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Skyglow relieves a crepuscular bird from visual constraints on being active

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Abstract

Artificial light at night significantly alters the predictability of the natural light cycles that most animals use as an essential *Zeitgeber* for daily activity. Direct light has well-documented local impacts on activity patterns of diurnal and nocturnal organisms. However, artificial light at night also contributes to an indirect illumination of the night sky, called skyglow, which is rapidly increasing. The consequences of this wide-spread form of artificial night light on the behaviour of animals remain poorly understood, with only a few studies performed under controlled (laboratory) conditions. Using animal-borne activity loggers, we investigated daily and seasonal flight activity of a free-living crepuscular bird species in response to nocturnal light conditions at sites differing dramatically in exposure to skyglow. We find that flight activity of European Nightjars (*Caprimulgus europaeus*) during moonless periods of the night is four times higher in Belgium (high skyglow exposure) than in sub-tropical Africa and two times higher than in Mongolia (near-pristine skies). Moreover, clouds darken the sky under natural conditions, but skyglow can strongly increase local sky brightness on overcast nights. As a result, we find that nightjars' response to cloud cover is reversed between Belgium and sub-tropical Africa and between Belgium and Mongolia. This supports the hypothesis that cloudy nights reduce individual flight activity in a pristine environment, but increase it when the sky is artificially lit. Our study shows that in the absence of direct light pollution, anthropogenic changes in sky brightness relieve nightjars from visual constraints on being active. Individuals adapt daily activities to artificial night-sky brightness, allowing them more time to fly than conspecifics living under natural light cycles. This modification of the nocturnal timescape likely affects behavioural processes of most crepuscular and nocturnal species, but its implications for population dynamics and interspecific interactions remain to be investigated.

Keywords: Nightjar, activity-logging, artificial light, time-niche, Anthropocene

This document: currently ~4000 words (excl. references) and 5 color figures

Introduction

Throughout the evolutionary history of animals, recurring cycles of light and darkness have remained relatively constant (Kronfeld-Schor et al., 2013; Kyba et al., 2017). As a result, most animals have evolved to use predictable changes in light conditions as an essential *Zeitgeber* for timing their daily activity (Berthold et al., 2003; Kronfeld-Schor et al., 2013) and to manage trade-offs between activities such as rest, reproduction, predation avoidance and foraging (Griffin et al., 2005; Kotler et al., 2010; Palmer et al., 2017; Ravache et al., 2020; Roeleke et al., 2018; York et al., 2014).

Since the introduction of electric-powered light sources, approximately 125 years ago, artificial night lighting has significantly altered the daily variation in light conditions by changing the physical properties of the twilight- and night environment (Gaston et al., 2013; Gaston and de Miguel, 2022; Longcore and Rich, 2004). Behavioural studies have given much attention to the effects of direct light emissions on a wide range of diurnal and nocturnal organisms, demonstrating that isolated or aggregated light sources that chronically or temporarily infiltrate local nocturnal habitats can alter the physiology, daily and seasonal activity patterns and life-history traits of individuals in various ways (Bennie et al., 2018; Rowan, 1925; Sanders et al., 2020; Senzaki et al., 2020; Stone et al., 2009; Vandersteen et al., 2020).

Artificial light at night also contributes to a diffuse illumination of the night sky, called skyglow. In contrast to the effects of direct artificial lighting on the environment, the indirect effects via skyglow remain poorly understood (Kyba et al., 2015). Skyglow arises when upwardly-emitted artificial night light is scattered back towards Earth by the atmosphere, creating an artificial night-time sky brightness, which in extreme cases can be comparable to – or even exceed – the illuminance of moonlit nights (up to about 0.3 lux (Hänel et al., 2018; Kyba et al., 2017, 2015; Torres et al., 2020)). Skyglow obscures celestial cues, such as the light of stars and the Milky Way (which produce 0.6-0.9 mlux (Hänel et al., 2018) on the ground) and polarized patterns of moonlight (Kyba et al., 2011).

The sky is artificially brightened by at least 8%, compared to starlight, over approximately 88% of the European and almost half of the United States' land area (Falchi et al., 2016; Kyba and Hölker, 2013), and the biological consequences of this environmental change are largely unknown (Garrett et al., 2020). Behavioural responses of animals to skyglow may differ substantially from those caused by more local sources of light. Direct lighting often has the effect of attracting or repelling individuals (Sanders et al., 2018). In contrast, skyglow lights up the entire sky over much larger areas than direct lighting, can be amplified up to hundred-fold during overcast nights near urbanized areas (Jechow et al., 2019; Kyba et al., 2011), and extends far into natural habitats tens of kilometres away from light sources (Garrett et al., 2020; Kyba and Hölker, 2013). A few studies, performed under controlled or

laboratory conditions, demonstrated that skyglow can interrupt orientation behaviour (in African dung beetle *Scarabaeus satyrus* Boheman (Foster et al., 2021) and in Sandhoppers *Talitrus saltator* (Torres et al., 2020)) and affect sleep patterns and the physiology of diurnal animals (e.g. in Barnacle Geese *Branta leucopsis* (van Hasselt et al., 2021) and Eurasian perch *Perca fluviatilis* (Kupprat et al., 2020)). Additionally, skyglow has been found to trigger or dampen nocturnal vocalisations in some diurnal bird species (Dickerson et al., 2022; Skorb et al., 2022) and change the perception of predation risk in the Eurasian curlew *Numenius arquata* (Jolkkonen et al., 2023).

We studied the impact of skyglow on the activity of a free-living bird, the Eurasian Nightjar (*Caprimulgus europaeus*, hereafter nightjar). Nightjars are medium-sized (~70g), visually-orienting, crepuscular aerial insectivores that also show nocturnal activity patterns in response to moonlight (Evens et al., 2020). Because they are adapted to exploit dim light conditions, we hypothesised that they might also be affected by skyglow. We equipped individuals with multi-sensor data loggers to study daily and seasonal variation in flight activity. We deployed the loggers at two sites that were not exposed to direct artificial night lighting, but that differed dramatically in skyglow-exposure (Fig. 1): (1) breeding sites in Belgium, with a clear sky brightness approximately four to six times brighter than a pristine starry sky, and (2) a Mongolian breeding site, with a night-time sky that is unaffected by artificially induced skyglow. After the breeding season, individuals migrated to sub-tropical Africa (Evens et al., 2017; Lathouwers et al., 2022b) where they spent the winter (November-February) under presumed near-pristine night-time sky conditions (Fig. 1). By comparing activity patterns during the breeding and non-breeding season and in areas that differed in the levels of skyglow-exposure, we investigated the impact of moonlight and skyglow on the individuals' behaviour.

Methods

We studied nightjars during the breeding season in a study site in Mongolia (48.6° N, 110.8° E; 2018–2020) and in three Belgian sites (51.1° N, 5.5° E; 2009–2022). The study sites differ dramatically in skyglow-exposure (Fig. 1; Supplementary Table S1), ranging from a night-time clear-sky brightness approximately six times brighter than a pristine starry sky (Belgian breeding sites; Fig. 1; Supplementary Table S1) to sites with a pristine night-time sky brightness (Mongolian breeding site; Fig. 1; Supplementary Table S1).

We captured all nightjars in their presumed territories during the breeding season using ultra-fine mist nets (Ecotone, 15 × 3 m) and tape lures, marked each individual with a unique alphanumeric ring and fitted a data logger dorsally between the wings using a full body harness with a 1 mm wide flat braided cord to avoid abrasion (Evens et al., 2020). In total, we tagged 78 adult males (Belgium = 49, Mongolia = 29) with a 1.4 g multi-sensor logger (SOI-GDL3pam; ± 2.2% of mean body mass) (Liechti et al., 2018).

At least one year later, after their long-distance migrations to sub-tropical Africa (Evens et al., 2017; Lathouwers et al., 2022a), we recovered 15 data loggers containing data of at least one breeding and one wintering season (Belgium = 10, Mongolia = 2). This resulted in a total return rate of 20%. One logger deployed in Mongolia recorded activity data during two breeding seasons and one wintering season. Two loggers deployed in Belgium recorded data during three breeding and two wintering seasons. Due to technical difficulties, we could not use the data from one logger for analysis.

Location estimates and activity data

The multi-sensor loggers record ambient light intensity (which can be used for geolocation, (Liechti et al., 2018)), body acceleration in one axis (z-axis), air pressure and air temperature in 5-min intervals and magnetic field in 4-h intervals. We used body acceleration data to measure flight activity (Evens et al., 2020) and ambient light intensity to estimate daily positions (longitude, latitude) of each individual (Lathouwers et al., 2022a). Absolute flight activity is measured as the sum of the absolute differences in acceleration on the z-axis and a summary variable is stored for each 5-min interval (Liechti et al., 2018). More specifically, acceleration along the z-axis is recorded every 5 min for 3.2 s with a frequency of 10 Hz and the summary measure of activity (approximate range = 0 - 65) is calculated by an on-board algorithm (Liechti et al., 2013). We categorized activity data into two classes, based on a previously defined threshold of 3.9, which is the (Evens et al., 2020). A 5-min period with activity equal or above the threshold is considered “active” (e.g., flight and foraging), a 5-min period with activity below the threshold is considered “inactive” (e.g., resting and roosting). [34] Due to the little overall activity in the absence of moonlight, we further transformed this binary dataset (active or inactive) to 15-minute intervals and counted the activity occurrences per interval to model individual activity patterns in relation to nocturnal darkness and cloud cover (see “statistical analysis”).

Ambient light measurements allowed us to estimate daily positions (longitude and latitude) based on sunset and sunrise events using the R-package PAMLR (Dhanjal-Adams et al., 2022). During the winter period (see definition below), we performed a Hill-Ekstrom calibration on the light-intensity measurements to model the error of sunrise/sunset events caused by shading of the light sensor by feathers. The location estimates were then refined using an Estelle model (250 iterations) in SGAT (Lisovski et al., 2019). This model is based on Markov chain Monte Carlo (MCMC) simulations and provides a probability distribution around each location estimate (two locations per day). The Estelle model was refined after three runs of 300 iterations with the following priors: (1) the deployment location of the logger, (2) the estimated sunrise/sunset error, (3) a distribution of probable flight speeds (relaxed gamma distribution of shape = 2.2 and rate = 0.08) and (4) a spatial probability mask

excluding stopovers over water. Finally, position estimates (with 97.5% confidence intervals) were calculated by running the Estelle model for 2000 iterations to ensure convergence.

For the purpose of this study, we only considered flight activity data from the breeding and wintering season. To determine these two seasons, we combined information from flight activity data and position estimates, similar to previous studies (Evens et al., 2020; Lathouwers et al., 2022a). We defined the wintering season as the period between the end of autumn migration and the onset of spring migration. Because nightjars remain at a single site during the entire winter, all position estimates of each individual during the winter were averaged to one location. We defined the breeding season as the period between the end of spring and the onset of autumn migration. Because male nightjars show high site fidelity, we used exact capture and recapture coordinates to determine Belgian and Mongolian breeding areas.

For each individual, we subdivided daily flight activity data into three groups: daytime (from sunrise until sunset), twilight (from sunset until nautical dusk; from nautical dawn until sunrise), and night (from evening nautical twilight until morning nautical twilight). [34]Of all 5-minute intervals (805572, including 489743 daytime intervals), 31,340 ($\pm 4\%$) were categorized as active, while the remaining 774,232 intervals were categorized as inactive. Of the 275329 nocturnal 5-minute intervals 11,649 ($\pm 4\%$) were categorized as active, and the remaining 263,680 intervals were categorized as inactive. Of the 36880 dusk intervals and 36812 dawn intervals, respectively 11470 ($\pm 45\%$) and 7306 ($\pm 25\%$) were categorized as active .

Environmental data

Exact geographic breeding locations were recorded at the time of deployment of the logger and wintering locations were estimated from the ambient light data recorded by each logger. For each breeding and wintering location we extracted clear sky luminance data from the World Atlas of artificial night sky brightness (Falchi et al., 2016). Clear sky luminance was transformed to light relative to starlight following the formula: $(WA + 0.174) / 0.174$. WA = world atlas sky luminance, 0.174 = natural sky luminance value of 0.174 mcd/m² (Falchi et al., 2016).

Data on the timing of day, night, and twilight (i.e., sunset and sunrise) were extracted for the known breeding sites and estimated wintering sites and for each 5-minute interval using the R-package “suncalc”. For each individual, data on moon and sun illuminance were extracted at 5-minute intervals using the R-package “Skylight” (Hufkens, 2022).

Data on total cloud cover were retrieved from the ERA5 reanalysis product (Hersbach et al., 2020) for the times (hourly resolution) and locations (within a 31 x 31 km grid size) of each individual during the

overwintering and breeding seasons. Other than cloud cover, we did not consider variation in local weather conditions for the analysis of flight activity. Not considering local weather leads to additional noise, and hence may weaken our results, rather than create systematic biases (Penteriani et al., 2010).

Statistical analysis

To discriminate between the influence of nocturnal light and daylight on nightjars' activity, we modelled nocturnal and crepuscular flight activity separately using Generalized Linear Mixed Models (GLMMs) with maximum likelihood using the R package glmmTMB version 0.2.3 (Brooks et al., n.d.).

For nocturnal flight activity, all models contained two sub-models: a model for the conditional mean and a zero-inflated model. Because only 4% of the nocturnal 5-minute intervals were categorized as active, the zero-inflated model allows modelling of the probability of excess zeros in the conditional part of the model. The zero-inflated models contained no predictors other than the overall mean, except for the nocturnal moonlight models, which also contained individual identity as random intercept. In a first version of the conditional model, we determined the influence of moonlight on flight probability ("nocturnal moonlight model"; Supplementary Tables S2-3). The results of this model suggested different flight probabilities between seasons and breeding locations during moonless parts of the night. Therefore, we created a second version of the conditional model to formally test for seasonal and location effects of flight probability during moonless parts of the night ("darkness model"; Supplementary Tables S4-5). Lastly, we ran a third version of the conditional model to investigate whether cloud cover explained the observed differences in flight probability between sites during moonless parts of the night ("cloud cover model"; Supplementary Tables S6-7). Cloud cover varied from zero (a clear sky) to 100% (a fully overcast sky). Clouds darken the sky under natural conditions, but skyglow can strongly increase local sky brightness on overcast nights near urban areas (Jechow et al., 2020, 2019).

The *nocturnal moonlight model* investigates seasonal flight probability, assumes clear sky conditions, and contains flight activity (categorical variable: presence or absence) as the dependent variable (binomial distribution) and an interaction between moon illuminance (continuous variable: log of local moon illuminance (lux)) and season (categorical variable: summer or winter) as the main predictors. We ran two nocturnal moonlight models, one for birds caught at their breeding site in Belgium (Supplementary Table S2) and one for birds caught in Mongolia (Supplementary Table S3). Similarly, we ran two *darkness models* to investigate nocturnal flight probability (dependent categorical variable: activity occurrences per 15-minute interval; Poisson distribution) in the absence of moonlight, also assuming clear sky conditions. The first model tests for seasonal variation in individuals caught in Belgium, and contains season as the explanatory variable (Supplementary Table S4). The second model

investigates summer flight activity, and contains origin (categorical variable: Belgium or Mongolia) as the explanatory variable (Supplementary Table S5). The two *cloud cover models* contain flight activity (categorical variable: activity occurrences per 15-minute interval) as the dependent variable (Poisson distribution). The first model assesses seasonal variation in flight activity for individuals caught in Belgium, and contains season, total cloud cover (continuous variable: ranging from 0% to 100%) and their interaction as explanatory variables (Supplementary Table S6). The second model assesses variation in summer flight activity, and contains origin, total cloud cover and their interaction as explanatory variables (Supplementary Table S7).

Models for crepuscular flight activity contain flight activity (categorical variable: presence or absence) as the dependent variable (binomial distribution) and period (categorical variable: dusk or dawn) and origin (categorical variable: Belgium or Mongolia) as the main predictors. We ran two crepuscular models, one for the breeding period (Supplementary Table S8) and one for the wintering period (Supplementary Table S9).

In all models, we included activity of the previous five-minute or 15-minute interval to control for temporal autocorrelation. In the nocturnal moonlight models and the cloud cover models, we included individual identity as random intercept and moon illuminance or cloud cover as random slope, to allow that individuals can vary in their response to variation in the explanatory variable. In the darkness models and the crepuscular models, we included individual identity as random intercept. Model specification problems were checked using the R-package “DHARMA”. We used post-hoc Tukey’s comparisons to test the significance of the difference between pairs of interactions between the main predictors using the R-package “emmeans”.

Results

Our data show that nightjars are affected by moonlight. In all individuals, nocturnal flight probability (hereafter activity) increases with increasing moonlight illumination, both during the summer and the winter (Fig. 2a,b; Supplementary Table S2,3). However, the activity patterns of nightjars in Belgium deviated from those at other locations. The probability that an individual flew during moonless periods of the night was four times higher in Belgium than in sub-tropical Africa (49.8% vs. 12.1% flight probability; Fig. 3a; $z = -25.1$, $p = <0.0001$; Supplementary Table S4) and two times higher than in Mongolia (59.9% vs. 30% flight probability; Fig. 3b; $z = -2.76$, $p = 0.006$; Supplementary Table S5). Caution is needed with the interpretation of the comparison of flight activity between breeding sites, because of the low number of Mongolian individuals. However, we assume that the relationship between flight activity and moon condition should be similar between breeding sites. Thus, our results suggest that the observed difference between individuals in Belgium and in sub-tropical Africa was not

only due to the overall higher nocturnal flight activity during the breeding season compared to winter, but potentially also due to artificial light.

To investigate whether artificial light caused the observed difference in flight activity, we also tested for an effect of skyglow by comparing the activity of nightjars during moonless periods of the nights in response to a gradient of cloud cover.[27,47] Our data show that nightjars' response to cloud cover is reversed between Belgium and sub-tropical Africa (overall country effect of cloud cover: $\chi^2 = 4.58$, $df = 1$, $p = 0.023$ [Supplementary Table S6]; overall slope difference: $t = 0.098$, $p = 0.032$ [Fig. 3c]) and between Belgium and Mongolia (overall country-specific effect of cloud cover: $\chi^2 = 5.16$, $df = 1$, $p = 0.023$ [Supplementary Table S7]; overall slope difference: $t = 0.82$, $p = 0.023$ [Fig. 3d]). Supporting the hypothesis that nightjars' activity is based on ambient light, the flight activity of nightjars in Belgium increased with cloud cover (Belgium vs. sub-tropical Africa: slope estimate Belgium $\pm$ SD = 0.106 ± 0.08 [Fig. 3c]; Belgium vs. Mongolia: slope estimate Belgium $\pm$ SD = 0.301 ± 0.181 ; [Fig. 3d]). This hypothesis also predicts that activity on cloudy nights should decrease in areas without skyglow. Increasing cloud cover was not associated with flight activity in sub-tropical Africa (slope estimate $\pm$ SD = -0.008 ± 0.085 [Fig. 3c]) and was associated with reduced flight activity in Mongolia (slope estimate $\pm$ SD = -0.521 ± 0.305 [Fig. 3d]).

Finally, our flight activity data show that, during the breeding season, nightjars in Belgium flew approximately 30% less during dusk and dawn compared to individuals in Mongolia (Mongolia vs. Belgium: $z = 0.578$, $p = 0.002$; Fig. 5a; Supplementary Table S8), while this difference in crepuscular flight activity between individuals from both populations was absent during the winter (Mongolia vs. Belgium: $z = 0.042$, $p = 0.814$; Fig. 5b; Supplementary Table S9).

Discussion

Activity data of nightjars demonstrate that in the absence of direct light, anthropogenic increases in sky brightness (particularly on cloudy nights) at approximately 5-10 km from urbanized areas relieve Belgian nightjars from visual constraints on being active. We show that moonlight determines nightjars' activity patterns, whereas during moonless and overcast periods skyglow may provide light conditions similar to the brightness of a moonlit night in areas affected by artificial night lighting (Fig. 4). When this occurs, individuals seem to respond quickly to this anthropogenic night-sky brightness by becoming more active. Individuals might also anticipate that they have additional time at night for being active (e.g. for foraging or display) and therefore decrease their flight activity at dusk. During the breeding season, nightjars in Belgium flew less during dusk and dawn compared to individuals in Mongolia (Fig. 5a; Supplementary Table S8), while this difference in crepuscular flight activity between individuals from both populations was absent during the winter (Fig. 5b; Supplementary Table S9).

Whether the differences in crepuscular flight activity during summer are due to different lighting conditions, or to other ecological conditions (e.g. differences in food availability, duration of the breeding season or noise) needs further investigation.

How this modification of nightjars' nocturnal "time-niche" (Gilbert et al., 2022) affects individual trade-offs between different behaviours remains unclear. Optimal foraging theory predicts that animals will adapt nocturnal foraging activity to maximize net energy gain (Pyke et al., 1977), because their food resources and daily available time are typically limited. Because nightjars are visual predators they require an illuminated sky to detect the silhouettes of flying insects (Cresswell and Alexander, 1992). At night, when prey activity decreases and active flight becomes hazardous, artificial night-sky brightness may counteract the adverse effects of low prey density by improving prey detectability, prolonging foraging activity and promoting energy-efficient foraging tactics. As a result, additional nocturnal foraging would enable individuals more time for other behaviours, such as territorial display, at dusk and dawn.

To understand the potential benefits or ecological trap-scenarios of rapid responses to artificially night-sky brightness, we need to better understand how skyglow affects interspecific interactions, such as predator-prey interactions. Currently, it is unclear how our findings translate to other groups of nocturnal animals. Many species, including seabirds (Rubolini et al., 2014), owls (San-jose et al., 2019), primates (Gursky, 2003) and carnivores (Preston et al., 2019), require the brightness of a moonlit night to orientate and/or to identify resources (Bachleitner et al., 2007; Grubisic et al., 2019; Moore et al., 2000; Warrant et al., 2004). We expect that such species will profit from artificial night-sky brightness, if it improves nocturnal visibility of prey, and allows them to increase nocturnal activity, adopt more efficient foraging tactics or adjust their space use. For example, visually-oriented carnivores relying on cursorial hunting techniques are more active during moonlit nights (Rasmussen and MacDonald, 2012), whereas the activity of species relying on ambush strategies is lower (Preston et al., 2019). Aerial-hawking noctule bats adjust their space use to open fields during moonlit nights to increase the success of hunting airborne insects (Roeleke et al., 2018).

At the same time, species may get disoriented from skyglow and prey and predators that do not rely on visual cues may become less active under increased light levels, to avoid being preyed upon (Haddock et al., 2019) which may then lead to reduced access to food resources (English et al., 2018). How artificial night-sky brightness affects abundance, orientation behaviour and seasonal polyphenism of nocturnal insects is largely unknown, yet it has been suggested that the global insect declines have been partly caused by various forms of light pollution (Bluthgen et al., 2022; Owens et al., 2020). Severe declines in populations of insectivorous birds, including several species of nightjars, have been

322 attributed to this global decline of nocturnal insects (Piano et al., 2020).[58,59]. However, in contrast,
323 several populations of European Nightjars in Western Europe show recent increases (Eaton et al., 2015;
324 Van Dijk et al., 2009; Vermeersch et al., 2020), coinciding with both intense conservation efforts to
325 restore breeding sites and increased skyglow. The latter could potentially benefit the species if it allows
326 individuals to compensate for the lower prey numbers by increasing their available foraging time at
327 night.

328 Using nightjars as a model organism, our study provides the first evidence that skyglow changes daily
329 activity patterns of animals. Human-induced “lighting up” of former dark parts of the night allows
330 individuals more time to be active compared to conspecifics living under natural light cycles. The wide
331 geographic distribution of study sites with an extreme difference in exposure to artificial light at night,
332 allowed us to investigate between- and within-individual variation in activity in relation to light
333 conditions. Using loggers with high-resolution GPS- and activity-data is now needed to investigate
334 spatiotemporal variation in behaviour within the same geographical region for individuals exposed to
335 different regimes of artificial light at night. Such studies are important, because skyglow is a persistent,
336 rapidly expanding and underestimated form of sensory pollution that can expand the time-niche of
337 crepuscular and nocturnal animals (this study), but with still unknown downstream biological
338 consequences.

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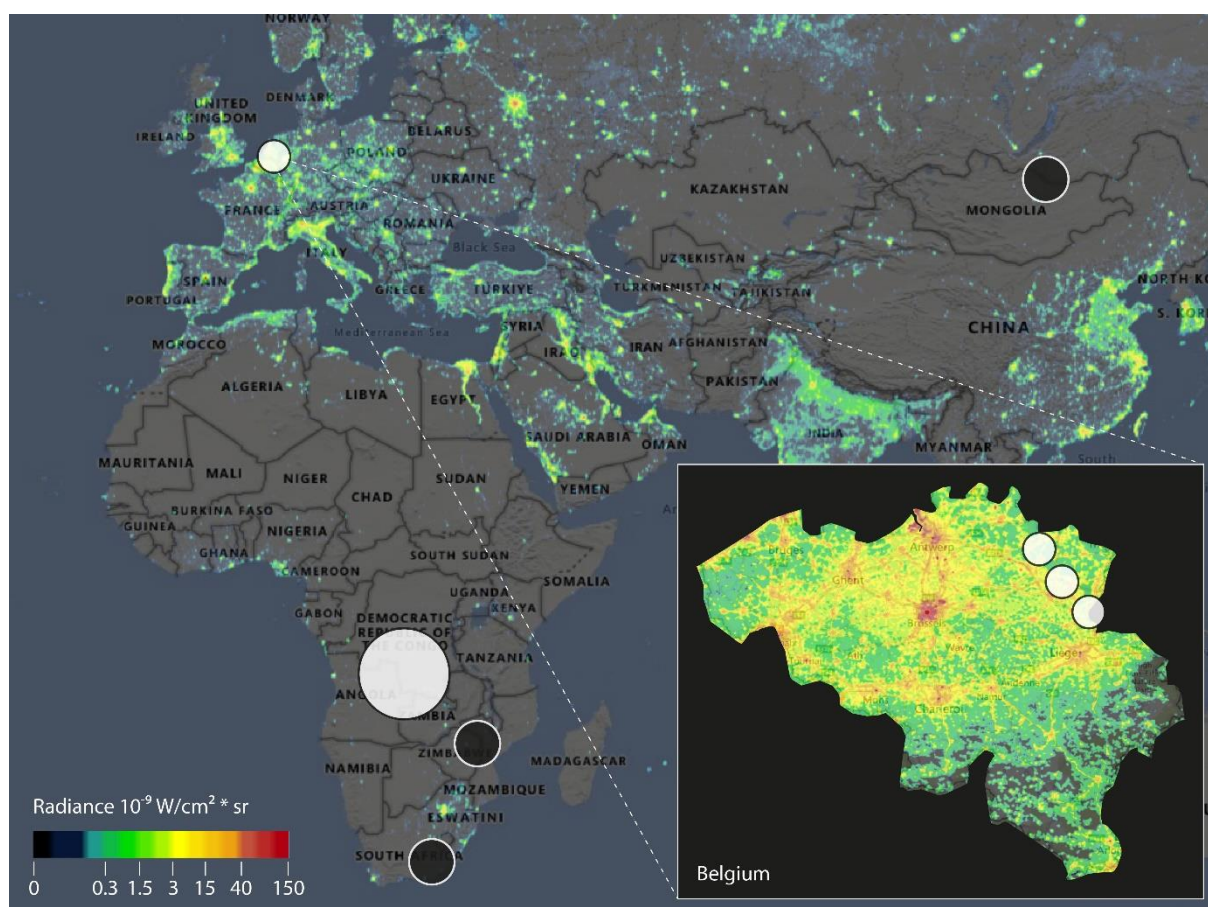
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353 **Fig. 1 Skyglow exposure in nightjar breeding and wintering areas.** Nocturnal sky luminance during
 354 clear and moonless skies for all breeding areas and sub-tropical wintering areas (Supplementary Table
 355 S1) identified for individuals caught during the breeding season in Belgium (circles with white fill) or in
 356 Mongolia (circles with black fill). Inset = light levels in three study sites in Belgium. Data on clear sky
 357 luminance was extracted from the World Atlas (Falchi et al., 2016). Shown is a radiance map, based on
 358 VIIRS-data, for 2019 from www.lightpollutionmap.info.

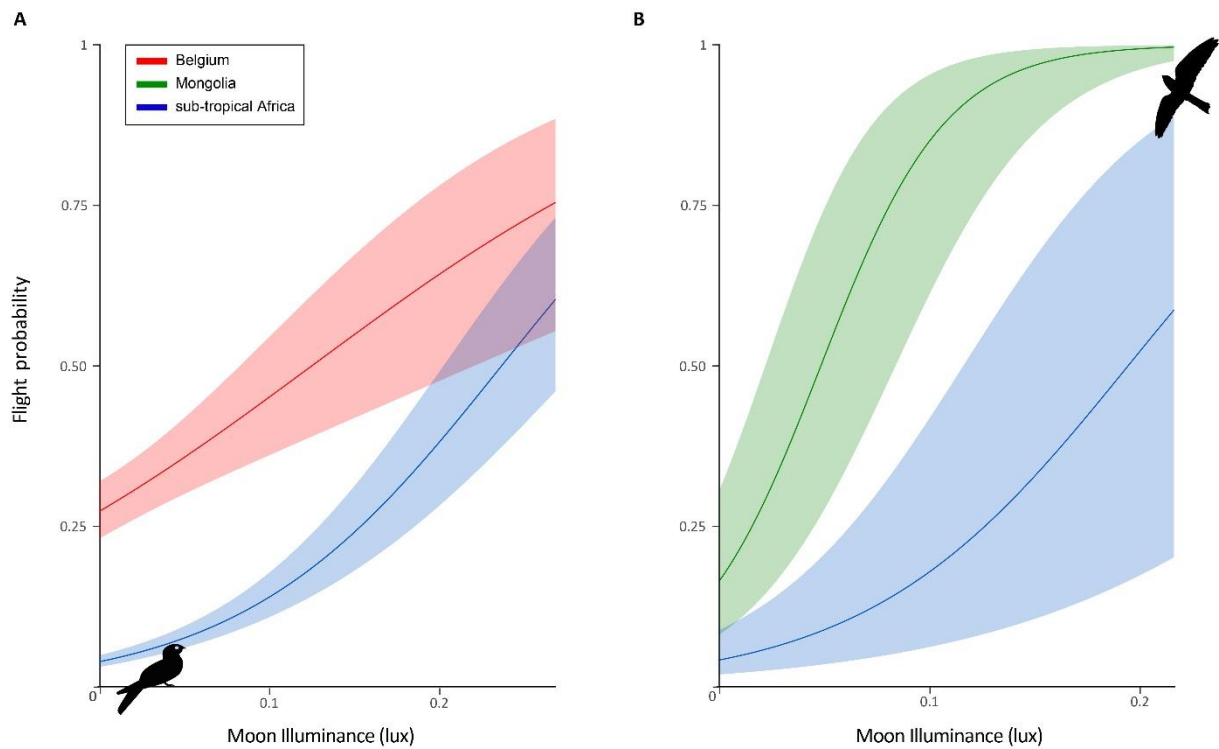


Fig.2 Nightjar flight activity in relation to moonlight. Nocturnal flight probability in relation to moon illuminance (full-night data, lux).. Flight probability is shown for the breeding season (red = Belgium; green = Mongolia) and during winter (a-b = blue) for individuals caught at their breeding site in Belgium (a; N = 12 individuals) or Mongolia (b; N = 3 individuals). Shown are estimates and 95% confidence intervals based on the models in Supplementary Table S2-3 (a,b).

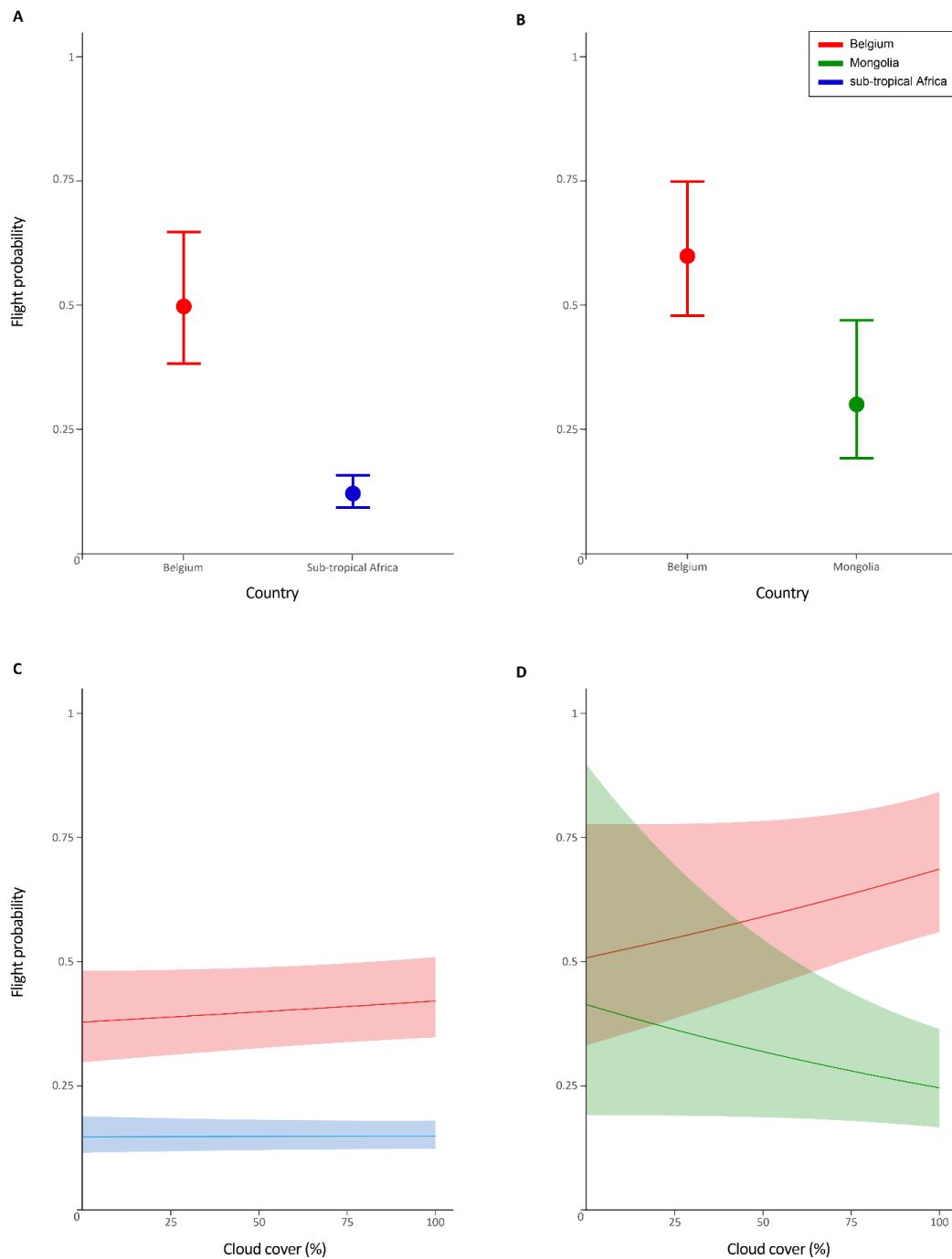
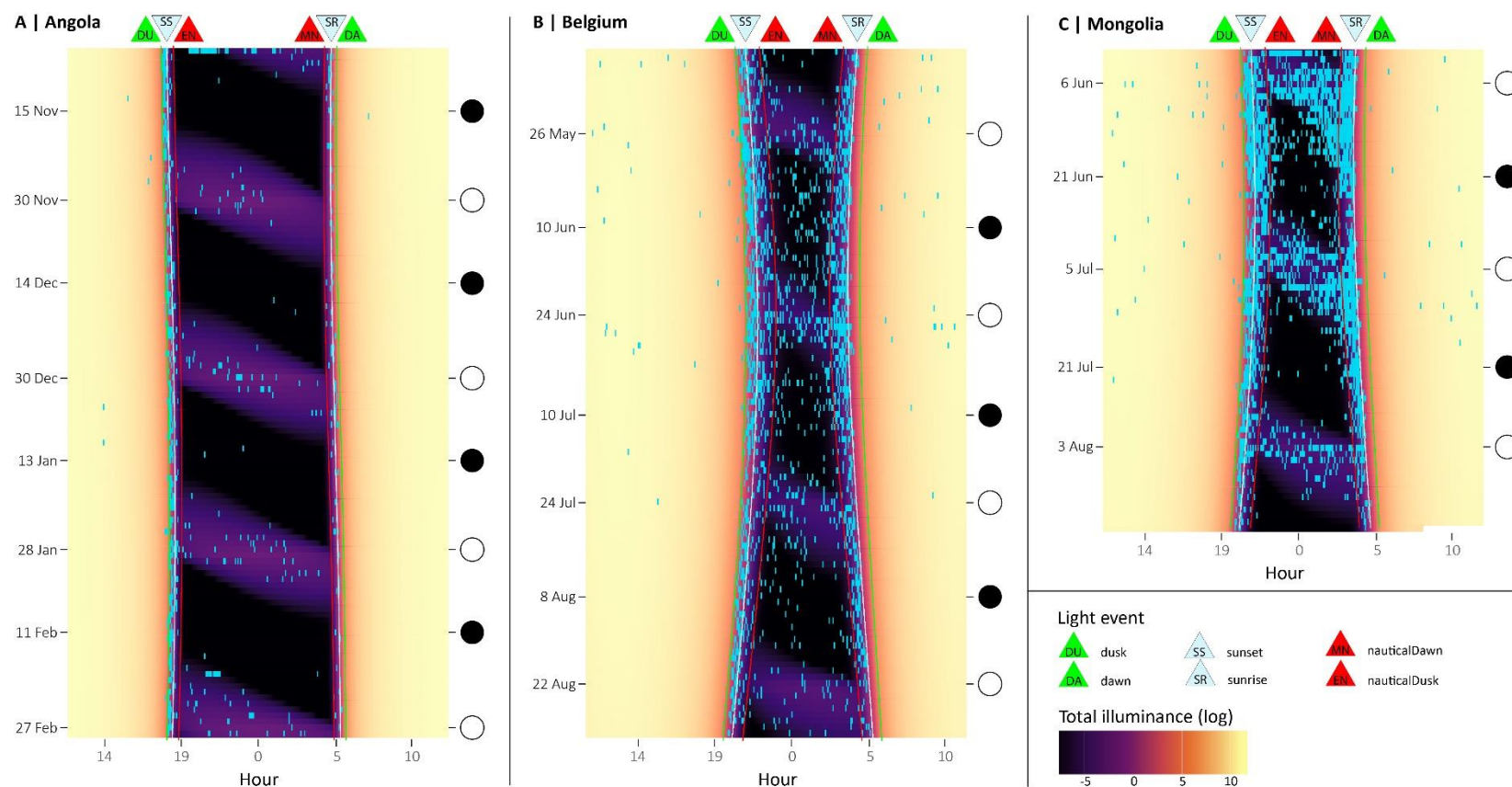
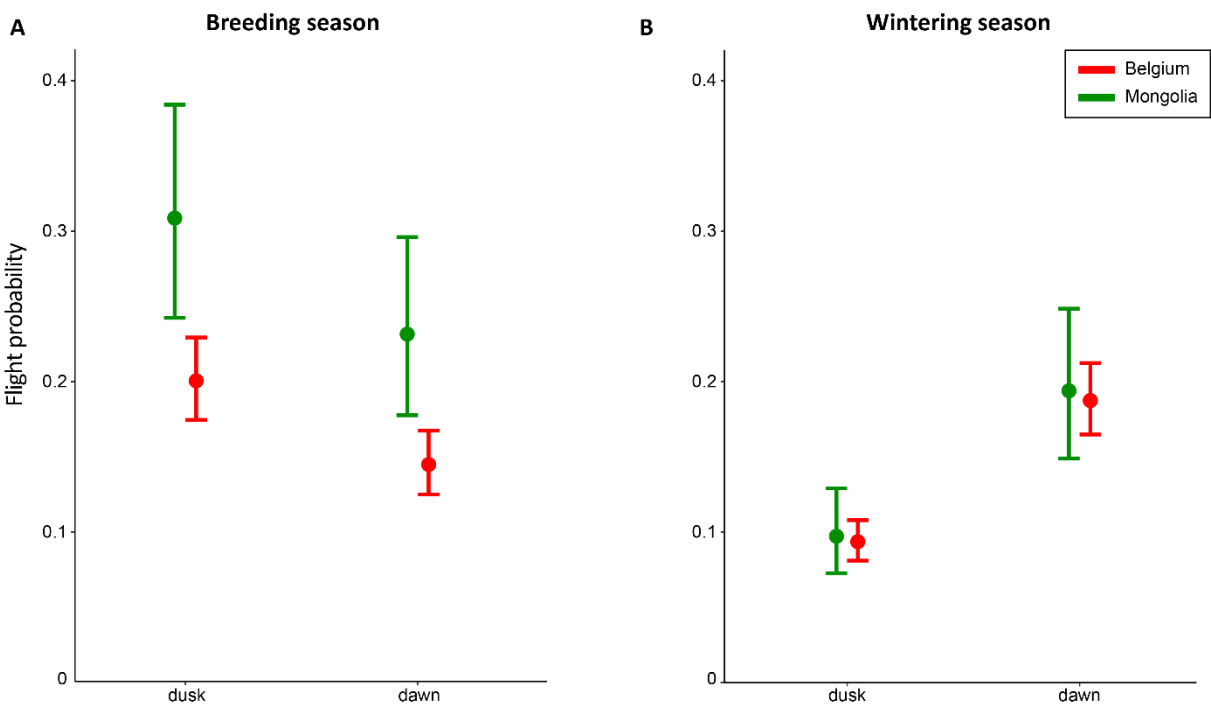


Fig.3 Nightjar flight activity in relation to darkness and cloud cover. Nocturnal flight probability during presumed clear and moonless parts of the nights (a, b) and flight activity in relation to cloud cover during moonless parts of the night nights (c, d). Flight probability and flight activity are shown for the breeding season (Belgium = red; Mongolia = green) and during winter (Sub-tropical Africa = blue) for individuals caught at their breeding site in Belgium (N = 12 individuals) or Mongolia (N = 3 individuals). Each panel shows estimates and 95% confidence intervals based on the two darkness models (a, b; Supplementary Table S4-5) and the two cloud models (c, d; Supplementary Table S6-7).



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374 **Fig. 4 Actograms of nightjar activity.** (a) Actogram of a nightjar caught at the breeding site in Belgium while wintering in sub-tropical Africa (2020-2021; four
 375 lunar cycles). (b) Actogram of the same individual subsequently breeding in Belgium (2021; three lunar cycles). (c) Actogram of a nightjar caught at its breeding
 376 site in Mongolia during the same breeding season (2020; two lunar cycles). Actograms show daily activity measured as flight activity per 5-min period (light
 377 blue) in relation to illuminance (lux; log transformed total illuminance) by the sun (day) and the moon (night). Each horizontal line shows one day with local
 378 midnight centred on the X-axis. Near-vertical curves represent local dusk (DU), sunset (SS), start of evening nautical twilight (EN), end of morning nautical
 379 twilight (MN), sunrise (SR) and dawn (DA). Open circles indicate (nights) with full moon, closed circles show nights with new moon.



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Fig.5 Nightjar flight activity during periods of twilight. Differences in flight activity between dusk and dawn during the breeding season (a) and during the winter (b) for birds caught at their breeding site in Belgium (red, N = 12 individuals) or in Mongolia (green, N = 3 individuals). Shown are model estimates and their 95% confidence intervals based on the model in Supplementary Table S8-9.

Ethical permit: The Mongolian and Belgian research protocols were approved by the Mongolian (Ministry of Environment and Tourism, license numbers: 06/2564 and 06/2862) and Belgian (Agency for Nature and Forest, license numbers: ANB/BL-FF/V18-00086, ANB/ BL-FF/19-00087-VB, ANB/ BL-FF/20-00114 and ANB/BL-FF/V22-00139) authorities. All protocols were carried out in accordance with the relevant guidelines and regulations.

Data and materials availability: Data available from the OSF Digital Repository: <https://osf.io/9s6ay>

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