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Migration departure strategies of shorebirds at a final pre-breeding stopover site

Kun Tan¹, Chi-Yeung Choi², Hebo Peng^{1,3,4}, David S. Melville⁵ and Zhijun Ma^{1*}

Abstract

Background: Departure decisions and behaviors of migratory birds at stopover sites are expected to maximize fitness by trade-offs among avoiding predators, optimizing refueling (energy) capacity, and matching other life-history events. We predict that species with different body sizes and migratory destinations will exhibit different behaviors when departing from the same stopover site. We also predict that with strong time constraint at the final pre-breeding stopover site, departure decisions may be less sensitive to exogenous factors, such as wind condition, compared to other stopover or nonbreeding sites.

Methods: We recorded migratory departures of four shorebird species, i.e. Eurasian Curlew (*Numenius arquata*), Bar-tailed Godwit (*Limosa lapponica*), Great Knot (*Calidris tenuirostris*), and Grey Plover (*Pluvialis squatarola*), at Yalujiang Estuary Wetlands in China, a final pre-breeding stopover site in the northern Yellow Sea, from 2011 to 2014. We compared flock sizes, departure time and departure directions between species, and investigated the effects of tide and weather conditions (rain and ground wind speed and direction) on the departure decision of shorebirds.

Results: We found that larger species departed in smaller flocks and were more variable in daily departure time. Departure trajectory of all four species appeared to be influenced by coastal topography. With the east–west coastline and intertidal mudflat on the south, birds exhibited westward or eastward deflection from the shortest migratory routes. Bar-tailed Godwit was the only species that deviated to the southeast and did not climb over the land. Birds avoided departure during precipitation, while their departure was not related to ground wind benefit or tidal condition.

Conclusions: Body size among species, which influences their vulnerability to predators, might be important in shaping shorebird departure strategies. Diverse departure directions could be the result of different wind use tactics in climbing stage. Narrow optimal time window of breeding might lead to reduced flexibility in departure date at a final pre-breeding site. Both endogenous and exogenous are important in shaping departure behaviors and decisions.

Keywords: Migration, Departure decision, Departure behavior, Shorebird, Stopover, Wader, East Asian–Australasian Flyway

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Background

Many migratory birds need one or more stopover sites to refuel and/or rest *en route*. They are expected to adjust departure decisions and behaviors at stopover sites to avoid predators, optimize energy deposition and match other annual life-history events (e.g. breeding) to maximize fitness (Newton 2010). Species subject to different predation pressure, energy demands, orientation cues, and climbing tactics could perform differently in the same environment. Therefore, we may compare departure strategies of different species departing from the same location in a similar migratory stage to assess which factors may influence their departure behaviors.

The relative effect of exogenous factors on departure decisions might also be related to migratory stage the bird is in. For example, departure from a final stopover site before arriving at the breeding ground will directly determine the arrival date at the breeding grounds and time window for breeding is relatively narrow, especially for birds breeding at high latitudes. In consequence, endogenous schedules might prevail over exogenous factors in this stage of the migration and birds might show less flexibility in date selection than those departing from non-breeding or other stopover sites (Warnock 2010; Hua et al. 2017; Shamoun-Baranes et al. 2017). Departure decisions from final stopover sites have been little studied (Greenberg and Marra 2005).

Flock sizes of birds are considered to be a trade-off between predator avoidance and foraging efficiency (O'Reilly and Wingfield 1995). Grouping might also be important for navigation (Simons 2004), migration initiation, breeding synchronization, and information acquisition and updating (Conradt and Roper 2005; Nemeth and Moore 2014). Larger groups may be associated with longer distance migration (Beauchamp 2011), but not in all cases (Kshatriya and Blake 1992).

Daily departure time selection involves safety, energy gain and orientation cues (Ydenberg et al. 2004; Alerstam 2009). Departure in the late afternoon or at night can maximize diurnal foraging time (Alerstam 2009) and avoid diurnal predators (Lank 1989). Sunrise and sunset is the time when skylight polarization is the strongest. Birds can use the polarized light for orientation or recalibration (Cochran et al. 2004; Åkesson and Hedenström 2007; Horváth 2014). The departure time of shorebirds which forage on tidal flats, has been linked to the tide cycle: by departing at high tide or on an incoming tide, birds could maximize their potential foraging time (Lank 1989); rising tide might also discourage foraging and encourage migration initiation (Battley 1997). Departure direction is generally used to deduce migration route and destination of shorebirds (Alerstam et al. 1990; Gudmundsson and Lindstrom

1992; Tulp et al. 1994). However, there might be some detour in climbing up, which is related to wind condition and topographic characters (Alerstam et al. 1990; Piersma et al. 1990).

Departure decision is strongly affected by weather conditions. Tail wind is usually favored as it can speed up migration (Liechti and Bruderer 1998), decrease energy expenditure (Åkesson and Hedenström 2007) and reduce risk of being blown off course (Battley et al. 2012). Bar-tailed Godwits' (*Limosa lapponica*) off-schedule departures and departure-track directions were associated with unfavorable wind (Gill et al. 2009). Red Knots (*Calidris canutus*) and Great Knots (*Calidris tenuirostris*) on pre-breeding migration tended to rest at stopover sites with low resources when facing headwind (Piersma and van de Sant 1992; Shamoun-Baranes et al. 2010; Ma et al. 2011). However, not all birds are sensitive to wind condition (Åkesson and Hedenström 2000; Alves et al. 2016). Precipitation is avoided as it causes weight increase and heat loss (Richardson 1978). Although multiple orientation cues may be applied by long-distance migratory birds which fly throughout both day and night, and because they need to cope with the absence of some cues in certain latitudes (Moore 1980, 1987; Gudmundsson and Sandberg 2000; Grönroos et al. 2010), it is easier to access light-relative cues, such as sun direction and skylight polarization when departing in clear sky.

Many shorebirds undertake long-distance journeys every year along the East Asian–Australasian Flyway. The Yalujiang Estuary Wetlands (hereafter YLE), located in the northern Yellow Sea, support over 150,000 shorebirds in the pre-breeding stopover period annually (Barter et al. 2000; Riegen et al. 2014; Bai et al. 2015). Those birds, especially large- to medium-sized shorebirds, such as Eurasian Curlew (*Numenius arquata*), Bar-tailed Godwit, Great Knot, and Grey Plover (*Pluvialis squatarola*) use this tidal flat as an important refueling site (Bai et al. 2015; Choi et al. 2015, 2017). Satellite-tracking records show that YLE is also the final pre-breeding stopover site for Bar-tailed Godwits (of both races *menzbieri* and *baueri*) (Battley et al. 2012) and Great Knots (Lisovski et al. 2016). This provides an opportunity to compare departure behaviors between species and explore possible factors related to migration decisions at the final stopover site (Table 1).

We examined the departure behaviors of shorebirds at YLE, with the aim is to explore the different departure strategies among species and deduce the possible causes for the difference, such as weather condition and tidal stages. We also investigated whether there was less flexibility in date selection under strong time constraints.

Table 1 Results of correlation analysis between departing individuals and wind benefits

| | 2013 | | | | 2014 | | | |
|-------------------|------------------|---------|------------------|---------|------------------|---------|------------------|---------|
| | Åkesson's method | | Piersma's method | | Åkesson's method | | Piersma's method | |
| | r value | p value |
| Eurasian Curlew | | | | | | | | |
| 1500 h | -0.05 | 0.84 | -0.05 | 0.84 | 0.01 | 0.94 | 0.01 | 0.94 |
| 1800 h | 0.11 | 0.63 | 0.11 | 0.63 | 0.00 | 0.98 | 0.00 | 0.98 |
| Bar-tailed Godwit | | | | | | | | |
| 1500 h | | | | | | | | |
| 4° | 0.24 | 0.26 | 0.31 | 0.24 | 0.02 | 0.76 | 0.08 | 0.76 |
| 35° | 0.39 | 0.06 | 0.42 | 0.04* | -0.08 | 0.75 | -0.13 | 0.60 |
| 92° | 0.25 | 0.26 | 0.25 | 0.26 | 0.08 | 0.94 | 0.02 | 0.94 |
| 1800 h | | | | | | | | |
| 4° | 0.06 | 0.79 | 0.11 | 0.61 | 0.13 | 0.61 | 0.11 | 0.68 |
| 35° | 0.08 | 0.71 | 0.13 | 0.55 | -0.02 | 0.93 | -0.20 | 0.42 |
| 92° | 0.06 | 0.79 | 0.11 | 0.61 | 0.13 | 0.61 | 0.11 | 0.68 |

Italic values indicate $p < 0.1$

* $p < 0.05$

Methods

Species

Eurasian Curlew (subspecies *orientalis*) has the largest body size among the four species (body length: 40–60 cm; wingspan: 80–100 cm), breeding in Eastern Siberia to Northeastern China and spending the non-breeding season mainly in Eastern and Southeastern Asia. Two subspecies of Bar-tailed Godwit (body length: 37–41 cm; wingspan: 70–80 cm): *L. l. baueri* breeds in Alaska and spends the non-breeding season mostly in eastern Australia and New Zealand, while *L. l. menzbieri* breeds in north-eastern Siberia and spends the non-breeding season mainly in northwestern Australia (Battley 1997). Grey Plovers (subspecies *tomkovichi* and *squatarola*; body length: 27–31 cm; wingspan: 71–83 cm) breed in Northeastern Siberia and spend the non-breeding seasons on the coasts of eastern and southeastern Asia and Australia. The Great Knot (body length: 26–28 cm; wingspan: 56–66 cm) is endemic to the East Asian–Australasian Flyway, breeds in northeastern Siberia and spends the non-breeding season mainly in Australia and south-east Asia (Piersma et al. 1996). The four species feed exclusively on tidal flats at YLE before departing for their breeding grounds (Choi et al. 2017).

Study site and field observation

Our study was conducted on the tidal flat of YLE (39°8'N, 123°9'E, Fig. 1a). The coastline in this area lies along an east–west axis with the tidal flat to the south (Fig. 1b). Tides are semidiurnal with each cycle about 12 h and

25 min long (Bai et al. 2008), with a range of about 7 m, resulting in tidal flats up to about 5 km wide being exposed on low spring tides.

Shorebird departures were recorded opportunistically during field work in April and May, 2010–2012, but observations were carried out by 1–2 observers from 8:00 to 18:00 h every day except those with heavy rains, as long as the tide flat was not fully covered from 7 April to 31 May 2013 and from 4 April to 26 May 2014. Flocks that were seen leaving from the tidal flats, as well as those observed flying past giving characteristic, loud, “migration” calls (Piersma et al. 1990; Tulp et al. 1994), were recorded. Departing shorebirds were followed with binoculars (8×) and spotting scopes (20–60×) until out of sight. Date, time, flock size, species composition and trajectory direction were recorded. A compass bearing was taken at the instant that the birds disappeared from view.

Data analysis

Surface wind direction, wind speed (1500 h, before departure peak, 1800 h, around departure peak, see below), and precipitation were collected from the Dandong weather station (39°6'N, 124°20'E) and downloaded from NOAA website (<http://gis.ncdc.noaa.gov>). Tide data of Dandong Port were obtained from China Oceanic Information Network (<http://www.nmdis.org.cn/>).

Kruskal–Wallis tests were conducted to determine if there were significant differences in flock sizes and daily departure time among species. Dunn's multiple comparisons were conducted when significant differences existed.

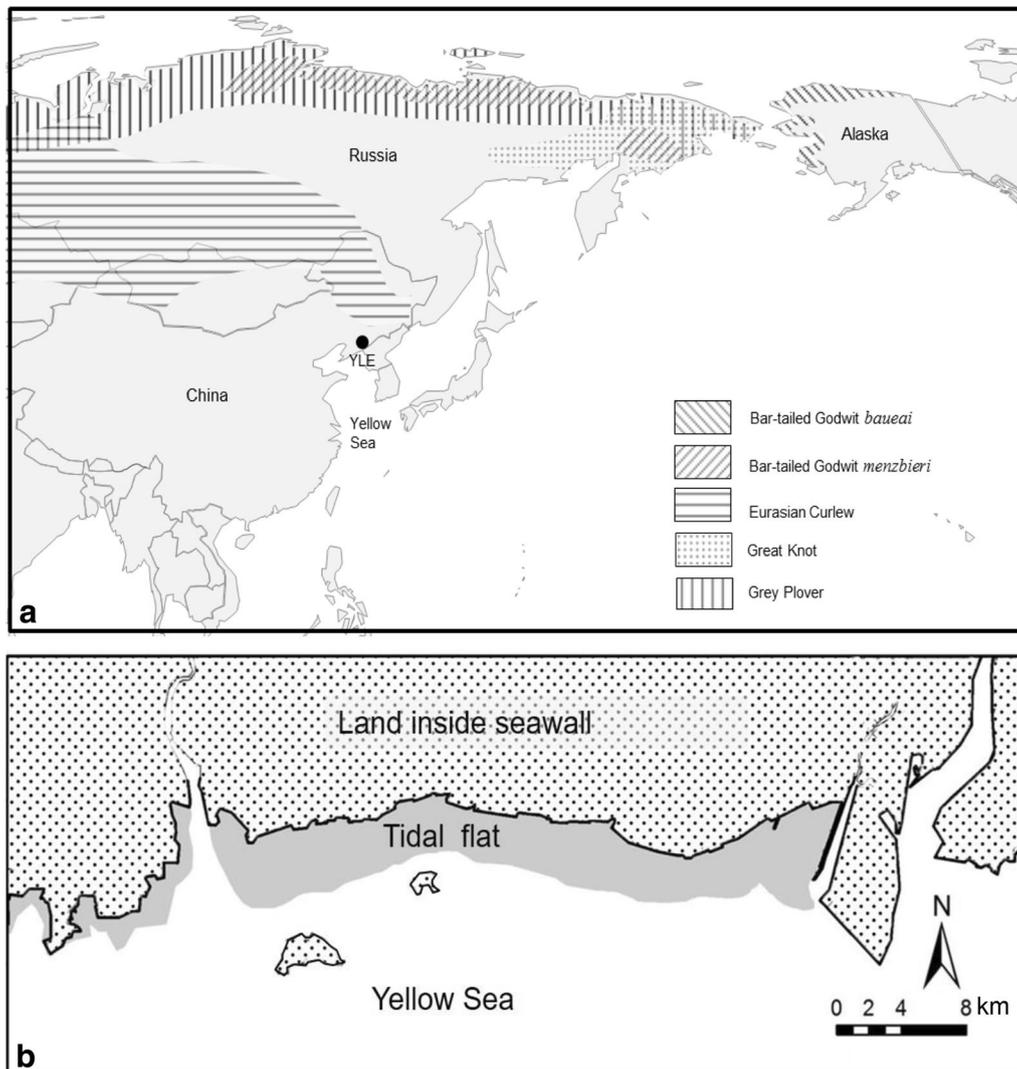


Fig. 1 Location of the Yalu Jiang Estuary Wetlands (YLE, the black dot) and the breeding grounds of the four species (a), and sketch map of YLE (b)

Nonparametric tests were used for the data did not coincide with normal distribution.

We calculated the initial bearing ranges if the birds were to follow the great circle (shortest distance routes) or rhumb line (routes with constant angle relative to magnetic north) towards their breeding ground. From these we could then determine if there was any detour in direction as the birds climbed during migratory departure. The two subspecies of Bar-tailed Godwits, *baueri* and *menzbieri* were analysed separately. Previous research showed that the departure peak of *menzbieri* was around 15 May (Choi et al. 2015), so we also summarized departure directions of Bar-tailed Godwits' departure flocks before and after this date in 2013 to assess possible differences between subspecies.

We used both Åkesson's and Piersma's methods to estimate the benefit birds may obtain from wind (Piersma and Jukema 1990; Åkesson and Hedenström 2000). Åkesson's method only includes tail wind components upon track direction, and the wind effects were calculated as $V_w \times \cos(\phi_t - \phi_w)$, where V_w is the wind velocity, ϕ_t is the mean preferred track direction of departing birds and ϕ_w is the wind direction. Piersma's method assumes that birds always try to remain on a fixed track direction when encountering side wind; the wind benefits are calculated as $V_w \times \cos(\phi_t - \phi_w) + (V_a^2 - (V_w \times \sin(\phi_t - \phi_w))^2)^{0.5} - V_a$, where V_a is the airspeed of the bird. In the latter formula, we assumed airspeed of shorebirds to be 65 km/h (Battley 1997). To test the possible influence of wind use, we

did correlation analyses between the number of migration birds and wind benefits, and compared the wind benefits between days with departure and days without. For Eurasian Curlew we used the actual observed direction of departure as the flight track direction for the direction we recorded was consistent with the direction of their breeding ground (See results below on departure direction). The migration goals of Bar-tailed Godwits were set as 5° (the shortest route to the center of the breeding ground of subspecies *menzbieri*) and 35° (subspecies *baueri*). We also used the actual observation directions in Bar-tailed Godwits (92°, average direction we observed) because the departure direction deviated from their destination (See results below). We excluded days with precipitation as we found that all the birds avoided departure in rain. The potential departure time window of each species was set from the third day before the day we observed the first departure flock in the year to the third day after the day the last departure flock was recorded.

In the analysis of relationship between departure decision and tide condition, we classified tide condition arbitrarily into five levels according to predicted tide height using 100 cm divisions (Tidal range is 0 to around 500 cm before the tide flat was almost fully covered). We then conducted Pearson correlation analyses between numbers of departing birds and tide heights to determine whether departure decisions were related to tide levels. For the analyses of tide cycle and weather, we only included Bar-tailed Godwit and Eurasian Curlew for which we had sufficient samples (> 50 flocks departing).

All statistics was performed in software R (R Development Core Team 2016).

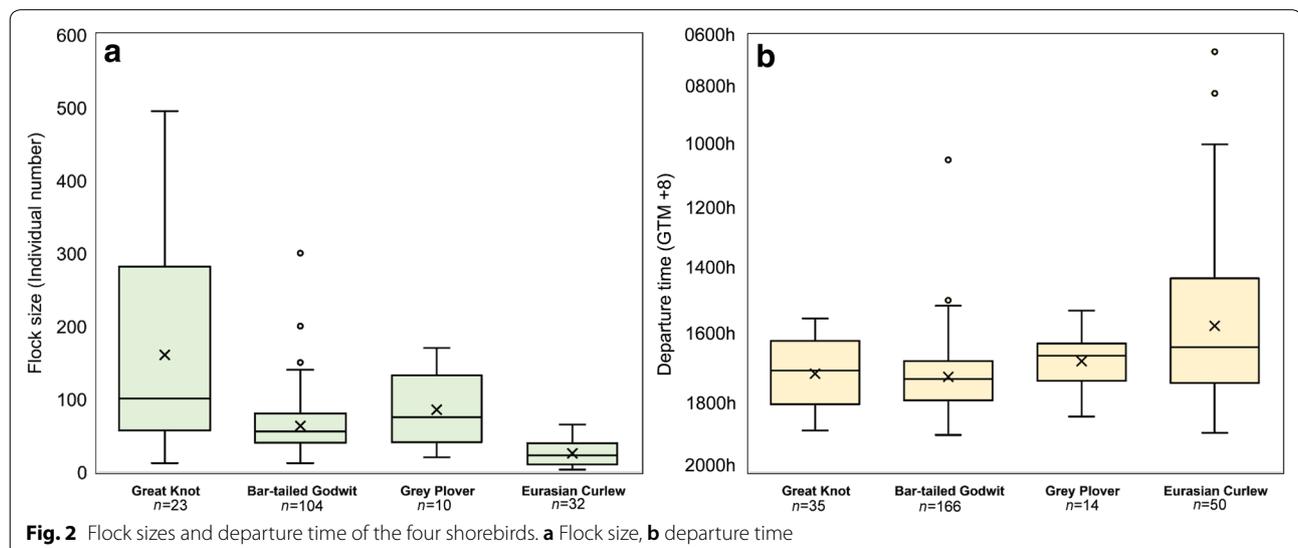
Results

Flock sizes and species composition

We recorded the departure of 10,604 Bar-tailed Godwits, 6458 Great Knots, 2443 Eurasian Curlews, and 1208 Grey Plovers. A total of 266 out of 272 departure flocks were composed of a single species. In the six mixed-species flocks, three were composed of Bar-tailed Godwits and Grey Plovers, two with Bar-tailed Godwits and Eurasian Curlews, and one with Bar-tailed Godwits and Dunlins (*Calidris alpina*). Great Knots occurred in the largest flocks (150 ± 114 individuals, medium = 100, range: 12–495, *n* = 23), followed by Grey Plovers (91 ± 48, medium = 75, range: 20–170, *n* = 10), Bar-tailed Godwits (66 ± 40, medium = 55.5, range: 12–300, *n* = 104) and Eurasian Curlews (31 ± 21, median = 22.5, range: 3–65, *n* = 32). Flock sizes of Grey Plovers were not significantly different from Bar-tailed Godwits or Great Knots; flock sizes between any other two species were significantly different ($\chi^2 = 43.137$, *p* < 0.01, Fig. 2a; Dunn test results see Additional file 1: Table S1).

Departure time and directions

All four species tended to depart from YLE in the late afternoon (Fig. 2b). Departure time of Eurasian Curlews (1518 h ± 161 min, *n* = 50, GTM + 8) was significantly earlier than Great Knots (1651 h ± 68 min, *n* = 36) and Bar-tailed Godwits (1657 h ± 62 min, *n* = 166), but not Grey Plovers (1627 h ± 59 min, *n* = 14; $\chi^2 = 19.67$, *p* < 0.01, Fig. 2b; Dunn test results see Additional file 1: Table S2). Departure time of Eurasian Curlews was also



more widely dispersed than other species, occurring in both the morning and around midday, as well as in the afternoon.

The average departure direction of Eurasian Curlew was 292° ($SD=20^\circ$, $n=32$; Fig. 3a), which is within the

range of the rhumb line ($267^\circ-46^\circ$) towards the breeding grounds, but not within the range of the great circle routes ($320^\circ-42^\circ$). Great Knots had a similar pattern: average departure direction ($54^\circ \pm 31^\circ$, $n=18$, Fig. 3b) within the rhumb line range ($0^\circ-55^\circ$), but not of the

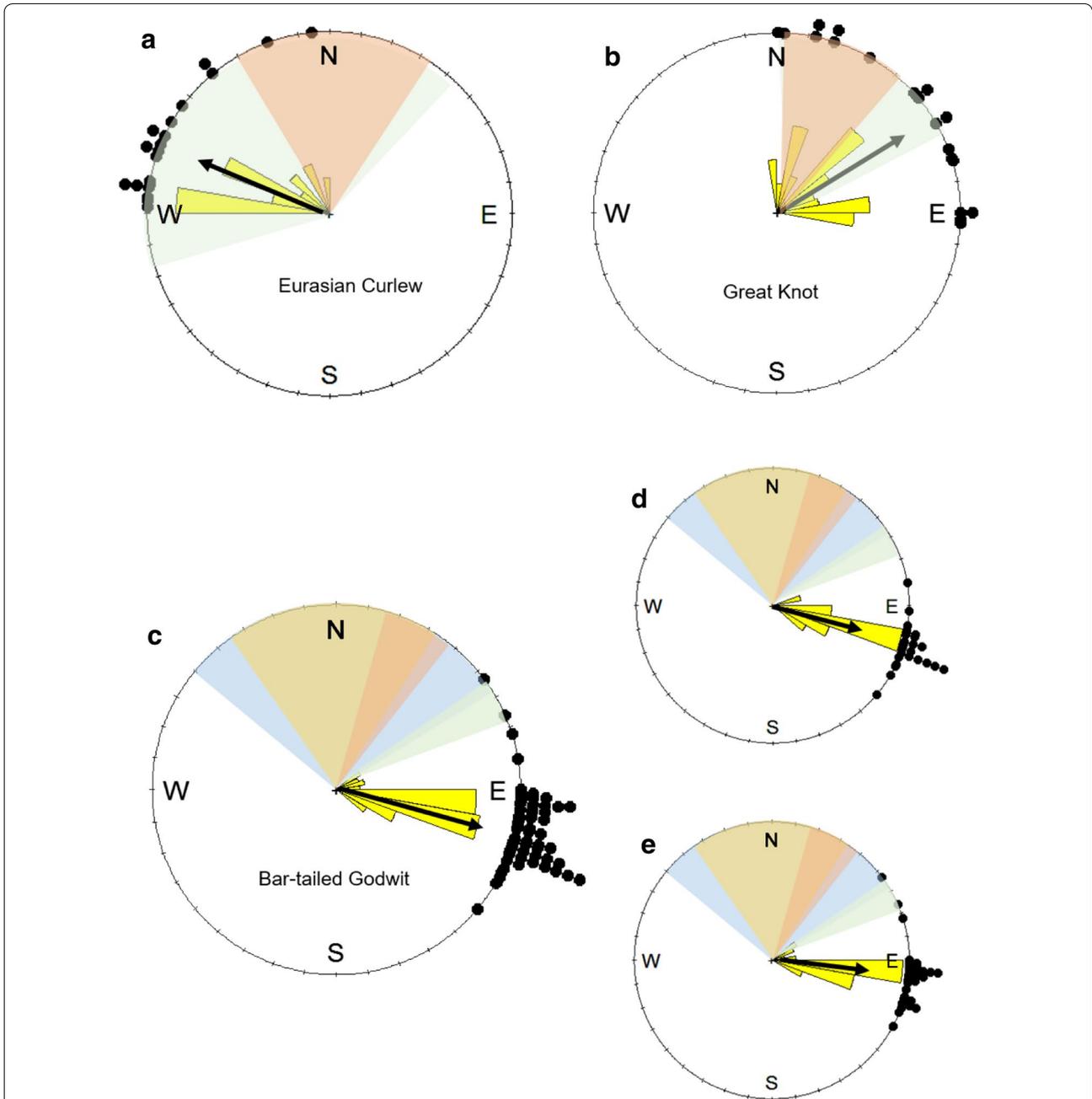


Fig. 3 Departure headings of Eurasian Curlew (a), Great Knots (b), Bar-tailed Godwits (c), Godwits departing before 15 May (d) and Godwits departing after 15 May (e). Black dots outside circles show departure direction of each flock, while the rose diagrams inside the circles show the distribution of individual departure direction. Arrows are the mean directions of all individuals. Light green sectors (light blue for *menzbieri* godwits in c–e) are the orientation range if birds fly following a rhumb line towards the breeding ground; orange sectors show the orientation range if following a great circle route (buff for *menzbieri* godwits in c–e)

great circle (0° – 35°). The trajectory patterns of Bar-tailed Godwits were distinctly different: they exhibited a southeastern detour ($103^{\circ} \pm 16^{\circ}$, $n=57$, Fig. 3c), fitting neither the rhumb line (53° – 73° for *baueri*, and 304° – 56° for *menzbieri*), nor the great circle line range (25° – 45° for *baueri* and 328° – 39° for *menzbieri*). There was only one dominant departure direction before late May ($107^{\circ} \pm 9^{\circ}$, $n=26$, Fig. 3d) while two direction peaks were found in late May ($96.48^{\circ} \pm 11.43^{\circ}$, $n=31$, Fig. 3e) in 2013, with the average direction turned northwards.

Wind effects and tide cycle

No departures occurred during periods of rainfall. One flock of Eurasian Curlews and two flocks of Bar-tailed Godwits migrated in the afternoon after a rainy morning.

The only significant positive relationship between wind benefit and number of individual birds migrating occurred in the day with the wind at 1500 h in 2013, with the migration goal set as 35° in Bar-tailed Godwits: wind benefit explained 39% (Åkesson's method, $n=25$, $p=0.06$) and 42% (Piersma's method, $n=25$, $p=0.04$; Table S3) of variation in the migration. There was no significant difference in wind benefits between days with and without migration in both Eurasian Curlews and Bar-tailed Godwits (Additional file 1: Table S3).

A total of 22 out of 43 flocks (51.2%) of Eurasian Curlew and 99 out of 173 flocks (57.2%) of Bar-tailed Godwit departed during an incoming flood tide. Flocks of Bar-tailed Godwits was not significantly related to tide heights ($p=0.29$), while Eurasian Curlews departure flocks departed more frequently at higher tide levels ($p=0.04$).

Discussion

Interspecific differences in migration departure behaviors

It appeared that both flock size and departure time were related with body sizes of the four species we analyzed: the largest-sized, Eurasian Curlew, formed the smallest flocks, and had a distinct pattern in departure time selection. This might be related to various extent of predator pressure among species. Generally smaller species are more vulnerable to predators, performing large flock and night migration to avoid predation (Gotmark and Post 1996; Møller and Nielsen 2007). Large flock size could be a by-product of clustered foraging and/or roosting. However, even when thousands of godwits foraged and roosted together, they separated into relatively small flocks when departing on migration from YLE; while the Grey Plovers, which foraged in relatively small, and scattered groups (usually less than 20 individuals), departed in relatively large flocks (K Tan, field observation). Although a bird in a large group is not necessarily better than a solo bird in terms of energy saving on

a long, non-stop migration (Kshatriya and Blake 1992), we cannot exclude the possibility that birds used aerodynamic up-wash from fellow birds, especially in Bar-tailed Godwits which usually flew in a V-shaped or echelon formation when departing (K Tan, field observation). Our result is contradicted in the flock size-body size relationship reported in former study (Piersma et al. 1990), which might be because either most of former records came from post-breeding migration when birds were more dispersed in migration date; or the smaller species, such as Ringed Plovers (*Charladies hiaticula*), Sanderlings (*Calidris alba*) were not tend to aggregate at stopover site before their departure.

All four species tended to depart in late afternoon, which is consistent with previous studies (Piersma et al. 1990). In our records, only the largest species, Eurasian Curlew, had a distinct pattern in departure time selection: they also departed in the morning or around midday. Additionally, we might have missed night-time departures of some shorebirds, especially Great Knots: in May 2013 we found that the population of Great Knots at YLE had decreased by about a half before we observed the first departure of a migratory flock. Furthermore, we rarely observed smaller waders, such as Dunlins, Red-necked Stints (*Calidris ruficollis*), and Sharp-tailed Sandpipers (*Calidris acuminata*) departed even though more than 50,000 individuals were counted in YLE during the boreal spring (Bai et al. 2015). This may occur because these species did not embark on long-distance departure from here, performed inconspicuous departure behaviors, or started migration at dusk. In fact, night departures in small birds have been recorded by radar and radio tracking extensively (Myres and Apps 1973; Åkesson et al. 2002). Higher predation pressure in the daytime could contribute to night departure of small birds (Alerstam 2009). Confronting a long non-stop journey, plus uncertainty of the duration caused by potentially adverse weather *en route*, neither the time saved for diurnal foraging before the migration nor gaining energy right after were expected to influence the departure decisions. Although departure in late afternoon has been connected with orientation use in sunset (Muheim et al. 2006), it remains unclear whether it is involved during the day time departure by shorebirds.

None of the departure directions of the four species coincided with the shortest route to the breeding ground. A possible explanation is wind use during their ascending stage. Some waders, such as Red Knots have been observed using soaring and gliding during the climbing phase (Alerstam et al. 1990). We have no records of this, however, we observed that the departure direction of Great Knots usually varied during ascent while other species maintained a consistent direction (K Tan, field

observation), possibly suggesting differences in aerodynamic tactics. Bar-tailed Godwit was the only species which exhibited a deviation from the direct route to the breeding ground. The more southerly departure track is consistent with satellite tracks of subspecies *baueri* flying to Alaska (Battley et al. 2012), which could be related to benefitting from greater wind assistance (Gill et al. 2014). The second direction peak in late May, which is thought to relate principally to migration of *menzbieri*, deviated from satellite tracking paths, being more southerly than expected (Battley et al. 2012). Part of this may be accounted for by the fact that some *baueri* are still present in the second half of May, which is to be expected as birds breeding on the North Slope of Alaska migrate some 30 days later than birds breeding in the southern part of the range (Conklin et al. 2010). However, the departure tracks of presumed *menzbieri* are still more southerly than expected, which may suggest that this only occurred in the initial climbing period. The detour could be the result of searching for favorable wind (Green et al. 2004), godwits have to be capable to “predict” prevailing wind on the ocean, realize the true navigation and change direction during migration on the ocean. Hence, it is not proper to deduce destination from departure direction.

The influence of tide and weather

Bar-tailed Godwit departures occurred equally in all tide conditions, but there was a positive relationship of tide height and observed Eurasian Curlew departing flocks. That difference might be due to different migratory stages between the two species: Bar-tailed Godwits use YLE as the final staging site (Gill et al. 2014), while Eurasian Curlews might make a further stopover after departing from YLE. However, we are inclined to consider the significant correlation as discovery bias of departing Eurasian Curlews: it is easier to notice the departure flocks when tide level was high and birds were aggregating in small and remaining dry area than those departed all over the bare mudflat during low tide. Meanwhile Godwits tended to aggregate on the mudflat beside the seawall before migration even during low tide (CY Choi and DS Melville, field observation), so that this kind of bias was likely to be much smaller. Strong selection for the time of day, together with the semidiurnal tide with a cycle of 12 h and 25 min, can reduce the chance of detecting correlation between departure and tidal height.

Wind benefits were not strongly related to departure dates of the species considered (Eurasian Curlews and Bar-tailed Godwits). Migration dates from the final stopover site can be constrained by the narrow optimal time window for arriving at breeding ground (Green et al. 2004; Both 2010). In addition, following a rigorous fuel deposition schedule at a stopover site (Schaub et al. 2008;

Hua et al. 2013) can reduce the date flexibility of pre-breeding departure. Departure in favorable winds does not mean they can always retain a tailwind during long migratory flight: wind is unstable in the middle latitude and it is more efficacious for birds to adjust their altitude and route to optimize wind assistance rather than day selection (Green 2004). Gill’s analysis based on individual show godwits departing Yellow Sea selected dates which provided significant wind assistances in their subsequent fly (Gill et al. 2014). It should be noted that analyses based on individuals assumed a specific time window around the actual migration date so it potentially ruled out part of the endogenous schedule constraint.

Conclusions

Our results suggest that for birds at the final pre-breeding stopover sites, the departure decisions are less sensitive to exogenous factors, which is different from departure decision at other stopover or nonbreeding sites. Moreover, departure behaviors were different among species with different body sizes and wind use strategies. This study highlights that understanding the spatial and temporal characteristics of the influence of endogenous and exogenous factors is important for clarifying the migratory strategies of birds.

Additional file

Additional file 1. The test results of flock sizes, departure time and wind benefits.

Authors’ contributions

KT and ZM designed the experiment, KT, HP, CC and DM conducted fieldwork, KT and ZM analyzed the data, KT led the writing with contribution from ZM, CC, DM and HP. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Consent for publication

Not applicable.

Ethics approval and consent to participate

All the fieldwork was conducted with the permission and support of the Yalujiang Estuarine Wetland Nature Reserve and was strictly complied with the requirement of Chinese Wild Animal Protection Law.

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