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A survey of nocturnality and risk for savanna chimpanzees at Assirik, Senegal

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Abstract – Chimpanzees (*Pan troglodytes*) in Senegal may use nocturnality to mitigate hyperthermia risk in semi-arid environments but the degree of nocturnality for such chimpanzees also in sympatry with large carnivores remains uncertain. We compared diel activity among chimpanzees and their potential predators at Assirik in Niokolo-Koba National Park and contextualized these findings relative to other unit-groups in savanna landscapes. From 2015-2018, we generated a predator inventory using multi-modal methods and monitored the diel activity of chimpanzees and predators with camera traps [$N = 2092$ camera trap (CT) days]. From 2015-2023, we also surveyed for evidence of predation during recce walks. Six potential nonhuman predators occur at Assirik, including lions (*Panthera leo*), leopards (*Panthera pardus*), spotted hyenas (*Crocuta crocuta*), African wild dogs (*Lycaon pictus*), Nile crocodiles (*Crocodylus niloticus*), and rock pythons (*Python sebae*). We documented one suspected case of a predator killing a chimpanzee. Nocturnality comprised 12.7% of CT events for chimpanzees and these events were more concentrated at twilight. Chimpanzees were more active during the day, predators were more active at night, and there was substantial temporal overlap among chimpanzees and potential predators during twilight intervals. Our findings support the hypothesis that savanna chimpanzees in Senegal are active at night in response to the extremely hot environment. We hypothesize that Assirik chimpanzees experience a tension between decreasing hyperthermia and increasing predation risk during nocturnality.

Keywords – nocturnal, *Pan troglodytes verus*, predation, Senegal, thermoregulation.

Introduction

In semi-arid climates where surface water and shade cover are seasonally scarce, savanna chimpanzees are at high risk of hyperthermia and may use nocturnality as a strategy to regulate body temperature (Pruetz, 2018; Wessling *et al.*, 2018a; Lindshield *et al.*, 2021). While nocturnality may decrease hyperthermia risk, it may also exacerbate predation risk at locales with sympatric large carnivores, such as Assirik (McGrew *et al.*, 2014; Lindshield *et al.*, 2019). To explore this possible trade-off, we investigate spatio-temporal aspects of diel activity for chimpanzees and large carnivores in a savanna environment.

PREDATION RISK

Predation pressures shape antipredator behavior in primates, including chimpanzees (Seyfarth *et al.*, 1980; van Schaik, 1983; Goodall, 1986; Boesch, 1991; Cartmill, 1992; Hart, 2007). Relative to most other primates, average mortality rate from predation is presumably low for chimpanzees due to their large body sizes (Tutin *et al.*, 1981). However, chimpanzees display adaptations to minimize predation because of its high cost to individual fitness (Klailova *et al.*, 2012). Examples of antipredator behaviors in chimpanzees include group living, flexibly increasing subgroup size in risky areas, risk-sensitive foraging, fleeing, alarm-calling, arboreal nesting, eavesdropping, and using tools as weapons (Kortlandt, 1962; Tutin *et al.*, 1981; Goodall, 1986; Boesch, 1991; Pruetz *et al.*, 2008; Lehmann and Dunbar, 2009; Stewart and Pruetz, 2013; McLester *et al.*, 2016; Lindshield *et al.*, 2017). Chimpanzees range within the intermediate size class of terrestrial mammals (van Valen, 1972), and mammals of this size are routinely killed by carnivores of the same or larger body classes (Carbone *et al.*, 1999). Verified chimpanzee killers include leopards (*Panthera pardus*: Boesch, 1991; Nakazawa *et al.*, 2013), lions (*Panthera leo*: Tsukahara, 1993), and humans (*Homo sapiens*: Hicks *et al.*, 2010).

Predation rates are difficult to estimate in chimpanzees and many other primates because direct observations of hunts and kills are rare (Isbell and Young, 1993; Hill *et al.*, 2001; Hart, 2007; this study), and predators that are deterred by the physical presence of researchers exacerbates this problem (Boesch, 1991; Isbell and Young, 1993). Alternatives to direct observation, including camera traps to capture evidence of cryptic predator species (Klailova *et al.*, 2013; Sylla *et al.*, 2022), passive acoustic sampling of alarm calls (Blumstein *et al.*, 2011), trace evidence of predation-sensitive foraging (Lindshield *et al.*, 2017), landscape analyses using remotely-sensed imagery of riskier and safer habitats (Willems *et al.*, 2009), and GPS-collaring of predator and prey species (Isbell *et al.*, 2018; but see Fedigan, 2010, for ethical aspects of darting) have contributed to a richer understanding of predation risk and antipredator strategies in primates.

HYPERTHERMIA RISK

Thermal adaptations to reduce hyperthermia occurrence in hot and dry environments are expected under natural selection (Kolka and Elizondo, 1983; Angilletta *et al.*, 2010). Physiological responses to hot conditions include evaporative cooling or sweating (Primates: Best and Kamilar, 2018) and panting (*Cebus imitator*: Campos and Fedigan, 2009). Behavioral thermoregulation is a proximate and flexible response to thermal sensitivity that is widespread in many primates, especially those inhabiting hot and dry environments (Brain, 1990; Brain and Mitchell, 1999; Hill *et al.*, 2004; Pruetz, 2007; Campos and Fedigan, 2009; Pruetz and Bertolani, 2009; McFarland *et al.*, 2014; Stewart *et al.*, 2018; Boyer-Ontl and Pruetz, 2020). To be effective, these behavioral strategies require predictable access to resources such as shade cover and water.

Savanna chimpanzees in Senegal exhibit higher frequencies and more varied forms of hyperthermia-related behaviors than other conspecifics (Lindshield *et al.*, 2021). These differences may be related to the higher average daily temperatures in Senegal relative to other areas of the species' geographic distribution (Tagg *et al.*, 2018; Wessling *et al.*, 2018b; van Leeuwen *et al.*, 2020). At Fongoli, behaviors that may minimize risk of hyperthermia include preferential use of shaded habitats, such as gallery forests (Pruetz and Bertolani, 2009) and caves (e.g., Pruetz, 2007; Boyer-Ontl and Pruetz, 2020), a higher time allocation to rest during daylight hours, especially during the dry season, relative to chimpanzees inhabiting landscapes with more forest cover (Pruetz and Bertolani, 2009), construction of sleeping nests that are thinner in hotter weather (Stewart *et al.*, 2018), a higher occurrence of nocturnal behavior relative to most other conspecifics (Kayan: Tagg *et al.*, 2018), and a higher time allocation to nocturnality during hotter and drier months of the year (Fongoli: Pruetz, 2018). These converging lines of evidence support the hypothesis that nocturnality, in certain contexts, is a form of behavioral thermoregulation.

NOCTURNALITY IN CHIMPANZEES

Chimpanzee activity during twilight and night periods, defined as nocturnality in this study and elsewhere (Pruetz, 2018; Tagg *et al.*, 2018; Lacroux *et al.*, 2022), is characteristically facultative because its occurrence is relatively low in frequency within a population and highly variable among populations (Tagg *et al.*, 2018). Nocturnality is widespread in wild chimpanzees but not universal (Janmaat *et al.*, 2014; Zamma, 2014; Pruetz, 2018; Tagg *et al.*, 2018; Lacroux *et al.*, 2022). In addition to sleeping and resting while in their nests at twilight and night, chimpanzees intermittently engage in various activities, inside and outside of their sleeping nests, arboreally and terrestrially (Zamma, 2014). Chimpanzees of all age and sex classes engage in nocturnality and display a suite of behaviors such as feeding, socializing, and traveling (Janmaat *et al.*, 2014; Zamma, 2014; Piel, 2018; Pruetz, 2018; Tagg *et al.*, 2018). There is high temporal variation in terrestrial nocturnality among chimpanzee groups, and they generally engage in terrestrial nocturnality around the twilight hours (Tagg *et al.*, 2018).

Hypotheses to explain nocturnality in chimpanzees include environmental pressures in hot and dry environments (i.e., minimizing hyperthermia risk), sleep disturbances from nonhuman predators and other sympatric mammals or humans, high moon illuminance that may improve visibility conditions during nocturnality, and minimizing feeding competition during daylight hours (Janmaat *et al.*, 2014; Krief *et al.*, 2014; Tagg *et al.*, 2018; Lacroux *et al.*, 2022). These hypotheses are not mutually exclusive. For example, it may be easier to forage and avoid predators on moonlit nights.

For savanna chimpanzees, specifically (*sensu* van Leeuwen *et al.*, 2020), higher frequencies of nocturnality are associated with seasonally hot and dry periods or climates (Issa: Piel, 2018; Fongoli: Pruetz, 2018), as predicted by the environmental stress hypothesis. In Senegal, nocturnality occurs at all times during the night and twilight periods (Fongoli: Pruetz, 2018; Kayan: Tagg *et al.*, 2018; cf. Issa, Tanzania: Tagg *et al.*, 2018). The habituated chimpanzees at Fongoli routinely socialize, travel, soak in water, and ingest food during twilight and night periods, with feeding frequency relatively high around dusk and dawn during the drier months (Pruetz, 2018).

STUDY AIMS

This study aims to investigate nocturnality in chimpanzees inhabiting a savanna biome with a rich predator guild and minimal anthropogenic habitat disturbance (Assirik, Senegal: Tutin *et al.*, 1981; Lindshield *et al.*, 2019) by exploring the potential tension between lower risk of hyperthermia and higher risk of predation. Tutin *et al.* (1981) reported that the unhabituated Assirik chimpanzees produced alarm calls at night after detecting a leopard, but they assumed that the Assirik chimpanzees remained mostly inactive and within their sleeping nests during the night. We aim to evaluate this perspective in light of new findings of chimpanzee nocturnality, enabled through behavior sampling of habituated savanna chimpanzees (Fongoli: Pruetz, 2018) and remote monitoring of terrestrial nocturnality with camera traps (e.g., Tagg *et al.*, 2018). Building on these foundational studies, we hypothesize that the Assirik chimpanzees engage in terrestrial nocturnality and, while doing so, are at risk of encountering large carnivores. Specifically, we analyze frequency and temporal patterns of terrestrial nocturnality in the Assirik chimpanzees collected with camera traps, develop a more robust assessment of predation risk from sympatric and potential predators, and survey for evidence of predation. Moreover, we contribute to the fast-growing frontier of nocturnality research on primates (reviewed in Fruth *et al.*, 2018), particularly nocturnality in chimpanzees (Piel, 2018; Pruetz, 2018; Stewart, 2018; Tagg *et al.*, 2018; Lacroux *et al.*, 2022), by evaluating our findings relative to nocturnality hypotheses involving hyperthermia and predation risks. The Assirik chimpanzee community occupies a landscape with the hottest and driest climate combined with the highest potential predator abundances of any study site known to us. Under these conditions, we expect to see strong selective pressure for behavioural strategies that mitigate the competing risks of hyperthermia and predation.

Materials and methods

STUDY SITE AND SUBJECTS

The study was conducted in the Assirik area of Niokolo-Koba National Park (UTM 28 N 1425758 m E 747165 m N) in southeastern Senegal (see Fig. 1 in Lindshield *et al.*, 2019). The study period included 20 cumulative months between 2015 and 2018 to determine predator species richness and survey for diel activity with camera traps (supplementary fig. S1), and an additional 41 cumulative months between 2019 and 2023 to survey for evidence of predators killing chimpanzees. Ground surveys by foot or vehicle occurred from approximately November or December until June or July of each year; this sampling period corresponds with the early dry until early wet seasons. The site was closed to researchers from the middle of the wet season into the dry season transition.

The savanna landscape at Assirik is mostly comprised of woodland and grassland vegetation, while a small proportion consists of evergreen forest (for more information, see McGrew *et al.*, 1981; Lindshield *et al.*, 2019). Senegal has one wet and one dry season per year (Fall *et al.*, 2006). We partitioned the year into three distinct periods, including wet, early-dry, and late-dry. The dry season was divided in two due to major differences in temperature and surface water availability (Pruetz and Bertolani, 2009; Stewart, 2011; Lindshield *et al.*, 2017) that are known to affect activity levels and habitat use (Pruetz and Bertolani, 2009; Boyer Ontl and Pruetz, 2020). During the wet period (June-October), surface water is readily available and the average monthly temperature ranges from 26 to 30°C (Fall *et al.*, 2006). In the early-dry period (November-February), the lowest average and minimum daily temperatures of the year occur, with the minimum dropping to 7°C in extreme cases (Stewart, 2011). Also, surface water gradually decreases but remains accessible in seasonal streams (Pruetz and Bertolani, 2009; Lindshield *et al.*, 2017; Wessling *et al.*, 2018a; Boyer Ontl and Pruetz, 2020). Average daily temperature increases as the dry season progresses, with averages ranging from 30 to 34°C (Fall *et al.*, 2006) and with a daily maximum routinely exceeding 40°C (Pruetz and Bertolani, 2009; Pruetz, 2018). In the late-dry period (March-May), water is limited to a few scattered springs (Pruetz and Bertolani, 2009; Lindshield *et al.*, 2017; Wessling *et al.*, 2018a; Boyer Ontl and Pruetz, 2020). Long-term trends demonstrate that May is a transitional month for precipitation, and it oftentimes marks the onset of the wet season (Pruetz and Bertolani, 2009). However, the early rains did not arrive until June between 2015 and 2018. Thus, the month of May was in the late-dry period for this study. This study did not evaluate the potential effects of food availability on nocturnality (Janmaat *et al.*, 2014; Pruetz, 2018; Lacroux *et al.*, 2022), and we suggest that future research include it.

Assirik is located within the park's interior with minimal human impacts (Lindshield *et al.*, 2019). From 2015-2018, visitors to the site (e.g., local residents, researchers, other tourists) were rare, other than our small team of 6-7 individuals. We found no evidence of farming, herding, timber extraction, charcoal production, or gold mining. Ndiaye *et al.* (2018) describe the frequency and distribution of these common land practices in unprotected areas of Senegal. For a discussion of humans killing chimpanzees in Senegal, which has been historically low, overall, and never reported in Niokolo-Koba National Park, see Lindshield *et al.* (2017, 2019). For these reasons, in addition to the use of remote and non-invasive methods for sampling animal activity (e.g., camera traps), we assumed that human impacts had a negligible but non-zero impact on chimpanzee and predator nocturnality.

A unit-group of approximately 26 unhabituated chimpanzees inhabit an area of approximately 90 km^2. Unit-group size and home range estimates are based on historic observations of sleeping nest locations, direct observations of unhabituated individuals, and geo-sourced genotypes extracted from fecal samples (Baldwin *et al.*, 1982; Tutin *et al.*, 1983; McGrew *et al.*, 2004). Historic records on unit-group size are consistent with contemporary observations at Assirik (Lindshield and Ndiaye, unpubl. data) and comparative records from the nearby Fongoli site (29-36 habituated individuals: Pruetz *et al.*, 2015; approximately 90 km^2 home range area: Pruetz, 2018). Additional research beyond the scope of this study is needed to improve estimates of unit-group size, home-range area, and proximity to neighboring unit-groups.

PREDATION

The large carnivore guild at Assirik includes putative and potential predators of chimpanzees. We defined putative predator species as those known to kill and ingest chimpanzees elsewhere, including lions and leopards (Boesch, 1991; Tsukahara, 1993; Nakazawa *et al.*, 2013). Limiting the inclusion standard to putative predators may underestimate predation risk from other nonhuman species, as killings are rarely observed (Tutin *et al.*, 1981; Hart, 2007). Moreover, while chimpanzees are not reported as preferred prey for any of the large predators at Assirik, these carnivores hunt opportunistically in other locations (Hayward and Kerley, 2005; Hayward, 2006; Hayward *et al.*, 2006a,b; Davidson *et al.*, 2013). To address this limitation, we included as potential predators those species that kill prey of similar body mass to wild and prime-age adult chimpanzees (approximately 30-60 kg: Smith and Jungers, 1997). This body mass range accounts for variation among *P. t. schweinfurthii*, *P. t. troglodytes*, and *P. t. verus* subspecies from both sexes. By calibrating this range to prime adults, we further assume that geriatric, young, injured, or ill chimpanzees have at least an equivalent risk of depredation from potential predators. Such potential predators at Assirik include hyenas (*Crocuta crocuta*), wild hunting dogs (*Lycaon pictus*), Nile crocodiles (*Crocodylus niloticus*), and rock pythons (*Python sebae*) (Cott, 1961; Broadley, 1983; Hayward, 2006; Hayward *et al.*, 2006a). These large carnivore species are mostly nocturnal (Spawls and Branch, 1995; Cozzi *et al.*, 2012; Behangana *et al.*, 2017; Mugerwa *et al.*, 2017), except for wild hunting dogs that may allocate about one-quarter of diel activity budget to nocturnality (Botswana: Cozzi *et al.*, 2012).

We used a multi-modal approach during 193 days of fieldwork from July 2015 to December 2018 to create the predator inventory at Assirik, including camera traps (Pebsworth and LaFleur, 2014), recce walks to record all direct encounters with potential predators (see White and Edwards, 2000; Kühl *et al.*, 2008), and opportunistic direct encounters while traveling on foot or by vehicle (Edwards *et al.*, 2000). Indices of predator activity (e.g., dung, prints, vocalizations) were not included in this survey but should be considered for future research. Recce surveys were conducted between 06:30-15:00 hours. Opportunistic encounters during vehicle travel occurred between 06:00-21:00 hours on 38 days. While in the vehicle, we followed the site access road and traveled at relatively low speeds (approximately 16-32 kph) in the Assirik area while scanning for wildlife. In the next section, we describe the camera-trap methods. All gallery forests at the Assirik site (see Lindshield *et al.*, 2019) were sampled during recce walks ($N = 149$ walks), which ranged in distance from approximately six to 22 km per walk, according to pedometer measurements. In addition to the surveys from 2015-2018, our team again used the recce method during an additional 412 walks between 2019-2023 to opportunistically survey for direct evidence of predators killing chimpanzees. One suspected case of predation was observed during this period.

DAY AND NIGHT ACTIVITY

We used the deliberately-biased placement method (Meek *et al.*, 2014) at focal points (e.g., surface water, liana tangles in gallery forests) to maximize detection of chimpanzees (see Fig. 1 in Lindshield *et al.*, 2019). As many as six Reconyx Hyperfire™ HC500 or Bushnell® Trophy Cam Aggressor HD camera traps (CT) with motion or infrared sensors monitored this area from 2015 to 2018 (2015 $N = 2$ months; 2016 $N = 5$ months; 2017 $N = 8$ months; 2018 $N = 5$ months). We aimed to uniformly sample among months at Assirik with CTs. Sampling effort (CT days) was uniform among the early-dry, late-dry, and wet periods but some months were underrepresented during the wet and early-dry periods due to road closures or funding gaps (supplementary fig. S1). We monitored the site with six active CTs during the dry periods and three CTs during the wet season, except in cases of CT repair and cleaning ($N = 2$ cases), or theft ($N = 1$ case).

Each site was monitored by a single CT and positioned at least 500 m Euclidean distance from its nearest neighbor. Geo-located CTs were positioned 50-100 cm above ground and out of direct sunlight. They were set to take three sequential still images followed by a 15-second delay, and this sequence was repeated until the individuals moved outside of the sensor's range. The relatively high position of the CT field-of-view was suitable for chimpanzees and large mammalian carnivores, this installation height may have been inadequate for sampling the shorter-statured reptilian carnivores. Each image was automatically tagged with a date, time, and temperature reading using internal instrumentation. Following Lindshield *et al.* (2019), one CT day was operationally defined as one 24 h monitoring period at one CT site.

This protocol was designed to maximize chimpanzee encounters by positioning CTs in their preferred habitats (closed tree-canopy areas: Pruetz and Bertolani, 2009) near water holes, liana tangles, and game trails. While the camera traps used in this study were relatively quiet to human observers and did not emit a white flash, they can be detectable to some diurnal and nocturnal animals and their effects on animal behavior deserve further study (e.g., Gregory *et al.*, 2014; Meek *et al.*, 2016). This sampling design is biased against species that preferentially use woodland and grassland vegetation at Assirik (see Discussion). Stratified random sampling with CT arrays minimizes this bias (TEAM, 2011) and it is an important method to consider for future research.

ABIOTIC CONDITIONS

The dates and times for each CT event were cross-referenced with visible light conditions from photographs as well as a localized day length calendar (suncalc.org) to classify the astronomical (sunrise, day, sunset, civil twilight, and night) condition of each event. We pooled nautical and astronomical twilight phases into the "night" category, as light levels at these times are relatively low, especially at CT sites in forested areas where vegetation obstructed the horizon. We classified "twilight" events as those occurring during civil twilight, when the center of the sun is six degrees below the horizon, as this light level reduces visual acuity in humans (Leibowitz and Owens, 1991), and the light level at these times triggered the infrared sensor on our cameras. Twilight and other darkness (night and nautical and astrological twilight) duration were downloaded from the U.S. Naval Observatory Astronomical Information Center (https://aa.usno.navy.mil/). Averages were calculated from reference year 2015 on the 1st and 15th of each calendar month. Following established protocols, we classified events as "nocturnal" when they were recorded at twilight and night (Pruetz, 2018; Tagg *et al.*, 2018; Lacroux *et al.*, 2022). For nocturnal events ($N = 39$), we further assessed visible light conditions with localized moon illuminance (%) estimates (mooncalc.org) for each species that had more than one nocturnal event during the study period (i.e., excludes wild hunting dogs). When the moon was below the horizon during nocturnal events, we assumed that illuminance was low (1% illuminance, $N = 22$ of 39 nocturnal events). This adjustment removed inflated estimates of illuminance, but also eliminated variation in low-illuminance values that certainly occurred (Krieg, 2021).

We used temperature estimates from CT internal sensors to measure the temperature conditions of each event. This method assumes that the temperatures at the CT sites were representative of the study site during the study period. This assumption is supported by the similarity in temperatures by season/period (table 1) to reports from other sites in the Kedougou region of Senegal (Pruetz and Bertolani, 2009; Wessling *et al.*, 2018a; Boyer Ontl and Pruetz, 2020).

Table 1. Temperature averages and variation among seasons/periods recorded for all chimpanzee CT events ($N = 110$).

Season	Average temperature °C ± standard deviation (range) $_{\text{sample size}}$		
	Day	True night and twilight	All events by season
Early-dry	31 ± 5 (16-39) $_{38}$	26 ± 3 (24-29) $_{3}$	31 ± 5 (16-39) $_{41}$
Late-dry	34 ± 8 (24-46) $_{22}$	27 ± 3 (24-31) $_{4}$	33 ± 8 (24-46) $_{26}$
Wet	30 ± 4 (23-40) $_{36}$	28 ± 2 (25-31) $_{7}$	30 ± 4 (23-40) $_{43}$
All events	31 ± 6 (16-46) $_{96}$	27 ± 2 (24-31) $_{14}$	31 ± 6 (16-46) $_{110}$

ANALYSES

To evaluate risk of hyperthermia and predation, we examined associations among animal detections (chimpanzees and their potential predators) from camera traps to environmental variables, including temperature, season, nocturnal phase, and moon illuminance. We further assessed predation risk by amalgamating species presence observations from the multimodal predator survey. Following Tagg *et al.* (2018), we classified CT events as independent when a period of $\geqslant$15 minutes elapsed between sets of images of the same individual or subgroup. In addition, we did not count a single individual (usually identified by unique physical traits; see Boyer Ontl and Pruetz, 2020) more than once per day/twilight/night within a 24-hour cycle. However, it was not possible to identify individuals from still images in $>$10% of independent events, and for this reason we excluded age and sex identifications from our descriptive statistics and statistical tests. We use an exploratory approach to examine social aspects of nocturnality; this analysis cautiously examines associations between subgroup size and diurnal-nocturnal activity due to two methodological limitations. First, the brightness of an image at night is limited to the reach of the camera's flash, and this illuminated area is smallest with infrared flash cameras (Wearn and Glover-Kapfer, 2017). The smaller illuminated area may cause researchers to neglect individuals outside of the illuminated area and underestimate subgroup size during nocturnality, in relation to diurnal events at the same location. Future studies may consider using cameras equipped with white flash to address this issue. Second, the presence of estrous females can be an important predictor of subgroup size in chimpanzees (Matsumoto-Oda, 1999) and nocturnality frequency (Pruetz, 2018) but we were unable to account for this effect.

Chimpanzees and their sympatric predators triggered camera traps on 144 independent occasions during 2,092 CT days. Sample sizes for chimpanzee detections and chimpanzee nocturnal events were within the reported ranges by Tagg *et al.* (2018). Sampling was approximately evenly distributed across the wet (34%, $N = 718$ days), early dry (34%, $N = 712$ days), and late dry (32%, $N = 662$ days) periods. We used a polar plot from the ggplot2 package in R version 3.4.3 (Wickham, 2016; R Core Team, 2017) to visualize CT events across the diel cycle for chimpanzees and potential predators. We used non-parametric tests to evaluate associations between nocturnality and risk of predation and hyperthermia, including the Mann-Whitney U test to compare temperature conditions during the day and twilight/night, and the Kruskal-Wallis test to compare temperature conditions across periods (early-dry, late-dry, wet). We used the Fisher's exact probability test to compare nocturnality across seasonal periods with the expected values calculated from a uniform distribution among periods (Freeman-Halton version), and across darkness phases (twilight and night) with expected values calculated from relative twilight and other darkness durations. We tested for differences in moon illuminance during nocturnal events among species with the Kruskal-Wallis test and the Mann-Whitney U test for differences

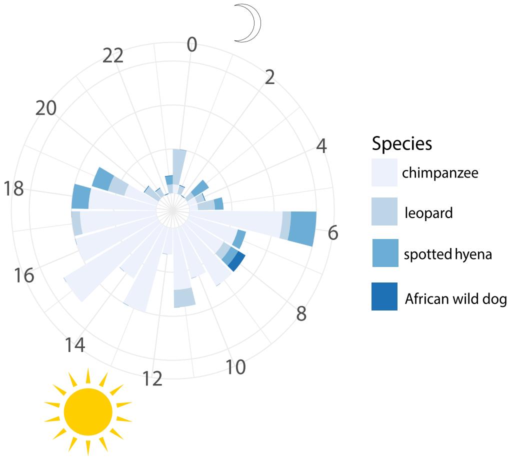

Figure 1. A comparison of day-night activity among chimpanzees and their potential predators. Activity frequencies by hour and species increase along the radial lines. Hours are reported in Arabic numerals around the perimeter.

between chimpanzees and their potential predators. The significance threshold was set to $\alpha = 0.05$.

Results

We recorded $N = 110$ independent CT events with chimpanzees (fig. 1), including 96 during daylight (87.3% of events) and 14 cases of nocturnality (12.7% of events). Nocturnality events were uniformly distributed during night (50.0%, $N = 7$) and twilight (50.0%, $N = 7$) stages but nocturnality occurred more often during twilight relative to other darkness (Fisher's exact test: $P = 0.02$) after adjusting for the relative duration of each (twilight daily average: 44 minutes, 6% of total darkness; other darkness daily average: 11 hours 6 minutes, 94% of total darkness). Average subgroup size was slightly higher during the day (day average: 3.4 ± 2.2 individuals, range: 1-13 individuals, $N = 96$; night average: 2.6 ± SD 2.2 individuals, range: 1-7; twilight average: 1.43 ± 0.5 individuals, range: 1-2 individuals).

PREDATION AND RISK

During the predator survey (2015-2018), we opportunistically encountered lions ($N = 1$ encounter), crocodiles ($N = 1$ encounter with skeletal remains), and pythons ($N = 2$ encounters) (supplementary fig. S2). We recorded 34 independent CT events with predators (fig. 1), including leopards ($N = 20$), hyenas ($N = 13$), and African wild dogs ($N = 1$). Each predator species was located within the chimpanzee unit-group's estimated home range.

Within the CT dataset, we found diel activity overlap among chimpanzees, leopards, hyenas, and African wild dogs, with the strongest overlap occurring in the early morning (06:00-09:00) and early evening (18:00-20:00) hours (fig. 1, supplementary table S1). In one case, an interval of 45 minutes separated at least three chimpanzees and one leopard at night (fig. 2). This chimpanzee subgroup minimally consisted of one likely adult female with an infant traveling on her back and one likely immature male.

During nocturnal CT events, predators were mostly active at times when moon illuminance was relatively low, usually when the moon was below the horizon (percent illuminance for leopards: average = 29%, median = 1%, range: 1-99%, $N = 16$; hyenas: average = 21%, median = 1%, range: 1-83%, $N = 9$). Moon illuminance was higher during chimpanzee nocturnality but chimpanzees were also active during low illuminance periods (average = 42%, median = 44%, range: 1-94%, $N = 14$) (supplementary fig. S3). There was not a significant difference in light condition during nocturnal events for chimpanzees versus leopards and hyenas combined (Mann-Whitney $U_1 = 210$, $P = 0.16$).

One suspected case of predation was discovered at 11:54 am on December 17, 2023. We encountered the fresh or recent remains of a chimpanzee, consisting of the distal portions of one or more limbs (fig. 3a), including an intact right foot that was disarticulated and defleshed at the ankle joint and a defleshed tibia and fibula (probable) as well as several tufts of hair and a piece of the viscera that was likely from the intestines. The body size was consistent with a mature or nearly mature individual. Scavengers removed the entire body before the skeletal elements could be collected for taphonomic and osteological analyses. Therefore, a better age estimate

Figure 2. Spatiotemporal and terrestrial overlap between a (a) leopard and (b, c) chimpanzees at Assirik. A 45-minute interval separates these two events. Photo credit: Recherche Chimpanzé Assirik and Direction des Parcs Nationaux du Sénégal.

Figure 3. Site of a suspected predation event at Assirik, including (a) the remains of a chimpanzee right foot and likely a distal tibia and fibula, and (b) a fresh chimpanzee nest located near the remains. Photo credits: Recherche Chimpanzé Assirik and Direction des Parcs Nationaux du Sénégal.

is not available. Moon illuminance ranged from 18.1-19.6% between sunset at 18:27 to 22:13 on 16 December. After 22:13, the moon was below the horizon and illuminance was $<1\%$ for the remaining night and twilight (dawn) intervals. Soon after encountering the remains, the field team detected an unhabituated chimpanzee, probably a juvenile, about 7 meters from the site. This individual climbed up a tree to hide from the team and later retreated from the site. A fresh nest (*sensu* Tutin and Fernandez, 1984) was observed above the remains (fig. 3b), but we did not observe fresh or recent feces, fresh urine, or any other fresh nests in the immediate area. The nest was positioned about four meters in height in the tree canopy and less than half a meter from an adjacent rock shelf. One side of the nest had partially collapsed.

HYPERTHERMIA RISK

The thermal minimums and maximums (averages and absolutes) were recorded by camera traps during the dry months (table 1), with minimums occurring in early-dry (average: 26°C, absolute: 16°C) and maximums in late-dry (average: 34°C, absolute: 46°C). Average day temperature differed among periods (Kruskal-Wallis $H_2 = 5.91$, $P = 0.05$) and day temperatures approaching or exceeding 40°C were recorded across all periods (table 1). As expected, temperatures during nocturnality events were significantly lower than day

Table 2. Distribution of day and night activity for chimpanzees among seasons/periods.

Season	Day	True night and twilight	All events by season
	Percentage and sample size (N) for CT events across seasons		
Early-dry	39.6% (38)	21.4% (3)	37.3% (41)
Late-dry	22.9% (22)	28.6% (4)	23.6% (26)
Wet	37.5% (36)	50.0% (7)	39.1% (43)
Total	100% (96)	100% (14)	100% (110)
	Percentage and sample size (N) for CT events within seasons		
Early-dry	93% (38)	7% (3)	100% (41)
Late-dry	84.6% (22)	15.4% (4)	100% (26)
Wet	83.7% (36)	16.3% (7)	100% (43)

events (diurnal versus nocturnal events: Mann-Whitney $U_1 = 311.5$, $P = 0.0006$); nocturnality was associated with 4°C lower temperatures than diurnality, on average (day average: 31 ± SD 6°C; range: 16-46; night average: 27 ± SD 2°C; range: 24-31; twilight average: 27 ± SD 2°C). Temperatures during nocturnality were equivalent across the periods (table 1). The frequency of nocturnal events was slightly but not significantly higher during the wet period (Fisher's exact test: $P = 0.07$; table 2). Within a season, the relative rate of nocturnality was lower during the early-dry (7%) period and similar between the wet and late-dry (16.3% and 15.4%, respectively) periods (table 2).

Discussion

TWILIGHT AND NIGHT ACTIVITY

This study verifies that chimpanzees at Assirik exhibit facultative nocturnality in an extremely hot and dry environment with sympatric large predators and minimal human activity. Assirik chimpanzees displayed high rates of nocturnality (12.7% of all chimpanzee CT events) in relation to 22 chimpanzee study sites reported in a cross-sectional study by Tagg *et al.* (2018) that used comparable methods to assess nocturnality (table 3 in Tagg *et al.*, 2018: average: 1.8%, median: 1.0%, range: 0-9.6%). The nocturnality rate at Assirik was higher in frequency than the highest value reported by these authors (9.6%) from a savanna landscape at Kayan, Senegal. At Issa, Tanzania, the other savanna landscape (van Leeuwen *et al.*, 2020; Lindshield *et al.*, 2021) with comparable data (Tagg *et al.*, 2018), the rate of nocturnality (3.4%) was about three or four times lower than for chimpanzees at Kayan or Assirik, respectively.

The differences in nocturnality frequency between Assirik, Issa, and Kayan may be due in part to methodological differences between studies. We used still images instead of video, and there could be a shorter delay between a chimpanzee triggering the CT and the CT recording the still image. If this was the case, then still images better represented nocturnality when chimpanzees were within the passive infrared sensor range for a few seconds or less. In addition, although both studies targeted suitable habitat frequented by chimpanzees, our research design may have included fewer camera traps than Issa and Kayan and, thus, potentially introduced methodological artifacts related to a smaller sample size (see Methods; Tagg *et al.*, 2018).

Regardless of these methodological differences, the relatively high frequency of nocturnality for Assirik chimpanzees converges with similar studies for Senegalese chimpanzees (Fongoli: Pruetz, 2018; Kayan: Tagg *et al.*, 2018), but not with savanna chimpanzees at Issa, Tanzania (Tagg *et al.*, 2018). There are important climate and landscape differences between the savanna landscapes in Senegal and Tanzania that may explain, in part, differences in nocturnality. Average temperatures at Issa are lower, ranging from 11-35°C and averaging 23°C (van Leeuwen *et al.*, 2020), or about 8°C cooler than the temperature average during CT events at Assirik (table 1). These lower temperatures indicate that chimpanzees at Issa experience an overall lower risk of hyperthermia in relation to savanna chimpanzees at Assirik, Fongoli, and Kayan. Alternatively, a funnel effect created by the deliberate placement of camera traps at focal points (e.g., surface water, liana tangles in gallery forests) to maximize animal detection (Kolowski and Forrester, 2017), may be exaggerated for chimpanzees in Senegal due to vegetation composition and physiognomy. Grassland vegetation is common (Assirik: 49-55% McGrew *et al.*, 1981; Lindshield *et al.*, 2019; Fongoli: 36% Pruetz and Bertolani, 2009) and mostly a type of habitat matrix that chimpanzees traverse through to access resources in woodland and forest vegetation (Fongoli: Pruetz and Bertolani, 2009). At Issa, in contrast, grassland vegetation comprises a smaller proportion (8%) of the landscape (Hernandez Aguilar, 2009). The larger areas of habitat matrix in Senegal may cause chimpanzees to reuse focal points in forests and woodlands more often in comparison to chimpanzees at Issa, and elsewhere, where habitat matrix covers smaller areas.

The largest cross-sectional study (Tagg *et al.*, 2018) of nocturnality provides another example of behavioral diversity among chimpanzee unit-groups/study sites, as these authors reported that chimpanzees in cooler and wetter climates with higher forest cover (e.g., Grebo: 3.33% of CT events) exhibited frequencies that were sometimes similar to hot and dry sites with lower forest cover (Issa: 3.42%; but see Kayan: 9.58%). Moreover, chimpanzees at Sebitoli in Kibale National Park, Uganda displayed a relatively high nocturnality rate (9.9% of CT events), which was mainly associated with crop-feeding (maize) near forest edges while farmers were not guarding their fields (Lacroux *et al.*, 2022). The lack of convergence on a single hypothesis indicates that there are multiple proximate causes of nocturnality.

PREDATION AND RISK

This study verifies that the Assisik chimpanzees are sympatric with six large predator species and provides evidence of a suspected predation event. The twilight period is the time of significant overlap in terrestrial activity among chimpanzees and their potential predators at Assirik (fig. 1). Elevated risk of predation for chimpanzees may occur during these intervals because encounter probability with a predator is likely higher and visual acuity is probably lower, relative to daylight, for chimpanzees (Ankel-Simons and Rasmussen, 2008). While the Assirik landscape is risky for this reason, chimpanzees are not a preferred prey species for any of these carnivores (Cott, 1961; Broadley, 1983; Hayward, 2006; Hayward and Kerley, 2006; Hayward *et al.*, 2006a,b). However, each of these potential predators has the capacity to hunt and kill chimpanzees under ideal conditions, and the presence of several antipredation behaviors in this great ape (Kortlandt, 1962; Tutin *et al.*, 1981; Goodall, 1986; Boesch, 1991; Pruetz *et al.*, 2008; McLester *et al.*, 2016; Lindshield *et al.*, 2017) indicates that predation pressure has had a non-trivial impact on their behavior.

The chimpanzee remains discovered in this study are largely consistent with a predation event. Additionally, the type of remains (i.e., distal limbs) and defleshed state are consistent with scavenging (M.Beasley, pers. comm.; K. Hunt, pers. comm.). Non-predation causes of death, such as disease or lethal aggression from conspecifics, followed by scavenging, cannot be eliminated. Although correlation is not causation, the discovery of the partially collapsed nest near the remains raises the possibility that the individual was attacked in their sleeping nest. The nest site was risky, as the nearby rock shelf could function as platform for a large predator to leap from during an attack (fig. 3b). Immediately following the death of a chimpanzee mother, her dependent offspring are known to stay close to her body (Fongoli: J. Pruetz and S. Lindshield, unpubl. data; Semliki, Uganda: K. Hunt, pers. comm.). The discovery of the young chimpanzee in close proximity to the remains, the lack of evidence that other members of the unit-group were nearby, and the general pattern of mothers often sleeping with young offspring in the same nest at night (Stewart and Pruetz,

2020) supports the idea that the deceased individual was its mother. In summary, this is a suspected, but not putative, case of predation that may have involved an adult female who was attacked in her sleeping nest.

Given that the life histories of chimpanzees include long life spans, inter-birth intervals, and juvenile development periods (Hill *et al.*, 2001; Emery Thompson, 2013), depredation on chimpanzees may affect unit-group size and demographic composition for several years after a chimpanzee killing. Furthermore, chimpanzees' likely reduced visual, olfactory, and auditory sensitivity, relative to primates who retain the retinal tapetum lucidum (Ankel-Simmons and Rasmussen, 2008), well-defined vomeronasal organ (Smith *et al.*, 2002), or high-performance hearing traits (e.g., tall and narrow outer ears: Coleman and Ross, 2004), respectively, may constrain their ability to detect predators in low-light conditions when many large carnivore species often hunt (Spawls and Branch, 1995; Cozzi *et al.*, 2012; Behangana *et al.*, 2017; Mugerwa *et al.*, 2017).

Our results indicate that predation risks for chimpanzees at Assirik are dynamic and context specific. There are potential positive and negative correlations between predation risk and chimpanzee nocturnality. Chimpanzees at higher risk of predator attacks may experience more sleep disturbances that lead to higher rates of terrestrial nocturnality (Tagg *et al.*, 2018). Moreover, chimpanzees may exhibit lower nocturnality rates by building nests that are more difficult for predators to access (Pruetz *et al.*, 2008; Stewart and Pruetz, 2013) and generally avoiding nocturnal terrestrial activity for fear of predator attacks. This latter process offers a potential explanation for the low rate of nocturnality within Issa chimpanzees (Tagg *et al.*, 2018), a unit-group also inhabiting a predator-rich savanna landscape (Stewart and Pruetz, 2013; Piel *et al.*, 2019). More research is needed to identify patterns in chimpanzee responses to predation threats and attacks at night.

We hypothesize that leopard depredation poses the highest risk at Assirik, as we captured still images of them more often than other predators (figs. 1-2), they share with chimpanzees a preference for forested vegetation and gallery forest, in particular (Boesch, 1991; Bailey, 1993; Pruetz and Bertolani, 2009), they are skilled climbers (Tutin *et al.*, 1981; Bailey, 1983) and they are known chimpanzee killers (Boesch, 1991; Nakazawa *et al.*, 2013). Lions probably pose a similar risk to the Assirik chimpanzees, given that their large body size, putative capacity to kill chimpanzees (Tsukahara, 1993), and gregarious hunting behaviors (Schaller,1972) allow for realistic scenarios where multiple hunters can simultaneously stalk unsuspecting chimpanzees. Although less is known about interactions between chimpanzees and other potential predators (Tutin *et al.*, 1981; Goodall, 1986; Zamma, 2011; McLester *et al.*, 2016), the pack hunting behaviors of hyenas (Kruuk, 1972) and wild hunting dogs (Creel and Marusha Creel, 1995), where several individuals coordinate during a hunt, may impose grave threats to chimpanzees when they are in vulnerable states, such as in open habitats with few escapes routes, or for young, geriatric, injured, or ill individuals with overall reduced escape capacity (McLester *et al.*, 2016).

The obligate or preferred use of aquatic habitats for crocodiles (Cott, 1961) and pythons (Broadley, 1983), respectively, places chimpanzees at higher risk of an ambush during visits to flowing rivers, streams, or water holes to drink water. Both species are cryptic in water and often aim for the vulnerable heads of their prey while they are drinking (Cott, 1961; Broadley, 1983). In general, chimpanzees drink at surface water from larger, riskier areas in addition to safer, smaller, and more numerous collection areas, such as tree holes and leaves (Goodall, 1986), and from preformed water (Lanjouw, 2002). Savanna chimpanzees could be more dependent on risky aquatic areas to source their drinking water, especially during the drier months, relative to conspecifics inhabiting wetter climates. We recommend that future studies develop more thorough assessments of predation risk dynamics by estimating predator population densities, comparing predator species evenness among sites, and measuring spatio-temporal overlap among chimpanzees and large carnivores.

Given that prey species are known to adjust nocturnal activity according to lunar phases, specific predators, and environmental contexts (Nash, 2007), it was hypothesized that chimpanzee nocturnality covaried with visible light levels. Supporting this idea, we found that nocturnality occurred more often during (civil) twilight. In addition, we predicted that chimpanzees would be active more often on nights when moon illuminance was higher to improve visible detection of predators, food, and group members (e.g., Pruetz, 2018; cf. Krief *et al.*, 2014). While directional differences in illuminance between chimpanzee (higher illuminance) and predator (lower illuminance) events matched expectations, this difference was surprisingly equivalent. It could be that our sample size and illuminance measurements lacked adequate statistical power. At a minimum, using an on-site illuminance meter and factoring cloud cover and rainfall into illuminance measurements (Krieg, 2021) will improve future research. Moreover, non-visual modes of predator detection are important to consider in the future, such as eavesdropping on the alarm calls of other nesting subgroups and other species (Byrne, 1981; Piel, 2018).

Lower rates of anthropogenic disturbances have been associated with higher frequencies of nocturnality for chimpanzees (cf. Lacroux *et al.*, 2022), perhaps due to the lower risk of encountering people who may hunt at night (Tagg *et al.*, 2018). Given that nocturnality frequency was relatively high and human activity was relatively low at Assirik, we cannot reject this anthropogenic disturbance hypothesis. However, Fongoli and Kayan chimpanzees also exhibit relatively high rates of nocturnality and these two savanna sites are more disturbed than Assirk. We suggest that this anthropogenic disturbance hypothesis is a poor predictor of nocturnality frequency in Senegalese chimpanzees, specifically, because these groups have been rarely hunted by local people (Pruetz and Kante, 2010). To test this idea, future studies may compare the effects of anthropogenic activity, hunting taboos, and predator diversity on nocturnality in savanna chimpanzees.

HYPERTHERMIA RISK

Our study reinforces the idea that savanna chimpanzees in Senegal occupy an environment that approaches the thermal maximum for this species (Assirik: McGrew *et al.*, 1981; Fongoli: Wessling *et al.*, 2018a,b), daytime temperatures approached or exceeded an ambient 40°C in closed-canopy vegetation across periods and the temperature reached a maximum of 46°C during CT events in the late-dry period (table 1). These maximum daily environmental temperatures are within range of the critical thermal maximum for human body temperature (Pluth Yeo, 2004) and heat-related deaths in humans (Green *et al.*, 2001). A regional pattern of high nocturnality in Senegal (Assirik: this study; Fongoli: Pruetz, 2018; Kayan: Tagg *et al.*, 2018) supports the hypothesis that chimpanzees in extremely hot and dry environments allocate time to feeding or other behaviors at night and twilight to compensate for inactivity during the hottest times of day.

In contrast to observations of Fongoli chimpanzees (Pruetz, 2018), we did not find evidence that nocturnality was higher during the dry season. However, the lowest relative nocturnality rate (% of nocturnal CT events within a period/season) occurred during the early-dry period at Assirik (table 2) when south-eastern Senegal experiences the lowest average and minimum daily temperatures. This pattern lends some support to the hyperthermia avoidance hypothesis. Unexpectedly, nocturnality occurred more often – but not significantly so – during the wet season at Assirik (table 2) when average diurnal event temperature was lowest and surface water was readily available. However, higher relative humidity restricts evaporative cooling potential from sweating (Buzan and Huber, 2020) and this factor may have offset any potential decreases in hyperthermia risk from lower temperatures during the wet season. For this reason, in part, human health and occupational safety programs use more complex measures of environmental heat to assess hyperthermia risk, such as the heat index and the wet bulb globe temperature, that account for the effects of relative humidity, shade, direct sunlight, windspeed, and cloud cover (Pluth Yeo, 2004; Morris *et al.*, 2019). We suggest that future research on nocturnality incorporate these more holistic measurements of heat.

We cannot rule out the possible effects of sampling design or low statistical power on the overall low occurrence of nocturnality during the hottest and driest months of this study (late-dry period in Senegal: Drambos: Boyer Ontl and Pruetz, 2020; Fongoli: Wessling *et al.*, 2018a). In our sample of 2,092 CT days, chimpanzees were recorded in about 2% of all still images, yielding 14 cases of nocturnality. In contrast, Pruetz (2018) recorded more than 700 signs of nocturnality, about half of which involved chimpanzees moving out of their sleeping nests during 40 nights of all-occurrence (Altmann, 1974) sampling. We could not replicate this methodology because the Assirik chimpanzees were not habituated, nocturnal research in this predator-rich landscape places our team at higher risk of injuries or fatalities at night, and CTs are one of a few technologies that meets ethical standards for conducting non-invasive research on wild chimpanzees (Piel, 2018; Tagg *et al.*, 2018). We recommend that sites with similar challenges continue to use CTs and integrate additional approaches, such as passive acoustic monitoring devices (e.g., Piel, 2018), to generate larger sample sizes.

Conclusion

This study provided the most comprehensive assessment of predation risk to Assirik chimpanzees and evaluated potential determinates of nocturnality in this risky landscape. Study findings support the hypothesis that nocturnality may be a widespread strategy to minimize hyperthermia risk for savanna chimpanzees in Senegal, even in the Assirik environment where predation risk from large nocturnal carnivores is relatively high. To further investigate this hypothesized tension between predation and hyperthermia risk, we recommend that future research use a cross-sectional approach to robustly measure nocturnality and environment, including multiple savanna chimpanzee sites that vary in predation and hyperthermia risks.

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Ethics

The Purdue IACUC board approved our research protocol. We followed the International Primatological Society's Code of Best Practices for Field Primatology (IPS, 2014) and the International Union for the Conservation of Nature's best practices for the prevention of disease transmission between researchers and great apes (Gilardi *et al.*, 2015). The Direction des Parcs Nationaux authorized this research.

Data availability

All data to support the findings of this study are available in supplementary table S1.

Supplementary material

Supplementary material is available online at: https://doi.org/10.6084/m9.figshare.26304979

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