Illuminating movement? Nocturnal activity patterns in chacma baboons

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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*) 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 heighted 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 suggests that although diurnal primates may periodically be active at night, but there is limited evidence for strategic use of the nocturnal phase even in highly seasonal environments.

Introduction

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-hour cycle (cathemeral) (Bennie *et al.*, 2014). Although activity patterns are generally constrained by physiology, morphology, and behaviour, many mammals exhibit remarkable flexibility in switching between nocturnal or diurnal activity patterns in relation to biotic or abiotic cues (Kronfeld-Schor & Dayan, 2003). Nevertheless, a range of factors may mask potential temporal shifts in activity such as competition avoidance (Carothers and Jaksić; 1984), predation (Lima and Dill, 1990), thermoregulation (Chappell & Bartholomew, 1981), and lunar luminosity (Kronfeld-Schor *et al.*, 2013). 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-hour cycle.

Animals often react to intensified moonlight by supressing their activity levels (Price, Waser & Bass, 1984; Hecker & Brigham, 1999; Prugh & Golden, 2014) with such lunar-phobic behaviour hypothesised to be an anti-predator defence (Clarke, 1983; Saldaña-Vázquez & Munguía-Rosas, 2013). In contrast, while diurnal mammals typically supress activity at night, there is increasing evidence that some species may exhibit heightened nocturnal behaviour as a response to intensified moonlight (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), while among cathemeral primates, increased activity on brighter nights may enhance foraging opportunities and predator detection (Kappeler and Erkert, 2003; Fernández-Duque, de la Iglesia and Erkert, 2010).

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). Behavioural plasticity in relation to climatic conditions is perhaps 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.*, 2003; Hill *et al.*, 2004b). For example, 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).

In primates, seasonal shifts in activity have been notably recorded in cathemeral species. 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 diurnal primates and whether such species can compensate for diurnal time budget constraints, particularly in winter, through nocturnal 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 and McGrew 1984; Stelzner and Hausfater 1986; although see Isbell *et al.*, 2017 and 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 (Global Positioning System) 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 and 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 dual axis accelerometers, we assessed whether temporal, environmental, and physiological factors impact 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 socialising (Dunbar, 1992; Hill *et al.*, 2003).

Despite being considered diurnal, baboons have been recorded becoming active at night as a response to lunar luminosity. For example, yellow baboons (*Papio cynocephalus*) at

Amboseli, Kenya, had periods of frequent alarm calling with increased nocturnal illumination (Altmann & Altmann, 1973), whereas Guinea baboons (*Papio papio*) in Sengal 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 and McGrew, 1984). Using accelerometers and GPS collars, Isbell and colleagues (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 whether populations living in a non-equatorial latitude exhibit nocturnal behaviour. Such populations are likely to experience significant ecological constraints on time at certain times of year (Hill *et al.*, 2003) such that the adaptive use of the nocturnal phase may allow them to compensate for limits in the diurnal activity period at these times.

Following an assessment that baboons exhibit quantifiable activity levels at night within the Soutpansberg Mountains, South Africa, we then test the following hypotheses:

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

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

H3: 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°06'45.14"S 29°11'37.10"E). Having a maximum elevation of 1748 metres above sea level (Mostert *et al.*, 2008) and running approximately 250 km from east to west and 15-60 kilometres 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 to February) and a winter dry season (May to 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 12.8-13.4°C (winter) and 18.6-19.1°C (summer). Day length fluctuates from approximately eleven hours in winter to over thirteen hours in summer.

Baboon Collaring Methods and Activity Data Collection

Baboons (N=3) from two groups were fitted with Vectronic GPS-PLUS collars (VECTRONIC Aerospace, Berlin, Germany) (N=4) between September 2013 and November 2015. One individual was collared twice during the study period. Collars were programmed to take GPS fixes every hour between 06:00 and 20:00 SAST except for one nocturnal fix at 22:00. All baboons were sedated with a combination of tiletamine/zolazepam (Zoletil, Virbac RSA (Pty) Ltd) and medetomidine (Domitor, Pfizer Laboratories (Pty) Ltd), delivered via remote injection dart (DanInject International SA) before being fitted with a collar. The GPS collars incorporated dual-axis activity sensors which captured acceleration on two axes (X-axis and Y-axis) in two-minute intervals. In this case, the X-axis represents forward and backward movements and the Y-axis sideward and rotary movements (Berger, Dettki & Urbano, 2014). 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). All GPS collars were designed to fall off 378 days after the collars were fitted, with data downloaded regularly through an Ultra High Frequency (UHF) terminal.

Predictor Variables

Data from between 20 minutes after the onset and 20 minutes 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). 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 (http://aa.usno.navy.mil/).

Local climatic data including rain, temperature, wind speed, and wind chill equivalent temperature were collected from an on-site SAEON (South African Environmental Observation Network) weather station. The wind chill equivalent temperature combines temperature and wind speed to estimate the perceived environmental temperature (Hill *et al.*, 2004a).

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 dataset. Lunar luminosity was continuous with values ranging between 0% (moon not visible) to 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.

Statistical Analysis

In order to test the three hypotheses, nocturnal activity data were separated into two different datasets (i) average activity throughout each night within the study period (dataset A) (N=777); or (ii) average activity in half hour intervals (i.e. the average activity within every half hour for each individual night) (dataset B) (N= 14019). The utilisation of two datasets allowed for both a coarse and fine scaled analysis of nocturnal activity. While a broad scale analysis (Model A) allowed for an overall analysis of seasonal trends, a fine scaled model (Model B) permitted the inclusion of environmental variables that may shift throughout the night.

A generalized linear mixed model (GLMM) with a gamma error structure and log link function (Bates *et al.*, 2015) was used to assess total activity levels across nights in RStudio (Version 0.98.1103; RStudio, Inc.). Activity data were transformed by adding a 1 to all values to fulfil the requirements for a gamma GLMM.

Day length was included in both coarse and fine-grained models to address 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). Temperature, wind speed (and the interaction between the two), and precipitation levels at half hour intervals were included to assess whether fluctuating environmental variables had a fine-grained influence on baboon nocturnal activity levels.

To account for intergroup, individual, and nightly variability, collar identity (N=4) specific groups (N=2), night (N=777), sleeping site identity (derived from the nocturnal GPS fix and ground-truthed with observational data, N=19) were included as random effects. 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 visualised with the aid of the ggplot2 package (Wickham, 2009).

Results

Although nocturnal activity levels were below those observed during the day (diurnal, N = 777, $\bar{x}$= 64.57, SE= 0.379; nocturnal, N=777, $\bar{x}$= 1.76, SE = 0.029), consistent, but low levels of activity were observed during the nocturnal phase, with more intermediate levels of activity in the twilight phases (Fig. 1).

Model A included lunar luminosity, wind-chill equivalent temperature, precipitation and day length as predictor variables (Table 1) and represented a significant improvement over the null model (the control variables, presence of an infant, day length, and random effects (likelihood ratio test: x^2 = 80.42, df = 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 exhibiting greater light intensity. There was no support for hypothesis 3 that lower perceived temperature (through wind chill) as well as 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, and temperature and wind speed and their interaction (Table 2). Overall, the full model was highly significant compared to the null model (including random effects, day length, and presence of an infant) (x^2 = 17.52, df = 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). In contrast of 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).

Discussion

Baboons in the western Soutpansberg Mountains, South Africa, show low yet consistent levels of nocturnal activity throughout the year. A coarse-grained model (Model A) indicated varying daylight hours and levels of lunar light intensity may alter nocturnal behaviour. In addition, a fine scale analysis demonstrated that temperature, the presence of the moon (coupled with lunar light intensity), as well as 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 all three hypotheses, with baboons appearing 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 living in seasonal environments (Hill *et al.*, 2003; Ménard *et al.*, 2013), it is possible that baboons may engage in social activities that may otherwise be severely constrained by shorter day lengths and increased diurnal foraging in winter. However, given the low nocturnal activity in general it is more likely such an increase is 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 more active activity bouts after dark.

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 a reduction in ambush cover that would otherwise be provided on darker nights (Sunquist & Sunquist, 1989).

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 specialised visual structure that aids in nocturnal vision (the *tapetum lucidum*). Although baboons in western Soutpansberg exhibited greater nocturnal activity patterns compared to those in equatorial Amboseli (Isbell *et al.*, 2017), there is still no evidence for any significant movement. This is reflected in the average distance moved between 20:00 and 22:00 as captured by GPS collars (avg: 67.99 m, N=625). As such, an increase in nocturnal activity with increased moonlight may simply reflect disturbed sleep patterns resulting from the increased nocturnal luminosity.

Female baboons in the western Soutpansberg increased their activity on nights with cooler temperatures, which supports 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, 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 and McGrew 1984). The significant effect of temperature on baboon activity in the western Soutpansberg may thus simply reflect localised conditions and sleeping site preference and a response to colder conditions by changing huddling positions throughout the night. Although Anderson and 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 noted 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; Altmann & Samuels, 1992). Interestingly, Barrett and colleagues (2006) found that baboons at De Hoop 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. It should be noted, however, that the activity sensors utilised in this study 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 utilised 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 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 utilised to assess nocturnal behaviours in diurnal species (Barrett *et al.*, 2004; Gula *et al.*, 2010; Thuppil & Coss, 2015) 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).

Baboons exhibited a consistent, yet very low increase in nocturnal activity when days were shorter, lunar luminosity was greater, and when temperatures were lower. 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 thus 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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Ethical approval

This study was approved by the Department of Anthropology Research Ethics sub-committee and the Animal Welfare Ethical Review Board at Durham University, and conducted with permission from the Limpopo Department of Economic Development, Environment and Tourism, South Africa.

Conflict of interest

The authors declare that they have no competing interests.

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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: 13h 31m). Activity levels range from 0 (low activity) to a maximum of 255 (high activity).

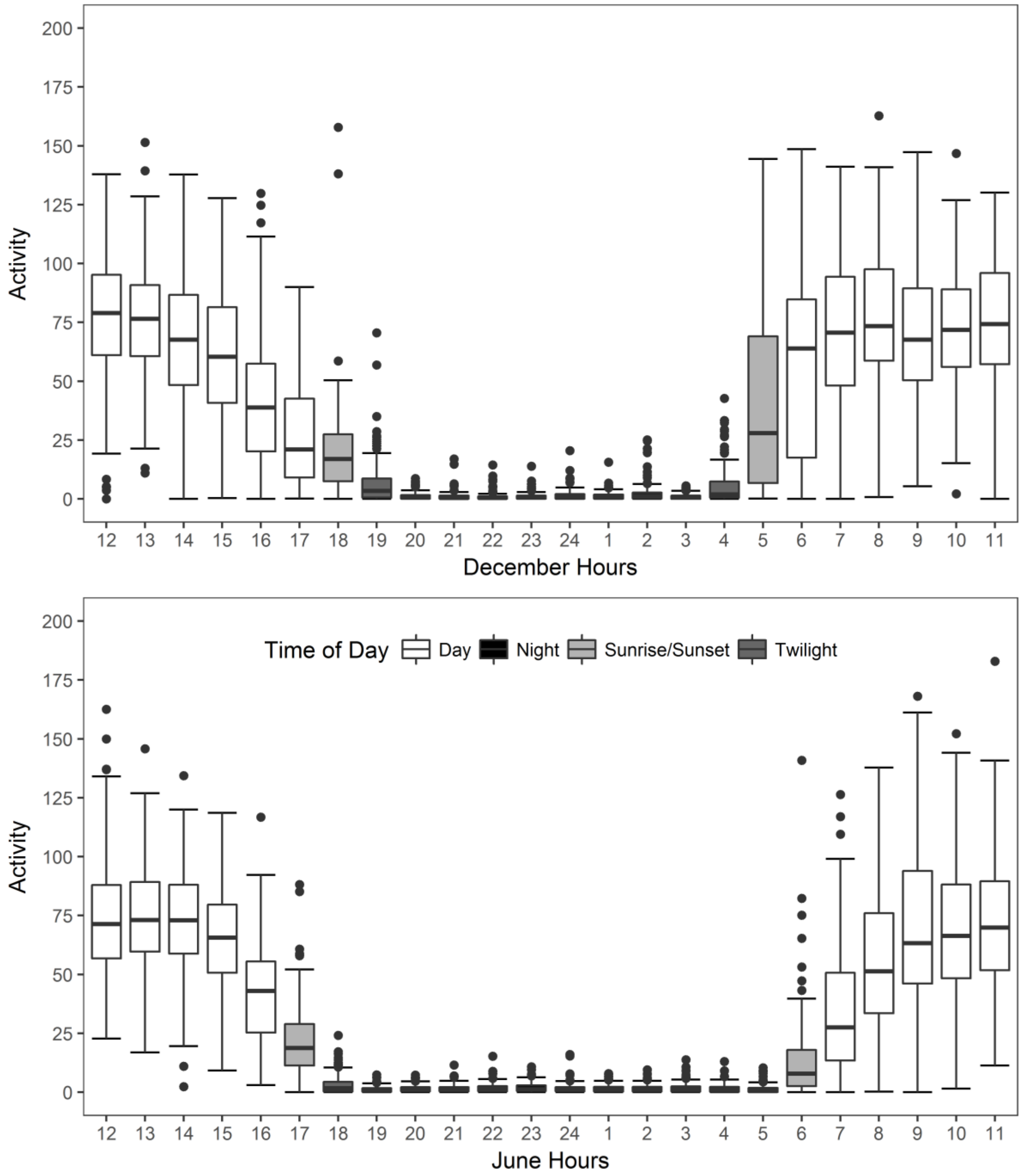
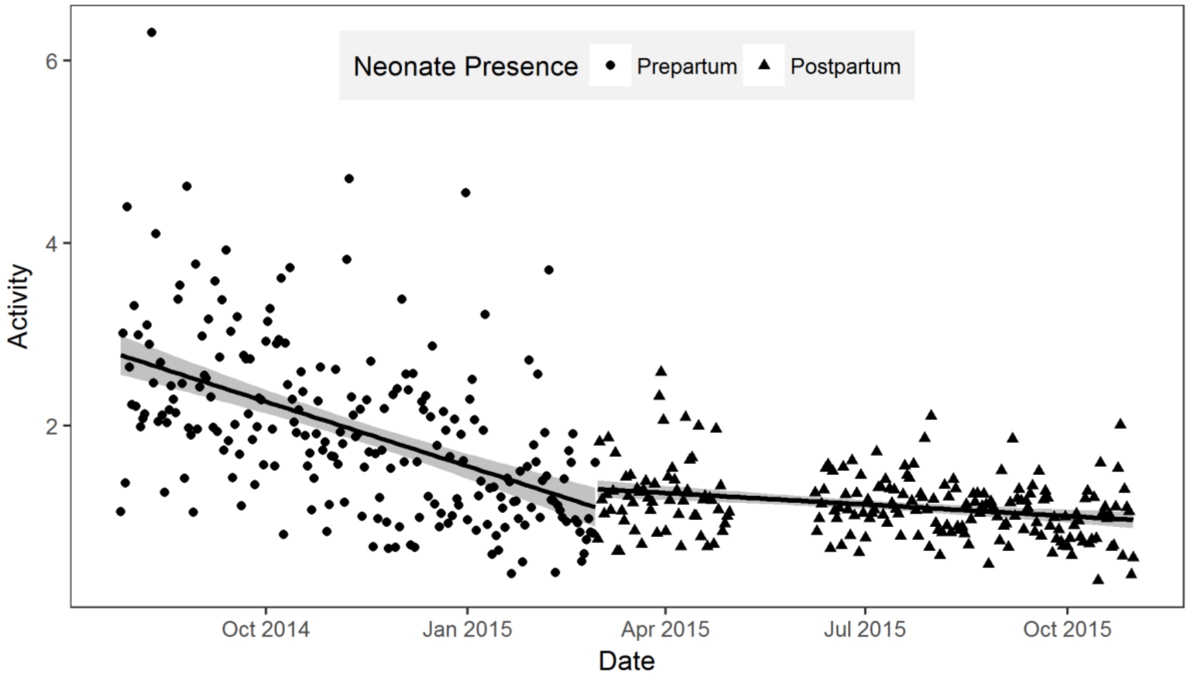


Figure 2 Relationship between nightly nocturnal activity levels and the presence of an infant (one activity value per night).



List of Tables

Table 1 Coefficients for coarse-grained analysis of seasonal nocturnal activity (Model A; 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	< **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**

Table 2 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**	**Std. Error**	**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**