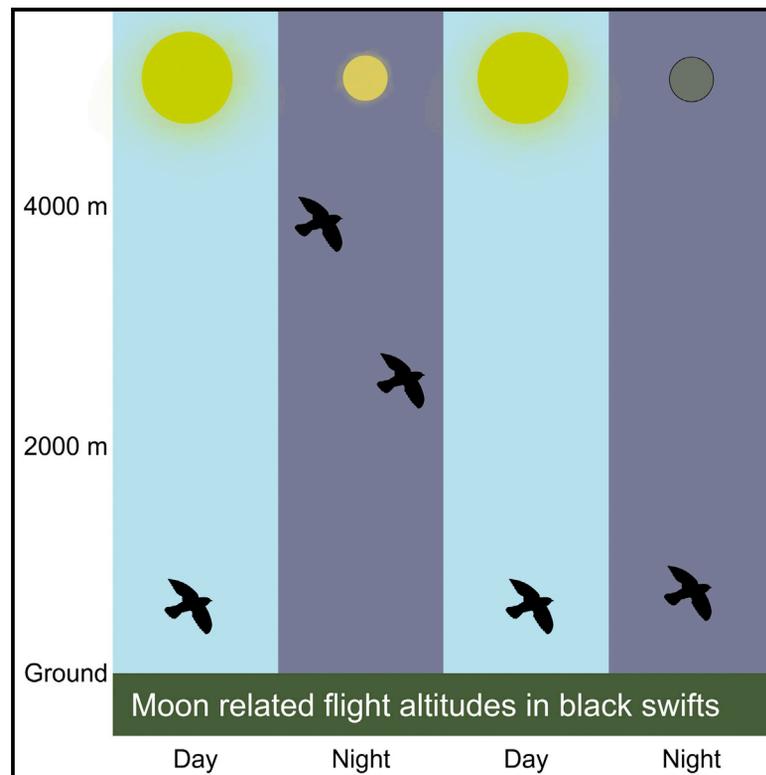


# Current Biology

## Moonlight drives nocturnal vertical flight dynamics in black swifts

### Graphical abstract



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### In brief

Migrating black swifts remain airborne for up to 8 months. Hedenström et al. show that they climb to 4,000 m and remain at 2,000 m during periods around full moon, when moonlight likely allows feeding on aerial insects. A lunar eclipse catalyzed a synchronized rapid descent by the swifts, showing the direct influence of light on their behavior.

### Highlights

- Black swifts are airborne for up to 8 months during their non-breeding period
- During nights around full moon, black swifts ascended to altitudes of 2–4,000 m
- Flight behavior during full moon nights suggests the swifts were actively foraging
- During a lunar eclipse the birds responded by immediately losing altitude



## Report

# Moonlight drives nocturnal vertical flight dynamics in black swifts

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## SUMMARY

Many animals have evolved a migratory lifestyle as an adaptation to seasonality,<sup>1,2</sup> ranging from insects<sup>3</sup> to fish,<sup>4</sup> terrestrial and marine mammals,<sup>5–7</sup> and birds.<sup>8</sup> Old World swifts have evolved an extraordinary aerial non-breeding life phase lasting for 6–10 months.<sup>9–11</sup> Swifts exploit the aerosphere in search of insects to meet the high energy demands of flight.<sup>12</sup> During this period they roost and likely also sleep in the open airspace. Nocturnal insectivores with restricted foraging time may use moonlight to increase energy intake.<sup>13</sup> Using multisensor data loggers that record light for geolocation, acceleration for flight activity, and pressure for flight altitude, we investigated if Northern black swifts, *Cypseloides niger borealis*, breeding in North America, also lead an aerial lifestyle similar to their Old World relatives. Individual flight activity showed they are airborne >99% of the time, with only occasional landings during their 8-month non-breeding period. Unexpectedly, during periods around the full moon, they conducted regular nocturnal ascents to altitudes up to >4,000 m (mean 2,000 m). A lunar eclipse triggered a synchronized descent, showing a direct effect of moonlight on flight altitude. This previously unknown behavior of nocturnal ascents during moonlight nights could be either a response to predator avoidance or that moonlight provides a foraging opportunity. Observed elevated nocturnal flight activity during periods of moonlight compared to dark nights suggests swifts were hawking for prey. Our finding of this novel behavior provides new perspectives on nocturnal flight behavior during periods surrounding the full moon.

## RESULTS

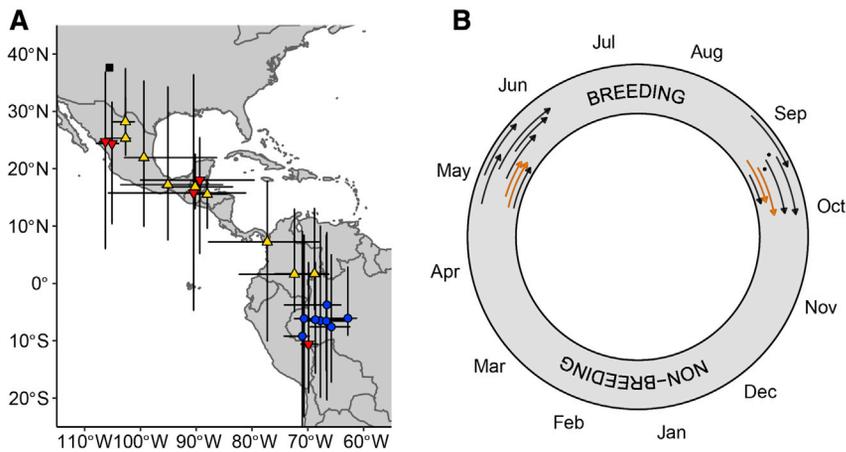
The American Northern black swift (henceforth black swift) and the Old World common swift *Apus apus* are very similar and both species are long-distance migrants.<sup>14,15</sup> Therefore, we hypothesized that black swifts are mainly airborne during the non-breeding period. The lunar cycle is known to affect the behaviors of many nocturnal animals,<sup>16</sup> where, for example, the reflected moonlight provides extended foraging opportunities in otherwise strictly crepuscular nightjars.<sup>13</sup> Assuming that black swifts are nocturnally active, i.e., flying, we hypothesized that moonlight may provide enough light to allow hawking for insects around full moon. We expected this to be manifested as increased flight activity compared with dark nights. To answer this question, we deployed custom-designed microdata loggers recording light for positioning, acceleration for flight activity, air pressure for flight altitude, and temperature to corroborate pressure measurements (STAR Methods). The black swifts migrated along similar routes during autumn and spring from Colorado via Central America to winter destinations in western Brazil (Figures 1 and S1). They left the breeding site from late August to early September as indicated by the abrupt switch from nocturnal

roosting in the nest to continuous flight (Figures 2A, 2B, S2A, S2B, S3A, and S3B) and by the time shift of diurnal flight activity in September, indicating a longitudinal displacement (Figures 2, S2, and S3). The duration away from the breeding site was on average 258 days (8 months, 14 days).

After leaving the breeding area, black swifts remained largely airborne for the entire non-breeding period, although occasional short inactivity periods occurred indicating terrestrial roosting. One individual remained inactive for 11 h on 29 March 2019 (Figure S3A). The total time when individual birds remained inactive varied between 9 and 23 h, corresponding to an average 0.24% of the non-breeding period. Mean flapping flight activity was generally higher in nighttime than daytime, suggesting a greater proportion of gliding/soaring during daytime than nighttime (Figures 2A, S2A, and S3A). Throughout the non-breeding period there was increased flapping activity around dusk and to a lesser degree near dawn (Figures 2B, S2B, and S3B). In addition, there was a periodicity in nocturnal flapping flight activity, with a period of approximately 1 month, seen as diagonal bands in the actograms (Figures 2B, S2B, and S3B).

Unexpectedly, the birds showed nocturnal ascents to relatively high altitudes of up to 5,000 m a.s.l. (above sea level),





**Figure 1. Migration route and wintering sites for black swifts**

Seasonal distribution of tracked black swifts (A) and timing of migration as estimated with light-level geolocation (B).

(A) Individual wintering locations (blue filled circles) and autumn (red triangles) and spring (yellow triangles) migration represent median latitudes and longitudes, respectively. Error bars show the full range of scatter in position estimates per 10-day sampling period (Figure S1). The black square indicates the breeding site. For separate maps of individuals, see Figure S1.

(B) Arrows illustrate the start and end (arrowhead) of autumn and spring migrations, respectively. The two dots mark the end of autumn migration of two birds that departed before the activation of the multi-sensor data loggers. Chestnut color indicates the individual with 2 years of data. See also Figure S1.

with a mean maximum altitude of 4,012 m ( $n = 7$  black swifts) reached during migration. This nocturnal behavior occurred periodically (Figures 2C, S2C, and S3C) and was strongly correlated with temperature data (Figures 2D, S2D, and S3D; LMM with individual as random intercept,  $t = 116.1$ ,  $p < 0.0001$ ). The ascents were associated with elevated flapping flight activity during early night (Figures 2B, 2C, 3D, S2B, S2C, S3B, and S3C; Table S1), indicative of continuous wing flapping required for climbing flight.

During the non-breeding period, there was a clear covariation between mean flight activity, altitude, and temperature (Figures 2B–2D, S2B–S2D, and S3B–S3D). The difference between day and night in these measures varied cyclically in relation to the lunar period, with the high-altitude nocturnal flights occurring mainly during a 10- to 11-day period between the first and third quarters, with maxima around full moon (Figures 2, 3, S2C, and S3C). Flight altitude correlated with the illuminated fraction of the moon and its altitude above the horizon (Figures 3B and 3C; Table S2). The absolute maximum altitudes reached during the non-breeding period of residency were about 4,400 m, while the mean of individual maximum nocturnal altitudes for each full-moon period was 2,741 m ( $n = 7$ , based on eight 11-day periods centered around full moon), and the mean of individual nightly mean altitudes was 2,050 m ( $n = 7$ ). Hence, the black swifts spent most of their night at altitudes near 2,000 m during moonlit nights. Nocturnal flight altitudes during 11-day periods centered around periods of new moon were 1,417 m (mean of individual maxima) and 719 m (mean of individual means). For comparison, the daytime flight altitudes for the same periods around full moon were 935 and 497 m. The corresponding daytime altitudes around new moon were 876 and 469 m, i.e., very similar to diurnal altitudes around full moon. An LMM analysis with altitude as response variable showed highly significant effects of moon phase, time of day (day/night), and their interaction (Table S3).

The level of activity among the birds, indicative for the ratio between flaps and glides,<sup>10</sup> also varied with the lunar cycle (Figure 3D; Table S1). The highest levels of activity were associated with the time of lunar ascent and around dusk and the lowest with the descending moon and during dark nights, respectively.

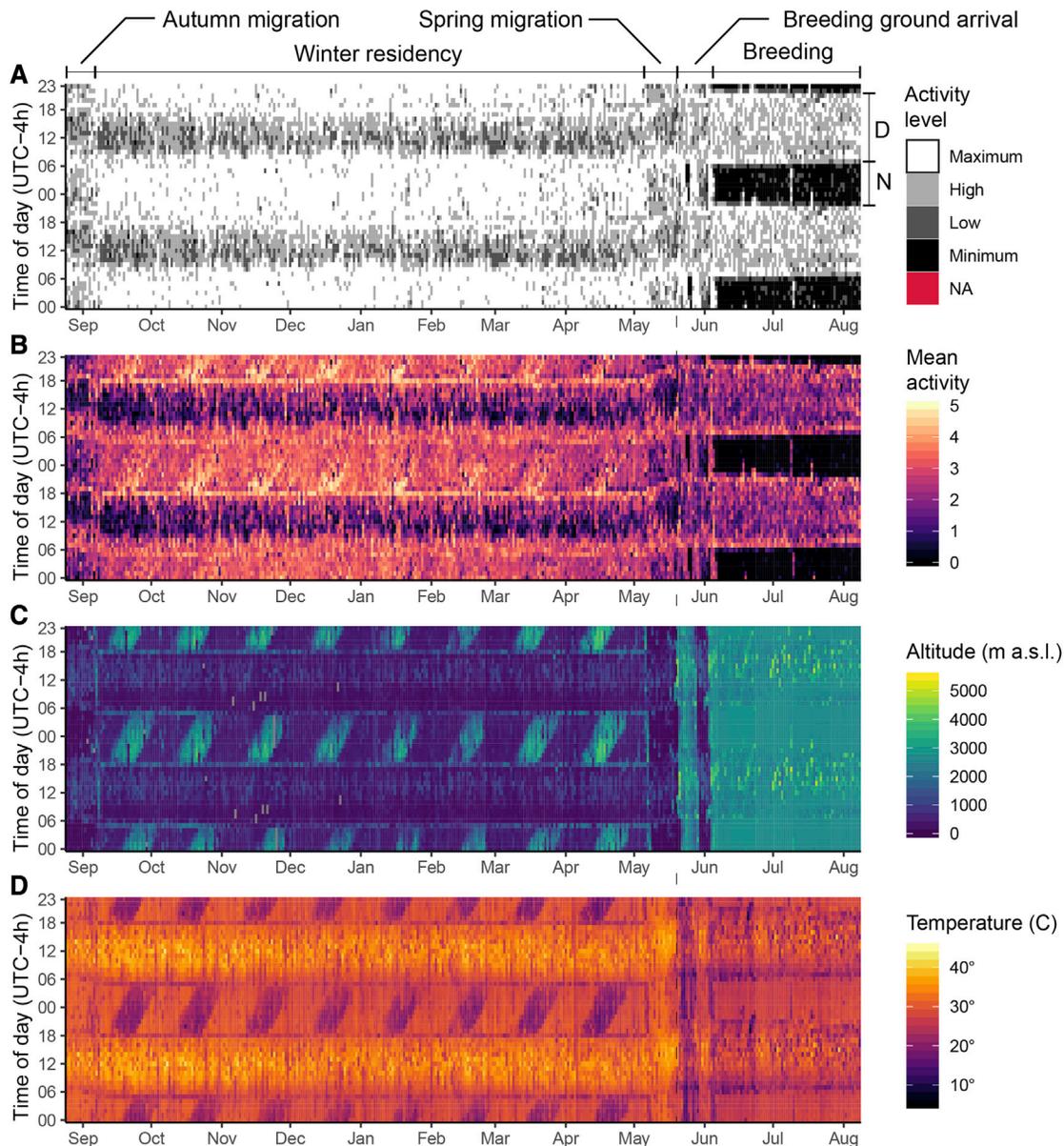
Periods around dawn and when the moon was more than 60° above the horizon, corresponding to relatively constant light and dark conditions, were associated with intermediate levels of activity. Lowest nocturnal flight activity was recorded during periods of descending moon and when the moon was below the horizon. The lunar-associated difference in flight activity (Figure 3D; Table S1) indicates that the birds make more maneuvers involving more active wing beats in moonlit than during dark nights.

On the night of 20–21 January 2019, a total lunar eclipse occurred between 04:37 and 05:48 (UTC) with maximum at 05:13 and a partial eclipse duration of 198 min, which corresponds to an onset of partial eclipse at 23:30 in the wintering area of our black swifts. At the time of eclipse maximum, the moon was 61.7° above the horizon. At dusk five birds for which pressure measurements were obtained climbed to altitudes of 3–4,000 m, as typical at full moon (Figure 4). Coincident with the lunar eclipse, all five birds lost altitude rapidly, which was a statistically unique event that was not repeated in any other night (Figure 4; Figure S4). Following termination of the lunar eclipse, the birds gained altitude again, resulting in two altitude peaks on this night (Figures 4 and S4). This “natural experiment” suggests an immediate influence of lunar light on nocturnal flight altitude in black swifts.

## DISCUSSION

Our data show that black swifts remain airborne during their entire non-breeding period, making only rare and brief landfalls, with individuals spending >99% of their time in flight. Such an aerial lifestyle is similar to a few migratory Old World swift species,<sup>9–11</sup> likely contributing to the longevity of swifts.<sup>17</sup> Our study included an individual that broke the black swift longevity record aged at 17 years. Although the New World black swift and Old World common swift have been separated for >20 million years,<sup>18,19</sup> they show a remarkable similarity in flight morphology and behavior (Table S4).

The increased flight activity near dusk and, to a lesser degree, near dawn throughout the non-breeding period is reminiscent of that observed in Old World swifts.<sup>9–11,20</sup> Altitudes reached by



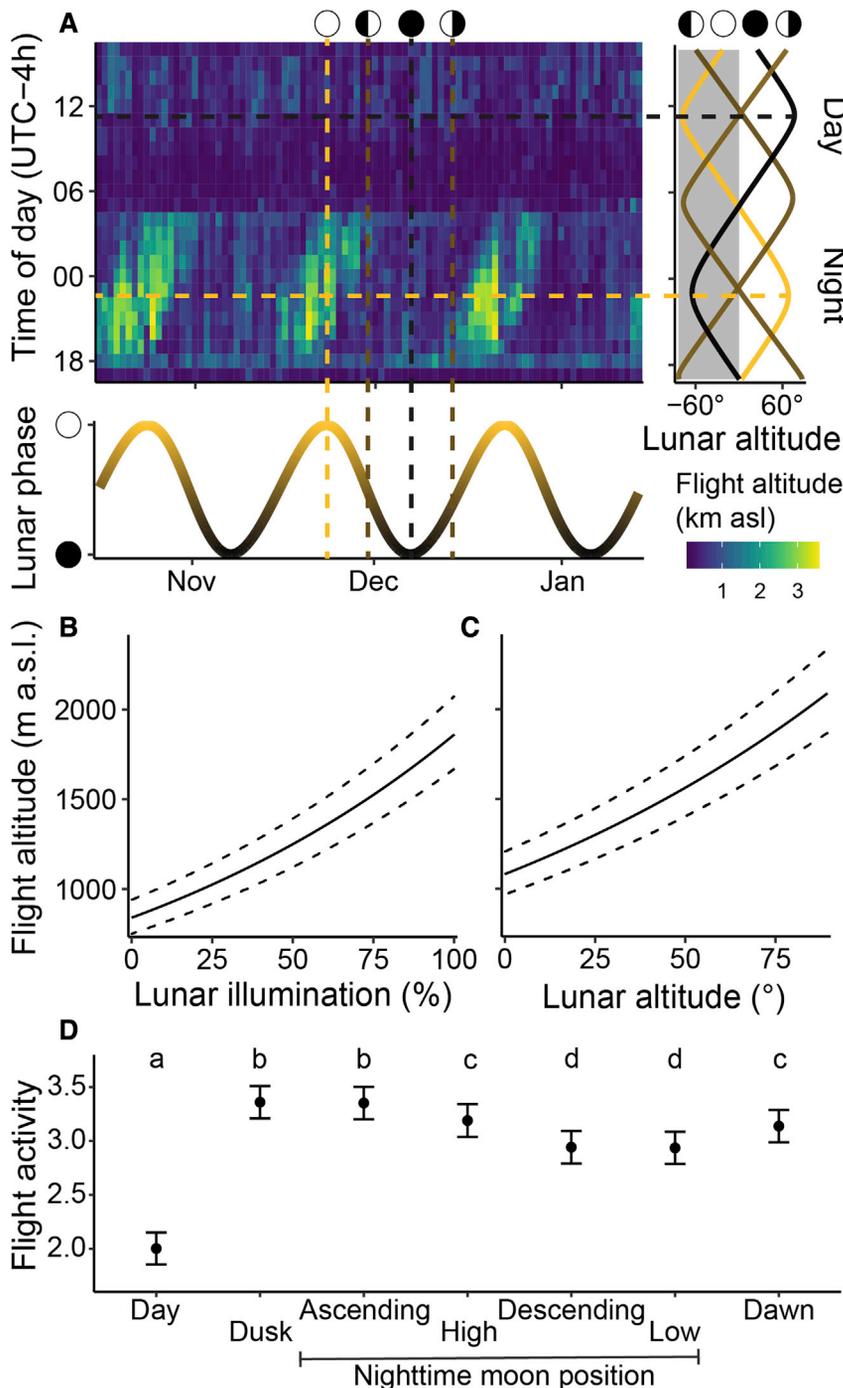
**Figure 2. Flight activity, altitude, and temperature for black swifts in relation to time of year**

Heatmap panels of 1-h resolution data collected from the multi-sensor data logger carried by a black swift (X01C) across the annual cycle (x axis) and over two consecutive days (y axis). From top, (A) categorical activity levels and (B) average activity as recorded by the accelerometer, (C) altitude estimates derived from ambient pressure, and (D) temperature registered on the logger. The data are time-shifted 4 h relative to UTC to correspond to the local day-night cycle at the longitude of the wintering area. Different episodes of the year are indicated at the top, and letters to the right of the top panel indicated day (D) and night (N). See also [Figures S2](#) and [S3](#).

black swifts are similar to those of common swifts during diurnal homing flights.<sup>21</sup> Our pressure data confirm the interpretation that elevated flight activity at dusk and dawn is associated with ascents, whose biological significance is still not well understood. Proposed functions include a need to re-orientate,<sup>22</sup> social behavior,<sup>20</sup> or that the birds take height to allow them to sleep during a gliding descent.<sup>10</sup>

The periodic altitudinal increases in relation to the moon cycle have never previously been observed in birds. There are other well-documented cases of lunar cycle effects on animal

behaviors,<sup>16</sup> including foraging flight in an avian nocturnal insectivore.<sup>13</sup> A similar immediate behavioral response to a celestial eclipse as we recorded has been observed in marine zooplankton during a solar eclipse.<sup>23</sup> It remains, however, to clarify if it is light per se that cause swifts to increase flight altitude, or if some other factor(s) covaries with moonlight that drives the swifts' behavior. At least two potential adaptive explanations related to ambient moonlight may cause swifts to climb. First, if insects are also climbing to high altitude as a response to moonlight, or if insects are present at high altitude



**Figure 3. Flight behavior of black swifts in relation to the moon cycle**

(A) Heatmap showing the recorded flight altitude of a black swift (X10C) during November–January. The dashed lines correspond to lunar maximum at full moon (yellow) and lunar minimum at new moon (black) dusk and dawn, respectively, at the estimated wintering location. The lower panel shows the illuminated fraction of the moon as observed from the same location, representing the lunar cycle during the same period. Dashed vertical lines correspond to a full moon, third quarter, new moon, and first quarter and correspond to the lines of the right-hand panel showing the altitude of the moon relative to the horizon over the course of the day. Colors of lines correspond to the illuminated fraction of the moon at the time.

(B) Effect on flight altitude of percentage lunar illumination (see Table S2 for statistics).

(C) Effect on flight altitude of lunar angular altitude above the horizon (see Table S2 for statistics).

(D) Comparison of model estimates of flight activity of five wintering black swifts between different periods of the day based on the position of sun and moon (STAR Methods). Error bars indicate 95% confidence limits of estimates. Different lowercase letters indicate significant differences in model means of flight activity (see Table S1 for test statistics): flight activity during daytime was the lowest among all categories. Highest flight activity was recorded around dusk and at nights during ascending moon while nights when the moon was high and periods around dawn were associated with intermediate level of flight activity. Lowest nocturnal flight activity was recorded during descending moon and during dark nights. See also Tables S1–S3.

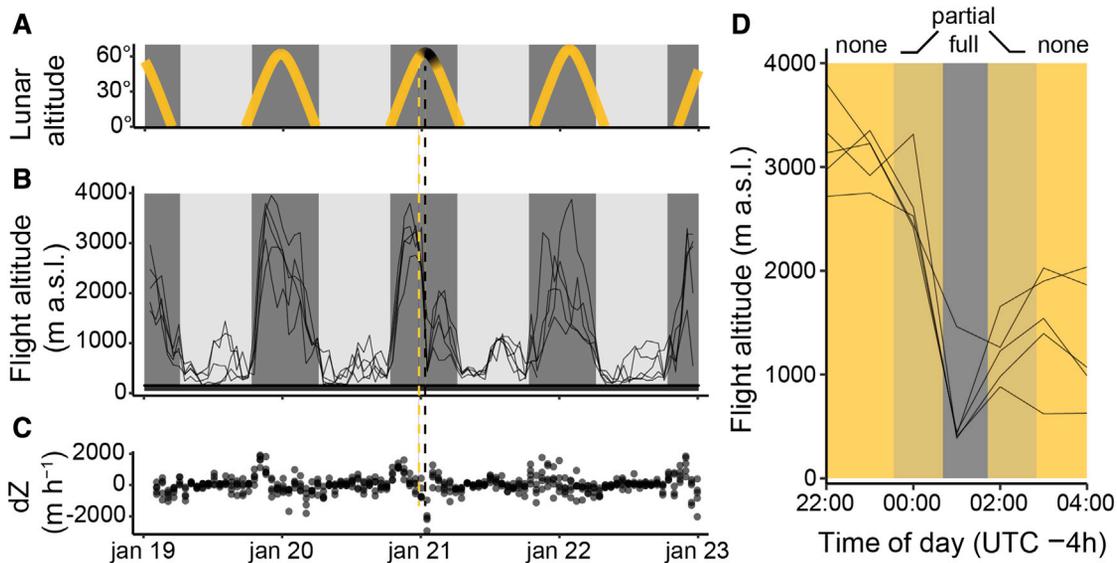
flight altitude. In daylight, the response of common swifts when attacked by falcons is to climb at maximum rate,<sup>26</sup> which could be a natural response to a perceived predation risk. Given the aerial lifestyle of black swifts, as shown here, they are likely striving to reduce energy expenditure by minimizing the amount of flapping. Prey capture, which involves accelerations and maneuvering by flapping flight, likely increases the activity level as recognized by the multisensor data loggers. Our results thus suggest that, as the nights change from dark to moonlit, black swifts increase their activity, indica-

but become visible to the swifts in moonlight, then the swifts' behavior could be a food tracking response. During the breeding season black swifts in Colorado feed opportunistically on a wide range of aerial insects,<sup>24</sup> though little is known about diet composition from the wintering area. Many aerial insects show a general trimodal lunar periodicity with one activity peak occurring near full moon,<sup>25</sup> potentially providing a reliable food source for swifts.

Second, if a crepuscular/nocturnal predator presents a threat to swifts in moonlight, they may escape predation by increasing

tive of changed behavior from energy-minimizing flight to foraging flight.

A potential predator of black swifts on the non-breeding grounds is the bat falcon (*Falco rugifigularis*), which inhabits tropical forests of Central and South America.<sup>27</sup> This falcon predaes on bats, birds, and insects, typically by hunting at dusk and dawn near the canopy of forests and in more open spaces. Highly aerial species like swifts are captured by bat falcons at some localities,<sup>28</sup> but the composition of prey species varies among individual falcons and localities depending on prey availability.<sup>29,30</sup>



**Figure 4. Daily flight altitude profiles in relation to lunar phase and a lunar eclipse**

(A) Lunar altitude measured as degrees above the horizon at the birds' average wintering location during 19–23 January 2019, including a complete lunar eclipse on 21 January 2019.

(B) Flight altitude of five black swifts during 19–23 January 2019.

(C) Vertical displacements (dZ) between successive altitude samples.

(D) Flight altitude of five black swifts during a total lunar eclipse on the night of 21 January 2019. Dark horizontal band represents ground level (B) and the pale and dark vertical bands correspond to the day and night (A and B), respectively. Dashed vertical lines show the timing of the onset of the partial (yellow) and full (black) lunar eclipse (A–C). The figure shows data for individuals X00F, X01A, X01B, X01C, and X01D.

See also [Figure S4](#).

There are no indications that bat falcons hunt at nighttime in moonlight.<sup>27</sup> In addition, the observed altitudes of 3–4,000 m reached by black swifts seem to constitute an unnecessarily wide safety margin to avoid predation. We therefore argue that predator avoidance is an unlikely driver for the periodic moon-related altitudinal shifts by swifts.

The lunar cycle has been reported to influence insect activity,<sup>25,31</sup> and a few studies found brood emergence to be synchronized with the full moon.<sup>32</sup> In New South Wales, Australia, migrating moths (Lepidoptera) appear to exploit wind assistance and reach altitudes up to 2,900 m a.s.l.<sup>33</sup> In Argentina, a meteorological radar detected flying insects up to 2,400 m a.s.l.,<sup>34</sup> while in Louisiana, USA, insect traps mounted on an airplane detected insects up to 4,500 m a.s.l.<sup>35</sup> Hence, even if little is known about flying insects over the Brazilian forest region, insects may occur at significant numbers at altitudes where swifts fly. Further indirect evidence of high-flying insects comes from radar observations of Brazilian free-tailed bats, *Tadarida brasiliensis*, which are found at altitudes up to 3,300 m a.g.l. (above ground level).<sup>36</sup> The altitudes where black swifts are mostly found during periods of moonlight were about 2,000 m, and therefore we argue that black swifts likely use the ambient light provided by the moon to hawk insects during nighttime. Support for this interpretation is provided by the increased flight activity recorded during moonlit nights compared with dark nights. While scientific probing into the ecology and behavior of many aerial organisms has been lingering due to technological obstacles, current sophisticated biologging technology now provides aeroecologists with the necessary tools to test novel hypotheses and make rapid progress in this field.

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- **KEY RESOURCES TABLE**
- **RESOURCE AVAILABILITY**
  - Lead contact
  - Materials availability
  - Data and code availability
- **EXPERIMENTAL MODEL AND SUBJECT DETAILS**
  - Study site
- **METHOD DETAILS**
  - Study species and logger deployment
  - Geolocation by light
  - Acceleration, pressure and temperature
- **QUANTIFICATION AND STATISTICAL ANALYSIS**
  - Flight characteristics relative to lunar cycle and time of day

## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2022.03.006>.

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#### AUTHOR CONTRIBUTIONS

Conceptualization, A.H. and R.A.S.; project leader and study coordination, R.A.S.; methodology, A.H., R.A.S., and G.N.; formal analysis, A.H. and G.N.; investigation, A.H., R.A.S., G.N., C.W., G.J.L., and S.Å.; writing – original draft, A.H.; writing – review & editing, A.H., R.A.S., G.N., C.W., G.J.L., and S.Å.; visualization, A.H. and G.N.; project administration, A.H. and R.A.S.; funding acquisition, A.H., R.A.S., and S.Å.

#### DECLARATION OF INTERESTS

The authors declare no competing interests.

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## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Moonlight drives nocturnal vertical flight dynamics in black swifts	This paper	Mendeley data: <a href="https://dx.doi.org/10.17632/zfw758v6sv.1">https://dx.doi.org/10.17632/zfw758v6sv.1</a>
Experimental models: Organisms/strains		
Northern black swift <i>Cypseloides niger</i>	Wild	N/A
Software and algorithms		
R	37–40	<a href="https://cran.r-project.org/">https://cran.r-project.org/</a>

### RESOURCE AVAILABILITY

#### Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Anders Hedenström ([anders.hedenstrom@biol.lu.se](mailto:anders.hedenstrom@biol.lu.se)).

#### Materials availability

This study did not generate any new unique materials.

#### Data and code availability

- Raw data from Figures 1, 2, 3, 4, and S1–S4 were deposited at Mendeley Data, <https://dx.doi.org/10.17632/zfw758v6sv.1>.
- This study did not generate any new code.

### EXPERIMENTAL MODEL AND SUBJECT DETAILS

#### Study site

Our study site was at Zapata Falls (37.619 N, 105.553 W), Colorado, which is situated at 2890 m a.s.l. The birds were trapped using mist nets in 2018–2020.

### METHOD DETAILS

#### Study species and logger deployment

The Northern black swift (*Cypseloides niger borealis*) breeds in western U.S.A. and Canada, where nests often are placed at high altitudes behind water falls or otherwise damp sites.<sup>41</sup> Seven birds were captured with mist-nets during the breeding site on four occasions between 1–25 August 2018. Six of the birds were recaptured one year later, three on 13 August, two on 14 August, one on 27 August 2019, and one on 8 August 2020. The loggers were still operating upon recapture, except for the logger retrieved in 2020 (X00F), which had stopped collecting data on 4 June 2020, but nevertheless contained data for two complete migrations. The black swift recaptured in 2020 with device X00F not only completed two migrations with the device but is also the oldest documented black swift. This individual was first banded in 2004 as an adult making it at least 17 years old, which is the oldest documented black swift thus far.

In August 2020 we took photos of the right wing and body with a ruler for reference length of nine individual black swifts, and from these we determined wing span and wing area<sup>42</sup> using ImageJ to calculate aspect ratio (wing span squared divided with wing area). The total wing area includes the area of the body between the wings.<sup>42</sup> Morphological data for these nine black swifts are shown in Table S4.

The multisensor data logger (MDL) comprises a real-time clock microcontroller, a memory, an accelerometer, temperature, pressure and light sensors. The accelerometer measures acceleration in 3D at a  $\pm 4g$  range at sampling rate of 100 Hz. Only the vertical axis (Z) acceleration was used for activity analysis. The MDLs were programmed to start recording data on 25 August 2018. The mass of the data logger was  $\leq 1.25$  g and on deployment the average body mass of the birds was 43.1 g, meaning the logger mass was 2.8% of the body mass on average.

### Geolocation by light

The MDLs were pre-programmed with a calendar defining when to run the light level measurements for position estimates.<sup>43</sup> This approach is different from the majority of geolocators in that our loggers only measured sequences of daily light cycles for a limited number of consecutive days. The reduction of measurement periods of light-level substantially reduces the amount of data to be stored, and prolongs operation time by minimizing the power consumption. In our study, we ran six measurement periods each of 10 days distributed over one year, starting on 1 September, 1 October, 1 January, 1 April, 1 May and 1 June, respectively. The timing of measurement sequences was selected to match residence periods previously identified by conventional geolocator measurements.<sup>15</sup>

The light-level data obtained from our data logger mainly serve as a control function to provide approximate locations of the swifts at key time periods of the year. When light measurements were activated, the device measured light intensity every minute and stored the maximum value recorded every 5-min. Transitions between night and day were distinguished by using a threshold level of 2 (on scale 1-256) in the software IntiProc v 1.03 (Migrate Technology). A sun angle of  $-6^\circ$  was selected for all loggers by matching the derived positions with the known positions at the breeding site and approximate locations during the winter.<sup>15</sup>

### Acceleration, pressure and temperature

Acceleration in the Z axis was sampled every 5 min with runs of 10 measurements at 5 time points, each separated by 5 s. Each measurement is a sample during 100 ms at 100 Hz in the range  $\pm 4g$ . For each run, the mean of the values was subtracted from each of the 10 measurements to compensate for static gravity, and the recorded acceleration was considered as indicative of flight if at least 3 of the 10 values were greater than  $|g/3|$ , where  $g$  is acceleration due to gravity. Each 5-min sample was assigned the number of runs that indicate flight behavior, i.e., (0, ..., 5). Every h a summary of results from all 12 runs were stored according to the distribution of the samples across the different activity categories (0, ..., 5). If the bird is perched and motionless the data stored will be (12, 0, 0, 0, 0, 0), and if it is flying with continuous wing beats the data are (0, 0, 0, 0, 0, 12). To illustrate flight activity in graphical actograms the hourly recordings are coded as 'white' to represent continuous flapping flight (0, 0, 0, 0, 0, 12), and 'black' to represent no flight (12, 0, 0, 0, 0, 0), with shades of gray representing intermediate activity levels. Please note that a bird in continuous gliding flight could in principle generate a signature indistinguishable from a bird resting on the ground, but when such periods are short and surrounded with activity recordings they most likely refer to gliding/soaring flight with no or few wing beats.<sup>10</sup>

The device had the auxiliary function of measuring ambient air pressure once per h. In addition to measuring altitude the pressure data were useful to corroborate flight behavior as recorded by accelerometry. Pressure data were converted into altitude ( $z$ ) using the formula of the Standard Atmosphere (SA; International Organization for Standardization 1975: ISO 2533:1975):

$$z = \frac{T_0}{L} \left( \left( \frac{P_0}{P} \right)^{\frac{LR_0}{g}} - 1 \right)$$

where  $T_0$  is temperature at sea level (assumed 288.15 K),  $L$  is the altitudinal lapse rate of temperature ( $-0.0065 \text{ deg K m}^{-1}$ ),  $P_0$  is standard atmospheric pressure at sea level (1013.25 hPa),  $P$  is measured air pressure,  $g$  is acceleration due to gravity ( $9.81 \text{ m s}^{-2}$ ) and  $R_0$  is the universal gas constant ( $287.053 \text{ J kg}^{-1} \text{ K}^{-1}$ ). Normal variation in sea level temperature and air pressure has a relatively small effect on estimated altitude. For example, at 4000 m altitude an increase at sea level temperature by  $5^\circ$  modifies the estimated altitude to 4069 m, while a sea level air pressure of 1020.25 hPa yields a calculated altitude of 4053 m. The temperature compensated pressure sensor we used (Bosch Sensortech BMP280) had an absolute accuracy of ca  $\pm 1$  hPa, corresponding to ca  $\pm 8$  m. Each pressure sensor was factory calibrated with a unique set of individual calibration parameters. Altitude data used for analyses refer to the standard atmosphere derived values, which are not corrected for local atmospheric conditions.

The device also recorded temperature and because the sensor was positioned on the side of the logger facing the bird body, the recorded values represent the combined effect of the ambient temperature and that of the bird's body. Hence, the temperature values cannot be used as measure of ambient air temperature, but rather used as a control function of changed flight altitude, as air temperature is expected to decline with increasing altitude.<sup>37</sup>

## QUANTIFICATION AND STATISTICAL ANALYSIS

All analyses are based on seven individuals tracked during eight full return migrations from the breeding site, i.e., one individual contributed data from two consecutive migrations. We used R<sup>38</sup> for all statistical calculations.

### Flight characteristics relative to lunar cycle and time of day

Data on lunar phase (quantified as the percentage of illuminated moon surface), lunar altitude (as degrees above horizon), and local solar position (relative to horizon) were downloaded for the wintering period using the *sunalc* package.<sup>39</sup>

To examine flight activity and trends of vertical displacements during different periods of the day we used the solar and lunar data to distinguish the following periods: 'Day' = sun  $\geq 15^\circ$  above horizon at the average wintering location, 'Dusk' =  $-15^\circ \leq \text{sun} \leq 15^\circ$  and descending, 'Ascending' = sun  $< -15^\circ$ ,  $0^\circ < \text{moon} \leq 60^\circ$  and ascending, 'High' = sun  $< -15^\circ$  and moon  $> 60^\circ$ , 'Descending' = sun  $< -15^\circ$ ,  $0^\circ < \text{moon} \leq 60^\circ$  and descending, 'Low' = sun  $< -15^\circ$  and moon  $\leq 0^\circ$ , and 'Dawn' =  $-15^\circ \leq \text{sun} \leq 15^\circ$  and ascending. We fitted a Linear Mixed Model (LMM) using the R package *lme4*<sup>40</sup> with flight activity as the response variable, period of day as a

factorial predictor, and bird identity and date as random intercepts (Figure 3D; Table S1). Significant differences among model means were assessed by a post hoc Tukey HSD using the R package *lsmeans*.<sup>44</sup>

We quantified the degree and covariation of vertical displacement for each h by testing the within-individual difference of subsequent altitude measurements using paired t test (Figures S4A and S4B).

We examined the relationship between lunar cycle and flight altitude of the black swifts using two separate approaches. First, we used the hourly dataset above. Before analyzing the lunar influence on the nocturnal flight altitude of the birds, we reduced the dataset by the following steps. We removed potentially erroneous altitude estimates below zero ( $n = 86$ ), as the ground level in the wintering area is  $> 100$  m a.s.l. and excluded registrations when the moon was below horizon ( $n = 15796$ ), or when the sun was above horizon ( $n = 8190$ ), resulting in a final dataset of 7775 registrations. We fitted a LMM with  $^{10}\log$  transformed flight altitude as the response variable. Predictors were the continuous variables lunar phase and lunar altitude. Bird identity was included as a random intercept (Figures 3B and 3C; Table S2).

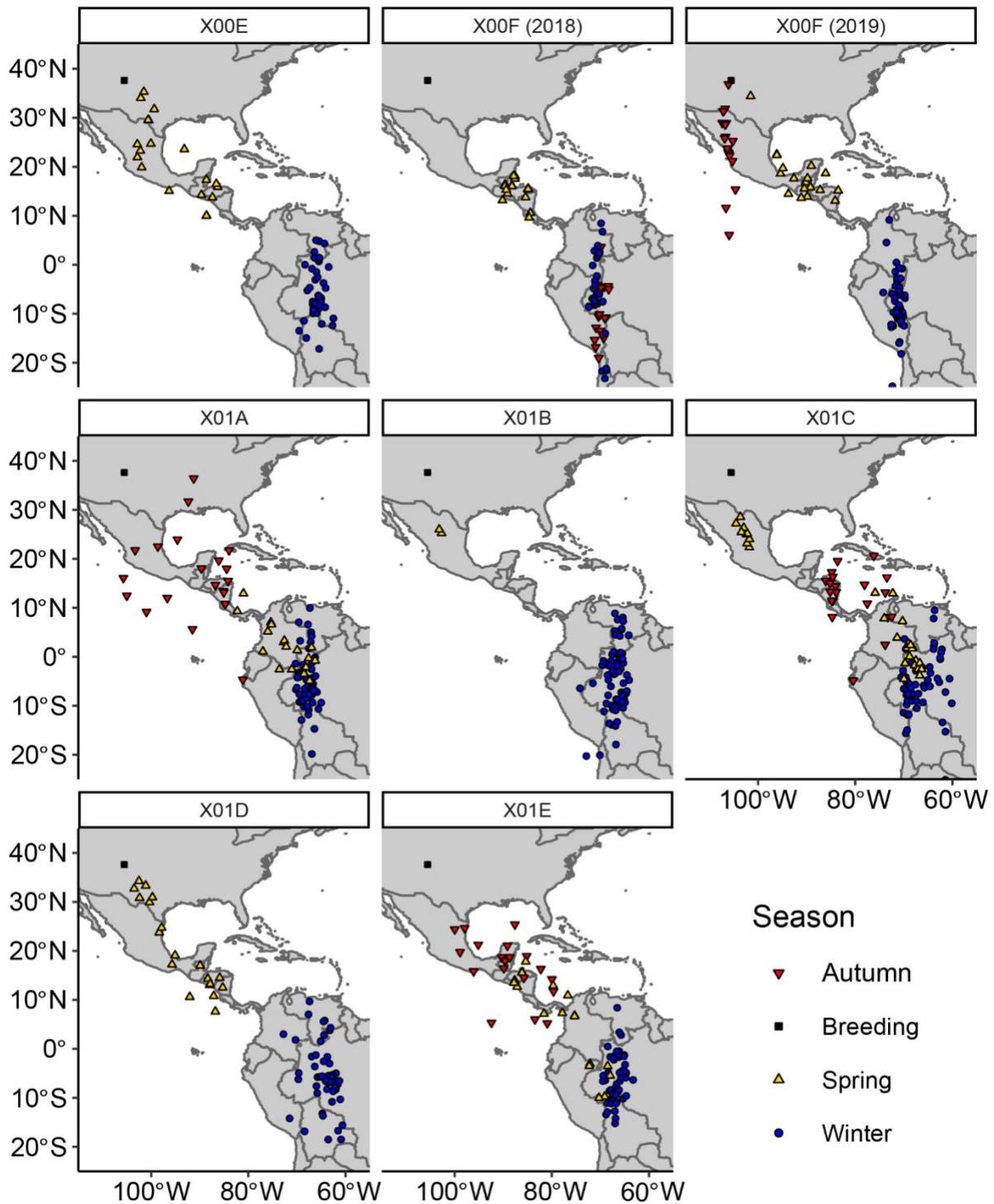
In our second approach, we extracted daily and nightly mean altitudes of the birds during 11-day periods around full moon and new moon, respectively. We ran a LMM with  $^{10}\log$ -transformed altitude as response variable, moon phase, time of day and the interaction (moon phase)\*(time of day) as factorial predictors, and with month and individual as random intercepts. We derived  $R^2$  values using the R package *MuMIn*<sup>45</sup> (Figures 2 and 3; Table S3).

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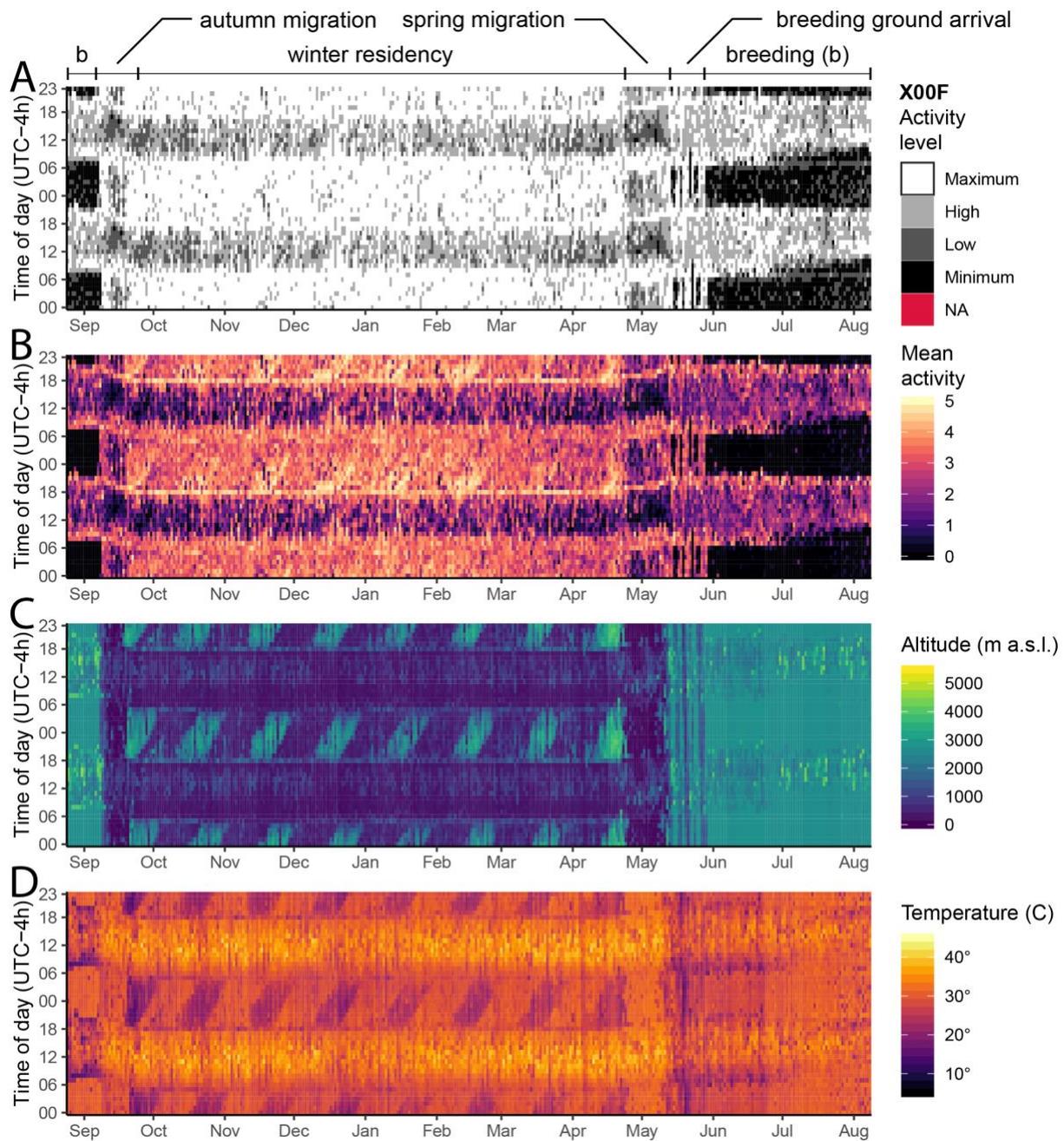
**Supplemental Information**

**Moonlight drives nocturnal vertical  
flight dynamics in black swifts**

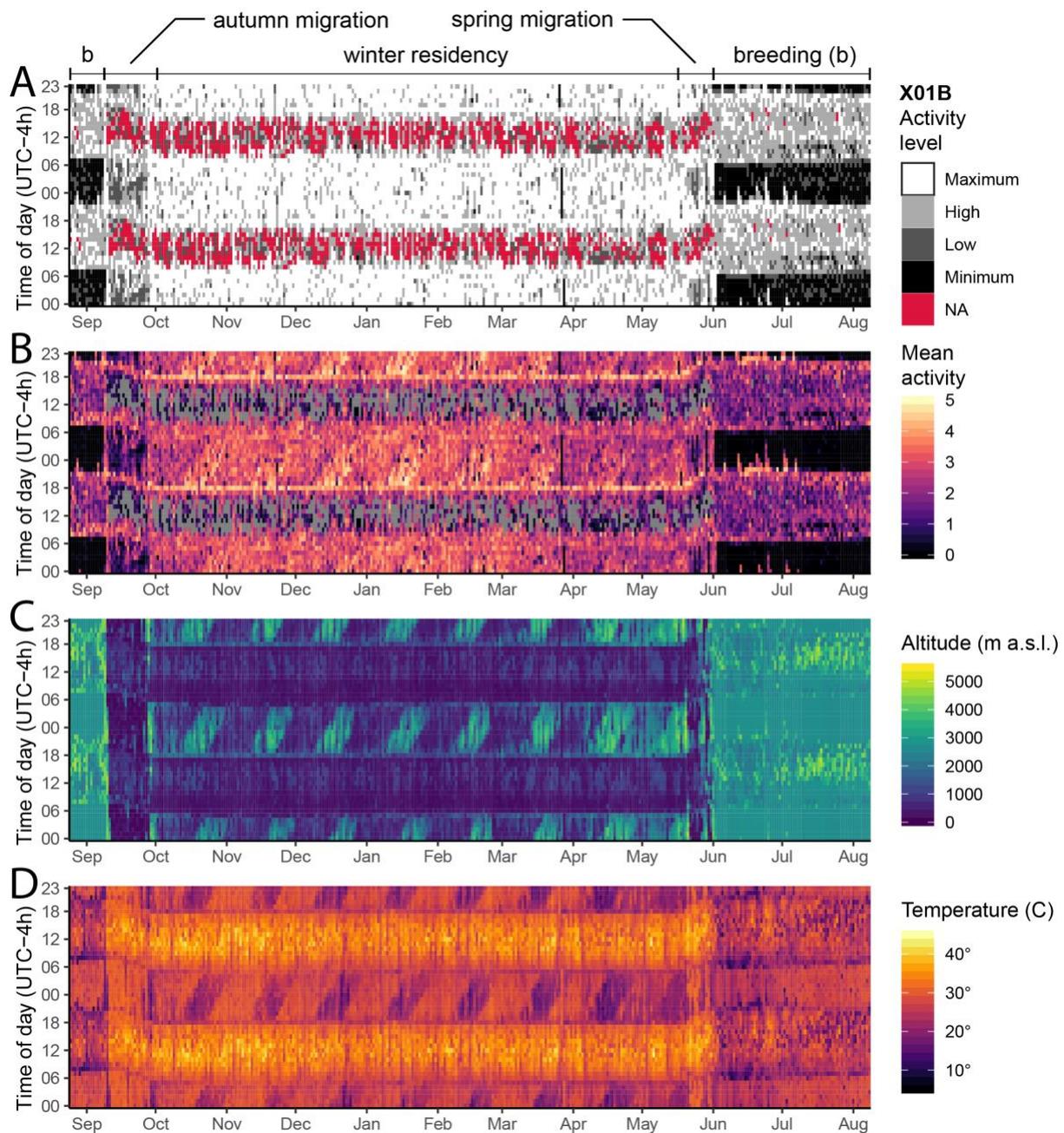
**Anders Hedenström, Robert A. Sparks, Gabriel Norevik, Colin Woolley, Greg J. Levandoski, and Susanne Åkesson**



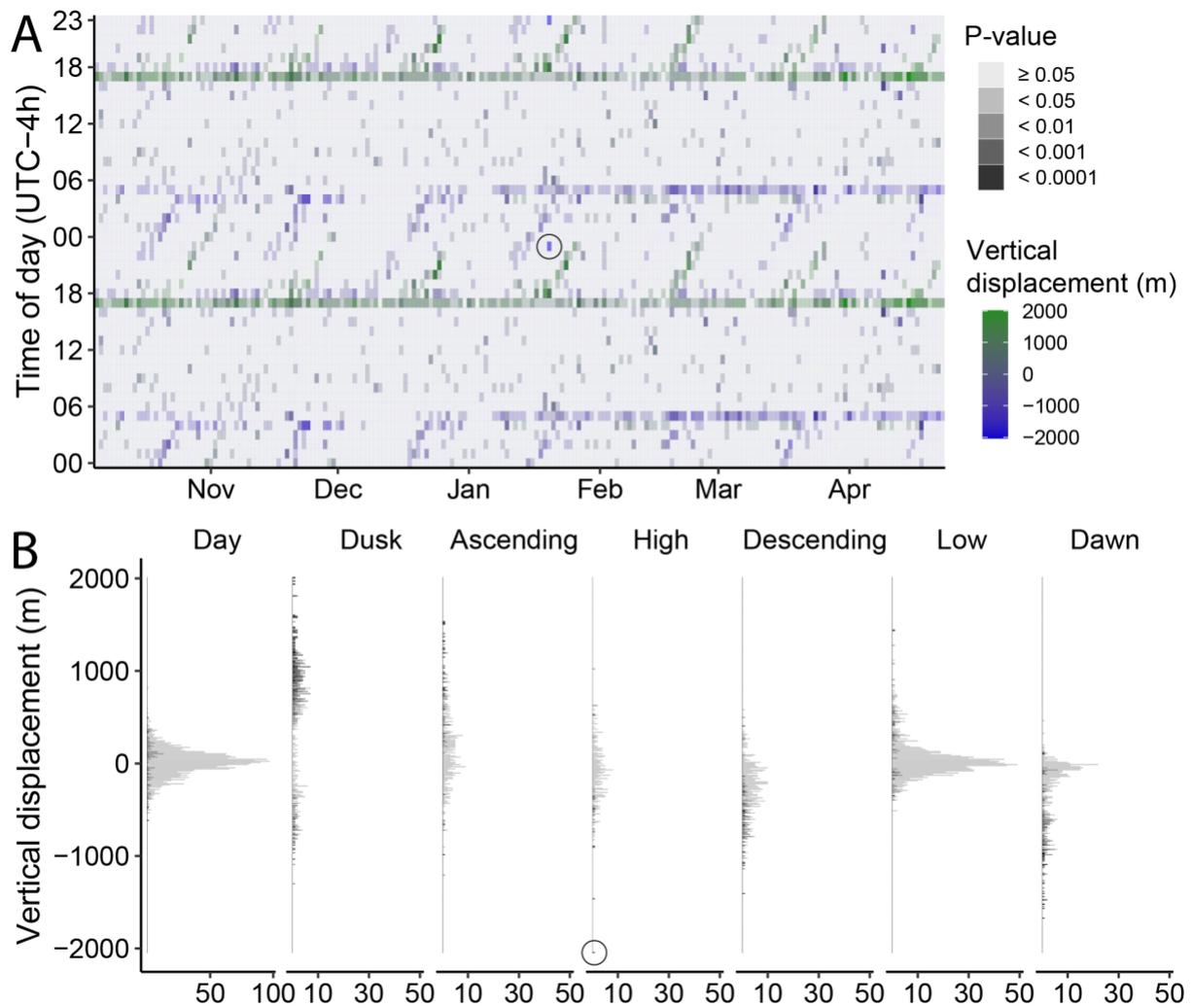
**Figure S1. Seasonal locations derived by geolocation for individual black swifts. Related to Figure 1.** Positions of individual Northern black swifts during migration and winter 2018-2019. Symbols show the seasonal distribution of the tracked birds as estimated with light-level geolocation. Symbols during wintering period (blue circles) and autumn (red triangles) and spring (yellow triangles), respectively, represent raw data points. The black square corresponds to the trapping location at the breeding site. One individual (X00F) with data for two migrations is represented by two maps, one for the 2018-2019 winter and one for the 2019-2020 winter.



**Figure S2. Flight activity, altitude and temperature for black swifts in relation to time of year. Related to Figure 2.** Heatmap panels of one-hour resolution data collected from a multi-sensor data logger carried by a Northern black swift (X00F) across the 2018-2019 annual cycle (x-axis) and over two consecutive days (y-axis). From top (A) categorical activity level and (B) average activity as recorded by the accelerometer, (C) altitude estimates derived from ambient pressure and (D) temperature registered on the logger. The data are time-shifted four hours relative to UTC to better correspond to the local day-night cycle on the longitude at the wintering area.



**Figure S3. Flight activity, altitude and temperature for black swifts in relation to time of year. Related to Figure 2.** Heatmap panels of one-hour resolution data collected from a multi-sensor data logger carried by a Northern black swift (X01B) across the 2018-2019 annual cycle (x-axis) and over two consecutive days (y-axis). From top (A) categorical activity level and (B) average activity as recorded by the accelerometer, (C) altitude estimates derived from ambient pressure and (D) temperature registered on the logger. The data are time-shifted four hours relative to UTC to better correspond to the local day-night cycle on the longitude at the wintering area. This individual roosted for 11 hours on 29-30 March 2019, during which time the pressure measurements indicated the bird remained stationary at an altitude of 166 m. The ground is about 100 m a.s.l. at the winter locations of this bird, suggesting it was roosting in a tall tree.



**Figure S4. Vertical displacements for black swifts during the non-breeding period.**

**Related to Figure 4.** Linear estimate of vertical displacements per hour of five black swifts during the wintering period (2018-10-05 – 2019-04-23). Hues illustrate p-values from t-tests in both heatmap and histograms. (A) Heatmap panel showing the distribution of synchronized vertical displacements over season and day. (B) Histograms showing distributions of vertical displacements during different periods of the day based on the position of sun and moon, respectively: ‘Day’ = sun  $\leq 15^\circ$  above horizon at the average wintering location, ‘Dusk’ =  $-15^\circ \leq \text{sun} \leq 15^\circ$  and descending, ‘Ascending’ = sun  $< -15^\circ$ ,  $0^\circ < \text{moon} \leq 60^\circ$  and ascending, ‘High’ = sun  $< -15^\circ$  and moon  $> 60^\circ$ , ‘Descending’ = sun  $< -15^\circ$ ,  $0^\circ < \text{moon} \leq 60^\circ$  and descending, ‘Low’ = sun  $< -15^\circ$  and moon  $\leq 0^\circ$ , and ‘Dawn’ =  $-15^\circ \leq \text{sun} \leq 15^\circ$  and ascending. Note different scale on ‘Day’. Vertical displacement data corresponding to the time of a lunar eclipse are encircled.

Linear null hypothesis	Estimate	SE	z	P-value
Dusk – Day = 0	1.3577	0.0141	96.30	< 0.001
Ascending – Day = 0	1.3450	0.0160	84.36	< 0.001
High – Day = 0	1.1872	0.0193	61.66	< 0.001
Descending – Day = 0	0.9396	0.0160	58.01	< 0.001
Low – Day = 0	0.9337	0.0104	89.66	< 0.001
Dawn – Day = 0	1.1356	0.0145	78.47	< 0.001
Ascending – Dusk = 0	-0.0079	0.0196	-0.406	1
High – Dusk = 0	-0.1705	0.0223	-7.645	< 0.001
Descending – Dusk = 0	-0.4180	0.0196	-21.38	< 0.001
Low – Dusk = 0	-0.4240	0.0153	-27.66	< 0.001
Dawn – Dusk = 0	-0.2221	0.0183	-12.11	< 0.001
High – Ascending = 0	-0.1626	0.0233	-6.990	< 0.001
Descending – Ascending = 0	-0.4101	0.0211	-19.41	< 0.001
Low – Ascending = 0	-0.4165	0.0174	-23.93	< 0.001
Dawn – Ascending = 0	-0.0214	0.0194	-10.80	< 0.001
Descending – High = 0	-0.2475	0.0230	-10.67	< 0.001
Low – High = 0	-0.2535	0.0206	-12.30	< 0.001
Dawn – High = 0	-0.0516	0.0225	-2.290	0.234
Low – Descending = 0	-0.0059	0.0173	-0.342	1
Dawn – Descending = 0	0.1960	0.0198	9.910	< 0.001
Dawn – Low = 0	0.2019	0.0157	12.90	< 0.001

**Table S1. Statistical comparisons of flight activity in black swifts between tie of day and lunar phases. Related to Figure 3D.** Comparisons of nocturnal mean activity of Northern black swifts during different periods of the day based on the position of sun and moon, respectively: ‘Day’ = sun  $\geq 15^\circ$  above horizon at the average wintering location, ‘Dusk’ =  $-15^\circ \leq \text{sun} \leq 15^\circ$  and descending, ‘Ascending’ = sun  $< -15^\circ$ ,  $0^\circ < \text{moon} \leq 60^\circ$  and ascending, ‘High’ = sun  $< -15^\circ$  and moon  $> 60^\circ$ , ‘Descending’ = sun  $< -15^\circ$ ,  $0^\circ < \text{moon} \leq 60^\circ$  and descending, ‘Low’ = sun  $< -15^\circ$  and moon  $\leq 0^\circ$ , and ‘Dawn’ =  $-15^\circ \leq \text{sun} \leq 15^\circ$  and ascending. Bird identity and date were included as random intercepts. Differences among means were assessed by *post hoc* Tukey HSD.

	Estimate	SE	t	P-value	R <sup>2</sup> cond./marg.
Intercept	2.79500	0.03190	111.24	< 0.0001	
Lunar phase (%)	0.00345	0.00010	34.00	< 0.0001	
Lunar altitude (°)	0.00320	0.00013	24.65	< 0.0001	0.28/0.24

**Table S2. Statistical analysis of nocturnal flight activity in relation to lunar properties. Related to Figures 3 B and C.** Summary statistics of Linear Mixed Model (LMM) relating nocturnal flight altitude of black swifts with the lunar phase and lunar altitude. Flight altitude was <sup>10</sup>log-transformed to normalize its distribution. Bird identity was included as random intercept. R<sup>2</sup> is presented as indicator of goodness of fit. SE - Standard error; t - t statistics.

	Estimate	SE	t	P-value	R <sup>2</sup> cond./marg.
Intercept	2.84100	0.02233	127.24	<0.0001	
Time Of Day (Day)	0.19380	0.00822	-23.58	<0.0001	0.82/0.78
Moon (Full)	0.44530	0.00824	54.10	<0.0001	
TOD : Moon	0.43180	0.01164	-37.11	<0.0001	

**Table S3. Statistical analysis of flight activity between day and night and lunar phase (full versus new). Related to Figures 2, 3.** Summary statistics of Linear Mixed Model (LMM) relating flight altitude during 11-day periods around full and new moon, respectively, of black swifts with the lunar phase ('full' or 'new'), categorical time of day ('day' or 'night') and the interaction between lunar phase and time of day. Flight altitude was <sup>10</sup>log-transformed to normalize its distribution. Month of the year and bird identity were included as random intercepts. R<sup>2</sup> is presented as indicator of goodness of fit. SE - Standard error; t - t statistics.

Individual	Body mass (kg)	Wing span (m)	Wing area (m <sup>2</sup> )	Wing loading (N/m <sup>2</sup> )	Aspect ratio
#1	0.046	0.398	0.01404	32.1	11.3
#2	0.415	0.382	0.01256	32.4	11.6
#3	0.0438	0.387	0.01188	36.2	12.6
#4	0.0416	0.383	0.01174	34.8	12.5
#5	0.0412	0.339	0.01040	38.9	11.1
#6	0.0489	0.345	0.01113	43.1	10.7
#7	0.043	0.398	0.01463	28.8	10.8
#8	0.0438	0.397	0.01359	31.6	11.6
#9	0.038	0.372	0.01125	33.1	12.3
<b>Mean</b>	<b>0.0431</b>	<b>0.378</b>	<b>0.01236</b>	<b>34.6</b>	<b>11.6</b>
<i>Apus apus</i>	<b>0.042</b>	<b>0.38</b>	<b>0.014</b>	<b>29.4</b>	<b>10.3</b>

**Table S4. Body mass and flight related morphology in black and common swifts.**

**Related to Figure 2.** Body mass and wing morphology of nine (#1, .., #9) Northern black swifts (*Cypseloides niger borealis*) and mean values for common swift (*Apus apus*)<sup>S1</sup>. Wing measurements follow the procedure recommended by Pennycuick<sup>S2</sup>, where the wing area includes the area of the body between the wings. The dimensionless aspect ratio is calculated as wing span squared divided with wing area, and wing loading is the weight (body mass times the acceleration due to gravity) divided with wing area with unit newtons per meter squared (N/m<sup>2</sup>).

## **Supplemental References**

- S1. Henningsson, P., Muijres, F. T., and Hedenström, A. (2011). Time -resolved vortex wake of a common swift flying over a range of flight speeds. *J. R. Soc. Interface* 8, 807-816.
- S2. Pennycuik, C. J. (2008). *Modeling the flying bird* (Academic Press, London).