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3 1 **ARTICLE TITLE:** Temporal patterns of chimpanzee loud calls in the Issa
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5 2 Valley, Tanzania: Evidence of nocturnal acoustic behavior in wild
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7 3 chimpanzees.
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27

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29
30 14 vocalization;
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28 INTRODUCTION

29 Many primates produce loud calls, which vary in function, from
30 advertising fitness to defending territorial boundaries (Wich and Nunn, 2002;
31 Delgado, 2006). Whilst the spatial distribution of those calls has been shown
32 to correspond to territorial defense (Wilson et al., 2007) and the coordination
33 of group movements (Boinski, 1993; Trillmich et al., 2004; Braune et al., 2005;
34 Byrne and da Cunha, 2006), far less is known about the temporal distribution
35 of calls, especially over 24h cycles. Understanding the temporal patterns of
36 animal vocal signals can reveal activity patterns at times and from places that
37 researchers traditionally cannot monitor, the evolution of inter- and intra-
38 specific communication systems, and more generally vocal competition in
39 complex acoustic environments (Pijanowski et al., 2012).

40 The timing of vocalization behavior is often a response to the caller's
41 physical environment. Vegetation and topography (Marten et al., 1977; Brown
42 et al., 1995; Mennill et al., 2006) as well as temperature, wind, humidity, and
43 ambient noise all change throughout the day and influence sound
44 transmission and thus when animals call. Specifically, temperature and wind
45 interact in important ways, affecting propagation differently across
46 atmospheric conditions (Heimann and Gross, 1999). Temperature inversions
47 can trap sound energy, promoting more efficient transmission across long
48 distances (Brown and Hall, 1978; Wilson et al., 2003), whereas wind may
49 attenuate sound, distorting or degrading calls that may otherwise transmit well
50 under calmer conditions (Hayes and Huntly, 2005). Further, intra- and inter-
51 specific acoustic competitors may deter vocalization behavior, with individuals
52 seeking to avoid their signals being spectrally or temporally masked by other

1
2
3 53 calls (Henry and Wells, 2010; Schmidt et al., 2012; Sinsch et al., 2012;
4
5 54 Villanueva-Rivera, 2014). That animals have evolved call types and call
6
7 55 behavior to optimise sound transmission has been termed the Acoustic
8
9 56 Adaptation Hypothesis (AAH) (Daniel and Blumstein, 1998). Whilst early work
10
11 57 did demonstrate support for the AAH in primates (Waser and Brown, 1986;
12
13 58 Brown et al., 1995), a more recent compilation of data across birds, anurans
14
15 59 and mammals found only minimal support (Ey and Fischer, 2009).

16
17
18 60 Despite inconsistent conformity to AAH predictions across the Order
19
20 61 Primates, along with many bird species (Staicer et al., 1996), many primates
21
22 62 also exhibit vocalization peaks at dawn and dusk (Table 1), with callers
23
24 63 exploiting low abiotic noise levels and ideal microclimates for long distance
25
26 64 sound transmission (Henwood and Fabrick, 1979). Most studies on primate
27
28 65 calling, however - and primate behavior more broadly - are limited to when
29
30 66 researchers are also active, during the day. Far less is known about primate
31
32 67 night-time activity (see Tagg et al., this issue), especially calling behavior of
33
34 68 diurnal primates.

35
36
37 69 There are good reasons to expect nocturnal behavior in diurnal
38
39 70 primates. First, nocturnally is likely the ancestral activity pattern for primates,
40
41 71 with subsequent shifts to diurnality and cathemerality attributed to speciation
42
43 72 events (Santini et al., 2015). Thus, there could be residual, nocturnal behavior
44
45 73 even in diurnal animals. Evidence for nocturnal activity can be seen in
46
47 74 differences between where study subjects are left late in one day, and where
48
49 75 they are found waking the subsequent morning (pers. observation),
50
51 76 suggesting night-time movement. In apes, this behavior has been explained
52
53 77 as a response to the social and environmental context. Socially, rank predicts
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3 78 mating opportunities in chimpanzees (Wroblewski et al., 2009), so low ranking
4
5 79 males may sneak copulations at night, hiding from protective alpha males that
6
7 80 would otherwise prevent the behavior. Finally, by definition, fission-fusion
8
9 81 animals are dispersed at various times during the day and night, and thus
10
11 82 calls may serve coordination and cohesive mechanisms (Leighty et al., 2008),
12
13 83 advertising a caller's location and facilitating reunions (e.g. fusion events) later
14
15 84 the next day. Environmentally, primates that live in hot climates may forage at
16
17 85 night to avoid high day-time temperatures (Pruetz, 2018). By being active
18
19 86 during periods of the night, animals can increase their foraging time and
20
21 87 ultimately, increase their caloric intake. Foraging at night may reduce feeding
22
23 88 competition for high quality foods from hetero-specifics as well (Donati et al.,
24
25 89 2009).

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28
29 90 There are costs to being active at night, however. Predation pressure is
30
31 91 generally higher at night compared to the day (Isbell, 1994) and many species
32
33 92 use highly conspicuous loud calls, which can reveal their location to potential
34
35 93 predators (Bergstrom and Lachmann, 2001). Given that diurnal animals
36
37 94 exhibit night-time activity, the advantages of this behaviour may outweigh any
38
39 95 risks.

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44 97 [Table 1 here]

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47
48 99 In great apes, despite decades of research describing vocalization
49
50 100 patterns (*Pongo*: MacKinnon, 1974; *Pan*: Marler and Hobbett, 1975), most
51
52 101 research has centered on acoustic analysis of call elements (Arcadi, 1996;
53
54 102 Riede et al., 2004; Lameira et al., 2012), context specific calls (Mitani and
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3 103 Nishida, 1993; Crockford and Boesch, 2005; Salmi et al., 2013), and how
4
5 104 communication informs the evolution of human language (Slocombe and
6
7 105 Zuberbühler, 2005; Slocombe and Zuberbuhler, 2007; Crockford et al., 2012;
8
9 106 Schel et al., 2013; Lameira et al., 2015, 2016). Save for extensive research
10
11 107 into gibbon call patterns (Tenaza, 1976; Geissmann and Nijman, 2006), little
12
13 108 work has focused on the temporal or environmental influences on ape loud
14
15 109 calls, especially at night when researchers are absent. Wild orang-utans
16
17 110 exhibit dramatic variation in nocturnal call rates between populations
18
19 111 (Hoepfner and Spillman, unpublished data), and it has been suggested that
20
21 112 population density, inter-male contests, or else female reproductive status
22
23 113 may drive increased call rates (Ross and Geissmann, 2009). Wild
24
25 114 chimpanzees (*P. troglodytes*) have been described to be awoken by
26
27 115 conspecifics making sounds at night (Zamma, 2014) and also to exhibit
28
29 116 various activity types (including calling) throughout the night (Pruetz, 2018;
30
31 117 Tagg et al., in press). Aside from these few studies, little is known about
32
33 118 nocturnal calling in chimpanzees.

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37 119 Night-time calling may potentially have been an important hominin
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39 120 behavior in adapting to a hotter, more open, but also sound-friendly savanna-
40
41 121 mosaic environment (Waser and Brown, 1986). Diurnal hominins could have
42
43 122 been driven to night activity by selective pressure to avoid high temperatures
44
45 123 during the day, or to avoid diurnal predators. However, Halle (2006) has
46
47 124 suggested that adaptation to one phase of the 24h cycle implies
48
49 125 maladaptation to the other, and thus vulnerability, especially to predation.
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51 126 Thus, hominins may have exhibited polyphasic activity (Halle, 2006) patterns
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1
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3 127 in response to very specific ecological conditions, without any specialized
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5 128 anatomical adaptations (Gerkema et al., 2013).

6
7 129 Like many other hominin behaviors, activity patterns do not fossilise,
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9 130 and thus studying extant great apes may be as close as we get to
10
11 131 reconstructing Pliocene hominin use of day-night periods. Similarly, it is
12
13 132 unlikely we will ever be able to directly test hypotheses concerning vocal
14
15 133 communication in hominins, but by investigating the phylogenetic spread and
16
17 134 proximate and ultimate functions of temporal (acoustic) behavior in
18
19 135 chimpanzees and other primates, we can inform hypotheses on hominin
20
21 136 adaptation, especially in those early species (e.g. *Australopithecus afarensis*)
22
23 137 that shared vocal anatomy similar to extant apes (Alemseged et al., 2006;
24
25 138 Boer, 2012).

26
27
28 139 One primary challenge to obtaining night-time data is following animals
29
30 140 at night. Remote monitoring technology has recently changed that, with
31
32 141 camera traps (Krief et al., 2014) and acoustic monitors (Kalan et al., 2015,
33
34 142 2016) now known to constitute reliable and effective means of identifying e.g.
35
36 143 caller presence and behavior when individuals are not followed (Spillmann et
37
38 144 al., 2015; Kalan et al., 2016). In the current study, I tested whether
39
40 145 chimpanzees were acoustically active across a 24h cycle. Broadly, I assumed
41
42 146 that chimpanzees were less active at night and so hypothesized that call-rates
43
44 147 would be lower than day-time rates. I then examined whether call production
45
46 148 was associated with optimum periods of sound transmission. Specifically, I
47
48 149 predicted that more calls would be produced during periods of low
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50 150 temperature, humidity, and wind. I then examined seasonal variation in day
51
52 151 and night call patterns, especially to test whether day rates predicted night
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3 152 rates. Discrepancies may suggest differences in grouping patterns. Finally, to
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5 153 investigate whether calls were likely serving intra- or inter-party functions, I
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7 154 tested whether counter-calls (those made within 60-seconds of a previous
8
9 155 call) were made from the same valley during day-time and night-time bouts.
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11 156 Similarly, I examined whether calls per night were associated with party size,
12
13 157 measured as the number of fresh nests in a cluster (within 100m of each
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15 158 other).
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20 160 **MATERIALS AND METHODS**

21 161 **Study site**

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23
24 162 I collected data between March 2009-Feb 2010 in the Issa valley, in
25
26 163 western Tanzania (Figure 1), one of the driest, most open habitats in which
27
28 164 chimpanzees live. The Issa valley, about 100km east of Lake Tanganyika,
29
30 165 consists of broad valleys separated by steep mountains and flat plateaus
31
32 166 ranging from 900-1800m above sea level. *Brachystegia* and *Julbernardia*
33
34 167 (*Fabaceae*) miombo woodlands dominate the vegetation, although the region
35
36 168 also has thin strips of evergreen gallery and thicket riverine forests as well as
37
38 169 grasslands and seasonally inundated swamps. There are two distinct
39
40 170 seasons: wet (October - April) and dry (May - September), with the heavy
41
42 171 rains beginning in December and continuing through late May typically.
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44 172 Temperatures ranged greatly over the study period (minimum: 13C;
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46 173 maximum: 32C).
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3 175 [Figure 1 about here]

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6 178 Chimpanzees were first studied in this area from 2001-2003

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8 179 (Hernandez-Aguilar, 2006), and continuously since 2005 (Piel et al., 2015). A

9
10 180 long-term research presence was initiated in 2008 and has been maintained

11
12 181 since then, with current studies of habituated red-tailed monkeys

13
14 182 (*Cercopithecus ascanius*) and yellow baboons (*Papio cynocephalus*), in

15
16 183 addition to chimpanzees.

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18
19 184

20
21 185 **Passive Acoustic Monitoring – Solar-Powered Acoustic Transmission**

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23 186 **Units (SPATUs)**

24
25 187 I deployed nine solar powered acoustic transmission units (SPATU),

26
27 188 arranged in modules to maximize coverage over ~ 12km² of the study area.

28
29 189 Devices consisted of an RF transmitter (model T301, Hamtronics, Inc.,

30
31 190 Rochester, NY, USA), interfaced with omnidirectional microphone, amplifier,

32
33 191 and housed in a Pelican case (model: 1600, Peli Products, Derbyshire, UK).

34
35 192 Each radio was powered by 10 2.4V High Temperature Rechargeable Nickel

36
37 193 Metal Hydride Cylindrical Cell batteries (model: GP400LAHT, Farnell

38
39 194 Distributors, UK), recharged by a solar panel (model: 10W Yingli solar

40
41 195 polycrystalline panel; SelectSolar, Ltd, Essex, UK), via a 10A DZ energy

42
43 196 charge controller (code: 07001DZ02, SelectSolar, Ltd, Essex, UK).

44
45 197 Transmitters were single channel VHF units (range 144-150MHz) that

46
47 198 provide 2-3W continuous duty output into a 50ohm antenna system. Channel

48
49 199 frequency was controlled by a synthesizer with DIP switch channel settings,

50
51 200 but were pre-ordered at specified frequencies and not altered. A TCXO

52
53 201 (temperature controlled xtal oscillator) provided a temperature stability of

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2
3 202 ±2ppm over a temperature range of -30°C to +60°C and the transmitters were
4
5 203 designed for narrow band FM with ±5 kHz deviation. Each transmitter was
6
7 204 then wired to its own 150-170MHz yagi, directional antenna (model: YA3VHF,
8
9 205 RW Badland Ltd, London, UK). Antennas were secured 2-3m from their
10
11 206 corresponding SPATU and pointed in the direction of the receiver antenna.
12
13 207 Vegetation was trimmed as needed to increase panel exposure to the sun.

14
15 208 All incoming signals first reached an omnidirectional receiver antenna,
16
17 209 secured 22m atop a *Brachystegia microfila* tree at camp. This antenna was
18
19 210 wired directly into a Peli case (model: 1610), from which the signals were
20
21 211 boosted through a 50ohm, medium high power wideband (2-500MHz)
22
23 212 amplifier. This amplifier was used to compensate for gain loss from splitting
24
25 213 incoming signals via a 24 way-0°, 50ohm, 1-200MHz power splitter (model:
26
27 214 ZFSC-24-11, MiniCircuits, New York, USA) into their respective channels.
28
29 215 Receivers were set in aluminium racks and powered through a 12V battery
30
31 216 and wired directly into one of three 8-channel MOTUs Ultralite Mk3 (Mark of
32
33 217 the Unicorn, Cambridge, MA, USA). MOTUs converted streaming RF signals
34
35 218 into audio and digital format, from where they were transmitted to a Panasonic
36
37 219 Toughbook CF-30 laptop via a PCMCIA card and read using Raven v.1.3
38
39 220 (Bioacoustics Research Program, Cornell University, Ithaca, NY, USA)
40
41 221 software.

42
43 222 SPATUs recorded continuously from April 2009 – February 2010, with
44
45 223 periodic breaks for maintenance.

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48
49 225 **Weather data**

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3 226 Weather data came from a HOBO (Onset Corp., Bourne, MA, USA) weather
4
5 227 station deployed in miombo woodland, halfway down a mountain <500m from
6
7 228 the research station. The HOBO recorded temperature, humidity, and wind
8
9 229 gust measurements at 30-minute intervals and data are averaged for each
10
11 230 hour (Figure 2). Rain data were also from a HOBO weather station, deployed
12
13 231 near the research station.

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15 232
16 233 [Figure 2 about here]
17 234

20 235 **Chimpanzee Nests**

21
22 236 Data on chimpanzee nests came from counts of age1 nests (Tutin and
23
24 237 Fernandez, 1984), defined as only those nests with fresh feces or urine in or
25
26 238 underneath them. In total, I collected data on 110 nest groups over the study
27
28 239 period. Of these, the majority were the result of opportunistic encounters
29
30 240 (recce walks) or from walking line transects.

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32
33 241

35 242 **Analyses**

36
37 243 Because callers were often hundreds of meters from recording units,
38
39 244 higher frequencies were not always recorded and I was not always able to
40
41 245 reliably discriminate different types of loud calls, i.e. screams from pant hoots.
42
43 246 These call types were thus consolidated into a single 'loud' category. I did not
44
45 247 consider whimpers or grunts. I manually located chimpanzee loud calls
46
47 248 (Figure 3) by scrolling through time series of sounds with the assistance of
48
49 249 Triton, a software package developed for analysis of large datasets (Wiggins
50
51 250 et al., 2010). Triton creates long-term spectrograms from a large group of
52
53 251 small (1GB) sequential data files. By (manually) scrolling through these long-
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3 252 term spectral averages, I was able to efficiently sieve the chimpanzee
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5 253 vocalizations, extracting them into a custom spreadsheet that allowed me to
6
7 254 include meta-data such as start and end time of vocalization, valley of origin,
8
9 255 etc. Sounds were considered separate if they were more than one second
10
11 256 apart and all calls less than three seconds were checked manually to ensure
12
13 257 the same vocalization was not documented on two different channels.
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17 259 [Figure 3 about here]
18 260

19
20 261 There are numerous ways to define the photoperiod between sunrise
21
22 262 and sunset, and definitions have historically varied with whether a study
23
24 263 species is inherently diurnal or nocturnal (Erkert, 2003). For this study, I used
25
26 264 a published figure¹ for the beginning of astronomical twilight in the morning
27
28 265 and evening of each day. I then categorised as 'Twilight' those calls made in
29
30 266 the one hour window 30 minutes before and 30-minutes after this time. 'Day'
31
32 267 calls were those made after the morning twilight window and before the
33
34 268 beginning of the evening twilight window. 'Night' calls were those made after
35
36 269 the evening twilight ended and before the morning window began.
37
38

39 270 I conducted statistical analyses using R Studio, version 1.0.143 (R
40
41 271 Development Core Team, 2015), and set significance to $p < 0.05$. For
42
43 272 temporal patterns, I first tested for multicollinearity in environmental variables
44
45 273 by using the Variance Inflation Factor (VIF) package. I then built a generalized
46
47 274 linear model (GLM) using the MASS package and a negative binomial
48
49 275 distribution to correct for overdispersion. I used call events - defined as the
50
51 276 number of loud calls per hour across all SPATUs - for a response variable and
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56 ¹ <https://www.timeanddate.com/>
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3 277 season, and hourly values of temperature, relative humidity, and wind gust
4
5 278 speed as fixed effects.

6
7 279 Pearson Chi Square tests addressed seasonal differences between
8
9 280 call rates during the three categories of time periods: diurnal, twilight,
10
11 281 nocturnal as well as whether night-time calls served intra- versus inter-party
12
13 282 communication purposes by comparing whether counter-calling behavior
14
15 283 (subsequent calls made within 60 seconds of a previous call) was similar
16
17 284 across the three time periods.

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20 285 Finally, Spearman's Rank tests assessed the relationship between
21
22 286 monthly mean call rate (calculated from the total calls/total days recording for
23
24 287 each month to control for sample bias) and monthly mean nest group sizes.

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26 288

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28
29 289 **Ethics Statement:**

30
31 290 This work was approved by the University of California, San Diego, Tanzania
32
33 291 Wildlife Research Institute (TAWIRI), and adhered to ethical considerations
34
35 292 described by the American Society of Primatologists.

36
37 293

38
39 294 **RESULTS**

40
41 295 SPATUs recorded 1573 loud vocalizations over 250 days of recording
42
43 296 (154 days in the dry; 96 days in the wet season). On 108 of these days at
44
45 297 least one chimpanzee loud vocalization was recorded, of which 43 included at
46
47 298 least one nocturnal vocalization and 28 included a call made during twilight
48
49 299 hours. A total of 1181 calls were recorded during diurnal hours and 392 during
50
51 300 twilight/night. SPATUs recorded at least one call each hour of the night over
52
53 301 the 250 days (Figure 4). Chimpanzees produced twilight and night-time calls
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3 302 in each month except for July (which had minimal days of coverage – Figure
4
5 303 5).

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7 304

8
9 305 [Figures 4 and 5 about here]

10 306

11 307

12
13 308 **Seasonal calling and environmental conditions**

14
15 309 There was a significant difference in the temporal distribution of calls between

16
17 310 dry and wet seasons, $\chi(2) = 20.34$, $p < 0.01$, which was driven by twilight calls,

18
19 311 produced more often in the dry, compared to wet season, $\chi(1) = 14.85$, $p <$

20
21 312 0.001. I found no collinearity between weather (VIF = <2 for all variables).

22
23 313 Chimpanzees produced more calls during warmer temperatures and lower

24
25 314 humidity, but there was no relationship between calling and wind gust or

26
27 315 rainfall (Table 2).

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30
31 317 [Table 2 here].

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34
35 319 Both monthly mean vocalization rates and nest group size peaked in

36
37 320 the late dry season (Aug-October) and I found a significant association

38
39 321 between them ($r_s(11) = 0.878$, $p < 0.001$; Figure 6). However, when I looked

40
41 322 more closely, this association only holds for calls made during the night

42
43 323 ($r_s(11) = 0.65$, $p = 0.03$), not for those made during the day ($r_s(11) = 0.24$,

44
45 324 $p = 0.38$) or during twilight ($r_s(11) = 0.31$, $p = 0.35$). The monthly number of calls

46
47 325 during the day did not predict the number of calls in either twilight ($r_s = 0.53$,

48
49 326 $p = 0.11$) or night-time ($r_s = 0.52$, $p = 0.11$), suggesting a different function,

50
51 327 potentially related to spacing behaviour. To test this, I then investigated

1
2
3 328 whether there was a similar difference between time of day and from where
4
5 329 counter calls were recorded. Counter-calls made from the same valley
6
7 330 (compared to a different valley) were significantly different across time
8
9 331 periods, $\chi(2) = 11.03$, $p < 0.01$, with twilight calls differing from both diurnal,
10
11 332 $\chi(1) = 9.41$, $p < 0.01$ and night-time calls, $\chi(1) = 5.23$, $p < 0.05$. Daytime and
12
13 333 night-time counter calls, however, did not differ from each other with respect
14
15
16 334 to the valley, $\chi(1) = .249$, $p = 0.61$.

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20 336 [Figure 6 about here]

21 337

22 338

23 339 **DISCUSSION**

24
25
26 340 In the current study, I used passive acoustic monitoring (PAM) to
27
28 341 assess vocal activity of wild, unhabituated chimpanzees in Tanzania across a
29
30 342 24h cycle. Whilst chimpanzees called at all hours of the day, including during
31
32 343 twilight and nocturnal periods, the majority of loud calls were produced during
33
34 344 the day with only an average of two calls/day outside of these hours. Call
35
36 345 rates were much lower during nights compared to days, revealing a diurnal
37
38 346 pattern of calling with crepuscular peaks (pre-dawn and after dusk). This
39
40 347 difference in rate suggests a different purpose for night-time calling. In one of
41
42 348 the few other studies systematically examining day vs. night calling in a social,
43
44 349 diurnal primate - howler monkeys (*Alouatta seniculus*) – individuals produced
45
46 350 more long calls at night and more short calls during the day, with vocal activity
47
48 351 throughout the 24h day (Vercauteren Drubbel and Gautier, 1993). The
49
50 352 authors speculated that the night-time preference for long calls suggested that
51
52 353 they function in inter-troop communication. I suggest a similar function for Issa
53
54 354 chimpanzee night-time calls (see below).

1
2
3 355 Calls at Issa did exhibit peaks in early morning and early evening
4
5 356 hours, as has been reported elsewhere for chimpanzees (Figure 7) and many
6
7 357 other primates such as howler (Sekulic, 1982) and colobus (Schel and
8
9 358 Zuberbühler, 2012) monkeys among other primates (Table 1). The traditional
10
11 359 explanation for such dawn/dusk chorusing is that animals call at these times
12
13 360 to exploit cool and quiet conditions for consistent sound quality transmission
14
15 361 (Brown and Handford, 2000; but see Hutchinson, 2002). Animals may also be
16
17 362 avoiding hetero-specifics, calling before overall environmental noise increases
18
19 363 as day breaks. Subsequent data revealing higher resolution of the Issa
20
21 364 soundscape will better contextualize chimpanzees in a broader acoustic
22
23 365 environment (Schneider et al., 2008), and especially whether chimpanzees,
24
25 366 like some birds, respond at night to changes in day-time noise levels (Fuller et
26
27 367 al., 2007).

30
31 368 In addition to morning and afternoon calling peaks, Issa chimpanzees
32
33 369 also exhibited a predawn peak around 0400, previously reported for gibbons
34
35 370 as well (Tenaza, 1976). In *Hylobates klossii*, predawn duets are thought to
36
37 371 advertise the occupation of high valued sleeping trees to competitors
38
39 372 (Tenaza, 1976). Pre-dawn calls in gibbons may also signal lengthy travelling
40
41 373 to come; Whitten (1982) reported a positive relationship between predawn
42
43 374 singing and the distance travelled to the first feeding tree, suggesting that
44
45 375 there is important information encoded in predawn calls related to food source
46
47 376 location. Testing of these ideas is not possible at Issa until full habituation is
48
49 377 achieved, but a preliminary check revealed that Issa chimpanzees produced
50
51 378 more predawn calls during the dry season, when they feed on more widely
52
53 379 dispersed foods (e.g. *Parinari*, *Strychnos* - Piel et al., 2017) compared to the
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3 380 wet season.
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6 382 [Figure 7 about here]
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9 384 In partial support of my hypothesis, chimpanzees called during warmer
10
11 385 temperatures and lower humidity, as would be expected if they called during
12
13 386 periods of optimal transmission. There was no relationship between calling
14
15 387 and rain or wind. I expected lower call rates during rain, but as much because
16
17 388 of limitations to recording as behavior. In one of the few studies on animal
18
19 389 sound transmission during rainfall, tawny owl (*Strix aluco*) sounds reached
20
21 390 only 1.7ha during rainfall, compared to 118ha during non-rain periods (a 69-
22
23 391 fold disadvantage) (Lengagne and Slater, 2002). Only data collected from
24
25 392 focal follows of chimpanzees during dry and wet seasons would reveal
26
27 393 chimpanzee calling patterns during wetter periods.
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31 394 Even with partial support for the AAH, it is likely that social, as well as
32
33 395 environmental factors influence chimpanzee calling. Chimpanzee vocal
34
35 396 behavior is influenced by party-composition and party-size, with individuals
36
37 397 often chorusing when in large parties (Mitani and Brandt, 1994; Mitani and
38
39 398 Gros-Louis, 1998; Fedurek et al., 2013). I found support for this with Issa
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41 399 chimpanzee grouping behavior positively associated with twilight call rates.
42
43 400 Day and night rates did not correspond to party, suggesting twilight calls are
44
45 401 the more useful proxy for group size.
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48 402 Without data on caller identity, I could not directly distinguish intra- from
49
50 403 inter-individual calling interactions; nonetheless, results from looking at the
51
52 404 location of counter-calls were informative. There was no difference between
53
54 405 the origins of counter-calls in day versus night periods, and so I found no
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3 406 support for nocturnal calls functioning differently than diurnal calls.
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5 407 Subsequent work using acoustic tomography will reveal caller location
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7 408 (Spillman et al. 2015) and provide higher resolution on call function, especially
8
9 409 in travel and reunions. Further, investigation into whether call types vary
10
11 410 between day-time and night-time calls would be informative, especially if
12
13 411 individuals are embedding other important information in their signals such as
14
15 412 identity (Levréro and Mathevon, 2013).

16
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18 413 Another social explanation for differences between day-time night-time
19
20 414 calling is if chimpanzees form small day-time parties and reunite in larger,
21
22 415 evening parties (Ogawa et al., 2007). This pattern may be reflected in
23
24 416 vocalization behavior, with individuals increasing vocal activity at dusk during
25
26 417 reunions and as sleeping clusters form (Hammerschmidt et al., 1994).
27
28 418 Hohmann and Fruth (1994) suggested that evening call peaks in bonobos (*P.*
29
30 419 *paniscus*) represented an attempt to gather individuals and “regulate and
31
32 420 maintain the social network”, which chimpanzees could be doing as well. In
33
34 421 this scenario, I may expect dawn and dusk calls to serve an intra-party
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36 422 function, whereas calls made during the night serve an inter-party function.
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41
42 424 **Nocturnal (acoustic) activity and implications for hominin activity**
43
44 425 **patterns**

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46 426 The primary advantage to flexibility in activity patterns (e.g.
47
48 427 cathemerality) is the allowance for an animal to exploit (or avoid) situations
49
50 428 that arise in either day or night-time only. This is most readily seen in
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52 429 chimpanzees in Senegal, where Fongoli chimpanzees exhibit night-time
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54 430 activity to escape soaring day-time temperatures (Pruetz, 2018), and in
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3 431 Uganda, where Kibale chimpanzees raid crops during the night to avoid fatal
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5 432 encounters with farmers during the day (Krief et al., 2014).
6

7 433 True cathemerality is most widespread in small mammals (Halle, 2006)
8
9 434 and in a few primate species, where it has been described in lemurs
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11 435 (Colquhoun, 1998; Curtis et al., 1999) and is likely part of the ancestral
12
13 436 condition of the earliest primates (Donati and Borgognini-Tarli, 2006; Santini
14
15 437 et al., 2015). Whilst the behaviour observed in both Issa and Fongoli
16
17 438 chimpanzees extends past daytime hours into especially twilight and during
18
19 439 some periods, nighttime, these are not cathemeral animals, but instead exhibit
20
21 440 primary activity during the day, with peaks of crepuscular calling during
22
23 441 morning and evening twilight periods. These correspond to waking and nest-
24
25 442 building periods, respectively, and thus calls may be used to orient listeners
26
27 443 with caller location. In the current study, I have presented evidence of
28
29 444 acoustic activity only; it is uncertain what other activity Issa chimpanzee
30
31 445 exhibit at night. Only by following individuals at night, either actively (Zamma,
32
33 446 2014; Pruetz, 2018) or remotely (Krief et al., 2014; Tagg et al., this issue) will
34
35 447 we learn whether Issa chimpanzee night-time acoustic activity corresponds to
36
37 448 other activities as well, e.g. foraging, traveling, etc. and moreover, reveal the
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39 449 regularity and type of such cryptic behavior.
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44 450 If subsequent data on other apes show similar patterns, we could be
45
46 451 looking at a phylogenetic signature in nocturnal behavior for a diurnal species.
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48 452 Issa and Fongoli are both characterised as mosaic landscapes with extreme
49
50 453 seasonality, and hot, dry, and open conditions with relatively poor floral
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52 454 diversity compared to tropical forests. Hominins likely confronted similar
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54 455 conditions during the Plio-Pleistocene transition to open environments. As a
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3 456 result, our challenge is to show how nocturnal behavior is an adaptive
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5 457 response, rather than an aberrant behavior. Whilst we may not be able to
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7 458 directly test these hypotheses in hominins, confirming the functional
8
9 459 significance of nocturnal activity in chimpanzees and other primates informs
10
11 460 whether similar conditions would have promoted the behavior in hominins.
12

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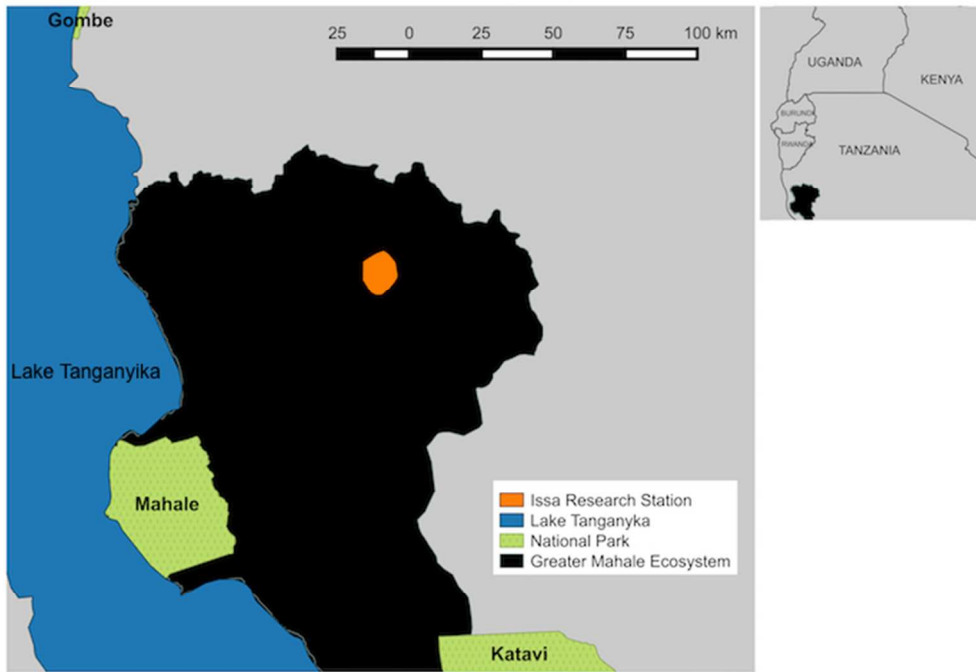
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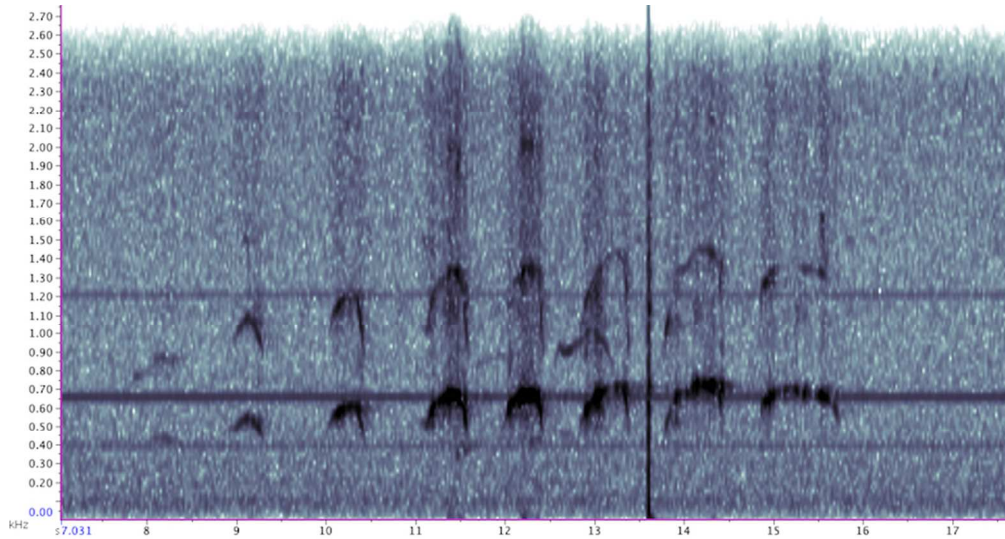
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Map of western Tanzania, including the study area (Issa Valley, center) and the surrounding National Parks, two of which - Gombe and Mahale Mountains - host chimpanzees

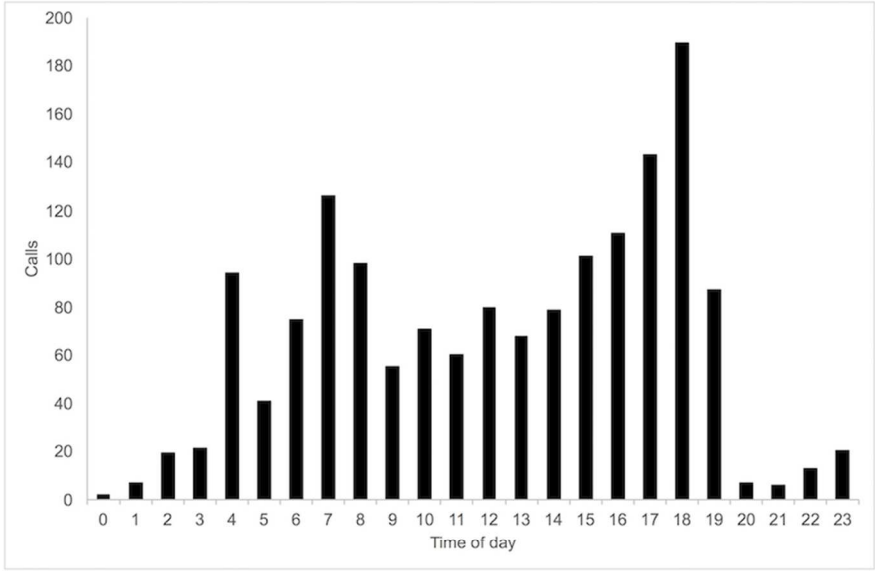
59x41mm (300 x 300 DPI)



A loud call recorded on a Solar Powered Acoustic Transmission Unit (SPATU) from the Issa Valley

23317x12446mm (1 x 1 DPI)

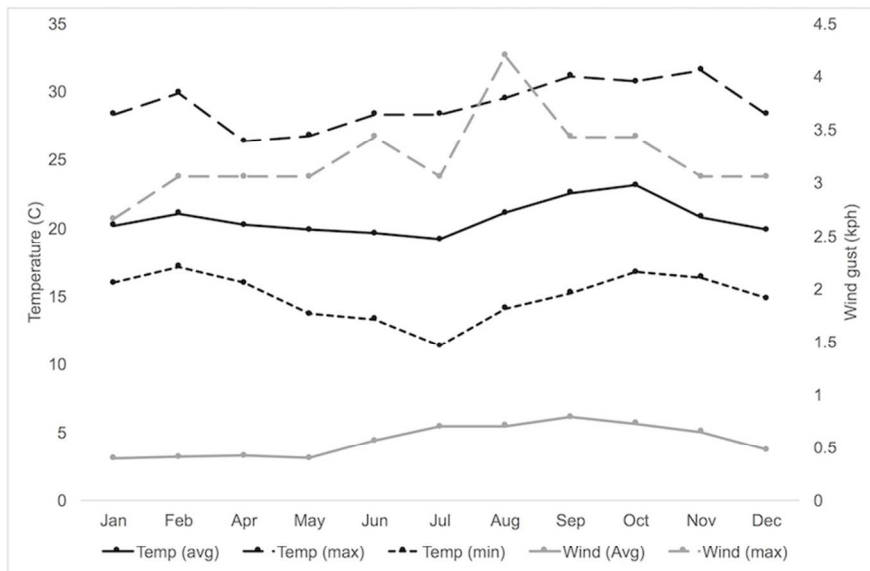
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Hourly distribution of vocalizations recorded across the study period

83x58mm (300 x 300 DPI)

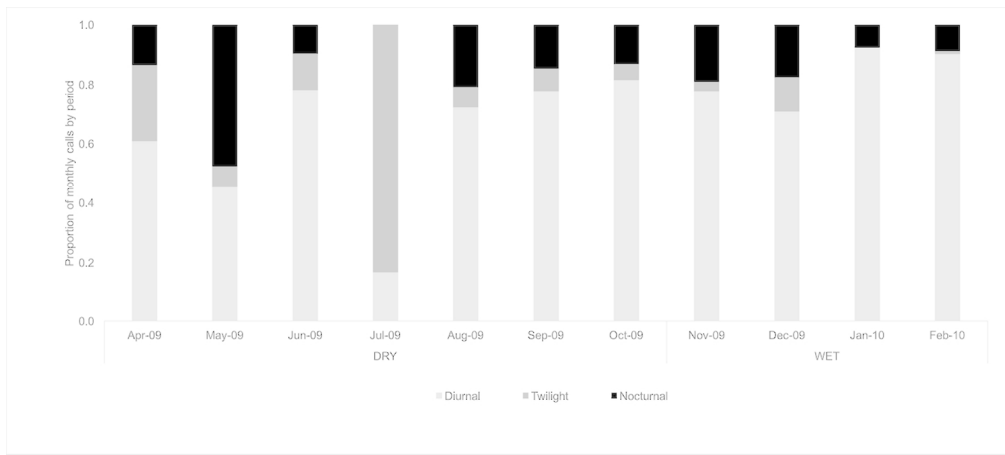
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Mean and maximum monthly temperature over the study period

83x58mm (300 x 300 DPI)

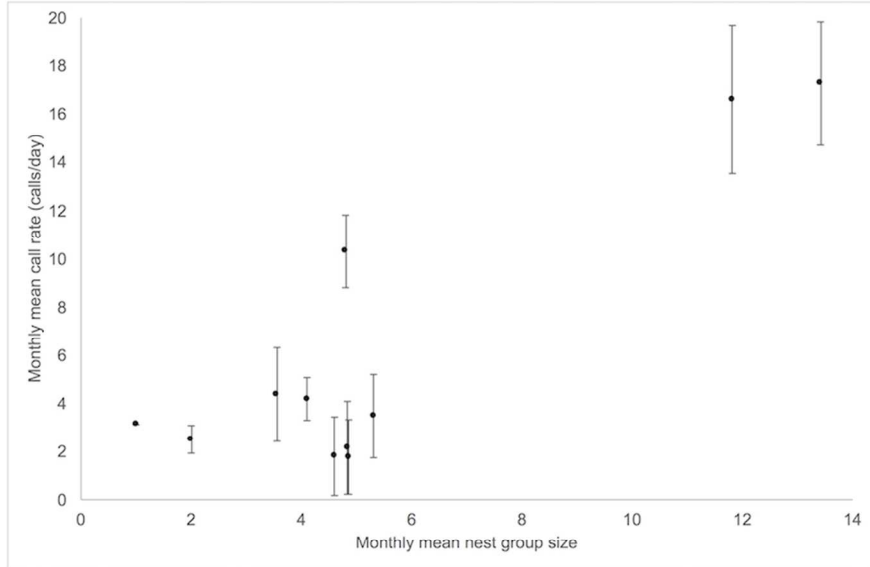
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Monthly call proportions during day, twilight, and night-time periods

245x109mm (150 x 150 DPI)

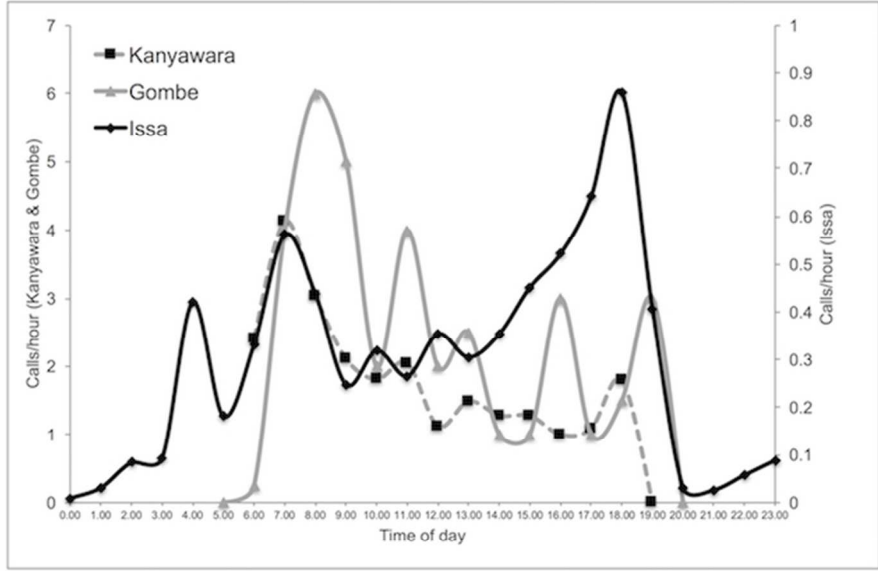
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Mean monthly call rate and chimpanzee nest group size. Error bars represent minimum and maximum nest groups for each month

83x58mm (300 x 300 DPI)

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Temporal calling patterns of three chimpanzee communities. Kanyawara data provided by M. Wilson; Gombe data from Wrangham (1975)

60x43mm (300 x 300 DPI)

Table 1 –Temporal calling peaks for various primate species

Common	Species	Call peak(s)	Reference
	<i>Cacajao melanocephalus</i>		(Bezerra, Souto, & Jones, 2010)
Common marmoset	<i>Callithrix jacchus</i>	0500-100	(Martins et al., 2009)
	<i>Callicebus torquatus</i>	615-630	(Kinzey & Robinson, 1983)
Black Howler	<i>Alouatta araya</i>	Sunrise	(Byrne & da Cunha, 2006)
Black Howler	<i>Alouatta pigra</i>	Morning	(Cornick & Markowitz, 2002)
Red Howler	<i>Alouatta seniculis</i>	730; 1330	(Sekulic, 1982)
Barbary macaque	<i>Macaca sylvanus</i>	2100	(Hammerschmidt, Ansorge, Fischer, & Todt, 1994)
Mentawai langur	<i>Presbytis potenziani</i>	700	
Purple faced langurs	<i>Trachypithecus vetulus nestor</i>	~545 ¹	(Schneider, Hodges, Fischer, & Hammerschmidt, 2008)
Mentawai leaf	<i>Simias concolor</i>	700	
Black and White Colobus	<i>Colobus guereza</i>	2h before dawn	(Marler, 1969; Schel & Zuberbühler, 2012)
Kloss gibbon	<i>Hylobates klossii</i>	400 (males); 800 (females)	(Tenaza, 1976)
Kloss gibbon	<i>Hylobates klossii</i>	800	(Schneider et al., 2008; Whitten, 1982)
Lar gibbon	<i>Hylobates lar</i>	500 (males); 700 (females)	(Raemaekers, Raemakers, & Haimoff, 1984)
Silvery gibbon	<i>Hylobates molloch</i>	0500 ²	(Geissmann & Nijman, 2006)
Orangutan	<i>Pongo pygmaeus</i>	0500; 0800; 1500	(Galdikas, 1983; Mitani, 1985)
Bonobo	<i>Pan paniscus</i>	1700	(Hohmann & Fruth, 1994)
Chimpanzee	<i>Pan troglodytes</i>	700	(Wilson, Hauser, & Wrangham, 2007)

¹ Earlier calls reported only² 500 peaks for males from Limng Asir, whilst data for females are from Ujung Kulon

Table 2 – Results of a General linear model with chimpanzee call rate as a response variable and temperature, relative humidity, and wind gust as fixed effects. Bolded values are significant (<0.05).

	Estimate	Standard error	t-value	p-value
Temperature	0.098	0.028	3.42	0.000
Relative humidity	-0.020	0.005	-3.72	0.000
Wind gust	0.056	0.081	0.69	0.489
Rainfall	-0.119	0.130	0.92	0.358
Seasonality	0.220	0.185	1.19	0.233