Journal of Ornithology (2019) 160:1109–1119
https://doi.org/10.1007/s10336-019-01683-6

ORIGINAL ARTICLE

Habitat use by migrating Whimbrels (*Numenius phaeopus*) as determined by bio-tracking at a stopover site in the Yellow Sea

Fenliang Kuang[1,2] · Wei Wu[3] · Wanjuan Ke[1] · Qiang Ma[3] · Weipin Chen[3] · Xuesong Feng[3] · Zhengwang Zhang[4] · Zhijun Ma[1]

Received: 8 December 2018 / Revised: 19 May 2019 / Accepted: 17 June 2019 / Published online: 27 June 2019

Abstract

Stopover sites are critical for refueling and resting by migrating birds. Clarifying the habitat requirements of migratory birds during stopover is important for understanding migration ecology and for conservation management. Habitat use by migratory birds at stopover sites, however, has been inadequately studied, and individual variation in habitat use among species is largely unexplored. We tracked the movement of migrating Whimbrels, *Numenius phaeopus*, using Global Positioning System–Global System for Mobile Communication tags at Chongming Dongtan, an important stopover site in the South Yellow Sea, China, in spring 2016 and in spring and autumn 2017. Multinomial logistic regression and multimodel inference were used to detect the effects of the individual bird, the diel factor (day vs. night), and tide height on the habitat use by Whimbrels during the stopover. The activity intensity of Whimbrels was lower during the night than during the day, while the maximum distance that tagged Whimbrels moved was similar between day and night. The saltmarsh and mudflat were intensively used by all of the individuals in all three seasons: > 50% and 20% of all records were obtained from the saltmarsh and mudflat, respectively. Habitat use significantly differed among individuals; the farmland and woodland were used by some individuals in spring 2016, while the restoration wetland near the intertidal area was used by some individuals in 2017. In general, the saltmarsh, farmland, and woodland were more frequently used in the daytime, while the mudflat was more frequently used at night. As tide height increased, the use of the mudflat decreased while the use of the saltmarsh increased. The results suggest that individual-based bio-tracking can provide detailed data on habitat use both during the day and at night. Differences in habitat use among individuals and periods highlight the importance of diverse habitats for bird conservation.

Keywords Individual difference · Diel variation · Tide height · Chongming Dongtan · Migration · Bird conservation

Communicated by T. Gottschalk.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10336-019-01683-6) contains supplementary material, which is available to authorized users.

✉ Zhijun Ma
zhijunm@fudan.edu.cn

1 Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Coastal Ecosystems Research Station of the Yangtze River Estuary Shanghai Institute of Eco-Chongming, Fudan University, Shanghai 200433, China

2 School of Chemistry and Life Sciences, Chuxiong Normal University, 546 South Road of Lucheng, Chuxiong, Yunnan 675000, China

3 Shanghai Chongming Dongtan National Nature Reserve, Shanghai 202183, China

4 Ministry of Education Key Laboratory for Biodiversity and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing 100875, China

Zusammenfassung

Habitat-Nutzung ziehender Regenbrachvögel (*Numenius phaeopus*): eine telemetrische Studie in einem Rastgebiet am Gelben Meer

Für ziehende Vögel sind die Rastgebiete sehr wichtig, um sich dort auszuruhen und neue Nahrung aufzunehmen. Das Verständnis der Ökologie des Vogelzugs zu verstehen und ein wirksames Naturschutz-Management anwenden zu können, hängen davon ab, die Anforderungen an die Rastgebiete möglichst gut zu kennen. Die Nutzung dieser Orte durch die Zugvögel ist bislang jedoch nur unzureichend untersucht worden, und über eine unterschiedliche Nutzung durch unterschiedliche Vogelarten weiß man nur sehr wenig. Im Frühjahr 2016 und Frühjahr und Herbst 2017 verfolgten wir mithilfe von GPS-GSM-Sendern die Ortsbewegungen ziehender Regenbrachvögel (*Numenius phaeopus*) bei Chongming Dongtan, einem wichtigen Rastgebiet am südlichen Gelben Meer in China. Mittels multinomialer logistischer Regressionsanalysen und Multimodel-Inferenz wurden prüften wir den Einfluss des Individuums, der Tageszeit (Tag vs. Nacht) und der Gezeitenhöhe auf die Habitatnutzung der Regenbrachvögel. Die Aktivitätsintensität der Regenbrachvögel war während der Nacht niedriger als am Tag, während die maximale Entfernung, die die markierten Tiere zurücklegten, zwischen Tag und Nacht ähnlich waren. Alle Tiere nutzten die Salzwiesen und Wattflächen intensiv in allen drei Zugzeiten: > 50% und 20% aller Nachweise stammten von den Salzwiesen bzw. dem Watt. Die Nutzung des Habitats variierte jedoch sehr stark zwischen den einzelnen Tieren. So nutzten im Frühjahr 2016 einige Vögel Ackerland und Buschland, während wiederhergestellte Feuchtbiotope nahe der Gezeitenzonen von manchen Tieren im Frühjahr 2017 genutzt wurden. Generell wurden die Salzwiesen, Acker- und Buschflächen stärker während des Tages besucht, das Watt öfters in der Nacht. Mit steigender Fluthöhe nahm die Nutzung des Watts ab und die der Salzwiesen zu. Diese Ergebnisse legen nahe, dass individuelle Telemetrie detaillierte Daten über die Habitatnutzung bei Tag und Nacht liefern kann. Die unterschiedliche Habitatnutzung von Einzeltieren und während verschiedener Perioden unterstreicht die Bedeutung unterschiedlicher Habitate für den Vogelschutz.

Introduction

Many migratory birds fly tens of thousands of kilometers between their breeding and non-breeding grounds every year. During these migrations, the birds generally stay temporarily at one or more stopover sites, where they consume large quantities of food and store a large amount of fuel (Newton 2008). To satisfy the requirement for rapid fuel deposition, the birds must optimize their habitat use during stopovers. Detecting how migratory birds use a variety of habitats at stopover sites is important for understanding migration ecology and selecting conservation measures.

Habitat use can be affected by both extrinsic and intrinsic factors. The extrinsic factors include habitat availability, habitat quality, predation risk, human disturbance, and intraspecific competition (Cody 1985; Pomeroy et al. 2006; Tuomainen and Candolin 2011; Murchison et al. 2016); The intrinsic factors include bird age (van den Hout et al. 2017), gender (Catry et al. 2012), and morphological characteristics (Duijns et al. 2015). Habitat use can also be affected by the character of individuals, as influenced by genetics or early life history (Alves et al. 2010; Holtmann et al. 2017; Spiegel et al. 2017). Although behavioral differences among individuals in the same population have been reported, studies on habitat use generally ignore the individual differences within a population because of the difficulty in tracking the movement of individuals.

Many shorebirds are long-distance migrants and require high-quality stopover sites for refueling during migration. During both migration and non-breeding periods, most shorebirds stay along coasts and forage on macrobenthos on intertidal habitats (Ens et al. 2004). It follows that habitat use is strongly affected by tide rhythm. Shorebirds on tidelands generally forage during low tide, when the intertidal habitats are exposed, and move outside the littoral region during high tide, when the shore is submerged (Dias 2009; Choi et al. 2014). Detecting the effects of tide on habitat use is an important aspect of understanding the habitat ecology of shorebirds.

To achieve the rapid fuel deposition required for migratory flight, most shorebirds forage both in the day and at night at stopover sites (Santiago-Quesada et al. 2014). Habitat use can differ greatly between day and night. On the one hand, the circadian rhythms of the macrobenthos on tidelands affect food availability (McNeil et al. 1995; Esser et al. 2008). On the other hand, many shorebirds are visual foragers, and their foraging efficiency is lower at night than during the day. Birds may improve their foraging efficiency by using different habitats in the day than at night (Beauchamp 2007). Habitat use in the day vs. night can also be affected by predation risk and human disturbance. At night, birds may forage on open habitats to facilitate the detection of nocturnal predators (Burton and Armitage 2005), or may forage on habitats lacking potential predators (Sitters et al. 2001). Because assessing bird activity at night is difficult, little is known about the difference in habitat use between day and night.

With the development of bio-tracking techniques, the movement of individuals can be recorded at fine spatial and temporal scales (Kays et al. 2015), thereby making it possible to detect habitat use by individuals in both the day and at night. In the current study, we analyzed the habitat use of migrating Whimbrels, *Numenius phaeopus*, at Chongming Dongtan (CMDT), a critical stopover site for shorebirds in the East Asian-Australasian Flyway (Barter 2002; Choi et al. 2009). Whimbrels are rather large-sized shorebirds. In the breeding season, they mainly forage in wet heaths, blanket bogs, farmlands, pastures, and serpentine heaths (Massey et al. 2016). In the non-breeding season, they forage along coastal wetlands, such as tidal flats, mangroves, and saltmarshes (Zwarts 1990; Turpie and Hockey 1993; McNeil and Rompre 2010; Watts and Truitt 2011). They can also use artificial habitats such as farmland during migration (Uhlig 1990). Whimbrels are visual foragers but can forage in both the day and at night (Zwarts 1990; Turpie and Hockey 1993). Although the habitat types used by Whimbrels have been well described for both the breeding [e.g., the UK in Massey et al. (2016)] and non-breeding grounds [e.g., South Africa (Turpie and Hockey 1993); the US (Watts and Truitt 2011); and Venezuela (McNeil and Rompre (2010)], habitat use by migrating Whimbrels at stopover sites is poorly understood and individual variation in habitat use has not been investigated. In the current study, we tracked the movements of Whimbrels using bio-tracking technology and analyzed the habitat use among individuals as affected by the diel changes (hereafter day/night) and by tide height.

Methods

Study area

CMDT (121°50′–122°05′E, 31°25′–31°38′N) is an estuarine wetland in the south Yellow Sea (Fig. 1). The tidal cycle is semi-diurnal, with two high tides and two low tides each day (Ma et al. 2011; Hua et al. 2017). The intertidal area is composed of a vegetated saltmarsh at the high and middle tidal flat and a bare mudflat at the low tidal flat. The dominant plants in the saltmarsh are *Scirpus mariqueter*, *Scirpus triqueter*, and *Phragmities australis*. The saltmarsh is submerged by tidewater during the high tide of the spring tide but is exposed in the neap tide and low tide of the spring tide. CMDT contains a large area of restoration wetland, which was created by removing the alien smooth cordgrass (*Spartina alterniflora*) and by providing habitats for waterbirds. The restoration wetland, which is near the natural tideland, has a dense reed community, open water, and dryland that provide foraging, resting, and

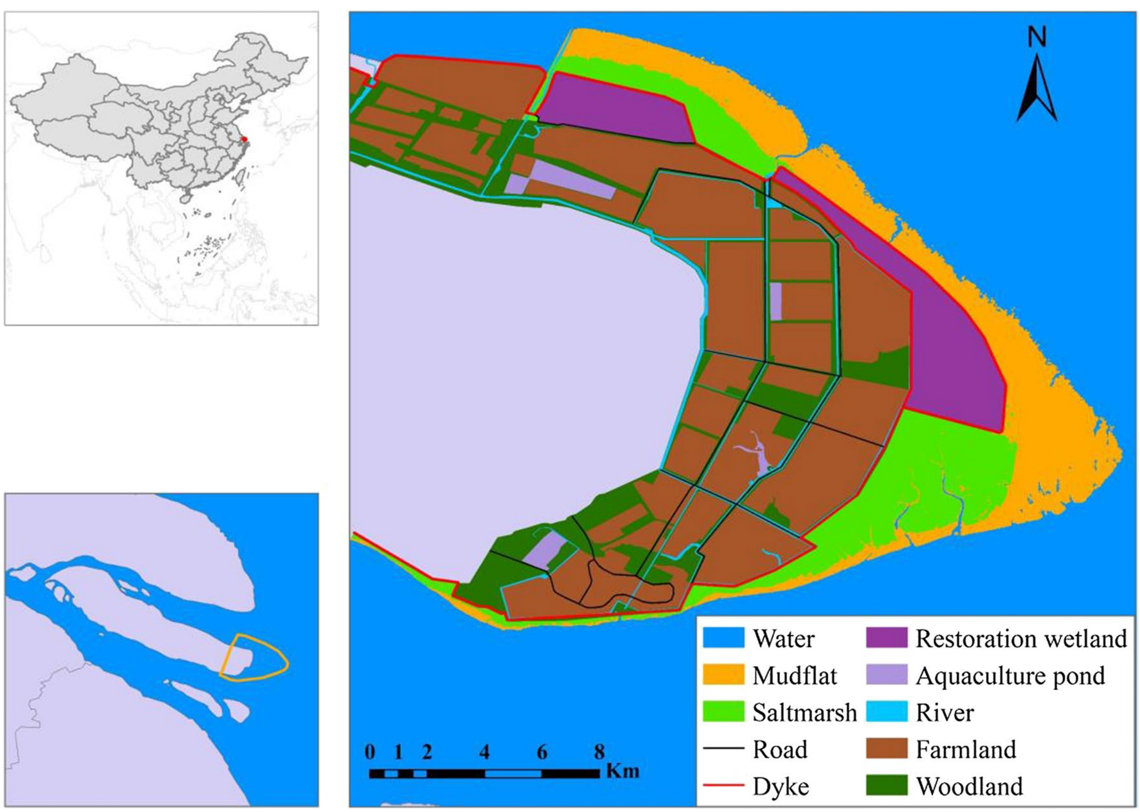

Fig. 1 Location of Chongming Dongtan (CMDT) in China (upper left) and in the Yangtze estuary (lower left), and distribution of habitat types at CMDT (right)

breeding habitats for many birds (Ma 2017). There is also a large area of farmland inside the seawall, where rice and wheat are the major crops. The farmland is usually ploughed in May for rice cultivation and in October for wheat cultivation. Woodland is patchily distributed near the farmland and along rivers at CMDT (Fig. 1).

The Whimbrel is a common migratory shorebird at CMDT. Along the East Asian-Australasian Flyway, the Whimbrel is subspecies *Numenius phaeopus variegatus*. This subspecies mainly breeds in eastern and central Siberia and winters in Southeast Asia and Australia (Barter 2002); about 1000 individuals are recorded in spring and autumn each year at CMDT. During their stopover at CMDT, Whimbrels mainly forage on the intertidal area, including both the saltmarsh and the mudflat (Ma et al. 2009).

Bird capture and tagging

Whimbrels were captured at CMDT using clap nets as part of a shorebird-banding program (Choi et al. 2009) during the northward migration of 2016 and during the northward and southward migration of 2017. After routine weighing, biometric measurement, and ringing of the birds, we attached a solar-powered Global Positioning System–Global System for Mobile Communication tag (model HQPG2009P, 9 g per tag; Hunan Global Messenger Technology, China) to each Whimbrel using a leg-loop harness. A total of 31 birds were tagged during the study period. All of the birds tagged were adults in spring but were first-year birds in autumn. The mass of each tag was 2.0–3.4% of the Whimbrel body mass [270–441 g; Electronic supplementary material (ESM), Table S1]. The tagged birds were placed in a cage for about 30 min and then released if no abnormal behavior was observed.

In accordance with the electric power supply, tags were programed to make one record at 1- to 3-h intervals. The records included information on time, geographic coordinates, instantaneous ground speed, and activity intensity. Activity intensity is an index of physical movement frequency of birds (Hunan Global Messenger 2018); a larger value indicates greater activity intensity. The records were downloaded from the data service platform provided by the manufacturer. We included those records with positioning error < 10 m (84.7% of the total).

We searched for the tagged Whimbrels after release according to their geographical position, and we monitored their behavior for 2–3 days in the field. We found no abnormal behavior among the tagged birds; the tagged birds always remained with other Whimbrels in flocks of about ten birds.

Habitat classification

During the study period, three satellite images (path/row = 118/38) were downloaded from US Geological Survey (USGS) (http://glovis.usgs.gov/). To obtain high resolution (15 m) data, the multi-spectral data and panchromatic data were sharpened using nearest neighbor diffusion after clipping, radiometric calibration, geometric correction, and atmospheric correction. Based on field surveys on habitat types in the study area, we identified main habitat types using supervised classification combined with artificial visual interpretation in ENVI 5.3 and Arcgis 10.3. The habitat type of each fix was then obtained by overlapping with the habitat layer in Arcgis 10.3. Tide height when the fix was recorded was determined from local tide tables (National Marine data and information service 2016, 2017).

Day and night division

The time of civil dawn and civil dusk each day was estimated using the maptools package (Bivand and Lewin-Koh 2017) in R (R Core Team 2016). Day (or daytime) was defined as the period between the beginning of civil dawn and the end of civil dusk, and night was defined as the period from the end of civil dusk to the beginning of civil dawn on the next day.

Data analysis

We collected data from tagged birds that stayed at CMDT for at least 15 days (an entire tide cycle). To avoid the effects of capture and tagging, we excluded data from the first day after capture from the analysis. Because birds might have different behavior and habitat use shortly before departure (Zwarts 1990; Pomeroy et al. 2008), records on the last day before departure were also excluded. In addition, if birds were moving with an instantaneous ground speed > 5 km/h when the fixes were recorded, these fixes were excluded from the analysis. Habitat types with fewer than five fixes (indicating only occasional use) were also excluded. Although the inference and prediction ability of habitat-use models could be affected by spatial autocorrelation, the minimum time interval between two consecutive fixes was never < 1 h, which reduced the dependence of the fixes (Sanzenbacher and Haig 2002).

Generalized linear mixed models (GLMM; family = Poisson, link = log) were used to compare the distance moved per hour of birds in the two major habitat types (saltmarsh and mudflat, see Results) and between day and night, with individual and date as random variables. To understand the difference in movement behavior of Whimbrels between day and night and at various tide heights, the distance moved and activity intensity per hour were calculated. The distance moved per hour was defined as the distance between the two consecutive fixes recorded at a 1-h interval and was calculated using the haversine formula (Sinnott 1984). The effects of tide height and day/night on distance moved and activity intensity were analyzed using GLMM with the lme4 package (Bates et al. 2015). Tide height, day/night, and their interaction were included as fixed effects, and habitat type, individual, time of day, and season were included as random effects.

The probability of habitat use by Whimbrels was estimated using multinomial logistic regression models in the nnet package (Venables and Ripley 2002). The models were separately constructed for each season because different individuals were tracked in different seasons. In each model, habitat type was used as the dependent variable, and individual, day/night, tide height, and their two-way interactions were used as independent variables. The saltmarsh was used as a reference for habitat-use comparison because all of the individuals were recorded in the saltmarsh during the study period. Similarly, the individual that used the most habitat types in each season was used as a reference for comparison of individuals (Agresti 2007). To identify the importance of the candidate models, we constructed a null model involving only the intercept.

The candidate models (ESM, Table S2) in each season were selected using Akaike's information criterion (AIC) in the MuMIn package (Bartoń 2017). The model with the lowest AIC was considered to have the best fit (Burnham and Anderson 2002). In addition, models with AIC difference (Δi; the difference in AIC value between the best-fit model and each of the other models) < 2 were considered to have substantial support (Burnham and Anderson 2002). Akaike weight and evidence ratio were used to evaluate the importance of each model (Burnham and Anderson 2002; ESM, Table S2). The significance of the independent variables and of the regression coefficients in the best-fit model was assessed by the Wald test (Agresti 2007). All statistical analyses were conducted in R (R Core Team 2016). Results are shown as mean ± SD.

Results

A total of 13 tagged Whimbrels remained at the stopover site for more than 15 days during the study period: four individuals in spring 2016, five in spring 2017, and four in autumn 2017 (Table 1). A total of 3020 high-resolution fixes were used for analysis in the current study, including 1864 in the day and 1156 at night. The mean number of recorded fixes was 232 ± 129 per bird (range 112–575; Table 1). During the study period, the tagged Whimbrels were recorded at five habitat types: mudflat, saltmarsh, restoration wetland, farmland, and woodland.

Movements of Whimbrels

The distance moved per hour by the Whimbrels was significantly longer in the daytime (median = 127 m, interquartile range IQR = 47 ~ 397 m, $n = 640$) than at night (median = 82 m, IQR = 19 ~ 530 m, $n = 372$) (U-test, $U = 133{,}470$, $P = 0.001$). The distance moved was significantly affected by tide height ($\chi^2 = 94{,}523$, $df = 1$, $P < 0.001$) and the interaction of tide height and diel ($\chi^2 = 11{,}582$, $df = 1$, $P < 0.001$) (ESM, Table S3). The distance moved per hour increased with tide height, and the increase was much greater at night than in the daytime (ESM, Fig. S1a).

Table 1 Numbers of fixes obtained for the 13 tagged Whimbrels at Chongming Dongtan according to habitat type and diel (day/night)

ID	Tracking days	Saltmarsh	Mudflat	Farmland	Restoration wetland	Woodland	Total
16S1	40	12/90	14/107	295/36	0/0	21/0	342/233
16S2	18	100/45	22/46	33/12	0/0	0/0	155/103
16S3	18	100/57	17/14	0/0	0/0	5/0	122/71
16S4	24	120/38	0/34	0/0	0/0	0/0	120/72
17S1	23	69/17	5/27	0/0	0/0	0/0	74/44
17S2	28	62/19	5/29	0/0	0/0	0/0	67/48
17S3	55	107/33	33/92	0/0	85/0	0/0	225/125
17S4	15	50/20	20/22	0/0	0/0	0/0	70/42
17S5	39	60/26	73/59	0/0	0/0	0/0	133/85
17A1	21	65/7	5/29	0/0	0/15	0/0	70/51
17A2	33	116/20	11/45	0/0	0/0	0/0	127/65
17A3	35	137/25	23/57	0/0	1/9	0/0	161/91
17A4	30	179/5	18/75	0/0	1/46	0/0	198/126
Mean	29.2	91/31	19/49	25/4	7/5	2/0	143/89
SD	11.2	43/23	19/28	82/10	24/13	6/0	78/52

There was no significant difference in the maximum distance moved per hour between daytime (median = 1184 m, IQR = 381 ~ 4499 m, $n = 64$) and night (median = 1481 m, IQR = 380 ~ 3283 m, $n = 59$) (U test, $U = 1875$, $P = 0.95$).

The activity intensity of Whimbrels in the daytime (median = 212, IQR = 5 ~ 818, $n = 640$) was greater than that at night (median = 179, IQR = 12 ~ 1260, $n = 372$) (ESM, Table S3). Moreover, the activity intensity of Whimbrels did not significantly change with tide height in the daytime ($\beta \pm \mathrm{se} = 0.156 \pm 0.215$, $t = 0.725$, $P = 0.469$) but significantly increased with tide height at night ($\beta \pm \mathrm{se} = 0.366 \pm 0.096$, $t = 3.823$, $P < 0.001$) (ESM, Fig. S1b).

Habitat type ($\chi^2 = 5065$, $df = 1$, $P < 0.001$) and the interaction between habitat type and diel ($\chi^2 = 10{,}197$, $df = 1$, $P < 0.001$) significantly affected the distance moved per hour by the Whimbrels. The distance moved per hour on mudflat was significant longer (median = 279 m, IQR = 74 ~ 882 m, $n = 34$) than that on saltmarsh (median = 117 m, IQR = 51 ~ 250 m, $n = 285$) in the daytime, while there was no significant difference in distance moved on mudflat (median = 67 m, IQR = 24 ~ 202 m, $n = 177$) and on saltmarsh (median = 83 m, IQR = 23 ~ 568 m, $n = 96$) at night (ESM, Fig. S2).

Habitat use by the Whimbrels

In spring 2016, most of the Whimbrel locations were recorded in the saltmarsh (59 ± 15%), followed by the mudflat (20 ± 2%), farmland (19 ± 14%), and woodland (2 ± 1%); no tagged Whimbrel was recorded in the restoration wetland. Habitat use was similar in spring and autumn of 2017: saltmarsh was the major habitat type (58 ± 6% in spring and 63 ± 3% in autumn), followed by mudflat (38 ± 5% in spring and 29 ± 1% in autumn) and restoration wetland (4 ± 4% in spring and 8 ± 3% in autumn). No tagged bird was recorded in the farmland or woodland in the two seasons of 2017 (Fig. 2).

Factors affecting habitat use by Whimbrels

Individual, day/night, tide height, and the interaction between individual and day/night, and between tide height and day/night significantly affected habitat use by the Whimbrels in all three seasons (Table 2).

Table 2 Wald tests for multinomial logistic regression models describing the effects of the independent variables on habitat use by tagged Whimbrels

Season and year	Independent variables	χ^2	*df*	*P*
Spring 2016	Bird ID	706.58	9	< 0.001
	Diel	440.88	3	< 0.001
	Tide height	128.47	3	< 0.001
	Bird ID × Diel	96.60	9	< 0.001
	Tide height × Diel	18.96	3	< 0.001
Spring 2017	Bird ID	251.22	8	< 0.001
	Diel	273.17	2	< 0.001
	Tide height	85.18	2	< 0.001
	Bird ID × Diel	28.00	8	< 0.001
	Tide height × Diel	11.87	2	0.003
Autumn 2017	Bird ID	57.99	6	< 0.001
	Diel	529.65	2	< 0.001
	Tide height	127.69	2	< 0.001
	Bird ID × Diel	22.25	6	0.001
	Tide height × Diel	11.29	2	0.004

The indicated combination of independent variables provided the best fit in the indicated season

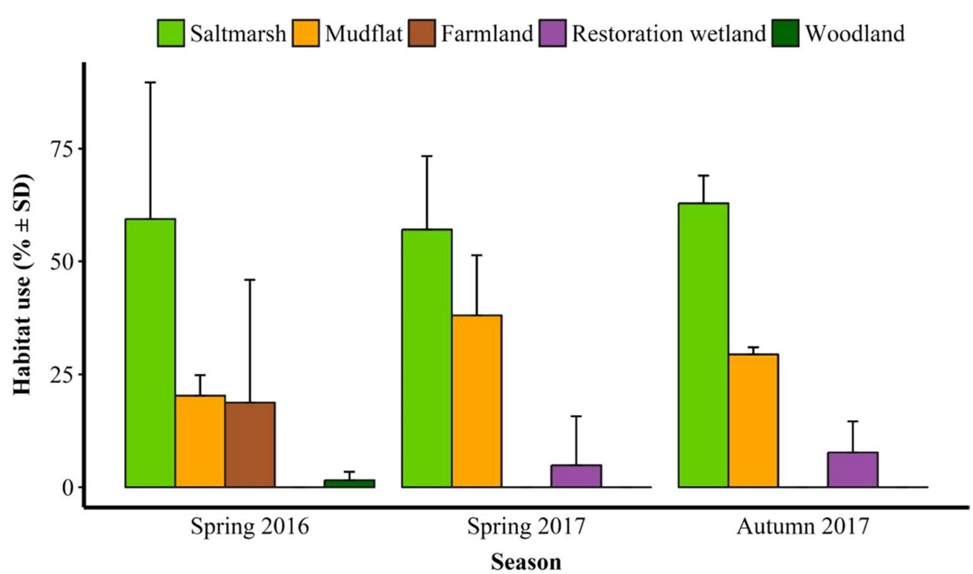

Fig. 2 Habitat use (mean + SD) by tagged Whimbrels in three seasons at CMDT

Individual differences in habitat use

Individuals significantly differed in habitat use in each season (ESM, Table S4, Fig. S3). Although the saltmarsh and mudflat were intensively used by all of the tagged birds, the use of the following habitats in the indicated seasons significantly differed among individuals: saltmarsh (spring 2016, $\chi^2=14.81$, $df=3$, $P=0.002$; spring 2017, $\chi^2=32.17$, $df=4$, $P<0.001$; autumn 2017, $\chi^2=50.91$, $df=3$, $P<0.001$); and mudflat (spring 2016, $\chi^2=82.72$, $df=3$, $P<0.001$; spring 2017, $\chi^2=141.75$, $df=4$, $P<0.001$; autumn 2017, $\chi^2=35.25$, $df=3$, $P<0.001$). In spring 2016, two of the four tagged Whimbrels were recorded in the farmland and two in the woodland. The bill lengths of the two birds recorded in the farmland were shorter than those of the two birds that were not recorded in the farmland (ESM, Table S1, Fig. S3). In 2017, one of the five tagged Whimbrels used the restoration wetland in spring, and three of the four tagged Whimbrels used the restoration wetland in autumn. Individual difference in habitat use was not affected by tidal height but was related to day/night (ESM, Fig. S3, S4).

Difference in habitat use between day and night

There was a significant difference in habitat use between day and night (Table 2, ESM, Table S5). The probability of saltmarsh use was generally higher in the day than at night, while the probability of mudflat use was generally higher at night than in the day. In spring 2016, the probability of farmland and woodland use was significantly higher in the day than at night. In 2017, restoration wetland was only used during the day in spring but was mainly used at night in autumn (ESM, Table S5).

Effect of tide height on habitat use

Tide height significantly affected the use of the saltmarsh and mudflat. As tidal height increased, the probability of saltmarsh use increased, but the probability of mudflat use decreased (Fig. 3, ESM, Table S5). The effect of tidal height on habitat use was related to day/night. Birds were more likely to use the mudflat at night than in the day during low tide, and more likely to use the saltmarsh during the day than at night during low tide (Fig. 3, ESM, Table S5). Moreover, the probability of saltmarsh and mudflat use was more strongly affected by tide height during the night than during the day (Fig. 3, ESM, Table S5). Use of the farmland, woodland, and restoration wetland was less affected than use of the saltmarsh and mudflat by tide height.

Discussion

The results of our study indicate that saltmarsh and mudflat are the major habitat types for migrating Whimbrels at CMDT. This finding may be explained by the distribution of crabs, which are the dominant macrobenthos in the saltmarsh and mudflat at CMDT (Zhu et al. 2007), and the major

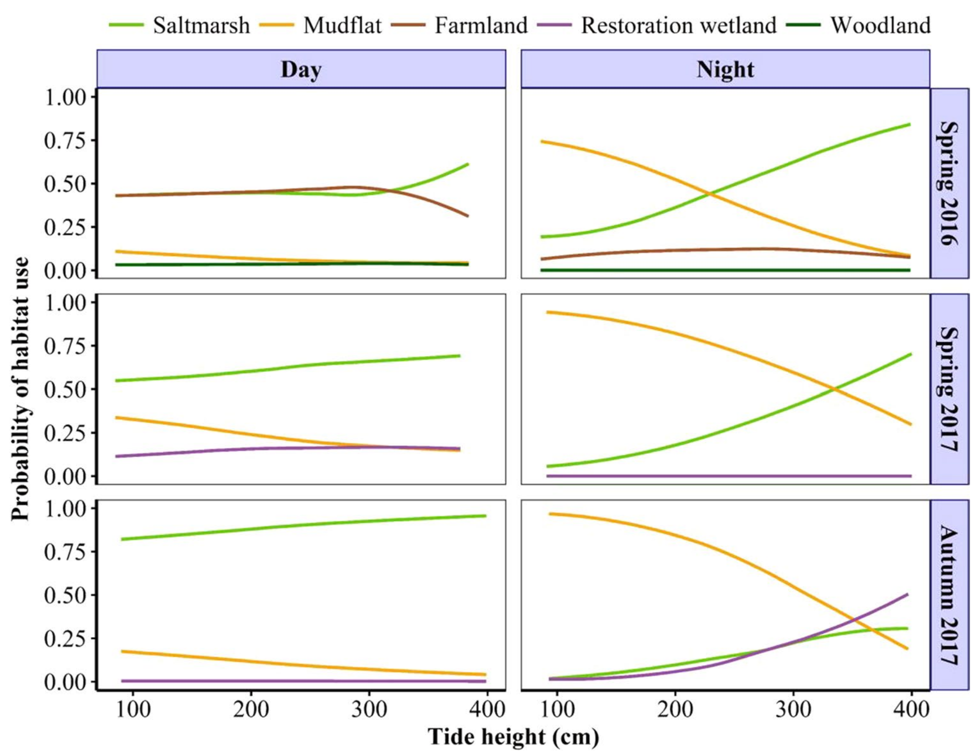

Fig. 3 Effect of tide height on habitat use in the daytime and at night by Whimbrels in spring 2016 and spring and autumn 2017

food for Whimbrels (Zwarts 1990; Turpie and Hockey 1993; Massey et al. 2016). The intensive use of saltmarshes and mudflats by Whimbrels has been reported at other stopover and non-breeding sites such as in Bulgaria (Uhlig 1990) and the US (Watts and Truitt 2011). We found that Whimbrels also used other habitat types, including farmland, woodland, and restoration wetland at CMDT, and that habitat use was affected by day/night and tide height. Moreover, Whimbrels exhibited seasonal differences in habitat use at CMDT. To our knowledge, the current report is the first to use high-resolution bio-tracking technology to document individual differences in habitat use by shorebirds. Our results suggest that individual-based tracking can provide detailed information for studies of habitat ecology.

Seasonal difference in habitat use

The results revealed seasonal differences in habitat use by Whimbrels at CMDT, with the main differences being in the use of the farmland, woodland, and restoration wetland. On the one hand, this might be related to seasonal differences in habitat conditions. The spring stopover period matches the cropping season of the farmland at CMDT. When the farmland is ploughed, some soil animals are exposed at the surface; this facilitated Whimbrel foraging in spring 2016. In spring 2017, however, the cropping season was postponed because of seawater encroachment (Mao 2017). As a result, the farmland was not ploughed during the stopover and therefore was unsuitable for foraging by Whimbrels. This appears to explain why some Whimbrels were frequently recorded in the farmland in spring 2016 but not in spring 2017. Moreover, the farmland in autumn is covered with dense crops and thus cannot be used by the Whimbrels. On the other hand, all of the tracked individuals were adults in spring but were first-year birds in autumn, and previous research has shown that age differences can also affect habitat use between seasons (Cody 1985; Van den Hout et al. 2017). Tracking the movements of the same adults in both spring and autumn should help clarify their seasonal difference in habitat use.

At CMDT, the restoration wetland near the intertidal area was still under construction in spring 2016. With its intensive human disturbance, the restoration wetland was an unsuitable habitat for the Whimbrels. After the construction was completed in early 2017, a large area of bare land and shallow water area provided foraging and roosting habitat for the Whimbrels. Apparently, as a consequence, some tagged Whimbrels were recorded in the restoration wetland after construction, especially during spring high tide in 2017 when the saltmarsh and mudflat were submerged by the tidewater. Tagged Whimbrels were also recorded in the restoration wetland in autumn 2017 after construction had been completed. This suggests that restoration wetland can provide an alternative habitat for Whimbrels.

Individual differences in habitat use

We found that individual Whimbrels exhibited clear differences in habitat use. This could be related to differences in gender or age (Catry et al. 2012; Van den Hout et al. 2017), character (Holtmann et al. 2017; Spiegel et al. 2017), behavioral plasticity (Tuomainen and Candolin 2011), and life experience (Gibelli and Dubois 2017). Habitat use can also differ among individuals because of differences in morphological characteristics, and especially because of differences in foraging organs (Block and Brennan 1993; Catry et al. 2012; Duijns et al. 2015). In spring 2016, the two tagged individuals that were not recorded in the farmland had longer bills than the two birds that were recorded there (ESM, Table S1). This might be because a long bill is advantageous for digging out deep-dwelling food in intertidal areas, while a short bill is advantageous for picking out surface-dwelling food on farmland. Further study on the food composition of birds in different habitats will help clarify the linkage between bill length and habitat use.

Difference in habitat use between day and night

Although the Whimbrel is a visual forager, it can still forage at night at non-breeding grounds (Turpie and Hockey 1993; McNeil and Rompre 2010). The tracking results indicated that the tagged Whimbrels moved frequently at night on intertidal habitat during low tide, suggesting that they were likely foraging at night. Foraging behavior at night has been reported in many shorebird species (Turpie and Hockey 1993; McCurdy et al. 1997; Santiago-Quesada et al. 2014). For migratory birds, nocturnal foraging can accelerate their fuel deposition during a stopover, which increases the probability of their successful migration and on-time arrival at the migratory destination; rapid fuel deposition at a stopover site is important because birds often face severe time constraints during migration (McCurdy et al. 1997; Santiago-Quesada et al. 2014).

The activity of Whimbrels was lower during the night than during the day, indicating that birds spend more time remaining still in the night than in the day. This is consistent with a study of Whimbrels at the non-breeding site at the Zwartkops Estuary Wetland in South Africa, where the frequencies of feeding and walking were found to be lower during the night than day (Turpie and Hockey 1993). In the current study, however, the maximum distance that tagged Whimbrels moved was similar between day and night. This could be related to the effect of the tide. On the intertidal area, birds generally remained in the saltmarsh during the day but stayed on the mudflat when the tide height was low at night (Fig. 3). When the mudflat was submerged by tidewater in the daytime or at night, however, the birds remained in the saltmarsh rather than move to the mudflat. The change of habitat from mudflat to saltmarsh at night increased the distance moved at night. This would also explain why the effect of tide was weaker on bird activity during the daytime than at night.

Information on habitat use at night is important for understanding the habitat requirements of birds (Gillings et al. 2005). Detecting birds at night using traditional methods is difficult but is now quite feasible with the development of bio-tracking equipment. We found a significant difference in habitat use by Whimbrels between day and night at CMDT, which is consistent with the finding for Whimbrels at a non-breeding ground in South Africa (Turpie and Hockey 1993) and for other shorebirds (Sitters et al. 2001; Burton and Armitage 2005). At CMDT, Whimbrels mainly used the saltmarsh during the day but the mudflat at night. Moreover, although only two tagged birds were recorded in farmland in spring 2016, we found that both stayed with other Whimbrels in flocks of about ten birds in the daytime (Z. J. Ma, field observation), suggesting that the use of farmland is not uncommon for Whimbrels. As noted earlier, this could be related to the macrobenthos on the tideland and to the soil animals in the farmland because the availability of both these important foods for Whimbrels follow diurnal rhythms. Crabs, for example, are the dominant macrobenthos in the saltmarsh and the major food for Whimbrels, and are more available in the day than at night (McNeil et al. 1995; Esser et al. 2008). Similarly, the ploughing of farmland, which almost always occurs in the daytime, brings soil animals to the soil surface. Thus, the saltmarsh and farmland provide good foraging habitat for Whimbrels in the daytime. Because it supports few predators and provides a wide field of vision, the mudflat is a relatively safe habitat at night. In heavily vegetated habitats, in contrast, it is difficult to detect nocturnal predators such as weasels (*Mustela sibirica*) and feral dogs. The difference in Whimbrel habitat use between day and night suggests a trade-off between feeding opportunity and predation risk (Sitters et al. 2001; Burton and Armitage 2005; Beauchamp 2007).

Effect of tide on habitat use

For waders foraging on coasts, tide obviously affects habitat availability (Fonseca et al. 2017) and food availability (McConkey and Bell 2005; Esser et al. 2008). At CMDT, the farmland, woodland, and restoration wetland were inside the seawall and thus were free of tidal influence; the saltmarsh and mudflat, however, were periodically submerged by tidewater. Therefore, the use of the mudflat and saltmarsh by Whimbrels was strongly influenced by tide height. In addition, because Whimbrels are more likely to remain on the mudflat at night, they were more affected by the tide during the night than during the day.

Conclusion

Habitat use by migrating birds has been well studied at the population level. Because of the difficulties in identifying and tracking individuals over a long period, however, it has been traditionally difficult to assess differences in habitat use among individuals within a population. This problem has been largely solved by the recent development of bio-tracking technology, which has been increasingly applied to the study of animal movement, especially long-distance migration. The results of the current study suggest that individual-based bio-tracking with a high accuracy of positioning can provide detailed data concerning the habitat use by individual birds during both the day and the night. This new technology will greatly improve our understanding of habitat use by birds and other animals.

The current results indicate that habitat use varies among individuals and that it can be affected by tide and day vs. night. These results highlight the importance of diverse habitat types for bird conservation. Further studies on the differences in physiology, morphology, behavior, and development among individuals could help clarify the causes of individual differences in habitat use. Long-term tracking of individuals will also increase our understanding of the fitness consequences of differences in habitat use.

Acknowledgements We thank the CMDT National Nature Reserve for supporting the fieldwork. We also thank Weiguo Jin, Guochang Ni, Hongxi Zang, Jingyao Niu, and the volunteers for their assistance in the fieldwork, and Xiaodan Wang for help in organizing the draft. We would like thank two anonymous reviewers and the editor for their constructive comments on the manuscript. This study was financially supported by the National Key Research and Development Program of China (2018YFC1406402), the National Natural Science Foundation of China (31830089 and 31772467), the Science and Technology Department of Shanghai (18DZ1205002), the World Wide Fund for Nature Beijing Office (10003881), and the MOE Key Laboratory for Biodiversity Science and Ecological Engineering. All of the fieldwork was conducted with the permission and support of the CMDT National Nature Reserve and strictly complied with the requirements of the Chinese Wild Animal Protection Law.

References

Agresti A (2007) An introduction to categorical data analysis, 2nd edn. Wiley, Hoboken

Alves JA, Lourenco PM, Piersma T, Sutherland WJ, Gill JA (2010) Population overlap and habitat segregation in wintering Black-tailed Godwits *Limosa limosa*. Bird Study 57:381–391

Barter M (2002) Shorebirds of the Yellow Sea: importance, threats and conservation status. Wetlands International, Canberra

Bartoń K (2017) MuMIn: multi-model inference. R package version 1.40.0. https://CRAN.R-project.org/package=MuMIn. Accessed 22 Oct 2017

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Beauchamp G (2007) Exploring the role of vision in social foraging: what happens to group size, vigilance, spacing, aggression and habitat use in birds and mammals that forage at night? Biol Rev 82:511–525

Bivand R, Lewin-Koh N (2017) Maptools: tools for reading and handling spatial objects. R package version 0.9-2. https://CRAN.R-project.org/package=maptools. Accessed 22 Aug 2017

Block WM, Brennan LA (1993) The habitat concept in ornithology: theory and applications. Curr Ornithol 11:35–91

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Burton NHK, Armitage MJS (2005) Differences in the diurnal and nocturnal use of intertidal feeding grounds by Redshank *Tringa totanus*. Bird Study 52:120–128

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

Choi CY, Gan XJ, Ma Q, Zhang KJ, Chen JK, Ma ZJ (2009) Body condition and fuel deposition patterns of calidrid sandpipers during migratory stopover. Ardea 97:61–70

Choi CY, Gan XJ, Hua N, Wang Y, Ma ZJ (2014) The habitat use and home range analysis of Dunlin (*Calidris alpina*) in Chongming Dongtan, China and their conservation implications. Wetlands 34:255–266

Cody ML (1985) Habitat selection in birds. Academic Press, New York

Dias MP (2009) Use of salt ponds by wintering shorebirds throughout the tidal cycle. Waterbirds 32:531–537

Duijns S, van Gils JA, Smart J, Piersma T (2015) Phenotype-limited distributions: short-billed birds move away during times that prey bury deeply. R Soc Open Sci 2:150073

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

Esser W, Voge S, Exo KM (2008) Day-night activity of intertidal invertebrates and methods to estimate prey accessibility for shorebirds. Senckenberg Marit 38:115–122

Fonseca J, Basso E, Serrano D, Navedo JG (2017) Effects of tidal cycles on shorebird distribution and foraging behaviour in a coastal tropical wetland: insights for carrying capacity assessment. Estuar Coast Shelf S198:279–287

Gibelli J, Dubois F (2017) Does personality affect the ability of individuals to track and respond to changing conditions? Behav Ecol 28:101–107

Gillings S, Fuller RJ, Sutherland WJ (2005) Diurnal studies do not predict nocturnal habitat choice and site selection of European Golden-Plovers (*Pluvialis apricaria*) and Northern Lapwings (*Vanellus vanellus*). Auk 122:1249–1260

Holtmann B, Santos ESA, Lara CE, Nakagawa S (2017) Personality-matching habitat choice, rather than behavioural plasticity, is a likely driver of a phenotype–environment covariance. Proc R Soc B 284:20170943

Hua N, Åkesson S, Zhou QY, Ma ZJ (2017) Springtime migratory restlessness and departure orientation of Great Knots (*Calidris tenuirostris*) in the south compared to the north Yellow Sea. Avian Res 8:20

Hunan Global Messenger (2018) Wild Animal Micro Tracker operation instruction. Version 3.02. http://www.hqxs.net/. Accessed 22 Oct 2018

Kays R, Crofoot MC, Jetz W, Wikelski M (2015) Terrestrial animal tracking as an eye on life and planet. Science 348:aaa2478

Ma ZJ (2017) The importance of habitat protection for bird conservation. Bull Biol 52:6–8

Ma ZJ, Wang Y, Gan XJ, Li B, Cai YT, Chen JK (2009) Waterbird population changes in the wetlands at Chongming Dongtan in the Yangtze River Estuary, China. Environ Manage 43:1187–1200

Ma ZJ, Hua N, Zhang X, Guo HQ, Zhao B, Ma Q, Xue WJ, Tang CD (2011) Wind conditions affect stopover decisions and fuel stores of shorebirds migrating through the south Yellow Sea. Ibis 153:755–767

Mao JW (2017) Ten thousand mu of paddy fields were killed by saltwater intrusion at Chongming Dongtan: the responsible party is entangled but when can the rice can be replanted? Shanghai Observer. https://www.shobserver.com/news/detail?id=57209. Accessed 22 Oct 2018

Massey K, Cosgrove P, Massey F, Jackson D, Chapman M (2016) Habitat characteristics of breeding Eurasian Whimbrel *Numenius phaeopus* on mainland Shetland, Scotland, UK. Bird Study 63:500–508

McConkey KR, Bell BD (2005) Activity and habitat use of waders are influenced by tide, time and weather. Emu 105:331–340

McCurdy DG, Boates JS, Forbes MR (1997) Diurnal and nocturnal foraging by Semipalmated Sandpipers *Calidris pusilla*. J Avian Biol 28:353–356

McNeil R, Rompre G (2010) Day and night feeding territoriality in Willets *Catoptrophorus semipalmatus* and Whimbrel *Numenius phaeopus* during the non-breeding season in the tropics. Ibis 137:169–176

McNeil R, Díaz OD, Ildefonso LA, José RRS (1995) Day- and night-time prey availability for waterbirds in a tropical lagoon. Can J Zool 73:869–878

Murchison CR, Zharikov Y, Nol E (2016) Human activity and habitat characteristics influence shorebird habitat use and behaviour at a Vancouver Island migratory stopover site. Environ Manage 58:386–398

National Marine Data and Information Service (2016) Tide tables. Ocean, Beijing

National Marine Data and Information Service (2017) Tide tables. Ocean, Beijing

Newton I (2008) The migration ecology of birds. Academic Press, London

Pomeroy AC, Butler RW, Ydenberg RC (2006) Experimental evidence that migrants adjust usage at a stopover site to trade off food and danger. Behav Ecol 17:1041–1045

Pomeroy AC, Seaman DAA, Butler RW, Elner RW, Williams TD, Ydenberg RC (2008) Feeding–danger trade-offs underlie stopover site selection by migrants. Avian Conserv Ecol 3:580–584

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/. Accessed 22 Jan 2017

Santiago-Quesada F, Estrella SM, Sánchez-Guzmán JM, Masero JA (2014) Why water birds forage at night: a test using Black-tailed Godwits *Limosa limosa* during migratory periods. J Avian Biol 45:406–409

Sanzenbacher PM, Haig SM (2002) Residency and movement patterns of wintering Dunlin in the Willamette Valley of Oregon. Condor 104:271–280

Sinnott RW (1984) Virtues of the Haversine. Sky Telesc 68:159

Sitters HP, Gonzalez PM, Piersma T, Baker AJ, Price DJ (2001) Day and night feeding habitat of Red Knots in Patagonia: profitability versus safety? J Field Ornithol 72:86–95

Spiegel O, Leu ST, Bull CM, Sih A (2017) What's your move? Movement as a link between personality and spatial dynamics in animal populations. Ecol Lett 20:3–18

Tuomainen U, Candolin U (2011) Behavioural responses to human-induced environmental change. Biol Rev 86:640–657

Turpie JK, Hockey PAR (1993) Comparative diurnal and nocturnal foraging behaviour and energy intake of premigratory Grey Plovers

Pluvialis squatarola and Whimbrels *Numenius phaeopus* in South Africa. Ibis 135:156–165
Uhlig R (1990) On the migration of the Whimbrel, *Numenius phaeopus*, in Bulgaria. Zool Middle East 4:33–38
Van den Hout PJ, Piersma T, Horn JT, Spaans B, Lok T (2017) Individual shifts toward safety explain age-related foraging distribution in a gregarious shorebird. Behav Ecol 28:419–428
Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York
Watts BD, Truitt BR (2011) Decline of Whimbrels within a Mid-Atlantic staging area (1994–2009). Waterbirds 34:347–351
Zhu J, Jing K, Gan XJ, Ma ZJ (2007) Food supply in intertidal area for shorebirds during stopover at Chongming Dongtan, China. Acta Ecol Sin 27:2149–2159
Zwarts L (1990) Increased prey availability drives premigration hyperphagia in Whimbrels and allows them to leave the Banc d'Arguin, Mauritania, in spring. Ardea 78:279–300