Global Ecology and Conservation 25 (2021) e01435



Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco



Original Research Article

Indicators of site loss from a migration network: Anthropogenic factors influence waterfowl movement patterns at stopover sites



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ARTICLE INFO

Article history:
Received 1 July 2020
Received in revised form 26 November 2020
Accepted 22 December 2020

Keywords:
Bird migration
Habitat configuration
Human activities
Animal movement
Wetland

ABSTRACT

A network of connected wetlands supports migratory movements of waterfowl. These networks are rapidly changing due to intensive human activities around natural habitats. Quantifying how anthropogenic factors change waterfowl movements via a reduction of habitat availability and quality can facilitate a better understanding of the dynamics of these migration networks, and provide early-warning signals for network collapse. Using satellite tracking data for greater white-fronted geese (*Anser albifrons*) in the East Asian-Australasian Flyway, we tested how environmental factors (i.e., anthropogenic and ecological factors) influence geese movement patterns at stopover sites. We found that these factors, e.g., percentage of farmlands in the landscape, and proximity index of wetland patches, accurately predicted percentage of flying time and the median movement distance of tracked geese at stopover sites. Farmlands may increase energy consumptions in stopover sites because the geese flew more frequently, made longer movements, and switched their behaviour more frequently in landscapes with a higher proportion of farmlands. Goose movements were constrained in natural habitats, as a higher proportion of water and wetlands increased their movements, and thereby increased flying time and median movement distances. We suggest that using environmental factors monitored by remote sensing techniques to predict bird movement patterns is a powerful quantitative tool to measure quality of stopover sites. The changes in environmental factors in these stopover sites can be used as an indicator for the probability of losing a site from a migration network, and thereby generates insights for setting priorities in conservation planning of migratory birds.

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https://doi.org/10.1016/j.gecco.2020.e01435
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1. Introduction

Human practices have both positive and negative effects on waterfowl survival and foraging success in local habitats (Fox et al., 2016; Yu et al., 2017), and ultimately modify the structure of their migration network (Xu et al., 2019b), i.e., a habitat network of non-breeding, breeding, and stopover sites (Xu et al., 2019a). Under global environmental changes, suitability of these sites may decrease over time, and consequently a site may be no longer used by migratory birds. Habitat loss and degradation reduce the connectivity of migration networks, negatively affecting migration success, and subsequent reproduction of migratory birds (Studds et al., 2017; Xu et al., 2019b). For instance, the population of greater white-fronted geese (*Anser albifrons*) have declined rapidly since 1950s (Syroechkovskiy 2006; Zhang et al., 2015), and the decreasing connectivity in their migration networks may be a crucial explanatory factor for this decline (Xu et al., 2019b). Other possible causes for the decline are the poor conservation status (Zhang et al., 2015), intensive human activities (Yu et al., 2017; Si et al., 2020), water level changes and land reclamation (Aharon-Rotman et al., 2017; Jia et al., 2018) in their non-breeding grounds. The human influence on waterfowl is increasing in recent decades. Human practices in areas around wetland sites, and urban sprawl are the major factors reducing local habitat availability and suitability for waterfowl (Sutherland, 1998).

However, in some cases, birds take advantage of human activities. For example, waterfowl utilizes agricultural lands in Europe and North America, where short, rapidly growing and high quality swards are created for cattle grazing by high input of fertilizer and sowing of specific early growing and high productive grass species (Van Eerden et al., 2005; Fox et al., 2016). In East Asia, geese also utilize croplands in their stopover sites as alternative foraging patches, although the natural resource patches (e.g., grasslands and wetlands) are preferred (Si et al., 2018; Zhang et al., 2018). Moreover, some bird species adapted to anthropogenic influences, as for instance, brent geese (*Brenta bernicla*) forage on heavily disturbed wintering habitats with high food availability (Mathers and Montgomery 1997). Also, shorebirds select flooded rice paddies over natural wetlands during their early stages of overwintering in Colusa National Wildlife Refuge (Barbaree et al., 2015). Calder et al. (2015) found that local movements of weaver birds was not restricted by the urban landscapes surrounding habitat patches, as the proximity between habitat patches was the dominant factor explaining movements.

Nevertheless, birds are often negatively affected by human activities in and around their habitats. Human-related disturbance may result in farther within-habitat movements, shorter foraging and roosting durations, and frequent switches between habitat patches., These responses could negatively affect their energy storage during migration, and subsequently impact their survival and breeding outputs (Lonsdorf et al., 2016; Tucker et al., 2019). Human disturbance triggers escape flights, and forces birds to spend more time on vigilance instead of foraging and roosting, which subsequently decreases the efficiency of their resting and refuelling, and increases their energy expenditure (Riddington et al., 1996). Some sensitive species might even shift their habitat from a highly disturbed area to a less disturbed but also less energy-profitable area, decreasing their foraging efficiency, or leading to suboptimal diets (Mathers and Montgomery 1997). In addition, wetland reclamation may result in habitat degradation and fragmentation, which impact migratory waterfowl by forcing them to move more frequently between smaller and more isolated habitat patches.

Although the habitat quality for birds is often evaluated through differences in bird densities, survival and reproduction rates, and patterns of habitat selection (Johnson 2007), their local movement patterns may also be used as a proxy for differences in habitat quality. Animals maximize their net energy intake rate and hence spend more time in relatively richer patches (Stephens et al., 2014). In areas with intensive human activities, e.g., farming (Si et al., 2020) and road traffic, birds spend more time on vigilant behaviour, or fly away, and seek shelter in less disturbed, but often also less profitable habitats (Riddington et al., 1996). Therefore, birds may stage for a shorter period in a low-quality stopover site, and spend a higher proportion of time on flying in such a site. Birds are also expected to switch their behaviours frequently and display more different types of behaviours in these low-quality stopover sites. In response to reduced habitat suitability in these stopover sites, movements of birds increase (Taft et al., 2008; Tucker et al., 2019). In addition, larger turning angles (i.e. deviations from a linear movement) are associated with foraging movements, and not with large distance displacements (Aben et al., 2012), so large turning angles can be used as an indicator of high foraging quality of stopover sites. Consequently, we assume that a high quality stopover site is correlated with a short movement distance, a short flying time, a long staging time, large turning angles, and a low frequency of switching between different behavioural classes.

Understanding how waterfowl movement patterns change in response to human activities and ecological factors generates insights into the effect these activities have on habitat quality, and can advance our understanding of how these factors influence the structure of the migration network by adding new stopover sites, or removing previously suitable sites. Thus, in this study, we investigated the effects of different human activities on waterfowl movements in and around different stopover sites to provide an integrated view of waterfowl responses to environmental (i.e. a combination of ecological and anthropogenic) factors (Fig. 1). To achieve this, satellite tracking data of greater white-fronted geese was separately analysed at each stopover site, and geese movement patterns were quantified as indicators of their responses to human activities and ecological factors. These geese are hypothesized to be negatively influenced by most anthropogenic practices including land reclamation, urbanization, and transportation, although they could also benefit from agricultural practices by grazing in croplands. The results can assist in setting priorities for conservation actions, in quantifying the probability of losing a site from a migration network, and in generating early warning signal for network collapse.

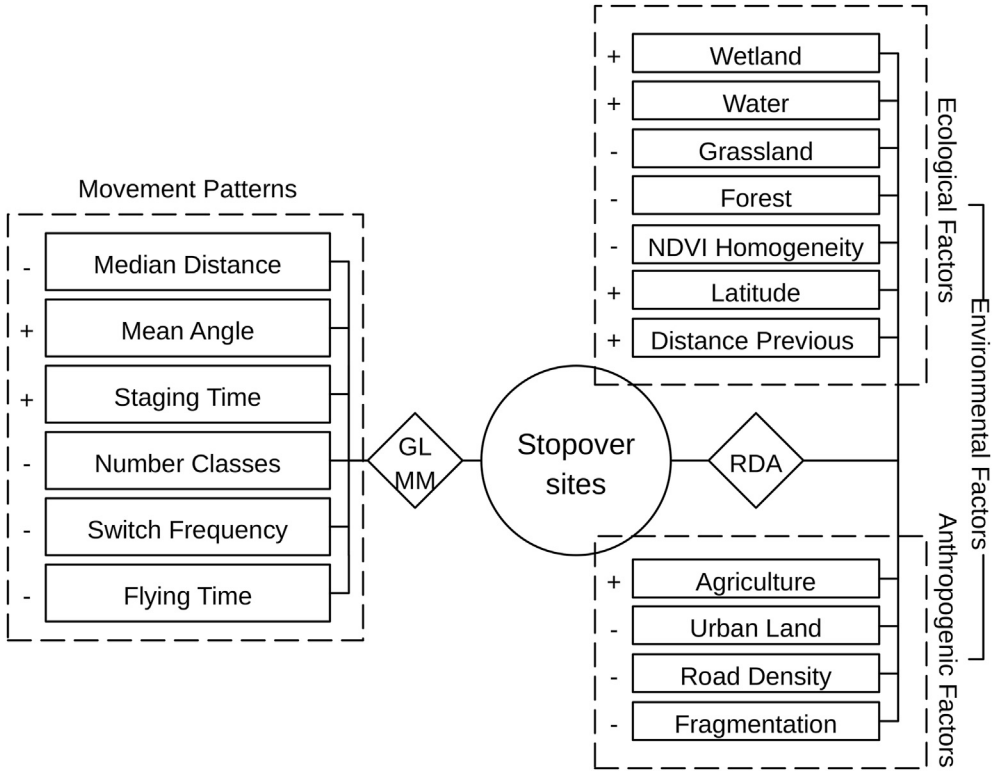


Fig. 1. A framework for the effects of human activities on waterfowl movements. GLMM = General Linear Mixed Model; RDA = Redundancy Analysis. A higher value of the movement patterns marked with "+" indicates a higher habitat quality with lower disturbance, while a higher value of those marked with "-" indicates a lower quality. The environmental factors marked with "+" were hypothesized to positively affect geese movement patterns related to high-quality habitats, while the ones marked with "-" were hypothesized to positively affect geese movement patterns related to low-quality habitats.

2. Methods

2.1. Tracking data and land cover map

The satellite tracking data for 21 greater white-fronted geese from 2015 to 2019 were used for movement pattern analysis in their stopover sites (Fig. 2). The geese were captured in Poyang Lake, Jiangxi, China (29°N, 116°E). The interval of GPS/GSM loggers was set as 1 position/2 h. The obtained mean daily count of GPS locations recorded was 10 positions per goose. We used latitude, longitude, date, and time of each GPS location for subsequent analyses. Details about geese capture, tracking, and ethical statements were shown in previous publications analysing this dataset (Si et al., 2018; Xu et al., 2019a).

We obtained 300-m resolution land cover maps for 2015 from ESA CCI Land Cover time-series v2.0.7 (1992–2015) dataset. Nine land cover types were included in subsequent analyses: wetlands (land cover code: 180), water (210), agriculture (10, 11, 12, 20, 30, 40), urban (190), forest (50, 60, 61, 62, 70, 80, 90, 100, 160, 170), and grasslands (110, 130). We also obtained 300-m resolution normalized density vegetation index (NDVI) maps from Copernicus Global Land Service for the years 2015–2019. The temporal resolution of these maps is 10 days/image, so we were able to select the NDVI maps that matched the period of geese staging in each of the stopover site. For road density estimation, we obtained road maps from the Global Roads Open Access Data Set v1 (1980–2010).

2.2. Identifying stopover sites

The study area included stopover sites utilized by tracked geese during their northward spring and southward autumn migrations. To identify these sites, we used the Guéguen method (Guéguen 2000) to distinguish migration movements from non-migration movements. The Guéguen method used a Bayesian division for movement tracks, assigning a track (moving trajectory within a defined time period) to several segments, based on the changes in bird movement patterns, i.e., migration or non-migration (Calenge 2011). The segments assigned to non-migratory movements, were defined as breeding/non-breeding/stopover sites. We only included defined sites that were used for $\geq$48 h for subsequent analyses, under the assumption that a stopover site is used for at least 2 days (Si et al., 2018). Because we only focused on bird movements in stopover sites, we removed the southernmost and northernmost segments to exclude breeding and non-breeding sites.

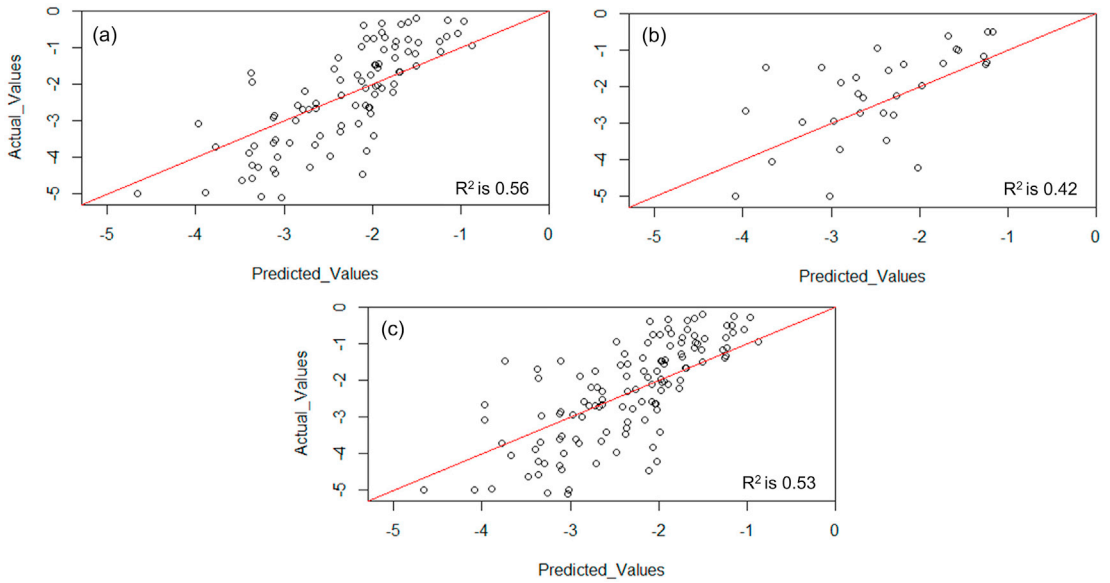


Fig. 2. Maps of geese movements from satellite tracking of the 21 greater white-fronted geese studied here. The maps show migration routes (a), local movement tracks in a farmland-dominant landscape in Zhenlai, China (b) and in a wetland-dominant landscape in Horqin Left Back, China (c).

2.3. Analysing movement pattern

We used the Guéguen method, again, to assign local movement tracks to different segments. These segments were classified into different movement patterns, ranging from 1 to 10, from little to no movement (class 1 and class 2), to intermediate and excessive movement (class 3 or higher). With these outputs, we quantified several indicators of bird movement patterns at each stopover site: median distance, percentage of flying time, mean angle, frequency of switches between behavioural classes, number of behavioural classes, and total staging time (Figure S1).

Duration and timing. The duration (days) of staging in a stopover site, termed *staging time* here, was calculated as one index to reflect the habitat quality. We quantified percentage of flying time (tracking points defined as 'flying' × sampling interval), as another index, by log (total amount of time a geese is flying/the total staging time per stopover site). We defined segments with intermediate and excessive movements (i.e. class 3 or higher) as 'flying'.

Distance and angle. We quantified the median flying distance (step length in kilometre) of each tracked bird in each stopover site. In addition, we calculated the median absolute turning angle for each tracked bird in each stopover site.

Behavioural switches. We quantified the frequency of behavioural switches, i.e. the frequency of switches between different behavioural classes (log-transformed). Additionally, we calculated the number of different behavioural classes a bird displayed within each stopover site.

2.4. Quantify environmental factors at different spatial scales

Quantification of the relationships between species and environment can be largely affected by spatial scales (De Knegt et al., 2011; Zhang et al., 2018). For a better understanding of the effect of environmental factors on bird movements, we therefore quantified the environmental factors that may affect the quality of a stopover site at different scales, i.e., 90%, 95%, and 99% areas defined as follows. We used dynamic Brownian Bridge Movement Models (dBBMM) (Kranstauber et al., 2012), which measure bird home ranges based on a probability of their space use, to define the utilized ranges for the tracked geese at each stopover site. According to previous satellite tracking studies on greater white-fronted geese in East Asia and visual inspection of the used data (Zhang et al., 2018; Si et al., 2018), we defined geographical ranges of 90%, 95%, and 99% isopleths of the utilization distributions as mostly used, frequently used, and total range of the utilized area for each site (Figure S2). For each of these scales in each site, we quantified the following environmental factors.

Anthropogenic factors. The main human-related effect agents for waterfowl include agricultural practices, land reclamation, urbanization, and transportation (Arzel et al., 2007) (Madsen 1998). We calculated the percentage of agriculture lands and urban lands at each scale in each stopover site. We also measured the road density (km/km^2), by the length of roads per square km, as another factor indicating the intensity of human activities. We quantified habitat fragmentation by the proximity index of wetlands. A lower value indicates that habitat patches within a single stopover site are relatively isolated from each other (Gustafson and Parker 1992).

Ecological factors. Wetland availability and vegetation heterogeneity, also influence waterfowl use of stopover sites, and were therefore also included in our models. We calculated the percentage of wetlands, water, grasslands, and forests at each scale in each stopover site (%). Water and wetlands are the most important natural habitats for geese (Davis et al., 2014), so we additionally calculated the percentage of wetlands plus water. To measure the availability of roosting habitat and food resources, we calculated a log-transformed area of water and a log-transformed area of wetlands plus grasslands (log km^2). We also measured surface area of stopover sites by the total area of each site in km^2. We included NDVI heterogeneity in each of the sites as an additional factor which represent heterogeneity of food resources for waterfowl in a landscape. NDVI heterogeneity was calculated by the standard deviation of NDVI values in landscape in and around each stopover site, excluding urban lands and water which can highly skew values. Moreover, because birds get closer to their destinations, i.e., breeding/non-breeding grounds, their movements patterns may change, for example, stage less or more at stopover sites (Kölzsch et al., 2016). We also calculated the mean latitude of all tracking points per stopover site. Lastly, we measured the distance to the previous stopover (or breeding/non-breeding) site by the distance from the first GPS location in the focal site to the last location in the previous site.

To select the best scale for an environmental factor to explain a movement pattern variable, we fitted General Linear Models (GLM) for each pair of the movement pattern variable (independent variable) and the environmental factor (dependent variable) at the 90%/95%/99% areas. Environmental factors at the areas with a lowest Akaike information criterion (AIC) in the model, i.e., the best-fitting scale, was applied in subsequent analyses.

2.5. Statistical analyses

To test the birds' responses to different ecological and anthropogenic factors, we fitted General Linear Mixed Models (GLMM) for each movement pattern variable (dependent variable) and all environmental factors (independent variables). The ID of tracked birds was used as a random factor in the GLMM. In case of a collinearity between the environmental factors, we maintained only environmental factors with variance inflation factors (VIF) ≤ 5 in the models. We selected the models with a lowest AIC for predicting movement patterns. To test how accurate these environmental factors can predict a site quality, we randomly selected 70% sites ($n = 90$) to train the models and used the remaining 30% sites ($n = 39$) to validate the models. To test the sensitivity of model outputs to these random selections of training (70%) and testing (30%) samples, each random selection was repeated for 5 times.

To summarize how environmental factors predict the site quality, we created a multivariate dataset consisting of movement pattern variables at different stopover sites and all environmental factors. Both positive and negative effects of different environmental factors were incorporated in a Redundancy Analysis (RDA), which analyses relationships between more than one response variable (i.e. movement pattern variable) and explanatory (i.e. environmental) variables. The derived canonical axes extract most of the variation in movement patterns, together with the environmental factors that are best correlated with the changes in geese movements. All movement pattern variables and environmental factors were standardized to range from 0 to 1 before running the RDA.

The analyses were conducted with packages 'vegan', 'lme4', and 'MuMIn' in R (www.r-project.org).

3. Results

3.1. Movement pattern responses to environmental factors

The median distance, number of behavioural classes, frequency of behavioural switches, and flying time increased with an increasing percentage of agriculture lands, which was in line with our expectations. Flying time increased with an increasing road density, and mean angle increased with an increasing percentage of urban lands. However, in some rare cases, human activities affected movement patterns in a different way, as the percentage of agricultural lands was negatively correlated with the mean angle, and the percentage of urban lands was negatively correlated with the median movement distance. The proximity of wetland patches within a stopover site (i.e. an index for fragmentation) was another important factor for predicting movement patterns of birds. However, in contrast to our predictions, proximity index was positively correlated with the number of behavioural classes (Table 1), frequency of behaviour switches, and flying time, while it had a negative effect on mean angle and staging time.

Among ecological factors, surface area was the most important factor for explaining movement patterns, which was positively correlated with staging time, flying time, median distance, and number of behavioural classes, and was negatively correlated with mean angle. The percentage of water was positively correlated with median distance and flying time, while it was negatively correlated with the mean angle. The percentage of wetlands/grasslands was positively correlated with all movement pattern variables. NDVI heterogeneity was positively correlated with staging time and frequency of behavioural switches, while it negatively affected flying time.

3.2. Validations for predictions of site quality

There was no significant difference between the five different random selections, so we explain here the results from the first random selection for model accuracy. The model for flying time made the most accurate prediction for the test dataset

Table 1
The effects of environmental variable on the movement variables of greater white-fronted geese, according to the best fitting models from each of five random selections. A "+" indicates that the environmental factor was positively correlated with the corresponding movement variable, while a "-" indicates a negative correlation. The number of "+"/"-" (max = 5) corresponds to the number of best fitting models that reported this relationship. "PR" shows predicted relationship between environmental factors and movement pattern variables.

	Scale (%)	Environmental factors																			
		Water				Agriculture				Urban				Forest				Wetland/Grass			
		PR	90	95	99	PR	90	95	99	PR	90	95	99	PR	90	95	99	PR	90	95	99
Movement pattern variables	Median distance	−	+			+	+		+	+	−			+	−			−	+	+	+
			+						+												
			+						+												
			+						+												
	Mean angle	+		−	−	−	−			−		+		−				+			+
	Staging time	+				−				−				−				+			+
																					+
	Behaviour classes	−	+		−	+			+	+				+	−		−	−			+
																	−				
																	−				
	Switch frequency	−				+	+			+				+				−			+
							+														+
							+														
							+														
							+														
	Flying time	−	+		+	+	+			+				+			+	−	+		
																	+				
	Scale (%)	Environmental factors																			
		Roads				Surface area				Proximity index				Lat		Lat diff		SD(NDVI)			
		PR	90	95	99	PR	90	95	99	PR	90	95	99	PR	/	PR	/	PR	90	95	99
Movement pattern variables	Median distance	+				+	+			−				−		−	+	+			
	Mean angle	−				−	−	−	−	+	−			+	+	+		−			
											−										
											−										
											−										
	Staging time	−				+			+++	+	−			−	−	+		−	+	+	
									+		−				−				+		
									+		−										
											−										
	Behaviour classes	+				+		+		−	+		+	−		−		+			
													+								
													+								
	Switch frequency	+				+				−			+	−		−		+		+	
													+							+	
													+							+	
	Flying time	+			+	+		+	+	−	+		++	−	+	−		+	−		
								+			+								−		
								+											−		

($R^2 = 0.42$; Fig. 3b). The model for the median distance generated the best prediction for the training dataset ($R^2 = 0.74$; Figure S3a) and the overall dataset ($R^2 = 0.63$; Figure S3c). Compared to other movement variables, the environmental factors explained the lowest amount of variation for the mean turning angle ($R^2 = 0.06$ for the overall dataset; Figure S4).

3.3. Multivariate analysis

The canonical axes were all significant at all areas (99%, 95%, and 90%). High quality sites were expected to be found in the top right quarter of the graphs at 99% and 95% areas (Fig. 4ab), and in the bottom right quarter at 90% area (Fig. 4c), associated with low median distance, low flying time, low frequency of behavioural switches, low number of behavioural classes, low mean angles, and with a higher total staging time. The percentage of agricultural lands and forests significantly explained the variation in movement patterns in different sites at all scales, whereas the percentage of water was only significant at the 95% and 99% scale. The percentage of agricultural lands was positively correlated with median distance, flying time, frequency of behavioural switches, and number of behavioural classes at all scales (Fig. 4). Other factors positively associated with these movement patterns include road density, area of grasslands, and area of wetlands plus grasslands. Percentage of water and percentage of forests were both negatively correlated with these four movement variables. Total staging time and mean angle were best extracted on the second RDA axis and were not strongly correlated with the other movement variables. A higher

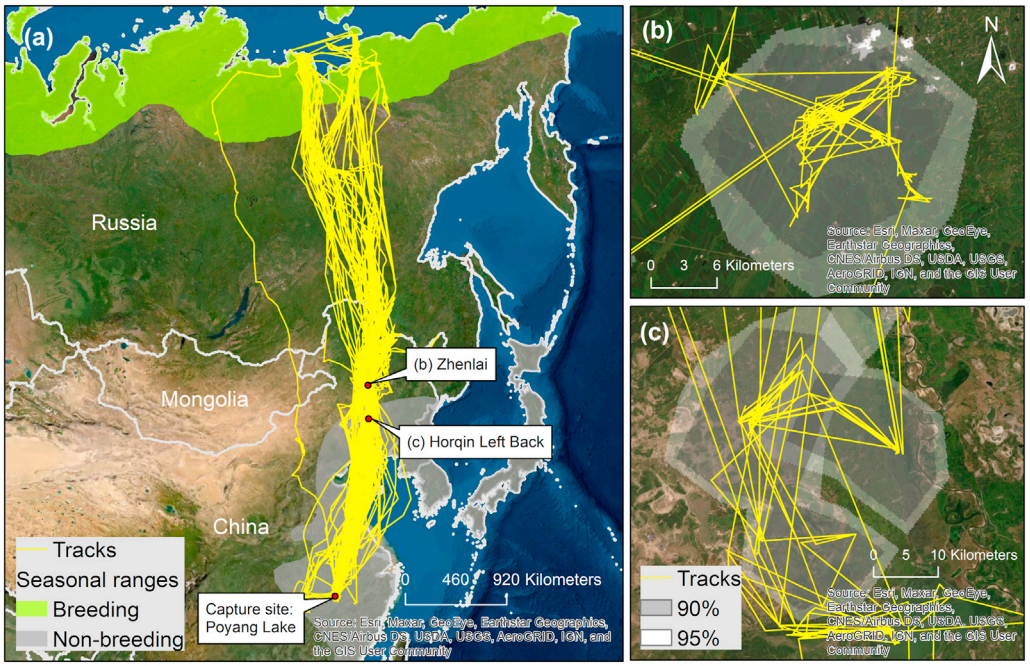


Fig. 3. The predicted values for the log-transformed flying time in a site by the best model, plotted against the observed values of this variable. (a) the model with original dataset (N = 90) which are the sites used to create the model, (b) the model with validation dataset (b; N = 39) which are the sites that were randomly selected for validation, (c) the model with all data (N = 129). The red lines indicate the X = Y line (i.e. a perfect prediction), with the R^2 value reflecting the accuracy of the model compared to this line.

percentage of agricultural lands and a higher percentage of wetlands were often related to a longer staging time in a site (Fig. 4).

4. Discussion

East Asian geese respond negatively to human activities, but in a different way compared to geese that have their North-South migration flyway through Europe or North America. Generally, farming activities negatively affect the habitat quality for these greater white-fronted geese in the East Asian-Australasian Flyway, as they fly more, make longer movements, and switch their behaviour more frequently in a stopover site with a higher proportion of agricultural lands (Table 1). Other human activities, i.e., development of urban lands and roads, did however not strongly affect their movement. Differently, many waterfowl species in Europe and North America take use of the abundant food resources in farmlands, creating conflicts between farmers and wild birds (Fox et al., 2016).

Hence, East Asian waterfowl prefer foraging on natural habitats, and are more disturbed in agricultural lands in China (Yu et al., 2017). This agrees with our results that the geese move more, and more frequently change their behaviour at stopover sites with a higher fraction of agricultural lands. Moreover, we found that geese expanded their movements (larger flight time and longer movement distances) in stopover sites with a higher water availability and a larger wetland proximity (Table 1). These natural land cover types may be their major habitats, and a larger area and a higher connectivity increases movements of waterfowl (Crooks and Sanjayan 2006; Zhang et al., 2018).

Hence, agriculture lands in China are not optimal habitats for waterfowl. Moreover, these farmlands are highly disturbed by human activities from resident settlements (1.0% are urban lands in these stopover sites), and hunting (Ma et al., 2012). Migratory geese in East Asia therefore prefer to use habitats with a lower human density (Li et al., 2017). Although 58% of the home range of the studied geese consists of farmlands, these agriculture lands may provide only limited food resources for waterfowl, as for example crops are frequently removed by free-ranging poultry from local farmers in non-breeding habitats in the Yangtze River Basin, Southeast China (Yu et al., 2017). A higher disturbance level increases energy expenditure while a lower food availability reduces intake rate, and as a result, these stopover sites are less attractive for resting and refuelling compared to those with a lower cover of agriculture lands.

Water bodies and wetlands are the main habitats for East Asian waterfowl. However, these natural habitats in the East Asian-Australasian Flyway are, at present, degrading rapidly (Studds et al., 2017; Xu et al., 2019b). Firstly, build-up of dams affect water level, and subsequently disrupt the natural phenology of recessional grasslands (Aharon-Rotman et al., 2017), which can result in a mismatch between the peak in forage availability and quality, and the arrival time of migratory waterfowl. Secondly, we found that a higher forest cover at stopover sites impeded goose movements indicated by a shorter

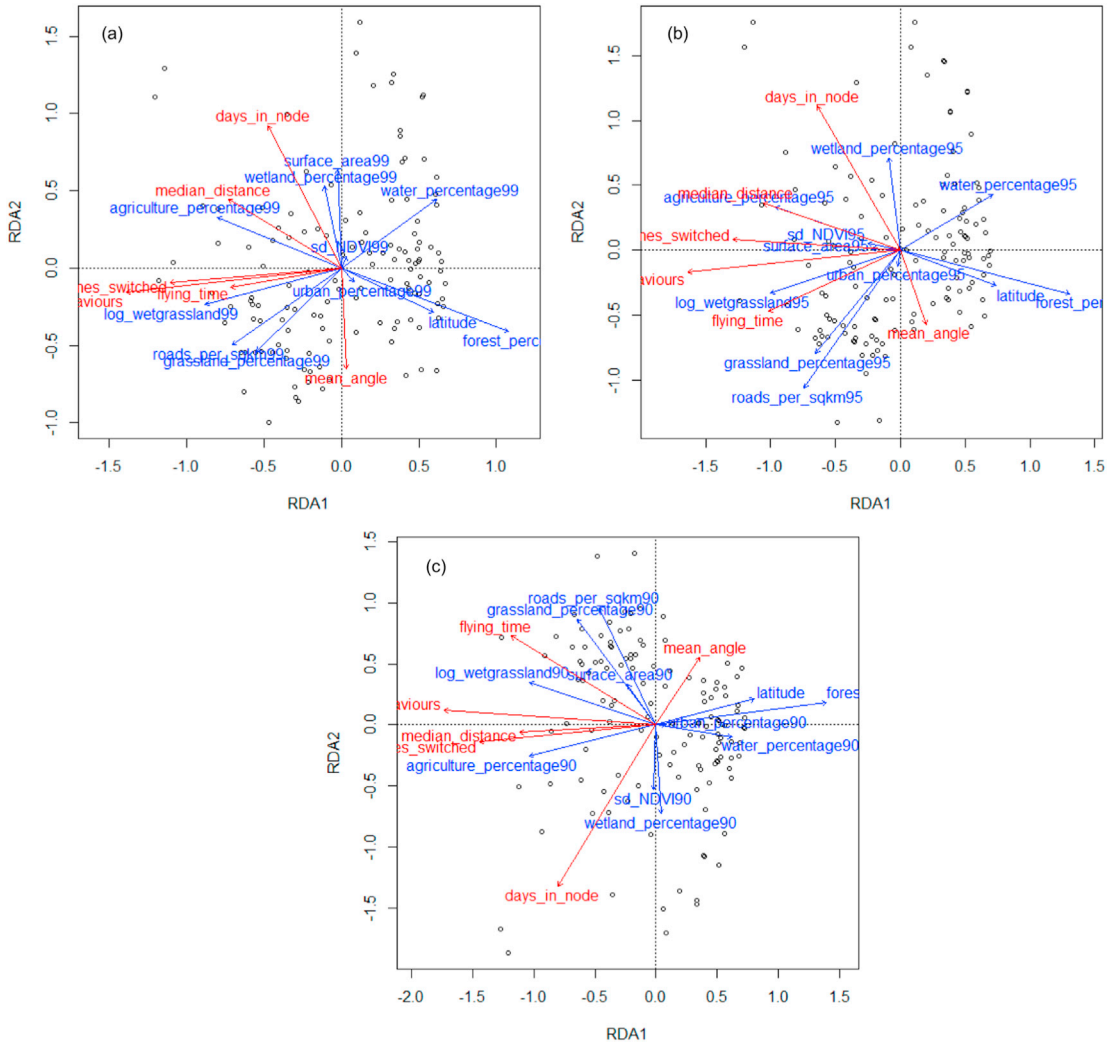


Fig. 4. Triplots from the three Redundancy Analyses (RDA) at the 99% (a), 95% (b), and 90% (c) area. The red arrows are movement variables, blue arrows represent environmental factors. The circles are sites. The first axis explained 11% of the variation at the 99% and 95% scale, and 12% at the 90% scale, and the second axis explained 6% of the variation at all scales.

median distance (Table 1). Wetland availability may decrease with expanding forest cover. Especially in Russia, staging sites became less suitable for geese because a large part of wetlands and grasslands have transformed to forest by economically driven land abandonment (Grishchenko et al., 2019). Thirdly, although not so much reflected in our results, an increasing proximity to human disturbance, e.g., urban expansion, road construction, and poaching, can also reduce the quality of natural habitats for waterfowl (Li et al., 2017; Zhang et al., 2018).

Therefore, migratory waterfowl in the East Asian-Australasian Flyway seem seriously threatened by land use changes related to anthropogenic practices. Consequently, unlike in Europe and North America where waterfowl population sizes boosted in the last decades (Fox et al., 2010; Rosenberg et al., 2019), East Asian waterfowl experienced a rapid population decline since 1950s (Syroechkovskiy 2006; Xu et al., 2019b). To effectively conserve these migratory species, it is pivotal to maintain or improve the connectivity of the stopover sites that they use during their migration (Xu et al., 2019b, Dhanjal-Adams et al., 2017). This requires thorough understanding of the network of connected stopover sites, and a temporal surveillance to quantify the dynamics of these networks that are under influence of the changes in the factors that influence habitat quality at stopover sites (resource quality and availability, fragmentation, disturbance levels, suitable roosting and foraging areas, etc.) (Xu et al., 2019a). This study can be used as a framework to analyse the entire migration network of a bird species. Moreover, the methodology in this study, i.e., using environmental factors in combination with movement variables as proxies for habitat quality in a migration network, is applicable to the surveillance of many migration networks, and can be used to evaluate network connectivity and to set priorities for conservation actions. To increase the prediction accuracy, we recommend using environmental factors that capture the landscape configuration and quantify the different aspects of

habitat quality for the bird species under study. This way, the entire migration network spreading over large geographical ranges can be studied efficiently, as a first step towards temporal surveillance of the network dynamics. This will enable us to detect important stopover sites that are crucial for an efficient migration and that contribute to the stability and resilience of the network (Xu et al., 2019a).

5. Conclusions

According to our results, the relationships between environmental factors and bird movement variables can be used to predict the quality of a stopover site. This enables scientists to generate early warning signals for network collapse, and simulate the effect of site removal from a migration network (Shimazaki et al., 2004; Xu et al., 2019c). Our methodology to predict habitat quality is expected to be reproduceable for other bird and mammal species who move in human dominated landscapes. Environmental factors were best in predicting flying time and median distance at stopover sites (Fig. 3; Figure S3), and thus, movement patterns related to flying distance and time can yield good indicators of the quality of a stopover site for migratory waterfowl. Turning angles could be poorly predicted by anthropogenic nor ecological factors in our study (Figure S4), and seem therefore not well suitable for predicting quality of stopover sites for waterfowl. This finding seems contrasting to the study of Aben et al. (2012) where the turning angle of forest birds was a good index for the encroachment of human dominant land use types. However, future studies can improve this method, by using tracking data with a higher temporal resolution, which may show another explanatory role of turning angles. For more specific behavioural classes, such as foraging, resting, or walking, the tracking interval could be optimised to obtain the highest accuracy for the classification (de Weerd et al., 2015). When sample sizes allow, this analysis may be improved by exploring more complex patterns in the data, like interaction terms between environmental factors. Further studies may also include secondary derived movement variables regarding the distribution of angles and distances (e.g., variance and skewness) and the changes thereof over time, which may be indicators for the stability of the system (Scheffer et al., 2015).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank F. Xu, W. Zhang, J. Wei, B. Wielstra, G. Liu, H. Luo, S. Balachandran, S.K. Behera, M. Ponnaian, Z. Lv, W. Wu, B. Gao, T. Zhang, and other members of the field crew for their supports in bird tracking. We thank J.A.J. Eikelboom for his insightful suggestions in movement analysis. Financial support was provided by the National Key R&D Program of China (No. 2017YFA0604404), the National Natural Science Foundation of China (No. 41471347), and China Scholarship Council (no. 201600090128).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01435.

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