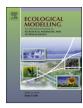
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Dynamic response of East Asian Greater White-fronted Geese to changes of environment during migration: Use of multi-temporal species distribution model



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ARTICLE INFO

Article history: Received 10 December 2016 Received in revised form 6 June 2017 Accepted 7 June 2017 Available online 14 July 2017

Keywords:
Species distribution model (SDM)
Satellite tracking
Spring migration
Habitat selection
Multi-temporal
Remote sensing
Dynamic water mask

ABSTRACT

Understanding how migratory species select habitats is essential for applied ecology and biological conservation. Although migratory species move across a wide range of environments during migration, their dynamic response to environments has rarely been considered. Taking advantage of the fine spatial-temporal resolution of satellite tracking data, we studied habitat selection of East Asian greater white-fronted geese (Anser albifrons) along their spring migration route from Yangtze River Basin to Lena Delta and Yana Bay. We developed a novel methodology to improve dynamic species distribution models (SDMs) by incorporating environmental variables derived from remotely sensed data precisely corresponding to migration time. Our results demonstrate that distance to the nearest water body, elevation, human population density and temperature contribute greatly to the models. Water-related and topographic factors (e.g., elevation, slope and distance to the nearest water body) were consistently associated with habitat selection of the geese from wintering area to breeding area, while the varied influences of temperature and human population density in different migration periods are closely related to their adaptation to local environments. In addition, response curves of vegetation index indicate that the geese are more strongly associated with food quality than quantity in wintering area and stopover sites. By building SDMs in different periods, we provide a unique dynamic perspective on how a long-distance migrant responds to different environments. The methodology proposed here could be integrated to future conservation management plans for predicting species relationship with fast changing environmental conditions.

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1. Introduction

Migratory birds move twice a year between breeding and non-breeding areas to take advantage of different habitats driven by life-history requirements and environmental change (Alerstam and Lindström, 1990; Berthold, 2001; Dingle, 2014). Migration is the

most risky period in the avian life cycle (Alerstam and Lindström, 1990; Si et al., 2015b; Sillett and Holmes, 2002) and the ability to adapt to different environments is crucial to the success of breeding. From the perspective of conservation, understanding habitat selection during migration is essential for effective conservation (Cox, 2010; Runge et al., 2014; Runge et al., 2016; Tottrup et al., 2008). Although migratory species move across a wide range of environments during migration, attention to the flexibility of habitat selection in response to changes of environments is rare (Franklin, 2009)

In recent years, the advancement of satellite tracking techniques provides increasing volumes of movement data for bird migration research (Cooke et al., 2004; Hebblewhite and Haydon, 2010). Bird tracking data help us better understand the detailed movements of avian migration as well as how species interact with others

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and local environments (Higuchi and Pierre, 2005; Robinson et al., 2010). Satellite tracking data have been used to monitor bird movements (Berthold et al., 2002; Bridge et al., 2011; Kanai et al., 2002), identify habitat utilization distribution (Hemson et al., 2005; Wood et al., 2000) and examine population dynamics (Klaassen et al., 2014; Trierweiler et al., 2014). However, satellite tracking data collected from a limited number of animals cannot directly represent general patterns of species movement and habitat requirement at a population level (Aarts et al., 2008; Hebblewhite and Haydon, 2010), which might lead to less rigorous inferences in movement ecology and resource selection (Hebblewhite and Haydon, 2010).

One popular approach to examining species-environment relationships is through species distribution models (SDM, for a review see Elith and Leathwick, 2009; Guisan and Zimmermann, 2000). SDMs link species occurrences at limited locations and environmental characteristics of those locations to gain ecological insights and predict species distributions (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000). Traditional species distribution data derived from atlas and field surveys used to fit the models are known to suffer from identification errors and geographic biases (Graham et al., 2008; Guralnick and Van Cleve, 2005; Hurlbert and White, 2005). In contrast, satellite tracking data are free of such weakness. Recent studies have successfully established SDMs using satellite tracking data despite a limited number of tracked individuals (Jiguet et al., 2010; Kassara et al., 2013; Limiñana et al., 2014).

The high spatial-temporal resolution of satellite tracking data further facilitates the use of dynamic predictors that precisely reflect the phenological fluctuations of the environments as species experienced during the tracking period, and make it possible to summarize dynamic species-environment relationships. The distribution of migratory species is dynamic (Roshier and Reid, 2003; Somveille et al., 2015), yet the species-environment relationships are often considered static (Pearman et al., 2008). Static SDMs often implicitly assume equilibrium (Elith and Leathwick, 2009) and only recently have multi-temproal SDMs been used to explore niche dynamics by distinguishing fundamental and realized niches (Pearman et al., 2008; Soberón and Nakamura, 2009). Notable attempts include examining the seasonal distribution changes of species (Edrén et al., 2010; Hayes et al., 2015), in response to changing environmental conditions (Gschweng et al., 2012) and plasticity in species-landcover associations (Zuckerberg et al., 2016).

The development of multi-temporal SDMs requires temporal consistency between species occurrences and corresponding environmental factors. Temporal mismatch between the species occurrences and their environments may have negative effects on evaluating the relationships between fast changing landscape characteristics and highly mobile migrants. This is for instance the case with water distribution. Water distribution is a crucial factor influencing habitat selection for waterfowl and therefore has been widely adopted in species distribution modelling (e.g., Moriguchi et al., 2013; Wisz et al., 2008a). However, the temporal changes in water bodies are not well characterised in static water databases such as Shuttle Radar Topography Mission (SRTM) Water Body Detection (SWBD; NASA/NGA, 2003), the Global Lakes and Wetlands Database (GLWD; Lehner and Döll, 2004), and Global Land Cover Facility (GLCF) water mask, MOD44W (Carroll et al., 2009). Since habitat selection of migrants like geese is strongly affected by water availability, using static water data in multi-temproal SDMs may fail to precisely describe the real environment conditions that migrants experience and lead to inaccurate species-environment relationships and species distibutions.

Greater white-fronted goose (*Anser albifrons*) is a long-distance migratory waterfowl that migrates across a diverse environment (Kear, 2005). In recent decades, the population wintering in China decreased markedly due to habitat loss and hunting mortality

(Barter et al., 2004; Cao et al., 2008). In Yangtze River Basin, where greater white-fronted geese mainly winter in China, its population fell from about 140,000 in 1987–1993 to about 18,000 in 2010 (Zhao et al., 2012). Nevertheless, the use of changing habitats by greater white-fronted geese along the spring migration route is hardly explored. In this study, we investigated the species-environment relationships of greater white-fronted geese using satellite tracking data and multi-temporal ensemble SDMs. Besides climate and vegetation indices that are considered as plausible predictors of bird occurrence, we also include a dynamic water layer in our models to represent the fast-changing environmental conditions. Our study aims to: (1) investigate what factor determines habitat selection of greater white-fronted geese under a wide range of environments; and (2) explore how greater white-fronted geese respond to different environmental determinants.

2. Materials and methods

2.1. Study area

We conducted this study from southeast China to northeast Russia ranging between 110°E-150°E, 25°N-80°N, which encompasses the core spring migration range and important stopovers of the population wintering in China along the East Asian-Australasian Flyway. In order to represent the different habitat conditions during migration, we divided the whole study area into four parts based on geese distribution in different life-history stages. The four stages including wintering spring-staging period (25°N-35°N), Northeast China Plain (NCP) stopover period (35°N-55°N), North Siberia lowland (NSL) stopover period (55°N-70°N), and breeding period in Lena Delta and Yana Bay (70°N-80°N) (Fig. 1). We adopted land cover data derived from MOD12Q1 (MODIS) as it represents the changes in habitat conditions (Pearson et al., 2004; Suárez-Seoane et al., 2002; Torres et al., 2014). Areas with unsuitable landcover classes were removed from our study (Appendix S1 in Supplementary Material: Table S1).

2.2. Satellite tracking data

During 1st - 4th February 2015, four greater white-fronted geese were captured using leg nooses and flat nets at their wintering sites in Poyang Lake, Jiangxi province, China (29°N, 116°E) (THU01, THU02, THU03, and THU05 were the tags given to the four captured geese). These birds were equipped with 22 g GPS-GSM (Global Positioning System – Global System for Mobile Communications), solar-powered neck loggers (IBIS series, location error 20 m, Ecotone Telemetry, Gdynia, Poland) and promptly released at the capture sites after transmitters were deployed. Approval for capture of and deploying transmitters on migratory birds was obtained from the Jiangxi Provincial Forestry Bureau (reference number: Ganlinban 201514) and the Animal Ethics Committee at Tsinghua University (reference number: IACUC15-SYL1). GPS positions were recorded every 2 h, and a total of 6056 locations (1724 for THU02, 1622 for THU03, 1589 for THU05 and 1125 for THU01) were collected from February to September. GPS locations were grouped into four periods (wintering spring-staging period, North China Plain period, Northeast Siberian lowlands period, and breeding period) based on birds' migration schedule (Table 1). All tracking data are stored in Movebank (http://www.movebank.org) under ID 52997422 and the study "2015 Tsinghua Greater White-fronted Goose (Yangtze)".

2.3. Environmentsal variables

Four static and five dynamic environmentsal variables were adopted in estimating species-environment relationships (Table 2).

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