RESEARCH ARTICLE

External environmental conditions impact nocturnal activity levels in proboscis monkeys (*Nasalis larvatus*) living in Sabah, Malaysia

Sophie J. Kooros[1,2] | Benoit Goossens[2,3,4] | Elisabeth H. M. Sterck[1,5] |
Richard Kenderdine[6] | Peter T. Malim[4†] | Diana A. Ramirez Saldivar[2,4‡] |
Danica J. Stark[2,7]

[1]Animal Behaviour and Cognition, Department of Biology, Utrecht University, Utrecht, The Netherlands

[2]c/o Sabah Wildlife Department, Danau Girang Field Centre, Kota Kinabalu, Sabah, Malaysia

[3]Organisms and Environment Division, School of Biosciences, Cardiff University, Cardiff, UK

[4]Sabah Wildlife Department, Kota Kinabalu, Sabah, Malaysia

[5]Animal Science Department, Biomedical Primate Research Centre, Rijswijk, The Netherlands

[6]Kenderdine Maths and Statistics, Bowral, New South Wales, Australia

[7]Wilder Institute/Calgary Zoo, Calgary, Alberta, Canada

Correspondence
Sophie Jane Kooros, Animal Behaviour and Cognition, Department of Biology, Utrecht University, Utrecht 3584CH, The Netherlands.
Email: sophkooros@gmail.com

Benoit Goossens, c/o Sabah Wildlife Department, Danau Girang Field Centre, Kota Kinabalu, Sabah, Malaysia.
Email: goossensbr@cardiff.ac.uk

Abstract

Recently, several diurnal nonhuman anthropoids have been identified displaying varying degrees of nocturnal activity, which can be influenced by activity "masking effects"—external events or conditions that suppress or trigger activity, temporarily altering normal activity patterns. Environmental masking characteristics include nocturnal temperature, rainfall, cloud cover, and moon brightness. Similarly, other ecological characteristics, including proximity to humans and predators and daytime activity, may also trigger or suppress nocturnal activity. Understanding the effects of external conditions on activity patterns is pertinent to effective species conservation. We investigated the presence of nocturnal activity and the influence of masking effects on the level of nocturnal activity displayed by wild proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysian Borneo. Dual-axis accelerometers were attached by collar to six male proboscis monkeys from different one-male, multi-female groups to record activity continuously (165–401 days each). We measured the monkeys' nocturnal and diurnal activity levels and investigated the effects of seven potential masking effects. Nocturnal activity was much lower than diurnal activity. Still, proboscis monkeys did display varying levels of nocturnal activity. Generalized linear mixed models identified higher nocturnal activity in the study individuals during nights with cooler temperatures, higher rainfall, and after higher diurnal activity. These three masking effects affected nocturnal activity levels during the observation period that informed our model, although they did not predict nocturnal activity outside of this period. While the generalizability of these results

remains uncertain, this study highlights the utility of accelerometers in identifying activity patterns and masking effects that create variability in these patterns.

KEYWORDS
accelerometer, activity pattern, diurnal primates, masking effects, nocturnal activity, proboscis monkeys

1 | INTRODUCTION

Most animals display regular diel activity patterns, meaning that they are routinely active during certain spans of the approximately 24-hour circadian period and not others (Fernández-Duque, 2003; Muñoz-Delgado et al., 2004). With regular activity patterns, behavior and physiology become adapted to the cyclical changes in the circadian period, thereby optimizing survival and reproductive fitness (Bartness & Albers, 2000; Krop-Benesch et al., 2013). The most common diel activity patterns exhibited by primate species are diurnal and nocturnal activity patterns, followed by cathemeral (activity occurring in bouts over the entire 24-h period), and crepuscular (active periods at dusk and dawn) activity patterns (Bray et al., 2017; Campera et al., 2019; Eppley & Donati, 2019; Fernández-Duque et al., 2010; Tattersall, 1987). Quantifying diel activity patterns and understanding activity pattern flexibility in primate species is pertinent to their conservation in a world where environments are being altered by anthropogenic disturbances such as habitat loss, artificial light changes, climate change, and human activities (Frey et al., 2017; Nowak & Lee, 2013). These anthropogenic changes may interrupt and change the timing of important activities like foraging, sleep, and antipredator strategies, which may have implications for individual survival and fitness (Costantini et al., 2017; Frey et al., 2017; Nowak & Lee, 2013).

In mammals, including primates, diel activity patterns are generally fixed, arising across an evolutionary timescale and result from internal and external mechanisms (Aschoff et al., 1982; Fernández-Duque, 2003; Gervasi et al., 2006). An internal clock acts as a pacemaker timing activity each day (Bartness & Albers, 2000). This internal clock is synchronized with, or entrained to, the circadian rhythm by external cues in the environment known as "zeitgebers" (Aschoff et al., 1982; Aschoff & von Goetz, 1988; Fernández-Duque, 2003). In general, the highly predictable daily light-dark cycle acts as the major zeitgeber on activity patterns (Ankel-Simons & Rasmussen, 2008; Muñoz-Delgado et al., 2004; Sharma & Chandrashekaran, 2005). However, factors such as temperature and social cues are examples of other potential zeitgebers (Aschoff et al., 1982).

While set internal clocks that are synchronized by external zeitgebers regulate activity patterns in primate species, activity patterns can have some flexibility in reaction to other external cues, which are known as temporary "masking effects" (Fernández-Duque, 2003; Nowak & Lee, 2013). These reactions to external cues help buffer an individual against changes in their environment through behavioral flexibility (Cristóbal-Azkarate & Arroyo-Rodríguez, 2007;

Jaman & Huffman, 2013; Nowak & Lee, 2013). External cues mask activity patterns by either triggering or suppressing activity because of conditions or events requiring the individual's immediate reaction (Aschoff, 1989; Aschoff et al., 1982). Some abiotic factors which can mask normal activity patterns include weather events (e.g. rain, wind, storms), temperature and moon brightness whereas some biotic factors include food availability, human presence, predator presence, sympatric species presence and intraspecific social behavior (Anderson, 2000; Gander & Moore-Ede, 1983; Mochida & Nishikawa, 2014; Nishikawa & Mochida, 2010; Pruetz, 2018; Silva et al., 2014). Understanding the degree to which a species' behavior is flexible can help predict how species will adapt to environments increasingly affected by humans, information that is critical to conservation efforts (Jaman & Huffman, 2013).

Anthropoid primates are widely regarded as solely diurnal primates, with the exception of the cathemeral and nocturnal owl monkeys (genus *Aotus*) of Central and South America (Fernández-Duque et al., 2010; Fernández-Duque & Erkert, 2006). As anthropoid primates have specialized diurnal vision, activity at night may be associated with higher risks because of poor nocturnal eyesight (Fruth et al., 2018; Kay & Kirk, 2000; Kirk & Kay, 2004; Santini et al., 2015; Van Schaik & Griffiths, 1996). Therefore, previous identification of nocturnal activity in some diurnal anthropoids is surprising and suggests further behavioral flexibility in these species than previously thought (Isbell et al., 2017). Varying degrees of nocturnal activity have been identified in anthropoids including chimpanzees (*Pan troglodytes*) (Pruetz, 2018; Tagg et al., 2018; Zamma, 2014), vervet monkeys (*Chlorocebus pygerythrus*) (Isbell et al., 2017), chacma baboons (*Papio ursinus*) (Ayers et al., 2020), olive baboons (*Papio anubis*) (Isbell et al., 2017), rhesus macaques (*Macaca mulatta*) (Vessey, 1973), Japanese macaques (*Macaca fuscata*) (Mochida & Nishikawa, 2014; Nishikawa & Mochida, 2010) and Guizhou snub-nosed monkeys (*Rhinopithecus brelichi*) (Tan et al., 2013).

Like other anthropoid primates, proboscis monkeys appear to be a diurnal species (Matsuda et al., 2009b). Proboscis monkeys (*Nasalis larvatus*) are folivore-frugivore, arboreal colobine anthropoid primates endemic to Borneo (Harding, 2015; Matsuda et al., 2008; Stark et al., 2018; Yeager, 1989). They typically live in one-male, multi-female groups (one male, several females, and their offspring), or all-male groups (Murai et al., 2007). Proboscis monkeys feed across the day, with most feeding occurring between 14:00 and 18:00 h and peak feeding between 15:00 and 17:00 h (Matsuda et al., 2009a, 2014). Proboscis monkey groups settle into sleeping sites, usually within 50 m of rivers, before sunset (Bernard et al., 2011; Matsuda

et al., 2014, 2009b; Thiry et al., 2016). A previous study identified that proboscis monkey groups were in the same sleeping site between 06:00 and 06:30 h as they had been observed settling into the evening before, further suggesting they are a solely diurnal species (Matsuda et al., 2014, 2009b).

Proboscis monkeys are listed as Endangered in the IUCN Red List and inhabit some of the most quickly degrading and fragmented habitats in Borneo (Meijaard & Nijman, 2000; Meijaard & Sheil, 2007; Sha et al., 2008; Toulec et al., 2020). Their habitats are impacted by illegal logging, fire, swamp to plantation conversion, increased tourism activity, agriculture, and aquaculture (Bismark, 2010; Boonratana, 2013; Sha et al., 2008; Stark et al., 2018; Toulec et al., 2020). Additionally, examples of proboscis monkey behavior being affected by human activity already exist. For example, they avoid sleeping sites close to tourism accommodation and boat landing activity (Boonratana, 2013). Therefore, understanding behavioral flexibility and how proboscis monkeys react to changes in their environment is critical to understanding how they live and will continue to do so in human-affected environments (Jaman & Huffman, 2013). However, little research on their nocturnal activity exists. Proboscis monkeys inhabit mangroves, riverine forests, and peat swamps, which are inherently challenging terrains for humans to follow monkeys, meaning that no studies focusing on nocturnal activity have been published to date (Kawabe & Mano, 1972; Matsuda et al., 2008).

Recent advances in accelerometer technologies have allowed circumvention of the difficulties faced by challenging observational environments. These devices allow for long-term, continuous data collection, that can give comprehensive insight into activity patterns across the 24-h circadian period in species and individuals (Zenone et al., 2020). Accelerometers, also known as activity sensors, are small devices (usually weighing a few grams) that register body movements by measuring acceleration (the rate of change in velocity) using a piezoelectric sensor on one to three axes (Brown et al., 2012, 2013; Costantini et al., 2017). When used on individuals, accelerometers can identify active behaviors such as locomotion, full-body movements, feeding and grooming (Papailiou et al., 2008; Starr et al., 2012) as well as inactive behaviors such as sleep, rest, and alertness (Starr et al., 2012).

In this study, we used accelerometers to investigate activity patterns in proboscis monkeys living in the Lower Kinabatangan Floodplain, Sabah, Malaysia. Specifically, we quantified the degree of nocturnal activity and the impact of several external cues on the nocturnal activity displayed by six male proboscis monkeys from different one-male, multi-female groups. The proboscis monkeys living in Sabah are the largest known population of proboscis monkeys, and only 15% of the monkeys in Sabah are living in fully protected areas (Sha et al., 2008). Therefore, this population remains of high conservation importance. We investigated the following six expectations.

1. We expected that proboscis monkeys would display very low levels of activity during the night compared to the day. Previous studies have identified that proboscis monkeys remain at the same sleeping sites from evening until the following morning, which suggests a diurnal activity pattern (Matsuda et al., 2009b, 2014). Furthermore, proboscis monkeys' diurnal-specialized eye morphology likely limits their nocturnal activity (Anderson, 2000; Kirk & Kay, 2004).

2. We expected that proboscis monkeys' nocturnal activity would exhibit flexibility and respond to weather conditions, as these would mask their diurnal activity patterns by disturbing sleep (Anderson, 2000). Specifically, we expected that proboscis monkeys would show more nocturnal activity in response to higher temperatures and higher rainfall (positive masking) (Anderson, 2000; Ayers et al., 2020; Pruetz, 2018; Tagg et al., 2018). Temperature and rainfall mask nocturnal activity in some anthropoid primates, likely because of thermoregulatory stress and sleep disturbance (Ayers et al., 2020; Muñoz-Delgado et al., 2004; Tagg et al., 2018).

3. We expected that brighter nights would trigger proboscis monkeys' nocturnal activity (positively masking activity patterns), influenced by both cloud cover and/or moon brightness (Aschoff & von Goetz, 1988). Thus, activity would occur during bright nights. Moonlight is a common mask of activity patterns in many anthropoid species, including chacma baboons, and rhesus macaques (Ayers et al., 2020; Vessey, 1973). Because of increased light, brighter moonlight conditions may allow anthropoids to extend daytime activity into the night (Anderson, 1984, 2000). Alternatively, sleep may be more often disturbed by sympatric species, predators, and humans during brighter moonlight, causing activity to be triggered (Anderson, 1984, 2000). Sunda clouded leopards (Neofelis diardi) are a predator of proboscis monkeys that may be more active during bright moonlight, potentially disturbing proboscis monkeys (Ampeng et al., 2018; Matsuda et al., 2008)

4. We expected that smaller distances to plantations would trigger proboscis monkeys' activity (positively masking activity patterns). Nights spent near plantations may be associated with higher human density, which could disrupt sleep or cause increased vigilance in proboscis monkeys (Gaynor et al., 2018; Leasor & Macgregor, 2004; Muñoz-Delgado et al., 2018; Tagg et al., 2018). Proboscis monkeys avoid sleeping sites near high human activity, which could indicate increased stress in the presence of humans and, thus, presence of nocturnal activity around plantations (Boonratana, 2013).

5. We expected that proboscis monkeys' activity would be triggered (positively masked) by the greater the distance that groups spent the night from rivers. Proboscis monkeys generally spend nights within 50 m of rivers and nights spent inland are uncommon for proboscis monkeys, potentially indicating increased external disturbance and consequently higher activity (Bernard et al., 2011; Matsuda et al., 2010; Thiry et al., 2016).

6. Lastly, we expected that high daytime activity levels would negatively mask nocturnal activity. Therefore, proboscis monkeys would be less active at night following days of high activity as reported in chimpanzees (Tagg et al., 2018).

2 | METHODS

2.1 | Study site and subjects

Six male proboscis monkeys from different one-male, multi-female groups were fitted with Lotek Biotrack GSM WildCellSD collars which weighed <2% of the individual's body weight (LotekWireless, 2011; Stark, 2018; Stark et al., 2017). These individuals were living in the Lower Kinabatangan Floodplain in Sabah, Malaysian Borneo (5°35′ N and 118°20′ E) and were studied between August 2011 and May 2015 (Stark, 2018). Individuals were collared more than 2 km apart or on different sides of the Kinabatangan River to limit overlap between home ranges (Stark, 2018). During the data collection period, average monthly minimum temperatures ranged between 23°C and 25°C, average monthly maximum temperatures ranged between 28°C and 36°C and average annual rainfall was 3004 mm (Stark, 2018). The Lower Kinabatangan Floodplain is approximately 280,000 hectares and has 42,000 hectares of protected land, including the Lower Kinabatangan Wildlife Sanctuary (Goossens et al., 2005; Hai et al., 2011). Collared individuals were living in lowland dry forest and seasonally flooded forest.

2.2 | Data collection

The Lotek Biotrack GSM WildCellSD collars collected GPS and accelerometer data for 165–401 days per individual (Table 1). Data collection ended for each individual either after the collar fell off at a pre-programmed time (after either 12 or 18 months), if the battery died prematurely or if the collar malfunctioned (Stark, 2018; Stark et al., 2017). The collars were programmed to collect GPS fixes hourly from 05:00 to 19:00 h (Stark, 2018). The accelerometer measured activity continuously, 24-h a day by the accelerometer on two axes (x and y) (LotekWireless, 2011). Every 5 min, the accelerometers recorded the average activity values from the previous 5 min per axis. The accelerometers were located on the back of an individual's neck. The x-axis recorded movement along the spine and y-axis recorded side-to-side movement.

All data preparation and further analysis were conducted using R (version 3.5.1) and Stata (version 8.2) (R Core Team, 2013; StataCorp, 2003). We divided the activity data set into day and night data sets. We decided to remove all twilight periods (civil, nautical, and astronomical twilight) from the data to incorporate only nocturnal and diurnal activity in analyses and not crepuscular activity. By removing civil twilight, nautical twilight and astronomical twilight, periods excluded were from when the sun was 0° below the horizon to when night began and the sun was 18° below the horizon (Bikos & Kher, n.d.). We organized the data into day and night data sets on R using the suncalc package and the "getSunlightTimes" function (Thieurmel & Elmarhraoui, 2019). During this study, day began between 05:55 and 06:35 h, and ended between 17:40 and 18:25 h. Night began between 19:05 and 19:50 h, and ended between 04:30 and 05:10 h.

2.3 | Activity data background

Acceleration was used as a proxy for animal activity. Acceleration is defined as the rate of change in velocity, referring to how quickly something is speeding up, slowing down, and/or whether something is changing direction. The Lotek accelerometer measured acceleration four times a second (4 Hz) on each axis separately (x and y) (LotekWireless, 2011). The sensor calculated the difference in acceleration between each time step and recorded this as activity per axis. Every 5 min, the collar saved the average activity value from the previous 5 min for each axis, together with the time and date. This accelerometer, which has an 8-bit encoder, encoded the analogue voltages generated by the sensor into a computer-readable (digital) value, taking a value of $2^8 = 256$ (or values from 0 to 255). This means that the accelerometer recorded 0 as no acceleration or activity, to 255 as maximum acceleration or highest measurable activity per axis. We combined the values from the x-axis

TABLE 1 Details on the six male proboscis monkeys collared in the Lower Kinabatangan Floodplain between 2011 and 2015, including date collared, number of days collared, and average nocturnal and diurnal activity values with standard deviation (SD) per individual and for the group overall

Individual	Date collared	Total 24-hour periods (days) collared	Average activity per night ± SD	Average activity per day ± SD
1	11/08/2011	364	1.86 ± 1.57	39.10 ± 7.85
2	16/05/2012	253	4.62 ± 4.28	54.29 ± 14.77
3	18/05/2012	165	1.17 ± 1.54	32.85 ± 5.82
4	24/09/2012	222	1.63 ± 1.14	40.09 ± 7.94
5	03/09/2013	366	3.09 ± 2.74	48.41 ± 15.27
6	28/04/2014	401	1.98 ± 1.86	44.60 ± 9.02
Group	–	177	2.42 ± 2.59	43.85 ± 12.52

Note: Activity values were unitless and could vary from 0 (no activity) to 510 (highest measurable activity).

and the y-axis, therefore, activity could vary from 0 (*no activity*) to 510 (*maximum activity*).

This accelerometer isolates dynamic acceleration without static acceleration, measurement noise and measurement bias by taking the difference in acceleration between two consecutive measurements. Since the orientation does not change significantly during the time interval between two measurements (0.25 s), and the bias is a constant, static acceleration and measurement bias cancel out, leaving only the dynamic acceleration and the measurement noise. Furthermore, the signal-to-noise ratio is increased by the square root of the number of measurements over which the averaging is performed (5 min). In our case, 4 Hz × 5 min × 60 s/minute = 1200 measurements per axis and so we increased the signal-to-noise ratio by a factor of approximately 35. Therefore, the measurement noise should be small compared to the dynamic acceleration, and this term can be considered negligible.

To measure activity per day or per night, we used the average accelerometer output during each day or night (Ayers et al., 2020; Erkert & Kappeler, 2004). Therefore, activity per day or night was measured as average activity and could range from 0 as no activity to 510 as the highest measurable activity per day or night. We focused on activity generally and not on specific behaviors. This is because the accelerometer records 5-min average values, which makes behavioral characterization difficult as it requires a higher temporal resolution (Petroelje et al., 2020).

2.4 | Masks of activity

We investigated the effects of seven factors that may mask any nocturnal activity in proboscis monkey individuals. These were temperature, rainfall, cloud cover, moon brightness, nightly distance from major waterways and from plantations, and daytime activity levels. Daytime activity levels were calculated as described in Section 2.4.

2.4.1 | Temperature, rainfall, and cloud cover

Temperature, rainfall, and cloud cover data were generated and adapted from the ERA5 reanalysis data set provided by the Copernicus Climate Change Service (Hersbach et al., 2019). The ERA5 reanalysis data set combines 12 hourly observations with model data across the entire globe to produce hourly estimates of atmospheric, land and oceanic conditions using the 4D-Var assimilation method (Hersbach et al., 2019; Tetzner et al., 2019). Temperature at 2 m, measured as the air temperature at 2 m above land, was measured in degrees Kelvin and converted to one average value of temperature per night in degrees Celsius (Hersbach et al., 2019). Rainfall was measured as the total amount of precipitation accumulated over an hour in meters, which was converted into total rainfall in mm/per night (Hersbach et al., 2019). Cloud cover was measured as the proportion of a grid box that is covered by cloud (from 0 [*no cloud*] to 1 [*no clear sky*]) (Hersbach et al., 2019). The data set has a resolution of 0.25° × 0.25° and all data were generated for the coordinates 5°18′ N–5°42′ N and 117°54′ E–118°33′ E and factored in night length (Hersbach et al., 2019).

2.4.2 | Moon brightness

Moon brightness was derived by multiplying the fraction of the moon visible on one night with the time the moon was above the horizon. Both the fraction of the moon visible and the time the moon was above the horizon were generated using the "getMoonIllumination" and "getMoonPosition" functions from the *suncalc* package in R for the coordinates of the Danau Girang Field Centre (located at 5°24′48.23″ N and 118°2′17.94″ E) (Thieurmel & Elmarhraoui, 2019). Moon fraction visible was recorded as a fraction between 0.0 and 1.0 per night, where 0.0 is a new moon and 1.0 is a full moon and moon position was recorded as the altitude of the moon above/below the horizon (Thieurmel & Elmarhraoui, 2019). We converted moon position to a binary form, where 1 indicated the moon was above the horizon and 0 was below the horizon. Moon position data were matched to every activity data point. For each night, the total proportion of 1's was calculated to give an overall fraction of how long the moon was above the horizon within one night.

We used the following formula to calculate moon brightness (Formula 1):

$$\text{brightness} = (\phi \cdot t_{up}), \tag{1}$$

where ϕ is the moon fraction and t_{up} is a fraction of how long the moon was above the horizon during the night.

2.4.3 | Distance from rivers and major waterways

The collars collected GPS locations every hour from 05:00 to 19:00 h. We used the 05:00 h GPS fix to assess the distance (m) between the sleeping site and major waterways such as rivers (distance from water) and from plantations (distance from plantations) during the previous night (Stark, 2018). There was little difference between the 19:00 and 05:00 h (<10 m) GPS fixes, thus the 05:00 h fix was selected.

2.5 | Statistical analysis

Activity levels across the entire 24-h period were visualized per individual using R package ggplot2 (Wickham, 2016). Nocturnal and diurnal activity were summarized with average and standard deviation values per individual and overall. Twilight data were not included in this summary or in the further analysis to focus on

nocturnal and diurnal activity only. Generalized linear mixed models (GLMM) were fit to the nocturnal activity data to identify potential masking effects on nocturnal activity presence. Stata software was used to fit gamma family GLMMs, utilizing the inverse link function, and maximum likelihood estimation (StataCorp, 2003). We used the robust standard errors option to estimate the variance. This allows for nonindependence of observations within individuals but independence between individuals. We considered gamma GLMMs as a good fit for this data set because the nocturnal activity data were right-skewed.

The nocturnal activity data were split into a "fit" data set (900 observations) and a "test" data set (829 observations). The data were allocated proportionally among the individuals, meaning that approximately the first half of the observations of each individual were assigned to the "fit" data set and the remainder to the "test" data set. The data were not split randomly because of data correlation within each individual's data (see Supporting Information: Figure S1). The individuals showed no evident patterns, except for individual 2 who showed a sudden elevation on average nocturnal activity (see Supporting Information: Figure S1). Plotting the potential masking effects over the observation time did not show any similar trends. This raised questions about the validity of the accelerometer data for individual 2, as one of the alternative explanations of a sudden elevation in activity values may be that the Lotek collar had come loose. We therefore decided to exclude this individual from the data set and subsequent GLMMs. With all observations from individual 2 omitted, 781 observations remained in the "fit" data set and 729 in the "test" data set.

We used an iterative approach to identify masking effects by including different variables as predictors when fitting the model with the "fit" data set (Table 2). The possible variables were temperature, rainfall, moon brightness, distance from waterways, distance from plantations, and diurnal activity values. The log of rainfall, and the squared values of cloud cover were used instead of the raw rainfall and raw cloud cover data to obtain a better spread in the data. We then used each fitted model to predict the nocturnal activity using the "fit" data set. To determine the performance of the model, we used the deviance values from the model. We used a reduction of deviance to determine whether additional variables should be included (one at a time). A lower deviance score indicates a better fitting model, where a model with a deviance of 0 indicates a perfect fit. If there was little or no reduction in deviance, or if the p-value of the predictor was larger than 0.05, the variable was not included in the model (Table 2). Based on deviance values, it initially appeared that model 8 was the best model (Table 2). However, on further inspection of the "distance from water" data, which identified extreme outliers, the inclusion of this variable was questioned. Because of the uncertainty combined with the low number of individuals in the model, we decided to not include this variable in the model. As such, model 4 was chosen as the final model (Table 2). The final model was validated by examining the distribution of the Anscombe residuals, and the scatter plot of deviance residuals against the linear predictor (see Supporting Information: Figures S2 and S3).

The final model was used to predict the nocturnal activity using the "test" data set (see Supporting Information: Figure S5).

TABLE 2 Models tested during the iterative approach to model selection with the "fit" data set

Model	Temp	Log (rain)	Daytime activity	Cloud cover squared	Moon brightness	Distance from plantations	Distance from water	Deviance
1	X							623
2		X						616
3	X	X						603
4	**X**	**X**	**X**					**595**
5	X	X	X	X (p > 0.05)				595
6	X	X	X		X (p > 0.05)			589
7	X	X	X			X (p>0.05)		594
8	X	X	X				X	589
9	X	X		X (p > 0.05)				602
10	X	X			X (p > 0.05)			597
11	X	X				X (p > 0.05)		602
12	X	X					X	598

Note: The X shows variables included in the model. A lower deviance indicates a better fitting model. If the inclusion of a variable decreased the deviance value, the variable was included in the model. If the p value of a variable was larger than 0.05, it was not included in the model, even if the deviance decreased. Model 4 (in bold) was the final model selected.

Supporting Information: Figure S4 shows a histogram of the residuals (actual−predicted). The residuals are left-centered, below 0, and thus indicate that the predicted values are larger than the actual values. The mean nocturnal activity of the "test" data set is 1.87, with a standard error of the mean of 0.08. The mean predicted value from the model is 2.07. This is approximately 2.6 times the standard error of the mean, and therefore it can be concluded that the model overestimates the activity, based on the fitted model. Marginal effects plots were created using the margins function in Stata [StataCorp, 2021]). For each of the three variables (rain, temperature, daytime activity), the other two were held at their median value.

## 3 | RESULTS

3.1 | Nocturnal activity presence

Nocturnal activity was much lower than diurnal activity (Table 1, Figure 1). Individuals varied in terms of location and spread of activity (Table 1). Activity values were unitless, ranging from 0 (no activity) to 510 (highest measurable activity). The average nocturnal activity of the proboscis monkeys ranged from 1.17 to 4.62 per individual, while the standard deviation varied between 1.14 and 4.28 (Table 1). Average diurnal activity ranged from 39.10 to 54.29 per individual, while the standard deviation varied between 5.82 and 15.27 (Table 1).

3.2 | Masking effects of activity

The final GLMM identified that temperature, rain and average activity during the day were masking effects that influenced nocturnal activity levels (AIC = 3.59, deviance = 595.17, deviance/df = 0.77, log pseudo-likelihood = −1399.41) (Table 3). Cooler temperatures, higher rainfall, and higher daytime activity predicted higher nocturnal activity (Figure 2a–c). Moon brightness and distance from plantations had all been eliminated earlier in the model fitting process and had no effect on activity. Poor results were obtained when the final fit of the model with the "fit" data was used to predict activity for the "test" data (see Supporting Information: Figures S4 and S5). This means that the masking effects are valid for the data range included in the "fit" data, but they may not be applicable to another group of similar individuals.

4 | DISCUSSION

Activity patterns in mammals are mostly constrained, with individualized flexibility to a certain degree to buffer against changes and disturbances in an environment (Jaman & Huffman, 2013; Nowak & Lee, 2013). Our results identified that the six male proboscis monkeys displayed diurnal activity patterns. However, proboscis monkeys can and do display some nocturnal activity in response to environmental disturbances. We found three possible weak effects of external factors on the levels of nocturnal activity displayed by five of
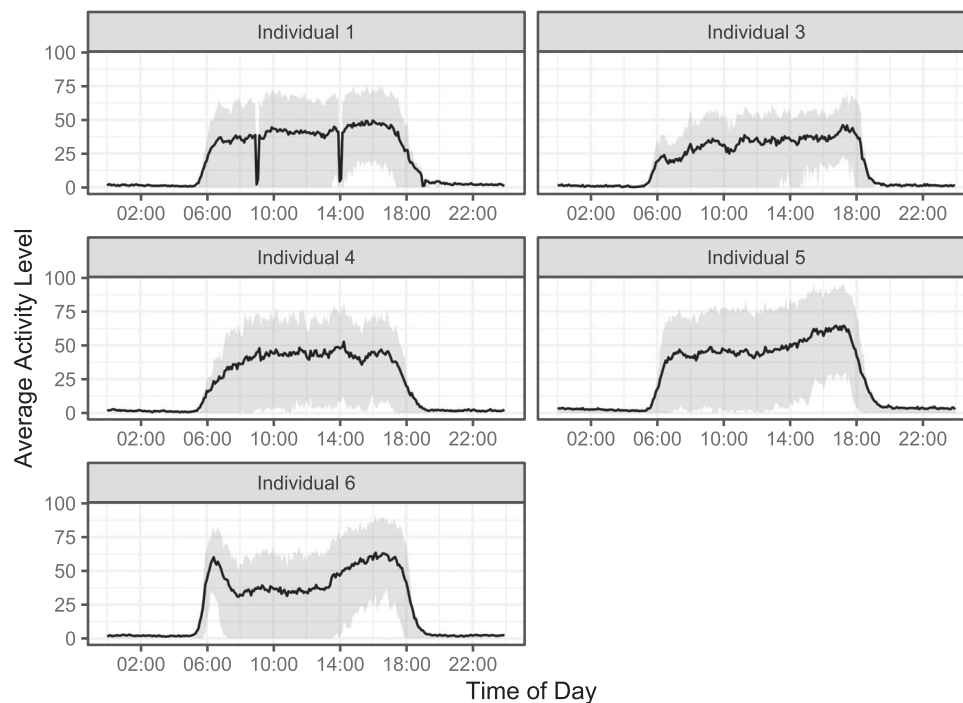
FIGURE 1 Average activity levels throughout the 24-h period per individual, including the interquartile range. Individual 2 was not included. This study was focused on nocturnal activity only, and thus the area of interest was approximately between 18:10 and 06:00 h. Activity values were unitless and could vary from 0 (no activity) to 510 (highest measurable activity)

the six proboscis monkeys: temperature during the night, rainfall during the night, and daytime activity. Our results provide a launchpad for other studies using accelerometers to understand masking effects in other species.

Contrary to our expectation, nocturnal activity was not higher during nights of warmer temperatures. Activity appeared to be higher on cooler nights, as was found with female chacma baboons in South Africa (Ayers et al., 2020). Thermoregulation is one of the main hypotheses behind nocturnal activity and sleep behaviors in many primate species (Ayers et al., 2020; Pruetz, 2018; Watanuki & Nakayama, 1993). The increase in activity on cooler nights could reflect an increase in the number of times individuals changed huddling and sleep positions (Ayers et al., 2020). However, because of the larger body size of proboscis monkeys, air temperature is not thought to majorly influence sleeping site selection (Matsuda et al., 2011). Additionally, temperatures varied only between 22°C and 26°C, and therefore, thermoregulation constraints may not impact the

changes in proboscis monkey activity (Anderson, 1984). Perhaps on cooler nights, proboscis monkeys can engage in more behaviors without heat stress, and therefore, extend their activity into the night.

As expected, higher rainfall appeared to be correlated with an increase in nocturnal activity levels in the five modeled individuals. Our results are some of the first to find a link between rainfall and nocturnal activity in anthropoids. Although rainfall is predicted to be a nocturnal disturbance that interrupts sleep in anthropoid primates, rainfall did not predict nocturnal activity presence in chacma baboons (Ayers et al., 2020) and chimpanzees (Tagg et al., 2018) and did not impact sleep in Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) (Anderson, 1984, 2000; Li et al., 2010). It may also be more difficult for proboscis monkeys to hear predators approaching in the rain, which could increase their vigilant behavior during the night (Ayers et al., 2020). Male proboscis monkeys in one-male, multi-female groups protect the female and young individuals (Kawabe & Mano, 1972), therefore, this explanation is plausible.

We expected that, similar to chimpanzees, activity at night would be lower after days of high activity (Tagg et al., 2018). Contrary to our expectation, high diurnal activity levels seemed to predict more nocturnal activity, suggesting that periods of disturbance may affect activity across the 24-h period. Quantifying diel activity patterns and their flexibility in primate species is pivotal to effective conservation management (Bismark, 2010; Nowak & Lee, 2013). This information may give clues about how species survive changes in their environment and will do so in the future. The three masking effect results (temperature, rainfall, and daytime activity) show some flexibility in proboscis monkey activity patterns and thus, proboscis monkey activity may change in the context of anthropogenic environments.

We split our accelerometer data into two data sets to identify if our model can be generalized to other proboscis monkeys. This

TABLE 3 Coefficients of the final generalized linear mixed model used to predict nocturnal activity in proboscis monkeys (AIC = 3.59, deviance = 595.17, deviance/*df* = 0.77, log pseudo-likelihood = −1399.41)

Fixed effects	Coef.	Std. err.	z Value	p > |z|	95% confidence intervals	
Temperature	0.085	0.038	2.22	0.026	0.010	0.160
logRain	−0.033	0.011	−2.98	0.003	−0.054	−0.011
Activity average day	−0.003	0.002	−1.91	0.056	−0.006	0.000
Constant	−1.411	0.894	−1.58	0.115	−3.163	0.341
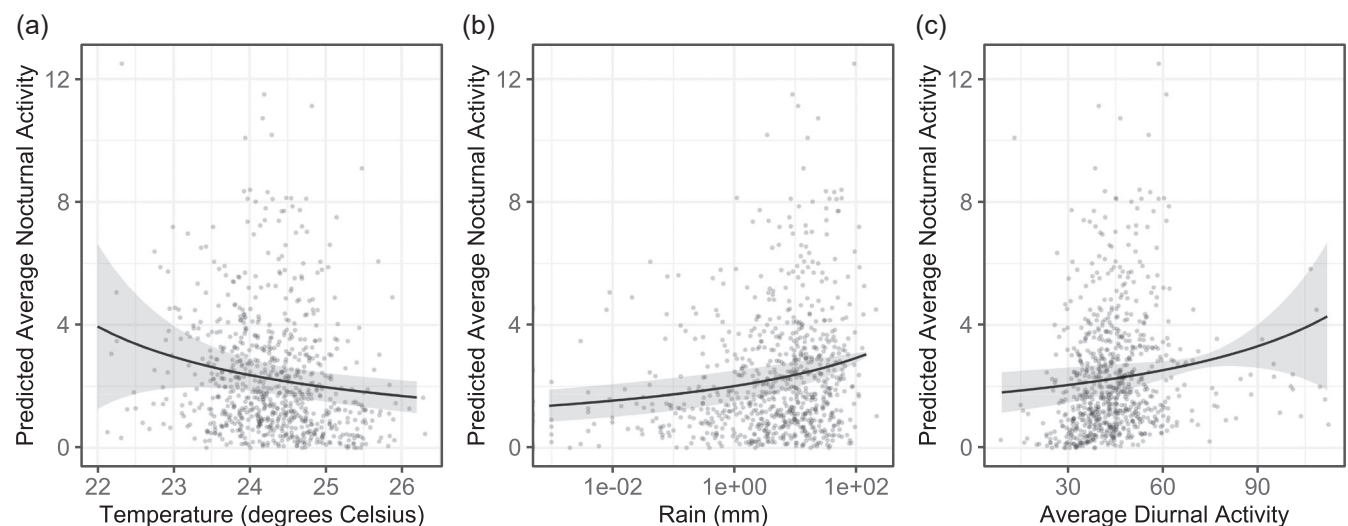
FIGURE 2 Marginal effects plots showing how nocturnal activity in proboscis monkeys related to (a) mean night-time temperature, (b) total rainfall during the night, and (c) mean diurnal activity in the period preceding the night of interest. Activity values were unitless and could vary from 0 (*no activity*) to 510 (*highest measurable activity*).

approach assumed that both the "fit" and "test" data were random samples from the same population. As the results of the fitted model with our "test" data did not indicate a good fit, it cannot yet be said whether our results apply to the wider population. The poor fit may be explained by the difference in behavior over the observation interval. Furthermore, we expected that the distance individuals spent the night from water would affect their nocturnal activity presence. Proboscis monkeys choose sleeping sites near rivers to reduce predation threats (Matsuda et al., 2008). However, we removed the distance from water data because of outliers that led to questions about its value in the model. The median distance from water was less than 35 m for all individuals, with outliers of over 1000 m. It was not known whether these distances were by choice or restrictions on availability of habitat.

We included seven factors that might mask activity patterns in proboscis monkeys. This was not an exhaustive list. In addition to the factors that we included, seasonality and social activity should be examined in future research (Nowak & Lee, 2013). Seasonality affects diel activity patterns in several anthropoids, including owl monkeys (Fernández-Duque, 2003), Yunnan snub-nosed monkeys (Li et al., 2010), spider monkeys (Muñoz-Delgado et al., 2004) and Guizhou snub-nosed monkeys (Tan et al., 2013). In Sabah, fruit availability is seasonal, and its availability influences the activity budgets of proboscis monkeys during the day and this effect may extend to nocturnal activity (Matsuda et al., 2009b, 2014). Additionally, proboscis monkey groups sleep together in one or multiple nearby trees each night, occasionally together with other groups, and social interactions are likely to influence on nocturnal activity (Bernard et al., 2011; Matsuda et al., 2008; Thiry et al., 2016). We studied male individuals from one-male, multi-female groups, however, understanding the activity patterns of other group members is another future goal. Apart from potentially displaying more vigilance, it appears that male proboscis monkeys sleep lower in the canopy than female and young individuals, which could lead to different disturbances experienced and thus, nocturnal activity displayed, by different individuals (Thiry et al., 2016).

Our study highlights the value of accelerometer data. The accelerometers allowed us to collect uninterrupted 24-h data, which would otherwise be impossible in the challenging riverine habitats that proboscis monkeys inhabit. We believe that, with the inclusion of more individuals, accelerometers are a robust method for studying activity patterns and behavioral flexibility. With the ability to collect large amounts of data, it is easier to quantify the effects of environmental disturbances on a species behavior, crucial to conservation planning (Bismark, 2010). These data can further be strengthened by incorporating GPS data, which is often collected alongside accelerometer data on the same device. We did not collect GPS data after 19:00 h and thus, we cannot say whether proboscis monkeys traveled during nights of activity. Collecting GPS data throughout the night could identify whether nocturnal activity coincides with travel away from and back to the sleeping site during the night (Gottardi et al., 2010; Isbell et al.,

2017). Such travel appears unlikely in the current study because GPS points were in the same location at 19:00 and 05:00 h the next day. Additionally, one can monitor specific behaviors by measuring activity in short continuous bursts, instead of as averages, which would add further dimensions to activity pattern studies (Costantini et al., 2017; Isbell et al., 2017; Petroelje et al., 2020).

In summary, we identified that six male proboscis monkeys in Sabah, Malaysia, displayed low but variable nocturnal activity, therefore displaying diurnal activity patterns. For the five modeled individuals, nocturnal activity levels appeared higher during nights with cooler temperatures, higher rainfall, and after higher diurnal activity. Our results cannot be generalized on the greater species-level scale. Further research into activity pattern masking effects, in particular into temperature, rainfall and daytime activity levels, in combination with data on seasonality and social activity, will further our understanding of nocturnal activity and behavioral flexibility in proboscis monkeys more generally. Proboscis monkeys in Sabah are a key population for the species and are severely impacted by habitat loss and habitat fragmentation (Sha et al., 2008). Understanding proboscis monkey's reaction to nocturnal masking effects, may provide insight in their reaction to human disturbances and help in their conservation.

AUTHOR CONTRIBUTIONS

Sophie Jane Kooros: conceptualization (equal); formal analysis (equal); writing – original draft (lead); writing – review & editing (equal). **Benoit Goossens**: conceptualization (equal); funding acquisition (lead); project administration (equal); supervision (equal); writing – review & editing (equal). **Elisabeth H. M. Sterck**: supervision (equal); writing – review & editing (equal). **Richard Kenderdine**: formal analysis (lead); writing – review & editing (equal). **Peter Titol Malim**: resources (equal); writing – review & editing (equal). **Diana Angeles Ramirez Saldivar**: data curation (equal). **Danica J. Stark**: conceptualization (equal); data curation (equal); supervision (equal); writing – review & editing (equal).

The authors state that neither the European Commission or European Centre for Medium-Range Weather Forecasts (ECMWF) is responsible for any use that may be made of the Copernicus information or data it contains. We dedicate this paper to the memory of co-authors Dr. Diana Angelez Ramirez Saldivar and Mr. Peter Titol Malim who devoted their lives to the conservation of wildlife in Sabah.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding authors upon reasonable request.

ETHICS STATEMENT
Animal handling was carried out in accordance with the current laws of Malaysia and Sabah Wildlife Department's Standard Operation Procedures on Animal Capture, Anaesthesia and Welfare. Permission was granted by Sabah Biodiversity Centre (permit JKM/MBS.1000-2/2 JLD.3 (73)). The work carried out during this study was in accordance with the Weatherall report (Weatherall, 2006), and followed the guidelines for nonhuman primates as described by Unwin et al. (2011). All efforts were made to ensure the welfare, and reduce stress of the animals, with the addition of full personal protective equipment worn by all team members throughout the process to prevent human-primate disease transmission. A veterinarian specialized in the capture and anesthesia of wildlife performed the darting, having previously conducted an evaluation of the area and target individual to minimize risk to the animals. Animals were anaesthetised using Zoletil 100 (Tiletamine + Zolazepam; 6 ± 10 mg/kg), and a prophylactic dose of Alamycin LA (20 mg/kg) and Ivermectin (0.2 mg/kg) was given as a preventative measure to assist in the post-anesthesia recovery. Anesthesia and vital signs were monitored throughout the procedure.

ORCID
Sophie J. Kooros https://orcid.org/0000-0002-1593-6392
Elisabeth H. M. Sterck http://orcid.org/0000-0003-1101-6027

REFERENCES
Ampeng, A., Shukor, M. N., Ahmad, S., Mohammad, H., Sabki, S., Liam, J., Osman, S., Bujang, M., Bujang, A., & Md-Zain, B. M. (2018). Preliminary findings on the activity patterns of the clouded leopard, *Neofelis diardi*, and its prey at Gunung Pueh National Park, Lundu, Sarawak. *Malaysian Applied Biology, 47*(3), 137–140.

Anderson, J. R. (1984). Ethology and ecology of sleep in monkeys and apes. *Advances in The Study of Behavior, 14*, 165–229. https://doi.org/10.1016/S0065-3454(08)60302-2

Anderson, J. R. (2000). Sleep-related behavioural adaptations in free-ranging anthropoid primates. *Sleep Medicine Reviews, 4*(4), 355–373. https://doi.org/10.1053/smrv.2000.0105

Ankel-Simons, F., & Rasmussen, D. (2008). Diurnality, nocturnality, and the evolution of primate visual systems. *American Journal of Physical Anthropology, S47*, 100–117. https://doi.org/10.1002/ajpa.20957

Aschoff, J., Daan, S., & Honma, K. -I. (1982). Zeitgebers, entrainment, and masking: some unsettled questions. In J. Aschoff, S. Daan, & G. Groos (Eds.), *Vertebrate circadian systems* (pp. 13–24). Springer. https://doi.org/10.1007/978-3-642-68651-1_2

Aschoff, J. (1989). Masking of circadian activity rhythms in canaries by light and dark. *Journal of Biological Rhythms, 4*(1), 29–38. https://doi.org/10.1177/074873048900400102

Aschoff, J., & vonGoetz, C. (1988). Masking of circadian activity rhythms in hamsters by darkness. *Journal of Comparative Physiology A, 162*(4), 559–562. https://doi.org/10.1007/BF00612521

Ayers, A. M., Allan, A. T., Howlett, C., Tordiffe, A. S., Williams, K. S., Williams, S. T., & Hill, R. A. (2020). Illuminating movement? Nocturnal activity patterns in chacma baboons. *Journal of Zoology, 310*(4), 287–297. https://doi.org/10.1111/jzo.12747

Bartness, T. J., & Albers, H. E. (2000). Activity patterns and the biological clock in mammals. In S. Halle, N. C. Stenseth (Eds.), *Activity patterns in small mammals. an ecological approach* (pp. 23–47). Springer. https://doi.org/10.1007/978-3-642-18264-8_3

Bernard, H., Matsuda, I., Hanya, G., & Ahmad, A. H. (2011). Characteristics of night sleeping trees of proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. *International Journal of Primatology, 32*, 259–267. https://doi.org/10.1007/s10764-010-9465-8

Bikos, K., & Kher, A. (n.d.). *Twilight, dawn, and dusk*. Retrieved January 26, 2022. https://www.timeanddate.com/astronomy/different-types-twilight.html

Bismark, M. (2010). Proboscis Monkey (*nasalis larvatus*): Bio-ecology and conservation. In S. Gursky-Doyen, & J. Stenseth (Eds.), *Indonesian primates* (pp. 217–233). Springer-Verlag https://doi.org/10.1007/978-1-4419-1560-3_12

Boonratana, R. (2013). Fragmentation and its significance on the conservation of proboscis monkey (*Nasalis larvatus*) in the Lower Kinabatangan, Sabah (North Borneo). In L. K. Marsh, & C. A. Chapman (Eds.), *Primates in fragments: Complexity and resilience* (2nd ed., pp. 459–474). Springer. https://doi.org/10.1007/978-1-4614-8839-2

Bray, J., Samson, D. R., & Nunn, C. L. (2017). Activity patterns in seven captive lemur species: Evidence of cathemerality in *Varecia* and *Lemur catta*? *American Journal of Primatology, 79*, 1–9. https://doi.org/10.1002/ajp.22648

Brown, D. D., Kays, R., Wikelski, M., Wilson, R. P., & Klimley, A. P. (2013). Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry, 1*, 1–16. https://doi.org/10.1186/2050-3385-1-20

Brown, D. D., Lapoint, S., Kays, R., Heidrich, W., Kümeth, F., & Wikelski, M. (2012). Accelerometer-informed GPS telemetry: Reducing the trade-off between resolution and longevity. *Wildlife Society Bulletin, 36*, 139–146. https://doi.org/10.1002/wsb.111

Campera, M., Balestri, M., Chimienti, M., Nijman, V., Nekaris, K. A., & Donati, G. (2019). Temporal niche separation between the two ecologically similar nocturnal primates *Avahi meridionalis* and *Lepilemur fleuretae*. *Behavioral Ecology and Sociobiology, 73*(5), 1–12. https://doi.org/10.1007/s00265-019-2664-1

Costantini, D., Sebastiano, M., Goossens, B., & Stark, D. J. (2017). Jumping in the night: An investigation of the leaping activity of the Western tarsier (*Cephalopachus bancanus borneanus*) using accelerometers. *Folia Primatologica, 88*, 46–56. https://doi.org/10.1159/000477540

Cristóbal-Azkarate, J., & Arroyo-Rodríguez, V. (2007). Diet and activity pattern of howler monkeys (*Alouatta palliata*) in Los Tuxtlas, Mexico: Effects of habitat fragmentation and implications for conservation. *American Journal of Primatology, 69*, 1013–1029. https://doi.org/10.1002/ajp.20420

Eppley, T. M., & Donati, G. (2019). Cathemeral. In V. Jennifer, & S. Todd (Eds.), *Encyclopedia of animal cognition and behavior* (pp. 1–2). Springer. https://doi.org/10.1007/978-3-319-47829-6

Erkert, H. G., & Kappeler, P. M. (2004). Arrived in the light: diel and seasonal activity patterns in wild Verreaux's sifakas (*Propithecus v.*

verreauxi; Primates: Indriidae). *Behavioral Ecology and Sociobiology*, 57(2), 174–186. https://doi.org/10.1007/s00265-004-0845-y

Fernández-Duque, E. (2003). Influences of moonlight, ambient temperature, and food availability on the diurnal and nocturnal activity of owl monkeys (*Aotus azarai*). *Behavioral Ecology and Sociobiology*, 54(5), 431–440. https://doi.org/10.1007/s00265-003-0637-9

Fernández-Duque, E., de la Iglesia, H., & Erkert, H. G. (2010). Moonstruck primates: Owl monkeys (*Aotus*) need moonlight for nocturnal activity in their natural environment. *PLoS ONE*, 5(9), 1–6. https://doi.org/10.1371/journal.pone.0012572

Fernández-Duque, E., & Erkert, H. G. (2006). Cathemerality and lunar periodicity of activity rhythms in owl monkeys of the argentinian chaco. *Folia Primatologica*, 77(1–2), 123–138. https://doi.org/10.1159/000089699

Frey, S., Fisher, J. T., Burton, A. C., & Volpe, J. P. (2017). Investigating animal activity patterns and temporal niche partitioning using camera-trap data: Challenges and opportunities. *Remote Sensing in Ecology and Conservation*, 3(3), 123–132. https://doi.org/10.1002/rse2.60

Fruth, B., Tagg, N., & Stewart, F. (2018). Sleep and nesting behavior in primates: A review. *American Journal of Physical Anthropology*, 166(3), 499–509. https://doi.org/10.1002/ajpa.23373

Gander, P. H., & Moore-Ede, M. C. (1983). Light-dark masking of circadian temperature and activity rhythms in squirrel monkeys. *American Journal of Physiology*, 245(6), R927–R934. https://doi.org/10.1152/ajpregu.1983.245.6.r927

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, 360(6394), 1232–1235. https://doi.org/10.1126/science.aar7121

Gervasi, V., Brunberg, S., & Swenson, J. (2006). An individual-based method to measure animal activity levels: A test on brown bears. *Wildlife Society Bulletin*, 34(5), 1314–1319. https://doi.org/10.2193/0091-7648(2006)34[1314:aimtma]2.0.co;2

Goossens, B., Chikhi, L., Jalil, M. F., Ancrenaz, M., Lackman-Ancrenaz, I., Mohamed, M., Andau, P., & Bruford, M. W. (2005). Patterns of genetic diversity and migration in increasingly fragmented and declining orang-utan (*Pongo pygmaeus*) populations from Sabah, Malaysia. *Molecular Ecology*, 14(2), 441–456. https://doi.org/10.1111/j.1365-294X.2004.02421.x

Gottardi, E., Tua, F., Cargnelutti, B., Maublanc, M. L., Angibault, J. M., Said, S., & Verheyden, H. (2010). Use of GPS activity sensors to measure active and inactive behaviours of European roe deer (*Capreolus capreolus*). *Mammalia*, 74(4), 355–362. https://doi.org/10.1515/MAMM.2010.058

Hai, T. C., Ng, A., Prudente, C., Pang, C., & TekChoonYess, J. (2011). Balancing the need for sustainable oil palm development and conservation: The Lower Kinabatangan Floodplains experience. ISP National Seminar 2001: Strategic directions for the sustainability of the oil palm industry.

Harding, L. E. (2015). *Nasalis larvatus* (Primates: Colobini). *Mammalian Species*, 47(926), 84–99. https://doi.org/10.1093/mspecies/sev009

Hersbach, H., Bell, B., Berrisford, P., Biavati, G., Horányi, A., MuñozSabater, J., Nicolas, J., Peubey, C., Radu, R., Rozum, I., Schepers, D., Simmons, A., Soci, C., Dee, D., & Thépaut, J. -N. (2019). *ERA5: Fifth generation of ECMWF atmospheric reanalyses of the global climate*. Retrieved April 12, 2022. https://doi.org/10.24381/cds.f17050d7

Isbell, L. A., Bidner, L. R., Crofoot, M. C., Matsumoto-Oda, A., & Farine, D. R. (2017). GPS-identified, low-level nocturnal activity of vervets (*Chlorocebus pygerythrus*) and olive baboons (*Papio anubis*) in Laikipia, Kenya. *American Journal of Physical Anthropology*, 164(1), 203–211. https://doi.org/10.1002/ajpa.23259

Jaman, M. F., & Huffman, M. A. (2013). The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (*Macaca mulatta*) in Bangladesh. *Primates*, 54(1), 49–59. https://doi.org/10.1007/s10329-012-0330-6

Kawabe, M., & Mano, T. (1972). Ecology and behavior of the wild proboscis monkey, *Nasalis larvatus* (Wurmb), in Sabah, Malaysia. *Primates*, 13, 213–227. https://doi.org/10.1007/BF01840882

Kay, R. F., & Kirk, E. C. (2000). Osteological evidence for the evolution of activity pattern and visual acuity in primates. *American Journal of Physical Anthropology*, 113(2), 235–262. https://doi.org/10.1002/1096-8644(200010)113:2.235::AID-AJPA7.3.0.CO;2-9

Kirk, E. C., & Kay, R. F. (2004). The evolution of high visual acuity in the anthropoidea. In C. F. Ross, & R. F. Kay (Eds.), *Anthropoid origins* (pp. 539–602). Kluwer Academic/Plenum. https://doi.org/10.1007/978-1-4419-8873-7_20

Krop-Benesch, A. R., Berger, A., Hofer, H., & Heurich, M. (2013). Long-term measurement of roe deer (*Capreolus capreolus*) (Mammalia: Cervidae) activity using two-axis accelerometers in GPS-collars. *Italian Journal of Zoology*, 80(1), 69–81. https://doi.org/10.1080/11250003.2012.725777

Leasor, C. H., & Macgregor, J. O. (2014). Proboscis monkey tourism: Can we make it "ecotourism"? In E. Russon, A, & J. Wallis (Eds.), *Primate tourism: A tool for conservation?* (pp. 56–75). Cambridge University Press. https://doi.org/10.1007/978-1-4419-8873-7_20

Li, D., Ren, B., Grueter, C. C., Li, B., & Li, M. (2010). Nocturnal sleeping habits of the Yunnan snub-nosed monkey in Xiangguqing, China. *American Journal of Primatology*, 72(12), 1092–1099. https://doi.org/10.1002/ajp.20871

LotekWireless Inc. (2011). *Lotek GPS4500/6000/7000/8000/IridiumTrack/GlobalStarTrack/Wildcell/MiniTrack User's Manual*.

Matsuda, I., Akiyama, Y., Tuuga, A., Bernard, H., & Clauss, M. (2014). Daily feeding rhythm in proboscis monkeys: A preliminary comparison with other non-human primates. *Primates*, 55(2), 313–326. https://doi.org/10.1007/s10329-014-0407-5

Matsuda, I., Tuuga, A., Akiyama, Y., & Higashi, S. (2008). Selection of river crossing location and sleeping site by proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. *American Journal of Primatology*, 70(11), 1097–1101. https://doi.org/10.1002/ajp.20604

Matsuda, I., Tuuga, A., & Bernard, H. (2011). Riverine refuging by proboscis monkeys (*Nasalis larvatus*) and sympatric primates: Implications for adaptive benefits of the riverine habitat. *Mammalian Biology*, 76(2), 165–171. https://doi.org/10.1016/j.mambio.2010.03.005

Matsuda, I., Tuuga, A., & Higashi, S. (2008). Clouded leopard (*Neofelis diardi*) predation on proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. *Primates*, 49(3), 227–231. https://doi.org/10.1007/s10329-008-0085-2

Matsuda, I., Tuuga, A., & Higashi, S. (2009a). Ranging behavior of proboscis monkeys in a riverine forest with special reference to ranging in inland forest. *International Journal of Primatology*, 30(2), 313–325. https://doi.org/10.1007/s10764-009-9344-3

Matsuda, I., Tuuga, A., & Higashi, S. (2009b). The feeding ecology and activity budget of proboscis monkeys. *American Journal of Primatology*, 71(6), 478–492. https://doi.org/10.1002/ajp.20677

Matsuda, I., Tuuga, A., & Higashi, S. (2010). Effects of water level on sleeping-site selection and inter-group association in proboscis monkeys: Why do they sleep alone inland on flooded days? *Ecological Research*, 25(2), 475–482. https://doi.org/10.1007/s11284-009-0677-3

Meijaard, E., & Nijman, V. (2000). The local extinction of the proboscis monkey *Nasalis larvatus* in Pulau Kaget Nature Reserve, Indonesia. *Oryx*, 34(1), 66–70. https://doi.org/10.1046/j.1365-3008.2000.00095.x

Meijaard, E., & Sheil, D. (2007). Is wildlife research useful for wildlife conservation in the tropics? A review for Borneo with global implications. *Biodiversity and Conservation*, 16(11), 3053–3065. https://doi.org/10.1007/s10531-007-9161-y

Mochida, K., & Nishikawa, M. (2014). Sleep duration is affected by social relationships among sleeping partners in wild Japanese macaques.

Behavioural Processes, *103*, 102–104. https://doi.org/10.1016/j.beproc.2013.10.010

Muñoz-Delgado, J., Corsi-Cabrera, M., Canales-Espinosa, D., Santillán-Doherty, A. M., & Erkert, H. G. (2004). Astronomical and meteorological parameters and rest-activity rhythm in the spider monkey Ateles geoffroyi. *Physiology and Behavior*, *83*(1), 107–117. https://doi.org/10.1016/j.physbeh.2004.07.015

Muñoz-Delgado, J., Pérez-Galicia, S., Sánchez-Ferrer, J. C., Canales Espinosa, D., Erkert, H. G. (2018). Diel and infradian (7-day) activity rhythms in Mexican spider monkeys (Ateles geoffroyi) kept with and without visitor contact. *American Journal of Primatology*, *80*(12), 1–11. https://doi.org/10.1002/ajp.22933

Murai, T., Mohamed, M., Bernard, H., Mahedi, P. A., Saburi, R., & Higashi, S. (2007). Female transfer between one-male groups of proboscis monkey (Nasalis larvatus). *Primates*, *48*(2), 117–121. https://doi.org/10.1007/s10329-006-0005-2

Nishikawa, M., & Mochida, K. (2010). Coprophagy-related interspecific nocturnal interactions between Japanese macaques (Macaca fuscata yakui) and sika deer (Cervus nippon yakushimae). *Primates*, *51*(2), 95–99. https://doi.org/10.1007/s10329-009-0182-x

Nowak, K., & Lee, P. C. (2013). "Specialist" Primates can be flexible in response to habitat alteration. In L. K. Marsh, & C. A. Chapman (Eds.), *Primates in fragments: Complexity and resilience* (2nd ed., pp. 199–211). Springer. https://doi.org/10.1007/978-1-4614-8839-2

Papailiou, A., Sullivan, E. L., & Cameron, J. L. (2008). Behaviors in rhesus monkeys (Macaca mulatta) associated with activity counts measured by accelerometer. *American Journal of Primatology*, *70*(2), 185–190. https://doi.org/10.1002/ajp.20476

Petroelje, T. R., Belant, J. L., Beyer, D. E., & Svoboda, N. J. (2020). Identification of carnivore kill sites is improved by verified accelerometer data. *Animal Biotelemetry*, *8*(18), 1–10. https://doi.org/10.1186/s40317-020-00206-y

Pruetz, J. D. (2018). Nocturnal behavior by a diurnal ape, the West African chimpanzee (Pan troglodytes verus), in a savanna environment at Fongoli, Senegal. *American Journal of Physical Anthropology*, *166*(3), 541–548. https://doi.org/10.1002/ajpa.23434

R Core Team, R. (2013). *A language and environment for statistical computing, version 3.5.1 (2018-07-02)*. http://www.r-project.org/

Santini, L., Rojas, D., & Donati, G. (2015). Evolving through day and night: Origin and diversification of activity pattern in modern primates. *Behavioral Ecology*, *26*(3), 789–796. https://doi.org/10.1093/beheco/arv012

Sha, J. C. M., Bernard, H., & Nathan, S. K. (2008). Status and conservation of proboscis monkeys (Nasalis larvatus) in Sabah, East Malaysia. *Primate Conservation*, *23*(1), 107–120. https://doi.org/10.1896/052.023.0112

Sharma, V. K., & Chandrashekaran, M. K. (2005). Zeitgebers (time cues) for biological clocks. *Current Science*, *89*(7), 1136–1146.

Silva, C. A. D., Pontes, A. L. B. D., Cavalcante, J. D. S., & Azevedo, C. V. M. D. (2014). Conspecific vocalisations modulate the circadian activity rhythm of marmosets. *Biological Rhythm Research*, *45*(6), 941–954. https://doi.org/10.1080/09291016.2014.939441

Stark, D. J. (2018). *Habitat use and movement of proboscis monkeys (Nasalis larvatus) in a degraded and human-modified forest landscape* [Unpublished doctoral dissertation]. Cardiff University, Cardiff.

Stark, D. J., Vaughan, I. P., Evans, L. J., Kler, H., & Goossens, B. (2018). Combining drones and satellite tracking as an effective tool for informing policy change in riparian habitats: A proboscis monkey case study. *Remote Sensing in Ecology and Conservation*, *4*(1), 44–52. https://doi.org/10.1002/rse2.51

Stark, D. J., Vaughan, I. P., Saldivar, D. A., Nathan, S. K., & Goossens, B. (2017). Evaluating methods for estimating home ranges using GPS collars: A comparison using proboscis monkeys (Nasalis larvatus).

PLoS ONE, *12*(3), 1–23. https://doi.org/10.1371/journal.pone.0174891

Starr, C., Nekaris, K. A., & Leung, L. (2012). Hiding from the moonlight: Luminosity and temperature affect activity of asian nocturnal primates in a highly seasonal forest. *PLoS ONE*, *7*(4), 1–8. https://doi.org/10.1371/journal.pone.0036396

StataCorp. (2003). *Stata statistical software: Release 8*. Retrieved July 17, 2021.

StataCorp. (2021). *Stata statistical software: Release 17 BE - Basic Edition*. Retrieved June 25, 2022.

Tagg, N., McCarthy, M., Dieguez, P., Bocksberger, G., Willie, J., Mundry, R., Stewart, F., Arandjelovic, M., Widness, J., Landsmann, A., Agbor, A., Angedakin, S., Ayimisin, A. E., Bessone, M., Brazzola, G., Corogenes, K., Deschner, T., Dilambaka, E., Eno-Nku, M., … Boesch, C.2018). Nocturnal activity in wild chimpanzees (Pan troglodytes): Evidence for flexible sleeping patterns and insights into human evolution. *American Journal of Physical Anthropology*, *166*(3), 510–529. https://doi.org/10.1002/ajpa.23478

Tan, C. L., Yang, Y., & Niu, K. (2013). Into the night: Camera traps reveal nocturnal activity in a presumptive diurnal primate, Rhinopithecus brelichi. *Primates*, *54*(1), 1–6. https://doi.org/10.1007/s10329-012-0318-2

Tattersall, I. (1987). Cathemeral activity in primates: A definition. *Folia Primatologica*, *49*, 200–202. https://doi.org/10.1159/000156323

Tetzner, D., Thomas, E., & Allen, C. (2019). A validation of ERA5 reanalysis data in the Southern antarctic peninsula–Ellsworth land region, and its implications for ice core studies. *Geosciences*, *9*(7), 1–17. https://doi.org/10.3390/geosciences9070289

Thieurmel, B., & Elmarhraoui, A. (2019). *Package 'suncalc', version 0.5.0*. https://github.com/datastorm-open/suncalc

Thiry, V., Stark, D. J., Goossens, B., Slachmuylder, J. L., Drubbel, R. V., & Vercauteren, M. (2016). Use and selection of sleeping sites by proboscis monkeys, Nasalis larvatus, along the Kinabatangan River, Sabah, Malaysia. *Folia Primatologica*, *87*(3), 180–196. https://doi.org/10.1159/000449219

Toulec, T., Lhota, S., Soumarová, H., Putera, A. K. S., & Kustiawan, W. (2020). Shrimp farms, fire or palm oil? Changing causes of proboscis monkey habitat loss. *Global Ecology and Conservation*, *21*, e00863. https://doi.org/10.1016/j.gecco.2019.e00863

Unwin, S., Ancrenaz, M., & Bailey, W. (2011). Handling, anaesthesia, health evaluation and biological sampling. In J. Setchell, & D. Curtis (Eds.), *Field and laboratory methods in primatology: A practical guide*. (2nd ed., pp. 147–168). Cambridge University Press. https://doi.org/10.1017/CBO9781139165105.010

Van Schaik, C. P., & Griffiths, M. (1996). Activity periods of Indonesian rain forest mammals. *Biotropica*, *28*(1), 105–112. https://doi.org/10.2307/2388775

Vessey, S. H. (1973). Night observations of free-ranging rhesus monkeys. *American Journal of Physical Anthropology*, *38*(2), 613–619. https://doi.org/10.1002/ajpa.1330380276

Watanuki, Y., & Nakayama, Y. (1993). Age difference in activity pattern of Japanese monkeys: Effects of temperature, snow, and diet. *Primates*, *34*(4), 419–430. https://doi.org/10.1007/BF02382651

Weatherall, D. (2006). The Weatherall report on the use of non-human primates in research. *London: The Royal Society*, 1–145.

Wickham, H. (2016). Ggplot2: Elegant graphics for data analysis (Package version: 3.3.2.). https://ggplot2.tidyverse.org

Yeager, C. P. (1989). Feeding ecology of the proboscis monkey (Nasalis larvatus). *International Journal of Primatology*, *10*(6), 497–530. https://doi.org/10.1007/BF02739363

Zamma, K. (2014). What makes wild chimpanzees wake up at night? *Primates*, *55*(1), 51–57. https://doi.org/10.1007/s10329-013-0367-1

Zenone, A., Ciancio, J. E., Badalamenti, F., Buffa, G., D'Anna, G., Pipitone, C., & Giacalone, M. V. (2020). Influence of light, food and

predator presence on the activity pattern of the European spiny lobster *Palinurus elephas*: An investigation using tri-axial accelerometers. *Ecological Indicators*, *113*, 106174. https://doi.org/10.1016/j.ecolind.2020.106174

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Kooros, S. J., Goossens, B., Sterck, E. H. M., Kenderdine, R., Malim, P. T., Ramirez Saldivar, D. A., & Stark, D. J. (2022). External environmental conditions impact nocturnal activity levels in proboscis monkeys (*Nasalis larvatus*) living in Sabah, Malaysia. *American Journal of Primatology*, 84, e23423. https://doi.org/10.1002/ajp.23423