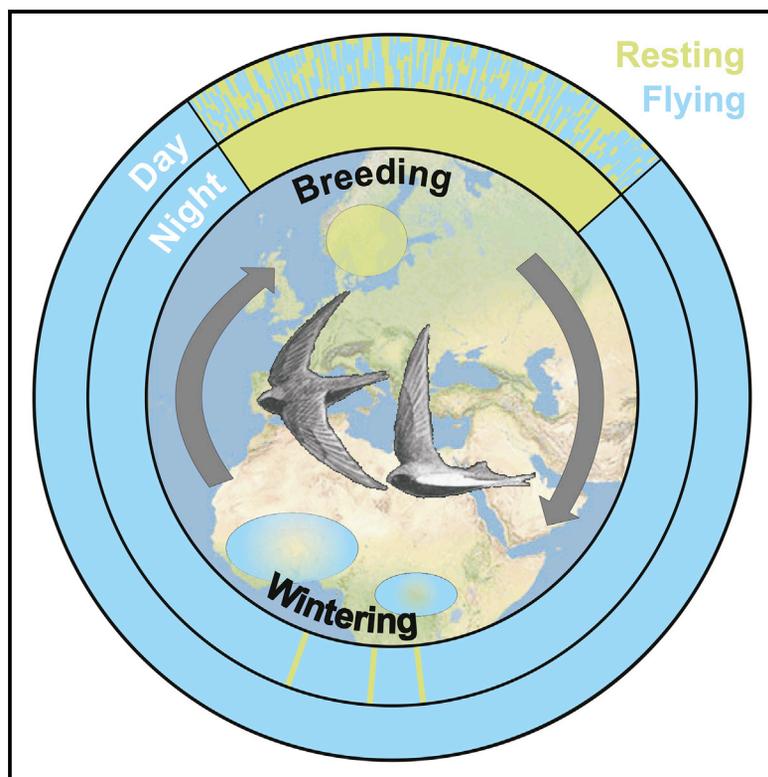


Current Biology

Annual 10-Month Aerial Life Phase in the Common Swift *Apus apus*

Graphical Abstract



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In Brief

Hedenström et al. show that common swifts almost never land during their 10-month migration and wintering periods. Occasional nightly landings occur in winter, but they are often brief, and accumulated time not flying is less than 1%. These findings provide evidence of a long-standing conjecture about the aerial lifestyle in common swifts.

Highlights

- Common swifts remain airborne for 10 months of their non-breeding period
- Dawn and dusk ascents occur throughout the migration and wintering periods
- Periodic nocturnal landings of short duration occur in most individuals
- A new micro data logger with optimized sampling routines made this research possible



Annual 10-Month Aerial Life Phase in the Common Swift *Apus apus*

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<http://dx.doi.org/10.1016/j.cub.2016.09.014>

SUMMARY

The common swift (*Apus apus*) is adapted to an aerial lifestyle, where food and nest material are captured in the air. Observations have prompted scientists to hypothesize that swifts stay airborne for their entire non-breeding period [1, 2], including migration into sub-Saharan Africa [3–5]. It is mainly juvenile common swifts that occasionally roost in trees or buildings before autumn migration when weather is bad [1, 6]. In contrast, the North American chimney swift (*Chaetura pelagica*) and Vaux's swift (*C. vauxi*) regularly settle to roost in places like chimneys and buildings during migration and winter [7, 8]. Observations of common swifts during the winter months are scarce, and roost sites have never been found in sub-Saharan Africa. In the breeding season, non-breeding individuals usually spend the night airborne [9], whereas adult nesting birds roost in the nest [1]. We equipped common swifts with a micro data logger with an accelerometer to record flight activity (years 1–2) and with a light-level sensor for geolocation (year 2). Our data show that swifts are airborne for >99% of the time during their 10-month non-breeding period; some individuals never settled, but occasional events of flight inactivity occurred in most individuals. Apparent flight activity was lower during the daytime than during the nighttime, most likely due to prolonged gliding episodes during the daytime when soaring in thermals. Our data also revealed that twilight ascents, previously observed during the summer [10], occur throughout the year. The results have important implications for understanding physiological adaptations to endure prolonged periods of flight, including the need to sleep while airborne.

RESULTS AND DISCUSSION

We equipped adult common swifts at two sites in southern Sweden with data loggers to record acceleration and monitor flight activity in 2013 and, in addition to acceleration, also light data for geolocation in 2014. The data loggers and sampling routine

were tailored for economic data storage of both activity and light data (see the [Supplemental Experimental Procedures](#)). We recaptured 11 birds in 2014 and eight birds in 2015. One data logger retrieved in 2015 was deployed in 2013 and contained activity recordings for 2 years. Of the retrieved loggers, two from 2014 showed technical problems and did not contain data. The light data showed that the swifts spent the winter in either West Africa (Liberia, Ivory Coast, and Ghana) or in Central Africa (Democratic Republic of Congo and Congo Brazzaville), with birds from both breeding sites wintering in the two main wintering areas ([Figure 1](#)). This is in agreement with previous results on Swedish swifts [4, 5].

For five birds we recorded flight activity for 2 years. From one bird we recovered a logger that had been attached for 2 years, including two breeding seasons ([Figure 2](#)), whereas the others were from birds that carried different loggers in two consecutive years, including one breeding season ([Figures 3](#) and [S1](#)). To confirm that the accelerometer data accurately represent flap-gliding flight versus no flight in common swifts, we simulated data acquisition by our sampling regime using a dataset of the wing-beat pattern obtained by radar echo signature (see the [Supplemental Experimental Procedures](#)). Breeding-season activity shows a characteristic pattern of nocturnal flight inactivity, with inactive periods during the daytime representing nest visits ([Figures 2, 3A, S1, and S2](#)). The accelerometer data also revealed when the bird was inactive in a near-vertical position (as the species is often depicted to do in field guides, which we consider as confirmed landings), which bird 1 did for two nights at the beginning of the 2014 breeding period ([Figure 2](#)), suggesting that it may have settled to roost outside the nest. There is a clear difference in the pattern of relative daytime flight inactivity between the two breeding periods in bird 1 ([Figure 2](#)), which may suggest that it had nestlings only in the second year, when it spent more time in the nest.

During migration and winter periods, there was almost a total lack of inactivity recordings, except for a few nights in February in 2014, when bird 1 settled in a vertical position during four whole nights (0.64% of the time from September–April) ([Figure 2](#)). In the second winter period, there were no indications of whole-night inactivity, with only one recorded stop of 2 hr (0.03% of time) ([Figure 2](#)), suggesting that this swift practically spent the entire non-breeding period airborne that year. In this case, the data suggest that the bird remained airborne for about 10 months (314 days). However, not all birds spent the entire non-breeding season airborne, as illustrated by bird 2, which showed signs of intermittent nocturnal flight inactivity from November–January in 2013–2014 ([Figure 3A](#)) and a similar pattern the following winter

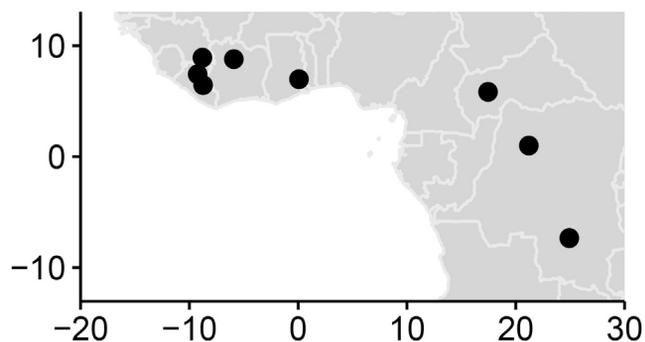


Figure 1. Winter Locations for Common Swifts in Africa

Map of the part of Africa showing the mean (February) wintering positions for individual common swifts equipped with activity loggers that, in addition to flight activity, also recorded light levels for geolocation between 2014 and 2015. See also [Figures S1](#) and [S3](#).

([Figure 3B](#)). The pattern for this bird was very similar, but not identical, between the 2 years, although flight behavior was recorded with two different sampling routines (see the [Supplemental Experimental Procedures](#)). This lends support for the

notion that the measurements accurately reflect flight behavior. However, the duration of landings was short, and in the 2013–2014 season no inactivity period was longer than 2 hr, whereas in 2014–2015 the bird was recorded as totally inactive for 23 hr (0.4% of the time September–April). Notice that during short periods of nocturnal inactivity, the swifts are not necessarily roosting with the body axis vertically aligned, but they may do so also with the body aligned near horizontal ([Figures 2](#) and [3](#)).

The remaining individuals show similar variation in flight behavior from being virtually completely airborne (birds 3, 7, 9, and 10; [Figures S1](#) and [S2](#)) to clear patterns of periodic nocturnal inactivity similar to that of bird 2 (birds 4–6, 8, and 11–13; [Figures S1–S3](#)), although the amount of inactivity periods varies between individuals. Five birds were tracked during two consecutive non-breeding periods, and they show similar, but not identical, flight activity between the 2 years ([Figures 2, 3](#), and [S1](#)). For example, bird 3 was largely airborne and had no inactivity periods longer than 2 hr in the 2 years, whereas birds 4 and 5 did show periods of nocturnal flight inactivity ([Figure S1](#)), although the accumulated duration of inactivity of 2 hr or more were only 9 and 11.5 hr, respectively. Nocturnal inactivity periods often seem to be of short durations, but whole-night inactivity was recorded

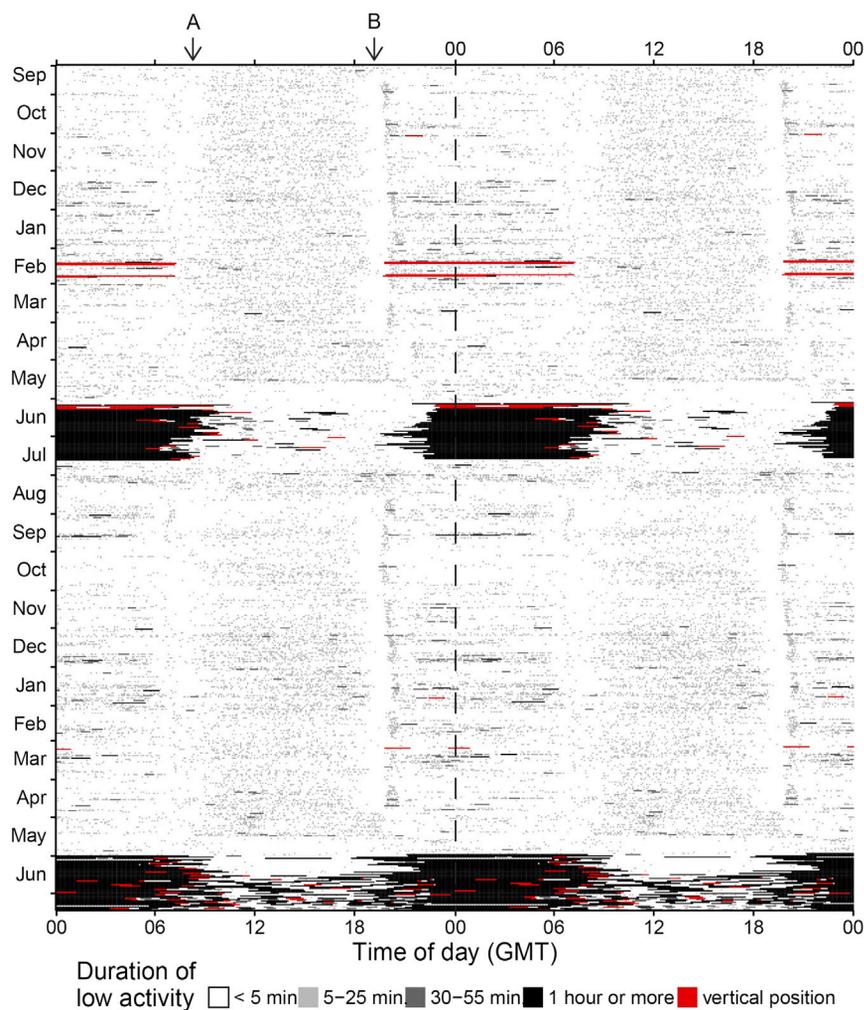


Figure 2. Flight Actogram Showing Flight Activity for a Common Swift

This bird (bird 1) was monitored during two successive years, 2013–2015, using logger type 1 (see the [Supplemental Experimental Procedures](#)). The figure shows data starting in September 2013 (top) running throughout June 2015 (bottom). Each horizontal line shows accelerometer data from two consecutive days, where the second day is duplicated as the first day on the next line to illustrate circadian patterns. Black horizontal bars show recordings indicative of non-flight, which in most cases are false indications due to the species' flap-gliding flight style. Red horizontal bars indicate that the bird's body orientation is near vertical, which means it is not flying. In the summer, the activity pattern shows alternate periods of foraging flight and nest visits. Arrows at the top indicate flight activity peaks around dawn (A) and dusk (B), respectively. See also [Figures S1–S3](#).

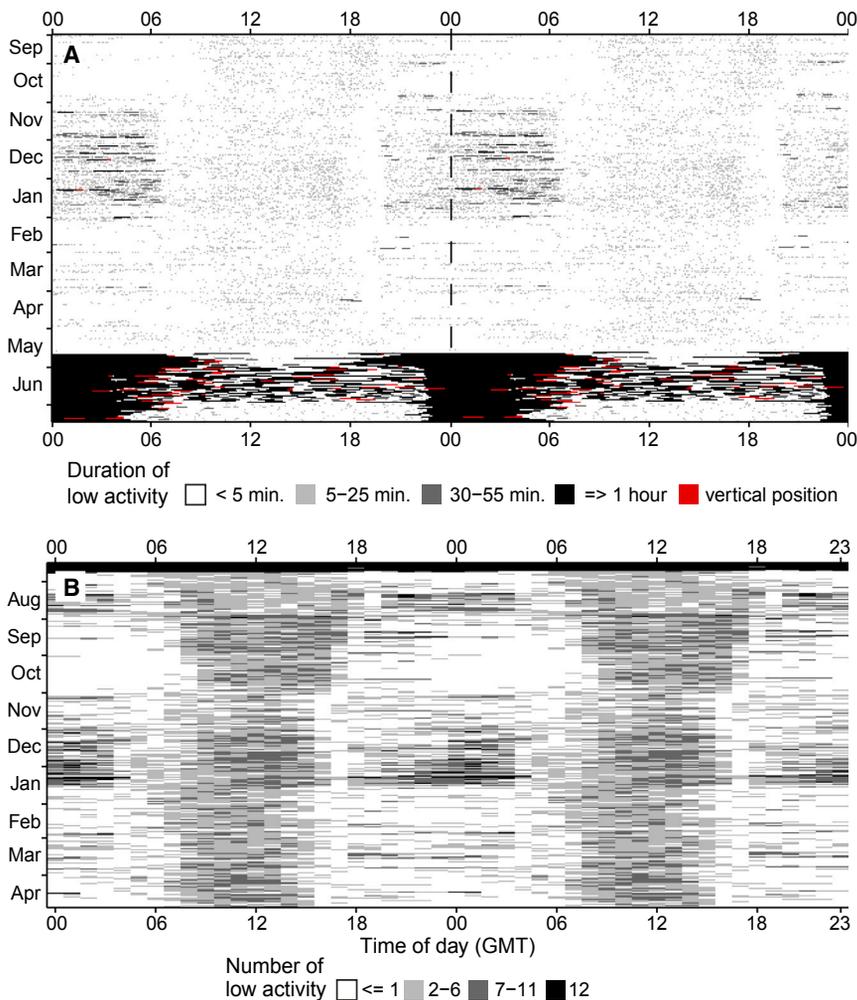


Figure 3. Flight Actogram for a Common Swift Monitored during 2 Years with Different Sampling Routines

The same common swift (bird 2) was monitored during 2 years using the two different logger types: type 1 during 2013–2014 (A) and type 2 during 2014–2015 (B) (see the [Supplemental Experimental Procedures](#)). In (A), logger started collecting data September 6, 2013; in (B), the logger started collecting data on July 15, 2014. See also [Figures S1–S4](#).

([Figures 2, 3, and S1–S3](#)). Immediately after the period of high flight activity around dusk, there is a short period of reduced flapping flight activity (denoted B in [Figure 2](#)), which is concordant with a gliding descent after a flapping flight ascent. The diurnal pattern of relatively more inactivity indications during daytime cannot be due to actual landings, since they are never recorded as indications of complete quiescent behavior and are much too short. Instead, we interpret this daily rhythm of relative flapping flight activity as a result of longer glide phases due to increased thermal soaring in daytime. This is contrary to the pattern observed in the Alpine swift, which appears to show longer glide phases during the nighttime than during the daytime [11].

The activity recorder used during the first year (2013–2014) allows us to illustrate seasonal differences in flight patterns. During autumn migration, the

proportion of active flight is generally high, in particular during the nighttime, with the slightly lower activity values in the daytime probably reflecting prolonged gliding flight periods when soaring ([Figure 4A](#)). In mid-winter, there is some variation between individuals in flight activity during the nighttime ([Figure 4B](#)), reflecting individual variation in the frequency of flight inactivity (cf. [Figure S1](#)), whereas daytime flight activity is similar to that during migration ([Figures 4A and 4B](#)). During spring migration, flight activity is very similar to that of autumn migration ([Figures 4A and 4C](#)). The breeding period shows a dramatic change in flight activity compared with the non-breeding period, reflecting the nightly roosting inside the nest and frequent nest visits during the daytime ([Figure 4D](#)).

in four birds (birds 1, 4, 10, and 13; [Figures 2, S1, and S3](#)). The amount of accumulated inactivity duration, including periods of 2 hr or more, during the non-breeding period (September–April) varied between 0% (birds 3, 7, and 9) and a maximum of 0.64% (bird 13; [Figures S1–S3](#)).

Inspection of the activity diagrams reveal two periods daily, one around 7–8 a.m. (denoted A in [Figure 2](#)) and another at 6–7 p.m. (denoted B in [Figure 2](#)), discerned as vertical bands of an almost complete lack of flight inactivity indications. These bi-daily periods that last for about 1.5 hr suggest an elevated proportion of flapping flight, which is consistent with climbing flight. Common swifts have been shown to perform ascents to altitudes up to 2,500 m around dusk and dawn in the summer [10], whereas our data suggest that common swifts make such ascents throughout the year. A similar pattern has been recorded in the Alpine swift (*Tachymarpis melba*) [11]. The reason for such ascending flights remains obscure, but it has been suggested they are involved in navigation rather than foraging [10]. Our results show that no matter what the reason for this behavior is, it occurs throughout the annual cycle.

Another diurnal rhythm in flight activity is a relatively higher proportion of gliding flight during the daytime compared to the nighttime, except for the occasions of nocturnal inactivity events

proportion of active flight is generally high, in particular during the nighttime, with the slightly lower activity values in the daytime probably reflecting prolonged gliding flight periods when soaring ([Figure 4A](#)). In mid-winter, there is some variation between individuals in flight activity during the nighttime ([Figure 4B](#)), reflecting individual variation in the frequency of flight inactivity (cf. [Figure S1](#)), whereas daytime flight activity is similar to that during migration ([Figures 4A and 4B](#)). During spring migration, flight activity is very similar to that of autumn migration ([Figures 4A and 4C](#)). The breeding period shows a dramatic change in flight activity compared with the non-breeding period, reflecting the nightly roosting inside the nest and frequent nest visits during the daytime ([Figure 4D](#)).

Adult common swifts typically molt their flight feathers in the winter [12], but sometimes they return to the breeding area with the outermost primary left unmolted. We recorded molt in 11 of the birds and divided these into one group that showed no or little flight inactivity during the winter (birds 1, 7, 9, and 10; [Figures 1, S2, and S3](#)) and one group that showed a pattern of periodic flight inactivity (birds 2, 4, 5, 8, and 11–13; [Figures 1 and S1–S3](#)). Of the birds in the mainly airborne group, all four had completed wing and tail molt during the preceding winter, whereas in the group of periodic nocturnal flight inactivity, all

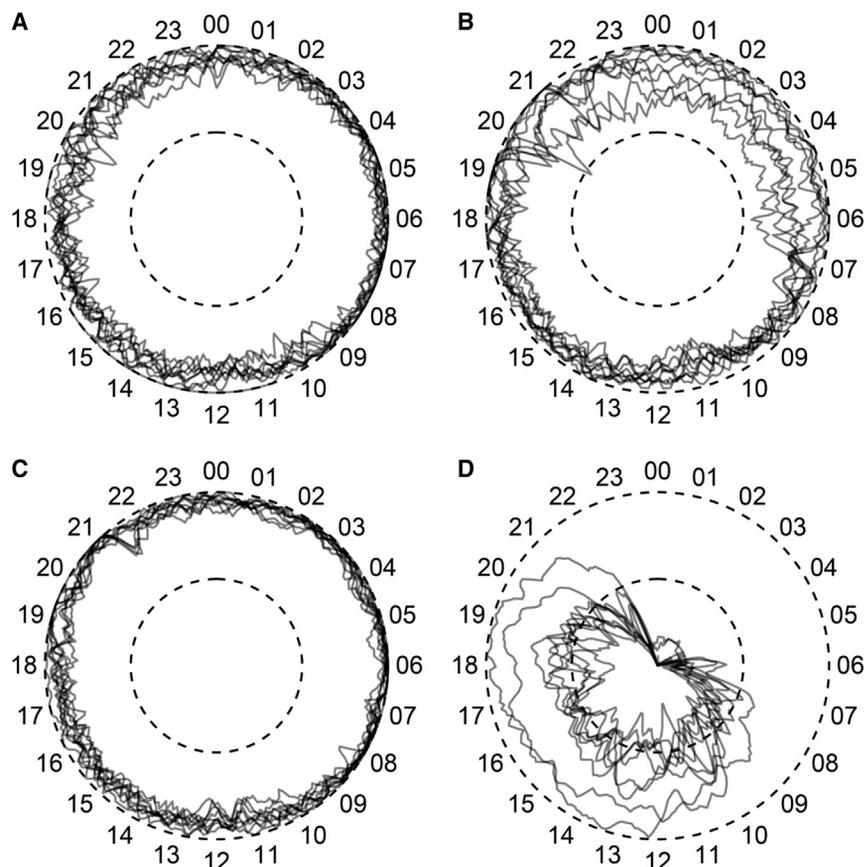


Figure 4. Seasonal Flight Activity in Common Swifts

Daily flight activity pattern during four periods recorded in 2013–2014 for nine individuals providing complete data. The circles show hourly means of flight activity, where the proportion of flight activity is measured as the proportion of 5 min periods representing flight. The dashed lines denote the 50% and 100% activity levels, respectively. Shown are autumn migration (September; A), winter residency (February; B), spring migration (April; C), and breeding (June; D). See also Figure S4.

but one out of seven birds retained unmolted outer primary. The difference between the groups is statistically significant ($p = 0.0152$, two-tailed Fisher's exact test). As molt is an energetically and aerodynamically costly process [13, 14], especially in an aerial bird, this suggests that there could be a physiological correlate explaining the pattern of nocturnal flight inactivity in the winter.

Conclusions

Our data resolved a long-standing enigma about non-breeding flight behavior in the common swift, which had been conjectured to remain airborne for the entire non-breeding period [2]. We show that individual birds may do so, but that regular events of flight inactivity do occur during the nighttime. However, even when swifts settle to roost, the amount of time not flying is very small. The Alpine swift also has an aerial lifestyle during the non-breeding period [11], but this period of about 10 months in common swifts is 3.5 months shorter in Alpine swifts. Such an extreme lifestyle raises questions related to a continuous high metabolic rate of flight [15] and its possible effects on immune function [16], as well as when and to what extent swifts need to sleep [17]. Great frigate birds (*Fregata minor*), which may stay aloft for up to 2 months [18], can sleep while airborne, although only for 7.4% of the time spent sleeping on land [19]. The minimal occurrence of full night inactivity and the fact that some individuals did not settle at all suggest that it is not a necessity for swifts to do so and is perhaps mainly a result of bad weather. It should therefore be of great interest to record sleep

activity in airborne swifts. The common swift has a streamlined body and high-aspect-ratio wings, which combined with a flap-glide flight style result in an efficient flight with low energy cost [20]. So, what are the main selective forces leading to such an extreme aerial lifestyle as found in swifts? One factor could be that specializing in high-altitude aerial insects as a main food source requires the suite of adaptations for efficient flight shown by swifts [21–23], which compromises terrestrial locomotion and make swifts vulnerable to predators and parasites had they been landing more often. Our data suggest that even if common swifts settle to roost occasionally, which

has been observed also in young swifts if the weather is bad [6], their predominant element during the 10-month non-breeding period is up in the air.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and four figures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.09.014>.

AUTHOR CONTRIBUTIONS

A.H. and S.Å. conceived the study; A.A. and J.B. designed the accelerometers and downloaded the data; G.N., A.H., and S.Å. conducted the fieldwork; K.W. simulated flight activity data; A.H., G.N., and S.Å. analyzed the data; A.H. drafted the manuscript; and all authors discussed the results and commented on the manuscript.

ACKNOWLEDGMENTS

We are grateful to David Winkler and an anonymous reviewer for comments on the manuscript. The research received supported from the Swedish Research Council to A.H. (621-2012-3585) and S.Å. (621-2013-4361), and the Centre for Animal Movement Research (CAnMove) was financed by a Linnaeus grant (349-2007-8690) from the Swedish Research Council and Lund University. This is contribution no. 297 from Ottenby Bird Observatory.

Received: August 22, 2016
 Revised: September 8, 2016
 Accepted: September 9, 2016
 Published: October 27, 2016

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Supplemental Information

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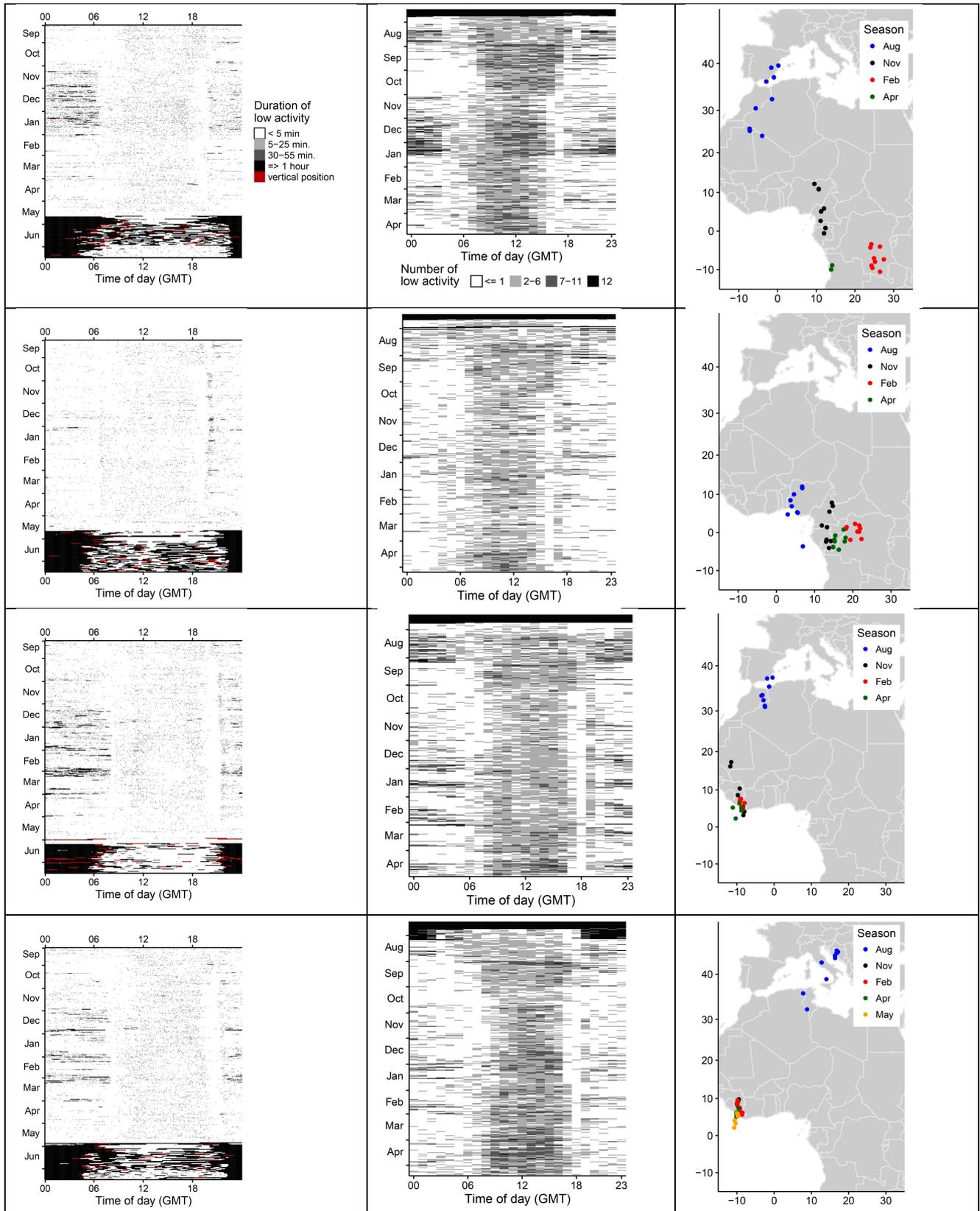


Figure S1. **Actograms and locations for common swifts tracked for two years.** Related to Figures 1-3. Upper row is bird #2, second row is bird #3, third row is bird #4, and bottom row is bird #5. Left column is year 2013-2014, middle column is year 2014-2015, and right column shows raw geolocation positions for 2014-2015.

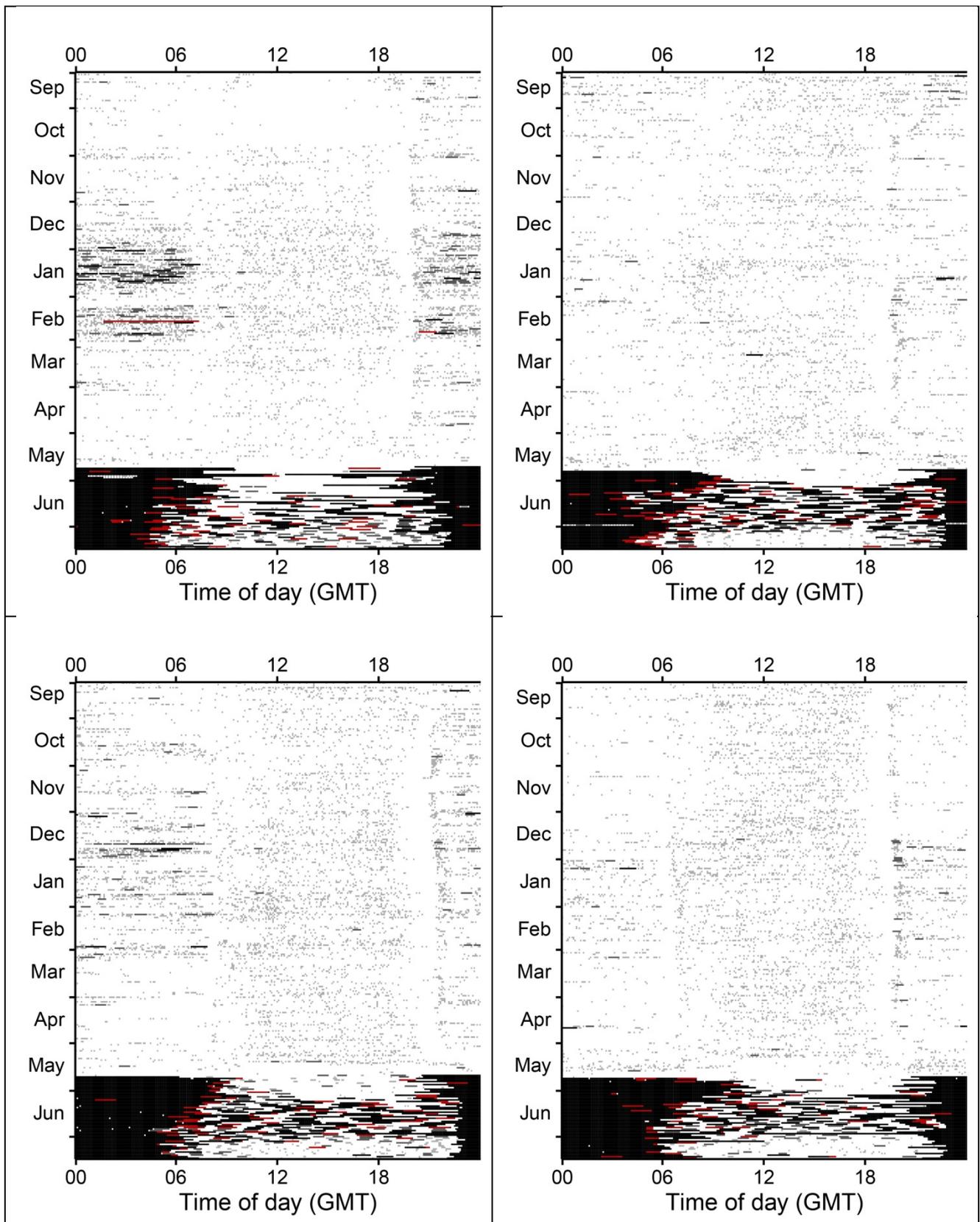


Figure S2. **Actograms for common swifts during 2013-2014.** Related to Figures 2-3. Upper left is bird #6, upper right is bird #7, lower left is bird #8, and lower right is bird #9.

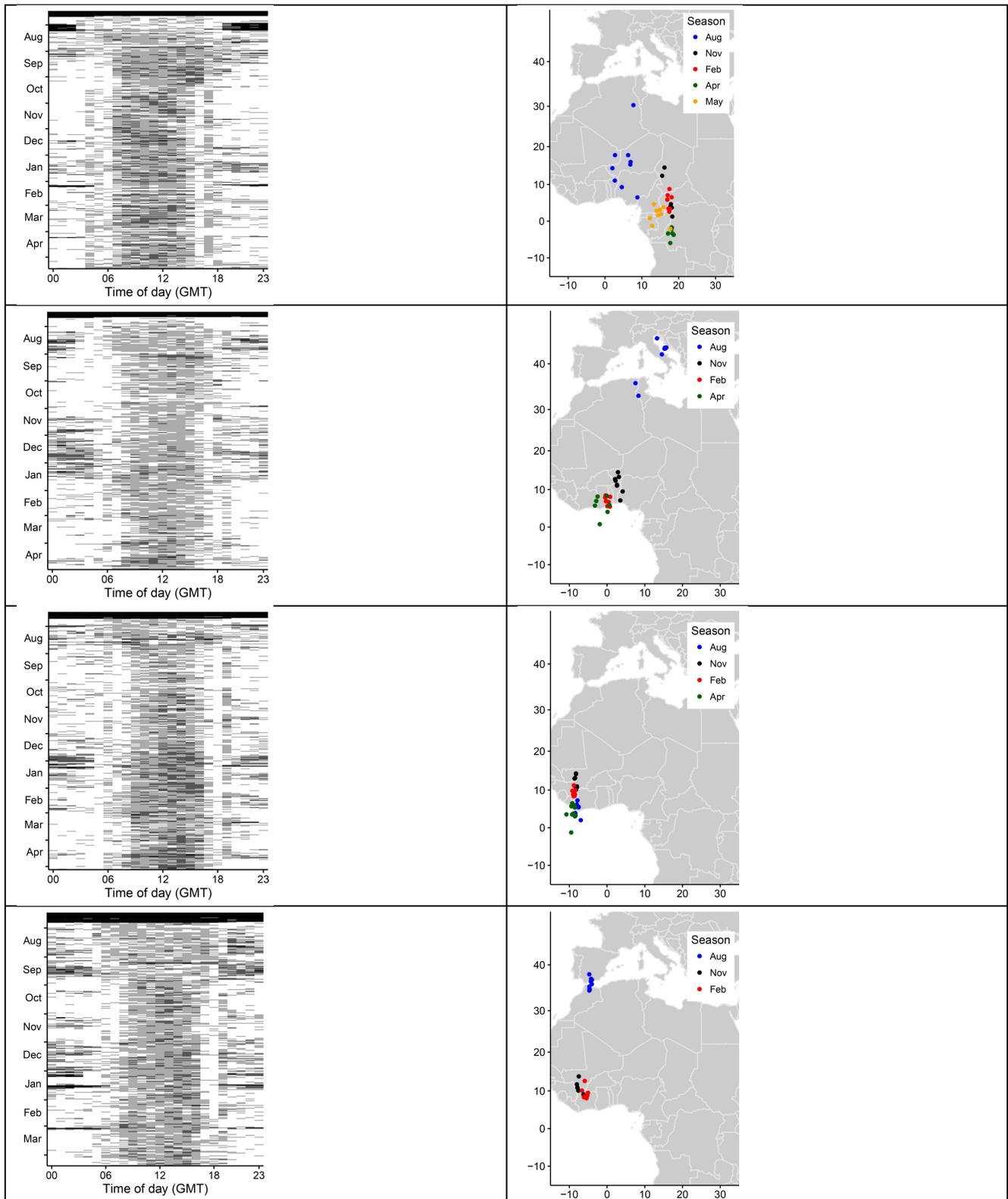


Figure S3. **Actograms and locations for common swifts tracked during 2014-2015.** Related to Figure 1-3. Annual activity pattern and raw geolocation positions for season 2014-2015. Upper row is bird #10, second row is bird #11, third row is birds #12, and bottom row is bird #13. Right column shows actograms and right column shows raw geolocation positions.

FIGURE S4

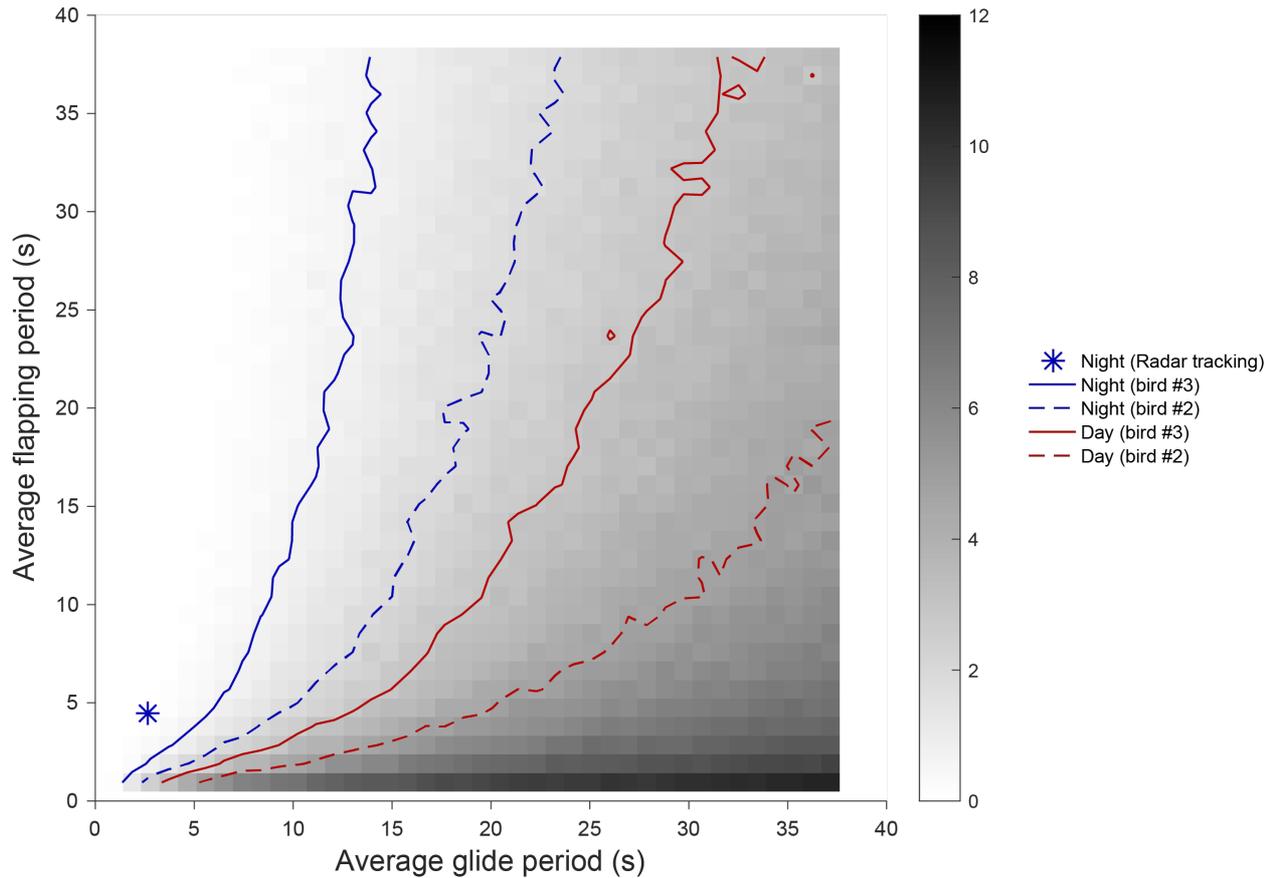


Figure S4. **Simulation of the sampling routine for type 2 loggers.** Related to Figure 3 and 4, and Supplemental Experimental Procedures. Simulated accelerometer measurements using flap-glide sequences generated from Weibull distributions (flapping period: $k_f=1.17$; gliding: $k_g=1.26$). λ is varied from 1-40 for both flapping and gliding, resulting in average periods of 0.95-37.9 s for flapping and 0.93-37.2 s for gliding. Background colour represents number of occurrences, per hour, of complete inactivity (all 5 measurements registered as “0”). Isolines show the average number of completely inactive periods every hour during day-time (9 a.m. – 3 p.m.) and night-time (8 p.m. – 3 a.m.) from 2014-09-01 for the most active (bird #3) and inactive (bird #2) individuals. Blue star represents the average value of Weibull distributions fitted to data of flap-glide sequences previously recorded by radar tracking.

SUPPLEMENTAL EXPERIMENTAL PROCEDURES

In 2013 and 2014 adult swifts (20 and 27) breeding at two sites in Sweden, Ås, Öland (56°14'17.40''N, 16°27'05.41''E) and Medhamn, Värmland (59°07'02.21''N, 13°58'31.70''E), were equipped with micro data loggers custom designed to record flight activity (2013) and in addition to flight activity also light level data for geolocation [S1, S2] in 2014. The birds were recaptured the year after deployment, except in one case where a logger deployed in 2013 was received in 2015. The data loggers were attached to the back of the birds using a body harness [S3]. The loggers were attached to the birds between 2013-07-16 and 2013-07-27, and started the sampling 2013-09-06, and between 2014-07-21 and 2014-07-23 with start of sampling 2014-07-15, respectively.

Hardware and sampling routines

The microprocessor-controlled data logger comprises an accelerometer, a memory and in 2014 also a light sensor. The logger measures acceleration in 3 dimensions at a $\pm 4g$ range with 8-bit effective resolution, with sampling rate set to 25Hz or 100 Hz to allow detection of the $\sim 7-8$ Hz wing flaps. Only the vertical axis (Z) acceleration was used for activity analysis. Z is the vertical axis – parallel to gravity – when the bird is flying level. If the bird roosts vertically acceleration due to gravity will be recorded by the X-axis. The weight of the data logger is $\leq 1.1g$.

Different sampling routines were used in the two years. The loggers deployed in 2013 (type 1) were programmed to wake up every 5 minutes, and collect 32 samples at 25Hz (equivalent to a 1.28s time period). The mean of the vertical axis values is calculated and subtracted from each Z-axis value to compensate for the static acceleration due to gravity (g). Then each of the 32 Z-values are compared with a threshold value indicative of powered flight, and the logger goes back to sleep if the result shows activity. The bird is considered flying (active) if 10 out of the 32 Z-values were outside $\pm g/3$. If inactivity is indicated, another measurement is made with a 10-second delay. The bird is considered inactive if 5 consecutive measurements with 10-second interval indicate lack of movement above the threshold. This measurement routine with appropriate threshold level was verified in 2013 on trials with birds on the breeding grounds. The activity (active = 1, inactive = 0) result is saved to memory, together with a timestamp, whenever there is a change in activity state, or else after 75 minutes at a constant state. Data from the axis in the horizontal plane (X) was saved for verification purposes whenever there was a shift in activity state or after an “inactivity” period 75 minutes or longer, when the maximum, minimum and mean value of the latest 1.2s period was saved to memory. Inactivity events where the X-value suggests the body axis is within 45° from vertical were considered as confirmed landings and depicted with red colour in the activity diagrams.

The loggers deployed in 2014 (type 2) were programmed to wake up every 5 minutes and make 5 short measurements (100 ms each) with 5-second interval. Each sample consisted of Z-axis acceleration sampled at 100 Hz in the range $\pm 4g$, i.e. 10 measurements each sample. The mean of the values was subtracted from each of the 10 measurements of a sample to compensate for static gravity, and the activity was considered as indicative of flight if at least 3 of the 10 values are greater than $|g/3|$. Each run of 5 samples is recorded as number of runs that indicate flight behaviour, i.e. (0, 1, ..., 5), where ‘0’ represents not flying and ‘5’ means that all samples suggested active flight. Every hour a summary of results from all 12 runs are stored that shows how many samples refer to the different activity categories (0,..., 5). If the bird is perched the results will be (12, 0, 0, 0, 0, 0) and if it is flying with continuous wing beats it is (0, 0, 0, 0, 0, 12).

Data interpretation

To investigate whether the results were consistent with continuous flight, we simulated the sampling regime using previously recorded radar echo signatures. The dataset consisted of lengths of the flapping (mean=4.5 s, SD=4.3 s, N=107,) and gliding (mean= 2.6 s, SD=2.0 s, N=84) portions of the flap gliding of nocturnally flying swifts in the breeding season in Sweden [S4]. Weibull distributions were fit to the data (flapping: $\lambda_f=4.75$, $k_f=1.17$; gliding: $\lambda_g=2.83$, $k_g=1.26$), as they were non-normal and right-skewed [S5]. Eight day long sequences of alternating flapping and gliding sequences were constructed by sampling from the Weibull distributions (using shorter sequences resulted in similar, although less smooth, results). To examine the effect of e.g. longer glides, we varied the λ parameter to allow for different lengths of the glide and flap periods. λ is a scale parameter that controls the spread of the distribution, while k determines its shape. Keeping the k constant ensures a right-skewed distribution. λ_f - and λ_g -values of 1-40 were used, corresponding to an average flap and glide period of 0.95-37.9 and 0.93-37.2 seconds, respectively. The sequences were then sampled using a similar

sampling regime as that of the accelerometers, as follows. Every fifth minute a sampling sequence was performed. A sequence consisted of five 0.1 second samples, with an interval of 5 seconds in between. If a flapping event occurred during these 0.1 seconds, a value of 1, or “true” was recorded. No differentiation was made between the cases: 1) flapping followed by gliding, 2) gliding followed by flapping, 3) continuous flapping and 4) a very short flapping event in between two gliding events. This sampling regime differs from that of the accelerometers in one aspect: while the loggers at the lowest sampling level measures the acceleration ten times and saves a value of 1 if the acceleration threshold has been exceeded at least three times, the simulated sampling always results in a ‘1’ if there is a flapping event during the 0.1 s interval. The number of 1:s, or “trues”, in the sampling sequence was counted, so that each 5-minute interval was assigned a value between 0 (“stationary”) and 5 (“actively flapping”). The average number of 0:s per hour (0-12) for every combination of λ_f and λ_g is displayed in Figure S2. In the same figure, isolines show the average number of 0:s per hour for the most active and the most inactive individuals during day-time (9 a.m. – 3 p.m.) and night-time (8 p.m. – 3 a.m.) from 2014-09-01. Day and night was defined as the largest time-span where all individuals lacked dawn/dusk flight behavior. All isolines correspond to λ_f - and λ_g -values larger than those of the data acquired using radar tracking. The simulations show that even for quite short glide periods the record data will appear as grey, i.e. there will be false indications of flight inactivity although the bird is flap-gliding. The difference between day and night, where daytime flying appears to involve more gliding flight than in the night, indirectly also suggest the loggers record flight behavior accurately since during daytime swifts are known to be on their wings.

Geolocation by light

The 2014 data logger model was pre-programmed with a calendar defining when to run the light level measurement for position estimates. This approach differs from the majority of geolocators in the way that our loggers did not measure and store light level data continuously, but only measured sequences of diurnal light cycles for a limited number of consecutive days. In our study we chose to run measurement sequences that lasted for 5 days, with 6 sequences distributed over one year. The timing of measurement sequences was selected to avoid the equinox periods and to cover periods where the swifts were more or less stationary. The stationary periods were previously identified by conventional light logger measurements [S3, S6]. The 5-day light measurement sequences were initiated on 26 August and 1 November in 2014, and in 2015 the sequences started 1 February, 25 April and 5 May. We also assumed that the swifts would never move outside the longitude interval 20°W to 50°E [S3], which covers the African continent and corresponds to a local time interval of 4h 40 min. By using a 5h long light measurement interval, we would make sure to record sunset/sunrise events and allow us to perform a light-threshold based position estimate [S1]. This significant limitation of measurement periods substantially reduces the amount of light-level data that needs to be collected and stored, and minimizes the power-on time of the data logger, which all saves energy. The light level data obtained from our data logger mainly have a control function to provide the approximate location of the bird at key time periods of the year, and a measurement scheme like this is only suitable when reasonable assumptions can be made about longitude ranges of wintering areas. When light measurements were active, we measured light intensity every minute and stored the maximum value recorded every 5-minutes. Transitions between night and day were distinguished by using a threshold level of 2 in the software IntiProc v 1.03 (Migrate Technology Ltd. 2015). A sun angle of -6 was selected for all loggers by matching the derived positions with previously know stationary areas in Europe and Sub-Saharan Africa [S1, S3].

Supplemental References

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