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UNIVERSITY OF CALIFORNIA, SAN DIEGO

Savanna Sounds: Using Remote Acoustic Sensing to Study
Spatiotemporal Patterns in Wild Chimpanzee Loud Vocalizations in the
Issa Valley, Ugalla, Western Tanzania

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy

in

Anthropology

by

Alexander Kenneth Piel

Committee in Charge:

Professor James J. Moore, Chair
Professor Daniel T. Blumstein
Professor John Hildebrand
Professor Margaret Schoeninger
Professor Shirley Strum

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Chair

University of California, San Diego

2014

DEDICATION

To MLB

EPIGRAPH

"The ideal situation is to have a recorder at each end of the long distance exchange and to record with both machines simultaneously throughout the exchange."

(Boehm, 1989:46)

TABLE OF CONTENTS

DEDICATION	iv
EPIGRAPH.....	v
TABLE OF CONTENTS	vi
LIST OF FIGURES	ix
LIST OF TABLES	xii
ACKNOWLEDGEMENTS.....	xiii
VITA	xvii
ABSTRACT OF THE DISSERTATION.....	xix
CHAPTER 1: INTRODUCTION	1
<i>Open-habitat chimpanzees</i>	<i>2</i>
<i>Vocal behavior in fission fusion societies</i>	<i>5</i>
<i>Passive Acoustic Monitoring (PAM)</i>	<i>9</i>
<i>Current study.....</i>	<i>12</i>
<i>Objective and aims.....</i>	<i>14</i>
<i>Broader impacts</i>	<i>16</i>
CHAPTER 2: SOLAR POWERED ACOUSTIC TRANSMISSION UNITS – AN ACOUSTIC REMOTE SENSING METHOD FOR THE STUDY OF WILD CHIMPANZEES (<i>PAN TROGLODYTES SCHWEINFURTHII</i>)	19
ABSTRACT	20
INTRODUCTION	21
<i>Why we need new technologies.....</i>	<i>23</i>
<i>The physical environment & sound transmission.....</i>	<i>25</i>
<i>Hypotheses.....</i>	<i>28</i>
METHODS.....	30
<i>Study site.....</i>	<i>30</i>
<i>Recording instrument – SPATU.....</i>	<i>31</i>
<i>Receiver</i>	<i>34</i>
<i>SPATU array</i>	<i>34</i>
<i>Playbacks</i>	<i>36</i>
<i>Data management & statistical analyses</i>	<i>38</i>
RESULTS	39
<i>Inter-SPATU variation and sub-sampling</i>	<i>39</i>
<i>Distance</i>	<i>43</i>
<i>Environmental (season and weather) conditions.....</i>	<i>44</i>
<i>Landscape features: vegetation and topography.....</i>	<i>45</i>
<i>The sound environment.....</i>	<i>46</i>
DISCUSSION	47
<i>Seasonality and environmental conditions as important variables</i>	<i>48</i>
<i>Optimal calling areas</i>	<i>49</i>

<i>Future Improvements</i>	53
<i>PAMs and Pan</i>	54
<i>Conservation applications</i>	56
CHAPTER 3: TEMPORAL PATTERNS OF CHIMPANZEE LOUD CALLS IN A SAVANNA WOODLAND	58
ABSTRACT	59
INTRODUCTION	60
<i>Savannas, sociality, and sounds</i>	65
<i>Why autonomous recording systems?</i>	66
METHODS	70
<i>Study site</i>	70
<i>Recording Instrument - Solar Power Acoustic Transmission Units (SPATUs)</i>	72
<i>Receiver</i>	73
<i>Characterizing the sound environment</i>	74
<i>Party size: chimpanzee nests</i>	75
<i>Data management and statistical analyses</i>	76
RESULTS	77
<i>Daily and monthly calling patterns</i>	79
<i>Calling and environmental conditions</i>	82
<i>Nest party size and calling rate</i>	84
<i>Chorusing or counter-calling?</i>	85
DISCUSSION	87
<i>Time of day</i>	87
<i>Issa and other ape calling patterns</i>	90
<i>Seasonal and environmental conditions</i>	90
<i>Sounds of sociality</i>	91
<i>Chorusing, counter-calling, and coordinating</i>	93
<i>Savanna soundscapes</i>	96
<i>Conclusions and Future Studies</i>	98
CHAPTER 4: LOCATING HIDDEN HOOTS: CHIMPANZEE SPATIAL DISTRIBUTION MONITORED BY REMOTE SENSING	101
ABSTRACT	102
INTRODUCTION	103
METHODS	107
<i>Study site</i>	107
<i>Recording Instrument – Solar Power Acoustic Transmission Units (SPATU)</i>	109
<i>Localization</i>	111
<i>Party size</i>	112
<i>Reconnaissance data</i>	113
<i>Vegetation classification and diet data</i>	114
<i>Data management and statistical analyses</i>	114
RESULTS	116
<i>Nesting across space and time</i>	119
<i>Predicting caller location...from other caller locations</i>	121
<i>Silent presence?</i>	122

DISCUSSION	122
<i>Calling and feeding down south.....</i>	<i>122</i>
<i>Silence and sociality on the savanna</i>	<i>124</i>
<i>Acoustic aggregation.....</i>	<i>126</i>
<i>Listening or walking?</i>	<i>126</i>
<i>Limitations and Future Studies.....</i>	<i>127</i>
CHAPTER 5: CONCLUSION	129
<i>Sound transmission: establishing efficacy.....</i>	<i>131</i>
<i>Timing and tuning</i>	<i>132</i>
<i>Sounds of savanna sociality</i>	<i>134</i>
<i>Silent absence.....</i>	<i>136</i>
<i>Acoustic evidence for ‘savanna adaptations’</i>	<i>137</i>
<i>Beyond behavior: additional applications</i>	<i>139</i>
<i>Listening ahead.....</i>	<i>140</i>
<i>Conserving Pan, deploying PAM</i>	<i>145</i>
REFERENCES	147

LIST OF FIGURES

CHAPTER 1

FIGURE 1 – THE CORE RESEARCH TEAM FOR THE DURATION OF THE STUDY	XV
FIGURE 2 - A PANT HOOTING CHIMPANZEE IN THE ISSA VALLEY, TANZANIA (PHOTO: J. HOSAK AND M. POLAK)	1
FIGURE 3 - MIOMBO WOODLAND IN THE ISSA VALLEY, WESTERN TANZANIA.....	3
FIGURE 4 - AN ISSA CHIMPANZEE IN MIOMBO WOODLAND (PHOTO: J. HOSAK AND M. POLAK).....	4
FIGURE 5 - HYPOTHETICAL MICROPHONE ARRAY (BLUE CIRCLES) AND SOUND ORIGIN (RED CIRCLE). LINES REPRESENT PARABOLAS ESTIMATING SOUND ORIGIN BASED ON TIME DELAYS TO EACH SENSOR (DIGBY, 2013)	10
FIGURE 6 - A SOLAR POWERED ACOUSTIC TRANSMISSION UNIT DEPLOYED AT ISSA	14
FIGURE 7 - THE ISSA VALLEY STUDY SITE	15
FIGURE 8 - SOUNDSCAPE ECOLOGY, HOW A SIGNAL (A) PROPAGATES WITHIN A COMBINATION OF (B) GEOPHONIC, BIOPHONIC, AND ANTHROPHONIC NOISE (FROM PIJANOWSKI ET AL., 2011)	18

CHAPTER 2

FIGURE 9 - A SOLAR POWERED ACOUSTIC TRANSMISSION UNIT (SPATU) DEPLOYED IN THE ISSA VALLEY	19
FIGURE 10 - MAP OF THE STUDY AREA (ISSA VALLEY) WITH THE TWO NATIONAL PARKS HOSTING CHIMPANZEES (GOMBE, MAHALE MOUNTAINS) ALSO LABELED	31
FIGURE 11 - A SOLAR POWERED ACOUSTIC TRANSMISSION UNIT DEPLOYED AT ISSA	33
FIGURE 12 - MAP SHOWING THE LOCATION OF ALL DEPLOYED RECORDING UNITS (SPATUs)	35
FIGURE 13 - AN EXAMPLE OF A PLAYBACK SOUND THAT REACHED FIVE DIFFERENT SPATUs. THE BOX REPRESENTS THE SAME CALL ELEMENT IN EACH.	42
FIGURE 14 – A MAP SHOWING THE SPATIAL DISTRIBUTION OF THE RECORDING UNITS AND THE PLAYBACK SOURCE ORIGIN FROM FIGURE 10.....	42
FIGURE 15 - GRAPH DESCRIBING THE PROPORTION OF SOUNDS RECEIVED ACROSS DIFFERENT TOPOGRAPHY AND VEGETATION COMBINATIONS.	44
FIGURE 16 - STUDY AREA ACCESSIBLE FOR USE OF SPATUs. YELLOW BALLOONS REPRESENT SPATUs. THE INTERNAL (GREEN) POLYGON SURROUNDING THE BALLOONS INDICATES APPROXIMATE CHIMPANZEE RANGE WITH ACOUSTIC COVERAGE, WHILST THE PERIPHERAL (RED) POLYGONS REPRESENT CHIMPANZEE RANGE WITHOUT ACOUSTIC COVERAGE, BUT WHERE WE ENCOUNTERED OTHER (NEST, FECAL, ETC.) EVIDENCE.	51

CHAPTER 3

FIGURE 17A AND B - PHOTOS CAPTURING EARLY MORNING (TOP) AND EVENING (BELOW) AT ISSA (PHOTO CREDITS: TOP: A. PIEL; BOTTOM: J. HOSAK, M. POLLAK)	58
FIGURE 18 - MAP OF WESTERN TANZANIA, INCLUDING THE STUDY AREA (ISSA VALLEY, CENTER) AND THE ONLY TWO NATIONAL PARKS IN TANZANIA WHERE CHIMPANZEES LIVE: GOMBE AND MAHALE MOUNTAINS, BOTH ALONG LAKE TANGANYIKA (MAP: L. PINTEA, THE JANE GOODALL INSTITUTE, USA)	71
FIGURE 19 - A SOLAR POWERED ACOUSTIC TRANSMISSION UNIT (SPATU), DEPLOYED IN THE ISSA VALLEY.....	73
FIGURE 20 - MAP DESCRIBING THE LOCATIONS OF SPL READINGS OF AMBIENT NOISE. YELLOW REPRESENTS DAYTIME LOCATIONS WHILST BLUE INDICATES LOCATIONS MEASURED IN THE EARLY EVENING (20H-22H).	76
FIGURE 21 – 2009-2013 AVERAGE MONTHLY RAINFALL AT ISSA	79
FIGURE 22 - TOTAL NUMBER OF CHIMPANZEE LOUD VOCALIZATIONS RECORDED FOR EACH HOUR DURING THE STUDY PERIOD	80
FIGURE 23 - CALL RATE OF ISSA CHIMPANZEE LOUD CALLS ACROSS MONTHS, WITH THE HIGHEST RATES BEING PRODUCED IN THE LATE DRY SEASON	81
FIGURE 24 - LOUD CALL HOURLY DISTRIBUTION ACROSS WET (BLACK) AND DRY (GREY) SEASONS	81
FIGURE 25 - AMBIENT NOISE LEVELS AND CHIMPANZEE CALL EVENTS PER HOUR.....	83
FIGURE 26 – A SIGNIFICANT CORRELATION WAS FOUND BETWEEN MEAN MONTHLY CALL RATE AND MEAN NEST GROUP SIZE.....	84
FIGURE 27 - THE TIME DELAY BETWEEN CHIMPANZEE CALLS OF JUST THOSE SOUNDS WITHIN ONE MINUTE OF THE PREVIOUS SOUND	86
FIGURE 28 - HOURLY BLOCK DISTRIBUTION OF CHIMPANZEE COUNTER-CALLS (SOUNDS MADE WITHIN ONE MINUTE OF A PREVIOUS SOUND)	86
FIGURE 29 - COMPARISON OF THREE PAN COMMUNITIES: <i>P. TROGLODYTES</i> FROM KANYAWARA (UGANDA) AND ISSA (TANZANIA), AND <i>P. PANISCUS</i> FROM LOMAKO, DEM. REP OF CONGO	90
FIGURE 30 - TWO EXAMPLES OF ISSA CHIMPANZEE CALLING EVENTS AND HOW THEY FIT INTO THE BROADER, BIOPHONAL SOUNDSCAPE	98

CHAPTER 4

FIGURE 31 - AN ISSA CHIMPANZEE WATCHING RESEARCHERS FROM A MIOMBO WOODLAND PERCH IN THE LATE DRY SEASON (PHOTO: N. COHEN).....	101
FIGURE 32 - MAP OF WESTERN TANZANIA, WITH THE STUDY AREA (ISSA VALLEY, CENTER), AND MAHALE AND GOMBE NATIONAL PARKS ALL MARKED WITH GREEN BOUNDARIES. CREDIT: L. PINTEA, JANE GOODALL INSTITUTE.....	108
FIGURE 33 – 2009-2013 AVERAGE MONTHLY RAINFALL AT ISSA	109
FIGURE 34 - THREE-DIMENSIONAL IMAGE OF THE STUDY AREA. YELLOW BALLOONS REPRESENT SPATU LOCATIONS.....	110
FIGURE 35 – TOP DOWN IMAGE OF THE STUDY AREA WITH NORTH/CENTRAL/SOUTH AREAS IDENTIFIED. YELLOW BALLOONS REPRESENT SPATU LOCATIONS.....	110

FIGURE 36 – A SPECTROGRAM WITH A PANT HOOT RECORDED ON THREE DIFFERENT CHANNELS. WHEN THIS OCCURRED, THE VALLEY WITH THE CHANNEL THAT RECORDED THE SOUND EARLIEST (HERE, CHANNEL 19) WAS DESIGNATED AS THE SOUND SOURCE.	112
FIGURE 37 - THE PROPORTION OF DAYS EACH MONTH WHEN AT LEAST ONE VOCALIZATION ("PRESENCE") WAS RECORDED VERSUS THE PROPORTION OF DAYS WHEN NONE ("ABSENCE") WAS RECORDED	117
FIGURE 38 - MEAN MONTHLY CALL RATE (CALL EVENTS PER DAY) USING JUST THOSE DAYS WHEN AT LEAST ONE CALL WAS MADE	117
FIGURE 39A AND B - SPATIAL DISTRIBUTIONS OF CHIMPANZEE VOCALIZATIONS IN THE DRY (LEFT) AND WET (RIGHT) SEASONS. SMALL CIRCLES REPRESENT 0-10% OF CALLS MADE, MEDIUM 11-25% AND LARGE, OVER 25%.....	118
FIGURE 40 - PROPORTION OF CHIMPANZEE VOCAL EVENTS IN EACH GEOGRAPHIC AREA, ACROSS TIME (MONTH) AND SPACE (NORTH, CENTRAL, SOUTH).	119

CHAPTER 5

FIGURE 41 - CAPTURING CHIMPANZEE CALLS AT ISSA, 2009-2010	129
FIGURE 42 – AN AUTONOMOUS SOUND LEVEL METER, FROM HTTP://WWW.CASELLAMEASUREMENT.COM/NEWS.HTM	143

LIST OF TABLES

TABLE 1 - TOTAL NUMBER OF PLAYBACK LOCATIONS AND IN WHAT VEGETATION TYPES AND TOPOGRAPHICAL LEVELS PLAYBACKS WERE BROADCAST	41
TABLE 2 - RESULTS FROM A BACKWARD STEPWISE LOGISTICAL REGRESSION THAT BEGIN WITH NINE POTENTIAL INFLUENCES ON WHETHER PLAYBACK SOUNDS ARRIVED AT SPATUs. SEVEN OF THE NINE WERE STATISTICALLY SIGNIFICANT, WHILST ONLY BROADCAST VOLUME (DB) AND HUMIDITY WERE NON-SIGNIFICANT.	46
TABLE 3 - SUMMARY OF THOSE PRIMATE SPECIES FOR WHICH CALL PEAK PERIODS HAVE BEEN DESCRIBED	63
TABLE 4 - RESULTS FROM A LOGISTICAL REGRESSION DESCRIBING THE INFLUENCE OF USING ENVIRONMENTAL VARIABLES TO EXPLAIN WHEN ISSA CHIMPANZEE PRODUCE LOUD CALLS	82
TABLE 5 - WILD CHIMPANZEE POPULATION DENSITIES IN FOREST- AND SAVANNA-DOMINATED HABITATS	106
TABLE 6 - RESULTS OF A GENERALIZED LINEAR MODEL FOR WHAT BEST PREDICTS THE PRESENCE OF NESTS RECORDED ON LINE TRANSECTS IN EITHER NORTH OR SOUTH REGIONS.	120
TABLE 7 - RESULTS OF A GENERALIZED LINEAR MODEL EXAMINING WHAT BEST PREDICTS IN WHICH VALLEY A VOCALIZATION WILL BE RECORDED	122

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Figure 1 – The core research team for the duration of the study

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The Nature Conservancy, \$81,200 – *Monitoring of priority areas for chimpanzees in the Greater Mahale Ecosystem* (w. F. Stewart)

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Selected publications

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Tapper, S., C. Johnson, A. Lenoel, A. Vining, F.A. Stewart, **A.K. Piel**. Riverine red-tails: Forest guenons in a savanna woodland habitat in the Issa Valley, Ugalla, western Tanzania. In: *Primates in Flooded Habitats: Ecology and Conservation*, (eds) A.A. Barnett, I. Matsuda & K. Nowak. In press.

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Kalousová, B., **A.K. Piel**, K. Pomajbíková, D. Modrý, F.A. Stewart, K.J. Petrželková. 2014. Gastrointestinal parasites of savanna chimpanzees (*Pan troglodytes schweinfurthii*) in Ugalla, Tanzania. *International Journal of Primatology* 35(2):463-475.

Piel, A.K. & F.A. Stewart. 2014. Greater Mahale Ecosystem Chimpanzee Survey Final Report. Report submitted to The Nature Conservancy. 74p

Piel, A.K. 2014. (Book review) Evolution of Emotional Communication: From Sounds in Nonhuman Animals to Speech and Music in Man. *Folia Primatologica*. DOI: 10.1159/000355041

Piel, A.K. F.S. Stewart, L. Pintea, Y. Li. M.A. Ramirez, D.A. Loy, P.A. Crystal, G.H. Learn, L.A. Knapp, P.M. Sharp, B.H. Hahn. 2013. The Malagarasi River does not form an absolute barrier to chimpanzee movement in western Tanzania. *PLoS One* 8(3).

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Rudicell, R. S., **A.K. Piel**, F.A. Stewart, G.Learn, Y. Li, J. Robertson, J.J. Moore. and B. Hahn. 2011. High prevalence of SIVcpz infection in a community of savanna chimpanzees. *Journal of Virology* 19:9918-28.

Stewart, F. A., **A.K. Piel**, and W.C. McGrew. 2011. Living archaeology: Artefacts of specific nest site fidelity in chimpanzees. *Journal of Human Evolution*. 61:388-95.

ABSTRACT OF THE DISSERTATION

Savanna Sounds: Using Remote Acoustic Sensing to Study
Spatiotemporal Patterns in Wild Chimpanzee Loud Vocalizations in the
Issa Valley, Ugalla, Western Tanzania

by

Alexander Kenneth Piel

Doctor of Philosophy in Anthropology

University of California, San Diego, 2014

Professor James J. Moore, Chair

Researchers who study unhabituated animals face a daunting task, that of locating and monitoring elusive subjects and, sometimes, conditioning them to human presence. With savanna-woodland chimpanzees (*Pan troglodytes*) in western Tanzania, this challenge is further exacerbated when one considers their hypothesized home range is over ten times larger than forest-dwelling populations and they live at one tenth the density. Consequently, alternative methods to study these apes are needed, especially to test hypotheses concerning behavioural adaptations necessary to cope with marginal, open-

habitat conditions. Results have implications for extant apes living in these drier habitats, and Plio-Pleistocene hominins that would have faced similar environments.

We designed and deployed an acoustic remote sensing system to continuously monitor chimpanzee vocalizations across space and time from April 2009 - February 2010. Results from a playback study examining sound propagation in the study area showed that sound carries farther through woodlands, slopes and mountain edges than from plateaus or through thicker, forest vegetation. Spatiotemporal analyses of chimpanzee loud calls revealed that individuals produced loud calls from non-random places and times, including exhibiting dawn and dusk peaks and during moonlit nights. Contrary to some of our hypotheses, we found no relationship between when chimpanzees call and optimal sound propagation conditions. Rather, the best predictor of when a vocalization was produced was the presence of a preceding call, both in predicting a call itself, and also from where it was emitted (e.g. in the same valley as the previous call). Significantly more calls were produced in the northern part of their range during the dry season, and more in the southern part, during the wet season. Additionally, mean monthly call rate (number of calls/day) correlated strongly with monthly mean nest party size, suggesting that vocalizations are a reliable predictor of grouping behaviour.

Whilst this dissertation describes spatiotemporal vocalization patterns, results from this terrestrial, remote passive acoustic monitoring have numerous other applications. These include using precise caller localizations to test hypotheses concerning the role of vocalizations in movement coordination, and establishing ecosystem-wide savanna soundscapes, to assess acoustic niche partitioning.

CHAPTER 1: INTRODUCTION

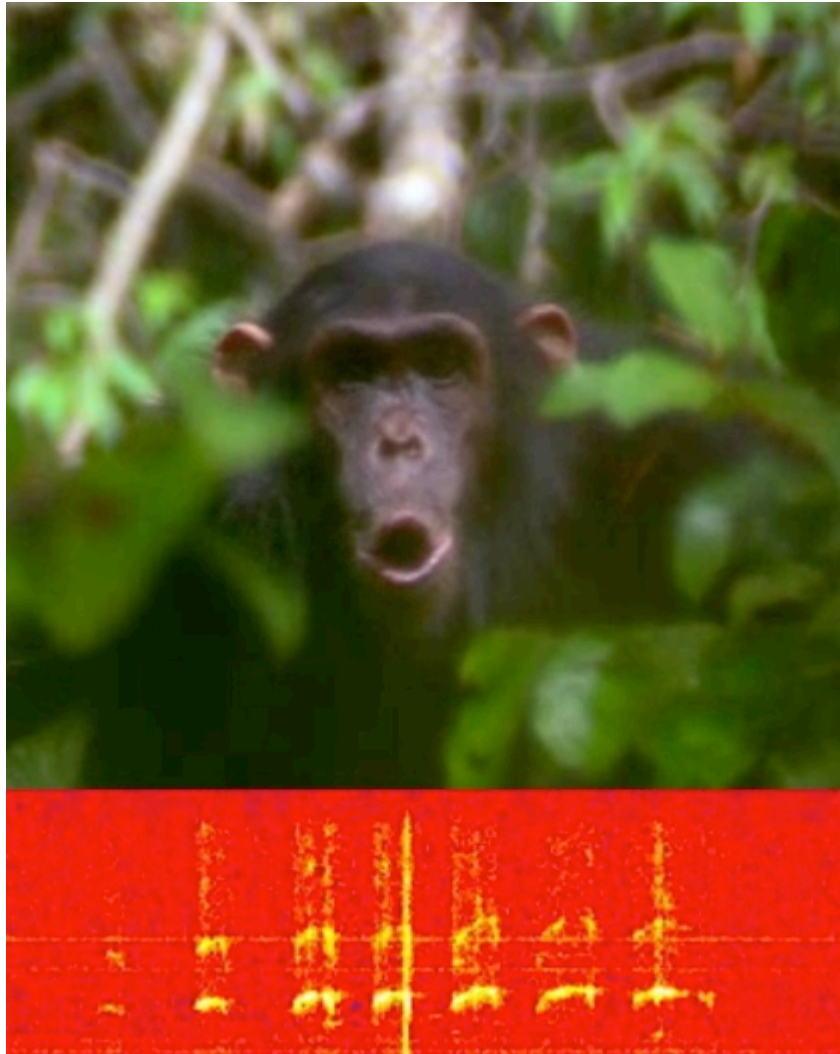


Figure 2 - A pant hooting chimpanzee in the Issa Valley, Tanzania
(photo: J. Hosak and M. Polak)

Open-habitat chimpanzees

Interest in savanna-woodland chimpanzees (*Pan troglodytes* sp.) as models for early human adaptations to open habitats dates to the earliest period of ape research. Studies across Africa from the pioneering ones of the 1960s in Tanzania (Izawa and Itani, 1966; Suzuki, 1969; Kano, 1971; reviewed in Nishida, 2011), across the continent to Senegal over a decade later (McGrew et al., 1979, 1981; Baldwin et al., 1982 a; Tutin et al., 1983) sought to first describe and then understand the behavioral adaptations of chimpanzees living in these hot, dry, arid landscapes. However, at all dry sites, researchers have reported low densities of chimpanzees (0.08 – 0.36 individuals/km²) (Hunt, 2000; Pruetz et al., 2002 a; reviewed in Moyer et al., 2006) and large home ranges (Samson, 2012; Skinner and Pruetz, 2012), resulting in few encounters, and thus failed habituation. Consequently, focus turned to forest-dwelling communities, which have been the primary sources of data on chimpanzees for the last half-century (Mitani et al., 2002). Today, research on open-habitat chimpanzees continues at three sites: Semliki (Uganda), Fongoli (Senegal), and Ugalla (Tanzania). While only at Fongoli has full habituation been achieved, unique behaviors not yet observed in forest-dwelling communities have been reported for all three sites. At Semliki, chimpanzees dig shallow wells in the sand of streambeds (McGrew et al., 2007, 2008). At Fongoli chimpanzees use caves when temperatures soar (Pruetz, 2007) and tools when hunting

small mammals (Pruetz and Bertolani, 2007). And at Ugalla chimpanzees obtain plant underground storage organs using digging tools (Hernandez-Aguilar et al., 2007) as well as show long-term, repeated use of nesting sites (Hernandez-Aguilar, 2009; Stewart et al., 2011), akin to 'home bases' found in the archaeological record (Sept, 1992).



Figure 3 - Miombo woodland in the Issa Valley, western Tanzania

Little else is known about the behavioral adaptations that early hominins made from moving from a predominantly arboreal, wet habitat to a terrestrial, dry one in the Plio-Pleistocene. With fossil and paleoecological evidence indicating Plio-Pleistocene hominids evolved in woodland habitats (WoldeGabriel et al., 1994; Reed, 1997; Schoeninger et al., 2003; White et al., 2010; Cerling et al., 2011 b), studying savanna-woodland (Figure 3 and Figure 4) chimpanzees allows

researchers to observe selection pressures similar to those that may have acted on early hominins and inform models of their adaptations to such habitats. Australopithecines (Berger and Tobias, 1996; Lovejoy et al., 2009; Venkataraman et al., 2013) and some early *Homo* species (Richmond et al., 2001) retained apelike post-cranial features (e.g. curved phalanges) and there is evidence that at least before *Homo* (Capasso et al., 2008), these ape-like hominins had vocal anatomy similar to those of extant apes (Alemseged et al., 2006), and thus we can assume that their communicative behavior was likely similar.

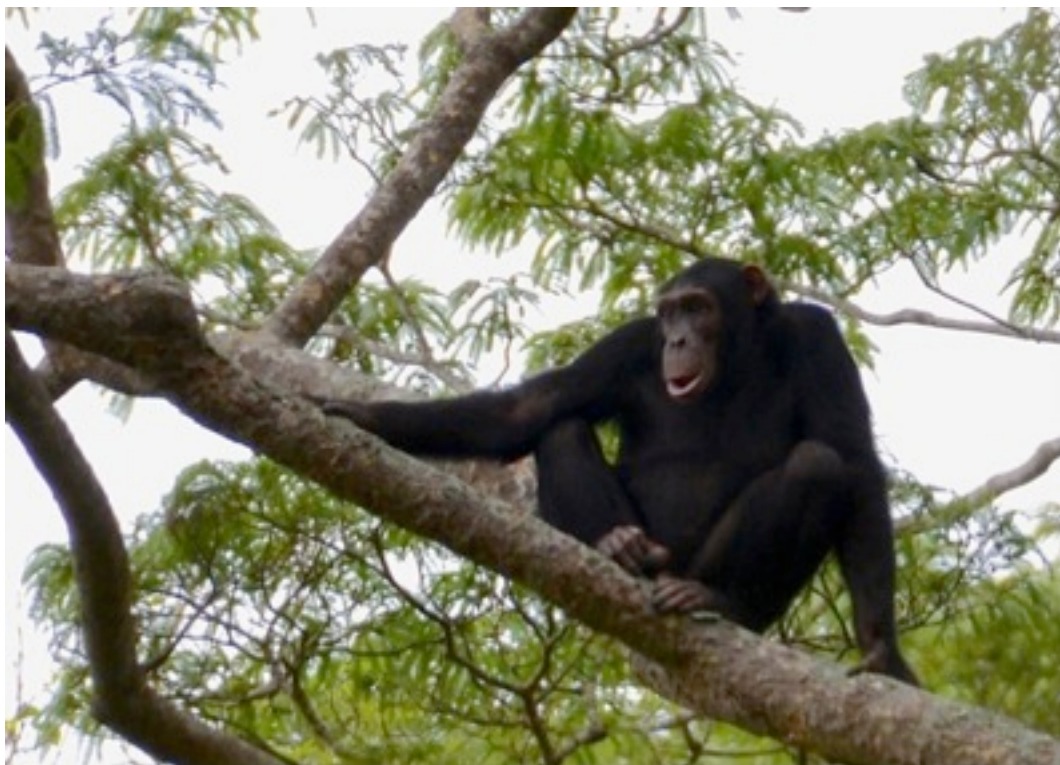


Figure 4 - An Issa chimpanzee in miombo woodland (photo: J. Hosak and M. Polak)

We also know little about what social adaptations low-density, wide-ranging chimpanzees exhibit, especially if and how their social organization may differ from forest-dwelling populations. For example, data from multiple studies report small average daily party sizes (Tutin et al., 1983; Ogawa et al., 2007) [compared to forest-dwelling communities (Jones and Sabaeter Pi, 1971; Newton-Fisher, 1999; Lehmann and Boesch, 2004)] and yet larger night nest parties (Baldwin et al., 1982 b; Ogawa et al., 2007). This suggests morning fission events and evening fusion events, likely at sleeping sites.

Given that forest-dwelling chimpanzees have been observed for over a half-century, that the aforementioned behaviors have only been reported in savanna populations supports Moore's (1992) suggestion of specific "savanna adaptations." Once more firmly documented, understanding of such adaptations will be useful in the application of chimpanzee 'models' to complement paleoanthropological research on early hominins (McGrew et al., 1981; Moore, 1996; but see Sayers and Lovejoy, 2008).

Vocal behavior in fission fusion societies

If fewer individuals are covering a larger area, long-distance communication may be even more important to maintaining relationships and coordinating movement and reunions. Modern humans rely on loud signals (calls, drums, or whistles) to communicate across large areas (Meyer, 2004), with combinations of loud signals

(e.g. calls plus drumming) used to augment or change the information embedded within a signal (Stern, 1957). Non-human primates also rely on vocal communication and loud calls – known for being the most distinctive in an animal's repertoire (Mitani and Stuht, 1998) – are especially important for fission fusion species where dispersed individuals form ephemeral sub-groups that respond to changing ecological and social dynamics. In these species, long call behaviour is important in (a) the coordination of sub-group reunions, especially at sleeping sites (Matthews and Aureli, 2003; Fischer and Zinner, 2011; I. Scahmberg, unpublished data), (b) increasing cohesion within the community (Hohmann and Fruth, 1994), (c) the advertisement of community membership (White, 2001), and (d) monitoring territory boundaries (Stern, 1957; Teixidor and Byrne, 1999; Watts and Mitani, 2001), among others.

Despite vocalizations being an inherently social behavior, few studies have attempted to situate calls in an exchange with group members. The logistics of monitoring an acoustic social network are often prohibitive, with callers and listeners distributed across areas often obscured by vegetation and potentially at various heights in the canopy. Nonetheless, those few studies that have described these exchanges reveal interesting patterns. For example, white bellied spider monkey (*Ateles belzebuth*) loud calls ("whinnies") are answered within 30 minutes by calls in a different location, and when such

counter-calls were emitted, smaller groups exhibited an increase in group size within one hour of the last call (Spehar and Fiore, 2013). Whinnies have also been shown to be individually distinctive and thus advertise sub-group composition (Chapman and Weary, 1990; Ramos-Fernández, 2005), with individuals vocally responding more often to the calls of preferred (even if visually obscured) social partners (Teixidor and Byrne, 1999; Spehar and Fiore, 2013). In investigating the role of vocalization in reunions, Matthews and Aureli (2003) demonstrated a significant increase in individual call rates during nighttime fusion events and interpreted this behavior as individuals assessing group composition when visibility is reduced, before deciding with whom to sleep.

In *Pan*, most research into vocalizations has centered on levels of variation and implications of call complexity and use for the evolution of language. Variation in (forest-dwelling) chimpanzee long calls – pant hoots – has been observed at the individual (Marler and Hobbett, 1975; Mitani et al., 1996; Kojima et al., 2003), community (Arcadi, 1996; Crockford et al., 2004), and population (Mitani et al., 1999) level. Chimpanzee hoot or scream types and/or rates have also been shown to change with caller location (Uhlenbroek, 1996; Wilson et al., 2007), target audience (Mitani and Nishida, 1993; Mitani and Brandt, 1994; Slocombe and Zuberbuhler, 2007), rank (Clark, 1993; Mitani and Nishida, 1993), and party composition (Mitani and Nishida, 1993;

Arcadi, 1996). Additionally, vocalization behavior changes with caller activity such as in feeding contexts (Wrangham, 1977; Clark and Wrangham, 1993) and before/after traveling (Mitani and Nishida, 1993; Uhlenbroek, 1996; Notman and Rendall, 2005; Gruber and Zuberbühler, 2013).

Overall, evidence supports a stronger social, rather than ecological influence on calling. Support comes from Clark and Wrangham (1993) who found no evidence of 'food-arrival' pant hoots, and suggested long calls instead broadcast social, rather than ecological information. Notman and Rendall (2005:184) later found evidence for specific reunion pant hoots, made "along the ground in small parties prior to joining up with other community members" (see also Gruber and Zuberbühler, 2013). Such context-specific flexibility has also been demonstrated in screams, where it is now well established that the audience (Slocombe and Zuberbuhler, 2007; Crockford et al., 2012) and caller's role in the social interaction (Slocombe and Zuberbuhler, 2005) influence call type.

Chimpanzees also combine signals, specifically pant hoots and drumming (Clark Arcadi et al., 2004; Arcadi and Wallauer, 2013), yet the function of this acoustic strategy remains unclear. Crockford and Boesch (2005) suggest that pant hoots may serve as individual signatures while complementary drumming, screaming, or grunting advertises specific social context (see also Arcadi et al., 1998), or adds

additional information, such as travel direction. Ideally, of course, we would like to know if such 'travel' calls actually coordinate later reunions, and if so, what, actually, in the call is signaling that information (I. Schamberg, pers. comm)?

Only Uhlenbroek's (1996) study of chimpanzee vocalizations at Gombe National Park, Tanzania attempted simultaneous multi-individual follows. She observed that chimpanzees produce different pant hoots in response to (1) perceived location of the caller (e.g. center or periphery of territory) and (2) to those from close allies, reinforcing the idea that counter-calling allows individuals to learn community-member's location (Marler, 1976). Hohmann and Fruth (1994:779) observed bonobos (*Pan paniscus*) to counter call "in more or less perfect alternation" and at similar spectral frequencies at Lomako, Democratic Republic of Congo, but simultaneous follows of multiple individuals were not conducted.

Passive Acoustic Monitoring (PAM)

When animals are heard, but not seen, passive acoustic monitoring (PAM) can provide information about otherwise elusive individuals. These non-invasive systems are composed of single or multiple (usually autonomous) units that record and store sounds, either continuously or on pre-programmed schedules. PAM systems are effective for the study of unhabituated, cryptic, or logistically difficult to study species, across marine (Mellinger et al., 2007), aerial (Mennill et

al., 2006, 2012), and more recently, terrestrial (Thompson et al., 2009 b; Wrege et al., 2010; Blumstein et al., 2011) habitats. In addition to identifying temporal patterns of animal vocalizations, PAM systems that are comprised of three or more sensors (also known as Acoustic Localization Systems – ALS) can also reveal high resolution caller use of space via sound time-delays-of-arrival (Mennill et al., 2006; Ali et al., 2008). These delays establish the location of a caller in

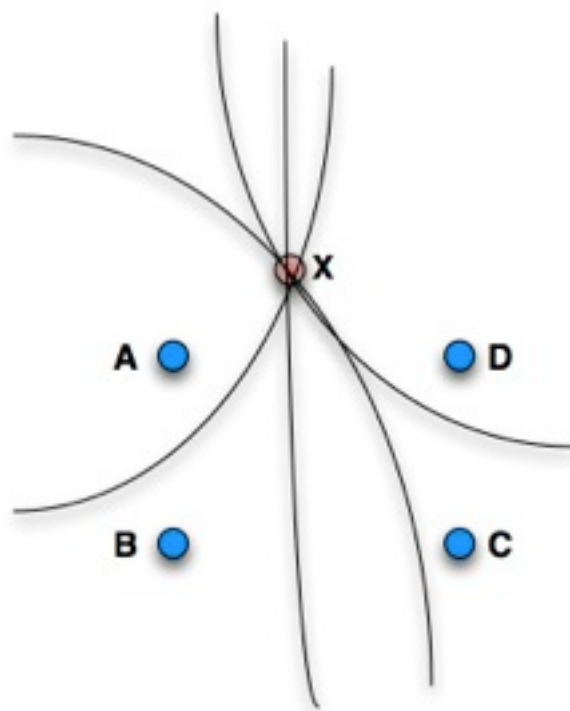


Figure 5 - Hypothetical microphone array (blue circles) and sound origin (red circle). Lines represent parabolas estimating sound origin based on time delays to each sensor (Digby, 2013)

two-dimensional (three sensors) or three-dimensional (four sensors) space (Figure 5). Such ALSs have been employed in the study of marine mammals to examine population densities, ranging, seasonal calling

and behavioral responses to anthropogenic noise as well, among others, and birds to examine duetting and territoriality (McGregor et al., 1997; Mennill et al., 2006; Fitzsimmons et al., 2008; Collier et al., 2010; Digby, 2013). PAM use with terrestrial species, however, remains in its infancy, with the so-called 'prospectus' only written in 2011 (Blumstein et al., 2011), almost four decades after some of the earliest work employing this method underwater (Watkins and Schevill, 1972).

Blumstein and colleagues (2011) describe the many advantages to these PAM systems, including the ability to study animals in their natural environment without disturbing them, track multiple individuals simultaneously across space and time, and monitor cryptic or nocturnal species adept at eluding researchers. Others have quantified improvement in spatial coverage between using off the shelf autonomous systems with traditional (manual) vocal counts, and described the benefits of reducing sampling bias with automated recording methods (Digby et al., 2013). Nonetheless, there exist abundant challenges to studying vocalization behavior in terrestrial environments. First, sound attenuates rapidly in air, compared to water, and thus recording units must be close to a caller to ensure sound recording. Autonomous units require maintenance checks to ensure they are functioning properly, and almost any system will be constrained by power and data capacity, although both have improved dramatically with recent technologies. Autonomous systems

are also fixed in space, which limits their spatial coverage (Digby et al., 2013). Further, in traditional systems sounds are identified and locations determined only weeks after a sound event, making those data unusable for real-time application (but see Klinck et al., 2012; Aide et al., 2013). Additionally, to localize a caller, multiple sensors must be time synchronized. Some teams achieved this by laying thousands of meters of cable to synchronize recording units (Fitzsimmons et al., 2008), or else developed wireless arrays (Collier et al., 2010; Mennill et al., 2012). Finally, the entire system needs to be affordable, which may be the biggest challenge for researchers in the behavioral biological sciences (Mennill et al., 2012)!

Despite these challenges, there are a number of PAM systems now available, with most designed either for large (spatial) scale monitoring of marine mammals or small scale monitoring of birds or small mammals. Until now, there is no known PAM system with real-time localization capability for wide-ranging, *terrestrial* animals.

Current study

Thompson et al.'s (2009 b) work using autonomous recording units (ARUs) to monitor African elephants (*Loxodonta africana*) in Ghana demonstrated both the uses and limitations of stationary units targeting wide-ranging animals, with all data stored internally on the recording units fastened to trees (see also Wrege et al., 2010). Deployments lasted only 38 days. Ali et al. (2008) described a small

wireless sensor system that was piloted using six nodes, each an independent processor, in a laboratory and with yellow bellied marmots in Colorado, USA as well. The objective of the study, however, was on localizing sound origins in a small ($\sim 1\text{km}^2$) area, rather than monitoring wider scale movements.

With chimpanzee home ranges in open habitats reaching unmanageable sizes for single research teams, encounters with parties are rarer than in forests, and thus we know little about chimpanzee behavioral responses to an open habitat, invaluable to our understanding of the flexibility of a fission-fusion system with a corresponding density difference up to 50 times lower. Behavioral strategies potentially include either a more cohesive social structure similar to what is observed in most monkeys, or a less cohesive structure with reduced inter-party encounters. Revealing which strategy chimpanzees use can only be addressed with simultaneous monitoring of multiple parties.



Figure 6 - A solar powered acoustic transmission unit deployed at Issa

Objective and aims

The primary objective of the current study was to design and deploy a custom developed PAM system to study Issa chimpanzee vocalization behavior and test hypotheses concerning their adaptations to a heterogeneous, open habitat in western Tanzania.. With colleagues, I designed and built Solar Powered Acoustic Transmission Units (SPATUs - Figure 6). In Chapter Two, we describe this system and discuss the results of a playback study aimed at assessing what environmental variables (e.g. temperature, wind, relative humidity) or habitat features (vegetation, topography) influence sound transmission in the study area. The playback study was further critical to assess the acoustic range boundaries of the microphone array.

We subsequently examined the temporal patterns of chimpanzee loud call production, investigating the environmental variables that best predicted loud call presence (Chapter Three). If loud calls are important for these chimpanzees to coordinate movement, for example, across large areas (Figure 7), we hypothesized that calls would be emitted during optimal transmission periods, much as observed in other species where calls are important in advertising fitness and/or territorial boundaries (Amrhein et al., 2004).



Figure 7 - The Issa Valley study site

Finally, in Chapter Four, we situated chimpanzee sound origins within specific regions (valleys) within the study area. Using sound origins as proxies for chimpanzee presence, we sought to test what best predicted from where chimpanzees call.

DISCLAIMER

There is substantial redundancy in the Methods between the middle three chapters. As Chapters Two, Three, and Four are all planned manuscript submissions, they have been written in active voice using “we” given that all are the result of contributed efforts of myself at least one other co-author. My goal here was to include in each chapter sufficient description about the recording device and microphone array for the chapters to stand on their own, but referring to Chapter 2 as a reference for more detailed information.

There is also overlap in an assessment of the recording system, which occurs in Chapter Two and also the Conclusion. Once again, this is due to my desire to reflect on this approach both in manuscript form, and also more holistically at the end of the dissertation.

My apologies in advance for this redundancy.

Broader impacts

In addition to addressing the above-described questions, the acoustic data obtained from SPATUs were simultaneously used in other important ways. For example, even knowing the valley of sound origin aided researchers in finding chimpanzee parties for parallel studies (Rudicell et al., 2011; Stewart et al., 2011; Kalousova et al., 2013) as well as create an auditory ‘soundprint’ (Figure 8) of a threatened ecosystem type - African savanna woodland (Syampungani et al., 2009) - that can be used to study biodiversity and to aid in conservation planning

and management (Laiolo, 2010; Dumyahn and Pijanowski, 2011). The emerging literature on soundscapes (Slabbekoorn and Bouton, 2008; Pijanowski et al., 2012; Servick, 2014) further underlines two additional benefits of long-term recording of entire acoustic ecosystems. First, acoustic databases may reveal the presence and abundance (Efford et al., 2009) of animals otherwise elusive to human observers and even camera traps. Second, sympatric homo- and hetero-specifics compete for a host of resources, including sound spaces, carving out acoustic niches to best communicate with conspecifics (Mossbridge, 1999; Schneider et al., 2008; Sinsch et al., 2012). A comprehensive database on such acoustic diversity at Issa allows for future study of these niches, and also how they change with anthropogenic disturbance (Rabin et al., 2003).

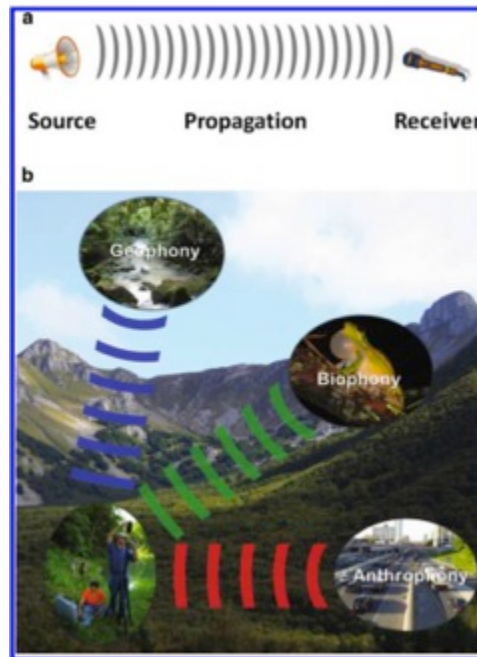


Figure 8 - Soundscape Ecology, how a signal (a) propagates within a combination of (b) geophonic, biophonic, and anthrophonic noise (from Pijanowski et al., 2011)

This system is the first of its type deployed for the study of primates, designed specifically to answer questions about how chimpanzees adapt a fluid social system to an open woodland habitat. In addition to examining the evolutionary origins of one of the defining characteristics of humans, complex communication, through investigation of its variability, use, and function in another hominoid, the current study will introduce and optimize a new field technology with many other wildlife and conservation applications.

CHAPTER 2: SOLAR POWERED ACOUSTIC TRANSMISSION UNITS – AN ACOUSTIC REMOTE SENSING METHOD FOR THE STUDY OF WILD CHIMPANZEES (*PAN TROGLODYTES SCHWEINFURTHII*)



Figure 9 - A solar powered acoustic transmission unit (SPATU) deployed in the Issa Valley

ABSTRACT

Researchers that study unhabituated animals face a daunting task, that of locating and monitoring elusive subjects and, sometimes, conditioning them to human presence. With savanna chimpanzees in western Tanzania, this challenge is further exacerbated when one considers that the hypothesized home range of savanna chimpanzees is over ten times larger than forested populations and that savanna chimpanzees live at one fiftieth the density of their forest cousins. Consequently, alternative methods to study these apes are needed. We describe here a system that uses a well-established method – passive acoustic monitoring – that has been modified to assist in locating and monitoring unhabituated chimpanzees. It relies on a solar-powered microphone array that uses radio frequency (RF) to transmit recorded sounds to a central computer. In total, twenty microphone units were deployed across a $\sim 12\text{km}^2$ area between April 2009 - March 2010 in western Tanzania, with half of the units used here to analyse playback sounds that simulated chimpanzee long calls (pant hoots). Under optimal conditions, sounds were recorded over three and a half kilometres from their source, with vegetation and topography significantly influencing transmission efficacy. The applications of this tool for studying an elusive, wide-ranging, and fission fusion species and also for conservation are discussed.

INTRODUCTION

For almost half a century passive acoustic monitoring (PAM) systems have been employed to address questions of animal calling behaviour across space and time (Watkins and Schevill, 1972). These non-invasive systems are composed of single or multiple (usually autonomous) units that record and store sounds, either continuously or on pre-programmed schedules. Animal sounds thus become the unit of analysis, rather than visual observations of the animal itself. Typically PAM systems are effective for the study of unhabituated, elusive, cryptic, or otherwise logistically difficult to study species, underwater (Mellinger et al., 2007), in the air (Mennill et al., 2012), and more recently, on the ground (Blumstein et al., 2011). When multiple sensors are used, the sound time-delay-of-arrival to each sensor can be used to establish the location of a caller to ask questions about coordinated movement and territoriality, among others. Acoustic systems have been employed in the study of marine mammals to examine population densities, ranging, seasonal calling and behavioral responses to anthropogenic noise as well. These studies have demonstrated the efficaciousness of PAM for monitoring animals otherwise not visible to researchers.

Blumstein and colleagues (2011) describe the many advantages to these PAM systems, including the ability to study animals in their

natural environment without disturbing them, track multiple individuals simultaneously across space and time, and monitor cryptic or nocturnal species adept at eluding researchers. However, there exist numerous challenges to studying vocalization behavior in terrestrial environments. First, sound attenuates rapidly in air, compared to water, and thus recording units must be close to a caller to ensure sound recording. Additionally, in order to localize, multiple units must be time synchronized, and the entire system, as for marine-based systems, needs to be affordable (Mennill et al., 2012). Further, autonomous units require maintenance checks to ensure they are functioning properly, and almost any system will be constrained by power and data capacity limits, although both have improved dramatically with recent commercial hardware. An important limitation of many PAM system is that they store data in the unit, with researchers only accessing acoustic data once units are retrieved and often, fieldwork is completed. That is, few systems allow researchers to access or evaluate data during recording. Some teams have sought to overcome these challenges, for example by laying thousands of meters of cable to synchronize recording units (Fitzsimmons et al., 2008) or else by deploying wireless microphone arrays (Mennill et al., 2012). To date, however, these approaches have either been over large scales for the study of marine mammals or on much smaller scales focused on birds or small terrestrial mammals.

Why we need new technologies

Despite the extensive history and diverse applications of PAM to study elusive animals, current designs are inadequate to track wide-ranging, terrestrial animals. Most systems store data internally and thus face both data and battery storage limitations. Thompson et al.'s (2009 b) work using autonomous recording units (ARUs) to monitor elephants in Ghana demonstrated both the uses and limitations of stationary units, with all data stored internally on the recording units fastened to trees, and deployments limited to 38 days. Ali et al. (2008) described a small wireless sensor system that was piloted using six nodes, each an independent processor, in a laboratory and with yellow bellied marmots in Colorado, USA as well. The objective of the study, however, was on localizing sound origins in a small ($\sim 1000\text{m}^2$) area. Such a system has not yet been deployed over a larger area to our knowledge.

We aimed to address the challenges of using PAM for terrestrial species through the development of a new type of PAM with improved power supply, data storage, and data-access. We developed this system with the goal of addressing behavioral questions of a wide ranging, terrestrial mammal, the eastern chimpanzee (*Pan troglodytes schweinfurthii*) in western Tanzania (Piel and Moore, 2007). The efficacy of the system was tested using playbacks. We also investigated sound transmission within the apes' habitat, examining the role of ambient

noise, topography and vegetation in sound transmission, to assess whether such a methodology could be applicable both for researchers and conservationists alike in studying an unhabituated, terrestrial population across a heterogeneous landscape.

Chimpanzees, like elephants, exhibit wide ranges ($>50\text{km}^2$), especially in savanna-woodland habitats. In the Issa Valley, these apes live in a very mountainous terrain, dominated by open, miombo woodlands. Combined, these landscape features present a heterogeneous environment through which to vocalize. Further, at Issa, individuals live at densities $1/50^{\text{th}}$ that of forest-dwelling communities, suggesting potential 'savanna adaptations' to living under such marginal conditions. Moore (1992) hypothesized that savanna chimpanzees may form small parties to forage efficiently, or else the opposite, exhibit increased cohesion in order for community members to maintain contact. To date, however, the logistical challenges of monitoring ephemeral subgroups over space and time has prohibited testing of these hypotheses.

Data from savanna chimpanzee populations are important for numerous reasons. They allow us to test hypotheses concerning behavioral diversity and the influence of a marginal habitat on behavior. Also, they provide a model for how early hominins may have adapted to dramatic landscape changes during the Plio-Pleistocene, namely a retraction of forest cover and shift to a more open habitat

(Cerling et al., 2011 b). Most savanna chimpanzees remain unhabituated, however, making the use of indirect methods, such as PAM, necessary to better understand these chimpanzees' ranging, social, and here, vocalization behavior. Nonetheless, there are significant challenges such as deployment and logistical difficulties that any PAM must overcome. For example, it must have renewable power to reduce maintenance needs. For researchers to locate calling parties for collection of additional data (e.g. party size, demographic information, etc.), the system must transmit sounds back to a central location for immediate access. We thus developed Solar Powered Acoustic Transmission Units (SPATU) to fulfill these requirements and aid in the study of a large, wide-ranging, terrestrial species such as savanna-woodland chimpanzees. To our knowledge, this is the first attempt at using remote acoustic monitoring to study wild primates.

The physical environment & sound transmission

Call types may also vary with locally specific habitat features. The Acoustic Adaptation Hypothesis (reviewed in Ey and Fischer, 2009) predicts that animal call structure and usage responds to the acoustic environment, especially to maximize transmission. However, all sounds degrade once emitted and even without additional sources of attenuation, spherical spreading results in a standard 6dB loss per doubling of distance from the sound source (Mockford et al., 2011). Habitat and overall environmental heterogeneity further degrade

signals, resulting in spectral, temporal, or structural changes to the sound. This can occur from changes in wind (refraction) and/or temperature (attenuation), among others and numerous studies have demonstrated the differences between (especially bird) vocalizations as a function of habitat (Dabelsteen et al., 1993).

In more closed habitats, call elements should exhibit lower durations, lower frequencies, and smaller frequency ranges compared to a similar call in an open habitat. Some studies have successfully shown a relationship between the physical environment and primate vocalizations, demonstrating the flexibility with which primates use their species-specific calls across varying vegetation types (*Cercopithecus mitis*, *Papio papio* - Brown et al., 1995; *Callithrix pygmaea* - de la Torre and Snowdon, 2002). Mitani et al. (1999) suggested that differences in forest structure (woodland-forest in Mahale, Tanzania versus closed-forest in Kibale, Uganda) could potentially explain why elements in the chimpanzee high amplitude call – the pant hoot – from Uganda had more energy at a lower frequency, than pant hoots from Tanzania. The authors conclude, however, that more data on the actual sound environment would be necessary to better explain this variation in pant hoot structure.

Given that many callers may have limited volition over how much they can modify the acoustic structure of their vocalization, studies have examined other ways callers might maximize signal

transmission efficacy. For example, non-anatomical, but behaviorally strategic ways to accomplish this may include adjusting the height from which callers emit sounds, their position, direction of call or time of day (Parris, 2002). Additionally, callers of some taxa (namely, birds) are well-known for exploiting optimal sound transmission conditions.

Temperature and wind interact in important ways with sound transmission, affecting propagation differently across atmospheric conditions (Heimann and Gross, 1999). Temperature inversions can trap sound energy in a ground-based duct, promoting more efficient sound transmission across long distances (Brown and Hall, 1978). Wind may further affect sound, distorting or degrading calls that would otherwise transmit well under calmer conditions.

Weather can also interact with topography, and the result can affect sound propagation. In contrast to flat areas, valley topography influences weather conditions – especially wind and temperature. Sound can refract upward and downward as a result of horizontal and vertical thermal and wind gradients. Winds that vary with the direction of the valley and/or unequal warming resulting from differential exposure to the sun, interact to produce slope winds that are perpendicular to the valley axis (Heimann and Gross, 1999). It is well established how birds adjust their location in response to some of these conditions (Parris, 2002), but similar phenomena have rarely been investigated in terrestrial animals, and not at all in primates.

The combined effect of local topography and environmental conditions can promote complex variation of the sound pressure level across any topographical gradient (Heimann and Gross, 1999). Larom et al. (1997 a) have shown the complex relationship between topography and temperature in modeling the acoustic behavior of African elephants (*Loxodonta africana africana*) in Etosha National Park, Namibia. The authors proposed that the presence of nocturnal (wind) jets over continuously rolling terrain that begin after sunset and continue until early morning may discourage elephant calling in otherwise optimal morning conditions. Given these complex behavior-sound interactions, a primary goal of the current study was to assess the so-called sound environment of the Issa Valley in Tanzania, as well as to assess the efficacy of a new monitoring tool for chimpanzees.

Hypotheses

To test the efficacy of the system, we conducted playbacks throughout the SPATU array. Because sound transmission is likely to be impaired in a mountainous and heterogeneous terrestrial environment, we tested the effect of environmental variables on (playback) sound transmission. Understanding the influence of these environmental variables is important in making predictions about chimpanzee calling behavior in the same area and asking how these apes exploit - or are limited by - their sound environment during calling.

Based on the pioneering work by Brown et al. (1978) and Marten et al. (1977 a) as well as more recent work by Renterghen and colleagues (2007), we expect that sounds broadcast from within open (woodland) vegetation types would travel further, and thus be received by more SPATUs (and theoretically, more chimpanzees if the origin was an actual caller) than those sounds broadcast from closed-canopy forests. Our playbacks are designed to (a) confirm these predictions and (b) establish quantitative parameters for e.g. attenuation differences to be used in interpretation of wild vocalizations.

We tested the hypothesis that playback. Similarly, we predicted that those sounds broadcast from hillside slopes would travel further and thus be received by more SPATU units than those broadcast from flat plateaus or valleys. Finally, we expected environmental variables to also affect sound transmission with positive relationships between temperature, but negative relationships between wind speed and relative humidity because these factors act to attenuate sound.

METHODS

Study site

The current study was conducted between April 2009-March 2010 in the Issa Valley, Ugalla, in western Tanzania (Figure 10), one of the driest, most open habitats in which chimpanzees are studied. The Issa Valley, >90km east of Lake Tanganyika, lies in the west of the Ugalla region, itself a 3300km² area consisting of broad valleys separated by steep mountains and flat plateaus ranging from 900-1800m above sea level. Ugalla vegetation is dominated by miombo woodland - *Brachystegia* and *Julbernardia* (Fabaceae), although also includes swamp, grassland, as well as evergreen and thicket, riverine closed-canopy forests. There are two distinct seasons: wet (October - April) and dry (May - September), with dry months defined as having <100 mm of rainfall. Rainfall averages ~1200 mm per annum (range: ~900-1400 from 2001; 2009-2013) and temperatures range from 11C to 35C (Hernandez-Aguilar, 2006; Stewart, 2011).

Chimpanzees were first studied in this area from 2001-2003 (Hernandez-Aguilar, 2006), and continuously since 2005. A long-term research presence was initiated in 2008 and has been maintained since then.

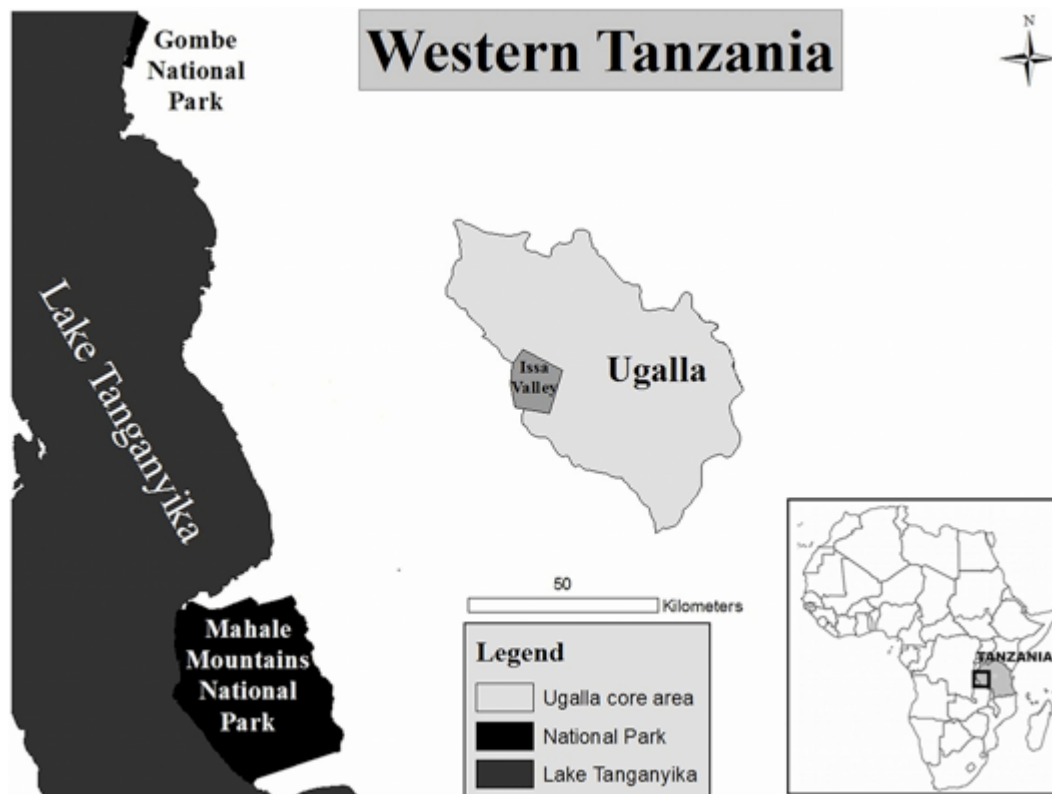


Figure 10 - Map of the study area (Issa Valley) with the two National Parks hosting chimpanzees (Gombe, Mahale Mountains) also labeled

Recording instrument – SPATU

We designed, built, and deployed a SPATU array in the Issa Valley study area. SPATUs consisted of an RF transmitter (model T301, Hamtronics, Inc., Rochester, NY, USA), interfaced with omnidirectional microphone (Cornell University) speech processor (model: VoiceMax, Telstar electronics, USA), and housed in a Pelican case (model: 1600, Peli Products, Derbyshire, UK) (Figure 11). Each radio was powered by 10 2.4V High Temperature Rechargeable Nickel Metal Hydride Cylindrical Cell batteries (model: GP400LAHT, Farnell Distributors, UK), and recharged by a solar panel (model: 10W Yingli solar polycrystalline panel; SelectSolar, Ltd, Essex, UK), via a 10A DZ energy charge

controller (code: 07001DZ02, Select Solar, Ltd, Essex, UK). Transmitters were wired to a yagi directional antenna (model: YA3VHF, RW Badland Ltd, London, UK).

Each omni-directional microphone was composed of ten small, highly sensitive electret microphones designed for high resistance to vibrations, which were soldered on circuit boards (20–20,000 Hz, model: Panasonic, WM-61A series) by Cornell University's Bioacoustics Research Program (Ithaca, NY, USA). 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 crystal oscillator) provided temperature stability of ± 2 ppm over a temperature range of -30°C to +60°C and the transmitters were designed for narrow band FM with ± 5 kHz deviation.

Because two-way radio communication relies on the modulation content within the signal, we also soldered a transceiver speech processor with a built-in Automatic Gain Control (AGC) circuit designed to stabilize the audio level, with <1% harmonic distortion. Noise gate levels – adjustable to block high levels of background or ambient noise - were set independently on each SPATU to maximize signal perception, and thus to extreme sensitivity in most cases. Units

were secured 4-6 metres up woodland trees, usually on plateau-edges overlooking valleys.

Each transmitter was then wired to its own 150-170MHz yagi, directional antenna via RG213 coaxial cable. Antennas were secured 2-3metres from their corresponding SPATU and pointed in the direction of the receiver antenna at the main camp. Vegetation was trimmed as needed to increase panel exposure to the sun and to reduce transmission interference.



Figure 11 - A solar powered acoustic transmission unit deployed at Issa

Receiver

Each SPATU had a corresponding receiver unit (model R302, Hamtronics, Inc., Rochester, NY, USA), designed for narrow band FM with ± 5 kHz deviation. It featured a positive acting, wide-range squelch circuit and additional output terminals for low level squelched audio and discriminator audio as well as COS. Squelch settings were adjusted individually on all receivers for maximum output.

All incoming signals first reached an omnidirectional receiver antenna, secured 22 meters above ground level in a *Brachystegia* sp. tree at the base station. This antenna was wired directly into a Peli case (model: 1610), from which the signals were boosted through a 50ohm, medium high power wideband (2-500 MHz) amplifier. This amplifier was used to compensate for gain loss from splitting incoming signals via a 24 way-0°, 50ohm, 1-200MHz power splitter (model: ZFSC-24-11, MiniCircuits, New York, USA) into their respective channels. Receivers were set in aluminum 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 digital format, from where they were transmitted to a Panasonic Toughbook CF-30 laptop.

SPATU array

The same configuration of SPATUs was used throughout the study, although the number of recorders ranged from 18-22 units due

to maintenance needs. These units acoustically covered $\sim 12\text{km}^2$, from April 2009-March 2010. SPATUs were deployed in modules - clusters of three units - when possible (Figure 12). Units within a cluster were always $<100\text{m}$ from each other, but the distance between clusters was usually ~ 1 kilometer (Piel and Moore, 2007). All units were deployed above valley forests and woodland slopes from where stimuli were broadcast and from where chimpanzees often call (pers. obs.).

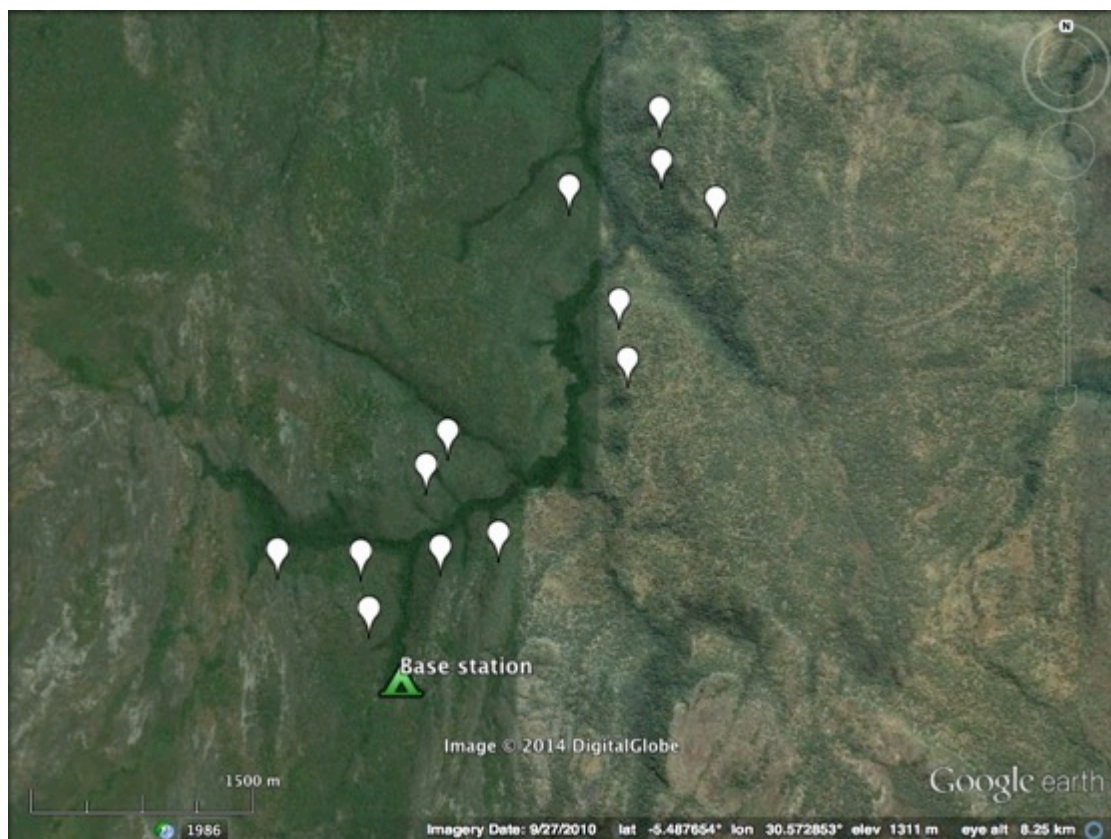


Figure 12 - Map showing the location of all deployed recording units (SPATUs)

Playbacks

We stored playback sounds as an .mp3 file on a digital playback device (Apple iPod nano, Cupertino, CA, USA). We then broadcast sounds from an omnidirectional speaker (model: Crate taxi TX 30E, St. Louis, MO, USA; output: 30W; frequency response: 20-20,000 Hz) at the approximate decibel level (~90-100dB) of the chimpanzee long call (Arcadi-Clark, pers. comm) - the pant hoot, a compound call comprised of several different phases. We conducted playbacks along linear transects starting 50 meters from the nearest SPATU, moving into the center of the nearest module, at ~150m intervals (although this was sometimes impossible due to topography).

For the actual sound played back, we used a tonal sequence rather than a recorded pant hoot from a wild chimpanzee to minimize disturbance to individuals that may have been within hearing range of playbacks (Herbinger et al., 2009; Kutsukake et al., 2012). Specifically, given that chimpanzees are territorial and xenophobic, there are inherent risks at broadcasting calls from unfamiliar individuals. Playback sounds thus consisted of a single, random tonal sequence that was created using the acoustic parameters of a wild chimpanzee pant hoot (range 500-1800Hz). Playbacks were conducted over three days (20 September; 4, 9 October) during the dry season, and over nine days (12-13, 29-31 January; 6-9 February) in the wet season.

We did not change the volume setting on either the iPod or amplifier during playbacks. Nonetheless, for all playbacks we used a sound pressure level meter (model: DT-805, Amateur Recording Technologies, Simi Valley, CA, USA; setting: slow response, C-weighting) to record the ambient noise level immediately prior to playback broadcast, and also for the onset of the broadcast (measured one meter from the speaker). The ambient noise level was recorded three times with an average later taken, as well as the highest reading during the playback.

Prior to initiating a playback session, we sat silently for 30 minutes listening for chimpanzee sounds. Any evidence of their presence (fresh nests or feces, vocalizations, etc.) terminated the playback session to avoid disturbing parties by broadcasting loudly played, unfamiliar sounds. We used human vocal cues (1,2 or 3 shouts), broadcast loudly about the same volume at playbacks, immediately prior to each broadcast to acoustically label each playback. Finally, we recorded various environmental data from each playback site, including a GPS point (model: GPS 130 Hcx; Garmin, Olathe, KS, USA), vegetation type (woodland, open or closed forest), and topographical level (valley, slope, plateau). We used a handheld Kestrel weather meter (model: 4500, KestrelMeters, USA) to record temperature (degree Celsius), wind speed (m/s) and relative humidity among others, as a data point at each playback location immediately prior to broadcast.

Data management & statistical analyses

All sounds were saved as multi-channel .aif files and converted to .wav files. After converting them, we used the sound analysis program Triton (Wiggins and Hildebrand, 2007) to identify recorded playbacks and reduce them to individual .wav files for future analyses. All playback and SPATU locations (GPS coordinates) were plotted on Google Earth, with horizontal distances between each playback and each SPATU measured manually and then entered into a database. Sound files of known playback events were then analyzed on Triton software to examine whether a particular SPATU received the sound. No attempt was made to examine sound strength; rather after both visually examining and listening to the time of the playback, we scored each playback event as either “present” or “absent” on each SPATU. The corresponding environmental data from each playback event were recorded for each SPATU score.

Logistical and linear regressions (conducted in R, v2.11.1 statistical software) were used to examine which environmental variables influence sound transmission across the study area. We included the following variables in the analysis: distance from sound origin to SPATU; ambient noise level and broadcast signal strength (both measured in SPL); vegetation; topography; season; wind gust speed, temperature, and relative humidity.

RESULTS

Inter-SPATU variation and sub-sampling

There were several sources of variation between SPATUs. First, microphone sensitivity and amplification levels were tuned on each unit, at each deployment location to address specific, sound environment variation (Fernandez-Juricic et al., 2005). Second, because SPATUs were individually custom built, rather than industrially manufactured, overall integrity varied between units. This 'integrity' varied from subtle differences in sound quality, likely a result of poor wire-connectivity, to overall malfunction of an entire unit, sometimes with no known explanation.

To address these differences, we sub-sampled which SPATUs to use for analysis. Some units were deployed at the initiation of the study, and never visited again until its completion, functioning effectively for the duration of the study. Other units, however, were regularly problematic (see "Future improvements" below), and we suspected that due to a number of reasons, these machines were not functioning consistently. Despite morning checks of all units on playback days, some tones of >95dB that were broadcast <50m from a SPATU produced no detectable signals on the streaming spectrogram at the predicted time. For this reason, we performed statistical analyses on a sub-sample of only 13 reliable units. That is, because our dependent variable was whether a sound was recorded on a unit, we analyzed

data only from SPATUs we were confident worked consistently throughout the study. Each valley had at least one reliable unit. Once the data were sub-sampled for only reliable data fitting the above criteria, the final sample size for analyses examining sound transmission fell from $n=3930$ to $n=2677$, of which 417 (15.6%) were successful transmissions.

In total, 213 playbacks from 113 different locations were analyzed for transmission efficacy (Table 1). Of these 113, 76% ($n=84$) were broadcast from open vegetation types, versus only 24% ($n=29$) from closed, whilst 30% ($n=34$) were broadcast from the tops of mountains (plateaus), 53% ($n=60$) from slopes, and 17% ($n=19$) from valleys. The mean SPL source level of all playbacks was 102.9dB (range: 92.2-114.4dB).

Table 1 - Total number of playback locations and in what vegetation types and topographical levels playbacks were broadcast

Date	Season	Locations	Open	Closed	Plateau	Slope	Valley
20-Sep-09	Dry	6	5	1	1	4	1
09-Oct-09		25	15	10	14	11	0
12-Jan-10	Wet	21	18	3	1	17	3
13-Jan-10		11	8	3	5	3	3
29-Jan-10		8	5	3	2	3	3
31-Jan-10		9	7	2	3	4	2
06-Feb-10		13	9	4	4	7	2
08-Feb-10		10	10	0	3	7	0
09-Feb-10		10	7	3	1	4	5

The total number of SPATUs deployed did not change in the course of a day during playback sessions, but the number of functioning units did vary from day to day (range 18-22) due to technical malfunctions. In total we measured 3930 different (horizontal) distances between broadcast location and SPATU units. Of these 3930 pairs (playback location-SPATU), 14.5% (n=570) were a successful sound transmission, whilst 3360 were not. Figure 13 and Figure 14 illustrate a given event for five selected channels that received a playback sound. The black rectangle marks a manual identification of a sound event. Note the time delay between the channels, a result of their

distance from the sound origin and the basis for future localization analyses (Freitag and Tyack, 1993; Mennill and Vehrencamp, 2008).



Figure 13 - An example of a playback sound that reached five different SPATUs. The box represents the same call element in each.

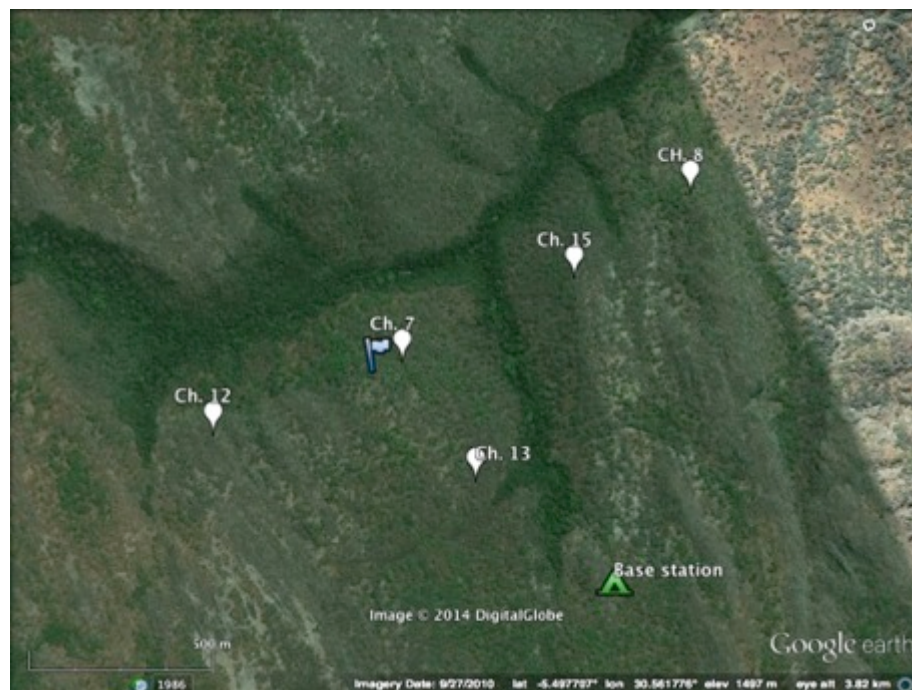


Figure 14 – A map showing the spatial distribution of the recording units and the playback source origin from Figure 10.

What affects transmission efficacy?

There are two ways to measure transmission efficacy: by examining whether a tone was recorded on a given SPATU, and also the distance that call traveled. In order to assess which variables influenced signal arrival, we conducted a logistical regression with nine independent variables (Table 2). Six of the nine variables measured had a significant effect, with only playback sound pressure level and humidity not being significant.

Distance

SPATUs were deployed at fixed distances, all within 4.5km of the base station. Of those broadcast sounds that reached SPATUs, the mean distance was 0.63km (range 0.019 – 3.63km, st dev = 0.44), with the majority within 1km (Figure 15). Over 60% of sounds broadcast from open habitats (flat and slope) between 0-500 meters were received versus less than 40% in closed habitats. After ~ one kilometer, there was a dramatic decrease in sound transmission, likely representing the upper limit of the effective distance between which chimpanzees call. Overall, distance had a significant effect on signal arrival, with unsuccessful playbacks broadcast farther ($\bar{X} = 2.27$, $SE=0.024$) from SPATU units than successful ones ($\bar{X}=0.63$, $SE=0.021$; $t(2675)=668$, $p<0.001$).

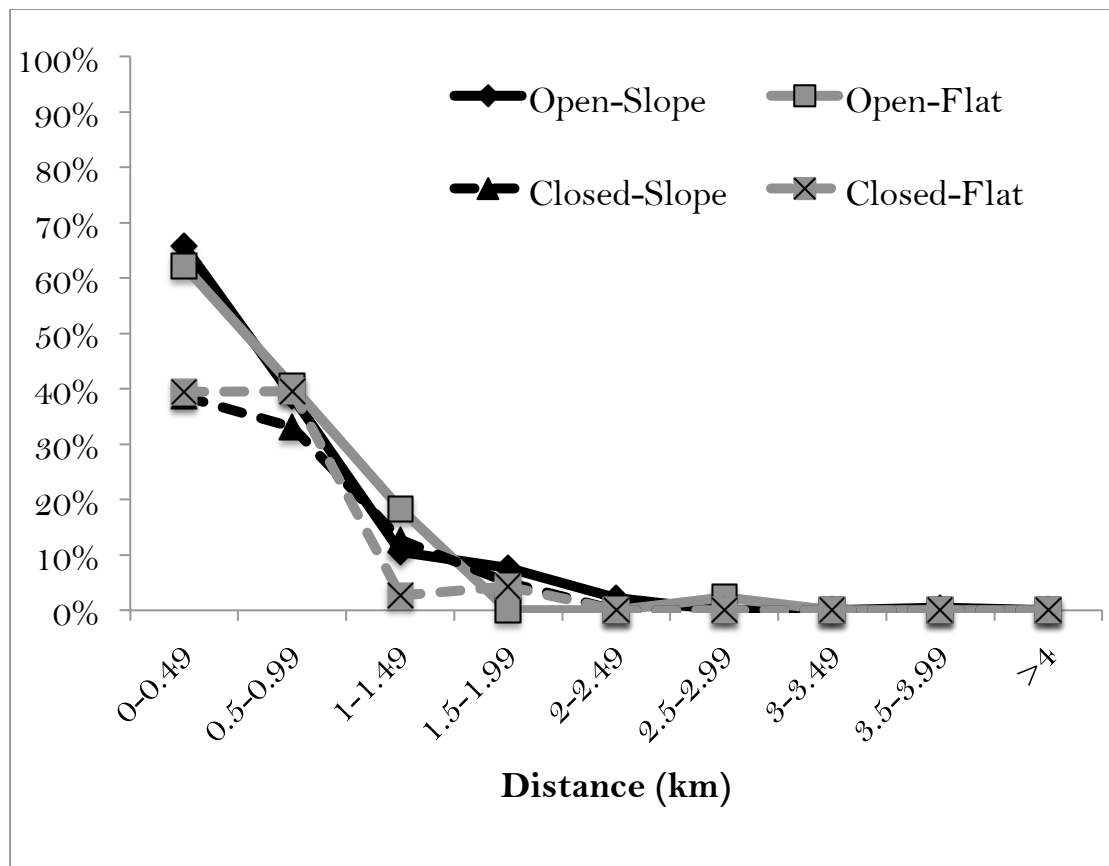


Figure 15 - Graph describing the proportion of sounds received across different topography and vegetation combinations.

Environmental (season and weather) conditions

When all playbacks were analyzed, there were significant effects of season, wind, and temperature, but not for humidity.

Proportionately, significantly more sounds reached the receivers during dry-season playbacks, than during wet season, $\chi^2(1, N = 2677) = 49.95, p < 0.001$. Further, the greater the wind speed and the higher the temperature, the less likely it was that sounds were recorded. There was no significant interaction between wind and temperature ($B=0.001$ (1),

NS) and no interaction between ambient noise and wind speed, $t(200) = -1.241$, NS.

When we looked further into how these environmental features compared across seasons, we found that two of the three measured variables were significantly different between wet and dry seasons. There was more wind in the dry ($\bar{X}=2.04$, $SE=0.318$) than the wet ($\bar{X}=0.47$, $SE=0.103$) season, $t(127)=4.689$, $p < 0.001$, and humidity was significantly higher in the wet ($\bar{X}=78.25$, $SE=1.385$) than the dry ($\bar{X}=45.64$, $SE=2.345$) season, $t(127)=-11.97$, $p < 0.001$. There was no significant difference in temperature between wet and dry seasons (wet mean = 24.82, $SE=0.227$; dry mean = 24.87, $SE=.404$, NS).

Landscape features: vegetation and topography

Given the heterogeneity of the Issa physical environment, we also tested whether sounds played from various vegetation types, and along different topographical gradients, transmitted with different efficacy. We categorized vegetation into either open (grassland or woodland) or closed (open or closed canopy riverine forest), and topography into either valley, plateau or slope (hillside). We found an influence of both vegetation and topography, with those sounds played from open habitats more likely to be received than those played from closed habitats, and similar for those from slopes compared to those from flat (plateau, valley) areas (Table 2).

The sound environment

The final two potential influences that we tested concerned the ambient noise level at the time of playback broadcast, as well as the source level (SPL) of the broadcast itself (which we deliberately sought to keep consistent). Whilst there was no effect of the source level of the playback broadcast, there was an effect of ambient noise level (range 31.4-73.2 dB – Table 2). Contrary to expectation, playback tones were more likely to be recorded when ambient level was higher, rather than lower. This, of course, was unexpected, and is discussed below.

Table 2 - Results from a backward stepwise logistical regression that begin with nine potential influences on whether playback sounds arrived at SPATUs. Seven of the nine were statistically significant, whilst only broadcast volume (db) and humidity were non-significant.

Independent Variable	B	SE	Wald	d.f.	Sig	Exp(B)
<i>Distance</i>	-2.809	0.166	284.671	1	$p \leq 0.001$	0.060
<i>Ambient SPL</i>	0.024	0.005	24.302	1	$p \leq 0.001$	1.025
<i>Vegetation</i>	-0.816	0.167	23.780	1	$p \leq 0.001$	0.442
<i>Topography</i>	0.171	0.064	7.225	1	$p \leq 0.01$	1.186
<i>Season</i>	0.601	0.210	8.193	1	$p \leq 0.01$	1.825
<i>Wind Gust (speed)</i>	-0.102	0.045	5.155	1	$p \leq 0.05$	0.903
<i>Temperature</i>	-0.147	0.029	26.073	1	$p \leq 0.001$	0.864

DISCUSSION

This study demonstrated the value of a new acoustic remote sensing monitoring system (SPATU) to study wild chimpanzee loud calls in western Tanzania. We found that environmental, landscape and sound environment features influenced the success of sound transmission, useful in understanding how these animals (acoustically) use their environment, e.g. when they call, from where, and under what conditions.

The effective range of sound transmission for a simulated tonal sequence akin to a chimpanzee pant hoot was around one kilometer. Under optimal sound conditions (woodland valleys) simulated pant hoots travel up to 3.6km, and under poor conditions (forested plateaus), even sounds from 200m fail to reach their receiver. These data are useful in at least two contexts. First, methodologically, they inform optimal recorder spatial distribution for future deployments of similar systems to acoustically monitor loud calling, wide-ranging terrestrial species (e.g. how many units are necessary, at what distance apart). Second, biologically, our results inform on the distance between which chimpanzees can vocally communicate in an open, wooded habitat, a critical component in our attempts to understand their sociality.

Seasonality and environmental conditions as important variables

There is a direct relationship between temperature and sound propagation. That playback tones were more likely to reach receivers during the dry season supports our hypotheses based on established experiments of sound propagation. That is, the relationship between wind and sound transmission may explain why, across sites, chimpanzee calling behavior peaks at dawn and dusk (Wrangham, 1975; Wilson et al., 2007), when wind is calmest, for example. Subsequent analyses from wild chimpanzee vocalization patterns at Issa support this, with significantly more calls made in the drier than wetter months, likely to take advantage of the acoustic conditions (Piel and Stewart, 2014 a). In the only study that we could find specifically addressing the influence of rain on animal vocalization behavior, Lengagne and Slater (2002) described a 69-fold advantage in sound propagation between dry seasons and rainy-conditions in the tawny owl (*Strix aluco*). They concluded that the constraints imposed by a rainy sound transmission path are likely what limit calling behavior. Although this relationship has not yet been studied in chimpanzees, we can expect the same influences on their long-call behavior.

Finally, we show that sounds played from slopes had a higher probability of reaching recording units than those played from flat areas, and sounds broadcast from open areas (woodlands) traveled farther than those broadcast from closed (riverine forests). These

patterns may explain why Issa chimpanzees often sleep in open habitat, woodland slopes, although other explanations abound (Hernandez-Aguilar et al., 2013; Stewart and Pruetz, 2013).

Unexpectedly, we found that more playback sounds were received when ambient noise was highest. We remain perplexed on why there was a positive relationship. Although we did not predict this and it is contrary to what is a well-established phenomenon in bioacoustics literature (Brumm and Slabbekoorn, 2005), it is possible that the combination of our selected broadcast volume (sounds played at ~100dB), coupled with low frequency signals (500-1800Hz), made ambient noise levels less relevant. The fact that there was a positive relationship found between noise and signal reception could be explained if playback sounds were enhanced by wind, which would have pushed sounds farther and ambient noise levels higher. Investigation into the direction of the speaker and wind would resolve this.

Optimal calling areas

When we combine our results from playbacks in open vs. closed, and flat vs. slope areas, we can quantify to what extent these elements are aiding sound transmission and which, of vegetation type and topography, contribute more to sound transmission efficacy in Ugalla. Figure 15 shows that for sounds made within 500 meters, calling in woodland (open) versus forest (closed) increases the likelihood of a

sound transmitting by 37%, whilst calling on slopes, versus flat areas, increases the likelihood 41%. Whilst overall, sounds transmitted farther when emitted from slope rather than flat areas, topographic variation had an unexpectedly minimal influence on transmission distance. The largest impact was seen between 1.5-2.5 kilometers where almost 10% of sounds were recorded, versus less than 1% from flat areas. After one kilometer, though, sounds from just about anywhere showed low likelihood of being recorded.

These results should be interpreted with caution. One reason that these numbers may not accurately reflect the direct impact of vegetation and topography on sound transmission relates to the acoustic path. That is, sound transmission is widely known to be most affected by (1) interference from ground reflection, (2) scattering (here, namely by branches and other foliage), and (3) absorption by those and also the air and ground (Huisman and Attenborough, 1991). By not measuring any of these influences, we cannot know how they varied from playback to playback. Subsequent tests could include these measurements, potentially even using remote sensing given known relationships between biomass and attenuation rates.

The current SPATU system sought to address the drawbacks of more traditional PAM systems used to date, first by transmitting acoustic data back to a central location for processing and storage, and to allow monitoring of system failure. Second, units still retain some

autonomy (versus being wired to a central base station receiver) and thus can be deployed across a much wider area, providing there is line-of-site to the base station. Third, SPATUs rely on solar power to recharge long-lived batteries. The result is a remote and non-invasive system requiring (in theory) low maintenance that streams incoming acoustic data in real-time, which can then be used for subsequent action, e.g. mobilization of research teams to the caller location.

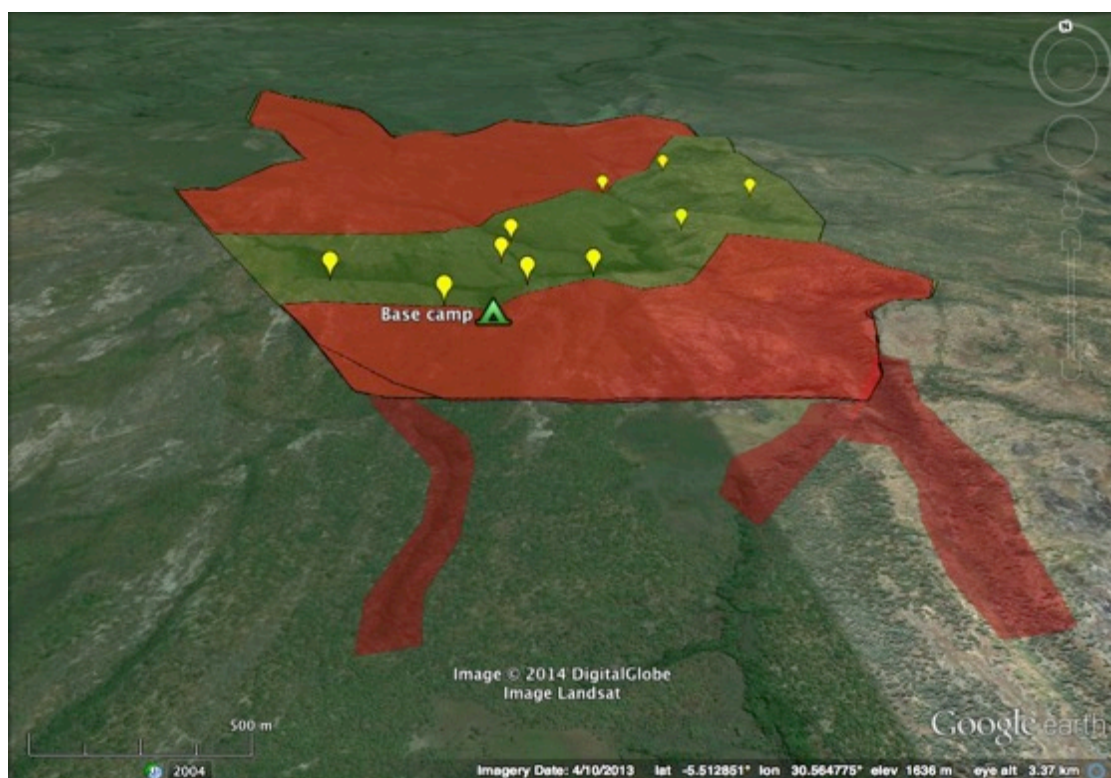


Figure 16 - Study area accessible for use of SPATUs. Yellow balloons represent SPATUs. The internal (green) polygon surrounding the balloons indicates approximate chimpanzee range with acoustic coverage, whilst the peripheral (red) polygons represent chimpanzee range without acoustic coverage, but where we encountered other (nest, fecal, etc.) evidence.

SPATUs, of course, have their own challenges. As described above, because this system relies on FM transmission, each unit requires line-of-site to the base station. As a result, certain portions of the study area could not be acoustically monitored (Figure 16). Finally, whilst battery capacity was calculated for the system and a three-day surplus power capacity included in system design, the Issa Valley wet season sometimes included over a week of overcast days that threatened SPATU power supply, as the solar panels could not generate sufficient energy. Consequently, numerous times, batteries needed either expedited recharging from the central base station system, or else multiple days of solar-charging at its deployment location.

Finally, streaming acoustic data averaged ~1GB/channel/day. Whilst portable hard-drives are increasingly cheap, durable, and small, data processing and organization remain a formidable challenge. Software such as Triton (Wiggins and Hildebrand, 2007), which can reduce large acoustic data sets to manageable visual patterns for faster, albeit manual, analysis became a necessary tool to data-mine and extract scientifically relevant vocalizations. And whilst automated call recognition software, which has revolutionized the way bioacousticians analyze large data sets for a host of species (Wiggins and Hildebrand, 2007; Aide et al., 2013), has obvious advantages, not all elements of playback sounds were necessarily received on each

SPATU. Thus, even sophisticated algorithms (Roch et al., 2013) do not eliminate the need for visual and/or acoustic examination of calls from at least neighboring units.

Future Improvements

Whilst we feel strongly that the SPATUs described here are an improvement on previously described systems, there are areas for further enhancement (see above). Even with long-lived batteries and 10W solar panels, power supplies ran low at times. This could be averted with circuits that sense low voltage and shut down the units automatically, leaving batteries to recharge until a certain voltage before activating again. One logistical challenge continues to be confirming whether system checks were successful. This involved having one researcher remain at the base station to confirm signal transmission before maintenance teams could leave a unit under repair. Incorporation of handheld receivers that could be tuned to various frequencies would allow maintenance teams to check, at location, whether a given SPATU was transmitting. This, of course, does not confirm that a signal is reaching the base station, but at least it would help eliminate some possible sources of malfunction. Finally, because each unit was adjusted manually at each location, the extent of inter-unit recording quality variability is unknown.

PAMs and *Pan*

Despite the pervasive deployment of PAMs in the study of cetaceans and birds alike, few times has this approach been tested with terrestrial mammals, and never with wild primates, nonetheless apes. This is surprising given that (savanna) chimpanzees share with many cetaceans a fluid, fission-fusion social system, large home ranges, and long call-behaviour that serves important functions for movement and sociality.

The heterogeneity of the Issa landscape means that chimpanzees may strategically exploit (or avoid) certain areas of their home range, especially for nesting or feeding. Chimpanzee nest-site preferences have been described as adaptations to building beds in more suitable trees (Hernandez-Aguilar et al., 2013) or else to avoid predation (Stewart and Pruetz, 2013). Additionally, sleeping on slopes, from where individuals typically call immediately before and after sleep (Fischer and Zinner, 2011), would promote increased sound transmission and thus may be one means by which individuals cope with (hypothesized) reduced intra-community interactions (Moore, 1992). This hypothesis is supported at Issa with the data presented here, where winds and temperature gradients significantly affect sound propagation, carrying sounds farther within the steep woodland slopes,

compared to plateau or valley ecotones which attenuate sounds more rapidly.

This system further has at least three more potential applications for the study of wild chimpanzees. First, often times the biggest challenge to collecting data on elusive animals is merely finding them. With real-time data accessible to researchers, caller locations are known immediately and research teams can be mobilize to collect subsequent data. Additionally, given chimpanzees are unlikely to travel at night, monitoring audio channels in the early evening for chimpanzee sounds allows researchers to know where parties will begin their day the following morning. Second, SPATUs simultaneously provide information on caller and receiver locations across space and time, and thus have the potential to inform on the role of loud calls in how especially social animals coordinate movement (Spehar and Fiore, 2013). Finally, there is a growing literature on soundscapes (Servick, 2014), yet little situating primates in their use of particular acoustic niches (but see Schneider et al., 2008). Acoustic monitoring of these complex and often threatened sound environments provides important data to researchers interested in how animals compete for calling space and to conservationists in understanding change in species composition in response to human disturbance.

Conservation applications

Historically, PAM has been successfully used across numerous conservation contexts. They have been deployed to monitor (1) cetacean responses to military training (Melcón et al., 2012), (2) elephant behavior to oil exploration (Wrege et al., 2010), (3) and migrating bird paths (Schrama et al., 2006) among others. Whilst we designed SPATUs with the eventual goal of studying temporal and spatial patterns of unhabituated, wild chimpanzee calling behavior, the current system has numerous additional applications for conservation, both in monitoring biodiversity and also threats. Like other systems (Aide et al., 2013), SPATUs do not discriminate which sounds to record and thus process a variety of other animal (mammal, bird, and amphibian - Piel and Moore, 2010) sounds. Previous studies have discussed at length how acoustic monitoring can provide census data on species (Bardeli et al., 2010), population (Cummings and Holliday, 1985), or even individual (Policht et al., 2009) levels, especially when using spatially explicit (acoustic) capture-recapture (SECR) statistical techniques (Borchers and Efford, 2008) to calculate densities.

We can see the potential application of acoustically generated data to inform on conservation strategies in preliminary SPATU evidence of ecosystem-wide threats at Issa (e.g. gunshots, illegal logging). One can imagine integrating real-time acoustic monitoring with government patrols, for example, to facilitate immediate action

on illegal activity, akin to what unmanned aerial vehicles (Koh and Wich, 2012) and motion triggered cameras are now doing. SPATU-generated acoustic censuses on biodiversity as well as real-time data on critical threats to wildlife represent just two of the additional applications of this technology across an expansive landscape such as Issa.

Chapter Two, in part, is a reprint of the material as it has been submitted to *Bioacoustics*. Piel, A.K., Stewart, F.A., "Solar powered acoustic transmission units: a method of remote sensing for the study of wild chimpanzees." The dissertation author was the primary investigator and author of this paper.

CHAPTER 3: TEMPORAL PATTERNS OF CHIMPANZEE LOUD CALLS IN A SAVANNA WOODLAND

(a)



(b)



Figure 17a and b - Photos capturing early morning (top) and evening (below) at Issa (Photo credits: Top: A. Piel; Bottom: J. Hosak, M. Pollak)

ABSTRACT

Understanding the temporal patterns of animal vocal signals can reveal much about an animal's adaptation itself, and about the evolution of communication systems, especially in complex acoustic environments. Whilst the social influences on especially chimpanzee vocalization patterns are well studied, the influence of the physical environment, especially conditions that propagate sound, has been rarely studied. We deployed a custom-designed passive acoustic monitoring system to study the temporal patterns of wild, savanna-woodland chimpanzee loud calls. Whilst we found no significant effect of either temperature or wind on when chimpanzees call, we did find that fewer calls were produced during high humidity, likely an effect of rain attenuating sound transmission. Further, 83.8% of all chimpanzee pant hoots were made within one hour of a previous call, and 37.8% within one minute, suggesting an important reciprocal element to calling. Most of these exchanges were made in the early mornings and evenings when chimpanzees combine or split. Call rate correlated significantly with party size, suggesting that PAMs are an accurate tool for assessing grouping behavior. The implications of using PAM to understand temporal patterns of chimpanzee calling are discussed, in addition to situating their sounds into a wider, savanna soundscape of acoustic niche partitioning.

INTRODUCTION

Many primates produce loud calls, which vary in function, from advertising fitness to 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 also the coordination of group movement (Boinski, 1993; Trillmich et al., 2004; Braune et al., 2005; Byrne and da Cunha, 2006; Gruber and Zuberbühler, 2013), far less is known about the temporal distribution of primate calls. Understanding the temporal patterns of animal vocal signals can reveal much about an animal's adaptation itself, and about the evolution of communication systems, especially in complex acoustic environments (Pijanowski et al., 2012).

The physical environment itself provides challenges to both callers and receivers. For example, whilst there exist clear hindrances to sound transmission in the form of vegetation and topography (Marten et al., 1977 b; Brown et al., 1995; Mennill et al., 2006; Piel and Stewart, 2014 b), other environmental features such as temperature and ambient noise – which change throughout the day - also influence when sounds are produced. Specifically, temperature and wind interact in important ways with sound transmission, affecting propagation differently across atmospheric conditions (Heimann and Gross, 1999). Temperature inversions can trap sound energy in a ground-based duct, promoting more efficient sound transmission

across long distances (Brown and Hall, 1978; Wilson et al., 2003). Wind may attenuate sound, distorting or degrading calls that may otherwise transmit well under calmer conditions (Hayes and Huntly, 2005). Whilst these two key environmental variables independently influence sound transmission, they also interact with each other and with the topography and vegetation over which sounds travel.

The combined effect of local topography and environmental conditions can promote complex sound pressure levels across a valley system (Heimann and Gross, 1999; Heutschi, 2006; Renterghem and Botteldooren, 2007). Larom et al. (1997 a; b) have shown the complexity of these variables in modeling the acoustic behavior of African elephants (*Loxodonta africana africana*) in Etosha National Park, Namibia. The authors proposed that the presence of nocturnal jets - which form over continuously rolling terrain (Zunckel et al., 1996) beginning after sunset and continuing until early morning - may discourage elephant vocalizations in otherwise optimal morning conditions on flat savanna landscapes. The same appears to be true for lions (Larom et al., 1997 a).

Numerous species across taxa exhibit vocalization peaks at dawn and dusk (Birds: Staicer et al., 1996; Dawn and Vehrencamp, 2005; Cetacea: Johnston et al., 2008; Primates: Maciej et al., 2011) (Table 3), with callers exploiting low abiotic noise levels and ideal microclimates for long distance sound transmission (Henwood and

Fabrick, 1979). Moonlight also influences call patterns. Studies of lunar philia and -phobia have shown that numerous (nocturnal) species change their activity patterns – feeding, vocalizing, and traveling – during full moons (Nash, 1986, *Lepilemur leocoptus* - 2007; *Aotus azarai* - Colquhoun, 1998; Bearder et al., 2002; *Tarsiers spectrum* - Gursky, 2003; Fernández-Duque et al., 2010; *Bubo bubo* - Penteriani et al., 2010). Finally, an emerging literature on soundscapes is demonstrating the complexity of acoustic niches, during both day and night, and thus acoustic competitors will also influence call types, rates, and temporal patterns (Schneider et al., 2008; Pijanowski et al., 2011).

Table 3 - Summary of those primate species for which call peak periods have been described

Common	Species	Call peak(s)	Reference
Common marmoset	<i>Callithrix jacchus</i>	0500	(Martins et al., 2009)
Collared titi	<i>Callicebus torquatus</i>	615-630	(Kinzey and Robinson, 1983)
Black Howler	<i>Alouatta araya</i>	Sunrise	(Byrne and da Cunha, 2006)
Black Howler	<i>Alouatta pigra</i>	Morning	(Cornick and Markowitz, 2002)
Red Howler	<i>Alouatta seniculis</i>	730; 1330	(Sekulic, 1982)
Barbary macaque	<i>Macaca sylvanus</i>	2100	(Hammerschmidt et al., 1994)
Mentawai langur	<i>Presbytis potenziani</i>	700	
Purple faced langurs	<i>Trachypithecus vetulus nestor</i>	~545 ¹	(Schneider et al., 2008)
Mentawai leaf	<i>Simias concolor</i>	700	
Black and White Colobus	<i>Colobus guereza</i>	2h before dawn	(Marler, 1972; Schel and Zuberbühler, 2012)
Kloss gibbon	<i>Hylobates klossii</i>	400 (males); 800 (females)	(Tenaza, 1976)
Kloss gibbon	<i>Hylobates klossii</i>	800	(Whitten, 1982; Schneider et al., 2008)
Lar gibbon	<i>Hylobates lar</i>	500 (males); 700 (females)	(Raemaekers et al., 1984)
Silvery gibbon	<i>Hylobates molloch</i>	0500 ²	(Geissmann and Nijman, 2006)
Orangutan	<i>Pongo pygmaeus</i>	0500; 0800; 1500	(Galdikas, 1983; Mitani, 1985)
Bonobo	<i>Pan paniscus</i>	1700	(Hohmann and Fruth, 1994)
Chimpanzee	<i>Pan troglodytes</i>	700	(Wilson et al., 2007)

¹ Earliest calls reported only

² 500 peaks for males from Limng Asir, whilst data for females are from Ujung Kulon

Despite decades of research describing great ape 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 ape communication informs on the evolution of human language (Slocombe and Zuberbühler, 2005; Slocombe and Zuberbühler, 2007; Crockford et al., 2012; Schel et al., 2013). Save for extensive research into gibbon vocal patterns (Tenaza, 1976; Geissmann and Nijman, 2006), little work into any of the apes has focused on the temporal or environmental influence on loud calls.

Further, most studies have addressed diurnal call patterns only. The few studies that have sought to address nocturnal patterns in diurnal animals have produced surprising results, from behaviorally and vocally active chimpanzees during full moons (Pruetz and Bertolani, 2009) to nocturnally singing robins (*Erithacus rubecula*) when daytime noise is high (Fuller et al., 2007). These reports add to a rich literature that already describes how moonlight can influence activity patterns – vocalizing, feeding and traveling – in various species (Nash, 1986; Colquhoun, 1998; Bearder et al., 2002; Gursky, 2003; Pruetz and Bertolani, 2009; Fernández-Duque et al., 2010). Given the multitude of biotic and abiotic factors that influence calling patterns, there is a need for comprehensive daytime and nighttime acoustic and

environmental monitoring of diurnal species, especially to learn if and how the acoustic world awakes when researchers sleep.

Savannas, sociality, and sounds

Wild chimpanzees live across a range of habitats across equatorial Africa, from moist tropical forests in the center of the continent to much drier savanna woodlands along their western (Baffing, Mali; Fongoli - Senegal) and eastern (Ugalla - Tanzania) distribution. The topography across this distribution also varies from environments that are remarkably flat (Fongoli) to mountainous (Nimba - Guinea, Conakry; Gombe, Mahale, Ugalla - Tanzania) landscapes. Open habitat populations (hereafter, 'savanna') live at extremely low densities and exhibit behaviors not otherwise seen in closed forest habitats - something we can say for certain because of over 250 years of combined studies of chimpanzees (Caldecott and Miles, 2005). For example, savanna chimpanzees use sticks to hunt for bushbabies in Fongoli (Pruetz and Bertolani, 2007) and to dig up underground storage organs at Issa (Hernandez-Aguilar et al., 2007). To cope with extreme conditions, they use caves (Pruetz, 2007) and dig wells in riverbeds (McGrew et al., 2007). Wherever they are studied, savanna chimpanzees also exhibit considerably larger home ranges than in forested communities: (minimal estimates) Fongoli - 65km² (Skinner and Pruetz, 2012); Semliki - 74km² (Samson and Hunt, 2012), Issa - 85km² (Stewart and Piel, 2014).

A characterizing feature of chimpanzee grouping behaviour is their fission-fusion social organization. The fluid nature of changes in sub-grouping composition and duration means that individuals have to maintain social relationships between conspecifics, despite spending (sometimes substantial) time apart. What are the options for this? In forest-dwelling populations, with manageable home ranges (Sonso, Budongo, Uanda, 6km² - Newton-Fisher, 2003), inter-party encounters are frequent, but in savanna populations, inter-party encounters are likely lower, just because there are fewer animals across a larger area (Moore, 1992).

Vocalizations, specifically long calls, may be an important part of the solution. Chimpanzees may rely on their long calls to efficiently coordinate reunions and overall maintain social cohesion with community members (for *Ateles*, see Spehar and Fiore, 2013) that otherwise are rarely seen. Ogawa and colleagues (2007) have proposed that savanna chimpanzees may disperse during the day, and reunite at sleeping sites. Vocalization peaks at nesting times or else “nesting calls” (I. Schamberg, unpublished data) would offer support for this hypothesis.

Why autonomous recording systems?

To be effective, individuals must transmit information to conspecifics, but studying this behavior has obvious limitations. In remote areas or with unhabituated animals, traditional means of

monitoring calling individuals preclude close range recording, and so researchers have relied on the deployment of autonomous acoustic recording units to document vocalization behavior over continuous periods. This approach has been most successful addressing small scales as with birds and small mammals (Blumstein et al., 2011; Mennill et al., 2012) and on large scales with cetaceans (Sousa-lima et al., 2013). Recent attempts with wide-ranging, terrestrial mammals such as elephants (Thompson et al., 2009 a) and chimpanzees (Piel and Moore, 2010) remain the first demonstrations of deploying remote sensing technology to study wide-ranging terrestrial mammals. Autonomous units have another important advantage. They can record at times, from places, and for durations that may simply be logistically impossible with traditional methods (Mennill et al., 2012). The data collected this way may reveal phenomena, like day-night patterns in vocalization behavior, not otherwise accessible without this technique.

Autonomous recording systems also allow the monitoring of entire acoustic networks, namely the ability to situate vocalizations within a social and acoustic network. Monitoring vocalizing animals for continuous periods may provide critical data, e.g. call rates, that can be used for modeling two other phenomena: animal densities and threat levels. Species-specific call rates can be logistically difficult to obtain, yet are a critical component to estimating population density via acoustic signals (Lee and Marsden, 2012), and in the employment

of spatially explicit capture-recapture models (Borchers and Efford, 2008; Borchers, 2010; Martin et al., 2013). Changes in call rates have also been used as a proxy for animal response to increased noise. For example, blue whales increase call rate during seismic testing (Di Iorio and Clark, 2010), whilst other cetaceans and some birds may cease to call altogether when noise levels increase (Brumm and Slabbekoorn, 2005). Establishing baseline levels of call rate may thus allow for later assessment of behavioral responses to stress.

Finally, within acoustic communities animals may occupy particular acoustic niches (Brown and Gomez, 1992; Schneider et al., 2008), competing with other biotic (sympatric species) and abiotic (water, wind, vegetation movements, etc.) noises, all of which, when combined, create a soundscape (Pijanowski et al., 2012). Thus, while the physical characteristics of the environment affect sound type, timing, and propagation, so, too, does the ambient noise create the (sound) environment, within which animals signal. Situating chimpanzee calls within this broader acoustic soundscape has important implications for the role of acoustic communication in chimpanzee sociality, but also on savanna soundscapes.

We studied the vocalization patterns of wild chimpanzees living in the Issa Valley, Ugalla. The study examined temporal patterns of calling including whether long calls corresponded to environmental conditions that facilitate efficient sound transmission across a

mountainous, open habitat. To do this required deploying 1) a passive acoustic monitoring system that continuously recorded and monitored loud vocalizations, 2) weather stations to monitor key environmental variables like temperature, humidity, and wind, and 3) sound meters to record the ambient noise levels at various times of day. The result was a comprehensive dataset of the sound environment, which was used to test whether Issa chimpanzees produce loud calls most often during optimal transmission times when either one or some combination of (1) ambient noise, (2) humidity, (3) temperature and (4) wind were lowest. We further tested whether counter-calling events – as a means of individuals remaining in contact over large distances – would be correlated with party size and when individuals may be coordinating travel (Gruber and Zuberbühler, 2013) (day) and sleeping (evening) reunions (Sugiura, 2001, 2007). This study is thus one of the first to use data recorded by a custom-designed remote sensing acoustic monitoring system to answer questions about the environmental influences on chimpanzee vocalization behavior. This will further serve as a model for other primate and non-primate species, in how to situate them in a broad acoustic soundscape that includes physical environment, ambient noise and sympatric hetero-specific callers.

METHODS

Study site

The study was conducted between April 2009-Feb 2010 in the Issa Valley, Ugalla, in western Tanzania (Figure 18), one of the driest, most open habitats in which chimpanzees have been studied. The Issa Valley, about 100km east of Lake Tanganyka, lies in the west of the Ugalla region, itself a 3300km² area consisting of broad valleys separated by steep mountains and flat plateaus ranging from 900-1800m above sea level. Ugalla vegetation is dominated by miombo woodland - *Brachystegia* and *Julbernardia* (Fabaceae), although also includes swamp, grassland, as well as evergreen gallery and thicket riverine forests. There are two distinct seasons: wet (October - April) and dry (May - September), with dry months defined as having <100 mm of rainfall. Rainfall averages ~1200 mm per annum (range: ~900-1400 from 2001; 2009-2013) and temperatures range from 11C to 35C (Hernandez-Aguilar, 2006; Stewart, 2011).

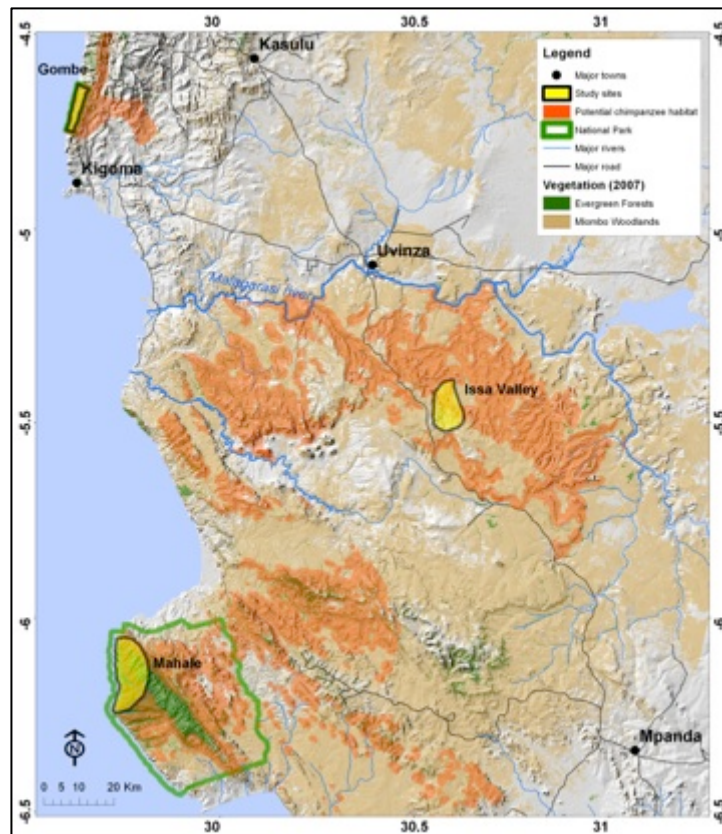


Figure 18 - Map of western Tanzania, including the study area (Issa Valley, center) and the only two national parks in Tanzania where chimpanzees live: Gombe and Mahale Mountains, both along Lake Tanganyika (map: L. Pintea, the Jane Goodall Institute, USA)

Chimpanzees were first studied in this area from 2001-2003 (Hernandez-Aguilar, 2006), and continuously since 2005 (Stewart and Piel, 2014). A long-term research presence was initiated in 2008 and has been maintained since then, with foci on resident red-tail monkeys (*Cercopithecus ascanius*) and yellow baboons (*Papio cynocephalus*), in addition to chimpanzees.

Recording Instrument - Solar Power Acoustic Transmission Units (SPATUs)

We deployed 18-22 acoustic monitoring devices (Figure 19) arranged in modules to maximize coverage over ~ 12km² 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, Select Solar, 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 ± 2 ppm 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 2-3metres 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.



Figure 19 - A solar powered acoustic transmission unit (SPATU), deployed in the Issa Valley.

Receiver

All incoming signals first reached an omnidirectional receiver antenna, secured 22metres atop a *Brachystgiai 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°, 50ohm, 1-200MHz power splitter (model: ZFSC-24-11, MiniCircuits, New York, USA) into their respective channels. Receivers were set in aluminum 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 PCMCIA 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 a 3 weeks break from 3-22 July 2009. The only other times when the entire system was suspended was during severe rainstorms when we sought to minimize the risk to the system in the event of a lightening strike to the receiver antenna.

See also Piel & Stewart (2014 b) for a more thorough description of SPATUs and overall microphone array geometry.

Characterizing the sound environment

The ambient noise level of the day and night environment was measured using an American Recorder Technologies Sound Level Meter (Radio Shack). SPL measurements were recorded three times (once a minute for three minutes) with the average value calculated later across 26 different locations: 12 different day-locations and 14-night locations (Figure 20). Values were recorded in both open and closed habitats (during the day).

We also deployed six HOBO (Onset Corp., Bourne, MA, USA) weather stations across the study site. One station each was placed in the plateau, on the slope, and in the valley topographic levels, and in each of those, in both open (woodland) and closed (forest) vegetation types. These stations recorded temperature, humidity, and wind gust measurements at 30-minute intervals. Finally, rain was recorded using a HOBO rain-gauge for the duration of the study. Lunar data came from published records.¹

Party size: chimpanzee nests

Data on chimpanzee nests came from counts of fresh nests, defined as only those nests with fresh feces or urine in or underneath them. In total, 110 groups were observed over the study period. Of these, the majority was the result of opportunistic encounters (recce walks) or from walking line transects. We identified very few of these groups from the previous evening's acoustic data, which would bias our sample to larger parties.

¹ <http://stardate.org/nightsky/moon>

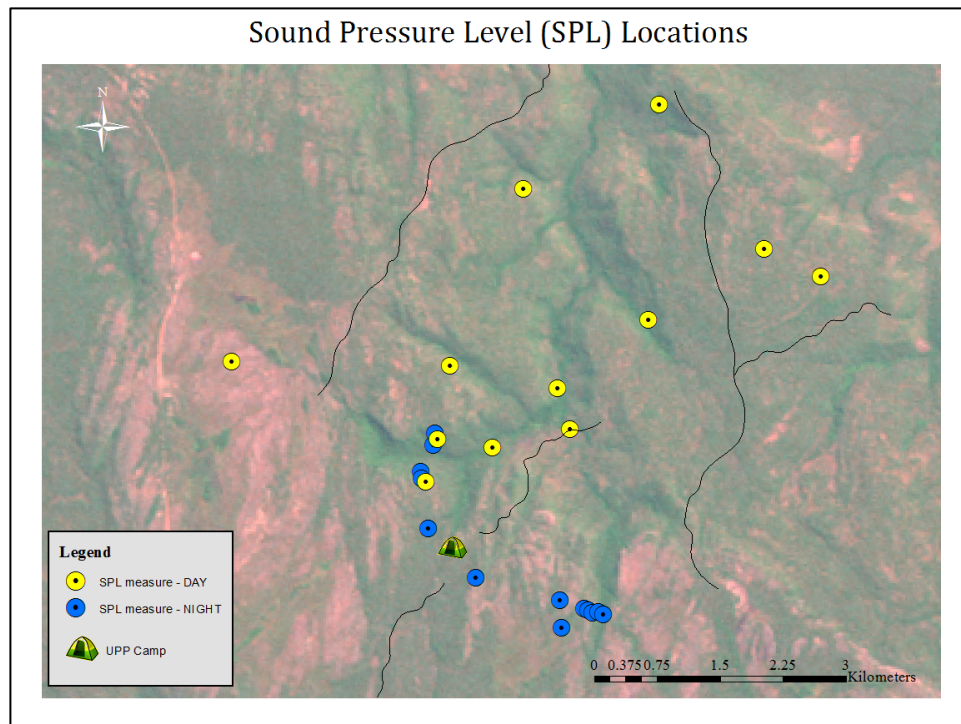


Figure 20 - Map describing the locations of SPL readings of ambient noise. Yellow represents daytime locations whilst blue indicates locations measured in the early evening (20h-22h).

Data management and statistical analyses

Because callers were often hundreds of meters from recording units, it could be difficult to discriminate screams from pant hoots and thus these were consolidated into a single 'loud' category. Whimpers and grunts were not considered. Chimpanzee loud calls were located manually 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, we were able to efficiently sieve the chimpanzee vocalizations, extracting them into a custom

spreadsheet that allowed us to include meta-data such as start and end time of vocalization, channel, etc. Additional information was then included for each call, such as whether it was a loud (pant hoot, scream) or soft (whimper, hoo) call (Clark and Wrangham, 1993). 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 recorded on two different channels.

Calls within one minute were considered for counter-calling/chorusing analyses. When counter-calling occurs between individuals within the same group, this behavior has long been described as *chorusing* (Mitani and Nishida, 1993; Mitani and Gros-Louis, 1998; Giacoma et al., 2010; Schel and Zuberbühler, 2012) versus individuals *counter-calling* from geographically separate areas as observed in various bird (Shackleton and Ratcliffe, 1994; Ascanio-Echeverria and Davis, 2000), bat (Behr et al., 2008), and hyrax (Koren et al., 2008) species.

Finally, this dataset was imported into R (v2.11.1 statistical software) for analyses.

RESULTS

SPATUs recorded sounds for a total of 227 days. 112 of these days recorded at least one chimpanzee loud vocalization. Of these 112, 54 included at least one nocturnal vocalization (defined as between

1900h-659h). We extracted 1573 loud vocalizations over the study period (April 2009 – February 2010). Of these, 1178 were recorded during the dry season, and only 397 during the wet season.

There were significant differences across seasons in all environmental variables that we measured: rain, temperature, humidity, and wind. Rainfall was actually detected in each month, even the late dry season, but clearly peaked between January-March (Figure 21). As has been reported previously (Hernandez-Aguilar, 2009; Stewart et al., 2011), temperatures were highest in the late dry season (August-October) and coolest in the early wet season. Average monthly wind gust speed exhibited parallel patterns to that of temperature.

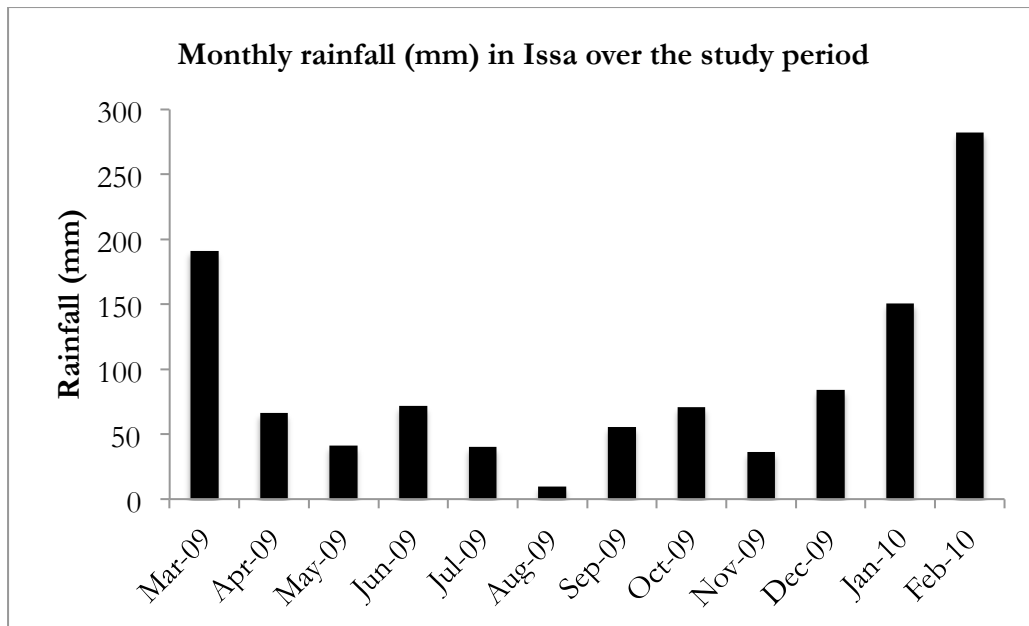


Figure 21 – 2009-2013 average monthly rainfall at Issa

Daily and monthly calling patterns

Issa chimpanzees exhibited three daily peaks in loud calling: 4am, 7am, and 7pm (Figure 22). We categorized the day into six blocks: early (3-7am) and late (7-11am) morning, early (11-3pm) and late (3-7pm) afternoon, and early (7-11pm) and late (11pm-3am) evening, and found that the number of calls differed significantly between blocks ($\chi^2 = 631.14$, $df = 5$, $p = .000$). Over half of all vocalizations were recorded in the early evening (1500h-1859h, 35%) and late morning (700h-1059h, 22%), with the fewest (2%) between 2300h-259h (late evening).

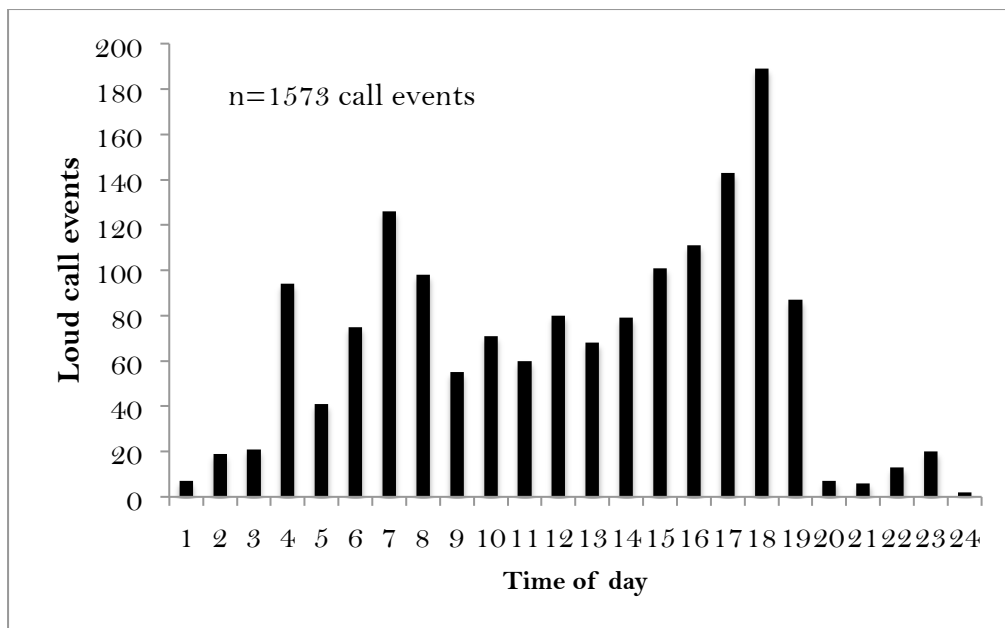


Figure 22 - Total number of chimpanzee loud vocalizations recorded for each hour during the study period

In addition to Issa chimpanzees producing an absolute number of more calls in the dry season, they also produced loud calls at a higher rate during this period as well. Specifically, Figure 23 describes call rate (total number of monthly calls/days recorded), with a dramatic increase in the peak dry season, rising from as low as 1.8 calls/day in the early-mid wet season (December) to as high as 17.1 calls/day in the mid-late dry season (August). However, a Wilcoxon signed rank test revealed no statistical difference in the distribution of loud calls over a 24h cycle between wet and dry seasons, $z = -0.257$, $p = 0.794$ (Figure 24).

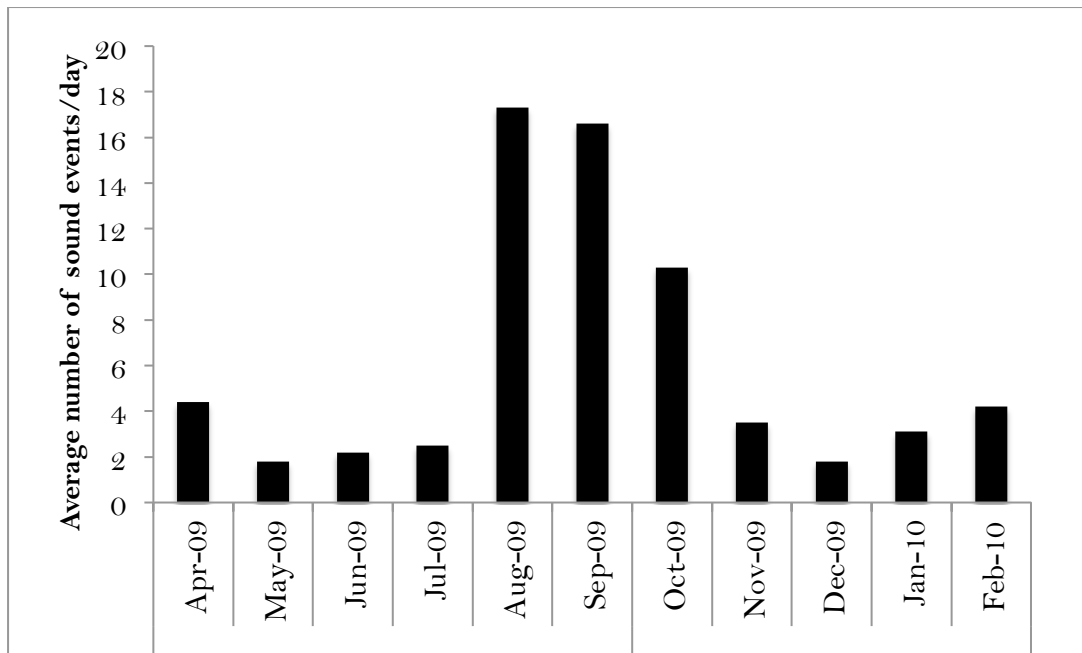


Figure 23 - Call rate of Issa chimpanzee loud calls across months, with the highest rates being produced in the late dry season

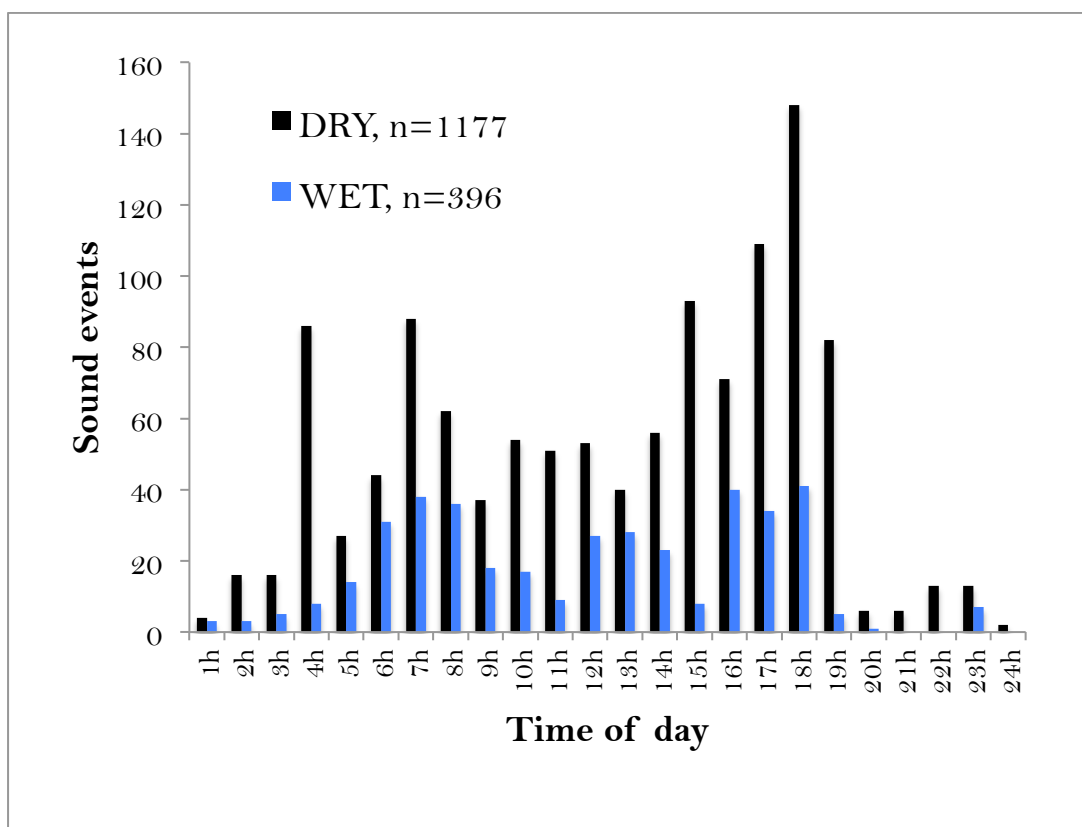


Figure 24 - Loud call hourly distribution across wet (black) and dry (grey) seasons

Calling and environmental conditions

There was no significant relationship between when chimpanzees produced loud vocalizations and either temperature or wind gusts, but relative humidity did significantly explain a proportion of the variation in call presence (Table 4). However, when we analyzed mean monthly call rate (calls/hour) in relation to environmental conditions, we found that wind (Beta = -0.561, $p=.001$), temperature (Beta = -0.946, $p=.000$), and relative humidity (Beta = -0.276, $p=.000$) all were significant predictors. The overall model fit was $r^2 = 0.658$. Given earlier studies examining the relationship between moonlit nights and primate activity patterns, we further examined whether chimpanzees called more often when there was moonlight, versus when the moon was absent. We found a significant difference between moonlit stages and chimpanzee calling, Pearson $\chi^2 (1, N = 6647), p = .000$, as chimpanzees were more likely to call on moonlit nights.

Table 4 - Results from a logistical regression describing the influence of using environmental variables to explain when Issa chimpanzee produce loud calls

Variable	Standard error	d.f.	Sig.	B
Temperature	-0.10	1	0.438	0.438
Relative Humidity	-0.41	1	0.000	0.000
Wind gust speed	-0.007	1	0.865	0.993

In addition to climatic variables discussed above, the acoustic environment for any calling animal includes ambient noise levels as well, influenced by insects, birds, and other mammals (Slabbekoorn, 2004; Pijanowski et al., 2012). We systematically recorded measurements of ambient noise levels (SPL) throughout the day, and in the early evening (Figure 25). When we examined chimpanzee call rate (number of loud calls/hour) in relation to ambient noise levels, we found a positive association, whereby both call rate and noise increased towards a peak at 1800h, then decreasing as evening fell.

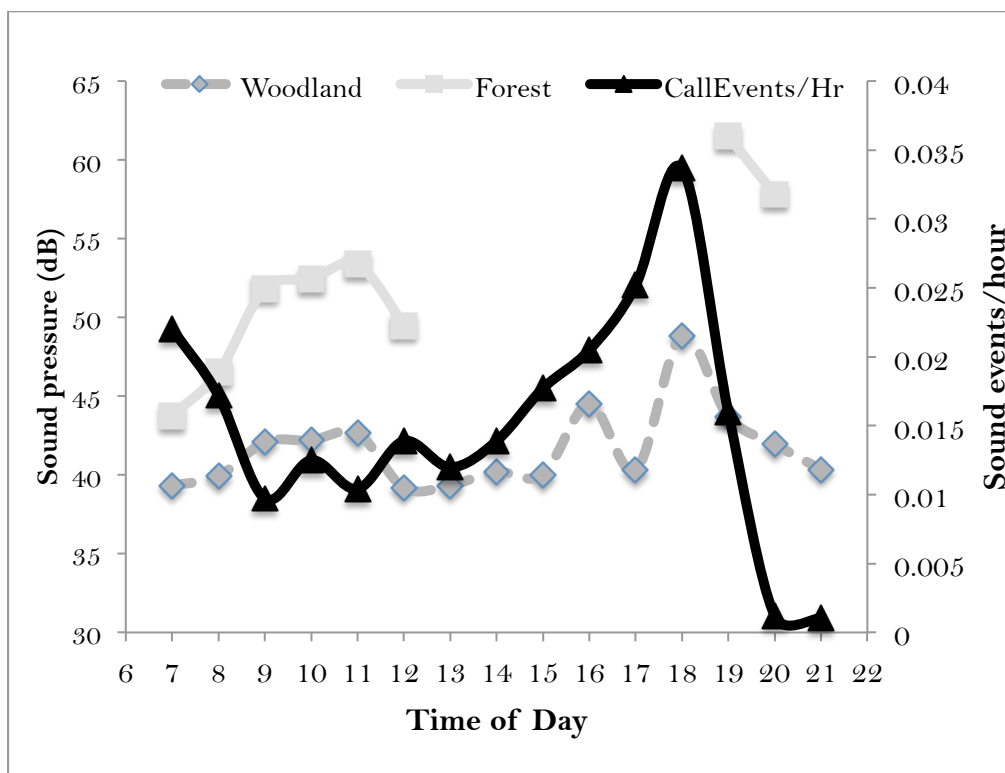


Figure 25 - Ambient noise levels and chimpanzee call events per hour

Nest party size and calling rate

Chimpanzee vocal behavior is influenced by party-composition and, specifically, who else is calling (e.g. 'chorus effect') (Mitani and Brandt, 1994; Mitani and Gros-Louis, 1998). Although chimpanzees at Issa are unhabituated, and thus daily party composition or size could not be reliably assessed, we were able to collect data from fresh chimpanzee nest groups (see Methods) and examine the relationship of nest party size to vocalization patterns. We correlated monthly mean vocalization rates to monthly mean nest group sizes. Both peak in the late dry season: Aug-October and we found a significant correlation between them ($r=0.878$, $n=11$, $p<0.001$; Figure 26).

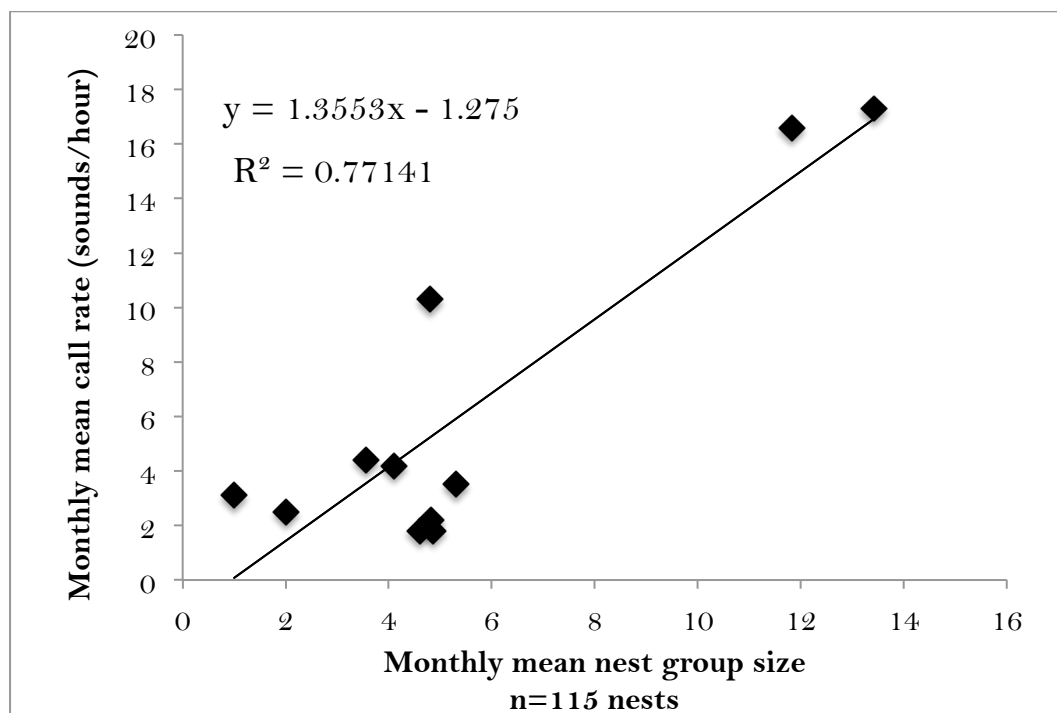


Figure 26 – A significant correlation was found between mean monthly call rate and mean nest group size

Chorusing or counter-calling?

At Issa, the time between the end of one vocalization and the beginning of a subsequent vocalization ranged from one second to multiple days, however the majority of calls that we recorded closely followed a previous call. Of 1573 vocalizations, 83.8% (n=1321) were made within one hour of a previous call. We found a significant effect for calling within an hour ($\chi^2 = 109.80$, df=1, $p < 0.001$) and also minute ($\chi^2 = 721.03$, df=1, $p < 0.001$) of a previous call. Further, 36.5% of all vocalizations (n=575) were made within the very first minute succeeding a previous call (Figure 27). When we analyzed these same patterns between seasons, we found the same pattern, that there were significantly more calls made within an hour (Mann Whitney U-test, $Z = -4.937$, $p < 0.001$) and minute ($Z = -6.430$, $p < 0.001$) in both wet and dry seasons.

We then examined whether there was a relationship between time of day and the immediacy of a counter call to address the question of whether subsequent calls were made equally throughout the day, or disproportionately high during morning and evening periods so that they might function for purposes of coordination and reunion. The sample consisted of calls produced within one minute of a previous call and their temporal distribution across six different four-hour time blocks. There was a significant difference ($\chi^2 = 325.64$, df=5, $p < 0.001$), with most counter calls (within one minute) produced

between 15h-18h ($n=234$, 40.3 %) and 7h-10h ($n=125$, 21.6%), compared to other times of day (Figure 28).

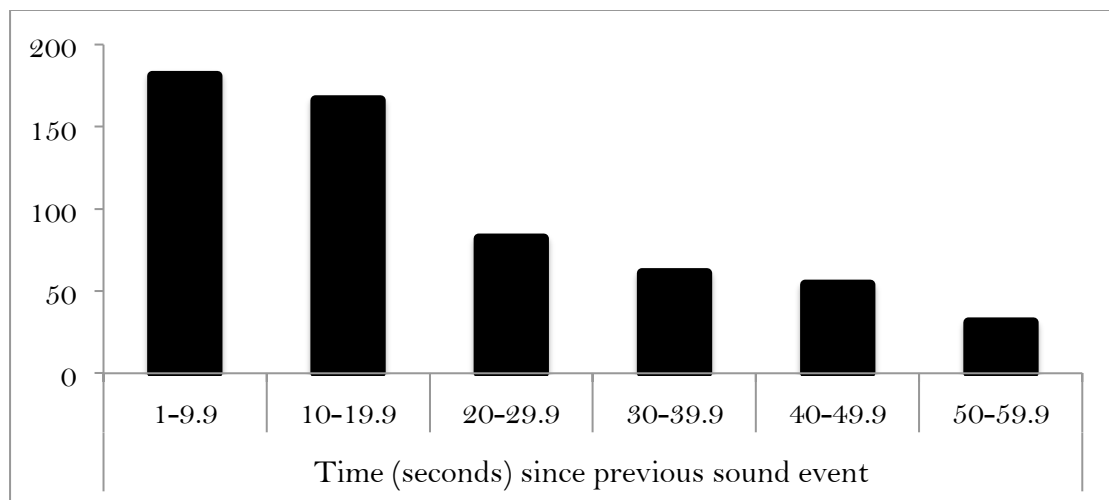


Figure 27 - The time delay between chimpanzee calls of just those sounds within one minute of the previous sound

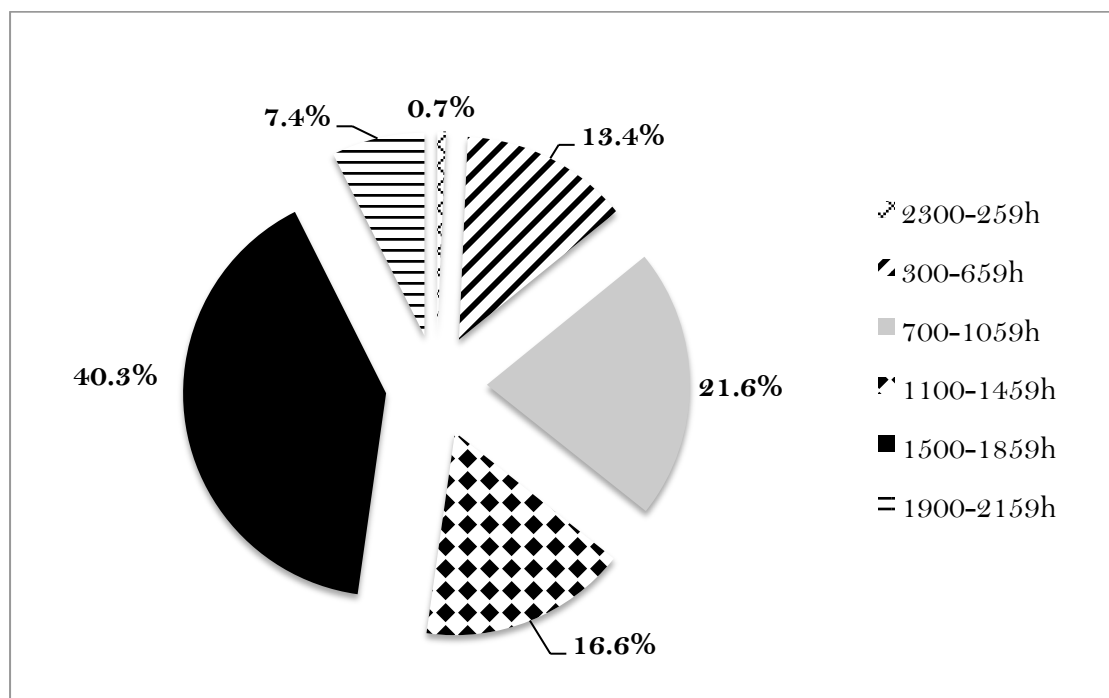


Figure 28 - Hourly block distribution of chimpanzee counter-calls (sounds made within one minute of a previous sound)

Finally, to test whether counter calling frequency correlated with party size, we categorized nest groups into small (1-3 individual nests), medium (4-7), and large (>8) and conducted a linear regression to investigate whether more calls were made within one minute as party size increased. We found a significant relationship only with large nest groups ($B=0.919$, $p=0.000$).

DISCUSSION

This study was unique because it examined the temporal calling patterns of unhabituated chimpanzees in the Issa Valley, Ugalla, western Tanzania using a modular acoustic monitoring system, allowing continuous monitoring vocalizations across space and time. The 18 recording units collected data for 11 months from April 2009 – February 2010 across ~12km². Our data allowed us to test hypotheses examining key questions about when, where and how chimpanzee loud calls are produced and their possible significance in savanna chimpanzee sociality. We could also address the question of whether chimpanzee vocalization patterns corresponded to optimal sound transmission periods.

Time of day

Many species exhibit predictable, temporal patterns of vocalizing. The 'dawn chorus' for example, has been extensively reported and studied in passerine birds (Henwood and Fabrick, 1979; Staicer et al., 1996; Dawn and Vehrencamp, 2005; Kunc et al., 2005),

where vocalizing is described in the context of territorial defense and sexual selection. Whilst similar temporal patterns have been reported in numerous primate species (Table 3), far less is known about the function of these morning and evening vocalizations. Early research tested the acoustic adaptation hypothesis, and found support for primate use of optimal sound windows (Waser and Waser, 1977) and vocalization characteristics specific to open or closed habitat types (Waser and Brown, 1984, 1986), although later studies found only minimal support for these patterns (Ey and Fischer, 2009).

Our data confirm what previous studies at Gombe (Wrangham, 1975) and Kanyawara, Uganda (Wilson et al., 2007) have shown, that chimpanzees call most in the early morning (7h-8h) and early evening (17h). Further, our continuous monitoring revealed four other patterns heretofore not described. First, we recorded at least one loud call at every hour of the day. Whilst historically, there has been little discussion of chimpanzee nocturnal activity, increasing reports suggest that they remain active throughout the night (Pruetz and Bertolani, 2009; Zamma, 2013). Second, our data reveal that not only are Issa chimpanzee vocally active, but also they seem to have a 3rd peak of vocal behavior at 4am. A closer look at weather does not suggest this as an optimal time to call, e.g. temperature is low but wind is high around this time, relative to other times of day. It may, however, be

that ambient noise is low at this time. Future studies would require continuous monitoring of the sound environment to address this.

Given this 4am peak, we also tested whether there was a significant relationship between when chimpanzees vocalize and corresponding lunar patterns. Although lunar-phobia has been widely reported across taxa (Daly et al., 1992; Mougeot and Bretagnolle, 2000), lunar-philía behavior is also common, both in birds (Penteriani et al., 2010) and primates (Nash, 1986, 2007; Gursky, 2003), where moonlit-night calling may actually be an artifact of increased activity (Schel and Zuberbühler, 2012). In the only other known report of lunar-philía in apes, Pruetz and Bertolani (Pruetz and Bertolani, 2009) suggested that Fongoli chimpanzees in southeastern Senegal increase activity – foraging and traveling - on moonlit nights as part of a suite of adaptations to cope with an extremely stressful (hot) savanna environment. Like Fongoli, Issa is also characterized by as an open habitat and thus chimpanzees may respond more to moonlight (here, measured with calling), compared to forest-dwelling populations. Indeed, we found a significant effect of the presence of moonlight and the likelihood of chimpanzees calling. Unfortunately, we could find no data from forested sites with which to compare the Issa lunar-philía. Finally, our data show that calls/hour incrementally increases from 12h until a peak at 17h, which may be suggestive of grouping patterns (see below).

Issa and other ape calling patterns

All apes distribute their calls in proportionally similar ways across the day (Galdikas, 1983; Hohmann and Fruth, 1994; Mitani, 1996; Geissmann and Nijman, 2006; Wilson et al., 2007). In fact, a test for distribution similarity across the Issa and Lomako studies that report hourly calls found no significant difference in distribution over the day, $K-S = 0.291$, $p=0.25$ (Figure 29).

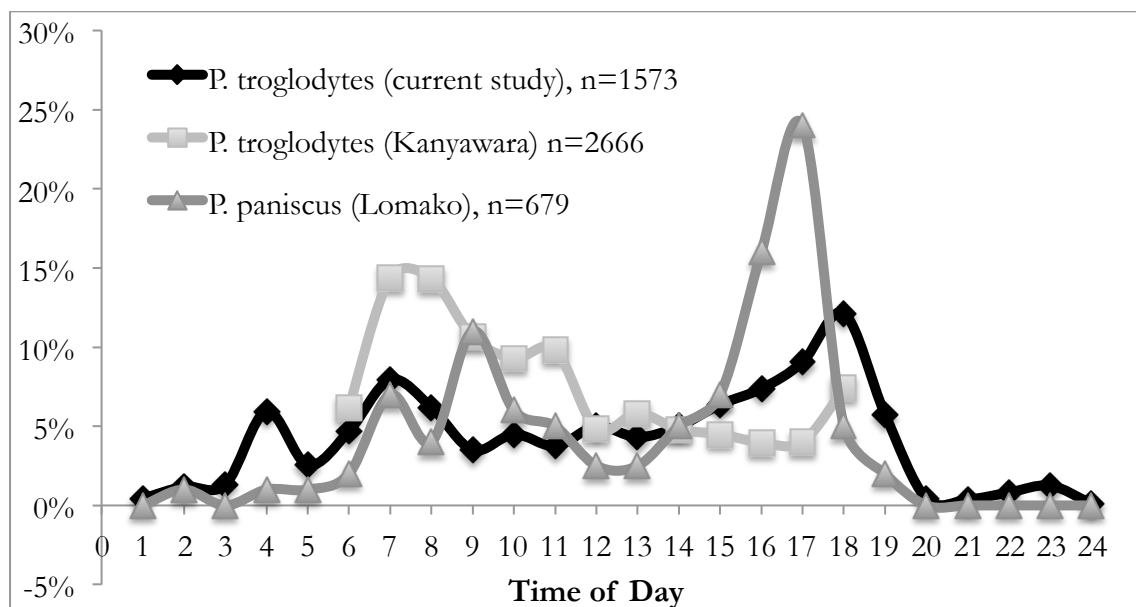


Figure 29 - Comparison of three Pan communities: *P. troglodytes* from Kanyawara (Uganda) and Issa (Tanzania), and *P. paniscus* from Lomako, Dem. Rep of Congo

Seasonal and environmental conditions

We recorded significantly more calls in the dry, than wet season, although calls in both seasons followed similar hourly fluctuations. The variation across seasons is likely due to seasonal differences in social grouping patterns, which is known to influence calling behavior in

chimpanzees (see below; Mitani and Nishida, 1993). A previous study (Piel and Stewart, 2014 b) that described (playback) sound transmission significantly affected by temperature, wind, and humidity was only partially supported here with data from wild calls. Whilst we found no relationship between temperature or wind and the timing of chimpanzee loud calling, we did find a significant inverse relationship between humidity and vocalizations. Our results support similar phenomena described in colobus monkeys (*Colous guereza* - Schel and Zuberbühler, 2012) and Kloos gibbons (*Hylobates klossii* - Whitten, 1982) where individuals called significantly less after cold, wet nights. Whilst we have shown that Issa chimpanzees call less *during* wet periods, rather than *after* them, in both cases wet periods predict lower calling rates.

It is not clear how reliable this effect is at Issa. Although we found a significant relationship between humidity and (an absence of) vocalizations, this may be due to our suspending recording during rain storms to reduce the impact of potential lightening strikes to the receiver antenna. Although this happened only a few times during the study and so does not likely explain this relationship between humidity and calling, further investigation is necessary to rule it out.

Sounds of sociality

The social role of chimpanzee loud calls may outweigh the environmental factors that may otherwise influence their temporal

distribution. Chimpanzees, like other fission-fusion primate societies may use vocalizations to coordinate movement (Gruber and Zuberbühler, 2013) and thus the social function of dawn and dusk vocalizations may be relevant for coordinating reunions, for example, between ephemerally separated sub-groups. Ramos-Fernandez (2005) and Spehar and DiFiore (2013) have argued for this phenomena in spider monkeys (*Ateles* sp.), similar to what has been suggested for silky sifakas (*Propithecus candidus* - Trillmich et al., 2004), white faced capuchins (*Cebus capucinus* - Boinski, 1993), pallid bats (*Antrozous pallidus* - Arnold and Wilkinson, 2011), bottlenose dolphins (*Tursiops truncatus* - Quick and Janik, 2012), and African elephants (*Loxodonta africana* - Leighty et al., 2008).

Ogawa and colleagues (2007) have suggested that Ugalla chimpanzees may distribute themselves into small parties during the day and reunite at evening. If so, this may be reflected in vocalization behavior. Hammerschmidt et al. (1994), for example, found that semi free-ranging Barbary macaques (*Macaca sylvanus*) exhibit increased vocal activity at dusk, specifically as sleeping clusters are forming. Hohmann and Fruth (1994) described the peak of wild bonobo calling in the early evening to represent a call to gather individuals and “regulate and maintain the social network” with larger nest than day party sizes. Our findings that Issa chimpanzees exhibit call peaks in early evening suggests these calls may function to unite subgroups otherwise

separated during the day. More data on day party sizes are necessary to more thoroughly test this hypothesis, though.

Chorusing, counter-calling, and coordinating

In a variety of loud calling species, there is minimal delay between the onset of one call and a subsequent call by a different individual (Tenaza, 1976; Whitehead, 1987; Hyman, 2003; Koren et al., 2008; Schel and Zuberbühler, 2012). The result of this counter call (or counter-singing) behavior are choruses, which have been described to function in male-male competition and territory defense (Marler, 1972; Wich and Nunn, 2002). Whilst chorusing is usually described for chimpanzees as those individuals within the same party (Mitani and Nishida, 1993; Fedurek et al., 2013), at Issa, where individuals live at low densities and range over large areas, we hypothesize that counter-calls are used to coordinate movement and advertise party composition between widely separated individuals. With unhabituated animals, however, we can only assess here the temporal patterns of (a) how often Issa chimpanzees wait before “responding” (e.g. time delay between calls) and also (b) how those counter-calls are distributed across time.

We tested not only the likelihood of one call being ‘answered’ by another (within one minute) and also how those counter-calling episodes were distributed across the day. We hypothesized that if such counter-calling was being used to coordinate movement, for example,

the majority of them would be produced in the early morning and late evening (e.g. morning travel; evening reunions), as seen in some other species (Kinzey and Robinson, 1983; Macedonia, 1993; Hohmann and Fruth, 1994; Kitchen et al., 2004).

We found that 37.8% of all recorded (loud) vocalizations were made within one minute of a previous call (and >83% within an hour) and further, those counter calls were made significantly more often between the hours of 3-6am and 15-18h (see Figure 28), when chimpanzees form daily and nesting associations, respectively. Whilst call peaks at these times have been reported in numerous other chimpanzee communities, we could find no study that has examined the temporal distribution of counter calling events. Thus, it is unclear if the pattern observed at Issa is an adaptation to living at low densities, or else a typical phenomenon across *Pan* communities. Further, until we incorporate the location of individual callers (unpublished data), we cannot test hypotheses of social coordination via loud calls.

We could find only few studies that described comparable data on time delays between counter calling primates, all of whom used traditional data collection methods (e.g. focal follows), rather than PAM. Whitehead (1987) claimed that around 70% of red howler monkey (*Alouatta palliata*) morning calls overlap with neighbor calls and Tenaza (1989) described 40% of male pig tail langur (*Simias concolor*) calls coming within 30 seconds of a previous one. Hohmann

and Fruth (1994) reported that wild bonobos respond acoustically to conspecific vocalizations 45% of the time, whilst 25% of heard calls elicited no (apparent) behavioral response. They did not discuss the time between vocalizations and behavior. More recently, Spehar and DiFiore (2013) showed that 32% (246/773) of Ecuadorian spider monkey (*Ateles belzebuth*) loud calls were made within 15 seconds of previous calls (and 60% within an hour) and subgroups were significantly likely to experience a change in size as a result of hearing a conspecific call. Most related to our study, Zamma (2013) spent five nights near chimpanzee nest sites in Mahale Mountains, Tanzania and reported that >75% of nocturnal vocalizations were responded to within five minutes.

Our observations of a relationship between larger party sizes and increased counter calling contradict those found previously for forest-dwelling chimpanzees. Mitani and Nishida (1993), for example, argued that chimpanzees at Mahale Mountains vocalize to maintain spatial contact between individuals, showing that individuals travel more before and after call events. They found no relationship, however, between party size and calling behavior, and instead suggested that proximity to close associates most reliably influences whether pant hoots are produced. Once again, there was no discussion of time delay between loud calls.

Regardless, the methodological differences between our study and those described above means that comparisons are tenuous at best. Most of the above studies used focal follows of individual, ensuring that each vocalization is documented, with results subject to high inter-individual variation. Remote sensing, on the other hand, monitors all callers, but only when they are in auditory range of recorders, and so time delays may actually represent vocal activity from distant callers rather than actual silence.

Savanna soundscapes

In birds and primates alike, explanations for the dawn-dusk chorus centre on optimal (atmospheric) calling conditions during early morning and early evening periods, with minimal insect noise and calmer winds. Our data reveal that chimpanzees call most often at 700h and 1800h, but also exhibit a peak at 4h. This final peak is unusual for chimpanzees, although is similar to what has been reported for silvery gibbons (Tenaza, 1976). Surprisingly, we found that ambient noise level was also highest around 1800h, when chimpanzees exhibit their second daily peak. Schneider et al. (2008) reported a similar relationship between high ambient noise and high calling activity in primates living in Siberut (southeast Asia), and they suggested that phylogeny explains why so many (closely related) species exhibit similar call patterns, but they do not address the unlikely relationship between simultaneous high ambient noise and increased calling activity. For

chimpanzees it may be that the social function of loud calls (i.e. night-time reunions promoting increased vocalizations) outweighs the cost any signal-loss due to high noise levels.

Alternatively, chimpanzees may be accommodating (and being accommodated by) other vocalizing fauna. That is, calling animals may exploit available frequencies not being occupied by sympatric vocal species (Naguib and Wiley, 2001; Nemeth et al., 2006).

Examination of this 'Soundscape' – the various sources of biophonic, geophonic, anthrophonic sounds within a single system – and overall sound distribution across space and time has been most recently used to assess the effect of human disturbance on landscapes (Slabbekoorn and Bouton, 2008; Pijanowski et al., 2011, 2012), but it may also explain some of the temporal variation in chimpanzee vocalizing at Issa. For example, Figure 30 below provides examples of two separate calling events at Issa, and places all callers in a larger, bioacoustic context, with other vocalizing fauna labeled. From these cases, we can see species-specific frequency ranges. Further studies should investigate to what extent callers are balancing abiotic (e.g. temperature, wind, etc.) and biotic (other animal vocalizations) sounds.

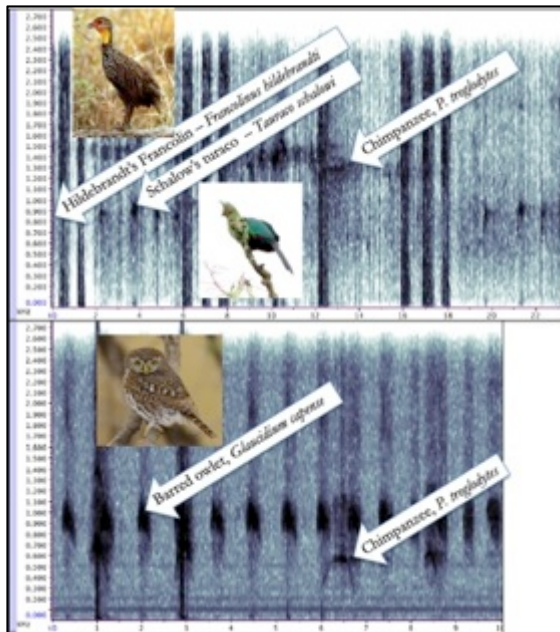


Figure 30 - Two examples of Issa chimpanzee calling events and how they fit into the broader, biophonal soundscape

Conclusions and Future Studies

This study has demonstrated the value of employing an established monitoring method in a novel context to address questions about chimpanzee adaptation to a savanna woodland environment. Eighteen recording units were deployed across ~12km² area and when combined with weather station data, reveal a unique data set on the temporal patterns of Issa chimpanzee loud calls. Chimpanzees produced most of their vocalizations in the early morning and early evening, and this pattern does not differ between seasons, although overall, far more calls were recorded in the dry season (especially August-September). There was no evidence that this peak was influenced by seasonally-specific weather patterns.

Instead, social factors may have influenced monthly call rate. The increase in call rate with nesting party size at this time of year suggests party size is the best predictor of chimpanzees calling, and that calls may be coordinating group movement (morning) or reunions (evening) (for *Pan*, see I. Schamberg, unpublished data; for *Ateles* see Spehar and Fiore, 2013). A closer look at the spatial distribution between callers will help resolve whether this pattern is a species-specific phenomenon, or else an important adaptation to living at remarkably low densities and covering large home ranges while maintaining their fission-fusion social system.

We have discussed elsewhere the numerous ways to improve the hardware (Piel and Stewart, 2014 b). For future studies, more systematic data on ambient noise levels may inform on the type of nocturnal peaks seen here, and more data on diurnal and nocturnal grouping patterns will better help address the question of how chimpanzee call rates change with grouping patterns. Further, it is unknown to what extent inter-individual variation may explain the current temporal variation. That is, sequential vocal events could be made by the same individual and thus not be examples of counter-calling or chorusing. Comparative data examining inter-individual call patterns in habituated chimpanzees may help address this. Finally, the inter-community comparisons described here are weakened due to poor methodological standardization in data collection e.g. active in

habituated sites, passive at Issa. Thus, future work would ideally deploy passive acoustic monitoring at a habituated site, to ensure data compatibility.

CHAPTER 4: LOCATING HIDDEN HOOTS: CHIMPANZEE SPATIAL DISTRIBUTION MONITORED BY REMOTE SENSING



Figure 31 - An Issa chimpanzee watching researchers from a miombo woodland perch in the late dry season (Photo: N. Cohen)

ABSTRACT

Chimpanzee spatiotemporal exploitation of their territory is a particularly important question for savanna-woodland dwelling populations that live in environments closely resembling those of human ancestors. To test hypotheses concerning chimpanzee space use and indications of their social organization in the Issa Valley, western Tanzania, we deployed a remote acoustic sensing monitoring system and used caller locations to reflect chimpanzee presence. Results showed that chimpanzees called more often from the southern portion of their range during the wet season, and less from the north, during the dry season. Despite this pattern, neither seasonality or geographic location (northern, central, or southern areas) best predicted from where a call was made; rather, the location of the previous call did, suggesting that chimpanzee long calls at Issa serve a highly social function, with call locations clustering over time and space. Finally, acoustic activity did significantly predict chimpanzee presence, as independently measured from ground-truthing, but overall, we argue that PAM is best used in conjunction with other methods (e.g. line transects) to best describe chimpanzee use of space.

INTRODUCTION

Chimpanzees (*Pan troglodytes*) spatially exploit their territories in response to changes in social and environmental resource distribution. In addition to spending more time near preferred feeding trees (Moscovice et al., 2010), male chimpanzees have been shown to spend more time along their territorial boundaries (Chapman and Wrangham, 1993; Wilson et al., 2007) and in their mother's core areas (Murray et al., 2008), whilst females' space use is influenced by dominance rank (Murray et al., 2007), in addition to high quality food sources. All chimpanzees are likely also influenced by the distribution of predators (Willems and Hill, 2009) and human activity (Last and Muh, 2013).

Chimpanzee spatio-temporal exploitation of their territory is a particularly important question for savanna-woodland dwelling populations. A central question in paleoanthropology concerns the social and behavioral consequences of human ancestors moving from a closed, moist environment to an open, drier one. If, as observed today in chimpanzees, open habitat hominin groups lived at lower densities (Table 5) and exhibited wider ranges than those from closed habitats, then we can make hypotheses about the costs to the traditionally described social unit ('party'), and more broadly, how a fission-fusion system is maintained. Hypotheses for these consequences include reduced inter-party encounters to more efficiently exploit

widely distributed food resources. Or, the opposite, more cohesive grouping patterns to maintain inter-individual relationships (McGrew et al., 1981; Baldwin et al., 1982 a; Tutin et al., 1983; Moore, 1996).

Monitoring spatial-temporal patterns in an extant community of savanna-dwelling chimpanzees may help us develop models on which, if either of these, extinct hominins exhibited.

In the current study, we deployed a custom designed passive acoustic monitoring (PAM) array in the Issa Valley, Ugalla, western Tanzania to study the spatial calling patterns of wild chimpanzees. PAM remains an unorthodox method for the study of wide ranging, terrestrial species (Piel and Stewart, 2014 b), although its application has now been successfully demonstrated in the study of at least two species (yellow-bellied marmots, *Marmota flaviventris* - Ali et al., 2008; elephants, *Loxodonta africana* - Thompson et al., 2009 b; Wrege et al., 2010) and as proof of concept with another (chimpanzees - Piel and Moore, 2007).

Using vocalization data as a proxy for chimpanzee presence, we monitored chimpanzee use of ten different contiguous areas within the Issa Valley for eleven months. The results of the study reveal how a passive, remotely deployed acoustic system can inform on if, when, and how a community of unhabituated, wide-ranging chimpanzees uses its home range. We hypothesized that Issa chimpanzees would (1) vocalize more often in areas where the majority of their food sources

were located (e.g. forested areas during the wet season, woodland areas during the dry season) (Hernandez-Aguilar, 2006; unpublished data). We also tested whether periods of acoustic silence indicate chimpanzee absence or else just quiet parties. We predicted that (2) when no chimpanzee sounds were recorded, field teams would also not find other evidence (feces, prints, nests) of their presence. Finally, if savanna chimpanzees exhibit a social organization unlike forest-dwelling communities, and exhibit more social cohesion, for example, then (3) vocalization events would cluster in time and space, suggesting individuals travel and forage together as a single unit, rather than fission and fusion as has been traditionally described for the species.

Table 5 - Wild chimpanzee population densities in forest- and savanna-dominated habitats

Community (Country)	Population Density (ind/km ²)	Reference
FOREST		
Nouabale Ndoki (Central African Republic)	2.65	Yamagiwa 1999
Odzala, Rep of Congo	2.74*	Bermejo 1995
Ngotto (Central African Republic)	0.29*	Brugière et al. 1999
Lope Forest (Gabon)	0.58	White 1994
Countrywide (Gabon)	0.32	Tutin & Fernandez 1984
Bili, DRC	0.6	Hicks 2009
Dzanga-Ndoki National Park (Central African Republic)	0.16	Blom et al. 2001
Compiled, E. Africa	0.73	Plumptre et al. 2010
Lagoas de Cufada Natural Park, Guinea Bissau	0.22	Carvalho et al. 2013
Tai Forest, Cote d'Ivoire	0.69-1.76	Kouakou et al. 2009
Republic of Congo	0.7	Poulsen & Clark 2004
Kalinzu Forest (Uganda)	4.71	Hashimoto 1995
Sonso, Budongo Forest Reserve (Uganda)	3.2-6.8	Newton-Fisher 2003
Ngogo, Kibale National Park (Uganda)	5.1	Potts et al. 2011
Kanyawara, Kibale NP (Uganda) -	1.4	Potts et al. 2011
Gombe National Park (Tanzania)	2.44	Williams et al. 2004
SAVANNA		
Fongoli, Assirik (Senegal)	0.09 – 0.13	Pruetz et al. 2002
Semliki (Uganda)	0.36	calculated from Hunt 2000
Ugalla (Tanzania)	0.08 – 0.26	Moyer et al. 2006; Piel & Stewart 2013; Yoshikawa et al. 2013; Moore & Vigilant 2013

* cited in Hicks 2009

METHODS

Study site

We collected data between April 2009-Feb 2010 in the Issa Valley, Ugalla, in western Tanzania (Figure 32), one of the driest, most open habitats in which chimpanzees are studied. The Issa Valley, <100km east of Lake Tanganyika, lies in the west of the Ugalla region, itself a 3300km² area consisting of broad valleys separated by steep mountains and flat plateaus ranging from 900-1800m above sea level. Ugalla vegetation is dominated by miombo woodland - *Brachystegia* and *Julbernardia* (Fabaceae), although also includes swamp, grassland, as well as evergreen gallery and thicket riverine forests. There are two distinct seasons: wet (mid October – mid April) and dry (late April – late September), with dry months defined as having <100 mm of rainfall. Rainfall averaged ~1400 mm per annum from 2009-2013 (Figure 33) and temperatures range from 11C to 35C (Hernandez-Aguilar, 2009; Stewart et al., 2011). Chimpanzees were studied first in this area from 2001-2003 (Hernandez-Aguilar, 2006), and continuously since 2005. A permanent research presence was initiated in 2008 and has been maintained since then.

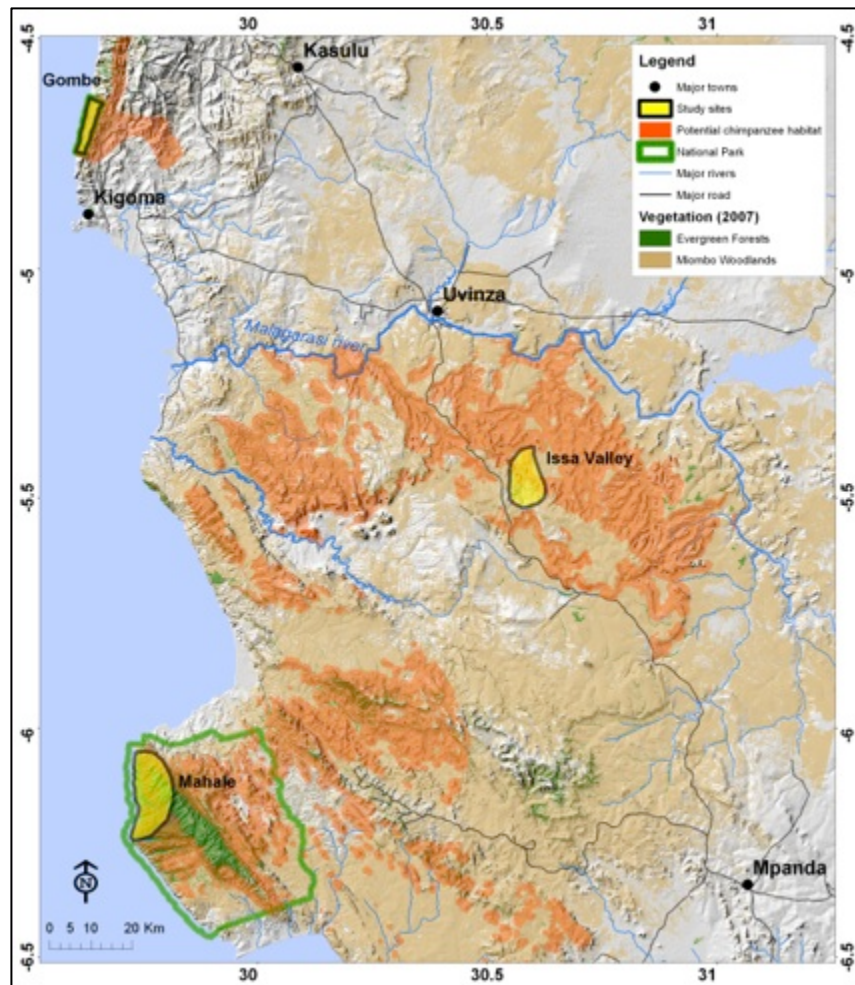


Figure 32 - Map of western Tanzania, with the study area (Issa Valley, center), and Mahale and Gombe National Parks all marked with green boundaries. Credit: L. Pintea, Jane Goodall Institute.

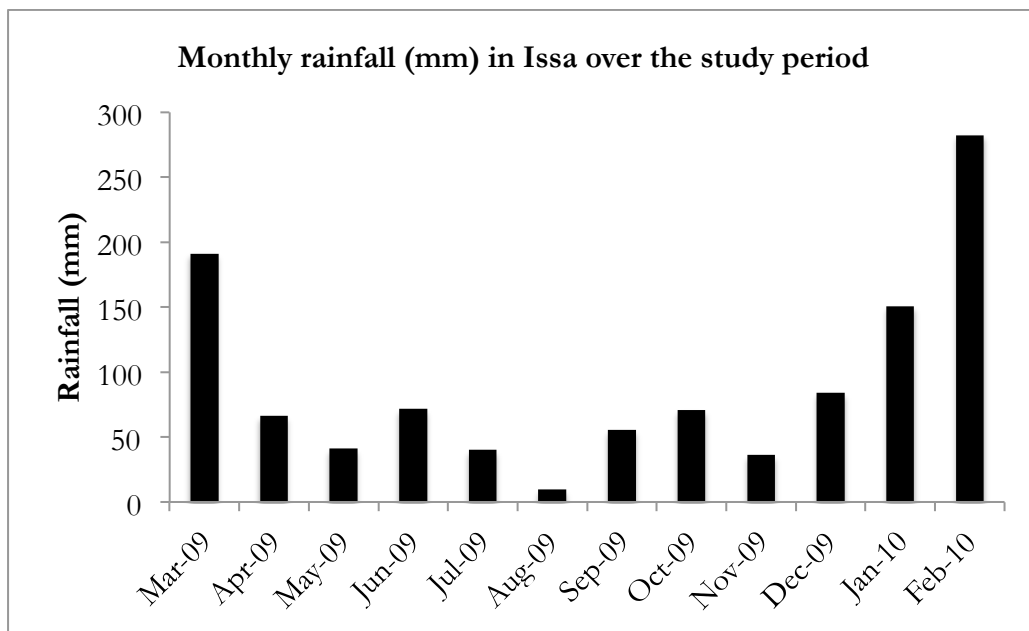


Figure 33 – 2009-2013 average monthly rainfall at Issa

Recording Instrument – Solar Power Acoustic Transmission Units (SPATU)

Acoustic data were recorded from ten acoustic monitoring devices, with each deployed atop mountains across the study area, covering ~ 12km² (Figure 34 and Figure 35). The average nearest-neighbor distance between SPATUs was 593m (range 0.56 – 1.07km). Details on SPATUs can be found elsewhere (Piel and Stewart, 2014 b).

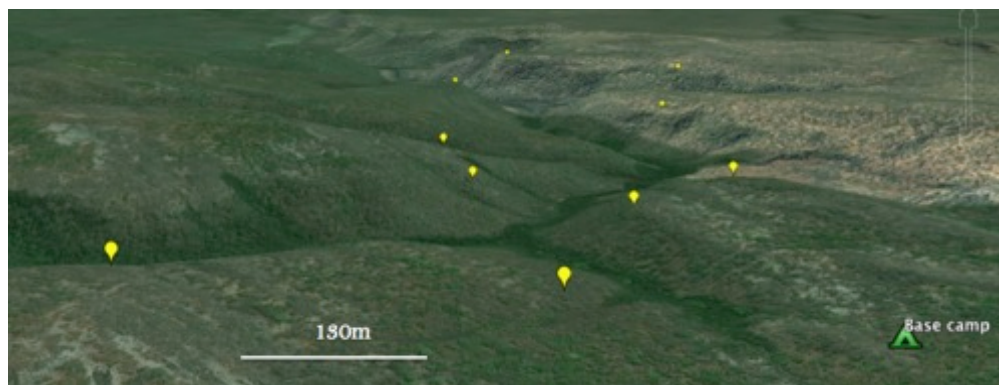


Figure 34 - Three-dimensional image of the study area. Yellow balloons represent SPATU locations.

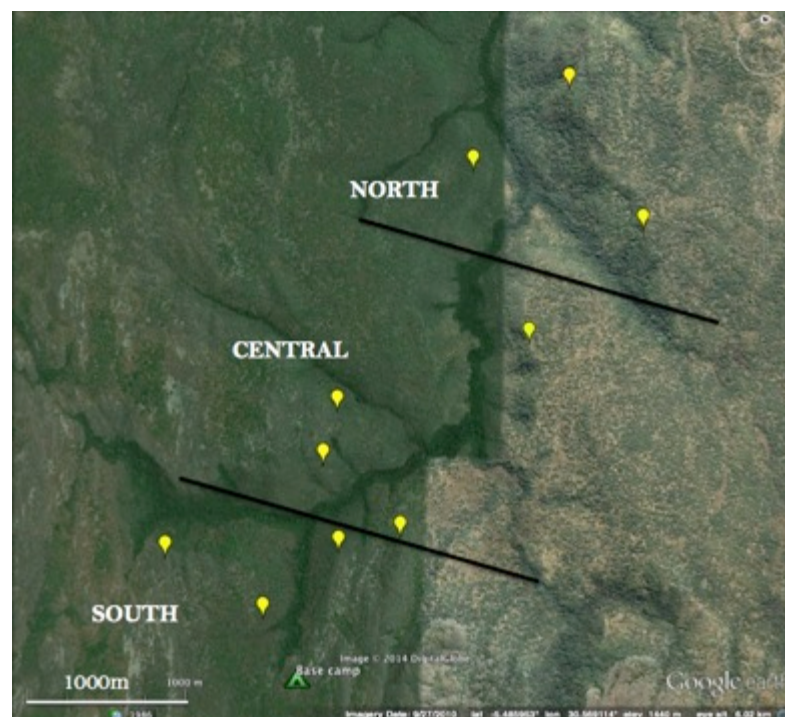


Figure 35 – Top down image of the study area with north/central/south areas identified. Yellow balloons represent SPATU locations.

Sounds were recorded as .aif files and then later converted into .wav files for analysis. We used the software program Triton (Wiggins et al., 2010) and manually identified all chimpanzee vocalizations. We then extracted only loud calls (e.g. pant hoots or screams). All calls less than three seconds were checked manually to ensure the same

vocalization was not recorded on two different channels and thus double-counted. We created a database that included other relevant information for each sound, including the channel that received the sound. The study area was then divided into ten different areas, each of which represented a single valley or entrance to a valley. Each area was monitored by a single SPATU, which recorded uninterrupted for the duration of the study.

Localization

Whilst it is possible with the current SPATU deployment to conduct acoustic tomography and localize callers, there are a number of challenges to this method (Reddy, 2011; Piel and Stewart, 2014 b) that need to be overcome first. Consequently, for the current study, sound events were assigned to a specific valley based on the SPATU location that received the sound first (Figure 36). Whilst this method provides only a crude location estimation, it was sufficient for placing callers in either south, central, or northern areas.

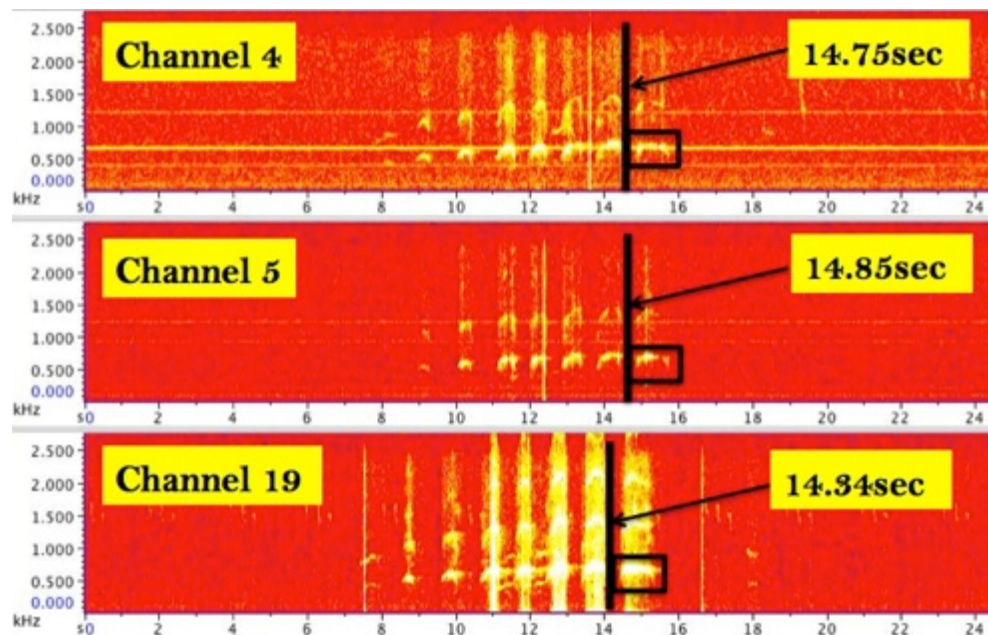


Figure 36 – A spectrogram with a pant hoot recorded on three different channels. When this occurred, the valley with the channel that recorded the sound earliest (here, Channel 19) was designated as the sound source.

Party size

Because at Issa, chimpanzees are not yet habituated to researchers, we used mean nest party size as a proxy for daily party size. We collected chimpanzee nest party size data from encounters with fresh nests, defined as only those nests with fresh feces or urine underneath them. In total, 110 fresh nest groups were observed over the study period. Of these, the majority was the result of opportunistic encounters (recce walks) or from walking line transects. We identified very few ($\sim <10$) of these groups from the previous evening's acoustic data, which would likely bias our sample to larger parties given vocal rate correlates with party size at Issa (Piel and Stewart, 2014 a).

We walked each of nine line transects (range: 3.8-6.1 km) twice-monthly, totaling 79.6 km/month. Transects all followed the same, randomly selected bearing, and were staggered 400-800 apart, crossing the study area. On each walk, we recorded all new evidence (from the previous walk) of large mammals, including feces, knuckle/foot prints, nests, etc. We attached metal tags to all trees with chimpanzee nests, as well as recording nest age, height, tree species, and perpendicular distance from the transect. To spatially analyze nest data across different parts of the study area (south, central, north), we needed to control for the effort spent on transects in each area. We used ArcGIS to calculate the total number of kilometers of each transect in each area.

Reconnaissance data

In addition to collecting data on all chimpanzee evidence whilst walking line transects, all research teams (usually two/day) also collected similar data on reconnaissance ("recce") walks. These walks varied in length, from less than two kilometers, to over 22, depending on the work of a given day (phenology, snare patrols, etc.). All feces, prints, and nests were aged (1 – new, 2 – recent, 3 – old), with vegetation and topography recorded as well. However, we used only data collected on fresh chimpanzee evidence to compare acoustic (e.g. calls) to silent (feces, prints, nests) presence, i.e. were chimpanzees present even when no vocalizations were recorded?

Vegetation classification and diet data

To examine whether vocalization patterns between northern and southern areas were related to feeding behavior, a vegetation classification was conducted of the entire study area using ArcGIS (v. 10.1, Redding, CA), with 1km x 1km cells being classified as either open (grassland, woodland, swamp) or closed (riverine forest), and in either the north, central, or southern portion of the area.

We inferred chimpanzee food consumption by analyzing all fresh fecal samples for known seeds and combining these data with unpublished data (Hernandez-Aguilar, 2006). Seeds were then identified by local botanists and field assistants and assigned to either open or closed vegetation types based on their host tree location in the study area.

Data management and statistical analyses

Because callers were often hundreds of meters from recording units, it could be difficult to discriminate screams from pant hoots and thus these were consolidated into a single 'loud call' category.

Whimpers and grunts were not considered. Chimpanzee loud calls were located manually 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, we

were able to efficiently sieve chimpanzee vocalizations, extracting them into a custom spreadsheet that allowed us to include meta-data such as start and end time of vocalization, channel, etc. Additional information was then included for each call, such as whether it was a loud (pant hoot, scream) or soft (whimper, hoo) call (Clark and Wrangham, 1993). 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 recorded on two different channels.

All tests were non-parametric and conducted in R. We conducted chi square tests on calling distributions across space (study site region) and time (dry vs. wet season), Spearman's correlations on the relationship between call patterns and rainfall, and between mean monthly nest party sizes and calling patterns. Finally, we built general linear models to examine what best predicted where chimpanzees nested and from where they vocalized, to assess whether these two indicators of chimpanzee presence responded to similar environmental variables.

RESULTS

In total, we extracted 1573 individual chimpanzee vocal events. There was tremendous variation in how the proportion of calls varied by valley: range $n=8$ calls (0.3%) to $n=403$ calls (26.2%). Three valleys (one north, one central, and one south) comprised 69.2% of all vocalizations. To examine more specifically how these calls were distributed across the study period, we needed to control for acoustic effort for each analysis. Morano et al. (2012) have argued that the proportion of days each month when at least one vocalization was recorded is a reliable measure of animal activity; Figure 37 reveals call peaks in August-October (late dry season), but also January-February (late wet season). Vocal activity, however, can also be measured as the number of calls/day (Figure 38), which shows the same dry seasonal pattern, but interestingly, nothing unusual for February.

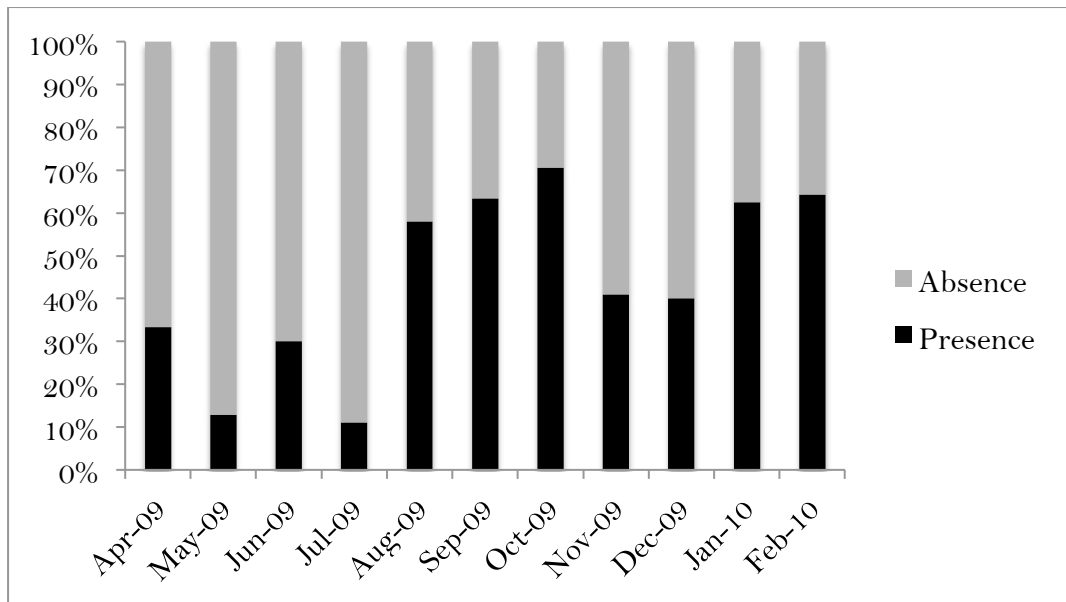


Figure 37 - The proportion of days each month when at least one vocalization ("presence") was recorded versus the proportion of days when none ("absence") was recorded

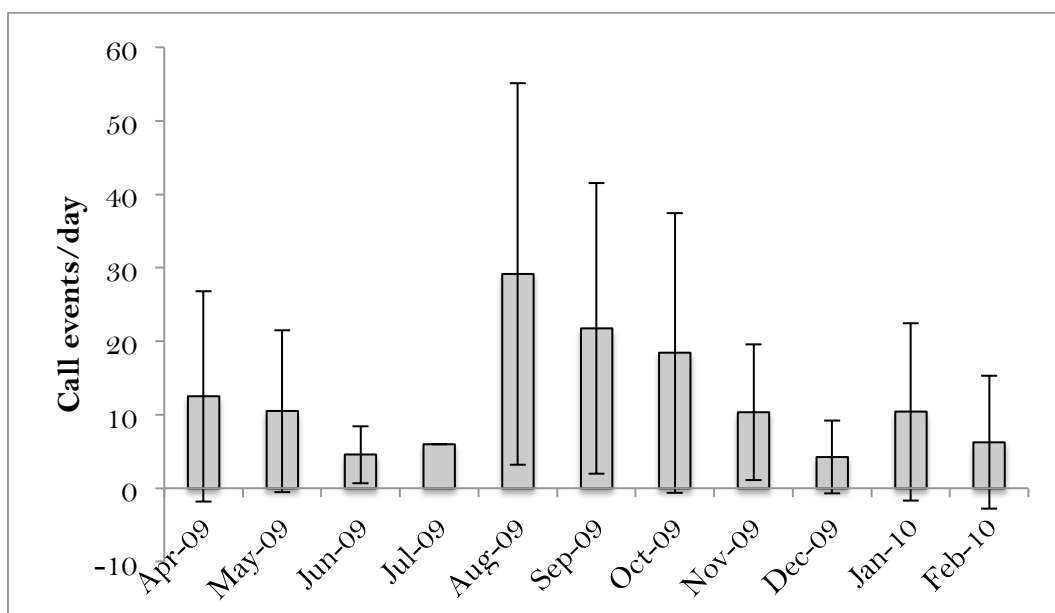


Figure 38 - Mean monthly call rate (call events per day) using just those days when at least one call was made

We recorded almost twice as many calls during the dry season as the wet ($n=1070$ calls over 131 recording days in the dry season = 8.17 calls/day; versus $n=502$ calls over 120 days in the wet season = 4.18

calls/day), and the calls were distributed differently across space between seasons (Figure 39). Chimpanzees produced more calls in the north of the study area during the dry season, and more in the south during the wetter months, $\chi^2(2) = 534.69$, $p < 0.001$. To examine if there was a relationship between rainfall and calling, we divided the number of vocal events and rainfall into two-week blocks. We found a significant positive relationship between the number of call events in the south of the study area and rainfall $r_s(20) = 3.41$, $p < 0.01$, and an inverse relationship between call events in the north and rainfall, $r_s(20) = 2.28$, $p < 0.05$).

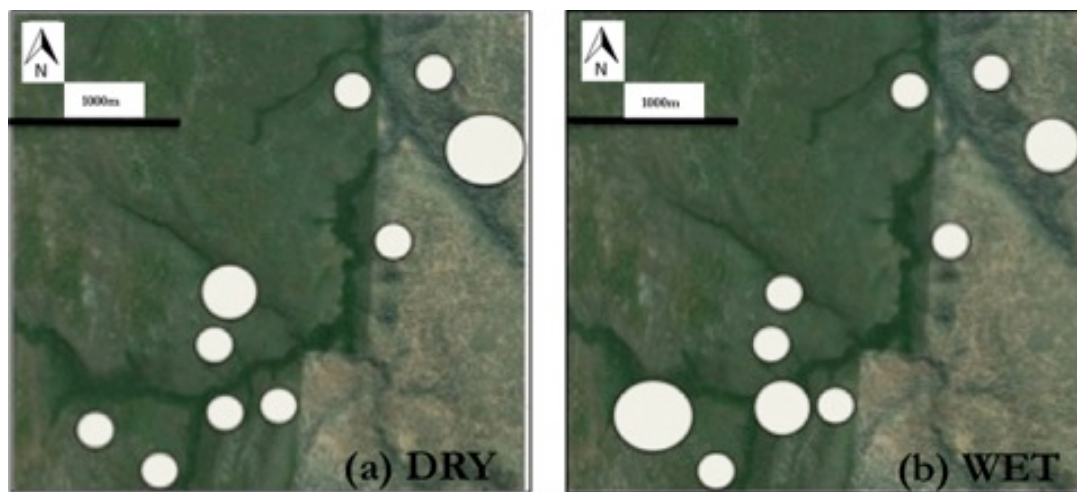


Figure 39a and b - Spatial distributions of chimpanzee vocalizations in the dry (left) and wet (right) seasons. Small circles represent 0-10% of calls made, medium 11-25% and large, over 25%.

When we examined the number of calls recorded per day across regions, we found the same geographic shift across time, whereby chimpanzees called significantly more frequently/day, [$\chi^2(2, N = 6) = 593.64$, $p < 0.001$] in the south, during the wet season, and likewise,

more frequently from the north, during the dry season (Figure 40). From vegetation classification, we also calculated more forest cover in the southern portion, than the northern portion of the study area.

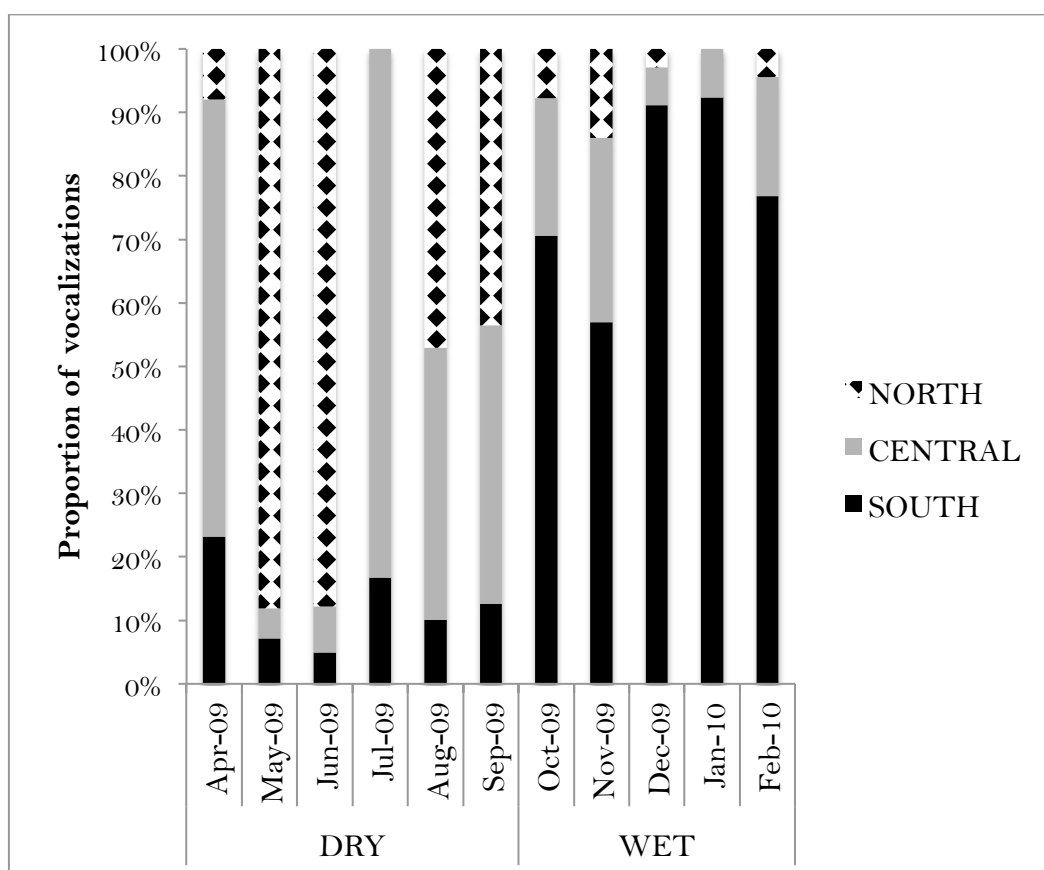


Figure 40 - Proportion of chimpanzee vocal events in each geographic area, across time (month) and space (north, central, south).

Nesting across space and time

We next examined whether the temporal and spatial patterning that we found in calling behavior was also present in nesting locations. In total, 265 nests were recorded on a total of 40.8km of nine line transects, each walked bi-weekly for the duration of the study. Of these 265 nests, 143 (53.9%) were recorded during the dry season. We first

looked at the seasonal effect of nesting in the north versus southern areas, and found that nests were more likely to be recorded in the south, during the wet season, and in the north, during the dry season, $t=-3.204$, $p<0.05$. When we looked further at whether temporal (month, seasonality), environmental (vegetation, topography), or behavioral (nest group size) variables predicted where nests were found (north or south), we found that seasonality and vegetation were the best predictors of whether nests were recorded in the north or south regions of the study area, although topography and nest group size showed a trend (Table 6). There was no interaction, however, between the most likely influences, e.g. season and nest group size ($t=-0.472$, $p=0.6386$) or season and vegetation ($t=-1.521$, $p=0.132$).

Table 6 - Results of a Generalized Linear Model for what best predicts the presence of nests recorded on line transects in either north or south regions.

Predictor	t-value	p-value
Season	-2.022	$p<0.05$
Vegetation	-3.095	$p<0.01$
Nest group size	1.912	$p=0.059$
Topography	1.812	$p=0.072$

Despite the parallel pattern of increased activity (vocal events and nest presence) in the southern areas during the wet season and northern area in the dry season, there was no relationship between how many nests and how many vocalizations were recorded per two-week period within a given area: north - $r_s(19) = 0.173$, $p=0.451$), central

- $r_s(19) = -0.043$, $p=0.851$), south - $r_s(19) = 0.034$, $p=.882$. In fact, we found that over 50% of the time (33/63), we recorded evidence of only one (vocal or nest) type of evidence.

Predicting caller location...from other caller locations

From Table 6, we learned that seasonality and vegetation were the best predictors of where a nest would be found in the study area. Nest location, however, did not predict caller location. We thus built a model to test whether the presence of a call in a given valley would reliably predict a subsequent call in that same valley. Using just those calls made within one hour of the previous call ($n=1320$), we found that 954 or 72.3% were made in the same valley as the previous call, whilst $n=366$ were produced in a different valley to the preceding call. Of those 366, $n=132$ were subsequently 'answered' by calls from the original valley, e.g. valley A \rightarrow valley B \rightarrow valley A pattern. When we combine these numbers, then, (of 1573 total calls), 92.3% of all Issa chimpanzee vocalizations are part of a social (vocal) exchange (see also Piel and Stewart, 2014 a). When we compared how strong the relationship was between succeeding calls in the same valley, we found that the presence of the previous call in a valley was the most reliable predictor of the next call also being in that same valley (Table 7).

Table 7 - Results of a Generalized Linear Model examining what best predicts in which valley a vocalization will be recorded

Predictor	z-value	P-value
Season	0.121	0.904
Month	-0.918	0.358
Time block	1.148	0.251
Valley	0.452	0.651
Previous call	9.987	$p < 0.001$

Silent presence?

To assess whether an absence of chimpanzee calls indicated an absence of chimpanzee themselves, we compared “silent” days (when no calls were recorded) with the presence of any other evidence of chimpanzees on that same day, e.g. fresh nests, fecal samples, or prints. We found that of the 143 days when no chimpanzee sounds were recorded, we observed no other evidence of chimpanzees in the forest on 93 (65.0%) of these. Acoustic silence is thus a reliable predictor of chimpanzee absence across the monitored area, $z = -5.08$, $p < 0.001$.

DISCUSSION

Calling and feeding down south

In the current study, we hypothesized that the seasonal location of callers would reflect where (north, central, south) chimpanzees were feeding at a given time of year. Our data support this hypothesis. We recorded significantly more calls in the south, during the wet season, and more from the north, during the dry season. Whilst feeding ecology

data are still under analysis, we know from previous studies (Hernandez-Aguilar, 2006) that chimpanzees consume more species from riverine forest during the wet season than the dry, and from our vegetation classification, that there is more riverine forest in the southern, than the northern parts of the study area. Whilst more detailed spatiotemporal analyses of food-species consumption is necessary, there is indirect, if weak, support for chimpanzees feeding more in the south than the north, during the wetter months.

There are, of course, alternative explanations. For example, chimpanzees could be responding to increased natural (carnivore) or anthropocentric threat presence in areas. Whilst various signs of human activity (logging, camps) were apparent during the initial period of our study, there was subsequently only a single snare and one fresh logging site observed over the course of the next eighteen months within the acoustically monitored area. And whilst lions and leopard are known predators of chimpanzees (Boesch, 1991; Tsukahara, 1993), and both present at Issa, we have no data on their distribution during the study period and so it is unknown what impact they have on chimpanzee movement. Third, chimpanzees have long been described to have 'core' ranges that impact fitness in important ways (Newton-Fisher, 2000; Thompson et al., 2007; Miller et al., 2014). It could be that such core area preferences are influencing our (arbitrarily) defined north and south in unknown ways. Relatedly, savanna-woodland

chimpanzees exhibit larger ranges than their forest-dwelling cousins. Thus, we have made the assumption here that it is the same individuals traveling up and down the valley, whereas it could actually be different chimpanzees, and thus not have anything to do with seasonality, but instead an ongoing rotation of individuals occupying various areas.

Silence and sociality on the savanna

Moore (1992) hypothesized a series of savanna adaptations unique to those chimpanzees living at low densities, with large home ranges, in dry habitats. One of those hypotheses concerned sociality, namely that chimpanzees living in marginal habitats may exhibit reduced inter-party encounters to efficiently forage over such a large home range, or exhibit increased cohesion, akin to Cercopithecine monkeys, to maintain relationships, monitor sexual opportunities, etc. Collecting data that informs on either of these scenarios (or an alternative) has heretofore not been attempted due to the logistical challenges of resolving these questions in unhabituated chimpanzees.

The current method of acoustic monitoring is one means of trying to address these competing hypotheses. Spatial (acoustic) data describing vocalization events distributed evenly across time and space would support the former hypothesis. Our results do not show this. Rather, we found clumping of call events, both in space (within valleys) and time (at certain times of year). Further, that 72% of

vocalizations are part of a social exchange answered within one hour (Piel and Stewart, 2014 a) suggests that at Issa, chimpanzees vocalize from within the same area at the same time, remaining in vocal contact with one another. The 28% of calls that were not followed by subsequent calls in the same valley could represent parties counter-calling from adjacent valleys and thus still coordinating movement, except over larger distances, or else individuals announcing their own presence. Additional time-spatial series analyses of these calls may reveal more about the function of them in a broader context.

Whilst the data that we describe here on spatial clumping of chimpanzee call events support earlier reports of temporal clumping (Piel and Stewart, 2014 a), we also found extended periods of silence, when no sounds were recorded (up to 19 days in one month) anywhere in the array. This acoustic silence is likely explained by one of two phenomena: either chimpanzees are present and not calling, or they are not present in the first place. We tested this by comparing periods of SPATU acoustic silence against other (non-acoustic) fresh evidence of chimpanzee presence, and found that in only 35% of cases, we found alternative evidence of chimpanzees the same day that chimpanzees were vocally silent, but that the majority of the time, acoustic silence significantly predicted ape absence. This supports the idea that Issa chimpanzees occupy a range outside the SPATU array, already $\sim 12\text{km}^2$.

Acoustic aggregation

The best predictor of where a vocalization would be heard was the location of the previous call, suggesting a large social component to chimpanzee loud calls (Mitani and Nishida, 1993). Whilst it is possible this suggests aggregations of callers across time and space, we cannot rule out the possibility that subsequent sounds were emitted by single individuals. Future localization analyses will assign higher resolution geographic locations (more specific than merely valleys) to callers, and thus allow us to test hypotheses concerning how individuals are distributed across space and time.

Listening or walking?

New nests observed from >40km of line transects walked bi-weekly for 12 months (a total of >960km walked) significantly correlate with vocalizations recorded in the same areas. Nonetheless, half of the time, only one type of evidence (sound or nest) was recorded, but not both. This discrepancy likely reflects differences in methodology, with transect data limited to observations of chimpanzee nests from a specific location, versus SPATUs, which offered larger spatial coverage. Each of these methods (acoustic and ground monitoring) contributes important data that informs on chimpanzee space use. Because solitary chimpanzees still construct a nightly nest, but are less likely to vocalize than when in larger parties (Mitani and Gros-Louis, 1998), conducting line transects provides presence data on these silent

individuals that would otherwise be missed by acoustic monitors. The opposite is true as well. Acoustic monitors, in turn, offer presence data on those individuals not leaving behind evidence in or near transects. Combined, then, these two methods provide a more robust means of monitoring seasonal presence of elusive chimpanzees than either on their own, especially in savanna-woodland habitats.

Limitations and Future Studies

A fundamental limitation of the current study is the crude means of assigning locations to call events. Given that pant hoots can travel >three kilometres under optimal conditions (Piel and Stewart, 2014 b), our means of using the first SPATU to receive the sound leaves room for spatial error. Higher precision of caller location using time-delay-of-arrival is preferred (Freitag and Tyack, 1993), although was not feasible for the current study. Secondly, northern, central, and southern areas were arbitrarily designated, and have no biological significance. They also do not represent the same amount of area (km²), such that there is not equal likelihood of receiving a call in each area. We created the borders as a broad way of dividing up the study area to assign a location in space, but a better way may be to use preferred feeding patches, to make the study more ecologically relevant. We also used feeding data from a study conducted over a decade ago (Hernandez-Aguilar, 2006), and within only part of the current study area. Current chimpanzee ranging patterns are likely different than

that from 2002, and heterogeneity in forest composition (unpublished data) suggests that not all forests provide similar amounts of feeding species for these apes. Current analyses of feeding species consumption from 2009-2010, combined with spatial distribution of those species is underway. Future studies will thus be able to more precisely map caller to known feeding locations and address some of these limitations.

CHAPTER 5: CONCLUSION



Figure 41 - Capturing chimpanzee calls at Issa, 2009-2010

In this study we have investigated the vocalization behavior of chimpanzees living in an open savanna-woodland in the Issa Valley, western Tanzania. As Issa's chimpanzees are unhabituated, we designed and deployed a custom designed, remote-sensing passive acoustic monitoring (PAM) system: solar powered acoustic transmission units (SPATUs) to address hypotheses concerning spatiotemporal vocalization patterns.

There is little agreement on the most accurate reconstruction of early hominin paleo-environments (White et al., 2010; Cerling et al., 2011 a; b; Domínguez-Rodrigo, 2014). Despite controversies in definition (Domínguez-Rodrigo, 2014) and reconstruction alike, we have used the term "savanna" here to represent an overall drying of the environment, especially as a catalyst for behavioral change in apes that adapted to a dramatic change in resource type, distribution, and quality (Wynn, 2004). Like most savanna chimpanzee populations, Issa chimpanzees live at low densities compared to their forest-dwelling cousins, and exhibit large home ranges. If these features also characterized early hominins who moved from a wetter, closed environment to an open, arid one during the Plio-Pleistocene then a better understanding of extant chimpanzees in this latter habitat may inform on the adaptations of some of the earliest human ancestors.

SPATUs revealed temporal and spatial patterns of loud call behavior. This system provided real-time, continuous radio transmission

of sounds over a $\sim 12\text{km}^2$ area, from which we extracted chimpanzee vocalization events and then situated them in a broader socio-ecological context. This Conclusion seeks to synthesize our findings and make recommendations for follow-up studies using remote acoustic sensing technologies for the study of wide-ranging terrestrial mammals (see also Blumstein et al., 2011; Mennill et al., 2012).

Sound transmission: establishing efficacy

Before we could contextualize chimpanzee calls, we first conducted a playback study to assess the efficacy of the system and characterize the sound environment. We found that under optimal conditions, sounds can carry as far as 3.6 kilometers, and both vegetation (woodlands more than forests) and topography (mountain slopes more than plateaus) facilitate sound transmission. Sounds broadcast under poor conditions degraded as little as 200m from their origin. In addition to helping establish the acoustic (monitoring) boundaries of SPATUs, especially for subsequent deployments of similar systems, there were additional implications to these results.

If loud calls are found to be important in maintaining social cohesion in these fission-fusion animals (cf: Spehar and Fiore, 2013; I. Schamberg, unpublished), then acoustic transmission limitations may inform on maximum inter-caller distances. The very unit of chimpanzee sociality, 'party', has traditionally been defined as either those individuals within a pre-defined space (Newton-fisher et al., 2000) or

else those that the researchers can see (Lehmann and Boesch, 2004). However, at Issa, the nature of having to exploit sparsely distributed resources may mean that individuals are more spatially distributed themselves, and outside of the visual space of both researcher and each other. Consequently, the social unit actually be those within vocal space, rather than visual space (Robinson, 1981).

Timing and tuning

If chimpanzee long calls at Issa were being used for coordination between widely spaced individuals, then we hypothesized that optimal sound transmission periods (e.g. low wind, ambient noise) would predict the presence of calls. Our next goal was thus to test whether acoustic data from wild chimpanzees would conform to hypotheses predicting that callers exploit these optimal periods. My hypotheses that chimpanzee calling would be most frequent under optimal conditions were not supported, as no relationship between temperature or wind significantly predicted call presence. We did find a significant, inverse relationship between relative humidity (RH) and call presence, but it is not clear how reliable this finding is. If we assume RH to represent rainfall, then another way to describe this relationship is that there was less calling during rainy periods. In other species, there is a dramatic influence of rain on sound (69-fold reduction on transmission distance - Lengagne and Slater, 2002), and it has been reported that primates emit fewer calls after wet

(and cold) nights (*Hylobates klossi* - Whitten, 1982; *Colours guereza* - Schel and Zuberbühler, 2012), so it is possible that chimpanzees did not vocalize during these periods. However, we also disengaged the entire system during heavy storms to minimize damage that would have resulted from a lightening strike. As a result, this relationship between RH and call absence could instead be an artifact of sample bias. A re-analysis of the data with these periods removed would address this.

Supporting previous studies that have reported chimpanzee temporal patterns of vocalizing (Wrangham, 1975; Wilson et al., 2007), we also found that Issa chimpanzees exhibit peak periods of calling in the early morning and evening, akin to dawn and dusk choruses observed in various taxa (Staicer et al., 1996; Schel and Zuberbühler, 2012). The continuous recording also revealed other interesting patterns, such as a third peak at 4h and calls made at least once during the study in every hour of the 24-hour day. We would have liked to incorporate ambient noise level measurements into this analysis as well, as the sound environment is composed of far more than just physical landscape features and weather (Pijanowski et al., 2012). We partially did this, collecting readings of ambient noise levels during the day and again from 1900h-2200h at bi-weekly intervals, but automated readings thorough the night would have added an important, additional component to analyses of chimpanzee calling patterns (see below).

In summary then, from our playback study we learned of the optimal times to produce loud calls at Issa. Data from the callers themselves, however, suggest there are other factors influencing when and from where individuals vocalize.

Sounds of savanna sociality

In addition to examining the temporal (ecological) influences on Issa chimpanzee calling, we assessed the social influences (Mitani and Nishida, 1993). First, we investigated the likelihood of one call being 'answered' by another (within one minute) and also how those counter-calling episodes were distributed across the day. We hypothesized that if such counter-calling was being used to coordinate movement, for example, the majority of them would be produced in the early morning and late evening (e.g. morning travel; evening reunions), as seen in some other species (Kinzey and Robinson, 1983; Macedonia, 1993; Hohmann and Fruth, 1994; Kitchen et al., 2004).

We found that over a third (37.8%) of all recorded loud vocalizations were made within one minute of a previous call (and >83% within an hour) and further, those counter calls were made significantly more often between the hours of 3h-6h and 15h-18h, when chimpanzees form daily and nesting associations, respectively. Given that we could find no previous study that described continuous recording of chimpanzee vocalizations, it is unclear if this daily distribution of chorusing is a savanna-specific phenomenon, or

something more broadly species-specific. Although we could find no data discussing the temporal distribution of chorusing episodes, the importance of short intervals between call events have been reported elsewhere for various other new world (*Alouatta palliata* - Whitehead, 1987; *Ateles belzebuth* - Spehar and Fiore, 2013) and old world (*Simias concolor* - Tenaza, 1989) primates.

In a second test of the social influences on calling patterns, we examined the relationship between grouping behaviour and mean calls/month. Because daytime encounters with chimpanzee parties yielded unreliable counts (individuals may have fled before we saw them), we used nest party sizes, and found a strong correlation between the mean monthly number of individuals in a (nest) party and the total number of calls. This differed from a previous study which showed that at Mahale Mountains, Tanzania, no such relationship existed (Mitani and Nishida, 1993). Whilst this difference may actually be a biological phenomenon, it is equally likely due to methodological differences between the current study, where all vocal events were considered, and that at Mahale Mountains National Park (Tanzania), where focal follows were conducted.

Finally, we explored the spatial distribution of Issa chimpanzee sound events, hypothesizing that the location of callers would reflect where in the study area chimpanzees were feeding at a given time of year. In fact significantly more calls were recorded in the south, during

the wet season, and more from the north, during the dry season. It is possible that this is due to the spatial distribution of chimpanzee preferred feeding species, but alternative explanations also exist. For example, chimpanzees could be responding to spatiotemporal patterns in natural (carnivore) or anthropocentric threat presence in these areas. We have also assumed here that it is the same individuals traveling up and down a valley, but that may not be the case. Instead, the differences in ape presence may be a result of individuals from different chimpanzee communities exhibiting 'core' ranges, as they do elsewhere (Newton-Fisher, 2000; Thompson et al., 2007; Miller et al., 2014).

Silent absence

The current method of acoustic monitoring is one means of trying to address competing hypotheses concerning how savanna chimpanzees adapt to an open habitat. Spatial (acoustic) data describing vocalization events distributed evenly across time and space would support fission-fusion organization, the traditionally described grouping behavior for chimpanzees (Lehmann and Boesch, 2004). My results do not show this. Rather, we found clumping of call events in space (within valleys) and time (at certain times of year). Almost three quarters (72%) of all vocalizations were part of a social exchange (answered within one hour).

We also found extended periods of silence (up to 19 days in one month) when no chimpanzee sounds were recorded anywhere in the array. This acoustic silence is likely explained by one of two phenomena: either chimpanzees were present and not calling, or they were not present in the first place. When we cross-referenced 'silent' days with any other data collected on chimpanzee presence that same day, we found that in almost two thirds of those days (65%), no other evidence was recorded, suggesting that when chimpanzees go silent, it is because they go elsewhere. They could, of course, be in pockets of the main study area obscured from acoustic coverage, or else areas peripheral to the main area, expanding their range beyond the PAM coverage.

Acoustic evidence for 'savanna adaptations'

Early estimates (~200 - 500km²: Kano, 1971, 1972; Baldwin et al., 1982 a) and current reports (>80km²: Samson, 2012; Skinner and Pruetz, 2012) of savanna chimpanzee home ranges are consistently vast compared to forest-dwelling communities. When combined with the remarkable low density of these apes (Table 5), such scale would provide a challenge to maintaining the traditionally described fission-fusion social organization of *Pan*. The earliest descriptions, in fact, of chimpanzees across these drier habitats foreshadowed what our acoustic data show here. Suzuki (1969) and Kano (1971) both described areas of high concentration of chimpanzee habitat use in

western Tanzania, and other areas still important in their range (namely for food sources), but rarely used. Whilst these early studies did not discuss the effort spent monitoring each, it is difficult to know how reliably these conclusions are.

The clumping of temporal and spatial call origins supports these early claims of non-random use of space, and also supports observations of another unhabituated, open habitat community from Mt. Assirik, Senegal. Over 35 years ago, Tutin and colleagues (1983:160) suggested that whilst fission fusion may still be exhibited in the savannas of west Africa, “chimpanzees of Mt. Assirik show sporadic, non-seasonal movements in large relatively stable parties over long distances.” It is unclear if the acoustic data actually represent either social or spatial “stability” given the absence of individual caller identification and a lack of exhaustive acoustic coverage. Nonetheless, subsequent work that integrates spatiotemporal patterns of chimpanzee activity and compares these to e.g. forest-dwelling chimpanzee patterns may help reveal whether these behaviors are in fact “savanna adaptations” (sensu Moore, 1992), informing on hominin evolution, or else byproducts of applying an unorthodox method to answer conventional hypotheses.

Importantly, chimpanzees are not frozen hominins, and so caution should always be taken when inferring *extinct* hominin behavior from any *extant* primate (Sayers and Lovejoy, 2008).

However, that the closest living relative to humans survives in a habitat resembling the one in which humans evolved suggests that insight can be gained into the various ways a large bodied, social ape adapts to a dramatic change in landscape.

Beyond behavior: additional applications

SPATUs have at least three more applications for the study of wild chimpanzees. First, often the biggest challenge to collecting data on elusive animals is merely finding them. With real-time data accessible to researchers, caller locations are known immediately and research teams can be mobilize to collect subsequent data (Filatova et al., 2006; Aide et al., 2013). Additionally, given chimpanzees are unlikely to travel at night, monitoring audio channels in the early evening for chimpanzee sounds allows researchers to know where parties will begin their day the following morning. Second, SPATUs simultaneously provide information on caller and receiver locations across space and time, and thus have the potential to inform on the role of loud calls in how social animals coordinate movement (Boinski, 1993; Spehar and Fiore, 2013; I. Schamberg, unpublished data). Finally, there is a growing literature on natural and disturbed soundscapes (Pijanowski et al., 2012; Servick, 2014), yet little situating primates in their use of particular acoustic niches (but see Schneider et al., 2008). Acoustic monitoring of these complex and often threatened sound environments provides important data to researchers interested in how animals compete for

call space and to conservationists in understanding change in species composition in response to human disturbance (Dumyahn and Pijanowski, 2011).

Listening ahead

The current SPATU system sought to simultaneously address (1) hypotheses about chimpanzee behavior and (2) the drawbacks of traditional PAM systems used to date, first by transmitting acoustic data back to a central location for processing and storage, and to allow monitoring of system failure. Second, units still retained some autonomy (versus being wired to a central base station receiver) and thus can be deployed across a much wider area than previous (wired) systems (Fitzsimmons et al., 2008). Third, SPATUs relied on solar power to recharge long-lived batteries. The result was a remote, non-invasive system that streamed incoming acoustic data in real-time, which could then be used, in theory, for subsequent action, e.g. mobilization of research teams to already known caller location.

This system does indeed address some of these challenges described by Mennill and colleagues (2012) in their review of terrestrial acoustic remote sensing microphone arrays. However, upon deployment, numerous challenges arose, and we discuss here how future systems can avoid such problems whenever possible. First, because the system relied on FM transmission, each SPATU required line-of-sight to the base station. As a result, large portions of the study

area where chimpanzees were known to range could not be acoustically monitored. This limitation could be addressed by erecting small towers on mountain ridges to relay signals from otherwise obscured areas (Porter et al., 2005).

Second, whilst battery capacity was calculated for the system and a three-day surplus power capacity included in system design, the wet season brought with it over a week of overcast days at times, which left SPATUs power-depleted and in need of replacement. Consequently, numerous times, batteries needed either expedited recharging from the central base station system, or else multiple days of solar-charging at their deployment location. The most effective solution to this problem would be to attach battery voltage regulators to each unit (Woodward and Bateman, 1994). Regulators de-activate SPATUs at custom chosen voltages allowing minimal time for units to return online when the sun eventually returns.

Third, streaming acoustic data averaged ~1GB/channel/day. Data processing and organization were thus a formidable challenge with files having to be moved every 1-2 days to portable hard drives. Software such as Triton (Wiggins and Hildebrand, 2007), which can reduce large acoustic data sets to manageable visual patterns for faster, albeit manual, analysis became a necessary tool to data-mine and extract scientifically relevant vocalizations. Even with Triton, we required the help of a research assistant and needed months of

extraction just to scan the dataset one time. Nonetheless, identifying Type II errors will still be necessary in the future. Automated call recognition software, which has revolutionized the way bioacousticians analyze large data sets for a host of species (Clemins et al., 2005; Wiggins and Hildebrand, 2007; Adi et al., 2010; Aide et al., 2013; Roch et al., 2013), is most effective for stereo-typical vocalizations, e.g. birds and marine mammals. Chimpanzees, however, present a challenge to this approach for two reasons. First, pant hoots exhibit high intra- and inter-individual variation in acoustic structure (Clark and Wrangham, 1993; Riede et al., 2004) and so algorithms that identify key parameters are difficult to write. Second, chimpanzees often chorus, which further complicates detectors (Brandes, 2008). To my knowledge, no detector has yet been written for chimpanzee sounds, but Artificial Neural Networks (ANNs) or Hidden Markov Models (HMMs) could be trained within known periods of chimpanzee sounds as a first step to automate call detection (*sensu* Pozzi et al., 2009).

Fourth, whilst it was necessary to build these units myself given the desired features, manual construction, especially by a novice, provides opportunity for subtle (and even not-so-subtle!) differences in electronics, microphone tuning, etc. which have unknown affects, from sensitivity to overall functionality. There are now various commercial options available for similar types of study, many which

offer guarantees to product quality and standardization of recording quality (Pieretti et al., 2011; Mennill et al., 2012).

Future studies should also consider incorporating additional data that were not collected here. For example, rather than bi-weekly walks to monitor ambient noise levels, autonomous sound level meters (Figure 42) are available that record such measurements on pre-determined schedules. Data from these units could then be used with other environmental data (e.g. wind, temperature) to model animal exploitation of optimal calling periods.



Figure 42 – An autonomous sound level meter, from <http://www.casellameasurement.com/news.htm>

Relatedly, one reason that my data may not accurately reflect the impact of vegetation and topography on sound transmission relates to the acoustic path. That is, sound transmission is widely known to be most affected by (1) interference from ground reflection, (2) scattering (here, namely by branches and other foliage), and (3)

absorption by those and also the air and ground (Huisman and Attenborough, 1991; Tunick, 2003). By not measuring any of these influences, we cannot know how they varied from playback to playback. Subsequent tests could include these measurements, potentially even using remote sensing given known relationships between biomass and attenuation rates (Martens, 1980).

One of the primary differences between this system and previous PAM arrays was the built-in RF transmission of signals back to the base station (see above). However, the Toshiba Toughbook used during the study lacked the necessary processing capacity to simultaneously allow data mining whilst processing incoming data. Consequently, we could not use the real-time feature as we would have liked. In subsequent deployments, we could remedy this by either using automated detectors (see limitations above, though), or else boosting processing capacity.

Finally, a primary goal of my study was not just to record chimpanzee sounds across a vast area (itself a debut for PAM with wild apes), but also to deploy microphone units in modules to maximize chances of sound localization based on time delay of arrival (Freitag and Tyack, 1993). Overall, we sought to identify savanna-specific social adaptations of chimpanzees to living at low densities, for example by investigating whether pant hoots coordinated inter-party movement across a large home range, and whether sleep-site calls exhibited

specific acoustic parameters (cf: Matthews and Aureli, 2003). Whilst the crude locations of sound origins that we presented here provide a general idea of caller spatial distribution, they are far too imprecise to inform on coordinated movement. Time and technical constraints prohibited localization analysis, but future work will offer higher resolution sound-localizations based on time of delay, as been successfully demonstrated in marine mammals (Freitag and Tyack, 1993; Filatova et al., 2006) and birds (Hayes et al., 2000; Collier et al., 2010) to address questions about the role that loud calls play in chimpanzee intra- and inter-party movement coordination.

Conserving *Pan*, deploying PAM

When combined with traditional methods of studying unhabituated apes, PAM offers data on ape movements across space and time that are otherwise logistically impossible in the same survey period, especially without habituation. We have shown that nestless areas may still be important for chimpanzees, as we identified periods when vocalizations, but no nests were recorded in specific valleys. Whilst it is well established that Issa chimpanzees exploit miombo woodlands as important nesting sites, especially in the wet season when woodland tress have the most leaves (Hernandez-Aguilar, 2009; Stewart et al., 2011), we have now shown that these woodlands also facilitate more efficient sound propagation (Piel and Stewart, 2014 b). Our data placing chimpanzees in valleys where other indirect

evidence was absent offers conservation planners additional areas that are important for these apes, but would otherwise not be detected using traditional means. Second, areas used only rarely may still be of great importance to the chimpanzees. For example, of 318 total vocalizations recorded from just one valley over the entire study period over 80% of those vocalizations were recorded in a 6-week period, suggesting that this area is used rarely, but in a highly concentrated way for a short period. Thus, the continuous monitoring of the sound environment provides data on chimpanzee ranging and aggregation patterns that may differ from our traditional understanding of (forest-dwelling) chimpanzee social organization.

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