

## Tracking the Stejneger's stonechat *Saxicola stejnegeri* along the East Asian–Australian Flyway from Japan via China to southeast Asia

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The East Asian–Australian Flyway spans from north Asia to Australia and is the world's richest birds' flyway because it involves > 40% of global migratory bird species. However, information is lacking on individual migratory routes and non-breeding grounds for small land birds using this flyway. Here, we present the first migration tracks of the songbird Stejneger's stonechat *Saxicola stejnegeri* from this part of the world using light-level geolocators. This species depends on grasslands during the entire annual cycle and was captured and equipped with tracking devices in Hokkaido, northern Japan. All individuals traveled through southern Primorye or eastern Heilongjiang (Russia/China) before flying southward via central China toward their major non-breeding grounds in southeast Asia (China, Laos, Cambodia, Thailand, and Vietnam). Individual stonechats spent 42–70 d en route during their autumn migration. Both the major non-breeding grounds and the stopover sites are likely to pose challenges to the persistence of this species, because these habitats are currently degraded and will likely be lost in the near future due to intensified agriculture and the establishment of permanent croplands. Moreover, the areas used by Stejneger's stonechat during migration largely overlapped with illegal trapping areas in northeastern China.

Grasslands and species that depend on this early-successional habitat are declining worldwide (Askins 2001, Boakes et al. 2010). Although the breeding habitats of grassland species can be successfully restored by forestry harvest (Yamaura et al. 2012b, King and Schlossberg 2014), factors outside the breeding season may have significant effects on the dynamics of the species population (Vickery et al. 2014, Rushing et al. 2016). For instance, the global decline of the yellow-breasted bunting *Emberiza aureola* is most likely due to rampant illegal trapping at sites where the species rests and feeds during migration in China (Kamp et al. 2015). Furthermore, deforestation in southeast Asia has been suggested to be a cause for the decrease in Japanese long-distance migratory birds that depend on mature forests during the non-breeding period (Yamaura et al. 2009). Hence, expanding conservation efforts from breeding to non-breeding periods is prerequisite to successfully conserve migratory species (Marra et al. 2015).

The East Asian–Australian Flyway is the most species-rich flyway in the world, hosting > 40% of global migratory bird species (Yong et al. 2015). However, the migration routes and non-breeding grounds of these species are completely unknown, particularly those of the entire suite of small

migratory land birds (Yong et al. 2015, but see Koike et al. 2016). Areas with high hunting pressure (Kamp et al. 2015) and ongoing significant land-use changes (Bradshaw et al. 2009) may overlap with the distributions of these species and threaten their persistence. Therefore, more information is warranted on how these bird populations use this particular flyway.

As a model species, we used here the Stejneger's stonechat *Saxicola stejnegeri*, breeding in grasslands from eastern Russia through the southern tip of Kamchatka to northeastern China, Korea, and Japan (Urquhart 2002). Its major non-breeding grounds are assumed to range from southeastern China through mainland southeast Asia to the Middle East (Urquhart 2002). In Japan, this species was generally suggested to be declining in the southern region (Endo and Hirano 1983), but they may be stable at the national scale (Yamaura et al. 2009) and are currently common in Hokkaido, northern Japan. Grassland species including stonechat are seen in early-successional stages of forestry plantations and are likely to be conserved by the forestry activities (Yamaura et al. 2012a, Toyoshima et al. 2013). Here, we identified the migratory routes, migration stopover sites, and major non-breeding grounds of 12 Stejneger's stonechats breeding

in Hokkaido. Their stopover sites and major non-breeding grounds would be essential information to the effective conservation of migratory songbirds in the Far East. This would allow us to attribute population dynamics to their migration routes, timing, and major non-breeding grounds.

## Material and methods

### Field survey

The study area was a 25-km long bank along the Ishikari and Tobetsu Rivers from Shinshinotsu village to Tobetsu town (43.12N, 141.57E; Japan). We captured 51 stonechats (46 males and 5 females) using spring and perch traps (TSB25 and PT30; Moudry, Říčany, Czech Republic) during 8–18 May, 2014. The sex was determined based on sexually dimorphic plumage coloration. Age was not ascertained; all were at least in their second calendar year. To estimate the migration routes, we used 0.50-g light-level geolocators (Intigeo P50B9-7-concord with 7-mm stalk; Migrate Technology, Cambridge, UK). The expected life of the battery was at least 9 months. Spring migration was not tracked since the batteries died in mid-February [22 February  $\pm$  22 d; mean  $\pm$  standard deviation (SD),  $n = 12$ ]. The devices were mounted on the birds using a leg-loop harness system (Rappole and Tipton 1991) with an elastic silicon rubber mixture (O-ring with 25.5-mm interdiameter and total weight of 0.65 g). The body weight of the tagged individuals was  $\geq 17.0$  g ( $n = 5$ ) for females and 14.9 g (SD = 0.65 g; range, 13.0–16.0 g,  $n = 46$ ) for males. Thus, the relative load of the geocator was clearly below the accepted 5% of the bird's body mass (Caccamise and Hedin 1985). The deployment procedure lasted  $< 15$  min. Geolocators and color rings were detached when the birds were recaptured in 2015.

### Data analysis

#### Estimating locations

Light-level geolocation data were analyzed in the R package 'GeoLight' ver. 2.01 (Lisovski and Hahn 2012) and 'SGAT' ver. 0.1-1 (Wotherspoon et al. 2015). The daily sunrise and sunset times were determined as the specific date and time when light intensity exceeded (sunrise) or fell below (sunset) a priori-defined light intensity threshold of 1.35 lux. To calibrate the individual geocator data series, we used the light intensities recorded after deployment and before 15 August when breeding stonechats are known to be stationary around their breeding sites (Fujimaki et al. 1994). Individual calibration periods ranged from 88 to 98 d. Using the individual calibration data, a log-normal density distribution was fitted to the zenith angle difference (twilight error) of each defined twilight time and the earliest/latest recorded sunrise/sunset time, e.g. the sunrise/sunset that has most likely been recorded without any interference of shading. Initial locations were estimated using the (modal) zenith angle at the maximum density of the defined log-normal distribution. This method corresponds to the often-called on-bird calibration (Lisovski et al. 2012). To correct for unrealistic positions caused by high-intensity shading events during twilight, we used a Bayesian framework within the 'SGAT' package that

incorporates the observed sunrise and sunset times and prior knowledge of the species' behavior to estimate location. Markov Chain Monte Carlo (MCMC) simulations permitted a spatial probability mask, a prior definition of the error distribution of twilight events (twilight model), and plausible flight speed values (behavioral model), which collectively allowed us to refine the tracks derived from the sunrise and sunset times (Sumner et al. 2009).

The spatial probability mask is based on the premise that stonechats are terrestrial birds and thus have a higher probability of occurring in a terrestrial habitat. However, the stonechats in our study population had to cross water during their migration; therefore, we allowed the location estimates to fall into the sea. These locations were associated with a lower probability that decreased with the distance to the coastline ( $d$ ) as follows:

$$P = 1 + 5 \times \exp(-(d/200\,000)^1).$$

Hence, locations  $> 200$  km from the nearest coastline had a four times lower probability ( $P$ ) of occurrence than locations on land. We used a freely available 1:75 000 spatial shoreline dataset (<http://shoreline.noaa.gov>). To parameterize the twilight model, we used the parameters (log-mean and log-standard deviation) of the individually defined log-normal density distribution. We assumed that migratory songbirds have a bimodal speed distribution for the behavioral model: stationary behavior during most of the year and traveling airspeeds of about  $8 \text{ m s}^{-1}$  (Bruderer and Boltd 2001) during active migration (gamma distribution for movement: shape = 9, scale = 0.25; periods of residency: shape = 1, scale = 0.2). We used the 'changeLight' function (from the R Package 'GeoLight') to define which of the two speed distributions should be used for a given location estimate. This analysis was based on a 'changepoint' analysis that quantified the probability of each sunrise and sunset to be different than the surrounding sunrise and sunset times and hence provides evidence for shifts/movement in the underlying locations. The sunrise and sunset times associated with a 'changepoint' probability greater than the 0.75 quantile of all probabilities were used to define the stationary periods separated by periods of movement. The 'changepoint' probability of 0.75 is a conservative estimate (Lisovski and Hahn 2012). We considered that times  $> 1.5$  d were changes in both location and location estimates that fell between stationary periods. We associated these changes with the active movement speed distribution. We drew 1500 samples to describe the posterior distribution for each individual using the above-described parameters. Based on the latter, we obtained the median track for each bird (e.g. median of the location estimates for each twilight time). These processes do not allow for convergence of the MCMC chains, as that would require a burn-in and tuning process before drawing a large sample. However, the large observed twilight error distribution during the calibration period resulted in unrealistic tracks (as far north as the arctic coastline) during the equinox, indicating that the observed twilight error did not reflect the twilight error during the movement and stopover periods. Therefore, we only used the method to slightly refine and, most importantly, to correct highly unrealistic location estimates, i.e. longer periods at sea or location estimates too far away from each other to be actually reachable by the birds.

### Defining the migration schedule

We used the 'changeLight' function to distinguish between periods of residency and movement based on the most likely track. First, we calculated the sunrise and sunset times for each estimated location along the track. Then, the periods of residency were defined as periods between sunrise and sunset that were associated with a probability of change  $> 0.8$  quantile of all probabilities and that were  $> 2$  d. This was rather conservative and often resulted in several spatially overlapping periods of residency. We then used the 'mergeSite' function from the R package 'GeoLight' to combine stationary periods, i.e. consecutive sites with median positions closer than 350 km. Light-level data and R codes are available at: [https://github.com/slivoski/Stonechat\\_Migration](https://github.com/slivoski/Stonechat_Migration).

## Results

Of the tagged males, 14 returned to the study area in 2015, i.e. a return rate of 30% (14/46). This was not significantly different from the return rate of a farmland study in eastern Hokkaido during 1977–1986 (Fujimaki et al. 1994), where 13 from 25 marked males returned to the breeding ground in the subsequent year ( $\chi^2 = 2.3$ ,  $DF = 1$ ,  $p = 0.13$ ). Two of our males had lost their geolocators before recapture. We successfully retrieved data from all 12 geolocators. Body mass did not differ significantly between the years (two-sample paired Wilcoxon signed-rank test:  $V = 62$ ,  $p = 0.08$ ,  $n = 12$ ) but was slightly lower by 2% in the year after deployment (Supplementary material Appendix 1). None of the five tagged females was observed in our study area in 2016. This was not significantly different from the return rate of the former study (7/36; Fujimaki et al. 1994):  $\chi^2 = 0.2$ ,  $DF = 1$ ,  $p = 0.65$ .

The mean ( $\pm$  SD) onset of autumn migration was 8 October, 2014 ( $\pm 7.7$  d). All individuals reached southeast Asia via the southern Primorye in the south Russian Far East or eastern Heilongjiang (Fig. 1a). Individuals used  $3.6 \pm 0.7$  stopover sites, and they stayed at each site for  $13 \pm 2.3$  d (see Supplementary material Appendix 1–2 for more details of individual routes, phenologies, and uncertainties in the stopover sites). Southern Primorye/eastern Heilongjiang, the North China Plain, and southern China were identified as mutual staging areas (Fig. 1, 2). The major non-breeding grounds were in southern China and mainland southeast Asia (Fig. 1, 2). The birds reached these areas on 2 December, 2014 ( $\pm 12$  d). Individuals spent  $55 \pm 9.2$  d migrating from Hokkaido to the non-breeding grounds. Only 17% ( $8.9 \pm 1.8$  d) of the time was spent actively migrating (Fig. 1b). Departure date of breeding grounds was positively correlated with the arrival date to the main non-breeding grounds (linear regression model:  $F_{1,10} = 7.6$ ,  $R^2 = 0.43$ , slope ( $\pm$  SE) =  $1.04 \pm 0.38$ ,  $p = 0.02$ ; Fig. 1c).

## Discussion

### Migratory route and schedule

Most stonechats departed from Hokkaido during early October and migrated to the continent and stopped over in

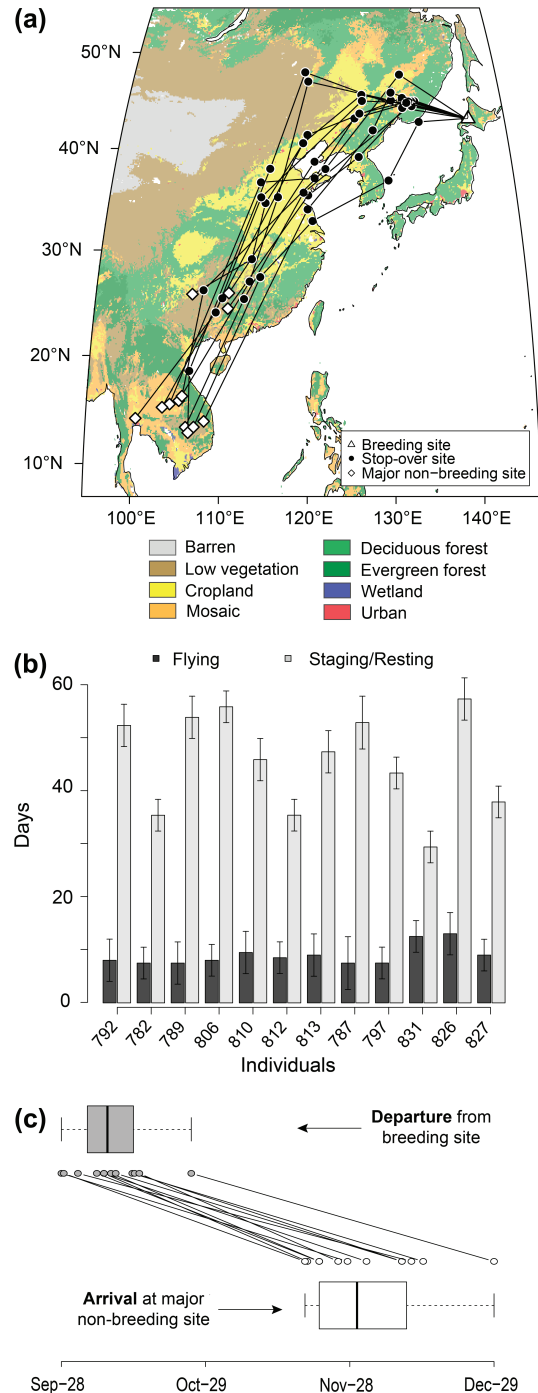


Figure 1. Migratory routes and schedules of 12 stonechats tagged on their breeding grounds in Hokkaido, northern Japan. (a) Simplified migration routes based on median posterior locations of the MCMC simulation during stationary periods (e.g. stopover sites and non-breeding sites). See Supplementary material Appendix 1 for individual tracks with uncertainty estimates. The underlying map represents land-use categories based on Broxton et al. (2014); see Supplementary material Appendix 2 for more details. (b) The amount of time each individual spent flying and resting/refueling during migration was calculated based on median posterior locations and the 'changeLight' analysis. Error bars represent the cumulative expected uncertainty of 0.5 d for each transition time between a stationary and a movement period. (c) Individual (open circles) departure dates from the breeding sites in Hokkaido and arrival dates at the major non-breeding sites.

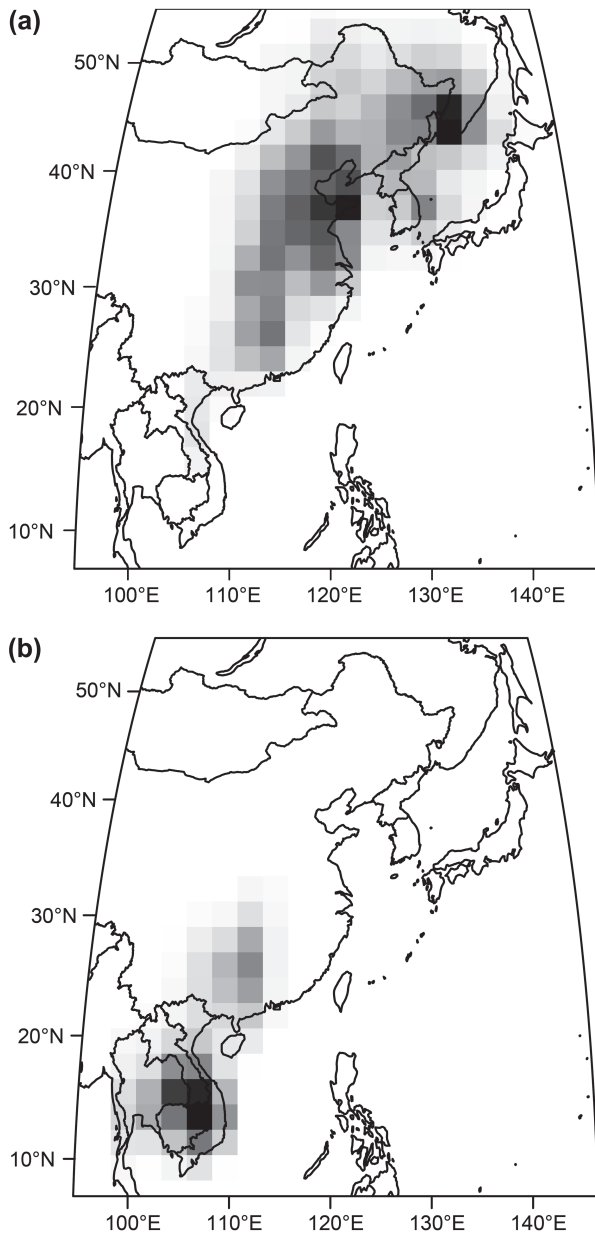


Figure 2. Relative time spent by all tracked individuals. Periods (a) on stopover sites and (b) on their non-breeding sites. The probability distribution is based on all MCMC chains (e.g. 1500 location estimates for each twilight). Grid size is  $250 \times 250$  km using a 'Mollweide' equal area map projection.

the southern Primorye or eastern Heilongjiang areas (Fig. 1, 2). The first snowfall can occur in lowland Hokkaido within the month of October (Sapporo Meteorological Observatory: <[www.jma-net.go.jp/sapporo/index.html](http://www.jma-net.go.jp/sapporo/index.html)>), and most plants in grasslands wither and associated arthropods disappear in October (Yamaura et al. unpubl.). We suggest that stonechats left Hokkaido before their food resources diminished significantly. The first stopover region in the continent is characterized by croplands, extensive agriculture, and wetlands surrounding Khanka Lake (Supplementary material Appendix 2). It likely represents a generally important stopover site for migratory land birds along the East Asian–Australian Flyway.

The North China Plain was visited by almost all of our stonechats (Fig. 1, 2a), where large-scale illegal and massive trapping of migratory early-successional birds occurs (Kamp et al. 2015). Stonechats traveled through China during October–November, which is a major trapping season for songbirds there (Kamp et al. 2015). This trapping and subsequent consumption ( $> 1$  million individuals  $\text{yr}^{-1}$ ) is potentially responsible for the unprecedented speed and extent of the decline of yellow-breasted buntings in the Palearctic (Kamp et al. 2015). Other migratory early-successional species are also hunted there (Kamp et al. 2015), and this may also include stonechats from Japanese breeding populations (Fig. 1, 2). Despite laws enacted to stop this type of bird hunting in China, hunting pressure is unlikely to change in the near future (S. Chan pers. comm.). Conserving stopover sites in southern Primorye/eastern Heilongjiang and reducing hunting pressure in China would be core conservation issues for migratory birds in the Far East.

Stonechats directly migrated to the continent from Hokkaido, although the migratory land birds in southern Japan (Honshu island) travel southward through the islands (Koike et al. 2016). During the last glacial period, Hokkaido was covered by vast grasslands due to the severe climates and connected by the continent via Skhalin as a grassland corridor (Adams 2002). Several bird species may have colonized from the continent by this grassland corridor, and the direct migratory route to the continent we found may have been maintained as a legacy of the last glacial period. This hypothesis seems to explain why Hokkaido harbors diverse grassland bird species dominated by migrants, including stonechats, grassland warblers (*Locustella ochotensis*, *L. lanceolata*), and yellow-breasted bunting.

Individuals departing early from their breeding grounds also arrived early at their major non-breeding grounds (Fig. 1c). This consistency of departure and arrival timing is also observed in other long-distance migrants within and among seasons (Schmaljohann et al. 2016). Correlated seasonal arrival dates at migratory goals suggest the importance of an individual-specific, endogenously controlled migratory program (Conklin et al. 2010) and may diminish the significance of total duration of migration to explain the variation in arrival dates. Total duration of migration was dominated by the stopover duration, as stonechats spent  $> 80\%$  of their migration period (Fig. 1b). This strong bias toward stopover than migratory flights is in line with theoretical predictions (Hedenström and Ålerstam 1997) and other studies on free-flying birds (Schmaljohann et al. 2012).

### Mainland southeast Asia as a major non-breeding ground

Mainland southeast Asia was identified as the major non-breeding ground of stonechats. This area is largely covered by farmland in the lowland areas and by a more heterogeneous (cropland/natural vegetation mosaic) landscape in the other areas (Supplementary material Appendix 2). Farmland, including rice paddy, and grasslands maintained by swidden agriculture (sensu Fox et al. 2012) are reportedly important habitats for buntings and stonechats in southeast Asia (Urquhart 2002, Yong et al. 2015). A significant



number of species, including stonechats, are dependent on extensively managed farmland worldwide, particularly in Asia (Wright et al. 2012a). Although species have evolved without farmland for most of their histories (Phalan et al. 2012), extensive farmland may be the only remaining habitat for these open-land species in the absence of naturally maintained open-lands (Wright et al. 2012b). It has also been suggested that man-made landscapes have been maintained for at least several thousand years in southeast Asia (Hunt and Rabett 2014).

However, forests, extensive farmland, and grasslands are currently decreasing in mainland southeast Asia (Fox et al. 2012), and they are being replaced by rubber plantations and permanent croplands (Warren-Thomas et al. 2015). The abundance of open-land species, including stonechats, may be higher in rubber plantations than that in secondary forests (Li et al. 2013), and the establishment of both rubber and possibly coffee plantations may provide some additional suitable habitats for open-land species. On the other hand, agricultural intensification in southeast Asia is required to meet the growing local and global food demands (Mueller et al. 2012). This is a clear dilemma for stonechats and other species that depend on farmland because agricultural intensification has a significant negative impact on many species (Flohre et al. 2011). Reconciling the increase in agricultural productivity and conservation of organisms dependent on farmland (sustainable intensification: Garnett et al. 2013) in southeast Asia may have major roles for bird conservation in the Far East.

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Supplementary material (Appendix JAV-01054 at <[www.avianbiology.org/appendix/jav-01054](http://www.avianbiology.org/appendix/jav-01054)>). Appendix 1–2.