



Skyglow facilitates prey detection in a crepuscular insectivore: Distant light sources create bright skies[☆]

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ABSTRACT

Light profoundly shapes ecosystems, influencing the behaviour and niche specialisation of many species. This is especially true for visual predators, particularly crepuscular and nocturnal animals, whose foraging depends on adequate illumination. Despite this, research on how animals perceive light sources and position themselves relative to these sources is scarce. Using a modified dead-reckoning protocol based on GPS, accelerometer, and magnetic compass data, we investigated the body orientation of foraging European Nightjars (*Caprimulgus europaeus*, hereafter nightjar) to determine their line of sight relative to bright sections of the nocturnal sky, created by natural or artificial light.

We found that nightjars are more likely to align themselves with brighter sections of the sky, although not necessarily with the brightest patch. On full moon nights, they positioned the moon within their line of sight when it was low on the horizon, but this likelihood decreased as the moon rose higher. During other moon phases, the likelihood of having the moon within line of sight increased linearly with moon altitude. During moonless parts of the night, nightjars appeared to use skyglow as a background for prey detection, but only when it was sufficiently bright. When both moonlight and skyglow were present, nightjars showed a preference for moonlight.

This study shows that European Nightjars use illuminated sections of the sky, including skyglow, as bright backgrounds to detect flying prey. This suggests that, in the absence of the moon, nightjars can actively take advantage of this form of light pollution while foraging. However, the success of their hunting under skyglow-induced lighting remains unclear. We hypothesise that the effectiveness of these backgrounds depends on their brightness and colour composition. Further research is needed to better understand the complex dynamics of contrast detection under varying lighting conditions.

1. Introduction

Light is a fundamental element of ecosystems, profoundly shaping the behavioural dynamics and niche specialisation of life on earth (Ausprey, 2021). Particularly for crepuscular and nocturnal animals, the subtle gradients of twilight and nighttime light significantly affect their

behaviour and physiology (Narendra et al., 2010; Maor et al., 2017; Cox et al., 2021; Salinas-Ramos et al., 2021; Cox & Gaston, 2024). Throughout the night, the lunar cycle introduces a dynamic interplay of light and darkness, transitioning through luminosities varying from less than 0.0006 lux to a maximum of 0.3 lux (Kyba et al., 2017; Aulsebrook et al., 2022; Śmielak, 2023). These variations in sky brightness can affect

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an animal's reliance on visual cues, influencing sensory functions essential for communication (Penteriani et al., 2010; Dickerson et al., 2020; Alonso et al., 2021), navigation (Dacke et al., 2004; Meschini et al., 2008; Zolotareva & Chernetsov, 2021), and foraging behaviour (Rubolini et al., 2014; Eberhart-Phillips, 2017; Roeleke et al., 2018; Ravache et al., 2020).

Since the advent of electric lighting, light pollution has dramatically altered the nighttime environment on a global scale (Santos et al., 2010), disturbing the delicate balance of natural light and darkness (Hölker et al., 2010a, 2010b; Gaston et al., 2013). While the majority of research on light pollution has focused on the localised effects of direct light sources on nocturnal habitats, skyglow is increasingly recognised as one of the most pervasive forms of sensory pollution (Davies & Smyth, 2018; Falchi et al., 2019). Skyglow occurs when artificial light is projected into the atmosphere and scatters on particles such as water and dust (Longcore & Rich, 2004; Owens & Lewis, 2018). Unlike direct lighting, which has a limited range, skyglow extends far beyond urban areas, affecting animals in their natural habitats (Garrett et al., 2020; Giavi et al., 2020). This brightening of nocturnal skies intensifies during overcast nights, erasing natural darkness and disrupting lunar brightness patterns (Kyba et al., 2011a; Jechow et al., 2017; Gaston and Holt, 2018). Both nocturnal and diurnal species have evolved to rely on natural light cycles to regulate their activities and behaviours, but skyglow now interferes with these processes, disrupting critical behaviours such as foraging (Becker et al., 2013; Bolton et al., 2017), reproduction (Witherington, 1992; Van Geffen et al., 2015), and migration (Torres et al., 2020; Horton et al., 2023).

Animals can intentionally use both natural and artificial light sources to assist in various activities (Salinas-Ramos et al., 2020; Adams et al., 2021). Perhaps the most well-known example of light exploitation by animals is the use of celestial cues, such as the moon, stars, and even the Milky Way, for navigation by insects (Ugolini et al., 2005; Dacke et al., 2013; Foster et al., 2018) and birds (Foster et al., 2018; Zolotareva & Chernetsov, 2021; Wiltschko & Wiltschko, 2023). Many insects also rely on polarised light from the moon or sun for orientation (Dacke et al., 2003, 2004; Warrant et al., 2006; Greiner et al., 2007; Warrant & Dacke, 2011). However, localised light pollution can interfere with nocturnal navigation by introducing new light sources into the nighttime environment, attracting animals like insects to streetlights (Firebaugh & Haynes, 2019; Foster et al., 2021; Degen et al., 2022a) and birds to illuminated buildings (Wang et al., 2011; Van Doren et al., 2017; Lao et al., 2020). Skyglow has been demonstrated to impede nocturnal navigation in urban areas by reducing the visibility of celestial cues (Falchi et al., 2016) and disrupting the polarised signals from moonlight (Kyba et al., 2011b). Only recently skyglow has been recognised as a potential light source that animals can intentionally exploit (Degen et al., 2022a, 2022b).

The foraging capabilities and activity patterns of visual predators are heavily influenced by light levels, as their ability to detect prey relies on sufficient illumination (Fraser & Metcalfe, 1997; Zimmer et al., 2008). According to optimal foraging theory, foraging individuals are expected to position light sources at angles that maximise prey detection and foraging efficiency (Pyke, 2019). However, to date, most research on light exploitation during foraging has focused on the effects of natural or direct light intensity on foraging activity (Eberhart-Phillips, 2017; Tidau et al., 2022; Willems et al., 2022), foraging efficiency (Ravache et al., 2020; Czarnecka et al., 2019; Luo et al., 2021; Moyse et al., 2023), and navigation towards foraging sites (Reid et al., 2011; Narendra et al., 2013; Zeale et al., 2018). Few studies have explored how animals perceive light sources from their own perspective (Degen et al., 2022b; Stöckl & Foster, 2022), likely due to the challenges of determining an animal's line of sight and the complex properties of light as it scatters across the sky. As a result, how foraging animals position themselves relative to light sources has, to the best of our knowledge, not yet been investigated.

Therefore, we here investigate light perception by a visually-

orienting, crepuscular insectivore, the European Nightjar (*Caprimulgus europaeus*, hereafter nightjar). The primary nocturnal foraging tactic of this bird species is a "sit-and-wait" tactic, also known as "flycatching" (Brigham & Barclay, 1995; Holyoak, 2001; Jackson, 2003), where the individual perches at an elevated position and waits for prey. Upon detecting an insect, the nightjar swiftly leaps up, capturing the prey from below in its wide mouth before returning to its perch (Camacho, 2013; Demmel Ferreira et al., 2019). The whole event usually lasts between 2 and 7 s (Cresswell & Alexander, 1992), with nightjars depending on light to discern flying insects as dark objects against a brighter background (Brigham & Barclay, 1995; Jackson, 2003). Recent studies have indicated that nocturnal flight activity of nightjars is correlated with both the altitude and illuminated fraction of the moon (Jetz et al., 2003; Evens et al., 2020a). Additionally, artificial skyglow from urbanised areas has the capacity to relieve nightjars from visual constraints, likely by increasing nocturnal sky brightness, thereby increasing their nocturnal activity during former dark parts of the night (Evens et al., 2023). The observed activity patterns in response to lunar- and skyglow-mediated sky brightness, along with nightjars' light-dependent foraging strategies, raise the question how nightjars may use different sources of sky brightness for prey detection during foraging.

Our study aims to determine how individuals position themselves with respect to bright sections of the nocturnal sky. By obtaining information on individuals' body orientation during flycatching events, using a modified dead-reckoning protocol that integrates GPS, acceleration and magnetic compass data, we expect to observe that individuals will strategically position themselves to keep the moon within their field of vision. This alignment would enable them to use the moonlit background to enhance prey detection. Conversely, during moonless periods of the night, artificial skyglow can illuminate large portion of the nocturnal sky, especially on overcast nights (Kyba et al., 2011a), potentially becoming an essential tool for prey detection.

2. Methods

2.1. Field methods

Nightjars were captured at four sites in Belgium (National Park Bosland: 51°11'3.628"N, 5°20'40.866"E; Oudsbergen: 51°3'57.053"N, 5°36'40.37"E; National Park Hoge Kempen: 50°58'48.622"N, 5°37'32.97"E; Kalmthoutse Heide: 51°11'3.628"N, 4°25'7.237"E) during the breeding season (May–August) of 2022 with techniques that were optimised during previous studies (Evens et al., 2017, 2024). We fitted male nightjars (n = 8) with a custom-designed combination of tracking devices: an activity logger (1.4g; Technosmart Axy5), a radio tag (0.4g; Biotrack Ltd.), and a GPS logger (1.8g; Pathtrack Ltd.), attached to the base of the tails with a simple drop-off mechanism (Evens et al., 2018a). The GPS loggers were programmed to record positions every 3 min, spanning from before sunset (9 p.m.) to after sunrise (6 a.m.). To ensure synchronised data collection, the activity loggers continuously recorded three-dimensional acceleration (g; 25 Hz) and magnetic field strength (μT ; 1 Hz) within the same timeframe. We calculated dynamic body acceleration by applying a 2-s rolling mean to the activity data, effectively removing static acceleration caused by the individuals' body angle in relation to gravity (Nathan et al., 2012). The absolute values of each dimension were then summed to derive the overall dynamic body acceleration (ODBA; Wilson et al., 2020). Visual examination of GPS tracks from 10 years of previous research revealed no evidence of abnormal behaviour or negative effects from the tracking devices.

2.2. Behaviour classification

The ODBA of four behavioural states (resting, flying, leaping, and singing) was examined, utilising previously annotated data (Evens et al., 2018b, 2020b; Eisenring et al., 2022) verified by field observations, sound recordings (Song Meters, Wildlife Acoustics), and thermal videos

(Pulsar Helion XQ38F Thermal Imaging Scope). These ODBA levels served as a basis for setting thresholds to distinguish the various behavioural states (Fig. 1). Stationary periods (resting) were differentiated from active periods using a threshold of $ODBA \leq 0.2$. Additionally, since flycatches typically last for 2–7 s (Cresswell & Alexander, 1992), active bouts within this duration were categorised as leaps. Singing behaviour consistently fluctuated between 0.5 and 1.1, hence continuous activity bouts falling within this ODBA range were classified as singing. The remaining active periods were classified as flying.

2.3. Calculating an individual's line of sight through dead-reckoning

Determining an individual's precise line of sight involves calculating its yaw, or the rotation around the individual's vertical axis, using magnetic field measurements (Bidder et al., 2015; Schoombie et al., 2023). However, to validate the accuracy of this calculation one would need exceptionally detailed GPS tracks. Therefore, to validate an individual's line of sight during foraging events and because our magnetic field data was measured at 1 Hz, we needed to increase the 3-min resolution of the GPS observations to a 1-s resolution. Dead-reckoning allows detailed reconstructions of flight paths by integrating activity data from tri-axial accelerometers and magnetic field data from magnetometers (e.g., with tilt-compensated compass method; Li et al., 2009; Gheorghe & Bodea, 2018). Dead-reckoning sequentially estimates the next position based on a previously determined position (i.e., the first GPS point of a 3-min interval), factoring in high-resolution estimates of heading and speed over a defined time period (i.e., 1-s measurements from activity loggers; Bidder et al., 2015; Beauregard & Haas, 2006; Walker et al., 2015).

To make a 1-s reconstruction of an individual's trajectory between two consecutive GPS observations (3-min resolution), we adapted a dead-reckoning protocol initially developed by Gunner et al. (2021; Fig. 2). First, we estimated travel distance per second, using ODBA as a proxy for speed (Bidder et al., 2012; Wilson et al., 2020). Continuous flight bouts between two GPS points enabled us to calculate the flight speed for each segment and correlate it with the measured ODBA recorded during these bouts. To refine the estimates of travel distance, we utilised the classified behavioural states to mark events when the individual was flying. This prevents the dead-reckoning process from mistakenly interpreting stationary intervals, such as during singing bouts, as movement solely based on ODBA readings. Since we assume that the nightjar returns to its perch after each flycatch, we classify the flycatch event as stationary as well. This ensures that the acceleration

during these events does not result in a positional shift during the dead-reckoning process. Second, we calibrated the magnetometer (including orthogonal rescaling, channel biases, correction for hard iron distortions, and de-rotation of the magnetometer by pitch and roll; Gunner et al., 2021; Williams et al., 2017), with which we finally calculated the yaw to determine the individual's line of sight. The yaw is calculated as the individual's bearing, which is the angle measured clockwise from the north direction (Bidder et al., 2015; Schoombie et al., 2023).

The accuracy of dead-reckoning relies heavily on precise estimation of both speed and line of sight. However, external factors such as temperature, humidity, and magnetic fields can affect the performance of loggers, leading to positional drift that accumulates over time. This drift impacts the precision and reliability of the collected data (Liu et al., 2015; Dewhirst et al., 2016). To mitigate these errors, we ground-truthed the estimated dead-reckoned tracks with a Verified Position (VP; Bidder et al., 2015; Wensveen et al., 2015; Andrzejczek et al., 2018), specifically the second GPS points from a 3-min interval, using the linear drift correction method (Gunner et al., 2021; Dewhirst et al., 2016; Shiomi et al., 2008). We calculated the difference between the VP and the dead-reckoned path segment at the second time point (the last-dead-reckoned segment of the 3-min interval) to derive a correction vector. This vector was then linearly applied between the two time points (start and stop of the 3-min interval) to adjust the length and heading of each dead-reckoned flight segment, aligning the endpoint of the estimated flight path with the VP along the actual path (Verified Position Correction, VPC). The corrected factors obtained through VPC provide reliable indicators for detecting consistent under- or over-estimations of speed and heading offsets. Due to the gradual accumulation of slight discrepancies over time, multiple iterations of the VPC may be necessary to align estimated and ground-truthed positions until the distance between these points is less than 1 m (Gunner et al., 2021).

2.4. Identification of foraging sites

We identified flycatching events using the classified behavioural data, marking the transition from a period of rest to a leap. For each identified flycatching event, the bird's location and line of sight during the resting period (i.e., while the bird is perched) were extracted from the dead-reckoned track. This line of sight represents the direction in which the nightjar's beak is pointing when facing straight ahead. It is important to note, however, that this line of sight does not necessarily indicate the direction that the nightjar is looking. Yet, with this line of

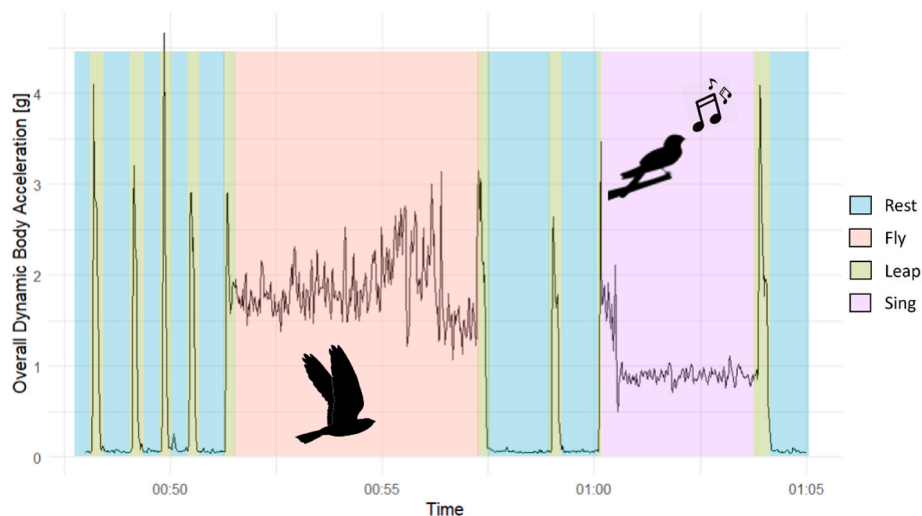


Fig. 1. Using ODBA thresholds to classify activity data into four behavioural states: resting (blue), flying (red), singing (purple), and leaping (green). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

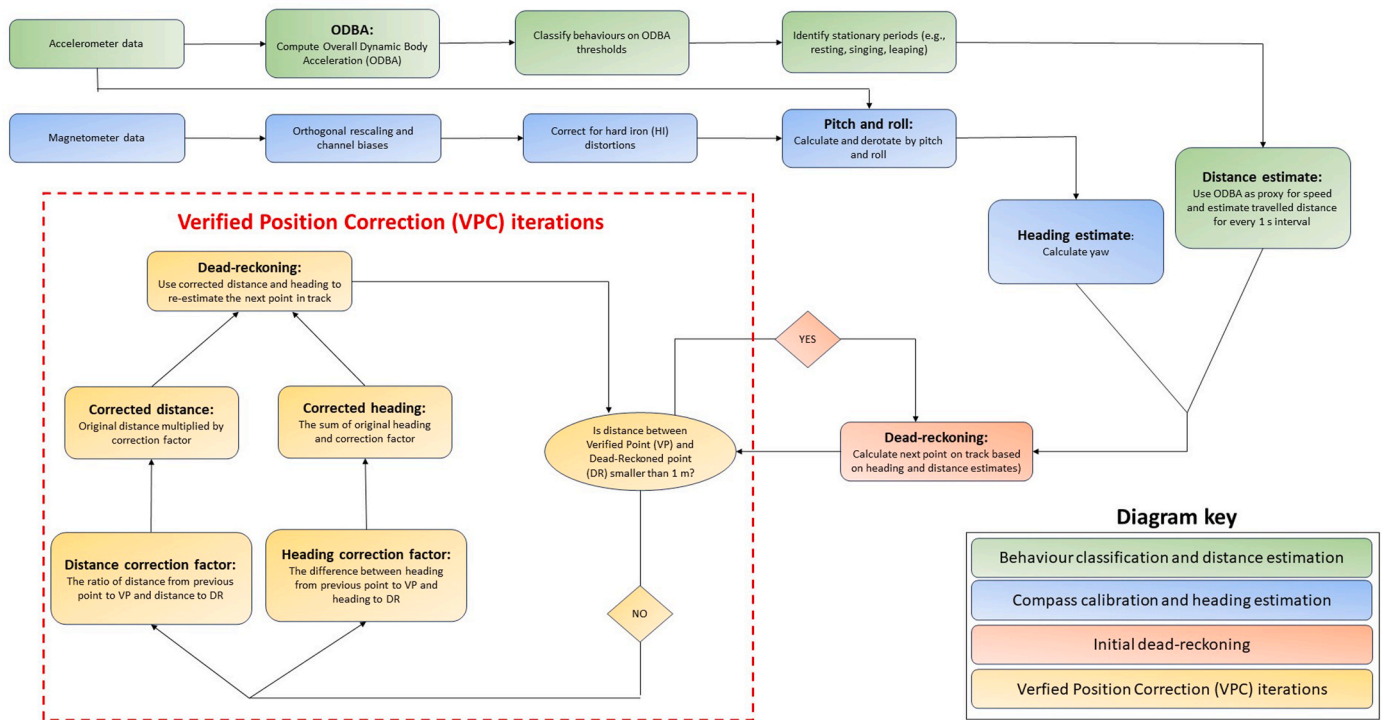


Fig. 2. Schematic overview of the dead-reckoning protocol.

sight we can estimate the bird’s field of view based on the known visual range of the Band-winged Nightjar (*Systellura longirostris*), which employs a similar foraging strategy (Salazar et al., 2020). The nightjar’s binocular vision extends 10° in each direction from its central line of sight, with an additional 130° of peripheral vision.

For each perch, we generated a Canopy Height Map (1 m resolution; QGIS v3.23.3) by subtracting the values of Digital Surface Model (DSM, 1 m resolution) from a Digital Terrain Model (DTM, 1 m resolution; both sourced from www.geopunt.be). Canopy height was then sampled within a 2-m radius, measuring at one-degree intervals around a full 360° circle. For each one-degree segment around the perch, we identified the presence of high vegetation (e.g., tree, bush, or other plant) if the vegetation height was at least 30 cm taller than the height of the perch, ensuring that the surrounding vegetation is higher than the perching nightjar (Holyoak, 2001).

2.5. Light sources

Using the ‘skylight’ R package (Hufkens et al., 2023), we gathered data on the brightness and position of the moon during nocturnal foraging events. We recorded the zenith sky brightness (lux), the relative position of the moon as the clockwise angle from the north (degrees), and the elevation angle relative to the horizon (degrees). Additionally, we created a general categorical variable to denote whether the sky during the foraging event was moonless or moonlit, based on whether the moon was respectively under or above the horizon. Finally, we categorised each foraging event into two moon phases: ‘full moon’ or ‘other moon phases’.

The ‘skylight’ package provides the relative position of the moon as clockwise angles from north. By recalculating these positions as angles from the nightjar’s line of sight, we can determine if the light sources fall within the bird’s field of vision (i.e., within 140° of its central line of sight; Salazar et al., 2020). If the light source is within the nightjar’s field of vision but aligns with areas of high vegetation (classified from the canopy height map), we assume the source is obscured by vegetation and thus not visible to the nightjar.

To identify potential sources of skyglow, we utilised a top-down Visible Infrared Imaging Radiometer Suite (VIIRS) satellite map (available at www.lightpollutionmap.info). This map depicts nocturnal radiance at a resolution of 300 m, measured in Watts per square centimetre steradian (10⁻⁹ W/cm² sr). For each perch location, we established 40 buffer zones, starting at 500 m and extending up to 20 km from the perch, with intervals of 500 m between each buffer zone. Radiance data was extracted at every 5-degree interval along the perimeter of each buffer zone. The brightest 2% of these points were identified as potential sources of skyglow for that perch. We determined this threshold by confirming that the identified sources are visible in the breeding areas using bottom-up, all-sky images (Canon EOS 7D MKII with Sigma 4.5 mm F/2.8 EX DC HSM fisheye lens; Jechow et al., 2019). With this information, we calculated the smallest angle between the nightjar’s line of sight and the nearest source of skyglow.

For each foraging event, we also included information on cloud cover, as dense cloud covers significantly increase skyglow-induced nocturnal brightness (Kyba et al., 2011a; Jechow et al., 2017). We interpolated sub-hourly cloud cover data from the hourly data provided by ECMWF’s Fifth-generation Reanalysis (ERA5; Hersbach, 2016). Given the substantial spatial variation in clouds, which greatly affects light scattering in the sky (Yao et al., 2020; Sciezor, 2020), we converted cloud cover data into clear-sky indices, measured in oktas (eights of the sky covered by clouds; Smith et al., 2017). We categorised the skies as clear (0–2 oktas), partly cloudy (3–6 oktas), or overcast (7–8 oktas; Smith et al., 2017; Davies et al., 2020). Due to the unpredictability of light scattering on partly cloudy nights, we excluded these events from our analysis.

2.6. Statistical analysis

In this study, we focused solely on nocturnal foraging events, defined as the period between astronomical dusk and astronomical dawn, when the sun is at least 12° below the horizon. Based on the knowledge that nightjars’ activity differs between moonless and moonlit parts of the night (Evens et al., 2023), we subdivided nocturnal foraging events into

two groups: moon above or below the horizon. Foraging events that occurred during moonlit nights were further subdivided into two groups: clear sky (0–2 okta) or overcast sky (7–8 okta), to account for the possible effect of cloud-mediated skyglow (Evens et al., 2023). For these five scenarios we developed a generalised linear mixed model, using the ‘glmmTMB’ package in R (Brooks et al., 2017), to investigate whether foraging nightjars orient themselves towards bright sections of the nocturnal sky. To account for variations among individual nightjars and the different nights of observation, random effects with nightjar nested within night were included in all models. Model assumptions were validated using the ‘DHARMA’ package in R (Hartig, 2022).

The first (clear sky) and second (overcast sky) model assesses the nightjar’s line of sight in relation to the moon during moonlit periods. Predictors include moon altitude (continuous: degrees above the horizon), moon phase (binary: full moon/other phases), and their interaction. In both models, the dependent variable is whether the perching nightjar positions itself so that the moon is within its field of vision (binary: yes/no), and this follows a binomial distribution.

The third (clear sky) and fourth (overcast sky) models evaluate the nightjar’s body position relative to sources of skyglow during moonlit periods when the moon is above the horizon. Predictors include moon altitude (continuous: degrees above the horizon), moon phase (binary: full moon/other phases), and their interaction. The dependent variable, modelled using a negative binomial distribution, is the minimum angle between the nightjar’s line of sight and the nearest source of skyglow during perching (continuous: degrees).

The fifth model examines periods without moonlight, specifically when the moon is below the horizon. Cloud cover is included as a continuous predictor. The dependent variable is the minimum angle between the nightjar’s line of sight and the nearest source of skyglow (continuous: degrees), modelled using a negative binomial distribution.

3. Results

We retrieved data from eight loggers spanning a total of 26 nights (4.25 ± 2.92 nights per individual). We identified 1043 flycatching events (59.14 ± 20.14 events per night). Out of the 26 recorded nights, eight were during a full moon, nine during waning moon and nine during waxing moon. No loggers were retrieved that recorded nights during a new moon. Ultimately, this resulted in 674 out of 1043 nightly foraging events occurring with the moon present above the horizon and 369 when the moon was below the horizon.

During clear, full moon nights (0–2 okta, $n = 182$ flycatching events), the probability that the nightjar positioned itself so that the moon was in its line of sight was highest when the rising or setting moon was at low altitudes above the horizon (Table 1, Model 1; Fig. 3A). This probability decreased linearly between moon altitudes of 5 and 15° above the horizon, levelling off at altitudes higher than 15°. During other moon phases, the probability that the nightjar positioned itself with the moon in its line of sight increased with moon altitude. During overcast, moonlit nights (7–8 okta, $n = 293$ flycatching events), the probability that the nightjar positioned itself with the moon within its line of sight decreased with increasing moon altitude (Table 1, Model 2; Fig. 3B).

During clear, moonlit nights (0–2 okta, $n = 182$ flycatching events), nightjars did not orient themselves towards distant sources of skyglow, as moon altitude showed to have no significant effect on the angle between the nightjar’s line of sight and the nearest potential source of skyglow (Table 1, Model 3). On overcast nights (7–8 okta, $n = 293$ flycatching events), this angle between the nightjar’s line of sight and the nearest potential source of skyglow was larger when the moon is low, and decreased as moon altitude increased (Table 1, Model 4; Fig. 4A). In other words, when the moon was low on the horizon, nightjars tended to orient away from the skyglow, likely facing the moon. Conversely, they will face more toward skyglow when the moon is higher in the sky and is potentially obstructed by clouds. During moonless nights ($n = 369$ flycatching events), the angle between a nightjar’s line of sight and the

Table 1

Model outputs of generalised mixed-effect models showing the effects of sun illuminance, moon altitude, moon phase, and cloud conditions, on how nightjars position themselves relative to bright sections of the sky during foraging. See Methods for model details.

Model	Response	Predictors	Estimate (SE)	z	p
1	Moon in field of vision	Intercept	−0.304 (0.38)	−0.80	0.423
		Moon altitude	0.046 (0.02)	1.93	0.053
		Moon phase ^a	2.466 (1.09)	2.27	0.024
		Moon altitude: moon phase	−0.277 (0.10)	−2.74	0.006
		Night: nightjar ^a	< 0.001 (< 0.001)		
2	Moon in field of vision	Intercept	1.051 (0.38)	2.77	0.006
		Moon altitude	−0.045 (0.02)	−2.02	0.044
		Moon phase ^a	−0.654 (0.52)	−1.26	0.207
		Night: nightjar ^a	0.452 (0.67)		
		Night: nightjar ^a	3.229 (0.14)		
3	Angle perch-skyglow	Intercept	0.002 (0.01)	0.31	<0.001
		Moon altitude	0.077 (0.14)	0.52	0.60
		Moon phase ^a	< 0.001 (< 0.001)		
		Night: nightjar ^a	0.077 (0.14)		
		Night: nightjar ^a	2.646 (0.36)		
4	Angle perch-skyglow	Intercept	0.062 (0.03)	1.67	0.093
		Moon altitude	0.847 (0.38)	2.21	0.026
		Moon phase ^a	−0.083 (0.03)	−2.14	0.032
		Moon altitude: moon phase	0.015 (0.12)		
		Night: nightjar ^a	3.662 (0.12)		
5	Angle perch-skyglow	Intercept	−0.380 (0.14)	−2.59	0.431
		Cloud cover	0.016 (0.12)		
		Night: nightjar ^a	0.016 (0.12)		
		Night: nightjar ^a	34.64		

Random intercept.

^a Estimates for full moon compared to other moon phases.

nearest potential source of skyglow decreased with cloud cover (Table 1, Model 5; Fig. 4B). In other words, nightjars oriented more toward the skyglow when the sky was overcast.

4. Discussion

The dead-reckoning of coarse GPS tracks allowed us to reconstruct the orientation of individual nightjars to investigate, at a 1-s resolution, how these crepuscular birds position naturally- and artificially-lit sections of the sky within their field of view during nocturnal foraging activities. This way, we demonstrate that nightjars in our study utilise sections of the sky illuminated by both moonlight and skyglow as bright background to facilitate the detection of flying prey at night.

Due to the limited knowledge of the prey detection mechanisms and visual system of the European Nightjar, we assume that nightjars perceive the bright background from a linear perspective from their perch, although their field of vision likely includes an upward component as well (Salazar et al., 2020). Little is known about the retinal morphology of nightjars. As a result, while we can make inferences about their overall field of view and line of sight, we cannot determine the direction of their highest visual acuity. Similarly, although accelerometer data can identify when a flycatching event occurs, it does not confirm whether an insect was successfully captured. Therefore, while we can draw conclusions about the types of backgrounds nightjars use for foraging, we cannot ascertain which backgrounds are most effective for successful prey capture.

Our study also exclusively includes male nightjars, as they are easily captured using tape lures and have higher logger recovery rates due to

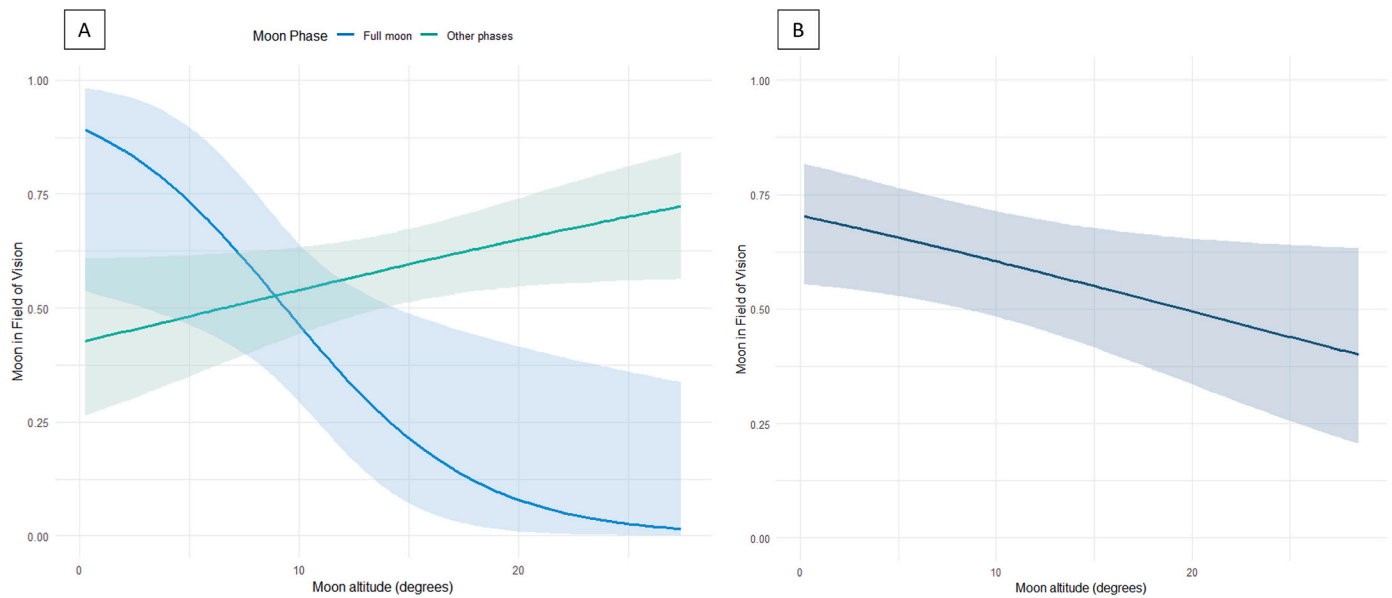


Fig. 3. Model predictions for the probability that the nightjar positions itself so that the moon is within its field of vision while perched on (A) moonlit, clear (0–2 okta) nights with either a full moon (blue) or another moon phase (green), or on (B) moonlit, overcast (7–8 okta) nights. Shaded areas indicate the 95% confidence intervals of the predictions. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

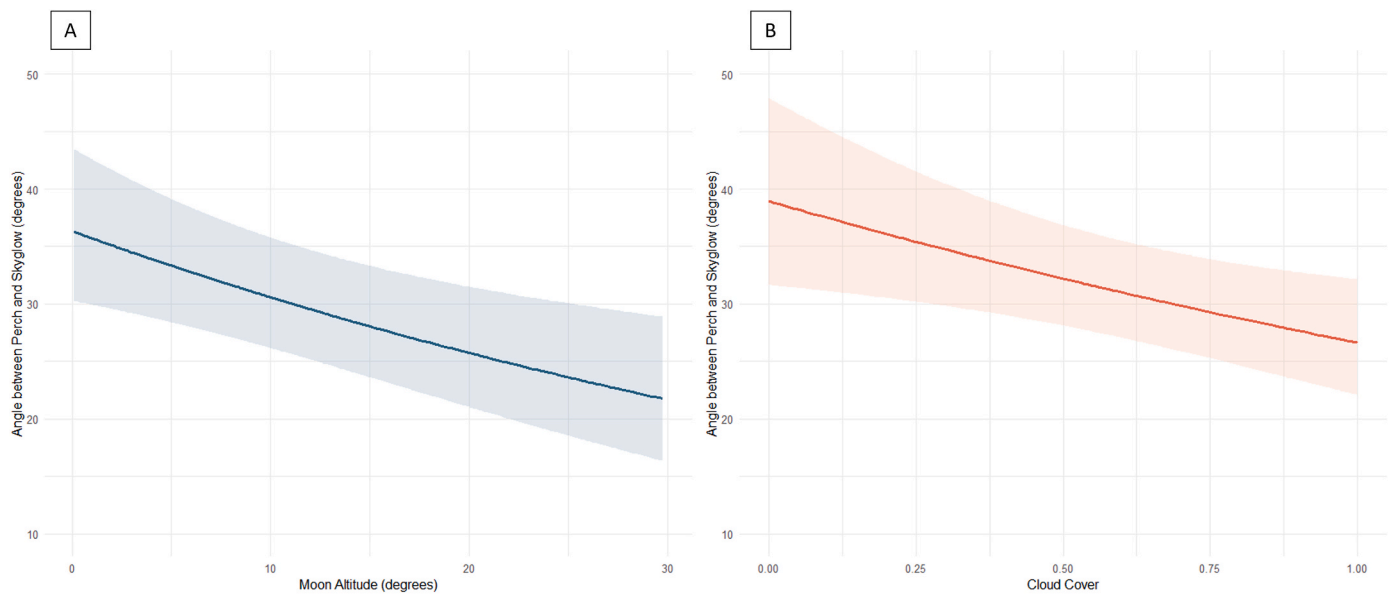


Fig. 4. Model predictions for the angle between the perch orientation and the nearest source of skyglow on (A) overcast, moonlit nights (7–8 okta) in function of moon altitude, and (B) moonless nights in function of cloud cover. Shaded areas illustrate the 95% confidence interval of each model prediction.

their site fidelity. However, we do not anticipate significant differences in the visual ecology between males and females, suggesting their strategic use of different backgrounds for prey detection is likely similar. Nevertheless, while the visual system of both sexes is likely similar, paired individuals alternate with chick rearing on the nest, so they forage at different times throughout the night, influencing their use and availability of bright backgrounds. Finally, comparing our results to other ecological studies is challenging. This difficulty arises not only due to the lack of similar studies (Gaston, 2019), but also from the severely unstandardised way of measuring nocturnal light conditions in different studies (e.g., the use of varying methods and units; Hänel et al., 2018). For this reason, we consider our results in the context of optimal illuminance levels, or the ideal spectral composition of light.

4.1. Moonlight as a bright background for prey detection during nocturnal foraging

During clear nights of a waxing and waning moon, the probability that nightjars position the moon within their field of view increases when the moon is higher above the horizon. Conversely, during a full moon this probability decreases when the moon is higher above the horizon (Fig. 3A). This seemingly contradictory response to the moon’s altitude may find its origin in the nonlinear progression of moonlight’s brightness and colour throughout the lunar cycle.

As the incoming moonlight is travelling through Earth’s atmosphere, it scatters upon atmospheric particles, a process known as Rayleigh scattering. This scattering causes the moonlight to spread through the sky. Shorter wavelengths, like blue and violet, scatter more intensely

than longer ones, such as red. The intensity of the scattered light also depends on the brightness of the moon: the brighter the moonlight, the more light there is available to scatter, enhancing the overall effect (Young, 1982; Spitschan et al., 2016).

During the waxing and waning phases of the moon, its illuminance increases linearly with its altitude. However, on full moon nights, illuminance levels increase exponentially, reaching at least twice the levels observed at similar altitudes during other phases (Kyba et al., 2017; Poon et al., 2024). When the full moon rises above 10°, we suspect that this exponential increase in illuminance creates a sufficiently bright nocturnal sky, filled with scattered light of shorter wavelengths due to the effects of Rayleigh scattering. This provides a well-lit background that aids in prey detection from all directions.

While full moons may create ideal conditions for nightjars to locate their prey, it is important to note that prey abundance does not necessarily peak during these times. The impact of lunar phases on moth activity, the primary prey for nightjars, remains a topic of ongoing discussion (Juddin et al., 2023). Evidence suggests that moth responses to moonlight might be species-specific (Nowinszky et al., 2010), with some species exhibiting reduced activity under bright conditions to avoid predation (Yela & Holyoak, 1997; Vásquez et al., 2020). Moreover, increased light levels can help prey detect and evade predators more effectively (Lang et al., 2006). As a result, although full moons enhance visibility for nightjars, their foraging success is not solely determined by moonlight, but also influenced by prey-specific factors.

With the full moon below 10° above the horizon, the brightness increase with moon altitude is comparable to other phases, yet we do not observe the same likelihood of nightjars positioning the moon within their field of vision. This suggests that additional factors may contribute to this behaviour. When the moon is low above the horizon, its light travels a longer distance through the atmosphere, resulting in more scattering on atmospheric particles (Veilleux & Cummings, 2012). The intensity of the shorter wavelengths that scatter from the moonlight will be dependent on both the brightness of the light and the proportion of shorter wavelengths in the light. Since the brightness of the moon at low altitudes is similarly dim for all moon phases, Rayleigh scattering will make for a red-shifted lunar disk, with scattered blue light close to the disk itself. However, the spectrum of moonlight “reddens” from the full moon to the quarter phases (Peacock, 1968; Kaydash et al., 2011). This causes the scattering of blue light to be more prominent during the full moon phases.

If we assume that nightjars orient themselves towards bright patches in the sky with predominantly shorter wavelengths (i.e., blue light) during the rising full moon, the only detectable blue light is that which surrounds the moon. When this full moon rises higher in the sky, its brightness increases exponentially and the scattered blue light is more likely to saturate the nocturnal landscape, reducing the necessity for the moon to be within the nightjar’s field of vision.

During the waxing and waning phases of the moon, the brightness of moonlight is dimmer, causing the scattered blue light to be detectable only near the moon itself. When these phases are thus high above the horizon, a suitable background for prey detection may exist in close vicinity to the moon. However, at lower altitudes, Rayleigh scattering is increased and the moon is dimmer and more red-shifted. The scattered blue light surrounding the moon might therefore be too faint to detect (Voudoukis & Oikonimidis, 2017). Additionally, when the moon is low above the horizon, red hues from skyglow, particularly from low-pressure sodium lamps, further red-shift the spectral composition (Gaston et al., 2014). This red-shifting may lead nightjars to rely more on brighter sources of skyglow or even direct light pollution.

4.2. Skyglow as alternative light source when moonlight is unavailable

On moonless nights, nightjars orient themselves closer towards sections of the sky that are lit by skyglow, especially during overcast nights (Fig. 4B), when the brightness of skyglow is known to significantly

increase (Jechow et al., 2017, 2020). This suggests that, within their natural habitats, nightjars can utilise artificial skyglow from distant cities or industrial areas as a luminous backdrop for prey detection under sufficiently bright conditions. Importantly, however, nightjars seem to prefer moonlight over skyglow sources for detecting prey as long as parts of the moonlit sky are visible (Figs. 3B and 4B). When cloud cover intensifies and obscures the moonlit sky, it reduces the likelihood that nightjars can use the (rising) moon’s light as a background for prey detection. Our data suggest that in such conditions, nightjars have adapted to redirect their attention towards artificial light sources. However, without data on the moon’s altitude relative to the clouds (i.e., whether the moon is actually obscured by clouds), we cannot conclusively prove this hypothesis.

The preference for moonlight over skyglow may arise from the notable differences in intensity and spectral composition between natural and artificial light. In Belgium, much of the skyglow originates from city centres or industrial areas illuminated by traditional sodium streetlights, which emit longer wavelengths, giving them their characteristic yellow hue (Elvidge et al., 2010; Davies et al., 2013). It is, however, noteworthy that the rapid transition to LED lights, which offer a broader spectrum of wavelengths, is now changing the nocturnal landscape (Dimovski & Robert, 2018; Alaasam et al., 2021). Nonetheless, our findings indicate that nightjars may resort to artificial lights when natural light is absent or insufficient for prey detection, despite being dominated by longer wavelengths.

How these increased opportunities influence the foraging success of nightjars remains unknown, as the effects of skyglow on moth activity remain poorly understood. Recent studies suggest that insects exhibit increased nocturnal activity during skyglow-induced brighter conditions and tend to shift their habitats toward more open areas (Dyer et al., 2023). While high-pressure sodium streetlights have been traditionally regarded as relatively unharmed to insects due to the spectral characteristics of their light (Eisenbeis, 2006), the widespread transition to LED lighting raises concerns about its impact on moth behaviour (Owens & Lewis, 2018). This shift underscores the need for further research to clarify how skyglow influences the spatial and temporal patterns of moth activity, and, consequently, the foraging success of nightjars.

Alternatively, when skyglow is insufficiently bright, nightjars may seek out direct sources of light pollution, such as streetlights, to capitalize on the heightened illumination provided by the lighting or the increased availability of flying moths (Macgregor et al., 2016). This hypothesis is supported by regular observations of individual nightjars foraging in city centres’ large industrial areas. Similar artificial light-mediated foraging behaviours have been observed in other visually-orienting nocturnal predators, such as some bat and wader species (Rydell, 1992; Santos et al., 2010; Lacoëuilhe et al., 2014).

4.3. Nightjars prefer bright, blue backgrounds for prey detection

Data on the orientation of nightjars towards lit sections of the nocturnal sky suggest that nightjars seem to prefer blue skies (i.e., scattered blue light from moonlight) for prey detection, although red-shifted backgrounds (i.e., skyglow) can serve as viable alternative when sufficiently bright. While it has been documented that certain crepuscular and nocturnal species exhibit heightened sensitivity to the blue end of the spectrum (Melin et al., 2012; Fuller et al., 2016; Höglund et al., 2019), the research exploring how these light sensitivities influence target detection against various backgrounds remains limited (Veilleux & Cummings, 2012). Nevertheless, the spectral tuning of photoreceptors in diurnal species has frequently been linked to their ability to detect targets against background radiance (Sumner & Mollon, 2000; Cummings, 2007). Given this, it is plausible that similar mechanisms operate in nocturnal species, potentially enabling them to develop nocturnal colour vision for target detection in varying light environments (Kelber & Roth, 2006; Kelber & Lind, 2010).

Despite the absence of direct empirical evidence demonstrating

nightjars' sensitivity to backgrounds of different colours, several studies might support this hypothesis. First, a comparative analysis of retinal morphology between Common Pauragues (*Nyctidromus albigollis*) and Oilbirds (*Steatornis caripensis*) demonstrates that Pauragues, which are closely related to nightjars, possess a notably high rod-to-cone ratio, indicative of their specialized adaptations to low light environments (Rojas et al., 2004). Pauragues also predominantly forage during twilight and moonlit nights through flycatching. The high rod-to-cone ratio likely enables the rapid detection of subtle brightness differences, which enhances their ability to swiftly detect contrast and motion, for example, in the form of a flying insect. Rods contain the rod opsin RH1, which is particularly sensitive to shorter wavelengths of light, peaking around 500 nm (cyan; Hart, 2001). This sensitivity contributes to the rods' effectiveness in low light conditions, as shorter wavelengths penetrate the atmosphere more efficiently, providing better stimulation of rod cells.

Second, the use of skyglow as a bright background for prey detection suggests that longer wavelengths (red and orange colours) can also be effective. Although little research has been done on the photoreceptors and visual system of European Nightjars, Ödeen and Håstad (2003, 2013) sequenced the SWS1 opsin genes of various bird species, including the European Nightjar, showing that they have colour vision extending into the violet range. Studies on related species, such as the Common Nighthawk (*Chordeiles minor*), Chuck-will's-widow (*Caprimulgus carolinensis*), and Jungle Nightjar (*Caprimulgus indicus*) reveal spectrally distinct types of cone oil droplets (Gondo & Ando, 1995; Hart, 2001), indicating likely tetrachromacy. This suggests that European Nightjars, despite their adaptation to low-light environments, are likely tetrachromatic as well.

During twilight, when light conditions and sky colours change rapidly, having multiple types of cones helps nightjars adapt and maintain effective prey detection. Additionally, in the presence of skyglow and artificial light, which often contain orange hues, these cones enable nightjars to distinguish prey against non-blue backgrounds. However, cones are only active above a certain brightness threshold (Barbur & Stockman, 2010), below which nightjars cannot rely on their colour vision. This aligns with our findings that skyglow can only serve as a suitable background for prey detection when its brightness is sufficiently high. The ability to detect prey against varying backgrounds provides nightjars with a significant survival advantage, allowing them to exploit different environmental conditions, whether under a blue moonlit sky or warmer skyglow hues.

5. Conclusion

Even with a small sample from our study population, data on an individual's orientation underscore the importance of natural and artificial light on the nightjars' foraging activities, while demonstrating the potential of dead reckoning course GPS-tracks with magnetometers to provide invaluable insights on individual behaviour. We show that the strategic use of naturally- and artificially-lit sections of the nocturnal sky highlights allow nightjars flexibility to forage under different environmental conditions, but also reveal the need to further examine skyglow-mediated animal behaviour. The rapid transition from high-pressure sodium lights to LEDs, for example, is rapidly changing the nocturnal sky with unknown effects on individuals' foraging efficiency and activity patterns.

CRedit authorship contribution statement

Jitse Creemers: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marcel Eens:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Eddy Ulenaers:** Conceptualization, Resources, Writing – review & editing. **Michiel Lathouwers:** Writing – review & editing, Validation, Methodology,

Data curation, Conceptualization. **Ruben Evens:** Writing – review & editing, Visualization, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Ethical permit

The research protocols were approved by the Belgian authorities (Agency for Nature and Forest, license numbers: ANB/BL-FF/V18-00086, ANB/BL-FF/19-00087, ANB/BL-FF/20-00114 and ANB/BL-FF/V22-00139). All protocols were carried out in accordance with the relevant guidelines and regulations.

Declaration of generative AI in scientific writing

During the preparation of this work, the authors did not use generative AI.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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