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Variability among autumn migration patterns of Mongolian Common Shelducks (*Tadorna tadorna*)

Xin Wang¹, Lei Cao^{1,2*}, Nyambayar Batbayar³ and Anthony David Fox⁴

Abstract

Background: Avian migrants moving between common breeding and wintering areas may adopt different migration routes, and consequently affect timing. However, this pattern has rarely been investigated, especially in waterbirds. Moreover, autumn migration patterns of the Common Shelduck (*Tadorna tadorna*) have never been studied.

Methods: We used GPS transmitters to track, for the first time, the autumn migration of the Common Shelduck in East Asia ($n = 14$).

Results: The Common Shelduck undertook a broadly northwest–southeast autumn migration, taking a mean of 91.7 ± 38.7 (SD) days to cover a mean distance of 1712.9 ± 450.5 km at a speed of 89.4 ± 226.5 km/day. The birds used 2.5 ± 1.8 stopover sites, and the total stopover duration was 81.9 ± 38.7 days. There were considerable between-individual variations in the onset (24 August to 28 September) and completion (29 September to 11 January) of migration, distance (1070.2–2396.4 km), speed (14.7–734.0 km/day), the index of straightness (0.6–1.0), duration (1.5–151.8 days), stopover times (0–5) and total stopover durations (0–148.1). More direct migration routes were associated with fewer and shorter stopovers ($p = 0.003$ in both cases). Post-breeding and wintering site habitat use was similar between individuals, whereas stopover site habitat use varied considerably within and between individuals.

Conclusions: Our study showed remarkable variability in Shelduck migration patterns, which was likely associated with refuelling patterns *en route*. To understand fully the migration diversity and flexibility of habitat-use, we need to track more birds to increase representativeness, using accelerometer-integrated transmitters to investigate behaviours in different habitats.

Keywords: Autumn migration, East Asian–Australasian flyway, Habitat use

Background

The power of flight enables birds to exploit temporally constrained food resource abundance in habitats separated by long distances by undertaking seasonal migration episodes (e.g. Stutchbury et al. 2009; Wang et al. 2018). As a result, birds tend to use widely geographically separate breeding and survival habitats (*sensu* Alerstam and Högstedt 1982). Birds move between these areas along migration routes using staging habitats along the

way, which are often shaped by the ecological barriers that separate breeding and wintering grounds (La Sorte et al. 2016) and the availability of suitable habitat patches that enable refueling after energy depletion along the way (Alerstam 1990). Long distance migratory waterbirds frequently concentrate at a narrow range of staging areas from very large breeding (e.g. Greater White-fronted Geese *Anser albifrons*, Wang et al. 2018) and wintering provenances (e.g. Red Knot *Calidris canutus*, Atkinson et al. 2005) at the continental scale. In addition, empirical observations have shown divergent migration patterns from single breeding or wintering areas via alternative routes and staging areas (migratory divides, Irwin and Irwin 2005) using ringing (Hedenstrom and Pettersson

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1987) and, more recently, geolocation (Delmore et al. 2012). Many passerines are known to undertake “broad-front” migration and show little between-year fidelity to staging sites (but see Catry et al. 2011; Buler and Dawson 2014). However, first indications suggest that some wetland specialist species, whilst demonstrating large differences in patterns of site use, show striking individual between-year fidelity to staging sites, as well as to breeding and wintering areas (Hasselquist et al. 2017).

Knowledge of individual variation in migration timing and use of staging areas is critical to the understanding of migration strategies (Tøttrup et al. 2012), and the link with resources and body condition (Weber et al. 1998; Bauer et al. 2010; Armstrong et al. 2016; Thorup et al. 2017). The localization of stopover sites and their importance to flyway populations of migratory species is also essential for their effective conservation and for mitigation against the effects of land use and climate change. However, for many waterbird populations we lack such knowledge of waterbird migration routes and site use. Furthermore, we lack information to link the timing and exploitation of migration routes and staging areas, because the application of ringing (Hedenstrom and Pettersson 1987), stable isotope (Toews et al. 2017) and molecular approaches (Battey et al. 2018) fail to describe the migration of individuals in time and space (but see Delmore et al. 2012). We especially lack knowledge about how individuals differ in their speed of migration and how this relates to refueling *en route*. Migration behaviour is shaped to a considerable degree by a species’ ability to accumulate energy stores to fuel migration episodes (Alerstam 2011), which is also affected by the range of available refueling sites. Birds may be forced to make detours and/or refuel *en route* if their accumulated energy stores are insufficient to undertake uninterrupted direct migratory flights (Hahn et al. 2014). For this reason, we predict that, for a species that can demonstrably accumulate fat stores to fuel a direct, nonstop autumn migration from its breeding area to the winter quarters, we would expect that the greater the number and duration of stopovers *en route*, the more tortuous its migratory route.

The Common Shelduck (*Tadorna tadorna*, hereafter Shelduck) has a widespread distribution in the Palearctic, divided into three populations, one in western Eurasia (Scott and Rose 1996) and two in East Asia (Miyabayashi and Mundkur 1999). Although these populations do not differ in morphology or plumage (Patterson 1982), they occupy very different habitats; the majority of western European birds breed and winter along shallow muddy shores and estuaries, with relatively few inland breeders. Birds breeding in semi-saline inland Mongolian waters migrate south and east to winter along Chinese and

Korean coasts (del Hoyo et al. 2017). Western European birds are largely sedentary, occupying territories, which become the breeding areas, in late winter, but most adults undertake a distinctive and direct moult migration in late summer to the German Wadden Sea or to smaller moult aggregations in the UK (Wernham et al. 2002). Mongolian Shelducks moult close to their breeding areas in Mongolia (Nowak 1970) before migrating across relatively inhospitable terrain to their marine winter quarters along Yellow and China Sea coasts (e.g. Cao et al. 2010).

Almost nothing is known of the migration of this species in East Asia, which must migrate across the semi-arid biomes of Mongolia and Inner Mongolia (China) and the intensively cultivated coastal plain of Liaoning, Hebei and Tianjin provinces to reach coastal wintering habitat. The interior regions have long been subject to major cycles in precipitation (Liu et al. 2003), exacerbated in recent times by development, agriculture, irrigation and climate change, which increasingly affect the number, size and quality of potential staging wetlands along the Shelduck migratory routes (Tao et al. 2015). For this reason, it is reasonable to expect individual migrating Mongolian Shelduck to adopt differing migratory trajectories to meet energy demands *en route*, because of the scarce and potentially variable and unpredictable nature of the autumn wetland habitats available along the migratory route.

In this study, we tracked the autumn migration of ten Shelducks using GPS transmitters for the first time in this flyway to compare fine-scale differences in individual spatial–temporal migration patterns. We also compared within- and between-individual habitat use in post-breeding, stopover and wintering sites. We predicted that Shelducks would show diversity in space and timing of migration and corresponding diversity in habitat use, in response to the diverse refueling requirements of birds and the scarce and unpredictable nature of habitat resource availability along their migration route. In contrast, we would also predict more homogenous habitat use on the post-breeding and wintering quarters in response to more stable conditions there.

Methods

Capture and satellite tracking of birds

Fourteen Common Shelducks were rounded up during the flightless moult period and captured at Bumbat Lake (48.12°N, 114.59°E), Mongolia, on 25–26 July 2017. Birds were fitted with Debut-15 GPS-GSM backpack transmitters (Druid Tech, China) following the methods of Roshier and Asmus (2009) and immediately released. Transmitters were programmed to record location, altitude and velocity every hour, depending on battery conditions (dependent on solar insolation via the in-built

solar cell). We only fitted transmitters to birds weighing more than 600 g to ensure the weight of transmitter (18 g) constituted less than 3% of the bird mass.

Migration parameters

In order to determine migration parameters, we first applied the methods of Wang et al. (2018) to segment migration tracks and identify post-breeding/stopover/wintering sites and periods, from 1 August 2017 to 1 February 2018. Briefly, this method was based on changes in movement pattern using first passage time (FPT), a secondary signal of movement tracks (Edelhoff et al. 2016). FPT estimates the minimum duration of an animal crossing a given radius along its path, which is high when an animal resides within a restricted area, and low when it is migrating. We identified the departure and arrival dates at breeding, stopover and wintering sites, and migrating segments, according to the shift between high (whilst on staging areas) and low FPT (observed during migration) using the penalized contrast method of Lavielle (2005). See Wang et al. (2018) for full details.

We defined the start/end of migration as the date individuals departed from/arrived at post-breeding/wintering sites. We defined post-breeding sites as the moulting sites where the birds were captured and all sites within 100 km of these and wintering sites as all sites within a 100 km distance of sites used continuously by individuals in winter. Migration duration was defined as the period from the start to the end of the migration. We defined a site where a bird stopped for more than 2 days as a stopover site (Kölzsch et al. 2015), and the number of stopovers was calculated accordingly. The stopover duration was derived as the sum of the days spent at each stopover site. We defined the migration distance as the cumulative distance flown from the departure from post-breeding sites until arrival at wintering sites. We delineated the path tortuosity of the autumn migration using the straightness index as the displacement from post-breeding to wintering sites divided by the migration distance (Benhamou 2004), a number constrained between zero and one. We calculated the migration speed as the migration distance divided by the migration duration.

Some migration tracks unavoidably contained gaps in data capture caused by low battery charge. In the results from this study, all such gaps occurred during migration and were confined either to long flights between two consecutive stopover sites or between the final stopover site and the ultimate wintering site. In these analyses, we have included these gaps in periods of rapid migration. This may overestimate the (1) duration of migration and (2) straightness index, and underestimate (1) migration distance, (2) number of stopovers, (3) stopover duration and (4) migration speed. However, this did not affect our

interpretation of flexibility in migration timing or diversity of migration routes.

Habitat use

We assessed individual habitat use by determining the land cover of bird locations at each of the post-breeding/stopover/wintering sites. We first excluded all points with an instantaneous velocity > 2 m/s, a threshold value derived from the frequency distribution of velocity, which excluded birds flying. We extracted the land cover type for each remaining location from the GlobeLand30 global land cover dataset (30 m high resolution accuracy) based on 2010 coverage (Brovelli et al. 2015; Chen et al. 2015), the most recent high-resolution land cover dataset available. Because the GPS transmitter's accuracy is high (< 10 m usually), high-resolution land cover dataset can show fine-scale habitat use, and reduce errors of misclassification of land cover. In order to evaluate the suitability of the outdated land cover dataset, we compared the land use patterns using the MODIS land cover type product (MCD12Q1) in 2010 and 2016. This product provides annual land cover data in 500-m resolution. We found that the patterns of land use between the 2 years were largely unchanged, and the between-individual diverse land use patterns did not change within either of the years (Additional file 1: Fig. S1).

The dataset is based upon ten land cover classification types, namely cultivated land, forest, grassland, shrubland, wetland, water bodies, tundra, artificial surfaces, bare substrate, permanent snow and ice. Within the post-breeding/stopover/wintering sites, the classes 'shrubland', 'tundra' and 'permanent snow and ice' were absent and the sea was classified as 'No Data' within the dataset, because it only considered the land cover in land area. 'Cultivated land' includes land used for agriculture, horticulture and gardens; 'forest' comprises land covered with trees, with vegetation cover $> 30\%$; 'grassland' is classified as land with $> 10\%$ grass cover; 'wetland' is land covered with wetland plants with restricted areas of open water; 'water bodies' refer to discrete water bodies within the land area; 'artificial surfaces' are land modified by human activities; 'bare substrate' is land with vegetation cover $< 10\%$.

Wetland predictability in the Shelduck migration range

Because it is known that drought affects wetland availability in the regions crossed by Shelducks on migration between their breeding and wintering areas, we attempted to assess the availability of predictable wetlands along their migration route. We measured the availability of predictable wetlands using the inter-annual recurrence of water surfaces of the global surface water dataset (Pekel et al. 2016), based on orthorectified

imagery from Landsat 5 Thematic Mapper, Landsat 7 Enhanced Thematic Mapper-plus and Landsat 8 Operational Land Imager from 1984 to 2015. The inter-annual recurrence of water surfaces is a measurement of the inter-annual variability in the presence of water, which describes how frequently water returned from one year to another in percentage. Within each 50 km × 50 km grid we summarized the number of pixels of water recurrence from 50% to 100% in the past 32 years.

Data analysis

All data analyses and remote sensing work were performed in R version 3.3.2 (R Development Core Team 2016). We used Spearman's rank correlation to investigate the correlation between number and duration of stopovers and straightness index.

Results

Overall, we obtained complete autumn migration tracks from ten of the 14 individuals (Table 1), including two 2nd-year male birds, five adult males, and three adult females. The body mass on capture ranged from 710 to 1240 g (mean 1022 ± 134.5 g SD).

All birds moulted in Bumbat Lake in Eastern Mongolia, and most of them used it and the surrounding lakes as post-breeding sites (Fig. 1). The autumn migration of individuals varied greatly in both time and space, although all undertook a broadly northwest–southeast migration (Fig. 1). Routes started to diverge immediately on migration initiation, most exploiting multiple stopover sites along the Mongolian border, southeast of the post-breeding sites. One bird (bird 2220) departed its moulting site and flew to a southwest stopover site for 11.5 days. As the migration proceeded, the migration routes, stopover sites and chronology became increasingly disparate. One bird (2247) was the last of the tagged birds to depart the post-breeding site, but flew directly to its ultimate wintering area, the only bird doing so, but confirming the ability of the species to reach the wintering quarters nonstop. Another bird, 2224 utilized a stopover site for 23 days, c. 720 km almost east of its moulting site; and 2229 used a site for 20 days 840 km due south of its moulting site. However, after initial stopovers, most birds continued directly to Bohai Bay coasts in eastern China. Three birds (2226, 2229, 2247) wintered here, including one bird that stopped over in the bay, 150 km to the northeast of the ultimate wintering site (2229). Seven other birds (2155, 2173, 2207, 2217, 2220, 2224, 2252) made stopovers in Bohai Bay, but continued to migrate further down the coast to ultimate wintering quarters. Five of them

(2155, 2207, 2217, 2224, 2252) made a single leg flight to winter on the south coast of Shandong Peninsula. Individual 2220 also flew there but then continued > 500 km further to winter on the Jiangsu coast. Some tracking data from 2173 were lost between Bohai Bay and the Yangtze Estuary, and this bird stopped over in the Yangtze Estuary for at least 3 days and wintered in Zhejiang coast, 300 km further south (Additional file 2: Table S1). The variation in the nature of individual autumn migrations can also be measured by migration parameters: the total migration distance ranged from 1070.2 to 2396.4 km (1712.9 ± 450.5 km), the straightness index ranged from 0.6 to 1.0 (0.9 ± 0.1) and the birds used an average of 2.5 ± 1.8 stopover sites (Table 1). The number and duration of stopover were negatively correlated with straightness index (Spearman's rank correlation, $S = 302.39$, $\sigma = -0.833$, $p = 0.003$, and $S = 308$, $\sigma = -0.867$, $p = 0.003$, respectively).

The patterns of individual autumn migration also showed high temporal variability. Most birds started autumn migration in late August or early September (Figs. 2, 3), but the departure date exhibited large variation (mean date 5 September 2017 ± 13.5 days). Consistent with the variable total migration distances, numbers of stopovers and their durations, migration duration varied considerably (91.7 ± 38.7 days, ranging from 1.5 to 151.8 days), resulting in high variability in date of migration completion and migration speed (Table 1).

In post-breeding sites, all birds used similar habitats, comprising of water, bare substrate, wetland and grassland (Fig. 4). During the progress of autumn migration, the birds showed highly variable habitat use within and among individuals (Fig. 5). Among birds which only stopped in coastal sites (2155, 2173, 2207, 2217, 2252), the habitats comprised mostly water, sea and wetland, rarely croplands (site 4 of 2224). For the birds that used terrestrial habitats, the habitats mostly exploited comprised water and grassland, less frequently bare substrates (2224, 2229) and croplands (2224, 2229). Although all the birds ultimately wintered along coasts, their habitat use showed moderate variation—most birds used sea and water, but 2207 and 2229 used high proportions of croplands, and 2217 and 2229 used high proportions of wetlands (Fig. 4).

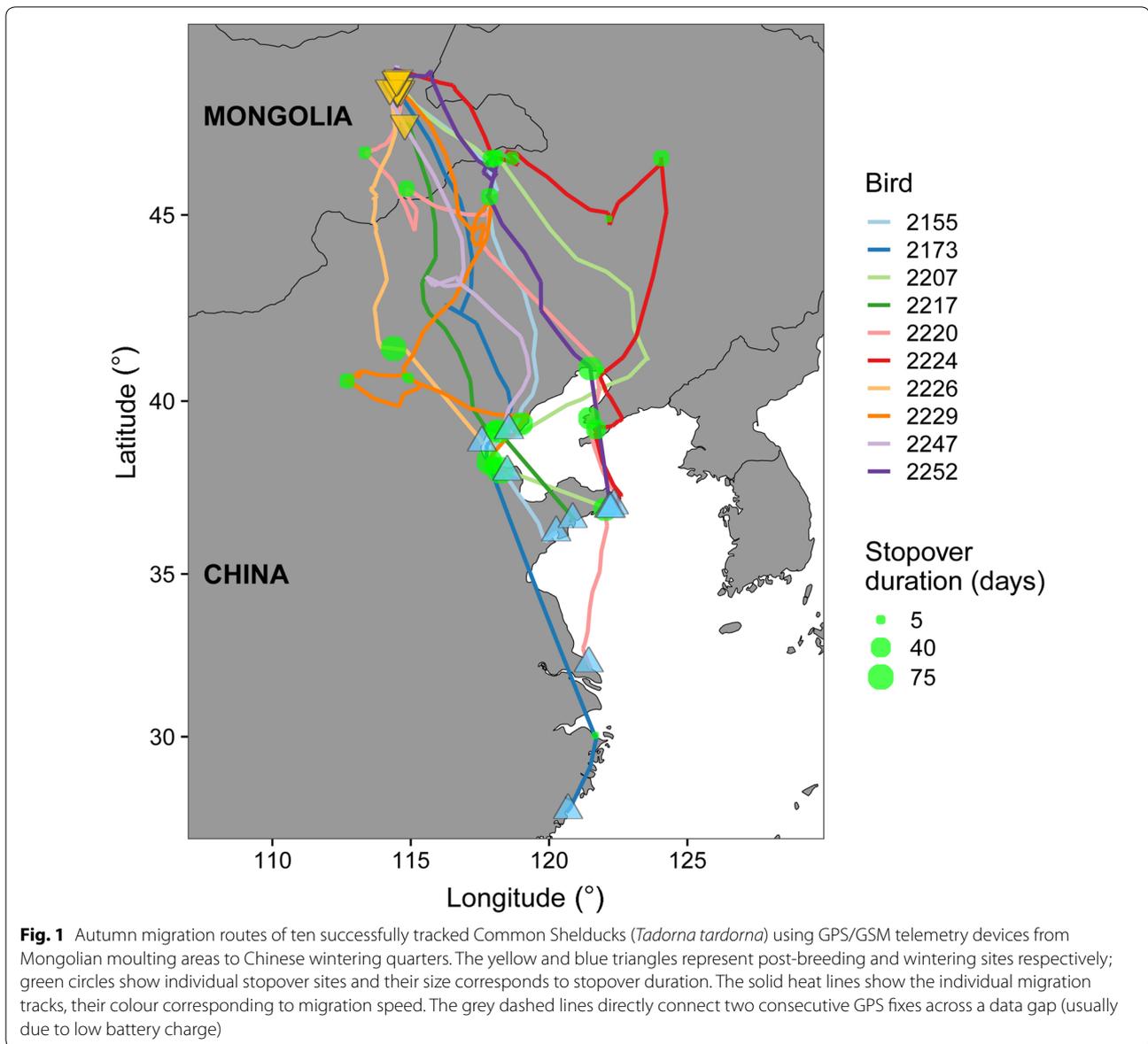
The migration episode from the post-breeding ground to the coast covered large area of low availability of predictable water surface, contrast with other major wintering or staging sites of waterbirds in East Asia, such as Northeast China and the Yangtze floodplain (Fig. 6).

Table 1 Bird information, individual and summarized autumn migration parameters of tracked Common Shelducks (*Tadorna tadorna*) based on tracking data retrieved on 16 March 2018

Logger	Captured date	Age	Sex	Body mass on capture (g)	Duration of tracking (days)	Start of migration	End of migration	Migration duration (days)	Migration distance (km)	Straightness index	No. stopovers	Stopover duration (days)	Mean \pm SD duration of stopovers (days)	Migration speed (km/day)
2252 ^a	7/25/2017	2cy	Male	980	203	8/24/2017	12/6/2017	103.5	1526.5	0.9	2	90.3	45.13 \pm 22.92	14.7
2247	7/26/2017	Adult	Male	1140	234	9/28/2017	9/29/2017	1.5	1070.2	1.0	0	0.0	0	734.0
2229	7/26/2017	Adult	Male	1240	233	9/10/2017	1/5/2018	116.8	1908.6	0.6	5	111.7	22.35 \pm 20.99	16.3
2226 ^a	7/26/2017	Adult	Male	1100	186	8/25/2017	11/14/2017	80.9	1189.7	0.9	1	71.7	71.75	14.7
2224	7/26/2017	Adult	Male	960	223	8/24/2017	12/13/2017	110.6	2092.1	0.7	5	104.1	20.82 \pm 13.46	18.9
2220	7/25/2017	Adult	Female	710	190	8/12/2017	1/11/2018	151.8	2114.0	0.9	5	148.1	29.62 \pm 24.62	13.9
2217 ^a	7/26/2017	Adult	Male	1100	210	9/10/2017	11/20/2017	70.9	1320.9	1.0	1	60.3	60.29	18.6
2207 ^a	7/25/2017	2cy	Male	1030	208	9/16/2017	12/22/2017	97.0	2018.0	0.7	2	65.5	32.77 \pm 10.75	20.8
2173 ^a	7/25/2017	Adult	Female	960	235	9/10/2017	12/11/2017	92.1	2396.4	1.0	2	77.3	38.65 \pm 50.41	26.0
2155	7/25/2017	Adult	Female	1000	217	9/10/2017	12/11/2017	92.3	1492.8	0.9	2	89.9	44.96 \pm 53.09	16.2
Mean				1022	213.9	9/5/2017	12/6/2017	91.7	1712.9	0.9	2.5	81.9	32.8	89.4
Standard deviation				134.5	17.7	13.5 days	29.6 days	38.7	450.5	0.1	1.8	38.7	25.1	226.5

^a "2cy" denotes the second-year bird

^a migration tracks containing data gaps, see the section "Methods" for more details



Discussion

This is the first satellite-tracking study of the Common Shelduck describing the autumn migration of this widespread species, providing the first descriptions of the individual diversity in movements, timing and habitat use on autumn migration from the post-breeding grounds prior to converging on the wintering quarters along Chinese coasts. The results conformed with studies of freshwater dabbling ducks in continental western Europe that also showed flexibility in navigation and movement patterns during autumn migration (van Toor et al. 2013; Gehrold et al. 2014). Notably, the early arrival in Bohai Bay or Shandong Peninsula by two females (2173, 2220)

allowed them to migrate southward to Zhejiang and Jiangsu coasts for winter. This extended movement is almost equal to the migration distance of many birds that wintered in Bohai Bay. This is in line with the broad wintering range along eastern China coasts (del Hoyo et al. 2017), and suggests that this distribution pattern is not necessarily caused by the occupancy of distinct populations (Scott and Rose 1996). It also supports the empirical observations of sex-biased wintering distribution of ducks (Owen and Dix 1986; Shao et al. 2016), which was attributed to competition (Choudhury and Black 1991). However, the seemingly sex-biased extended movement remains speculative because the difference was not

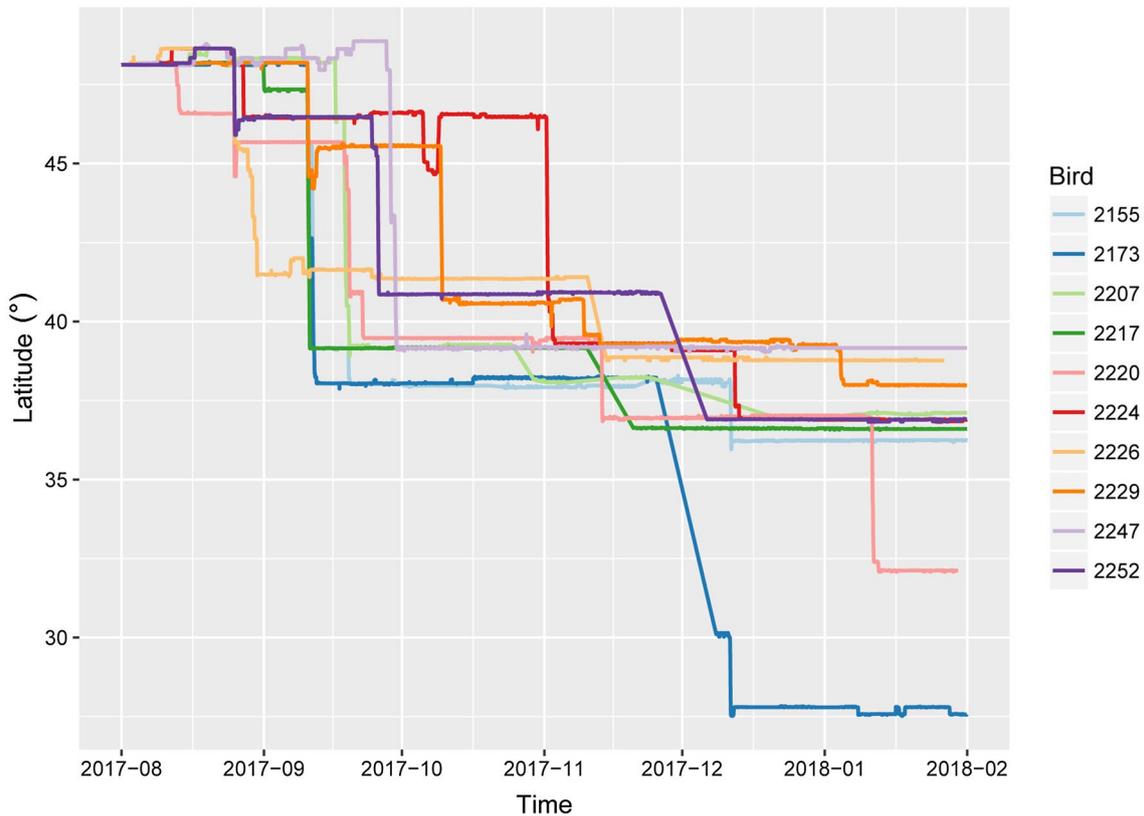


Fig. 2 Individual latitudinal movement tracks of the ten tracked Common Shelducks from Mongolian post-breeding sites to Chinese wintering sites. Numbers relate to the individuals referred to in detail in the text and Table 1

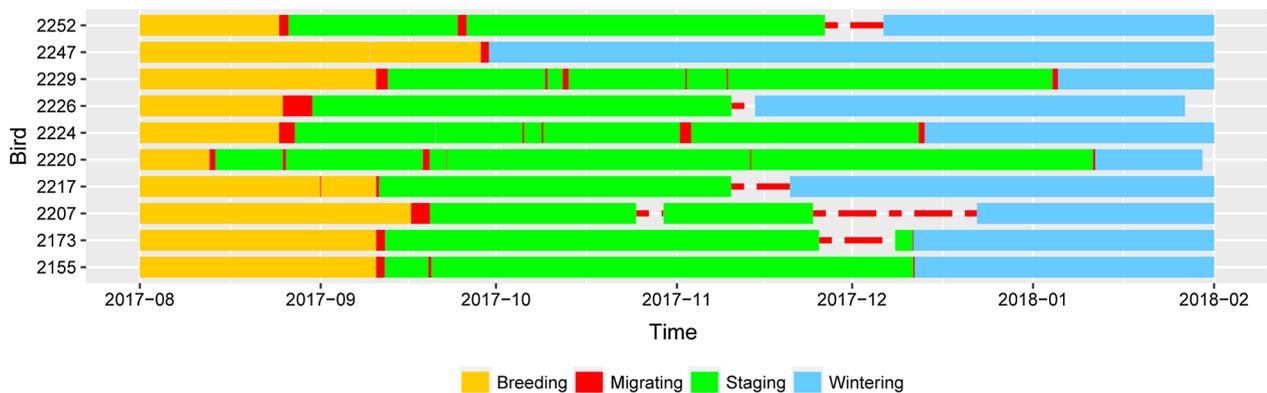


Fig. 3 Autumn migration schedules of the ten tracked Common Shelducks from Mongolian breeding areas to Chinese wintering quarters. Red bands indicate periods of prolonged migration; the horizontal red dashed line represents periods of missing data caused by low battery power. Numbers relate to the individuals referred to in detail in the text and Table 1

significant based on *t*-tests because of the limited sample size. What appears unique about the results from the Shelduck tracking is the diversity of migration routes, stopover sites, stopover duration and habitat use taken by different individuals drawn from a common moulting

site *en route* to a cluster of wintering sites. Moreover, the birds showed highly flexible migration timing. Notably, the individual 2247 migrated from the moulting areas non-stop to wintering grounds, but no other birds did so. This bird left the moulting site very late, taking 1.5 days

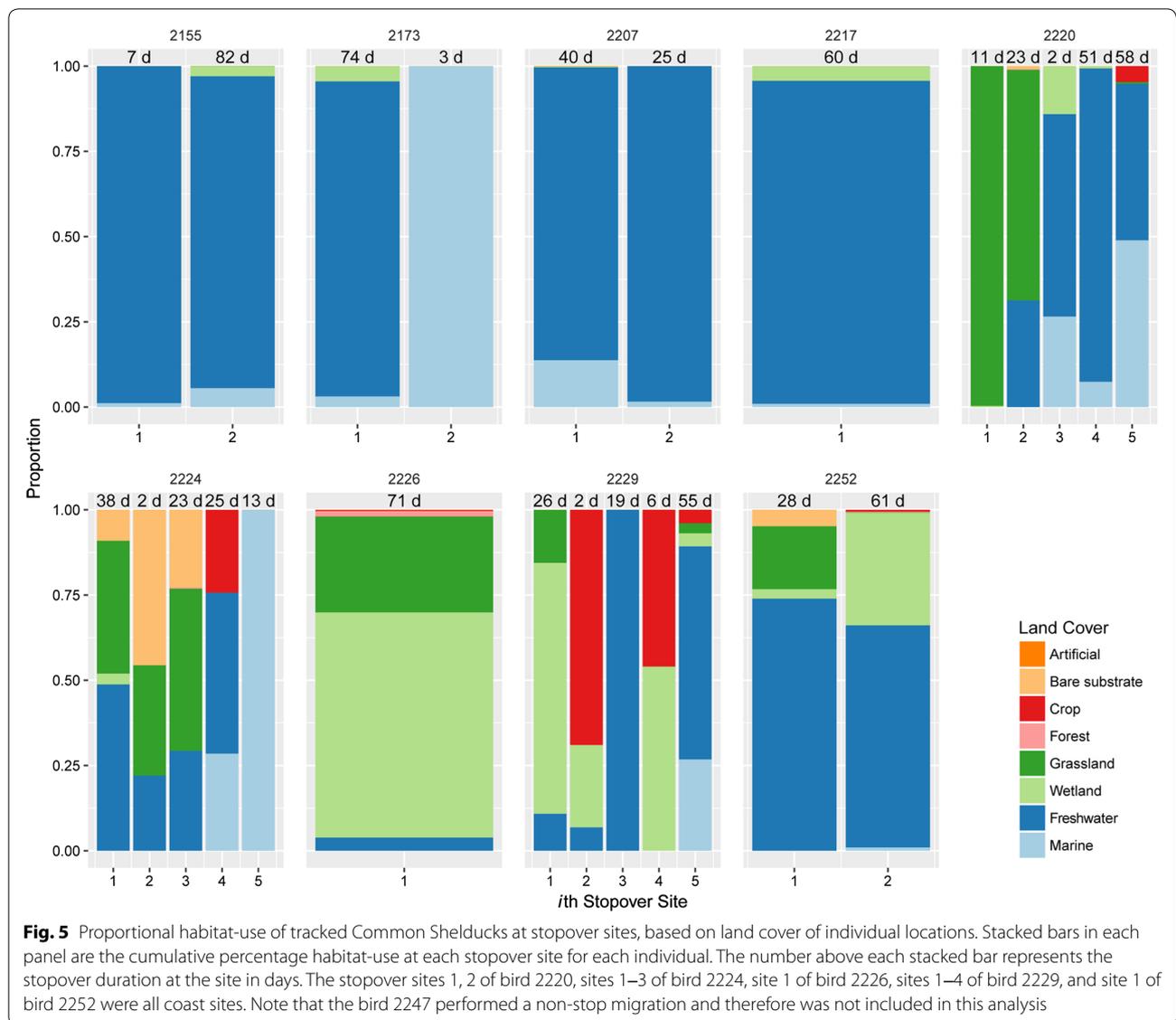


to cover 1070 km, in a speed of 734.0 km/day. This individual was an extreme case for the timing flexibility, as all the other individuals migrated for at least 70.9 days at a speed of at most 26.0 km/day. The variability in overall migration timing would decrease if the bird 2247 was excluded. However, given the reasonably high occurrence (one in ten), we argue that the observed movements of the bird 2247 represents one type of migration strategy of this population, and legitimately contributes to the temporal variability during migration.

Many factors may explain the diverse pattern of autumn migration of Mongolian Common Shelduck. Firstly, energy store and refueling demands of birds can result in diverse site use and timing of migration. Autumn migration has been considered to be less time-constrained than in spring when birds are pressed to arrive earliest to breeding areas (Kokko 1999; Alerstam 2011). Therefore, given adequate fat stores, tracked birds were capable of making a one-step flight to complete their migration to wintering quarters, such as 2247; birds potentially failing to fully achieve such body stores might take long detours to utilize distant habitats, such as 2224, 2229 to derive fuel stores for onward movement. Secondly, the unpredictable nature of many wetlands within

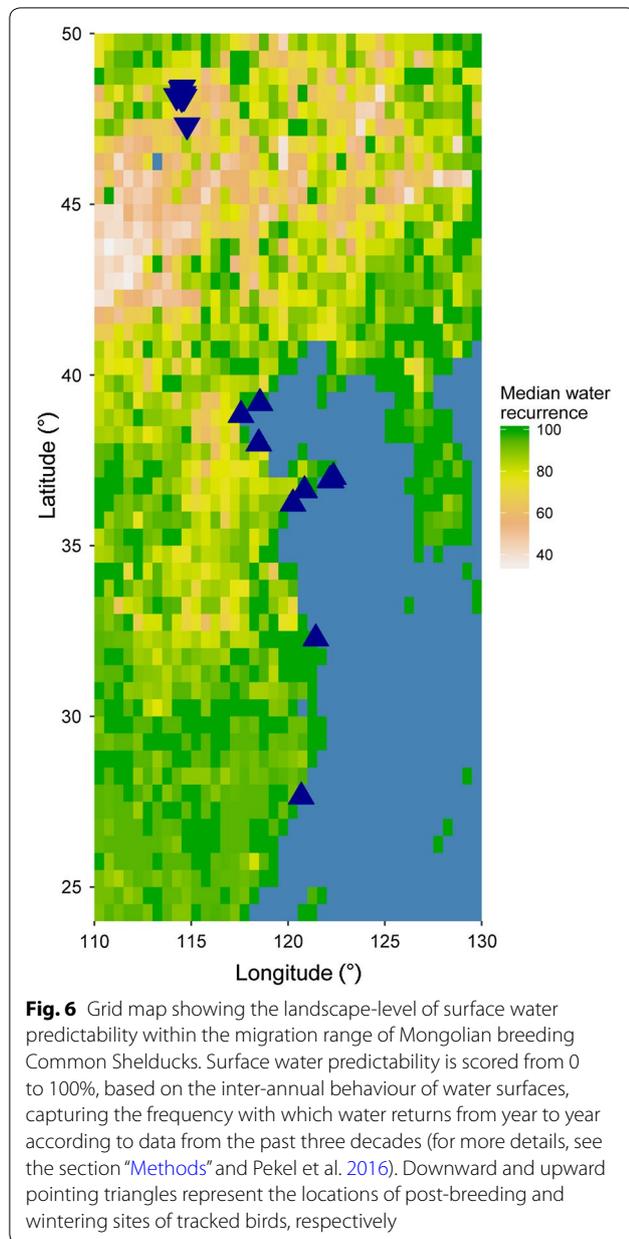
the reach of Shelduck migrating towards their wintering areas (Fig. 6) likely contributed to the degree of variability in site use and migration routes. Habitat unpredictability can generate high levels of variation in individual migration strategies, which are likely the product of differential search patterns and the benefit of previous experience (e.g. Roshier et al. 2008). Birds making no apparent detours used no stopover sites *en route* to the coast after departing the China–Mongolia border until they reached the sea, corroborated by the significant correlation between number and duration of stopover and straightness index. These differences suggest the general lack of suitable habitats in this vast area and the need to refuel to compensate for the search needed to locate suitable refueling habitats.

To better address such questions, more migratory Shelducks need to be tracked in this flyway to describe the full range of migration patterns and the reasons behind the observed differences in individual responses. We advocate modelling the effects of individual energy store accumulation at the end of the post-breeding season (adjusted for body size and sex) on subsequent migration strategy, in terms of numbers and duration of migration stopovers. Such



tracking should use transmitters incorporating accelerometers, to simultaneously record instantaneous behaviour of the migrating birds. Such transmitters will help to understand the behaviour of birds at stopover sites, and provide data on energy expenditure and income during migration. Such information could contribute critical support to validate our hypothesis that these birds adopt diverse migration patterns to meet the refueling demands of a given migration episode. We would also advocate a better understanding of the habitat use of different individuals. Although the land cover dataset used here was high-resolution and new (Brovelli et al. 2015; Chen et al. 2015), it is restricted to ten crude land cover types, hindering

insights into more detailed habitat selection. Ground fieldwork could verify more fine-grained habitat selection and their relative energetic profitability, which may change seasonally (Chudzinska et al. 2015). Such detailed studies would provide enlightened possibilities to compare these patterns with migration strategies of Shelduck in other parts of the world, contrast the behaviour of birds in different environments and test our hypothesis that the availability and predictability of habitats contribute directly to the diversity of migration patterns witnessed in individuals. Finally and most importantly, all the above efforts will also support the future conservation of this species, by revealing their distribution, habitat use and



requirements, and potentially the impact of human activities on the birds and their refueling areas along the flyway.

Conclusions

We showed for the first time the autumn migration patterns of the Mongolian Common Shelduck. The results showed remarkable variability in Shelduck migration patterns, which was likely associated with refuelling patterns *en route*. To understand fully the migration diversity and flexibility of habitat use, we need to track

more birds to increase representativeness, using accelerometer-integrated transmitters to investigate behaviours in different habitats.

Additional files

Additional file 1: Fig. S1. Comparison of land use patterns at each site of Common Shelduck (*Tadorna tadorna*) individuals, based on MODIS land cover dataset (MCD12Q1) in 2010 and 2016.

Additional file 2: Table S1. Detailed migration timing and site location of tracked Common Shelducks.

Authors' contributions

XW and ADF conceived the idea and wrote the manuscript. NB led the fieldwork. XW analyzed the data. LC obtained funding, coordinated fieldwork and provided important input during the manuscript preparation. All authors read and approved the final manuscript.

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Acknowledgements

We thank Junjian Zhang for managing transmitters and satellite-tracking data, Fanjuan Meng for coordinating fieldwork, and the biologists and workers that participated in the fieldwork.

Competing interests

The authors declare they have no competing interests.

Availability of data and materials

The data generated or analysed during this study are included in this published article and its Additional files.

Consent for publication

Not applicable.

Ethical approval and consent to participate

This study was examined and approved by the Animal Ethics Committee, Research for Eco-Environmental Sciences, Chinese Academy of Sciences, and was conducted under permission No. rcees-ddll-001.

Funding

The study was supported by the National Key Research and Development Program of China (Grant No. 2017YFC0505800), the National Natural Science Foundation of China (Grant Nos. 31661143027, 31670424, 31500315), and China Biodiversity Observation Networks (Sino BON).

Received: 15 October 2018 Accepted: 7 December 2018

Published online: 14 December 2018

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