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Multi-scale habitat selection by two declining East Asian waterfowl species at their core spring stopover area

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ABSTRACT

Animals respond to their environment at multiple spatial scales that each require different conservation measures. Waterbirds are key bio-indicators for globally threatened wetland ecosystems but their multi-scale habitat selection mechanisms have rarely been studied. Using satellite tracking data and Maximum entropy modeling, we studied habitat selection of two declining waterfowl species, the Greater White-fronted Goose (*Anser Albifrons*) and the Tundra Bean Goose (*A. serrirostris*), at three spatial scales: landscape (30, 40, 50 km), foraging (10, 15, 20 km) and roosting (1, 3, 5 km). We hypothesized that the landscape-scale habitat selection was mainly based on relatively coarse landscape metrics, while more detailed landscape features were taken into account for the foraging- and roosting- scale habitat selection. We found that both waterfowl species preferred areas with a larger percentage of wetland and waterbodies at the landscape scale, aggregated waterbodies surrounded by scattered croplands at the foraging scale, and well-connected wetlands and well-connected middle-sized waterbodies at the roosting scale. The main difference in habitat selection for the two species occurred at the landscape and foraging scale; factors at the roosting scale were similar. We suggest that conservation activities should focus on enhancing the aggregation and connectivity of waterbodies and wetlands, and developing less aggregated cropland in the surroundings. Our approach could guide waterbird conservation practices and wetland management by providing effective measures to improve habitat quality in the face of human-induced environmental change.

1. Introduction

The importance of spatial scale in ecology is increasingly recognized (Levin, 1992; McGarigal et al., 2016; Schneider 2001; Wiens, 1989). Habitat is characterized by a multidimensional structure (Wiens and Kotliar, 1990), in which species perceive and respond to their surroundings across a range of spatial scales (Wiens, 1989). Hence, drawing conclusions from any single-scale at which all observations are measured may result in an overestimation of those observations that drive system behavior (Decesare et al., 2012; Mayor et al., 2009). Multi-scale analysis provides important theoretical insight into ecological patterns and processes, and facilitates effective conservation and management (Chave, 2013; Cunningham et al., 2014; Wiens et al., 1987). Conservation goals also vary at different spatial scales, from dealing with large-scale biodiversity threats to restoring finer-scale habitat, and hence different conservation activities are required at different spatial scales (Cabeza et al., 2010). In recent decades, scale-dependent habitat selection by birds has been increasingly studied (Lemaître et al., 2012; Mayor et al., 2009; McGarigal et al., 2016; Spautz et al., 2006; Wiens, 1989), improving conservation planning at different scales (Benítez-López et al., 2017; Cao et al., 2015; du Toit 2010). While most studies have focused on forest and grassland birds (Doherty et al., 2010; Rae et al., 2014; Timm et al., 2016), multi-scale habitat selection of waterbirds is rarely studied (but see review in McGarigal et al., 2016; Becker and Beissinger, 2003, Bellier et al., 2010; Timm et al., 2016; Benítez-López et al., 2017). Furthermore, wetlands are of economic importance, and in the meantime are eco-sensitive and heavily threatened (Turner et al., 2000). Hence, assessing the multi-scale habitat selection of waterbirds, which are key bio-indicators for wetland ecosystems (Amat and Green, 2010), provides crucial insight for wetland management and conservation.

Species distribution modeling, also known as ecological niche modeling, has been widely applied to quantify the relationship between species distribution and environmental factors and predict potentially

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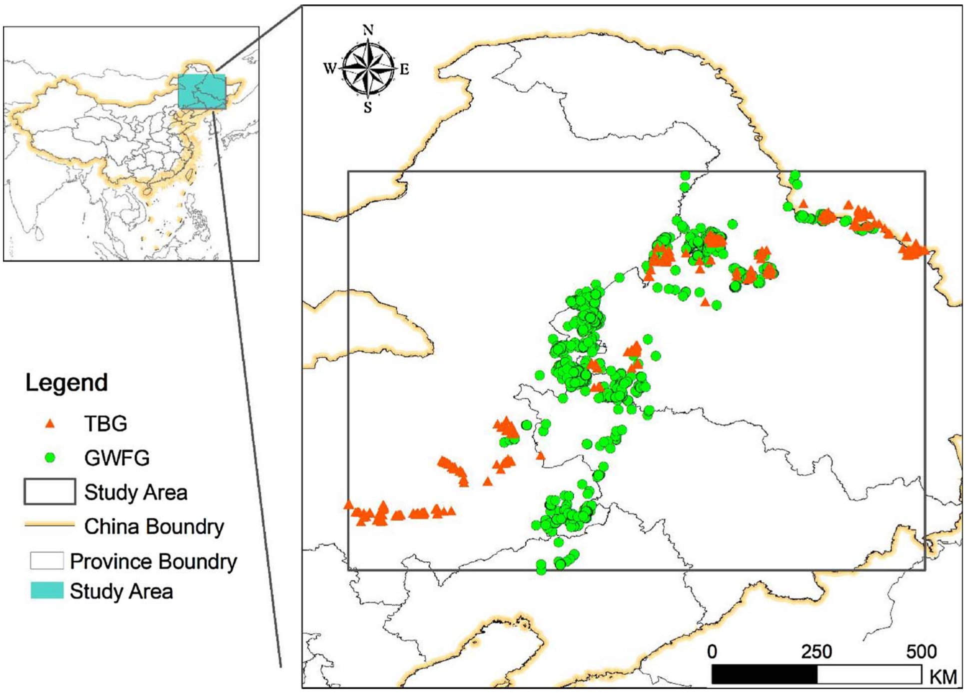

Fig. 1. Map of the study area in the Northeast China Plain (NCP). Red triangles and green circles represent the satellite tracking points. TBG refers to Tundra Bean Goose (*A. serrirostris*). GWFG refers to Greater White-fronted Goose (*Anser Albifrons*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

suitable area (Guisan and Thuiller 2005; Peterson, 2006). Species distribution models can also be used to estimate the response function and contribution of environment factors (Razgour et al., 2011) and thus can reflect the habitat selection process (Benítez-López et al., 2017). In species distribution models, environmental variables such as food resources, meteorological factors, elevation and human disturbance, have been frequently used to explore bird-environment relationships and predict suitable habitat (Bridge et al., 2015; Osborne et al., 2001; Rosin et al., 2012; Zhang et al., 2016). Moreover, landscape features can influence bird distribution and their habitat selection considerably (Cushman and McGarigal, 2002; Resetarits and Silberbush, 2016). For instance, landscape composition can influence species distribution (McGarigal and McComb, 1995; Sanza et al., 2012) and shifts therein (Brandolin and Blendinger, 2016; Bruun and Smith, 2003). Landscape fragmentation can cause population declines, especially for area-sensitive species (Herkert, 1994). Therefore, the effect of landscape features needs to be considered in analyzing habitat selection mechanisms and developing management measures (Kosicki, 2017).

The process of habitat selection of migratory birds at their stopover area remains poorly understood (Arzel et al., 2006; Drent et al., 2006). The Northeast China Plain (thereafter NCP) is a core spring stopover area for waterbirds wintering in China (Li et al., 2017), where they spent an extended period of time to accumulate energy before traveling to their breeding grounds in Siberia (Li et al., 2017). However, natural wetlands in the NCP have deteriorated drastically since the 1980s (Gong et al., 2010; Niu et al., 2012). This may explain the considerable decline of East Asian waterfowl wintering in China. The landscape and microhabitat in the NCP is highly heterogeneous (Lu et al., 2016; Niu et al., 2012; Wang et al., 2011). This calls for conservation measures considering the effect of landscape features and environmental factors at different spatial scales.

Using satellite tracking data, we investigate the habitat selection of two migratory waterfowl species, the Greater White-fronted Goose (GWFG, *Anser Albifrons*), and the Tundra Bean Goose (TBG, *A. serrirostris*), in the NCP at three spatial scales: landscape, foraging, and roosting. Waterfowl may first select an area to settle at a broad scale, and later gather more precise information at a finer scale (Beatty et al., 2014; Leopold and Hess, 2013). Therefore, we hypothesize that at the landscape scale, habitat selection is mainly based on relatively coarse landscape metrics such as the percentage of relevant land cover types, while at the foraging and roosting scale, more detailed landscape features, such as shape and aggregation indices of relevant land cover type are taken into account.

2. Methods and materials

2.1. Study area

The Northeast China Plain (NCP) is a low elevation plain (< 250 m asl) surrounded by mountains, located in the northeastern part of China, covering the Heilongjiang, Jilin and Liaoning Provinces and Eastern Inner Mongolia (Huang et al., 1998). We define the range of the study area (between 42°02′N – 50°34′N and 118°05′E – 130°27′E) based on the maximum extent of bird tracking data at this core stopover site (Fig. 1). The climate in this region is continental temperate monsoon and is characterized by cold winters, warm summers and abundant rainfall (Zhao et al., 2015a, 2015b). The mean annual temperature is 1.4–4.3 °C, with an average maximal of 21–22 °C and an average minimal −18 °C (Shen et al., 2009). The mean annual precipitation is 400–1000 mm, and 80% of the precipitation is concentrated between May and September (Chen et al., 2012). Although wetlands only account for less than 10% of the area (Lu et al., 2016), it serves as a core stopover area for waterfowl (Li et al., 2017). Besides, the NCP is also an important crop production area (Shen et al., 2009). The main crops in the NCP include rice, corn and soybean, with the sown acreage of soybean being the largest (Liu et al., 2008).

2.2. Bird tracking data

In 2014 and 2015, a total of 24 GWFG and 13 TBG were captured at their wintering ground in Poyang Lake along the Yangtze River Floodplain, Jiangxi Province, China and equipped with GPS-GSM (Global Positioning System – Global System for Mobile Communications), solar-powered loggers (20-necked IBIS series, Ecotone Telemetry, Gdynia, Poland; 15-necked HQNG series, Hunan Global Messenger Technology Co. Ltd., Xiangtan, China; and 2-backed ANIT series, Blueoceanix Technology Co. Ltd., Tianjin, China). The loggers were programmed to record GPS positions every 2 h and send the data back every other day by Short Messaging Service (SMS).

We have obtained 9305 GPS locations from 14 GWFG and 5 TBG during their stopover in the NCP during their 2015 and 2016 spring migration. All data are stored in Movebank (http://www.movebank.org) under ID 52997422, study '2015 Tsinghua waterfowl (Yangtze)'.

2.3. Radius of landscape, foraging, and roosting scales

We determined the radius of three spatial scales (landscape, foraging, and roosting) based on the distribution utilization of geese calculated by the dynamic Brownian Bridge Movement Model (dBBMM) (Kranstauber et al., 2012). As waterfowl mostly forage by day, we first labeled daytime and nighttime points as the foraging and roosting locations respectively, using the sunrise and sunset time for each location based on algorithms provided by the National Oceanic & Atmospheric Administration (NOAA) (https://www.esrl.noaa.gov/), Then we built three dBBMMs using 1) all locations, 2) foraging locations, and 3) roosting locations, to calculate the utilization distributions at the landscape, foraging and roosting scales. The landscape scale is defined as the potential distribution area. The foraging scale is defined as the highly utilized area where most foraging activities occur. The roosting scale was regarded as the most intensively utilized area for roosting. The optimal value for the selection of percentage volume contours varies among scales and species. Thus, based on visual inspection of our data, the 99%, 90% and 75% isopleths of the utilization distribution were adopted to represent areas used at the landscape, foraging and roosting scales. We then calculated the radius of the three scales based on the average radius of multiple utilization-area patches at each scale.

The radius of three spatial scales for both species were calculated and no significant difference was found between species (Shapiro-Wilk normality test, p values < 0.05; Mann-Whitney test, all p-values > 0.3). We calculated the mean radius of both species at each scale: the landscape scale 34.60 km (95% CI = 28.6 ~ 40.6 km), foraging scale 13.82 km (95% CI = 12.02 ~ 15.62 km) and roosting scale 1.89 km (95% CI = 1.52 ~ 2.26 km). Based on this, a gradient of 30 km, 40 km and 50 km at the landscape scale, 10 km, 15 km and 20 km at the foraging scale, and 1 km, 3 km and 5 km at the roosting scale were adopted.

2.4. Environmental data

We used five environmental datasets that are ecologically relevant to habitat selection of waterfowl, including the differential Enhanced Vegetation Index (EVI; Bridge et al., 2015), land cover maps (Fox et al., 2005), elevation (Leopold and Hess 2013), land surface temperature (Li et al., 2017) and precipitation (Webb et al., 2010).

Herbivorous waterfowl mainly utilize spring growing grasses along their migration routes to store energy (Si et al., 2015a). We adopted the differential Enhanced Vegetation index (EVI_{diff}) to measure plant growth (Bridge et al., 2015). The global Moderate Resolution Imaging Spectroradiometer (MODIS) enhanced vegetation index (EVI) product with a 250 m and 16 day resolution (MOD13Q1; https://lpdaac.usgs.gov) was used to calculate EVI_{diff}. For each bird location, we extracted the EVI value from the map with the closest date and the EVI value 32 days before the former map. The difference between these two EVI values is EVI_{diff}.

To generate a land cover map, we applied the same classification scheme as Li et al., 2016, which used the finer resolution observation and monitoring of global land cover (FROM-GLC) (Gong et al., 2013) and the Food and Agriculture Organization (FAO) Land Cover Classification System (Di Gregorio and Jansen, 2000) legends. Because most bird locations were recorded in 2016 (7359/9305), a total of 456 Landsat 8 Operational Land Imager (OLI) images of 2016 were used to generate a 30-m land cover map. The overall accuracy of the map was 77.84% (Zhao et al., 2014). Wetlands are hard to characterize by automatic classification methods due to their rapid changes (Yu et al., 2017). Hence, to reduce confusion between wetland and cropland or grassland, the land cover map was improved with a 20-m wetland map for 2008, which used human interpretation and multi-temporal imagery as a reference (Gong et al., 2010; Niu et al., 2012). Pixels in the original land cover map were reclassified as wetland if they were identified as wetland in the resampled 30-m wetland map. The land cover types include forest, grassland, wetland, waterbody, cropland, impervious layer, and bare land. For each land cover type, we created a distance map which measure the closest distance to the corresponding land cover type from every grid cell in the land cover map. This procedure was processed in R 3.3.3 using 'rgeos' and 'rgdal'.

Based on Advanced Spaceborne Thermal Emission and Reflection Radiometer Global Digital Elevation Model (ASTER GDEM) data (Available: https://lpdaac.usgs.gov/node/1079), we extracted elevation, slope and aspect maps at 30-m resolution. Average monthly precipitation data was obtained from WorldClim Version 2.0 (http://www.worldclim.org) at a spatial resolution of 1 km^2. We used the MODIS Global Land Surface Temperature product (MOD11A2; https://lpdaac.usgs.gov) at 1-km and 8 day resolution to extract temperature.

2.5. Landscape metrics

Landscape metrics used in this study (Table 1) were selected to simplify analysis and clarify guidelines for conservation and management (Cunningham and Johnson, 2011). For each scale, we generated a buffer for each point to calculate the landscape metrics. The radius of the buffer equals the corresponding scale. All the landscape metrics were calculated in R 3.3.3 using 'SDMTools'.

We mainly focused on land cover types and landscape metrics that are ecologically relevant to the life-history traits of herbivorous waterfowl. Focal land cover types included grassland, cropland, wetland, waterbody and bare land (Black et al., 1991; Kaminski and Elmberg, 2014; Li et al., 2017; Madsen, 1985; Si et al., 2011). The percentage cover of each land cover type (PO) and Shannon's diversity index (SHDI) were considered as coarse landscape metrics. PO reflects the general composition of the landscape. SHDI measures the diversity of land cover types, and a higher SHDI indicates a larger number of different land cover types or a more equal distribution of each land cover type (McGarigal and Marks, 1995).

Detailed landscape metrics included patch density (PDO), edge density (EDO), mean patch area (MPAO), landscape shape index (LSIO), mean shape index (MSIO), aggregation index (AIO), landscape division index (LDIO) and patch cohesion index (PCO), of the focal land cover types. PDO is a general index of spatial heterogeneity of the entire landscape mosaic, and a higher value indicates a higher density. EDO standardizes edge to a per unit area basis and facilitates comparisons among landscapes of varying size (Morgan and Gates, 1982; Paton, 1994; Strelke and Dickson, 1980). LSIO and MSIO are in relation to configuration, while AIO and LDIO are used to measure the landscape fragmentation. AIO increases as the focal land cover type becomes increasingly aggregated and reaches its maximal value when the land cover type is aggregated into one single patch (McGarigal and Marks, 1995). LDIO is interpreted as the probability that two randomly chosen cells in the landscape are not situated in the same patch of the corresponding land cover type (Jaeger, 2000). PCO is used to measure the physical connectedness of the focal land cover type and increases as the landscape becomes less subdivided and more connected (Schumaker, 1996).

2.6. Habitat selection modeling

To investigate the habitat selection of both waterfowl species at three spatial scales and each scale with three radii, we built a total of 18 Maximum entropy (MaxEnt) models. MaxEnt compares the environmental features at presence points to those of pseudo absences to discriminate the suitable area (Phillips et al., 2006). MaxEnt builds models

Table 1
Environmental variables and landscape metrics used to measure the habitat selection of the Greater White-fronted Goose (*Anser Albifrons*) and Tundra Bean Goose (*A. serrirostris*) at landscape, foraging and roosting scales.

Scale	Detailed/ Coarse	Variable	Abbreviation	Description
Landscape, foraging & roosting		***Landscape metrics***		
	Coarse	Percentage of focal land cover type	PO	Percentage cover of each patch type in the landscape (%)
	Coarse	Shannon diversity index	SHDI	$SHDI = -\sum_{i=1}^{n} P_i{*}lnP_i$, where n is the number of land cover types and P_i is percentage of land cover i
	Detailed	Patch density of focal land cover types	PDO	PDO (/km^2): divide the total number of the particular land cover type by the total landscape area (km^2)
	Detailed	Edge density of focal land cover types	EDO	EDO (m/km^2): the sum of the length of all edge segments of a particular land cover type, divided by the total landscape area
	Detailed	Landscape shape index of focal land cover types	LSIO	A standardized measure of the total edge adjusted by the size of the landscape for one particular land cover type
	Detailed	Mean patch area of focal land cover types	MPAO	The average patch area of each land cover type (m^2)
	Detailed	Mean shape index of focal land cover types	MSIO	The average shape index of each patch from a particular land cover type
	Detailed	Aggregation index of focal land cover types	AIO	The interspersion of the focal land cover type
	Detailed	Landscape division index of focal land cover types	LDIO	$LDIO = 1 - \left(\sum_{j=1}^{m} a_j\right)^2$, where a_j is the area of each patch and m is the number of patches
	Detailed	Patch cohesion index of focal land cover types	PCO	$PCO = 1 - \left(\sum_{j=1}^{m} p_j \;/\; \sum_{j=1}^{m} p_j\sqrt{a_j}\right)\left(1 - \frac{1}{\sqrt{A}}\right)^{-1}$, where m is the number of patches of a particular land cover type, a_j is the area of patch j, p_j is the perimeter of patch j and A is the total landscape area
		Environmental variables		
Landscape	Coarse	Elevation, Slope, Aspect	ELE, SLO, ASP	Elevation (m), slope (°) and aspect (°)
Landscape	Coarse	Temperature	TEM	Temperature of land surface (°C)
Landscape	Coarse	Precipitation	PRE	Mean monthly precipitation (mm)
Foraging & roosting	Detailed	Differential Enhanced Vegetation index	EVI_{diff}	Plant growth in a month
Foraging & roosting	Detailed	Distance to a particular land cover type	DISTO	Closest distance to each land cover type (m)

using a generative approach and thus has an inherent advantage over a discriminative approach, especially when the amount of training data is small (Phillips et al., 2006). Due to its good performance compared to other species distribution modeling techniques, MaxEnt is widely used in biogeography and conservation biology (Elith et al., 2006).

We used both foraging and roosting points together as the input for the landscape scale model, foraging points only for the foraging scale model and roosting points only for the roosting scale model. While the number of pseudo absence should not be too large, it needs to capture the environmental features sufficiently well. Hence, 10,000 random points (the default number in MaxEnt model) outside the 99% isopleths of the utilization distribution were generated as background points. Duplicate points falling into the same 30 × 30 m pixel were eliminated to avoid pseudoreplication. The relative Variance Inflation Factors (VIFs) were used to test multicollinearity among variables (Marquardt 1970). Highly correlated variables were excluded by sequentially removing the variable that has high collinearity with other variables (VIF > 10) and the least ecological relevance. We then recalculated the VIFs and repeated this process until all VIFs were smaller than 10 (Si et al., 2010).

Model performance was evaluated by the Area Under the Curve (AUC) of the Receiver Operator Characteristic (ROC), which is a threshold-independent measurement for discrimination ability between presence and random points (Phillips et al., 2006). When the AUC value is higher than 0.75, the model was considered good (Elith et al., 2006). The radius of the best performing model (highest AUC value) at each scale was considered as the proper radius at the relevant scale.

We ran the MaxEnt model using default settings, but with 1000 instead of 500 maximum iterations. For each model, we ran 20 bootstrap replications, and each time 75% of locations were selected at random as training samples, while the remaining 25% were used as validation samples. We used the Jackknife to test the relative importance of each variable, and a logistic curve to measure the response curve of each variable. Only variables that contributed to the model over 1% were included. The top three important variables of the best model at each scale based on Jackknife were used to analyze the habitat selection process. All analyses were performed in R 3.3.3 using the packages 'dismo', 'rgdal', 'vegan', 'move', 'usdm' and 'GSIF'.

3. Results

Model performance for GWFG and TBG at each scale is summarized in Table 2. The regularized training gain of Jackknife of the best

Table 2
The average performance of MaxEnt models at three different scales for the Greater White-fronted Goose (GWFG, *Anser Albifrons*) and Tundra Bean Goose (TBG, *A. serrirostris*) of each radius at the landscape, foraging, and roosting scales. AUC is the mean value of the Area Under the Curve of the Receiver Operator Characteristic and Std. Dev is the standard deviation. The best perform models are marked in bold.

Scale	Radius (km)	AUC_{GWFG}	Std. Dev	AUC_{TBG}	Std. Dev
Landscape	30	0.875	0.00038	0.942	0.00014
	40	**0.889**	**0.00061**	**0.947**	**0.00123**
	50	0.866	0.00071	0.935	0.00107
Foraging	10	0.820	0.00106	0.914	0.00308
	15	0.831	0.00073	0.941	0.00130
	20	**0.855**	**0.00047**	**0.948**	**0.00187**
Roosting	1	0.632	0.00054	0.800	0.00286
	3	0.800	0.00094	0.902	0.00309
	5	**0.840**	**0.00112**	**0.917**	**0.00321**

Fig. 2. Variable importance in MaxEnt models for Greater White-fronted Goose (*Anser Albifrons*; a, b, c) and Tundra Bean Goose (*A. serrirostris*; d, e, f) at the landscape scale (a, d), foraging scale (b, e) and roosting scale (c, f) based on Jackknifing. Variables marked in bold represent coarse ones and underlined represent detailed ones.

performing model at each scale was used to test variable importance (Fig. 2).

For both goose species, the best performing models at the landscape scale were at a 40-km radius (Table 2). For GWFG, the elevation and percentage cover of wetland and waterbody are the most important variables (Fig. 2), contributing 65% to model performance (Table S1). GWFG prefer areas with low elevation and a high percentage cover of wetland and waterbody (Fig. 3). For TBG, the most important variables are the percentage cover of cropland, wetland and waterbody (Fig. 2), contributing 69% to model performance (Table S2). TBG prefer for areas with about 70% percentage cover of croplands, as well as a high percentage cover of wetland and waterbody (Fig. 3).

At the foraging scale, the best performing models for both species had a 20 km radius (Table 2). For GWFG, the most important variables are mean patch area of cropland, aggregation index of waterbody and the closest distance to waterbody (Fig. 2), contributing 58% to model performance (Table S1). GWFG prefer areas close to waterbodies of high aggregation index with small croplands (Fig. 4). For TBG, the landscape division of cropland, average patch area and aggregation index of waterbody are the most important variables (Fig. 2), contributing 63% of model performance (Table S2). TBG prefer areas with middle-sized waterbodies of high aggregation index and scattered

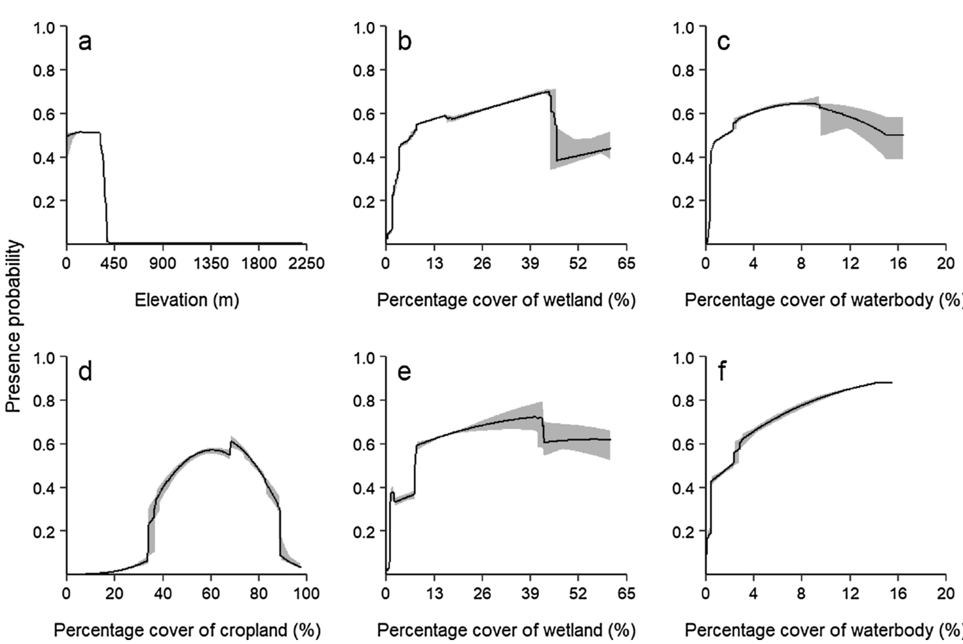

Fig. 3. The probability of presence and the most important variables for Greater White-fronted Goose (*Anser Albifrons*; a, b and c) and Tundra Bean Goose (*A. serrirostris*; d, e and f) at the landscape scale.

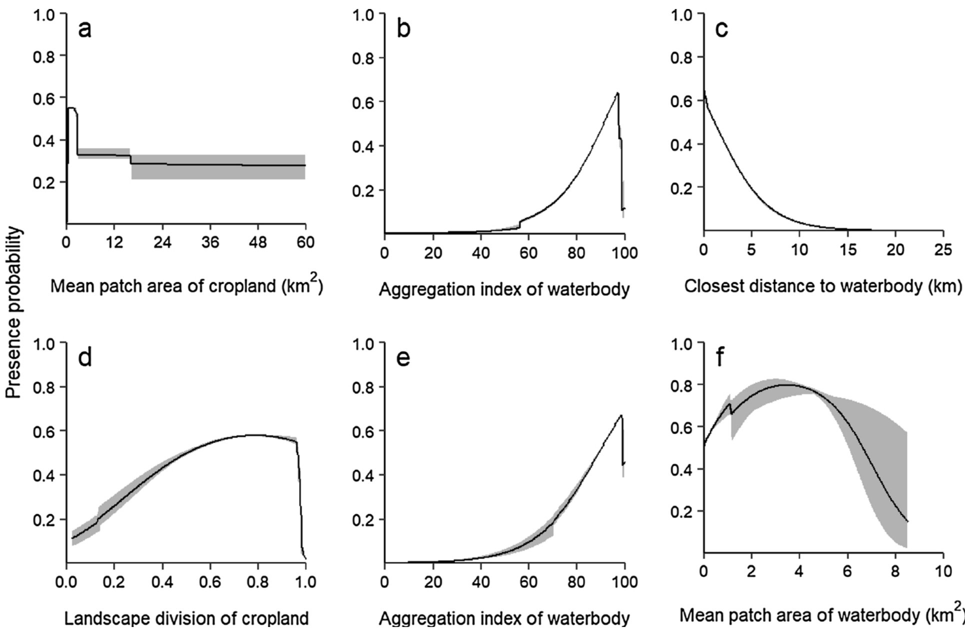

Fig. 4. The probability of presence and the most important variables for Greater White-fronted Goose (*Anser Albifrons*; a, b and c) and Tundra Bean Goose (*A. serrirostris*; d, e and f) at the foraging scale.

croplands (Fig. 4).

At the roosting scale, the best performing models of both species were found in models using a 5-km radius (Table 2). For both species, the most important variables are patch cohesion of wetland, patch cohesion index and percentage cover of waterbody (Fig. 2), contributing 76% (GWFG) and 61% (TBG) to model performance (Table S1 & S2). Both species prefer an intermediate percentage cover of waterbodies and wetlands with high patch cohesion index (Fig. 5).

4. Discussion

This study investigates the multi-scale habitat selection of two waterfowl species at their stopover area using species distribution modeling. We find that coarse variables explain the most variation at the landscape scale while detailed variables explain most variation at the foraging and roosting scales. Both species prefer areas with a larger percentage of wetland and waterbodies at the landscape scale, aggregated waterbodies surrounded by scattered croplands at the foraging scale, and well-connected wetlands, well-connected middle-sized waterbodies at the roosting scale. The main difference in habitat selection for the two species is found at the landscape and foraging scale; habitat selection at the roosting scale is similar. At the landscape scale, GWFG also prefer lowland, while Tundra Bean Goose TBG prefer an intermediate percentage cover of croplands. At the foraging scale, being close to waterbodies is important to GWFG, as well as middle-sized waterbodies to TBG. Our results contribute to a better understanding of waterfowl response to scale-dependent habitat conditions and offer suggestions on how to improve habitat quality in bird-human conflict areas (Si et al., 2015b).

We find that a higher percentage cover of waterbody and wetland is of great importance to the landscape-scale habitat selection of waterfowl species. This finding indicates that when searching potential habitat at the broader-landscape scale, geese are more likely to choose an area based on the coverage of relevant land cover types, rather than

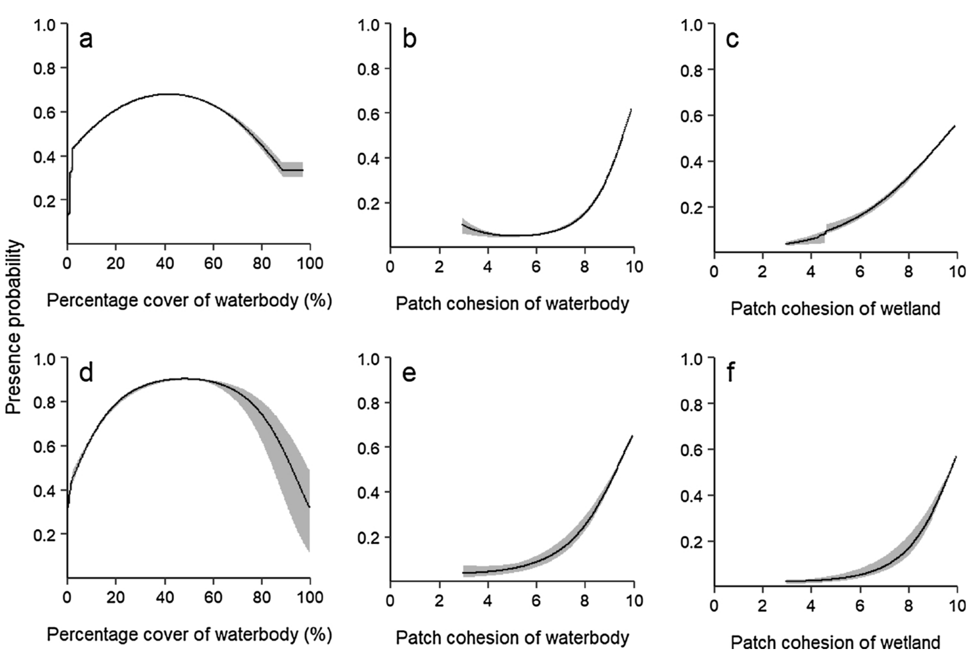

Fig. 5. The presence probability and the most important variables for Greater White-fronted Goose (*Anser Albifrons*; a, b and c) and Tundra Bean Goose (*A. serrirostris*; d, e and f) at the roosting scale.

complicated landscape features. This finding is in accord with previous research that found that the percentage cover of particular land cover types is a more broadly useful landscape metric than more complex measures in explaining the responses of woodland bird species to shifts in the landscape (Cunningham and Johnson, 2011).

At the foraging scale, both waterfowl species prefer aggregated waterbodies surrounded by small and scattered croplands, and the rate of habitat use for GWFG declines as the distance to waterbody increases. This foraging strategy supports the central-place foraging hypothesis (Orians and Pearson, 1979; Rosenberg and Mckelvey, 1999; Van Gils and Tijsen, 2007) which poses that the rate of habitat use declines as the distance from the roosting site increases as species often congregate at roosting sites during some period of the day to rest. The main landscape of the NCP is cropland (Lu et al., 2016). During the waterfowl staging period, the leftover cereal grains after harvest (Liu et al., 2013) make a good source of food (Reinecke et al., 1989). This may explain why cropland features show a strong influence on the habitat selection. Furthermore, the waterfowl are foraging in a highly dynamic and heterogeneous agriculture landscape in the NCP. Compared to waterbody and wetland, food availability in cropland changes rapidly; therefore, the waterfowl are unlikely to have sufficient information on patch quality (Amano et al., 2006). To reduce searching time and energy expenditure, the waterfowl species tend to select scattered cropland near their roosting waterbodies and wetlands.

At the roosting scale, we found that the two waterfowl species prefer well-connected wetlands and an intermediate percentage cover of waterbodies. The percentage cover of waterbodies, which is considered as a coarse factor, is an important factor determining roosting site selection. However, as the percentage cover of waterbody was calculated within a 5-km buffer around each night location, it is basically equivalent to the area of roosting waterbody, which could be considered as a detailed factor. Generally, larger waterbodies offer birds a better opportunity to spot predators (Owen, 1972; Radtke and Dieter, 2010) and allow for more and larger flocks to roost. However, the benefit of bigger flocks to avoid predators will not increase after flocks reach a certain size (Spilling et al., 1999). Therefore, choosing a middle-sized waterbody to roost balances the tradeoff between roosting safety and competition. Compared to a previous report that roost occurrence is positively correlated with waterbody size (Jankowiak et al., 2015), our findings help to further understand the roosting selection mechanism of geese.

Although the habitat selection mechanism is similar for GWFG and TBG, we found some difference at the landscape and foraging scales. GWFG tend to select low-elevated habitat and TBG prefer area with an intermediate percentage cover of croplands at the landscape scale. Moreover, the distance to waterbodies plays a more important role in foraging-land selection by GWFG than by TBG. The low elevation gradient habitats are usually closer to waterbodies and provide high quality spring-growing meadows for geese (Olff et al., 1997; Zhang et al., 2016). However, soybean is less nutritious for waterfowl in comparison to other grains and young meadows (Reinecke et al., 1989). This difference could be explained by the Jarman-Bell Principle (Bell, 1970; Jarman, 1974) that larger body-size herbivores (here TBG in comparison to GWFG) can afford to utilize more diverse food resources, including relatively low-quality ones due to their lower metabolic demands. Given that both species are grazing birds, there is some overlap in their ecological niche. However, GWFG mainly use wet meadows and TBG use both meadows and croplands, explaining how these two waterfowl species can coexist.

There are limitations to species distribution modeling due to the theoretical assumptions of species-environment equilibrium and niche conservatism, which implies the current suitable area of the species is fully occupied and the niche envelope remains unchanged over space and time (Jackson et al., 2009; Wiens et al., 2009). Moreover, the selection of pseudo absences in species distribution modeling strongly affects the validation of the resulting models (Acevedo et al., 2012; Barve et al., 2011). AUC often increases with the number of pseudo-absence points that have environment characteristics distant from the species requirement (Acevedo et al., 2012; Chefaoui and Lobo, 2008). However, MaxEnt requires that the expected value of each environmental feature should match its empirical average (Phillips et al., 2006). The number of pseudo absences thereby should be sufficient to fully reflect environmental features. To balance the tradeoff between MaxEnt's ability to minimize the potential bias towards pseudo absences while sufficiently capturing the variance of environment features, we investigated the change of the number of pseudo absence on the representation of environmental features (Fig. S1) and model performance (Fig. S2). We found that 10,000 pseudo-absence points can well capture the environment characteristics and AUC leveled off after the number of pseudo absence reached 10,000. Nevertheless, the bias towards pseudo absences needs to be considered when interpreting the results. Although we have reduced the pseudoreplication by recording goose locations every 2 h and removed the duplicated points within one grid cell of the land cover map, it still exists due to relatively limited number of individual birds. A higher number of tracked individuals should be used to further reduce pseudoreplication in future studies.

5. Management and conservation implications

Wetland ecosystems provide important services but are extremely vulnerable and have suffered serious degradation (Niu et al., 2012). Waterfowl are sensitive to the changes of wetland habitat and can act as bio-indicators for the health of wetland ecosystems. Therefore, our findings on scale-dependent waterbird habitat selection mechanisms can contribute to the conservation of wetland ecosystems and waterbirds. Both waterfowl species prefer a high percentage of waterbody and wetland at the landscape scale, and this information can help identify the national- or regional-level priority conservation areas. The habitat selection mechanism at the foraging and roosting scales can further contribute to the local management of these priority conservation areas. At the foraging scale, both species prefer aggregated waterbody surrounded by scattered croplands, while at the roosting scale they prefer well-connected wetlands and well-connected middle-sized waterbodies. This multi-scale habitat selection suggests a potential habitat selection process in which waterfowl first target a region based on coarse landscape features (percentage cover of suitable habitats), and then gather more detailed information (complex landscape features) to select foraging and roosting areas. Therefore, when managing the local habitat, the larger-scale context should be considered; and vice versa. However, due to the difficulty of increasing the percentage cover of waterbody and wetland in most wetland ecosystems, we suggest that management actions should focus on improving local habitat quality by enhancing the aggregation and connectivity of waterbodies and wetlands, and develop less aggregated cropland in the surroundings.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolind.2017.12.035.

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