



Activity and migratory flights of individual free-flying songbirds throughout the annual cycle: method and first case study

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We describe a method and device (<1.2 g) for recording, processing and storing data about activity and location of individuals of free-living songbirds throughout the annual cycle.

Activity level was determined every five minutes from five 100 ms samples of accelerometer data with 5 s between the sampling events. Activity levels were stored on an hourly basis throughout the annual cycle, allowing periods of resting/sleep, continuous flight and intermediate activity (foraging, breeding) to be distinguished. Measurements from a light sensor were stored from preprogrammed key stationary periods during the year to provide control information about geographic location.

Successful results, including annual actogram, were obtained for a red-backed shrike *Lanius collurio* carrying out its annual loop migration between northern Europe and southern Africa. The shrike completed its annual migration by performing > 66 (max. 73) nocturnal migratory flights (29 flights in autumn and > 37, max. 44, in spring) adding up to a total of > 434 (max. 495) flight hours. Migratory flights lasted on average 6.6 h with maximum 15.9 h. These flights were aggregated into eight travel episodes (periods of 4–11 nights when flights took place on the majority of nights). Daytime resting levels were much higher during the winter period compared to breeding and final part of spring migration. Daytime resting showed peaks during days between successive nocturnal flights across Sahara, continental Africa and the Arabian Peninsula, indicating that the bird was mostly sleeping between these long migratory flights.

Annual activity and flight data for free-living songbirds will open up many new research possibilities. Main topics that can be addressed are e.g. migratory flight performance (total flight investment, numbers and characteristics of flights), timing of stationary periods, activity patterns (resting/sleep, activity level) in different phases of the annual cycle and variability in the annual activity patterns between and within individuals.

It has been known for two hundred years that migratory songbirds in captivity spontaneously show increased activity during the migratory seasons, by fluttering intensively during the nights. This was reported by Naumann (1795–1817; cited from Berthold 1996) and Ekström (1826). However, it was not until the 1930s that experimental techniques were developed to quantify the activity of caged birds, by Wagner (1930) and Palmgren (1935; see also reviews by Dorst 1962, Berthold 1996), making it possible to investigate how the migratory restlessness ('Zugunruhe') is determined by endogenous and environmental (food, weather, photoperiod) factors. This technique of recording activity patterns of caged migratory birds for several years paved the way for major discoveries of the circannual rhythms in different species of long- and short-distance songbird migrants by

Gwinner (1967, 1969; reviewed by Gwinner 1986, 1990, Gwinner and Helm 2003) and Berthold (1973; reviewed by Berthold 1996, 2001). The assumption that migratory restlessness reflect motivation to depart on migratory flights has been confirmed by correlations between birds' restlessness in cages and their behaviour in the field with respect to departure probability (Eikenaar et al. 2014) and response to wind (Eikenaar and Schmaljohann 2015).

While much knowledge has accumulated from studies of caged birds concerning annual activity patterns during day and night (including patterns of sleep; cf. Rattenborg et al. 2004), such information has until now not been possible to obtain for free-living songbirds on an annual basis and we still lack knowledge about activity patterns for individual songbirds in the wild (Thorup et al. 2010). The available knowledge about activity patterns of free-living songbirds is based on short-term studies of foraging, flight and resting behaviour by field observations, radar and radio telemetry (Cochran 1970, 1985, Newton 2008, Chernetsov 2012). For larger birds, data loggers that measure acceleration have

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been used to provide detailed information about behaviour and energy expenditure, and such loggers have also been used in combination with GPS tracking systems allowing activity records for large birds over long periods of time (Wilson et al. 2006, Bouten et al. 2013, Brown et al. 2013).

Despite the difficulties associated with following free-flying small birds over long distances, new microelectronic techniques have made it possible to use ultralight sensors, batteries, memories and programming circuits to record and store information in dataloggers carried by free-living small birds throughout the annual cycle (Bridge et al. 2011, Kays et al. 2015). Geolocators represent such a new powerful technique to reveal the geographic patterns of movement (annual migration routes, stopover sites and winter quarters) of songbirds from light-level measurements (Stutchbury et al. 2009, Tøttrup et al. 2012). Furthermore, activity sensors (accelerometers) and geolocators have been used to reveal that Alpine swifts (a medium-sized non-passerine species) stay airborne for a major part of the non-breeding season in tropical west Africa (Liechti et al. 2013). Temperature data provided by geolocators (in addition to the light-level information) were used by Arlt et al. (2015) to indicate behavioural changes in a songbird. However, these authors also pointed out that accelerometer data would be more useful for that purpose.

Here we describe a method for recording activity and migratory flights of an individual songbird carrying an ultralight datalogger (< 1.2 g) with activity and light-level sensors and software that stores economized information throughout the annual cycle. The method is new in the sense that existing technology has been miniaturized and that programming has been adapted to economize data storage and to facilitate interpretation of activity patterns. We also present the first successful results for a male red-backed shrike *Lanius collurio*, providing information about timing and durations of migratory flights and about variation in resting/sleep and activity levels for every hour throughout its annual long-distance migratory cycle. The continuous activity recordings have been combined with light-level measurements during six periods of the annual cycle to provide control information about the individual's geographic location. The detailed flight information and activity patterns that can be obtained for free-flying songbirds by this method open up several new research dimensions (as addressed in Discussion), providing long-awaited crucial complementary information to the extensive available knowledge about circannual activity rhythms as recorded for caged songbirds.

This study presents a new technology using a combination of physical sensors that have the potential to reveal many details about the annual behavior in migrating birds. We illustrate this with data from only one bird, and inferences and conclusions about birds' general behaviour patterns during the year must of course await results from many more individuals.

Material and methods

The purpose of the datalogger was to continuously monitor the relative activity of the bird and to determine the position of the bird at pre-programmed occasions.

A total of 17 red-backed shrikes were trapped in Gribkov (55.98°N, 12.33°E), Denmark, between 3 June and 16 July 2014 and equipped with small (< 1.2 g) dataloggers. The dataloggers were attached by using leg-loop harnesses as described in Naef-Daenzer (2007). The recapture of only one (and an additional bird with logger being observed but not recaptured) out of 17 birds was less than the recapture rate of birds with geolocators during earlier years (15–20%; Tøttrup et al. 2012). This low recapture rate was probably an unfortunate accidental occurrence, since the present datalogger was not significantly different in either mass, size or attachment procedure from the geolocators used earlier and we can see no reasons to expect lowered return rates compared to geolocators of equal mass and size.

The dataloggers consisted of a primary battery, a microcontroller, a real-time clock, a non-volatile memory, an accelerometer and a light sensor. Measured accelerometer values revealed the level of activity of the bird carrying the datalogger and light-levels allowed us to estimate a position by using a geolocation-by-light procedure (Afanasyev 2004). The hardware components of the datalogger (Fig. 1) were battery, microcontroller, real-time clock, memory, accelerometer and light sensor as described in Supplementary material Appendix 1.

The recording device had two functions. The main task was to monitor relative movement of the animal carrying the platform and the other was to estimate position by measuring changes in diurnal light intensity (geolocation-by-light, Hill and Braun 2001, Afanasyev 2004). The datalogger had a programmable startup delay that made it possible to attach the logger well before measurements began. Our datalogger was set to start measuring on 15th of July at 00:00.

Activity measurements

Unlike some other studies, we did not attempt to classify certain behaviours from the characteristics of raw accelerometer data, since lengthy sequences needed for advanced analysis (Brown et al. 2013) cannot be stored in the small memory of the datalogger. We sampled very short repeated sequences (100 ms) and used a threshold model to determine whether the animal was moving or not (Fig. 2). Still, we



Figure 1. The activity data logger ready to be mounted on a bird. Most of the mass and volume is the button-cell battery (flat circular 10 mm structure to the left). The upward-pointing structure is the 'light-stalk', an acrylic tube that conducts ambient light down to a light sensor mounted inside the logger.

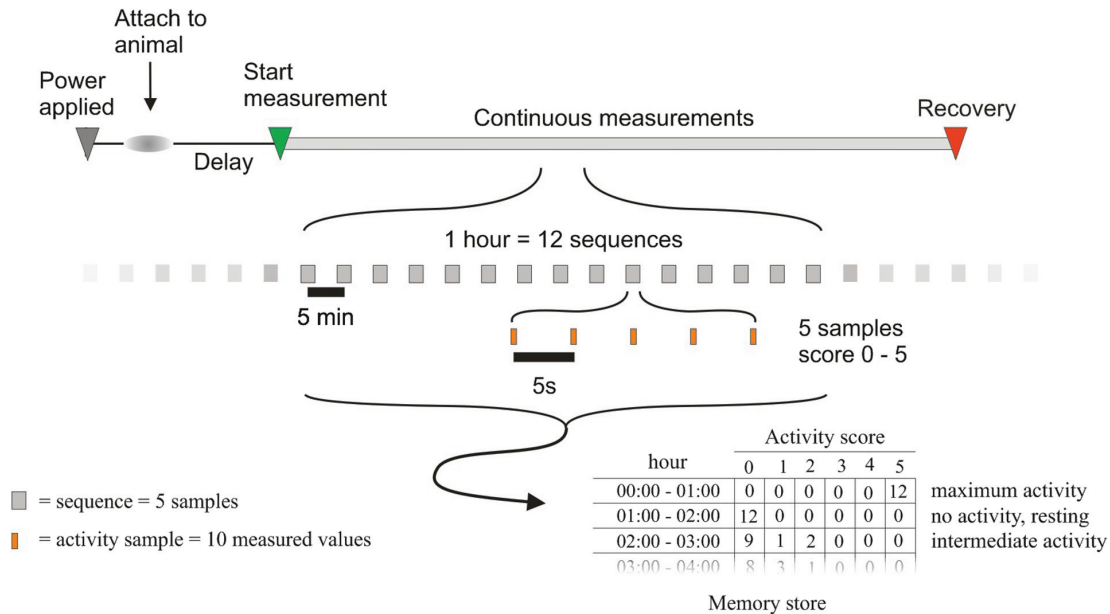


Figure 2. Estimation of activity classes. The activity measurements run continuously with a measurement sequence every 5 min. Each sequence consists of 5 samples. If all samples show no activity, the sequences scores a '0' and if all samples show activity it scores a '5', and intermediate cases give scores '1' to '4'. Every hour, number of scores of each value are counted and stored in a table that summarizes activity scores during the preceding hour. The sum of score counts for each hour is always 12, which is the number of 5-min intervals in an hour. In the example table above, all 12 sequences scored '5' in the first line (00:00–01:00), indicating continuous movement. In the second line (01:00–02:00) all sequences scored '0' which means no movement at all. The third line (02:00–03:00) shows that during nine of the sequences there was no activity. One of the sequences scored '1', meaning that one out of five samples in a sequence showed activity. Two of the sequences in this hour interval scored '2' which means that two out of five samples showed activity. Finally, no sequences scored '3', '4' or '5' between 02:00 and 03:00.

could estimate the overall level of activity from this sampling scheme which allowed inferences about different types of behaviour such as resting/sleep, continuous flight etc.

The wing-beat frequency of a red-backed shrike is approximately 10 Hz (Bruderer et al. 2010). We programmed the accelerometer to read values with a frequency of 100 Hz. A sampling duration of 100 ms yielded 10 values in a sample and covered an entire wing-beat cycle. We calculated the average acceleration in the sample in order to subtract the static acceleration caused by gravity. We counted the number of values deviating from average acceleration by more than 0.25 g. If 3 values or more passed this threshold, we regarded the bird as moving at that moment. Earlier field trials with common swifts *Apus apus* have shown that this simple threshold model is quite reliable to detect flight (own unpubl. data) and we think it is reasonable to believe that the same procedure should work for a red-backed shrike since this species is only slightly smaller than a common swift.

We developed a data reduction method in order to reduce the amount of stored data. Still, we wanted to be able to distinguish different levels of activity on a reasonably high resolution time scale. The method we applied was to compile activity for every hour, using a number of activity classes. The activity classes ranged from 0 (no activity) to 5 (maximum activity). See Fig. 2 for details on calculations.

Light measurements

The datalogger described here differs from the majority of geolocators in the way that it only measures sequences of

diurnal light cycles for a limited number of consecutive days. We also pre-programmed the device with a calendar of when to run the light level measurement sequences. In our study we chose to run measurement sequences that lasted for 5 d, with 6 sequences (yellow boxes in Fig. 3 and 5) distributed over one year. The timing of measurement sequences was selected according to known staging area schedules from previously published data (Tøttrup et al. 2012).

The 5-d light measurement sequences were initiated on 16 July, 18 August and 13 October in 2014 and in 2015 the sequences started 1 January, 13 April and 1 May.

In order to further reduce the number of measurements and amount of data, we assumed that the red-backed shrikes breeding in Denmark would never move outside the longitude interval 20°W to 50°E (corresponding to a local time interval of 4 h 40 min). By using a 5 h long light measurement interval, we would record sunset/sunrise as long as the bird is within 20°W to 50°E longitude. This would allow us to at least perform a light-threshold based position estimate (Lisovski and Hahn 2012). Using a measurement scheme like this is possible when reasonable assumptions can be made about longitude ranges of wintering areas. A limited measurement period can substantially reduce the amount of light-level data that needs to be collected and also minimizes the power-on time of the light sensor, which saves energy. This also means that the light level data obtained from our datalogger has mainly a control function to validate the location of the bird at key time periods of the year. Hence, it is preferable to have access to more detailed geographic results based on the existing continuous geolocator technique

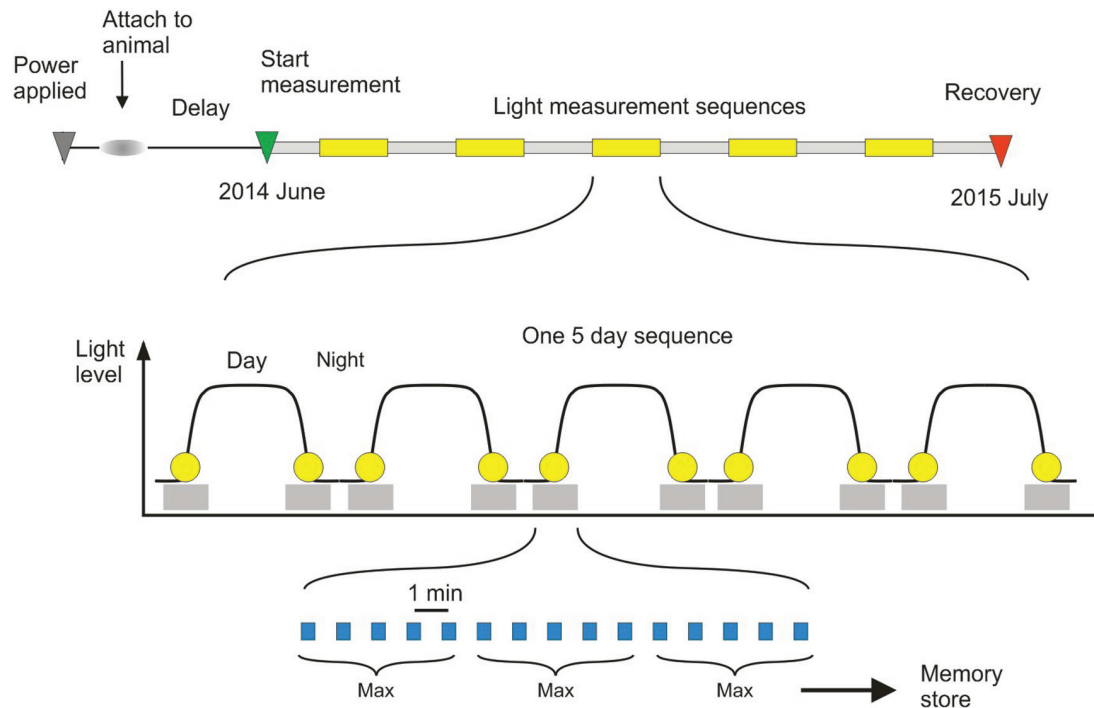


Figure 3. Algorithm illustration for light measurements. Activation times are pre-defined by a calendar in the datalogger. We measured light levels in six sequences during the annual cycle (yellow boxes). Each sequence is 5 d long and every day is made up by one morning and one afternoon event of light measurements (grey boxes). An event lasts for 5 h, long enough to include sunrise/sunset (yellow circles). Within an event, light is measured once every minute (blue squares) and the maximum light intensity sample value within a 5-min period is saved to memory.

for programming the timing of light measurement periods of the combined accelerometer/light logger described in this study (as we did based on earlier geolocation data for red-backed shrikes; Tøttrup et al. 2012).

Estimating positions

Positions were estimated from the light-level recordings using the software Intiproc (Migrate Technology 2015). To define twilight events we used a threshold light-level value of 2 corresponding to the sun being below the horizon (Supplementary material Appendix 2).

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.34dn2>> (Bäckman et al. 2016).

Results

The first case study: the annual activity cycle of a red-backed shrike

Data presented in this paper originates from the first recovered trial version of the datalogger carried by a red-backed shrike.

The annual actogram

The annual actogram for the red-backed shrike based on hourly mean levels of activity is shown in Fig. 4. Hours with no activity (activity level zero for all twelve measurements during an hour; white in Fig. 4) presumably often reflect

sleep, and occurred dominantly during the dark hours of the night but also as more fragmented inactivity during daytime to a varying degree in different phases of the annual cycle. Of course we cannot distinguish sleeping from resting (when the bird is awake but motionless) or from a foraging mode when the bird is on motionless lookout for prey for long periods. Hence, the interpretation of inactivity (activity class zero) cannot be made as strictly (although of course most likely reflecting resting/sleep if it occurs during long continuous periods) as the highest activity levels (activity class 4 and 5) which were apparently strict indicators of continuous flight (see below). During daytime the hourly mean activity was most often between 0 and 3 (as indicated by intensities of green colour in Fig. 4) with the highest mean levels during the breeding period and part of the autumn and spring.

The start and end of the daily activity period were determined primarily by the times of sunrise and sunset, which depended on both the time of year and the location of the bird. The dawn and dusk periods seemed to be shifted to the earliest GMT times in April and early May when the bird was at its most easterly longitudes in NE Africa and Arabian Peninsula (Fig. 4, 5). During the end of May and in June and July the nights were short at the northerly breeding latitudes and the bird was active during a very long daytime period, spending only a few hours sleeping during the short summer nights.

The highest activity levels (4 and 5) were associated with migratory flights which occurred during night-time, and most nights with migratory activity were aggregated into rather well-defined travel episodes (see below).

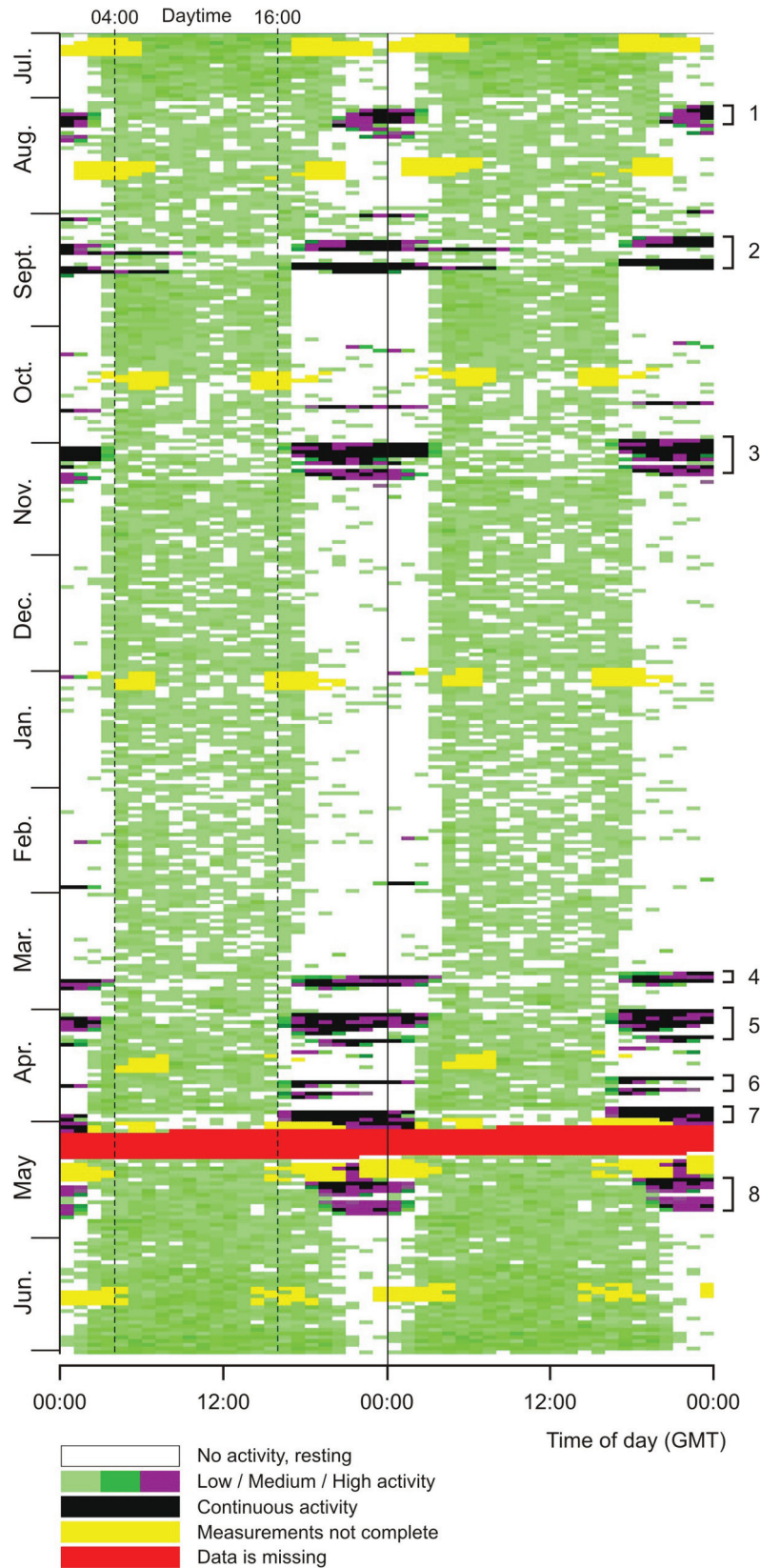


Figure 4. Annual activity pattern for a red-backed shrike, monitored from 15 July 2014 (top) until 2 July 2015 (bottom). Each horizontal line represents accelerometer data from two consecutive days, where the second day is repeated as the first day on the next line. Mean activity level was calculated for each hour ranging from 0 = no activity (white) to 5 = continuous flight throughout the hour (black) with intermediary levels in colour (see text). Activity data was missing from the period 3–9 May. Activity data were not complete (less than the expected sum of 12 activity scores per hour) during periods indicated in yellow. Marked periods 1–8 indicate the different travel episodes (see text and Fig. 5).

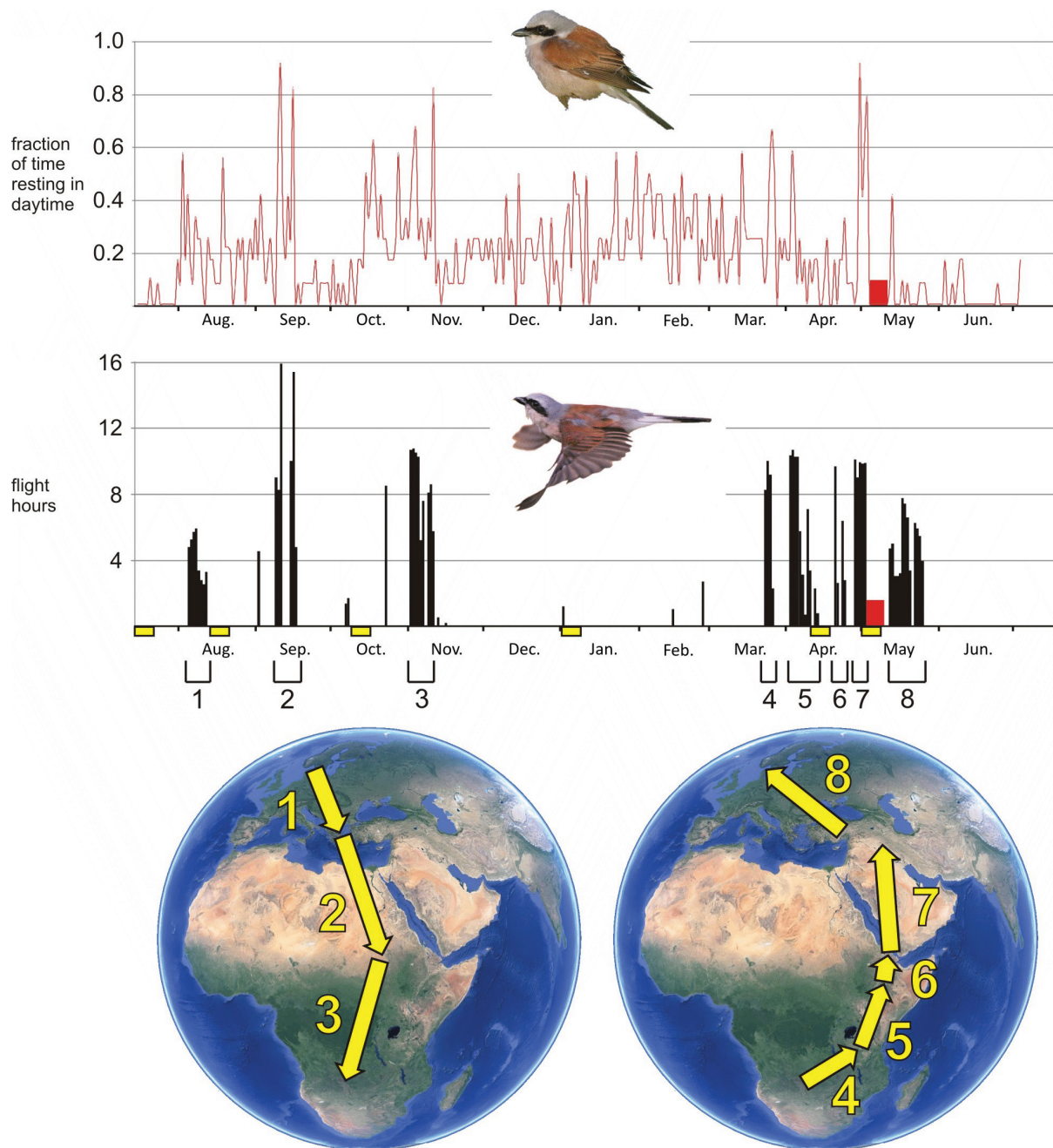


Figure 5. Resting and flight of a red-backed shrike during the annual cycle. The upper diagram shows the fraction of daytime hours 04:00–16:00 GMT (period indicated in Fig. 4) with no activity. The lower diagram shows the duration of 69 flights that were recorded during the year. The flights were aggregated into three travels episodes during autumn migration (episodes 1–3) and five travel episodes during spring migration (episodes 4–8). The schematic geographic interpretation of autumn and spring travel episodes are shown in the two maps (see Table 1, text and Supplementary material Appendix 1–4). Light-level data for geolocation were recorded during six five-day periods during the annual cycle (indicated in yellow along the time axis of flight diagram) and activity data was missing from the period 3–9 May (indicated in red).

Resting and flight throughout the annual cycle

Mean daytime levels of resting (fraction of hours between 04 and 16 h GMT with no activity) are shown along the annual time axis in Fig. 5. The occurrence of migratory flights and their durations throughout the annual cycle are also shown in this figure. The geographic movement associated with the different travel episodes (numbers 1–8 in

Fig. 5 and Table 1) were derived on the basis of light-level measurements for travel episodes 1–3 and from earlier geolocator tracking results for travel episodes 4–8 (when light-level data were poor for the focal individual). Hence, the geographic interpretation of movements during travel episodes 4–8 must be regarded as more provisional, although the red-backed shrikes previously tracked by geolocators (from the same breeding population as the focal individual)

Table 1. Travel episodes and flights recorded by accelerometer during the annual cycle of a red-backed shrike. (A) Main steps of migration were completed during travel episodes when flights took place during the vast majority of nights. Dates, number of nights with and without flights and flight times are given for travel episodes during autumn (1–3) and spring (4–8) migration. The geographic movement associated with each episode (measured or judged by estimation) is shown in Fig. 5. The occurrence of isolated flights outside main travel episodes is given in the right-hand column (see also Fig. 4 and 5 for flight data throughout the annual cycle). (B) Characteristics (dates, numbers, total time, mean time with variation and range) of migratory flights recorded by accelerometer for the red-backed shrike.

(A)

Travel episode	Dates	Number of nights with flights	Number of nights without flights	Total flight time (h)	Flights in between travel episodes
Autumn					
1	4–11 Aug	8	0	33.4	1 Sep (4.5 h)
2	8–16 Sep	6	3	63.3	6–7 Oct (1.3 + 1.7 h)
3	1–10 Nov	9	1	77.4	22 Oct (8.5 h)
Spring					
4	23–26 Mar	4	0	29.7	12 Nov (0.5 h)
5	2–13 Apr	11	1	64.4	15 Nov (0.2 h)
6	20–24 Apr	4	1	21.3	1 Jan (1.2 h)
7 ¹	28 Apr–2 May	5	0	48.7	14 Feb (1.0 h)
8 ^{1, 2}	12–25 May	13 ²	1	78.6 ²	26 Feb (2.7 h)

(B)

	First flight	Last flight	Number of flights	Total flight time (h)	Flight time mean (h)	Flight time SD (h)	Flight time range (h)
Autumn	4 Aug	15 Nov	29	190.8	6.6	4.1	0.2–15.9
Spring ¹	23 Mar	25 May	37 (44 ³)	242.7 (303.9 ³)	6.6	3.1	0.7–10.7
Total ⁴			69	438.4	6.4	3.6	0.2–15.9

¹Missing data for seven nights 3–9 May.

²Five flights 12–16 May may have been underestimated by maximally 15 h total flight time because of lack of start/end times for flights (missing data for some hours).

³Estimate of maximum for spring migration by adding 7 flights of mean duration 6.6 h (46.2 h total duration) during seven nights with missing data 3–9 May, and adding 15 h possibly underestimated flight time 12–16 May.

⁴Including flights 1 Jan, 14 and 26 Feb.

showed a high degree of consistency between individuals in their spring migration routes across NE Africa and the Arabian Desert, with a final leg across Europe from Turkey (Tøttrup et al. 2012).

Daytime resting levels were lowest during the breeding period (end of May, June and July; mean fraction of resting = 0.04, 95%CI = 0.01–0.06, $n = 58$ d), during the initial stay in the Sahel region of Africa (late September, early October) and during the final part of spring migration (mid–end May). These were periods when the bird probably foraged intensively (refuelling during migratory stopover) and/or engaged in breeding activities (the long days during the breeding season and final part of spring migration further enhanced the total daily activity during these periods; cf. Fig. 4).

Daytime resting showed distinct peaks during a few days that were immediately preceded and followed by long migratory flights across Sahara (travel episode 2), across continental Africa (travel episode 3) and across the Arabian desert (travel episode 7), indicating that the bird was spending the days inactive and resting/sleeping between these long migratory flights. Daytime resting was also at a high level during the final part of the bird's stay in Sahel (end October) and throughout the winter stay from December to March (mean fraction of resting during winter period = 0.23, 95%CI = 0.21–0.25, $n = 132$ d).

Characteristics of migratory flights

Activity levels 4 and 5 reflected continuous flight, which occurred only during the night (in two cases the flights lasted into the first part of the day, see below). Since activity levels 4 and 5 did not occur during daytime (except in the two cases mentioned) we can be quite certain that they refer exclusively to continuous flight, allowing us to distinguish efficiently between continuous flight and other activity associated with e.g. foraging or breeding, even when these other activities were intensive. In the vast majority of nights with flight activity (60 out of 69) there seemed to be only one flight for which the start and end times could be calculated from the fraction of activity level 4 and 5 during the first and last hour with flight activity. During intervening hours, activity level was always 4 or 5, indicating continuous flight. Total flight time could thus be calculated as the sum of hours with 100% activity level 4 and 5 and the fractions of time with these activity levels during the initial and final hours of flight activity (and start and end times for the flights could thus be estimated with an accuracy of five minutes). In two of these 60 flights there were missing data for a few hours around midnight with flight activity recorded before and after this gap, and in these cases the intervening hours were included in the flight time by interpolation (assuming that there was no interruption in the nocturnal flight which was clearly the most common pattern, recorded

during 58 of 62 flights with complete activity coverage). During four nights with flight activity the time pattern was irregular, indicating that the bird had landed and started again one or more times, and for these nights the sum of hourly fractions with activity levels 4 and 5 were used as total flight time. During five nights with flight activity (within the period 12–16 May) there were partially missing activity data that made it impossible to determine the start and/or end times of the flight, and the total duration of these flights may have been underestimated by maximally 15 h (cf. Table 1). Records of activity level 4 and 5 during only one isolated measurement (out of the twelve measurements that were made each hour) occurred in nine cases but were not included as flights. Thus, the minimum flight time corresponded to two measurements of activity level 4 and 5 during an hour ($2/12 = 0.17$ h duration).

A total of 69 nocturnal flights were recorded during the annual cycle, with 29 flights during autumn migration, 37 flights during spring migration and three flights during the winter period. Due to missing data from seven days and nights during spring migration, the number of spring flights may have been underestimated by maximally seven nights (using an average flight duration of 6.6 h, the corresponding number of flight hours may have been underestimated by $7 \times 6.6 = 46$ h; cf. Table 1).

Durations of the flights ranged from 0.2 to 15.9 h with a mean of 6.4 h (SD = 3.6 h). Flights were of similar mean duration during autumn and spring migration, while the three nocturnal flights during the winter season were all short (1.2, 1.0 and 2.7 h, respectively). Flight durations showed a rather uniform distribution up to 11 h, above which there were only two cases with longer flight durations (15.9 and 15.4 h, respectively). These two unusually long flights took place on 10–11 and 15–16 September, respectively (not ending until 09.19 and 08.04 h GMT, respectively, which corresponded to about 11 and 10 h local time since the position of the bird was at approx. 30°E longitude), and were associated with the crossing of the Sahara desert (travel episode 2; Fig. 4 and 5; see about prolonged flights over desert in Schmaljohann et al. 2007, Adamik et al. 2016, Ouwehand and Both 2016).

During travel episode 2, when the bird crossed the main barriers of the Mediterranean Sea and the Sahara desert, it stopped for three days and nights after having flown for three nights and before flying for another three nights (total flight time was 63 h for the barrier passages associated with travel episode 2). During these three days the bird was active at a moderate level, suggesting that it had stopped to forage in an oasis in Sahara. In contrast, the crossing of the Arabian desert in spring (travel episode 7) was completed by five long flights (each flight lasted approximately ten hours) during five nights in succession (and with mainly resting during daytime periods; Fig. 4 and 5).

The total flight time for spring migration, between 243 h (minimum) and 304 h (maximum; cf. Table 1), clearly exceeded that for autumn migration (191 h) by 27–59%. This is partly explained by the fact that the spring route is on average 22% longer than the autumn route according to earlier estimates from geolocator tracking data (Tøttrup et al. 2012). Using these distance measurements to estimate the average ground speed of flight gives a higher ground speed

for autumn migration ($9719 \text{ km}/191 \text{ h} = 51 \text{ km h}^{-1}$) compared to spring migration (min $11862 \text{ km}/304 \text{ h} = 39 \text{ km h}^{-1}$, max $11862 \text{ km}/243 \text{ h} = 49 \text{ km h}^{-1}$), indicating that less favourable wind conditions during spring compared to autumn may be an important contributory explanation for the longer total flight time in spring.

Technical issues

The datalogger contained a nearly complete year of data. However, there were some technical issues with the logger. One issue was an interruption in operation from 3 May until 9 May where we assume that the logger stopped because of a near empty battery associated with a phase of more intense measurements (light and accelerometer recording simultaneously). After a period of recovery, the battery was able to deliver energy for the last couple of weeks with lower measurement intensity (no programmed light recordings). Since the datalogger was operating when it was recovered and stopped, we could reconstruct the time of measurements back to where the logger restarted after the interruption. Another issue was an interference with accelerometer measurements during light measurements, probably due to temporary battery overload. This resulted in cases where the sum of activity was not complete, meaning that one or more measurements failed. It is rather obvious when inspecting data that in a majority of cases, only one or a few measurements have actually failed (see complete data file in Supplementary material Appendix 4). These problems have been solved in more recent versions of the datalogger by improving separation of measurement cycles to avoid a temporary strain of the battery. The light stalk has been redesigned to minimize the risk of detachment (Supplementary material Appendix 2).

Discussion

New research dimensions based on individual activity recordings during the annual cycle

The new method of recording rather detailed activity combined with position data during the annual cycle of free-flying songbirds opens up new research dimensions. It makes it possible to define and quantify migratory flight performance, stationary periods and activity patterns throughout the annual cycle as illustrated by the case study of the red-backed shrike (see above). We point out four main topics to exemplify how the new activity measurements will have a profound importance for new insights (Fig. 6).

Flight

The activity recorder allows detailed measurements of the total flight performance during the migratory journey (number of flights as well as flight duration), allowing critical comparisons of total flight investments between migratory seasons (spring and autumn), different species and populations, as well as between different categories of individuals (depending on e.g. age, sex, condition). It will be possible to find out if flights are aggregated into clearly defined bouts or episodes of travel (as for the red-backed

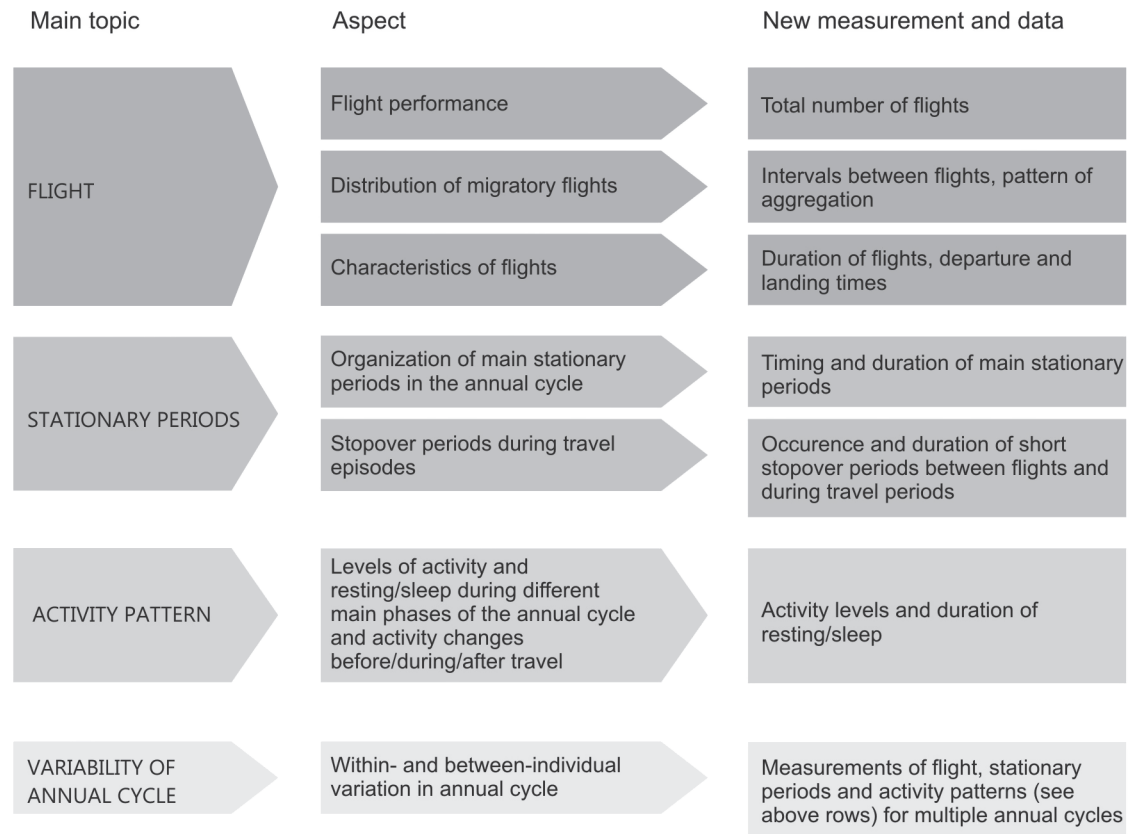


Figure 6. Main topics and aspects that can be addressed by analyzing the new measurements and data provided by the activity recorder. See main text for further explanation.

shrike in the case study) or if songbirds also migrate by a more regular alternation between flights and intervening stopover/stationary periods. The new possibility of accurately determining flight duration will open up possibilities to answer a suite of unsolved questions about duration and timing of migratory flights of songbirds (e.g. how these are affected by weather and potential barriers and how departure and landing times vary) and to integrate with movement/decision data for birds of known condition during specific stopover and passage occasions (Cohen et al. 2012, Deppe et al. 2015).

Stationary periods

With a more precise knowledge of the stationary periods during the annual cycle (and the activity levels during these periods indicating e.g. intensity of foraging versus amount of rest) it will become possible to analyze how stationary periods are linked to seasonal resource peaks at different sites along the migratory circuit. Furthermore, for shorter stopover periods it will be possible to investigate how important weather and winds are in causing interruption of flights during travel episodes and to what degree the birds spend the stopover time foraging or resting/sleeping.

Activity patterns

Activity levels and the level of resting/sleep will reveal time budgets for the individual during its different annual phases. For the red-backed shrike the much higher activity level

during breeding season compared to non-breeding season clearly revealed a high performance level for the bird during breeding, while its time at the winter quarters was much more relaxed. Another striking finding for the red-backed shrike was the change in activity level during the long stationary period in Sahel (about 1.5 months) from a high foraging intensity during the first half of this stay to much more resting during the later half. On a shorter time scale, activity patterns before/during/after travel episodes will help to reveal the importance of foraging/refueling between flights (such intensive day-time foraging between successive flights was indicated for the red-backed shrike during the final part of spring migration, episode 8) or if birds rest/sleep between the flights (as indicated for the red-backed shrike during the crossing of desert barriers, episodes 2 and 7, supporting the findings of Bairlein 1985, Biebach et al. 1986, Biebach 1990, Schmaljohann et al. 2007 and Adamik et al. 2016, but see Ouwehand and Both 2016). Such analyses will also help to understand to what degree sleep is suppressed during travel periods (cf. Fuchs et al. 2006, Németh 2009) and intensive phases in the annual cycle and if birds show more activity investment during spring compared to autumn migration, as would be expected if birds are time-selected to a higher degree in spring but more energy-selected in autumn (Nilsson et al. 2013).

Variability of annual cycle

Multi-year recording of the annual cycle will open up possibilities to analyze the degree of individuality in the

organization of the annual cycle and in migratory habits. This will reveal the flexibility within and between individuals in different features related to flight, stationary periods and activity patterns.

Future development

Future development should include the improvement of methods for on-board processing and analysis of accelerometer data. This would allow identification of more types of specific behaviour (calibration studies of more specific accelerometer signatures in relation to the birds' behaviour, such as simultaneously recorded by video and visual observations in the field, are underway). Most commonly, analyses and classifications of behaviour by larger birds and other animals have been made by post-processing raw data that was downloaded from the datalogger (as reviewed by Brown et al. 2013). Dataloggers of 1 g mass cannot store large amounts of raw data, so processing has to be done in real-time. With our method of reducing data volumes, operations are usually limited by available energy and not limited by memory storage. A potential disadvantage of reduced light measurement periods could be that some more elaborated analysis methods require complete diurnal light cycles or at least entire dusk/dawn light transitions. For applications that require the best possible position estimates, it can be necessary to extend the light measurement scheme.

A promising option is to improve software, such as further optimised operation algorithms or improved data compression. We are certain that it is possible to save energy by making more targeted measurements, e.g. performing a light-level measurement only when the accelerometer data has indicated a number of days without migratory flight behaviour to increase the probability that measurements are taken during stationary periods. This would help to reduce the size of the battery, which is the largest and heaviest component, and would make it possible to construct combined activity/position loggers that could be mounted on even smaller passerines.

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References

- Adamik, P., Emmenegger, T., Briedsi, M., Gustafsson, L., Henshaw, I., Krist, M., Laaksonen, T., Liechti, F., Procházka, P., Salewski, V. and Hahn, S. 2016. Barrier crossing in small avian migrants: individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy. – *Sci. Rep.* doi: 10.1038/srep21560
- Afanasyev, V. 2004. A miniature daylight level and activity data recorder for tracking animals over long periods. – *Memoirs Natl Inst. Polar Res.* 58: 227–233.
- Arlt, D., Olsson, P., Fox, J. W., Low, M. and Pärt, T. 2015. Prolonged stopover duration characterises migration strategy and constraints of a long-distance migrant songbird. – *Anim. Migr.* 2: 47–62.
- Bäckman, J., Andersson, A., Alerstam, T., Pedersen, L., Sjöberg, S., Thorup, K. and Tøttrup, A. P. 2016. Data from: Activity and migratory flights of individual free-flying songbirds throughout the annual cycle: method and first case study. – *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.34dn2>.
- Bairlein, F. 1985. Body weights and fat deposition of Palearctic passerine migrants in the central Sahara. – *Oecologia* 66: 141–146.
- Berthold, P. 1973. Relationships between migratory restlessness and migration distance in six *Sylvia* species. – *Ibis* 115: 594–599.
- Berthold, P. 1996. Control of bird migration. – Chapman and Hall.
- Berthold, P. 2001. Bird migration. A general survey, 2nd ed. – Oxford Univ. Press.
- Biebach, H. 1990. Strategies in trans-Sahara migrants. – In: Gwinner, E. (ed.), *Bird migration, physiology and ecophysiology*. Springer, pp. 352–367.
- Biebach, H., Friedrich, W. and Heine, G. 1986. Interaction of body mass, fat, foraging and stopover period in trans-Sahara migrating passerine birds. – *Oecologia* 69: 370–379.
- Bouten, W., Baaij, E. W., Shamoun-Baranes, J. and Camphuysen, K. C. J. 2013. A flexible GPS tracking system for studying bird behaviour at multiple scales. – *J. Ornithol.* 154: 571–580.
- Bridge, E. S., Thorup, K., Bowlin, M. S., Chilson, P. B., Diehl, R. H., Fleron, R. W., Hartl, P., Kays, R., Kelly, J. F., Robinson, W. D. and Wikelski, M. 2011. Technology on the move: recent and forthcoming innovations for tracking migratory birds. – *Bioscience* 61: 689–698.
- Brown, D. D., Kays, R., Wikelski, M., Wilson, R. and Klimley, A. P. 2013. Observing the unwatchable through acceleration logging of animal behaviour. – *Anim. Biotelemetry* 1: 20.
- Bruderer, B., Peter, D., Boldt, A. and Liechti, F. 2010. Wing-beat characteristics of birds recorded with tracking radar and cine camera. – *Ibis* 152: 272–291.
- Chernetsov, N. 2012. Passerine migration. Stopovers and flight. – Springer.
- Cochran, W. W. 1970. Long-distance tracking of birds. – In: Galler, S. R., Schmidt-Koenig, K., Jacobs, G. J. and Belleville, R. E. (eds), *Animal orientation and navigation*. National Aeronautics and Space Administration, Special Publication 262, pp. 39–69.
- Cochran, W. W. 1985. Orientation and other migratory behaviours of a Swainson's thrush followed for 1500 km. – *Anim. Behav.* 35: 927–929.
- Cohen, E. B., Moore, F. R. and Fischer, R. A. 2012. Experimental evidence for the interplay of exogenous and endogenous factors on the movement ecology of a migrating songbird. – *PLoS One* 7: e41818.
- Deppe, J. L., Ward, M. P., Bolus, R. T., Diehl, R. H., Celis-Murillo, A., Zenal Jr, T. J., Moore, F. R., Benson, T. J., Smolinsky, J. A., Schofield, L. N., Enstrom, D. A., Paxton, E. H., Bohrer, G., Beveroth, T. A., Raim, A., Obringer, R. L., Delaney, E. and Cochran, W. W. 2015. Fat, weather and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. – *Proc. Natl Acad. Sci. USA* 112: E6331–E6338.
- Dorst, J. 1962. The migrations of birds. – Heinemann.
- Eikenaar, C. and Schmaljohann, H. 2015. Wind conditions experienced during the day predict nocturnal restlessness in a migratory songbird. – *Ibis* 157: 125–132.

- Eikenaar, C., Klinner, T., Szostek, K. L. and Bairlein, F. 2014. Migratory restlessness in captive individuals predicts actual departure in the wild. – *Biol. Lett.* 10: 20140154.
- Ekström, C. U. 1826. Strödda anteckningar om svenska flyttfoglarna, och i synnerhet tiden för deras ankomst och afflyttning i Södermanland. (Notes about Swedish migratory birds, especially their times of arrival and departure in the province of Södermanland.) – *Kungliga Vetenskaps Akademiens Handlingar* 1826: 153–168, in Swedish.
- Fuchs, T., Haney, A., Jechura, T. J., Moore, F. R. and Bingman, V. P. 2006. Daytime naps in night-migrating birds: behavioural adaptation to seasonal sleep deprivation in the Swainson's thrush, *Catharus ustulatus*. – *Anim. Behav.* 72: 951–958.
- Gwinner, E. 1967. Circannuale Periodik der Mauser und der Zugunruhe bei einem Vogel. – *Naturwissenschaften* 54: 447.
- Gwinner, E. 1969. Untersuchungen zur Jahresperiodik von Laubsängern. – *J. Ornithol.* 100: 1–21.
- Gwinner, E. 1986. Circannual rhythms. – Springer.
- Gwinner, E. 1990. Circannual rhythms in bird migration: control of temporal patterns and interactions with photoperiod. – In: Gwinner, E. (ed.), *Bird migration. Physiology and ecophysiology*. Springer, pp. 257–268.
- Gwinner, E. and Helm, B. 2003. Circannual and circadian contributions to the timing of bird migration. – In: Berthold, P., Gwinner, E. and Sonnenschein, E. (eds), *Avian migration*. Springer, pp. 81–95.
- Hill, C. and Braun, M. J. 2001. Geolocation by light level – the next step: latitude. – In: Sibert, J. R. and Nielsen, J. (eds), *Electronic tagging and tracking in marine fisheries*. Kluwer Academic Publishers, pp. 315–330.
- Kays, R., Crofoot, M. C., Jetz, W. and Wikelski, M. 2015. Terrestrial animal tracking as an eye on life and planet. – *Science* 348: 1222–1225.
- Liechti, F., Witvliet, W., Weber, R. and Bächler, E. 2013. First evidence of a 200-day non-stop flight in a bird. – *Nat. Commun.* 4: 2554.
- Lisovski, S. and Hahn, S. 2012. GeoLight – processing and analysing light-based geolocator data in R. – *Methods Ecol. Evol.* 3: 1055–1059.
- Migrate Technology 2015. – *IntiProc Geolocation Processing Software* 1–11.
- Naef-Daenzer, B. 2007. An allometric function to fit leg-loop harnesses to terrestrial birds. – *J. Avian Biol.* 38: 404–407.
- Németh, Z. 2009. Observation of day-time sleep-like behaviour in a migratory songbird during stopover. – *Wilson J. Ornithol.* 121: 644–646.
- Newton, I. 2008. *The migration ecology of birds*. – Academic Press.
- Nilsson, C., Klaassen, R. H. G. and Alerstam, T. 2013. Differences in speed and duration of bird migration between spring and autumn. – *Am. Nat.* 181: 837–845.
- Ouwehand, J. and Both, C. 2016. Alternate non-stop migration strategies of pied flycatchers to cross the Sahara desert. – *Biol. Lett.* 12: 20151060.
- Palmgren, P. 1935. Ein einfacher Apparat zur Registrierung der Intensitätsvariation der Zugunruhe bei gekäfigten Vögel. – *Ornis Fenn.* 12: 55–58.
- Rattenborg, N. C., Mandt, B. H., Obermeyer, W. H., Winsauer, P. J., Huber, R., Wikelski, M. and Benca, R. M. 2004. Migratory sleeplessness in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). – *PLoS Biol.* 2: e212.
- Schmaljohann, H., Liechti, F. and Bruderer, B. 2007. Songbird migration across the Sahara: the non-stop hypothesis rejected! – *Proc. R. Soc. B* 274: 735–739.
- Stutchbury, B. J. M., Tarof, S. A., Done, T., Gow, E., Kramer, P. M., Tautin, J., Fox, J. W. and Afanasyev, V. 2009. Tracking long-distance songbird migration by using geolocators. – *Science* 323: 896.
- Thorup, K., Holland, R. A., Tøttrup, A. P. and Wikelski, M. 2010. Understanding the migratory orientation program of birds: extending laboratory studies to study free-flying migrants in a natural setting. – *Integr. Comp. Biol.* 50: 293–304.
- Tøttrup, A. P., Klaassen, R. H. G., Strandberg, R., Thorup, K., Kristensen, M. W., Jørgensen, P. R., Fox, J., Afanasyev, V., Rahbek, C. and Alerstam, T. 2012. The annual cycle of a trans-Equatorial Eurasian-Africa passerine migrant: different spatio-temporal strategies for autumn and spring migration. – *Proc. R. Soc. B* 279: 1008–1016.
- Wagner, H. O. 1930. Über Jahres- und Tagesrhythmus bei Zugvögel. – *Z. Vergleichende Physiol.* 12: 703–723.
- Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R. and Butler, P. 2006. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. – *J. Anim. Ecol.* 75: 1081–1090.

Supplementary material (Appendix JAV-01068 at <www.avianbiology.org/appendix/jav.01068>). Appendix 1–4.