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METHODS PAPER

# Biologically meaningful moonlight measures and their application in ecological research

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**Abstract**

Light availability is one of the key drivers of animal activity, and moonlight is the brightest source of natural light at night. Moon phase is commonly used but, while convenient, it can be a poor proxy for lunar illumination on the ground. While the moon phase remains effectively constant within a night, actual moonlight intensity is affected by multiple factors such as disc brightness, position of the moon, distance to the moon, angle of incidence, and cloud cover. A moonlight illumination model is presented for any given time and location, which is significantly better at predicting lunar illumination than moon phase. The model explains up to 92.2% of the variation in illumination levels with a residual standard error of 1.4%, compared to 60% explained by moon phase with a residual standard error of 22.6%. Importantly, the model not only predicts changes in mean illumination between nights but also within each night, providing greater temporal resolution of illumination estimates. An R package *moonlit* facilitating moonlight illumination modelling is also presented. Using a case study, it is shown that modelled moonlight intensity can be a better predictor of animal activity than moon phase. More importantly, complex patterns of activity are shown where animals focus their activity around certain illumination levels. This relationship could not be identified using moon phase alone. The model can be universally applied to a wide range of ecological and behavioural research, including existing datasets, allowing a better understanding of lunar illumination as an ecological resource.

**Significance statement**

Moon phase is often used to represent lunar illumination as an environmental niche, but it is a poor proxy for actual moonlight intensity on the ground. A model is therefore proposed to estimate lunar illumination for any given place and time. The model is shown to provide a significantly better prediction of empirically measured lunar illumination than moon phase. Importantly, it also has much higher temporal resolutions, allowing to not only detect selectiveness for light levels between nights but also within each night, which is not achievable with moon phase alone. This offers unprecedented opportunities to study complex activity patterns of nocturnal species using any time-stamped data (GPS trackers, camera traps, song meters, etc.). It can also be applied to historical datasets, as well as facilitate future research planning in a wide range of ecological and behavioural studies.

**Keywords** Moonlight · Lunar cycle · Moon phase · Illumination · Temporal partitioning

## Introduction

### Moonlight as an ecological resource

Although the ecological niche, defined as a multidimensional space of environmental conditions and resources, has remained one of the core concepts in ecological studies (Hutchinson 1957), 'time' has only recently gained attention as an important niche dimension (Hut et al. 2012). Temporal partitioning is believed to be an adaptive mechanism driven by foraging, competition and predation (e.g. Kronfeld-Schor and Dayan 2003). With the advance in technology such as camera traps and other automated monitoring devices that provide precisely time-stamped records of animal activity, it is possible to further investigate this topic (Frey et al. 2017). It is likely, however, that what is measured as temporal patterns of activity also reflects the selectiveness of other resources, such as illumination. As light levels change throughout the night, especially around dawn and dusk, nocturnal species likely seek

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'optimal' light levels for foraging, but these could conflict with the necessity to avoid competition and predation.

Moon is the brightest natural light source at night (Kyba et al. 2017) and is an important factor influencing animal behaviour. Two main hypotheses aim to explain the response to changing moonlight in respect of predator avoidance. The first one predicts that under bright moonlight, predators are potentially more successful, while the second one predicts that prey species can visually detect predators and forage more efficiently, e.g. mammals that orientate primarily visually increase their activity on brighter nights, while species using other senses decrease it (Prugh and Golden 2014). Response to moonlight is likely to be a result of a complex trade-off between 'seeing' (improved resource harvesting and predator detection) and 'not being seen' (remaining cryptic and reducing encounters by predators and predator lethality).

The impact of the moon cycle on animal behaviour has been widely studied across most taxonomic groups; however, researchers mostly use simple measures of light levels based on moon phase or visibility of the moon. Neither of these measures take the changes in illumination throughout a night into account, which is a function of both brightness and the position of the moon in the night sky. Moreover, for experimental studies where simulated moonlight is used as a cue for predation risk (e.g. measuring giving-up densities), artificial lighting often neither matches the intensity nor changes of real moonlight (Aulsebrook et al. 2022).

Ideally, in ecological studies, actual values of moonlight intensity on the ground should be used, and this can be measured in the field using photometers. In practice, this is difficult, as light loggers capable of measuring very low light intensities are difficult to obtain and expensive and for some applications have to be custom-built. In astronomy and light pollution research, specialty light measuring devices have been used, such as the Sky Quality Meter (Unihedron, Ontario, Canada). While very sensitive, these devices measure the brightness of a specific portion of the sky rather than illumination on the ground.

Theoretical models estimating moonlight intensity have been used in astronomy (e.g. Krisciunas and Schaefer 1991), but they are too complex for practical application in ecological studies, and a simpler approach for calculating moonlight illuminance on the earth's surface is needed. Austin et al. (1976) proposed such a model, predicting illumination relative to an 'average' full moon rather than estimating absolute illumination values. Although not widely adopted, this approach simplifies calculations while maintaining the ecological relevance of model output. Here, an improved model was developed to predict relative moonlight illumination on the ground, which incorporates major variables (position of the moon, the brightness of the moon face and several physical properties of light propagation) and is relatively simple yet precise and easy to use in a wide range of ecological studies.

This paper argues why several ecologically relevant measures of moonlight should be used and proposes an approach for data with various temporal resolutions. An R package *moonlit*, a new tool for studying the ecological impacts of moonlight, is also introduced.

## Understanding the moon cycle

The moon's sidereal period (one full orbit of earth) is around 27.3 days. However, the earth is also orbiting the sun, and therefore, the synodic period (one full lunar cycle) repeats, on average, every 29.5 days (Lang 1992). Because of the asynchrony between the sidereal and synodic periods, a lunar day (time from moonrise to moonrise) is approximately 50 min longer than a solar day; thus, moonrise is delayed every day, on average, by approximately 50 min, and it changes seasonally in predictable manner.

As times of moonrise and lunar noon (upper meridian transit time, i.e. the moment when the moon is highest in the sky and brightest on a given night) progress through the lunar cycle, on most nights, the moon is below the horizon for part of the night. In the first half of the cycle, the moon rises before sunset and peaks before midnight, and as a result, the second part of the night has no moonlight. The opposite is true for the second part of the cycle (Fig. 1).

As the moon is orbiting the earth, the illuminated part of the lunar surface visible from the earth gradually increases and decreases in a cyclic pattern. Conventionally starting with new moon, when the visible side of the moon is dark, the proportion of the face that is illuminated increases towards a full moon when the entire moon face is lit and then decreases back towards new moon. Two points of the cycle, when exactly half of the moon is illuminated, are called first and last quarter and additional phases can be used to describe intermediate parts — waxing and waning, crescent and gibbous. These qualitative terms are referred to as the moon's primary phases and can also be represented quantitatively as a fraction of the visible moon face illuminated by the sun, ranging from 0 for a new moon to 1 for a full moon. A complete sequence of lunar phases is called a lunar month or lunation.

Moon phase is an intuitive and convenient term. It depends solely on the position of the moon in its orbit and therefore is independent of the position of the observer. For practical purposes, it is often considered constant over a single night (hourly change does not exceed 0.4%). The trajectory of the moon, however, does not follow an intuitive pattern. Not only does the moon's position change constantly, but the lunar trajectory also changes through the year and is dependent on the observer's location. For example, beyond latitude 28°, the moon never reaches the zenith. Additionally, the maximum altitude of a full moon, which impacts illumination on the ground, fluctuates with approximately a 12-month cycle, and the amplitude of these fluctuations increases with latitude

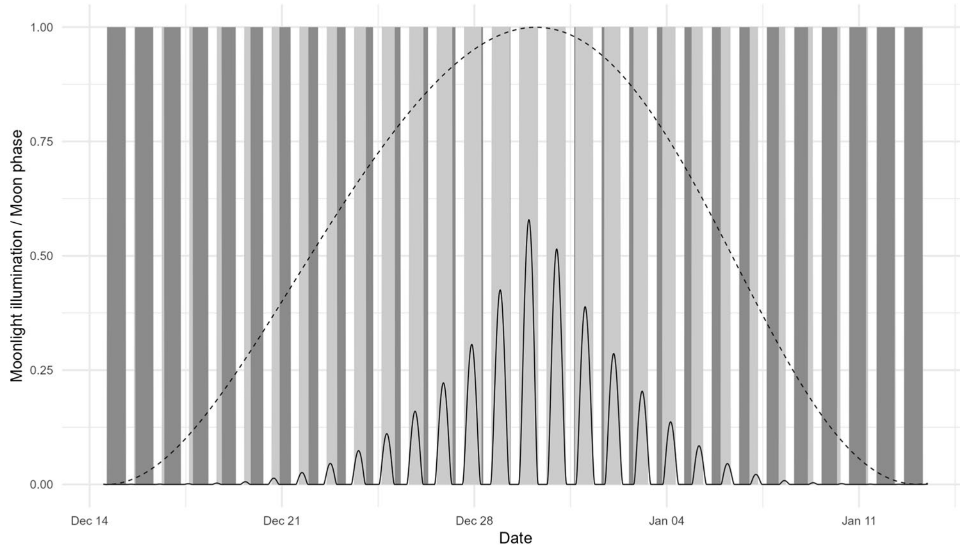


**Fig. 1** Lunar phase (dashed line) and moonlight intensity on the ground (solid line). Grey bars in the background represent night, with light grey representing parts of the night when the moon is visible and dark grey representing parts of the night when there is no moonlight. Data represent a single lunar cycle in Białowieża, Poland, in December 2020 and January 2021 (values generated using the proposed model)

(Kyba et al. 2017). As a result, while on the equator, the maximum illumination of a full moon is relatively constant over the year; as latitude increases, a full moon in winter can be significantly brighter than a full moon in summer (Fig. 2). Predicting lunar position for a given observer's location and time, therefore, requires computation using astronomical models (e.g. using the R package *suncalc* (Agafonkin and Thieurmel 2018)).

## Modelling moon illumination on the ground

The illumination by the moon on the ground can be modelled based on optical processes and mechanics of light propagation and extinction. Moonlight intensity depends predominantly on two factors: the amount of light reaching the atmosphere and how this light is subsequently refracted and absorbed (Austin et al. 1976; Krisciunas and Schaefer 1991). The amount of light reaching the atmosphere depends

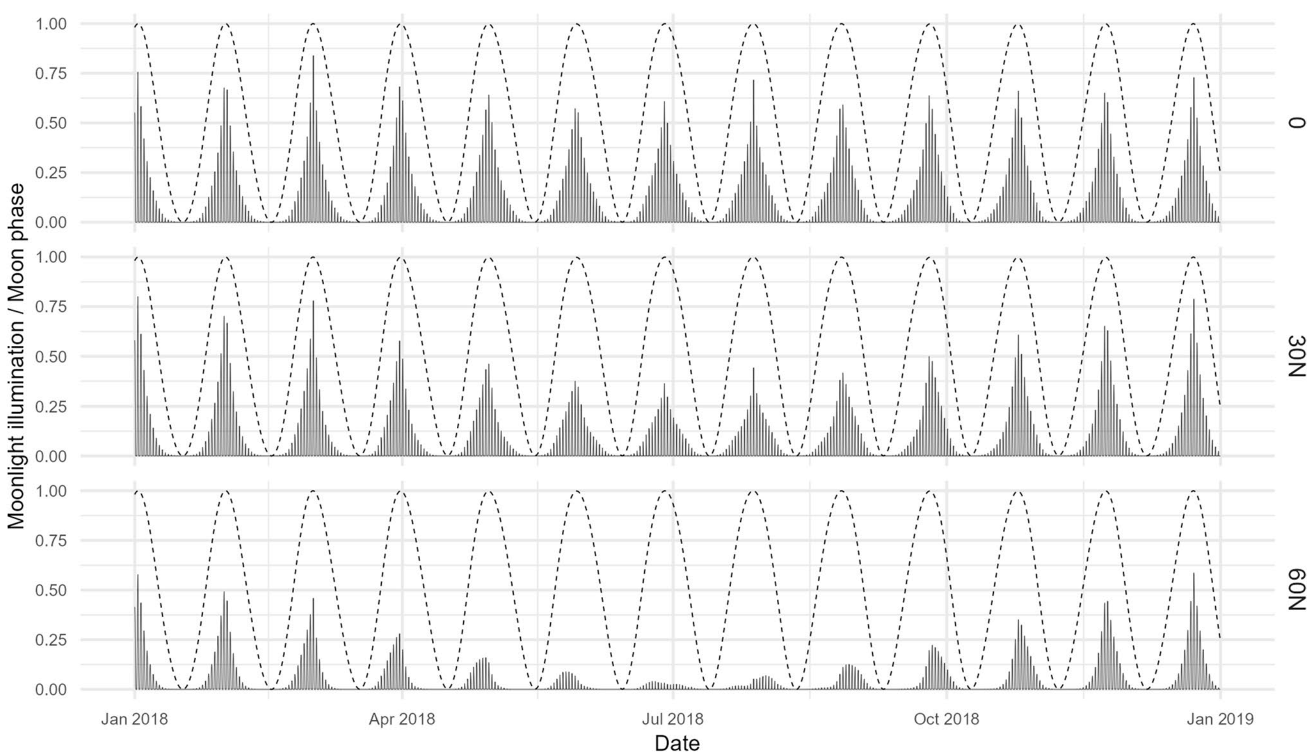


**Fig. 2** Changes in modelled moonlight intensity (solid line) in relation to moon phase (dashed line) over the year 2018 for the longitude of 0° and latitudes of 0° (top), 30° N (middle) and 60° N (bottom). As the observer moves away from the equator, changes in monthly maximum moonlight intensity increase

on the brightness of the moon face and the distance between the earth and the moon. The proportion of the light reaching the earth's surface depends on the altitude of the moon in the sky which affects atmospheric absorption and refraction, while the angle of incidence further affects illumination levels. Similar to Austin et al. (1976), the unit used is brightness relative to full moon in zenith at mean moon distance. This is a biologically sound approach as the moon is the brightest natural object in the night sky reaching maximum at approximately 0.3 lx, and starlight is relatively constant and at least two orders of magnitude dimmer than a full moon (Kyba et al. 2017). Model output can therefore be interpreted as moonlight intensity standardised to the range of 0 to 1. It can easily be converted to lux by multiplying by 0.3. For a comprehensive comparison of light levels provided by different sources and their relevance in ecological context, refer to Aulsebrook et al. (2022).

### Lunar disk brightness — moon phase and opposition effect

As mentioned previously, moon phase refers to the fraction of the illuminated moon surface that is visible from the earth. Importantly, however, the brightness of the lunar disk is not a linear function of moon phase. There is very little change in brightness for moon phases from 0 to 25%. At half-moon, when 50% of the visible surface is illuminated, the brightness is only 8% of that of a full moon. Peak brightness can be observed at full moon with nearly 40% change in a single day before and after a full moon (Fig. 3). This so-called opposition surge is caused by shadow hiding and coherent backscatter, a result of topographic irregularities and reflective properties of the lunar surface (Hapke et al. 1998). Values for disk-integrated brightness (brightness measured over the entire visible surface of a sphere, seen as a disk by the observer) at various lunar phases have been experimentally measured, and in the model, data collated from empirical lunar observations (Buratti et al. 1996) are used.

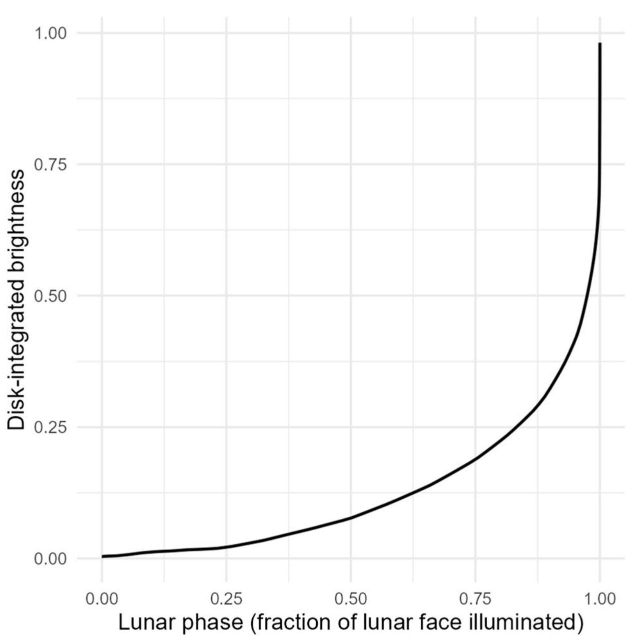


**Fig. 3** Moon phase vs measured disk-integrated brightness. Note a spike of brightness (opposition effect) visible close to full moon (after Buratti et al. 1996)

### Distance to the moon

The distance between the earth and the moon varies from 357,000 to 407,000 km, with an average of 384,400 km (Williams 2017). The propagation of light follows the inverse square relationship with distance; therefore, the difference in perceived brightness can vary by 30% between perigee (closest approach) and apogee (farthest distance) and is accounted for by a correction factor:

$$D = \left(\frac{d_1}{384400}\right)^{-2}$$

where $d_1$ is the distance between the moon and the Earth at a given time.

### Atmospheric extinction and moon visibility

Before reaching the earth's surface, light reflected by the moon must travel through the atmosphere where it is scattered, refracted and absorbed (Horvath 1993). The amount of air along the line of sight is shortest when the moon is in zenith, and light travels through the atmosphere perpendicular to the earth's surface. This shortest distance is referred to as one air mass. Distance travelled through atmosphere increases with lower moon elevations, subsequently reducing the intensity of light reaching the surface (Fig. 4). For a given elevation, the distance travelled can

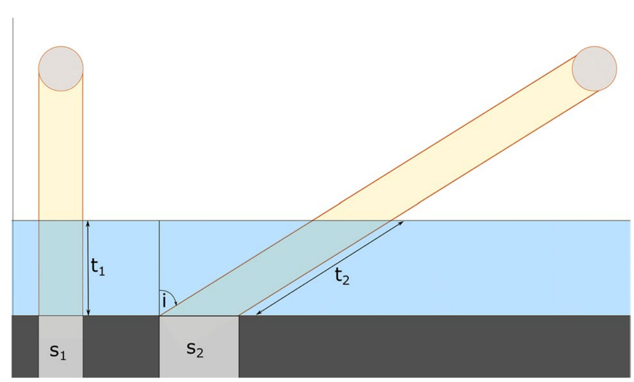


**Fig. 4** The angle of incidence (i) and the air mass thickness (*t*), both impact illumination on the ground

be calculated using astronomical equations (Meeus 1991). Compared to the zenith, light transmission is reduced to approximately 80% at a moon angle of 45° and to just 20% at an angle of 5°. At the horizon, light is travelling through 40 air masses (i.e. 40 times longer than at zenith), the maximum possible distance. Moreover, the coefficient of extinction changes with the observer's elevation above sea level as well as with season (cleaner and dryer air in winter means a lower extinction rate). For the model, a simple function to calculate atmospheric extinction (the proportion of light lost to scattering, refraction and absorption) is used based on the thickness of the atmosphere. Average extinction coefficients have been adapted for elevations of 0, 0.5, 1 and 2 km above sea level (Green 1992). An appropriate coefficient must be provided as model input. A correction factor is also used for moon visibility (0 when the moon is below the horizon, 1 when the moon is above the horizon).

### Angle of incidence

When the moon is in the zenith, the angle of incidence (i.e. the angle of rays reaching the surface, $i$) is 0, and the radiant flux of the light is scattered over the smallest surface area ($s_1$). The surface area illuminated increases with the angle of incidence, and the irradiance decreases (Fig. 4). A correction factor is therefore applied, relative to irradiance in zenith: $I = \sin(i)$.

### Final model

The model output — relative moonlight intensity — is calculated using all the correction factors explained in the previous section, following the equation:

$$M = B * D * A * v * I$$

where $M$ = relative moonlight intensity, $B$ = lunar disk brightness, $D$ = correction for the distance to the moon, $A$ = correction for atmospheric extinction, $v$ = correction for moon visibility, and $I$ = correction for the angle of incidence.

### Twilight solar illumination

The proposed model estimates lunar illuminance on the ground. It must be considered relative to other sources of light, particularly the sun. The sun is approximately 400,000 times brighter than the moon and solar light scattered in the atmosphere continues to illuminate the surface even after sunset. When no moonlight is present and without light pollution, absolute minimum light levels are reached at a solar elevation below − 18°, which is referred to as astronomical twilight. The remaining background light level, coming from the airglow and stars, is in millilux levels (Spitschan et al. 2016). At higher solar angles, the relative contribution of moonlight depends on the lunar disk brightness, the position of the moon and the solar elevation. For example, when the sun is 8° below the horizon, moonlight contributes less than 1% of total illumination at moon phase 0.2, around 15% at phase 0.75 and about 50% at full moon, while for a solar elevation of − 12°, for a moon phase of 0.5 and above, moonlight contributes nearly 100% of total illumination (Palmer and Johnsen 2015). Because of these rapid and continuous changes in total and relative illumination, no single definition of 'night' exists, and different solar elevations can be used as a cut-off point, depending on the circumstances of a particular study.

This approach, however, has limitations. In higher latitudes, the twilight is significantly longer than at the equator. Locations with latitude of 48.6° and above observe no true night around the summer solstice, which equals an all-night astronomical twilight. In locations closer to the poles in summer, the sun does not fall lower than 6° below the horizon, which means there is an all-night civil twilight (i.e. 'white nights'). While these are fairly extreme cases, the setting sun does contribute to overall illumination, and it can be of importance to both nocturnal and crepuscular animals: it defines lower and upper illumination levels, therefore affecting their activity, and should be taken into account where relevant.

A simple estimate of the intensity of scattered sunlight, based on the empirical measurements of light intensity after sunset, collected in the past to create illumination curves (MacInnis et al. 1995), is thus proposed. These illumination curves, however, present absolute values in lux, while the moonlight model provides relative values of moonlight illumination. To relate moonlight and solar twilight, a value of 0.32 lx is used as a reference for a 'mean full moon' (Kyba et al. 2017). With this assumption, sunlight intensity, total twilight illumination and relative contribution of moonlight are provided as model output.

## Verifying model accuracy

### Methods

To assess the accuracy of the model, its output was compared with empirically measured values of moonlight intensity from three independent sources — a commercially available weather station with a light logger, a light pollution monitoring station and a custom-built moonlight logger. Datasets were collected at different times and locations.

For each of the loggers, daylight records were removed, and a subset of observations was created representing night. Moonlight model was then used to predict illumination for each nocturnal data point recorded by a logger. To account for scattered solar light, an arbitrary threshold was set at solar elevation of − 11° at which measured sunlight was negligible for each of the loggers, and subsequently, measurements taken at higher solar elevations were discarded. Model predictions, as well as the lunar phase (proportion of moon illuminated), were then compared with measured values using best-fitting polynomial models, which in each case was a cubic polynomial regression fit. Models were fitted using the lm() function in base R version 4.0.2 (R Core Team 2013). Data and code are provided in GitHub repository (see Data availability statement).

### Weather station

Data were collected with a commercially available TR-74Ui Illuminance UV recorder (T&D Corporation, Matsumoto, Japan) operating in the range, 0–130 k lx, with a resolution of 0.01 lx and unspecified field of view, deployed at the Centre for Animal Research and Teaching at the University of New England, Armidale, New South Wales, Australia (30.48S, 151.64E). The facility is located on a hill above the university campus and is mostly shielded by trees, but there is artificial lighting and light pollution present from the campus and nearby town. The logger was programmed to collect measurements at 10-min intervals from June 17, 2016, to May 8, 2017, with a total of 49,832 data points, from which 21,567 night-time records were used.

### Sky Quality Meter logger

Night sky brightness data were collected as a part of a light pollution monitoring network in southern Switzerland (Osservatorio Ambientale della Svizzera Italiana 2019). Sky brightness data were collected every 30 min using a Sky Quality Meter. The monitoring station in Gnosca village (46.23 N, 9.02E) was selected because it had the lowest light pollution levels. A total of 41,377 measurements were extracted from the database (from March 2015 to April 2019), with 28,999 night-time measurements used in the model. For comparison, data were converted from apparent magnitude measured in visual mags arcsecond$^{-2}$ to luminance measured in cd m$^{-2}$ following the equation provided by the manufacturer ([value in cd m$^{-2}$] = $10.8 \times 10^4 \times 10$ ^ (− 0.4 × [value in mag arcsec$^{-2}$]).

### Custom logger

Data were collected by a custom moonlight logger built by G. Koertner and MKS (for details, see supplementary materials). Above a certain illumination level, the photoresistor was saturated, and the voltage value of 2.5 V was recorded. Saturated data points were removed from the dataset as they were uninformative. The logger was deployed at Guy Fawkes River National Park (30.07S, 152.15E) and set to record illumination every 5 min from June to October 2015. A total of 17,952 non-saturated records were obtained, with 17,093 night-time records used in the model.

## Results

For each dataset, the moonlight illumination model was significantly better at predicting illumination than the moon phase, and residual standard error was an order of magnitude smaller for model predictions (Fig. 5). The model best fitted the data from the custom-built logger where modelled predictions explained over 92% of the variance in measured light values with residual standard error of 1.4% (Table 1). This was likely because the photoresistor used in the logger had the widest field of view, and its measurements were closer to true ambient light than the other two devices. The national park site also likely had the lowest level of artificial light pollution. Interestingly, the fitted curve for the custom logger differs from the other two devices (concaves down) which could be attributed to the non-linear response curve of the photoresistor. While a response curve for the photoresistor model used in the logger was not provided by the manufacturer, the response curves of similar photoresistors are non-linear. Both the weather station and SQM loggers appeared to underestimate medium illumination values. This was explained by their narrower field of view, which in the case of SQM covered only 40° around the zenith. Since in middle latitudes the moon never actually reaches the zenith, this kind of logger should be expected to underestimate illumination except for the rare occasions when the moon is high enough in the sky to enter the field of view.

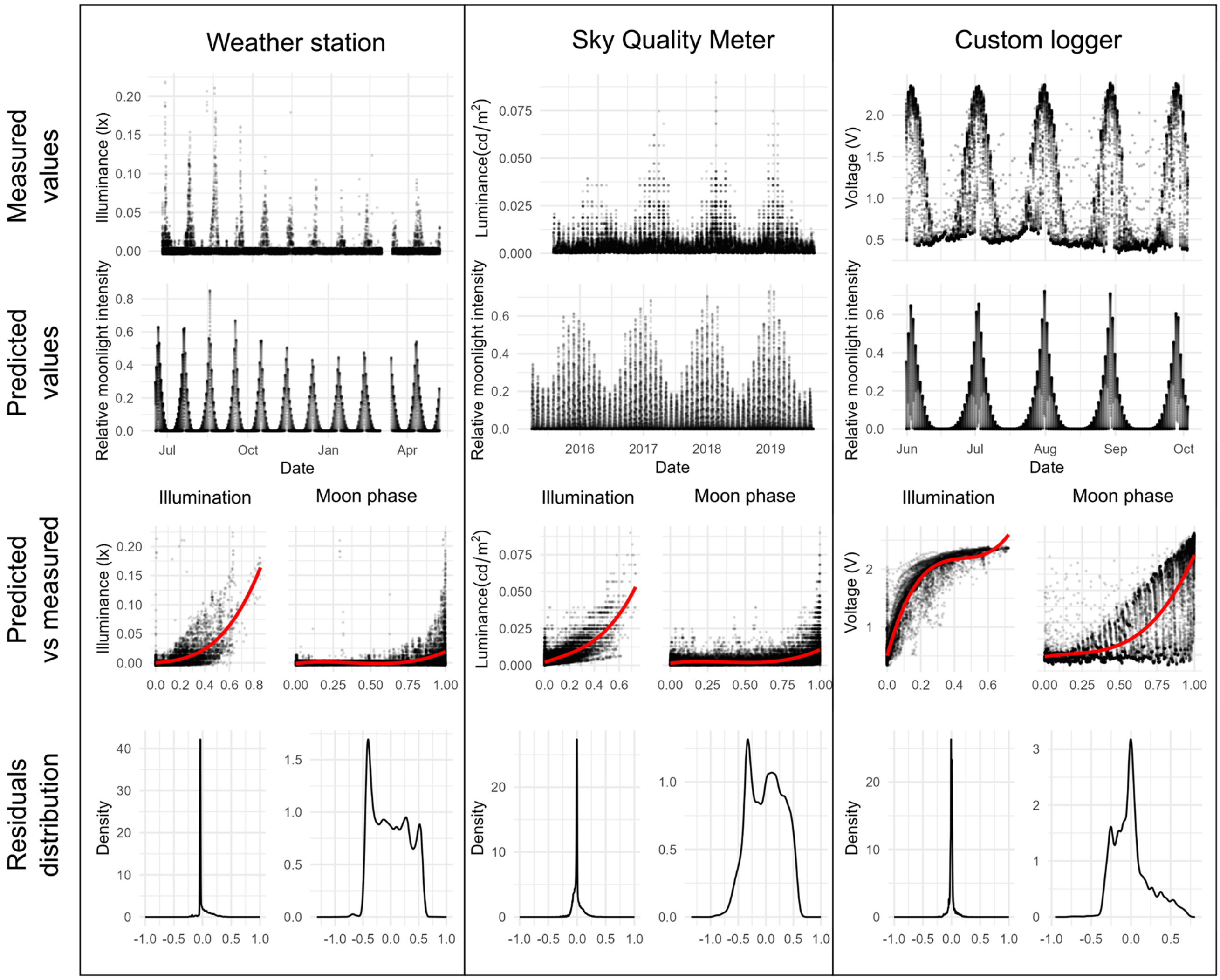


**Fig. 5** Comparison of measured (first row) and predicted (second row) illumination values, regression fits for measured illumination against modelled values and moon phase (third row) and distribution of residuals (fourth row) for each of the loggers (columns)

**Table 1** Comparison of coefficients of determination and residual standard errors for cubic polynomial regressions of empirically measured illumination values on predicted moonlight values and moon phase, for each device

| Device | Multiple $R^2$ | | Residual standard error | |
|---|---|---|---|---|
| | Moonlight model | Moon phase | Moonlight model | Moon phase |
| Weather station | 0.543 | 0.190 | 0.029 | 0.319 |
| Sky Quality Meter | 0.566 | 0.228 | 0.023 | 0.311 |
| Custom logger | 0.922 | 0.600 | 0.014 | 0.226 |

## *moonlit*: an R package for predicting moonlight intensity

As the model was effective in predicting biologically relevant changes in moonlight intensity, its core functions have been integrated into a dedicated statistical package, *moonlit*. With growing recognition of the importance of code availability and reproducibility of research, the open-source programming environment, R (R Core Team 2013), was chosen. R has become the most popular tool in ecological data analysis (Lai et al. 2019). Releasing the code as an R package should facilitate greater uptake of this new tool, while also allowing its development to be greatly simplified by using existing packages, such as *suncalc*, as dependencies. As suggested by Kyba et al. (2020), it will hopefully encourage biologists to apply more precise moonlight measures in their studies.

Following the open-source philosophy of the R project, the package *moonlit* is released under a GNU General Public License version 3, and the current version of the package is available on the project's website https://github.com/msmielak/moonlit.

Currently, the *moonlit* package contains two core functions that can be used to study the impact of moonlight on animal behaviour: (1) calculateMoonlightIntensity() which predicts moonlight intensity for a given place and time using the model described here and (2) calculateMoonlightStatistics() which calculates mean moonlight intensity values for a given night (from sunset to sunrise). For detailed documentation of each function, please refer to the project's repository.

## Ecological implications and case study

As the proposed model allows moonlight intensity to be calculated more accurately and provides higher temporal resolution than moon phase alone, it has the potential to improve studies of the impact of moonlight on animal behaviour at different temporal scales. Species might show a preference for brighter or darker nights within the moon cycle, and this has already been studied broadly, usually using moon phase as a proxy in various groups of nocturnal mammals, particularly bats, rodents and primates (Saldaña-Vázquez and Munguía-Rosas 2013; Prugh and Golden 2014). It has also been investigated in birds in the context of night singing (Dickerson et al. 2020), hunting behaviour (San-Jose et al. 2019) and flight patterns (Hedenström et al. 2022).

However, as mentioned above, changes in moon brightness throughout the lunar cycle are not linear and there are long periods, particularly around the new moon, when there is virtually no variation in moonlight intensity for many days. It is possible that some species, particularly smaller-bodied ones with higher energetic requirements, cannot cease activity for such a long period and therefore will show little to no preference for moon phases. The model, however, allows prediction not only of changes in moon brightness between nights but also changes in on-ground illumination within each night. During evenings when there is moonlight, light levels change continuously, providing an opportunity for animals to show resource selection by choosing optimal illumination levels. Activity data of a nocturnal mammal were therefore used to test for selectiveness of certain moonlight intensity levels both between and within nights.

## Methods

A dataset of 4,518 records of common brushtail possum (*Trichosurus vulpecula*) in Guy Fawkes River National Park (30.07S, 152.15E) was used. Data were collected from December 15, 2015, to December 20, 2017 as part of a predator–prey study (MKS et al., unpublished data) and represented individual detections of possums with a 5-min threshold (i.e. subsequent detections within a 5-min period were ignored) at 27 on-trail camera traps, spaced at 1-km intervals along management and fire trails in the Paddys Land section of the park.

The common brushtail possum is a medium-sized (1.2–4.5 kg) nocturnal marsupial native to Australia. In this study site, possums were exposed to a range of native and introduced mammalian predators such as wild dogs (*Canis familiaris*), red foxes (*Vulpes vulpes*), feral cats (*Felis catus*) and spotted-tailed quolls (*Dasyurus maculatus*) and likely exhibited at least some temporal partitioning of nocturnal activity in response to predation risk. This dataset was used to test the effect of illumination on possum activity, in particular if possum were more likely to be detected (a) on nights with certain moon phases and moonlight intensities, and (b) under certain illumination levels within each night.

### Nightly detection rates

To test if nightly possum activity was affected by moon phase and mean moonlight intensity, two generalized linear models with a log link function and negative binomial error distribution were built. The response variable was the number of events (independent detections) for a given night, and the explanatory variables were (a) moon phase and (b) mean moonlight intensity, respectively. Because of the length of the study, there was a long-term trend in nightly detections and data were de-trended by adding days from the beginning of the study as a random variable. Models were fitted using the R package 'glmmTMB' (Magnusson et al. 2020). The marginal coefficient of determination (a pseudo-R-squared value of fixed terms in the model) was also calculated using the r.squaredGLMM() function from the package MuMIn (Bartoń 2020).

### Possum selectivity of within-night moonlight intensity levels

To test if possums showed a preference for certain illumination levels within a night, for each possum detection, the difference between illumination levels at times of recorded activity and the mean illumination level for that night was calculated. The difference is referred to as 'moonlight preference' as it indicated selection of light levels lower (negative) or higher (positive) than the mean value for that night.

For the null hypothesis that possums show no selectivity for light levels within a night, 'moonlight preference' should, on average, equal zero. However, as mean moonlight intensity increases, so does the variance (a wider range of illumination levels is available), so fitting a standard linear model was not possible due to violation of the assumption of homoscedasticity. To mitigate this, two types of analysis were conducted. Firstly, the data were divided into groups based on mean relative moonlight levels (0–0.1, 0.1–0.2, 0.2–0.3, 0.3–0.4 and > 0.4) and each group was tested to see if moonlight preference differed from zero using a *t*-test. Secondly, the darkest nights were excluded when no preference could be shown, and the subset of nights was analysed when relative mean moon illumination was > 0.02 (528 out of 959 nights, 56% of total detections) by fitting a linear model using generalized least squares, with a varConstPower variance function (constant plus power of a variance covariate) using the gls() function in the nlme package (Pinheiro et al. 2021).

## Results

Mean moonlight intensity was a better predictor of the number of detections than moon phase (Table 2; Fig. 6). While the fixed term was statistically significant in both models, the pseudo-$R^2$ value was higher in the moonlight intensity model. This measure represents how well the data fit the regression model and can be used as an estimator for effect size. It is worth noting that while higher in the second model, it still represented a small effect size.

Mean illumination at activity was overall higher than mean illumination for the night. This 'moonlight preference' increased as nights got brighter and the distribution of moonlight preference values shifted to the right (Fig. 7a; Table 3). This was further confirmed by the fitted linear model which showed that except for the darkest nights, possums preferred illumination values higher than the mean for the night, and the preference was stronger on nights with higher mean moonlight intensity (Fig. 7b; Table 4).

**Table 2** Comparison of two negative binomial GLMs of daily detection rates using different predictors, moon phase and mean moonlight intensity

| | Moon phase | | | Moonlight intensity | | |
|---|---|---|---|---|---|---|
| Predictors | Log-Mean | CI | *P* | Log-mean | CI | P |
| (Intercept) | 1.21 | 1.10–1.31 | < 0.001 | 1.23 | 1.15–1.32 | < 0.001 |
| Explanatory variable | 0.22 | 0.06–0.37 | 0.006 | 2.32 | 1.21–3.44 | < 0.001 |
| Observations | 1092 | | | 1092 | | |
| Pseudo-$R^2$ | 0.007 | | | 0.03 | | |

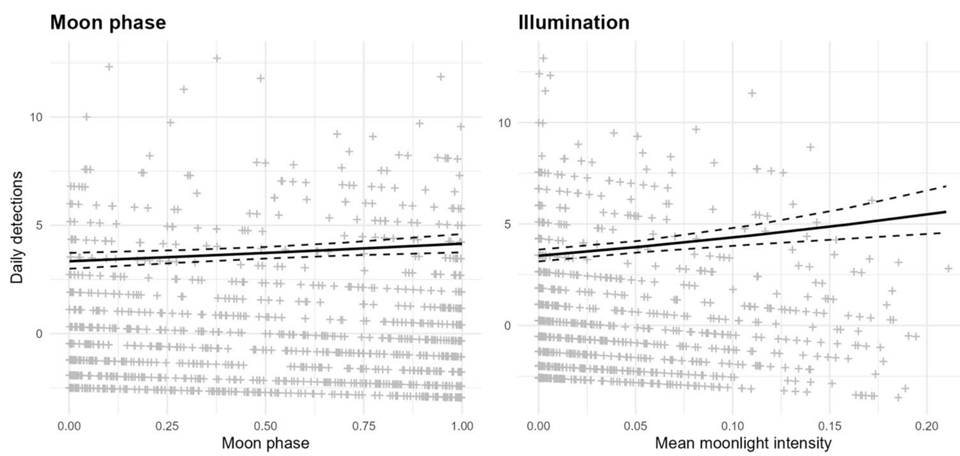


**Fig. 6** Effect plots for two negative binomial GLMs of daily detection using different predictors — moon phase or mean moonlight intensity. Grey crosses represent model residuals. Dashed lines represent the 95% confidence intervals around the predicted response (continuous line)

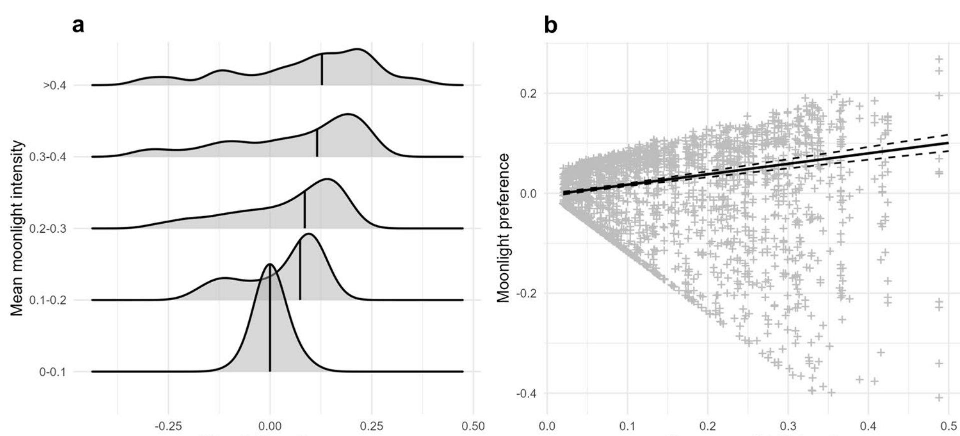


**Fig. 7** Moonlight preference at different moon brightness levels. In (**a**), the distribution of preference values is presented for various mean moonlight intensities, with vertical lines representing median values; in (**b**), the linear response (generalized least squares regression) is plotted as a function of mean moonlight intensity. Grey crosses represent model residuals, and dashed lines represent the 95% confidence interval

**Table 3** Results of *t*-test for within-night moonlight preference

| Mean moon-light level | Moonlight preference | | | |
|---|---|---|---|---|
| | Observations | Estimates | CI | *P* |
| 0–0.1 | 3093 | 0.003 | 0.002–0.004 | < 0.001 |
| 0.1–0.2 | 566 | 0.029 | 0.022–0.037 | < 0.001 |
| 0.2–0.3 | 471 | 0.043 | 0.032–0.055 | < 0.001 |
| 0.3–0.4 | 229 | 0.061 | 0.041–0.082 | < 0.001 |
| > 0.4 | 43 | 0.084 | 0.031–0.137 | 0.002 |
| Sum | 4518 | | | |

**Table 4** Results of the linear model of changes in moonlight preference with mean moonlight intensity levels

| Predictors | Moonlight preference | | |
|---|---|---|---|
| | Estimates | CI | *P* |
| (Intercept) | − 0.00 | − 0.01–0.00 | 0.001 |
| Mean moonlight intensity | 0.21 | 0.17–0.25 | < 0.001 |
| Observations | 2,370 | | |
| $R^2$ | 0.041 | | |

## Discussion

Changes in moonlight intensity are complex and depend on multiple factors. Moon phase, while convenient and generally well understood, is a poor proxy for moonlight intensity because on-ground illumination demonstrably does not show a simple correlation with moon phase. At the study location, for 85% of the moon cycle, lunar illumination on the ground does not exceed 5% of the maximum, and 50% of the maximum illumination and above is only present for approximately 0.6% of the lunar cycle. The model proposed here provides significantly better predictive power and estimates light levels with errors at least an order of magnitude lower than moon phase alone. Importantly, the model provides greater temporal precision, which can be adjusted by the user to match specific needs and allowing changes to be tracked at various temporal scales. While moon phase allows coarse comparisons of brightness between nights, it does not provide information on changes in light levels within nights, between lunar cycles or between seasons. Furthermore, the model can be used with historical data retrospectively, providing an opportunity for reanalysis of old datasets, as well as to predict future moonlight intensity values, which may be useful in experimental design and planning. It also has an advantage over stationary moonlight loggers as it can be used to predict light levels for any location which can be particularly useful when studying species on move, such as migrating birds travelling long distance.

The model is not without limitations. While moon face brightness and position can be modelled precisely, the actual intensity on the ground further varies with vegetation and cloud cover. This limitation, however, also applies to the use of moon phase. It is also relevant to empirical measurements of light intensity, as values measured by a logger in an open area might differ significantly from simultaneous values measured under the canopy. It can be mitigated by using cloud cover and vegetation structure as covariables in analysis. Global cloud cover estimates can be obtained, for example, from the NCEP/NCAR Reanalysis 1 project, accessible with an R package RNCEP (Kemp et al. 2020), while different vegetation structure datasets are available on a global and regional scale. The advantage of including them in statistical analysis in interaction terms with moonlight rather than incorporating them directly in moonlight model output is that both cloud cover and vegetation structure affect not only illumination levels, but also likely have a direct impact on animal activity as well as indirect impacts through other environmental variables. For example, temperature drops more slowly on cloudy nights because some of the earth's radiant heat is reflected back towards the ground, trees reduce wind speed, etc. In an area with complex topography, such as steep slopes, gullies and gorges, it is possible to further improve model predictions by including topographic corrections to moon visibility. Visibility analysis can be performed using a digital elevation model, and as the model already includes the position of the moon in the sky, a correction can be applied for times when the moon is above the horizon but obscured by the terrain. This functionality will be introduced in future versions of the model.

As shown in the common brushtail possum case study, modelled moonlight intensity is a better predictor of possum activity levels than moon phase. Even at the temporal scale of a single night, mean modelled brightness performed better than moon phase. This was expected as it has been demonstrated both theoretically and empirically that moon phase is a poor proxy for light intensity as it overestimates light level changes for most of the lunar cycle and underestimates changes in light levels around full moon. Moreover, moon phase does not account for changes in maximum moon brightness between lunar cycles. It is unlikely that a medium-sized mammal like a common brushtail possum can reduce or cease activity for an entire night, let alone the multiple nights required for large changes in mean brightness at certain times of the lunar cycle and year. Moreover, other environmental factors such as temperature, wind and rainfall have a significant impact on possum activity (van den Oord et al. 1995; Herbert and Lewis 1999). This is likely why while significantly better than moon phase, moonlight intensity only predicts a small fraction of the variance in detection rates, suggesting that more complex models incorporating other environmental factors are needed to better understand drivers of possum behaviour.

For species that need to remain active on most or all nights, the choice to be active can be achieved not between nights but rather within a single night. Each night, moonlight intensity oscillates between a nightly minimum (usually equal to zero when the moon is below the horizon) and a nightly maximum. This model provides a tool to detect patterns of preference when animals select illumination levels that are low or high relative to the mean value on a given night. In the example provided, illumination values at the time of activity ('selected' light levels) were compared with the mean nightly illumination value ('available' light levels), and a clear preference was detected for above-average illumination levels. This has hardly been tested before on wild animals as most studies use moon phase as the measure of moonlight intensity, which does not allow analysis of changes in moonlight within a night.

There have been attempts to mitigate these limitations in ecological studies. For example, using day of the lunar cycle gives an indication if light was present early (waxing) or late (waning) in the night. Another way is to combine moon visibility over the horizon with moon phase (Stokes et al. 2001; Huck et al. 2016; Palmer et al. 2017). Within-night selectivity, however, is rarely considered, and few studies have attempted to assess it. The study by Perea et al. (2011) is worth mentioning as the authors used linear interpolation between the lowest (moonrise) and highest (lunar noon) moonlight intensity to estimate changes in relative brightness values for each night. While changes in brightness are not linearly correlated with the position of the moon, this method allowed them to determine that rodents showed within-night preferences for relatively lower light levels. Another study (Pratas-Santiago et al. 2017) incorporated moon transit times in their model and also found that prey species avoided the brightest parts of the night. For insectivorous bats, however, differences in moon phase rather than changes in moon brightness within a single night appeared to affect activity patterns (Appel et al. 2017). Even more precise methods to estimate moonlight intensity were applied in some studies, using more complex formulas (Upham and Hafner 2013; Pajot et al. 2021), but these are rare. In one of the very few studies where measurements of illumination were collected using a precise light meter, Fernández-Duque et al. (2010) found that nocturnal activity of Azara's owl monkeys (*Aotus azarae*) increased with greater moonlight illumination and abruptly stopped during total lunar eclipse. In this case, moonlight patterns were shown, like the case study presented, to modulate the circadian rhythmicity. Similarly, European nightjars (*Caprimulgus europaeus*) were found to increase nocturnal activity with both moon phase and lunar altitude, showing that their activity was not only highest on brightest nights, but also focused around the brightest part of each night (Evens et al. 2020).

It is also worth noting that light levels should be considered in a wider context of the lunar cycle. Changes in lunar illumination are cyclical and predictable and depending if the moon is waxing or waning, the same light level can be followed by either an increase or a decrease in nightly average illumination. This means that animals can anticipate upcoming changes in predation risk and/or foraging opportunities and adjust timing of their activity accordingly. Study on Allenby's gerbils (*Gerbilus andersoni allenbyi*) found that at similar light levels, gerbils spent on approximately 2.5 times more time foraging in waning than in waxing moon, suggesting that following a period of high risk (full moon), gerbils needed to increase foraging to compensate for loss in state (Kotler et al. 2010).

While there is no 'one-size-fits-all' solution to studying the ecological impacts of moonlight, including moonlight intensity (measured or predicted with a model such as the one presented here) provides an opportunity to not only use a more biologically relevant moonlight proxy but also to answer more complex research questions. A tool and examples of how it can be used are provided here but as it is adopted, other applications will be found, as both new and historical data are analysed.

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**Data availability** Code and data used for model testing are available in the author's GitHub repository (https://github.com/msmielak/moonlit).

## Declarations

**Ethics approval** Common brushtail possum activity data were collected during a study carried out under the auspices of the University of New England Animal Ethics Committee, permit AEC14-079. Data collection methods followed all applicable guidelines set out in the Australian Code for the Care and Use of Animals for Scientific Purposes.

**Conflict of interest** The author declares no competing interests.

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