

# 1 Illuminating Movement? Nocturnal Activity Patterns in Chacma 2 Baboons

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## 19 **Keywords**

20 Diurnal, Cathemeral, Day Length, Lunar Cycle, Constraints, Time Budgets

21

## 1 **Abstract**

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

## 1 **Introduction**

2 Diel activity patterns typically refer to when a species is primarily active. While most  
3 mammals are active at night (nocturnal), several taxa have evolved to be active during  
4 daylight hours only (diurnal), at intermediate light conditions (such as at dawn and dusk:  
5 crepuscular), or throughout the 24-hour cycle (catheMERal) (Bennie *et al.*, 2014). Factors that  
6 influence diel activity patterns may vary between species and include physical characteristics  
7 such as the structure of visual systems (Veilleux & Kirk, 2014) to a range of environmental  
8 factors including weather conditions (such as temperature) (Herman, 1977; Dussault *et al.*,  
9 2004), predation (Lima & Dill, 1990), and competition avoidance (Carothers & Jaksić,  
10 1984). Although behaviour is generally constrained to the active period, it is important to  
11 understand how extrinsic (environmental) variables enhance or constrain the potential for  
12 behavioural flexibility and for activity to extend into other phases of the 24-hour cycle.

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

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

1 means to avoid thermal stress (Herman, 1977; Dussault *et al.*, 2004; Bourgoin *et al.*, 2011;  
2 Hetem *et al.*, 2012). Behavioural plasticity in relation to climatic conditions may be best  
3 illustrated in species that live in seasonal environments where fluctuating climatic conditions  
4 coupled with limited daylight hours have the potential to alter activity budgets (Dunbar,  
5 1992; Hill *et al.*, 2003; Hill *et al.*, 2004b).

6 In primates, seasonal shifts in activity have been recorded in cathemeral species, who are  
7 found to regularly shift their activity patterns throughout the 24-hour diel cycle. Mongoose  
8 lemurs (*Eulemur mongoz*) living in seasonally dry forests became more diurnal during the  
9 wet season due to lower night time light intensity and yet became chiefly nocturnal during the  
10 dry season when day length was shorter (Curtis, Zaramody & Martin, 1999). In less  
11 predictable environments that are characteristic of south-eastern Madagascar, brown collared  
12 lemurs (*Eulemur collaris*) shifted their activity levels in response to food availability and thus  
13 became more diurnally active when ripe fruit was more readily available (Donati *et al.*,  
14 2007). Despite this remarkable seasonal plasticity, there has been no formal investigation to  
15 date of whether such flexibility extends to the use of the nocturnal phase in anthropoids (who  
16 are considered strictly diurnal with the exception of *Aotus*) residing in seasonal environments  
17 and whether such species can compensate for diurnal time budget constraints, particularly in  
18 winter, through nocturnal activity.

19 In diurnal primates, nocturnal activity in response to increased lunar luminosity has been  
20 reported for ring-tailed lemurs (*Lemur catta*) (Parga, 2011; Donati *et al.*, 2013). Chimpanzees  
21 (*Pan troglodytes*) have been recorded engaging in behaviours such as feeding (Chivers,  
22 1987), mating (Nishida, 1994), and traveling (Pruetz & Bertolani, 2010) under increased  
23 moonlight, although a recent analysis by Tagg (*et al.*, 2018) found that lunar luminosity had  
24 no effect on nocturnal activity in chimpanzees from 22 different populations. Nevertheless,  
25 Krief (*et al.*, 2014) found that chimpanzees in Kibale National Park, Uganda, were more

1 likely to crop raid under moonless nights as a possible means to prevent detection from  
2 humans. The interactions between lunar luminosity and nocturnal behaviour in diurnal  
3 species is thus not straightforward.

4 Despite being considered diurnal, baboons have been recorded becoming active at night as a  
5 response to lunar luminosity. For example, yellow baboons (*Papio cynocephalus*) in Kenya,  
6 had periods of frequent alarm calling with increased nocturnal illumination (Altmann &  
7 Altmann, 1970), whereas Guinea baboons (*Papio papio*) in Sengal were found to regularly  
8 move throughout the night and to leave sleeping sites earlier in the morning during the dry  
9 season when nocturnal illumination was greater (Anderson and McGrew, 1984). Using  
10 accelerometers and GPS collars, Isbell and colleagues (2017) found low levels of nocturnal  
11 activity in a group of olive baboons (*Papio anubis*) in Laikipia, Kenya, with movement found  
12 to occur on 15% of nights, but there was no clear indication that baboons responded to  
13 increased moonlight. Although nocturnal activity may be marginal in equatorial baboons,  
14 there has yet to be a formal assessment of nocturnal activity in non-equatorial populations.  
15 Such populations are likely to experience significant ecological constraints on time at certain  
16 times of year (Hill *et al.*, 2003) such that the adaptive use of the nocturnal phase may allow  
17 them to compensate for limits in the diurnal activity period at these times (although  
18 decreasing temperatures during winter months may impose thermoregulatory constraints that  
19 may lead to a decrease in activity).

20 Due to practical constraints ranging from inadequate visibility to unintentionally altering  
21 natural sleeping habits, previous research on nocturnal activity patterns in diurnal anthropoids  
22 has been primarily limited to anecdotal observations (Vessey 1973; Anderson and McGrew  
23 1984; Stelzner and Hausfater 1986; although see Isbell *et al.*, 2017; Tan *et al.*, 2013).

24 However, recent advances in radio-telemetry have allowed for the collection of activity data  
25 through dual axis accelerometers attached to GPS (Global Positioning System) collars.

1 Accelerometers have been especially useful in allowing researchers to monitor the behaviour  
2 of cryptic species such as pumas (*Puma concolor*) (Williams *et al.*, 2014), badgers (*Meles*  
3 *meles*) (McClune *et al.*, 2014) and lynx (*Lynx lynx*) (Podolski *et al.*, 2013) as well as activity  
4 patterns during time periods where behavioural observations are difficult (Cooke *et al.*, 2004;  
5 Brown *et al.*, 2013). Accelerometers have also proven effective on primates (including  
6 baboons; Markham and Altmann 2008; Fehlmann *et al.* 2017; Isbell *et al.* 2017) and have  
7 been employed to assess intragroup (Mann *et al.*, 2005) as well as seasonal variability in  
8 activity patterns (Erkert & Kappeler, 2004; Muñoz-Delgado *et al.*, 2005; Eppley, Ganzhorn &  
9 Donati, 2015).

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

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

1 H1: Baboons will respond to shorter day lengths in winter by extending their activity into the  
2 nocturnal phase.

3 H2: Nocturnal activity will increase on nights exhibiting greater lunar luminosity (i.e. during  
4 a full moon) due to increased visual acuity.

5 H3: Environmental variables will impact nocturnal activity levels due to thermoregulatory  
6 constraints. Specifically, activity will decrease as temperature and the wind-chill equivalent  
7 temperature decreases and wind-speed increases, and as precipitation increases.

## 8 **Materials and methods**

### 9 **Study Site**

10 This study was based at the Lajuma Research Centre in the western Soutpansberg Mountains,  
11 Limpopo Province, South Africa (23°06'45.14"S 29°11'37.10"E). Having a maximum  
12 elevation of 1748 metres above sea level (Mostert *et al.*, 2008) and running approximately 250  
13 km from east to west and 15-60 kilometres from north to south (Berger *et al.*, 2003), the  
14 Soutpansberg Mountains are a topographically complex environment consisting of numerous  
15 habitats ranging from closed woodlands, mistbelt forests, bushveld complexes, as well as  
16 relatively open and rocky sub-alpine mountain bushveld and sourveld ecosystems (Mostert *et*  
17 *al.*, 2008; Kirchof *et al.*, 2010). The study site has a mean annual rainfall of 724 mm with a  
18 summer rainy season (December to February) and a winter dry season (May to August)  
19 (Willems, Barton & Hill, 2009). Mean daily minimum and maximum seasonal temperatures  
20 throughout the study period ranged from 16.8-17.6°C in winter to 21.2-22.0°C in summer.  
21 Mean nightly minimum and maximum temperatures ranged from 12.8-13.4°C (winter) and  
22 18.6-19.1°C (summer). Day length fluctuates from approximately eleven hours in winter to  
23 over thirteen hours in summer.

## 1 **Baboon Collaring Methods and Activity Data Collection**

2 Adult female baboons (N=3) from two groups were fitted with Vectronic GPS-PLUS collars  
3 18 (VECTRONIC Aerospace, Berlin, Germany) between September 2013 and November  
4 2015 (Table 1). One individual was collared twice during the study period and only females  
5 were collared since males periodically transfer between groups.

6 All baboons were sedated with a combination of 1 - 1.4mg/kg tiletamine/zolazepam (Zoletil,  
7 Virbac RSA (Pty) Ltd) and 0.02 - 0.03mg/kg medetomidine (Domitor, Pfizer Laboratories  
8 (Pty) Ltd), delivered via remote injection dart (DanInject International SA) before being  
9 fitted with a collar. After all procedures were completed, the medetomidine was antagonised  
10 with an intramuscular dose of atipamezole (Antisedan, Pfizer Laboratories (Pty)), given at 0.1  
11 - 0.15mg/kg and the animals were allowed to recover in a crate before being released near to  
12 their group.

13 Collars were programmed to take GPS fixes every hour between 06:00 and 20:00 SAST with  
14 one nocturnal fix at 22:00 (N = 11129; mean fixes per day 15.43 (96.4%). The GPS collars  
15 incorporated dual-axis activity sensors which captured acceleration on two axes (X-axis and  
16 Y-axis) at 4Hz, with the data processed and stored as 120s averages. Accelerometers were  
17 located at the top of GPS collars and near the back of the animals' neck. Direction of the X  
18 axis sensors moved from front to back whereas the direction of the Y axis from side to side as  
19 the animals moved. In this case, the X-axis represented forward and backward movements  
20 and the Y-axis sideward and rotary movements ("body roll movement") (Berger, Dettki &  
21 Urbano, 2014). Our collars did not have accelerometers that incorporate the Z-axis (up and  
22 down movements). Given the strong positive correlation found between the X-axis and the Y-  
23 axis (Pearson's  $r = 0.953$ ,  $p = < 0.0001$ ), only the X-axis data were used in analysis  
24 (following Heurich *et al.*, 2014). Activity values derived from sensors range from 0 (no  
25 activity) to 255 (high activity).



1 Most GPS collars fell off when designated (378 days after the collars were fitted) with the  
2 exception of one collar which fell off earlier than expected. All data were downloaded  
3 regularly through an Ultra High Frequency (UHF) terminal.

4

## 5 **Predictor Variables**

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

15 Local climatic data including rain, temperature, wind speed, and wind chill equivalent  
16 temperature were collected from an on-site SAEON (South African Environmental  
17 Observation Network) weather station. The wind chill equivalent temperature combines  
18 temperature and wind speed to estimate the perceived environmental temperature (Hill *et al.*,  
19 2004a). Precipitation was measured as the rainfall in a half-hour interval or the average  
20 nightly rainfall depending on the analysis (see Statistical Analysis).

21 Lunar luminosity, defined as the percentage of the lunar sphere that is visible due to  
22 illumination by the sun was used to assess whether moonlight influenced baboon nocturnal  
23 activity. Lunar luminosity, daily moonrise and set times, and day length (being the period in  
24 which the Earth receives illumination from the sun) were downloaded from NASA's data

1 services (<https://data.nasa.gov/>) and synchronized to the dataset. Lunar luminosity was  
2 continuous with values ranging between 0% (moon not visible) to 100% (fully visible). Since  
3 lunar luminosity is constrained to times in which the moon is visible in the night sky (above  
4 the horizon), lunar luminosity values were constrained by moonrise and set times each night.  
5 Unfortunately, cloud coverage data could not be obtained for these analyses.

## 6 **Statistical Analysis**

7 In order to test the three hypotheses, nocturnal activity data were separated into two different  
8 datasets. Dataset A consisted of average activity throughout each night within the study  
9 period (N=777) and allowed a broad scale analysis (Model A) for an overall assessment of  
10 seasonal trends. Dataset B (N=14019) comprised of average activity in half hour intervals  
11 (i.e. the average activity within every half hour for each individual night). Dataset B  
12 permitted a fine scaled model (Model B) with the inclusion of environmental variables that  
13 may shift throughout the night.

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

21 Day length was included in both coarse and fine-grained models to assess whether baboons  
22 responded to shorter days by extending their nocturnal activity levels throughout the night  
23 (H1). To assess the impact that the lunar cycle had on baboon activity levels (H2), lunar  
24 luminosity was included in the coarse-grained model (Model A), with the luminescence value

1 corrected for the presence of the moon combined in Model B (fine-grained model). Mean  
2 nightly wind chill temperatures and precipitation levels were included in Model A to assess  
3 the impact of weather variables (H3). We used mean instead of lowest temperature for Model  
4 A since the meteorological data allowed us to account for the variability in temperatures  
5 across each half hour interval rather than using a single coldest value for the night.  
6 Temperature, wind speed (and the interaction between the two), and rainfall levels at half  
7 hour intervals were included to assess whether fluctuating environmental variables had a fine-  
8 grained influence on baboon nocturnal activity levels (Model B).

9 To account for intergroup, individual, and nightly variability, collar identity (N=4) specific  
10 groups (N=2), night (N=777), sleeping site identity (derived from the nocturnal GPS fix and  
11 ground-truthed with observational data, N=19) were included as random effects. Collar  
12 identity was preferred as a random effect over individual identity due to possible differences  
13 in collar performance. As one collared female gave birth during data collection, the presence  
14 of an infant was thus included as a factor to account for the costs of maternal care such as  
15 infant carrying, suckling and increased vigilance (Altmann & Samuels, 1992; Rendall,  
16 Cheney & Seyfarth, 2000; Maestriperi, 2011) impacting on nocturnal activity. Subsequent  
17 results were analysed in RStudio and visualised with the aid of the ggplot2 package  
18 (Wickham, 2009).

## 19 **Results**

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

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

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

## 1 **Discussion**

2 A coarse-grained model (Model A) indicated that varying daylight hours and levels of lunar  
3 light intensity may alter nocturnal activity in baboons (N=3) in the western Soutpansberg  
4 Mountains. In addition, a fine scale analysis demonstrated that temperature, the presence of  
5 the moon (coupled with lunar light intensity), as well as day length impacted baboon activity  
6 levels throughout the course of the night. For both analyses, the presence of an infant had a  
7 significant negative effect on the nocturnal activity levels of the adult female. Collectively,  
8 these analyses appear to support two out of the three hypotheses (H1 and H2), with baboons  
9 seeming to respond to environmental conditions through changes in nocturnal behaviour.  
10 However, the fact that levels of nocturnal activity are very low throughout the year, suggests  
11 that such patterns could simply reflect intermittent sleep disturbances rather than specific  
12 activity by the baboons.

13 In support of hypothesis 1, baboons increased their nocturnal activity levels in response to  
14 shorter day lengths in winter. As previous studies have described the importance of day  
15 length in constraining the activity budgets of diurnal primates living in seasonal environments  
16 (Hill *et al.*, 2003; Ménard *et al.*, 2013), it is possible that baboons may engage in activities  
17 such as social behaviour that may otherwise be severely constrained by shorter day lengths  
18 and increased diurnal foraging in winter. Our data are not at a resolution to allow us to  
19 explore this formally, but given the low nocturnal activity in general it is more likely that  
20 activity increases are simply due to longer nights during winter exceeding the time needed for  
21 sleep. As such, although baboons exhibited higher activity levels during these periods, this  
22 could simply reflect the fact that the animals are awake and shifting position slightly rather  
23 than exhibiting heightened activity after dark.

24 If baboons are not compensating for short day lengths with increased activity at night, one  
25 expectation might be that the animals should start moving sooner in winter as soon as light

1 becomes available. Interestingly our results suggest that the baboons became active earlier in  
2 summer (Figure 1), complementing previous studies showing that primates wake up earlier in  
3 summer (Erkert & Kappeler, 2004; Urbanski, 2011). This could be a strategy to be active  
4 earlier to avoid higher midday temperatures (Huang *et al.*, 2003; Hill, 2006; Zhou *et al.*,  
5 2007; Aublet *et al.*, 2009; Paulo & Lopes, 2014), although it is important to note that earlier  
6 summer activity may not be associated with an earlier departure from the sleeping site.  
7 Unfortunately our GPS data are not at a sufficient resolution to determine the timing of  
8 departure in relation to sunrise. Hall (1962) found that the baboons at Cape Point, South  
9 Africa, began their active day earlier during the winter months, although subsequently  
10 concluded that emergence times were independent of sunrise. However, Davidge, (1978)  
11 reported that the baboons rested longer immediately following emergence from their sleeping  
12 site during the winter months, possibly as a response to a need to warm up in direct sunshine  
13 (see Stelzner & Hausfater, 1986)). Thermoregulatory considerations may thus mask any  
14 movement response to the constraints of short days and long nights in winter.

15 Lunar luminosity had a positive effect on nocturnal activity levels in both models, supporting  
16 hypothesis 2. Baboons were more active on nights exhibiting greater lunar light intensity, but  
17 only at times when the moon was visible above the horizon. Baboons did not travel or forage  
18 with increased lunar luminosity and remained on their relatively narrow sleeping cliffs at  
19 night. Although baboons in the western Soutpansberg Mountains have been recorded being  
20 predated on by leopards (*Panthera pardus*) on their sleeping sites at night, it seems likely that  
21 lunar luminosity may inhibit leopards from attacking. This is primarily because ambush  
22 predators (such as felids) are generally less successful at hunting at such times due a  
23 reduction in ambush cover that would otherwise be provided on darker nights (Sunquist &  
24 Sunquist, 1989; Martins & Harris, 2013). Nevertheless, Bidner, Matsumoto-Oda & Isbell,  
25 (2018) found that lunar luminosity did not influence leopard visitation rates at sleeping sites

1 in Laikipia, Kenya, suggesting that some elements of predator behaviour are not influenced  
2 by the lunar cycle.

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

9 Although our data do not show significant movement away from the sleeping site between  
10 20:00 and 22:00 (median 10.24 m, range: 0.00-773.26 m, GPS accuracy = 5 m or less,  
11 N=623), baboons in western Soutpansberg exhibited seemingly greater nocturnal activity  
12 patterns compared to those in equatorial Kenya (Isbell *et al.*, 2017). Nevertheless, there were  
13 several nights where baboons moved greater distances (> 100m; N=57) with anecdotal  
14 observations, particularly alarm vocalisations, suggesting they may have been driven from  
15 their sleeping sites by the presence of a predator (unpublished data). Even so, there was no  
16 correlation between distance moved and activity levels in those 2 hours ( $r=-0.05$ , N= 605,  $p =$   
17  $0.218$ ), suggesting that this cannot account for our results. Despite occasionally moving large  
18 distances, therefore, the generally low activity levels at night appear to simply reflect  
19 disturbed sleep patterns.

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

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

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

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



1 (Dunbar & Dunbar, 1988; Altmann & Samuels, 1992). Interestingly, Barrett and colleagues  
2 (2006) found that baboons at De Hoop Nature Reserve (South Africa) did not increase time  
3 spent feeding as a response to infant rearing but instead suppressed their diurnal activity  
4 levels by resting more frequently during the day (possibly due to general fatigue after giving  
5 birth). The results here suggest that females with infants may also increase resting and  
6 inactivity at night, although it is important to note that the activity sensors we used were not  
7 able to pick up subtle behaviours associated with infant suckling. Nevertheless, the fact that  
8 nocturnal activity also declines across pregnancy suggests that there are energetic  
9 consequences of pregnancy and infant rearing that are reflected in increased resting  
10 requirements at night.

11 Despite having been effective in the assessment of primate movement (Papailiou, Sullivan &  
12 Cameron, 2008; McFarland *et al.*, 2013), the data derived from accelerometers in this  
13 analysis can only be utilised to assess how overall trends in nocturnal activity are impacted  
14 by a specific attribute. Since the GPS collars attached to the baboons only collected a single  
15 fix late at night it was not possible to supplement this information with additional behavioural  
16 data. While the rise in nocturnal activity after shorter days and on moonlit nights probably  
17 points to baboons making small adjustments, additional data are needed to assess whether  
18 baboons reallocate specific behaviours to the nocturnal period. Infrared cameras have  
19 successfully been utilised to assess nocturnal behaviours in diurnal species (Barrett *et al.*,  
20 2004; Gula *et al.*, 2010; Thuppil & Coss, 2015) and may therefore be valuable for remotely  
21 determining temporal trends in nocturnal activity. In addition, fine-scale GPS data in  
22 conjunction with accelerometers should also permit more refined analysis (Fehlmann *et al.*,  
23 2017). Finally, we suggest that future research should ideally use accelerometers that  
24 incorporate the Z axis (up and down movements) when assessing the movement patterns of

1 terrestrial mammals. This would not only allow for a more refined assessment of movement  
2 patterns, but may also allow the identification of specific behaviours (Shepard *et al.*, 2010).  
3 Results from two generalized linear mixed models show that shorter days, increased lunar  
4 luminosity and lower temperatures had a weak (but positive) effect on nocturnal activity  
5 levels in chacma baboons. Given that the effect sizes of the relationships were modest, it  
6 seems likely that sleep was simply more interrupted under conditions of long winter nights,  
7 high lunar illumination and at cold temperatures. Future research should focus on identifying  
8 the precise behaviours exhibited during heightened activity in the nocturnal phase to better  
9 understand how diurnal primates living in temperate latitudes respond to fluctuating  
10 environmental conditions.

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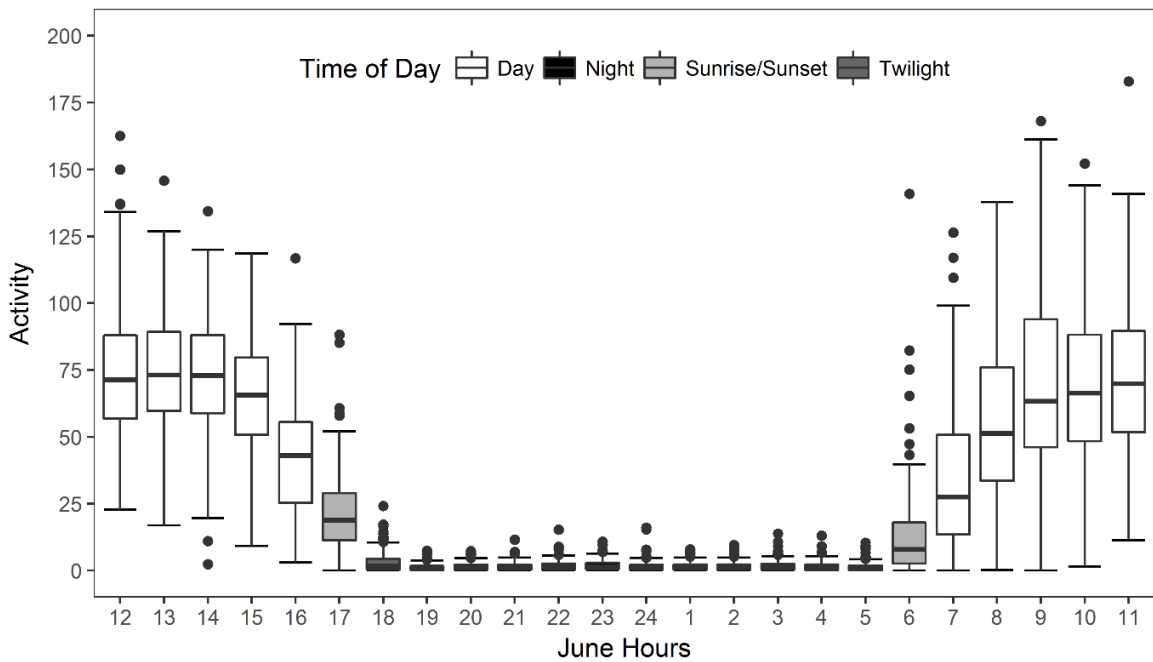
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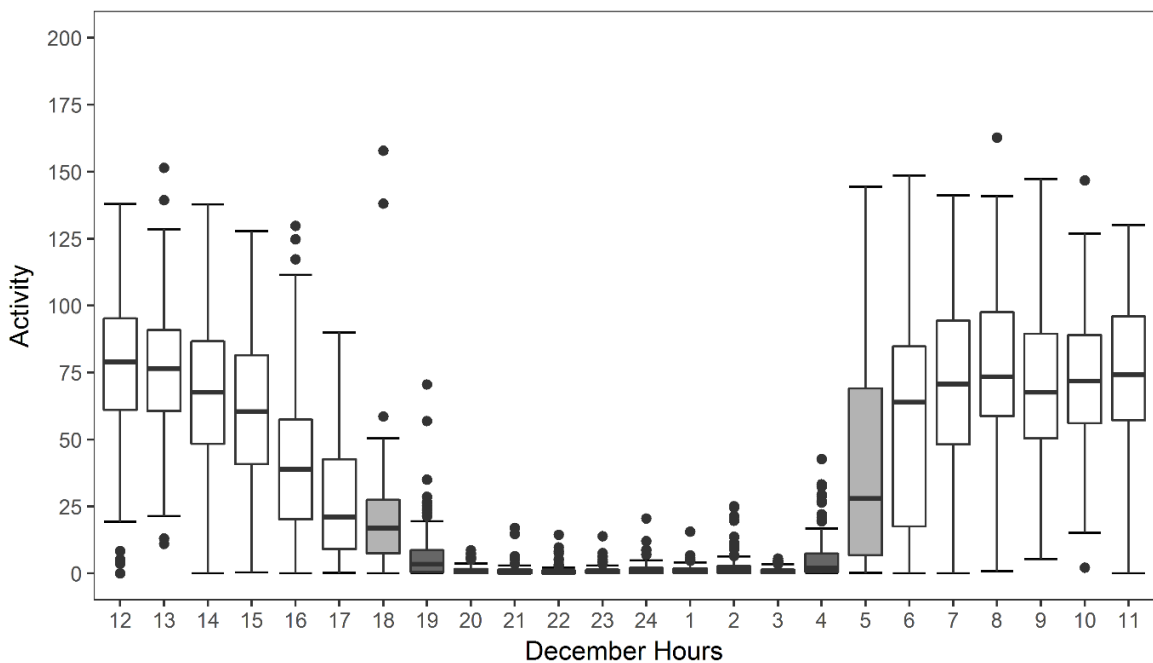
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- 18

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



7

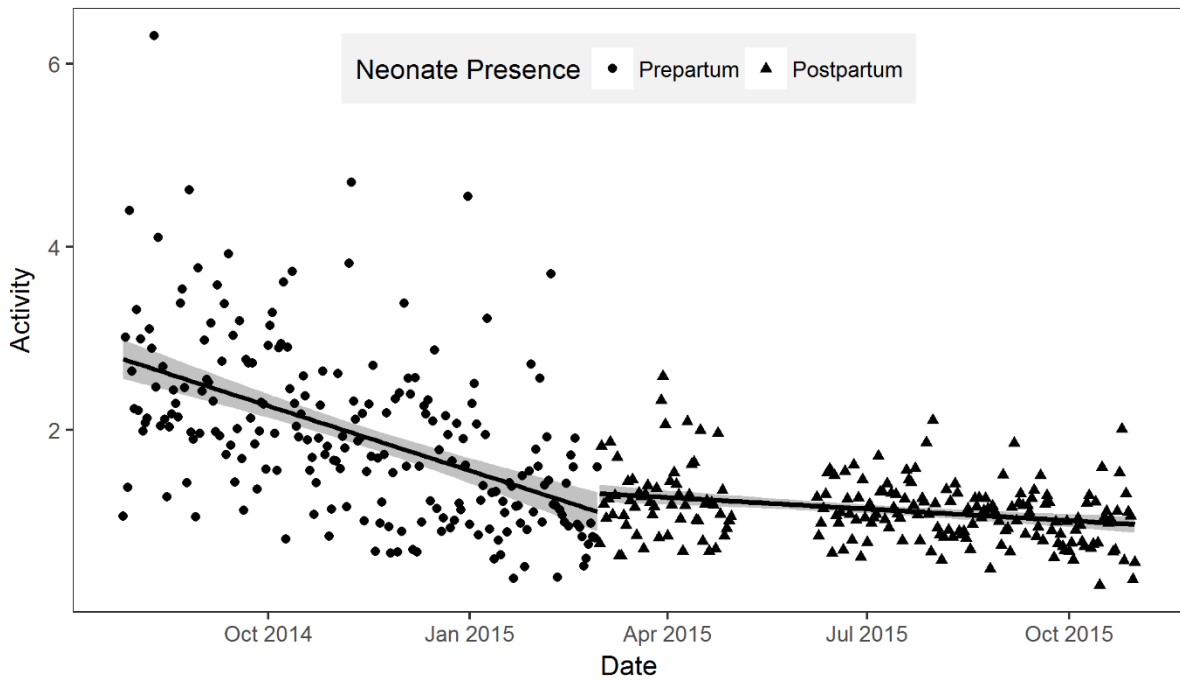


8



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

3



4



## 1 List of Tables

### 2 Table 1 GPS 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.

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3

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

Fixed Effects	Estimate	Std. Error	t value	Pr(> z )
Intercept	2.0286	0.1665	12.179	< <b>0.0001</b>
Lunar luminosity	0.0741	0.0259	2.859	<b>0.0042</b>
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	< <b>0.0001</b>
Infant presence	-0.3312	0.0399	-8.288	< <b>0.0001</b>

3

**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).

<b>Fixed Effects</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; z )</b>
Intercept	2.3390	0.1662	14.071	<b>&lt; 0.0001</b>
Lunar luminosity	0.0483	0.0210	2.297	<b>0.0216</b>
Temperature	-0.0079	0.0029	-2.661	<b>0.0077</b>
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	<b>&lt; 0.0001</b>
Infant presence	-0.3021	0.0369	-8.168	<b>&lt; 0.0001</b>

1

2