PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Hufkens K *et al.* 2023 Evaluating the effects of moonlight on the vertical flight profiles of three western palaearctic swifts. *Proc. R. Soc. B* **290**: 20230957.
https://doi.org/10.1098/rspb.2023.0957

Received: 26 April 2023
Accepted: 9 October 2023

Subject Category:
Behaviour

Subject Areas:
behaviour, ecology

Keywords:
migration, resource and habitat use, foraging, flight altitude, night-time schedule, light pollution

Author for correspondence:
Koen Hufkens
e-mail: koen.hufkens@gmail.com

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.6888257.

THE ROYAL SOCIETY
PUBLISHING

Evaluating the effects of moonlight on the vertical flight profiles of three western palaearctic swifts

Koen Hufkens[1], Christoph M. Meier[2], Ruben Evens[3], Josefa Arán Paredes[4,5], Hakan Karaardiç[6], Stef Vercauteren[7], Ann Van Gysel[7], James W. Fox[8], Carlos Miguel Pacheco[9], Luis P. da Silva[9,10], Sandra Fernandes[11], Pedro Henriques[12], Gonçalo Elias[13], Luís T. Costa[14], Martin Poot[15] and Lyndon Kearsley[1,16]

[1]BlueGreen Labs (bv), Kloetstraat 48, 9120 Melsele, Belgium
[2]Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland
[3]Department of Biology, Behavioural Ecology and Ecophysiology Group, University of Antwerp, Wilrijk, Belgium
[4]Institute of Geography, University of Bern, Hallestrasse 12, 3012 Bern, Switzerland
[5]Oeschger Centre for Climate Change Research, University of Bern, Falkenplatz 16, 3012 Bern, Switzerland
[6]Education Faculty, Math and Science Education Department, Alanya Alaaddin Keykubat University, Alanya, Turkey
[7]Locus Developments bv, Gent, Belgium
[8]Migrate Technology Ltd, Cambridge, UK
[9]Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO), InBIO Laboratório Associado, Universidade do Porto, 4485-661 Vairão, Portugal
[10]BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, 4485-661 Vairão, Portugal
[11]Department of Biology, Faculty of Sciences, Universidade do Porto, 4099-002 Porto, Portugal
[12]31 Rua do Sol, Queluz 2745-052, Portugal
[13]44 Rua de São Pedro, Castelo de Vide 7320-163, Portugal
[14]Nature Returns, Av D Sebastião 101, 2825-408 Costa da Caparica, Portugal
[15]Martin Poot Ecology, Culemborg, The Netherlands
[16]Belgian Ornithological Research Association, Steenweg Hulst-Lessen 29, 9140 Temse, Belgium

KH, 0000-0002-5070-8109; CMM, 0000-0001-9584-2339; JAP, 0009-0006-7176-2311; LK, 0000-0003-4526-1872

Recent studies have suggested the presence of moonlight mediated behaviour in avian aerial insectivores, such as swifts. Here, we use the combined analysis of state-of-the-art activity logger data across three swift species, the common, pallid and alpine swifts, to quantify flight height and activity in responses to moonlight-driven crepuscular and nocturnal light conditions. Our results show a significant response in flight heights to moonlight illuminance for common and pallid swifts, i.e. when moon illuminance increased flight height also increased, while a moonlight-driven response is absent in alpine swifts. We show a weak relationship between night-time illuminance-driven responses and twilight ascending behaviour, suggesting a decoupling of both crepuscular and night-time behaviour. We suggest that swifts optimize their flight behaviour to adapt to favourable night-time light conditions, driven by light-responsive and size-dependent vertical insect stratification and weather conditions.

1. Introduction

Relatively constant cycles of daylight and nocturnal darkness have shaped animal behaviour throughout evolutionary history [1–3]. Whereas most animals use photonic information from twilights as an external cue (i.e. zeitgeber) for daily activity, many crepuscular and nocturnal animals also use moonlight to trade off behaviours associated with rest, reproduction, predation risk and foraging [4–8]. Nocturnal activity and changes in foraging tactics in response to moonlight through improved prey detectability have been typically

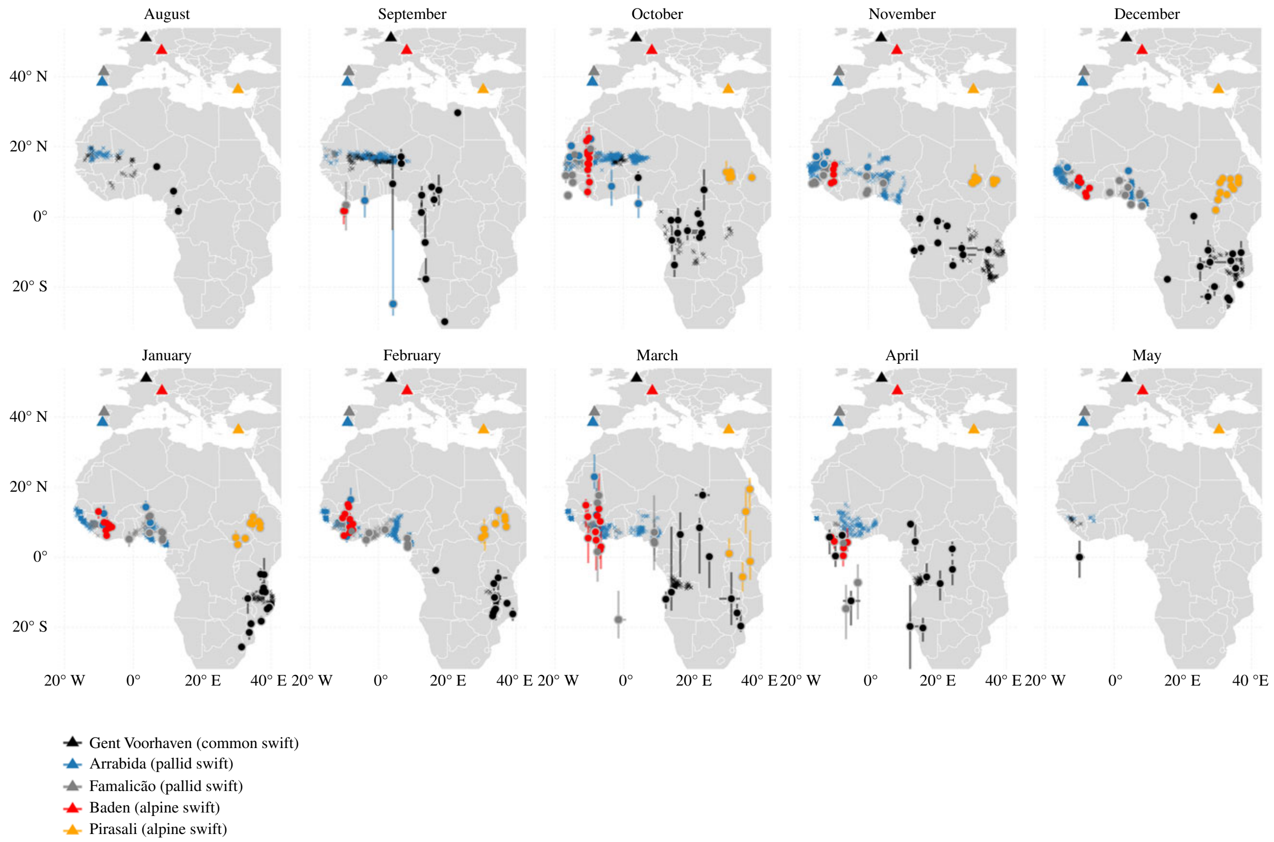

Figure 1. Overview map of monthly positions of both the GPS locations and the geolocator-based estimated location data, and this for the five sites (colour triangles) and three swift species (i.e. the common swift or *Apus apus*, the pallid swift or *Apus pallidus* and the alpine swift or *Tachymarptis melba*). Small X show GPS positions during stationary periods while positions during migration are omitted. Geolocator based locations, for the whole non-breeding season, were clustered using a breakpoint analysis dividing migration and stationary periods. Note that equinox positions have not been excluded. Large closed circles show the median location of the cluster, with error bars showing one standard deviation around the mean for each month.

attributed to nocturnal predators, such as nightjars, pelagic seabirds and owls [9,10]. For example, a comparison between 21 seabirds showed widely diverging responses to moonlight, depending on foraging and migratory tactics [11].

In the case of insectivorous bird species, nightjars have been shown to increase flight activity during moonlit nights, suggesting continued foraging when higher light levels facilitate prey detectability [4,6]. A study of northern black swifts (*Cypseloides niger borealis*) suggests that moonlit nights are used to continue foraging [7]. Although the common (*Apus apus*) and pallid swifts (*Apus pallidus*) are known to forage under night-time light pollution [12] or at times increase night-time flight altitude and activity [13,14], neither has of yet shown a clear link to moonlight.

Flight patterns of small insectivorous bird species, such as swifts, also show large variations during twilight. Twilight ascents, with birds ascending to high altitudes during both dusk and/or dawn, have been documented for the common swift using radar during the breeding season [15,16]. Observations using multi-sensor geolocators across the non-breeding season for alpine swifts (*Tachymarptis melba*) show similar results [17]. However, it remains uncertain if twilight behaviour is influenced by moonlight illuminance.

At the same time, many species of airborne insects on which swifts prey show increased activity during twilight and moonlit nights [18–20], determining the behaviour of their predators. Aerial feeders such as swifts are heavily dependent on these insects and select prey size according to their own body size [21]. Not only does insect activity increase during twilight and moonlit nights, their distribution is also strongly vertically stratified, shaping food availability, with small insects flying higher than larger ones [22]. It therefore follows that different species would find their prey at different altitudes.

A study of New World northern black swifts suggests that moonlit nights are used to continue foraging [7]. The strong similarity in flight behaviour between the Old World common swift and the New World black swift, despite an evolutionary divergence of over 20 Myr [23,24], puts forward the question if this nocturnal behaviour translates to Old World swifts. As such, it remains uncertain if aerial insectivores such as the common, pallid or alpine swifts extend their foraging behaviour into the night when natural (moonlight) illumination conditions are favourable.

Here, we use the combined analysis of state-of-the-art data-logger data (i.e. both from global positioning systems (GPS) and multi-sensor data loggers (MDLs)), investigating multiple lines of evidence, across three western palaearctic swift species to quantify flight height and activity responses to crepuscular and nocturnal light conditions and food availability. We hypothesize that swift species with different size dependent prey preferences [21], as derived from the literature, might show different responses to crepuscular and nocturnal light conditions.

2. Methods

We deployed two types of data loggers at five sites across Portugal (two), Belgium (one), Switzerland (one) and Turkey (one), for pallid, common and alpine swifts, respectively (figure 1). The Portuguese pallid swifts breed in the ceiling of a seaside cave in the Serra da Arrábida Natural Park south of Lisbon (38.47° N, 8.97° W, from hereon referred to as Arrábida), and a second colony is housed in a municipal building in the town of Vila Nova de Famalicão (41.41° N, 8.52° W, from hereon referred to as Famalicão) approximately 20 km inland and to the north of Porto. Belgian common swifts nest in built-in nest-boxes installed in a relatively new housing development (51.08° N, 3.73° E) along a dockside in the Ghent Voorhaven, Belgium (https://swifts.be/). The alpine swifts nested under the roof of a historical town gate in Baden, central Switzerland, (47.47° N, 8.31° E), and in crevices of natural rocks along the coastline of Pirasali island in southern Turkey (36.34° N, 30.53° E, from hereon referred to as Pirasali). For a detailed list of sites, loggers deployed and measurements made we refer to electronic supplementary material, appendix tables S1 and S2.

(a) Logger deployment

We used two lines of evidence based on separate animal tracking technologies across most sites. We used MDLs for light level geolocation, pressure and activity logging together with state of the art nanoFix micro-GPS loggers (figures 2 and 3).

MDLs (Intigeo-BAR & CAR, Migrate Technology Ltd, Cambridge, UK; BAR: approx. 0.37 g including harness, approx. 18 × 6 × 4.3 mm and CAR: approx. 0.43 g including harness, approx. 18 × 6 × 4.3 mm) were deployed on pallid swifts for five birds at the Arrábida site, and on 10 birds at the Famalicão site (with two and five recaptured, for Arrábida and Famalicão, respectively). Similarly, nine data loggers were deployed on Voorhaven birds, with seven retrieved. We tagged eight alpine swifts at the Swiss site and 26 at the Turkish Pirasali island with MDLs from the Swiss Ornithological Institute (SOI-GDL3pam, 1.4 gm including harness; approx. 24 × 12 × 9 mm, with four and 11 recaptured, respectively). All MDL sensors logged light levels, pressure and temperature, while a number also logged activity (electronic supplementary material, appendix table S1). Light intensity data were logged at 5 min intervals while all other variables were recorded every 5 or 30 min (details in electronic supplementary material, appendix table S3 and [25]). Data were logged across four seasons from 2018 to 2021 (electronic supplementary material, appendix table S1). Of a total of 58 MDLs deployed across all sites, 29 were retrieved during the following breeding season (electronic supplementary material, appendix table S5 for details).

GPS tagging, with nanoFix micro-GPS loggers with solar trickle charging (PathTrack Ltd, Otley, UK, approx. 1.04 g including harness, approx. 21 × 12 × 4.5 mm plus external added whip antenna of 45 mm) across the two Portuguese sites and the Belgian site were carried out in parallel with the geolocator tagging. We deployed 19 loggers on adult pallid and common swifts of which six at both the Arrábida and Famalicão site, as well as seven at Gent Voorhaven (of which five, three and four were recaptured, respectively). Swift diurnal positions and altitude were tracked throughout a full migration season, at regular 6 h intervals. Logging starts at 1 h Greenwich mean time (GMT) for the Arrábida site, while Famalicão and Gent Voorhaven sites start logging at midnight (0 h and/or 2 h GMT). Data were logged over three seasons but with varying deployment dates (2019–2022, electronic supplementary material, appendix tables S2–S4). Of 19 GPS loggers deployed across sites, 11 were retrieved during the following breeding seasons. At the Famalicão site, two GPS loggers failed shortly after deployment and are therefore not included in our analysis. At the Gent Voorhaven site, two GPS loggers were recovered but only a partial track was used for Tag 21 900 due to an age-related gradual battery failure (electronic supplementary material, appendix table S1). Raw data were forwarded to PathTrack Ltd for high precision processing.

Across all available data, we find overall mean recapture rates of approximately 55% and approximately 57% for MDL and GPS loggers, respectively. We acknowledge that recapture rates vary widely across deployed loggers and locations (from 40 to 83%, electronic supplementary material, appendix table S5). Differences in recapture rates are due to a combination of the true return frequency of swifts as influenced by recapture protocols, weather conditions and potential tag effect [26,27]. Most recapture rates are similar or exceed those of (long-term) ringing studies [28] or control groups. For detailed recapture statistics, we refer to electronic supplementary material, appendix table S5. All loggers were deployed late in the breeding season to avoid breeding disturbance and followed the ongoing ringing protocol at the Portuguese colony [28], and a similar approach at the Voorhaven site, i.e. using a full body harness with a 1 mm wide flat braided soft terylene cord to avoid abrasion. Alpine swift protocols followed ringing and sensor deployment protocols as described in Meier *et al.* [17,25], installing loggers at the end of the breeding season and collecting them before egg-laying started. Returning swifts were examined and no abrasion or skin damage was found.

(b) Data pre-processing

(i) Location

GPS sensors provide near absolute positional accuracy in three dimensions [14]. GPS data analysis separated stationary (area-restricted search) from migration movements using a hidden Markov model (HMM). The non-breeding season analysed in this study was defined as all movements lower than 23.4° N, i.e. the Tropic of Cancer, constraining data to continental Africa below the Sahara desert. Swift movements were categorized as migration (corridor movements) and stationary (area-restricted search) using a two-state HMM [29], with missing positions filled using continuous-time correlated random walk data [30] to create a homogeneous 6 h time series (see electronic supplementary material, appendix; [14]). GPS positions were divided into 'coastal' and 'continental' positions, where a coastal position is defined as the two positions preceding and following a position above marine waters, with the coastline defined by 1:10 m Natural Earth data (www.naturalearthdata.com). GPS time in GMT was corrected to local time using the longitudinal offset and centred on midnight.

Data were downloaded from MDLs and the approximate location of the common and pallid swifts was determined using geolocation by light using the 'GeoLight' R package [31]. MDL data were constrained to the non-breeding season, determined by uninterrupted acceleration measurements and clear diurnal light patterns (electronic supplementary material, appendix table S1). To mark twilight events, we used a threshold of 1.5 on log-transformed and clock drift adjusted light level data. Clock drift was assumed to be linearly accumulating and was calculated from the difference between the on-board clock of the tag and a reference time. On a logger-by-logger basis, we selected the most suitable sun-angle in half-degree steps by comparing derived positions with known GPS-based stationary locations and published relevant literature (electronic supplementary material, appendix table S1 and figure S1; [13,14,25,27].

The median longitudinal difference between the breeding site and stationary positions were used to correct logger time to standardized local (solar) time, with a 4 min per degree time difference. Location estimates were clustered in stationary and migration periods using a breakpoint analysis (i.e. changeLight in the 'GeoLight' R package, quantile parameter set to 0.9). For the processing of the Swiss and Turkish sites, we refer to procedures described in Meier *et al.* [25]. We assigned the median longitude and latitude across a stationary cluster of dates to best

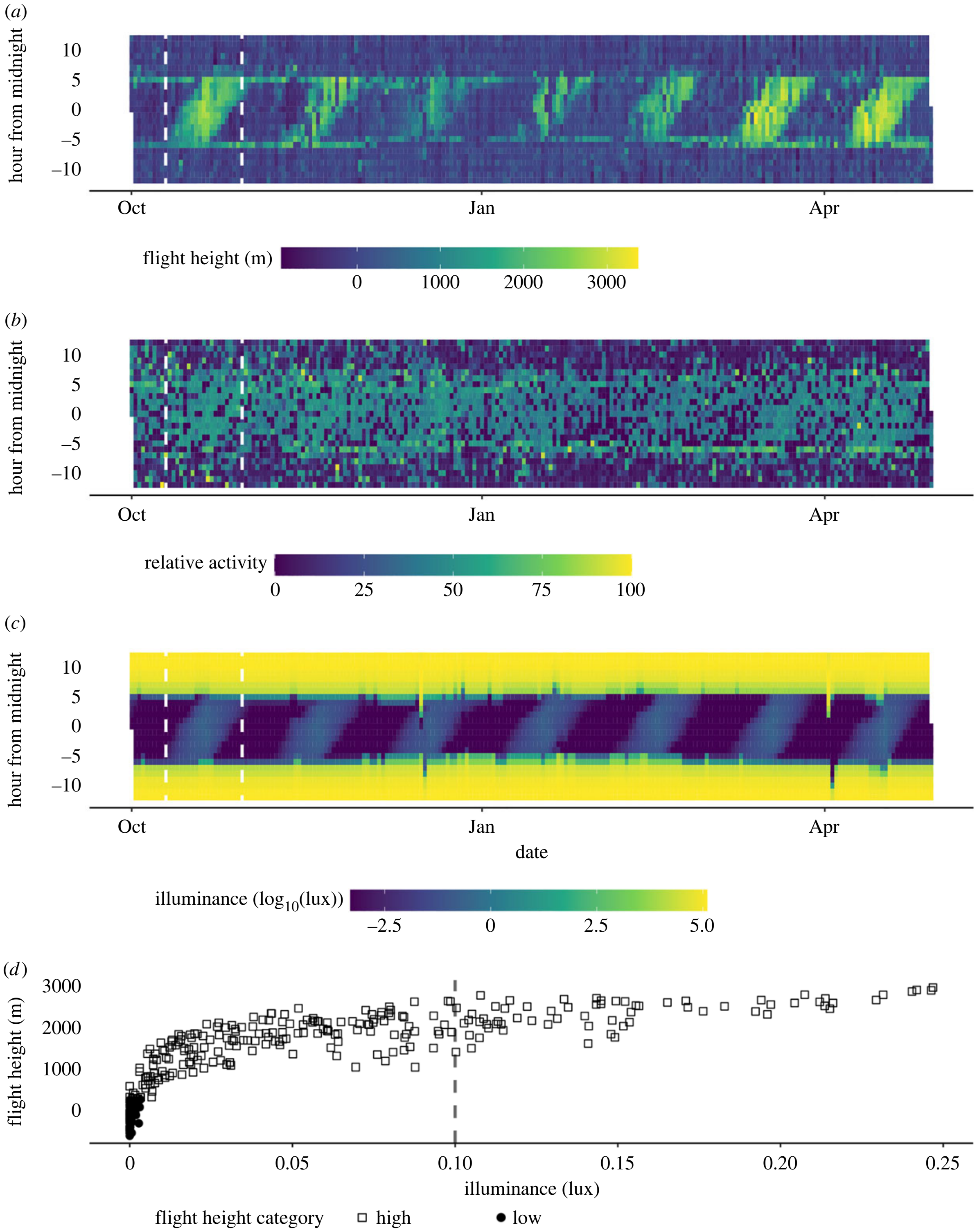

Figure 2. Continuous multi-sensor data logger (normalized) flight height (*a*) and relative activity (*b*) measurements for common swift (*Apus apus*) tag CC895 compared with modelled illuminance (log(lux)) values, *c*). In (*a*–*c*) each column represents a day of data with time centred on midnight, where negative hours indicate hours before midnight and positive values hours after midnight. Half-hourly values are represented by a pixel, with its colour representing the measurement value (see colour legends for scale). Relative activity is a proxy for motion, i.e. wing beats, and scales between 0 and 100 (unitless). And (*d*), a scatterplot of the flight height changes in response to changing night-time illuminance values over the course of a lunar cycle of October 2021. Sampled dates of the scatterplot (*d*) are outlined by two white dashed lines in (*a*–*c*), where flight height categories are marked with open rectangles and closed circles, for high and low flights, respectively. A grey vertical line specifies the moonlight illuminance value at which a approximately 50% probability of a high flight is exceeded (as modelled using a generalized linear model (GLM)).

approximate a swift's location during that time. Missing location estimates (e.g. during equinoxes) were linearly interpolated from adjacent median cluster coordinates (figure 1).

(ii) Flight altitude and activity

GPS logger processing can lead to spurious values due to limited reception, which results in negative altitudes or locking values to 250 m intervals if no clear altitude solution is found (PathTrack Ltd 2021, personal communications). Therefore, we excluded all negative altitude values and those rounded to 250 m increments. Flight altitudes were corrected for topography to flight height using NASADEM digital elevation model (DEM) data [32], with values below terrain level removed.

The MDL accelerometer reads bursts along x- and z-axis during a set measurement time interval (either 30 or 5 min,

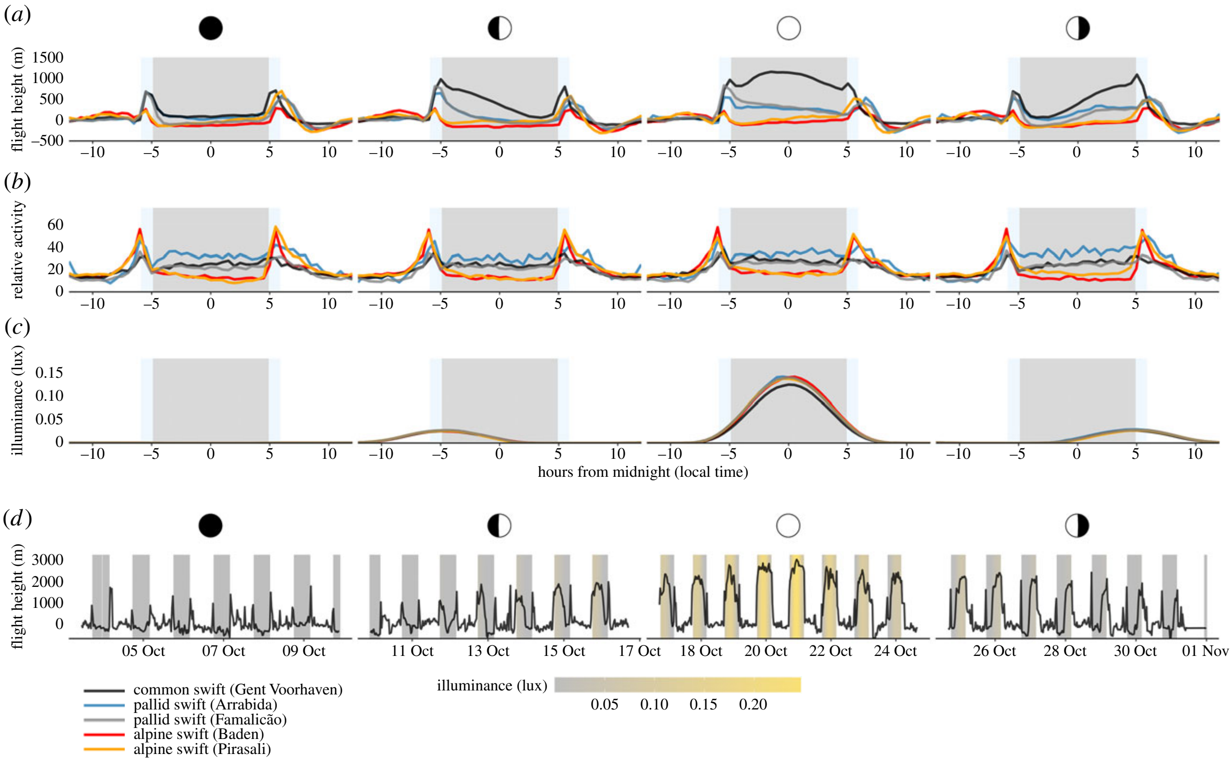

Figure 3. Average flight height (elevation in metres, centred on a daytime mean of 0), the flight activity and derived moon illuminance (lux) centred on midnight during moon phases (*a*–*c*). Different sites and species (i.e. the common swift or *Apus apus*, the pallid swift or *Apus pallidus* and the alpine swift or *Tachymarptis melba*) are indicated by the colour of the full lines. The grey rectangles in plots (*a*–*c*) indicate the average astronomical night, where light blue rectangles approximate twilight as mean dusk and dawn ± 1 s.d., respectively. In addition, a full time series of a lunar cycle (*d*) showing the progression of flight heights is shown in combination with moon illuminance values (daytime values are not shown, as orders of magnitude higher than the maximum illuminance of a full moon approx. 0.23 lux). We show time series for common swift tag CC895. Moon phases from left to right are indicated by their respective icons and are as follows: new moon, first quarter, full moon and last quarter. Relative activity (*b*) values are scaled on a tag-by-tag basis.

for Migrate Technology Intigeo-CAR or Swiss Ornithological Institute GDL sensors respectively, see electronic supplementary material, appendix). Activity measurements capture the accumulated up–down movements of the body of a bird relative to gravity (*z*-axis) and should be seen as a proxy for motion, i.e. wing beats. The values reported are relative activity (normalized by tag between 0 and 100, unitless) and are a trade-off of technical constraints, measurement resolution and species specific characteristics [33,34]. To ensure temporal consistency across loggers, we resampled the 5 min GDL activity and pressure measurements to half-hourly intervals. Atmospheric pressure recorded was converted to altitude (in metres) using the international standard atmosphere (International Organization for Standardization ISO 2533:1975, see electronic supplementary material, appendix). We did not correct for local weather conditions (pressure and temperature) as it only marginally affects altitude estimates [7].

Half-hourly MDL pressure and activity data were joined with the corresponding daily location estimates. GPS data highlighted considerable topographic differences across locations, e.g. common swifts fly over a mean topography of greater than 500 m.a.s.l., approximately 250 m higher than pallid swifts (electronic supplementary material, appendix table S3). Visually comparing absolute flight altitudes between species is therefore difficult, and flight altitudes should be normalized for the underlying land surface elevation. Uncertainty on MDL positions limits correction of flight altitudes using DEM data. We accounted for day-to-day changes in underlying topography by subtracting the mean daytime altitudes on a day-by-day basis, using daytime (see below) flights as a fixed baseline (assuming relatively stable low flights during this period; e.g. [15]). This method retains absolute diurnal altitude differences as a proxy for true flight heights, but might at times give rise to negative flight heights (figure 2; electronic supplementary material, appendix figures S1 and S2).

We further divided flight heights into two classes using a threshold value based on the mean and standard deviation of daytime flight heights. Night-time flight heights exceeding the mean daytime flight height plus one standard deviation, per individual (tag), were considered ‘high’ flights and all others as ‘low’ flights. This approach normalizes responses between individuals (tags), allowing for a comparison across species irrespective of underlying topography and allows for an easy interpretation of statistical results.

(iii) Sun and moon parameters

To facilitate further analysis, all data were divided into distinct periods according to the sun's location. Here, ‘daytime’ was defined as values with a sun angle above 0° (above the horizon). ‘Dawn’ and ‘dusk’ were specified as times where the sun angle is between 0° to 18° below the horizon (the end of astronomical twilight) on the sun's rising or setting direction. All other times are set to ‘night-time’.

Moon fraction and moon altitude are a poor substitute for moonlight illuminance in animal studies [35,36]. We therefore improve upon general approaches using moon elevation and moon illuminated fraction by calculating moonlight illuminance according to Janiczek & DeYoung [37] for all positions using the ‘skylight’ R package [38]. We used MDL loggers' median positions per stationary cluster (figure 1), or absolute GPS position to calculate moonlight illuminance. Due to the large uncertainties on MDL light level geolocation, we did not account for local weather (cloud) conditions as this might weaken results rather than address any biases [6]. We acknowledge that geolocation is not free of uncertainty. As such, estimated illuminance values are dependent on the accuracy of measured light-derived geolocation, which might in turn influence our modelling efforts. Yet, visual inspection of data centred on local midnight shows an expected centred twilight timing (electronic supplementary material, appendix figure S1–S4). We calculated an additional parameter for our crepuscular analysis, in particular the 'twilight flight timing'. Twilight flight timing is defined as the timing of maximum flight height relative to timing of civil dusk or dawn, i.e. when the sun is 6° under the horizon (as calculated for a given location). Deviations of this twilight flight timing in response to moonlight illuminated night-time conditions would suggest an illuminance sensitivity in twilight behaviour. This behaviour would avoid additional ascents during moonlit nights potentially saving energy, at the expense of sleep cycles as proposed by Liechti *et al.* [33].

(c) Statistical analysis

In our statistical analysis, we test if flight activity and altitudes are influenced by moon illuminance. We divide our analysis into two parts. First, we question if natural nocturnal light affects night-time flight height using both MDL and GPS sensors; and second, we test if nocturnal light affects twilight (dusk/dawn) activity, i.e. the effect on flight height when moving into or out of twilight periods.

To quantify the response of moon illuminance on the state of the flight height (high or low), we fitted a generalized linear mixed effects model (GLMM) with a binomial link function and using moon illuminance and lagged altitude, i.e. the altitude as measured at the previous time step, to account for temporal autocorrelation, and species as fixed effects (glmmTMB, [39]). Including the lagged altitude at a previous time step accounts for temporal autocorrelation by allowing the model to consider a previous flight state, in addition to slow varying moon illuminance values. The tag is nested within species as a random intercept to account for species and bird specific behaviour. For all MDL measurements, we only considered stationary periods. We did not include activity explicitly, as activity monitoring is logger profile and species dependent [34], making the reuse of activity data from various loggers and species in the same model challenging. Activity was also not measured in all tags, which would reduce our dataset significantly (electronic supplementary material, appendix table S1). Across night-time values, activity and flight height were poorly correlated (absolute Pearson's correlation coefficient $|\rho| < 0.15$, electronic supplementary material, appendix table S7). For the GPS data, we used the same model. However, GPS measurements were measured at a low temporal frequency and therefore no correction for autocorrelation (i.e. lagged altitude) was applied. In our analysis, we only retained continental positions. Coastal flight of predominantly pallid swifts were excluded, as previously described coastal flight patterns [14] might skew the analysis.

The influence of night-time moonlight conditions on twilight behaviour, i.e. the flight behaviour moving into or out of twilight periods, is described by a linear mixed effects model with the twilight flight timing as response variable, moon illuminance as a fixed effect, with tag nested within species as a random intercept. Similarly, we use a linear mixed effects model to quantify flight activity between species and the time of day (daytime versus night-time). We modelled differences in flight activity as a function of time-of-day (day- versus night-time) interacting with species as a fixed effect, while accounting for species and bird specific behaviour as random effects.

All statistics were carried out in R [40] using 'glmmTMB', 'lme4', 'lmerTest' and 'ggeffects' packages, where visualizations were supported by the 'tidyverse', 'patchwork', 'ggtext' packages [39,41–46].

Table 1. Model output of quantifying high or low flights in response to moon illuminance, using generalized linear mixed effects model and multi-sensor data logger (MDL) data. The model used moon illuminance, lagged altitude, to account for temporal autocorrelation, and species as fixed effects. The tag is nested within species (i.e. the common swift or *Apus apus*, the pallid swift or *Apus pallidus* and the alpine swift or *Tachymarptis melba*) as a random intercept to account for species and bird specific behaviour.

predictors	estimate	s.e.	*z*	*p*-value
intercept	−0.51356	0.36989	−1.39	0.1650
moon illuminance	8.90868	0.26969	33.03	<0.0001
previous altitude	1.97752	0.02047	96.59	<0.0001
species: pallid swift	−1.77630	0.52346	−3.39	<0.0001
species: alpine swift	−4.27890	0.49564	−8.63	<0.0001
random effect	**variance**	**s.d.**		
tag within species	0.9549	0.97719		
species	<0.000	0.0004		

3. Results

All swifts showed known migration patterns, with the pallid swifts foraging in western Africa during the non-breeding season [13,14,27,47], while the common swifts moved further to southeast Africa (figure 1, [48]. Alpine swifts migrated to either western or eastern Africa depending on their breeding sites, as previously described by Meier *et al.* [25]. We logged a total of 7235 GPS and 209 565 MDL positions with reliable data for statistical analysis. The MDL geolocation patterns of stationary clusters correspond with those registered by GPS, despite the uncertainty on light level geolocation (figure 1).

Distinct differences in maximum flight height are still noticeable between species (figure 3*a*), despite normalizing flight altitude data. Common swifts reach a maximum nocturnal flight height during a full moon of 1623 ± 873 m, while pallid swifts on average flew at 929 ± 519 m and 896 ± 494 m for the Famalicão and Arrabida sites, respectively. Alpine swifts did not show high nocturnal flights, with new moon night-time flights not differing greatly from full moon ones (331 ± 264 and 406 ± 334 m for Pirasali and 196 ± 183 and 253 ± 209 m for Baden, figure 3*a*).

Across moon phases, we observe consistent patterns in changes in flight height and activity, and this for both GPS or MDL sensors. MDL flights are high when moonlight illuminance is high (figure 3*a*,*c*,*d*; electronic supplementary material, appendix table S3) for the pallid and common swifts. By contrast, alpine swifts do not show a response to moonlight figure 3*a*). Our MDL (GLMM) model showed a marginal R^2 of 0.70 for the explanatory power of the fixed effects alone, with a significant effect of moon illuminance, temporal lag and species (table 1). A similar model using GPS data, but omitting the lagged altitude response, shows that the explanatory power related to the fixed effects alone (marginal R^2) is weak at 0.15, with a positive and significant effect of moon illuminance; yet no significant effect of species was found (table 2). Our model results show different species responses, with common and pallid swift showing a strong response to moonlight illuminance (figure 3), while alpine swifts lack such a response (figures 3*a* and 4*a*). Two sensor

Table 2. Model output of quantifying high or low flights in response to moon illuminance, using a generalized linear mixed effects model as measured from GPS data. The model used moon illuminance and species as fixed effects. The tag is nested within species (i.e. the common swift or *Apus apus*, the pallid swift or *Apus pallidus* and the alpine swift or *Tachymarptis melba*) as a random intercept to account for species and bird specific behaviour.

predictors	estimate	s.e.	*z*	*p*-value
intercept	−2.1526	0.3991	−5.392	<0.0001
moon illuminance	15.3049	1.0566	14.485	<0.0001
species: pallid swift	0.2165	0.4509	0.48	0.631
random effect	**variance**	**s.d.**		
tag within species	0.338	0.579		
species	<0.000	<0.000		

technologies provide two lines of evidence and robust and consistent hypothesis support, where the high frequency of MDL data complements high accuracy of GPS-based data.

Twilight ascents are especially pronounced for common swifts with very brief (1 h) long climbs up to an average maximum flight height of 2221 ± 629 m, and climbing on average 1807 ± 551 m (figures 2*d* and 3*c*). Twilight flights for pallid and alpine swifts are generally lower, only rising to average maximum flight heights of approximately 1500 m, and climbing approximately 1000 m (average maximum flight height: 1537 ± 656 m and 1464 ± 534 m, average flight height increase of 1187 ± 633 m and 897 ± 278 m, for pallid and alpine swifts, respectively). When testing if nocturnal light affects a shift towards night-time away from civil twilight (for dusk and dawn) using a linear mixed effects model we found our model's explanatory power weak (conditional $R^2 = 0.03$, table 3; electronic supplementary material, appendix figure S9), with a statistically significant effect of both fixed effects, moon illuminance and twilight period (dusk/dawn).

For the common and pallid swifts, dusk marked the start of a period of sustained high activity continuing throughout the night until dawn with peaks during both twilight periods (figure 3*b*). A formal test comparing daytime with night-time flight activity shows a marginal R^2 of 0.7 for fixed effects alone. Where, for both the common and pallid swift the interaction effect between time-of-day (day versus night) and species is statistically significant and positive, this interaction is statistically significant and negative for alpine swifts (electronic supplementary material, appendix table S6 and figure S9).

4. Discussion

Several aerial insectivores have shown to profit from night-time illuminance conditions, either from artificial sources or through moonlight. These favourable illumination conditions allow for prolonged foraging behaviour. Direct observations of common swifts show documented prolonged flight activity in the presence of intense urban light pollution [12], while it has been hypothesized that northern black swifts (*Cypseloides niger borealis*) use favourable night-time light conditions to continue foraging [7]. In this study, we explored if three western palaearctic swift species, the common, pallid and alpine swift, show divergent night-time behaviour across their African non-breeding season in response to moonlight illuminance.

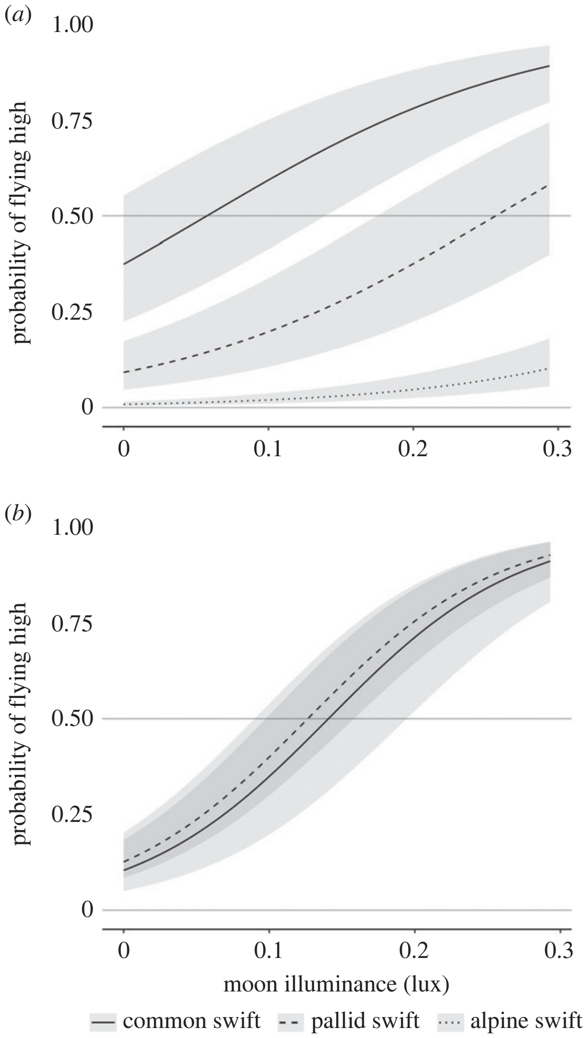

Figure 4. Marginal effect sizes by species (i.e. the common swift or *Apus apus*, the pallid swift or *Apus pallidus* and the alpine swift or *Tachymarptis melba*) for the generalized linear mixed effects logistic models relating moon illuminance with flight height for both MDL, i.e. showing the probability of a high night-time flight relative to daytime flight altitudes for MDL (*a*) and GPS (*b*). Grey 95% confidence intervals (CIs) were computed using a Wald z-distribution approximation and a standardized dataset.

Table 3. Model output of a linear mixed effects model comparing the timing of maximum twilight flight height (in minutes from civil twilight) in response to night-time moonlight illuminance using multi-sensor data logger (MDL) data. Moon illuminance is a fixed effect with tags nested within species (i.e. the common swift or *Apus apus*, the pallid swift or *Apus pallidus* and the alpine swift or *Tachymarptis melba*) as a random intercept.

predictors	estimate	s.e.	*t*	*p*-value
intercept	8.562	1.141	7.507	<0.005
moon illuminance	130.408	8.036	16.228	<0.0001
random effect	**variance**	**s.d.**		
tag within species	13.675	3.698		
species	1.977	1.406		

Our results show that moonlight-driven night-time responses are strongly species and context dependent. We note the strongest response (absolute flight heights and moonlight illuminance sensitivity) in the common swift, a reduced response in pallid swifts and no response in alpine swifts. Species responses fall along a gradient in body and prey size, and previously described flight patterns [21,22]. We show a weak relationship between night-time illuminance-driven responses and twilight ascending behaviour across all species, suggesting a decoupling of both behaviours, separating night-time foraging from social, zeitgeber and orientation-focused behaviour.

We used both GPS and MDL data to test our hypothesis. The combined approach, using two lines of evidence, allowed us to validate hypotheses using two independent measurements and led to a more nuanced analysis. Where MDL-based model output suggest diverging responses for common and pallid swifts, the GPS results showed no significant species effect, potentially related to unaccounted-for effects of (coastal) weather systems (see below, [14], electronic supplementary material, appendix figure S10). Our approach highlights the strength of combining both sensor technologies to gain a better understanding of species behaviour. In contrast to common approaches using moon elevation angles and phase [6,7], we used moon illuminance values, which provide more robust model results [36]. To ensure reproducibility, we made our implementation of the sky illuminance model by Janiczek & DeYoung [37] freely available to the community as the ‘skylight’ R package [38].

(a) Night-time moonlight response

Our study found three distinct night-time flight patterns in response to changing moonlight illuminance. This varying sensitivity in the probability of a high night-time flight suggests that the magnitude and frequency of night-time moonlight responses are highly species and context specific.

In common swifts, the strong synchrony of nocturnal flight behaviour with moon illuminance showed a pronounced non-linear relationship in their flight height response, with a low threshold value relative to their mean daytime flight behaviour (figures 2*d* and 4*a*). This behaviour was limited in flight height (figures 2*d* and 3*d*), but still allowed the common swifts to rise more than 1500 m. Little change in moonlight is therefore required to trigger a change in their flight height. Research on the American black swift has shown that responses to decreasing moon illuminance, in response to a moon eclipse, are indeed fast and reversible [7]. Our analysis corroborates these observations where moonlight-synchronized flight patterns are at times abruptly interrupted, only to be resumed later in the night (figure 2*a*, months of January and February). Conversely, during the new moon, in absence of any moonlight, flights remained consistently low. For pallid swifts, higher illuminance values are required to trigger a higher flight (figure 4*a*,*b*) as shown by our model results of MDL data.

Less pronounced moonlight-driven behaviour in pallid swifts is probably due to common low-altitude coastal foraging behaviour around sea breeze fronts [14], which limits the ability to rise to greater heights. Here, offshore winds at higher altitudes (greater than 1000 m) would push birds away from land. GPS data shows that common swifts rarely position themselves near or over coastal waters, as shown by only 14 registered locations, while almost a quarter of the positions of the pallid swifts are coastal foraging locations ([14], electronic supplementary material, appendix table S2). This suggests that moonlight illuminance-driven responses are mediated by synoptic and macroscale weather. By contrast, inland continental positions showed higher night-time flights of pallid swifts (table 1 in [14]). It was speculated that these flights could be linked to common aggregation of insects at inversion layers at the dry side of the Intertropical Convergence Zone (ITCZ) [49,50]. Our current analysis puts these results in a different perspective, and shows a strong connection to moonlight illuminance. However, we cannot exclude the influence of weather and seasonal changes in frequency of the moonlight illuminance responses for both the common and pallid swifts. Overview plots show that the response is weakest from December to February (figure 2; electronic supplementary material, appendix S1 and S2). These time windows correspond with time spent in tropical regions where cloud conditions or large frontal systems might obscure or influence moonlight-driven flight responses. We suggest that clouds and a swift’s geographic position with respect to seasonal (local) weather, might limit moon illuminance responses in more cloudy tropical areas.

In contrast to the behaviour of both the common and pallid swift, the alpine swift does not show a moonlight illuminance-driven response in flight height and activity (figures 3*a*,*b* and 4*a*). Despite being a small aerial insectivore, which is continuously on the wing [17], they are twice the size of both the common and pallid swift, weighing approximately 100 g compared with approximately 40 g [21]. Body size positively correlates with prey size across seven species of swifts, with the alpine swift targeting consistently larger prey than *Apus sp.* [21]. It is a well-observed phenomena that insects increase their flight height and activity during moonlit nights [19,20,51], and insect size distributions are strongly vertically stratified based, with small insects flying higher than large ones [22,52]. As such, alpine swift, preferring larger (low flying) insects, would naturally forage at lower altitudes than the common and pallid swifts, which prefer high flying smaller insects. We show that cyclical moonlight-driven increases in flight height in search for prey seems plausible, where swift flight patterns follow a size-dependent continuum in (insect) prey size [22,52].

While moonlight may determine flight height in common and pallid swifts, it does not affect flight activity. During all nights flight activity remained high, suggesting more intense flapping activity and conversely less soaring flights (figure 3*b*, [53]). In contrast, alpine swifts do not show sustained high activity during the night, with activity values similar to those during the day (figure 3*b*). The lack of thermals during night-time might explain some of this dynamic, although the contrasting behaviour of the alpine swift puts this hypothesis in question. Past research has suggested long nocturnal gliding intervals with low flapping frequency, suggesting roosting on the wing [33]. We argue that alpine swift, due to their critical energy budget, might not preclude low intensity opportunistic night-time feeding. A strong moonlight-driven decrease in activity, as mentioned by Hedenström *et al*. [7], is missing in all our observations (electronic supplementary material, appendix figures S3–S5).

Although the spatial distribution of swift species seems to follow a size-dependent vertical distribution of insects during the night, we cannot exclude predator avoidance as part of the moonlight illuminance-driven response. The Eleonora’s falcon shares overlapping regions with all three species during the non-breeding period [54], and is known to hunt at night under favourable artificial or moonlight conditions [55]. Escaping from falcons by rising flights is a common predator evasion strategy in swifts [56]. Giant noctule bats (*Nyctalus lasiopterus*) have been shown to feed upon passerine birds during migration [57,58]. Noctule bats show considerable flexibility in foraging timing and space use in response to food availability. However, contrasting flight strategies and/or prolonged periods of high flights across swifts would make this scenario less likely.

Furthermore, the observed patterns question the notion that birds roost throughout the night, on the wing [59]. Nocturnal moonlight-driven changes in flight height and activity for the common and pallid swifts suggest that, at least, these species adapt their waking flights to the light environment. This suggests plasticity in their sleep–wake cycle, where it has been suggested that descending twilight flights might serve as a time for rest [7,48].

(b) Twilight behaviour

For all species, we find pronounced twilight ascents aligning with a period of high flight activity. For both the common and pallid swifts this high activity continues through the night regardless of light-driven changes in flight height (figure 2*a*,*b*). In contrast, alpine swifts show isolated peaks during twilight, with activity values similar to daytime values during the night.

Maximum twilight flight heights are attained before civil dusk or right after civil dawn (figure 3). Given our current data, we do not show strong support for a shift in twilight flight timing in relation to moon illuminance. While it would be energetically favourable to not descend when high moonlight illuminance conditions follow later in the night (or conversely moonlight illuminance is followed by twilight conditions), we do not observe such behaviour. Swifts do not seem to anticipate a future moonlit night or coming twilight conditions (figures 2*b* and 3*a*). All swifts descend after their twilight ascent, even briefly, before any moonlight illuminance response. Due to the short duration of twilight events, the sampling rate and the uncertainty on twilight events linked to positional accuracy the statistical power of our analysis is limited.

The full scope of the twilight behaviour, and its connection to night-time activity, remains poorly understood. It has been shown that pallid swifts overtop sea-breeze fronts using higher twilight and night-time flights in order to retain a favourable foraging position [14]. Therefore, an alternative hypothesis exists for at least a part of the non-breeding season of pallid swifts, while for other species other factors cannot be excluded. A weak moonlight illuminance sensitivity, moving into and out of twilight conditions does not exclude the reorientation hypothesis [60,61] with flights linked to the timing of maximum sunlight polarization. The most pronounced twilight ascends are recorded for the common swift. This species crosses the equator and would benefit the most from a twilight-recalibrated compass [62]. Strong twilight ascending flights could suggest reorientation events. However, past analysis of alpine swift data showed social bonding through screaming parties dominated over reorientation [17]. Foraging behaviour cannot be fully excluded either. Both moonlight illuminance [19,20,51] and twilight conditions have been linked to increased insect activity of small swarming insects such as mosquitoes, flies and ants [52], making up a sizeable proportion of the diet of small aerial insectivore (tropical) bats [63,64]. During the breeding season, common swifts have been observed to prey on swarming insects at twilight near the Afsluitdijk, The Netherlands [15]. However, limited observational evidence exists of such behaviour during the non-breeding season. Finally, due to the continued active behaviour in moonlit nights, the hypothesis of descending twilight flights as a resting phase [7,48] needs consideration as this behaviour is pronounced and consistent across all three permanently airborne swift species [13,17,33,48].

In the assessment of both the night-time moonlight illuminance responses and twilight behaviour, there is a need for co-located measurements of insect prey to confirm a distinct foraging aspect over potential social, sleep, orientation or predator avoidance-based behaviour. The co-occurrence of swift along an insect prey size-dependent distribution, following behaviour of insects as described in literature, would call into question if, like nightjars [65], at least the common and pallid swifts might be considered crepuscular-nocturnal aerial insectivores.

5. Conclusion

We show that both the common and pallid swifts engage in night-time ascending behaviour in the presence of moonlight, while no such behaviour is observed in alpine swifts. These flight patterns follow a weight to prey-size vertical stratification of insects as described in the literature. Our analysis changes the interpretation of the diurnal movements of night-time ascents of pallid swifts previously described, and suggests similarities between both common and pallid swift behaviour and the behaviour observed in both the northern black swift and nightjars. All these species seem to extend their night-time foraging behaviour in the presence of moonlight. As all swift species considered (so far) have documented continuous flights during the non-breeding season, we suggest that swifts optimize their flight behaviour to adapt to favourable night-time light conditions, weather conditions and a size-dependent (vertical) insect prey distribution.

Ethics. Swiss loggers were attached under a ringing licence of the Federal Office for the Environment FOEN and ethical approval of the veterinary office of canton of Aargau under the licence 26552/LU0415. All research at the Arrabida/Famalicão sites was carried out under all the required legal requirements of the ICNF (Portuguese Institute for the Conservation of Nature and Forests), ringing licences 134/2021 and 144/2022. For research at the Gent Voorhaven site, the licence was issued by the Agency for Nature and Forest, Belgium (Flanders) number ANB/BL-FF/VERG/11-00316.

Data accessibility. The manuscript's database and code supporting our findings is made available on Github at: https://bluegreen-labs.github.io/swift_lunar_synchrony/ and a matching Zenodo Digital Repository: https://doi.org/10.5281/zenodo.7814214 [66] under a CC-BY 4.0 licence.

Supplementary material is available online [67].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. K.H.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing—original draft, writing—review and editing; C.M.M.: conceptualization, data curation, formal analysis, investigation, methodology, resources, validation, visualization, writing—original draft, writing—review and editing; R.E.: conceptualization,

investigation, methodology, writing—review and editing; J.A.P.: formal analysis, investigation, methodology, validation, writing—review and editing; H.K.: data curation, resources, writing—review and editing; S.V.: resources, writing—review and editing; A.V.G.: resources, writing—review and editing; J.W.F.: data curation, resources, software, writing—review and editing; C.M.P.: resources, writing—review and editing; L.P.S.: resources, writing—review and editing; S.F.: resources, writing—review and editing; P.H.: resources, writing—review and editing; G.E.: investigation, resources, writing—review and editing; L.T.C.: investigation, resources, writing—review and editing; M.P.: resources, writing—review and editing; L.K.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. The GPS loggers were financed by the Belgian Ornithological Research Association (Belora vzw) as was a portion of the travel expenses (L.K.) for initial deployment (2019). R.E. was funded by the FWO (project number 12T3922N). L.P.S. was funded by FCT through the research contract CEECIND/02064/2017. C.M.M. acknowledges the Swiss federal office for the environment (FOEN) for financial support for the development of the tags (grant no. UTF 400.34.11) and the Wolfermann-Nägeli foundation granted support for fieldwork. J.W.F. and Migrate Technology Ltd provided assistance in the form of a research and development collaboration, covering design and trial of the prototype MDL loggers. All aspects of data processing by K.H. were privately financed on a voluntary basis.

Acknowledgements. Belora vzw, Locus Developments bv (Gent) and the Municipal government of Vila Nova de Famalicão funded GPS loggers. We are grateful for the support by Migrate Technology Ltd for providing prototype multi-sensor data loggers in a research and development collaboration. We thank PathTrack Ltd for their custom data processing, and discussions regarding data quality. Moon phase icons were taken from the Emoji One BW v. 2.0 library from JoyPixels (https://joypixels.com/).

References

1. Aschoff J. 1989 Temporal orientation: circadian clocks in animals and humans. *Anim. Behav.* **37**, 881–896. (doi:10.1016/0003-3472(89)90132-2)
2. Alerstam T, Pettersson S-G. 1991 Orientation along great circles by migrating birds using a sun compass. *J. Theor. Biol.* **152**, 191–202. (doi:10.1016/S0022-5193(05)80452-7)
3. Guilford T, Taylor GK. 2014 The sun compass revisited. *Anim. Behav.* **97**, 135–143. (doi:10.1016/j.anbehav.2014.09.005)
4. Smit B, Boyles JG, Brigham RM, McKechnie AE. 2011 Torpor in dark times: patterns of heterothermy are associated with the lunar cycle in a nocturnal bird. *J. Biol. Rhythms* **26**, 241–248. (doi:10.1177/0748730411402632)
5. Appel G, López-Baucells A, Magnusson WE, Bobrowiec PED. 2017 Aerial insectivorous bat activity in relation to moonlight intensity. *Mamm. Biol.* **85**, 37–46. (doi:10.1016/j.mambio.2016.11.005)
6. Evens R *et al.* 2020 Lunar synchronization of daily activity patterns in a crepuscular avian insectivore. *Ecol. Evol.* **10**, 7106–7116. (doi:10.1002/ece3.6412)
7. Hedenström A, Sparks RA, Norevik G, Woolley C, Levandoski GJ, Åkesson S. 2022 Moonlight drives nocturnal vertical flight dynamics in black swifts. *Curr. Biol.* **32**, 1875–1881.e3. (doi:10.1016/j.cub.2022.03.006)
8. Pérez-Granados C, Schuchmann K-L, Marques MI. 2022 Addicted to the moon: vocal output and diel pattern of vocal activity in two Neotropical nightjars is related to moon phase. *Ethol. Ecol. Evol.* **34**, 66–81. (doi:10.1080/03949370.2021.1886182)
9. Cruz SM, Hooten M, Huyvaert KP, Proaño CB, Anderson DJ, Afanasyev V, Wikelski M. 2013 At–sea behavior varies with lunar phase in a nocturnal pelagic seabird, the swallow-tailed gull. *PLoS ONE* **8**, e56889. (doi:10.1371/journal.pone.0056889)
10. San-Jose LM *et al.* 2019 Differential fitness effects of moonlight on plumage colour morphs in barn owls. *Nat. Ecol. Evol.* **3**, 1331–1340. (doi:10.1038/s41559-019-0967-2)
11. Bonnet-Lebrun A-S *et al.* 2021 Seabird migration strategies: flight budgets, diel activity patterns, and lunar influence. *Front. Mar. Sci.* **8**, 683071. (doi:10.3389/fmars.2021.683071)
12. Amichai E, Kronfeld-Schor N. 2019 Artificial light at night promotes activity throughout the night in nesting common swifts (*Apus apus*). *Sci. Rep.* **9**, 11052. (doi:10.1038/s41598-019-47544-3)
13. Hedenström A, Norevik G, Boano G, Andersson A, Bäckman J, Åkesson S. 2019 Flight activity in pallid swifts *Apus pallidus* during the non-breeding period. *J. Avian Biol.* **50**, 1–8. (doi:10.1111/jav.01972)
14. Kearsley L *et al.* 2022 The aeroecology of atmospheric convergence zones: the case of pallid swifts. *Oikos* **2022**, e08594. (doi:10.1111/oik.08594)
15. Dokter AM, Åkesson S, Beekhuis H, Bouten W, Buurma L, van Gasteren H, Holleman I. 2013 Twilight ascents by common swifts, *Apus apus*, at dawn and dusk: acquisition of orientation cues? *Anim. Behav.* **85**, 545–552. (doi:10.1016/j.anbehav.2012.12.006)
16. Nilsson C, Bäckman J, Dokter AM. 2019 Flocking behaviour in the twilight ascents of Common Swifts *Apus apus*. *Ibis* **161**, 674–678. (doi:10.1111/ibi.12704)
17. Meier CM, Karaardıç H, Aymí R, Peev SG, Bächler E, Weber R, Witvliet W, Liechti F. 2018 What makes Alpine swift ascend at twilight? Novel geolocators reveal year-round flight behaviour. *Behav. Ecol. Sociobiol.* **72**, 45. (doi:10.1007/s00265-017-2438-6)
18. Williams CB, Singh BP. 1951 Effect of moonlight on insect activity. *Nature* **167**, 853–853. (doi:10.1038/167853a0)
19. Bowden J, Gibbs DG. 1973 Light-trap and suction-trap catches of insects in the northern Gezira, Sudan, in the season of southward movement of the Inter-Tropical Front. *Bull. Entomol. Res.* **62**, 571–596. (doi:10.1017/S0007485300005472)
20. Danthanarayana W. 1986 *Insect flight: dispersal and migration*. Berlin, Germany: Springer.
21. Collins CT, Tella JL, Colahan BD. 2009 Food habits of the alpine swift on two continents: intra- and interspecific comparisons. *Ardeola* **56**, 259–269.
22. Helms JA, Godfrey AP, Ames T, Bridge ES. 2016 Predator foraging altitudes reveal the structure of aerial insect communities. *Sci. Rep.* **6**, 28670. (doi:10.1038/srep28670)
23. Jordan Price J, Johnson KP, Clayton DH. 2004 The evolution of echolocation in swiftlets. *J. Avian Biol.* **35**, 135–143. (doi:10.1111/j.0908-8857.2004.03182.x)
24. Jarvis ED *et al.* 2014 Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* **346**, 1320–1331. (doi:10.1126/science.1253451)
25. Meier CM, Karaardıç H, Aymí R, Peev SG, Witvliet W, Liechti F. 2020 Population-specific adjustment of the annual cycle in a super-swift trans-Saharan migrant. *J. Avian Biol.* **51**, jav.02515. (doi:10.1111/jav.02515)
26. Morganti M *et al.* 2018 Effect of light-level geolocators on apparent survival of two highly aerial swift species. *J. Avian Biol.* **49**, jav-01521. (doi:10.1111/jav.01521)
27. Norevik G, Boano G, Hedenström A, Lardelli R, Liechti F, Åkesson S. 2019 Highly mobile insectivorous swifts perform multiple intra-tropical migrations to exploit an asynchronous African phenology. *Oikos* **128**, 640–648. (doi:10.1111/oik.05531)
28. Costa LT, Elias GL. 1998 Biometrics and survival rates of Pallid Swifts *Apus pallidus* in Portugal. *Ringing Migr.* **19**, 59–64. (doi:10.1080/03078698.1998.9674167)
29. McClintock BT, Michelot T. 2018 momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods Ecol. Evol.* **9**, 1518–1530. (doi:10.1111/2041-210X.12995)
30. Johnson DS, London JM, Lea M-A, Durban JW. 2008 Continous-time correlated random walk model for animal telemetry data. *Ecology* **89**, 1208–1215. (doi:10.1890/07-1032.1)
31. Lisovski S, Hahn S. 2012 GeoLight: processing and analysing light-based geolocator data in R. *Methods*

Ecol. Evol. **3**, 1055–1059. (doi:10.1111/j.2041-210X.2012.00248.x)

32. Nasa J. 2020 *NASADEM Merged DEM Global 1 arc second V001* [Dataset]. See https://cmr.earthdata.nasa.gov/search/concepts/C1546314043-LPDAAC_ECS.html.
33. Liechti F, Witvliet W, Weber R, Bächler E. 2013 First evidence of a 200-day non-stop flight in a bird. *Nat. Commun.* **4**, 2554. (doi:10.1038/ncomms3554)
34. Yu H, Muijres FT, Te Lindert JS, Hedenström A, Henningsson P. 2023 Accelerometer sampling requirements for animal behaviour classification and estimation of energy expenditure. *Anim. Biotelemetry* **11**, 28. (doi:10.1186/s40317-023-00339-w)
35. Kyba CCM, Mohar A, Posch T. 2017 How bright is moonlight? *Astron. Geophys.* **58**, 1.31–1.32. (doi:10.1093/astrogeo/atx025)
36. Kyba CCM, Conrad J, Shatwell T. 2020 Lunar illuminated fraction is a poor proxy for moonlight exposure. *Nat. Ecol. Evol.* **4**, 318–319. (doi:10.1038/s41559-020-1096-7)
37. Janiczek PM, DeYoung JA. 1987 *Computer programs for sun and moon illuminance with contingent tables and diagrams*. Washington, DC: United States Naval Observatory.
38. Hufkens K. 2022 skylight: a simple sky illuminance model. *Zenodo*. (doi:10.5281/zenodo.7222045)
39. Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM. 2017 glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**, 378. (doi:10.32614/RJ-2017-066)
40. R Core Team. 2023 *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
41. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
42. Kuznetsova A, Brockhoff PB, Christensen RHB. 2017 lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* **82,** 1–26. (doi:10.18637/jss.v082.i13
43. Wickham H. 2017 *tidyverse: Easily Install and Load the 'Tidyverse'*. See https://cran.r-project.org/web/packages/tidyverse/index.html.
44. Lüdecke D. 2018 ggeffects: tidy data frames of marginal effects from regression models. *J. Open Source Softw.* **3**, 772. (doi:10.21105/joss.00772)
45. Pedersen TL 2022 *patchwork: The Composer of Plots*. See https://cran.r-project.org/web/packages/patchwork/index.html.
46. Wilke CO. 2022 *ggtext: Improved text rendering support for ggplot2*. See https://cran.r-project.org/web/packages/ggtext/index.html.
47. Finlayson S, Holmes TL, Finlayson G, Guillem R, Perez C, Bensusan K, Finlayson C. 2021 Birds with multiple homes: the annual cycle of the pallid swift (*Apus pallidus brehmorum*). *PLoS ONE* **16**, e0259656.
48. Hedenström A. 2016 Annual 10-month aerial life phase in the common swift *Apus apus*. *Curr. Biol.* **26**, 3066–3070. (doi:10.1016/j.cub.2016.09.014)
49. Reynolds DR, Smith AD, Chapman JW. 2008 A radar study of emigratory flight and layer formation by insects at dawn over southern Britain. *Bull. Entomol. Res.* **98**, 35–52. (doi:10.1017/S0007485307005470)
50. Nicholson SE. 2009 A revised picture of the structure of the 'monsoon' and land ITCZ over West Africa. *Clim. Dyn.* **32**, 1155–1171. (doi:10.1007/s00382-008-0514-3)
51. Brown ES, Taylor LR. 1971 Lunar cycles in the distribution and abundance of airborne insects in the equatorial highlands of East Africa. *J. Anim. Ecol.* **40**, 767. (doi:10.2307/3449)
52. Jansson S, Malmqvist E, Mlacha Y, Ignell R, Okumu F, Killeen G, Kirkeby C, Brydegaard M. 2021 Real-time dispersal of malaria vectors in rural Africa monitored with lidar. *PLoS ONE* **16**, e0247803. (doi:10.1371/journal.pone.0247803)
53. Hedrick TL, Pichot C, de Margerie E. 2018 Gliding for a free lunch: biomechanics of foraging flight in common swifts (*Apus apus*). *J. Exp. Biol.* **221**, jeb186270. (doi:10.1242/jeb.186270)
54. Vansteelant WMG, Gangoso L, Bouten W, Viana DS, Figuerola J. 2021 Adaptive drift and barrier-avoidance by a fly-forage migrant along a climate-driven flyway. *Mov. Ecol.* **9**, 37. (doi:10.1186/s40462-021-00272-8)
55. Buij R, Gschweng M. 2017 Nocturnal hunting by Eleonora's falcons *Falco eleonorae* on their breeding and non-breeding grounds. *Acta Ornithol.* **52**, 35–49. (doi:10.3161/00016454AO2017.52.1.004)
56. Hedenstrom A. 2001 Predator versus prey: on aerial hunting and escape strategies in birds. *Behav. Ecol.* **12**, 150–156. (doi:10.1093/beheco/12.2.150)
57. Popa-Lisseanu AG, Delgado-Huertas A, Forero MG, Rodríguez A, Arlettaz R, Ibáñez C. 2007 Bats' conquest of a formidable foraging niche: the myriads of nocturnally migrating songbirds. *PLoS ONE* **2**, e205. (doi:10.1371/journal.pone.0000205)
58. Ibáñez C, Popa-Lisseanu AG, Pastor-Beviá D, García-Mudarra JL, Juste J. 2016 Concealed by darkness: interactions between predatory bats and nocturnally migrating songbirds illuminated by DNA sequencing. *Mol. Ecol.* **25**, 5254–5263. (doi:10.1111/mec.13831)
59. Rattenborg NC, Voirin B, Cruz SM, Tisdale R, Dell'Omo G, Lipp H-P, Wikelski M, Vyssotski AL. 2016 Evidence that birds sleep in mid-flight. *Nat. Commun.* **7**, 12468. (doi:10.1038/ncomms12468)
60. Muheim R. 2011 Behavioural and physiological mechanisms of polarized light sensitivity in birds. *Phil. Trans. R. Soc. B* **366**, 763–771. (doi:10.1098/rstb.2010.0196)
61. Muheim R, Schmaljohann H, Alerstam T. 2018 Feasibility of sun and magnetic compass mechanisms in avian long-distance migration. *Mov. Ecol.* **6**, 8. (doi:10.1186/s40462-018-0126-4)
62. Cochran WW, Mouritsen H, Wikelski M. 2004 Migrating songbirds recalibrate their magnetic compass daily from twilight cues. *Science* **304**, 405–408. (doi:10.1126/science.1095844)
63. Racey PA, Swift SM. 1985 Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *J. Anim. Ecol.* **54**, 205. (doi:10.2307/4631)
64. Pavey CR, Burwell CJ, Grunwald J-E, Marshall CJ, Neuweiler G. 2001 Dietary benefits of twilight foraging by the insectivorous bat *Hipposideros speoris*. *Biotropica* **33**, 670–681. (doi:10.1111/j.1744-7429.2001.tb00224.x)
65. Jetz W, Steffen J, Linsenmair KE. 2003 Effects of light and prey availability on nocturnal, lunar and seasonal activity of tropical nightjars. *Oikos* **103**, 627–639. (doi:10.1034/j.1600-0706.2003.12856.x)
66. Hufkens K *et al.* 2023 Moonlight synchronous flights across three western palearctic swifts mirror size dependent prey preferences. Zenodo Digital Repository. (doi:10.5281/zenodo.7814214)
67. Hufkens K *et al.* 2023 Evaluating the effects of moonlight on the vertical flight profiles of three western palaearctic swifts. Figshare. (doi:10.6084/m9.figshare.c.6888257)