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Article

Consistent habitat preference underpins the geographically divergent autumn migration of individual Mongolian common shelducks

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Abstract

While many avian populations follow narrow, well-defined "migratory corridors," individuals from other populations undertake highly divergent individual migration routes, using widely dispersed stopover sites en route between breeding and wintering areas, although the reasons for these differences are rarely investigated. We combined individual GPS-tracked migration data from Mongolian-breeding common shelduck *Tadorna tadorna* and remote sensing datasets, to investigate habitat selection at inland stopover sites used by these birds during dispersed autumn migration, to explain their divergent migration patterns. We used generalized linear mixed models to investigate population-level resource selection, and generalized linear models to investigate stopover-site-level resource selection. The population-level model showed that water recurrence had the strongest positive effect on determining birds' occupancy at staging sites, while cultivated land and grassland land cover type had strongest negative effects; effects of other land cover types were negative but weaker, particularly effects of water seasonality and presence of a human footprint, which were positive but weak or non-significant, respectively. Although stopover-site-level models showed variable resource selection patterns, the variance partitioning and cross-prediction AUC scores corroborated high inter-individual consistency in habitat selection at inland stopover sites during the dispersed autumn migration. These results suggest that the geographically widespread distribution (and generally rarity) of suitable habitats explained the spatially divergent autumn migrations of Mongolian breeding common shelduck, rather than the species showing flexible autumn staging habitat occupancy.

Key words: common shelducks, habitat selection, individual variation, resource selection function

It is axiomatic that the high mobility of migratory birds potentially enables them to use widely dispersed stopover sites by following divergent routes from single breeding or wintering areas within populations (Irwin and Irwin 2005). Many passerines seem to follow this pattern, for instance, willow warblers *Phylloscopus trochilus* (L.) breeding in Scandinavia spread along the Mediterranean during migration and throughout central and south Africa in winter (Hedenstrom and Pettersson 1987). Western North American Swainson's thrushes *Catharus ustulatus* from relatively restricted breeding areas showed dramatic inter-individual divergent migration routes *en route* to wintering areas in Mexico, Central and South America (Delmore et al. 2012). Despite this, telemetry studies show many migratory waterbirds follow well-defined corridors (e.g., Green et al. 2002; Wang et al. 2018b), while other populations of the same species do not (e.g., van Wijk et al. 2012) and yet others show flexibility in migration routes (van Toor et al. 2013; Gehrold et al. 2014; Wang et al. 2018a). Investigating why species adopt variable migration strategies is of major importance to understanding their evolution and ecology and of direct importance to management for their effective conservation (Delmore et al. 2012).

Extensive contiguous wetland systems are rare in nature, so migratory waterbirds tend to migrate between "islands" of wetland habitats isolated by intervening tracts of unsuitable terrestrial habitat that offer little in food and shelter to such species. Hence, habitat selection during dispersed migration episodes is critical to understand the mechanisms underlying the adoption of such a strategy, yet rarely studied in waterbird populations. Dispersed migration may result from the ability of a population to utilize a diversity of habitat/resource types. In this case, we would predict individuals in such flexible populations would show variable habitat and resource selection at different stages during the annual cycle (e.g., Chudzinska et al. 2015; Zurell et al. 2018). Alternatively, birds may adopt dispersed migration patterns because their high mobility enables them to exploit the availability of very specific habitat/resource types which are restricted geographically (Alerstam and Högstedt 1982). In this case, we would expect very consistent habitat preference/selection between individuals, yet such associations between habitat selection and dispersed migrations are rarely investigated. The recent development of advanced lightweight GPS transmitters now enables us to record individual bird movements at high spatiotemporal resolution to enable us to test for such different inter-individual habitat selection patterns.

In a previous study, we showed that tracked Mongolian breeding common shelduck *Tadorna tadorna* (hereafter shelduck, a Least Concern species according to IUCN 2018) performed highly dispersed and contrasting patterns of individual autumn migration (Wang et al. 2018a). Individuals from congruent summering areas in semi-saline inland habitats in Mongolia showed highly divergent routes and dispersed stopover sites in time and space *en route* to their ultimate coastal wintering areas in China (Wang et al. 2018a). Most notably, individuals used highly variable habitat types at stopover sites, but used a relatively narrow set of habitat types at post-breeding and wintering sites. Such inter-individual variation in the use of migration routes, stopover sites, and habitat types seems rarely reported in the literature and the reasons for this were not obvious. Shelducks might be expected to prefer habitats which are predictable, as they tend to utilize wetlands with open water that are a persistent feature of the land surface over many years when migrating across the semi-arid biomes of Mongolia and Inner Mongolia (Wang et al. 2018a). On the other hand, the arid environment and relative scarcity of wetlands means that they select for highly productive, but ephemeral seasonal wetlands, as do other waterbird species in East Asia (Jia et al. 2018). However, such a strategy carries a risk. Use of such wetlands to recoup depleted energy stores for onward migration may be critical (McNamara et al. 2011), but birds risk arrival to *desiccated* sites from which they must leave with inadequate fuel stores for the onward journey. Hence, selecting less predictable habitats may have profound fitness consequences for the individual. Moreover, when birds migrate across the intensively cultivated plains of Northeast China, human activities may also play an additional role, by creating disturbance and modifying habitats as elsewhere in East Asia (Yu et al. 2017; Zhang et al. 2019).

In this study, we test the role of habitat type and predictability in the landscape in determining shelduck autumn stopover site selection using resource selection functions. We evaluated the inter-individual consistency in habitat selection by examining the predictability of individual resource selection models on other individuals. We predicted that given their consistent reliance on aquatic foods, they would show high inter-individual consistency, rather than flexibility in habitat selection, and that they would prefer predictable and seasonal habitats associated with water and with low human disturbance, as is the case with other waterbirds elsewhere in East Asia.

Materials and Methods

Study area and bird movement data

Wang et al. (2018a) described shelduck movement data from 14 birds captured at Bumbat Lake (48.12°N, 114.59°E) in Mongolia during the molting period in July 2017 to which GPS–GSM transmitters (<3% of the birds' body mass, see Wang et al. [2018a] for full details of methods) were attached. In autumn, the birds migrated generally southwards from Northeast Mongolia but showed considerable diversity in their orientation and directness of migration overland to their ultimate wintering grounds along the eastern China coast (fully reported in Wang et al. [2018a], but reproduced here in Figure 1). Among the 10 individuals with complete autumn migration tracks, 9 used a total of 25 stopover sites *en route* for refueling, including 14 coastal and 11 inland sites (Table 1, see Wang et al. [2018a] for details). We identified stopover sites as sites where a bird did not displace >30 km for at least 48 h (van Wijk et al. 2012). Five individuals migrated directly to the coast without using inland stopovers, but all tracked shelducks ultimately staged at coastal stopover sites in Bohai Bay or along the Shandong Peninsula (Wang et al. 2018a). The coastal stopover sites used by all birds overlapped with wintering sites. Use of these coastal stopover sites did not considerably contribute to the variation in migration routes taken by individuals, because headings taken by migrating shelducks diverged almost immediately on departing their summering areas and converged to the coastal zone. For this reason, we focused only on the 11 inland stopover sites of the 5 individuals using inland stopover sites to analyze and compare fine-grained habitat selection (Table 1).

Habitat variables

To characterize the wetlands used by tracked shelducks, we used water recurrence and water seasonality measures from the Global Surface Water dataset (30 × 30 m resolution, Pekel et al. 2016). Water recurrence describes how frequently water returned from 1 year to another (expressed as a percentage) and in this study, we used this property as an assessment of inter-annual environment predictability. Water seasonality provides information concerning the intra-annual pattern of water existence for 2014–2015, measured in months. We used Global Terrestrial Human Footprint maps 2009 to measure cumulative anthropogenic pressures on the environment (1 × 1 km resolution, Venter et al. 2016). This data set combined 1) built environments, 2) population density, 3) electricity infrastructure, 4) crop lands, 5) pasture lands, 6) roads, 7) railways, and 8) navigable waterways to generate a general measure of human footprint and disturbance. The values ranged between 0 (no

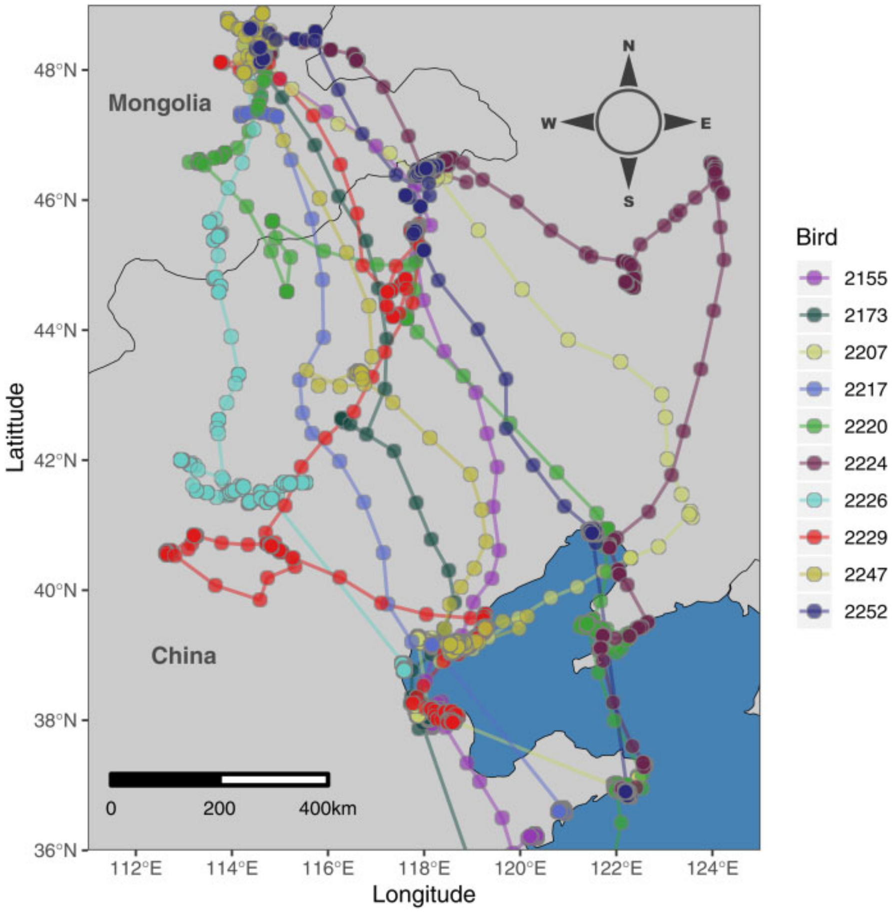

Figure 1. Locations of GPS telemetry positions and inferred tracks (i.e., shortest distance between sequential GPS positions) of the Mongolian common shelduck *Tadorna tadorna* tracked during the autumn migration between the summering sites in Northeast Mongolia and the eastern China coast. Open sea is shown as dark blue and national boundaries in black.

Table 1. The location and duration of stopover sites used by tracked Mongolian common shelduck *Tadorna tadorna* during autumn migration

Stopover site ID	Bird ID	Longitude	Latitude	Arrival date	Departure date	Number of GPS locations used for analyses[a]
1	2220	113.35	46.58	13 August 2017	25 August 2017	265
2	2220	114.84	45.67	26 August 2017	18 September 2017	549
3	2224	118.20	46.45	27 August 2017	5 October 2017	897
4	2224	122.29	44.79	5 October 2017	8 October 2017	66
5	2224	124.06	46.49	9 October 2017	1 November 2017	525
6	2226	114.37	41.36	30 August 2017	10 November 2017	1,638
7	2229	117.85	45.54	12 September 2017	9 October 2017	623
8	2229	114.81	40.69	9 October 2017	12 October 2017	57
9	2229	112.63	40.57	13 October 2017	2 November 2017	452
10	2229	114.79	40.70	2 November 20172	9 November 2017	156
11	2252	117.96	46.47	26 August 2017	24 September 2017	663

The stopover site IDs correspond to those shown in Figure 2. For each site, the number of GPS telemetry locations associated with each individual there is also provided (after filtering out positions when the bird was traveling at speed).

[a] We only retained GPS fixes associated with a velocity $<0.5\ \mathrm{m{\cdot}s^{-1}}$ to exclude locations when birds were moving rapidly over a location, such as flying or running, which did not reflect true habitat use.

disturbance) and 25.95 (maximum level of disturbance). We used the GlobeLand30 land cover dataset of 2017 (an updated version of Gong et al. [2013], available from http://data.ess.tsinghua.edu.cn/fromglc2017v1.html) to determine the land use type of the sites used by the birds. To our knowledge, this is the highest resolution (30 × 30 m) and most up-to-date land cover dataset currently available. The dataset is based upon 10 land cover classification types, namely cultivated land, forest, grassland, shrubland, wetland, water bodies, tundra, artificial surfaces, bare substrate, permanent snow, and ice (tundra, permanent snow and ice are absent from areas used

Table 2. Variance inflation factors (VIFs) of variables of final population-level and stopover-site-level models

Stopover site ID	Water recurrence	Water seasonality	Human footprint	Land cover: cultivated land	Land cover: grassland	Land cover: water bodies	Land cover: artificial surfaces	Land cover: bare substrate
All	1.40	1.67	1.07	1.43	2.61	1.83	1.23	2.74
1	1.79	1.45	1.13		1.21			
2	2.10	1.90	1.03		1.28			
3	2.78	2.92	1.01	1.00	1.07			1.27
4	2.57	2.72	1.48	1.00	1.49		1.78	1.36
5	3.33	5.23	1.36	2.31	2.21	4.65		
6	1.28	1.46	1.26	1.37	1.95			2.58
7	3.30	2.86	1.07		3.26			1.66
8	1.75	1.27	1.09	1.02	1.00		1.61	
9	1.00	2.01	1.27	1.89	1.83	1.99		
10	1.49	1.52	1.06	1.00	1.11		1.03	
11	1.48	1.49	1.02	1.00	1.00			1.10

If any VIF was larger than 10 in a model, we performed a step-wise procedure to remove such variable(s) (see the “Materials and Methods” section for details). The stopover site IDs correspond to those identified in Table 1 and Figure 2. Stopover site ID “All” denotes the population-level resource selection generalized linear mixed model.

by shelducks). Unlike many habitat selection analyses, we excluded landscape variables such as elevation and slope, because shelducks almost exclusively used water bodies and wetlands (del Hoyo et al. 2019), where these landscape variables were irrelevant.

We excluded rare land cover types (<5% of total land use by either use or availability data points), namely forest, shrubland, and wetland, to avoid model convergence problems recognized below these levels (Altman et al. 2004). For each model, we checked multicollinearity of variables by examining the variance inflation factors (VIFs), and performed a step-wise removal of VIF > 10 variables, from the least to most used land cover types at the stopover site by the birds (all the VIF > 10 variables were land cover variables). We obtained final models when VIF of all variables were smaller than 10 (all <6, see Table 2).

Resource selection modeling

We used generalized linear models (GLMs) with a binomial error structure to evaluate stopover-site-level resource selection with use/availability as response variable, and environment variables as explanatory variables. We retained all GPS fixes of the birds with a velocity $<0.5\,\mathrm{m{\cdot}s^{-1}}$ as constituting site use, in order to exclude birds showing substantial movement (flying), which did not reflect genuine resource use by the birds. Transmitters were programmed to record locations at hourly intervals to reduce autocorrelation (Signer et al. 2019).

In order to generate availability data (i.e., pseudo-absence data) at each stopover site, we generated 100% minimum convex polygons (MCPs based on positions for tagged individuals), and extended these outwards by 19 km (the average maximum hourly displacement for all individuals at all stopover sites) to represent the area potentially available to staging birds. We then randomly selected locations from the extended MCP for each stopover site as pseudo-absence data. We maintained the use: availability data ratio as 1:20, in order to obtain stable and unbiased parameter estimates (Northrup et al. 2013).

We used generalized linear mixed models (GLMMs) with a binomial error structure to analyze the population-level resource selection during autumn migration. The model structure was based on the stopover-site-level models with the stopover site ID nested in bird ID as the random effect on intercept.

In order to estimate the effect size of explanatory variables, we rescaled variables using the “standardize” function in “arm” package in R (Gelman and Su 2018), following the method of Gelman (2008). The effect size was then evaluated by comparing coefficients of the rescaled models: larger positive/smaller negative coefficients suggest larger positive/negative effects on the model.

We used 2 approaches to estimate the inter-individual consistency/variation in habitat selection. First, we compared the variance explained by fixed effects (environment variables) and random effects (individuals and stopover sites) in the population-level resource selection model. The variance explained by fixed effects was expressed as the marginal R^2, and the variance explained by random effects was calculated by subtracting the marginal R^2 from conditional R^2 (the variance explained by fixed and random effects). Marginal and conditional R^2 were calculated based on the methods of Nakagawa and Schielzeth (2013). Lower variance explained by random effects suggests lower inter-individual variance in habitat selection. We also tested the cross-prediction accuracy of each of the stopover-site-level resource selection models, and the population-level resource selection model, on each of the stopover sites, by estimating the area under the receiver operating characteristic (ROC) curve (AUC). Values for the AUC can range between 0 and 1, with 0.5 indicating predictions no better than chance, 1 indicating perfect discrimination, and 0.7 generally indicating reasonable predictions (Hosmer and Lemeshow 1989). If habitat selection were consistent among individuals and stopover sites, the AUC values of each model would be high. In addition, we generated the predictive probability surface of expected use within the overall migration range of the birds, based on the environment variables and the population-level resource selection models with random effects set to zero.

Results

All 11 inland stopover sites used by 5 tracked shelducks during the autumn migration originating in eastern Mongolia *en route* to the Chinese coast, in 2017, were scattered throughout northeast China (Figure 2).

All 5 Mongolian shelduck shared similar patterns of habitat use at inland stopover sites (Figure 3), all locations used by birds showed consistently high water recurrence, and relatively high water seasonality. In contrast, these values at corresponding available locations

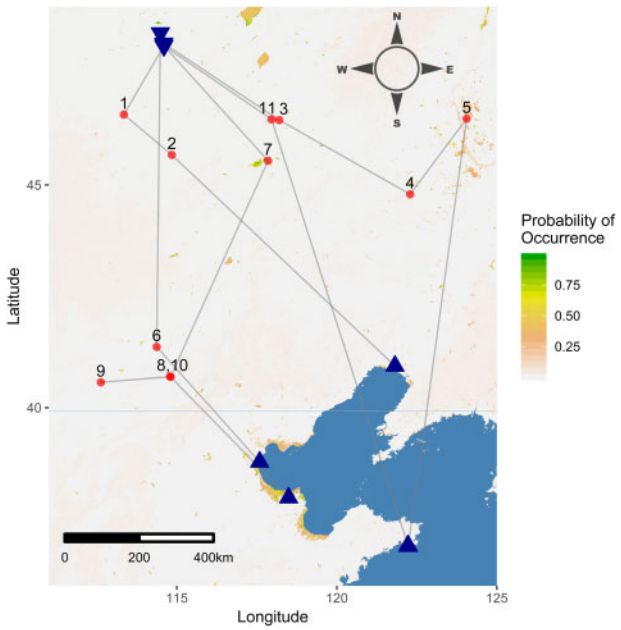

Figure 2. Inland stopover sites and probability of occurrence of the Mongolian common shelduck. The up and down triangles denote summering and first coastal stopover/wintering sites, respectively. Red dots denote the location of inland stopover sites subject to analysis here. Gray lines, showing the progression of autumn migration progress for each bird, connect sites used by the same individuals. The numbers adjacent to stopover sites correspond to the stopover site ID shown in Table 1. Ocean is shown in dark blue; the probably of occurrence of shelduck throughout the entire area is presented as a color gradient as illustrated in the key.

in the area around the stopover sites were low. The levels of human footprint were highly variable but tended to be similar between used and available locations. We also found a diverse pattern of used/available land cover types at different stopover sites, consistent with our previous findings (Wang et al. 2018a). The birds mainly used bare substrate and water bodies, whereas grassland and cultivated land dominated the available locations.

The population- and stopover-site-level resource selection models showed similar variable selection (Table 3). In the population-level resource selection model, water recurrence had strongest positive effect, and cultivated land and grassland land cover types had the strongest negative effects in determining birds' occupancy of locations. The effect of water seasonality was positive but weak; the effect of land cover types of cultivated land, grassland, water bodies, artificial surfaces, and bare substrate were all negative. The birds showed no significant selection for human footprint. Although some variables were missing in some stopover-site-level resource selection models because of lack of changes in the values or due to high multicollinearity, birds showed similar habitat selection at different stopover sites. At most sites, birds preferred high water recurrence, and avoided cultivated land and grassland. At the few sites at which water bodies and artificial surfaces were included in the models, birds tended to show avoidance of these 2 habitats. The birds did not show consistent preference/avoidance for water seasonality, human footprint, or bare substrate. The population- and stopover-site-level models showed generally high explanatory power. Specifically, in the population-level model, the fixed effects explained 46% of total variance, whereas the random effects only explained 11%.

The one population- and 11 stopover-site-level models showed high predictive power (Table 4). Most models obtained AUC scores >0.75 using the training and the 11 remaining prediction datasets. Among the 144 AUC scores, only 6 were <0.75, including 4 generated by the model of stopover site No. 2 and 2 by the model of stopover site No. 5. Inland locations, which experienced a high probability of shelduck occurrence, were very widely distributed in the form of small patches, within the migration range used by this species, but overall were extremely rare features within the total landscape (Figure 2).

Discussion

Combining the high-resolution GPS tracking data of the Mongolian shelduck during autumn migration from post-breeding sites to coastal wintering sites, with a variety of remote-sensing environmental datasets, we investigated the pattern and inter-individual consistency of habitat selection at inland stopover sites during migration. Although we should be prudent about concluding too much from a relatively small sample size, our results showed a previously unreported high level of inter-individual consistency in habitat selection, which rather contradicted the general diversity of habitats used by this population (Wang et al. 2018a). While we cannot fully reject the fact that deployment of devices on shelducks may have affected their behavior, there was nothing to suggest their migratory behavior was in any way aberrant. Hence, these results show that the divergent migration routes taken by different individuals to broadly reach the same ultimate wintering grounds result from the specific selection of features (i.e., wetlands with high between-year predictability). These habitats are generally extremely scarce in the landscape, which they traverse on autumn migration (see Figure 2).

Counter-intuitively, tracked shelducks neither strongly selected for high water seasonality nor avoided areas affected by the human footprint. Seasonal water creates productive inundation areas, known to support larger, more diverse waterbird communities (Aharon-Rotman et al. 2017; Jia et al. 2018). However, we suggest that for Mongolian shelducks, selection for water seasonality was less important, because within this semi-arid and highly unpredictable part of their migration range (Wang et al. 2018a), water recurrence was likely the overriding factor involved in habitat selection. Agriculture and human communities require water. The rarity of water bodies in the semi-arid migration range of the Mongolian shelduck may actually result in the concentration of humans and agriculture around more permanent, and therefore predictable water bodies. In this way, the human footprint associated with habitats used by shelduck was enhanced, while they avoided cultivated land, grassland, artificial surfaces, and bare substrate, conforming to their general patterns of behavior (Kear 2005; del Hoyo et al. 2019). The rare inclusion of water bodies in stopover-site-level models indicated their scarce occupancy by shelducks, also seems counter-intuitive, given the species reliance on water. However, this is probably because the land cover dataset was based on satellite images not necessarily gathered during the wet season. In the dry season, many seasonal water bodies dry up and, at the time they were captured on imagery, might be classified as bare substrate. Shelducks habitually forage in shallow water, which are typical of such seasonally recharged wetlands in this region. Unfortunately, there is no seasonal land cover dataset specifically generated during the migration season, so we cannot improve the quality of land cover classification.

The population-level model also provides a deeper understanding of the combined effects of water-related variables, i.e., water recurrence and water bodies. These 2 variables showed large effect sizes in opposite directions. On the surface, this pattern seems

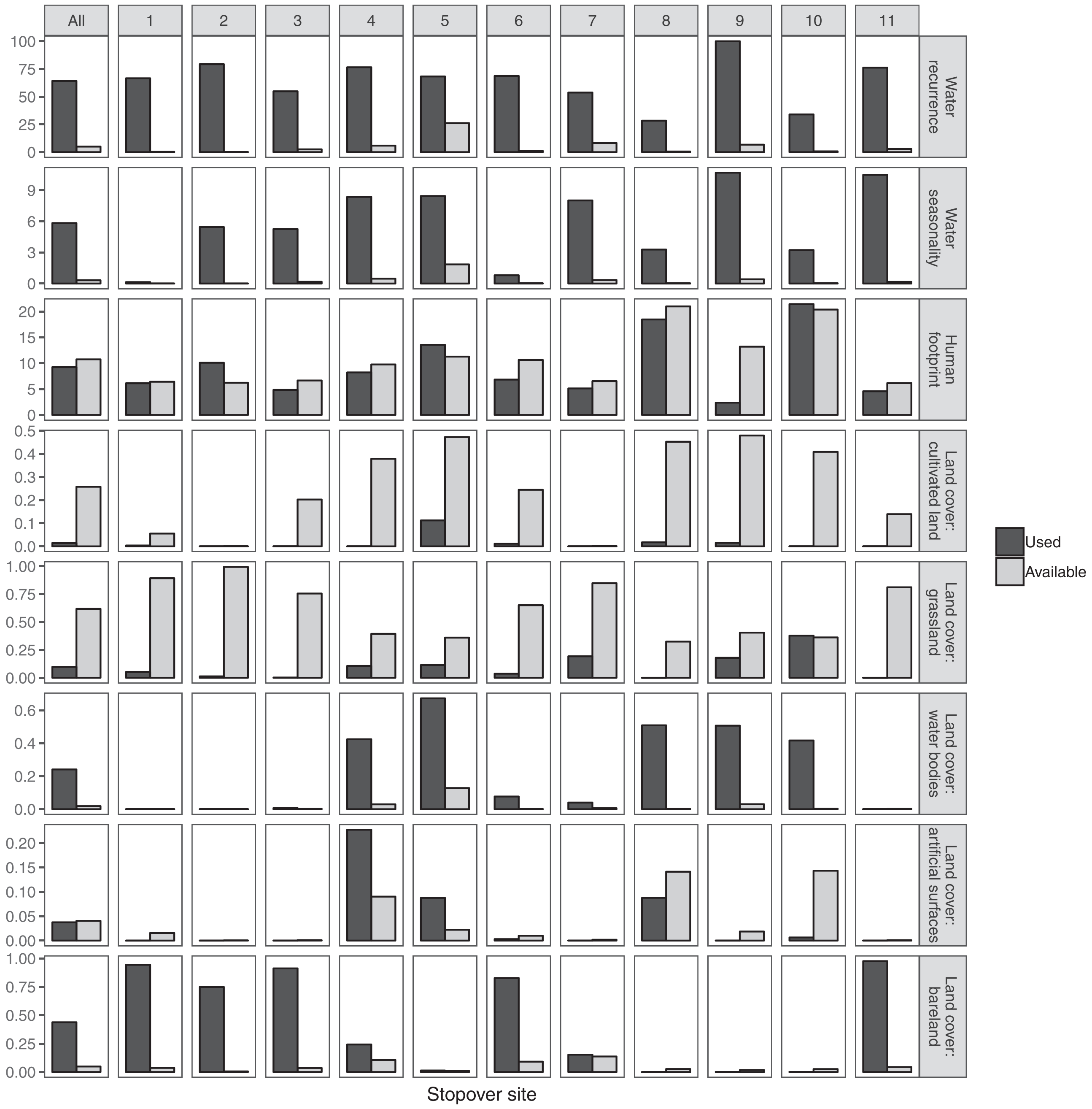

Figure 3. Available (gray) and used resources (black) at all and each of the stopover sites used during the autumn migration of the telemetry tracked Mongolian common shelduck. The stopover site IDs correspond to those identified in Table 1 and Figure 2. Stopover site ID "All" denotes the population-level resource selection generalized linear mixed model. Note that the axis scale differs between panel rows.

confusing. However, water bodies classified by the land cover dataset as such were almost certainly permanent lakes, which are continuous features in the landscape, characterized by deep water and steep edges (such as artificial reservoirs), features avoided by staging shelduck. Deep water is associated with high water recurrence, a feature preferred by the shelduck, but high water recurrence is not confined to deep permanent lakes, because the landscape is characterized by seasonal shallow water lakes also with high water recurrence. Such water bodies would show high predictability, and positive accumulated effect size (i.e., with high water recurrence but are not classified as water bodies). In contrast, because shelduck show no preference for deep water (by definition with highly recurrence) the effects of water bodies and water recurrence counteract each other in the models. Hence, despite an apparent contradiction, these model-based extrapolations conform to our prediction based on the feeding ecology of the species, which forages largely in shallow ephemeral waters. We also suspect that a proportion of seasonal water bodies were misclassified in this land-use classification (see above). Areas of bare substrate and water seasonality are also likely features of ephemeral water bodies potentially attractive to staging shelduck, but their relatively small effect size could result from their weak selection for or avoidance of these features, as well as their weak contribution to identifying these types of water features in the landscape.

Table 3. Coefficients and effect size of resource selection models for each stopover site, and all combined, based on rescaled explanatory variables

Stopover site ID	Intercept	Water recurrence	Water seasonality	Human footprint	Land cover: cultivated land	Land cover: grassland	Land cover: water bodies	Land cover: artificial surfaces	Land cover: bare substrate	R^2 of fixed effects	R^2 of random effects
All	**−5.10**	**2.11**	**0.29**	−0.08	**−4.04**	**−3.51**	**−2.26**	**−2.15**	**−0.46**	0.46	0.11
1	**−5.34**	**3.10**	**−0.51**	**−1.20**		**−2.35**				0.80	
2	**−7.81**	**1.82**	**0.85**	**2.01**		**−5.81**				0.95	
3	−10.6	**0.81**	**−0.17**	**−1.83**	−18.35	**−7.19**			**0.99**	0.71	
4	−12.67	**2.83**	0.22	**−5.69**	−18.43	**−1.63**		0.96	0.12	0.64	
5	**−4.39**	0.36	**1.34**	**2.10**	**−2.24**	**−1.70**	−0.39			0.32	
6	**−5.89**	**2.42**	**−0.30**	**−1.05**	**−2.98**	**−3.08**			−0.27	0.75	
7	**−4.24**	**0.32**	**1.05**	**−1.24**		**−2.89**			**−2.35**	0.50	
8	−9.96	**1.31**	0.35	**−1.13**	**−5.08**	−19.54		**−3.10**		0.64	
9	−212.53	146.93	−0.25	**−1.51**	**−4.95**	−0.29	**−2.00**			0.74	
10	−10.28	**0.92**	**0.80**	**0.74**	−18.74	**−1.24**		**−4.51**		0.49	
11	−20.7	**1.06**	**1.34**	**−1.53**	−15.84	−15.92			**3.54**	0.82	

Values in bold denotes $P < 0.05$; blank cells denote that the variable was excluded from the model because of rare occupancy or high VIF values. The stopover site IDs correspond to those identified in Table 1 and Figure 2. Stopover site ID "All" denotes the population-level resource selection generalized linear mixed model. R^2 of fixed effects is the marginal R^2 of the model, i.e., the variance explained by fixed effects; R^2 of random effects is the difference between conditional R^2 (the variance explained by fixed and random effects) and marginal R^2 of the model. R^2 of random effects only applies to mixed models.

Table 4. Cross-prediction results (AUC scores) of resource selection models of all and each stopover site during autumn migration of the Mongolian common shelduck *Tadorna tadorna*.

	The stopover site ID of prediction dataset											
The stopover site ID of model training dataset	All	1	2	3	4	5	6	7	8	9	10	11
All	**0.97**	**0.99**	**>0.99**	**0.96**	**0.95**	**0.95**	**0.99**	**0.96**	**0.96**	**0.97**	**0.95**	**0.99**
1	**0.95**	**0.99**	**0.96**	**0.96**	**0.93**	**0.88**	**0.98**	**0.89**	**0.95**	**0.92**	**0.95**	**0.94**
2	**0.88**	**0.99**	**>0.99**	**0.95**	**0.86**	0.63	**0.92**	**0.93**	0.42	0.74	0.47	**0.98**
3	**0.96**	**0.99**	**0.96**	**0.97**	**0.96**	**0.95**	**0.99**	**0.89**	**0.95**	**0.96**	**0.95**	**0.98**
4	**0.95**	**0.98**	**0.93**	**0.96**	**0.96**	**0.90**	**0.98**	**0.88**	**0.95**	**0.97**	**0.95**	**0.96**
5	**0.94**	**0.95**	**0.95**	**0.95**	**0.95**	**0.95**	**0.94**	**0.95**	0.71	**0.95**	0.74	**0.95**
6	**0.95**	**0.99**	**0.98**	**0.95**	**0.96**	**0.87**	**0.99**	**0.90**	**0.95**	**0.94**	**0.95**	**0.95**
7	**0.95**	**0.95**	**0.96**	**0.95**	**0.93**	**0.88**	**0.95**	**0.97**	**0.95**	**0.95**	**0.95**	**0.95**
8	**0.96**	**0.99**	**>0.99**	**0.97**	**0.95**	**0.84**	**0.99**	**0.90**	**0.97**	**0.94**	**0.97**	**0.97**
9	**0.95**	**0.95**	**0.95**	**0.95**	**0.96**	**0.94**	**0.95**	**0.94**	**0.95**	**0.97**	**0.95**	**0.95**
10	**0.96**	**0.97**	**>0.99**	**0.96**	**0.96**	**0.84**	**0.97**	**0.95**	**0.97**	**0.97**	**0.98**	**0.98**
11	**0.96**	**0.95**	**0.96**	**0.96**	**0.96**	**0.95**	**0.95**	**0.95**	**0.95**	**0.96**	**0.95**	**0.99**

The stopover site IDs correspond to those identified in Table 1 and Figure 2. Stopover site ID "All" denotes the population-level resource selection generalized linear mixed model. AUC scores were highlighted in bold if they were >0.75, suggesting good predictive power.

Although the stopover-site-level resource selection models showed considerable variance in effect direction and sizes of different variables, in the population-level model, individual variance only explained a small proportion of total model variance, although the environmental (fixed) factors explained much more (Table 3). The cross-prediction AUC scores of population- and stopover-site-level resource selection models were, in general, very high. Both corroborated the high inter-individual consistency in habitat selection during the dispersed autumn migration of the Mongolian shelduck. These modeling results complied with our biological knowledge of this species, which mostly feeds on aquatic invertebrates in shallow water and mud in riverine environments, marshes, and shallow lake margins (Kear 2005; del Hoyo et al. 2019). This high inter-individual consistency contrasts with other species/taxa that showed considerable individual variation in environmental requirements during certain stages in the annual cycle (e.g., Leclerc et al. 2016; Zurell et al. 2018). This result, and the map of occurrence probability based on the population-level model, indicate that the divergent migration routes and scattered inland stopover sites used can be explained by the wide and dispersed distribution of suitable habitats *en route*, rather than by the flexibility shown by birds in their habitat use.

Our analysis showed that the highly scattered, relative rarity, and temporary nature of its staging habitat represents a potential bottleneck in a region that has been subject to rapid economic growth and pressure on water resources. The shelduck is currently abundant and widespread and globally maintains a relatively good conservation status (Least Concern, IUCN 2018) including those birds occurring in East Asia (Kear 2005; del Hoyo et al. 2019). However, the results also showed the vulnerability of the species to threats to the recurrence of autumn staging wetlands (and hence their predictability as refueling sites) and increasing human disturbance (affecting their ability to effectively acquire energy stores for onward migration). This is especially critical given existing pressures on this population during the breeding season from rapid lake loss caused by human activities and climate change (Tao et al. 2015) and the massive reclamation of intertidal mudflats along the eastern China coast (Ma et al. 2014; Murray et al. 2014) which constitutes their wintering area. As we have shown, inland staging areas are also rare and threatened by hydrological pressures, which make adequate site safeguard a priority in this region, for shelducks and other migratory waterbirds.

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Authors' Contributions

F.M., X.W., and A.D.F. conceived the study and wrote the manuscript. F.M. and X.W. prepared and analyzed the data. F.M., L.C., and N.B. coordinated the fieldwork. N.B., T.N., B.D., and I.D. conducted the fieldwork and obtained the field data. L.C. provided the critical input during manuscript preparation. All authors contributed to the development of ideas and approved the final version of the manuscript.

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