

GPS-identified, low-level nocturnal activity of vervets (*Chlorocebus pygerythrus*) and  
olive baboons (*Papio anubis*) in Laikipia, Kenya

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- 24 Number of text pages: 13; number of figures: 6
- 25 Abbreviated title: nocturnal activity of vervets and baboons
- 26 Key words: nocturnality; evolution of diurnality; anthropoid primates
- 27 Grant sponsorship: National Science Foundation; L.S.B. Leakey Foundation; Wenner-
- 28 Gren Foundation; University of California, Davis; Japan Society for the Promotion of
- 29 Science (JSPS)

## **ABSTRACT**

### **Objectives**

Except for owl monkeys (*Aotus* spp.), all anthropoid primates are considered strictly diurnal. Recent studies leveraging new technologies have shown, however, that some diurnal anthropoids also engage in nocturnal activity. Here we examine the extent to which vervets (*Chlorocebus pygerythrus*) and olive baboons (*Papio anubis*) are active at night.

### **Materials and Methods**

We deployed GPS collars with tri-axial accelerometer data loggers on 18 free-ranging adult females: 12 vervets spread among five social groups, and six olive baboons spread among four groups. Their locations were recorded every 15 min, and their activity levels, for three sec/min over 7.5 mos. We also employed camera traps at seven sleeping sites that were triggered by heat and movement.

### **Results**

Travel was detected on 0.4% of 2029 vervet-nights involving three vervets and 1.1% of 1109 baboon-nights involving five baboons. Travel was mainly arboreal for vervets but mainly terrestrial for baboons. During the night, vervets and baboons were active 13% and 15% of the time, respectively. Activity varied little throughout the night and appeared unaffected by moon phase.

### **Discussion**

Our results confirm the low nocturnality of vervets and olive baboons, which we suggest is related to living near the equator with consistent 12-hr days, in contrast to other anthropoids that are more active at night. Since anthropoid primates are thought to have

evolved in northern latitudes, with later dispersal to tropical latitudes, our results may have implications for understanding the evolution of anthropoid diurnality.

It is well established that the size of the eye orbits is a reliable indicator of diel activity in primates, with nocturnally active species having larger orbits than diurnally active species (Ankel-Simons and Rasmussen, 2008; Kay and Kirk, 2000; Kirk, 2006; Ross and Martin, 2007; Ross et al., 2006). Recent studies have shown that some strepsirrhine primates in Madagascar do not fit neatly into these two activity categories. *Eulemur* and *Hapalemur* are now known to be cathemeral, i.e., active at any time during the day or night (Colquhoun, 1998; Curtis and Rasmussen, 2002; Donati et al., 2001; Kappeler and Erkert, 2003; Tattersall 1987) and their orbits overlap in size between nocturnal and diurnal species (Kay and Kirk, 2000). The discovery of cathemerality was made only fairly recently in the history of primatology because human observers are diurnal and tend to conduct their research during the daytime.

Technological advances have now made it possible to monitor animal movements and activity throughout the 24-hour cycle via camera traps and biotelemetry collars that record locational data (via GPS) as well as orientation and three-dimensional movement (via tri-axial accelerometers). While GPS/accelerometer collars have been deployed on many animal taxa, this approach is rarely used on primates, especially diurnal species, because most are easily observed without recourse to trapping and sedation, interventions that are necessary for collar deployment. However, studies using such remote sensing methods have revealed surprising results. For instance, although accelerometer data confirm that Verreaux's sifakas (*Propithecus verreauxi*) are strictly diurnal (Erkert and

Kappeler, 2004), nocturnal observations, camera trap imagery, and GPS monitoring reveal that ring-tailed lemurs (*Lemur catta*), also traditionally considered strictly diurnal (Jolly, 1966), exhibit substantial nocturnal activity and spatial displacement (Donati et al., 2013; LaFleur et al., 2014; Parga, 2011). Perhaps future work will reveal that other Malagasy strepsirrhines are also flexible in their diel patterns.

In contrast to strepsirrhines, all anthropoid primates except owl monkeys (*Aotus* spp.) are considered strictly diurnal. Thus it is even more surprising that two anthropoid species (chimpanzees, *Pan troglodytes*, and Guizhou snub-nosed monkeys, *Rhinopithecus brelichi*) have shown nocturnal travel and activity (Krief et al., 2014; Tan et al., 2013). This opens up the possibility that other anthropoid primates may also be more active at night than expected. We investigated this possibility in sympatric vervets (*Chlorocebus pygerythrus*) and olive baboons (*Papio anubis*), two African anthropoid species that tend to live in tropical, semi-arid environments. As the subjects of many studies over the years, they are considered strictly diurnal. However, to the best of our knowledge they have not yet been studied to assess nocturnal activity. Here we employ remote GPS/accelerometer technology to assess the extent to which vervets and olive baboons are active at night. Discovery of frequent activity at night would be relevant for studies of energetics and social behavior. For instance, a population of chimpanzees was discovered to engage in crop-raiding at night, thus supplementing their energy intake from wild foods (Krief et al., 2014). It has also been argued that group-living primates are constrained in the time required to invest in social relationships via social grooming to the extent that it limits group size (Dunbar, 1991; Lehmann et al., 2007). Nocturnal activity involving grooming could, presumably, reduce this pressure. Reports of

nocturnal activity in animals whose vision is adapted for sunlight might also stimulate research on their effectiveness in seeing at night and lead to greater understanding of visual processes.

## MATERIALS AND METHODS

### Study site and subjects

We conducted this research at the Mpala Research Centre on the Laikipia Plateau of central Kenya (0.29° N, 33.90° E), a semi-arid environment (total rainfall in 2014: 443.2 mm) that includes riverine habitat along the Ewaso Nyiro River, dominated by *Acacia xanthophloea*, and bushlands away from the river, dominated by *A. etbaica*, *A. mellifera*, *A. brevispica*, and *Boscia angustifolia*. The study area supports a nearly full complement of wild mammals (Young et al., 1998; Isbell and Bidner, 2016).

We monitored five groups of vervets and four groups of olive baboons with GPS and VHF/GPS radio-collars, respectively, all with tri-axial accelerometer data loggers (Savannah Tracking, Inc., Nairobi, Kenya). The goal was to place collars on two adult females in each study group. Females were targeted because they are philopatric and served as representatives of their groups. We trapped vervets in drop-traps modified from Grobler and Turner (2010) and baboons in wire cage traps placed near regular sleeping sites (Jolly et al. 2003). The traps were pre-baited with dried maize prior to trapping for 4–24 days. When an adult female entered a trap, we caught vervets by pulling the prop away using a rope tied to it, and baboons, by releasing a taut rope attached to the wire cage door, both from inside a vehicle at least 20 m away. Trapped primates were immobilized with 10mg/kg ketamine administered via hand injection or

blow dart. After weighing and measuring the animals, and fitting the collars on them, we returned them to cage traps or to two drop-traps stacked together to recover from immobilization. We fitted nine vervets and six olive baboons with collars in January 2014, and fitted three more vervets with collars in March 2014.

### **Data Collection**

The data collection period reported here spanned 7.5 months from 16 January - 31 August 2014. We programmed the collars to take GPS fixes every 15 min, and accelerometer recordings for three sec/min at 32 Hz, continuously throughout the study. When we were within UHF range of each collar, we downloaded the collar's GPS and accelerometer data using a base station (E-obs GmbH, Gruenwald, Germany) fitted with either an omnidirectional marine antenna (cxl 900-3LW: Procom, Frederikssund, Denmark) or a nine-element yagi antenna (YAGI-869A: Low Power Radio Solutions, Witney, United Kingdom).

We also monitored terrestrial activities of primates at or near seven sleeping sites with camera traps (Reconyx Hyperfire PC900 and Rapidfire RM45; Reconyx, Inc., Holmen, WI, USA) that ran continuously day and night. Body heat or movement triggered the cameras to take bursts of three photographs at the rate of one/sec. All cameras used infrared illumination for nocturnal photos.

### **Data Analysis**

“Travel” and “activity” are measures that both involve movement. Travel was identified via GPS data and always involved spatial displacement of the collared

individual greater than the precision of our GPS units. Activity was identified based on accelerometer data and involved bodily movement (McFarland et al., 2013) that could, but did not have to, involve spatial displacement. For example, a primate engaged in grooming, local foraging, scratching, or body shifting would be scored as active but not traveling in our analysis. To quantify individual activity patterns, we calculated the overall dynamic body acceleration (ODBA), an aggregate measure that combines data from all three accelerometer axes. We first generated a histogram of ODBA values during the daytime, from which we identified a threshold ODBA value for distinguishing active from inactive states (see Fig. 4). We then applied this threshold to the nighttime ODBA values to estimate the proportion of ODBA measures that were above this threshold (and thus the proportion of time spent active).

**Travel.** We extracted GPS data from 3138 primate-nights between 2000 hrs and 0400 hrs, inclusive (local time). We limited our analyses to these hours in order to avoid confounding effects from animals arriving late at their sleeping trees or leaving particularly early. We first explored the characteristics of GPS units left *in situ* where vegetation was either sparse or wooded for 1-4 days to examine the accuracy of the units. We found that when the GPS unit's internal horizontal inaccuracy estimate was  $> 23\text{m}$  for a given point, the error of the point became unpredictable. In contrast, when the value was  $< 23\text{m}$ , the location error had a 95% error range of 11m (but up to about 20m error). Thus, we expect about 95% of the location estimates for a stationary GPS collar to lie within a 22m-diameter circle of the collar's true location.

To determine whether animals traveled during the night, we developed and applied a spatiotemporal clustering algorithm to identify changes in the centroid of consecutive



observations. This algorithm involved first calculating the distance between consecutive points (step length) and multiplying this by the time between points (in minutes). We then applied a hierarchical clustering algorithm (using the complete linkage algorithm) to these distances to generate a hierarchical tree in which the branch length is equal to the spatiotemporal distance between clusters of observations. We found that the distribution of between-cluster distances was bimodally distributed, and applying a cut-off of 45m (which is twice the maximum GPS error) as the minimum spatiotemporal distance between clusters enabled us to generate an *a priori* set of candidate travel nights (Fig. 1). The two modes in the distribution of travel nights are shown in Figure 1, with most nights having very little travel (gray) and fewer nights potentially having some travel (red). These candidate travel nights ( $n = 577$ ) included many false positives, so we visually examined the nightly travel tracks for each animal-night found in the right-hand half of that distribution to manually extract the ones that showed clear evidence for travel (i.e., two clusters with separated centroids) in the movement plots.

[Insert Fig. 1 here]

When trying to characterize nightly travel of these diurnal primates, we found that there was no simple way of classifying distance traveled into movement vs. non-movement due to GPS noise. For example, we found the log of the distance between each consecutive GPS point to be normally distributed. This suggests that there were no cases where an individual moved a distance in a 15-min period that was larger than GPS error (or at least they were very rare). Had individuals made significantly larger movements than the size of the GPS error during the course of a night, e.g., hundreds of meters, these points would have appeared as a second ‘hump’ in the distribution of

between-point distances (step lengths) and thus would have been clearly identifiable.

**Activity.** The total time spent active, pooled across individuals for each species, was estimated using data taken from 3D accelerometers integrated into the GPS collars. For each 3-sec measurement of activity, we calculated ODBA by summing the total acceleration across all three axes of the accelerometer (Wilson et al., 2006). We then calculated the frequency distribution of  $\log(\text{ODBA})$  values, and found that these were clearly bimodal (see Fig. 4). Comparing the nighttime distribution of  $\log(\text{ODBA})$  values to those from the daytime suggested that “active” and “non-active” were clearly different modes, and that an ODBA threshold value of  $\log(992) = 6.9$  would separate out observations of active individuals from those of non-active individuals. This number represents the mean minima between distributions across all individuals. Thus, to calculate total time spent active for each night, we calculated the proportion of  $\log(\text{ODBA})$  values above 6.9. We calculated the moon phase for each night using the R package *lunar* (Lazaridis, 2014) to examine rates of activity relative to moon phase.

## RESULTS

### Travel

We analyzed 3138 primate-nights (vervets:  $n = 2029$ ; baboons:  $n = 1109$ ), and found evidence of nighttime travel on only 21 of these nights (vervets:  $n = 9$ ; 0.4% of vervet-nights; baboons:  $n = 12$ ; 1.1% of baboon-nights). Only three of 12 baboons, all in different groups, ever traveled at night. In contrast, five out of six baboons, representing all four study groups, engaged in nighttime travel at least once. Baboons traveled on significantly more nights than vervets ( $\chi^2 = 4.33$ ,  $p = 0.04$ ). On travel nights, vervets

moved an average of 29.7m (range: 11.5m-66.5m, SD: 21.5m) whereas baboons moved  
 an average of 22.8m (range: 11.6m-54.8m, SD: 17.2m). Figures 2 and 3 provide  
 examples of nights with and without travel in each species. None of the camera traps  
 ever revealed primates on the ground at night. Inspection of GPS locations on those  
 nights using Google Earth indicates that vervets remained in the trees on six nights, but  
 on three nights the same vervet did not move into her sleeping trees until 21:00-03:00.  
 On these nights, before ascending she was in the same bushland area, suggesting that  
 there might have been a unique refuge at that particular location, but we cannot identify  
 it. One night of arboreal travel may have been in response to a leopard, which was  
 caught on camera at the sleeping site that night. Baboons were located on kopjes (rocky  
 outcrops) on nine of the baboon-nights in which they traveled, indicating terrestrial  
 travel. On one night, two females from the same group crossed the river together,  
 suggesting the possibility of a predator attack. On another night, a female appears to  
 have descended to the ground before returning to the trees.

(Insert Figs. 2 and 3 here)

### Activity

Figure 4 contrasts high activity during the daytime with low activity during the  
 nighttime for vervets and baboons. Separating out the “active” state (the right-hand peak)  
 from the “inactive” state (the left-hand peak) on the daytime plot, and then applying this  
 same threshold to the nighttime reveals that vervets were active 13% of the night, and  
 baboons, 15%. Activity varied little throughout the night (Fig. 5) and was also not  
 obviously affected by moon phase (Fig. 6).

(Insert Figs. 4-6 here)

## DISCUSSION

Until fairly recently, it was widely thought that if a primate is active during the day it would not be active at night. The increasing awareness of cathemeral primates now challenges this view sufficiently that it is worth investigating nocturnal behavior in what have always been considered strictly diurnal primates. The availability of remote, automated technology to monitor the movements of animals throughout the 24-hr cycle now makes it possible to determine to what extent “strictly diurnal” primates are active at night. Our results confirm limited nocturnality in vervets and olive baboons, two cercopithecoid primate species traditionally considered strictly diurnal. Camera traps, accelerometer, and GPS data reveal that once vervets and olive baboons in Laikipia are settled down for the night, they rarely travel from their nighttime locations and are active at night no more than 15% of the time. Their level of nighttime activity is similar to that of humans with normal sleep patterns (Zhang et al., 2012). We were unable to identify specific types of nocturnal activity. To discriminate behaviors based on accelerometer data requires substantial time-matched data on behavioral states from direct observations. A recent study has used accelerometer data to delineate a more complete behavioral ethogram from remotely sensed data (Fehlmann et al., 2017). Time-matched data on behavioral states from direct observations are difficult to collect at night, however, because our vision is adapted for sunlight.

We propose that the rarity of nocturnal activity in vervets and olive baboons at our study site is linked to living near the equator where environmental influences vary little

over time. At our study site, sunrise and sunset vary by 31 min and 11 min, respectively, over the course of a year. In 2014 the shortest day was 12.07 hrs and the longest, 12.17 hrs (United States Naval Observatory (USNO) (<http://aa.usno.navy.mil>)). Similarly, temperatures are consistently mild in this semi-arid environment, with mean monthly minimum and maximum temperatures of 9° C and 32° C, respectively, and fluctuating by 20° C at most, during the dry season months of January-March when cloud cover at night is uncommon (Isbell, 2013).

In contrast, snub-nosed monkeys living in China's temperate environment were active at night in 25% of all camera trap events, and their nocturnal activity was attributed to living in a temperate environment where sunlight fluctuates more and seasonality is stronger (Tan et al., 2013). Among owl monkeys, those species living in tropical habitats with low seasonality are nocturnal (Khimji and Donati, 2014) whereas *A. azarai* living in highly seasonal, subtropical Argentina (Fernandez-Duque et al., 2002) is more active during the day after nights when moonlight is reduced as well as during colder months (Fernandez-Duque and Erkert, 2006). Full cathemerality, with its more uniform diel activity, has been found thus far only in Malagasy strepsirrhines, whose environment has been described as hyper-variable in rainfall and fruit productivity (Dewar and Richard, 2007), but which also includes variable hours of sunlight across the year (Curtis and Rasmussen, 2002; Donati and Borgognini-Tarli, 2006). One way to test the effects of variable day length on nocturnal activities would be to investigate nighttime activity in vervets and baboons living in southern Africa where day length is not constant across the year (Hill et al., 2003). To our knowledge, this has not yet been done.

Our findings have implications for the evolution of diurnality in primates. Like other early placental mammals, the lineage leading to primates is thought to have been nocturnal (Hall et al., 2012; Isbell, 2009; Ross and Martin, 2007; Ross et al., 2006). Primates of modern aspect first appeared during the Paleocene and Eocene in the northern latitudes (Fleagle, 2013), and included diurnal primates based on orbit size relative to body size and diel activity of extant primates (Kay and Kirk, 2000). Although these latitudes were tropical in climate, daylight would have varied across the year much more than in the tropical latitudes (23.5 degrees north and south of the equator) where most primates now live (Ankel-Simons and Rasmussen, 2008; Bennie et al., 2014). Both conventionally diurnal and nocturnal extant primate species living outside the tropics are revealing greater flexibility in diel activity, and perhaps extinct strepsirrhines living north of the tropics had similar flexibility. There is also growing evidence that anthropoids evolved in Asia (Beard, 2006). In Hubei Province, China where *Archicebus* was discovered (Ni et al., 2013), daylight fluctuates annually by four hrs (USNO: <http://aa.usno.navy.mil>). It is worth exploring the possibility that the visual systems of the first anthropoids evolved under dim light conditions (Melin et al., 2013) and that the strict diurnality that is seen in today's anthropoids evolved only after they spread to tropical latitudes.

## ACKNOWLEDGMENTS

This research was approved and conducted under IACUC protocol #17477 at the University of California, Davis. Permission to conduct research in Kenya was granted upon affiliation with the Kenya Wildlife Service (KWS) and approval from the

governmental agencies NCST and NACOSTI (permit No. P/15/5820/4650). The field research was supported by the National Science Foundation (BCS 99-03949 and BCS 1266389), L.S.B. Leakey Foundation, and the University of California, Davis to LAI, and from the Wenner-Gren Foundation to LRB, and the Japan Society for the Promotion of Science (grant numbers 23405016, 10H05776) to AMO. MCC and DRF were supported by the NSF (EAGER-IOS-1250895 and III-1514174 to MCC); DRF also received support from the BBSRC (BB/L006081/1 to B.C. Sheldon). We thank Mpala Research Centre Director Margaret Kinnaird and staff for logistical support, Mathew Mutinda and George Omondi for veterinary assistance, and Wilson Longor, Matt Snider, and Eric Van Cleave for field assistance. This manuscript was improved by thoughtful comments and suggestions from the associate editor, an anonymous reviewer, and R. McFarland.

**Author Contributions:** L.A.I. conceived the study and wrote the manuscript. L.R.B. compiled the data and contributed to the manuscript. D.R.F. executed analyses and contributed to the manuscript. A.M.O. and M.C.C. contributed to the manuscript. GPS and accelerometer data are deposited at <https://www.movebank.org>.

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