design in a long-distance migrating molluscivore: how fast-fuelling red knots in Bohai Bay, China, get away with small gizzards. J. Exp. Biol. 216, 3627–3636. https://doi.org/10.1242/jeb.083576.

Yasué, M., 2005. The effects of human presence, flock size and prey density on shorebird foraging rates. J. Ethol. 23, 199–204. https://doi.org/10.1007/s10164-005-0152-8.

Zhang, A., Yuan, X., Yang, X., Shao, S., Li, J., Ding, D., 2016. Temporal and spatial distributions of intertidal macrobenthos in the sand flats of the Shuangtaizi Estuary, Bohai Sea in China. Acta Ecol. Sin. 36, 172–179. https://doi.org/10.1016/j.chnaes.2016.04.003.

Zhao, M., Christie, M., Coleman, J., Hassell, C., Gosbell, K., Lisovski, S., Minton, C., Klaassen, M., 2017. Time versus energy minimization migration strategy varies with body size and season in long-distance migratory shorebirds. Mov. Ecol 5, 23. https://doi.org/10.1186/s40462-017-0114-0.

Zharikov, Y., Skilleter, G.A., 2003. Nonbreeding Eastern Curlews *Numenius madagascariensis* do not increase the rate of intake or digestive efficiency before long-distance migration because of an apparent digestive constraint. Physiol. Biochem. Zool. 76, 704–715. https://doi.org/10.1086/376427.

Zharikov, Y., Skilleter, G.A., 2004. Why do eastern curlews *Numenius madagascariensis* feed on prey that lowers intake rate before migration? J. Avian Biol. 35, 533–542. https://doi.org/10.1111/j.0908-8857.2004.03275.x.

Zheng, G.M., 2017. A Checklist on the Classification and Distribution of the Birds of China, third ed. Science Press, Beijing.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.

Zwarts, L., Esselink, P., 1989. Versatility of male curlews *Numenius arquata* preying upon *Nereis diversicolor* deploying contrasting capture modes dependent on prey availability. Mar. Ecol. Prog. Ser 56, 255–269. https://doi.org/10.3354/meps056255.