Migratory connectivity of Swan Geese based on species' distribution models, feather stable isotope assignment and satellite tracking

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Abstract

Aim: Understanding connectivity between avian breeding and non-breeding areas is essential to understand processes affecting threatened migrants throughout their annual cycle. We attempted to establish migratory connectivity and flyway structure of the IUCN vulnerable Swan Geese (Anser cygnoides) by combining citizen science species' distribution models (SDMs) and feather stable isotope analysis.

Locations: Russia, Mongolia and China.

Methods: We established migratory origins and movements of 46 Swan Geese from five wintering locations by integrating citizen science SDMs and feather stable hydrogen isotope (δ²H) measurements by linking feathers to precipitation isoscapes in a Bayesian probability framework.

Results: We determined multiple summering origins among Swan Geese from the most important wintering location, Poyang Lake, Jiangxi Province, China. As predicted, we found no evidence for sex-biased differences in δ²H measurements. Four geese tracked with GPS/GSM loggers all migrated to moulting areas, which confirmed the accuracy of our predictions from δ²H assignments. Differences between summering ranges inferred from historical and modern samples coincided with major wetland loss in northeastern China since the 1950s. Despite limited historical data, we contend that this supports the hypothesis that the summering range prior to 1950 was much wider than that of the current population.

Main conclusions: This was the first Asian study to establish migratory origins of wintering Anatidae based on stable isotopes and citizen science SDMs. We advocate the wider combined application of SDMs, telemetry studies and stable isotopes to investigate effectively avian migratory connectivity, as the results from this study provided important contributions to the development of conservation measures for this threatened and declining species in East Asia.
1 | INTRODUCTION

Migratory connectivity describes the movement of individuals between summer and winter home ranges, as well as use of intermediate stopover sites (Webster, Marra, Haig, Bensch, & Holmes, 2002). Defining connectivity for migratory species is essential to differentiate discrete populations as a basis for comprehending their population dynamics and life-history strategies (Pekarsky et al., 2015; Rolshausen, Segelbacher, Hobson, & Schaefer, 2009). This need is more urgent for declining taxa. More than 30% of all vertebrates species are reported to be declining (Thompson, Klütsch, Manseau, & Wilson, 2019), rising to at least 40% among birds (McLaren et al., 2018). More than 40% of global avian species undertake annual migrations (Newton, 2007), during which they interact with a series of local environments and provide a variety of ecosystem services (e.g. Duarte, Laura, Willem, & Jordi, 2016; Tian et al., 2015). However, with increasing pressure on migratory birds at multiple points along their annual flyway corridors, understanding connectivity is becoming more urgent in order to develop effective conservation strategies, especially for the most rapidly declining populations (Hobson & Wassenaar, 2019).

Multiple techniques have been employed to describe the geo-spatial movement of individual birds. The extensive application of passive extrinsic markers such as metal rings and neck collars has provided great historical insights into migration patterns, but is limited by extremely low reporting rates (Hobson, Norris, Kardynal, & Yohannes, 2019). Recent innovation has provided devices that can be mounted on birds that record time-stamped positions with great accuracy using the global positioning system facility, with data downloaded via the mobile telephone system, albeit with potential effects on tagged individuals (Bodey et al., 2018).

In contrast, intrinsic markers (such as the stable isotope ratios of body tissues) do not require device attachments but rely solely on features of the birds’ physiology and ecology, as well as our ability to decode the information via the comparison of these features with known geophysical spatial isotopic patterns. As a result, intrinsic markers may be less subject to bias (e.g. towards easily accessible regions for trapping and marking of birds), as well as being relatively less costly to implement. The stable hydrogen isotope ratio ($\delta^2$H) of avian tissue has become a popular intrinsic marker to infer bird movements (Hobson et al., 2019; Vander Zanden et al., 2018). Natural variation in $\delta^2$H in precipitation ($\delta^2$Hp) can be characterized across space and time (López-Calderón, Van Wilgenburg, Roth, Flasphohler, & Hobson, 2019; Vander Zanden et al., 2018). Values of $\delta^2$H$_p$ reflect hydrogen taken up and incorporated into plant tissues and by their primary consumers, both of which will be assimilated into the organs of birds via their food. As a result, the specific isotopic value in any given feather ($\delta^2$H$_p$) reflects the amount-weighted, mean annual $\delta^2$H$_p$ at the natal or moult location (Fox et al., 2017). It is therefore possible to create assignment models by comparing $\delta^2$H$_p$ values and prevailing environmental values in amount-weighted, time-averaged $\delta^2$H$_p$. Nevertheless, while $\delta^2$H-based methods are highly tractable and pragmatic, their assignments are generally coarse as large geographical regions share similar $\delta^2$H$_p$ values.

Resolution of $\delta^2$H-based assignments can be improved by incorporating prior sources of information. These include ring-recovery data (Guillemain, Van Wilgenburg, Legagneux, & Hobson, 2014; Procházka, Van Wilgenburg, Neto, Yosef, & Hobson, 2013), genetic markers (Chabot, Hobson, Van Wilgenburg, McQuat, & Lougheed, 2012; Clegg, Kelly, Kimura, & Smith, 2003) and predictions from species’ distribution models, SDMs (Fournier, Drake, & Tozer, 2017; Pekarsky et al., 2015). While it can be difficult to incorporate systematic genetic and ring-recovery data at a comprehensive scale, the extensive data collected by citizen scientists can be used to generate SDMs that provide excellent utility for refining isotopic assignments of migratory connectivity (Fournier, Sullivan, et al., 2017; Pekarsky et al., 2015). Citizen science enlists (often non-professional) observers to collect and/or process data, some of which extend over several decades (Bonney et al., 2009; Bonney, Phillips, Ballard, & Enck, 2015). For example, eBird (eBird, 2017) engages the global bird-watching community to collect more than 5000,000 bird observations every month, submitted to a central database. These data have been used in at least 90 peer-reviewed publications on various topics (Bonney et al., 2014). Despite data quality issues related to citizen science (Hunter, Alabri, & van Ingen, 2013; Kosmala, Wiggins, Swanson, & Simmons, 2016), observation records from these repositories can be effectively employed in presence-only species distribution modelling to generate valuable priors which, in our case, can be used to subsequently refine isotopic assignment of individuals to localities. This is essential for understanding the distribution range and population dynamics of migratory species, especially for those populations that are confined to fragmented and/or remote regions.

The Swan Goose (Anser cygnoides) is an Asian endemic species, which is listed as vulnerable in the Red List of Threatened...
Species of the International Union for Conservation of Nature (IUCN). This species is formerly thought to have bred in a continuous band from Zaysan Lake (eastern Kazakhstan 48°2′N, 83°52′E) across Far East Russia to Sakhalin island and as far north as Ayan (56°30′N, 138°10′E; BirdLife International, 2019; Dementiev & Gladkov, 1952). However, by the early 1990s, its breeding range was increasingly restricted to Mongolian steppe wetlands, in the west extending into neighbouring Tuva in the Russian Federation and in the east extending into Russian Chita and northeast China. Elsewhere in Russia, there remain a few breeding birds around Khanka Lake, another group around Lake Udyl and the coast at Schastye Bay and perhaps a few on Sakhalin Island (Fox & Leafloor, 2018; Kear, 2005; Poyarkov, Klenova, & Kholodova, 2010). Swan Goose wintering range also once traversed Korea, Japan and much of China, but in recent years, this has contracted to China and concentrated increasingly there at Poyang Lake in Jiangxi Province (Fox & Leafloor, 2018). To date, there is limited information on the migration connectivity of this species. Initial tracking studies demonstrated that most marked geese from northeastern Mongolia followed more indirect and energetically costly autumn migration pathways than the expected direct flight to the winter quarters, which was potentially explained as the result of adverse landscape changes in east China affecting historical migratory behaviour (Batbayar et al., 2011). More recent tracking has confirmed connections between Swan Geese breeding in Far East Russia and disjunct wintering areas on the southeastern coast of China (Minjiang River Estuary, Fujian Province, C. Y. Choi, personal communication), the subject of prolonged speculation (Choi et al., 2016; Poyarkov, 2005; Poyarkov et al., 2010). These studies, however, were confined to restricted areas of the breeding grounds, and the recent rapid consolidation of the species at Poyang Lake makes it imperative to undertake a broader study of the movements of remaining Swan Geese.

In this study, we develop a framework for generating spatially explicit predictions of the breeding/moultng origins for Asian large-bodied waterbirds, by integrating SDMs, constructed from citizen science and systematic survey data, with stable isotope analysis of feathers from individual birds. We test this framework on Swan Goose caught on their winter quarters to trace their summer origins. Given that more than 95% of the total population seems now to occur at Poyang Lake (Fox & Leafloor, 2018) and the characteristic long-term pair bonds of the species, we made two predictions. (1) That feathers from individuals captured at Poyang Lake would differ significantly in their δ²Hf values reflecting the different δ²Hf isoscape values representing the summer moult locations. (2) There would be no difference between sexes. Furthermore, the breeding range is thought to have become more fragmented in recent times (Poyarkov, 2005). Increased human population density and urbanization in eastern China (Batbayar et al., 2011), as well as severe loss of natural wetlands in northeastern China (Lu et al., 2016; Xu et al., 2019) have also likely affected the migratory routes followed by Swan Geese in recent years. We therefore also tested the prediction that wintering Swan Geese in China have altered their historical summering distribution range, using δ²Hf measurements from museum specimens.

2 | METHODS

We analysed δ²H values for feathers collected from breeding and wintering grounds (Figure 1). Because feather keratin is metabolically inert after formation, feathers sampled in the summer should reflect isotopic environments occupied during post-breeding feather growth (Scordato et al., 2019). Probable origins of wintering birds were determined by (1) construction of season-specific SDMs representing the prior probability of Swan Goose occurrence; (2) construction of a spatially explicit δ²Hf isoscape for
Swan Goose based on a derived relationship between measured δ²Hf and δ²Hp, primarily from the International Atomic Agency (IAEA) Global Network of Isotopes in Precipitation (GNIP); and (3) application of a Bayesian assignment algorithm to depict spatially explicit probability of origin surfaces for Swan Geese based on their δ²H values.

2.1 | Telemetry and feather sample collection

Ninety-six feathers of birds from 12 summering (July) and five wintering sites (November to February) were obtained between 2010 and 2017 (Table 1). On the moulting areas, we rounded up flightless geese using boats, gently pushed them into corrals and nets on land. Secondary median wing coverts from captured adults were plucked (feather base intact) and stored in separate paper envelopes. Wing coverts were chosen as they are regrown with (Kear, 2005) or after (Ashton, 2012) primaries and secondaries, reducing the risk of impairing flight due to sampling flight feathers. Wintering geese were caught using static mist nets or by pursuit in boats with strong lamps to catch geese with hand nets at roost sites (see Aharon-Rotman et al., 2017 for full details). Four wintering geese (Table S1; Sample ID: #1, #33, #36, #42) were fitted with GPS/GSM loggers before releasing to identify their subsequent moulting locations. Feather specimens from two museums were also included in analyses (Table 1). Feather bases were removed for sex identification based on DNA analysis (Dawson, Dos Remedios, & Horsburgh, 2016), while feather vane material was used for δ²H analysis. Based on this, the δ²H in feathers grown during the previous summer provided information on (1) the approximate latitude of natal origin in the case of one-year-old birds or (2) approximate previous post-breeding moult location in the case of older birds (Hobson, Wassenaar, & Bayne, 2004). Goose captures in Mongolia were carried out under licenses provided by the Ministry of Nature, Environment and Tourism of Mongolia (Nos. 06/2008 and 06/2862), and elsewhere in accordance with the guidance and permission (No. rcees-ddll-001) of the Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences.

| Time of year | Locations | Sampling period | N   |
|--------------|-----------|-----------------|-----|
| Moulteting   | Airag Lake, Mongolia | 31 July 2010 | 7   |
| Moulteting   | Baruunereennuuriinburd, Mongolia | 25 July 2016 | 2   |
| Moulteting   | Buir Lake, Mongolia | 20 July 2017 | 7   |
| Moulteting   | Bus Lake, Mongolia | 29 July 2014 | 4   |
| Moulteting   | Chukh Lake, Mongolia | 31 July 2014 | 2   |
| Moulteting   | Davsantsagaan, Mongolia | 22 July 2016 | 1   |
| Moulteting   | Galuut lake, Mongolia | 28 July 2014 | 3   |
| Moulteting   | Galuut lake, Mongolia | 23 July 2016 | 4   |
| Moulteting   | Gurmen lake, Mongolia | 16 July 2015 | 5   |
| Moulteting   | Khaichiin Tsagaan Lake, Mongolia | 30 July 2014 | 1   |
| Moulteting   | Ugii lake, Mongolia | 12 July 2017 | 9   |
| Moulteting   | Uvs Lake, Mongolia | 6 July 2017 | 2   |
| Moulteting   | Hulun Lake, Inner Mongolia, China | 7–11 July 2017 | 3   |
| Wintering    | Minjiang Estuary, Fujian Province, China | 2006  | 2   |
| Wintering    | Chenyao Lake, Anhui Province, China | 16 November to 12 December 2015 | 3   |
| Wintering    | Chenyao Lake, Anhui Province, China | 7 November 2016 | 3   |
| Wintering    | Chongming Island, Shanghai City, China | 6 February 1960; 11 April 1976 | 2   |
| Wintering    | Dongting Lake, Hunan Province, China | 6 September 2016 | 1   |
| Wintering    | Poyang Lake, Jiangxi Province, China | 3 March 2015 | 18  |
| Wintering    | Poyang Lake, Jiangxi Province, China | 9–13 December 2015 | 16  |
| Wintering    | Poyang Lake, Jiangxi Province, China | 1 January 2017 | 1   |

Abbreviation: N, number of individuals.

*Represents for museum samples.
2.2 | Species distribution modelling

Species’ distribution models are widely used to predict the probability of occurrence for species across the landscape based on the relationship estimated between species’ observation records and their corresponding environmental characteristics (Elith et al., 2011; Hijmans, 2012). There is now a plethora of methods for modelling species’ distributions, among which maximum entropy (MaxEnt) models are commonly used (Radosavljevic & Anderson, 2014) because they generate robust results using sparse, irregularly sampled data with minor locational errors (Elith et al., 2006; Kramer-Schadt et al., 2013). Moreover, MaxEnt has the advantage of using presence-only data, avoiding the need for confirmed absence records (Elith et al., 2006), making it especially suitable for rare species and/or those with a fragmented range.

2.2.1 | Spatial filtering of occurrence data and correction for sampling bias

We defined the flightless moult period as 16 June to 16 September (Batbayar et al., 2011). A probability surface for Swan Goose moulting areas was generated based on presence records during this period (Table S2) from three main sources: (1) sampling locations of feather collections; (2) moulting locations described elsewhere; and (3) records downloaded from the eBird and GBIF citizen sciences databases (https://ebird.org/home; https://www.gbif.org/).

We chose Maxent version 3.3.3k (Phillips, Anderson, & Schapire, 2006) for species distribution modelling for two main reasons. Firstly, we are constrained to use a presence-only modelling approach because the majority of our records (68.69%, Table S2) were collected with unknown sampling effort. Hence, it is impossible to incorporate covariates that account for heterogeneity in detectability, effort and reporting (duration spent searching for birds, start time, distance travelled, etc.) when constructing SDMs (Johnston et al., 2019). Secondly, Maxent is documented to outperform other presence-only modelling approaches (Ruan et al., 2018; Townsend Peterson, Papeş, & Eaton, 2007). A fundamental assumption in Maxent is that the entire area of interest has been systematically sampled. However, most data sources (e.g. from museums and citizen science programmes) exhibit strong spatial bias in survey effort (Stolar & Nielsen, 2015), as some sites are more likely to be surveyed than others (Ruizgutierrez & Zipkin, 2011). This can severely impact model quality (Phillips et al., 2009) by over-representation of certain environmental features of more accessible and extensively surveyed areas.

To overcome such sampling bias, the entire dataset was spatially filtered and a bias grid was generated to modify the random selection of background points using tools from the SDM toolbox (Brown, 2014) implemented in ArcMap 10.3 (ESRI). The bias grid was created using the SDM toolbox Gaussian Kernel Density of Sampling Localities tool loaded with all presence points (with a sampling bias distance of 50 km). This radius was chosen because the mean home range size of moulting individual Swan Geese was mostly well below this threshold based on data from the tracking study (I. Damba, H. Li, X. Wang, K. Yi, X. Li, N. Batbayar, T. Natsagdorj, B. Davaasuren, L. Cao, personal communication). Spatial filtering of independent occurrence records (n = 915, data not shown) used the SDM toolbox Spatially Rarefy Occurrence data for SDMs tool to remove duplicate occurrence points within a radius of 50 km. The resulting spatially filtered presence data (n = 99, Table S2) and bias grid were utilized in Maxent as the occurrence data and bias file, respectively.

2.2.2 | Environmental variables

Twenty-four raster layers (Table S3) representing four groups of variables (bioclimatic parameters, vegetation, human influence and topographical attributes) potentially related to habitat suitability of the Swan Goose were selected as candidate variables. We included 19 bioclimatic variables from WorldClim 2.0 (http://www.worldclim.org/), which integrated the effects of latitude, longitude and elevation (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). The Climate Change Initiative LC dataset (CCI-LC) from ESA (https://maps.elie.ucl.ac.be/CCI/viewer/; 2008–2012 centred on 2010; 300 m resolution) was used as a categorical variable of vegetation type. Human influence index regarding human impacts was downloaded from Last of the Wild (Wildlife Conservation Society-WCS & University, 2005). Slope and aspect were extracted from an ASTER GDEM V2 30 m resolution digital elevation model (DEM; http://www.gscloud.cn/), by using the Surface Analyst Tool of ArcGIS 10.3 (ESRI). To reduce multicollinearity, we calculated Pearson’s correlation (r) between each variable pair for 6,000 random points from throughout the geographical range. Tightly correlated (r > .80) and redundant variables were removed, favouring those more temporally inclusive (e.g. BIO08–Mean Temperature of Wettest Quarter versus BIO05–Max Temperature of Warmest Month) or relevant to ecology of Swan Goose in the field (e.g. land cover vs. elevation), finally five variables (Table S3) were retained for further modelling. All grids were clipped to match the distribution range of the Swan Goose, with a resampling resolution of 1 km.

2.2.3 | Correlative modelling

Criterion-based model selection was conducted by assessing different combinations of the feature class types (FC) and regularization multiplier (RM) using the software ENMTOOLS version 1.3 (Warren, Glor, & Turelli, 2010). We constructed models for Swan Geese by applying alternate FCs (e.g. L = linear; LQ = linear and quadratic; H = hinge; LQH = linear, quadratic and hinge; LQHPT = LQH, product and threshold; LQHP) and RMs ranging from zero to 15.0 at 0.5 intervals. In sum, we tested 186 alternate models (6 FCs × 31 RMs) and identified optimum model settings using corrected Akaike information criterion (Hope et al., 2016). The final modelling was conducted with 20 replicates, log-scale outputs, 5,000 iterations and a
default convergence threshold of 0.00001. For replicate modelling, the occurrence dataset was randomly partitioned into two groups, with 75% for training and the remaining 25% for validation. MAXENT produces a set of continuous surfaces, and we used the mean of replicated models to represent the suitability or likelihood (Guillera-Arroita et al., 2015; Hope et al., 2016).

2.3 | Stable isotope analysis

Feather samples were cleaned with 2:1 chloroform–methanol solution and dried at room temperature in a fume hood. Distal sub-samples (~350 µg) of feather vane were prepared and analysed for δ²H at the Stable Isotope Hydrology and Ecology Laboratory of Environment Canada in Saskatoon, Canada, using the comparative equilibration method (Wassenaar & Hobson, 2003) through the calibration of keratin δ²H reference materials (CBS: −197‰; KHS −54.1‰). All non-exchangeable H isotope fractions are reported in VSMOW-SLAP standard scale. Based on within-run replicate measurements of standards (five each), we estimated measurement error to be ~2‰.

2.4 | Statistical analyses

We tested for differences in δ²Hf from the same location, but from different years at Poyang Lake and Chenyao Lake (Table S1). The δ²Hf data from Poyang Lake in March (n = 18) and December (n = 16) of 2015 were both tested for normal distribution (Shapiro–Wilk’s test; α = 0.05) with equal variance (Levene’s test; α = 0.05), after which they were compared using t tests. For Chenyao Lake, the effect of year was tested using a nonparametric Wilcoxon rank sum test/Mann–Whitney U test because of small sample size (n = 3 for both 2015 and 2016). To assess the potential sex difference in wintering occurrence of δ²Hf, we applied nonparametric Kruskal–Wallis analyses of variance to multiple sex groups, after which we used Dunn’s test to assess post hoc pairwise differences with group settings to test for year effects. Only groups with sample size exceeding three were included in the statistical analysis. All the statistical analyses were performed in the R statistical computing environment v3.2.2 (R Core Development Team, 2015).

2.5 | Identifying goose origins

An appropriate rescaling relationship between δ²Hf and δ²Hp is a prerequisite for stable isotope-derived geographical assignments (Vander Zanden et al., 2018). The calibration set used to determine the relationship between δ²Hf and δ²Hp comprised a set of 50 feathers from 12 moulting locations. We regressed the δ²Hf against mean annual growing season δ²Hp at the site of sampling locations and further used this relationship to convert a GIS-based model of δ²Hp across the study area into a spatially explicit raster depicting mean expected δ²Hf values (Bowen, Wassenaar, & Hobson, 2005).

Due to sources of variance inherited from the regression model, δ²Hf values expected from any given pixels are best characterized as a distribution of potential values rather than a single value; hence, we reported the origins of a given bird as a normal density function (Hope et al., 2016; Pekarsky et al., 2015):

\[
f(y|\mu, \sigma) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{1}{2\sigma^2}(y-\mu)^2\right)
\]

where \(f(y|\mu, \sigma)\) is the probability that any given cell on the isoscape represents a potential origin for an individual with δ²Hf value of \(y\), with an expected mean \(\mu\) of δ²Hf and expected standard deviation \(\sigma\) based on the rescaling equation. The \(\sigma\) value was estimated using the standard deviation of the residuals from the regression equation, given that this accounts for the deviation of the δ²Hf from the expected geographical pattern, which is present in the ambient water, thus representing the variance in the predicted value within the calibrated isoscape.

We incorporated the SDM as prior information for the stable isotope assignment using Bayes’ rule:

\[
f(b|y) = \frac{f(y|b) \cdot f(b)}{\sum_{b'} f(y|b') \cdot f(b')}
\]

where \(f(b|y)\) is the posterior probability a given pixel on the raster represents the origin of a bird, \(f(b)\) represents the spatially explicit prior probabilities of the location being an origin of each individual based on SDM, and \(f(y|b)\) is estimated from Equation 1.

To depict the likely origins of each population, we assigned each individual separately and converted the raster to a binary surface using a 2:1 odds ratio (Fox et al., 2017; Procházka et al., 2013), where isoscape cells in the upper 66.7% of probabilities were considered as likely (1) and, otherwise, unlikely (0) origins. Assignments to each cell throughout the distribution range were generated in this way, which were subsequently “stacked” together for all individuals in the wintering samples to depict potential moulting origins for each wintering group. Each cell value represented the sum of these individual-level binary grids, summed and then normalized by dividing by the number of geese in each group, thus obtaining the posterior probability surface of origin for the group. Digital file manipulation and assignment to origin analyses were conducted using multiple R packages including “raster” (Hijmans et al., 2015) and “maptools” (Bivand & Lewin-Koh, 2015).

2.6 | Assignment verification via satellite tracking

Moulting locations of the four tracked Swan Geese were identified given the unique pattern of restricted movements recorded during their flightless period. Observations during 16 June to 16 September (Batbayar et al., 2011) when the birds remained within a radius of...
30 km for at least 21 days (Kölzsch et al., 2019) were identified as moulting. The central location of the data points during moulting period was considered as the moulting point and was plotted on the origin prediction map of corresponding capture group along with the tracking routes of each individual to verify the prediction power of the Bayesian models.

3 | RESULTS

3.1 Differences in feather stable isotopes

There was a significant difference between the two sets of samples from Poyang Lake (from March and December 2015; two-sided t-test, $t = 3.32, df = 32, p = .002$). Geese from two consecutive winters (2015 and 2016) caught at Chenyao Lake did not differ significantly ($W = 0.85, p = .17$). For this reason, all subsequent Poyang Lake analyses were performed separately with those caught in March 2015 designated as winter 2014/15 and those from December 2015 as 2015/16, Figure 2), while all the samples from Chenyao Lake were treated as one group. Kruskal–Wallis tests suggested marginally significant differences between the six testing groups ($\chi^2 = 11.2, p = .0048$), while none of the pairwise sex groups exhibited significant difference according to the $P$ values after Bonferroni correction (Table S4).

3.2 Species’ distribution models

Some spatial bias was detected in the moulting observations for the Swan Goose. Within the summering range, sampling intensity was highest in eastern Mongolia the adjacent Daurian area located along the boundary of China, Russia and Mongolia, while the potential moulting areas in western Mongolia and eastern Kazakhstan were less sampled (Figure S1). Although SDM without spatial bias correction could accurately predict the test presence locations as demonstrated by their high area under the curve (AUC) of the receiver operating characteristic curve (ROC) values (Figure S2), this is largely because they predicted a higher presence in the more densely sampled eastern Mongolia and adjacent Daurian region. This spatial bias in observations was translated into environmental bias by providing the bias grid as an “environmental covariate” to Maxent when constructing the moulting SDMs.

3.3 Assignment of moulting area provenance

Significant correlation was found between $\delta^{2}H_f$ and $\delta^{2}H_p$ of known-provenance geese ($\delta^{2}H_f = 1.7084 \delta^{2}H_p + 9.0279, \sigma = 8.89, r^2 = .431, p = 2.3e^{-7}$). Most uncertainty in the relationship arose from deviation in the expected $\delta^{2}H_f$ among sites (Figure 3a). In addition, there was a significant negative relationship between $\delta^{2}H_f$ and the longitude of sampling location ($\sigma = 10.29, r^2 = .238, p = .0032$; Figure 3b).

By generating a separate assignment map for each independent capture group, Swan Geese wintering in Poyang Lake were predicted to originate mainly from the Kherlen River, which derives from eastern Mongolia before emptying into Hulun Lake in China. Adjacent areas of eastern Mongolia, Hulun Lake and northern East Ujimqin Banner in Inner Mongolia, China, as well as the Songnen Plain in northeast China were other moulting origins of high probability. Western and central Mongolia were also potential origins for geese in Poyang Lake, but those geese sampled in the winter of 2015/16 (Figure 4b) were seemingly more widely distributed during moulting period than those sampled in the spring of 2014/15 (Figure 4a). The predicted provenance for wintering geese in Chenyao Lake, Anhui Province was similar with those from Poyang Lake combined for both years (Figure 4c), but with eastern Tuva (especially the neighbouring area around Yenisei River), Shilka River, Chita region in Russia and

![FIGURE 2](image-url) Comparisons of stable hydrogen isotope ratio in the feathers of Swan Geese Anser cygnoides among different wintering groups. The first three letters for the legends stand for the sampling locations (PYL for Poyang Lake in Jiangxi Province; CYL for Chenyao Lake in Anhui Province) in China, numbers correspond to the moulting year (2014 and 2015, respectively) for the feather samples taken at Poyang Lake. The letters following the underline indicate males (M) and females (F). The global statistical significance level generated by Kruskal–Wallis tests is shown in the upper-left corner.
the eastern-most border between China and Russia represent other highly probable origins (Figure 4d).

Although the southeastern Transbaikalia region in Russia (especially the Chita area) seems to be the common summering origin for both coastal (Figure 5c,d) and inland geese (Figure 5a), the historical moulting range in the summer for Swan Geese was quite different from that of modern ones despite the relatively small and uneven sample size. Feathers taken from museum specimens of geese which wintered along the Chinese coast (Chongming Island in Shanghai City) were predicted to have grown sampled flight feathers in environments farther north and east (Figure 5d) of areas within its current breeding/moulting range based on the recent feather assignment data, especially in the western and central parts of the summering range. Far East Russia, northern Sakhalin Island and the Ussuri River region were also inferred as potential hotspots of high probability for the summer provenances for geese sampled in the 1960 and 1970s. However, geese sampled at the beginning of the 21st century (from Fujian Province, Figure 5c) show no such linkages with Far East Russia and seem to exhibit a transition state of summering origins between historical and modern patterns.

3.4 | Comparing telemetry tracks and stable isotope predictions

Among the four tracked geese, one from Poyang Lake and another from Chenyao Lake (#36 and #42, respectively; Table S1) migrated to western Mongolia for the subsequent breeding season (Figure 4b,d), both moulting in the northeastern corner of Uvs Lake, the largest saline lake in Mongolia. Two other Poyang Lake marked geese went to Inner Mongolia, China (Figure 4b,c) but one moulted in Hulun Lake (#1; Table S1) while another stopped in East Ujimqin Banner (#33; Table S1). The final moulting destinations for all these four geese showed a high coincidence with the regions predicted by our assignment model. Nevertheless, because numbers of tracked individuals were few, there was no evidence of moulting provenance for those hotspots located in central Mongolia (Figure 4b), Chita region in Russia (Figure 4c), northeastern China (Figure 4b) and the Qixing–Naoli River in Shuangyashan City, Heilongjiang Province (Figure 4d).

4 | DISCUSSION

Using a Bayesian framework to combine SDMs derived from citizen science observations with δ²H assignments to produce high-resolution estimates of the origins of Swan Geese, we provided evidence to support the known contraction in range of the species on their Russian and Mongolian breeding areas (Batbayar et al., 2011; Goroshko, 2001). This is the first case study in Asia to successfully define the migratory origin of the wintering Anatidae based on a species-specific rescaling relationship between δ²Hf and δ²Hp, confirmed by satellite telemetry.

The integration of SDMs greatly improved the accuracy of stable hydrogen isotope assignments for Swan Geese. To demonstrate the improvement, we depicted the probable origin surface of all the wintering geese caught in China. Model uncertainty exacerbates the natural lack of resolution in stable isotope-based assignment (Figure 5b), for which the probable origin of birds extended over a vast area from Western Mongolia as far north as southern Baikal Lake region and east to the lower reaches of the Amur River, with
low resolution. Conditioning isotope assignments on the moult-specific SDM greatly enhanced geographical assignment (Figure 5a), which confined the final predicted areas of origin to adjacent areas distributed between eastern Mongolia, China and the Chita region of Russia as well as central and western parts of Mongolia. Given that we suspect that the current breeding/moulting distribution range of the Swan Goose is severely fragmented compared to that in the recent past, we thus conclude that the prediction power of the Bayesian approach had benefitted by integrating the moult-specific SDM.

Combining SDMs and δ²H data, we predicted the potential moulting origins for 46 geese sampled on their Chinese winter quarters, including the currently most important wintering location, Poyang Lake in Jiangxi Province, as well as museum specimens wintering along the coast from the 1960s and 1970s. Our results confirmed the absence of sex effect on δ²H values among the tested groups, but revealed differences in moulting provenance of Swan Geese between feathers sampled from contemporary and historically derived geese despite the potential limitations associated with the relatively small sample size among the latter. We contend that while the improvement of the sample size would provide more confidence in the precision of the geospatial assignment of historical individuals, in all likelihood the historical summering range extended further to the north and east than that of the current population.

4.1 | Multiple moulting origins among Poyang Lake wintering geese

Two groups of Swan Geese sampled in the same year but in subsequent seasons at Poyang Lake exhibited significantly different δ²H values, demonstrating multiple moulting origins for geese sampled there. Batbayar et al. (2011) showed that telemetry tracked geese from eastern Mongolia mainly migrated to Poyang Lake in winter, while those from central and eastern Mongolia were likely to appear
The loss of submerged macrophytes in Anhui Lakes (Fox et al., 2011) has reduced the carrying capacity for tuber-consuming birds, altering the distribution and abundance of the *Vallisneria* tuber-feeding avian guild. This has notably affected the Swan Goose, which is perhaps more specialized in this respect than other species (Chen, Zhang, Cao, De Boer, & Fox, 2019; Fox et al., 2011). At Shengjin Lake, wintering Swan Goose numbers decreased more than 10-fold between 2003 and 2008 (Zhang et al., 2011). The wintering range continues to contract (Cao, Zhang, Barter, & Lei, 2010; Zhang et al., 2011), concentrating at Poyang Lake, where more than 95% of the world population currently occurs (Fox & Leafloor, 2018). It is therefore not surprising that Poyang Lake supports wintering Swan Geese of increasingly diverse breeding provenance. These include birds from known important summering areas, distributed between China and Mongolia (Ganbold et al., 2017; Goroshko, 2004; Songtao, Xinhai, & Gerilechaoketu, 2014), the southeastern Transbaikalia region in Russia (Goroshko, 2001; Goroshko, Cornely, & Bouffard, 2008), and in western/central Mongolia and northeast China (Tian, Jia, Tao, & Li, 2010).

### 4.2 Changes in moulting distribution in northeast China

The distinctive differences in the predicted geographical origins between historical and modern feather samples potentially indicate a change in distribution of summering Swan Geese despite the relatively small sample size available from museum specimens. The Swan Goose formerly bred in the Tuva republic, the Nanweng River wetlands in Heilongjiang Province, and the Ergun wetlands in Inner Mongolia in the central and western parts of its former range (Poyarkov, 2005). In addition, the species has almost completely disappeared in summer from the Amur-Heilong River Basin, the Ussuri River and Khanka Lake as well as throughout Far East Russia, so our data from museum samples from Fujian Province suggesting links with that area may reflect the transient state at that time. This reflects documented major environmental change in the area: for example, Swan Geese were common at Lake Kizi (Lower Amur region) in the 1930s, but the site was abandoned by geese in the 1950–1960s as a result of extensive timber cutting operations along the lake shore (Poyarkov, 2005). Cultivation and agricultural intensification forced...
Support abundant Swan Geese (Li, 1996), but where the species is fowl, is particularly severe in Heilongjiang Province, which used to continuous loss of natural wetlands in northeast China, which used to

Rozenfeld, S. Moriguchi, A. Zhan, L. Cao, A. D. Fox, personal commu-

Zhao, K. Yi, N. Batbayar, T. Natsagdorj, B. Davaasuren, X. Wang, S.

is therefore not surprising to find local fine-scale genetic structure among birds sampled on the breeding grounds (Q. Zhu, I. Damba, Q. Zhao, K. Yi, N. Batbayar, T. Natsagdorj, B. Davasauren, X. Wang, S. Rozenfeld, S. Moriguchi, A. Zhan, L. Cao, A. D. Fox, personal communication) which might also transfer to the wintering quarters.

4.3 | Lack of sex-linked provenance and moulting strategy

Lack of a sex effect on the $\delta^{2}H$, values of wintering geese and the significant negative relationship between $\delta^{2}H$, and longitude of sampling locations suggest similar provenance and moulting strategy for both genders. This is hardly surprising for a monogamous species that pairs for life (BirdLife International, 2019; Kear, 2005) in contrast to many seasonally monogamous duck species where females undertake brooding rearing and parental care alone (Salomonsen, 1968). Non-breeders undertake moult migration to large open-water bodies with adequate food resources (Batbayar et al., 2011), while breed-

ers remain together with goslings until fledging (Poyarkov, 2005) and moult in the vicinity of their nesting site (Salomonsen, 1968). However, even in favourable breeding seasons, non-breeding Swan Goose aggregations in the Daurian region still constitute c.70% of the world population (Goroshko, 2004). Lifetime pair-bond duration and extended parental care are typical of goose species (Ely, Wilson, & Talbot, 2017), enabling Swan Geese to maintain social bonds with conspecific and even family groups (Robertson & Cooke, 1999). It is therefore not surprising to find local fine-scale genetic structure among birds sampled on the breeding grounds (Q. Zhu, I. Damba, Q. Zhao, K. Yi, N. Batbayar, T. Natsagdorj, B. Davasauren, X. Wang, S. Rozenfeld, S. Moriguchi, A. Zhan, L. Cao, A. D. Fox, personal communication) which might also transfer to the wintering quarters.

4.4 | The value of combining telemetry and isotope approaches

The contribution from using stable isotope methods to interpret migratory connectivity is now well documented (Fournier, Drake, et al., 2017; Symes & Woodborne, 2010; Van Wilgenburg & Hobson, 2011) and verified by our study. Thanks to the predictable natural variation in $\delta^{2}H$, we see the potential of using $\delta^{2}H$ as a means of compensating for the lack of long-term research and monitoring and especially traditional capture–mark–recapture approaches to determine levels of migratory connectivity in waterbirds in East Asia. There are likely to be further advantages in analysing for multiple elements to further improve the prediction resolution and accuracy of moulting provenance based on feather stable isotopes as demonstrated elsewhere (Fox et al., 2017; Pekarsky et al., 2015).

Although the application of telemetry devices to waterbirds has proved invaluable for describing individual migration patterns, given the general patterns of lifetime site fidelity in these species, the broader application of this technique to determining migratory connectivity within and between population remains limited. Nevertheless, we see advantages in the complementary use of telemetry and stable isotopes in this context. Firstly, stable isotope analyses could identify potentially high-connectivity areas based on feather samples from unmarked birds. Sites believed to be key nodes in the connectivity matrix can then be investigated further by enhanced telemetry tracking to enlighten us about breeding provenance, habitat use and migration strategies to fully characterize migratory movements. Secondly, for species with a fragmented breeding range, applying tracking devices on more individuals to estimate the probability of their migration to each distinct breeding patch would generate an improved set of priors to apply within a Bayesian framework to greatly improve on current knowledge.

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DATA AVAILABILITY STATEMENT

All the relevant data necessary for this study are included in the Supporting Information.

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**BIOSKETCH**

The Wetland and Biodiversity Research Group (http://sourcedb. rceeas.cn/yw/yyj/201510/I20151026_4444979.html) is interested in wetland biodiversity ecology and conservation, and the movement ecology of wetland birds. We have a strong focus on the ecology and conservation of migratory species in the East Asian–Australasian Flyway (EAAF). By deploying cutting-edge avian telemetry devices, we have initiated tracking programmes within China and across Far East Asia. We are also coordinating a national monitoring and research network of bird-tracking in China. We work with local partners to ensure that our scientific findings are transferred to on-the-ground conservation action.

Qin Zhu is a PhD candidate in the Wetland and Biodiversity team, whose primary interests lie in explaining and modelling spatial patterns of biodiversity of waterfowl species at various scales for use in systematic conservation planning and risk assessment.

Author contributions: Q.Z., A.D.F., L.C., J.G., Q.Z. and Y.Z. designed the theoretical and methodical framework; I.D., N.B., T.N., B.D., X.W., L.C. and A.D.F. carried out fieldwork and collected samples in Mongolia, Q.Z. and L.F. in China; Q.Z., L.F. and J.G. conducted sample preparation and statistical analyses; K.A.H. conducted stable isotope analyses; Q.Z., I.D. and A.A. jointly collected occurrence records; Q.Z. drafted the manuscript; A.D.F., K.A.H., A.A., Q.Z. and L.C. revised the manuscript: all authors read the draft and contributed to the discussion and completion of the final manuscript.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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