Original Research Article

Using geolocator tracking data and ringing archives to validate citizen-science based seasonal predictions of bird distribution in a data-poor region

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ABSTRACT

Unstructured citizen-science data are increasingly used for analysing the abundance and distribution of species. Here we test the usefulness of such data to predict the seasonal distribution of migratory songbirds, and to analyse patterns of migratory connectivity.

We used bird occurrence data from eBird, one of the largest global citizen science databases, to predict the year-round distribution of eight songbird taxa (*Agropsar philippensis*, *Calliope calliope*, *Cecropis daurica*, *Emberiza aureola*, *Hirundo rustica*, *Locustella certhiola*, *Oriolus chinensis*, *Saxicola torquatus stejnegeri*) that migrate through East Asia, a region especially poor in data but globally important for the conservation of migratory land birds. Maximum entropy models were built to predict spring stopover, autumn stopover and wintering areas. Ring recovery and geolocator tracking data were then used to evaluate, how well the predicted occurrence at a given period of the annual cycle matched sites where the species were known to be present from ringing and tracking data.

Predicted winter ranges were generally smaller than those on published extent-of-occurrence maps (the hitherto only available source of distribution information). There

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was little overlap in stopover regions. The overlap between areas predicted as suitable from the eBird data and areas that had records from geolocator tracking was high in winter, and lower for spring and autumn migration. Less than 50% of the ringing recoveries came from locations within the seasonal predicted areas, with the highest overlap in autumn. The seasonal range size of a species affected the matching of tracking/ringing data with the predictions. Strong migratory connectivity was evident in Siberian Rubythroats and Barn Swallows. We identified two migration corridors, one over the eastern mainland of China, and one along a chain of islands in the Pacific.

We show that the combination of disparate data sources has great potential to gain a better understanding of the non-breeding distribution and migratory connectivity of Eastern Palearctic songbirds. Citizen-science observation data are useful even in remote areas to predict the seasonal distribution of migratory species, especially in periods when birds are sedentary and when supplemented with tracking data.

1. Introduction

Species distribution models (SDMs) have been proven to be useful tools to understand the spatio-temporal occurrence of species, and allow to predict their distribution in areas that are poorly covered by observational data (Guisan and Thuiller, 2005). Observations from citizen scientists are available in ever-increasing numbers, and commonly used for SDMs (Kéry et al., 2010; van Strien et al., 2013; Tye et al., 2017; Fink et al., 2020). However, the usefulness of such data for assessing abundance and distribution remains controversial (Conrad and Hilchey, 2011; Kamp et al., 2016), as several systematic errors can affect the results. First, species identification might be wrong (Lotz and Allen, 2007). Second, the data might be biased towards conspicuous species (due to uneven detection probability), towards species-rich or easy-to-reach areas (resulting in spatial bias), and towards certain times of the day or year (resulting in temporal bias) (Boakes et al., 2010; Bird et al., 2014). To increase data quality, some citizen-science databases have established standard protocols and a rigorous quality check (Bonter and Cooper, 2012; Freitag et al., 2016). Novel analytical techniques allow to correct for observer bias (Johnston et al., 2018, 2020), spatial bias (Hochachka et al., 2012) and differences in detection probability (Isaac et al., 2014; Guillera-Arroita, 2017).

The prediction of seasonal distributions or periods of movement for highly mobile and migratory species remains challenging. Species may widen or change their niche during different times of the annual cycle, which is a common pattern in migratory fish (Forseth et al., 1999; Weng et al., 2005), mammals (Cherel et al., 2007, 2009) and birds (e.g. Martínez-Meyer et al., 2004; Nakazawa et al., 2004). Phenological changes in behaviour (such as density-dependent singing activity during the breeding season and on spring migration in songbirds) can cause variation in detection probability (Warren et al., 2013).

The combination of tracking and citizen-science data holds a high potential to improve species distribution models. Laughlin et al. (2013) used observation data from different sources to determine habitat use and stopover sites of Tree Swallows *Tachycineta bicolor*. However, the authors did not model the spatial distribution based on the observation data, but used them only to analyse temporal migration patterns. In contrast to field observations based on citizen science, individual tracking data are spatially unbiased, and can therefore be used to model species distributions in regions of low observer density (Jiguet et al., 2011; Gschweng et al., 2012; Williams et al., 2017). But the availability of tracking data is usually limited to larger species and few individuals (Bridge et al., 2011). Alternatively, bird ringing data can be used to predict seasonal distributions, but information on recovery probabilities needs to be available (Thorup and Conn, 2009). In many parts of the world, few ringing recoveries are available for most species (Clark et al., 2009).

The increasing spatial and temporal resolution of citizen-science data allows the modelling of migratory movements in unprecedented temporal and spatial resolution (Hurlbert and Liang, 2012; Sullivan et al., 2014; Supp et al., 2015). The potential for predicting seasonal priority areas for the conservation of rare species by using citizen-science observations is huge (Devictor et al., 2010). However, the inclusion of individuals from resident populations might affect the predictions (Supp et al., 2015), and biased predictions might result in ineffective conservation measures (Loiselle et al., 2003). Citizen-science based models of seasonal distributions have not been evaluated by comparing the predictions with spatially unbiased tracking data so far.

The East Asian-Australasian flyway holds the highest number of migratory land birds, including the highest number of globally threatened species of any flyway (Yong et al., 2015). Habitat loss due to deforestation (Brooks et al., 1999; Wilcove et al., 2013; Estoque et al., 2019), the conversion to cropland and agricultural management intensification are major drivers of biodiversity loss (Kehoe et al., 2017; Zhao et al., 2006). During the past four decades such land use change happened across vast areas in East and South East Asia and has been linked to declines in migratory land birds (Higuchi and Morishita, 1999). Russia, where most of the migratory species breed (Ravkin and Ravkin, 2005; Yong et al., 2015), showed an opposite development with large scale abandonment of agricultural land since the break-down of the Soviet Union (Lesiv et al., 2018). Unsustainable trapping for consumption (Kamp et al., 2015), cage bird trade (Shepherd et al., 2016) and religious purposes

("merit release", Gilbert et al., 2012) has further contributed to the rapid population declines of several songbird species that move along the East Asian flyway.

Species-specific causes and mechanisms for these declines are still poorly understood, as knowledge on land bird migration routes, stopover sites and wintering grounds in East and South-East Asia is still rudimentary (Amano and Yamaura, 2007; Yong et al., 2015). Key to the conservation of migratory animals is the linking of breeding, stopover and wintering areas, known as migratory connectivity (Marra et al., 2011). For Asia, data is available for large birds such as geese (Palm et al., 2015) and bustards (Combreau et al., 2011), but data on migratory connectivity in songbirds is lacking (Yong et al., 2015).

Several million birds have been marked with metal rings in Asia since the 1950's. However, the last large-scale analysis of ringing and recovery data from Asia was published almost 50 years ago (McClure, 1974). Moreover, new technology has revolutionized bird migration research: Light-level based geolocators enable us to follow the migration of songbirds down to 10 g body weight, which are too small to carry satellite transmitters (Bridge et al., 2011). Dozens of geolocation studies were conducted in the American and European-African flyways, but only few published results are available for the Asian migration routes (McKinnon and Love, 2018).

Here, we use observational data from citizen scientists to predict the seasonal distribution of songbird species that migrate along the East Asian route. We then validate the predicted distributions with bird ringing and tracking data.

Our aims were A) to test the usefulness of citizen-science observation data to predict the seasonal distribution of migratory species in a data-poor region by validating it with ringing and tracking data, and B) to analyse migratory connectivity and patterns of non-breeding distribution of a set of East Asian songbirds.

2. Materials and methods

2.1. Study region

Our study region covered the area that is likely to be reached by birds migrating in the East Asian flyway: eastwards from the Ural Mountains to Kamchatka (from 60° to 160° longitude) and northward from Indonesia to the Arctic Circle ($-10°-60°$ latitude).

2.2. Predicting seasonal species' distributions

We built maximum entropy (MaxEnt) models, a class of SDMs allowing to model the geographic distribution with presence-only data (Phillips et al., 2006), using the R package dismo (Hijmans et al., 2016b).

To feed our models, we used unstructured citizen science data from eBird, the world's largest database of bird observations (Sullivan et al., 2009; La Sorte and Somveille, 2019). We selected all land bird species for which also tracking data were available (see below), namely Yellow-breasted Bunting *Emberiza aureola*, Siberian Rubythroat *Calliope calliope*, Pallas's Grasshopper Warbler *Locustella certhiola*, Barn Swallow *Hirundo rustica*, Red-rumped Swallow *Cecropis daurica*, Black-naped Oriole *Oriolus chinensis*, Stejneger's Stonechat *Saxicola torquatus stejnegeri* and Chestnut-cheeked Starling *Agropsar philippensis*. We downloaded all observations available up to October 2018. We defined April and May as spring migration, September and October as autumn migration, and November to March as wintering periods. We used two approaches to correct for spatial bias in the eBird observation data. First, we randomly selected only one observation per grid cell (see below) for each species and season (Kramer-Schadt et al., 2013). Such systematic sampling has been shown to be the most efficient method for correcting sampling bias (Fourcade et al., 2014). Second, we included a bias file (representing the sampling probability surface based on available species records, Fourcade et al., 2014) as most observations come from densely populated areas and places where birdwatchers congregate (Boakes et al., 2010). Models containing a bias file had a poorer fit than those without bias correction (Suppl. 1), therefore the bias grid was not used in the final models. An overview of the sample sizes per species and season is given in Table 1. MaxEnt models rely on a comparison of probability densities of presence-only records with background data (Elith et al., 2011). For each model, we sampled 10,000 random points across the study area and considered these background locations.

Table 1
Sample sizes for eBird observations, geolocation data and ringing recoveries for the selected target species (excluding data from the breeding season). The number of recoveries of ringed birds is based on data of the ringing schemes of Russia and Japan until 2017.

Species	eBird observations (autumn/winter/spring)	Geolocation (individuals/positions)	Ringing (long-distance recoveries)
Yellow-breasted Bunting	101/113/93	3/9	3
Siberian Rubythroat	334/467/430	10/21	136
Pallas's Grasshopper Warbler	129/173/183	1/3	0
Barn Swallow	2619/3328/3475	1/1	200
Red-rumped Swallow	1095/1555/1442	1/1	1
Black-naped Oriole	506/562/621	1/7	0
Stejneger's Stonechat	168/223/219	12/55	1
Chestnut-cheeked Starling	87/41/127	16/145	8

As predictors, we used climatic variables (Fick and Hijmans, 2017) and altitude (Jarvis et al., 2008), which are the main factors that determine large-scale distributional patterns in birds (Rahbek and Graves, 2001). From the BioClim dataset (Fick and Hijmans, 2017), we extracted mean monthly precipitation, maximum monthly temperature and mean monthly water vapour pressure, and calculated the average mean for all seasons (autumn, winter, spring) for all available years (1970−2000). We also calculated the mean Normalized Difference Vegetation Index (NDVI) for each season based on the MODIS product MOD13C1 (Didan, 2015). Many songbirds are known to track seasonal resource availability (Thorup et al., 2017), and the NDVI has been shown to be correlated with migration phenology (Robson and Barriocanal, 2011), including in Siberian Rubythroats migrating along the East Asian flyway (Heim et al., 2018). Additionally, we included land cover (10 classes, 30 m resolution) as a predictor variable (downloaded from http://www.globallandcover.com, Chen et al., 2017) as it influences species distributions on regional scales (Thuiller et al., 2004). All layers were resampled to a resolution of 0.05° (approximately 5.55 by 5.55 km at equator) using the *resample* function from the R package raster.

We built separate models for spring migration, autumn migration and winter based on the seasonal records from eBird as defined above, including the climatic and NDVI data from the respective months (Williams et al., 2017). For land cover and altitude, the same layers were used for all seasons.

Model performance was assessed using the area under a receiver-operator curve (AUC) and Cohen's Kappa (Manel et al., 2001). We used three different thresholds to translate the gradual predictions of habitat suitability into binary presence-absence maps to map the range predicted as suitable: maximum kappa, maximum specificity and sensitivity, and zero omissions of presence points from the predicted range. Predicted values above the corresponding threshold were interpreted as suitable range, while values below the threshold were interpreted as unsuitable range (Jiménez-Valverde and Lobo, 2007). We chose the most sensitive threshold for each seasonal model that would minimize the predicted range to gain maximum specificity. Preparation of the layers was done using the R packages raster (Hijmans et al., 2016a), rgdal (Bivand et al., 2015), rJava (Urbanek, 2009) and rgeos (Bivand et al., 2016).

2.3. Validating predictions of seasonal distributions

To validate the MaxEnt seasonal range predictions, we used different sources of data (Fig. 1): Published and unpublished geolocation tracking data, and ringing recoveries. Geolocation data are spatially unbiased, but the precision of the location estimates varies strongly due to shading by vegetation, bird behaviour, length of stay at a given site and time of the year (Lisovski et al., 2012). Ringing recovery data are spatially biased towards areas of higher activities of ringers and more densely populated areas with a higher detection probability of dead birds (Thorup et al., 2014).

Geolocation data were available from our own field studies (6 species, Heim et al., 2018, Heim et al. unpublished, Fig. 2) and were analyzed using the R package GeoLight (Lisovski and Hahn, 2012). All positions with a minimum stopover duration of five days were considered, for details see Suppl. 2 and Heim et al. (2018). Geolocation data for two more species were gathered from publications (Koike et al., 2016; Yamaura et al., 2017).

Ringing data were obtained from the national ringing archives of Russia (Bird Ringing Centre of Russia, Moscow) and the ringing recovery archive of the Ministry of the Environment, Tokyo, Japan, managed by the Yamashina Institute for Ornithology, Abiko, Chiba, Japan. Additional ringing recovery data were gathered from McClure (1974). We only included long-distance recoveries (≥200 km between ringing and recovery site) within our study area.

To identify out-of-range predictions, we overlaid our predictions with coarse extent-of-occurrence (EOO) maps available from BirdLife International (BirdLife International, 2019). These maps were available for winter distribution as well as for spring and autumn combined. We calculated the overlap between the predictions and the EOO maps using the *gArea* function
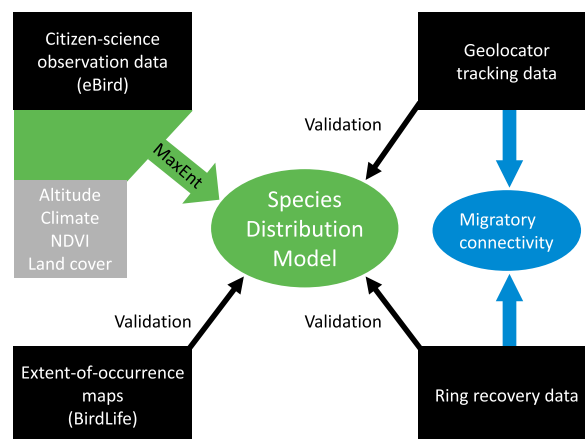

Fig. 1. Overview on the data sources used for fitting our seasonal species distribution models, for the validation of these models and for analyzing migratory connectivity.
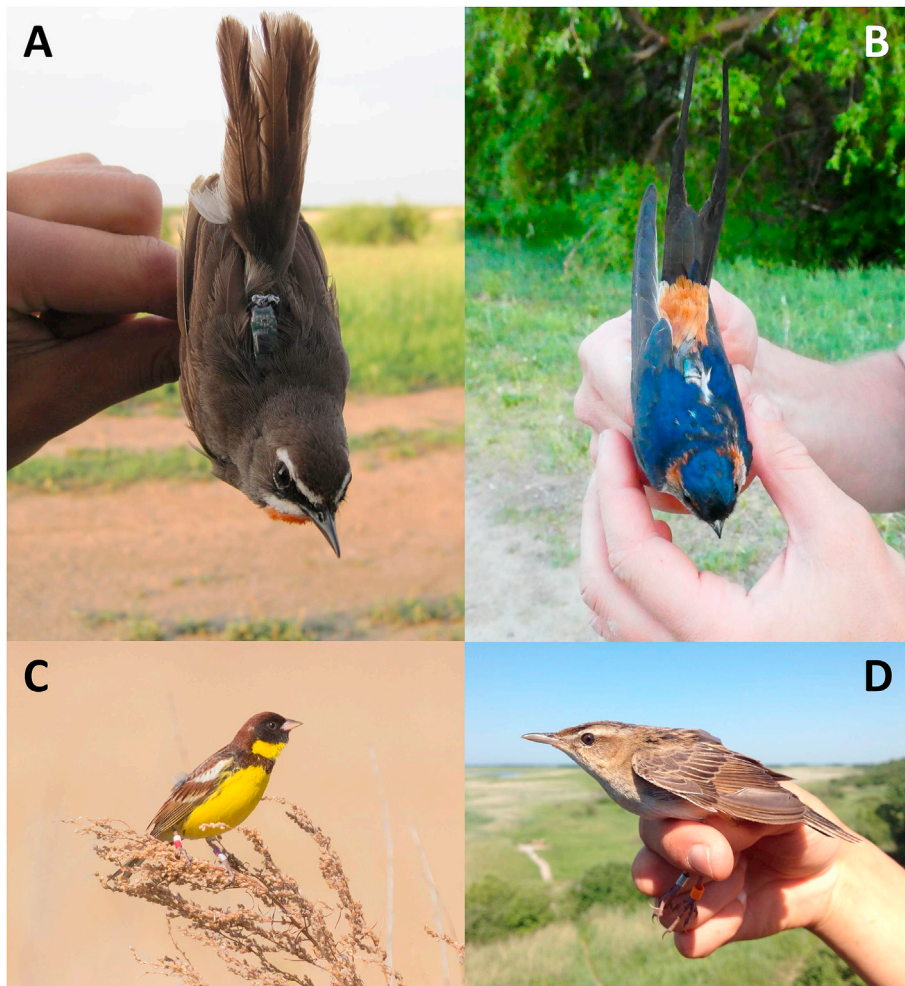
Fig. 2. Light-level geolocators mounted with leg-loop harnesses on the back of A) Siberian Rubythroat, B) Red-rumped Swallow, C) Yellow-breasted Bunting and D) Pallas's Grasshopper Warbler. Note that the devices are well visible from above (A—B) but are hardly visible in more natural postures (C—D). Color-ring combinations were used to identify individual birds in the field (C—D). Photographs by R. J. Heim, L. Fuhse, A. Heim and W. Heim (from A to D). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

in R package rgeos (Bivand et al., 2016). We give both the percentage of the predicted areas covered by the EOO maps, and the percentage of the EOO map extent covered by the predictions.

To externally validate our seasonal range predictions, we calculated the proportion of geolocator positions and ring recoveries that fell onto the area predicted as suitable in the given season (for season definitions see above). For geolocator positions, we used mean coordinates (Suppl. 3). To incorporate uncertainty associated with the estimated mean coordinate, we identified the area covered by the range of the latitude and longitude standard deviation of the mean coordinate (resulting in polygons of varying size). We then evaluated whether these polygons showed any overlap with the area predicted as suitable by the MaxEnt model.

In a second step, we modeled the probability of our validation locations to fall within the predicted ranges using generalized linear mixed-effect models (GLMMs) in R package lme4 (Bates et al., 2014). We used models with a binomial error distribution and logit link (i.e. binary logistic regression). Locations that fell within the predicted range were considered successes (1), locations that were out of range were considered failures (0). Data type (geolocator or ringing data), season (winter, spring and autumn) were fitted as fixed independent effects. The extent of the seasonal predicted range was fitted as covariate. Species identity was included as random effect. We built two sets of candidate models, one defining the matching/non-matching of the tracking locations with the predicted distribution by the mean coordinates of the geolocation fixes, the other using a polygon of the mean coordinate plus the area added by considering the standard deviation. Model assumptions were graphically tested using residual plots in the DHARMa package (Hartig, 2019). Goodness of fit was examined with the conditional and marginal R^2 (Nakagawa and Schielzeth, 2013).

2.4. Connectivity analyses

We analyzed migratory connectivity by correlating the longitude of the location during breeding season with the longitude during the non-breeding season for ring recoveries and geolocation positions (Trierweiler et al., 2014) using a Pearson's product moment correlation coefficient. A significant correlation would indicate high migratory connectivity, i.e. the use of population-specific routes (Finch et al., 2017). If more than one site was available for one individual, we chose the final winter site with the longest duration of stay. To estimate the strength of migratory connectivity we conducted a Mantel test (with 9999 random permutations) using the R package ade4 (Dray and Dufour, 2007; Ambrosini et al., 2009).

3. Results

3.1. Predicted distributions

The predicted non-breeding ranges covered almost exclusively South and South-East Asia in all species, only very few suitable areas were predicted in Russia, Kazakhstan, Mongolia and NW China (Fig. 3). A migration corridor through Central Asia, appearing as a high predicted suitability in spring and/or autumn west of the Himalayas, was only found for Barn Swallow and Red-rumped Swallow (Fig. 3). The predictive performance of the models varied across seasons and species, but was acceptable in all cases (AUC > 0.75, Table 2). Models with more presence points exhibited the best fit (Table 2). The predicted ranges were smallest when using the threshold that maximized kappa (Suppl. 1). This threshold was used for all range maps and further calculations. The size of the predicted ranges varied considerably (range: 22–900 grid cells) and seasonal differences were also species-specific (Fig. 3). Smallest ranges were predicted for the Chestnut-cheeked Starling during autumn and winter and for the Yellow-breasted Bunting during autumn, largest ranges were predicted for Barn Swallow and Red-rumped Swallow in all seasons.

3.2. Geolocator tracks

We gathered 171, 43 and 28 geolocation positions of 8 species for autumn, winter and spring, respectively (Table 1, Suppl. 3).

All individuals of all species tagged in the Russian Far East migrated south-westward in autumn, stopped over in China and wintered in South-East Asia (Fig. 3). No movements were detectable during winter, except for one Yellow-breasted Bunting which moved in February from southern Myanmar to the north of the country. All winter locations were located on the Indochinese peninsula and adjacent China (Yunnan province), except for the Yellow-breasted Buntings, which wintered more to the west in Myanmar or northeast India. Spring migration data were only available for three species: one single Pallas's Grasshopper Warbler and one Black-naped Oriole used almost identical stopover areas for their return migration, whereas all Siberian Rubythroats moved slightly more to the east, with the stopover sites situated in southern China and not in northern China as during autumn migration.

The standard deviation of positions was highest for latitude during autumn (Suppl. 3), as most species migrate around the autumnal equinox.

3.3. Ring recoveries

Long-distance ring recoveries were available for six of the included species (Table 1). Siberian Rubythroats and Barn Swallows ringed during the breeding season or on migration in Japan and easternmost Russia (Sakhalin, Kamchatka) were mainly recovered in winter in Taiwan and the Philippines, and vice versa (Fig. 3). A Yellow-breasted Bunting ringed on the breeding grounds in Kamchatka was recovered during autumn migration near Beijing in mainland China, and one Stejneger's Stonechat migrated from southern Japan to South Korea in autumn. Birds ringed in the Russian Far East (mainland) were exclusively recovered on the South-East Asian mainland, and vice versa. For Barn Swallow, Red-rumped Swallow and Chestnut-cheeked Starling geolocation and ringing recovery data were available from the same areas of origin, and the main direction of migratory movements was similar in all cases.

3.4. Validation

The predicted ranges were generally smaller than the distribution ranges given by BirdLife, and on average covered only 40% (±28%, range: 5–80%) of the BirdLife winter distributions (Table 4). On average, only 61% (±29%, range: 7–90%) of the area predicted as suitable ranges were within the BirdLife ranges. Very low overlap (<10%) was found for the Chestnut-cheeked Starling, whereas good concordance (>70%) was evident for Siberian Rubythroat and Red-rumped Swallow.

The proportion of the mean geolocation positions that fell onto the predicted range was rather low in all seasons for all species combined (23, 35 and 18% for autumn, winter and spring, respectively, Table 3). We found species-specific differences – between 0 and 100% of the exact positions (without standard deviation of the coordinates) were within the predicted species' ranges. When including the standard deviation of the geolocation positions, most of the positions were within the predicted range (51, 67 and 78% for autumn, winter and spring, respectively, Table 3). SDM prediction showed highest overlap
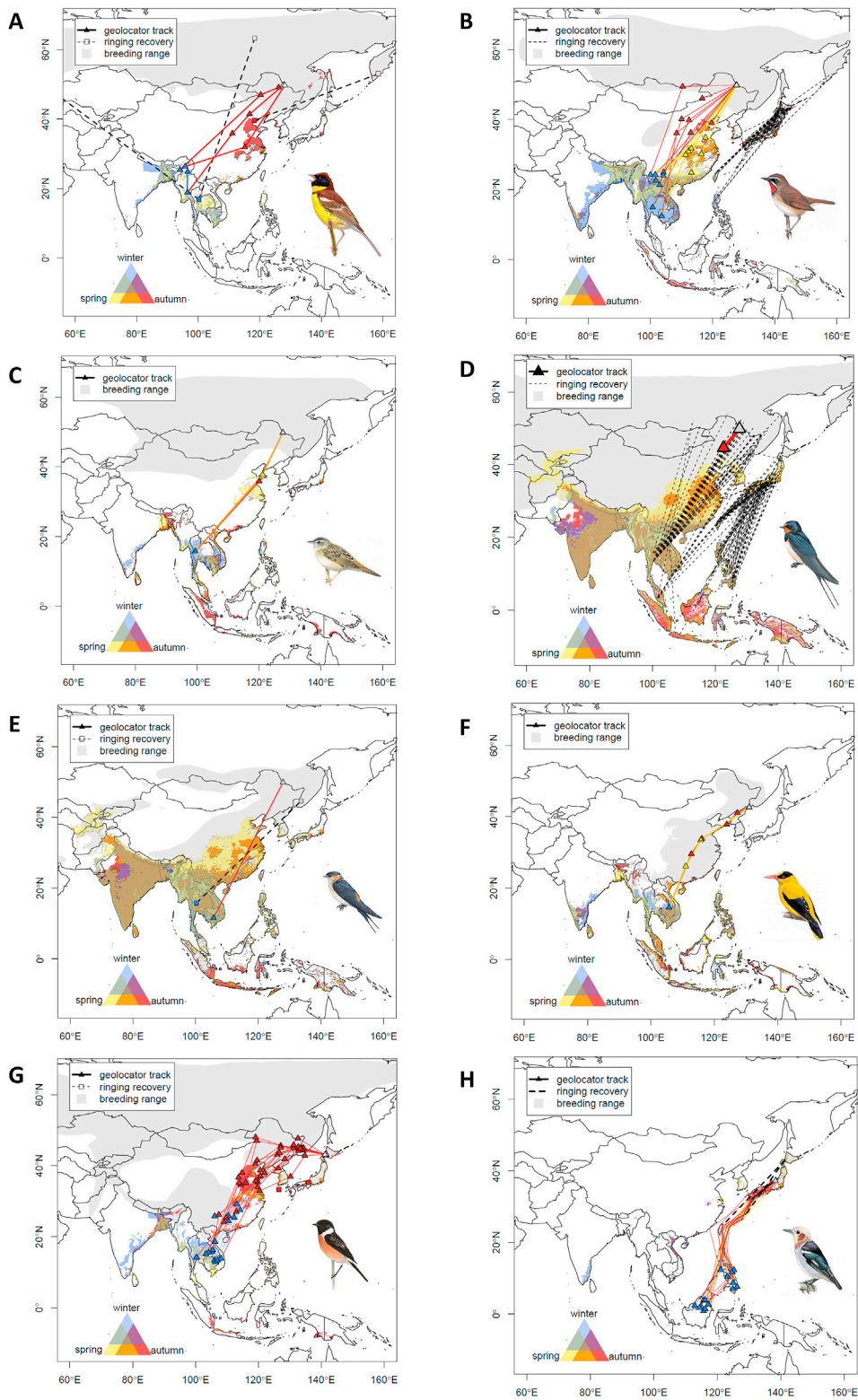
Fig. 3. Predicted ranges in autumn, winter and spring, geolocator positions and ring recoveries for A) Yellow-breasted Bunting, B) Siberian Rubythroat, C) Pallas's Grasshopper Warbler, D) Barn Swallow, E) Red-rumped Swallow, F) Black-naped Oriole, G) Stejneger's Stonechat and H) Chestnut-cheeked Starling. The species' breeding ranges (following BirdLife, 2019) are shaded grey. Note that only winter positions are depicted for Chestnut-cheeked Starling. Bird pictograms reproduced with permission of Lynx Edicions. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Predictive performance of the MaxEnt species distribution models. Given is the number of eBird presence points used for each of the seasonal models (n) and the respective AUC and kappa statistics.

Species	Autumn			Winter			Spring		
	n	AUC	kappa	n	AUC	kappa	n	AUC	kappa
Yellow-breasted Bunting	101	0.82	0.29	113	0.93	0.31	93	0.91	0.30
Siberian Rubythroat	334	0.89	0.39	467	0.95	0.55	430	0.86	0.40
Pallas's Grasshopper Warbler	129	0.90	0.22	173	0.97	0.56	183	0.89	0.35
Barn Swallow	2619	0.87	0.56	3328	0.91	0.69	3475	0.82	0.51
Red-rumped Swallow	1095	0.88	0.50	1555	0.93	0.68	1442	0.85	0.46
Black-naped Oriole	506	0.91	0.48	562	0.96	0.66	621	0.91	0.51
Stejneger's Stonechat	168	0.91	0.35	223	0.95	0.50	219	0.90	0.40
Chestnut-cheeked Starling	87	0.96	0.53	41	0.95	0.30	127	0.96	0.50

Table 3
Overlap of the seasonal predictions with the coordinates of mean geolocation positions ("geolocation points"), polygons based on the standard deviation around mean geolocation positions ("geolocation points + SD") and the position of ringing recoveries. The first column for each species and season indicates how many of the available points were within the predicted range, the second column the percentage (in %).

Species	Autumn		Winter		Spring	
Geolocation points	n	%	n	%	n	%
Yellow-breasted Bunting	0/5	0.0	1/4	25.0	0/0	NA
Siberian Rubythroat	0/7	0.0	5/8	62.5	4/6	66.7
Pallas's Grasshopper Warbler	0/1	0.0	1/1	100.0	0/1	0.0
Barn Swallow	0/1	0.0	0/0	NA	0/0	NA
Red-rumped Swallow	0/0	NA	1/1	100.0	0/0	NA
Black-naped Oriole	0/4	0.0	1/1	100.0	0/2	0.0
Stejneger's Stonechat	6/43	14.0	6/12	50.0	0/0	NA
Chestnut-cheeked Starling	34/110	30.9	0/16	0.0	1/19	5.3
Total	40/171	23.4	15/43	34.9	5/28	17.9
Geolocation points + SD	*n*	*%*	*n*	*%*	*n*	*%*
Yellow-breasted Bunting	3/5	60.0	4/4	100.0	0/0	NA
Siberian Rubythroat	5/7	71.4	8/8	100.0	6/6	100.0
Pallas's Grasshopper Warbler	0/1	0.0	1/1	100.0	1/1	100.0
Barn Swallow	0/1	0.0	0/0	NA	0/0	NA
Red-rumped Swallow	0/0	NA	1/1	100.0	0/0	NA
Black-naped Oriole	0/4	0.0	1/1	100.0	0/2	0.0
Stejneger's Stonechat	23/43	53.5	9/12	75.0	NA	NA
Chestnut-cheeked Starling	NA	NA	5/16	31.3	NA	NA
Total	31/61	50.8	29/43	67.4	7/9	77.8
Ringing recoveries	*n*	*%*	*n*	*%*	*n*	*%*
Yellow-breasted Bunting	1/1	100.0	2/2	100.0	0/0	NA
Siberian Rubythroat	77/236	32.6	4/25	16.0	0/9	0.0
Pallas's Grasshopper Warbler	0/0	NA	0/0	NA	0/0	NA
Barn Swallow	40/77	51.9	39/114	34.2	32/80	40.0
Red-rumped Swallow	0/0	NA	1/1	100.0	0/0	NA
Black-naped Oriole	0/0	NA	0/0	NA	0/0	NA
Stejneger's Stonechat	1/1	100.0	0/1	0.0	0/2	0.0
Chestnut-cheeked Starling	0/4	0.0	0/0	NA	1/6	16.7
Total	119/319	37.3	46/143	32.2	33/97	34.0

Table 4
Validation of the seasonal predictions ("SDM") with existing extent-of-occurrence maps ("EOO", BirdLife International, 2019). Note that we had to combine the predictions for spring and autumn ("Migration") to analyse overlap with the BirdLife EOO maps. The spatial overlap is given in %.

Species	Migration		Winter	
	SDM covered by EOO map	EOO covered by SDM	SDM covered by EOO map	EOO covered by SDM
Yellow-breasted Bunting	NA	NA	55.7	33.5
Siberian Rubythroat	29.2	9.2	70.9	76.2
Pallas's Grasshopper W.	24.7	11.6	29.6	16.0
Barn Swallow	NA	NA	90.2	58.1
Red-rumped Swallow	NA	NA	85.3	80.0
Black-naped Oriole	NA	NA	73.7	34.3
Stejneger's Stonechat	NA	NA	75.1	19.3
Chestnut-cheeked Starling	NA	NA	6.9	5.0
Total (mean)	**26.9**	**10.4**	**60.9**	**40.3**

with the geolocator positions in winter, and least overlap in autumn. Highest overlap was found for the Siberian Rubythroat, whereas most locations were outside of the predicted range for the Chestnut-cheeked Starling.

Only around a third of the ringing and recovery sites were situated within the corresponding seasonal predicted range (37, 32 and 34% for autumn, winter and spring, respectively, Table 3). Species-specific differences were high, ranging from 0 to 100%, but seasonal differences were low. Detailed results of the comparisons can be found in Table 3 and Supplement 5.

Our models revealed that the probability of a point falling onto the predicted range was dependent on the seasonal range size (Table 5), while the random factor *species* explained little or no variance. Seasonal effects on the probability were only found when the mean coordinates of geolocation positions were considered, while the data type had only a significant effect when the standard deviation around geolocation points was included (Table 5). However, both models explained only very little of the overall variance ($R^2 < 0.05$, Table 5).

3.5. Migratory connectivity

We had sufficient data to analyse migratory connectivity in two species. The longitudes of breeding and non-breeding sites were positively correlated in both Siberian Rubythroat (Pearson's, r = 0.91, p < 0.001, n = 14 individuals) and Barn Swallow (r = 0.53, p < 0.001, n = 110). We found evidence of strong migratory connectivity in the Siberian Rubythroat and to a lesser degree in the Barn Swallow (Mantel correlation coefficients of 0.80 (p < 0.001) and 0.25 (p < 0.001), respectively).

4. Discussion

4.1. Predicted seasonal distributions

We predicted the spatio-temporal occurrence of a set of Eastern Palearctic Passerines during autumn, winter and spring based on unstructured citizen-science data. The predicted distributions varied significantly in their extent. For some species (e.g. Barn and Red-rumped Swallows), huge parts of the study region were predicted suitable, with high overlap between seasons. This pattern is most likely caused by the existence of sedentary populations in the south of the range (BirdLife International, 2019), which may bias seasonal predictions (Supp et al., 2015). Strong seasonal differences in occurrence can be more easily detected in true long-distance migrants (Supp et al., 2015), such as Yellow-breasted Bunting, Pallas's Grass-hopper Warbler and Stejneger's Stonechat in our study. In some of the species, migration of the northernmost breeding populations might take place outside of the migration periods that we used for our models (e.g. June and August), and therefore observations of migrating individuals might have been disregarded or mixed up with breeding season observations from southern populations (Supp et al., 2015). This might be the case for the Black-naped Oriole, for which only areas in South-East Asia were predicted suitable, but no stopover areas further north during spring or autumn migration. Our geo-location data revealed pronounced differences in the timing of migration between and within species. For example, some Siberian Rubythroats have already arrived in October at their wintering sites, but one only in December. The precision of the predictions could have been increased by building monthly or full-year models instead of seasonal models (Williams et al., 2017). However, fitting a full-year model would have required many more data points for all months, which were not available from the eBird dataset for most of the studied species. A limited number of presence points will often result in poorer model outcomes, and single erroneous observations can have a stronger impact on the predicted ranges when low numbers of presence records are available for modeling (Wisz et al., 2008). Observations of birds outside their usual geographic range, known as vagrants, tend to get more comprehensively reported by birdwatchers (Callaghan et al., 2018). This might explain the model result for the Chestnut-cheeked Starling, where single observations of vagrants from the South-East Asian mainland outside of the known wintering range (Robson, 2008) affected our model strongly, leading to a limited overlap of the BirdLife range with our predictions. Furthermore, caused by the rather coarse resolution of our background layers, many coastal sites might have been classified as water (and therefore as unsuitable for the species) by our SDMs. For all other species, the larger part of the predicted distributions overlapped with the BirdLife EOO maps, suggesting an overall good fit. The BirdLife ranges are coarser, and is expected to include unsuitable habitats within the area of occurrence, whereas our modeled predictions might depict the actual distribution more precisely (Graham and Hijmans, 2006; Hurlbert and Jetz, 2007; Cantú-Salazar and Gaston, 2013).

Our SDMs predicted some regions to be suitable for most of the studied songbirds, and those might therefore constitute important areas for the conservation of migratory land birds in East Asia (Fig. 3), although the set of species included here is

Table 5
Effects of data type, season and range size on the probability of our validation locations to fall within the predicted ranges using GLMMs. Significant effects are highlighted in bold.

Model	Data type	Season	Range size	R^2
1 (point data)	$Chi^2 = 0.456$ p = 0.500	$Chi^2 = 7.700$ p = **0.021**	$Chi^2 = 10.497$ p = **0.001**	$R_{cond} = 0.03$ $R_{marg} = 0.03$
2 (polygons)	$Chi^2 = 26.767$ p < **0.001**	$Chi^2 = 4.093$ p = 0.129	$Chi^2 = 4.700$ p = **0.030**	$R_{cond} = 0.05$ $R_{marg} = 0.05$

small and not necessarily representative for all East Asian songbirds. During winter, the south-eastern end of mainland South-East Asia and the Ganges-Brahmaputra floodplain in Bangladesh were predicted as suitable for many of the species. Hebei province, surrounding the Chinese capital Beijing, was predicted as the main autumn stopover area for Siberian Rubythroat, Stejneger's Stonechat, Barn Swallow and the critically endangered Yellow-breasted Bunting. The lower Yangtze River valley was predicted to be an important stopover area during spring for Pallas's Grasshopper Warbler, and during both spring and autumn seasons for Yellow-breasted Bunting, Siberian Rubythroat, Barn and Red-rumped Swallow as well as Stejneger's Stonechat. Many of the key stopover areas in eastern China are currently not protected (Lei et al., 2019). However, the lack of citizen-science records from western China, where birds might utilize different stopover habitats (caused by climate-driven differences in habitat availability), and the overrepresentation of observations from the densely populated Shanghai and Beijing areas might have biased our predictions (Guillera-Arroita, 2017), despite our correction for sampling bias.

Parts of the predicted areas of occurrence well beyond the known range limits of the species' might be suitable, but might not have been colonized so far or are not reachable during migration by the studied species (Engler et al., 2014). This is most likely true for predicted areas outside of the BirdLife range maps in Indonesia for Siberian Rubythroat and Pallas's Grasshopper Warbler and for areas in South-East India for Siberian Rubythroat, Pallas's Grasshopper Warbler, Stejneger's Stonechat and Chestnut-cheeked Starling (Fig. 3).

4.2. Validation of the predictions

The validation with spatially unbiased geolocation positions, ring recoveries and with the available BirdLife range maps suggested that our predictions were more accurate for winter compared to spring or autumn migration. This might be explained by the fact that our study species are much less mobile during winter compared to the migration seasons − only one of the geolocator-tagged birds moved over a longer distance in winter. During migration, birds temporarily use a variety of sites and habitats, which could lead to a decreased precision in model predictions (Williams et al., 2017). The stronger overlap of the model predictions with tracking data during winter might also be caused by inherent seasonal differences in the precision of geolocation data. First, latitude can hardly be estimated during equinox periods (Fudickar et al., 2012), a time coinciding with autumn and spring migration for most species. Second, location errors are decreasing with the length of the stationary period, so that short stopovers during migration can less precisely be determined than long stays on the wintering grounds (Rakhimberdiev et al., 2016).

On the contrary, based on our GLMMs, season had no or only a weak effect on the probability that our validation points fell into the predicted ranges. Instead, the range extent was the best predictor. This is most likely linked to seasonal differences in the size of the predicted ranges: in our study, smaller ranges were predicted for autumn migration (Suppl. 4). Narrower distributional ranges or ecological niches during periods of migration are known from many species (e.g. Suárez-Seoane, de la Morena, Prieto, Osborne and de Juana, 2008).

We also found a better overlap of the predicted ranges with point locations of ring recoveries than with the mean geolocation points. While geolocation data are spatially unbiased, the probability of recovery of a ringed bird is linked to human density or targeted ringing activities (Thorup and Conn, 2009). The bird ringing data used in our study mainly reflects the high activity of Japanese ringing groups, whereas only few recoveries were available for birds migrating over the Asian mainland. The lack of ringing recoveries from e.g. Indonesia is most likely related to limited awareness about bird ringing studies in these regions (McClure, 1974). The same spatial bias might be inherent in the eBird data used for our predictions: most major cities are located along the coasts of East Asia and this is where most birdwatchers are concentrated. This likely led to the perception, that songbirds mainly migrate along coastal flyways (see map in Yong et al., 2015). In particular, geolocator tracking revealed that most of our study species likely migrated over the Asian mainland, with no evidence for migration along the coastlines or long-distance sea crossings (with the exception of the Chestnut-cheeked Starling). This pattern has rarely been demonstrated for Asian songbirds before. There are only few studies that provide data on songbird migration over the East Asian mainland, for example from the Fenghuang mountains in southern China (Han et al., 2007), and from a bird ringing site in south-east Mongolia (Sukhbaatar, 2019). The avoidance of sea crossings and migration over mainland is likely a typical, but so far poorly evidenced, characteristic of most East Asian land bird migrants.

All birds tracked from mainland East Russia wintered in South-East Asia, but for some of the species, a much larger wintering range was predicted by our models, extending westwards into India. Birds wintering in these areas might originate from the western part of their breeding distribution, from which we lack data. Barn Swallows and Red-rumped Swallows reach India through Central Asia (Gavrilov et al., 2002), but due to the lack of observations from this area it seems unlikely that other species such as the Siberian Rubythroat or Yellow-breasted Bunting would use the Central Asian route across high mountain ranges as well.

4.3. Migratory connectivity

The combination of different data types allowed us to quantify migratory connectivity in selected East Asian songbirds for the very first time. The two analyzed species, Barn Swallow and Siberian Rubythroat, seem to use multiple, population-specific routes. This is unexpected, as high migratory connectivity was found to be uncommon among long-distance migrants from Neotropic and Afro-Palearctic flyways (Finch et al., 2017). Two main migration corridors were used in East Asia: Individuals belonging to populations breeding in mainland East Russia migrate through mainland China and spend the winter

in South-East Asia ("mainland corridor"), while birds ringed during the breeding season or on migration in Japan and easternmost Russia (Sakhalin, Kamchatka) were mainly recovered in winter in Taiwan and the Philippines, and vice versa ("island corridor").

We found a higher degree of connectivity in the Siberian Rubythroat than in the Barn Swallow. This could be explained either by the lower sample size for the Siberian Rubythroat or by the availability of data from a wider range of different populations (no data were available for Barn Swallows from Kamchatka). Another issue could be the obvious differences in ringing effort, especially during the non-breeding season, which might have affected the results, and the fact that some records in our data set refer to individuals which were still on migration (Ambrosini et al., 2009).

Low migratory connectivity could be expected for species in which multiple populations use a common route (Finch et al., 2017). We found that Yellow-breasted Buntings from mainland East Russia use the same autumn stopover area in north-east China as an individual ringed in Kamchatka (Fig. 3). The wintering sites of the geolocator-tagged birds from East Russia are close to the recovery sites of ringed Yellow-breasted Buntings from the northernmost and westernmost ends of its breeding distribution. Therefore, it seems likely that all populations of the Yellow-breasted Bunting use the same migration corridor in East Asia. This could explain why unsustainable harvest in China has led to a disproportionally wide-ranging decline in this species (Kamp et al., 2015). Another taxon, which might share this migration pattern, is the Stejneger's Stonechat - birds from Hokkaido are known to jump to the East Asian mainland before starting to migrate southwards (Yamaura et al., 2017), most likely along the same route as their conspecifics from the mainland.

The remaining study species likely use only one migration route through East Asia, since they breed either only on the mainland (mainland corridor: Pallas's Grasshopper Warbler, Black-naped Oriole, Red-rumped Swallow) or only on the Japanese archipelago and adjacent Russian islands (island corridor: Chestnut-cheeked Starling).

4.4. Conclusions

The combination of SDMs, ringing and tracking data provided a valuable set of tools to understand the spatio-temporal distribution of birds in a data-poor region. We found that species occurrence during stationary periods in winter can be rather accurately predicted with unstructured citizen-science observation data, while predictions of occurrence during the migration periods were less precise. Ringing and tracking data on the other hand can provide valuable insights into migration routes and migratory connectivity, but sample sizes are often small, and the spatial resolution varies. We argue that all available data sources should be included when assessing seasonal distribution of migratory species.

Our results highlight several regions as potential hotspots for migratory land birds, but further studies using geolocators or transmitter tracking will be necessary to pin-point important stopover areas to inform the conservation of Eastern Palearctic Passerines.

Authors' contributions

W.H. and J.K. designed the study, with contributions by P.K. and K.T.; W.H. planned and undertook the fieldwork for the geolocation studies, with additional data from O.A.B. and I.M.T.; I.B., R.J.H., M.M.S., S.M.S., S.S., An.T., Al.T., K.T. and M.W. were involved in the fieldwork; Y.G., K.O. and I.P. provided the ringing recovery data, W.H. analyzed the data, under supervision of J.K., W.H. wrote the manuscript with contributions by all authors.

Data availability statement

All observation data are available from eBird (www.ebird.org). All location data (ringing recoveries and geolocation positions) are available in the electronic supplement of this article.

Declaration of competing interest

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

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Appendix A. Supplementary data

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