Migration timing influences the responses of birds to food shortage at their refuelling site

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Short communication

Migration timing influences the responses of birds to food shortage at their refuelling site

WAN-JUAN KE,[1] PENG HE,[1] HE-BO PENG,[1,2,3]
CHI-YEUNG CHOI,[4] SHOU-DONG ZHANG[1,2,3]
DAVID S. MELVILLE[5] & ZHIJUN MA[1]*
[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 (SIEC), Fudan University, Shanghai 200433, China*
[2]*Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC, Groningen, The Netherlands*
[3]*NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems and Utrecht University, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands*
[4]*School of Environmental Science and Engineering, Southern University of Science and Technology, Shenzhen 518055, China*
[5]*Global Flyway Network, Nelson, 7096, New Zealand*

Because migration is highly time-constrained and migration timing varies among individuals, the responses of migrants to food shortage at a refuelling site could differ between individuals that arrive early and late at the site. To test this hypothesis, we compared the stopover decision, in terms of occurrence and length of stay (LOS), of radiotagged Great Knots *Calidris tenuirostris* before (2012) and after (2015) a dramatic decline in food supply at a critical spring final pre-breeding refuelling site in the northern Yellow Sea. The probability of occurrence at the refuelling site was consistent between the two years, whereas the average LOS significantly shortened in the year of food shortage in late-arriving individuals. This suggests migration timing intensifies the influence of food shortage in late-arriving individuals, which might be more sensitive and vulnerable to food shortage at refuelling sites compared with early-arriving individuals.

*Corresponding author.
Email: zhijunm@fudan.edu.cn

Keywords: length of stay, migratory birds, spring migration, stopover decision, stopover site, Yellow Sea.

Food resources are fundamental to the survival and reproduction of animals (White 2008). Food shortage decreases the carrying capacity of habitats and excludes some individuals that fail to acquire enough food to sustain themselves (Gill *et al.* 2001, Lourenco *et al.* 2010). Migratory species, such as many shorebirds, generally form temporary flocks at food-rich refuelling sites during migration (Warnock 2010). When facing food shortage at a refuelling site, migratory shorebirds are able to alter their stopover decisions, i.e. they can move to a different refuelling site (Weber *et al.*1999, Verkuil *et al.* 2012) or reduce their length of stay (LOS) (Stöcker-Segre & Weihs 2014). Because loss and degradation of refuelling sites seriously threaten migratory shorebirds (Baker *et al.* 2004, Piersma *et al.* 2016), understanding their responses to food shortages at those sites is critical for their conservation management.

During migration many migrants spend the majority of their time at stopover sites (Alerstam 1990). LOS at stopover sites determines migration speed and even migration success (Hedenström & Alerstam 1997). Both extrinsic factors (e.g. food abundance, weather conditions and predators) (Jenni & Schaub 2003, Ma *et al.* 2011) and intrinsic factors (e.g. fuel stores and migration timing) (Newton 2006, Arizaga *et al.* 2008, Goymann *et al.* 2010) affect LOS at a stopover site. For example, birds delayed their departure and thus increased their LOS when facing disadvantageous weather condition (Ma *et al.* 2011), but departed earlier and thus shortened their LOS when facing high predation risk (Fransson & Weber 1997). LOS is longer for birds arriving with lower fuel stores (Arizaga *et al.* 2008) and late arrivals exhibit shorter LOS than early arrivals (Ma *et al.* 2013).

For birds breeding at high latitudes, all individuals within a species that breed at the same sites should depart from the final pre-breeding refuelling site within a narrow time window because of the time constraint at the breeding sites (Ma *et al.* 2013, Peng *et al.* 2015). However, the timing of departure from non-breeding grounds is generally quite variable among individuals (Conklin *et al.* 2013, Ma *et al.* 2013). This suggests that early arriving individuals at refuelling sites have longer LOS than those arriving later. As a consequence, individuals with different migration timing could suffer different pressures when food is limited at the refuelling site; early arrivals might have more time to exploit limited food, whereas late arrivals have less time for foraging and may face a food supply already depleted by the early arrivals (Weber *et al.* 1999, Newton 2006). Compared with early arrivals, late arrivals might suffer stronger pressures from food shortage and are predicted to be more likely to look for food at other refuelling sites if they cannot reach the threshold of departure fuel load (Alerstam & Lindström 1990, Weber *et al.* 1999). However, there is still a lack of empirical evidence regarding the influence of migration timing on the responses of migratory species to food shortage under natural conditions.

Here, we investigated the stopover decisions of migrating Great Knots *Calidris tenuirostris* at the Yalujiang estuarine wetland (YLE), a critical final pre-breeding refuelling site in the northern Yellow Sea (Ma *et al.* 2013; Fig. 1). The Great Knot is an endemic shorebird in the East Asian-Australasian Flyway. It is highly dependent on small bivalves for its food at the refuelling site, where the birds double their body mass before departing for their breeding grounds (Ma *et al.* 2013, Choi *et al.* 2017). The arrival period of the Great Knots at YLE lasts for 1 month, and most birds depart from YLE within about 1 week and thus there is great variation in LOS among individuals, with the early arrivals staying for nearly 2 months, whereas late arrivals stay for only 1 month (Ma *et al.* 2013). The food of Great Knots at YLE has dramatically declined since 2013, with available food in 2015 (average 97 bivalves per m^2) being less than one-fifth of that in 2012 (average 697 bivalves per m^2) (Zhang *et al.* 2018). This caused an 85% reduction in daily food intake rate and thus it is unlikely for birds to store sufficient fuel at departure for a successful migration to the breeding grounds (Zhang *et al.* 2018, 2019). This provided an opportunity to compare the stopover decisions, in terms of occurrence and LOS, of Great Knots between 2012 and 2015 to test the hypothesis that individuals with different migration timing responded differently to food shortage, i.e. the LOS of late arrivals would shorten more than early arrivals at YLE.

MATERIALS AND METHODS

During spring migration, Great Knots often make a non-stop flight, or make only a short stop during the journey, from their major non-breeding grounds in Australia to their major stopover site in the Yellow Sea, and then fly

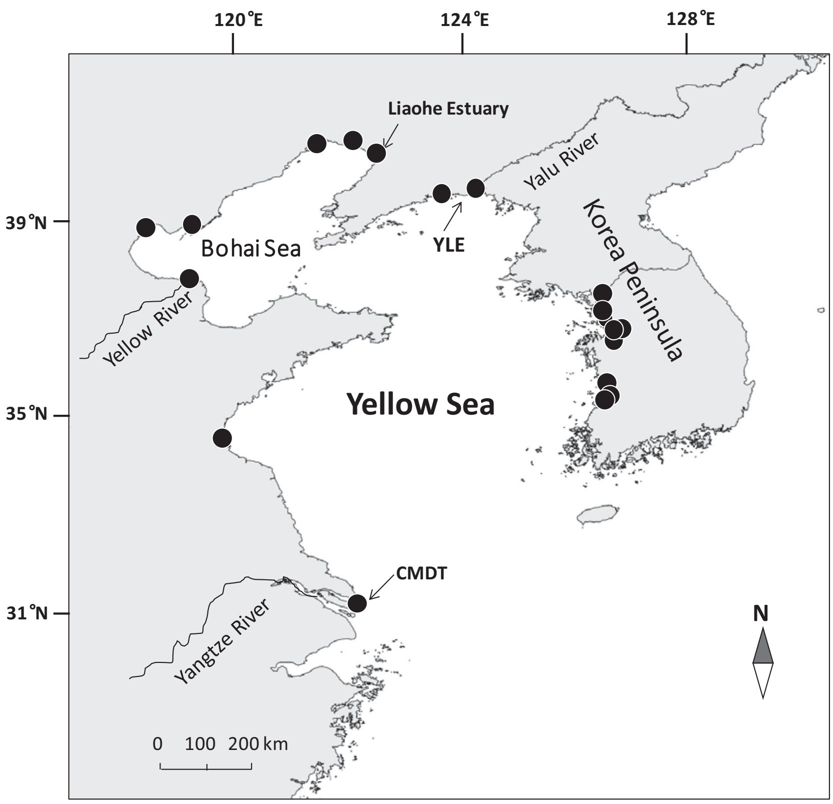

Figure 1. Locations of Chongming Dongtan wetland (CMDT) and Yalujiang estuarine wetland (YLE) in the south and the north part of the Yellow Sea, China. Both arrival and departure windows of the Great Knot population span from late March to late April at CMDT; the arrival window of the population spans from late March to late April and departure window occurs in mid-May at YLE. Black circles mark the key stopover sites of Great Knots in the region.

directly from there to their breeding grounds in Siberia in mid-May (Battley *et al.* 2000, Lisovski *et al.* 2016). Many Great Knots make a brief stopover at the southern Yellow Sea, such as the Chongming Dongtan wetland (CMDT, 31.5°N, 121.9°E), before moving to the northern Yellow Sea, such as the YLE (39.8°N, 123.9°E), for a more extended fuelling stopover (Battley *et al.* 2000, Ma *et al.* 2013, Fig. 1). Great Knots were captured using clap-nets (Choi *et al.* 2009) at CMDT every day except on rainy days from late March to late April in 2012 and 2015. A total of 40 and 78 Great Knots were randomly selected and fitted with radiotags (BD-2, Holohil Systems, ON, Canada, 2.45 g per tag) in 2012 and 2015, respectively, using the method described by Warnock and Warnock (1993).

Tagged birds were tracked throughout the entire region between CMDT and YLE along fixed routes every day (except on rainy days) after being released in both years (Ma *et al.* 2013). At CMDT, we stopped searching for a particular bird only if we could not detect it for five consecutive days, or if the bird had been recorded at YLE. At YLE, we searched for all birds tagged at CMDT every day until the end of the migratory season, so we could find the birds tagged at CMDT as soon as they arrived at YLE. Birds that could not be recorded for five consecutive days were considered to have departed the day after they were last detected (Peng *et al.* 2015). There was no significant difference in the median capture dates at CMDT between the two years (31 March in 2012, $n = 406$; 2 April in 2015, $n = 472$, Wilcoxon rank sum test, $W = 1736.5$, $P = 0.31$). The first day a bird was detected at YLE was used as the arrival date at YLE (D_{YLE}). Because the detection probability (the total number of days a bird was detected/days from the first to the last record of the tagged bird except for the rainfall days without tracking) of tagged birds was high (90% in 2012 and 87% in 2015) (Ma *et al.* 2013) and we used the same methods in both years, we did not correct for detection probability in analysis. The LOS at YLE was calculated as the number of days recorded for each tagged bird. We adjusted the LOS at YLE for the rainy days without detection in 2012 based on detection probability (Ma *et al.* 2013, Fig. S1); there was no rainfall during the day at YLE during the study period in 2015. The interval between arrival at CMDT and arrival at YLE (INT_{CY}) was estimated as the number of days between the capture date at CMDT and the first day when a bird was recorded at YLE.

Generalized linear models (GLMs, family = binomial, link = logit) were used to assess the effects of arrival date at CMDT (D_{CMDT}), Year (2012 or 2015), body mass at capture (M), and the two-way interactions between D_{CMDT} and Year, and between D_{CMDT} and M on the occurrence of tagged birds at YLE. GLMs (family = Gaussian, link = identity) were used to test the effects of variables above on INT_{CY} of tagged birds that occurred at YLE. Inter-annual difference of M of birds that were detected at YLE was tested using GLMs (family = Gaussian, link = identity) accounting for D_{CMDT}, Year and the interaction between them. Linear models were further used to assess the effects of D_{YLE}, Year and their interaction on the LOS of birds at YLE. LOS was logarithmically transformed to improve normality; an outlier data point in 2012 (one bird was not detected after 12 April, whereas all other birds departed on 17 May ± 2 days, $n = 11$) was excluded from the analysis. Data analysis was performed with the R software, version 3.5.1 (R Development Core Team 2018). We used $P < 0.05$ to establish statistical significance and means ± sd are given.

RESULTS

Of the tagged birds at CMDT, 30% (12 of 40) were detected at YLE in 2012 and 28% (22 of 78) in 2015. There was no significant difference in the probability of occurrence at YLE between the two years ($\chi^2 = 0.04$, df = 1, $P = 0.84$). D_{CMDT} affected the probability of occurrence at YLE, with late arrivals at CMDT being less likely to be detected at YLE than early arrivals ($\chi^2 = 11.71$, df = 1, $P < 0.001$, Fig. 2a).

For the birds detected at YLE, there was no significant interannual difference in M ($\chi^2 = 2.26$, df = 1, $P = 0.13$), INT_{CY} ($\chi^2 = 1.96$, df = 1, $P = 0.16$) or D_{YLE} ($\chi^2 = 0.01$, df = 1, $P = 0.98$; Fig. 3). However, there was a significant shortening of LOS at YLE in 2015 (16.0 ± 11.6 days, $n = 22$) compared with that in 2012 (29.5 ± 4.9 days, $n = 11$) ($F = 7.71$, df = 1, $P = 0.01$, Fig. 3) and later arrivals exhibited shorter LOS than early arrivals ($F = 4.70$, df = 1, $P = 0.04$, Fig. 2b). Furthermore, the interaction between the variables of Year and D_{YLE} significantly affected the LOS at YLE ($F = 4.50$, df = 1, $P = 0.04$), with the late arrivals exhibiting shorter LOS in 2015 than in 2012 (Fig. 2b). The η^2 for the interaction term was 0.07, suggesting that the effect was not strong. Most tagged birds (92%, 11 of 12) stayed at YLE until mid-May in 2012, compared with only 32% (7 of 22) in 2015.

DISCUSSION

Great Knots refuel in the Yellow Sea each year during spring migration (Lisovski *et al.* 2016, Piersma *et al.* 2016). Although a dramatic decline in food availability has occurred at their traditional refuelling site at YLE since 2013 (Zhang *et al.* 2018), the probability of occurrence at YLE was similar between the tagged birds in 2012 and 2015, suggesting persistent use of the refuelling site by Great Knots. This might be explained by strong site fidelity, which has been documented for many waterbird species including shorebirds (Taylor & Bishop 2008, Buchanan *et al.* 2012). Moreover, the late

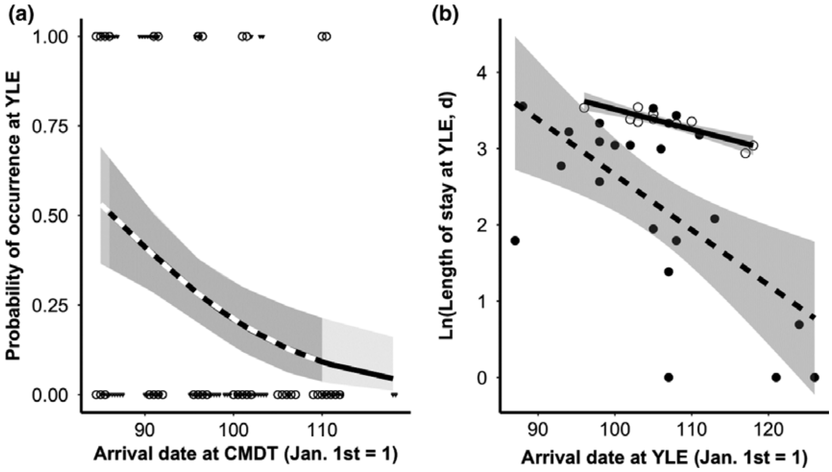

Figure 2. (a) The probability of occurrence at Yalujiang estuarine wetland (YLE) of tagged Great Knots in 2012 (dashed line, n = 40) and 2015 (solid line, n = 78) as a function of arrival date at Chongming Dongtan wetland (CMDT). Occurrence data (0 = not detected and 1 = detected at YLE) of tagged birds in 2012 (open circles) and 2015 (filled triangles). Some data were modified (± 0.5 days in 2012 and ± 0.3 days in 2015) to avoid overlap of individuals. (b) The length of stay (LOS) of tagged Great Knots at YLE as a function of arrival date at YLE in 2012 (filled circles, n = 11) and 2015 (open circles, n = 22).

arrivals at CMDT exhibited a lower probability of occurrence at YLE in both years, suggesting that early and late migrants are following different migration strategies and use different refuelling sites irrespective of food abundance.

Tracking the migration of Great Knots indicates that birds departing from the Yellow Sea flew directly to the breeding grounds during their northward migration (Lisovski *et al.* 2016), suggesting there is lack of adequate refuelling sites further north and birds were required to deposit large amounts of fuel in the Yellow Sea for their non-stop flight of several thousand kilometres (Ma *et al.* 2013). This is supported by the observation of Great Knots departing from YLE by mid-May with their body mass being doubled during stopover (Ma *et al.* 2013). In 2015, however, only one-third of tagged birds stayed at YLE until mid-May. Because the time window for breeding at high latitudes is narrow, arriving too early at the breeding site can mean experiencing cold weather and food shortage (Klaassen 2003). Thus, birds that left earlier than usual were likely to have moved to other refuelling sites in the Yellow Sea instead of flying to the breeding grounds. Indeed, six tagged birds were detected at Liaohe Estuary, about 160 km further west, after leaving YLE in 2015 (P. He pers. obs.), whereas in 2012, no tagged birds were detected at other stopover site in the northern Yellow Sea after departure from the YLE. Although the peak numbers of Great Knots in late April were similar in the two years at YLE, the count in May 2015 was lower than in 2012 (Zhang *et al.* 2018). This further supports the finding that some individuals left YLE earlier in 2015 than in 2012.

Tagged birds exhibited similar body mass at capture, interval between arrival at CMDT and arrival at YLE, and arrival date at YLE in the two years. Moreover, there was no interannual difference in weather conditions (in terms of daily mean temperature and wind assistance, Table S1) and predation pressures (C.-Y. Choi pers. obs.) at YLE, suggesting that birds experienced similar environmental condition in the two years, except for the changed food conditions at YLE. Compared with 2012, when food was more abundant, the mean LOS of tagged birds significantly shortened in 2015 when food dramatically declined. This could be largely due to the late arrivals shortening their LOS. This suggests that food shortage at a staging site reduces stopover duration, and migration timing could amplify the impact. The effects of interaction between the year and arrival date on the LOS, however, was not very strong, but this may be due to the small sample size.

With shorter stopover duration at YLE, late arrivals require a higher refuelling rate than early arrivals to deposit enough fuel for their next stage of migratory flight (Atkinson *et al.* 2007, Ma *et al.* 2013). However, food is usually depleted by early arrivals, and thus late arrivals could be penalized by a reduced refuelling rate (Weber *et al.* 1999, Newton 2006). Theoretical studies have predicted that reduced refuelling rate will delay the departure date, especially if a high departure fuel load is required (Weber *et al.* 1999). However, birds will miss the breeding time window if they depart from YLE too late. When they cannot achieve a high fuelling rate to deposit enough fuel before the departure window, late arrivals might explore other unfamiliar

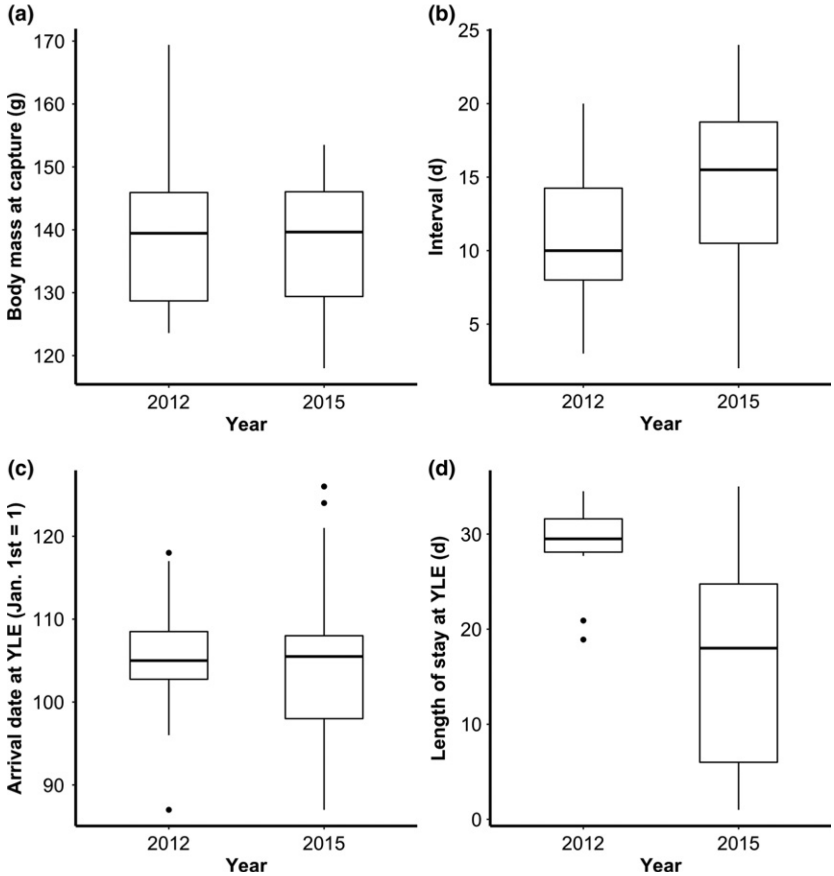

Figure 3. Body mass at capture (a) and interval between arrival at Chongming Dongtan (CMDT) and arrival at the Yalujiang estuarine wetland (YLE) (b), arrival date at YLE (c) and length of stay at YLE (d) of tagged Great Knots recorded at YLE in 2012 (n = 11) and 2015 (n = 22). Horizontal lines show the median, and upper and lower hinges of box plots represent the first and third quartiles. Lower whiskers represent the value greater than lower hinge + 1.5 × interquartile range and upper whiskers represent the value less than upper hinge + 1.5 × interquartile range.

refuelling sites. Early arrivals, by contrast, have a relatively long stopover period and a relatively good food status in the early period, and thus might exploit familiar refuelling sites (Alerstam & Lindström 1990). This supports the theoretical prediction that late arrivals are more vulnerable to food decline at refuelling sites compared with early arrivals (Weber *et al.* 1999). By integrating migration timing and body state, individuals might be able to assess food condition and fuel deposition rate at a refuelling site to decide whether to exploit the familiar site or to search for a new site (Weber *et al.* 1999, Katz & Naug 2015).

Birds can use alternative refuelling sites as a buffer against loss and degradation of traditional refuelling sites (Weber *et al.* 1999). In this study, although some individuals apparently changed their refuelling sites to cope with the food shortage at YLE, it remains unclear whether they can deposit sufficient fuel at other sites to complete migration successfully. Time constraints on late arrivals might make them more vulnerable than early arrivals to food shortage at a refuelling site, which could affect both survival and breeding via a domino effect (Baker *et al.* 2004). Tracking the full annual cycle of individuals will help to clarify the fitness consequences of food shortage at refuelling sites.

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SUPPORTING INFORMATION

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

Table S1. Comparison of weather conditions in terms of daily mean temperature (T) and wind effects (ΔW) during spring stopover of Great Knots (from March 26 to May 22) at YLE between 2012 and 2015.

Figure S1. Tracking records of tagged Great Knots at Chongming Dongtan (CMDT, open squares), Yalujiang Estuarine wetland (YLE, circles) in 2012 (a) and 2015 (b). The solid vertical lines indicate those days on which the tracking was completely suspended and the dotted lines indicate those days on which the tracking covered part of the study area at YLE (thus some individuals were recorded) due to rain.