

Combining modern tracking data and historical records improves understanding of the summer habitats of the Eastern Lesser White-fronted Goose *Anser erythropus*

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Abstract

The Lesser White-fronted Goose (*Anser erythropus*), smallest of the “grey” geese, is listed as Vulnerable on the IUCN Red List and protected in all range states. There are three sub-populations, with the least studied being the East Asian sub-population, shared between Russia and China. The extreme remoteness of breeding enclaves makes them largely inaccessible to researchers. As a substitute for visitation, remotely tracking birds from wintering grounds allows exploration of their summer range. Over a period of three years, and using highly accurate GPS tracking devices, eleven individuals of *A. erythropus* were tracked from the key wintering site of Dongting Lake, China, to breeding, molting, and staging sites in north-eastern Russia. Data obtained from that tracking, bolstered by ground survey and literature records, were used to model the summer distribution of *A. erythropus*. Although earlier literature suggests the summer range is patchy, the model confirms a contiguous summer range. The most suitable habitats are located along the coasts of the Laptev Sea, primarily the Lena-Delta, in the Yana-Kolyma Lowland, and smaller lowlands of Chukotka with narrow riparian extensions upstream along major rivers such as the Lena, Indigirka and Kolyma. The probability of *A. erythropus* presence is related to sites with altitude less than 500 m with abundant wetlands, especially riparian habitat, and a climate with precipitation of warmest quarter around 55 mm and mean temperature of wettest quarter around 14°C. Human disturbance also affects site suitability, with a gradual decrease in species presence starting around 160 km from human settlements. Remote tracking of animal species can bridge the knowledge gap required for robust estimation of species distribution patterns in remote areas. Better knowledge of species’ distribution is important in understanding the large-scale ecological consequences of rapid global change and establishing conservation management strategies.

Introduction

The Lesser White-fronted Goose *Anser erythropus* is the smallest of the so-called “grey” geese of the genus *Anser* (BirdLife International 2018). Excluding threatened taxa, grey geese are traditionally used for subsistence and sport hunting in Eurasia. Arctic nations especially continue to consider geese as a sustainable source of fresh meat in spring. However, hunting bans in many European countries, Republic of Korea and Japan have allowed the various species of grey geese to become part of agricultural landscapes. In contrast,

several species of grey geese in China prefer to winter on wetlands with typically low levels of human use, rather than exploiting agricultural lands that are densely populated by people and their livestock (Deng *et al.* 2018). Since 1994, following rapid population reduction, *A. erythropus* has been globally listed as Vulnerable in the IUCN Red List (BirdLife International 2018).

Three sub-populations can be distinguished: Fennoscandian, West Asian, and East Asian, with potential overlap of the breeding grounds between the West and East Asian sub-populations (Jones *et al.* 2008). Aarvak and Oien (2018) note that the Fennoscandian sub-population appears on the brink of extinction with only 30-35 pairs left, despite captive breeding and restocking in Finland and Sweden during 1981 – 1999 (Ruokonen *et al.* 2000; Andersson and Holmqvist 2010). The number of the West Asian sub-population assessed from counts at stop-over sites during autumn migration has risen from an estimated 10,000-21,000 in early 2000s (Fox *et al.* 2010) to 30,000-34,000 in 2015 (Cuthbert and Aarvak 2016) and perhaps as high as $48,580 \pm 2,820$ in 2017 (Rozenfeld *et al.* 2019). However, this increase could be attributed to additional survey efforts for *A. erythropus* at previously infrequently or un-visited staging sites in Kazakhstan. The most recent estimate of the East Asian sub-population is 14,000-19,000 individuals (Jia *et al.* 2016), accounting for around 25% of the global *A. erythropus* population (Jia *et al.* 2016 and Rozenfeld *et al.* 2019). The eastern sub-population of *A. erythropus* extends from the Taymyr Peninsula eastward to Chukotka region (Morozov 1995; Morozov and Syroechkovski -Jr 2002; Lei *et al.* 2019a), and in common with other subpopulations, is declining (BirdLife International, 2018). A range of threats, including habitat loss and degradation along the migration route and on the wintering grounds proposed to fragmentation of the formerly continuous breeding range, have all been identified being responsible for past population declines (Madsen *et al.* 1984; Grishanov 2006; Morozov 2006). In addition, illegal and accidental hunting (i.e. the genuine confusion with the similar looking Greater White-fronted Goose *A. albifrons*, a species that can be hunted legally in Russia) are also threats to population viability.

Quantitative knowledge of a species spatial distribution is the cornerstone for its effective conservation. Due to the remoteness and restricted accessibility, historical observations of the summer range of the East Asian sub-population are rather scarce (Ruokonen *et al.* 2004, Morozov 1995; Morozov and Syroechkovski -Jr 2002; Lei *et al.* 2019a) Further, there are no systematic surveys covering the potential range of eastern sub-population of *A. erythropus* (Fig. 1). Current knowledge on the breeding distribution and habitat preference of *A. erythropus* is therefore limited (Egorov and Okhlopov 2007, Solovieva and Vartanyan, 2011, Degtyaryev *et al.* 2014). In the last 25 years, ornithologists generally considered that the East Asian *A. erythropus* had a patchy breeding distribution, and the number, position and shape of those areas changed as new knowledge was acquired from occasional visits to remote sites in East Siberia as illustrated in Figure 1. Furthermore, an intensive multi-year survey in the area adjacent to the breeding grounds along the Rauchua River, West Chukotka, helped locate a number of breeding/molting groups and separated broods, suggesting that the entire survey area was populated by *A. erythropus* (Fig. 2). This suggests that a single survey in one year, the usual method employed to study distribution of geese in remote areas of East Siberia (Egorov and Okhlopov 2007, Solovyeva and Vartanyan 2011), may not allow for an effective understanding of the summering distribution, limiting potential conservation actions for the species.

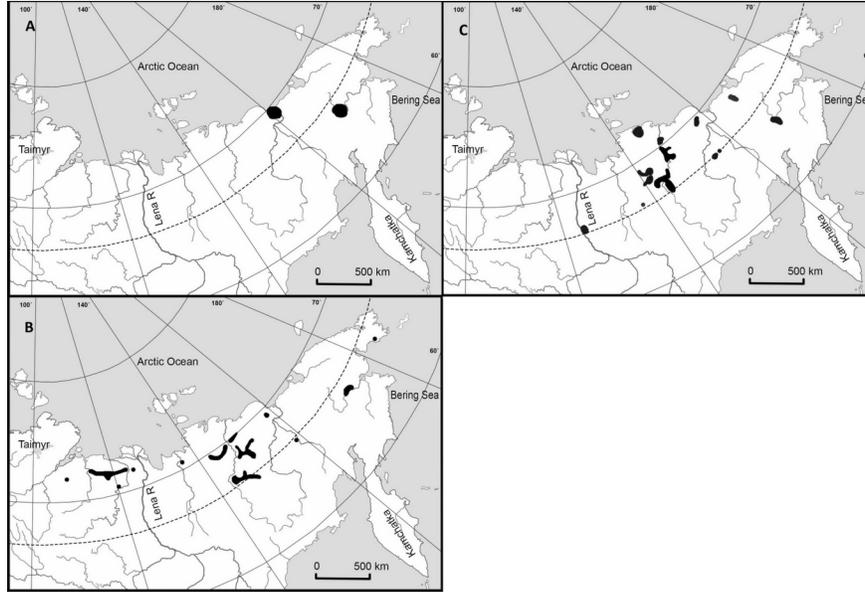


Figure 1 Historical summer (breeding and molting) range of the eastern sub-population of Lesser White-fronted Goose. Black contours indicate known breeding or molting enclaves. A) from Morozov 1995; B) from Morozov and Syroechkovski-Jr 2002; and C) from Cao *et al.* 2018.

As new tracking technologies have developed, the investigation and quantification of spatial and temporal distributions of wide-ranged migratory species, such as *A. erythropus*, now typically involve the deployment of telemetric tracking devices (Jiguet *et al.* 2011; Pimm *et al.* 2015). Rapid accumulation of tracking data offers new insights to assess distribution ranges and to explore habitat preferences (Kays *et al.* 2015). For example, tracking data can be linked with environmental conditions and used in ecological niche models to predict the overall space use by a population (Jiguet *et al.* 2011). In this context, this paper aimed to quantify to the potential summering range of the East Asian *A. erythropus* sub-population by combining GPS tracking data, historical ground survey records, and literature sources. Using bioclimatic, geomorphological, land cover, and human disturbance layers, we used Maxent (a niche modelling technique, Elith *et al.* 2006), to predict the summering habitats of *A. erythropus* within East Siberia in an ensemble forecast framework, i.e. averaging predictions from many models (100 in this study) to account for data uncertainties and model variability (Pearson *et al.* 2006). Niche models using both historical records and recent tracking data could help to get better understanding of the summering distribution of the East Asian *A. erythropus* sub-population, and provide more accurate information for conservation plans including identifying potential threats and prioritizing management actions.

Materials and methods

Study Area

The study area was in northeast Siberia, extending eastwards from Olenyok R (119.2 E) to the watershed between the Pacific and Arctic drainage basins, including Republic of Sakha, Magadanskaya Oblast and Chukotskiy Autonomous Okrug. *A. erythropus* was never reported in in the Arctic Archipelagos, these island areas are excluded in our study.

Surveys in West Chukotka, Russia

During July-August 2002-2019 surveys were undertaken along rivers and lake habitats in the area of 19,260 km² of assumed *A. erythropus* range in Chukotka (Figure 2). Brood-rearing adult *A. erythropus* with their brood or flocks of molting adult *A. erythropus* were counted during downstream travel in a motorboat from the upper reaches of rivers, which were reached by helicopter. A description of the study area and survey results of 2002-2010 have been previously published (Solovieva and Vartanyan 2011). No *A. erythropus* were found on lakes and only surveys along rivers have been used in this study (Figure 2). Positions and numbers of *A. erythropus* were given as (1) middle point and peak number for each river from surveys in multiply years; (2) middle point and number per river from single survey for the rivers surveyed once. As rivers of the study area are relatively small (up to 320 km) and uniform by habitat type, we considered each river as one data point for the niche modelling. These surveys provided 11 records for the model comprising eight breeding records and three molting records.

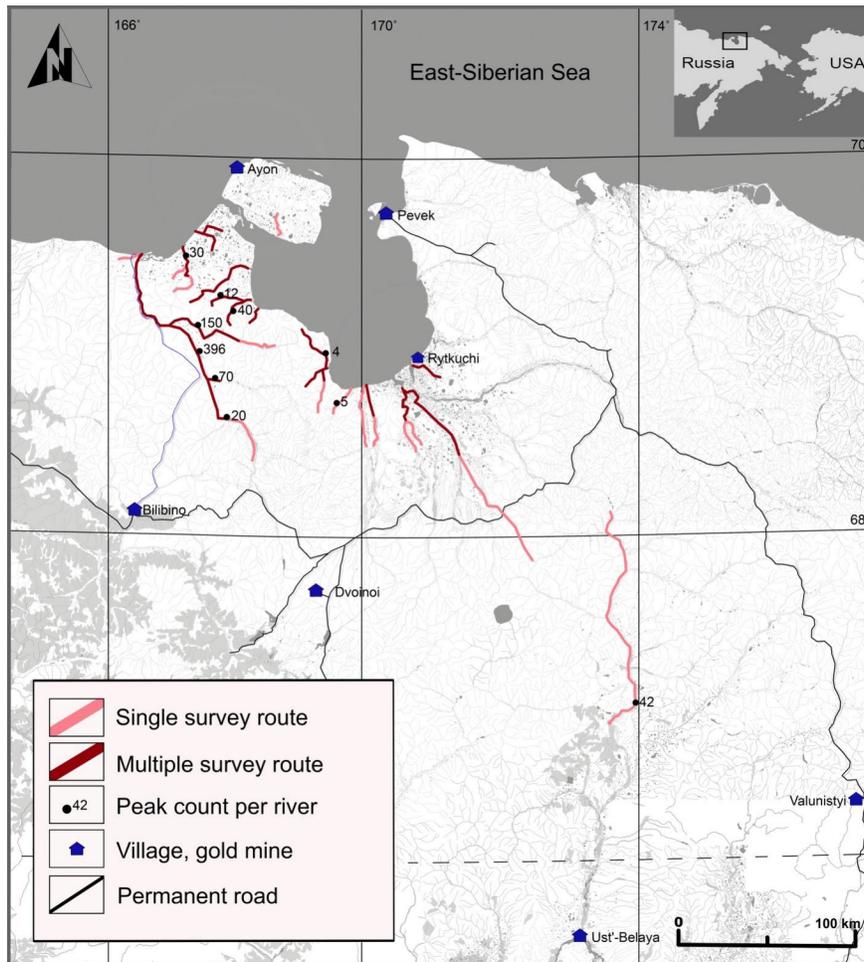


Figure 2 Survey route and peak counts of the Lesser White-fronted Geese on the rivers of West Chukotka, 2002-2019.

Data extraction from published sources

A total of 13 records of breeding or molting *A. erythropus* were compiled from historical surveys along the rivers dated after 1998. Originally 11 of these records were not attributed to GPS coordinates and to

geo-reference them, we converted descriptions of records (river name and distance to the nearest village) to coordinates.

Capture methods and data tracking

Using techniques described in Lei *et al.* (2019a), individual *A. erythropus* captured, during the winter of 2016/17 at East Dongting Lake, China. This lake is the most important wintering site for the species, supporting more than 70% of the East Asian sub-population (Wang *et al.* 2012). A Total of 88 *A. erythropus* were captured and tagged by experienced hunters using baited clap traps, and 11 individuals returned with a completed wintering-migration-summering-migration-wintering cycle (Table 1).

Table 1. Summary of eleven tagged Lesser White-fronted Geese used for this study.

ID	Capture Date	GPS Start Date	GPS End Date	Nb days	Nb summers	Nb of GPS fixes
BFUL041	20.11.2016	23.11.2016	16.04.2018	509	1	7,227
BFUL044	30.11.2016	02.12.2016	09.06.2018	554	1	8,459
BFUL050	25.11.2016	27.11.2016	19.05.2018	538	1	8,351
BFUL057	30.11.2016	02.12.2016	17.07.2018	592	1	4,093
BFUL059	30.11.2016	02.12.2016	29.12.2017	392	1	4,050
BFUL065	05.12.2016	07.12.2016	05.09.2017	272	1	4,832
BFUL068	15.12.2016	16.12.2016	28.05.2018	528	1	9,347
BFUL051	25.11.2016	28.11.2016	25.12.2018	757	2	7,812
BFUL061	30.11.2016	02.12.2016	12.05.2019	891	2	11,490
BFUL074	15.01.2017	19.01.2017	14.05.2019	845	2	6,932
BFUL062	08.12.2016	11.12.2016	27.11.2019	1081	3	17,848

Birds were fitted with transmitters (Hunan Global Messenger Technology Company, China) programmed to record GPS position and speed every 1-3 hours depending on the battery condition. Transmitters were solar powered to enable the global system for mobile communication (GSM) to transmit data *via* the short message service (SMS). These back-pack design transmitters were 55x36x26 mm in size and weighed 22g (appr. 1.6% of the bird's body mass; Lei *et al.* 2019a). As Mobile network coverage is sparse or non-existent in summering sites of North-East Russia, the stored data obtained from that area were downloaded when birds returned to China.

GPS records of locations (accuracy of <1000 m) were used in the analysis of *A. erythropus* journeys to Russia. For non-breeding *A. erythropus* (the longest one-way migration recorded was 16,172 km in 60 days, Lei *et al.* 2019b), it was assumed the spring migration turned to summering activities when the trans-latitudinal movement became mostly trans-longitudinal. Like spring migration, we assumed summering was terminated when a pronounced southbound movement was detected. For breeding birds, the date of arrival at a breeding site was used to indicate the start of summering. The site was classified as staging if the bird stayed at a location for more than four days.

Environmental predictors

To model the potential summering habitat, a range of environmental variables were used including bioclimatic, geomorphological, land production and human disturbance.

Bioclimatic Bioclimatic variables were taken from the 30 second WorldClim (v2.1) climate data, downloaded from <http://www.worldclim.org>, which were generated through interpolation of monthly mean temperature and rainfall data from weather stations for the period of 1970-2000 (Hijmans *et al.* , 2005). We selected five variables that are relevant to geese summering including Max Temperature of Warmest Month (Bio5), Mean

Temperature of Wettest Quarter (Bio8), Mean Temperature of Warmest Quarter (Bio10), Precipitation of Wettest Month (Bio13) and Precipitation of Warmest Quarter (Bio18).

Geomorphological Topographic heterogeneity is important for species distribution (Austin and Van Niel 2011). Three topographic variables were included in the modelling, namely elevation, LDFG (Local Deviation from Global Mean) and TRI (terrain ruggedness index). The global 1 km resolution digital elevation model (DEM) for the study area was downloaded from (<http://srtm.csi.cgiar.org/>) and cropped with the study. Based on the DEM, LDFG and TRI were calculated as:

$$LDFG = y_i - y \quad (1)$$

where y is mean evaluation of the 3 by 3 window, and y_i is the elevation of the focus grid. Positive LDFG values represent locations that are higher than the average of their surroundings, as defined by the neighborhood (ridges). Negative LDFG values represent locations that are lower than their surroundings (valleys). LDFG values near zero are either flat areas (where the slope is near zero) or areas of constant slope (where the slope of the point is significantly greater than zero).

$$TRI = (\sum (Z_c - Z_i)^2)^{1/2} \quad (2)$$

where Z_c is the elevation of the central grid and Z_i is the elevation of one of the eight neighboring grids. The terrain ruggedness index (TRI) is a topographic measurement developed by Riley, *et al.* (1999) to quantify topographic irregularities in a region.

As *A. erythropus* is ecologically dependent on wetlands, and often observed breeding along river valleys (Solovieva *et al.* 2011), we included a layer of distance to steams in the modelling. We generated the raster using polylines in the Global River Widths from Landsat (GRWL) dataset (George, 2018) as the central lines. The polylines were checked to be a good represent of the rivers in the study area.

Land production To characterize land production, we calculated three variables (EVI_{max} , EVI_{hom} and EVI_{range}) using EVI (Enhanced Vegetation Index) time series (2000-2009). The 10-day global EVI images with 333×333 m resolution were downloaded from Copernicus Global Land Service (<https://land.copernicus.eu/global/products/ndvi>, data downloaded on 28 August 2019). EVI_{max} is an indicator of peak land productivity and was calculated as the 10-year mean of annual max EVI. EVI_{range} is the range of land productivity (i.e. $EVI_{max} - EVI_{min}$). EVI_{hom} is the similarity of EVI between adjacent eight pixels, and was computed as (Tuanmu and Jetz 2015):

$$EVI_{hom} = \sum_{i,j=1}^m \frac{P_{i,j}}{1+(i-j)^2} \quad (3)$$

where m is the number of all possible scaled EVI values (i.e. 100) and $P_{i,j}$ is the probability that two adjacent pixels have scaled EVI values of i and j , respectively. Both EVI_{hom} and EVI_{range} can be indicator of habitat diversity.

Human Disturbance Human disturbance can lead to declines and local extinctions of avian species as well as habitat loss (Vollstädt *et al.* 2017). The inclusion of human disturbance data can increase the performance and accuracy of SDM (species distribution model - Stevens and Conway, 2020). We compiled a database of all human settlements including villages and towns in the study area (i.e. Republic of Sakha, Magadanskaya Oblast and Chukotskiy Autonomous Okrug) and generated a layer of distance to settlements as a proxy of human disturbance. Settlements with zero registered inhabitants (abandoned and closed before 2011) were excluded.

Land Cover Forcey *et al.* (2011) found that land use has strong effects on waterbird distribution, and the percentage of waterbird abundance is positively related to the area of wetland. In this study, we used the 2015 global land cover map derived from satellite observations by Land Cover Climate Change Initiative (CCI) and available from <https://maps.elie.ucl.ac.be/CCI/viewer/download.php>. The map classifies the global terrestrial system into 28 major classes using United Nations Food and Agriculture Organization's land cover classification system (Di Gregorio 2005).

R (R Core Team, 2019) packages “raster” (Hijmans *et al.* . 2015) and spatialEco (Evans and Ram, 2018) were used for raster manipulation and calculation.

Modeling

A total of 96 geo-referenced records were compiled by combining the tracking data and historical surveys (post 1999) (Table S2 in Supplementary). To analyze the potential breeding range, maximum entropy implemented in the Maxent package (version 3.4.1) was used. Maxent is among the most robust and accurate SDM techniques (Elith *et al.*, 2006). In the past two decades, it has gained popularity in conservation studies, partly because the technique is less sensitive to the number of recorded sites and uses presence-only data (Elith *et al.*, 2011). In developing the SDM, the program was set to take 75% of the occurrence records randomly for model training and the remaining 25% for model testing. The mean area under the receiver operating characteristic curve (AUC) was used to evaluate model performance, and AUC values > 0.75 are considered as suitable for conservation planning (Lobo *et al.*, 2008). The modelling process was replicated 100 times and we reported the mean as summering ranges to reduce the sampling bias (Merow *et al.* ., 2013).

Although collinearity is less of a problem for machine learning methods in comparison with statistical methods (Elith *et al.* ., 2011), minimizing correlation among predictors prior to model building is recommended (Merow *et al.* ., 2013). We used VIF (Variance inflation factor) to select predictors (Dupuis and Victoria-Feser, 2013). Nine variables with VIF less than 10, including two bioclimatic variables (Bio10 and Bio18), two topographic variables (DEM and LDFG), two productivity variables (EVI_{hom} and EVI_{range}), land cover, Distance to stream, and Distance to settlement, were included in model building.

Using the logistic outputs of MaxEnt, we applied the minimum training presence threshold (MTP) to produce binary habitat map. MTP threshold finds the lowest predicted suitability value for an occurrence point and ensures that all occurrence points fall within the area of the resulting binary model (Elith *et al.* ., 2011).

Results

Potential summering range of the East Asian sub-population of *A. erythropus*

The mean training AUC of the 100 models was 0.9510 suggested these models are very useful (Swets 1988) for predicting the summering range of *A. erythropus* . The standard deviation of AUC was very small (0.0007) indicating the models were stable. Moreover, the mean testing AUC was 0.9356 (SD = 0.0739), which was comparable to the training AUC, suggesting excellent predictive power of the fitted model (Lobo *et al.*, 2008).

The average of summering distribution prediction of the 100 models was presented in Figure 3. The most suitable habitats are located along the coasts of the Laptev Sea, primarily the Lena-Delta, in the Yana-Kolyma Lowland, and smaller lowlands of Chukotka with narrow strips extended upstream to catchments of major rivers such as the Lena, Indigirka, and Kolyma (Fig. 3). The binary map (Fig. 4) produced using the criteria of minimum training presence threshold indicated that 36.44% of the study area was suitable summering habitats.

Lowland wetlands including large deltas, estuaries, tundra, and swampy floodplains (i.e. floodplain contains numerous ponds and shallow lakes), which extend from the Lena Delta at the west to the Kolyma River at the east, provide the most extensive and continuous breeding ground for *A. erythropus* in our study area (Figs. 3 and 4). This is particularly the case for the very large Lena Delta (~29,000 km², Schneider *et al.* . 2009), where the predicted summering habitats include tundra together with numerous interlaced channels and lakes (Dutta *et al.* . 2006).

Most of predicted breeding habitats are covered by a range of plant types including grasses, sedges, herbs, as well as abundant mosses and lichens. This tundra vegetation is also characterized by widely spaced shrubs

(e.g. *Betula nana* (s.l.), *Dushecia fruticosa* and several species of *Salix*) (Yurkovskaya 2011). Such tundra vegetation along major rivers within the taiga biome also have potential to be suitable habitat (Fig. 3).

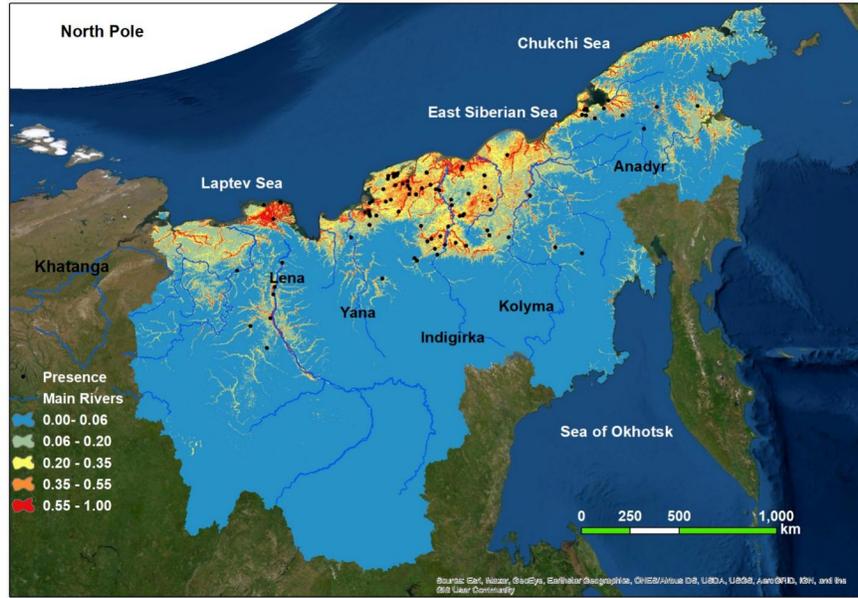


Figure 3 Fitted Maxent model showing the probability of summering habitats of the Eastern population of the Lesser White-fronted Goose. Red color indicates the strongest probability, with orange and yellow less so. Background: Aerial Imagery from ESRI (<http://services.arcgisonline.com/arcgis/rest/services>). Projection: Asia North Albers Equal Area Conic.

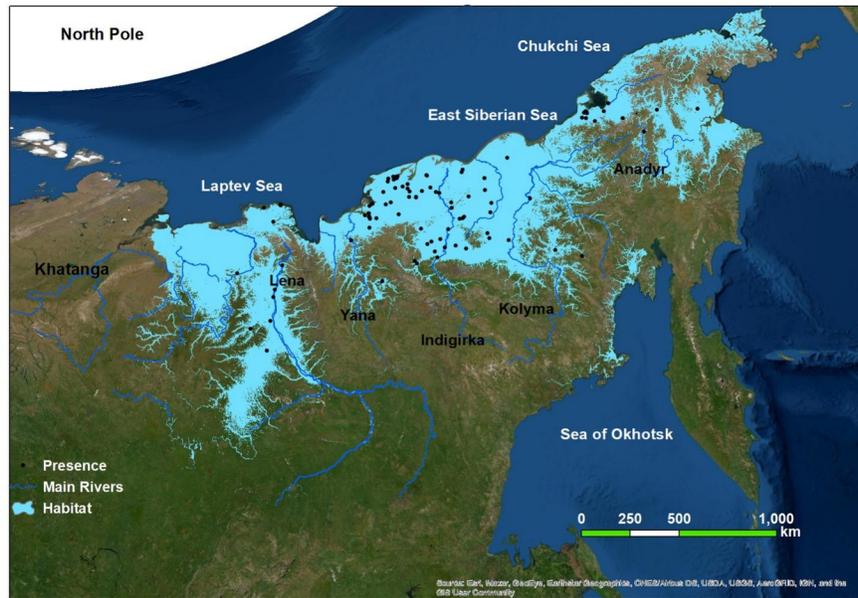


Figure 4 Breeding habitats of the Eastern population of the Lesser White-fronted Goose based on the minimum training presence threshold. Projection: Asia North Albers Equal Area Conic. Background:

World Imagery from ESRI (<http://services.arcgisonline.com/arcgis/rest/services>).

Effects of environmental factor on the summering range of *A. erythropus*

Of the nine environmental variables included in model building, elevation was the most important, strongly contributing to the scaling of the Maxent model (59.7% based on the model gain and 50.1% based on re-evaluation of the random permutation of training presence and background data, Table 2). Other highly influential variables (with more than 5% permutation contribution) include precipitation of the warmest quarter, distance to streams, and mean temperature of the warmest quarter (Table 2).

Although highly correlated environmental predictors were excluded from model fitting, there are still collinearities in the remaining variables. For example, the Pearson r between Bio10 (precipitation of the warmest quarter) and Bio18 (mean temperature of the warmest quarter) is relatively high (-0.82) in the study area. Thus, the variable contributions in Table 2 should be interpreted with caution (Phillips 2005).

Table 2 Relative contributions of the environmental variables to the breeding habitat distribution of *A. erythropus* ranked by permutation importance.

Predictor	Percent contribution	Permutation importance
Elevation	59.4	54.3
Precipitation of warmest quarter	5.0	25.2
Distance to streams	20.3	6.5
Mean temperature of warmest quarter	5.2	5.8
Range_EVI	0.9	2.6
Distance to settlement	2.4	2.2
Land cover	5.5	2.0
Homogeneity_EVI	1.0	0.8
Local deviation from global	0.2	0.6

The marginal effects of the predictors on habitat suitability of *A. erythropus* (i.e. occurrence probability responds to changes in a specific explanatory variable while other covariates are assumed to be held constant as mean) were presented in Figure 5. The response curves showed that the effects of environmental factors on the occurrence of *A. erythropus* were strongly nonlinear.

For topographic variables, the probability of *A. erythropus* presence declines with increasing elevation up to 500 m, with locations higher than 500 m elevation were virtually devoid of *A. erythropus* (Fig 5A). Also, the response curve of LDFG indicated that the geese prefer relatively flat sites (Fig 5I). In terms of bioclimatic variables, the probability of *A. erythropus* presence increases with precipitation of the warmest quarter to around 55 mm and mean temperature of the warmest quarter to around 14°C, after which there is a sharp decrease (Fig. 5B, Fig. 5D). Human disturbance also influences summering habitat, with suitability increasing the further the site is from human settlement (Fig. 5F). The response curve of habitat occurrence probability to distance from rivers (Fig. 5C) suggests that the geese were highly dependent on wetlands and riparian areas (Fig. 5C). Within the riparian zone, the summering habitat suitability decreases sharply with increasing distance from water courses, and after about 4.5 km virtually no birds are found. *A. erythropus* generally prefers land cover types waters (code 210) and shrubland (120; Fig. 5G). The modeling results suggest that the probability of occurrence increases with land productivity range (Fig. 5E) and homogeneity (Fig. 5H).

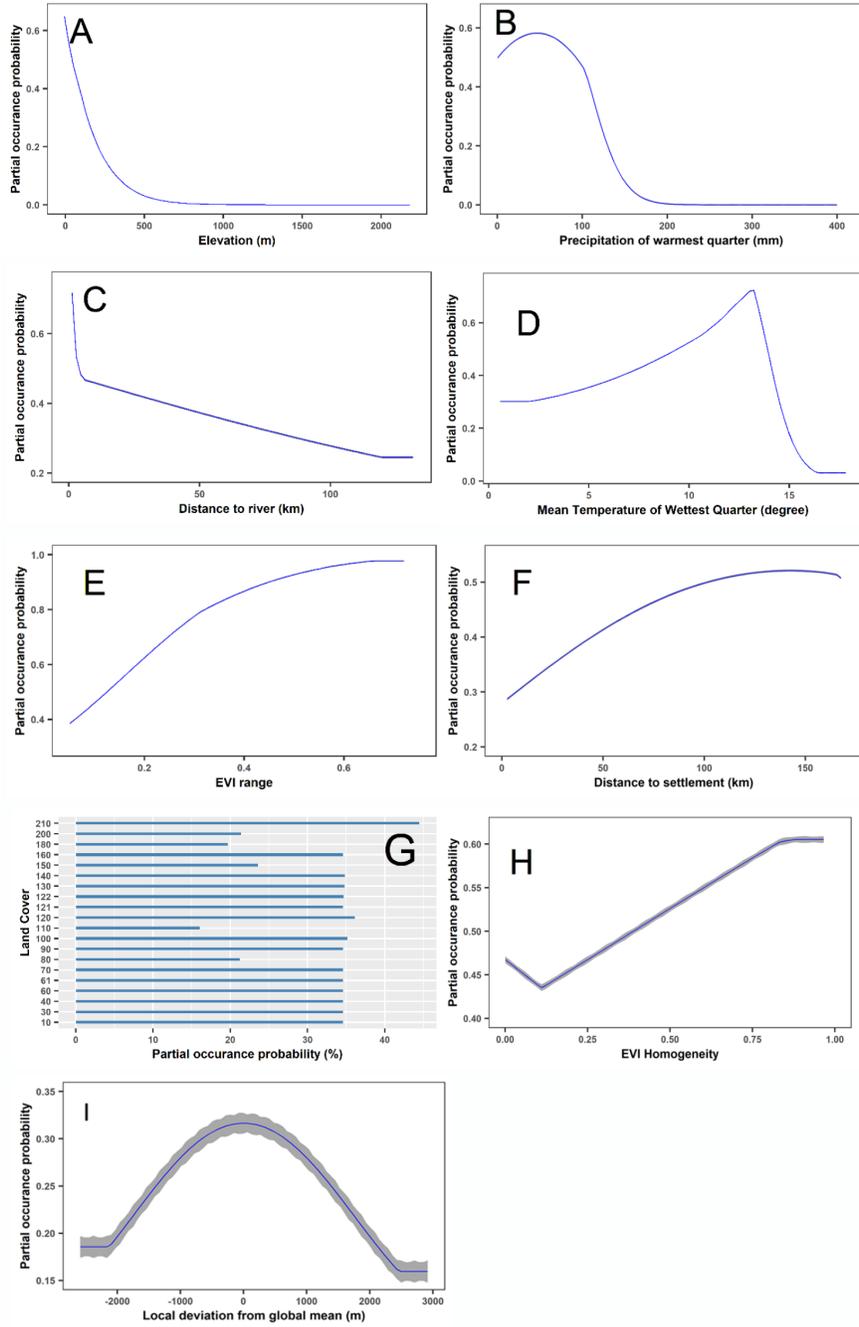


Figure 5 The relationships between the probability of *A. erythropus* occurrence and the top ten environmental variables based on permutation. Blue lines are mean response curves, and grey shades are 1 standard deviation.

Discussion and Conservation Implications

Due to the remoteness and restricted accessibility, there are few historical observations of the summering ground of this population (Ruokonen *et al.* 2004), and our current knowledge on the breeding distribution and habitat preference is limited (Fig. 1 and see Artiukhov and Syroechkovski-Jr. 1999; Egorov and Okhlopkov 2007; Solovieva and Vartanyan, 2011). In this context, rapid development of animal tracking technologies offers new insights to determine distribution range and habitat preferences (Kays *et al.* 2015). In this study, we combined historical records with recent tracking data to model potentially suitable areas of the east sub-population of *A. erythropus* across the more than 7,400,000 km² of arctic and subarctic of north-eastern Russia. Our findings assist conservation of this threatened species by identifying the most suitable breeding grounds and assessing existing and future threats. As *A. erythropus* often co-occurs with other geese (e.g. Greater White-fronted goose (*A. albifrons*), Bean Goose (*A. fabalis*) and Brent Goose (*Branta bernicla*) and other waterfowl including ducks and tundra swan (Hodges and Eldridge, 2001; Pozdnyakov, 2002; Krechmar and Kondratiev 2006), the breeding habitat map could also be used for prioritizing waterbird conservation including through identification of high-priority conservation areas.

Model accuracy and breeding range

In recent years, animal tracking point data have been used in SDM construction either through direct use for model fitting (Williams *et al.* 2017) or for validating the output of the model (Pinto *et al.* 2016). By combining three-year tracking data and historical surveys, our dataset represents the most comprehensive presence record and offers a solid basis to delineate the breeding range of the poorly-known eastern sub-population of *A. erythropus*. The cross-validation results showed that the training and testing AUC are both high (i.e. greater than 0.92) and comparable, suggesting that the output is highly reliable (Phillips and Dudík 2008).

The Maxent output suggested a continuous rather than patchy breeding range of the *A. erythropus* on the plains adjusted to the Laptev, East-Siberian and Chukchi Seas and in the Anadyr Lowland. Within this over 4,000 km area of coastal plains, the Lena Delta, the wide Yana-Kolyma Lowland and smaller lowlands of Chukotka represent the most extensive breeding area with the highest probability of occurrence (Figures 3 and 4). While there are suggestions that breeding ranges of West and East Asian sub-populations overlap between 103 and 118 E, our work did not confirm this. The flat and rolling subarctic tundra is among the most productive wetland system in north-eastern Russia (Gilget *et al.* 2000). Vegetation characteristic in this area is typical tundra, southern tundra with shrubs and forest-tundra with sparse patches of larch (*Larix spp.*) Yurkovskaya (2011). A current IBA (Important Bird Area), including the four main deltas (i.e. the Kolyma, Indigirka, Yana and Lena), covers about 34% of the modeled breeding range (BirdLife International, 2017). However, the majority of the coastal plains, extending up to 450 km inland (Figures 3 and 4), and valleys of large rivers are not included in this IBA. Although there are several Wetlands of International Importance under the Ramsar Convention on the Kamchatka Peninsula, the closest to the study area (Parapolsky Dol) does not contain habitat the modelling suggests as suitable. Highly suitable habitats in the study areas have legal protection through declaration as Federal (State) Nature Reserves: Ust-Lenskiy, Olekminskiy and Magadanskiy, and also by Kytalyk and Beringia National Parks.

Environmental characteristics of breeding habitat

The selection of environmental variables is a critical step in SDM (Araujo and Guisan 2006; Fourcade *et al.* 2018), and hundreds of environmental factors have been utilized in Maxent (Bradie and Leung 2017). These predictor variables can be loosely grouped into four main groups: limiting factors that control the ecophysiology of the species concerned (e.g. temperature, precipitation, pH); resource factors (e.g. vegetation, water areas), which are supplies needed by the organisms to survive; disturbance factors including anthropogenic and natural perturbations in the environment; and landscape factors, which can be related to the species dispersal limitations (Guisan and Thuiller 2005; Vuilleumier and Metzger 2006).

The geomorphological predictors (i.e. elevation, distance to streams and local deviation from global) collectively contributed to 61.4% of the model gain based on permutation test. This level of relative importance was considered very high for Maxent modeling (Bradie and Leung 2017). The decisive role of topography in controlling the distribution of summering grounds might be attributed to strong preference of river valleys and lowlands, especially considering reduced mobility of geese during breeding and molting periods (Akeson and Raveling 1982). Kosicki (2017) demonstrated the importance of topography for modeling the distribution of both lowland and upland bird species, and omitting topographic variables could lead to substantial overestimation of distribution range, especially for rare species. The response curves show that *A. erythropus* selects lowlands with a concave shape as preferred habitat, which is consistent with field observations (e.g. Artiukhov and Syroechkovski-Jr. 1999; Egorov and Okhlopkov 2007; Solovieva and Vartanyan 2011), which reported the bird bred and molt in river valleys.

The majority of Maxent models include climate variables as limiting factors, and most studies found temperature and precipitation were very important variables (Bradie and Leung 2017) as climate is believed to be the most important factor for species distributions (Gaston, 2003). It is therefore not surprising that climate variables including precipitation and temperature were also important for *A. erythropus*. A significant finding of the study is that there was an optimal window of mean summer temperature in 9-14°C (Fig. 5D) and dry continental or high Arctic precipitation of the wettest quarter in 55 mm (Fig. 5B), within which the habitat suitability is maximized.

Land cover is also important and contributes strongly to model performance (Table 2). The response curve indicates that two land cover types are favored by *A. erythropus* including shrubland and open-water areas. The land-cover preference can be linked to the requirement of nest shelters during breeding season (Hilton *et al.* 2004) and food resources. In terms of food resources, the *A. erythropus* is an herbivorous browser, i.e. it tends to increase the portion of the selective resources in their feeding range (Markkola *et al.* 2003). The wet sedge meadows on the alluvial floodplains that are preferred by herbivorous geese (Sedinger and Raveling 1984), and are critical for brood rearing (Markkola *et al.* 2003) offer a range of highly nutritious species with an adequate protein–water ratio and low portions of cellulose and lignin, (e.g. grasses *Puccinellia phryganodes*, *Phragmites australis* and sedges

Carex spp.).

Finally, the most suitable habitats had higher land productivity heterogeneity (Fig. 5E and 5H) which was expected as species richness and abundance often increases with habitat diversity (Chasko and Gates 1982; Wen *et al.* 2015). Although human disturbance can sometimes increase diversity in such wetland systems, here the habitat suitability decreases with human disturbance (Fig. 5F), reflecting the negative impacts of human presence (Lei *et al.* 2019b).

Conservation challenges

The results of this study highlight a major challenge from future climate change on the *A. erythropus*. First, many climate change models predict increasing spring temperatures and earlier snow melting (IPCC 2014), which will lead to flooding, submergence, permafrost erosion and loss and change in low-lying coastal wetlands (Prowse *et al.* 2006). As the predicted summering habitats were concentrated in the lowland coastal zone of the Laptev and East Siberian Seas, the projected sea level rise (IPCC 2014; Wrona *et al.* 2016) and increasing river flows (Karlsson *et al.* 2012; Wrona *et al.* 2016) could cause extensive habitat loss. The response curves of habitat suitability to topographic variables suggest that the relatively hilly and rugged landscape would restrict extension of suitable habitat landward and such “habitat squeeze” (Leo *et al.* 2019) would be highly detrimental to *A. erythropus*. Second, the models suggested that there was an “optimal window” in terms of mean summer temperature and precipitation, which could be interpreted as the realized climatic niche of *A. erythropus* (Merow *et al.* 2016). Rising temperatures under future climate change scenarios means that the temperature niche could shift northerly, which is sea. Third, studies have shown that encroachment of shrubs following projected climate change (e.g. *Salix ovalifolia* and *Dushecia*

fruticosa) into the wet meadows (Carlson *et al.* 2018), would likely decrease quantity and quality of available food resources.

Finally, there is the threat from increasing anthropogenic disturbance; *A. erythropus* avoids locations near active mines (although can colonize such areas after mining is finished) (Egorov and Okhlopkov 2007; Solovieva and Vartanyan 2011). Currently, human population levels in the predicted summering range is among the lowest in the world, and the coastal areas of this region are some of the least explored. However, the coast of the Russian Arctic is likely to undergo rapid development as there are reserves of oil, gas, metals and other natural resources which could be exported, with additional infrastructure, through the North-East Passage to European and Asian ports (Martini *et al.* 2019), more information on these potential developments can be found at <http://ecoline-eac.com/proekty/peschanka/deposit.html>, and these developments present perhaps the most difficult challenges to the future of eastern sub-population of *A. erythropus*.

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