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ORIGINAL ARTICLE

Full annual cycle tracking of a small songbird, the Siberian Rubythroat *Calliope calliope*, along the East Asian flyway

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Abstract

We used light-level-based geolocation to study the spatio-temporal behaviour of Siberian Rubythroats *Calliope calliope* breeding in the Amur region of the Russian Far East. Three retrieved devices revealed long-distance migrations, with southwestward movement from Amur through Northeast China in autumn, with the tracked individuals reaching their wintering grounds in southern China and Indochina without major detours and apparently on a route slightly further west than that of the return migration in spring. A single stopover occurred in two of the three birds in both spring and autumn in China. Migration was faster in spring compared to autumn. The birds spent most of their time in seasonal habitats on their temperate breeding sites, and in less seasonal habitats on their tropical wintering grounds. Departure from and arrival at their breeding site coincided with decreasing and increasing vegetation greenness, respectively. This is the first study presenting year-round tracking data for a songbird migrating from mainland Eurasia to Southeast Asia along the East Asian flyway.

Keywords Migration · Geolocation · Passerine · Land bird · Normalised difference vegetation index · Spatio-temporal behaviour

Zusammenfassung

Aufenthaltsorte des Rubinkehlchens *Calliope calliope* entlang des Ostasiatischen Zugweges im Jahresverlauf Mit Hilfe von Geolokatoren haben wir das Raum-Zeit-Verhalten von am Amur im Fernen Osten Russlands brütenden Rubinkehlchen *Calliope calliope* untersucht. Wir stellen damit erstmalig Positions-Daten zum Herbst- und Frühjahrszug einer Singvogelart vor, welche vom eurasischen Festland entlang des Ostasiatischen Zugweges nach Südostasien zieht. Der Langstreckenzug von drei Individuen konnte erfolgreich verfolgt werden. Im Herbst zogen die Vögel in südwestlicher Richtung über Nordost-China ab. Die Winterquartiere lagen im südlichen China und in Indochina und wurden ohne Umweg erreicht. Die Daten der ausgelesenen Geolokatoren deuten darauf hin, dass der Heimzug im Frühjahr weiter östlich als der Wegzug stattfindet. Die Zuggeschwindigkeit der beloggerten Individuen war im Frühjahr höher als im Herbst. Je ein Zwischenrastplatz während des Herbst- und Frühjahrszug konnte für zwei der drei Individuen in China lokalisiert werden. Die meiste Zeit verbrachten die verfolgten Rubinkehlchen im temperaten Brutgebiet, und in Gebieten mit schwacher Saisonalität im tropischen Winterquartier. Der Abzug vom und die Ankunft im Brutgebiet fallen in die Zeit der stärksten Ab- beziehungsweise Zunahme der NDVI-Werte (Normalized Difference Vegetation Index) - die Vögel passten also die Vegetationsperiode in Fernost Russland ab.

Introduction

Of all the major bird migration systems, the Asian flyways are exceedingly data poor (Kirby et al. 2008; Yong et al. 2015), even though they host the greatest diversity and largest populations of migratory birds and the highest number of globally threatened species (Yong et al. 2015). Little is known about the migration routes of Asian species, and

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research is biased towards larger birds (McKinnon et al. 2013) such as birds of prey (Higuchi et al. 2005), shorebirds (Piersma et al. 2016; Szabo et al. 2016) and other large waterbirds (Takekawa et al. 2010; Tian et al. 2015), while information on land birds (including the majority of songbirds) remains scarce (Yong et al. 2015). Bird ringing efforts in East Asia are limited, and the last large-scale ringing recovery analysis contained only a few long-distance recoveries (McClure 1974). Also, only two songbird species have been tracked on the East Asian flyway so far (Koike et al. 2016; Yamaura et al. 2016) compared to > 100 on the American and African-Palearctic flyways (McKinnon et al. 2013). In both cases, populations breeding in Japan were studied and no information is available for species breeding in mainland Asia. Recent studies have demonstrated that populations of songbirds migrating along the East Asian flyway have crashed during past decades (Edenius et al. 2017; Kamp et al. 2015; Tamada et al. 2017). A better understanding of their spatio-temporal behaviour is therefore urgently required for effective conservation measures all along the flyway.

The Siberian Rubythroat *Calliope calliope* (hereafter: Rubythroat) is a widespread breeding bird in northern Eurasia, occurring from the Ural Mountains in the west to Chukotka in the east (BirdLife International 2017). The species is genetically divided into a western and an eastern clade, which overlap during the non-breeding season in Southeast Russia (Spiridonova et al. 2013). The global population is believed to be stable in the absence of any data proving decline (BirdLife International 2017). Little is known about the migration of the Rubythroat: despite thousands of individuals being ringed at several ringing stations, no long-distance recoveries have been recorded (e.g. McClure 1974; own data). The known wintering area covers South China, Southeast Asia and North India (BirdLife International 2017). By using stable isotopes, Weng et al. (2014) identified birds wintering in Taiwan as originating from the southern part of the breeding range. The authors considered this a leapfrog migration pattern, with birds breeding in the northernmost part of their range occupying the southernmost wintering sites (Weng et al. 2014). However, the resolution of the isoscape maps for the vast Siberian breeding grounds remains coarse, limiting the inference from the isotope results (Weng et al. 2014).

The aim of our study was to obtain more accurate information on the year-round distribution of songbird migrants in East Asia, based on light-level geolocation. Here, we present the first migration tracks of Rubythroats, covering stationary sites during their full annual cycle. Furthermore, we compare the observed pattern with the change in vegetation greenness (normalised difference vegetation index; NDVI) on their stationary sites, as seasonal vegetation conditions are often thought to drive the evolution of migration timing of insectivorous land birds, enabling birds to track resources throughout their annual cycle (Thorup et al. 2017).

Methods

Fieldwork

Our study was conducted from 2016 to 2017 as part of the Amur Bird Project at Muraviovka Park (49°55′N, 127°40′E), a nature reserve in the Amur region of the Russian Far East (Heim and Smirenski 2013). Rubythroats are common breeding birds (> 100 pairs) in the study area (6500 ha), inhabiting willow shrubs and forest edges along wetlands. We targeted only territorial males since past ringing studies suggested that females are less site faithful and/or harder to recapture (own data). They were trapped with song recordings and mist nets (Ecotone, Poland) in their breeding territories from 4 to 6 June 2016. A total of 12 birds were equipped with light-level geolocators (Intigeo W65Z11; Migrate Technologies, Cambridge, UK), with two 1-mm-wide tubes on each side, regular coating and without a stalk. The devices were mounted with a leg-loop harness (Rappole and Tipton 1991) and had a total weight of 0.8 g, which corresponds to less than 4% (3.2–3.6%) of each bird's body weight (mean 23.6 g, range 22.0–25.0 g). The tagged birds were marked with three plastic colour rings and a metal ring of the Moscow Bird Ringing Centre.

Recaptures and resightings were carried out from 30 April to 11 July 2017. We had to change the recording used for luring the birds to the net since the marked birds would not respond to the playback used in the previous year. All three resighted birds were recaptured. All of them still carried the device and were in good physical condition. The return rate (3/12, 25%) did not differ significantly from the return rate of colour-ringed-only birds re-trapped in the previous year (4/12; $\chi^2 = 0$, $df = 1$, $p = 1$). The weight of the birds did not differ significantly between that at first capture in 2016 and recapture in 2017 (mean, 23.6 vs. 24.7 g; two-sample paired Wilcoxon signed-rank test—$V = 1$, $p = 1$, $n = 3$). One of the returned birds (BA152) had already been ringed as a juvenile at the study site on 26 August 2015, revealing natal philopatry. Two geolocators were still actively collecting data, while in one of the devices the battery power had expired in mid-February (BA152).

Geolocation data analysis

Geolocation data were analysed using the R package GeoLight (Lisovski and Hahn 2012). Data were log transformed and a threshold of 0.3 was used to determine twilights. Data were first adjusted for clock drift. Then, erroneous twilights from the dataset were determined by visual inspection of plots comparing each twilight to the twilight on the previous and following day, and these were deleted using the BAStag package (Wotherspoon et al. 2013). Positions were estimated using the coord function in GeoLight and latitudinal estimates for up to 3 weeks on each side of the equinox were excluded (tolerance = 0.17). A total of eight, 11 and 19 additional twilights were removed for individuals BA131, BA140 and BA152, respectively, which were randomly distributed. An on-bird breeding site calibration was used to determine the sun elevation angle for each individual. However, this resulted in highly unlikely positions for stopover and wintering sites (e.g. on the Tibetan plateau or the open sea), even when excluding the early phase on the breeding grounds when birds are exposed to more light while singing on a perch. We therefore used a Hill-Ekstrom calibration (Ekstrom 2004; Hill and Braun 2001), and selected the sun elevation angle where the latitude during the stationary period on the wintering grounds showed minimum variation. This resulted in higher sun elevation angles (− 3 to − 1 compared to − 5 to − 4 for breeding site calibration). The reason for this pattern might be a change in behaviour by the birds during the non-breeding season (more skulking) or by using less open habitats (e.g. forests instead of willow shrubs) (Fudickar et al. 2012; Lisovski et al. 2012). The migration schedule was determined with the changeLight function in GeoLight version 2.0.0, with a quantile of 0.95 and a minimum number of 5 days (Lisovski and Hahn 2012). However, obviously identical positions on the breeding grounds were subsequently merged manually. Great-circle distances between breeding and wintering grounds were calculated using the rdist.earth function in fields version 9.0 (Nychka et al. 2017). Minimum total migration speed was calculated by dividing the distance between the breeding grounds and the corresponding wintering grounds by the number of days required for migration, including stopover days. The difference in migration speed between autumn and spring was tested with a paired *t*-test.

Comparison with vegetation data

NDVI shape files (MOD13C1) were downloaded from the MODIS server by using the R packages MODIS version 1.1.0, gdalUtils version 2.0.1.7 and XML version 3.98-1.9 (Greenberg and Mattiuzzi 2015; Lang 2017; Mattiuzzi et al. 2017). The values of the rasters were scaled to an index ranging from − 1 to 1 with a extent of 2° × 2° to match the resolution of the tracking data with the R package raster version 2.5-8 (Hijmans et al. 2016). For each cell a biweekly NDVI value was computed for the time during which the birds were tracked (in total 23 periods from 1 June 2016 to 1 June 2017). As the SE of many of the overall average positions during the non-breeding season was rather high, cells of 4° longitude × 5° latitude were used for the analysis. The change in NDVI during arrival or departure events from stationary sites was measured by subtracting the NDVI value of the biweekly period before the event from the biweekly NDVI value after the event. Therefore, negative values show decrease in NDVI, while positive values show increase (Supplement 2). Experienced greenness was computed as the corresponding biweekly NDVI value for the individual bird's locality (Thorup et al. 2017). To investigate whether the birds utilized favourable conditions on sites, we computed the local surplus NDVI for each locality by subtracting the value of each biweekly period from the mean NDVI value on this site during the study period (1 June 2016 to 1 June 2017). Values above 0 indicate values higher than the average, while values below 0 indicate values below the average in this area. All analyses were conducted in the statistical software R (R Core Team 2017).

Results

We present data for autumn migration and wintering grounds for three males and spring migration for two. All three birds migrated initially westward and wintered in Southeast Asia—one in southern China (Yunnan province), one in the border region between Laos and Vietnam and one individual in Cambodia (Fig. 1). During spring, the birds migrated along a more easterly route. All long stopovers were in China, in autumn in Northwest China (Nei Mongol, Ningxia or Shaanxi provinces) and during spring in Central China (Henan, Hubei or Hunan provinces). The three males left the breeding grounds between 20 and 30 September, and arrived at their wintering site between 15 and 28 November (Table 1). Two birds left their wintering grounds on 30 March and 8 April, while one logger stopped recording before departure on 15 February. The two birds arrived on the breeding grounds on 25 April and 2 May, respectively (details about the migration schedule and length of stationary periods are given in Fig. 1 and Supplement 1). The minimum total migration speed was higher in spring compared to autumn migration speed (mean, 171 vs. 72 km/days, $t = -10.765$, $df = 1$, $p = 0.059$).

The NDVI of their northern temperate breeding area showed high seasonal variation, while the NDVI of their wintering sites in tropical forests showed only slight annual changes and stayed relatively high throughout the year (Fig. 2). All birds left the breeding area as well as their autumn stopover sites before NDVI reached its lowest values. In spring, birds arrived at their stopover sites and the breeding grounds when NDVI increased. Positive change in NDVI around migration events occurred for departure from the breeding area, for arrival at the wintering grounds, departure from the spring stopover sites and arrival at the breeding area. The largest changes in NDVI were experienced around

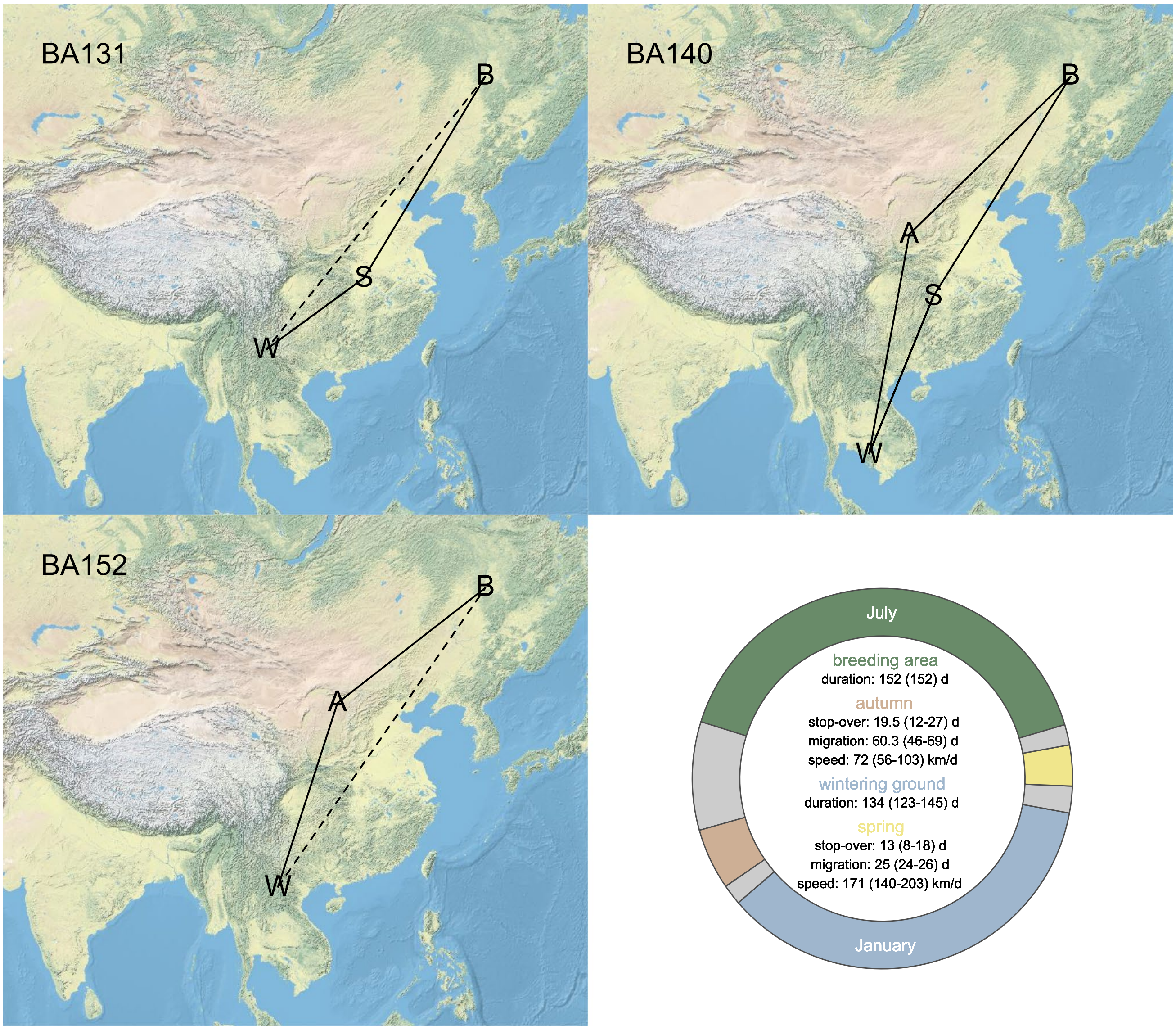

Fig. 1 Migration routes of three individual Siberian Rubythroats *Calliope calliope* from their breeding sites (*B*) to their wintering grounds (*W*). If applicable, positions of long stopover sites during autumn (*A*) and spring (*S*) migration are indicated. *Dashed lines* are drawn if no stopover site was found, while *solid lines* connect known stationary positions. The *inset* below on the *right* shows the life cycle. The *colours* of the mean stationary periods correspond to the colour of the headings within the ring chart. Mean migration periods are shown in *grey*. Mean values (range in *parentheses*) for duration of stay during stationary periods are given as number of days (*d*). Note that short stopovers (<5 days) cannot be detected with the method applied. The indicated migration periods likely consist of short stopovers and flights. The same colour scheme is used in Fig. 2 (colour figure online)

Table 1 Age in the year of capture (2 2nd year, 2+ after 2nd year) of the three male Rubythroats *Calliope calliope* with tags, their capture date in 2016 and recapture date in 2017, and their migration details obtained from the geolocators they carried

Logger	Age	Tagged 2016	Retrieved 2017	Departure breeding	Arrival wintering	Departure wintering	Arrival breeding	Distance[a] (km)
BA131	2+	6 Jun	16 May	23 Sep	28 Nov	30 Mar	25 Apr	~ 7400
BA140	2+	5 Jun	23 May	30 Sep	15 Nov	8 Apr	2 May	~ 9600
BA152	2	4 Jun	23 May	20 Sep	28 Nov	NA	NA	~ 7800

[a]Distance is the minimum travelled distance between breeding ground, stopover areas, wintering grounds and back to the breeding ground using a most direct route

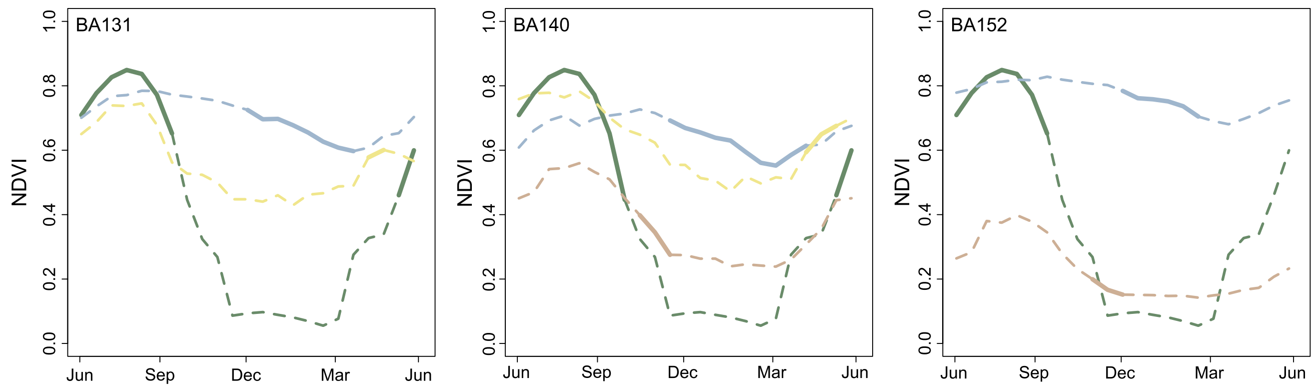

Fig. 2 Normalised difference vegetation index (*NDVI*) values for all stationary sites for three individual Siberian Rubythroats *C. calliope*. The *colour scheme* corresponds to Fig. 1, with the breeding ground in *green*, wintering grounds in *blue*, autumn stopover in *brown* and spring stopover in *yellow*. *Solid lines* indicate that the individual was present at the given site, and *dashed lines* that it was absent (colour figure online)

departure from and arrival at the breeding grounds (Supplement 2). During their stay on the breeding grounds the birds experienced surplus greenness (surplus NDVI 0.20–0.45, mean 0.36), while the NDVI values of the sites visited during the non-breeding season were slightly below the average of these areas (surplus NDVI − 0.09 to 0.02, mean, − 0.03).

Discussion

This is the first study presenting year-round tracking data for a songbird migrating from mainland Eurasia to Southeast Asia. The tracked Rubythroats followed rather straight paths without major detours towards their final winter destinations, similar to the routes proposed by Tugarinov (1931). When initiating migration in autumn, the three individual Rubythroats moved westward, with stationary sites far away from the shore. The routes were further inland than suggested by McClure (1974), who assumed the main East Asian passerine migration route to be closer to the Chinese coasts. Our tracks support recent studies, which have demonstrated that many passerine migrants, including Rubythroats, regularly cross mountains in Southwest China (Han et al. 2007) and even the Himalayas (Delany et al. 2017).

The wintering locations differed considerably among the three individuals, covering a large area across Southeast Asia from southern China (24°N) to Cambodia (12°N) within the species´ known wintering range (BirdLife International 2017). This suggests low migratory connectivity between breeding and stopover sites in this species, which implies that habitat loss, e.g. across the non-breeding range, could negatively affect multiple breeding populations (Finch et al. 2017). In addition, the interdependence of events occurring at sites visited throughout the annual cycle indicates that management across multiple sites is needed to maintain viable populations of migratory birds (Runge et al. 2015).

The tracked Rubythroats spent most of their time in seasonal habitats on their temperate breeding grounds in Russia, and in less seasonal habitats on their wintering grounds in tropical Southeast Asia. Experienced greenness was high throughout the year, with occurrence on the breeding grounds related to surplus greenness (Thorup et al. 2017). Departure and arrival matched changes in greenness, especially in spring. Such apparent resource tracking was found in other terrestrial insectivorous long-distance migrants in the Palearctic-African and American flyway systems as well (Bridge et al. 2016; Thorup et al. 2017), including the closely related Common Nightingale *Luscinia megarhynchos* (Emmenegger et al. 2014). Future changes in vegetation phenology caused by climate change might therefore entail the risk of mistiming for Rubythroats and other migratory songbirds (Emmenegger et al. 2016).

All three individuals stayed on the breeding grounds until late September, where they probably finished their full body moult (Glutz von Blotzheim 1988). Our birds timed their migration similar to nominate *C. calliope calliope* in the very southeast of Russia, for which a main migration peak was found during the end of September, whereas birds of the *Calliope calliope* '*anadyrensis*' type were found migrating during early October (Maslovsky et al. 2014).

The birds migrated faster in spring than in autumn, which was presumably related to time pressure of the breeding schedule (Nilsson et al. 2013). Similar results were found for closely related species like Bluethroat *Luscinia svecica* (Lislevand et al. 2015) and Thrush Nightingale *Luscinia luscinia* (Thorup et al. 2017).

Due to inherent limits of geolocation (Lisovski et al. 2018), only long stopovers (> 5 days) were detected. However, we assume that the tracked Rubythroats made numerous short stopovers during migration (Fig. 1). Some stopover sites were used for up to 27 days, similar to *Luscinia* species migrating from Europe to Africa or Asia (Emmenegger et al. 2014; Lislevand et al. 2015; Thorup et al. 2017). The function of these long stopovers is unknown, as Rubythroats moult on the breeding grounds, and no obvious ecological barriers have to be crossed during migration. All detected stopover sites were situated in mainland China, highlighting the importance of this country for the conservation of this species. Rubythroats are intentionally trapped during the non-breeding season as food and for use as caged birds (Weng et al. 2014) due to their beautiful song and plumage, which could lead to population declines (Kamp et al. 2015).

Our results give valuable insights into the annual life cycle of a long-distance migrant along the East Asian flyway, providing relevant information for future conservation measures. Geolocation has proven to be a valuable tool for the study of the spatio-temporal behaviour of small songbird migrants, and more studies on multiple populations of Asian passerines using this technique are desirable.

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