

Illuminating movement? Nocturnal activity patterns in chacma baboons

A. M. Ayers^{1,2} , A. T. L. Allan^{1,2}, C. Howlett^{1,2,3}, A. S. W. Tordiffe⁴, K. S. Williams^{1,2}, S. T. Williams^{1,2,5,6} & R. A. Hill^{1,2,5}

¹ Department of Anthropology, Durham University, Durham, UK

² Primate and Predator Project, Lajuma Research Centre, Makhado, South Africa

³ School of Anthropology and Conservation, The University of Kent, Canterbury, Kent, UK

⁴ Department of Paraclinical Sciences, Faculty of Veterinary Science, University of Pretoria, Onderstepoort, South Africa

⁵ Department of Zoology, University of Venda, Thohoyandou, South Africa

⁶ Institute for Globally Distributed Open Research and Education (IGDORE), Thohoyandou, South Africa

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Correspondence

Alec M. Ayers, Department of Anthropology, Durham University, Durham, DH1 3LE, UK.
Emails: ayers.alec@gmail.com

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Abstract

Recent analyses have shown that typically diurnal primates may periodically exhibit some levels of activity at night. Despite this, there have been few studies that have explored whether diurnal primates living in temperate environments will extend their activity budgets to the nocturnal phase as a response to seasonal constraints. Using dual-axis accelerometers, we explored whether chacma baboons (*Papio ursinus*; $N = 3$) in the western Soutpansberg Mountains, South Africa, responded to seasonally fluctuating levels of day length, lunar illumination, wind speed, precipitation and temperature by heightening or lowering nocturnal activity levels. Our results showed that chacma baboons engaged in low levels of activity at night throughout the year. Although baboons had heightened nocturnal activity as a response to shorter days, moonlit nights and lower temperatures, these responses were most likely due to disturbed sleeping patterns rather than more active movement. Nocturnal activity significantly dropped in a female baboon throughout the course of her pregnancy and remained low after giving birth suggesting that females with infants must increase resting. Our results compliment previous analyses which suggest that although diurnal primates may periodically be active at night, there is limited evidence for strategic use of the nocturnal phase even in highly seasonal environments.

Introduction

Diel activity patterns typically refer to when a species is primarily active. While most mammals are active at night (nocturnal), several taxa have evolved to be active during daylight hours only (diurnal), at intermediate light conditions (such as at dawn and dusk: crepuscular) or throughout the 24-h cycle (cathemeral) (Bennie *et al.*, 2014). Factors that influence diel activity patterns may vary between species and include physical characteristics such as the structure of visual systems (Veilleux & Kirk, 2014) to a range of environmental factors including weather conditions (such as temperature) (Herman, 1977; Dussault *et al.*, 2004), predation (Lima & Dill, 1990) and competition avoidance (Carothers & Jaksic, 1984). Although behaviour is generally constrained to the active period, it is important to understand how extrinsic (environmental) variables enhance or constrain the potential for behavioural flexibility and for activity to extend into other phases of the 24-h cycle.

Although diurnal animals typically suppress activity at night, there is increasing evidence that some diurnal animals may increase their activity at night due to factors ranging from migration (Newton, 2008), human avoidance (Graham *et al.*, 2009) and lunar luminosity (Kronfeld-Schor *et al.*, 2013). Among carnivores, increased activity on moonlit nights has been suggested to aid hunting efficiency (Cozzi *et al.*, 2012; Rasmussen & MacDonald, 2012; Broekhuis *et al.*, 2014).

Climatic variables including weather patterns such as wind speed, rain and temperature have the potential to place thermal constraints on animals by altering their core body temperature (Stelzner & Hausfater, 1986; Hill, 2006; Webster *et al.*, 2008). As a response to harsh climatic conditions, endothermic animals (including primates) will alter their behaviour and activity budgets as an attempt to maintain homeothermy (Hill, 2006; Donati *et al.*, 2011; Majolo *et al.*, 2013; Gestich, Caselli & Setz, 2014). Ungulates and rodents living in environments with high summer temperatures will often switch to foraging at night as a means to avoid thermal stress (Herman, 1977;

Dussault *et al.*, 2004; Bourgoin *et al.*, 2011; Hetem *et al.*, 2012). Behavioural plasticity in relation to climatic conditions may be best illustrated in species that live in seasonal environments where fluctuating climatic conditions coupled with limited daylight hours have the potential to alter activity budgets (Dunbar, 1992; Hill *et al.*, 2003a; Hill *et al.*, 2003b; Hill *et al.*, 2004b).

In primates, seasonal shifts in activity have been recorded in cathemeral species, which are found to regularly shift their activity patterns throughout the 24-h diel cycle. Mongoose lemurs (*Eulemur mongoz*) living in seasonally dry forests became more diurnal during the wet season due to lower night-time light intensity and yet became chiefly nocturnal during the dry season when day length was shorter (Curtis, Zaramody & Martin, 1999). In less predictable environments that are characteristic of south-eastern Madagascar, brown collared lemurs (*Eulemur collaris*) shifted their activity levels in response to food availability and thus became more diurnally active when ripe fruit was more readily available (Donati *et al.*, 2007). Despite this remarkable seasonal plasticity, there has been no formal investigation to date of whether such flexibility extends to the use of the nocturnal phase in anthropoids (who are considered strictly diurnal with the exception of *Aotus*) residing in seasonal environments and whether such species can compensate for diurnal time budget constraints, particularly in winter, through nocturnal activity.

In diurnal primates, nocturnal activity in response to increased lunar luminosity has been reported for ring-tailed lemurs (*Lemur catta*) (Parga, 2011; Donati *et al.*, 2013). Chimpanzees (*Pan troglodytes*) have been recorded engaging in behaviours such as feeding (Chivers, 1987), mating (Nishida, 1994) and travelling (Pruettz & Bertolani, 2010) under increased moonlight, although a recent analysis by Tagg *et al.* (2018) found that lunar luminosity had no effect on nocturnal activity in chimpanzees from 22 different populations. Nevertheless, Krief *et al.* (2014) found that chimpanzees in Kibale National Park, Uganda, were more likely to crop raid under moonless nights as a possible means to prevent detection from humans. The interactions between lunar luminosity and nocturnal behaviour in diurnal species are thus not straightforward.

Despite being considered diurnal, baboons have been recorded becoming active at night as a response to lunar luminosity. For example, yellow baboons (*Papio cynocephalus*), in Kenya, had periods of frequent alarm calling with increased nocturnal illumination (Altmann & Altmann, 1970), whereas Guinea baboons (*Papio papio*) in Senegal were found to regularly move throughout the night and to leave sleeping sites earlier in the morning during the dry season when nocturnal illumination was greater (Anderson & McGrew, 1984). Using accelerometers and global positioning system (GPS) collars, Isbell *et al.* (2017) found low levels of nocturnal activity in a group of olive baboons (*Papio anubis*) in Laikipia, Kenya, with movement found to occur on 15% of nights, but there was no clear indication that baboons responded to increased moonlight. Although nocturnal activity may be marginal in equatorial baboons, there has yet to be a formal assessment of nocturnal activity in non-equatorial populations. Such populations are likely to experience significant ecological constraints

on time at certain times of year (Hill *et al.*, 2003a; Hill *et al.*, 2003b) such that the adaptive use of the nocturnal phase may allow them to compensate for limits in the diurnal activity period at these times (although decreasing temperatures during winter months may impose thermoregulatory constraints that may lead to a decrease in activity).

Due to practical constraints ranging from inadequate visibility to unintentionally altering natural sleeping habits, previous research on nocturnal activity patterns in diurnal anthropoids has been primarily limited to anecdotal observations (Vessey, 1973; Anderson & McGrew, 1984; Stelzner & Hausfater, 1986; although see Isbell *et al.*, 2017; Tan *et al.*, 2013). However, recent advances in radio telemetry have allowed for the collection of activity data through dual-axis accelerometers attached to GPS collars. Accelerometers have been especially useful in allowing researchers to monitor the behaviour of cryptic species such as pumas (*Puma concolor*) (Williams *et al.*, 2014), badgers (*Meles meles*) (McClune *et al.*, 2014) and lynx (*Lynx lynx*) (Podolski *et al.*, 2013) as well as activity patterns during time periods where behavioural observations are difficult (Cooke *et al.*, 2004; Brown *et al.*, 2013). Accelerometers have also proven effective on primates (including baboons; Markham & Altmann, 2008; Fehlmann *et al.*, 2017; Isbell *et al.*, 2017) and have been employed to assess intragroup (Mann *et al.*, 2005) as well as seasonal variability in activity patterns (Erkert & Kappeler, 2004; Muñoz-Delgado *et al.*, 2005; Eppley, Ganzhorn & Donati, 2015).

Through the aid of accelerometers, we assessed whether temporal and environmental factors, as well as pregnancy, impacted nocturnal activity patterns in chacma baboons (*Papio ursinus*) found in the western Soutpansberg Mountains, Limpopo Province, South Africa. Living in large complex multi-male/multi-female groups, baboons are some of the most widespread primates in Africa (Henzi & Barrett, 2005) inhabiting a variety of different environments that vary significantly in terms of seasonality, food availability and habitat types (Dunbar, 1992). Chacma baboons respond to environmental pressures including seasonal changes in food availability, temperature and day length by not only altering their diet, but also by reallocating their time spent engaging in necessary tasks including resting, feeding and socializing (Dunbar, 1992; Hill *et al.*, 2003b).

Here, we define 'activity' as any movement that is recorded, regardless of the animal's position and behavioural state (Scheibe *et al.*, 1998). Following an assessment that baboons exhibit quantifiable activity levels at night within the Soutpansberg Mountains, South Africa, we then test the following hypotheses:

Hypothesis 1

Baboons will respond to shorter day lengths in winter by extending their activity into the nocturnal phase.

Hypothesis 2

Nocturnal activity will increase on nights exhibiting greater lunar luminosity (i.e. during a full moon) due to increased visual acuity.

Hypothesis 3

Environmental variables will impact nocturnal activity levels due to thermoregulatory constraints. Specifically, activity will decrease as temperature and the wind chill equivalent temperature decreases and wind speed increases, and as precipitation increases.

Materials and methods

Study site

This study was based at the Lajuma Research Centre in the western Soutpansberg Mountains, Limpopo Province, South Africa ($23^{\circ}06'45.14''S$ $29^{\circ}11'37.10''E$). Having a maximum elevation of 1748 m above sea level (Mostert *et al.*, 2008) and running c. 250 km from east to west and 15–60 km from north to south (Berger *et al.*, 2003), the Soutpansberg Mountains are a topographically complex environment consisting of numerous habitats ranging from closed woodlands, mistbelt forests, bushveld complexes, as well as relatively open and rocky sub-alpine mountain bushveld and sourveld ecosystems (Mostert *et al.*, 2008; Kirchhof *et al.*, 2010). The study site has a mean annual rainfall of 724 mm with a summer rainy season (December–February) and a winter dry season (May–August) (Willems, Barton & Hill, 2009). Mean daily minimum and maximum seasonal temperatures throughout the study period ranged from 16.8–17.6°C in winter to 21.2–22.0°C in summer. Mean nightly minimum and maximum temperatures ranged from 12.8 to 13.4°C (winter) and 18.6 to 19.1°C (summer). Day length fluctuates from c. 11 h in winter to over 13 h in summer.

Baboon collaring methods and activity data collection

Adult female baboons ($N = 3$) from two groups were fitted with Vectronic GPS-PLUS collars 18 (VECTRONIC Aerospace, Berlin, Germany) between September 2013 and November 2015 (Table 1). One individual was collared twice during the study period, and only females were collared since males periodically transfer between groups.

All baboons were sedated with a combination of 1–1.4 mg kg⁻¹ tiletamine/zolazepam (Zoletil; Virbac RSA (Pty) Ltd, Halfway House, South Africa) and 0.02–0.03 mg kg⁻¹ medetomidine (Domitor; Pfizer Laboratories (Pty) Ltd, Maywood, NJ, USA), delivered via remote injection dart (DanInject International, Pietermaritzburg, South Africa) before being fitted with a collar. After all procedures were completed, the medetomidine was antagonized with an intramuscular dose

of atipamezole (Antisedan; Pfizer Laboratories (Pty)), given at 0.1–0.15 mg kg⁻¹, and the animals were allowed to recover in a crate before being released near to their group.

Collars were programmed to take GPS fixes every hour between 06:00 and 20:00 SAST with one nocturnal fix at 22:00 ($N = 11\,129$; mean fixes per day 15.43 (96.4%). The GPS collars incorporated dual-axis activity sensors which captured acceleration on two axes (*x*-axis and *y*-axis) at 4 Hz, with the data processed and stored as 120s averages. Accelerometers were located at the top of GPS collars and near the back of the animals' neck. Direction of the *x*-axis sensors moved from front to back, whereas the direction of the *y*-axis from side to side as the animals moved. In this case, the *x*-axis represented forward and backward movements and the *y*-axis sideward and rotary movements ('body roll movement') (Berger, Dettki & Urbano, 2014). Our collars did not have accelerometers that incorporate the *z*-axis (up and down movements). Given the strong positive correlation found between the *x*-axis and the *y*-axis (Pearson's $r = 0.953$, $P = <0.0001$), only the *x*-axis data were used in analysis (following Heurich *et al.*, 2014). Activity values derived from sensors range from 0 (no activity) to 255 (high activity).

Most GPS collars fell off when designated (378 days after the collars were fitted) with the exception of one collar which fell off earlier than expected. All data were downloaded regularly through an ultra high frequency terminal.

Predictor variables

Data from between 20 min after the onset and 20 min before the conclusion of astronomical twilight were extracted for analysis in order to completely ensure that only nocturnal data were included (Bearder, Nekaris & Curtis, 2006) (night-time hours in these analyses range from 13 h in winter and 10.45 h in summer, $N = 777$). Astronomical twilight defines a time range when the sun (disc) is 18° below the horizon such that the data selection ensured that baboons could not see without additional illumination. Times for the onset and conclusion of astronomical twilight across the duration to this study derived from the National Aeronautics and Space Administration (NASA) database (<https://www.usno.navy.mil/>).

Local climatic data including rain, temperature, wind speed and wind chill equivalent temperature were collected from an on-site South African Environmental Observation Network (SAEON) weather station. The wind chill equivalent temperature combines temperature and wind speed to estimate the perceived environmental temperature (Hill *et al.*, 2004a). Precipitation was measured as the rainfall in a half-hour interval or the average nightly rainfall depending on the analysis (see Statistical analysis).

Table 1 Global positioning system collared baboon information

Collar ID	Date collared from	Data collected until	Sex	Group	Notes
11941	09/03/2013	05/02/2014	F	Habituated	—
11940	11/06/2015	14/08/2015	F	Unhabituated	—
11942	27/07/2014	30/05/2015	F	Habituated	Gave birth to infant in March 2015
11938	04/06/2015	18/7/2015	F	Habituated	Same individual as Collar ID 11942

Lunar luminosity, defined as the percentage of the lunar sphere that is visible due to illumination by the sun, was used to assess whether moonlight influenced baboon nocturnal activity. Lunar luminosity, daily moonrise and set times, and day length (being the period in which the Earth receives illumination from the sun) were downloaded from NASA's data services (<https://data.nasa.gov/>) and synchronized to the data set. Lunar luminosity was continuous with values ranging between 0% (moon not visible) and 100% (fully visible). Since lunar luminosity is constrained to times in which the moon is visible in the night sky (above the horizon), lunar luminosity values were constrained by moonrise and set times each night. Unfortunately, cloud coverage data could not be obtained for these analyses.

Statistical analysis

In order to test the three hypotheses, nocturnal activity data were separated into two different datasets. Data set A consisted of average activity throughout each night within the study period ($N = 777$) and allowed a broad-scale analysis (Model A) for an overall assessment of seasonal trends. Data set B ($N = 14\,019$) comprised of average activity in half-hour intervals (i.e. the average activity within every half-hour for each individual night). Data set B permitted a fine-scaled model (Model B) with the inclusion of environmental variables that may shift throughout the night.

Generalized linear mixed models (GLMM) with a gamma error structure and log-link function (Bates *et al.*, 2015) were used to assess total activity levels (both broad scale (Model A) and fine scale (Model B) across nights in RStudio (Version 0.98.1103; RStudio, Inc., Boston, MA, USA). A gamma error structure was selected for all GLMMs given the continuous and positive structure of the data as well as the near-constant variance found on the log scale. Log-link functions are generally used with gamma error structures. Activity data were transformed by adding 1 to all values to fulfil the requirements for a gamma GLMM.

Day length was included in both coarse and fine-grained models to assess whether baboons responded to shorter days by extending their nocturnal activity levels throughout the night (H1). To assess the impact that the lunar cycle had on baboon activity levels (H2), lunar luminosity was included in the coarse-grained model (Model A), with the luminescence value corrected for the presence of the moon combined in Model B (fine-grained model). Mean nightly wind chill temperatures and precipitation levels were included in Model A to assess the impact of weather variables (H3). We used mean instead of lowest temperature for Model A since the meteorological data allowed us to account for the variability in temperatures across each half-hour interval rather than using a single coldest value for the night. Temperature, wind speed (and the interaction between the two) and rainfall levels at half-hour intervals were included to assess whether fluctuating environmental variables had a fine-grained influence on baboon nocturnal activity levels (Model B).

To account for intergroup, individual and nightly variability, collar identity ($N = 4$) specific groups ($N = 2$), night ($N = 777$) and sleeping site identity (derived from the

nocturnal GPS fix and ground-truthed with observational data, $N = 19$) were included as random effects. Collar identity was preferred as a random effect over individual identity due to possible differences in collar performance. As one collared female gave birth during data collection, the presence of an infant was thus included as a factor to account for the costs of maternal care such as infant carrying, suckling and increased vigilance (Altmann & Samuels, 1992; Rendall, Cheney & Seyfarth, 2000; Maestripieri, 2011) impacting on nocturnal activity. Subsequent results were analysed in RStudio and visualized with the aid of the ggplot2 package (Wickham, 2009).

Results

Although nocturnal activity levels were far below those observed during the day, consistent, but low levels of activity were observed during the nocturnal phase [diurnal defined as the hours after sunrise and before sunset ($N = 777$, $\bar{x} = 64.57$, $SE = 0.379$) and nocturnal as the hours after sunset and before sunrise ($N = 777$, $\bar{x} = 1.76$, $SE = 0.029$)]. During the twilight phases, when the sun still has an impact on the illumination available, activity was 16% of that observed during the diurnal period ($N = 765$, $\bar{x} = 10.65$, $SE = 0.285$; Fig. 1).

Model A included lunar luminosity, wind chill equivalent temperature, precipitation and day length as predictor variables (Table 2) and represented a significant improvement over the null model (the control variables, presence of an infant, day length and random effects (likelihood ratio test: $\chi^2 = 80.42$, d.f. = 4, $P < 0.0001$). In support of Hypothesis 1, a significant negative relationship between day length and nocturnal activity levels suggests that baboons increase nocturnal activity as day length declines. In support of Hypothesis 2, there was a significant positive relationship between baboon activity levels and lunar luminosity with baboons more active on nights with greater light intensity. There was no support for Hypothesis 3 that perceived temperature (through wind chill) or higher levels of nightly precipitation impacted baboon activity patterns throughout the night. Nocturnal activity significantly decreased with the presence of a dependent infant.

Model B assessed a fine-scale analysis of activity throughout the night and included combined moon presence and lunar luminosity as well as temperature and wind speed and their interaction (Table 3). Overall, the full model was highly significant compared with the null model (including random effects, day length and presence of an infant; $\chi^2 = 17.52$, d.f. = 5, $P = 0.003$). In support of Hypothesis 2, lunar light intensity had a significant positive effect on baboon nocturnal activity levels, with activity increasing with higher nocturnal illumination. There was no support for wind speed or precipitation impacting nocturnal activity levels nor the interaction between temperature and wind speed (Hypothesis 3). Contrary to expectations, there was a significant negative relationship between temperature and activity levels, with activity increasing when night-time temperatures were coldest. The reduction in activity levels in the presence of an infant remained significant, as was the relationship with day length (Hypothesis 1).

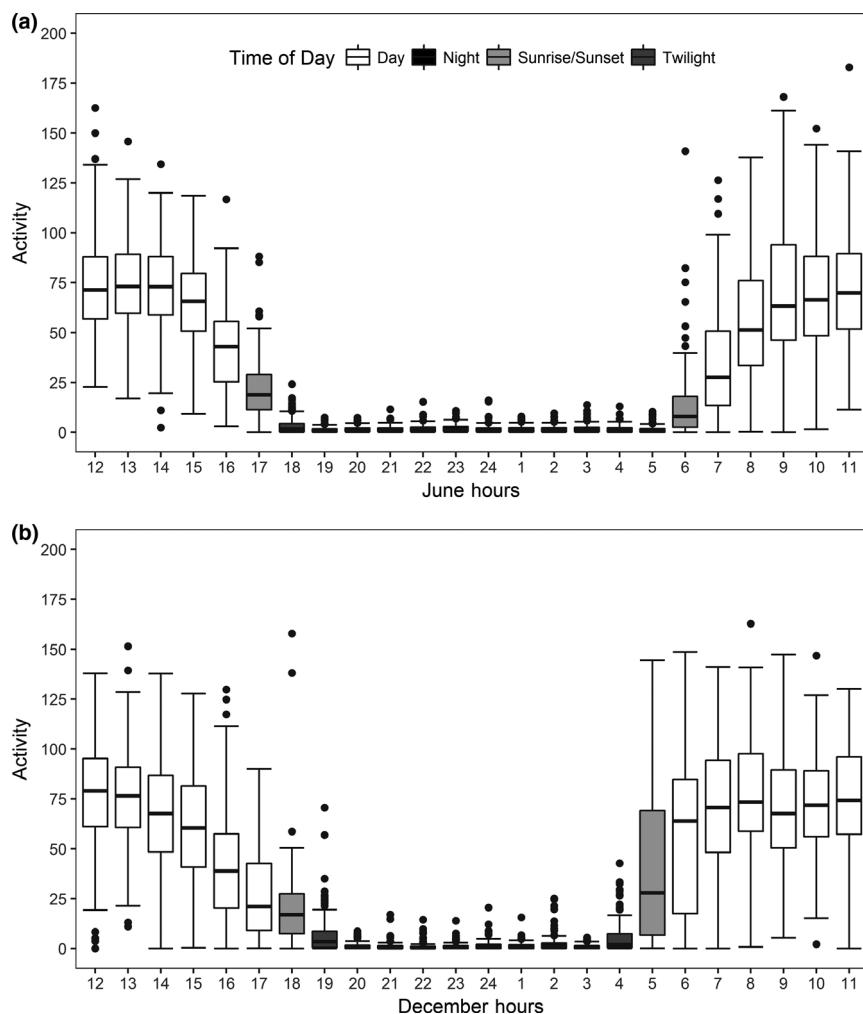


Figure 1 Boxplots (median, lower and upper quartiles, and one standard error) of activity levels across the 24-hr cycle under conditions of (a) minimum day length/maximum night length in winter (June; mean day length: 10h 44m) and (b) maximum day length/minimum night length in summer (December; mean day length: 13 h 31 min). Twilight hours for (a) (winter) are 5:00 and 18:00. Twilight hours for (b) (summer) are 4:00 and 19:00. Activity levels range from 0 (low activity) to a maximum of 255 (high activity).

Table 2 Coefficients for coarse-grained analysis of seasonal nocturnal activity (Model A; random effects include individual, night, sleeping site and baboon group)

Fixed effects	Estimate	SE	t value	Pr(> z)
Intercept	2.0286	0.1665	12.179	<0.0001
Lunar luminosity	0.0741	0.0259	2.859	0.0042
Wind chill	-0.0010	0.0024	-0.421	0.6734
Precipitation	0.0526	0.0407	1.292	0.1964
Day length	-2.2643	0.3176	-7.129	<0.0001
Infant presence	-0.3312	0.0399	-8.288	<0.0001

Significant coefficients are highlighted in bold.

Discussion

A coarse-grained model (Model A) indicated that varying day-light hours and levels of lunar light intensity may alter nocturnal activity in baboons ($N = 3$) in the western Soutpansberg

Mountains. In addition, a fine-scale analysis demonstrated that temperature, the presence of the moon (coupled with lunar light intensity) and day length impacted baboon activity levels throughout the course of the night. For both analyses, the presence of an infant had a significant negative effect on the nocturnal activity levels of the adult female. Collectively, these analyses appear to support two out of the three hypotheses (H1 and H2), with baboons seeming to respond to environmental conditions through changes in nocturnal behaviour. However, the fact that levels of nocturnal activity are very low throughout the year suggests that such patterns could simply reflect intermittent sleep disturbances rather than specific activity by the baboons.

In support of Hypothesis 1, baboons increased their nocturnal activity levels in response to shorter day lengths in winter. As previous studies have described the importance of day length in constraining the activity budgets of diurnal primates

Table 3 Coefficients for fine-grained analysis of trends in activity throughout the night (Model B; random effects include individual, night, sleeping site and baboon group)

Fixed effects	Estimate	SE	t value	Pr(> z)
Intercept	2.3390	0.1662	14.071	<0.0001
Lunar luminosity	0.0483	0.0210	2.297	0.0216
Temperature	-0.0079	0.0029	-2.661	0.0077
Wind speed	-0.0042	0.0050	-0.843	0.3992
Precipitation	-0.0084	0.0163	-0.516	0.6061
Temperature: wind speed interaction	0.0005	0.0003	1.574	0.1154
Day length	-2.4552	0.3468	-7.079	<0.0001
Infant presence	-0.3021	0.0369	-8.168	<0.0001

Significant coefficients are highlighted in bold.

living in seasonal environments (Hill *et al.*, 2003b; Ménard *et al.*, 2013), it is possible that baboons may engage in activities such as social behaviour that may otherwise be severely constrained by shorter day lengths and increased diurnal foraging in winter. Our data are not at a resolution to allow us to explore this formally, but given the low nocturnal activity in general it is more likely that activity increases are simply due to longer nights during winter exceeding the time needed for sleep. As such, although baboons exhibited higher activity levels during these periods, this could simply reflect the fact that the animals are awake and shifting position slightly rather than exhibiting heightened activity after dark.

If baboons are not compensating for short day lengths with increased activity at night, one expectation might be that the animals should start moving sooner in winter as soon as light becomes available. Interestingly, our results suggest that the baboons became active earlier in summer (Fig. 1), complementing previous studies showing that primates wake up earlier in summer (Erkert & Kappeler, 2004; Urbanski, 2011). This could be a strategy to be active earlier to avoid higher midday temperatures (Huang *et al.*, 2003; Hill, 2006; Zhou *et al.*, 2007; Aublet *et al.*, 2009; Paulo & Lopes, 2014), although it is important to note that earlier summer activity may not be associated with an earlier departure from the sleeping site. Unfortunately, our GPS data are not at a sufficient resolution to determine the timing of departure in relation to sunrise. Hall (1962) found that the baboons at Cape Point, South Africa, began their active day earlier during the winter months, although subsequently concluded that emergence times were independent of sunrise. However, Davidge (1978) reported that the baboons rested longer immediately following emergence from their sleeping site during the winter months, possibly as a response to a need to warm up in direct sunshine (see Stelzner & Hausfater, 1986). Thermoregulatory considerations may thus mask any movement response to the constraints of short days and long nights in winter.

Lunar luminosity had a positive effect on nocturnal activity levels in both models, supporting Hypothesis 2. Baboons were more active on nights exhibiting greater lunar light intensity, but only at times when the moon was visible above the horizon. Baboons did not travel or forage with increased lunar luminosity and remained on their relatively narrow sleeping cliffs at night. Although baboons in the western Soutpansberg Mountains have been recorded being predated on by leopards

(*Panthera pardus*) on their sleeping sites at night, it seems likely that lunar luminosity may inhibit leopards from attacking. This is primarily because ambush predators (such as felids) are generally less successful at hunting at such times due to a reduction in ambush cover that would otherwise be provided on darker nights (Sunquist & Sunquist, 1989; Martins & Harris, 2013). Nevertheless, Bidner, Matsumoto-Oda & Isbell, (2018) found that lunar luminosity did not influence leopard visitation rates at sleeping sites in Laikipia, Kenya, suggesting that some elements of predator behaviour are not influenced by the lunar cycle.

While many nocturnal and cathemeral primates exhibit higher activity levels on full moons (Gursky, 2003; Kronfeld-Schor *et al.*, 2013), it seems likely that for many species, nights exhibiting greater light intensity may simply have a stimulating effect that supersedes standard circadian activity patterns (i.e. positive masking) (Donati *et al.*, 2013). Such an effect may be especially true in primate species such as chacma baboons that lack a specialized visual structure that aids in nocturnal vision (the *tapetum lucidum*).

Although our data do not show significant movement away from the sleeping site between 20:00 and 22:00 (median 10.24 m, range: 0.00–773.26 m, GPS accuracy = 5 m or less, N = 623), baboons in western Soutpansberg exhibited seemingly greater nocturnal activity patterns compared with those in equatorial Kenya (Isbell *et al.*, 2017). Nevertheless, there were several nights where baboons moved greater distances (>100 m; N = 57) with anecdotal observations, particularly alarm vocalisations, suggesting they may have been driven from their sleeping sites by the presence of a predator (unpublished data). Even so, there was no correlation between distance moved and activity levels in those 2 h ($r = -0.05$, N = 605, $P = 0.218$), suggesting that this cannot account for our results. Despite occasionally moving large distances, therefore, the generally low activity levels at night appear to simply reflect disturbed sleep patterns.

A number of factors have been found to reduce sleep quality in non-human primates, including weather conditions (such as wind and rain) and disturbance by either predators or members of their own group (Anderson, 2000). Our results suggest that lunar luminosity may possibly cause sleep disturbances in baboons and altered sleep patterns due to environmental conditions (Navara & Nelson, 2007) and increased nocturnal light exposure in urban environments have been found in humans

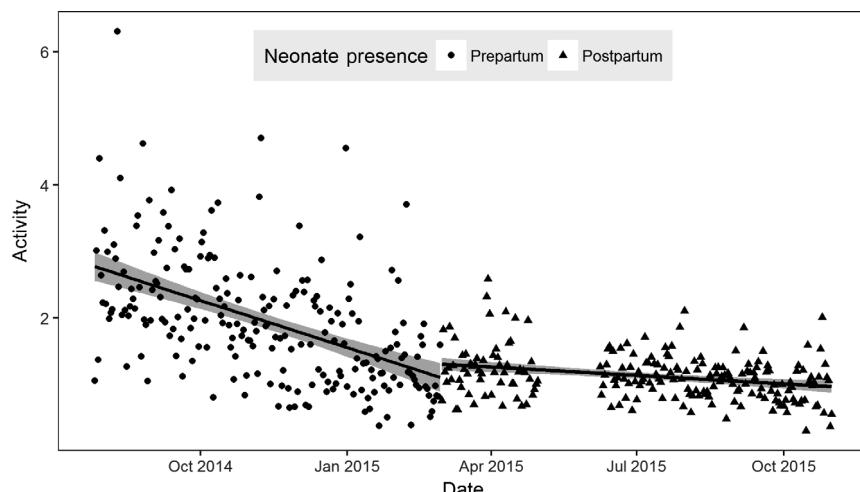


Figure 2 Relationship between nightly nocturnal activity levels and the presence of an infant (one activity value per night).

(Muniezawa *et al.*, 2011; Ohayon & Milesi, 2016). Interestingly, melatonin (a hormone that regulates sleep and wake patterns) suppression in humans can be achieved after being exposed to 90 min of light levels equivalent to a full moon (Brainard *et al.*, 2001) leading to a loss in quality of sleep. Baboons sleeping on cliffs, therefore, may experience similar issues with lower sleep quality on moonlit nights.

Female baboons in the western Soutpansberg increased their activity on nights with cooler temperatures, contrary to our predictions for Hypothesis 3. Baboons, like other primates and mammals, are known to respond to thermoregulatory constraints by huddling with one another (Gilbert *et al.*, 2010). While such a strategy allows for heat conservation and leads to the prediction that activity should decline at low temperatures, previous research on Guinea baboons suggests that individuals may often alter their positions throughout the night as a response to changing climatic conditions (such as wind speed and rain) (Anderson & McGrew, 1984). The significant effect of temperature on baboon activity in the western Soutpansberg may thus simply reflect localized conditions and sleeping site preference and a response to colder conditions by changing huddling positions throughout the night. Although Anderson & McGrew (1984) did not find temperature to have an effect on postural adjustments, it should be noted that the relatively warmer conditions that are characteristic of Niokolo Koba National Park, Senegal, may negate the need for such behaviours.

An interesting outcome of our analyses was that nocturnal activity levels for one female dropped significantly after giving birth (Fig. 2). While this might be in contrast to predictions that infant presence may increase activity, it should be recognized that with the exception of one non-human primate study (Fite *et al.*, 2003), such expectations were driven primarily from research involving maternal sleep disturbances in human mothers (Nishihara & Horiuchi, 1998; Dennis & Ross, 2005; Goyal, Gay & Lee, 2007). In the context of baboons, there have been several studies highlighting the costly demands associated with infant rearing (Dunbar & Dunbar, 1988; Altman & Samuels, 1992). Interestingly, Barrett *et al.* (2006)

found that baboons at De Hoop Nature Reserve (South Africa) did not increase time spent feeding as a response to infant rearing but instead suppressed their diurnal activity levels by resting more frequently during the day (possibly due to general fatigue after giving birth). The results here suggest that females with infants may also increase resting and inactivity at night, although it is important to note that the activity sensors we used were not able to pick up subtle behaviours associated with infant suckling. Nevertheless, the fact that nocturnal activity also declines across pregnancy suggests that there are energetic consequences of pregnancy and infant rearing that are reflected in increased resting requirements at night.

Despite having been effective in the assessment of primate movement (Papailiou, Sullivan & Cameron, 2008; McFarland *et al.*, 2013), the data derived from accelerometers in this analysis can only be utilized to assess how overall trends in nocturnal activity are impacted by a specific attribute. Since the GPS collars attached to the baboons only collected a single fix late at night, it was not possible to supplement this information with additional behavioural data. While the rise in nocturnal activity after shorter days and on moonlit nights probably points to baboons making small adjustments, additional data are needed to assess whether baboons reallocate specific behaviours to the nocturnal period. Infrared cameras have successfully been utilized to assess nocturnal behaviours in diurnal species (Barrett *et al.*, 2004; Gula *et al.*, 2010; Thuppil & Coss, 2016) and may therefore be valuable for remotely determining temporal trends in nocturnal activity. In addition, fine-scale GPS data in conjunction with accelerometers should also permit more refined analysis (Fehlmann *et al.*, 2017). Finally, we suggest that future research should ideally use accelerometers that incorporate the *z*-axis (up and down movements) when assessing the movement patterns of terrestrial mammals. This would not only allow for a more refined assessment of movement patterns, but may also allow the identification of specific behaviours (Shepard *et al.*, 2010).

Results from two generalized linear mixed models show that shorter days, increased lunar luminosity and lower temperatures

had a weak (but positive) effect on nocturnal activity levels in chacma baboons. Given that the effect sizes of the relationships were modest, it seems likely that sleep was simply more interrupted under conditions of long winter nights, high lunar illumination and at cold temperatures. Future research should focus on identifying the precise behaviours exhibited during heightened activity in the nocturnal phase to better understand how diurnal primates living in temperature latitudes respond to fluctuating environmental conditions.

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