

# Nocturnal behavior by a diurnal ape, the West African chimpanzee (*Pan troglodytes verus*), in a savanna environment at Fongoli, Senegal

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## Abstract

**Objectives:** I report on the nocturnal behavior of Fongoli chimpanzees in a savanna mosaic during different seasons and lunar phases and test the hypothesis that hot daytime temperatures influence activity at night. I predicted that apes would be more active at night during periods of greater lunar illuminosity given diurnal primates' lack of visual specializations for low-light conditions and in dry season months when water scarcity exacerbated heat stress.

**Materials and Methods:** I observed chimpanzees for 403 hrs on 40 nights between 2007 and 2013 and categorized their activity as social, movement, or vocalization. I scored their activity as occurring after moonrise or before moonset and considered the influence of moon phase (fuller versus darker phases) as well as season on chimpanzee nocturnal behavior in the analyses.

**Results:** Results indicate that apes were more active after moonrise or before moonset during fuller moon phases in the dry season but not the wet season. Most night-time activity involved movement (travel or forage), followed by social behavior, and long-distance vocal communication.

**Discussion:** Animals in highly seasonal habitats often exhibit thermoregulatory adaptations but, like other primates, chimpanzees lack physiological mechanisms to combat thermal stress. This study provides evidence that they may exhibit behaviors that allow them to avoid high temperatures in a savanna environment, such as feeding and socializing at night during the hottest time of year and in the brightest moon phases. The results support theories invoking thermal stress as a selective pressure for hominins in open environments where heat would constrain temporal foraging niches, and suggest an adaptability of sleeping patterns in response to external factors.

## KEYWORDS

ape, seasonality, thermal stress

## 1 | INTRODUCTION

Although many mammals are nocturnal, crepuscular or cathemeral, the majority of primate species, including humans, are diurnal, with the exception of most strepsirhines, tarsiers (*Tarsius* spp.), and the owl monkey (*Aotus* spp.). Our understanding of diurnal primates' nocturnal behavior is limited given our own emphasis on diurnality, as well as the tendency to dichotomize species into either category (Curtis & Rasmussen, 2006) and assume that corresponding rest periods consist mainly of sleep (Santini et al., 2015). There has been minimal investigation into the flexibility of sleep patterns in most wild primate species save for

the nocturnal and cathemeral species (e.g., Bearder et al., 2006; Savagian & Fernandez-Duque, 2017; Starr et al., 2012). The lack of such study also perhaps stems from primatologists' tendency to assume their diurnal subjects sleep throughout the night as is common in modern humans. This does not appear to be the case, in fact, for captive chimpanzees (Videan, 2006) or for humans in many cultures nor probably for much of human history (see Samson & Nunn, 2015), but the nature of nocturnal sleep in other diurnal primates is relatively unknown.

Reports of nocturnal activity by wild, diurnal primates are mainly anecdotal and include reports of vocalizations as well as activity such as foraging or traveling. Numerous studies have reported nocturnal

movement for diurnal primates (*Alouatta pigra*: Dahl & Hemingway, 1988; *Cebus capucinus*: cited in Bearder et al., 2006; *Theropithecus gelada*: Kawai & Iwamoto, 1979; *Macaca mulatta*: Vessey, 1973; *M. fuscata*: Nishikawa & Mochida, 2010; *M. sinica*: cited in Bearder et al., 2006; *Pongo pygmaeus*: MacKinnon, 1974; *Pan troglodytes*: Goodall, 1962, 1968; Pruetz & Bertolani, 2009; Zamma, 2014) as well as diurnal strepsirrhines (*Lemur catta*: Donati et al., 2013). Primates heard vocalizing at night include Barbary macaques (*M. sylvanus*: Hammerschmidt et al., 1994) and chimpanzees (Goodall, 1968; Izawa & Itani, 1966; Tutin et al., 1981), and gorillas (*Gorilla beringei*) chest-beat at night (Schaller, 1963).

Diurnal primates lack the visual adaptations for low-light conditions, such as those characterizing strepsirrhine primates (Bearder et al., 2006; Santini et al., 2015). Because most primates lack these adaptations, nocturnal activity in diurnal monkeys and apes is associated with risks and, presumably, with some benefit. Even among nocturnal and crepuscular species, there is variation according to how lunar illuminosity affects activity. In a review of moonlight effects on nocturnal activity in various mammals, Bearder et al. (2006) showed activity changes with increased lunar illuminosity in 9 of 14 studies. In species belonging to the genera *Aotus*, *Galago*, *Tarsius*, and *Eulemur*, activity increased with fuller moon phases but in five of the studies, including *Eulemur*, *Lepilemur*, *Microcebus*, and *Loris* species, no change occurred (Bearder et al., 2006). The nature of primate sleep may also influence nocturnal activity.

All great ape species build night nests, which may allow for a more restful night's sleep. Chimpanzees exhibit REM sleep, and studies of these apes in captivity indicate variation in whether they remain relatively stationary (Riss & Goodall, 1976) or move around at night and sleep in bouts of a few hours at a time (Morimura et al., 2012). Zamma (2014) found that wild chimpanzees at Mahale, Tanzania, were frequently disturbed at night. Although occasional nocturnal activity because of disturbance is expected, other circumstances such as nocturnal crop raiding by chimpanzees (*P.t. schweinfurthii*) in Uganda (Krief et al., 2014), appear to cause diurnal primates to adjust their normal activity patterns and expand their temporal niche. While numerous studies have recognized the sleep-wake cycle in humans (Dijk, 2002), patterns exhibited by other primates remain little known, and those of apes living in hot, dry, and open environments are especially informative regarding the evolution of sleep patterns in hominids.

Two of the hypotheses that have received the most attention in studies of sleep in primates focus on predation stress and thermoregulatory stress (Savagian & Fernandez-Duque, 2017). Predation pressure on diurnal animals is especially strong at night (Packer et al., 2011), and most predators of nonhuman primates are nocturnal felids, especially the major predators of the large-bodied apes (Hart and Sussman, 2005). Small, cryptic primates are lunar phobic during the cool dry season nights of greater lunar illuminosity (*Nycticebus pygmaeus*, Starr et al., 2012; *Tarsius spectrum*, Gursky, 2003). The risk of moving terrestrially at night, even for great apes that routinely make arboreal night nests may be significant.

In savanna environments, where chimpanzees are less studied, one of the major stresses is heat. A study of white-faced capuchins in a seasonal dry forest in Costa Rica found that these primates avoided heat

stress by resting more and traveling less (Campos & Fedigan, 2009), similar to Fongoli chimpanzees at the hottest time of year (Pruetz & Bertolani, 2009). We hypothesized that chimpanzees at Fongoli, Senegal, adjust behaviorally to heat stress, as they drink on most days during the dry season, use caves to rest in where temperatures are cooler, and soak in pools of water during the early rainy season when temperatures are high (Pruetz & Bertolani, 2009). This corresponds to what Stelzner and Hausfater (1986) termed heat stress avoidance or behavioral thermoregulation. At Fongoli, heat stress may exert stronger pressure on chimpanzees than risk of predation pressure. The predator guild at Fongoli is reduced compared to other savanna sites, in that lions (*Panthera leo*) and wild dogs (*Lycaon lycaon*) have been locally exterminated (Lindshield et al., in prep.). However, leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*) are resident in the area, and Fongoli chimpanzees mob both these species (Pruetz and Boyer-Onti, in prep.).

Thermoregulatory costs in a hot, dry, and open environment are well known for a number of species, but less so for nonhuman primates. Even animals that do not exhibit adaptations to highly seasonal environments adjust to stresses associated with changes in temperature (e.g., Kelley et al., 2016; *Lemur catta*; Savagian & Fernandez-Duque, 2017; *Aotus azarae*). Foraging behavior in diurnal desert rodents (*Acomys russatus*) depends more so on water requirements than on predation risk (Levy et al., 2016). Studies of baboons provide some of the best examples of the effects of heat stress on diurnal primates. Hill (2006) found that chacma baboons (*Papio hamadryas ursinus*) rested and groomed more during periods of high heat stress, while Brain and Mitchell (1999) showed that desert baboons (*P.h. ursinus*) in Namibia adjusted to hotter days where they did not drink with sand-bathing behavior, which functioned to cool their body temperature.

Based on preliminary evidence that chimpanzees in the savanna habitat of Fongoli, Senegal, were leaving their night nests before dawn and moving some distance, I began spending the night with chimpanzee subjects to test the hypothesis that these apes can be active at night. Specifically, I predicted that they would be more active on moonlit nights during the dry season when chimpanzees minimize daily activity by spending significant portions of the day resting (Pruetz & Bertolani, 2009). This stems from Wheeler's (1984, 1990, 1991a,b, 1992) physiological model, which seeks to explain the origins of bipedalism in hot, dry, and open environments as a thermoregulatory advantage (Wheeler, 1984, 1990, 1991a,b, 1992). Given the thermoregulatory costs associated with pressures in such habitats, the daytime activity scheduling associated with basic needs would be limited. Similarly, based on limits to daytime activity budgets and on preliminary data indicating social activity at night when estrous females were present, I predicted that chimpanzees would be more active on nights when there was at least one estrous female in the sleeping party.

## 2 | METHODS

### 2.1 | Study site

The Fongoli chimpanzee community ranges within the Kedougou (formerly Tambacounda) region in southeastern Senegal (12°40N,

12°13W), approximately 50 km SW of the Niokolo Koba National Park. Chimpanzees here live outside of protected areas in Senegal and share their range with people of the Malinke, Diahanke, Bassari, Puhlar, and Bedik groups. The savanna environment at Fongoli is a mosaic of woodland, grassland, bamboo, and gallery forest habitats (Pruetz, 2006). The majority of the chimpanzee community's approximately 90 km<sup>2</sup> home range comprises woodland and grassland habitat types, with gallery and ecotone forest accounting for about 3% of the area and anthropogenic disturbance such as crop fields, villages, dirt roads, and artisanal mines accounting for approximately 5% (Pruetz, 2006).

The extensive dry season at Fongoli lasts for over seven months, from October through May. The short rainy season occurred in June through September during initial years of the long-term Fongoli Savanna Chimpanzee Project (FSCP) study, but rainfall patterns have been erratic in recent years. For this study, the dry season included the month of May based on rainfall data. Rainfall at Fongoli usually averages less than 1,000 mm annually, although there is variation in recent years especially (Pruetz and Bertolani, 2009; Pruetz, unpublished data). Maximum temperature in the dry season often exceeds 40°C (Pruetz, 2007).

## 2.2 | Study subjects

The Fongoli chimpanzee community varied annually between 28 and 36 individuals from 2005 to 2016, averaging 32 individuals. Systematic all-day follows of study subjects began in 2005 after we habituated adult males to allow nest-to-nest follows, but the adult females remained semi-habituated, in that they exhibited signs of nervousness around observers when adult males were absent. I did not follow adult females apart from when they were in mixed-sex parties, but collected data on females when in the presence of males. I identified all females by January 2006. Daily party size at Fongoli is higher than at other sites, averaging 15 individuals overall, with larger parties (mean 17.7 chimpanzees) characterizing dry season months and smaller parties (mean 12.1 chimpanzees) characterizing wet season months (Pruetz & Bertolani, 2009). If the daytime party fissioned before nesting, I defined nesting party size as the number of individuals detected via auditory and visual clues at dusk.

## 2.3 | Data collection—behavior

Data were collected on chimpanzee nocturnal behavior (defined as behavior occurring following sunset and before dawn) between 2007 and 2013, with most observations occurring in 2010 ( $n = 35$ ). Observations began between 1805 and 1935 hrs ( $n = 40$ ) and ended between 542 and 640 hrs for full nights ( $n = 34$ ). On six nights, observations were abandoned early, usually because of rain (at 2020, 2035, 2130, 0310, 0027, and 0120 hrs), which made visibility difficult and reliable detection of behavior impossible. However, incomplete nights were included in analyses unless they were statistical outliers. I spent 28 dry season nights and 12 wet season nights with Fongoli chimpanzees.

I spent the night with chimpanzee parties following an all-day follow of a focal male subject, and I attempted to find a space for

nocturnal observation near multiple individuals before dark but after individuals started making nests, so that chimpanzees were aware of my presence. Each night, I noted the number of individuals within a 10 to 35 m radius from me, along with their age and sex class and individual identity, if possible. In rare cases, the closest individuals were farther. In a single case, where individuals were at the edge of a plateau, and I placed myself farther than usual (80 m) from the closest individuals, who were an adult female and her infant. These data were included in analyses unless they were statistical outliers.

I began data collection when low-light conditions required using a flashlight (with red bulb) to write. Unlike Zamma (2014), I did not use chimpanzees' nesting behavior as an indication to start data collection on nocturnal behavior, as Fongoli chimpanzees often nested well after dark, especially during the dry season. Therefore, data collection included behavior that occurred before nesting began but after darkness fell as well as behavior following nesting, presumed sleeping and then waking. My definition coincided more closely with nautical twilight than astronomical twilight, which I argue is more biologically relevant for chimpanzee behavior given their lack of visual traits associated with low-light conditions. Krief et al. (2014) define nautical twilight as complete darkness, when the sun is less than 12° below the horizon. In 16 of the 40 nights of observation, my definition entailed beginning data collection before astronomical twilight began, while 24 nights comprised sessions beginning at astronomical twilight. On average, I started these observations 34 min before astronomical twilight ( $n = 16$  nights, range 4–92 min). More of these nights occurred during the wet season ( $n = 11$ ) compared to the dry season ( $n = 5$ ), when cloud cover resulted in earlier darkness. Darkness fell between 1839 and 1944 hrs, varying somewhat with season ( $n = 40$ ).

Behaviors that I recorded during the night included any vocalizations, as well as other sounds such as chimpanzees exiting nests and any observations or sounds associated with other animals or rain, thunder, and high winds indicating the onset of a storm. I recorded data in an all-weather data book using a red light flashlight to minimize disturbance of chimpanzee subjects. I recorded all occurrences of activity and scored them according to three general categories that I could score reliably, even in low-light conditions. Data were summarized post-hoc following Zamma (2014), one of the few studies of nocturnal behavior in wild chimpanzees. I considered activities occurring less than 5 min apart as dependent and lumped them into a single record of activity (Zamma, 2014). Behavioral categories also followed Zamma (2014) with modification, including “chimpanzee vocalizations and activity-related sounds” (CVAs) to enable comparison between studies. However, I modified these categories to indicate behavior within and outside of nests. Operational definitions of behaviors followed Nishida et al. (1999) and conservatively distinguished between activities in which at least one chimpanzee was not in a nest (movement, social behavior, social vocalizations) and those that did not necessarily indicate that a chimpanzee was out of a nest (long-distance vocalizations). The main categories were (1) movement: a behavior that did not involve auditory communication, such as shifting in, exiting, modifying, or building nest, locomotion within a tree crown or on the ground, feeding, and soaking in water, (2) long-distance vocalization: common

calls such as pant hoots, and “waaa” barks, which could have been emitted from nest and were not observed in chimpanzees that had exited nests, (3) social behavior: agonism or affiliation, including sexual behavior, and (4) social vocalizations, which included vocalizations that indicated interactions between chimpanzees where it was likely that at least one chimpanzee had exited their nest. Common vocalizations in this category were submissive pant-grunts, pant-barks, and screams, which subordinates usually give in the immediate vicinity of dominant individuals (Nishida et al., 1999). Pant-hoots, vocal displays, and buttress-drumming communications were included in this category when the observer could detect that chimpanzees had exited their nest. Chimpanzee vocalizations accompanied most social behavior usually, and these two latter categories were subsequently lumped together. In addition to visual observation of nonvocal activity, I based the coding of many behaviors on sounds of walking, climbing, and feeding. I scored categories as one-half or one-third of a CVA if more than one type of CVA was recorded during a 5-minute interval. The maximum number of CVAs I could record in a single hour was 12, although multiple individuals could be active during one CVA. Using CVA as the dependent variable is a conservative measure of activity that controlled for the observer’s inability to detect all individuals active at one time.

## 2.4 | Data collection—environmental variables

Environmental variables considered to influence nocturnal behavior included lunar phase, season, and whether the moon had risen or set during observations. Disturbances were recorded that could have influenced chimpanzee behavior, whether they were seen or heard, and these were defined as a stimulus that elicited a visible or auditory reaction from chimpanzees.

## 2.5 | Data analyses

I categorized moon phase as darker (new or quarter moon) or lighter (half, three-fourths or full moon) for analyses. I used these categories as a comparative measure of luminosity when the moon was above the horizon. I scored individual CVAs according to whether they were recorded when the moon was up versus when it had set or not yet risen (via <http://mooncalc.org>). I analyzed activity according to season, availability of moonlight, and moon phase as well as activity according to time of night on raw data files, using individual CVAs for analyses rather than nightly averages, so that these data are not necessarily independent. In analyses, I controlled for the time the moon was visible above the horizon for dry (51% of observation time) and wet (55% of observation time) season nights. The three behavioral categories (non-social move, social, nonsocial vocalize) were converted to an hourly mean according to time observed.

Independent variables abiotic in nature included moon phase, season, and moonlight availability. Dependent variables in analyses included the total number of CVAs per night while the moon was above the horizon. I used nonparametric tests to assess the influence of season, moon phase and moonlight availability on overall nocturnal activity.

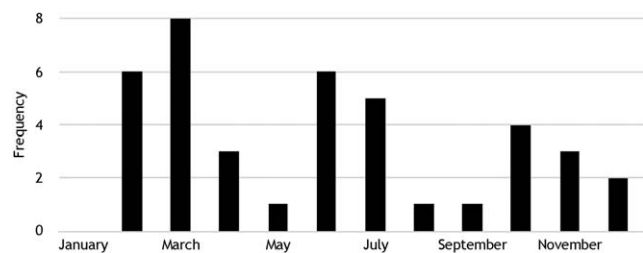


FIGURE 1 Number of nights spent with chimpanzees according to month (all years included)

## 3 | RESULTS

I recorded a total of 712 CVAs during 403.98 hrs on the 40 different nights spent observing Fongoli chimpanzees (Figure 1) or 705 CVAs (range 3–58) during 403.15 hrs on the 39 nights when I eliminated the outlier case comprising 50 min of observation time. I predicted that season would influence the activity of chimpanzees at night. On wet season nights, I spent 123.21 hrs with chimpanzees, and 280.72 hrs with chimpanzees at night during the dry season. Fongoli chimpanzees exhibited, on average, 2.105 CVAs per hr ( $n = 591$  CVAs) in the dry season versus 0.982 per hr ( $n = 121$  CVAs) in the wet season.

Overall, chimpanzees were more active when the moon was visible ( $n = 424$  CVAs) than when it had set or not yet risen ( $n = 301$  CVAs). When the moon was visible, **Fongoli chimpanzees were more active in the dry season during fuller moon phases ( $X^2 = 30.6746$ ,  $df = 1$ ,  $p < 0.001$ ) but also in darker phases ( $X^2 = 11.6757$ ,  $df = 1$ ,  $p < 0.005$ ) compared to the wet season** (fuller phases:  $X^2 = 2.1493$ ,  $df = 1$ ,  $p > 0.1$ ; darker phases:  $X^2 = 0.0333$ ,  $df = 1$ ,  $p > 0.5$ ) (Figure 2).

The number of individuals within proximity of the observer averaged 4 (range 1–11,  $SD \pm 2.33$ ,  $n = 38$ ). Nesting party size ranged from 3 to 32 individuals (mean 20.82 chimpanzees,  $SD \pm 5.80$ ,  $n = 39$ ). There were, on average, 7.03 adult males (range 1–11,  $SE \pm 1.89$ ) and 4.23 females (range 1–7,  $SD \pm 1.86$ ) in nesting parties ( $n = 39$ ). The average number of estrous females in nesting parties was 1.72 (range 0–4,  $SD \pm 1.34$ ,  $n = 39$ ). Average observation time per night was 10.34 hrs (range 1.17–12.33 hrs,  $SD \pm 2.55$ ,  $n = 39$ ). The overall mean for the daily maximum temperature the day before a nocturnal observation took place was 37.1°C (range 28–44°C,  $SD \pm 3.55$ ,  $n = 40$ ).

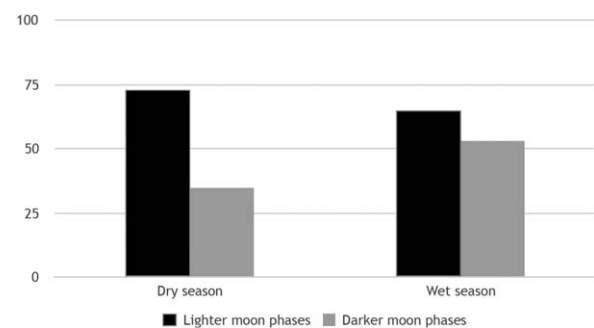


FIGURE 2 Percentage of nocturnal activity (CVA) according to season and lunar phase (darker or lighter) when moon was above horizon

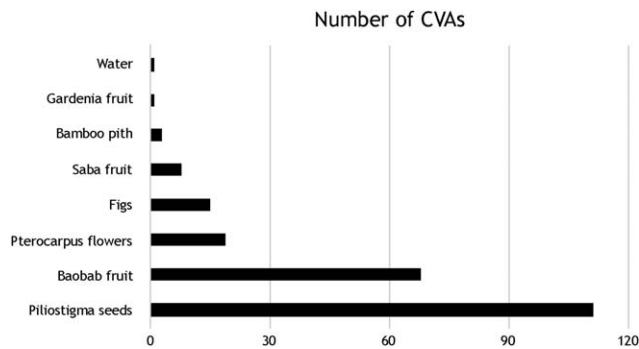


FIGURE 3 Nocturnal feeding behavior by Fongoli chimpanzees

Chimpanzees were disturbed by other animals or weather conditions, such as rain, thunder, and high winds, approximately once a night (mean 0.95 disturbances per night, range 0–5,  $n = 39$  nights). Disturbances that were abiotic in nature included rain, thunder, or high winds that preceded a storm and accounted for slightly over one-third of disturbances ( $n = 13$ ). Disturbances by the presence of other animals such as cows (*Bos taurus*), Senegal bushbabies (*Galago senegalensis*), genets (*Genetta genetta*), warthogs (*Phacochoerus africanus*), and unidentified animals ( $n = 12$ ) accounted for almost one-third of cases. Disturbances in the form of vocalizations by domestic dogs (*Canis familiaris*), bushbucks (*Tragelaphus sylvaticus*), baboons (*Papio papio*), vervets (*Chlorocebus aethiops*), spotted hyenas, long-tailed glossy starlings (*Lamprotornis caudatis*), and wattled plovers (*Vanellus senegallus*) accounted for another one-third of cases ( $n = 13$ ). In many cases, these were warning calls (plovers, starlings, vervets, baboons, bushbuck), suggesting the possibility that a predator was also present.

Chimpanzees exhibited a mean number of 16.9 CVAs per night ( $n = 34$ ), excluding six partial nights. The mean rate of CVAs per hr was 1.845 ( $n = 39$ ; range 0.117–8.583,  $SD \pm 1.536$ ). Of the 712 CVAs recorded, vocalizations such as pant-grunts, pant barks, and screams that indicated social interaction in proximity to another individual accounted for 16.3%. Almost 30% of the activities recorded included long-distance vocalizations such as pant-hoots and alarm barks. These did not necessarily indicate that chimpanzees had left their night nest. Over half of all CVAs included nonsocial movement outside of the night nest, such as soaking in water, feeding, or socializing (55.1%). Of the 455 CVAs recorded as moving, one-half included feeding behavior (50.1%,  $n = 228$ ). Feeding was recorded primarily during dry season

months (figs, [*Ficus* sp.] baobab [*Adansonia digitata*] fruit, *Piliostigma* seeds, *Pterocarpus* flowers), but some feeding was also observed during the wet season (*Saba* fruit) (Figure 3). Within this category, the least active behavior, shifting in nest, accounted for only 1.1% of CVAs ( $n = 8$ ).

Fongoli chimpanzees were active at all hours of the night, but there were peaks in activity immediately following nightfall, immediately preceding dawn and in the middle of the night. Chimpanzees showed an active peak immediately following dusk, when they fed on important foods like baobab and *Piliostigma* seeds during the dry season months when nesting began later and they woke up earlier, and chimpanzees exited nests to socialize during the middle of the night. I also used an ANOVA (SYSTAT, v. 13) to assess the effects of different variables on the time of night that I recorded CVAs, based on individual CVA records per night. The number of estrous females in a nesting party (Mean Squares = 413.967,  $F$ -ratio = 6.575,  $df = 1$ ,  $p = 0.011$ ) but not season (Mean Squares = 1.936,  $df = 1$ ,  $F$ -ratio = 0.031,  $p = 0.861$ ) influenced the hour of night when chimpanzees were active (Figure 4).

#### 4 | DISCUSSION

A number of variables influenced Fongoli chimpanzees' nocturnal activity, reflecting a complex set of interactions among both abiotic and demographic factors. In addition to season, I predicted that moon phase would influence apes' nocturnal activity. Fongoli chimpanzees spent more time active during fuller moon phases when the moon was above the horizon during the dry season. The number of individual chimpanzees in a nesting party positively correlated with the presence of estrous females, with the latter influencing nocturnal behavior, where chimpanzees in nesting parties with estrous females were significantly more active at certain times of night.

Based on the significant influences of season, moonlight availability, and lunar phase on chimpanzee nocturnal activity at Fongoli, apes here appear to adjust to environmental stresses via flexibility in their diel (i.e., day and adjoining night) activity patterns. During the dry season, Fongoli chimpanzees were more likely to socialize or move at night. Apes fed on important foods in their diet, such as baobab fruits and *Piliostigma* seeds as well as *Saba senegalensis* fruits, *Pterocarpus erinaceus* flowers, and figs. Such feeding behavior under low-light conditions is similar to what Yamashita et al. (2005) found for trichromatic species in their comparison of light

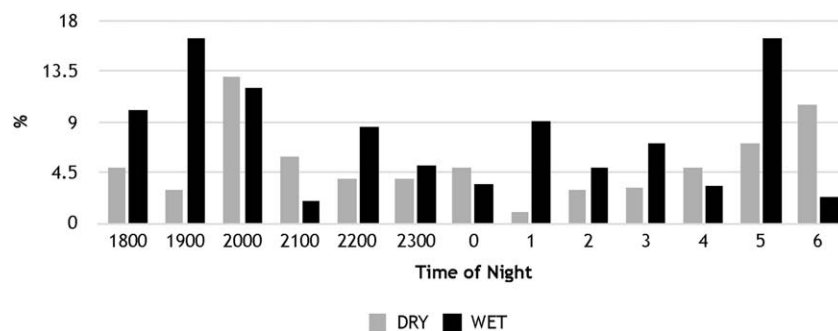


FIGURE 4 Frequency of CVA events according to time of night and season



levels used by primates of varying visual abilities. The foods eaten at night by Fongoli chimpanzees, baobab and *Saba* fruits, *Piliostigma* seed (pods), and flowers, are all nongreen foods, with the exception of unripe figs and unripe *Saba* fruits, which apes may have consumed along with riper fruits during the feeding bouts recorded here. Yamashita et al. (2005) found that nongreen foods were eaten more so than green foods under lower light conditions by a diurnal monkey species (*Cercopithecus ascanius*) in Kibale, Uganda. The authors concluded that primates with trichromatic color vision might be more flexible in seeing color at all light levels (Yamashita et al., 2005). **Thus, arboreal feeding at night by Fongoli chimpanzees may be less challenging than daytime feeding under high heat stress.** Captive chimpanzees also engage in nonsocial behavior at night, including foraging, drinking, and vigilance (Videan, 2006). Zamma (2014) conducted his study during a low illuminosity moon phase, demonstrating that apes can be active at night even under low-light conditions. Although chimpanzees at Fongoli were more active at night during the dry season, they engaged in nocturnal activity during the rainy season as well, specifically nonsocial vocalization, which included long-distance auditory communication. Such activity does not necessarily entail exiting one's night nest, but the significance of greater movement and social behavior during the dry season, especially, warrants explanation.

Feeding at night, in addition to other activities such as social behavior, may be beneficial in the thermally challenging habitat at Fongoli, especially if the relatively low predator density at this site releases them from predation pressure at night. Alternatively, they could be avoiding humans by engaging in nocturnal behavior as other species do (George & Crooks, 2006; Kitchen et al., 2000; Sonnichsen et al., 2013). This latter explanation is supported by recent research on Fongoli chimpanzees' feeding behavior in regards to the presence of humans (Lindshield et al., 2017), where adult males were not deterred from feeding near anthropogenic disturbance but exhibited higher levels of anti-predator behavior when feeding there. Other species in Senegal have changed their temporal foraging niches in response to predation pressure by humans, including warthogs (pers. obs.), Giant Derby Eland (*Taurotragus derbianus*) and elephants (*Loxodonta africana*) (P. Stirling, pers. comm.). Additionally, chimpanzees in larger nesting parties were more active at night, which conforms to theories of social grouping as an anti-predator strategy in primates (Isbell, 1994). It is likely that at least older individuals in the Fongoli chimpanzee community co-existed with lions at this site (M. Camara, pers. comm.), such that residual anti-predator behavior still exists. Trade-offs regarding such risks as higher predation, including humans as a type of threat, seem to incur fewer costs than those associated with the extreme thermal environment at Fongoli.

Chimpanzees living at the species' limit in the savannas of Senegal can serve as sentinel populations for understanding the effects of climate change and increasing temperatures on this endangered species. As climate change results in extreme weather and increasing temperatures in Senegal, understanding how species adjust to such stresses is critical (Moyer-Horner et al., 2015). As the West African chimpanzee has been recently uplisted to Critically Endangered (IUCN Redlist version 3.1, <http://www.iucnredlist.org/details/15935/0>), this becomes especially important for chimpanzees here. Even captive chimpanzees in South Africa utilize shade as a thermoregulatory resource while living outside

of their geographical range and at lower temperatures than chimpanzees in Senegal (Duncan & Pillay, 2013). Similarly, Videan (2006) found that maximum and minimum overnight humidity significantly influenced captive chimpanzee sleep patterns, with total sleep duration and quality—the latter negatively correlated with waking—decreasing with increased maximum humidity. As Moyer-Horner et al. (2015) note for American pika (*Ochotona princeps*), behavioral adjustments to tolerate heat stress are expected for animals that cannot change their altitudinal or latitudinal ranging patterns. Such species may change their microclimate use patterns (Moyer-Horner et al., 2015) or, as is hypothesized here, change their activity patterns as a response to heat stress. Fongoli individuals rest significantly more during the day than chimpanzees living in forested environments during dry season months especially, while they spend significantly less time feeding but an almost equivalent amount of time traveling (Pruetz & Bertolani, 2009). Chimpanzees here also feed on baobab fruit at faster rates in open canopy habitats (Lindshield et al., 2017), perhaps as a means to reduce thermal stress.

Revisiting the two hypotheses for explaining nocturnal behavior presented here initially illustrates the usefulness of using savanna chimpanzee studies, in an argument from homology as well as ecology, to help understand early hominin behavior in similar environments. The habitat similarities between savanna chimpanzee habitats and early hominin ones (White et al., 2009) make such apes especially relevant to anthropological inquiries into the nature of traits such as sleep patterns. The nocturnal activity of chimpanzees at Fongoli can in particular provide some insight into hominin evolution in terms of potential nocturnal behavior in similarly dry, open and hot environments, especially regarding those hominins predating fire domestication. A key development during the course of human evolution was the control and use of fire, in part because this allowed earlier hominins to lengthen their day more safely (Burton, 2009). Burton (2009) and other scholars who assert that hominins initially domesticated fire because of its value as a light resource largely overlook daytime heat as selective pressure, however. Conversely, low night-time temperatures could also explain higher activity levels if such activity helped to keep subjects warmer. The nocturnal behavior of Fongoli chimpanzees lends support for Wheeler's physiological model (1984, 1990, 1991a,b, 1994), which maintains that high heat stress in open environments would temporally restrict foraging niches for hominins. The implications include support for the hypothesis that early fire use and control could have been a means to deal with predator pressure at night, for example (Burton, 2009), as hominins expanded their foraging niche temporally. This may be especially significant for hominins compared to other primates, given recent research on people living in savanna environments today (Nunn, in press, this issue).

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