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

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Abstract (194/300 words)

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 days 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.

Keywords: East Asian–Australian Flyway; geocator; stonechat *Saxicola stejnegeri*

43

Introduction

44 Grasslands and species that depend on this early-successional habitat are declining
45 worldwide (Boakes et al. 2010, Askins 2001). Although the breeding habitats of
46 grassland species can be successfully restored by forestry harvest (Yamaura et al. 2012b,
47 King and Schlossberg 2014), factors outside the breeding season may have significant
48 effects on the dynamics of the species population (Vickery et al. 2014, Rushing et al.
49 2016). For instance, the global decline of the yellow-breasted bunting (*Emberiza*
50 *aureola*) is most likely due to rampant illegal trapping at sites where the species rests
51 and feeds during migration in China (Kamp et al. 2015). Furthermore, deforestation in
52 Southeast Asia has been suggested to be a cause for the decrease in Japanese
53 long-distance migratory birds that depend on mature forests during the non-breeding
54 period (Yamaura et al. 2009). Hence, expanding conservation efforts from breeding to
55 non-breeding periods is prerequisite to successfully conserve migratory species (Marra
56 et al. 2015).

57 The East Asian–Australian Flyway is the most species-rich flyway in the world,
58 hosting >40% of global migratory bird species (Yong et al. 2015). However, the
59 migration routes and non-breeding grounds of these species are completely unknown,
60 particularly those of the entire suite of small migratory land birds (Yong et al. 2015, but
61 see Koike et al. 2016). Areas with high hunting pressure (Kamp et al. 2015) and
62 ongoing significant land-use changes (Bradshaw et al. 2009) may overlap with the
63 distributions of these species and threaten their persistence. Therefore, more information
64 is warranted on how these bird populations use this particular flyway.

65 As a model species, we used here the Stejneger's stonechat (*Saxicola stejnegeri*),
66 breeding in grasslands from eastern Russia through the southern tip of Kamchatka to
67 northeastern China, Korea, and Japan (Urquhart 2002). Its major non-breeding grounds

68 are assumed to range from southeastern China through mainland Southeast Asia to the
69 Middle East (Urquhart 2002). In Japan, this species was generally suggested to be
70 declining in the southern region (Endo and Hirano 1983), but they may be stable at the
71 national scale (Yamaura et al. 2009) and are currently common in Hokkaido, northern
72 Japan. Grassland species including stonechat are seen in early-successional stages of
73 forestry plantations and are likely to be conserved by the forestry activities (Yamaura et
74 al. 2012a, Toyoshima et al. 2013). Here, we identified the migratory routes, migration
75 stopover sites, and major non-breeding grounds of 12 Stejneger's stonechats' breeding
76 in Hokkaido. Their stopover sites and major non-breeding grounds would be essential
77 information to the effective conservation of migratory songbirds in the Far East. This
78 would allow us to attribute population dynamics to their migration routes, timing, and
79 major non-breeding grounds.

80

81 Materials and Methods

82 Field survey

83 The study area was a 25-km long bank along the Ishikari and Tobetsu Rivers
84 from Shinshinotsu village to Tobetsu town (43.12 N, 141.57 E; Japan). We captured 51
85 stonechats (46 males and 5 females) using spring and perch traps (TSB25 and PT30;
86 Moudry Ltd., Říčany, Czech Republic) during May 8–18, 2014. The sex was
87 determined based on sexually dimorphic plumage coloration. Age was not ascertained;
88 all were at least in their second calendar year. To estimate the migration routes, we used
89 0.50-g light-level geolocators (Intigeo P50B9-7-concord with 7-mm stalk; Migrate
90 Technology Ltd., Cambridge, UK). The expected life of the battery was at least 9
91 months. Spring migration was not tracked since the batteries died in mid-February [22
92 February \pm 22 days; mean \pm standard deviation (SD), $n = 12$]. The devices were

93 mounted on the birds using a leg-loop harness system (Rappole and Tipton 1991) with
94 an elastic silicon rubber mixture (O-ring with 25.5-mm interdiameter and total weight of
95 0.65 g). The body weight of the tagged individuals was ≥ 17.0 g ($n = 5$) for females and
96 14.9 g (SD = 0.65 g; range, 13.0–16.0 g, $n = 46$) for males. Thus, the relative load of the
97 geolocator was clearly below the accepted 5% of the bird's body mass (Caccamise and
98 Hedin 1985). The deployment procedure lasted < 15 min. Geolocators and color rings
99 were detached when the birds were recaptured in 2015. Field work was permitted on the
100 river bank by the Iwamizawa and Sapporo River Offices, and capture of stonechats was
101 permitted by Hokkaido Prefecture (#1666 in 2014 and #1358 in 2015). In addition, the
102 overall study program was approved by the animal ethics committee of Hokkaido
103 University (#14-0024).

104

105 Data analysis

106

106 Estimating locations

107 Light-level geolocation data were analyzed in the R package “GeoLight” ver.
108 2.01 (Lisovski and Hahn 2012) and “SGAT” ver. 0.1–1 (Wotherspoon et al. 2015). The
109 daily sunrise and sunset times were determined as the specific date and time when light
110 intensity exceeded (sunrise) or fell below (sunset) a priori-defined light intensity
111 threshold of 1.35 lux. To calibrate the individual geolocator data series, we used the
112 light intensities recorded after deployment and before August 15 when breeding
113 stonechats are known to be stationary around their breeding sites (Fujimaki et al. 1994).
114 Individual calibration periods ranged from 88 to 98 days. Using the individual
115 calibration data, a log-normal density distribution was fitted to the zenith angle
116 difference (twilight error) of each defined twilight time and the earliest/latest recorded
117 sunrise/sunset time, e.g., the sunrise/sunset that has most likely been recorded without

118 any interference of shading. Initial locations were estimated using the (modal) zenith
119 angle at the maximum density of the defined log-normal distribution. This method
120 corresponds to the often-called on-bird calibration (Lisovski et al. 2012). To correct for
121 unrealistic positions caused by high-intensity shading events during twilight, we used a
122 Bayesian framework within the “SGAT” package that incorporates the observed sunrise
123 and sunset times and prior knowledge of the species’ behavior to estimate location.
124 Markov Chain Monte Carlo (MCMC) simulations permitted a *spatial probability mask*,
125 a prior definition of the error distribution of twilight events (*twilight model*), and
126 plausible flight speed values (*behavioral model*), which collectively allowed us to refine
127 the tracks derived from the sunrise and sunset times (Sumner et al. 2009).

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

$$134 \quad P = 1 + 5 * \exp(-(d/200,000)^1).$$

135 Hence, locations >200 km from the nearest coastline had a four times lower
136 probability (P) of occurrence than locations on land. We used a freely available
137 1:75,000 spatial shoreline dataset (<http://shoreline.noaa.gov>). To parameterize the
138 *twilight model*, we used the parameters (log-mean and log-standard deviation) of the
139 individually defined log-normal density distribution. We assumed that migratory
140 songbirds have a bimodal speed distribution for the *behavioral model*: stationary
141 behavior during most of the year and traveling airspeeds of about 8 m/s (Bruderer and
142 Boldt 2001) during active migration (gamma distribution for movement: shape = 9,

143 scale = 0.25; periods of residency: shape = 1, scale = 0.2). We used the “changeLight”
144 function (from the R Package “GeoLight”) to define which of the two speed
145 distributions should be used for a given location estimate. This analysis was based on a
146 “change point” analysis that quantified the probability of each sunrise and sunset to be
147 different than the surrounding sunrise and sunset times and hence provides evidence for
148 shifts/movement in the underlying locations. The sunrise and sunset times associated
149 with a “change point” probability greater than the 0.75 quantile of all probabilities were
150 used to define the stationary periods separated by periods of movement. The
151 “change point” probability of 0.75 is a conservative estimate (Lisovski and Hahn 2012).
152 We considered that times >1.5 days were changes in both location and location
153 estimates that fell between stationary periods. We associated these changes with the
154 active movement speed distribution. We drew 1,500 samples to describe the posterior
155 distribution for each individual using the above-described parameters. Based on the
156 latter, we obtained the median track for each bird (e.g., median of the location estimates
157 for each twilight time). These processes do not allow for convergence of the MCMC
158 chains, as that would require a burn-in and tuning process before drawing a large
159 sample. However, the large observed twilight error distribution during the calibration
160 period resulted in unrealistic tracks (as far north as the arctic coastline) during the
161 equinox, indicating that the observed twilight error did not reflect the twilight error
162 during the movement and stopover periods. Therefore, we only used the method to
163 slightly refine and, most importantly, to correct highly unrealistic location estimates, i.e.,
164 longer periods at sea or location estimates too far away from each other to be actually
165 reachable by the birds.

166

167

Defining the migration schedule

168 We used the “changeLight” function to distinguish between periods of
169 residency and movement based on the most likely track. First, we calculated the sunrise
170 and sunset times for each estimated location along the track. Then, the periods of
171 residency were defined as periods between sunrise and sunset that were associated with
172 a probability of change >0.8 quantile of all probabilities and that were >2 days. This
173 was rather conservative and often resulted in several spatially overlapping periods of
174 residency. We then used the “mergeSite” function from the R package “GeoLight” to
175 combine stationary periods, i.e., consecutive sites with median positions closer than 350
176 km. Light-level data and R codes are available at:
177 https://github.com/slisovski/Stonechat_Migration.

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Results

181 Of the tagged males, 14 returned to the study area in 2015, i.e., a return rate of
182 30% (14/46). This was not significantly different from the return rate of a farmland
183 study in eastern Hokkaido during 1977–1986 (Fujimaki et al. 1994), where 13 from 25
184 marked males returned to the breeding ground in the subsequent year ($\chi^2 = 2.3$, $df = 1$, p
185 $= 0.13$). Two of our males had lost their geolocators before recapture. We successfully
186 retrieved data from all 12 geolocators. Body mass did not differ significantly between
187 the years (two-sample paired Wilcoxon signed-rank test: $V = 62$, $p = 0.08$, $n = 12$) but
188 was slightly lower by 2% in the year after deployment (see Appendix 1). None of the
189 five tagged females was observed in our study area in 2016. This was not significantly
190 different from the return rate of the former study (7/36: Fujimaki et al. 1994): $\chi^2 = 0.2$,
191 $df = 1$, $p = 0.65$.

192

The mean (\pm SD) onset of autumn migration was October 8, 2014 (\pm 7.7 days).

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

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Discussion

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Migratory route and schedule

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Most stonechats departed from Hokkaido during early October and migrated to the continent and stopped over in the southern Primorye or eastern Heilongjiang areas (Figs. 1, 2). The first snowfall can occur in lowland Hokkaido within the month of October (Sapporo Meteorological Observatory: <http://www.jma-net.go.jp/sapporo/index.html>), and most plants in grasslands wither and associated arthropods disappear in October (Yamaura et al. personal observation). 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 (Appendix 2). It likely

218 represents a generally important stopover site for migratory land birds along the East
219 Asian–Australian Flyway.

220 The North China Plain was visited by almost all of our stonechats (Figs. 1, 2a),
221 where large-scale illegal and massive trapping of migratory early-successional birds
222 occurs (Kamp et al. 2015). Stonechats traveled through China during October–
223 November, which is a major trapping season for songbirds there (Kamp et al. 2015).
224 This trapping and subsequent consumption (>1 million individuals per year) is
225 potentially responsible for the unprecedented speed and extent of the decline of
226 yellow-breasted buntings in the Palearctic (Kamp et al. 2015). Other migratory
227 early-successional species are also hunted there (Kamp et al. 2015), and this may also
228 include stonechats from Japanese breeding populations (Figs. 1, 2). Despite laws
229 enacted to stop this type of bird hunting in China, hunting pressure is unlikely to change
230 in the near future (S. Chan, personal communication). Conserving stopover sites in
231 southern Primorye/eastern Heilongjiang and reducing hunting pressure in China would
232 be core conservation issues for migratory birds in the Far East.

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

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

254

255 *Mainland Southeast Asia as a major non-breeding ground*

256 Mainland Southeast Asia was identified as the major non-breeding ground of
257 stonechats. This area is largely covered by farmland in the lowland areas and by a more
258 heterogeneous (cropland/natural vegetation mosaic) landscape in the other areas
259 (Appendix 2). Farmland, including rice paddy, and grasslands maintained by swidden
260 agriculture (sensu Fox et al. 2012) are reportedly important habitats for buntings and
261 stonechats in Southeast Asia (Yong et al. 2015, Urquhart 2002). A significant number of
262 species, including stonechats, are dependent on extensively managed farmland
263 worldwide, particularly in Asia (Wright et al. 2012a). Although species have evolved
264 without farmland for most of their histories (Phalan et al. 2012), extensive farmland
265 may be the only remaining habitat for these open-land species in the absence of
266 naturally maintained open-lands (Wright et al. 2012b). It has also been suggested that
267 man-made landscapes have been maintained for at least several thousand years in

268 Southeast Asia (Hunt and Rabett 2014).

269 However, forests, extensive farmland, and grasslands are currently decreasing
270 in mainland Southeast Asia (Fox et al. 2012), and they are being replaced by rubber
271 plantations and permanent croplands (Warren-Thomas et al. 2015). The abundance of
272 open-land species, including stonechats, may be higher in rubber plantations than that in
273 secondary forests (Li et al. 2013), and the establishment of both rubber and possibly
274 coffee plantations may provide some additional suitable habitats for open-land species.
275 On the other hand, agricultural intensification in Southeast Asia is required to meet the
276 growing local and global food demands (Mueller et al. 2012). This is a clear dilemma
277 for stonechats and other species that depend on farmland because agricultural
278 intensification has a significant negative impact on many species (e.g., Flohre et al.
279 2011). Reconciling the increase in agricultural productivity and conservation of
280 organisms dependent on farmland (sustainable intensification: Garnett et al. 2013) in
281 Southeast Asia may have major roles for bird conservation in the Far East.

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283

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411 Supplementary material (Appendix JXXXXXX at

412 <www.oikosoffice.lu.se/appendix>). Appendix 1–2.

413

414 Figure captions:

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416 Fig. 1. Migratory routes and schedules of 12 stonechats tagged on their breeding
417 grounds in Hokkaido, northern Japan. (a) Simplified migration routes based on median
418 posterior locations of the MCMC simulation during stationary periods (e.g., stopover
419 sites and non-breeding sites). See Appendix 1 for individual tracks with uncertainty
420 estimates. The underlying map represents land-use categories based on Broxton et al.
421 (2014); see Appendix 2 for more details. (b) The amount of time each individual spent
422 flying and resting/refueling during migration was calculated based on median posterior
423 locations and the “changeLight” analysis. Error bars represent the cumulative expected
424 uncertainty of 0.5 days for each transition time between a stationary and a movement
425 period. (c) Individual (open circles) departure dates from the breeding sites in Hokkaido
426 and arrival dates at the major non-breeding sites.

427

428 Fig. 2. Relative time spent by all tracked individuals. Periods (a) on stopover sites and
429 (b) on their non-breeding sites. The probability distribution is based on all MCMC
430 chains (e.g., 1,500 location estimates for each twilight). Grid size is 250×250 km using
431 a “Mollweide” equal area map projection.

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