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The value of coastal saltpans for migratory shorebirds: conservation insights from a stable isotope approach based on feeding guild and body size

Weipan Lei[1], Jose A. Masero[2], Caroline Dingle[3], Yang Liu[4], Ziwen Chai[1], Bingrun Zhu[1,5], Hebo Peng[5,6], Zhengwang Zhang[1] & Theunis Piersma[5,6]

1 Key Laboratory for Biodiversity Science and Ecological Engineering, National Demonstration Center for Experimental Life Sciences & Biotechnology Education, College of Life Sciences, Beijing Normal University, Beijing, China
2 Ecology in the Anthropocene, Associated Unit CSIC-UEX, Zoology, Faculty of Sciences, University of Extremadura, Badajoz, Spain
3 Division of Ecology & Biodiversity, School of Biological Sciences, The University of Hong Kong, Hong Kong S.A.R., China
4 State Key Laboratory of Biocontrol, School of Ecology, School of Life Sciences, Sun Yat-sen University, Guangzhou, China
5 Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, The Netherlands
6 Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Texel, The Netherlands

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Correspondence
Jose A. Masero, Ecology in the Anthropocene, Associated Unit CSIC-UEX, Zoology, Faculty of Sciences, University of Extremadura, Badajoz, Spain.
Email: jamasero@unex.es

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Abstract

Migratory shorebirds are among the most threatened groups of birds. They rely on natural intertidal habitats outside the breeding season, but, to some extent have adjusted to using man-made habitats. Here, we assessed the importance of coastal saltpans – a type of anthropogenic wetland – for feeding in migratory shorebirds during their northward migration along the East Asian-Australasian Flyway (EAAF). We combined low tide counts on intertidal flats and nearby saltpans at the Luannan coastal wetland complex (Bohai Bay, China) with Bayesian mixing model analyses (BMMs) based on stable isotopes to evaluate the relative importance of coastal saltpans versus natural intertidal habitats as foraging grounds for migrating species. We grouped shorebird species (n = 24) according to feeding guild and body size, and found that both predictors explained the broad-scale patterns of foraging use of saltpans by shorebirds at low tide. The guild of water-surface foraging species (e.g. stilts and avocets), independently of body size, mostly fed in saltpans, and the small-medium visual (e.g. plovers) and tactile-surface (e.g. sandpipers) foraging species consumed a significant portion of their diet in this habitat. In contrast, most large tactile-surface foraging species barely foraged in saltpans at low tide. BMMs showed that shorebirds had a greater reliance on saltpans than did traditional counts of foraging birds in each habitat at low tide. Saltpan food is rich in essential fatty acids, so the contribution of saltpans to the diet of shorebirds should not be considered only in absolute values, but also in the quality of this contribution. Saltpans may therefore help conserve declining shorebirds if properly managed – for example by controlling water levels – to serve the specific feeding guilds that rely on them. While our focus is in the EAAF, the findings are relevant for other flyways and other non-tidal anthropogenic wetlands.

Introduction

Habitat loss is the greatest threat to biodiversity (e.g. Brooks *et al*., 2002; Gaston, Blackburn & Goldewijk, 2003). The situation is critical in the East Asian-Australasian Flyway (EAAF), as approximately 65% of intertidal flats along the coast of the Yellow Sea have been lost in the past five decades (Murray *et al*., 2014; Piersma *et al*., 2016). Among the global flyways, the EAAF supports both the highest number of migratory shorebirds (a minimum of 7.3 million birds) and threatened shorebird species (more than 17 species) (Conklin, Verkuil & Smith, 2014; Hua *et al*., 2015; BirdLife International, 2020a). Up to 40% of these migratory shorebirds rely on Yellow Sea intertidal flats during migration (Hua *et al*., 2015) and the loss of these intertidal flats has been suggested to be the main driver of shorebird population declines (Piersma *et al*., 2016; Studds *et al*., 2017). In this context, to predict relative levels of resilience, we need to assess the ability of migratory shorebird species to adapt and make use of altered habitat types (Newbold *et al*., 2013).

Shorebirds show a variety of prey detection mechanisms (e.g. Martin & Piersma, 2009) and foraging modes including pecking, probing or sweeping (e.g. Barbosa & Moreno, 1999). Many migratory shorebirds can exploit a range of prey items by using different foraging modes depending on prey type and availability (e.g. Baker & Baker, 1973; Zwarts & Esselink, 1989; Skagen & Oman, 1996; Gerwing *et al*., 2016). Species will deal with particular contexts of prey availability as far as their sensory, cognitive and mechanical capacities allow (Zhang *et al*., 2019). This flexibility in foraging methods would enable some degree of buffering against variation in natural feeding conditions and facilitate the exploitation of new, man-made, environments.

Coastal saltpans are anthropogenic non-tidal wetlands used for producing salt by the solar evaporation of seawater (Rocha *et al*., 2017). Coastal saltpans of the Yellow Sea, as in other regions such as the Mediterranean basin and Inner Gulf of Thailand, have been part of the coastal landscape for centuries (Wang, 2012; Green *et al*., 2015), and at least since the last century, these man-made wetlands support important populations of migratory waterbirds, including shorebirds (Britton & Johnson, 1987; Masero, 2003; Dias *et al*., 2014; Jackson *et al*., 2020). This fact is probably related to the destruction and impact on natural habitats and/or opportunistic foraging of waterbirds, as the flooded ponds of coastal saltpans are rich in prey items such as chironomid larvae, brine flies or brine shrimps (e.g. Britton & Johnson, 1987; Masero *et al*., 1999; Sánchez, Green & Castellanos, 2006), which represent a natural food for migratory shorebirds in many natural brackish and salt lakes (e.g. Jehl, 1994; Verkuil *et al*., 2003).

The importance of coastal saltpans for shorebirds in the EAAF and on other flyways is increasingly recognized (e.g., Takekawa, Lu & Pratt, 2001; Masero, 2003; Sripanomyom *et al*., 2011; Green *et al*., 2015; Lei *et al*., 2018; Jackson *et al*., 2020). Shorebirds that depend on intertidal areas for feeding may move to the adjacent saltpans and continue foraging at high tide, or may even prefer to remain in the saltpans during the low tide phase instead of moving back to the exposed intertidal areas (Velasquez & Hockey, 1992; Masero *et al*., 2000; Dias *et al*., 2014). However, some shorebirds, e.g. bar-tailed godwits (*Limosa lapponica*), rarely feed in saltpans (Masero *et al*., 2000; Lei *et al*., 2018). To date, virtually all data on the relative use of coastal saltpans versus natural intertidal areas as foraging grounds are based on comparisons of numbers (e.g. Sripanomyom *et al*., 2011; Lei *et al*., 2018; Jackson *et al*., 2020) or on visual estimates of their energy intake rates in each habitat type (e.g. Masero & Pérez-Hurtado, 2001; Masero, 2003). These approaches do not account for the fact that, for example, some species may feed in the saltpans at night (Masero *et al*., 2000).

In contrast to conventional dietary analyses, which often reflect ingestion rather than assimilation, stable isotopes reflect assimilated protein (Inger & Bearhop, 2008) and may more reliably estimate the actual importance of saltpans versus intertidal flats to shorebird diet (e.g. Lourenço *et al*., 2017). Here, we provide species-specific assessments of the contribution of saltpan foraging to the diet of shorebird species during northward migration. We sampled birds in intertidal mudflats and nearby saltpans at the Luannan coastal wetland complex (Bohai Bay, China) and assessed the importance of each habitat type by combining (i) abundance counts of foraging birds at low tide in both habitats with (ii) Bayesian mixing models (BMMs) based on stable isotope analysis of blood fractions to determine the relative contribution of prey from each habitat to shorebird diet at different time-scales (plasma: 1–7 days; red cells: 14–30 days) (e.g. Klaassen *et al*., 2010). In non-tidal coastal wetlands, foraging patterns by waterbirds, including shorebirds, are not species-specific but vary depending on feeding guild and body size (Ntiamoa-Baidu *et al*., 1998). Thus, we expected that feeding guilds, i.e., groups of species that exploit the same resources in a similar way (Root, 1967), based on predominant foraging modes and body size, would have a significant role in driving broad-scale patterns of foraging use of saltpans by shorebirds. This feeding guild approach provides an operational unit between the individual species and the community as a whole (Root, 1967) and denotes the most basic approach to true multiple-species management (Block, Finch & Brennan, 1995).

Materials and methods

Study area

The Luannan coastal wetland complex is located in the northern region of Bohai Bay, Yellow Sea (39°N, 118°E) (Figure S1). It is a key staging site for migratory shorebirds within the EAAF (Yang *et al*., 2011; Lei *et al*., 2018). Our study area included the Nanpu Saltpans (290 km^2) and the adjacent intertidal flats (57 km^2) (Figure S1). Similar to other industrial saltpans, the Nanpu Saltpans consist of shallow, interconnected pans of varying sizes (range: 0.6–1 685 ha) separated by dikes. There are three types of ponds: storage, evaporation and crystallization ponds. Seawater is pumped into storage ponds, and from here, water is circulated through a number of evaporation ponds by gravity or with the help of pumps. As water flows, salinity gradually increases by solar evaporation to near saturation point and the brine is pumped to the crystallization ponds. Previous research in the study area showed that for feeding, migratory shorebirds mainly used evaporation ponds (2.4–18.0 km from tidal flats) (Lei *et al*., 2018). These evaporation ponds (hereafter ‘inland ponds’) exclusively consist of artificial salt pans with different water surface areas (range: 37–724 ha) and salinities (range: 40‰–120‰). There are two water management regimes for inland ponds: in one, saltworkers maintain a high and constant water level from 60 to 100 cm, and in the other, they keep a lower water level, ranging from 40 to 60 cm. In the latter, water depths are variable with management practices and it is common to find water depths less than 20 cm and even drained ponds, which are used by shorebirds to feed (Lei *et al*., 2018).

Bohai Bay has a semidiurnal tide, and the average tidal amplitude is 2.5 m (HPDLR, 2007). The tidal flats are 1–3 km wide at low tide depending on tidal amplitude (Yang *et al*., 2011). For the shorebird abundance counts, the tidal flats were divided into four sectors: Beipu (14 km^2), Nanpu

(22 km^2), Double Bridge (10 km^2) and Zuidong (11 km^2). More detailed information about saltpans in the area can be found in Lei *et al*. (2018).

Bird counts and sample collections

Low tide counts

The number of shorebirds using inland ponds and adjacent intertidal flats were counted two to six times during each northward migration season (April to early June) from 2014 to 2018 (except 2017). There was at least a 1-week interval between successive counts. The counted inland pond area occupied 86 km^2, i.e. 30% of the total surface of Nanpu Saltpans. The surface of intertidal flats at low tide was 57 km^2. Surveys were performed by one or several experienced teams in each habitat, depending on the number of migrating shorebirds. During each count, the whole inland pond area was surveyed using the network of accessible non-paved roads, by car or by foot. To avoid double counting birds, inland ponds and tidal flats were counted simultaneously from 3 hours before to 3 hours after low tide, with teams communicating throughout by radio or cell phone. The sequence of road itineraries was changed from count to count to keep points from being sampled systematically at the same time of the low tide period. The tidal flats were surveyed in a similar way while teams drove along the road inside of dike borders of the intertidal area during the outgoing tide, when all birds were close to the dike.

All species of shorebirds in tidal flats were counted except in 2015, when only red knots (*Calidris canutus*), great knots (*Calidris tenuirostris*), sanderlings (*Calidris alba*) and bar-tailed godwits were counted due to logistic constraints. As most shorebirds were feeding during low tide in both tidal flats ans saltpans (Lei *et al*., 2018), we did not discriminate between feeding and roosting individuals.

Guild structure

We characterized the foraging modes of shorebirds (24 species) and grouped them into different feeding guilds (*sensu* Ntiamoa-Baidu *et al*., 1998) based on individual feeding style and sensory mechanism used to detect prey. The following feeding guilds were used, following Ntiamoa-Baidu *et al*., (1998): (i) tactile-surface foraging and (ii) visual-surface foraging, two groups of surface foragers which predominantly use tactile and visual means to find their prey, respectively, and (iii) water-surface foraging species, which forage in the water layer and use visual as well as tactile senses to detect their prey. We further classified each species by their body size (inferred from body length, measured from bill to tail; Del Hoyo *et al*., 2019), grouping them as large (body size ≧37 cm), medium (20 cm < body size <37 cm), or small (body size ≦20 cm) birds (Fig. 1).

Sample collections of stable isotopes

During the 2016 northward migration (from 17 April to 5 May), we caught shorebirds in both intertidal flats and saltpans using mist nets, walk-in traps and wind-assisted clap nets. We collected blood samples (70–200 μL) from each individual captured; samples were centrifuged within six hours after capture to separate the plasma and red cells. Due to different turnover rates of both tissues, the δ^{15}N and δ^{13}C values in the plasma and red cells reflect the diet for approximately the previous 1–7 days and 14–30 days, respectively (e.g. Klaassen *et al*., 2010). Samples were stored at −20°C in the field station and then transferred and stored at −80°C in the Beijing Normal University laboratory until analysis. The plasma and red cells of a total of 12 shorebird species were used in BMMs (Table S1). Although large numbers of marsh sandpipers occur in the area, we only caught two individuals for stable isotope analysis, so we also sampled pectoral muscle of marsh sandpipers (n = 6) killed by predators

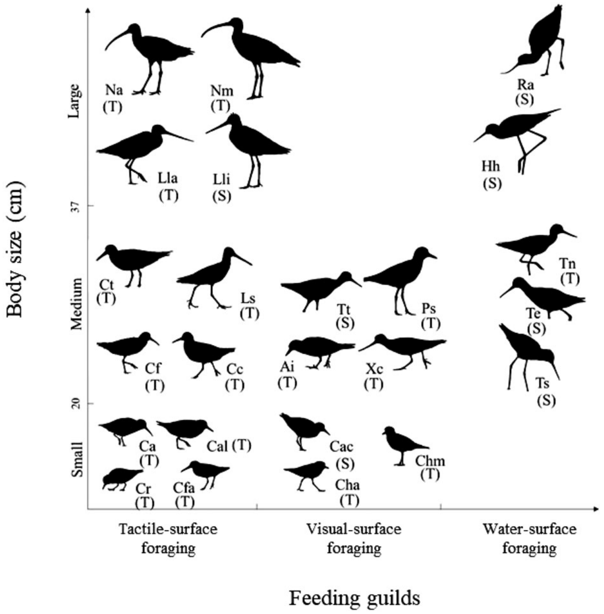

Figure 1 Feeding guilds and body size categories of shorebirds using Luannan coastal wetland complex (Bohai Bay, China). Ai: ruddy turnstone (*Arenaria interpres*), Ca: dunlin (*Calidris alpina*), Cal: sanderling (*Calidris alba*), Cac: sharp-tailed sandpiper (*Calidris acuminate*), Cc: red knot (*Calidris canutus*), Cf: curlew sandpiper (*Calidris ferrugínea*), Cfa: broad-billed sandpiper (*Calidris falcinellus*), Cha: Kentish plover (*Charadrius alexandrinus*), Chm: lesser sand-plover (*Charadrius mongolus*), Cr: red-necked Stint (*Calidris ruficollis*), Ct: great knot (*Calidris tenuirostris*), Hh: black-winged Stilt (*Himantopus himantopus*), Lla: bar-tailed godwit (*Limosa lapponica*), Lli: black-tailed godwit (*Limosa limosa*), Ls: Asian dowitcher (*Limnodromus semipalmatus*), Na: Eurasian curlew (*Numenius arquata*), Nm: Eastern curlew (*Numenius madagascariensis*), Ps: grey plover (*Pluvialis squatarola*), Ra: pied avocet (*Recurvirostra avosetta*), Te: spotted redshank (*Tringa erythropus*), Tn: common greenshank (*Tringa nebularia*), Ts: marsh sandpiper (*Tringa stagnatilis*), Tt: common redshank (*Trina tetanus*), Xc: Terek sandpiper (*Xenus cinereus*). (T) indicated the mean number was higher in intertidal flats than in saltpans, and (S) indicated the mean number was higher in saltpans than in tidal flats.

or by cars for estimating the diet contribution by BMMs (Figure S2).

During the northward migration period in 2015 and 2016, we collected potential prey from inland ponds and intertidal mudflats for δ^{15}N and δ^{13}C analysis. The invertebrates were collected by hand or by using sampling cores and sieving (0.5 mm mesh-size) the sediment. In the saltpans, potential food sources included brine shrimps (*Artemia* spp.), brine flies (*Ephydra glauca*; larvae pupa, and adult individuals) and chironomid larvae (*Chironomus salinarius*). In the intertidal mudflats, potential prey items included bivalves, gastropods, crustaceans and polychaetes. We collected 1–20 samples for each species or prey type, and each sample consisted of a pool of 1–70 individuals (Table S2). A total of 81 samples from tidal flats and 20 samples from saltpans were analysed (Table S2).

Stable isotope analysis

The plasma and red cell samples were freeze-dried at −80°C for 48 hr. The potential prey items and marsh sandpiper muscle were thawed, lightly rinsed with deionized water, dried at 70°C to constant weight and then ground to powder in a tissue homogenizer (FastPrep-24, MP Biomedicals).

Lipids within samples may impact the measurements of δ^{13}C due to their more negative δ^{13}C values relative to other biochemical compounds related to their *de novo* synthesis in organisms (Martínez del Rio *et al*., 2009). Most species sampled were small-sized shorebirds, and red cell and plasma samples were not delipidated due to the small quantities of blood that we collected by puncturing the brachial vein. Nevertheless, lipid component of avian blood (whole blood and red cells) generally is very low (<1% of the total wet mass), and it is unlikely to be of sufficient magnitude to influence the overall δ^{13}C value (Bearhop *et al*., 2000). Thus, several studies suggested that there is no need to extract lipids in avian blood (e.g. Bearhop *et al*., 2002; Cherel, Hobson & Hassani, 2005; Phillips *et al*., 2011; Kowalczyk *et al*., 2014; Barrionuevo *et al*., 2020). Nevertheless, high C:N mass ratios in plasma could influence results (see Discussion).

The potential impact can be lessened either by lipid removal prior to analysis or by a post-hoc corrections (Kiljunen *et al*., 2006; Logan *et al*., 2008). Lipid correction equations by Logan *et al*., (2008) were used to correct the potential impact of lipid content on isotope values in potential prey items other than polychaetes. In the case of polychaete worms, we collected enough amount for extracting lipids and knew, from previous data (Castro *et al*., 2008), that this prey type contains about 14% lipids. This also was the case of pectoral muscle samples of marsh sandpiper, and they could be delipidated. For this step, in both cases, we prepared two aliquots of each sample: one aliquot was immediately prepared for stable isotope analysis without any procedure to remove lipids (see below) and in the second aliquot, lipids were removed before analysis. This was done by soaking and rinsing the sample several times with a chloroform-methanol [2:1] solution to reduce variability due to differential content of lipids. We analysed δ^{13}C and δ^{15}N in both aliquots (Logan *et al*., 2008), and used the results to quantify the impact of lipid extraction on both δ^{13}C and the carbon-to-nitrogen (C:N) ratio.

Subsamples of the powdered materials for each sample type were weighed (range: 0.5–1.2 mg) before being placed into tin capsules for analysis. The carbon and nitrogen isotope analyses were carried out at the Stable Isotope Laboratory of the University of Hong Kong using a EuroVector (EA3000) coupled with a Nu Instruments Perspective IRMS (Isotopes Ratio Mass Spectrometry). Samples of potential food from saltpans were analysed at the Institute of the Quality Standard and Testing Technology for Agro-Products of CAAS (Chinese Academy of Agricultural Sciences), via elemental analyzer (Flash 2000) and IRMS (Delta V, Thermo). The average reproducibility for δ^{13}C and δ^{15}N was ±0.2 ‰, based on replicate analyses. The stable isotope ratios are presented conventionally as δ values in parts per thousand (‰) relative to the Vienna PeeDee Belemnite for δ^{13}C, and atmospheric nitrogen (N^2) for δ^{15}N.

Data analysis

Data exploration followed the protocol described by Zuur, Hilbe & Ieno (2013). Specifically, Cleveland dotplots were used to inspect for potential outliers in both response and predictor variables (see Table S3 for the variables description). Data exploration indicated that none of the variables contained outliers.

As the number of total shorebirds in the study area differed in several orders of magnitude between species (from hundreds to several thousands), we modelled how the proportion (%) of foraging shorebirds in the saltpans at low tide changed as a function of different predictors, using a beta-binomial mixed model with logit link (Harrison, 2015).

We calculated generalized variance inflation factors (GVIF) using the ‘car’ package in R version 3.6.1 (Fox & Weisberg, 2011; R Core Team, 2019) to evaluate potential collinearity among predictors. Species was removed as predictor variable due to multicollinearity with feeding guild and body size (Zuur, Leno & Elphick, 2010); GVIF values of predictors then decreased below 2. Thus, we included as potential predictors feeding guild (tactile, visual and water-surface foraging), body size (small, medium, large), tidal amplitude (continuous) and Julian date (continuous) as fixed effects. We included tidal amplitude (vertical difference in height between consecutive high and low waters over a tidal cycle) because within periods of low tidal range, tidal amplitude may influence shorebird abundance on intertidal flats (e.g. Fonseca *et al*., 2017; Basso *et al*., 2018). Julian date (day 1 = 10 April) was included as quadratic effect so as to allow for potential non-linear patterns across the migration season. Year (four levels) was included as random effect.

We did not model all of the combinations of these predictors or their interactions, as it is important to maintain clear biological hypotheses about which combinations might be important. We therefore only modelled 10 combinations (Table 1) to investigate different hypotheses associated with

Table 1 Models predicting variation in proportion of foraging shorebirds in saltpans at low tide

Model	df	logLik	AICc	ΔAICc	*wi*
FG + BS	7	−950.07	1914.52	0	0.63
FG + BS + T	8	−950.07	1916.62	2.09	0.22
FG + BS + T + D	9	−949.82	1918.24	3.72	0.10
FG + BS + T + D + D^2	10	−949.82	1920.38	5.86	0.03
FG + BS + T + D + D^2 + BS × T	12	−949.31	1923.7	9.17	0.01
FG + BS + T + D + D^2 + FG × T	12	−949.79	1924.65	10.12	0
FG + BS + T + D + D^2 + FG × T + BS × T	14	−949.12	1927.68	13.16	0
FG	5	−966.29	1942.79	28.26	0
BS	5	−1006.84	2023.88	109.35	0
Null model	3	−1011.13	2028.33	113.81	0

Relationships were modelled using GLMM with a beta binomial distribution and the logit link function. Models were ranked using the Akaike Information Criterion for small sample sizes (AICc). Only a model met the selection criterion ΔAICc <2. All candidate models included a random term of year. Feeding guild (FG), body size (BS), tidal amplitude (T) and date (D; as quadratic effect) were used as explanatory variables. '×' denotes interaction effect, 'df' denotes degrees of freedom of the model, 'logLik' is the log-likelihood, 'ΔAICc' is the difference in AICc between a given model and the model with the lowest AICc; *wi* is the weight value for each model.

specific effects of feeding guild, body mass, tide and date. We used an information theory approach using Akaike's information criterion (AIC) as our basis for selecting among competing models (Burnham, Anderson & Huyvaert, 2011). We used the 'MuMIn' package (Barton, 2019) to rank models using Akaike's corrected information for small sample size (AIC_C), and Akaike's weight (w_i) to select the most parsimonious models (Burnham & Anderson, 2004). All models with a ΔAIC_C value <2 were considered as having effectively equivalent levels of support (Burnham & Anderson, 2004). If only one model met the selection criterion, we would not perform averaging but provide estimates and 95% confidence intervals of this model. GLMMs were fitted using the 'glmmTMB' package (Magnusson *et al.*, 2017). 'ggeffects' package was used to predict estimated marginal means (Lüdecke *et al.*, 2021). Lastly, we verified the validity of our model using functions from the 'DHARMa' package (Hartig & Lohse, 2021); we tested for uniformity of residuals, under and over dispersion, outliers and zero-inflation and found no significant problems in our model fit.

Prey items were grouped into seven categories: three from the saltpans, and four from tidal flats. Multiple food sources could yield highly uncertain estimates when only two isotope elements are used (Phillips, Newsome & Gregg, 2005). The standard approach for reducing the number of sources in a mixing model is to combine sources (Ward *et al.*, 2011). When source isotope signatures are similar and the combined source group has some biological significance, source reduction through combination can improve mixing model tractability and inference (Phillips *et al.*, 2005). We found that the prey categories within each habitat type had similar $\delta^{13}C$ and $\delta^{15}N$ values (Figure S3, Table S2), so as we were interested in the relative contribution of habitat to the diet of shorebirds rather than the contribution of a specific type of food, we pooled the seven categories of prey items in those two categories to improve the model's performance (Phillips, Newsome & Gregg, 2005; Parnell *et al.*, 2010).

Dual-isotope BMMs were used to estimate the contributions of saltpans and intertidal food sources to shorebirds diet. The 'simmr' package, a Bayesian stable isotope mixing model implemented in R (version 3.6.1), was used to produce all mixing models (Parnell & Inger, 2016). Mean and SD of $\delta^{13}C$ and $\delta^{15}N$ values of two groups of potential food sources, and individual $\delta^{13}C$ and $\delta^{15}N$ values of shorebird plasma and cells were used in the models. The diet-tissue trophic discrimination factors (mean ± SD) used for plasma, red cells and muscle were $\delta^{15}N = 3.07 \pm 0.83$, $\delta^{13}C = -0.09 \pm 0.65$; $\delta^{15}N = 2.78 \pm 0.74$, $\delta^{13}C = 0.91 \pm 1.22$; $\delta^{15}N = 1.7 \pm 1.04$, $\delta^{13}C = 0.92 \pm 0.77$, respectively. These discrimination factors were averaged from the values listed in several studies (Table S4).

Pearson correlations were used to explore the relationship between diet contribution from saltpans based on BMMs and the proportion (%) of foraging shorebirds using this habitat at low tide. All tests were two-tailed, and the significance levels were set at $P < 0.05$. The values given are the means ± SD unless otherwise indicated.

Results

Relative use of intertidal flats and saltpans

Comparison of competing models provided strong support for a single model with ΔAICc <2, which included feeding guild and body size as predictors (Table 1; see Table S5 for mean number of foraging individuals for each species in each habitat at low tide). The proportion of foraging shorebirds in the saltpans at low tide was significantly higher in water-surface foraging species that in tactile and visual foraging species, while this proportion of foraging shorebirds in the saltpans was higher in small-bodied shorebirds than in medium and large species (Table 2, Fig. 2).

Table 2 Parameter estimates (±SE) from the best-supported model predicting variation in proportion of foraging shorebirds in saltpans at low tide

Variable	Estimate	SE	95% CI	*Z*-value	*P*-value
Intercept	2.13	0.46	1.22, 3.04	4.60	0.00
Tactile-surface foraging[a]	−2.99	0.29	−3.56, −2.42	−10.26	<0.001
Visual-surface foraging[a]	−2.82	0.33	−3.47, −2.16	−8.44	<0.001
Medium body size[b]	−1.38	0.24	−1.55, −0.40	−5.65	0.00
Large body size[b]	−0.97	0.29	−1.86, −0.90	−3.33	0.00

Note: Variance and SD of random effect (year) were 0.36 and 0.60, respectively. Overdispersion parameter was 0.413.

[a] Reference level: water-surface foraging guild.

[b] Reference level: small body size.

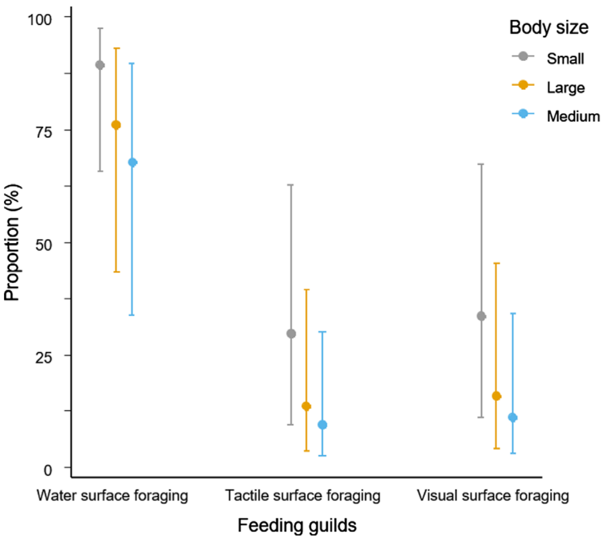

Figure 2 Estimated marginal means (best supported model; see Table 1) of the proportion (%) of foraging shorebirds at low tide in the saltpans of each feeding guild and body size. Marginal means are shown with 95% CI. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

Diet reconstructions

δ^{15}N values of potential prey items differed significantly ($t_{39.88} = -21.64$, $P < 0.001$) between intertidal areas (10.89 ± 1.93‰) and saltpans (2.78 ± 1.37‰). δ^{13}C values from intertidal areas (−17.43 ± 4.10‰) were significantly different ($t_{84.82} = 4.21$, $P < 0.001$) from those from the saltpans (−15.04 ± 1.50‰) (Fig. 3). C:N ratios were statistically similar ($t_{45.72} = -0.72$, $P = 0.48$) in the two habitats (intertidal area: 6.76 ± 3.04‰; saltpans: 7.39 ± 4.82‰) (see Table S2).

The water-surface foraging species (marsh sandpiper), small visual and tactile-surface foraging species (red-necked stints *Calidris ruficollis*, sanderling, Kentish plovers *Charadrius alexandrinus*, except dunlin *Calidris alpina*) had δ^{15}N and δ^{13}C values of plasma that closely matched the food available in the saltpans (Fig. 3), which suggested that prey from saltpans provide the greatest contribution to diet in these species (means >50%) (Fig. 4; see also Figure S4, Figure S5, and Table S6). This high contribution of saltpan resources was especially high for the red-necked stint (82% – 95%) (Table S6). In contrast, δ^{15}N and δ^{13}C plasma values of large and medium visual and tactile-surface foraging species (Terek sandpiper *Xenus cinereus*, ruddy turnstone *Arenaria interpres*, great knot, red knot and bar-tailed godwit, except curlew sandpiper and common redshank) closely matched the intertidal isotopic values (Fig. 3), suggesting that prey from intertidal flats contribute the most to the dietary intake of these feeding guilds (means >50%) (Fig. 4; see also Figure S4, Figure S5, and Table S6).

The plasma isotopic signatures reflected a more saltpans diet than red cells isotopic signatures, supporting that diet contribution from saltpans increased with time for all species except great knot (decreased by 2.3%). The increase was obvious in water-surface foraging species (19.5%) and small visual and tactile-surface foraging species (16.6–22.5%), and less noticeable in large and medium visual and tactile-surface foraging species (0.4–12.0%) (Fig. 4; see also Figure S4, Figure S5, and Table S6).

The mean diet contribution from the saltpans based on the BMMs (for both plasma and red cells) was higher than expected based on the number of birds observed foraging in these artificial habitats at low tide (except for marsh sandpiper) (Fig. 5a,b; Table S6). This diet contribution from the saltpans was highly correlated with the proportion of each shorebird species foraging in the saltpans at low tide (plasma: $r = 0.70$, $P < 0.05$; red cells: $r = 0.57$, $P = 0.05$) (Fig. 5a,b). Diet contribution of saltpans obtained from both blood fractions were also significantly correlated ($r = 0.89$, $P < 0.001$), with plasma values showing a higher contribution of saltpans to shorebird diet during migration than red cell values (Fig. 5c).

Discussion

Using low tide count data combined with stable isotope data (analysed using dual-isotope BMMs) we demonstrated that prey items from saltpans are a large and integral part of the diet for water-surface foraging species, and to a lesser but still important extent for visual and tactile-surface foraging species characterized by small and medium body size. In the tactile-surface foraging red-necked stint, prey from saltpans contributed more than 85% to the assimilated diet. Overall, our model showed a reasonably good fit with the data collected, and exhibited satisfactory power for explaining the foraging use of saltpans at low tide by shorebirds. This model suggested that feeding guild and body size were important factors in explaining this foraging use of saltpans by migratory shorebirds.

Different use of saltpans between guilds

In saltpans and natural hypersaline lagoons, most shorebirds feed on small prey items suspended in the water column

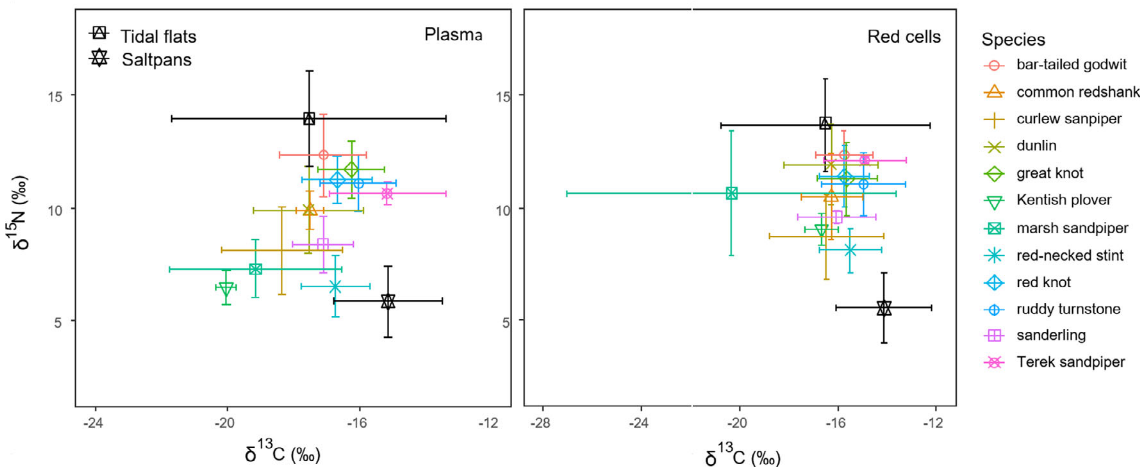

Figure 3 Mean (± SD) nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) values in plasma and red cells of shorebird blood and food sources (saltpans and intertidal flats) in Luannan wetlands during northward migration. Values were adjusted using trophic discrimination factors (see Table S4). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

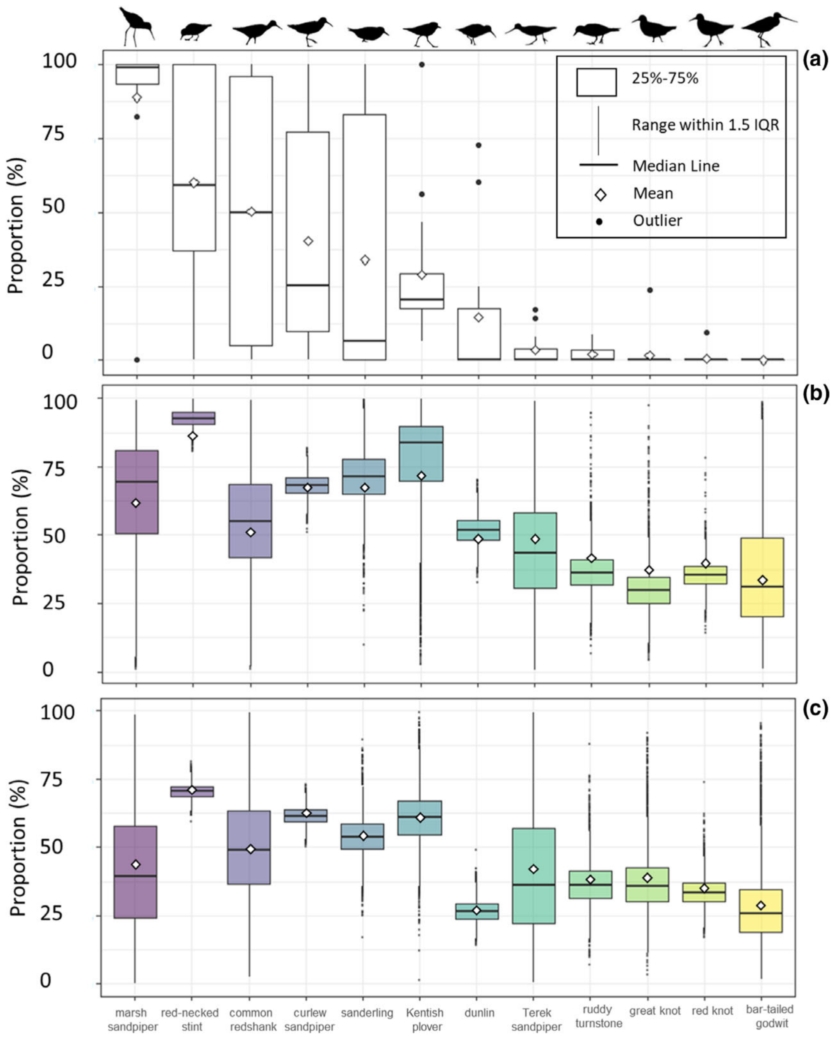

Figure 4 Proportion (%) of the total population of each species that chose to forage in the saltpans at low tide rather than in the adjacent intertidal mudflats (a). Food contribution (%) from saltpans to shorebird diet based on stable isotope analyses (Bayesian mixing models) of plasma (b), and red cells (c). The shorebird species are ordered from highest to lowest foraging use-food contribution of saltpans. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

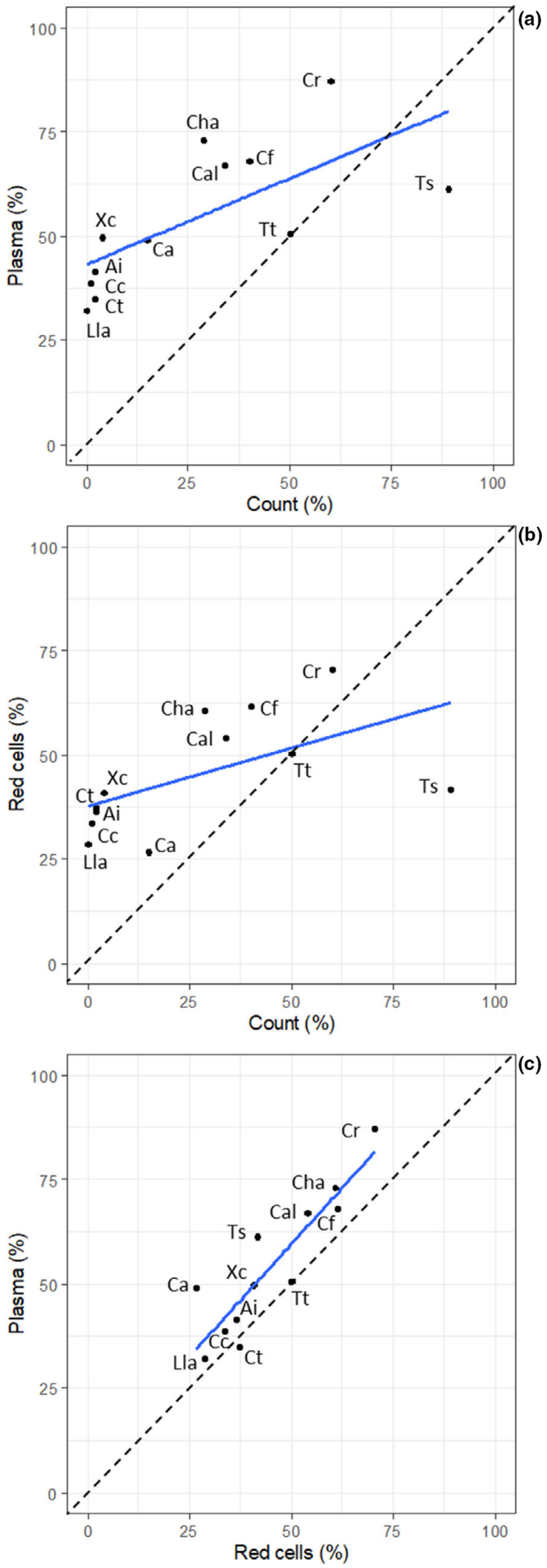

Figure 5 Relationship between proportion (%) of the total population of each species foraging in the saltpans at low tide based on bird counts (*X*-axis) and food contribution (%) from saltpans based on isotope analysis of plasma (a) and red cells (b) (*Y*-axis). The bottom panel (c) shows the relationship between food contribution of saltpans based on isotope analysis of plasma and red cells. Broken lines indicate *X* = *Y*. For acronyms of species names see Fig. 1. Variation of the mean values were excluded for clarity (they are shown in Fig. 4 and Table S2). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

(Verkuil *et al*., 2003; Estrella & Masero, 2007; Estrella, Masero & Pérez-Hurtado, 2007). Shorebird species whose diet was dependent on saltpan food to a significant extent – water-surface foraging species, small-medium visual and tactile-surface foraging species – are equipped with needle-shaped bills. This bill morphology is necessary to use surface tension transport (STT) (alone or in conjunction with rhynchokinesis), a feeding mechanism that allows efficient feeding on small prey items suspended in water such as brine shrimps or copepods, and that probably limits the ingestion of hypersaline water (e.g. Verkuil *et al*., 2003; Estrella *et al*., 2007). The food supply available in the ponds may therefore be particularly important for migrating species equipped with these needle-shaped bills, independently of taxonomic affiliation. These species would include not only shorebirds but also medium-sized species of bird groups such as gulls or terns. For example, back-headed gull (*Chroicocephalus ridibundus*) and white-winged tern (*Chlidonias leucopterus*) are seen feeding in large numbers in the saltpans (Lei *et al*., 2018).

The water-surface foraging species did not commute between the intertidal flats and saltpans to forage, and in general, chose inland ponds to meet their high energy requirements during migration. Low tide counts corroborated that the saltpans' food contributed mostly to water-surface foraging species' diet. In the case of the marsh sandpiper, most birds were found foraging in the inland ponds, but stable isotope analysis in red cells (but not plasma) suggested that prey from the intertidal flats contributed over 50% of this species' diet. We assume that this inconsistency is due to the small sample size for blood samples, since dual-isotope BMMs using muscle tissue (Figure S2) showed that they fed mostly in saltpans. Unfortunately, half of the sampled species, including marsh sandpiper, had a low sample size (2-4 individuals), so stable isotope results for these species should be interpreted with caution and not in isolation.

Most visual-surface and tactile-surface foraging species of small and medium body size foraged in lower or similar numbers in saltpans than in tidal flats. However, our isotope analysis suggested that saltpans are an important foraging ground for both guilds. In addition to feeding in tidal flats at low tide, shorebird species also may feed in saltpans during the high tide phase (i.e. when intertidal mudflats are unavailable to shorebirds) in Nanpu Saltpans (Lei *et al*., 2018), or even at night, as they do in southern European saltpans (Masero *et al*., 2000). This may explain why in some cases diet contribution from saltpans based on the BMMs was higher than expected from relative low tide counts.

Some shorebird species included in this study do not appear to use the saltpans as foraging grounds at low tide. Overall, large shorebirds ignore most small prey items because of low handling efficiency (Zwarts & Wanink, 1993). As most of the food supply available for shorebirds in ponds is limited to small prey items (e.g., Britton & Johnson, 1987; Masero *et al*., 1999; Sánchez *et al*., 2006), large species or species with thick bills, would be predicted to feed only opportunistically on these small prey items. In our study, this seemed to be the case with large species (Eastern curlew *Numenius madagascariensis*, Eurasian curlew *Numenius arquata* and bar-tailed godwit) or medium-sized species (Asian dowitcher *Limnodromus semipalmatus*, grey plover *Pluvialis squatarola*, red knot, and great knot) which could have the disadvantage of having thick bills to feed on small prey items suspended in the water column such as brine shrimps (Masero, 2002). The exception was the black-tailed godwit, a large species that fed extensively by shallow probes in the ponds. This species feeds efficiently in hypersaline ponds by selecting the greatest length classes of *Chironomus salinarius* larvae (Estrella & Masero, 2010). The chironomid and brine larvae and this prey-size selection could explain why this large species used saltpans preferentially as foraging grounds. Nevertheless, there are other factors that could also influence the foraging patterns of shorebirds using intertidal flats and adjacent supratidal saltpans, such as density-dependent effects in habitat occupancy (Masero & Pérez-Hurtado, 2001).

During neap tides, the surface of exposed intertidal flats at low tide is severely reduced in relation to spring tides, and shorebird numbers on the intertidal flats may decrease significantly (e.g. Fonseca *et al*., 2017; Basso *et al*., 2018). We did not find support for a significant role of tidal amplitude in explaining the use of saltpans at low tide by foraging shorebirds, but we cannot rule out this possibility because most counts were performed during spring tides.

Different between plasma and red cells

Isotope analysis of plasma showed a greater contribution from saltpans than red cells, probably indicating that birds shifted its feeding habits over time (Hobson & Clark, 1993; Podlesak, McWilliams & Hatch, 2005). Assuming most individuals of sampled species arrived at the study area in early April (i.e., they stayed at Nanpu for two weeks as minimum), this suggests that diet contribution from saltpans may increase over the migration period for almost all species. The increasing use of saltpans over the season may be due to increasing food abundance in saltpans (authors' unpublished data). This increase in the contribution of saltpans to the diet of shorebirds differed between feeding guilds and indicates that water-surface foraging species, small-medium visual and tactile-surface foraging species have a more positive response to the increase of food abundance in saltpans. Nevertheless, C:N ratio of plasma was higher than C:N ratio of red cells, so the increasing use of saltpans over the season must be interpreted with caution.

Conservation implications

Yellow Sea tidal mudflats are a threatened ecosystem that has decreased by >65% in recent decades (Studds *et al*., 2017). We showed that coastal saltpans act as primary or supplementary feeding habitats for several species of migratory shorebirds that rely on natural wetlands in the Yellow Sea, many of which are rapidly declining in the EAAF. Curlew sandpiper and red-necked stint populations have declined by 80% and 29%, respectively, over the last three generations, and both species were listed recently as Near Threatened on IUCN Red List (Studds *et al*., 2017; BirdLife International, 2020b). The coastal saltpans offer them natural trophic resources that they exploit during a critical period such as migration, especially during neap tides, allowing them to refuel quickly (increase feeding time, reduce commute energy) and ensuring a successful migration. In addition, some prey types in saltpans (e.g. brine shrimp) are richer in certain types of long-chain fatty acids such as DHA (docosahexaenoic acid) and EPA (eicosapentaenoic acid) than marine invertebrates such as polychaete worms or bivalves (Kharchenko & Lykova, 2014). The availability of DHA and EPA is an important determinant of bird performance (e.g. Klaassen *et al*., 2012; Twining *et al*., 2016). So diet contribution from saltpans, even in low proportions, may have a relevant role in the migratory performance of shorebirds. The increasing pressure on coastal wetlands by urbanization and sea-level rise (e.g. Ma *et al*., 2014; Iwamura *et al*., 2013) has led to the degradation and loss of saltpans along the EAAF (Melville, Chen & Ma, 2016; Jackson *et al*., 2020). Conserving the functionality of active or abandoned saltpans is an economical way to preserve alternative habitats for migratory shorebirds (e.g. Masero, 2003; Lourenço *et al*., 2017; Barnagaud *et al*., 2019).

In the saltpans of the Mediterranean basin or South America, the lowest salinity (deep) ponds are often drained for artisanal fishing, at which time the shorebirds feed in the benthic macrofauna of the exposed mudflat (Rocha *et al*., 2017). The food supply of these exposed mudflats after draining is similar to that of the natural intertidal areas, and large numbers of shorebirds, independent of their body mass, bill shape or foraging strategy, feed extensively on these drained ponds (Rocha *et al*., 2017). In the saltpans located in the EAAF, including Nanpu, there are no such uses, and the benthic fauna of the deepest ponds is only occasionally available to shorebirds, so small-sized shorebirds are limited to foraging along the shorelines. It is important to note that in our study system, the surface of saltpans was disproportionately larger than that of the adjacent intertidal mudflats, and that only 30% of that surface of the saltpans potentially functioned as foraging area for migratory shorebirds. The functionality of coastal saltpans for shorebirds conservation within EAAF would increase for shorebirds by integrating low-cost and easy management practices, such as artisanal fishing or similar uses within that large surface of unused saltpans, a procedure that would not increase costs or affect salt production.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Map of Luannan wetlands.

Figure S2. Contribution from tidal flats and saltpans to marsh sandpiper diet (n=6) based on muscle tissue isotope analysis (BMM).

Figure S3. Mean values (±SD) of δ^{13}C and δ^{15}N of the different potential food groups we considered (tidal flat: bivalve, crustacean, gastropod, polychaete; saltpans: brine shrimp, brine fly, chironomid).

Figure S4. Posterior probability densities of the proportional dietary contribution of saltpans and tidal flats to shorebird populations in Luannan Wetlands as generated by Bayesian mixing models based on plasma.

Figure S5. Posterior probability densities of the proportional dietary contribution of saltpans and tidal flats to shorebird populations in Luannan Wetlands as generated by Bayesian mixing models based on red cells.

Table S1. Mean (±SD) values of δ^{15}N, δ^{13}C, N%, C% and C:N in plasma and red cells of shorebird caught during northward migration at Luannan wetlands.

Table S2. Mean (±SD) values of δ^{13}C and δ^{15}N and C:N ratio in potential food sources from saltpans and tidal flats at Luannan wetlands.

Table S3. List of variables used in the analyses.

Table S4. Description of discrimination factors obtained from literature, sorted by tissue type and year.

Table S5. Mean number (±SD) of shorebirds using saltpans (inland ponds) and tidal flats at low tide during northward migration in Luannan wetlands.

Table S6. Diet contribution (%) from saltpans and tidal flats estimated by isotope analyses (BMMs) based on lipid-corrected and uncorrected potential food sources.