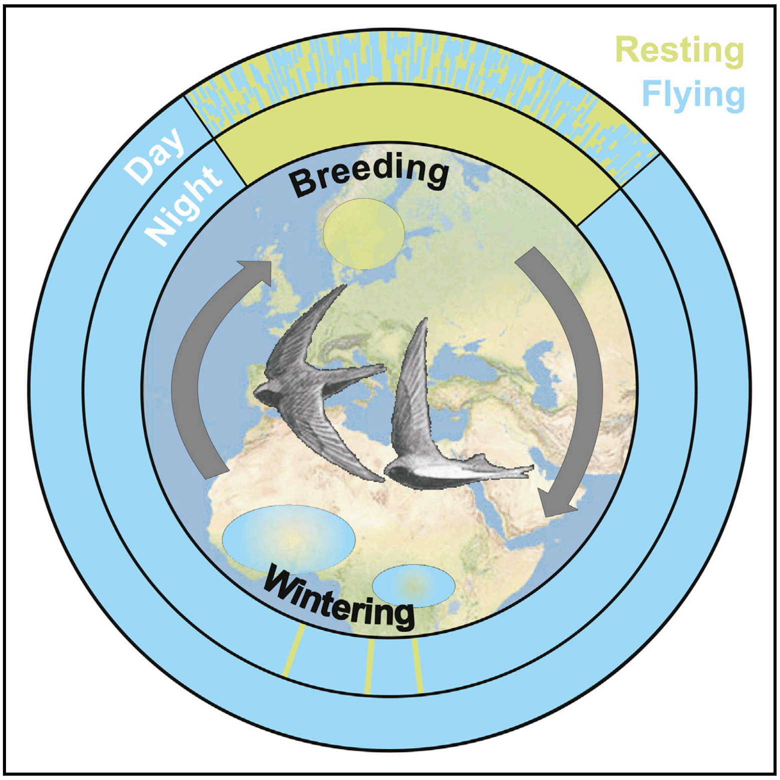
Report

Current Biology

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

Graphical Abstract



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

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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.

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

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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 breading 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

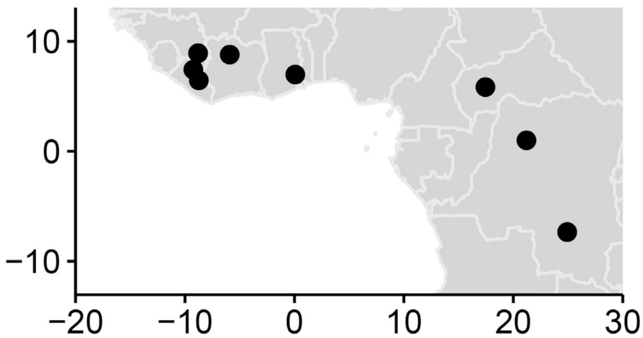

Figure 1. Winter Locations for Common Swifts in Africa

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

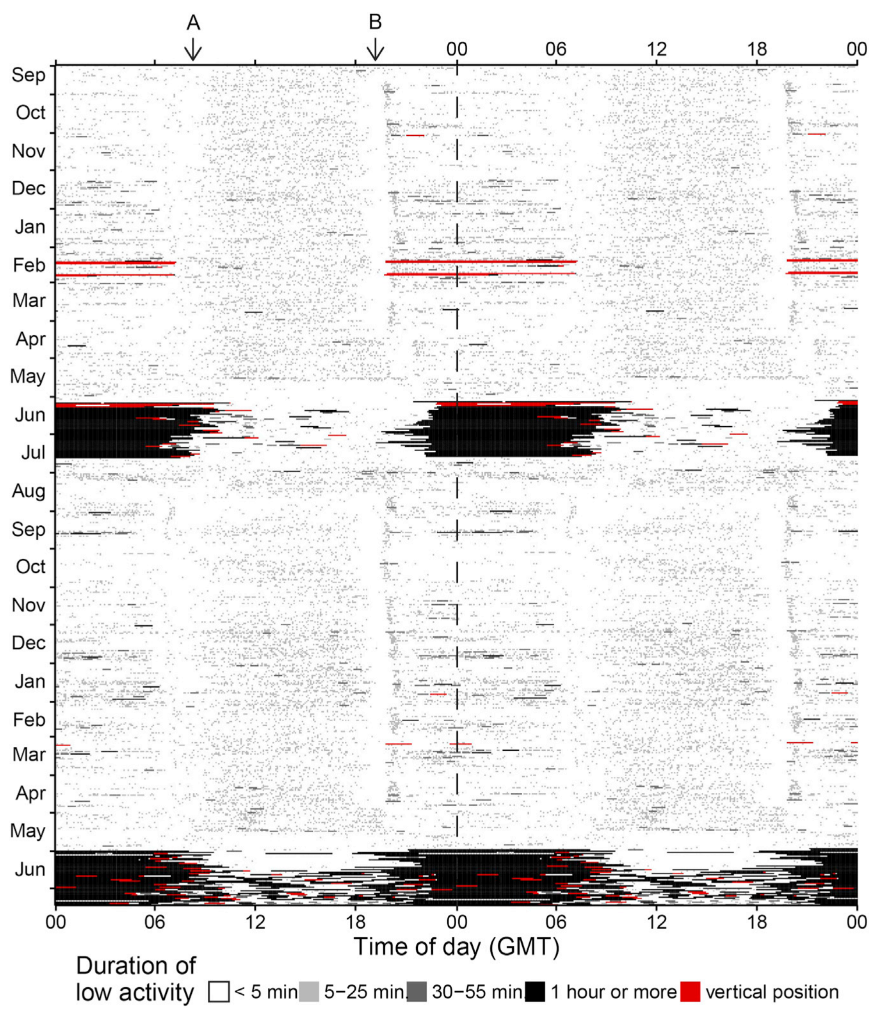

Figure 2. Flight Actogram Showing Flight Activity for a Common Swift

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.

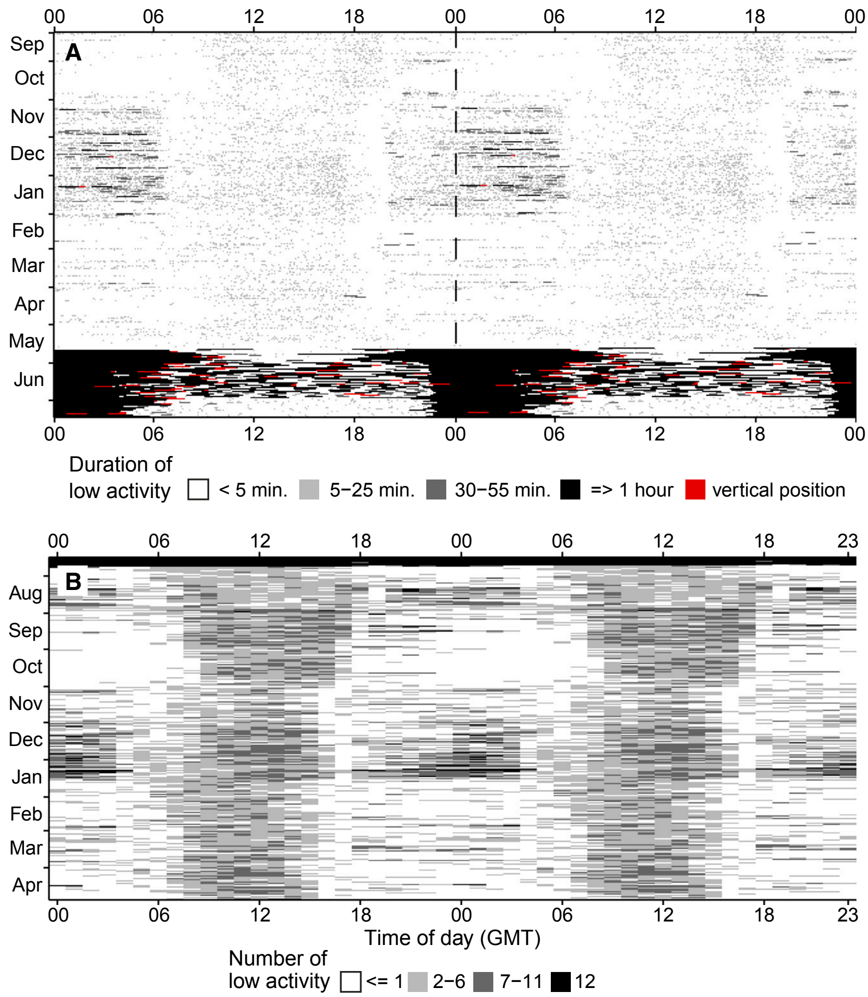

Figure 3. Flight Actogram for a Common Swift Monitored during 2 Years with Different Sampling Routines

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.

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 (*Tachymarptis 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 (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).

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

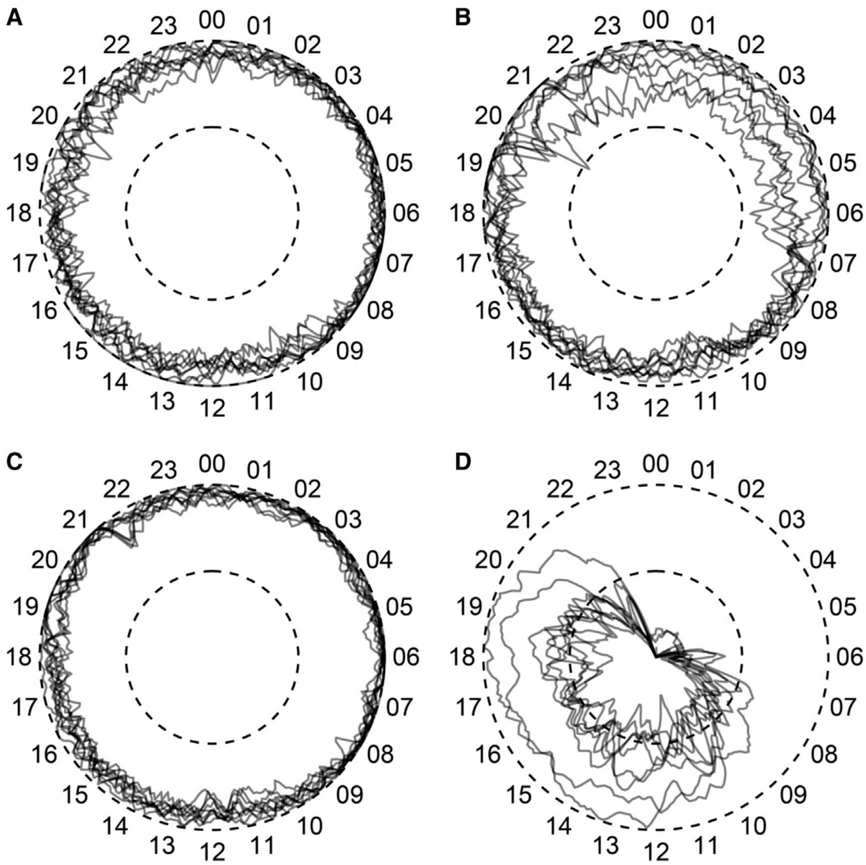

Figure 4. Seasonal Flight Activity in Common Swifts

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.

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