Geolocators reveal three consecutive wintering areas in the thrush nightingale

Abstract
The winter distribution of many migratory birds wintering in tropical Africa is poorly known. After the crossing of the Sahara Desert, some long-distance migrants typically stay in the Sahel zone for an extended period before continuing migration to their main wintering areas south of the equator. Here we show how two thrush nightingales (Luscinia luscinia) fitted with light-level geolocators, after a six to seven week long stay in the Sahel zone of Sudan, moved to an intermediate area in northern Kenya for a month-long stay before continuing to their final wintering areas in southern Africa. These data indicate that thrush nightingales may use three consecutive wintering sites during their stay in Africa. The migratory movements in Africa between wintering sites are well-coordinated with high precipitation in these areas, suggesting that thrush nightingales track peaks of insect abundance occurring after rains. This three-stage wintering strategy has, to our knowledge, previously not been described, and shows that long-distance migrants can have complex wintering behaviour.

Keywords
Bird migration • Africa • Sahel region • Geolocator • Stopover • Wintering pattern • Thrush nightingale • Luscinia luscinia

Introduction
Knowledge about wintering areas in Africa is patchy and incomplete for many long-distance migratory birds. The vast areas to search, together with an often rudimentary infrastructure and sometimes political instability, have made it difficult for researchers to paint a detailed picture of the wintering distribution and strategies of migrants in the African continent. Bird ringing, together with visual observation in different parts of the African continent, has for decades been the major source of information about migratory movements in Africa. The development of smaller and smaller tracking devices has recently revolutionized the possibility to gain novel information about bird migration by tracking individual birds throughout the year. Miniature, light-level, archival loggers, hereafter “geolocators”, are lightweight enough to be fitted on small passerines, which comprise the majority of long-distance migrating bird species wintering in Africa. Geolocators register light intensity. The data they collect can be used to calculate geographical locations based on the timing of sunrise and sunset at different latitudes and longitudes [1].

Recent use of geolocators has revealed detailed information on the migration of several small songbirds. For example, previously unknown wintering [2–4] and breeding sites [5], loop migration [6,7], cross-hemisphere migration [8], as well as the use of two wintering sites in one season [7,9] have been described in different species.

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The thrush nightingale (Luscinia luscinia) breeds in an area that stretches from Norway in the west through the Russian interior to approximately 90° E [10]. They prefer dense bush vegetation and are often found in association with rivers and wetlands. Thrush nightingales are insectivorous and forage mainly on the ground under bushes [11]. Information from bird ringing suggests an easterly entry into Africa during autumn migration [12]. Wintering has been described as a two-step migration where the thrush nightingales, as well as several warbler species, cease migration after having passed the Sahara Desert, entering the Sahel zone at the end of summer to take advantage of the food resources following the rains in the region [13]. They are assumed to continue migration after a few months to their final wintering site south of the equator. This second leg of the journey has been indicated by the very large numbers of thrush nightingales caught annually during migration in November and December at Ngulia Lodge in Tsavo National Park in southeast Kenya [13,14].

On the African continent, insect abundance, as well as vegetation cover, fluctuates greatly between seasons, with insects peaking during the rainy season and dramatically dropping in abundance during the following dry periods [15–17]. Precipitation is governed by the oscillating movements of the Intertropical Convergence Zone, which reaches its most northerly distribution during the northern summer (July-September), covering the Sahel zone, before turning south and penetrating...
far south of the equator during the northern winter (January-March) [18]. The onset and completion of the rains in different parts of the African continent has been proposed to shape the winter distribution of migratory birds [19]. However, detailed knowledge about avian migration on the African continent is scarce. Bird ringing, the main source of information on passerine migration, renders information about migration on a species level, where the resolution of the dataset is restricted to the number of ring recoveries for each species, which are quite rare in the lower latitudes. Our aim in this study was to describe the migration routes and wintering sites for the thrush nightingale at the individual level, using geolocators, and hence contribute detailed information about the species’ migratory movements in Africa.

Methods

In spring 2010, we caught 35 male thrush nightingales, using mist nets and tape lures at their breeding territories, at four different locations in Sweden: Sundre, Gotland (56° 54’ N, 18° 10’ E), Aspa (58° 56’ N, 17° 6’ E), Nynäshamn (58° 54’ N, 17° 57’ E) and Tyresö (59° 14’ N, 18° 20’ E). The average body mass of the birds was 25.8 ± 1.9 g (mean ± SD, max. 30.6 g, min. 23.0 g). We fitted the birds with MK12-S geolocators, manufactured by the British Antarctic Survey (BAS), using a leg-loop harness [20]. The weight of the device with the leg-loop harness was 0.9 g. The weight of the geolocator represented approximately 3.5% (range: 2.9 – 3.9) of the body mass of the birds.

In spring 2011, we retrieved two geolocators; one in the Sundre area (bird 1) and one in the Aspa area (bird 2); both birds were recaptured in the same area where they were initially trapped. One other bird was trapped which had lost its geolocator. No other birds were sighted carrying geolocators, although the species is not easily observed in the breeding habitat. Spring arrival of thrush nightingale to Sweden in 2011 was delayed approximately two weeks (Bird Ringing Centre, Swedish Museum of Natural History, unpublished data). This may have affected the number of individuals returning and thus the low recovery rate in this study. Both of the retrieved geolocators ran out of battery power shortly after the birds had begun the spring migration, after approximately ten months of use, but both delivered intact information of the autumn migration.

Data analysis

To derive location estimates from changes in light intensities, a specific level of light during sunrise and sunset has to be matched to a sun elevation corresponding to the point where the sun is still well below the horizon but the light is changing most rapidly [20]. Through calibration at a known location, the relationship between a light-level threshold and a sun elevation can be established. We calibrated the geolocators using post-deployment data from a fourteen-day period after tagging, when the birds were assumed to be stationary in their territory. Due to the relatively dark environment inhabited by the birds, a light threshold level of 2 was chosen, which corresponded to a sun elevation of 3.4 and 3.6 degrees below the horizon for bird 1 and 2 respectively. We calculated local sunrise and sunset with Transedit2 software, and noon and midnight locations were estimated using Locator software (BASTrack software suite, British Antarctic Survey, Cambridge, UK). This way, two positions were obtained for each day. Latitude is derived from the length of day/night, and longitude from the absolute time of local noon and midnight on a given date. Accuracy of the geolocator is influenced by shading events, weather conditions or behaviour of the bird, as well as the time of year and latitude (accuracy decreases closer to the equator) [21]. The accuracy of geolocators on birds inhabiting forest habitats has been estimated to 143 ± 62 km for latitude and 50 ± 34 km for longitude [22]. Around the equinoxes, when the difference in day and night length is minimal, estimates on latitude are impossible [23]. Estimates on latitude were ignored for a period of 14 days prior to and after the equinoxes (autumn: September 23, spring: March 20). Longitude is largely unaffected by day length and data on longitude was included in the analysis during these periods [24]. We smoothed the location data twice following Pütz [25], a procedure which has been shown to increase accuracy of the estimated locations [26]. Clearly unrealistic latitudes from a few locations at the European sites, as well as for some at the third African site, were rejected from the analysis. These latitude estimates were probably subject to interference from the equinoxes even though they were outside the two-week boundaries set around the equinoxes. Clear shifts in longitude over several consecutive days marked movements between stationary sites, i.e. stopover sites and wintering sites. Difference in longitude between the stationary sites was also tested statistically using Mann-Whitney U-test. Only large-scale movements (> 1000 km) could be distinguished. Small-scale movements within the stationary periods and short stopovers during migratory movements were obscured by the variation in the dataset.

The derived location estimates were mapped onto a base map (Mercator projection) using QGIS desktop ver.1.7.2 (Quantum GIS Development Team, 2011. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org) and we calculated the mean latitude and longitude (± SD) for the stationary periods as well as the great-circle distance between the mean positions and total migration range. Precipitation contour maps for four months (September-December) with a one-degree resolution on precipitation normals (data from at least a ten-year period) were collected from the Global Precipitation Climatology Projects (GPCC) data visualizer (http://kunden.dwd.de/GPCC/Visualizer).

Ethics statement

Birds were captured with permission from the Swedish Bird Ringing Centre, Swedish Museum of Natural History (permission no. 619). The procedure of this study was reviewed and approved by the regional Swedish ethical committee (permit Stockholm Södra djurförsökssetiska nämnd Dnr S 41-10).
Results

Data from the two birds show the use of three sites south of the Sahara Desert (Figure 1) and there were significant differences in longitude between the consecutive sites (Table 1). The two birds began their autumn migration in mid-August, (17 and 18 Aug. respectively, Figure 1). Each made a stopover in southern Europe (Figure 1) that lasted 24 and 23 days respectively (Table 1) in

![Figure 1. Autumn migration routes of two thrush nightingales. Filled circles represent mean positions of stationary sites. Solid lines represent migration between stationary sites and dashed lines represent migratory movements undertaken during the autumn equinox. Dates indicate time spent at stationary sites.](image)

Table 1. Summary statistics of stationary sites of the two thrush nightingales as determined from geolocators. The difference in sample size between longitude and latitude is a result of the uncertainty in latitude during the equinox periods.

| Bird | Arrival at site | Departure from site | Mean longitude (±SD) | Difference in longitude to previous site* | n(lon.) | Mean latitude (±SD) | n(lat.) | Location of mean position | Number of days at site | Distance from last site (km) |
|------|----------------|---------------------|----------------------|------------------------------------------|---------|---------------------|---------|------------------------|----------------------|---------------------------|
| 1    | 21 August      | 13 September        | 15° 55' E ± 1° 59'   | <0.001                                   | 48      | 39° 1' N ± 4° 27'  | 30      | Italy                  | 24                   | 2000                      |
|      | 20 September   | 30 October          | 34° 34' E ± 1° 2'    |                                          | 82      | 22° 15' N ± 8° 11' | 50      | S Egypt                | 41                   | 2570                      |
|      | 3 November     | 9 December          | 37° 46' E ± 0° 55'   |                                          | 74      | 3° 5' N ± 2° 59'  | 74      | N Kenya                | 37                   | 2160                      |
|      | 16 December    | 16 March            | 32° 32' E ± 1° 6'    |                                          | 182     | 12° 2' S ± 3° 26' | 138     | E Zambia               | 91                   | 1780                      |
| 2    | 21 August      | 12 September        | 19° 26' E ± 2° 23'   | <0.001                                   | 46      | 38° 51' N ± 2° 24' | 15      | Greece                 | 23                   | 2230                      |
|      | 16 September   | 3 November          | 33° 58' E ± 1° 8'    |                                          | 98      | 15° 57' N ± 6° 48' | 64      | E Sudan                | 49                   | 2900                      |
|      | 19 November    | 8 December          | 37° 37' E ± 0° 39'   |                                          | 60      | 2° 19' N ± 2° 53' | 60      | N Kenya                | 30                   | 1570                      |
|      | 17 December    | 21 March            | 34° 49' E ± 1° 21'   |                                          | 190     | 12° 40' S ± 4° 17' | 134     | N W Mozambique         | 95                   | 1700                      |

*P-value from Mann-Whitney U-test
have been suggested to stopover in the Sahel region, taking advantage of the rich food resources available after the rains in this region before moving south to the main winter destination [13,19,27]. However, our data suggests that wintering in the thrush nightingale begins when the birds reach the Sahel region in Sudan, and that the birds use three consecutive wintering areas, tracking seasonal rain and vegetation. Similarly, in a study of migratory behaviour of the red-backed shrike (Lanius collurio), the authors classify the long staging period (34-71 days) of the birds after crossing the Sahara Desert as a resident period rather than a stopover during migration [7]. The seasonal pattern of the rains has been suggested to be the main driving force in the distribution of wintering areas of long-distance migrants [19], and is probably also the explanation for the use of three wintering areas in the thrush nightingales. Insect abundance in Africa is closely linked to the rainy periods [16], causing a fluctuation in time and space of available food resources for insectivorous bird species. As a result, long-distance migrants are forced to adapt their migratory strategies to follow the seasonal availability of food resources.

The birds remained in the Sahel zone of Sudan for 41 and 49 days respectively (Table 1). They then moved to a second site (Figure 2), located in northern Kenya (mean latitude 3° 5' N ± 2° 59' and 2° 19' N ± 2° 53', Table 1). They remained in this area for 37 and 30 days (Table 1) before continuing migration to a third site south of the equator (mean latitude 12° 2' S ± 3° 26' and 12° 40' S ± 4° 17', Table 1, Figure 2). Here they remained stationary until the beginning of the spring migration in the middle of March (Table 1). Total distance travelled during autumn migration by the two birds was approximately 8500 and 8400 km, calculated as the sum of the legs of migration.

The migratory movements between the three sites coincide with the passing of the rains in these areas (Figure 3). The birds arrived in the Sahel zone at the end of the rainy season (Figure 3a-b) and stayed several weeks. When the dry season started in the Sahel (at the end October and beginning of November) the birds moved on to the second site, in Kenya (Figure 3c), when the first annual rainy period begins. During this time, the rain has not yet reached the third site south of the equator and therefore that region is probably inhospitable to the species. The last migratory step which takes them to their third and final site takes place when the rain has reached these lower latitudes (Figure 3d).

Discussion

We show that two independent thrush nightingales make use of three spatially separate locations during the winter stay in Africa. The length of stay in the two northerly areas represents almost half the time spent in Africa before spring migration, and none of the sites were used for less than four weeks. We define a stopover site as a location during migration where the bird’s main activity is to refuel for the next migratory flight. Thus, these areas are not used solely as stopover sites en route to a distant wintering site, but rather function as short-term wintering areas. Several long-distance migrants using the eastern migration path have been suggested to stopover in the Sahel region, taking advantage of the rich food resources available after the rains in this region before moving south to the main winter destination [13,19,27]. However, our data suggests that wintering in the thrush nightingale begins when the birds reach the Sahel region in Sudan, and that the birds use three consecutive wintering areas, tracking seasonal rain and vegetation. Similarly, in a study of migratory behaviour of the red-backed shrike (Lanius collurio), the authors classify the long staging period (34-71 days) of the birds after crossing the Sahara Desert as a resident period rather than a stopover during migration [7]. The seasonal pattern of the rains has been suggested to be the main driving force in the distribution of wintering areas of long-distance migrants [19], and is probably also the explanation for the use of three wintering areas in the thrush nightingales. Insect abundance in Africa is closely linked to the rainy periods [16], causing a fluctuation in time and space of available food resources for insectivorous bird species.
Figure 3. Mean precipitation (September-December) across the wintering range of the thrush nightingale (based on GPCC’s Normals V. 2011 focusing on the period 1951-2000, 1.0 x 1.0° resolution). Open circles represent stationary sites of bird 1 and filled circles bird 2. Stationary sites are shown as mean with standard deviation in longitude and latitude. Dates indicate the time periods the birds are stationary at each site.
species. The birds in our study stayed in the Sahel region for a period of six to seven weeks after the passage over the desert. They arrived when the rainy season was drawing to an end in this region and then they stayed and took advantage of the green vegetation and food resources which followed the rain. This is in concordance with literature on migration strategies for the species in this area. Thrush nightingales are commonly found around the Nile system in the southeast Sudan during August and September ([28], Figure 2). They seem to anticipate the rains when moving to their second winter site in northern Kenya at the beginning of November, an area crisscrossed by dry riverbeds which fill during the rains. When the birds abandon the Sahel and move south to the second wintering area it is still several weeks before the rain reaches their third and southernmost wintering site, and a month-long stay at the intermediate site prevents them from arriving too early to dry and barren areas. The migration to the second winter site has previously not been described in detail. Ash [29] reported wintering thrush nightingales in south Ethiopia at around seven degrees latitude, caught mainly in October to November, which may represent this second step in the species wintering strategy. The first rainy season in Kenya ends in December [27] and the birds in our study seem to have stayed on for the duration of the rain. During November and December the rain has moved further south and the birds resumed migration to their third wintering site.

At this point it is not known how important the second site is for a successful winter stay in this species. The habitat of thrush nightingales is linked to moist shrub vegetation and it may be that this area serves as a refuge when the northerly site becomes too dry but the southernmost site has not yet received enough rain to become habitable for them.

Large numbers of thrush nightingales are caught on migration at Ngulia Lodge in southeast Kenya during November and December ([14], Figure 2) which coincides well with the timing of the second movement within Africa of our birds with geolocators. Previously, it has not been known from where birds caught at Ngulia begin their flight, but our findings suggest that the onset of migration may start fairly close to the north.

Based on substantial ringing recoveries, northern Egypt has been proposed to be a major preparation area for the Sahara crossing for this species [12]. The birds in this study prepared for the Sahara crossing much further to the northwest than was earlier believed for this species. The short period of time used for the Sahara crossing indicates that if these birds passed northern Egypt, it was only for a day’s stopover.

Even though sample size in this study is small, the fact that the two thrush nightingales, trapped at two different locations in Sweden, show very similar patterns in both timing and location during migration and wintering, suggests that this may describe a general pattern for the species. Furthermore, thrush nightingales from the entire breeding range seem to converge in a restricted wintering area in eastern Africa [10], and large numbers pass through Ngulia Lodge in late November-early December [14], indicating that moving between several wintering sites may be a general pattern for the species.

It is intriguing to ponder which cues govern this three-step migration in Africa. Could it be that thrush nightingales solely respond to a deteriorating habitat around them, pushing them further south and stopping at the first benign site they find? Or are they guided by an innate response to an internal clock advising them to move during specific times [30]? The non-random distribution of ring recoveries of thrush nightingales in the eastern Mediterranean area suggests that the species, at least in this area, use external cues for finding species-specific stopover areas [12]. Also, fuelling behavior of thrush nightingales has been shown to be influenced by geomagnetic fields during autumn migration, indicating the use of more precise external cues [31-33]. We suggest a more precise spatio-temporal migration programme during the wintering period in thrush nightingales, just as has been suggested for the red-backed shrike [7].

In conclusion, rather than staying in the Sahel region for an extended period before moving south to the main and second wintering area south of the equator, thrush nightingales appear to use three subsequent wintering areas, taking advantage of the available food sources produced by the rains. Our results thus show that long-distance migrants can have a more complex wintering behaviour than previously described.

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