Nocturnal activity in wild chimpanzees (Pan troglodytes): evidence for flexible sleeping patterns and insights into human evolution

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ABSTRACT

Objectives – We investigated occurrences and patterns of terrestrial nocturnal activity in wild chimpanzees (*Pan troglodytes*) and modelled the influence of various ecological predictors on nocturnal activity.

Methods – Data were extracted from terrestrial camera-trap footage and ecological surveys from 22 chimpanzee study sites participating in the Pan African Programme: The Cultured Chimpanzee. We described videos demonstrating nocturnal activity, and we tested the effects of the percentage of forest, abundance of predators (lions, leopards and hyenas), abundance of large mammals (buffalos and elephants), average daily temperature, rainfall, human activity, and percent illumination on the probability of nocturnal activity.

Results – We found terrestrial nocturnal activity to occur at 18 of the 22 study sites, at an overall average proportion of 1.80% of total chimpanzee activity, and to occur during all hours of the night, but more frequently during twilight hours. We found a higher probability of nocturnal activity with lower levels of human activity, higher average daily temperature, and at sites with a larger percentage of forest. We found no effect of the abundance of predators and large mammals, rainfall, or moon illumination.

Discussion – Chimpanzee terrestrial nocturnal activity appears widespread yet infrequent, which suggests a consolidated sleeping pattern. Nocturnal activity may be driven by the stress of high daily temperatures and may be enabled at low levels of human activity. Human activity may exert a relatively greater influence on chimpanzee nocturnal behavior than predator presence. We suggest that chimpanzee nocturnal activity is flexible, enabling them to respond to changing environmental factors.

An animal's socio-biology is shaped by the environmental conditions experienced during diurnal or nocturnal activity. Diurnal animals exhibit activity during the day and sleep during the night, in contrast to nocturnal animals that are active at night and sleep during the day (Smale, Lee and Nunez, 2003). Animals are adapted to the differing conditions of the parts of the day or night during which they are awake; for example, nocturnal animals tend to have eyes that are specially adapted to absorbing as much light as possible, in order to maximise upon the contrast of low light levels in the shade of the night (Ankel-Simons and Rasmussen, 2008; Smolka et al., 2016). Similarly, the period of day or night that animals are active may be shaped by the animal's socio-biology; for example, some rodents exhibit crepuscular activity (i.e., during dusk and dawn) as a response to inter-specific resource competition (Kronfeld-Schor and Dayan, 2003).

Categorizing animals as diurnal or nocturnal may lead to observational bias, which is likely to lead to biases in the assumptions we make about animals and their behavior patterns. For example, all anthropoids, except owl monkeys (*Aotus*; Fernandez-Duque and Erkert, 2006; Wright, 1994), are categorised as diurnal and are, therefore, generally not studied during night hours as they are ubiquitously assumed to be inactive throughout the night. However, numerous accounts suggest that wild diurnal monkey species exhibit various types of activity during night-time hours, including traveling by gelada baboons (*Theropithecus gelada*; Kawai and Iwamoto, 1979), olive baboons (*Papio anubis*) and vervet monkeys (*Chlorocebus pygerythrus*; Isbell, Bidner, Crofoot, Matsumoto-Oda and Farine, 2017); playing, eating, and mating by rhesus macaques (*Macaca mulatta*; Vessey, 1973); feeding by Guizhou snub-nosed monkeys (*Rhinopithecus brelichi*; Tan, Yang and Niu, 2013); vocalizing by Barbary macaques (*M. sylvanus*; Hammerschmidt, Ansorge, Fischer and Todt, 1994); and moving sleeping sites by Japanese macaques (*M. fuscata yakui*; Nishikawa and Mochida, 2010).

In the wild, great apes have generally been assumed to remain for the 12-hour duration of the night in their nests from the time they first enter, around dusk, until their departure, around dawn (e.g., for chimpanzees, Goodall, 1962). However, many researchers have gathered anecdotal accounts of night-time vocalizations in wild-living great apes. For example, chimpanzees pant hoot (*Pan troglodytes*; Izawa and Itani, 1966; van Lawick-Goodall, 1968; Zamma, 2013), gorillas chest-beat (*Gorilla sp.*; Schaller, 1963; authors' obs.), and orangutans call (*Pongo pygmaeus;* pers. comm.: Brigitte Spillman). There have also been anecdotal visual observations of great apes being active out of their nests at night, including mating, social grooming, and play in bonobos (*Pan paniscus*; Fruth and Hohmann, 1993, 1994); and mating, feeding, and travelling in chimpanzees at Gombe, Tanzania (van Lawick-Goodall, 1968) and Mahale, Tanzania (Zamma, 2013).

Such nocturnal activity in diurnal species which do not exhibit morphological adaptations to nocturnal activity is interesting, yet the logistical and practical obstacles of conducting night-time observations have meant that investigations of the drivers of such activity in primates are very few (but see, e.g., Pruetz and Bertolani, 2009; Tan et al., 2013). However, new technologies and behavioral data collection methods, such as the use of acoustic sensors, camera trapping, and GPS collars, have overcome some of the practical and logistical obstacles to studying diurnal primates at night. These advancements are permitting new insights into the occurrence and flexibility of nocturnal activity in diurnal species and contributing to a broader understanding of the species' socio-ecology (e.g., Isbell et al., 2017; Pruetz and Bertolani, 2009; Tan et al., 2013; Zamma, 2013). Camera trapping is a relatively new methodology, but one which is increasingly widely used in the study of primates (Boyer-Ontl and Pruetz, 2014; Estienne, Mundry, Kühl and Boesch, 2017; Gregory, Carrasco Rueda, Deichmann, Kolowski and Alonso, 2014; Head, Robbins, Mundry, Makaga and Boesch, 2012; Isbell et al., 2017), and which can continuously collect data at places and times inaccessible to human observers.

Describing chimpanzee nocturnal activity can contribute to our understanding of sleep patterns, revealing possible insights into our evolutionary interpretation of human sleep and the evolution of human cognition. Chimpanzees are among humans' closest living evolutionary relatives, having shared a common ancestor 7–8 million years ago (Langergraber et al., 2012), and thus exhibit a range of physiological similarities, including characteristics of sleep. For example, all great apes experience muscle atony during sleep which necessitates a recumbent sleeping position and does not enable limb-sleeping, as seen in small primates (Anderson, 2000; Fruth and McGrew, 1998). Chimpanzees commonly nest in trees (van Lawick-Goodall, 1968; Tutin and Fernandez, 1984) and it is likely that early hominins (species of *Australopithecus* and *Homo*) also did so, encouraged by their arboreality and enabled by their light body size. Increasing body size in *Homo erectus* would have necessitated ground sleeping, which was further enabled by the discovery of fire (Coolidge and Wynn, 2006; Sabater Pi, Vea` and Serrallonga, 1997), reflecting the tree-to-ground transition that we see around this time. The safer and more comfortable sleeping conditions on the ground could have enabled better sleep quality: longer duration, higher proportion of rapid-eye movement (R.E.M.) sleep (Fruth and Hohmann, 1996), and fewer disturbances. While early hominin societies and technologies were developing (Coolidge and Wynn, 2006), improved sleep quality may have enabled increased or improved consolidation of learning. Sleep is therefore likely to have played an important role in the evolution of learning, memory, and creativity in early humans (Coolidge and Wynn, 2006; Fruth and Hohmann, 1996; Fruth, Tagg and Stewart, in press; Rasch and Born, 2013).

We can study wild great ape sleep patterns to shed light on ancestral, as well as present day, human sleep. In the pre-industrial West (before the 17th century), people appear to have commonly exhibited a pattern of fragmented sleep (Ekirch, 2006), whereby sleep onset occurs early in the evening and the night's sleep is divided into two or more bouts separated by periods of wakefulness (de la Iglesia and Lee, 2015; Wehr, 1992). Benefits may have included alertness to dangers in the depths of the night, social advantages, creativity, and innovativeness (Ekirch, 2006). In the modern day, humans generally exhibit a consolidated (one-phase) sleeping pattern, with sleep durations of 7–8 hours recommended for adults (Hirshkowitz et al., 2015) and sleep onset usually occurring several hours after nightfall. It has been argued that the 'freedom' to exhibit fragmented sleep has been lost in modern societies because of technological advances, such as artificial lighting (Moreno et al., 2015), and modern pressures, such as long working days. However, a significant body of evidence is building (Eban-Rothschild, Giardino and de Lecea, 2017; Vyazovskiy, Achermann and Tobler, 2007; Wehr, Aeschbach and Duncan, 2001) that the ancestral sleep pattern was consolidated, as observed in traditional societies today (Yetish et al., 2015). The fragmented sleep phenomenon evident in the pre-industrial West may have developed as a temporary pattern as humans moved into northern latitudes 46–50,000 years ago (Oppenheimer, 2012) and the long, cold nights encouraged early sleep onset. With the beginning of the industrial era, street lighting and policing overnight would have made after-dark activities safer, delaying sleep onset and allowing sleep to revert to a consolidated pattern (Ekirch, 2006). To assist us in further investigating this assertion that ancestral humans are likely to have exhibited a consolidated sleep pattern, we can investigate sleeping patterns in our sister taxa, the great apes: evidence of a non-fragmented sleep pattern may support our hypothesis. Using data and footage from terrestrial camera traps collected as part of the Pan African Programme: The Cultured Chimpanzee (henceforth PanAf) (Kühl et al., 2016; Vaidyanathan, 2011), this study addresses the following hypotheses concerning the possible predictors of terrestrial nocturnal activity in diurnal chimpanzees:

1) Nocturnal activity will occur infrequently and irregularly in wild chimpanzees, and will not be biased towards the middle of the night, thus revealing a consolidated sleeping pattern.

2) Building upon this, we predict that nocturnal activity will instead be influenced by environmental factors, such as temperature, rainfall, and light levels:

i) Nocturnal activity may be more likely to occur under extreme environmental conditions, such as in hot and dry savanna habitats, which may hinder effective/sufficient feeding or other behaviors during the day. For example, at Fongoli, Senegal, frequent nocturnal activity is suggested to be the result of environmental stresses (Pruetz and Bertolani, 2009). We therefore hypothesize more nocturnal activity with higher temperatures, lower rainfall, and in savanna habitats.

ii) Nocturnal activity may also be facilitated by light from the moon, as chimpanzees which are physiologically adapted to light conditions will be able to see better and navigate their environment under nightfall. Among primates, rates of vocalizations increase (Anderson, 1984) and physical activity increases in chimpanzees (Izawa and Itani, 1966; Pruetz and Bertolani, 2009; van Lawick-Goodall, 1968; pers. comm.: Koichiro Zamma) and rhesus monkeys (Vessey, 1973) with increased moon illumination. Indeed, many of the early anecdotal observations of nocturnal activity in wild great apes were made in periods of high proportion of illumination by the moon (Anderson, 1984; Nishida, 1996; Pruetz and Bertolani, 2009). Owl monkeys, the only nocturnal anthropoid, have been shown to require moonlight in order to forage effectively during periods of nocturnal activity (Fernandez-Duque, de la Iglesia and Erkert, 2010). In humans, certain sleep parameters are reduced during a full moon, with shorter sleep durations and lower proportions of REM sleep being exhibited (Cajochen et al., 2013), suggesting an increase in the likelihood of wakefulness during moonlit nights. If this influence on sleep is also experienced by great apes, apes might be more active during a full moon; we therefore hypothesize more nocturnal activity with higher moon illumination.

3) Nocturnal activity may be a result of physical or perceived disturbance at night, either by predators, other large animals, or by human activity.

i) Large carnivores constitute natural predators of chimpanzees (Stewart and Pruetz 2013) and documented events involve leopards (*Panthera pardus*; Boesch, 2009; Nakazawa, Hanamura, Inoue, Nakatsukasa and Nakamura, 2013) and lions (*Panthera leo*; Nishida, 2012). Chimpanzees are likely to vocalize at night in response to the presence of such potential predators (Tutin, McGrew and Baldwin, 1981), as well as to hyena (*Crocuta crocuta*), suggesting an influence of predators on chimpanzee behavior at night. Furthermore, arboreal nesting may be partly driven by predator avoidance in chimpanzees and gorillas (e.g., Carvalho, Meyer, Vicente and Marques, 2015; Pruetz et al., 2008; Stewart and Pruetz, 2013; Yamagiwa, 2001), and gorilla females and juveniles were assumed to avoid ground nesting as a result of their relative vulnerability to predation (Yamagiwa, 2001). Therefore, we hypothesize that higher abundances of predators will increase nocturnal activity.

ii) Similarly, sleeping chimpanzees could be disturbed by other large mammals living sympatrically, specifically elephants (*Loxodonta africana*) and buffalos (*Syncerus caffer*). To our knowledge, no empirical evidence is available supporting disturbance of chimpanzees by these species; however, chimpanzees can be competitively excluded by sympatric elephants when fruit availability is low (Head et al., 2012). Therefore, we hypothesize that higher abundances of elephants and buffalos will increase nocturnal activity.

iii) Evidence exists that wild chimpanzees perceive humans as a threat across their range, as they exhibit lower densities closer to human settlements (Clark, Poulsen, Malonga and Elkan, 2009; Kano and Asato, 1994; Walsh et al., 2003), alter their behavior (Lindshield, Danielson, Rothman and Pruetz, 2017), and avoid areas of human disturbance (Arnhem, Dupain, Vercauteren, Devos and Vercauteren, 2008; Rabanal, Kühl, Mundry, Robbins and Boesch, 2010; Stokes et al., 2010; Tagg and Willie, 2013). Therefore, human activity overnight may also cause disturbance to sleeping chimpanzees. Hunters frequently operate at night and in twilight hours (Astaras, Linder, Wrege, Orume and Macdonald, 2017); the gunshots and movements of people below nest sites, for example, may pose a threat to chimpanzees. We therefore hypothesize more nocturnal activity with higher levels of human activity.

METHODS

The PanAf (Kühl et al., 2016; Vaidyanathan, 2011) was established to collect a range of ecological, social, demographic, and behavioral data to study evolutionary–ecological drivers which contribute to behavioral diversity in chimpanzee (*Pan troglodytes*) populations and to evaluate potential evolutionary scenarios central to questions of cultural evolution. The PanAf was motivated to address the knowledge gaps resulting from minimal field sites dedicated to studying wild chimpanzees. It set out to understand the evolutionary–ecological drivers that have generated the behavioral diversity found between populations of chimpanzees across their range. It wanted to investigate the vast array of possible explanatory variables, such as resource availability, historic landscape effects, predation, and disease pressure as well as inherent population dynamics influencing trait invention and loss. The PanAf therefore studies a large number of populations with a cross-sectional sampling approach. It quantifies a broad spectrum of the ecological parameters that possibly contribute to generating behavioural diversity in chimpanzees. The PanAf has included 39 long-term and temporary research sites located within the chimpanzee range since January 2010. Data from 22 of these sites were available at the time of the study (Table 1); the available data were obtained from studies of varying durations (7 to 22 months). As part of the standardized data collection at all sites, we set grids comprising 20 to 96 1×1 km cells for distribution of sampling units (to cover a minimum of 20–50 km² in rainforest and 50–100 km² in woodland savannah). We placed an average of 29 (range 5 to 41) movement-triggered Bushnell cameras per site. We placed one camera per grid cell where possible; however, in larger grids we placed cameras in alternate cells. If certain grid cells did not contain suitable habitat, such as in heterogenous sites, we placed two cameras as far away from each other as possible in the cells containing suitable habitat to maximise coverage. According to the PanAf objectives, in cases of specific locations of interest (e.g., termite fishing sites), we placed a second camera at the same location to capture the same scenes from a different angle. We placed cameras about 1m high, in locations that were frequently used by chimpanzees (e.g. trail, feeding tree). This method ensured a strategic installation of cameras, with maximal chance of capturing footage of terrestrial activity of chimpanzees. We recorded GPS location and habitat type of the location. We set cameras to 60-s video mode with a 1-s interval between triggers, and we visited and maintained cameras, and downloaded videos, every one to three months throughout the study periods (for further detail see http://panafrican.eva.mpg.de/pdf/Pan_African_Field_Protocol_July2014_final2.pdf, henceforth PanAf protocol).

[Table 1 here]

Camera-trap video data

We extracted all camera-trap videos containing chimpanzees in the night time from 10 sites that had been uploaded, prior to February 2017, onto a web-based citizen science platform, Chimp&See (https://www.chimpandsee.org/#/; Arandjelovic et al., 2016), hosted by Zooniverse (Cox et al., 2015).

On the Chimp&See platform, volunteers identified animals present in the PanAf videos. We considered a video analysed when either three volunteers marked the video as blank, seven volunteers unanimously agreed on the identity of the animal present, or 15 volunteers annotated the video. Project scientists and moderators then further assessed videos that were classified as containing chimpanzees and extracted those videos which were filmed at night and appeared dark for inclusion in this study. We also included camera-trap data from an additional 12 PanAf sites in the present study, totaling 22 sites. We watched all videos containing chimpanzees from each of these sites and extracted all those which were filmed at night and appeared dark. For each site, we calculated the camera-trapping effort (i.e., the number of cameras active throughout the study period and the number of days they were active), the number of videos filmed, and the number of videos containing chimpanzees.

We extracted date and time of each video from the timestamp of the video (if the timestamp was not present, we extracted date and time from the metadata of the video file; if this information was incorrect due to camera malfunction, we accessed date and time using the installation data recorded by the field data collectors). We excluded duplicate videos captured by one of a set of paired cameras. We calculated site- and date-specific time of sunset or sunrise (depending on whether the video was filmed before midnight or after midnight, respectively) using the US Navy web tools http://aa.usno.navy.mil/data/index.php, and classified each video of nocturnal activity as having occurred in true night (>30 min after sunset or before sunrise) or in twilight hours (within 30 min of sunset or sunrise). Similarly, we determined the moon phase (percent illumination) using the same tools, and classified each video in terms of whether or not the moon was up at the time of recording.

To identify individual chimpanzees (and assign age class and sex), we used two methods. First, for videos that had been uploaded to Chimp&See, we relied on previously assigned identifications of individual chimpanzees by citizen scientists. Citizen scientists identified each chimpanzee according to their age class and sex, described them according to individual characteristics (e.g., scars, distinctive pigmentation patterns), and assigned a unique identifying code for reference. Following independent observations in at least two distinct events, and after consensus between at least two citizen scientists and confirmation from a PanAf researcher with chimpanzee identification experience, individual identification codes (using online hashtags in any associated videos) were assigned to individual chimpanzees. Citizen scientists subsequently hashtagged any additional video captures of the same individual chimpanzee following consensus agreement from at least three people. For non-Chimp&See sites, researchers reviewed nocturnal video clips and assigned age class, sex, and individual identification codes (the latter by M. McCarthy only) for all chimpanzees exhibiting identifiable features, as above for Chimp&See sites. We defined a nocturnal activity ‘event’ as a series of consecutive videos captured by the same camera within 15 min of the previous video (Boesch et al., 2017). We further defined a ‘chimpanzee-event’ as each distinct chimpanzee (identified and non-identified individuals) appearing in the event.

For each nocturnal activity chimpanzee-event, we described the main behavior. We observed a variety of nocturnal activities, but to facilitate interpretation we grouped all activities into four main categories: ‘movement’ (including walking and running into and/or out of the camera view during the video); ‘on location’ (including ascending or descending a tree, sitting or standing); ‘social’ (including playing, grooming, displaying); and ‘feeding’.

Transect, habitat and climate data

We placed line transects to cross through the middle of each grid cell in a north-south or east-west direction across the grid. We walked transects regularly in each site (1 to 6 times per site, mean=3) during the study. We achieved an average line transect survey effort across all sites of 81.6 km, ranging from 14.2 km (Bili, Democratic Republic of the Congo) to 237.7 km (Issa, Tanzania) (Appendix 1).

We carried out surveys for animal and human signs during the regular line transect walks. We recorded all direct and indirect observations, including footprints, tracks, and feeding remains. Human signs included all (non-research related) direct observations and indirect signs of human presence, including machete cuts, camps, snares, gunshots, and spent cartridges. For each site, we calculated 'encounter rates' (signs per kilometer of transect) for elephants (*Loxodonta africana*), buffalos (*Syncerus caffer*), predators (lions, *Panthera leo,* leopards, *Panthera pardus* and hyenas, *Crocuta crocuta*), and humans using the total number of signs of each target species/group of species divided by the total line transect survey effort (km). Survey efforts per site and encounter rates per kilometer for buffalos, elephants, predators, and humans are given in Appendix 1.

During transect walks, we recorded habitat type at every observation and whenever the habitat changed during line transect walks. Habitat was classified according to the characteristics of the vegetation (e.g., size/density of trees, closed/openness of canopy), the predominant ground type (e.g., *terra firma*, swamp), and the age of the habitat (e.g., old versus young secondary), following definitions given in the PanAf protocol (Appendix 2; White and Edwards, 2000). For most sites, we summed the distance between every observation made along the first round of line transects within each habitat type. For one site (Issa), where habitat data were particularly scarce for the first round of line transects, we restricted the analysis to four transects, created mean start and end coordinates for each transect, and pooled the observation data from six rounds. We then grouped occurrences of different habitat types to subsequently calculate a percentage of forest versus savanna (Table 2) for each site, to assess habitat type as a predictor of nocturnal activity. Most sites (16 of 22) exhibited a higher percentage (>50%) of forest habitat; the remaining six sites (Bakoun, Guinea; Boé, Guinea Bissau; Geprenaf, Ivory Coast; Kayan, Senegal; Sobeya, Guinea; and Issa, Tanzania) exhibited a higher percentage of savanna habitat.

[Table 2 here]

Finally, we obtained climate data for each site. We calculated the daily average temperature from the minimum and maximum temperatures recorded the day after nocturnal activity, thus reflecting the values recorded over the preceding 24 hr. We extracted the total rainfall volume for the day preceding the night during which each nocturnal activity event occurred.

Data analysis

Occurrence and timing of nocturnal activity. For each site, we calculated the proportion of chimpanzee nocturnal activity as: (the number of chimpanzee nocturnal activity videos / the total number of all chimpanzee activity videos) × 100. We wanted to assess whether nocturnal activity occurred throughout the night or was more likely at certain times. To be comparable between different geographic locations and times of year, we scaled the recording time of the videos from 0 (sunset) to 1 (sunrise), considering its distance to sunset and the night duration on that day at that location (x = (Tvideo−Tsunset) / night duration). To understand the number of videos occurring across sites in different phases of the night, we plotted the number of videos falling in the following phases: phase 1 (1 hour after/before sunset/sunrise), phase 2 (within 2 hours of twilight), phase 3 (2 hours of early morning and late-night occurrences), phase 4 (2 hours around midnight).

Behavior during nocturnal activity. For each behavior category (movement, on location, social, feeding), we determined the number of events of nocturnal activity in which these behaviors were exhibited. Data are presented together (true night and twilight hours pooled) and separately for true night and twilight hours.

Predictors of chimpanzee terrestrial nocturnal activity. To fit a model estimating what drove terrestrial nocturnal activity of chimpanzees, we needed to avoid pseudo-replication arising from the same individual chimpanzee appearing in multiple videos and events, and multiple cameras recording at each site (Hurlbert, 1984). Hence, we first extracted, for each site, all identified chimpanzees who were clearly visible and to whom identifying features could be assigned observed at night and the nights during which at least one chimpanzee was seen. We then constructed a data set which, separately for each site, included one row for each combination of chimpanzee ID and night, indicating whether the respective chimpanzee was detected in the respective night. For sites where no single nocturnal detection was made, we included one dummy chimpanzee and one dummy night during which the dummy chimpanzee was not detected. Note that such a data set is very conservative since it only considers a minimum number of non-detections; that is, chimpanzees never being detected (likely varying in number among sites) and nights during which no detection was made, did not contribute anything to these data (except for the one dummy chimpanzee not seen during the one dummy night). Consequently, the data underestimate the magnitude of differences between sites; however, given the high risks associated with pseudo-replication we feel that this approach was the best option.

We estimated the magnitude of the effects of the different environmental predictors on the probability of chimpanzees being detected at night using a Generalized Linear Mixed Model (Baayen, 2008) with binomial error structure and logit link function (McCullagh and Nelder, 1989). Into this we included, as fixed effects, percentage of forest, abundance of predators, abundance of large mammals, average daily temperature, amount of rainfall on the day prior to the night in question, amount of human activity, and percentage illumination. The percentage of savanna was highly collinear with the percentage of forest (Variance Inflation Factor, VIF = 27.1; Field 2005; Quinn and Keough, 2002), so we excluded it from the model. As random effects, we included site, individual chimpanzee, and night; the latter two were nested within site. To keep the type I error rate at the nominal level of 0.05, we included random slopes (Barr, Levy, Scheepers and Tily, 2013; Schielzeth and Forstmeier, 2009) of average daily temperature and percent illumination within chimpanzee and site ID into the model (other random slopes were not identifiable because the respective fixed effects did not vary within chimpanzee or site ID). Originally, we also included the correlations among random intercepts and slopes. However, these appeared unidentifiable as indicated by all absolute correlation parameters being close to one (Matuschek, 2017); therefore, we removed them from the model.

To avoid the issue of multiple testing due to the multitude of fixed effects (Forstmeier and Schielzeth, 2011), we compared the fit of the full model with that of a null model lacking them but having an identical random effects structure. We estimated model stability by excluding the levels of the random effects one at a time, fitting the full model as described above to these subsets of data, and comparing the estimates derived with those obtained for the full data set. This did not reveal any severe stability issues. To rule out collinearity problems, we determined VIF for a standard linear model lacking the random effects. With a maximum VIF of 3.40, collinearity did not appear to be a severe issue. We obtained bootstrapped confidence intervals of the estimated model coefficients by means of a parametric bootstrap. We fitted the model in R (version 3.4.1 R Core Team 2016) using the function glmer of the package lme4 (version 1.1-13; Bates, Maechler, Bolker and Walker, 2015) with the optimizer 'bobyqa'. We conducted bootstraps using the function bootMer of the package lme4, and determined Variance Inflation Factors using the function vif of the package car (version 2.1-4; Fox and Weisberg, 2011). We determined P-values for the individual effects by comparing the full model with reduced models lacking the fixed effects one at a time (Barr et al., 2013) using a likelihood ratio test (Dobson, 2002). We also tested the significance of the random slopes by comparing the full with reduced models lacking random slopes, one at a time, using likelihood ratio tests. Prior to fitting the model, we checked whether the predictors had roughly symmetrical distributions; however, several did not because they were comprised of many zeros. Therefore, we were unable to find a transformation to alleviate the issue. Results of model stability, however, indicated that the model did not suffer from highly influential cases. Prior to fitting the model, we z-transformed all predictors to a mean of zero and a standard deviation of one to achieve comparable estimates and to increase the likelihood of model convergence. The sample size was a total of 989 data points (140 detections and 849 non-detections) of 119 chimpanzee-events during 103 nights (nested in site) and at 22 sites.

RESULTS

Occurrence and timing of chimpanzee nocturnal activity

We identified 143 videos containing evidence of terrestrial nocturnal activity (including true night and twilight) (Figs. 1 and 2). These made up 119 independent events (i.e., a distinct individual or a series of videos of the same individual captured by the same camera within 15 min of the previous video). These events represent 235 chimpanzee-events (i.e., event × number of distinct individuals present in the event; Table 3). When considering the site-specific and date-specific sunrise and sunset times, we observed 59 events of nocturnal activity (77 videos) in true night and 60 events (66 videos) in twilight.

[Figure 1 here]

[Figure 2 here]

[Table 3 here]

Although activity during the twilight periods was very common, we found nocturnal activity to occur in all phases of the night (Fig. 3). We observed nocturnal activity during both twilight and true night hours in 14 sites, with no twilight activity occurring in Taï R (Ivory Coast), and no true night activity in Bili (Democratic Republic of Congo), Boé (Guinea Bissau), and Taï E (Ivory Coast). We found nocturnal activity in the deeper phases of the night (i.e., phases 3 and 4, early morning, and late night occurrences and within 2 hours either side of midnight) in three sites only: Geprenaf (Ivory Coast), Issa (Tanzania), and Kayan (Senegal) (Fig. 3).

[Figure 3 here]

We found nocturnal activity to occur at an average overall proportion of 1.80% of all chimpanzee activity (day and night) observed in camera-trap footage (all sites pooled). We observed nocturnal behavior at 18 of the 22 sites (Fig. 2), with no night activity observed in Conkouati (Republic of Congo), Gashaka (Nigeria), Korup (Cameroon), and La Belgique (Cameroon) (Table 3).

We found the highest frequency of occurrence of nocturnal activity in Kayan, Senegal with 19 events, followed by Sobeya, Guinea (16), Issa, Tanzania (14), and Budongo, Uganda (13; Table 3). We found the lowest frequency in Taï E, Ivory Coast (1), Taï R, Ivory Coast (1), Djouroutou, Ivory Coast (1), and Bakoun, Guinea (2). In considering nocturnal activity as a proportion of overall (nocturnal and diurnal) activity observed in camera-trap videos (Table 3, column F), we also found the highest proportion of nocturnal activity in Kayan (9.58%), followed by Geprenaf, Ivory Coast (3.73%), and Grebo, Liberia (3.33%). We found the lowest proportion in Bakoun (0.14%).

We observed nocturnal activity in three of the four chimpanzee subspecies, with *Pan troglyodytes elliotі* not being recorded to exhibit this behavior. Our camera-trapping effort of *P. t. ellioti* was lower than for the other subspecies (just over 17,000 camera-days [number of cameras × number of days each camera was active], whereas the camera-trapping effort total for the other subspecies ranged from 29,000–94,000 camera-days; Table 3), which may account for the lack of nocturnal activity observed. We observed more nocturnal activity events for *P. t. verus* compared to other subspecies (Table 3). However, the high camera-trapping effort (94,000 camera-days) for this subspecies may contribute to this, as we found the lowest proportion of overall chimpanzee activity in *P. t. verus* (and *P. t. ellioti*) compared to other subspecies (Table 3, column D).

Demographics and behavior of chimpanzee nocturnal activity

We found immature individuals to be the most represented in terrestrial nocturnal activity events (40% of individuals, n=235) followed by adult males (29.8%) then females (with and without infants; 20%) (Table 4; Fig. 4). We found most nocturnal activity events to comprise only one individual (52.9%, n=119). We also found a relatively high proportion of events to comprise two or three individuals (24.4 and 14.3%, respectively), and a low proportion of events comprising four individuals or more (0.8–1.7%). We found adult males to appear more often alone in an event than with others (55.7% of males appeared alone, n=70), and to be alone more often than other age-sex groups (61.9% of individuals appearing alone were males, n=63). We found that females were more often observed with infants and immatures than without (e.g., 68.1% of females were carrying infants, n=47). Immature individuals and females with infants (63.2 and 26.3%, respectively) constituted the majority of individuals appearing in events comprising eight individuals or more (n=19). We were unable to compare the proportions of males to females or of different age groups observed in nocturnal videos with those proportions observed in all chimpanzee (diurnal) activity videos as these site-level comparative data are not currently available from the PanAf.

We found the most predominant behavior exhibited by chimpanzees during nocturnal activity to be ‘movement’ (80.9% of chimpanzee-events, n=235), followed by ‘on location’ (14.9%) (Table 5). We found both ‘social’ and ‘feeding’ behaviors to feature rarely (2.6 and 1.7%, respectively). We found movement and social behaviors to occur more often in true night than in twilight (movement: 52.6 and 47.4%, respectively, n=190; social: 83.3 and 16.7%, respectively, n=6), but on location behavior to occur more often in twilight than true night (68.6 and 31.4%, respectively, of on location chimpanzee-events, n=35). We observed no feeding behaviors in twilight hours. We found the majority of movement behaviors to be exhibited by immature individuals, and the majority of on location behaviors to be exhibited by adult males (in both twilight and true night). We observed feeding and social behaviors to be exhibited only by adult males and immature individuals, in all phases of the night (Table 5). Again, we were unable to compare the proportions of behavior patterns observed in nocturnal videos with those proportions observed in all chimpanzee (diurnal) activity videos as these site-level comparative data are not currently available from the PanAf.

[Figure 4 here]

[Tables 4 & 5 here]

Predictors of chimpanzee nocturnal activity

Overall, we found the fixed effects to impact the probability to detect terrestrial nocturnal activities (full-null model comparison: χ^2=28.762, df=8, p=0.001). More precisely, we found higher levels of nocturnal activity at sites with lower levels of human activity, increased average daily temperatures, and a higher percentage of forest (Table 6; Fig. 5). We found none of the other predictors to have a significant effect on the probability of nocturnal activity (Fig. 5). We found no indication for the effects of percent illumination or daily temperature to vary among sites (Appendix 3). Given the low transect survey effort of two sites in particular, Bili and Sapo, we removed them and re-ran the model but found no difference in the overall results and significant effects (Appendices 4 and 5).

[Table 6 here]

[Figure 5 here]

DISCUSSION

Occurrence of chimpanzee nocturnal activity

We investigated terrestrial nocturnal activity in chimpanzees (*Pan troglodytes*) using footage from movement-triggered camera traps. There are considerable advantages to using such technology, such as the noninvasive nature, the ability to study unhabituated animals, and the ability to obtain information in places and at times inaccessible to human observers, such as at night (Boyer-Ontl and Pruetz, 2014; Estienne et al., 2017; Head et al., 2012). However, limitations of camera trapping should be carefully considered when interpreting results; the limitations will be presented within the subsequent discussion.

Overall, we found a low level of terrestrial nocturnal activity to be widespread across chimpanzee populations, occurring in the majority of research sites studied. In four of the sites studied we did not observe any nocturnal activity in camera-trap footage. Camera-trapping efforts of these four sites were not particularly low, and—apart from at Gashaka (Nigeria)—the proportions of videos containing chimpanzees at the other three sites (La Belgique, Korup, Cameroon; and Conkouati, Republic of Congo) were also not low, suggesting that the chimpanzees of these sites are not particularly elusive compared to other sites. However, it should be noted that data used in the study were restricted in some cases due to the availability of data through the PanAf (e.g., not always spanning all seasons), so it is possible that with additional camera-trapping effort and an extended investigation, nocturnal activity could be observed in these sites. In fact, initial investigations of more recent camera-trap footage from La Belgique that was not included in this study indicates some terrestrial nocturnal activity in chimpanzees (author's obs.: N. Tagg). Similarly, proportion of nocturnal activity at some sites may not be precise: for example, at Boé (Guinea Bissau) only part of the PanAf data collection period and associated data were available for use in the study, and initial observations suggest that the percentage of chimpanzee nocturnal activity at this site might be increased if the full PanAf data collection period could have been included. Similarly, at Loango (Gabon) it is suspected that the number of chimpanzee videos may be a conservative measure.

The overall proportion of nocturnal activity observed was low (1.80% of all chimpanzee occurrences in videos); however, this rate of observation is likely to be an underestimation. First, chimpanzees are a predominantly arboreal species across many parts of their range and some nocturnal activity may occur exclusively or predominantly in the trees (Goodall, 1962; Izawa and Itani, 1966; Mitani and Nishida, 1993; van Lawick-Goodall, 1968; Zamma, 2013). The terrestrial nature of the camera-trapping methodology does not allow us to investigate arboreal activity, so it is likely that arboreal nocturnal activity could have been missed. Both the degree of terrestriality and the observability of terrestrial activity are likely to vary between sites, depending on the openness of the habitat and the denseness of the understory vegetation. Second, it is likely that camera-trap capture rates are reduced in dark conditions, so it might be possible for chimpanzees to move about at night without triggering a camera; or that chimpanzees are sensitive to the light or sound emitted by cameras, which may be heightened at night when the contrast may be greater, and cameras may be avoided. Third, not all sites exhibited the same camera-trapping effort, and a low number of camera traps at some sites will have reduced the likelihood of observing nocturnal activity. However, the study supports the long-held belief that chimpanzees are largely diurnal, and that this observed terrestrial nocturnal activity is rather infrequent. This corroborates studies on other primates, such as olive baboons and vervet monkeys, which exhibit nocturnal activity on only 1.1% and 0.4% of the nights during which the animals were being observed, respectively (Isbell et al., 2017).

We observed this infrequent nocturnal activity in three of the four chimpanzee subspecies, with the highest number of events of nocturnal activity occurring in *P. t. verus*, followed by *P. t. schweinfurthii*, then *P. t. troglodytes*. We did not observe nocturnal activity in *P. t. ellioti*; however, this may be due to the relatively low camera-trapping effort for this subspecies (i.e., fewer camera-days and only at two sites). Therefore, overall, we found a low level of terrestrial nocturnal activity to occur in the majority of research sites studied and in three of the four subspecies of chimpanzee, suggesting this infrequent behavior pattern to be widespread in chimpanzees. This further suggests that nocturnal activity may be also present in other diurnal primate species (e.g., Isbell et al., 2017).

Demographics and behavior

We found chimpanzee terrestrial nocturnal activity to be exhibited more often by lone adult males. Males have a larger body size compared to females which may afford them more security for night-time activity, as is argued for male gorillas nesting closer to the ground than females (e.g., Yamagiwa, 2001). It is possible that males may wake more at night due to the nature of the activities carried out at night: males, for example, may be more likely to engage in territory patrols and this can occur at night (e.g., Boesch et al., 2007). However, many females and immature individuals were also observed exhibiting nocturnal activity, so it is not solely an adult male activity. Observations of chimpanzee crop raiding by night in Kibale, Uganda, have demonstrated more females to be involved in the activity (Krief et al., 2014). Furthermore, it is possible that male–female and age group ratios observed in camera-trap footage may be an artefact of the camera-trapping method (to address this we would need to know the probability of males versus females being recorded by camera traps). Alternatively, the sex ratio in nocturnal videos may reflect the structure of the population or group—particularly important if the sex-age composition of certain sites is skewed, for example at Fongoli (Senegal; Pruetz, Ontl, Cleaveland, Lindshield, Marshack and Wessling 2017)—and may not be specific to nocturnal activity; information regarding real demographic structure including ratios of various age classes would be necessary.

We found 'movement' to be the most common behavior exhibited during terrestrial nocturnal activity, including walking and running into and/or out of view of the camera. Travelling on the ground at night has previously been observed at Fongoli, Senegal (Pruetz and Bertolani, 2009), Mahale, Tanzania (Zamma, 2013), and Gombe, Tanzania (Goodall, 1986; van Lawick-Goodall, 1968). Olive baboons and vervet monkeys were observed travelling at night (Isbell et al., 2017). Movement behavior patterns could be explained as the individual moving to a new nest site (for example if disturbed; Zamma, 2013), as seen in Japanese macaques (Nishikawa and Mochida, 2010), moving away or back to the nest before or after night-time feeding/foraging (e.g., Goodall, 1986; van Lawick-Goodall, 1968), or fulfilling some social requirement, such as mating (chimpanzees: Nishida, 1996; rhesus macaques: Vessey, 1973) and territory patrol/aggressions (e.g., Boesch et al., 2007 and see Nishida, 1996; pers. obs.: Shelley Masi, from Krief et al., 2014, p. 2). Wild bonobos (*Pan paniscus*) have been observed to exhibit sex, social grooming, and play overnight (Fruth and Hohmann 1993, 1994). 'On location' behaviors (including sitting/standing in view, or ascending, descending a tree, etc), and 'social' behaviors were observed at a low rate, including some play (immature individuals), both during twilight hours and during true night. On location behaviors could reflect movement behaviors, whereby the animal paused; however, they could also indicate having fed or being in search of a food source, or leaving or arriving at a nest. It is possible that chimpanzees wake early for early arrival at ephemeral fruit trees in Taï National Park, Ivory Coast (Janmaat, Polansky, Ban, and Boesch, 2014). Similarly, other studies have demonstrated feeding to be the main reason for activity during night hours, for example, crop raiding in Kibale, Uganda (Krief et al., 2014). In our case, it was not possible to corroborate the location of nesting sites or feeding trees in conjunction with the data from camera-trap footage. Furthermore, in our study, 'feeding' behaviors were not observed at all during twilight hours and only very rarely during true night hours. We observed rare social behavior patterns during nocturnal activity. We did not observe any social grooming between individuals, but we did observe some play behavior between adolescents and infants while the mother chimpanzee exhibited a standing (on location) behavior. However, the frequent movement behaviors observed could similarly reflect individuals moving to or from feeding locations and crucially, as most feeding occurs arboreally, we would not expect to observe high rates of feeding in nocturnal activity videos captured by terrestrial camera traps. Furthermore, behaviors exhibited by individuals appearing in the same event will be non-independent, which may have further skewed the high proportions of certain behavior types observed.

Timing of nocturnal activity

We observed terrestrial nocturnal activity taking place during all phases of the night, but the majority of observations occurred during twilight. Activity during these phases likely represents an extension of daytime activities—i.e., during twilight after sunset chimpanzees may still be seeking a suitable nesting site, or moving from their last location to their selected nesting site. This has been demonstrated in Guizhou snub-nosed monkeys, at a site where fluctuating day length and food availability have led to flexible twilight feeding behaviors (Tan et al., 2013). Chimpanzees at Fongoli have been observed to remain active late into the evening, particularly in the dry season when temperatures are higher and nights are longer (Pruetz and Bertolani, 2009). During twilight before sunrise, active chimpanzees may represent those who have recently arisen early from their nest sites for early arrival at a food source (Janmaat et al., 2014). However, all videos of nocturnal activity in these twilight phases display a dark sky, thus rendering this extension of daytime activities into the night an interesting observation. Future research could investigate the possibility of a latitudinal effect for nocturnal behavior: nocturnal activity may be seasonal, for example, occurring more during periods when nights are longer, as observed in Fongoli (Pruetz and Bertolani, 2009).

Insights into human evolution. Activity in deeper phases of the night (phases 3 and 4 in Fig. 3) are more likely to represent cases whereby individuals awoke from sleep and left their night nest, and/or were likely to nest (again) before rising the next morning. This type of nocturnal activity could suggest a fragmented sleeping pattern (de la Iglesias and Lee, 2015) that has rarely been previously empirically documented in chimpanzees (but see Zamma, 2013). There is some evidence that fragmented sleep reflects the ancestral pattern in humans: some traditional societies (e.g., in Nigeria; Bohannan, 1953; Ekirch, 2006) exhibit high levels of activity around midnight, and use the terms "first sleep" and "second sleep"; and modern humans living under experimental, short (10 h) photoperiods begin to exhibit fragmented sleep (Wehr, 1992). However, we observed relatively very few events of nocturnal activity in these deeper phases of the night, and only in a few sites. If early hominin night-time sleep was fragmented, we would expect to see more waking in the middle of the night in chimpanzees in between ‘bouts’ of sleep; instead, we found chimpanzee nocturnal activity to occur at all hours of the night and more commonly during twilight. We would also expect to see a higher proportion of night waking (e.g., by more individuals on more nights), but the study found nocturnal activity overall to occur at a very low proportion, suggesting that the majority of chimpanzees on the majority of nights do not exhibit nocturnal activity. Therefore, although some habitat- or site-specific exceptions may exist, we find support for the hypothesis that wild chimpanzee sleep is commonly consolidated. This finding is in line with interpretations by human sleep scientists who argue that fragmented sleep is likely to lead to cognitive disadvantages (Eban-Rothschild et al., 2017): when compared to short, fragmented sleep epochs, long, consolidated sleep epochs have been demonstrated to have increased recovery power in humans (Vyazovskiy et al., 2007). Similarly, in orangutans, more nocturnal calls (suggesting interrupted sleep) were associated with poorer sleep quality (Samson, Hurst and Shumaker, 2014). Human sleep literature shows that cyclical pressures exerted by the circadian and homeostatic processes in humans favor an extended and consolidated bout of nocturnal sleep (de la Iglesias and Lee, 2015), with a biological dusk and dawn in human natural rhythms (Wehr et al., 2001), and with no evidence of physiological drivers for waking in the middle of the night. Several studies support this by presenting evidence of consolidated sleep in traditional societies, where people exhibit sleep onset a few hours after dark and then sleep through the night (e.g., Yetish et al., 2015).

Predictors of nocturnal activity

Our study revealed higher levels of terrestrial nocturnal activity with lower levels of human activity encountered at the site, with higher temperatures, and in sites with a higher percentage of forest.

Human activity. Although there is some evidence for chimpanzees finding ways to persist in human-dominated landscapes (see Hockings et al., 2015), there is considerable evidence that wild chimpanzees perceive humans as a threat across their range (Arnhem et al., 2008; Clark et al., 2009; Kano and Asato, 1994; Rabanal et al., 2010; Stokes et al., 2010; Tagg and Willie, 2013; Walsh et al., 2003). Hunters frequently operate at night and in twilight hours (Astaras et al., 2017). The movement and actions of people in chimpanzee sites at night may pose a threat to chimpanzees; indeed, humans have arguably become the principal predator of chimpanzees across much of their range. Our study suggests that lower rates of human activity in a site may facilitate or enable higher rates of nocturnal activity in chimpanzees, as the threat posed by encountering a human is reduced (Tagg, Willie, Petre, and Haggis, 2013). The signs of human activity recorded in the present study comprised evidence of hunting, gathering, illegal logging, etc., but not of research activity, thus supporting the suggestion that these types of human pressures are perceived by chimpanzees as a threat.

We did not, however, observe the same effect with regard to predators (lions, *Panthera leo*; leopards, *P. pardus*; and hyena, *Crocuta crocuta*) or to other large mammals (elephants, *Loxodonta africana*; and buffalos, *Syncerus caffer*) that could pose a threat to chimpanzees at night. We therefore cannot conclude that a potential reduction in the risk of injury at night via an encounter with a large mammal or predator might enable terrestrial nocturnal activity, nor that chimpanzees might be disturbed from sleep by the activity of large mammals below the nest. The lack of influence of predator abundance in particular is surprising, given the array of previous evidence for the disturbance of chimpanzees by predators (Carvalho et al., 2015; Pruetz et al., 2008; Stewart and Pruetz, 2013; Tutin et al., 1981). Generally, predator abundances were low if detected at all (maximum abundance rate: 0.121 signs per kilometer at Taï R, Ivory Coast). Fourteen of 22 sites did not identify predator presence on the transects although we have reason to believe that, for example, leopards are present in Gashaka (author's obs.: V. Sommer). Our proxy variable used to represent predator pressure may not have been adequately representative, or the transect survey effort in some sites was quite low, and further studies may serve to refute or elaborate on these observations, particularly if able to consider site-specific conditions. These inaccuracies may have weakened the influence of predators as measured in the present study. However, humans are arguably the most significant predator of chimpanzees in most of their range, even in areas where poaching is rare (see Lindshield et al., 2017). Thus, it is perhaps not surprising that we found no effect of non-human predators on nocturnal activity, whereas we did find an effect of human activity.

Habitat. We found the probability of chimpanzee nocturnal activity to increase in forested habitats compared to savanna habitats. This is surprising given the previous evidence of nocturnal activity in chimpanzees living in savanna habitats (e.g., Pruetz and Bertolani, 2009). However, these results are not consistent with some of our site-specific observations of nocturnal activity in the study. Six of the sites included in the study were categorized as savanna sites, constituting a higher percentage of savanna than forest, and three of these savanna sites (Sobeya, Guinea; Kayan, Senegal; and Geprenaf, Ivory Coast) accounted for most of the nocturnal activity occurring during the deeper phases of the night. Kayan, in particular, which is characterized by nearly 75% savanna, exhibited the most nocturnal activity (in terms of number of videos, events and distinct individuals exhibiting nocturnal activity) of all sites, thus appearing to support previous observations of a high occurrence of nocturnal activity in savanna habitats (i.e., at Fongoli; Pruetz and Bertolani, 2009). It could be argued that such open habitats may necessitate increased terrestrial activity, thus leading to an increased capture rate of nocturnal activity; however, the overall (day and night) chimpanzee capture rates at these sites were not higher than at forested sites. Furthermore, two other sites, Budongo and Ngogo (Uganda), comprised very high percentages of forest (100 and 85%, respectively) but also exhibited some nocturnal activity in true night; the markedly high percentage of forest habitats at these sites might explain the strength of the forest variable in predicting nocturnal activity.

Temperature. We found higher levels of nocturnal activity with higher average daytime temperatures. This observation is supported by previous literature. Chimpanzees in the savanna habitats of Fongoli, Senegal have developed behavioral strategies, such as soaking in pools of water and seeking refuge in caves, to counter the effects of the high daytime temperatures (Pruetz, 2001, 2007; Pruetz and Bertolani, 2009). The thermoregulatory costs associated with daytime foraging (Lindshield et al., 2017) have been suggested to explain subsequent nocturnal feeding activity observed (Pruetz and Bertolani, 2009). Similarly, chimpanzees at Gombe, Tanzania, have been observed to visit feeding areas and water sources at night, possibly because of the daytime heat at the site (van Lawick-Goodall, 1968). It is expected for extreme temperatures to influence nocturnal activity: in humans, temperature may influence sleep duration in traditional populations, possibly as a mechanism of maintaining a low body–environment temperature differential to reduce energy needed to stay warm (Yetish et al., 2015). We did not detect an effect of rainfall on nocturnal activity, despite the link between temperature and rainfall and the evidence for extremes of such climatic conditions to lead to nocturnal behavior. Savanna chimpanzees in Comoé, Ivory Coast, have been filmed dipping for water in tree holes during periods of low rainfall, with one sequence of this behavior occurring throughout the night (Lapuente, Hicks and Linsenmair, 2017). As there are vast differences in environmental conditions and habitat composition of the study sites spanning the entire longitudinal range of the chimpanzee in Africa, it is possible that the environmental and habitat-related drivers of nocturnal activity may differ between sites and the overarching statistical model employed in the present study would not be able to detect site- or season-specific predictors. In addition, nocturnal activity may be influenced by season, which was not considered in the study due to the already small sample sizes. However, we made a start by including climate variables (temperature and rainfall) in our model. Further studies which consider the effects of environmental conditions varying among and within sites could contribute to elucidating their possible influences on the occurrence of nocturnal activity in chimpanzees.

Other factors. Moonlight was frequently suggested to be a strong determinant of night-time activity levels in primates (Fernandez-Duque et al., 2010; Izawa and Itani, 1966; Pruetz and Bertolani, 2009; van Lawick-Goodall, 1968; pers. comm.: Koichiro Zamma). However, the present study found no support for moonlight enabling or being a prerequisite of night waking as there was no significant influence of percent illumination on the occurrence of nocturnal activity. The illumination intensity range for feeding activity in chimpanzees (and other great apes) is 1–85 lux, whereas the illuminance (the measure of the incident light illuminating a surface) during a full-moon night amounts to about 0.3 lux (Erkert, 2003, 2008); this is one of the criteria used to categorize great apes as diurnal. Cover from trees and other vegetation will reduce this even further. Therefore, even during a full moon it would not be easy for chimpanzees to navigate and function safely at night. Furthermore, nocturnal activity has also been described to occur on non-moonlit nights in wild chimpanzees (e.g., Krief et al., 2014), thus suggesting that moon illuminance neither encourages nor necessarily facilitates nocturnal activity, consistent with the results of the present study. It should be noted, however, that the present study did not account for cloud cover affecting the actual amount of light reaching the forest floor regardless of the percent moon illumination for that night.

As highly social animals, it is very likely that social factors will influence many aspects of chimpanzee behavior, both overnight as well as during diurnal activity. We were not able to investigate the influence of social factors on nocturnal activity, but we did observe a couple of events of play behavior during nocturnal activity. Previous studies offer great support for social factors driving chimpanzee behavior. For example, cortisol levels and rates of aggression can be higher in both males and females during the times that females are in estrus in chimpanzees and bonobos (Emery Thompson and Wrangham, 2008; Surbeck, Deschner, Schubert, Weltring and Hohmann, 2012); such tensions may even lead to lethal aggression (e.g., Pruetz et al., 2017). It is possible that males would expend more effort in maintaining contact with estrous females, even at night—especially if they are also limited by environmental factors, such as avoiding activity during the hottest times of the day. Furthermore, chimpanzees may attempt to avoid intragroup competition for important resources by waking up early to access food resources and have been demonstrated to plan the previous night's nesting sites accordingly (Janmaat et al., 2014).

Given the multi-faceted functions of sleep as well as all behavioral repertoires in a behaviorally complex species such as the chimpanzee, it is likely that nocturnal activity is driven by a combination of factors. Despite the limitations of our study, we show that terrestrial nocturnal activity occurs infrequently, but was evident in most of the sites and in three of the four chimpanzee subspecies studied, lending support to the notion that nocturnal awakening is a widespread and flexible behavior across all populations, and can be influenced by environmental pressures. The decision of whether to sleep or be awake at any time is a trade-off between the benefits and costs of sleeping versus being awake (Siegel, 2005; Starr, Nekaris and Leung, 2012). The ability to alter nocturnal behavior depending on short- and long-term changes in the environment enables an individual to constantly 'trade off' between the benefits (memory consolidation) and costs (loss of time awake, vulnerability) of sleep, and the opportunities (learning, social development, feeding) and costs (reduction in effectiveness) of wakefulness. Furthermore, such a flexibility of sleeping and night-time behavior may have implications for the capacity of chimpanzee populations, and of the species, to adapt to changing conditions or pressures in their environment (e.g., Krief et al., 2014), including environmental conditions, such as high temperatures, as well as threats and disturbances, such as those posed by humans.

Flexible sleeping behaviors likely contributed to early hominins' ability to respond and adapt to changing conditions, facilitating spread into new environments and survival under extreme conditions. The ability to maximize advantages of sleep against those of wakefulness could have contributed both to the fitness of individuals, and the survival of the species. We advocate additional research into the occurrence and predictors of nocturnal activity in wild chimpanzees across their range, and highlight the importance of direct observations and an investigation of arboreal nocturnal activity. We also recommend research in other wild great ape species and a range of primate species, to frame humans within a comparative context and inform human sleep patterns and the evolution of human cognition.

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AUTHOR CONTRIBUTIONS

F. Stewart and N. Tagg developed the concept for the study; G. Bocksberger, P. Dieguez, M. McCarthy, N. Tagg, J. Widness, and J. Willie processed, compiled, and extracted data; M. McCarthy performed identification of all individuals appearing in videos for all sites; G. Bocksberger and J. Willie produced the figures; R. Mundry and J. Willie designed and performed statistical analyses; A. Landsmann and J. Widness moderated the Chimp&See videos; N. Tagg wrote the paper with input from all co-authors; M. Arandjelovic, C. Boesch, and H. Kühl enabled the study via the PanAf. Field site collaborators were: T. Deschner, A. Goedmakers, K. E. Langergraber, V. Lapeyre, E. Normand, A. Piel, V. Sommer, F. Stewart, N. Tagg, M. ter Heegde, H. Vanleeuwe, V. Vergnes, E. Wessling, R.

M. Wittig, and K. Zuberbuehler. Data were collected in the field by: A. Agbor, S. Angedakin, A. E. Ayimisin, M. Bessone, G. Brazzola, K. Corogenes, E. Dilambaka, M. Eno-Nku, H. Eshuis, A.-C. Granjon, J. Head, V. Hermans, S. Jones, P. Kadam, M. Kambi, J. Lapuente, K. Lee, V. Leinert, G. Maretti, S. Marrocoli, A. Meier, S. Nicholl, L. J. Ormsby, O. Robinson, A. Tickle, E. Ton, and J. van Schijndel. All field data collection protocols comply with all regulations, institutional or governmental, regarding the ethical treatment of research subjects.

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FIGURE CAPTIONS

Figure 1 – Snapshots from videos of nocturnal activity: A. Kayan 01:46 hours (04/08/2013); B. Issa 06:01 hours (07/09/2014).

Figure 2 – Locations of sites included in the present study: 1. Kayan (Senegal), 2. Boe (Guinea Bissau), 3. Bakoun, 4. Sobeya (Guinea), 5. East Nimba, 6. Grebo, 7. Sapo (Liberia), 8. Djouroutou, 9. Geprenaf, 10. Tai E, 11. Tai R (Ivory Coast), 12. Gashaka (Nigeria), 13. Korup, 14. Campo Ma'an, 15. La Belgique (Cameroon), 16. Loango (Gabon), 17. Conkouati (Republic of Congo), 18. Bili (Democratic Republic of Congo), 19. Budongo, 20. Bwindi, 21. Ngogo (Uganda), 22. Issa (Tanzania). The size of the dot indicates the relative occurrence of nocturnal activity from 0 to 20 videos. Colored patches represent the range of the four subspecies of chimpanzee, from west to east: purple: *Pan troglodytes verus*, pink: *P. t. ellioti*, blue: *P. t. troglodytes*, green: *P. t. schweinfurthii*.

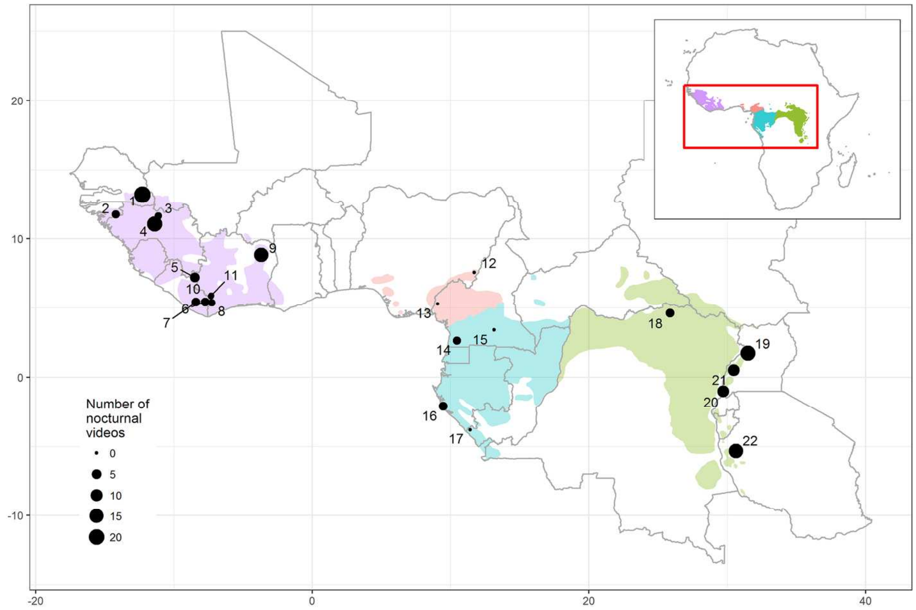
Figure 3 – Video capture of chimpanzees through the night at 18 sites. To be comparable between different geographic locations and times of year, the recording time of the videos was scaled from 0 to 1 based from the time difference from sunset on that day (or the previous day for videos captured after midnight) and night duration (x = (Tvideo−Tsunset) / night duration). Panel A displays the night videos through the night per site. Each dot represents a video (N=143), sized by the maximum number of individuals present in the video. The vertical grid indicates **approximately** an hour. Panel B shows the total number of videos through the night. Night time was separated into four phases represented by the horizontal black bars at the bottom: phase 1 (1 hour after/before sunset/sunrise), phase 2 (within 2 hours of twilight); phase 3 (2 hours of early morning and late night), phase 4 (2 hours around "midnight").

Figure 4 – Density distribution of age–sex categories within nocturnal events with various numbers of participants. Females are accounted for in two different ways: either without or with infant. The class 'immature' includes adolescent, juveniles and infants. Each dot represents a nocturnal event captured by camera traps.

Figure 5 – Probability of nocturnal activity (y-axes) as a function of the percentage of forest (a), human activity (b), and mean daily temperature (c; x-axes). Indicated are the fitted model (dashed line) and its confidence interval (dotted lines). Points represent the proportions of data points with nocturnal activity (per bin of the respective predictor); the area of the points is proportionate to the number of data points in the respective bin of the predictor (range, a: 1 to 270; b: 7 to 270; c: 7 to 133).

Figure 1 – Snapshots from videos of nocturnal activity: A. Kayan 01:46 hours (04/08/2013); B. Issa 06:01 hours (07/09/2014).

255x82mm (300 x 300 DPI)



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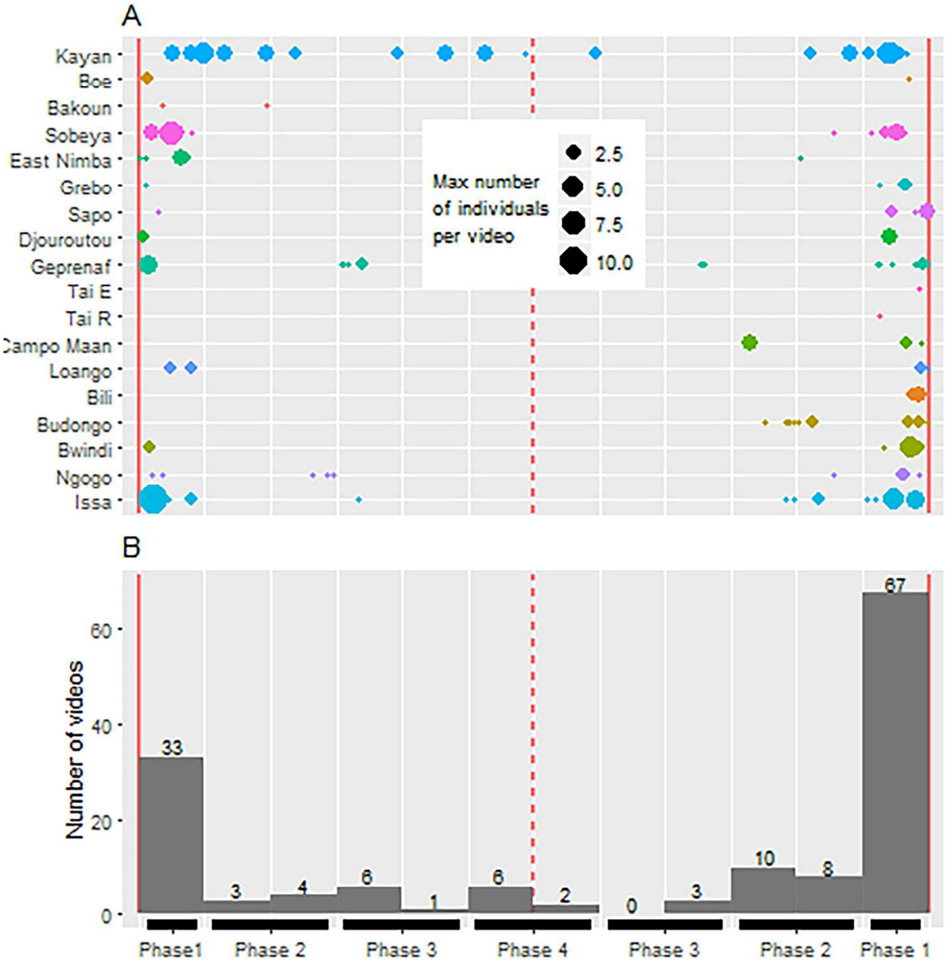
177x108mm (300 x 300 DPI)



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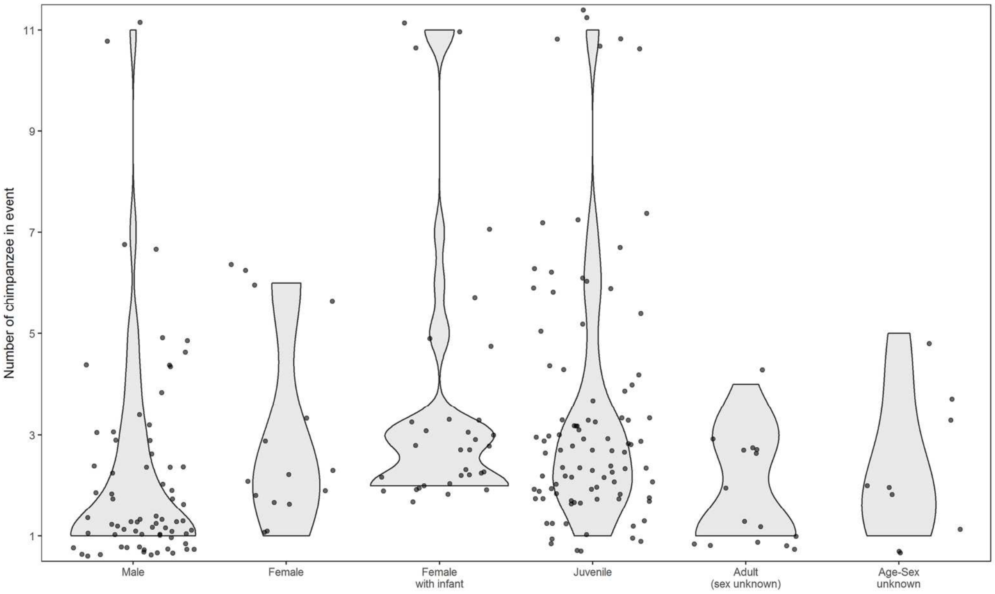
169x169mm (300 x 300 DPI)



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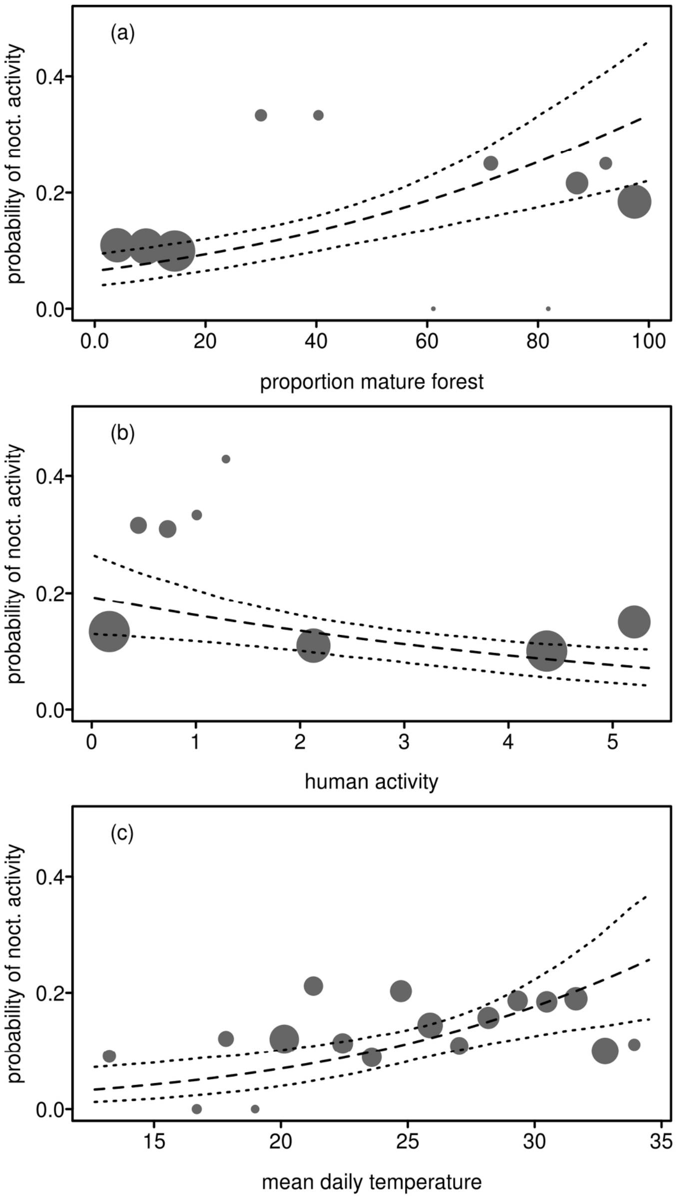
177x108mm (300 x 300 DPI)



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133x233mm (300 x 300 DPI)

Table 1 – Study sites of the Pan African Programme: The Cultured Chimpanzee (PanAf), that were included in the study, ordered according to country listed from west to east Africa, and showing the chimpanzee subspecies present at the site, and whether videos were uploaded to Chimp&See (C&S) or not (non-C&S).

Country	**Site name**	**Chimpanzee (*Pan troglodytes*) sub-species**	**Chimp&See (C&S) or non-Chimp&See (non-C&S)**
Senegal	**Kayan** (temporary research site)	*P. t. verus*	C&S
Guinea Bissau	**Boé** (Beli)	*P. t. verus*	Non-C&S
Guinea	**Bakoun** Classified Forest	*P. t. verus*	Non-C&S
Guinea	**Sobeya** (temporary research site)	*P. t. verus*	Non-C&S
Liberia	**East Nimba** Nature Reserve	*P. t. verus*	C&S
Liberia	**Grebo** National Park (Sala)	*P. t. verus*	C&S
Liberia	**Sapo** National Park	*P. t. verus*	C&S
Ivory Coast	**Djouroutou**, Tai National Park	*P. t. verus*	C&S
Ivory Coast	**Geprenaf** (temporary research site)	*P. t. verus*	Non-C&S
Ivory Coast	**Tai E** (Ecotourism Site), Tai National Park	*P. t. verus*	C&S
Ivory Coast	**Tai R** (Research Site), Tai National Park	*P. t. verus*	C&S
Nigeria	**Gashaka**-Gumti National Park	*P. t. ellioti*	Non-C&S
Cameroon	**Korup** National Park	*P. t. ellioti*	Non-C&S
Cameroon	**Campo Ma'an** National Park	*P. t. troglodytes*	Non-C&S
Cameroon	**La Belgique**, Dja Biosphere Reserve	*P. t. troglodytes*	Non-C&S
Gabon	**Loango** National Park	*P. t. troglodytes*	Non-C&S
Republic of Congo	**Conkouati**-Douli National Park	*P. t. troglodytes*	Non-C&S
Democratic Republic of Congo	**Bili**, Gangu Forest	*P. t. schweinfurthii*	C&S
Uganda	**Budongo** Forest	*P. t. schweinfurthii*	C&S
Uganda	**Bwindi** Impenetrable Forest National Park	*P. t. schweinfurthii*	C&S
Uganda	**Ngogo**, Kibale National Park	*P. t. schweinfurthii*	Non-C&S
Tanzania	**Issa** (Issa Valley), Ugalla	*P. t. schweinfurthii*	Non-C&S

Table 2 – Proportions of forest and savanna per site. Shaded cells indicate the habitat type (forest or savanna) which exhibits the highest proportion in the site (i.e., more than 50%).

Site	Forest (%)	Savanna (%)	Other habitat types (%)
Kayan	12.1	74.5	13.4
Boe	38.4	50.4	11.2
Bakoun	11.75	72.5	15.75
Sobeya	1.5	81.5	17.0
East Nimba	87.5	0.0	12.5
Grebo	97.2	0.0	2.8
Sapo	94.7	0.0	5.3
Djouroutou	100.0	0.0	0.0
Geprenaf	30.7	68.4	0.9
Tai E	100.0	0.0	0.0
Tai R	100.0	0.0	0.0
Gashaka	63.5	36.5	0.0
Korup	95.9	0.0	4.1
Campo Ma'an	88.3	0.0	11.7
La Belgique	81.2	0.0	18.8
Loango	72.7	18.2	9.1
Conkouati	85.4	11.5	3.1
Bili	99.3	0.7	0.0
Budongo	100.0	0.0	0.0
Bwindi	98.4	0.0	1.6
Ngogo	84.6	8.7	6.7
Issa	6.8	90.6	2.6

Table 3 – Sampling effort (camera-days), number of camera trap videos, number of chimpanzee videos, rate of chimpanzee occurrence in all videos (%), number of chimpanzee nocturnal activity videos, proportion of chimpanzee nocturnal activity (%), number of events of chimpanzee nocturnal activity (i.e., a video or a series of videos captured >15 mins apart from the next), and number of chimpanzee-events of nocturnal activity (i.e., number of distinct individuals appearing in events), per site (see Methods section for explanation of events and chimpanzee-events).

	A	**B**	**C**	**D=C/B*100**	**E**	**F=E/C*100**	**G**	**H**
Site name	**Camera days**	**Number of videos**	**Number of chimpanzee videos**	**Chimpanzee occurrence (%)**	**Number of chimpanzee nocturnal activity VIDEOS**	**Chimpanzee nocturnal activity (%)**	**Number of chimpanzee nocturnal activity EVENTS**	**Number of nocturnal CHIMPANZEE-EVENTS**
Kayan	9904.6	16,737	240	1.43	23	9.58	19	51
Boe	4613.0	17,791	747	4.20	3	0.40	3	4
Bakoun	8641.2	27,366	1461	5.34	2	0.14	2	2
Sobeya	8525.4	14,666	715	4.88	19	2.66	16	35
East Nimba	9968.7	7,498	286	3.81	5	1.75	5	8
Grebo	9365.9	7,210	120	1.66	4	3.33	4	5
Sapo	8329.0	9,421	275	2.92	4	1.45	4	7
Djouroutou	7004.3	8,308	220	2.65	2	0.91	2	5
Geprenaf	6994.8	8,881	429	4.83	16	3.73	8	11
Tai E	6904.1	9,706	253	2.61	1	0.40	1	1
Tai R	10,571.8	15,471	220	1.42	1	0.45	1	1
Gashaka	7384.5	14,571	132	0.91	0	NA	0	0
Korup	9710.2	8,664	466	5.38	0	NA	0	0
Campo Ma'an	8445.5	6,823	484	7.09	3	0.62	3	6
La Belgique	7332.0	10,512	216	2.05	0	NA	0	0
Loango	11,825.0	4021	391	9.72	4	1.02	4	7
Conkouati	10,715.1	9,457	351	3.71	0	NA	0	0
Bili	3113.0	4,895	94	1.92	4	0.46	4	7

Budongo	2788.8	6,764	655	9.68	18	2.75	13	17
Bwindi	7346.1	16,141	717	4.44	9	1.26	9	21
Ngogo	7452.8	15,114	1215	8.04	9	0.74	7	10
Issa	8323.5	18,112	468	2.58	16	3.42	14	37
TOTAL / *AVERAGE*	**175,259.3**	**258,129**	**10,155**	*4.15*	**143**	*1.77*	**119**	**235**
Sub-species								
P. t. troglodytes	**42,930.0**	**48,604.0**	**2189**	*5.36*	**10**	*0.41*	**10**	**17**
P. t. verus	**94,533.3**	**143,376.0**	**4687**	*3.16*	**92**	*2.52*	**76**	**154**
P. t. schweinfurthii	**29,024.2**	**61,026**	**3149**	*5.33*	**56**	*2.48*	**47**	**86**
P. t. ellioti	**17,094.7**	**23,235**	**598**	*3.14*	**NA**	*NA*	**NA**	**NA**

Table 4 – The number of individuals appearing per nocturnal activity event, and the breakdown of sex and age group of these individuals. Note: the number of individuals does not imply distinct individuals outside of event; i.e., the same individual(s) may occur in subsequent event(s).

Number of individuals in event	**Number of events**	**Number of sites exhibiting this composition**	**Number of individuals**						
			Adult male	**Adult female with infant**	**Adult female no infant**	**Adult sex unknown**	**Juvenile**	**Unidentifiable**	**Total**
1	63	17	39	0	2	7	12	3	**63**
2	29	14	12	11	6	1	25	3	**58**
3	17	9	8	10	3	6	23	1	**51**
4	2	2	3	0	0	1	3	1	**8**
5	2	2	1	2	0	0	7	0	**10**
6	2	2	1	1	4	0	5	1	**12**
7	2	2	4	3	0	0	7	0	**14**
8	1	1	0	2	0	0	6	0	**8**
11	1	1	2	3	0	0	6	0	**11**
All events	**119**	**18**	**70**	**32**	**15**	**15**	**94**	**9**	**235**

Table 6 – Results of the Generalised Linear Mixed Model of the probability of nocturnal activity detection (estimated effects together with standard errors, confidence limits, likelihood ratio tests, and model stability estimates)

Term[1]	Estimate	SE	lower CI	upper CI	χ^2	df	P	min	max
Intercept	-1.975	0.136	-2.317	-1.755			[2]	-2.039	-1.665
Percent forest	0.774	0.158	0.474	1.127	20.641	1	<0.001	0.684	0.879
Predator abundance	0.064	0.165	-0.319	0.443	0.151	1	0.697	-0.099	0.307
Buffalo abundance	-0.166	0.137	-0.494	0.140	1.525	1	0.217	-0.465	-0.010
Elephant abundance	0.007	0.088	-0.328	0.169	0.006	1	0.939	-0.407	0.104
Human activity	-0.437	0.139	-0.755	-0.156	8.474	1	0.004	-0.515	-0.320
Mean daily temperature	0.527	0.159	0.214	0.874	9.788	1	0.002	0.381	0.600
Rainfall day before	-0.033	0.125	-0.376	0.178	0.069	1	0.793	-0.081	0.137
Percent illumination	-0.041	0.149	-0.363	0.212	0.080	1	0.777	-0.141	0.064

(1) All predictors were z-transformed to a mean of zero and a standard deviation of one; mean (standard deviation) of the original variables were 34.494 (39.556) (Percent forest), 0.014 (0.014) (Predator abundance), 0.066 (0.233) (Buffalo abundance), 0.266 (1.174) (Elephant abundance), 2.549 (2.053) (Human activity), 25.867 (5.002) (Mean daily temperature), 1.774 (5.257) (Rainfall day before), and 53.512 (34.784) (Percent illumination).

(2) Not indicated because of having a very limited interpretation