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Piel, AK (2018) Temporal patterns of chimpanzee loud calls in the Issa Valley, Tanzania: Evidence of nocturnal acoustic behavior in wild chimpanzees. Amercian Journal of Physical Anthropology, 166 (3). pp. 530-540. ISSN 0002-9483

ARTICLE TITLE: Temporal patterns of chimpanzee loud calls in the Issa Valley, Tanzania: Evidence of nocturnal acoustic behavior in wild chimpanzees.

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PAGES: 29

ABBREVIATED TITLE: Nocturnal acoustic activity in chimpanzees

KEY WORDS: Pant hoot; passive acoustic monitoring; great ape; vocalization;

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GRANT SPONSORSHIP: National Science Foundation, Wenner-Gren Foundation, Royal Anthropological Institute Ruggles Gates Fund, University of

California, San Diego; Salk/UCSD Center for Academic Research and Training in Anthropogeny (CARTA)

INTRODUCTION

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

The timing of vocalization behavior is often a response to the caller's physical environment. Vegetation and topography (Marten et al., 1977; Brown et al., 1995; Mennill et al., 2006) as well as temperature, wind, humidity, and ambient noise all change throughout the day and influence sound transmission and thus when animals call. Specifically, temperature and wind interact in important ways, affecting propagation differently across atmospheric conditions (Heimann and Gross, 1999). Temperature inversions can trap sound energy, promoting more efficient transmission across long distances (Brown and Hall, 1978; Wilson et al., 2003), whereas wind may attenuate sound, distorting or degrading calls that may otherwise transmit well under calmer conditions (Hayes and Huntly, 2005). Further, intra- and inter-specific acoustic competitors may deter vocalization behavior, with individuals seeking to avoid their signals being spectrally or temporally masked by other calls (Henry and Wells, 2010; Schmidt et al., 2012; Sinsch et al., 2012; Villanueva-Rivera, 2014). That animas have evolved call types and call behavior to optimise sound transmission has been termed the Acoustic Adaptation Hypothesis (AAH) (Daniel and Blumstein, 1998). Whilst early work did demonstrate support for the AAH in primates (Waser and Brown, 1986; Brown et al., 1995), a more recent compilation of data across birds, anurans and mammals found only minimal support (Ey and Fischer, 2009).

Despite inconsistent conformity to AAH predictions across the Order Primates, along with many bird species (Staicer et al., 1996), many primates also exhibit vocalization peaks at dawn and dusk (Table 1), with callers exploiting low abiotic noise levels and ideal microclimates for long distance sound transmission (Henwood and Fabrick, 1979). Most studies on primate calling, however - and primate behavior more broadly - are limited to when researchers are also active, during the day. Far less is known about primate night-time activity (see Tagg et al., this issue), especially calling behavior of diurnal primates.

There are good reasons to expect nocturnal behavior in diurnal primates. First, nocturnally is likely the ancestral activity pattern for primates, with subsequent shifts to diurnality and cathemerality attributed to speciation events (Santini et al., 2015). Thus, there could be residual, nocturnal behavior even in diurnal animals. Evidence for nocturnal activity can be seen in differences between where study subjects are left late in one day, and where they are found waking the subsequent morning (pers. observation), suggesting night-time movement. In apes, this behavior has been explained as a response to the social and environmental context. Socially, rank predicts mating opportunities in chimpanzees (Wroblewski et al., 2009), so low ranking males may sneak copulations at night, hiding from protective alpha males that would otherwise prevent the behavior. Finally, by definition, fission-fusion animals are dispersed at various times during the day and night, and thus calls may serve coordination and cohesive mechanisms (Leighty et al., 2008), advertising a caller's location and facilitating reunions (e.g. fusion events) later the next day. Environmentally, primates that live in hot climates may forage at night to avoid high day-time temperatures (Pruetz, 2018). By being active during periods of the night, animals can increase their foraging time and ultimately, increase their caloric intake. Foraging at night may reduce feeding competition for high quality foods from hetero-specifics as well (Donati et al., 2009).

There are costs to being active at night, however. Predation pressure is generally higher at night compared to the day (Isbell, 1994) and many species use highly conspicuous loud calls, which can reveal their location to potential predators (Bergstrom and Lachmann, 2001). Given that diurnal animals exhibit night-time activity, the advantages of this behaviour may outweigh any risks.

[Table 1 here]

In great apes, despite decades of research describing vocalization patterns (*Pongo*: MacKinnon, 1974; *Pan*: Marler and Hobbett, 1975), most research has centered on acoustic analysis of call elements (Arcadi, 1996; Riede et al., 2004; Lameira et al., 2012), context specific calls (Mitani and

Nishida, 1993; Crockford and Boesch, 2005; Salmi et al., 2013), and how communication informs the evolution of human language (Slocombe and Zuberbühler, 2005; Slocombe and Zuberbuhler, 2007; Crockford et al., 2012; Schel et al., 2013; Lameira et al., 2015, 2016). Save for extensive research into gibbon call patterns (Tenaza, 1976; Geissmann and Nijman, 2006), little work has focused on the temporal or environmental influences on ape loud calls, especially at night when researchers are absent. Wild orang-utans exhibit dramatic variation in nocturnal call rates between populations (Hoepfner and Spillman, unpublished data), and it has been suggested that population density, inter-male contests, or else female reproductive status may drive increased call rates (Ross and Geissmann, 2009). Wild chimpanzees (*P. troglodytes*) have been described to be awoken by conspecifics making sounds at night (Zamma, 2014) and also to exhibit various activity types (including calling) throughout the night (Pruetz, 2018; Tagg et al., in press). Aside from these few studies, little is known about nocturnal calling in chimpanzees.

Night-time calling may potentially have been an important hominin behavior in adapting to a hotter, more open, but also sound-friendly savanna-mosaic environment (Waser and Brown, 1986). Diurnal hominins could have been driven to night activity by selective pressure to avoid high temperatures during the day, or to avoid diurnal predators. However, Halle (2006) has suggested that adaptation to one phase of the 24h cycle implies maladaptation to the other, and thus vulnerability, especially to predation. Thus, hominins may have exhibited polyphasic activity (Halle, 2006) patterns in response to very specific ecological conditions, without any specialized anatomical adaptations (Gerkema et al., 2013).

Like many other hominin behaviors, activity patterns do not fossilise, and thus studying extant great apes may be as close as we get to reconstructing Pliocene hominin use of day-night periods. Similarly, it is unlikely we will ever be able to directly test hypotheses concerning vocal communication in hominins, but by investigating the phylogenetic spread and proximate and ultimate functions of temporal (acoustic) behavior in chimpanzees and other primates, we can inform hypotheses on hominin adaptation, especially in those early species (e.g. *Australopithecus afarensis*) that shared vocal anatomy similar to extant apes (Alemseged et al., 2006; Boer, 2012).

One primary challenge to obtaining night-time data is following animals at night. Remote monitoring technology has recently changed that, with camera traps (Krief et al., 2014) and acoustic monitors (Kalan et al., 2015, 2016) now known to constitute reliable and effective means of identifying e.g. caller presence and behavior when individuals are not followed (Spillmann et al., 2015; Kalan et al., 2016). In the current study, I tested whether chimpanzees were acoustically active across a 24h cycle. Broadly, I assumed that chimpanzees were less active at night and so hypothesized that call-rates would be lower than day-time rates. I then examined whether call production was associated with optimum periods of sound transmission. Specifically, I predicted that more calls would be produced during periods of low temperature, humidity, and wind. I then examined seasonal variation in day and night call patterns, especially to test whether day rates predicted night rates. Discrepancies may suggest differences in grouping patterns. Finally, to investigate whether calls were likely serving intra- or inter-party functions, I tested whether counter-calls (those made within 60-seconds of a previous call) were made from the same valley during day-time and night-time bouts. Similarly, I examined whether calls per night were associated with party size, measured as the number of fresh nests in a cluster (within 100m of each other).

MATERIALS AND METHODS

Study site

I collected data between March 2009-Feb 2010 in the Issa valley, in western Tanzania (Figure 1), one of the driest, most open habitats in which chimpanzees live. The Issa valley, about 100km east of Lake Tanganyika, consists of broad valleys separated by steep mountains and flat plateaus ranging from 900-1800m above sea level. *Brachystegia* and *Julbernardia* (Fabaceae) miombo woodlands dominate the vegetation, although the region also has thin strips of evergreen gallery and thicket riverine forests as well as grasslands and seasonally inundated swamps. There are two distinct seasons: wet (October - April) and dry (May - September), with the heavy rains beginning in December and continuing through late May typically. Temperatures ranged greatly over the study period (minimum: 13C; maximum: 32C).

[Figure 1 about here]

Chimpanzees were first studied in this area from 2001-2003 (Hernandez-Aguilar, 2006), and continuously since 2005 (Piel et al., 2015). A long-term research presence was initiated in 2008 and has been maintained since then, with current studies of habituated red-tailed monkeys (*Cercopithecuas ascanius*) and yellow baboons (*Papio cynocephalus*), in addition to chimpanzees.

Passive Acoustic Monitoring – Solar-Powered Acoustic Transmission Units (SPATUs)

I deployed nine solar powered acoustic transmission units (SPATU), arranged in modules to maximize coverage over ~ 12km^2 of the study area. Devices consisted of an RF transmitter (model T301, Hamtronics, Inc., Rochester, NY, USA), interfaced with omnidirectional microphone, amplifier, and housed in a Pelican case (model: 1600, Peli Products, Derbyshire, UK). Each radio was powered by 10 2.4V High Temperature Rechargeable Nickel Metal Hydride Cylindrical Cell batteries (model: GP400LAHT, Farnell Distributors, UK), recharged by a solar panel (model: 10W Yingli solar polycrystalline panel; SelectSolar, Ltd, Essex, UK), via a 10A DZ energy charge controller (code: 07001DZ02, SelectSolar, Ltd, Essex, UK).

Transmitters were single channel VHF units (range 144-150MHz) that provide 2-3W continuous duty output into a 50ohm antenna system. Channel frequency was controlled by a synthesizer with DIP switch channel settings, but were pre-ordered at specified frequencies and not altered. A TCXO (temperature controlled xtal oscillator) provided a temperature stability of

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

All incoming signals first reached an omnidirectional receiver antenna, secured 22m atop a *Brachystegia microfila* tree at camp. This antenna was wired directly into a Peli case (model: 1610), from which the signals were boosted through a 50ohm, medium high power wideband (2-500MHz) amplifier. This amplifier was used to compensate for gain loss from splitting incoming signals via a 24 way-0^o, 50ohm, 1-200MHz power splitter (model: ZFSC-24-11, MiniCircuits, New York, USA) into their respective channels. Receivers were set in aluminium racks and powered through a 12V battery and wired directly into one of three 8-channel MOTUs Ultralite Mk3 (Mark of the Unicorn, Cambridge, MA, USA). MOTUs converted streaming RF signals into audio and digital format, from where they were transmitted to a Panasonic Toughbook CF-30 laptop via a PCMCI card and read using Raven v.1.3 (Bioacoustics Research Program, Cornell University, Ithaca, NY, USA) software.

SPATUs recorded continuously from April 2009 – February 2010, with periodic breaks for maintenance.

Weather data

Weather data came from a HOBO (Onset Corp., Bourne, MA, USA) weather station deployed in miombo woodland, halfway down a mountain <500m from the research station. The HOBO recorded temperature, humidity, and wind gust measurements at 30-minute intervals and data are averaged for each hour (Figure 2). Rain data were also from a HOBO weather station, deployed near the research station.

[Figure 2 about here]

Chimpanzee Nests

Data on chimpanzee nests came from counts of age1 nests (Tutin and Fernandez, 1984), defined as only those nests with fresh feces or urine in or underneath them. In total, I collected data on 110 nest groups over the study period. Of these, the majority were the result of opportunistic encounters (recce walks) or from walking line transects.

Analyses

Because callers were often hundreds of meters from recording units, higher frequencies were not always recorded and I was not always able to reliably discriminate different types of loud calls, i.e. screams from pant hoots. These call types were thus consolidated into a single ‘loud’ category. I did not consider whimpers or grunts. I manually located chimpanzee loud calls (Figure 3) by scrolling through time series of sounds with the assistance of Triton, a software package developed for analysis of large datasets (Wiggins et al., 2010). Triton creates long-term spectrograms from a large group of small (1GB) sequential data files. By (manually) scrolling through these long-term spectral averages, I was able to efficiently sieve the chimpanzee vocalizations, extracting them into a custom spreadsheet that allowed me to include meta-data such as start and end time of vocalization, valley of origin, etc. Sounds were considered separate if they were more than one second apart and all calls less than three seconds were checked manually to ensure the same vocalization was not documented on two different channels.

[Figure 3 about here]

There are numerous ways to define the photoperiod between sunrise and sunset, and definitions have historically varied with whether a study species is inherently diurnal or nocturnal (Erkert, 2003). For this study, I used a published figure[1] for the beginning of astronomical twilight in the morning and evening of each day. I then categorised as ‘Twilight’ those calls made in the one hour window 30 minutes before and 30-minutes after this time. ‘Day’ calls were those made after the morning twilight window and before the beginning of the evening twilight window. ‘Night’ calls were those made after the evening twilight ended and before the morning window began.

I conducted statistical analyses using R Studio, version 1.0.143 (R Development Core Team, 2015), and set significance to $p < 0.05$. For temporal patterns, I first tested for multicollinearity in environmental variables by using the Variance Inflation Factor (VIF) package. I then built a generalized linear model (GLM) using the MASS package and a negative binomial distribution to correct for overdispersion. I used call events - defined as the number of loud calls per hour across all SPATUs - for a response variable and

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[1] https://www.timeanddate.com/

season, and hourly values of temperature, relative humidity, and wind gust speed as fixed effects.

Pearson Chi Square tests addressed seasonal differences between call rates during the three categories of time periods: diurnal, twilight, nocturnal as well as whether night-time calls served intra- versus inter-party communication purposes by comparing whether counter-calling behavior (subsequent calls made within 60 seconds of a previous call) was similar across the three time periods.

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

Ethics Statement:

This work was approved by the University of California, San Diego, Tanzania Wildlife Research Institute (TAWIRI), and adhered to ethical considerations described by the American Society of Primatologists.

RESULTS

SPATUs recorded 1573 loud vocalizations over 250 days of recording (154 days in the dry; 96 days in the wet season). On 108 of these days at least one chimpanzee loud vocalization was recorded, of which 43 included at least one nocturnal vocalization and 28 included a call made during twilight hours. A total of 1181 calls were recorded during diurnal hours and 392 during twilight/night. SPATUs recorded at least one call each hour of the night over the 250 days (Figure 4). Chimpanzees produced twilight and night-time calls in each month except for July (which had minimal days of coverage – Figure 5).

[Figures 4 and 5 about here]

Seasonal calling and environmental conditions

There was a significant difference in the temporal distribution of calls between dry and wet seasons, $\chi(2) = 20.34$, $p<0.01$, which was driven by twilight calls, produced more often in the dry, compared to wet season, $\chi(1) = 14.85$, $p < 0.001$. I found no collinearity between weather (VIF = <2 for all variables). Chimpanzees produced more calls during warmer temperatures and lower humidity, but there was no relationship between calling and wind gust or rainfall (Table 2).

[Table 2 here].

Both monthly mean vocalization rates and nest group size peaked in the late dry season (Aug-October) and I found a significant association between them (*rs(11)*=0.878, p<0.001; Figure 6). However, when I looked more closely, this association only holds for calls made during the night (*rs(11)* = 0.65, p=0.03), not for those made during the day (*rs(11)* = 0.24, p=0.38) or during twilight (*rs(11)* = 0.31, p=0.35). The monthly number of calls during the day did not predict the number of calls in either twilight (r_s = 0.53, p=0.11) or night-time (r_s = 0.52, p=0.11), suggesting a different function, potentially related to spacing behaviour. To test this, I then investigated whether there was a similar difference between time of day and from where counter calls were recorded. Counter-calls made from the same valley (compared to a different valley) were significantly different across time periods, $\chi(2) = 11.03$, $p < 0.01$, with twilight calls differing from both diurnal, $\chi(1) = 9.41$, $p<0.01$ and night-time calls, $\chi(1) = 5.23$, $p<0.05$. Daytime and night-time counter calls, however, did not differ from each other with respect to the valley, $\chi(1) = .249$, $p = 0.61$.

[Figure 6 about here]

DISCUSSION

In the current study, I used passive acoustic monitoring (PAM) to assess vocal activity of wild, unhabituated chimpanzees in Tanzania across a 24h cycle. Whilst chimpanzees called at all hours of the day, including during twilight and nocturnal periods, the majority of loud calls were produced during the day with only an average of two calls/day outside of these hours. Call rates were much lower during nights compared to days, revealing a diurnal pattern of calling with crepuscular peaks (pre-dawn and after dusk). This difference in rate suggests a different purpose for night-time calling. In one of the few other studies systematically examining day vs. night calling in a social, diurnal primate - howler monkeys (*Alouatta seniculus*) – individuals produced more long calls at night and more short calls during the day, with vocal activity throughout the 24h day (Vercauteren Drubbel and Gautier, 1993). The authors speculated that the night-time preference for long calls suggested that they function in inter-troop communication. I suggest a similar function for Issa chimpanzee night-time calls (see below).

Calls at Issa did exhibit peaks in early morning and early evening hours, as has been reported elsewhere for chimpanzees (Figure 7) and many other primates such as howler (Sekulic, 1982) and colobus (Schel and Zuberbühler, 2012) monkeys among other primates (Table 1). The traditional explanation for such dawn/dusk chorusing is that animals call at these times to exploit cool and quiet conditions for consistent sound quality transmission (Brown and Handford, 2000; but see Hutchinson, 2002). Animals may also be avoiding hetero-specifics, calling before overall environmental noise increases as day breaks. Subsequent data revealing higher resolution of the Issa soundscape will better contextualize chimpanzees in a broader acoustic environment (Schneider et al., 2008), and especially whether chimpanzees, like some birds, respond at night to changes in day-time noise levels (Fuller et al., 2007).

In addition to morning and afternoon calling peaks, Issa chimpanzees also exhibited a predawn peak around 0400, previously reported for gibbons as well (Tenaza, 1976). In *Hylobates klossii*, predawn duets are thought to advertise the occupation of high valued sleeping trees to competitors (Tenaza, 1976). Pre-dawn calls in gibbons may also signal lengthy travelling to come; Whitten (1982) reported a positive relationship between predawn singing and the distance travelled to the first feeding tree, suggesting that there is important information encoded in predawn calls related to food source location. Testing of these ideas is not possible at Issa until full habituation is achieved, but a preliminary check revealed that Issa chimpanzees produced more predawn calls during the dry season, when they feed on more widely dispersed foods (e.g. *Parinari*, *Strychnos* - Piel et al., 2017) compared to the wet season.

[Figure 7 about here]

In partial support of my hypothesis, chimpanzees called during warmer temperatures and lower humidity, as would be expected if they called during periods of optimal transmission. There was no relationship between calling and rain or wind. I expected lower call rates during rain, but as much because of limitations to recording as behavior. In one of the few studies on animal sound transmission during rainfall, tawny owl (*Strix aluco*) sounds reached only 1.7ha during rainfall, compared to 118ha during non-rain periods (a 69-fold disadvantage) (Lengagne and Slater, 2002). Only data collected from focal follows of chimpanzees during dry and wet seasons would reveal chimpanzee calling patterns during wetter periods.

Even with partial support for the AAH, it is likely that social, as well as environmental factors influence chimpanzee calling. Chimpanzee vocal behavior is influenced by party-composition and party-size, with individuals often chorusing when in large parties (Mitani and Brandt, 1994; Mitani and Gros-Louis, 1998; Fedurek et al., 2013). I found support for this with Issa chimpanzee grouping behavior positively associated with twilight call rates. Day and night rates did not correspond to party, suggesting twilight calls are the more useful proxy for group size.

Without data on caller identity, I could not directly distinguish intra- from inter-individual calling interactions; nonetheless, results from looking at the location of counter-calls were informative. There was no difference between the origins of counter-calls in day versus night periods, and so I found no support for nocturnal calls functioning differently than diurnal calls. Subsequent work using acoustic tomography will reveal caller location (Spillman et al. 2015) and provide higher resolution on call function, especially in travel and reunions. Further, investigation into whether call types vary between day-time and night-time calls would be informative, especially if individuals are embedding other important information in their signals such as identity (Levréro and Mathevon, 2013).

Another social explanation for differences between day-time night-time calling is if chimpanzees form small day-time parties and reunite in larger, evening parties (Ogawa et al., 2007). This pattern may be reflected in vocalization behavior, with individuals increasing vocal activity at dusk during reunions and as sleeping clusters form (Hammerschmidt et al., 1994). Hohmann and Fruth (1994) suggested that evening call peaks in bonobos (*P. paniscus*) represented an attempt to gather individuals and “regulate and maintain the social network”, which chimpanzees could be doing as well. In this scenario, I may expect dawn and dusk calls to serve an intra-party function, whereas calls made during the night serve an inter-party function.

Nocturnal (acoustic) activity and implications for hominin activity patterns

The primary advantage to flexibility in activity patterns (e.g. cathemerality) is the allowance for an animal to exploit (or avoid) situations that arise in either day or night-time only. This is most readily seen in chimpanzees in Senegal, where Fongoli chimpanzees exhibit night-time activity to escape soaring day-time temperatures (Pruetz, 2018), and in

Uganda, where Kibale chimpanzees raid crops during the night to avoid fatal encounters with farmers during the day (Krief et al., 2014).

True cathemerality is most widespread in small mammals (Halle, 2006) and in a few primate species, where it has been described in lemurs (Colquhoun, 1998; Curtis et al., 1999) and is likely part of the ancestral condition of the earliest primates (Donati and Borgognini-Tarli, 2006; Santini et al., 2015). Whilst the behaviour observed in both Issa and Fongoli chimpanzees extends past daytime hours into especially twilight and during some periods, nighttime, these are not cathemeral animals, but instead exhibit primary activity during the day, with peaks of crepuscular calling during morning and evening twilight periods. These correspond to waking and nest-building periods, respectively, and thus calls may be used to orient listeners with caller location. In the current study, I have presented evidence of acoustic activity only; it is uncertain what other activity Issa chimpanzee exhibit at night. Only by following individuals at night, either actively (Zamma, 2014; Pruetz, 2018) or remotely (Krief et al., 2014; Tagg et al., this issue) will we learn whether Issa chimpanzee night-time acoustic activity corresponds to other activites as well, e.g. foraging, traveling, etc. and moreover, reveal the regularity and type of such cryptic behavior.

If subsequent data on other apes show similar patterns, we could be looking at a phylogenetic signature in nocturnal behavior for a diurnal species. Issa and Fongoli are both characterised as mosaic landscapes with extreme seasonality, and hot, dry, and open conditions with relatively poor floral diversity compared to tropical forests. Hominins likely confronted similar conditions during the Plio-Pleistocene transition to open environments. As a result, our challenge is to show how nocturnal behavior is an adaptive response, rather than an aberrant behavior. Whilst we may not be able to directly test these hypotheses in hominins, confirming the functional significance of nocturnal activity in chimpanzees and other primates informs whether similar conditions would have promoted the behavior in hominins.

ACKNOWLEDGEMENTS

Many thanks to Nikki Tagg and Fiona Stewart for inviting this contribution to the special issue of nocturnal activity in great apes, and to the Tanzanian Wildlife Research Institute (TAWIRI) and Commission for Science and Technology (COSTECH) for permission to carry out research in Tanzania. Kimmy Kissinger helped with extraction of calls and funding was provided by the National Science Foundation, Wenner-Gren Foundation, and the Royal Anthropological Institute - Ruggles Gates Fund. The Salk/UCSD Center for Academic Research and Training in Anthropogeny (CARTA) provides long-term support for the Greater Mahale Ecosystem Research and Conservation (GMERC) Project and none of this would be possible without their support and that of the GMERC field assistants. The manuscript was significantly improved by the very helpful feedback from an anonymous reviewer.

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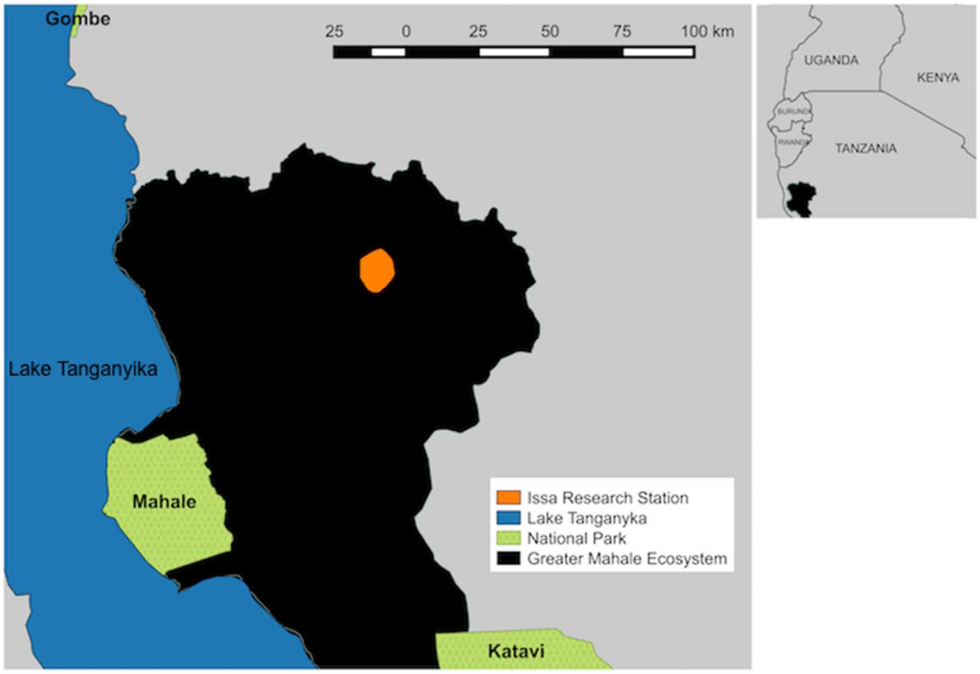
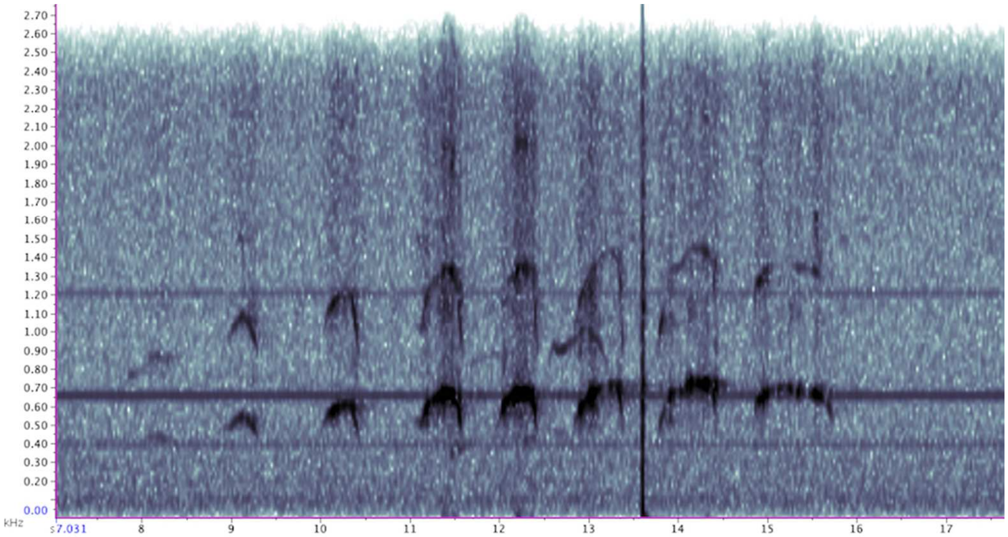


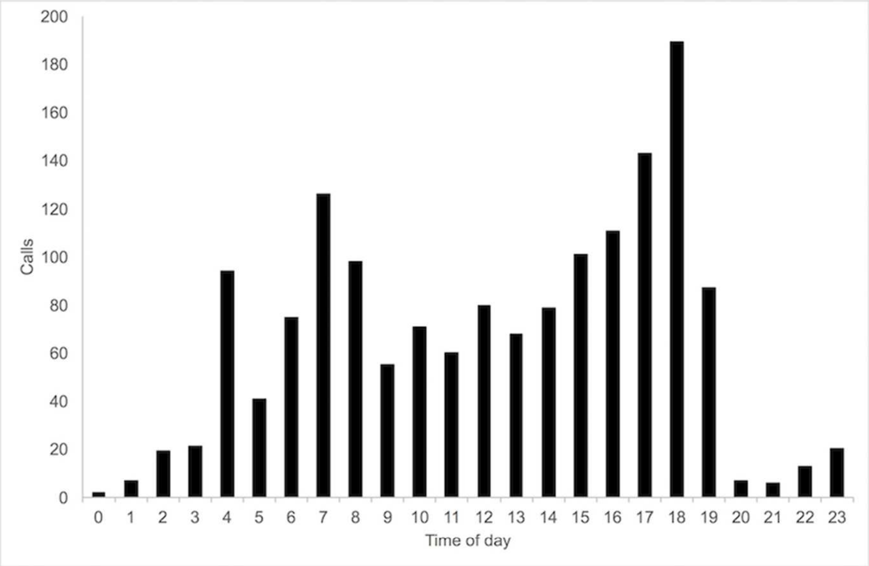
Map of western Tanzania, including the study area (Issa Valley, center) and the surrounding National Parks, two of which - Gombe and Mahale Mountains - host chimpanzees

59x41mm (300 x 300 DPI)



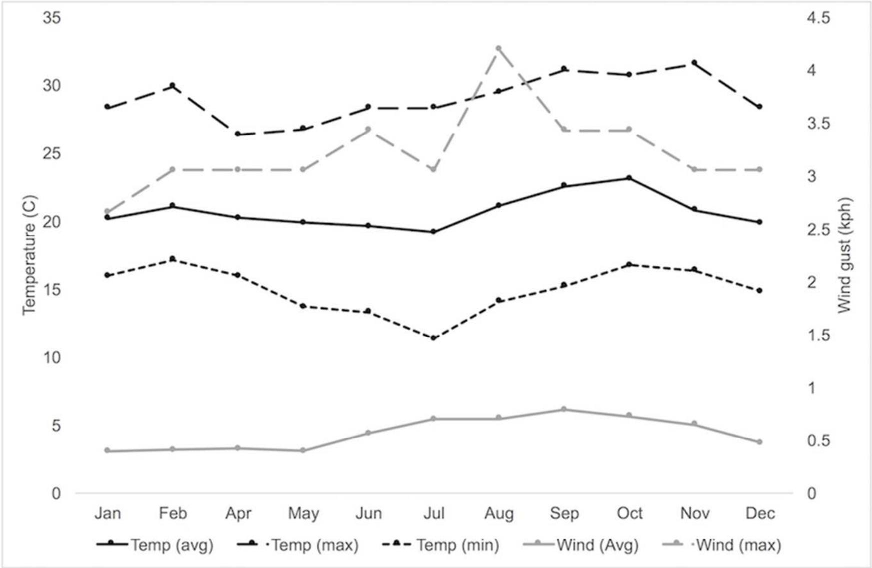
A loud call recorded on a Solar Powered Acoustic Transmission Unit (SPATU) from the Issa Valley

23317x12446mm (1 x 1 DPI)



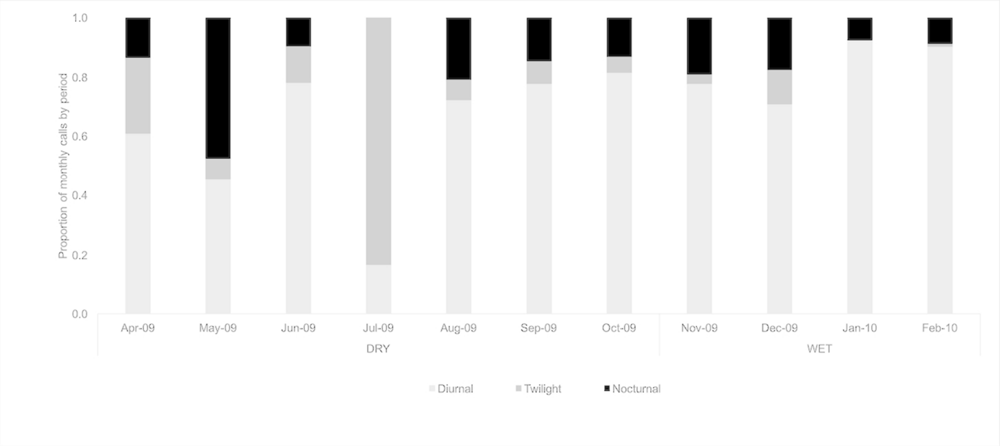
Hourly distribution of vocalizations recorded across the study period

83x58mm (300 x 300 DPI)



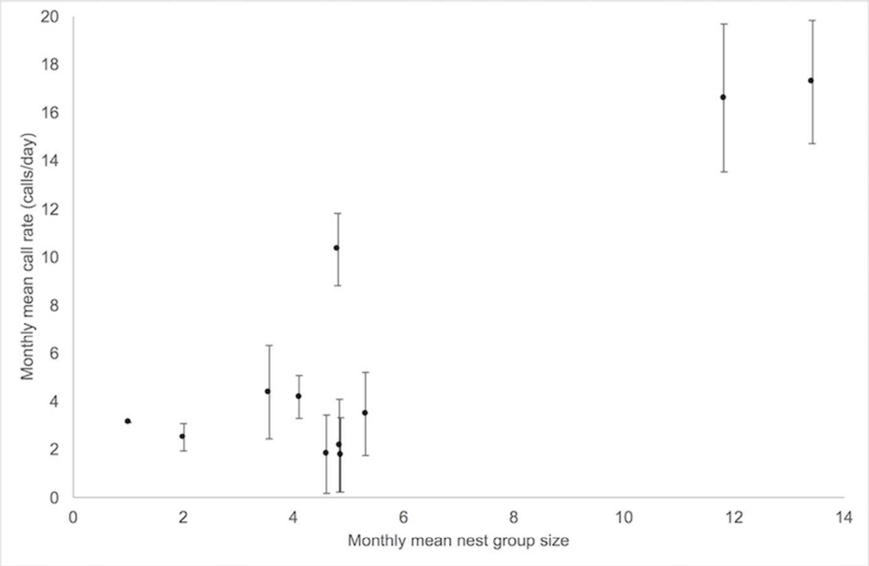
Mean and maximum monthly temperature over the study period

83x58mm (300 x 300 DPI)



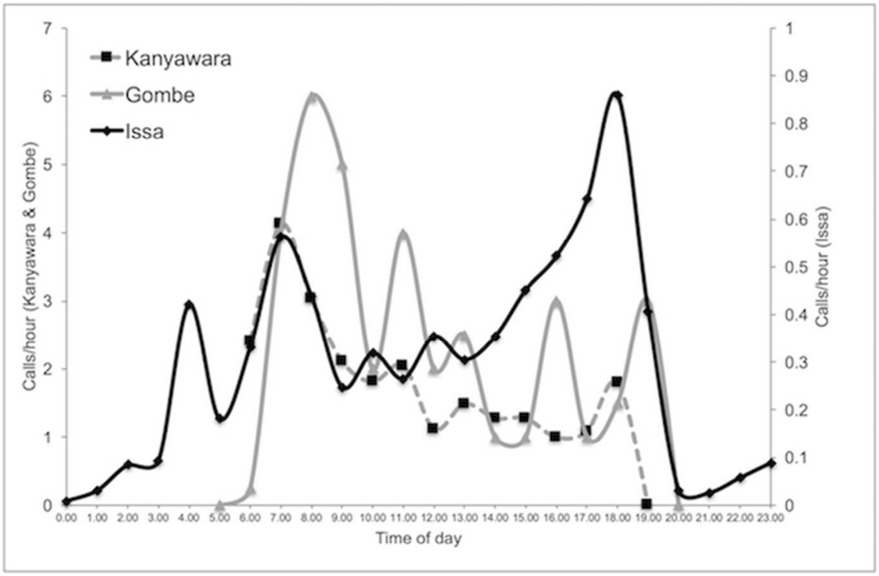
Monthly call proportions during day, twilight, and night-time periods

245x109mm (150 x 150 DPI)



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)



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

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[1] Earlier calls reported only

[2] 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