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SHORT REPORT

Following year-round movements in Barn Swallows using geolocators: could breeding pairs remain together during the winter?

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Capsule The spatio-temporal schedule provided by geolocators suggests that a pair of Barn Swallows could have remained together during the non-breeding period. Data from four birds, of which two were a breeding pair, showed winter quarters from West to Central Africa. The tracks of the paired individuals coincided both spatially and temporally at a scale of <200 km throughout the non-breeding period, in contrast to the tracks of an unpaired male and female from the same region.

The Barn Swallow Hirundo rustica is a common songbird with a widespread breeding area in the Northern Hemisphere (Cramp 1985). European Barn Swallows winter in sub-Saharan African in open habitats (Zwarts et al. 2009). Ring-recovery analyses of Barn Swallows ringed in Europe have revealed large-scale connectivity with their wintering areas (Ambrosini et al. 2009, 2011, Zwarts et al. 2009). During the non-breeding period, Barn Swallows show highly gregarious behaviour (Turner 2010), congregating in communal roosts both during the migration period and in the winter (Rubolini et al. 2002, Zwarts et al. 2009). This behaviour could facilitate mated pairs remaining together during the non-breeding season. Passerines with common foraging and roosting places rarely hold territories, and long-term pair maintenance could potentially occur. This would not necessarily be due to year-round mate-fidelity, but could be because the pair joined the same flock after breeding and would remain within it for the rest of the non-breeding period. However, this has not been studied among small, long-distance, gregarious migratory passerines.

Light-level geolocators have enabled us to study year-round individual movements of even small birds (Stutchbury et al. 2009, Tøttrup et al. 2012). Here, we used light-level geolocators to study the migration and investigate the possibility of winter pair association in Barn Swallows. The relatively low accuracy of this type of device (errors of up to more than 200 km) prevents a stronger test of this phenomenon (e.g. pair association). However, the temporal scheduling of events can be determined with greater accuracy and coinciding scheduling throughout the non-breeding is unlikely for separated mates. Thus, we test for simultaneous timing of events to indicate possible pair maintenance during the non-breeding period with spatial locations providing a supplementary test.

Fifty breeding Barn Swallows (25 pairs) were tagged with archival light-level loggers (geolocators) in June and July (breeding season) of 2012 at the Urdaibai Biosphere Reserve in the North of Spain (43°20′N 02°40′W). The geolocators used in this study were provided by Biotrack (UK) (model: MK6540C, 0.6 g). Geolocators were attached with a leg-loop backpack harness. Once a nest with chicks was found the two adults were captured with mist nets and ringed, weighed (body mass, ±0.1 g accuracy) and tagged with a geolocator. The weight (0.5 g) of the geolocators was 2.6–3.2% of Barn Swallow body mass. Body mass of Barn Swallows in 2012 (mean ± sd: 17.7 ± 1.4 g, n = 6)
did not differ significantly from the body mass when recaptured in 2013 (mean ± sd: 19.0 ± 2.6 g, n = 6; paired t-test: t = 0.91, P = 0.41).

During the breeding period of 2013, geolocators were retrieved from 6 Swallows, corresponding to a return rate of 12%. This rate is below the one reported in untagged Swallows (Scandolara et al. 2014). However, we have no data on local return rates from untagged birds at Urdaibai. Data from two geolocators that failed before the birds left their breeding grounds were excluded. Two of the four remaining Barn Swallows (two males and two females) belonged to a single breeding pair, marked and recaptured one year later in the same nest.

Geolocator data were analysed with the BASTRAK software suite. We defined sunrises and sunsets using the threshold method, with a sun angle estimated for each individual. We used a threshold level of 2 (arbitrary units) and found the individual corresponding sun angle (range: −3.4° to −2.2°) by calibrating the data with the Hill–Ekstrom calibration (Ekstrom 2004). When incorrect sun angles are used, the error in latitude increases when approaching the equinox due to the decreasing day length variation with latitude (so latitudinal data are lost due to the equinox). We have used this characteristic and the sun angle producing the least variation in latitude during the longest stationary period (determined from longitude) between autumn and spring equinoxes was applied.

The migration periods coincided, both in autumn and spring, with the equinoxes. Accordingly, we were unable to determine locations during migration (we removed all latitudes within three weeks on each side of the equinoxes). Alternatively, we used longitudinal data to assess possible routes of migration (e.g. to estimate whether the Swallows migrated parallel to the West African coastline or, alternatively, across the Sahara). Stationary periods were defined as those where longitude did not change more than 3° in a consistent matter. Departure and arrival dates were defined as the last or first day within 1° longitude of the preceding or following stopover (see Online Supplementary Material, Fig. S1). We also calculated departure and arrival times using a change point function. We used the changeLight function in the R package GeoLight (Lisovski & Hahn 2012) using a 0.9 quantile and a minimum stopover duration of five days. We subsequently lumped all successive stationary periods with a difference in mean longitude less than 2°. The results are compared to the stationary periods found by evaluating longitudes in Fig. S1 (see Online Supplementary Material). Overall, both approaches provided very similar results, but in a few cases the changeLight function identified new stopovers or extends duration of stopovers into obvious periods of movement. This was probably caused by differences in levels of noise among individuals (for some individuals a higher or lower quantile would perform better). For this reason, we assessed each stationary period by evaluating the estimated longitude, rather than by using the changeLight function. We define a stopover as a stationary period of more than five days (Tøttrup et al. 2012). To estimate the location of the stopovers, the mean of all estimated latitudes (if possible) and longitudes within the period was calculated.

Because of the lack of information on latitudes during migration, total migration distances were calculated as the minimum migration distances, i.e. the great circle route (orthodrome) from breeding to winter quarters. We defined the shortest (minimum) duration of migration as the time elapsed between the last position at breeding quarters and the first one at the winter quarters for the autumn migration period, and the opposite for the spring migration period. Travel speeds were calculated as the distance of migration divided by duration of migration. Thus, our estimates for distances and speeds are likely to be conservative.

Three Barn Swallows wintered in West Africa, likely along the coast of Liberia (Fig. 1). Another bird wintered in Central Africa, either in West Gabon or between Gabon and Congo (Fig. 1).

The Swallows departed from Spain 09–12 September (Table 1). For three birds wintering in West Africa, the autumn migration period took only 10–11 days, whilst it took 26 days for the bird wintering in Central Africa (Fig. 2). The birds reached their wintering sites 28 September–09 October (Table 1), and stayed from 151 (Central Africa) to 184–190 (West Africa) days. Swallows from West Africa left the area 20–28 March (Table 1), whilst the Central African bird left 08 March. The spring migration period was also very fast, taking 10–13 days for the birds in West Africa and 26 days for the bird in Central Africa. Arrival at the breeding area occurred 31 March–11 April.

Based on longitudes, all Swallows seemed to follow a flyway parallel to the West African coast in autumn (Fig. 2). The westernmost longitudinal position of each bird occurred in mid-September. Also in the spring the flyway was apparently parallel to the West African coast (Fig. 2). The westernmost longitudinal position of each bird in spring was late March–early April.
Long stopovers (>5 days) were only detected for the bird wintering in Central Africa, which was found to stop over for 9 days (22–30 March), likely somewhere in West Africa (longitude: 8.2°W). Orthodromes from breeding to winter quarters were 4053–5278 km, resulting in a mean speed of migration of 363 km/d in autumn (range: 203–463 km/d), and 320 km/d (range: 203–417 km/d) in spring. Speeds in spring did not differ from the autumn speeds (Wilcoxon paired test: $Z = 1.604$, $P = 0.11$). Excluding the stopover period, the bird wintering in Central Africa travelled at 310 km/d in spring.

The pair left the breeding area the same day (09 September), whilst the other two Swallows departed one day before and three days after, respectively. The individuals from the pair were assessed to arrive at their wintering sites with a difference of one day (this is within the accuracy of the geolocators), whilst the other bird wintering in West Africa arrived 2–3 days before and the bird wintering further east arrived 18–19 days after the pair. The members of the pair departed from their wintering areas on the same day (28 March), arriving in the breeding quarters 10 and 11 April. The other two birds arrived 6–7 and 10–11 days earlier than the pair.

Barn Swallows breeding in the North of Spain wintered across a widely scattered area from West to Central Africa, supporting only large-scale connectivity (Cresswell 2014). Individuals from the same breeding pair showed similar temporal schedules throughout the non-breeding period, in contrast to the male and female not associated as a pair during the breeding season. This temporal timing is highly unlikely to occur by chance for individuals that are not associated, and suggests that they could have migrated and wintered together. Geolocator positions have a high degree of uncertainty, hence we focus on the timing similarities of the pair. The estimated positions provide additional support for this claim although it remains unproven.

All four Barn Swallows seemed to follow a flyway parallel to the West African coast, both in autumn and spring, which would allow them to avoid the risks associated with the Sahara crossing (Biebach 1990) or the crossing of the Atlas mountains (Liechti et al. 2012). Other populations or individuals cross the Sahara far from the coast (Zwarts et al. 2009). Including the detour along the coast of Africa, migration distances of more than 5000 km (or even

Table 1. Key dates from the four birds recaptured in 2013. Stopovers were defined as those sites where birds stayed >5 days.

<table>
<thead>
<tr>
<th>Individual</th>
<th>Sex</th>
<th>Attach date 2012</th>
<th>Depart. breeding</th>
<th>Arrival wintering</th>
<th>Depart. wintering</th>
<th>Arrival breeding</th>
<th>Stopovers</th>
</tr>
</thead>
<tbody>
<tr>
<td>01 (pair)</td>
<td>Female</td>
<td>02 Jul</td>
<td>09 Sep</td>
<td>21 Sep</td>
<td>28 Mar</td>
<td>11 Apr</td>
<td>No</td>
</tr>
<tr>
<td>08 (pair)</td>
<td>Male</td>
<td>02 Jul</td>
<td>09 Sep</td>
<td>20 Sep</td>
<td>28 Mar</td>
<td>10 Apr</td>
<td>No</td>
</tr>
<tr>
<td>22</td>
<td>Male</td>
<td>17 Jul</td>
<td>08 Sep</td>
<td>18 Sep</td>
<td>20 Mar</td>
<td>31 Mar</td>
<td>No</td>
</tr>
<tr>
<td>46</td>
<td>Female</td>
<td>2 Jul</td>
<td>12 Sep</td>
<td>09 Oct</td>
<td>08 Mar</td>
<td>04 Apr</td>
<td>Yes*</td>
</tr>
</tbody>
</table>

* A single spring stopover from 22 to 30 March in West Africa.
>6000 km for the bird that wintered in Central Africa) were likely.

The wintering area for the three birds in West Africa fits the general wintering pattern for the European populations of Barn Swallows (Zwarts et al. 2009). However, exceptions are likely common, as one bird out of four was observed to winter as far as Gabon–Congo. Barn Swallows commonly congregate in huge communal roosts before and during migration, as well as when they are in their wintering areas. Populations obviously mix at these sites (Zwarts et al. 2009), hence birds from one population may potentially continue their migration following birds from other populations, giving rise to even larger scale connectivity (Cresswell 2014).

All Barn Swallows migrated rather fast (>300 km/d), which allowed these birds to reach their wintering areas in West Africa in <2 weeks, and the wintering site in Central Africa in <1 month. The birds from this study were found to show faster total migration speed (i.e. including stopovers) compared to other relatively small-sized species (Bächler et al. 2010, Åkesson et al. 2012). The total speed of migration of the Swallows (including potential short stopovers) is comparable to the speed found for Common Swifts Apus apus from Sweden in spring, but twice the speed of the Swifts in autumn (Åkesson et al. 2012). Both Swallows and Swifts feed on the air and, therefore, they can feed during migration. However, Swallows fatten up before migration (Rubolini et al. 2002).

In conclusion, although in part constrained by the low accuracy of the archival light-level geolocators used for small passerine birds, we obtained data suggesting that a pair of Barn Swallows could have remained together for a full annual cycle, including the migration period both in autumn and spring. Such behaviour has apparently not been reported before in a long-distance migrating songbird. Palaearctic birds wintering south of the Sahara can show a high degree of stochasticity in choosing their wintering sites at a large scale, especially with regard to first-year birds (Cresswell 2014). Adults, however, may re-use these sites year after year, especially if they experience good conditions.

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SUPPLEMENTAL MATERIAL

Figures illustrating the change in estimated logitude with date for each of the four Swallows can be accessed at 10.1080/00063657.2014.998623

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