Barometer logging reveals new dimensions of individual songbird migration

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Abstract

Recent advances in tracking technology are based on the use of miniature sensors for recording new aspects of individual migratory behaviour. In this study, we have used activity data loggers with barometric and temperature sensors to record the flight altitudes as well as ground elevations during stationary periods of migratory songbirds. We tracked one individual of red-backed shrike and one great reed warbler along their autumn migration from Europe to Africa. Both individuals performed their migration stepwise in travel segments and climbed most metres during the passage across the Mediterranean Sea and the Sahara Desert and least metres during the first flight segment in Europe. The great reed warbler reached its highest flight altitude of 3950 m above sea level (a.s.l). during the travel segment from Europe to west Africa, while the red-backed shrike reached 3650 m a.s.l as maximum flight altitude during its travel segment from Sahel to southern Africa. Both individuals used both lowlands and highlands for resting periods along their migrations. Furthermore, temperature decreased with increasing altitude during migratory flights for both individuals, highlighting the potential to determine flight duration from temperature measurements. Finally, we discuss how barometric data could be used to investigate birds' responses to changes in air pressure as a cue for departures on migratory flights. This new technique, i.e. using a miniature data logger with barometric pressure sensor to estimate flight altitudes and ground elevations, will open up new avenues for research and importantly advance our understanding on how small birds behave during migratory flights.

Introduction

During the last decades, advances in tracking techniques have revealed previously unknown spatiotemporal patterns of songbird migration (Bridge et al., 2011). With the use of activity-recording data loggers we are now also able to measure individual migratory behaviours, and give precise estimates of flight and stopover durations in small birds (Bäckman et al., 2017a, 2017b) which have previously only been possible in larger birds able to carry heavier tracking devices (Bridge et al., 2011). However, the degree to which individual songbirds change and regulate their flight altitude within and between flights remains unclear.

Radar has been used to estimate flight altitudes since the 1950s (Eastwood, 1967), and studies have revealed that migrants show a large variation in flight altitudes with regular flight altitudes up to 6-7000 m above sea level (a.s.l.; Liechti & Schaller, 1999, Bruderer et al., 2018). Different types of radars provide snapshots of the altitudinal distribution of birds at a site, yet, it gives us no insight at the individual level, at least not over longer distances. There have been a few attempts to record flight altitudes of individual birds, with various resolutions and flight durations. Altimeters based on α–particle radiation have been used to measure altitudes (range and maximum altitude) of single flights in pigeons and swifts at their breeding grounds (Gustafson et al., 1973, 1977). Cochran & Kjos (1985) used triangulation from ground of signals from Swainson's thrushes *Catharus ustulatus* tracked with radiotelemetry to give rough estimates of altitudes at a few occasions during a migratory flight. The first high resolution altitudinal tracks came with GPS satellite receivers, but these receivers are still too heavy to be carried by a small songbird (Bridge et al., 2011). Miniaturized barometric pressure sensors were first used in a radiotelemetry study where Swainson's thrushes were tracked during entire nights of flight with high temporal resolution (every 15 - 30 s; Bowlin et al., 2015). Those tracks clearly illustrated a complexity in altitudinal flight behaviour that previously had been completely unknown due to the difficulties in studying individual flight behaviour. Recently, barometric sensors have been used to record year-round flight behaviour of a medium sized bird, the alpine swift *Apus melba* (Meier et al., 2018).

In this study we use data loggers to monitor pressure, movement and temperature along the whole autumn migratory journey of two individual songbirds, one red-backed shrike *Lanius collurio* and one great reed warbler *Acrocephalus arundinaceus*. Both these species breed in Europe and winter in sub-Saharan Africa (Tøttrup et al., 2012, Lemke et al., 2013, Hasselquist et al., 2017). We illustrate four aspects of songbird migration that become

available for analysis based on the new combined barometer/accelerometer/temperature information – (1) flight altitudes, (2) ground elevations where the birds stay and forage before and after migration as well as during stopover and resting in between the migratory flights, (3) relationships between barometric pressure changes and the birds' probability of departure on migratory flights and (4) relationships between flight altitude or ground elevation (when the bird is on the ground and not in migratory flight) and data logger temperature. The latter relationships are useful as a basis for using temperature data to indicate flight/non-flight of songbirds equipped with other data loggers limited to measuring light and temperature.

Methods

20 data loggers were deployed on red-backed shrikes in 2016 (10 females and 10 males) in Gribskov forest, Denmark (55.988 N, 12.338 E) during the breeding season May-July and four males were recaptured in the following year. One data logger contained useful data. 25 data loggers were deployed on great reed warblers in 2016 at Lake Kvismaren (59.10 N, 15.24 E) and eight individuals (five males and three females) were recaptured in 2017. Only one data logger had useful data. The return rate of 20% for red-backed shrikes is similar to that of a control group with colour rings (27%, n = 15) and corresponds to previous studies using geolocators on this species (Tøttrup et al., 2012, 2017). The return rate of 32% for great reed warblers exceeded that of a colour ringed control group (24.5%, n= 57). Leg-loop harnesses were used to mount accelerometers data loggers on the back of all birds. The weight of the data logger (mass 1 - 1.2 g) represented maximum 4.5% of the body weight (red-backed shrike: mean ± SD: 30.5 ± 3.78g, great reed warbler 33.3 ± 2.43g). The data logger from the red-backed shrike contained activity and barometric data from Jul 15 until April 3, and the logger from the great reed warbler contained accelerometer data from Jul 10 until Feb 7 but barometric data only until the last flight of the second flight segment (Sept 10). As only two nights of flight were recorded for the red-backed shrike during spring, we only included autumn flight data of the red-backed shrike to facilitate direct comparison between the species. However, wintering season barometric data is included in the discussion of altitudes of stationary periods of the red-backed shrike.

Data loggers

The data loggers used in this study carried an accelerometer, sensors for pressure, temperature and light, a real-time clock and memory. Each sensor could be configured with its own measurement schedule. Barometric pressure from the pressure sensor were used to calculate altitudes and to investigate the birds' departure behaviour in relation to changes in air pressure and we used the data from the accelerometer to identify flight schedule and calculate flight durations. Temperature data were analysed to investigate if temperature patterns can be used to identify flights.

Barometric pressure and temperature were measured once every hour. The sensor used was a Bosch Sensortec BMP280 with temperature compensation and an absolute accuracy of $\pm$ 1 hPa. The temperature and pressure sensor was mounted on the side of the logger that was facing the bird. This means that the temperature values are influenced by the body heat from the bird and do not truly reflect the ambient atmospheric temperature.

Activity measurements were performed using the accelerometer which measured movement every 5 min at a $\pm$ 4 g range, giving 12 measurement sequences per hour. Accelerometer values were collected along one axis, on a flying bird approximately in parallel with gravity. At each measurement sequence, 5 samples of 100 ms duration with 5 s between samples were recorded. If none of these five samples showed activity, the sequence scores a "0" and if all samples show activity it scores a "5", and intermediate cases give scores "1" to "4". Every hour a summary of results from the last 12 measurement sequences are stored showing how many sequences that refer to the different activity categories (0 - 5). If the bird is perched and motionless the hourly result will be (12, 0, 0, 0, 0, 0), if it is flying with continuous wing beats the result will be e.g. (0, 0, 0, 0, 0, 12) and an example of an intermediate score would be (8, 3, 1, 0, 0, 0). Accelerometer range settings and sampling were chosen on the basis of field validations with red-backed shrikes and common swifts *Apus apus* (own unpubl. data). The detailed operation of the activity recording and data compression is somewhat intricate and has been described thoroughly in Bäckman et al. (2017a; see especially figure 2 in that paper).

The data loggers also provided position estimates on 6 5-day periods distributed over one year by using the geolocation-by-light method. In this study we did not use these data since some light level recordings either had failed or were of poor quality. When approximating regions for comparison of standard atmosphere estimates and geopotential heights of altitudes (see below), and when describing the flight segments of the birds, we used

earlier published spatiotemporal patterns from individuals of the same populations of red-backed shrikes (Tøttrup et al., 2012) and great reed warblers (Lemke et al., 2013; Hasselquist et al., 2017).

Data treatment and analyses

Altitudes were calculated from the measured barometric pressure according to the International Standard Atmosphere model (International Organization for Standardization 1975: ISO 2533:1975) from the following equation:

$$H = -\frac{T_0}{L} \cdot \left(1 - \left(\frac{P}{P_0}\right)^{\frac{1}{5.2561}}\right)$$

where H = altitude (m), P = pressure from the barometric sensor (hPa or mb), P_0 = air pressure at sea level (hPa or mb), T_0 = temperature at sea level (Kelvin) and L = Lapse rate (temperature change per meter increase in altitude, deg/m). To solve this equation, we used the standard sea level conditions $P_0 = 1013.25$ hPa, $T_0 = 288.15$ K (= 15.15^0 C) and standard L = -0.0065 deg/m.

The resulting standard atmosphere (SA) estimates of altitudes will deviate from true altitudes because of differences in local atmospheric conditions from the SA model. The error in SA altitude estimates may be several hundred meters in extreme low and high pressure weather systems at ground levels. At higher levels of several kilometres true altitudes may differ by more than $\pm$ 10 % from the SA estimates of altitude. To estimate the error in SA altitude one may use data of atmospheric conditions at the times and regions of the birds' estimated locations. We used the NCEP/NCAR Reanalysis Data of actual atmospheric conditions, available from US Department of Commerce, NOAA (http://www.esrl.noaa.gov/psd/data/composites/hour/) for this purpose. We compared geopotential heights (virtually identical to true geometric altitude) of three pressure levels (925, 850 and 700 hPa) at the times and regions of the birds' travel segments with the SA heights (being 762, 1457 and 3012 m a.s.l. for the three pressure levels, respectively). The travel segments were three segments in Europe and Africa for the red-backed shrike and two segments for the great reed warbler (Table 1, Fig. 1; the birds' regional locations were broadly estimated from the autumn migratory routes as demonstrated by earlier geolocator studies in Tøttrup et al. 2012 , Lemke et al. 2013 and Hasselquist et al. 2017). Both birds completed all travel segments in high pressure conditions and the comparison showed that the SA heights were underestimated for the times and regions of the two individuals in this study. The SA heights should be multiplied with a factor between 1.02

and 1.09 (average 1.055) to obtain the best estimates of true (geopotential) altitude. Applying a general factor of 1.055 for these two birds with barometer data thus gives estimates of true altitude with an error of $\pm$ 3% depending on variation in local atmospheric conditions. For ground levels and low flight altitudes ($\leq$ 300 m a.s.l.) we estimated altitude error by comparing geopotential height of the 1000 hPa level (http:www.esrl.noaa.gov/psd/data/composites/hour/) with the SA height (111 m a.s.l.) for the relevant regions and time periods. SA altitudes at the breeding sites and the European stopover regions of the great reed warbler and red-backed shrike were on average close to true altitudes with an error margin of about $\pm$ 50 m.

We determined flight altitudes based on all hourly barometric pressure data when the birds were flying continuously according to accelerometer information. One flight of the red-backed shrike that lasted only 40 min is removed from all analyses including barometric pressure data since no pressure measurement was taken during this time (see below for calculation of flight duration from activity data). For each flight we identified the maximum altitude and calculated mean altitudes for the total flight time. We subsequently used these data to calculate mean and max altitudes for the flights in different travel segments and for all flights during autumn migration (see Table 1). Climb altitude (height over starting altitude) was calculated by subtracting the starting altitude from the flight altitude. To obtain a measurement of the total number of climbed meters, cumulative climbing was calculated by adding together all positive differences between consecutive measurements of climbing altitude. Cumulative climb was then divided by maximum climb altitude for each flight to get an estimate of changes in altitude during flights (with ratios > 1 indicating repeated climbs or descents during the flight, to an increasing extent with increasing ratio). For this calculation, all flights with duration < 3h were excluded since at least 3 altitude measurements of flight as well as starting altitude are needed to identify a repeated climb. Flight durations were calculated by summing up the number of 5 minute periods with level 4 and 5 from the activity data for the red-backed shrike similar to what has been described in Bäckman et al. (2017a). For the great reed warblers we summed up periods with activity level 3 − 5, as the periods of continuous nocturnal activity had overall lower activity scores compared to the red-backed shrike. This could have several causes, e.g. differences in flight pattern, a low set threshold value to identify activity or differences in the attachment of the logger making the logger less horizontal while the bird is in flight. Isolated sporadic activity measurements with high activity scores 5 - 30 min were not regarded as migratory flights. As we made the assumption that the number of 5 min periods with activity score 4-5 (red-backed shrike) or 3-5 (great red

warbler) in the hour before and after hours with 100% flight activity were part of the same migratory flight, we got a 5 min resolution for flight duration (as well as for start and end times for the flights; see Bäckman et al. 2017a). Hence, we have a different resolution for activity and pressure and temperature data. To investigate the effects of changes in air pressure on departure decision we compared the trend (increase or decrease) in air pressure at 17:00 UTC at departure days with the day before. Only departures following at least one stationary day was included in the analysis. Since changes in air pressure are correlated with different upcoming weather systems depending on the climate zone (in a stationary bird), we do not expect the birds to react to changes in air pressure in the same way in temperate Europe and tropical Africa. Hence, the data were divided into, "Europe" and "Africa". For the great reed warbler analyses were applicable only for departures within Europe.

See supplementary methods for methods regarding flight and flight time identification by temperature data.

All statistics was performed using R version 3.2.3 (R Development Core Team 2015).

Results

Flights

The red-backed shrike divided its migration in three travel segments with 5, 11 and 17 flights, respectively, while the migration of the great reed warbler was divided in two travel segments, with 7 and 8 flights, respectively (table 1; Fig. 1). In total, the red-backed shrike spent 190.3 h on flights from the breeding area to the final non-breeding area in Namibia/Angola (table 1). The longest flight lasted 13.7 h during the second flight segment from south eastern Europe to the Sahel region while mean flight duration for the 33 flights was 5.8 h ± 3.3 h (mean ± SD). The great reed warbler spent in total 121.3 h from breeding to wintering ground, with a mean flight duration of 8.1 ± 2.2 h for the 15 flights (max flight duration = 11 h).

Overall, mean flight altitude of the red-backed shrike was lowest during the first flight segment within Europe (Fig. 1a) and highest during the third flight segment from Sahel to southern Africa (ANOVA: $F_{2,27} = 5.70$, $P = 0.0086$; table 1). Also the highest flight altitude of 3480 m a.s.l. (corrected geopotential altitude: 3650 m a.s.l.) was also reached during the last flight segment. The maximum flight altitude of the first flight segment was 1600 m a.s.l. (corrected geopotential altitude: 1740 m a.s.l.) while flight altitudes reached 3202 m a.s.l. (corrected geopotential altitude: 3340 m a.s.l.) in the

second flight segment. The red-backed shrike flew at higher maximum altitudes (ANOVA: $F_{2,29} =$ 4.94, $P = 0.014$) and climbed higher (ANOVA: $F_{2,29} = 4.52$, $P = 0.020$) during the second flight segment than during the last flight segment; and the first segment was still lower in all aspects (table 1). Similar to the red-backed shrike, all aspects of flight and climb altitudes of the great reed warbler were lowest during the first travel segment within Europe (ANOVA: $F_{2,12} = 11.65$, $P = 0.0051$; table 1; Fig. 1c). The highest flight altitude of 3757 m a.s.l. (corrected geopotential altitude: 3950 m a.s.l.) was reached during the second flight segment crossing the Mediterranean Sea and Sahara while the highest flight altitude during the European travel segment was 2186 m a.s.l. (corrected geopotential altitude: 2290 m a.s.l.). Furthermore, the great reed warbler reached higher maximum altitudes (ANOVA: $F_{1,12}$ $= 13.04$, $P = 0.0036$), and climbed higher distances (ANOVA: $F_{1,12} = 8.20$, $P = 0.014$) during the second flight segment from Europe to western Africa.

Cumulative climb did not differ between the segments for any of the birds (ANOVA; red-backed shrike: $F_{2,22} =$ 1.88, $P = 0.18$; great reed warbler: $F_{1,12} = 4.31$, $P = 0.060$). However, both individuals climbed higher during longer flights (linear regression; red-backed shrike: $F_{1,30} = 22.45$, adj-$R^2 = 0.41$, $n = 32$, $P < 0.001$; great reed warbler: $F_{1,12} = 16.09$, adj-$R^2 = 0.54$, $n = 14$, $P < 0.01$; Fig. 2). The ratio of total climb to maximum climb was 1.23 ± 0.41 m (mean $\pm$ SD) for the red-backed shrike and 1.35 ± 0.32 m for the great reed warbler. None of the individuals changed altitude more often during longer flights (linear regression; red-backed shrike: $F_{1,23} =$ 0.000030, adj-$R^2 = -0.043$, $n = 25$, $P = 1.00$; great reed warbler: $F_{1,12} = 2.95$, adj-$R^2 = 0.13$, $n = 14$, $P = 0.11$).

Stationary periods

Both individuals spent the breeding period and the first stopover in Europe in areas close to sea level (mean $\pm$ SD; breeding and first stopover, respectively; red-backed shrike: -9 ± 32 and 42 ± 40 m a.s.l.; great reed warbler: 23 ± 51 and -55 ± 35 m a.s.l.; Fig. 1b, d). During the stopover in Sahel, the red-backed shrike stayed at 622 ± 15 m a.s.l. and the winter location was in an area at 1132 ± 20 m a.s.l. The resting periods between flights in the travel segments took place at -55 to 1448 m a.s.l. for the red-backed shrike and at -53 to 640 m a.s.l. for the great reed warbler. The negative altitudes are within the error margin and may in fact have been close to sea level (see Methods).

Departure decision

There was no difference in trend in air pressure between departure days and the day before in either Europe (both birds grouped; Fisher's exact test: $P = 0.11$, $n = 13$; Fig. 3) or for red-backed shrikes, in Africa (Fisher's exact test: $P = 0.37$, $n = 18$).

Temperature as indicator of flights

There was a strong and significant negative correlation between altitude and temperature for the red-backed shrike when flying from the breeding grounds in Denmark to the stopover site in southern Europe (Pearson's correlation: $r = -0.88$, $P <0.001$, $n = 24$; Fig. 4A, yellow), from southern Europe to the stopover site in Sahel (Pearson's correlation: $r = -0.85$, $P <0.001$, $n = 75$; Fig. 4A, blue) and from Sahel to the wintering grounds in Namibia/Angola (Pearson's correlation: $r = -0.75$, $P <0.001$, $n = 92$; Fig. 4A, dark blue). The same was true for the great reed warbler when flying from the breeding grounds in Sweden to the stopover site in southern Europe (Pearson's correlation: $r = -0.85$, $P <0.001$, $n = 41$; Fig. 4B, yellow) and from southern Europe to the wintering grounds in western Africa (Pearson's correlation: $r = -0.96$, $P <0.001$, $n = 70$; Fig. 4B, red).

Discussion

Flight altitudes

Understanding flight altitudes is essential to understand physical capabilities of migrants and crucial to fully understand migration flight strategies and the costs of migratory flights. Migrants have been shown to be selective for favourable winds and to adapt flight altitude to favourable wind layers whilst in flight (e.g. Cochran & Kjos, 1985, Bruderer et al., 1995). By selecting favourable winds birds can increase flight range and reduce energetic and water costs for a certain flight to a highly significant degree (Liechti & Bruderer, 1998). Swainson's thrushes tracked during their migratory flights made extensive adjustments in flight altitudes (>100m) regularly during the flight (Bowlin et al., 2015). Changes in wingbeat frequency indicated that the variations were active changes in altitude made by the birds, but the reasons for these changes are yet to be understood. Likewise, both the red-backed shrike and the great reed warbler in this study changed flight altitudes several times during their nocturnal flights, clearly illustrating that songbird migrants do not maintain a constant (preferred) cruising altitude, as has often been assumed in migration models (e.g. Alerstam 1990, Newton 2008,

Pennycuick, 2008). The resolution of one estimate per hour cannot be used to show the frequent changes in altitudes recorded in high resolution data of single flights (Bowlin et al. 2015). However, our data support the observations of a complex behaviour with surprising changes of flight altitudes. Both individuals climbed to higher altitudes during longer flights (Fig 2). This is unexpected if birds in the beginning of a flight climb high to sample the different wind layers before continuing on a preferred cruising altitude (Cochran & Kjos, 1985). Rather, the positive correlation in Fig 2 illustrates the tendency of the birds to climb high also later during their flights, leading to an increased probability of high altitude with increasing flight duration. The low flight altitudes, and the relatively short flight durations in Europe compared to Africa further contributes to explain the pattern of higher altitudes on longer flights. Relatively low flight altitudes in Europe during autumn migration have previously been observed, and are suggested to be energetically beneficial due to unfavourable strong westerly winds at high altitudes (e.g. Shamoun-Baranes et al., 2017, Bruderer et al., 2018). An altitude increase of the lower part of migration has been observed before, during and after mountain crossings in Europe (Bruderer et al., 2018), and it has been suggested that birds generally increase flight altitude when crossing barriers, e.g. over oceans and deserts (Newton 2008). Both individuals in this study climbed most metres during the crossing of the Mediterranean Sea and the Sahara Desert. However, the red-backed shrike reached higher flight altitudes closer to its main wintering area when flying from Sahel to south Africa.

Elevation while on ground

Both individuals used both highlands and lowlands as resting sites during their migration. The great reed warbler more often used lowland areas, reflecting the habitat preferences of the species (wetlands), but during its second travel segment from Europe to western Africa it also rested at sites at higher elevations. Also the red-backed shrike mostly stayed in lowland areas until departure from the stopover site in southeast Europe, but used resting sites located at nearly 1500 m a.s.l. during the last travel segment from Sahel to southern Africa, and wintered in a highland area. Seasonal differences in conditions en route are suggested as a driver of loop migrations (Newton, 2008) and spring phenology differs between different elevations. Hence, migrants have been suggested to take advantage of early spring in lowlands resulting in differences in elevation for staging periods during spring and autumn migration (La Sorte et al., 2014).

Barometric pressure as a trigger for departure

Prevailing weather conditions are known to affect how long a bird stay at a stopover site, with unfavourable flight conditions delaying departures (strong opposing winds and precipitation; e.g. Åkesson & Hedenström, 2000). Birds are able to perceive small changes in air pressure (Kreithen & Keeton, 1974, Breuner et al., 2013), and it has been suggested that migrants use changes in air pressure to predict changes in flight conditions (Newton, 2008). The limited sample size from these two individuals of red-backed shrike and great reed warbler provides only some highly provisional data, and we did not find a significant difference in air pressure trends between departure days and the day before. However, six out of seven departures in Europe for both birds took place in increasing air pressure (three of three departures in the red-backed shrike and three of four departures in the great reed warbler; Fig. 3 The high proportion of departures in increasing air pressure support earlier observations. Reed warblers *Acrocephalus scirpaceus* departing from Falsterbo, Sweden (Åkesson et al., 2002), and European robins *Erithacus rubecula* departing from Rybachy, the Courish spit (Buluyk & Tsvey, 2013), have been observed to have a higher departure probability in high or increasing air pressure. Northern wheatears *Oenanthe oenanthe* migrating between Alaska and Africa have been observed to have higher departure probability in rising air pressure in interaction with decreasing remaining migratory distance and increasing flow assistance during spring migration, while departures during autumn were associated with low air pressure in the beginning of the migration and high air pressure in the end of the migration (Schmaljohann et al., 2017)

Temperature as indicator of flights

In addition to collecting more information from each individual by using data loggers with multiple sensors, there is also a gain when data can be validated between the different sensors. We used activity and pressure data to show that the temperature data could potentially be used to identify migratory flights and flight times. Temperature decreased with increasing altitude for both birds when they were actively flying during migration (Fig. 4 and Fig. S1). Therefore, a significant decrease in temperature is a good indication that the bird has been flying. By applying certain rules (supplementary methods; Fig. S2 and S3), we calculated the flight time for the two birds using temperature data and compared it to the accelerometer data. Although some flights were misidentified or unidentified based on only temperature data, most of the flights were identified correctly when compared with the activity data (Tables S1 and S2). However, flight numbers and flight time could be underestimated or overestimated if only identified using temperature data because of sudden changes in ambient temperature or overheating of temperature sensor. This is especially true for short flights (Table S2). Also, if the

bird was flying at low altitudes the temperature sensor might not register big differences in temperature values and such flights would not be identified. Temperature data could not only potentially be used to identify flights and flight times, but also improve the estimation of bird's departure and arrival dates if e.g. departure and arrival dates were calculated using only geolocation data.

General conclusion

By using miniature data loggers recording barometric pressure, we have shown that it is now possible to record also the third dimension, altitude, during the whole season of migration even for individuals of small songbirds. Altitude estimates calculated form a Standard Atmosphere model may deviate from true geopotential altitudes by several hundred metres depending on the specific atmospheric conditions at the times and regions of the birds' locations. However, these possible errors may be corrected for by considering geopotential height data as shown in this study, reducing altitude error to $\pm$ 100 m or less. Altitude information will give new insights not only about birds' flight behaviour with respect to their individual flexibility and adaptability in flight altitude, but also about other aspect of their migratory life –ground levels, responses to pressure changes and exposure to temperatures etc. It is too early to draw general conclusions from the results of only two individual songbirds during their autumn migration from Europe to Africa. However, we believe that the examples of possible analyses given in this first study indicate a promising future for data loggers with multiple miniature sensors recording barometric pressure, acceleration, temperature and light in studies of individual songbird migration.

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Figure Legends

Fig 1. Flight altitudes, and altitudes of stationary periods, in a great reed warbler (a-b) and a red-backed shrike (c-d). Migratory routes, and breeding, stopover and wintering areas, of the great reed warbler and the red-backed shrike are indicated on the topographic map (e; modified from Tøttrup et al., 2012; Lemke et al., 2013; Hasselquist et al., 2017). Colours indicate the different travel segments: the first segment within Europe for both individuals (yellow), the second segment to western Africa (red) for the great reed warbler, and the second segment (blue) and the last segment from Sahel to southern Africa (dark blue) for the red-backed shrike. Flight altitudes (a & c) are plotted only for the flight periods including start and landing altitude; hence, each flight is separated by a gap, but there could be differences in time between each flight. Stopover altitudes (b & d) are plotted excluding the flights, and each flight is replaced by a gap. Each flight period (the line in a & c; by block in b & d) is coloured in relation to the same travel segment, and the time scale is the same in (a) and (c), and in (b) and (d). Flight altitudes were schematically calculated from barometric pressure according to standard atmosphere conditions. Multiplying with a correction factor of 1.055 gives best estimates of true (geopotential) altitude (with error range ± 3%) for the actual times and places of the flight segments of the birds (see Methods).
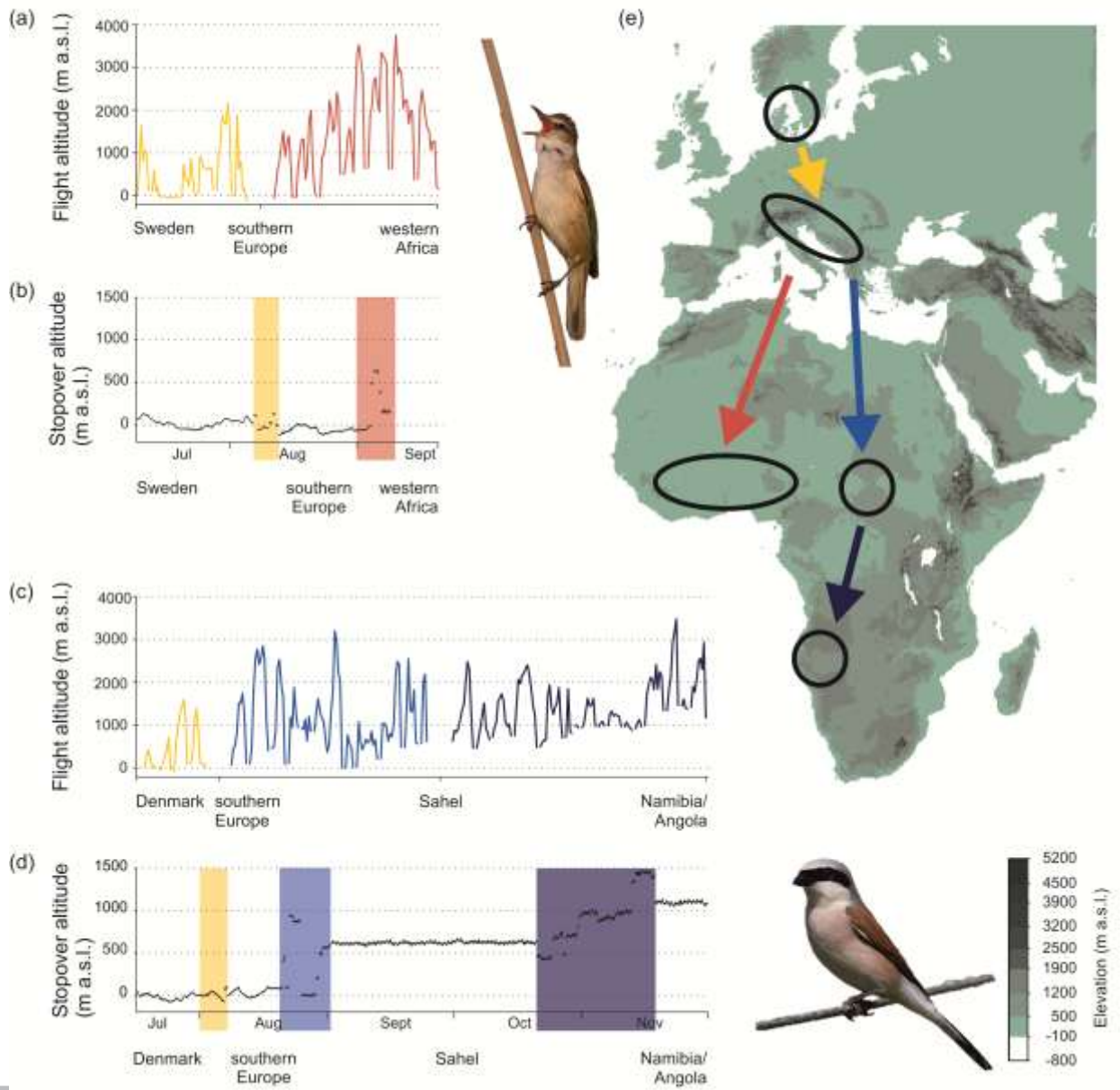
Fig 2. Correlation between maximum climb altitude (i.e. maximum altitude minus start altitude) and flight

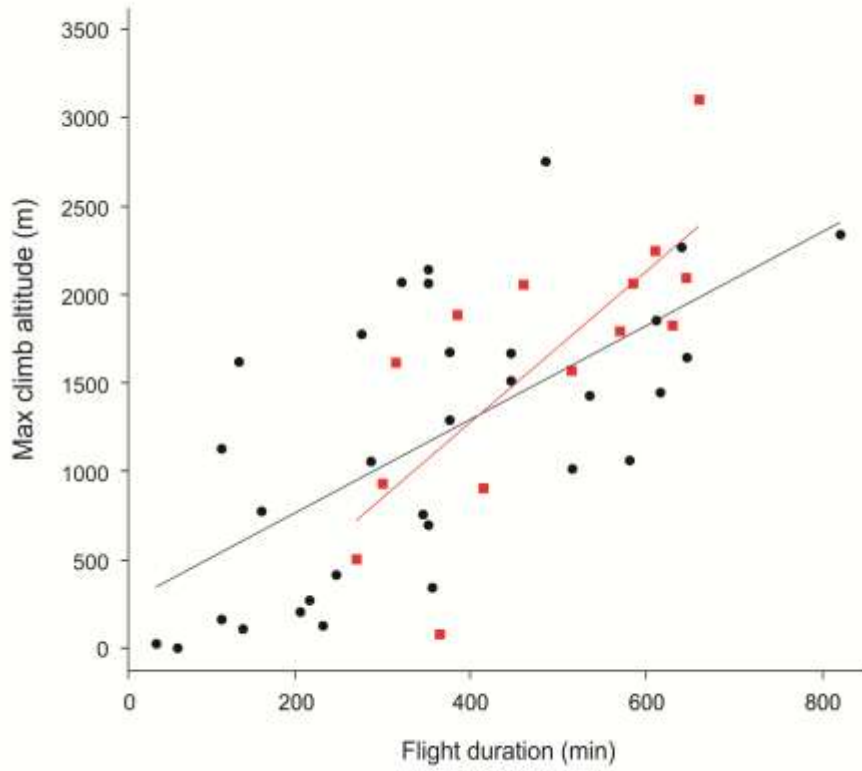duration for the red-backed shrike (black circles) and the great reed warbler (red squares).

Fig 3. Air pressure at 17:00 UTC at departure day and the days preceding the departure event, following a stationary day or period, within Europe. The red-backed shrike (black circles) made three departures and the great reed warbler (red squares) four within their travel segments in Europe, each departure event is connected with lines.
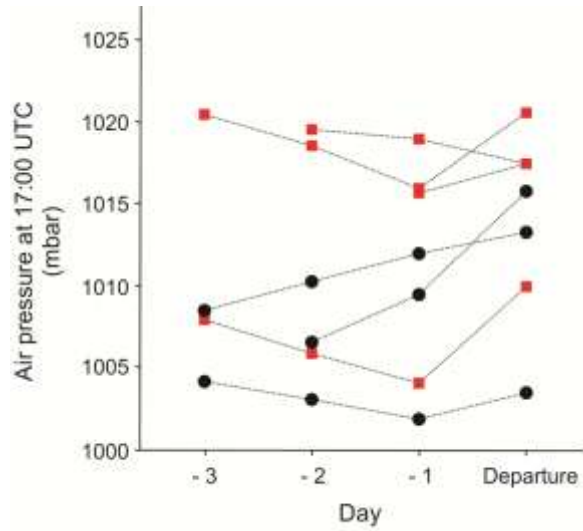
Fig 4. Correlation between temperature and altitude (m a.s.l.) for the red-backed shrike (a) and the great reed warbler (b) when the birds were actively flying during migration. Altitude and temperature were measured with an activity recording data logger. Colours indicate travel segment, the travel segment within Europe for both individuals (yellow), the second segment for the red-backed shrike (blue), followed by the last segment from Sahel to southern Africa (dark blue), and the second segment to western Africa (red) for the great reed warbler. Temperatures reflect ambient air temperatures but with an influence from the body temperature of the bird.
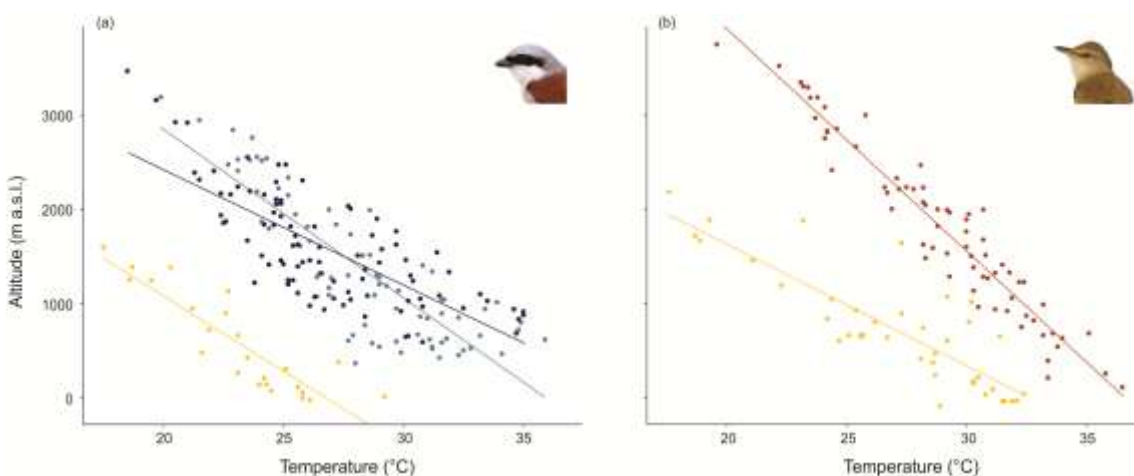
Table Legend

Table 1. Migratory flights of a red-backed shrike and a great reed warbler as recorded by accelerometer and barometer measurements during autumn migration. Flight altitudes were schematically calculated from barometric pressure according to standard atmosphere conditions. Multiplying with a correction factor of 1.055 gives the best estimates of true (geopotential) flight altitude (with error range ± 3%) for the actual times and places of the flight segments of the birds (see Methods).

Ind	Travel segment, dates	No of flights	Flight hours	Flight duration mean (SD) (h)	Flight altitude[a] mean (SD) (m a.s.l.)	Max altitude mean (SD) (m a.s.l.)	Max climb[b] mean (SD) (m)	Cumulative climb mean (SD) (m)
Red-backed shrike	1, 1-7 Aug	5	23.0	4.6 (2.1)	573 (381)	831 (591)	830 (591)	849 (589)
	2, 19 Aug- 3 Sept	11	73.8	6.7 (3.4)	1357 (479)	2044 (742)	1697 (704)	2067 (846)
	3, 19 Oct- 18 Nov	17[c]	93.6	5.5 (3.3)	1514 (487)	1848 (699)	998 (639)	1132 (772)
	Total 1-3	33	190.3	5.8 (3.3)	1331 (562)	1757 (809)	1212 (745)	1418 (917)
Great reed warbler	1, 5-12 Aug	7	41.8	6.0 (1.0)	665 (492)	1167 (708)	1141 (685)	1340 (754)
	2, 30 Aug- 11 Sept	8[d]	79.5	9.9 (0.8)	1771 (622)	2720 (780)	2106 (462)	3123 (685)
	Total 1-2	15	121.3	8.1 (2.2)	1218 (788)	1944 (1076)	1623 (758)	2232 (1146)

[a] Based on means for each flight, flights below 1 h excluded

[b] Max altitude above start altitude

[c] One flight of 40 min excluded from analyses regarding pressure sensor data, see methods.

[d] Barometric data is only recorded for the first 7 flights