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

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**Nocturnal activity in wild chimpanzees (*Pan troglodytes*):
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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.

23 An animal's socio-biology is shaped by the environmental conditions experienced during diurnal or
24 nocturnal activity. Diurnal animals exhibit activity during the day and sleep during the night, in
25 contrast to nocturnal animals that are active at night and sleep during the day (Smale, Lee and Nunez,
26 2003). Animals are adapted to the differing conditions of the parts of the day or night during which
27 they are awake; for example, nocturnal animals tend to have eyes that are specially adapted to
28 absorbing as much light as possible, in order to maximise upon the contrast of low light levels in the
29 shade of the night (Ankel-Simons and Rasmussen, 2008; Smolka et al., 2016). Similarly, the period of
30 day or night that animals are active may be shaped by the animal's socio-biology; for example, some
31 rodents exhibit crepuscular activity (i.e., during dusk and dawn) as a response to inter-specific
32 resource competition (Kronfeld-Schor and Dayan, 2003).

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

45 In the wild, great apes have generally been assumed to remain for the 12-hour duration of the night in
46 their nests from the time they first enter, around dusk, until their departure, around dawn (e.g., for
47 chimpanzees, Goodall, 1962). However, many researchers have gathered anecdotal accounts of night-
48 time vocalizations in wild-living great apes. For example, chimpanzees pant hoot (*Pan troglodytes*;
49 Izawa and Itani, 1966; van Lawick-Goodall, 1968; Zamma, 2013), gorillas chest-beat (*Gorilla sp.*;
50 Schaller, 1963; authors' obs.), and orangutans call (*Pongo pygmaeus*; pers. comm.: Brigitte Spillman).
51 There have also been anecdotal visual observations of great apes being active out of their nests at
52 night, including mating, social grooming, and play in bonobos (*Pan paniscus*; Fruth and Hohmann,
53 1993, 1994); and mating, feeding, and travelling in chimpanzees at Gombe, Tanzania (van Lawick-
54 Goodall, 1968) and Mahale, Tanzania (Zamma, 2013).

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

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

88 We can study wild great ape sleep patterns to shed light on ancestral, as well as present day, human
89 sleep. In the pre-industrial West (before the 17th century), people appear to have commonly exhibited a
90 pattern of fragmented sleep (Ekirch, 2006), whereby sleep onset occurs early in the evening and the
91 night's sleep is divided into two or more bouts separated by periods of wakefulness (de la Iglesia and
92 Lee, 2015; Wehr, 1992). Benefits may have included alertness to dangers in the depths of the night,
93 social advantages, creativity, and innovativeness (Ekirch, 2006). In the modern day, humans generally
94 exhibit a consolidated (one-phase) sleeping pattern, with sleep durations of 7–8 hours recommended
95 for adults (Hirshkowitz et al., 2015) and sleep onset usually occurring several hours after nightfall. It
96 has been argued that the 'freedom' to exhibit fragmented sleep has been lost in modern societies
97 because of technological advances, such as artificial lighting (Moreno et al., 2015), and modern
98 pressures, such as long working days. However, a significant body of evidence is building (Eban-
99 Rothschild, Giardino and de Lecea, 2017; Vyazovskiy, Achermann and Tobler, 2007; Wehr,
100 Aeschbach and Duncan, 2001) that the ancestral sleep pattern was consolidated, as observed in
101 traditional societies today (Yetish et al., 2015). The fragmented sleep phenomenon evident in the pre-
102 industrial West may have developed as a temporary pattern as humans moved into northern latitudes
103 46–50,000 years ago (Oppenheimer, 2012) and the long, cold nights encouraged early sleep onset.
104 With the beginning of the industrial era, street lighting and policing overnight would have made after-
105 dark activities safer, delaying sleep onset and allowing sleep to revert to a consolidated pattern
106 (Ekirch, 2006). To assist us in further investigating this assertion that ancestral humans are likely to
107 have exhibited a consolidated sleep pattern, we can investigate sleeping patterns in our sister taxa, the
108 great apes: evidence of a non-fragmented sleep pattern may support our hypothesis. Using data and
109 footage from terrestrial camera traps collected as part of the Pan African Programme: The Cultured
110 Chimpanzee (henceforth PanAf) (Kühl et al., 2016; Vaidyanathan, 2011), this study addresses the
111 following hypotheses concerning the possible predictors of terrestrial nocturnal activity in diurnal
112 chimpanzees:

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

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3 115 2) Building upon this, we predict that nocturnal activity will instead be influenced by environmental
4 116 factors, such as temperature, rainfall, and light levels:
- 5
6 117 i) Nocturnal activity may be more likely to occur under extreme environmental conditions, such as
7 118 in hot and dry savanna habitats, which may hinder effective/sufficient feeding or other behaviors
8 119 during the day. For example, at Fongoli, Senegal, frequent nocturnal activity is suggested to be the
9 120 result of environmental stresses (Pruetz and Bertolani, 2009). We therefore hypothesize more
10 121 nocturnal activity with higher temperatures, lower rainfall, and in savanna habitats.
- 11
12 122 ii) Nocturnal activity may also be facilitated by light from the moon, as chimpanzees which are
13 123 physiologically adapted to light conditions will be able to see better and navigate their environment
14 124 under nightfall. Among primates, rates of vocalizations increase (Anderson, 1984) and physical
15 125 activity increases in chimpanzees (Izawa and Itani, 1966; Pruetz and Bertolani, 2009; van Lawick-
16 126 Goodall, 1968; pers. comm.: Koichiro Zamma) and rhesus monkeys (Vessey, 1973) with increased
17 127 moon illumination. Indeed, many of the early anecdotal observations of nocturnal activity in wild
18 128 great apes were made in periods of high proportion of illumination by the moon (Anderson, 1984;
19 129 Nishida, 1996; Pruetz and Bertolani, 2009). Owl monkeys, the only nocturnal anthropoid, have
20 130 been shown to require moonlight in order to forage effectively during periods of nocturnal activity
21 131 (Fernandez-Duque, de la Iglesia and Erkert, 2010). In humans, certain sleep parameters are reduced
22 132 during a full moon, with shorter sleep durations and lower proportions of REM sleep being
23 133 exhibited (Cajochen et al., 2013), suggesting an increase in the likelihood of wakefulness during
24 134 moonlit nights. If this influence on sleep is also experienced by great apes, apes might be more
25 135 active during a full moon; we therefore hypothesize more nocturnal activity with higher moon
26 136 illumination.
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30 137 3) Nocturnal activity may be a result of physical or perceived disturbance at night, either by predators,
31 138 other large animals, or by human activity.
- 32
33 139 i) Large carnivores constitute natural predators of chimpanzees (Stewart and Pruetz 2013) and
34 140 documented events involve leopards (*Panthera pardus*; Boesch, 2009; Nakazawa, Hanamura,
35 141 Inoue, Nakatsukasa and Nakamura, 2013) and lions (*Panthera leo*; Nishida, 2012). Chimpanzees
36 142 are likely to vocalize at night in response to the presence of such potential predators (Tutin,
37 143 McGrew and Baldwin, 1981), as well as to hyena (*Crocuta crocuta*), suggesting an influence of
38 144 predators on chimpanzee behavior at night. Furthermore, arboreal nesting may be partly driven by
39 145 predator avoidance in chimpanzees and gorillas (e.g., Carvalho, Meyer, Vicente and Marques,
40 146 2015; Pruetz et al., 2008; Stewart and Pruetz, 2013; Yamagiwa, 2001), and gorilla females and
41 147 juveniles were assumed to avoid ground nesting as a result of their relative vulnerability to
42 148 predation (Yamagiwa, 2001). Therefore, we hypothesize that higher abundances of predators will
43 149 increase nocturnal activity.
- 44
45
46 150 ii) Similarly, sleeping chimpanzees could be disturbed by other large mammals living
47 151 sympatrically, specifically elephants (*Loxodonta africana*) and buffalos (*Syncerus caffer*). To our
48 152 knowledge, no empirical evidence is available supporting disturbance of chimpanzees by these
49 153 species; however, chimpanzees can be competitively excluded by sympatric elephants when fruit
50 154 availability is low (Head et al., 2012). Therefore, we hypothesize that higher abundances of
51 155 elephants and buffalos will increase nocturnal activity.
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54 156 iii) Evidence exists that wild chimpanzees perceive humans as a threat across their range, as they
55 157 exhibit lower densities closer to human settlements (Clark, Poulsen, Malonga and Elkan, 2009;
56 158 Kano and Asato, 1994; Walsh et al., 2003), alter their behavior (Lindshield, Danielson, Rothman

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3 159 and Pruetz, 2017), and avoid areas of human disturbance (Arnhem, Dupain, Vercauteren, Devos
4 160 and Vercauteren, 2008; Rabanal, Kühl, Mundry, Robbins and Boesch, 2010; Stokes et al., 2010;
5 161 Tagg and Willie, 2013). Therefore, human activity overnight may also cause disturbance to
6 162 sleeping chimpanzees. Hunters frequently operate at night and in twilight hours (Astaras, Linder,
7 163 Wrege, Orume and Macdonald, 2017); the gunshots and movements of people below nest sites, for
8 164 example, may pose a threat to chimpanzees. We therefore hypothesize more nocturnal activity with
9 165 higher levels of human activity.

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METHODS

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15 168 The PanAf (Kühl et al., 2016; Vaidyanathan, 2011) was established to collect a range of ecological,
16 169 social, demographic, and behavioral data to study evolutionary–ecological drivers which contribute to
17 170 behavioral diversity in chimpanzee (*Pan troglodytes*) populations and to evaluate potential
18 171 evolutionary scenarios central to questions of cultural evolution. The PanAf was motivated to address
19 172 the knowledge gaps resulting from minimal field sites dedicated to studying wild chimpanzees. It set
20 173 out to understand the evolutionary–ecological drivers that have generated the behavioral diversity
21 174 found between populations of chimpanzees across their range. It wanted to investigate the vast array of
22 175 possible explanatory variables, such as resource availability, historic landscape effects, predation, and
23 176 disease pressure as well as inherent population dynamics influencing trait invention and loss. The
24 177 PanAf therefore studies a large number of populations with a cross-sectional sampling approach. It
25 178 quantifies a broad spectrum of the ecological parameters that possibly contribute to generating
26 179 behavioural diversity in chimpanzees. The PanAf has included 39 long-term and temporary research
27 180 sites located within the chimpanzee range since January 2010. Data from 22 of these sites were
28 181 available at the time of the study (Table 1); the available data were obtained from studies of varying
29 182 durations (7 to 22 months). As part of the standardized data collection at all sites, we set grids
30 183 comprising 20 to 96 1×1 km cells for distribution of sampling units (to cover a minimum of 20–50
31 184 km² in rainforest and 50–100 km² in woodland savannah). We placed an average of 29 (range 5 to 41)
32 185 movement-triggered Bushnell cameras per site. We placed one camera per grid cell where possible;
33 186 however, in larger grids we placed cameras in alternate cells. If certain grid cells did not contain
34 187 suitable habitat, such as in heterogenous sites, we placed two cameras as far away from each other as
35 188 possible in the cells containing suitable habitat to maximise coverage. According to the PanAf
36 189 objectives, in cases of specific locations of interest (e.g., termite fishing sites), we placed a second
37 190 camera at the same location to capture the same scenes from a different angle. We placed cameras
38 191 about 1m high, in locations that were frequently used by chimpanzees (e.g. trail, feeding tree). This
39 192 method ensured a strategic installation of cameras, with maximal chance of capturing footage of
40 193 terrestrial activity of chimpanzees. We recorded GPS location and habitat type of the location. We set
41 194 cameras to 60-s video mode with a 1-s interval between triggers, and we visited and maintained
42 195 cameras, and downloaded videos, every one to three months throughout the study periods (for further
43 196 detail see http://panafrican.eva.mpg.de/pdf/Pan_African_Field_Protocol_July2014_final2.pdf,
44 197 henceforth PanAf protocol).

45 198 [Table 1 here]

46 199

Camera-trap video data

47 200 We extracted all camera-trap videos containing chimpanzees in the night time from 10 sites that had
48 201 been uploaded, prior to February 2017, onto a web-based citizen science platform, Chimp&See
49 202 (<https://www.chimpandsee.org/#/>; Arandjelovic et al., 2016), hosted by Zooniverse (Cox et al., 2015).

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3 203 On the Chimp&See platform, volunteers identified animals present in the PanAf videos. We
4 204 considered a video analysed when either three volunteers marked the video as blank, seven volunteers
5 205 unanimously agreed on the identity of the animal present, or 15 volunteers annotated the video. Project
6 206 scientists and moderators then further assessed videos that were classified as containing chimpanzees
7 207 and extracted those videos which were filmed at night and appeared dark for inclusion in this study.
8 208 We also included camera-trap data from an additional 12 PanAf sites in the present study, totaling 22
9 209 sites. We watched all videos containing chimpanzees from each of these sites and extracted all those
10 210 which were filmed at night and appeared dark. For each site, we calculated the camera-trapping effort
11 211 (i.e., the number of cameras active throughout the study period and the number of days they were
12 212 active), the number of videos filmed, and the number of videos containing chimpanzees.

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15 213 We extracted date and time of each video from the timestamp of the video (if the timestamp was not
16 214 present, we extracted date and time from the metadata of the video file; if this information was
17 215 incorrect due to camera malfunction, we accessed date and time using the installation data recorded by
18 216 the field data collectors). We excluded duplicate videos captured by one of a set of paired cameras. We
19 217 calculated site- and date-specific time of sunset or sunrise (depending on whether the video was filmed
20 218 before midnight or after midnight, respectively) using the US Navy web tools
21 219 <http://aa.usno.navy.mil/data/index.php>, and classified each video of nocturnal activity as having
22 220 occurred in true night (>30 min after sunset or before sunrise) or in twilight hours (within 30 min of
23 221 sunset or sunrise). Similarly, we determined the moon phase (percent illumination) using the same
24 222 tools, and classified each video in terms of whether or not the moon was up at the time of recording.

25
26
27 223 To identify individual chimpanzees (and assign age class and sex), we used two methods. First, for
28 224 videos that had been uploaded to Chimp&See, we relied on previously assigned identifications of
29 225 individual chimpanzees by citizen scientists. Citizen scientists identified each chimpanzee according
30 226 to their age class and sex, described them according to individual characteristics (e.g., scars, distinctive
31 227 pigmentation patterns), and assigned a unique identifying code for reference. Following independent
32 228 observations in at least two distinct events, and after consensus between at least two citizen scientists
33 229 and confirmation from a PanAf researcher with chimpanzee identification experience, individual
34 230 identification codes (using online hashtags in any associated videos) were assigned to individual
35 231 chimpanzees. Citizen scientists subsequently hashtagged any additional video captures of the same
36 232 individual chimpanzee following consensus agreement from at least three people. For non-
37 233 Chimp&See sites, researchers reviewed nocturnal video clips and assigned age class, sex, and
38 234 individual identification codes (the latter by M. McCarthy only) for all chimpanzees exhibiting
39 235 identifiable features, as above for Chimp&See sites. We defined a nocturnal activity 'event' as a series
40 236 of consecutive videos captured by the same camera within 15 min of the previous video (Boesch et al.,
41 237 2017). We further defined a 'chimpanzee-event' as each distinct chimpanzee (identified and non-
42 238 identified individuals) appearing in the event.

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46 239 For each nocturnal activity chimpanzee-event, we described the main behavior. We observed a variety
47 240 of nocturnal activities, but to facilitate interpretation we grouped all activities into four main
48 241 categories: 'movement' (including walking and running into and/or out of the camera view during the
49 242 video); 'on location' (including ascending or descending a tree, sitting or standing); 'social' (including
50 243 playing, grooming, displaying); and 'feeding'.

51 52 244 **Transect, habitat and climate data**

53
54 245 We placed line transects to cross through the middle of each grid cell in a north-south or east-west
55 246 direction across the grid. We walked transects regularly in each site (1 to 6 times per site, mean=3)

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2
3 247 during the study. We achieved an average line transect survey effort across all sites of 81.6 km,
4 248 ranging from 14.2 km (Bili, Democratic Republic of the Congo) to 237.7 km (Issa, Tanzania)
5 249 (Appendix 1).

6
7 250 We carried out surveys for animal and human signs during the regular line transect walks. We
8 251 recorded all direct and indirect observations, including footprints, tracks, and feeding remains. Human
9 252 signs included all (non-research related) direct observations and indirect signs of human presence,
10 253 including machete cuts, camps, snares, gunshots, and spent cartridges. For each site, we calculated
11 254 'encounter rates' (signs per kilometer of transect) for elephants (*Loxodonta africana*), buffalos
12 255 (*Syncerus caffer*), predators (lions, *Panthera leo*, leopards, *Panthera pardus* and hyenas, *Crocuta*
13 256 *crocuta*), and humans using the total number of signs of each target species/group of species divided
14 257 by the total line transect survey effort (km). Survey efforts per site and encounter rates per kilometer
15 258 for buffalos, elephants, predators, and humans are given in Appendix 1.

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18 259 During transect walks, we recorded habitat type at every observation and whenever the habitat
19 260 changed during line transect walks. Habitat was classified according to the characteristics of the
20 261 vegetation (e.g., size/density of trees, closed/openness of canopy), the predominant ground type (e.g.,
21 262 *terra firma*, swamp), and the age of the habitat (e.g., old versus young secondary), following
22 263 definitions given in the PanAf protocol (Appendix 2; White and Edwards, 2000). For most sites, we
23 264 summed the distance between every observation made along the first round of line transects within
24 265 each habitat type. For one site (Issa), where habitat data were particularly scarce for the first round of
25 266 line transects, we restricted the analysis to four transects, created mean start and end coordinates for
26 267 each transect, and pooled the observation data from six rounds. We then grouped occurrences of
27 268 different habitat types to subsequently calculate a percentage of forest versus savanna (Table 2) for
28 269 each site, to assess habitat type as a predictor of nocturnal activity. Most sites (16 of 22) exhibited a
29 270 higher percentage (>50%) of forest habitat; the remaining six sites (Bakoun, Guinea; Boé, Guinea
30 271 Bissau; Geprenaf, Ivory Coast; Kayan, Senegal; Sobeya, Guinea; and Issa, Tanzania) exhibited a
31 272 higher percentage of savanna habitat.

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35 273 [Table 2 here]

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37 274 Finally, we obtained climate data for each site. We calculated the daily average temperature from the
38 275 minimum and maximum temperatures recorded the day after nocturnal activity, thus reflecting the
39 276 values recorded over the preceding 24 hr. We extracted the total rainfall volume for the day preceding
40 277 the night during which each nocturnal activity event occurred.

41 42 278 **Data analysis**

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44 279 **Occurrence and timing of nocturnal activity.** For each site, we calculated the proportion of
45 280 chimpanzee nocturnal activity as: (the number of chimpanzee nocturnal activity videos / the total
46 281 number of all chimpanzee activity videos) \times 100. We wanted to assess whether nocturnal activity
47 282 occurred throughout the night or was more likely at certain times. To be comparable between different
48 283 geographic locations and times of year, we scaled the recording time of the videos from 0 (sunset) to 1
49 284 (sunrise), considering its distance to sunset and the night duration on that day at that location ($x =$
50 285 $(T_{\text{video}} - T_{\text{sunset}}) / \text{night duration}$). To understand the number of videos occurring across sites in
51 286 different phases of the night, we plotted the number of videos falling in the following phases: phase 1
52 287 (1 hour after/before sunset/sunrise), phase 2 (within 2 hours of twilight), phase 3 (2 hours of early
53 288 morning and late-night occurrences), phase 4 (2 hours around midnight).

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3 289 ***Behavior during nocturnal activity.*** For each behavior category (movement, on location, social,
4 290 feeding), we determined the number of events of nocturnal activity in which these behaviors were
5 291 exhibited. Data are presented together (true night and twilight hours pooled) and separately for true
6 292 night and twilight hours.

7
8 293 ***Predictors of chimpanzee terrestrial nocturnal activity.*** To fit a model estimating what drove
9 294 terrestrial nocturnal activity of chimpanzees, we needed to avoid pseudo-replication arising from the
10 295 same individual chimpanzee appearing in multiple videos and events, and multiple cameras recording
11 296 at each site (Hurlbert, 1984). Hence, we first extracted, for each site, all identified chimpanzees who
12 297 were clearly visible and to whom identifying features could be assigned observed at night and the
13 298 nights during which at least one chimpanzee was seen. We then constructed a data set which,
14 299 separately for each site, included one row for each combination of chimpanzee ID and night,
15 300 indicating whether the respective chimpanzee was detected in the respective night. For sites where no
16 301 single nocturnal detection was made, we included one dummy chimpanzee and one dummy night
17 302 during which the dummy chimpanzee was not detected. Note that such a data set is very conservative
18 303 since it only considers a minimum number of non-detections; that is, chimpanzees never being
19 304 detected (likely varying in number among sites) and nights during which no detection was made, did
20 305 not contribute anything to these data (except for the one dummy chimpanzee not seen during the one
21 306 dummy night). Consequently, the data underestimate the magnitude of differences between sites;
22 307 however, given the high risks associated with pseudo-replication we feel that this approach was the
23 308 best option.

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27 309 We estimated the magnitude of the effects of the different environmental predictors on the probability
28 310 of chimpanzees being detected at night using a Generalized Linear Mixed Model (Baayen, 2008) with
29 311 binomial error structure and logit link function (McCullagh and Nelder, 1989). Into this we included,
30 312 as fixed effects, percentage of forest, abundance of predators, abundance of large mammals, average
31 313 daily temperature, amount of rainfall on the day prior to the night in question, amount of human
32 314 activity, and percentage illumination. The percentage of savanna was highly collinear with the
33 315 percentage of forest (Variance Inflation Factor, VIF = 27.1; Field 2005; Quinn and Keough, 2002), so
34 316 we excluded it from the model. As random effects, we included site, individual chimpanzee, and night;
35 317 the latter two were nested within site. To keep the type I error rate at the nominal level of 0.05, we
36 318 included random slopes (Barr, Levy, Scheepers and Tily, 2013; Schielzeth and Forstmeier, 2009) of
37 319 average daily temperature and percent illumination within chimpanzee and site ID into the model
38 320 (other random slopes were not identifiable because the respective fixed effects did not vary within
39 321 chimpanzee or site ID). Originally, we also included the correlations among random intercepts and
40 322 slopes. However, these appeared unidentifiable as indicated by all absolute correlation parameters
41 323 being close to one (Matuschek, 2017); therefore, we removed them from the model.

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45 324 To avoid the issue of multiple testing due to the multitude of fixed effects (Forstmeier and Schielzeth,
46 325 2011), we compared the fit of the full model with that of a null model lacking them but having an
47 326 identical random effects structure. We estimated model stability by excluding the levels of the random
48 327 effects one at a time, fitting the full model as described above to these subsets of data, and comparing
49 328 the estimates derived with those obtained for the full data set. This did not reveal any severe stability
50 329 issues. To rule out collinearity problems, we determined VIF for a standard linear model lacking the
51 330 random effects. With a maximum VIF of 3.40, collinearity did not appear to be a severe issue. We
52 331 obtained bootstrapped confidence intervals of the estimated model coefficients by means of a
53 332 parametric bootstrap. We fitted the model in R (version 3.4.1 R Core Team 2016) using the function
54 333 `glmer` of the package `lme4` (version 1.1-13; Bates, Maechler, Bolker and Walker, 2015) with the
55 334 optimizer 'bobyqa'. We conducted bootstraps using the function `bootMer` of the package `lme4`, and

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3 335 determined Variance Inflation Factors using the function `vif` of the package `car` (version 2.1-4; Fox
4 336 and Weisberg, 2011). We determined P-values for the individual effects by comparing the full model
5 337 with reduced models lacking the fixed effects one at a time (Barr et al., 2013) using a likelihood ratio
6 338 test (Dobson, 2002). We also tested the significance of the random slopes by comparing the full with
7 339 reduced models lacking random slopes, one at a time, using likelihood ratio tests. Prior to fitting the
8 340 model, we checked whether the predictors had roughly symmetrical distributions; however, several did
9 341 not because they were comprised of many zeros. Therefore, we were unable to find a transformation to
10 342 alleviate the issue. Results of model stability, however, indicated that the model did not suffer from
11 343 highly influential cases. Prior to fitting the model, we z-transformed all predictors to a mean of zero
12 344 and a standard deviation of one to achieve comparable estimates and to increase the likelihood of
13 345 model convergence. The sample size was a total of 989 data points (140 detections and 849 non-
14 346 detections) of 119 chimpanzee-events during 103 nights (nested in site) and at 22 sites.

17 347 RESULTS

19 348 Occurrence and timing of chimpanzee nocturnal activity

21 349 We identified 143 videos containing evidence of terrestrial nocturnal activity (including true night and
22 350 twilight) (Figs. 1 and 2). These made up 119 independent events (i.e., a distinct individual or a series
23 351 of videos of the same individual captured by the same camera within 15 min of the previous video).
24 352 These events represent 235 chimpanzee-events (i.e., event \times number of distinct individuals present in
25 353 the event; Table 3). When considering the site-specific and date-specific sunrise and sunset times, we
26 354 observed 59 events of nocturnal activity (77 videos) in true night and 60 events (66 videos) in twilight.

28 355 [Figure 1 here]

29 356 [Figure 2 here]

30 357 [Table 3 here]

31 358 Although activity during the twilight periods was very common, we found nocturnal activity to occur
32 359 in all phases of the night (Fig. 3). We observed nocturnal activity during both twilight and true night
33 360 hours in 14 sites, with no twilight activity occurring in Taï R (Ivory Coast), and no true night activity
34 361 in Bili (Democratic Republic of Congo), Boé (Guinea Bissau), and Taï E (Ivory Coast). We found
35 362 nocturnal activity in the deeper phases of the night (i.e., phases 3 and 4, early morning, and late night
36 363 occurrences and within 2 hours either side of midnight) in three sites only: Geprenaf (Ivory Coast),
37 364 Issa (Tanzania), and Kayan (Senegal) (Fig. 3).

38 365 [Figure 3 here]

39 366 We found nocturnal activity to occur at an average overall proportion of 1.80% of all chimpanzee
40 367 activity (day and night) observed in camera-trap footage (all sites pooled). We observed nocturnal
41 368 behavior at 18 of the 22 sites (Fig. 2), with no night activity observed in Conkouati (Republic of
42 369 Congo), Gashaka (Nigeria), Korup (Cameroon), and La Belgique (Cameroon) (Table 3).

43 370 We found the highest frequency of occurrence of nocturnal activity in Kayan, Senegal with 19 events,
44 371 followed by Sobeya, Guinea (16), Issa, Tanzania (14), and Budongo, Uganda (13; Table 3). We found
45 372 the lowest frequency in Taï E, Ivory Coast (1), Taï R, Ivory Coast (1), Djouroutou, Ivory Coast (1),
46 373 and Bakoun, Guinea (2). In considering nocturnal activity as a proportion of overall (nocturnal and
47 374 diurnal) activity observed in camera-trap videos (Table 3, column F), we also found the highest

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3 375 proportion of nocturnal activity in Kayan (9.58%), followed by Gprenaf, Ivory Coast (3.73%), and
4 376 Grebo, Liberia (3.33%). We found the lowest proportion in Bakoun (0.14%).

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6 377 We observed nocturnal activity in three of the four chimpanzee subspecies, with *Pan troglodytes*
7 378 *elliotti* not being recorded to exhibit this behavior. Our camera-trapping effort of *P. t. elliotti* was lower
8 379 than for the other subspecies (just over 17,000 camera-days [number of cameras × number of days
9 380 each camera was active], whereas the camera-trapping effort total for the other subspecies ranged from
10 381 29,000–94,000 camera-days; Table 3), which may account for the lack of nocturnal activity observed.
11 382 We observed more nocturnal activity events for *P. t. verus* compared to other subspecies (Table 3).
12 383 However, the high camera-trapping effort (94,000 camera-days) for this subspecies may contribute to
13 384 this, as we found the lowest proportion of overall chimpanzee activity in *P. t. verus* (and *P. t. elliotti*)
14 385 compared to other subspecies (Table 3, column D).

16 17 386 **Demographics and behavior of chimpanzee nocturnal activity**

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19 387 We found immature individuals to be the most represented in terrestrial nocturnal activity events (40%
20 388 of individuals, n=235) followed by adult males (29.8%) then females (with and without infants; 20%)
21 389 (Table 4; Fig. 4). We found most nocturnal activity events to comprise only one individual (52.9%,
22 390 n=119). We also found a relatively high proportion of events to comprise two or three individuals
23 391 (24.4 and 14.3%, respectively), and a low proportion of events comprising four individuals or more
24 392 (0.8–1.7%). We found adult males to appear more often alone in an event than with others (55.7% of
25 393 males appeared alone, n=70), and to be alone more often than other age-sex groups (61.9% of
26 394 individuals appearing alone were males, n=63). We found that females were more often observed with
27 395 infants and immatures than without (e.g., 68.1% of females were carrying infants, n=47). Immature
28 396 individuals and females with infants (63.2 and 26.3%, respectively) constituted the majority of
29 397 individuals appearing in events comprising eight individuals or more (n=19). We were unable to
30 398 compare the proportions of males to females or of different age groups observed in nocturnal videos
31 399 with those proportions observed in all chimpanzee (diurnal) activity videos as these site-level
32 400 comparative data are not currently available from the PanAf.

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35 401 We found the most predominant behavior exhibited by chimpanzees during nocturnal activity to be
36 402 ‘movement’ (80.9% of chimpanzee-events, n=235), followed by ‘on location’ (14.9%) (Table 5). We
37 403 found both ‘social’ and ‘feeding’ behaviors to feature rarely (2.6 and 1.7%, respectively). We found
38 404 movement and social behaviors to occur more often in true night than in twilight (movement: 52.6 and
39 405 47.4%, respectively, n=190; social: 83.3 and 16.7%, respectively, n=6), but on location behavior to
40 406 occur more often in twilight than true night (68.6 and 31.4%, respectively, of on location chimpanzee-
41 407 events, n=35). We observed no feeding behaviors in twilight hours. We found the majority of
42 408 movement behaviors to be exhibited by immature individuals, and the majority of on location
43 409 behaviors to be exhibited by adult males (in both twilight and true night). We observed feeding and
44 410 social behaviors to be exhibited only by adult males and immature individuals, in all phases of the
45 411 night (Table 5). Again, we were unable to compare the proportions of behavior patterns observed in
46 412 nocturnal videos with those proportions observed in all chimpanzee (diurnal) activity videos as these
47 413 site-level comparative data are not currently available from the PanAf.

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51 414 [Figure 4 here]

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53 415 [Tables 4 & 5 here]

54 55 416 **Predictors of chimpanzee nocturnal activity**

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3 417 Overall, we found the fixed effects to impact the probability to detect terrestrial nocturnal activities
4 418 (full-null model comparison: $\chi^2=28.762$, $df=8$, $p=0.001$). More precisely, we found higher levels of
5 419 nocturnal activity at sites with lower levels of human activity, increased average daily temperatures,
6 420 and a higher percentage of forest (Table 6; Fig. 5). We found none of the other predictors to have a
7 421 significant effect on the probability of nocturnal activity (Fig. 5). We found no indication for the
8 422 effects of percent illumination or daily temperature to vary among sites (Appendix 3). Given the low
9 423 transect survey effort of two sites in particular, Bili and Sapo, we removed them and re-ran the model
10 424 but found no difference in the overall results and significant effects (Appendices 4 and 5).

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13 425 [Table 6 here]

14 426 [Figure 5 here]

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DISCUSSION

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Occurrence of chimpanzee nocturnal activity

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20 429 We investigated terrestrial nocturnal activity in chimpanzees (*Pan troglodytes*) using footage from
21 430 movement-triggered camera traps. There are considerable advantages to using such technology, such
22 431 as the noninvasive nature, the ability to study unhabituated animals, and the ability to obtain
23 432 information in places and at times inaccessible to human observers, such as at night (Boyer-Ontl and
24 433 Pruetz, 2014; Estienne et al., 2017; Head et al., 2012). However, limitations of camera trapping should
25 434 be carefully considered when interpreting results; the limitations will be presented within the
26 435 subsequent discussion.

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29 436 Overall, we found a low level of terrestrial nocturnal activity to be widespread across chimpanzee
30 437 populations, occurring in the majority of research sites studied. In four of the sites studied we did not
31 438 observe any nocturnal activity in camera-trap footage. Camera-trapping efforts of these four sites were
32 439 not particularly low, and—apart from at Gashaka (Nigeria)—the proportions of videos containing
33 440 chimpanzees at the other three sites (La Belgique, Korup, Cameroon; and Conkouati, Republic of
34 441 Congo) were also not low, suggesting that the chimpanzees of these sites are not particularly elusive
35 442 compared to other sites. However, it should be noted that data used in the study were restricted in
36 443 some cases due to the availability of data through the PanAf (e.g., not always spanning all seasons), so
37 444 it is possible that with additional camera-trapping effort and an extended investigation, nocturnal
38 445 activity could be observed in these sites. In fact, initial investigations of more recent camera-trap
39 446 footage from La Belgique that was not included in this study indicates some terrestrial nocturnal
40 447 activity in chimpanzees (author's obs.: N. Tagg). Similarly, proportion of nocturnal activity at some
41 448 sites may not be precise: for example, at Boé (Guinea Bissau) only part of the PanAf data collection
42 449 period and associated data were available for use in the study, and initial observations suggest that the
43 450 percentage of chimpanzee nocturnal activity at this site might be increased if the full PanAf data
44 451 collection period could have been included. Similarly, at Loango (Gabon) it is suspected that the
45 452 number of chimpanzee videos may be a conservative measure.

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49 453 The overall proportion of nocturnal activity observed was low (1.80% of all chimpanzee occurrences
50 454 in videos); however, this rate of observation is likely to be an underestimation. First, chimpanzees are
51 455 a predominantly arboreal species across many parts of their range and some nocturnal activity may
52 456 occur exclusively or predominantly in the trees (Goodall, 1962; Izawa and Itani, 1966; Mitani and
53 457 Nishida, 1993; van Lawick-Goodall, 1968; Zamma, 2013). The terrestrial nature of the camera-
54 458 trapping methodology does not allow us to investigate arboreal activity, so it is likely that arboreal
55 459 nocturnal activity could have been missed. Both the degree of terrestriality and the observability of

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3 460 terrestrial activity are likely to vary between sites, depending on the openness of the habitat and the
4 461 denseness of the understory vegetation. Second, it is likely that camera-trap capture rates are reduced
5 462 in dark conditions, so it might be possible for chimpanzees to move about at night without triggering a
6 463 camera; or that chimpanzees are sensitive to the light or sound emitted by cameras, which may be
7 464 heightened at night when the contrast may be greater, and cameras may be avoided. Third, not all sites
8 465 exhibited the same camera-trapping effort, and a low number of camera traps at some sites will have
9 466 reduced the likelihood of observing nocturnal activity. However, the study supports the long-held
10 467 belief that chimpanzees are largely diurnal, and that this observed terrestrial nocturnal activity is rather
11 468 infrequent. This corroborates studies on other primates, such as olive baboons and vervet monkeys,
12 469 which exhibit nocturnal activity on only 1.1% and 0.4% of the nights during which the animals were
13 470 being observed, respectively (Isbell et al., 2017).

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16 471 We observed this infrequent nocturnal activity in three of the four chimpanzee subspecies, with the
17 472 highest number of events of nocturnal activity occurring in *P. t. verus*, followed by *P. t.*
18 473 *schweinfurthii*, then *P. t. troglodytes*. We did not observe nocturnal activity in *P. t. ellioti*; however,
19 474 this may be due to the relatively low camera-trapping effort for this subspecies (i.e., fewer camera-
20 475 days and only at two sites). Therefore, overall, we found a low level of terrestrial nocturnal activity to
21 476 occur in the majority of research sites studied and in three of the four subspecies of chimpanzee,
22 477 suggesting this infrequent behavior pattern to be widespread in chimpanzees. This further suggests that
23 478 nocturnal activity may be also present in other diurnal primate species (e.g., Isbell et al., 2017).

24 479 **Demographics and behavior**

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28 480 We found chimpanzee terrestrial nocturnal activity to be exhibited more often by lone adult males.
29 481 Males have a larger body size compared to females which may afford them more security for night-
30 482 time activity, as is argued for male gorillas nesting closer to the ground than females (e.g., Yamagiwa,
31 483 2001). It is possible that males may wake more at night due to the nature of the activities carried out at
32 484 night: males, for example, may be more likely to engage in territory patrols and this can occur at night
33 485 (e.g., Boesch et al., 2007). However, many females and immature individuals were also observed
34 486 exhibiting nocturnal activity, so it is not solely an adult male activity. Observations of chimpanzee
35 487 crop raiding by night in Kibale, Uganda, have demonstrated more females to be involved in the
36 488 activity (Krief et al., 2014). Furthermore, it is possible that male–female and age group ratios observed
37 489 in camera-trap footage may be an artefact of the camera-trapping method (to address this we would
38 490 need to know the probability of males versus females being recorded by camera traps). Alternatively,
39 491 the sex ratio in nocturnal videos may reflect the structure of the population or group—particularly
40 492 important if the sex-age composition of certain sites is skewed, for example at Fongoli (Senegal;
41 493 Pruetz, Ontl, Cleaveland, Lindshield, Marshack and Wessling 2017)—and may not be specific to
42 494 nocturnal activity; information regarding real demographic structure including ratios of various age
43 495 classes would be necessary.

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47 496 We found ‘movement’ to be the most common behavior exhibited during terrestrial nocturnal activity,
48 497 including walking and running into and/or out of view of the camera. Travelling on the ground at night
49 498 has previously been observed at Fongoli, Senegal (Pruetz and Bertolani, 2009), Mahale, Tanzania
50 499 (Zamma, 2013), and Gombe, Tanzania (Goodall, 1986; van Lawick-Goodall, 1968). Olive baboons
51 500 and vervet monkeys were observed travelling at night (Isbell et al., 2017). Movement behavior
52 501 patterns could be explained as the individual moving to a new nest site (for example if disturbed;
53 502 Zamma, 2013), as seen in Japanese macaques (Nishikawa and Mochida, 2010), moving away or back
54 503 to the nest before or after night-time feeding/foraging (e.g., Goodall, 1986; van Lawick-Goodall,
55 504 1968), or fulfilling some social requirement, such as mating (chimpanzees: Nishida, 1996; rhesus

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3 505 macaques: Vessey, 1973) and territory patrol/aggressions (e.g., Boesch et al., 2007 and see Nishida,
4 506 1996; pers. obs.: Shelley Masi, from Krief et al., 2014, p. 2). Wild bonobos (*Pan paniscus*) have been
5 507 observed to exhibit sex, social grooming, and play overnight (Fruth and Hohmann 1993, 1994). ‘On
6 508 location’ behaviors (including sitting/standing in view, or ascending, descending a tree, etc), and
7 509 ‘social’ behaviors were observed at a low rate, including some play (immature individuals), both
8 510 during twilight hours and during true night. On location behaviors could reflect movement behaviors,
9 511 whereby the animal paused; however, they could also indicate having fed or being in search of a food
10 512 source, or leaving or arriving at a nest. It is possible that chimpanzees wake early for early arrival at
11 513 ephemeral fruit trees in Tai National Park, Ivory Coast (Janmaat, Polansky, Ban, and Boesch, 2014).
12 514 Similarly, other studies have demonstrated feeding to be the main reason for activity during night
13 515 hours, for example, crop raiding in Kibale, Uganda (Krief et al., 2014). In our case, it was not possible
14 516 to corroborate the location of nesting sites or feeding trees in conjunction with the data from camera-
15 517 trap footage. Furthermore, in our study, ‘feeding’ behaviors were not observed at all during twilight
16 518 hours and only very rarely during true night hours. We observed rare social behavior patterns during
17 519 nocturnal activity. We did not observe any social grooming between individuals, but we did observe
18 520 some play behavior between adolescents and infants while the mother chimpanzee exhibited a
19 521 standing (on location) behavior. However, the frequent movement behaviors observed could similarly
20 522 reflect individuals moving to or from feeding locations and crucially, as most feeding occurs
21 523 arboreally, we would not expect to observe high rates of feeding in nocturnal activity videos captured
22 524 by terrestrial camera traps. Furthermore, behaviors exhibited by individuals appearing in the same
23 525 event will be non-independent, which may have further skewed the high proportions of certain
24 526 behavior types observed.

27 28 29 527 **Timing of nocturnal activity**

30 528 We observed terrestrial nocturnal activity taking place during all phases of the night, but the majority
31 529 of observations occurred during twilight. Activity during these phases likely represents an extension of
32 530 daytime activities—i.e., during twilight after sunset chimpanzees may still be seeking a suitable
33 531 nesting site, or moving from their last location to their selected nesting site. This has been
34 532 demonstrated in Guizhou snub-nosed monkeys, at a site where fluctuating day length and food
35 533 availability have led to flexible twilight feeding behaviors (Tan et al., 2013). Chimpanzees at Fongoli
36 534 have been observed to remain active late into the evening, particularly in the dry season when
37 535 temperatures are higher and nights are longer (Pruetz and Bertolani, 2009). During twilight before
38 536 sunrise, active chimpanzees may represent those who have recently arisen early from their nest sites
39 537 for early arrival at a food source (Janmaat et al., 2014). However, all videos of nocturnal activity in
40 538 these twilight phases display a dark sky, thus rendering this extension of daytime activities into the
41 539 night an interesting observation. Future research could investigate the possibility of a latitudinal effect
42 540 for nocturnal behavior: nocturnal activity may be seasonal, for example, occurring more during
43 541 periods when nights are longer, as observed in Fongoli (Pruetz and Bertolani, 2009).

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47 542 **Insights into human evolution.** Activity in deeper phases of the night (phases 3 and 4 in Fig. 3) are
48 543 more likely to represent cases whereby individuals awoke from sleep and left their night nest, and/or
49 544 were likely to nest (again) before rising the next morning. This type of nocturnal activity could suggest
50 545 a fragmented sleeping pattern (de la Iglesias and Lee, 2015) that has rarely been previously
51 546 empirically documented in chimpanzees (but see Zamma, 2013). There is some evidence that
52 547 fragmented sleep reflects the ancestral pattern in humans: some traditional societies (e.g., in Nigeria;
53 548 Bohannan, 1953; Ekirch, 2006) exhibit high levels of activity around midnight, and use the terms "first
54 549 sleep" and "second sleep"; and modern humans living under experimental, short (10 h) photoperiods
55 550 begin to exhibit fragmented sleep (Wehr, 1992). However, we observed relatively very few events of

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3 551 nocturnal activity in these deeper phases of the night, and only in a few sites. If early hominin night-
4 552 time sleep was fragmented, we would expect to see more waking in the middle of the night in
5 553 chimpanzees in between 'bouts' of sleep; instead, we found chimpanzee nocturnal activity to occur at
6 554 all hours of the night and more commonly during twilight. We would also expect to see a higher
7 555 proportion of night waking (e.g., by more individuals on more nights), but the study found nocturnal
8 556 activity overall to occur at a very low proportion, suggesting that the majority of chimpanzees on the
9 557 majority of nights do not exhibit nocturnal activity. Therefore, although some habitat- or site-specific
10 558 exceptions may exist, we find support for the hypothesis that wild chimpanzee sleep is commonly
11 559 consolidated. This finding is in line with interpretations by human sleep scientists who argue that
12 560 fragmented sleep is likely to lead to cognitive disadvantages (Eban-Rothschild et al., 2017): when
13 561 compared to short, fragmented sleep epochs, long, consolidated sleep epochs have been demonstrated
14 562 to have increased recovery power in humans (Vyazovskiy et al., 2007). Similarly, in orangutans, more
15 563 nocturnal calls (suggesting interrupted sleep) were associated with poorer sleep quality (Samson,
16 564 Hurst and Shumaker, 2014). Human sleep literature shows that cyclical pressures exerted by the
17 565 circadian and homeostatic processes in humans favor an extended and consolidated bout of nocturnal
18 566 sleep (de la Iglesias and Lee, 2015), with a biological dusk and dawn in human natural rhythms (Wehr
19 567 et al., 2001), and with no evidence of physiological drivers for waking in the middle of the night.
20 568 Several studies support this by presenting evidence of consolidated sleep in traditional societies, where
21 569 people exhibit sleep onset a few hours after dark and then sleep through the night (e.g., Yetish et al.,
22 570 2015).

26 571 **Predictors of nocturnal activity**

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28 572 Our study revealed higher levels of terrestrial nocturnal activity with lower levels of human activity
29 573 encountered at the site, with higher temperatures, and in sites with a higher percentage of forest.

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31 574 **Human activity.** Although there is some evidence for chimpanzees finding ways to persist in human-
32 575 dominated landscapes (see Hockings et al., 2015), there is considerable evidence that wild
33 576 chimpanzees perceive humans as a threat across their range (Arnhem et al., 2008; Clark et al., 2009;
34 577 Kano and Asato, 1994; Rabanal et al., 2010; Stokes et al., 2010; Tagg and Willie, 2013; Walsh et al.,
35 578 2003). Hunters frequently operate at night and in twilight hours (Astaras et al., 2017). The movement
36 579 and actions of people in chimpanzee sites at night may pose a threat to chimpanzees; indeed, humans
37 580 have arguably become the principal predator of chimpanzees across much of their range. Our study
38 581 suggests that lower rates of human activity in a site may facilitate or enable higher rates of nocturnal
39 582 activity in chimpanzees, as the threat posed by encountering a human is reduced (Tagg, Willie, Petre,
40 583 and Haggis, 2013). The signs of human activity recorded in the present study comprised evidence of
41 584 hunting, gathering, illegal logging, etc., but not of research activity, thus supporting the suggestion that
42 585 these types of human pressures are perceived by chimpanzees as a threat.

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45 586 We did not, however, observe the same effect with regard to predators (lions, *Panthera leo*; leopards,
46 587 *P. pardus*; and hyena, *Crocuta crocuta*) or to other large mammals (elephants, *Loxodonta africana*;
47 588 and buffalos, *Syncerus caffer*) that could pose a threat to chimpanzees at night. We therefore cannot
48 589 conclude that a potential reduction in the risk of injury at night via an encounter with a large mammal
49 590 or predator might enable terrestrial nocturnal activity, nor that chimpanzees might be disturbed from
50 591 sleep by the activity of large mammals below the nest. The lack of influence of predator abundance in
51 592 particular is surprising, given the array of previous evidence for the disturbance of chimpanzees by
52 593 predators (Carvalho et al., 2015; Pruetz et al., 2008; Stewart and Pruetz, 2013; Tutin et al., 1981).
53 594 Generally, predator abundances were low if detected at all (maximum abundance rate: 0.121 signs per
54 595 kilometer at Taï R, Ivory Coast). Fourteen of 22 sites did not identify predator presence on the

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3 596 transects although we have reason to believe that, for example, leopards are present in Gashaka
4 597 (author's obs.: V. Sommer). Our proxy variable used to represent predator pressure may not have been
5 598 adequately representative, or the transect survey effort in some sites was quite low, and further studies
6 599 may serve to refute or elaborate on these observations, particularly if able to consider site-specific
7 600 conditions. These inaccuracies may have weakened the influence of predators as measured in the
8 601 present study. However, humans are arguably the most significant predator of chimpanzees in most of
9 602 their range, even in areas where poaching is rare (see Lindshield et al., 2017). Thus, it is perhaps not
10 603 surprising that we found no effect of non-human predators on nocturnal activity, whereas we did find
11 604 an effect of human activity.

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14 605 **Habitat.** We found the probability of chimpanzee nocturnal activity to increase in forested habitats
15 606 compared to savanna habitats. This is surprising given the previous evidence of nocturnal activity in
16 607 chimpanzees living in savanna habitats (e.g., Pruetz and Bertolani, 2009). However, these results are
17 608 not consistent with some of our site-specific observations of nocturnal activity in the study. Six of the
18 609 sites included in the study were categorized as savanna sites, constituting a higher percentage of
19 610 savanna than forest, and three of these savanna sites (Sobeya, Guinea; Kayan, Senegal; and Geprenaf,
20 611 Ivory Coast) accounted for most of the nocturnal activity occurring during the deeper phases of the
21 612 night. Kayan, in particular, which is characterized by nearly 75% savanna, exhibited the most
22 613 nocturnal activity (in terms of number of videos, events and distinct individuals exhibiting nocturnal
23 614 activity) of all sites, thus appearing to support previous observations of a high occurrence of nocturnal
24 615 activity in savanna habitats (i.e., at Fongoli; Pruetz and Bertolani, 2009). It could be argued that such
25 616 open habitats may necessitate increased terrestrial activity, thus leading to an increased capture rate of
26 617 nocturnal activity; however, the overall (day and night) chimpanzee capture rates at these sites were
27 618 not higher than at forested sites. Furthermore, two other sites, Budongo and Ngogo (Uganda),
28 619 comprised very high percentages of forest (100 and 85%, respectively) but also exhibited some
29 620 nocturnal activity in true night; the markedly high percentage of forest habitats at these sites might
30 621 explain the strength of the forest variable in predicting nocturnal activity.

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34 622 **Temperature.** We found higher levels of nocturnal activity with higher average daytime temperatures.
35 623 This observation is supported by previous literature. Chimpanzees in the savanna habitats of Fongoli,
36 624 Senegal have developed behavioral strategies, such as soaking in pools of water and seeking refuge in
37 625 caves, to counter the effects of the high daytime temperatures (Pruetz, 2001, 2007; Pruetz and
38 626 Bertolani, 2009). The thermoregulatory costs associated with daytime foraging (Lindshield et al.,
39 627 2017) have been suggested to explain subsequent nocturnal feeding activity observed (Pruetz and
40 628 Bertolani, 2009). Similarly, chimpanzees at Gombe, Tanzania, have been observed to visit feeding
41 629 areas and water sources at night, possibly because of the daytime heat at the site (van Lawick-Goodall,
42 630 1968). It is expected for extreme temperatures to influence nocturnal activity: in humans, temperature
43 631 may influence sleep duration in traditional populations, possibly as a mechanism of maintaining a low
44 632 body–environment temperature differential to reduce energy needed to stay warm (Yetish et al., 2015).
45 633 We did not detect an effect of rainfall on nocturnal activity, despite the link between temperature and
46 634 rainfall and the evidence for extremes of such climatic conditions to lead to nocturnal behavior.
47 635 Savanna chimpanzees in Comoé, Ivory Coast, have been filmed dipping for water in tree holes during
48 636 periods of low rainfall, with one sequence of this behavior occurring throughout the night (Lapunte,
49 637 Hicks and Linsenmair, 2017). As there are vast differences in environmental conditions and habitat
50 638 composition of the study sites spanning the entire longitudinal range of the chimpanzee in Africa, it is
51 639 possible that the environmental and habitat-related drivers of nocturnal activity may differ between
52 640 sites and the overarching statistical model employed in the present study would not be able to detect
53 641 site- or season-specific predictors. In addition, nocturnal activity may be influenced by season, which

642 was not considered in the study due to the already small sample sizes. However, we made a start by
643 including climate variables (temperature and rainfall) in our model. Further studies which consider the
644 effects of environmental conditions varying among and within sites could contribute to elucidating
645 their possible influences on the occurrence of nocturnal activity in chimpanzees.

646 **Other factors.** Moonlight was frequently suggested to be a strong determinant of night-time activity
647 levels in primates (Fernandez-Duque et al., 2010; Izawa and Itani, 1966; Pruettz and Bertolani, 2009;
648 van Lawick-Goodall, 1968; pers. comm.: Koichiro Zamma). However, the present study found no
649 support for moonlight enabling or being a prerequisite of night waking as there was no significant
650 influence of percent illumination on the occurrence of nocturnal activity. The illumination intensity
651 range for feeding activity in chimpanzees (and other great apes) is 1–85 lux, whereas the illuminance
652 (the measure of the incident light illuminating a surface) during a full-moon night amounts to about
653 0.3 lux (Erkert, 2003, 2008); this is one of the criteria used to categorize great apes as diurnal. Cover
654 from trees and other vegetation will reduce this even further. Therefore, even during a full moon it
655 would not be easy for chimpanzees to navigate and function safely at night. Furthermore, nocturnal
656 activity has also been described to occur on non-moonlit nights in wild chimpanzees (e.g., Krief et al.,
657 2014), thus suggesting that moon illuminance neither encourages nor necessarily facilitates nocturnal
658 activity, consistent with the results of the present study. It should be noted, however, that the present
659 study did not account for cloud cover affecting the actual amount of light reaching the forest floor
660 regardless of the percent moon illumination for that night.

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

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

688 conditions, such as high temperatures, as well as threats and disturbances, such as those posed by
689 humans.

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

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723 **AUTHOR CONTRIBUTIONS**

724 F. Stewart and N. Tagg developed the concept for the study; G. Bocksberger, P. Dieguez, M.
725 McCarthy, N. Tagg, J. Widness, and J. Willie processed, compiled, and extracted data; M. McCarthy
726 performed identification of all individuals appearing in videos for all sites; G. Bocksberger and J.
727 Willie produced the figures; R. Mundry and J. Willie designed and performed statistical analyses; A.
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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 ($x = (T_{\text{video}} - T_{\text{sunset}}) / \text{night duration}$). 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)

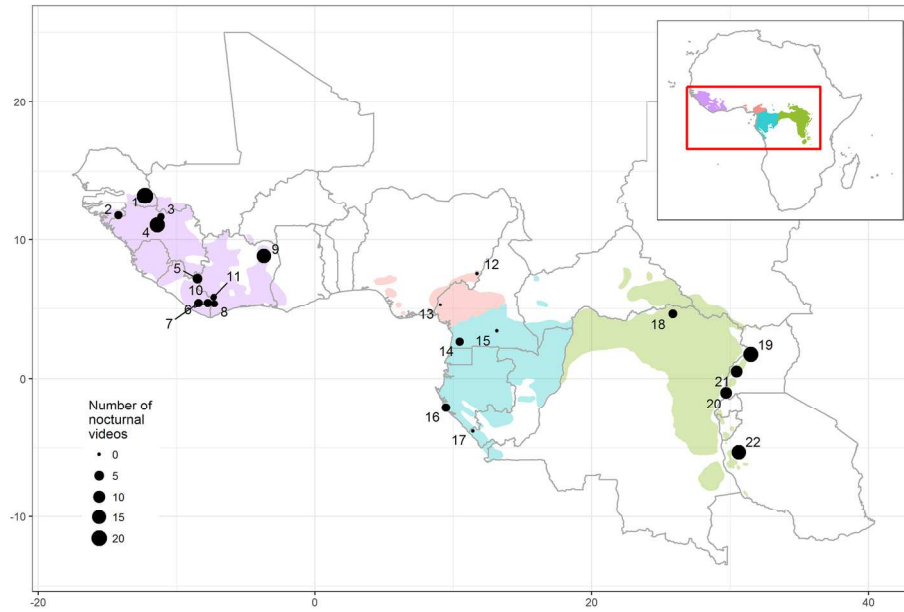


Figure 2 – Locations of sites included in the present study: 1. Kayan (Senegal), 2. Boe (Guinea Bissau), 3. Bakoun, 4. Sobeya (Guinea), 5. East Nimba, 6. Grebo, 7. Sapo (Liberia), 8. Djouroutou, 9. Geprenaf, 10. Tai E, 11. Tai R (Ivory Coast), 12. Gashaka (Nigeria), 13. Korup, 14. Campo Ma'an, 15. La 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*.

177x108mm (300 x 300 DPI)

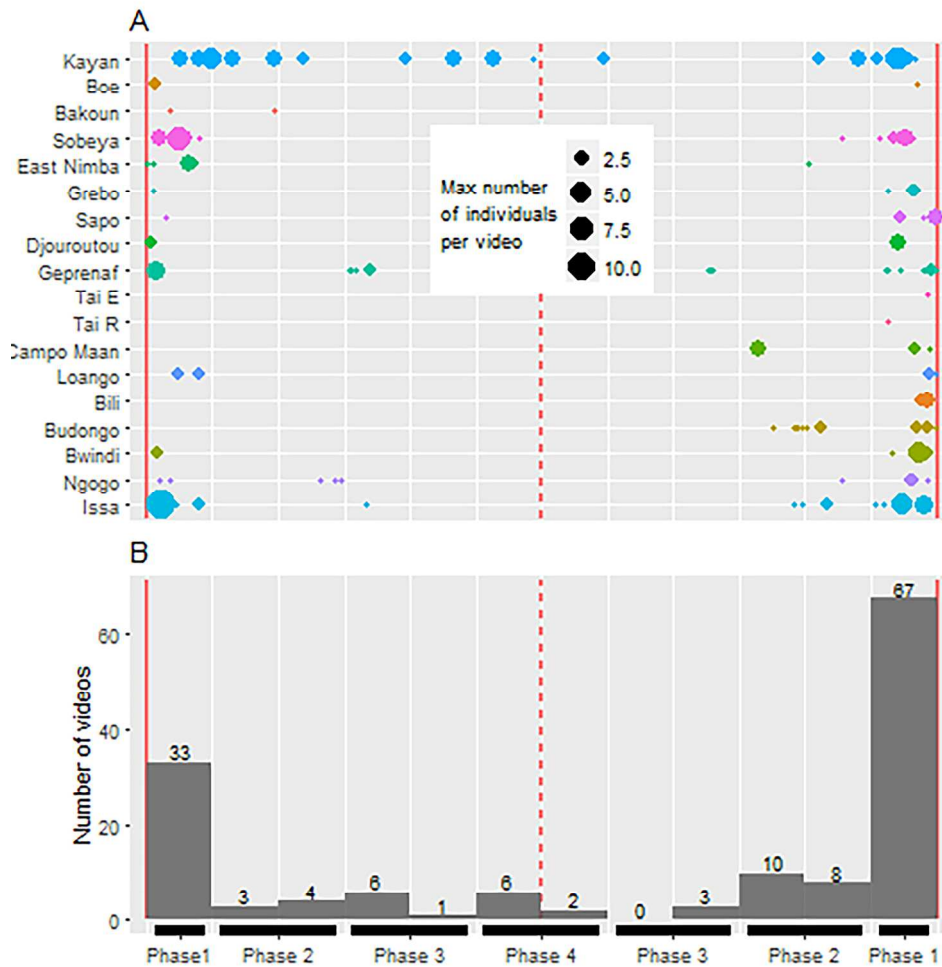


Figure 3 – Video capture of chimpanzees through the night at 18 sites. To be comparable between different geographic locations and times of year, the recording time of the videos was scaled from 0 to 1 based from the time difference from sunset on that day (or the previous day for videos captured after midnight) and night duration ($x = (T_{\text{video}} - T_{\text{sunset}}) / \text{night duration}$). 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”).

169x169mm (300 x 300 DPI)

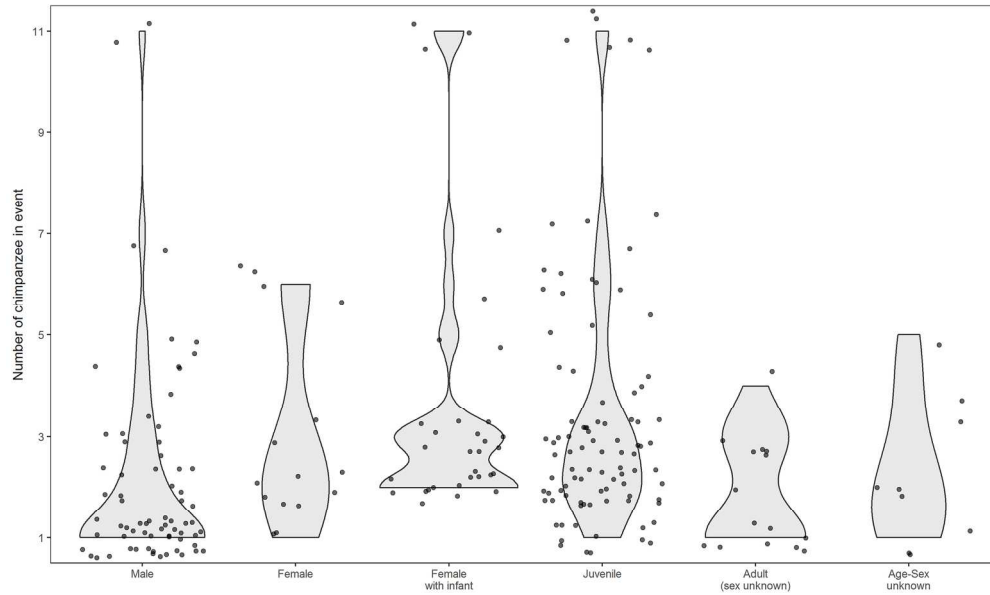


Figure 4 – Density distribution of age–sex categories within nocturnal events with various numbers of participants. Females are accounted for in two different ways: either without or with infant. The class ‘immature’ includes adolescent, juveniles and infants. Each dot represents a nocturnal event captured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

177x108mm (300 x 300 DPI)

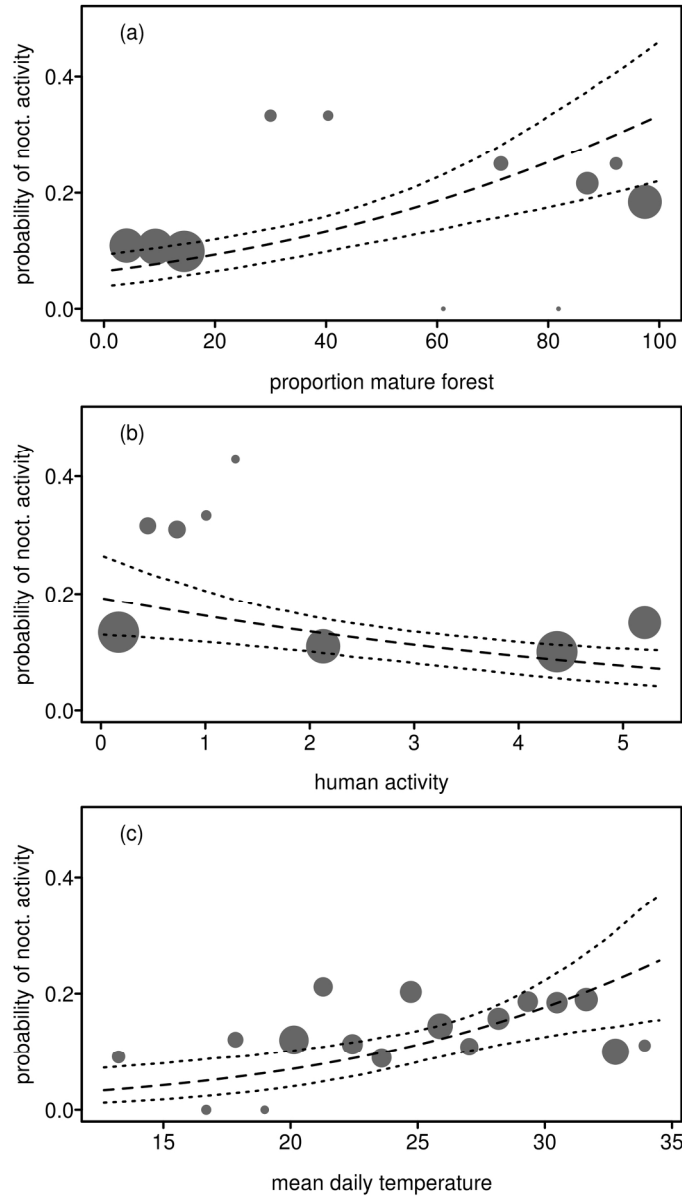


Figure 5 – Probability of nocturnal activity (y-axes) as a function of the percentage of forest (a), human activity (b), and mean daily temperature (c; x-axes). Indicated are the fitted model (dashed line) and its confidence interval (dotted lines). Points represent the proportions of data points with 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).

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 (<i>Pan troglodytes</i>) sub-species	Chimp&See (C&S) or non-Chimp&See (non-C&S)
Senegal	Kayan (temporary research site)	<i>P. t. verus</i>	C&S
Guinea Bissau	Boé (Beli)	<i>P. t. verus</i>	Non-C&S
Guinea	Bakoun Classified Forest	<i>P. t. verus</i>	Non-C&S
Guinea	Sobeya (temporary research site)	<i>P. t. verus</i>	Non-C&S
Liberia	East Nimba Nature Reserve	<i>P. t. verus</i>	C&S
Liberia	Grebo National Park (Sala)	<i>P. t. verus</i>	C&S
Liberia	Sapo National Park	<i>P. t. verus</i>	C&S
Ivory Coast	Djouroutou , Tai National Park	<i>P. t. verus</i>	C&S
Ivory Coast	Geprenaf (temporary research site)	<i>P. t. verus</i>	Non-C&S
Ivory Coast	Tai E (Ecotourism Site), Tai National Park	<i>P. t. verus</i>	C&S
Ivory Coast	Tai R (Research Site), Tai National Park	<i>P. t. verus</i>	C&S
Nigeria	Gashaka-Gumti National Park	<i>P. t. ellioti</i>	Non-C&S
Cameroon	Korup National Park	<i>P. t. ellioti</i>	Non-C&S
Cameroon	Campo Ma'an National Park	<i>P. t. troglodytes</i>	Non-C&S
Cameroon	La Belgique , Dja Biosphere Reserve	<i>P. t. troglodytes</i>	Non-C&S
Gabon	Loango National Park	<i>P. t. troglodytes</i>	Non-C&S
Republic of Congo	Conkouati-Douli National Park	<i>P. t. troglodytes</i>	Non-C&S
Democratic Republic of Congo	Bili , Gangu Forest	<i>P. t. schweinfurthii</i>	C&S
Uganda	Budongo Forest	<i>P. t. schweinfurthii</i>	C&S
Uganda	Bwindi Impenetrable Forest National Park	<i>P. t. schweinfurthii</i>	C&S
Uganda	Ngogo , Kibale National Park	<i>P. t. schweinfurthii</i>	Non-C&S
Tanzania	Issa (Issa Valley), Ugalla	<i>P. t. schweinfurthii</i>	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								
<i>P. t. troglodytes</i>	42,930.0	48,604.0	2189	<i>5.36</i>	10	<i>0.41</i>	10	17
<i>P. t. verus</i>	94,533.3	143,376.0	4687	<i>3.16</i>	92	<i>2.52</i>	76	154
<i>P. t. schweinfurthii</i>	29,024.2	61,026	3149	<i>5.33</i>	56	<i>2.48</i>	47	86
<i>P. t. ellioti</i>	17,094.7	23,235	598	<i>3.14</i>	NA	<i>NA</i>	NA	NA

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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