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Chimpanzees (*Pan troglodytes schweinfurthii*) in the Northern Democratic Republic of the Congo Adapt their Long-Distance Communication Behavior to Human Hunting Pressure

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Abstract

We systematically recorded all long-distance chimpanzee vocalizations and tree drums over an 18-month study-period to the north of The Uele River in The Democratic Republic of the Congo and a 13-month period to the south. We found that the frequency of chimpanzee vocalizations and tree-drums was greatly reduced in areas of high human hunting pressure, and these sounds were also mostly limited to the early morning hours. The chimpanzees appeared to have the behavioral flexibility necessary to modify their behavior in areas where humans were a major threat. However, it is also likely that the social systems of these gregarious apes may be negatively affected by the 'enforced silence' they are obligated to maintain in the vicinity of humans.

Introduction

Chimpanzees (*Pan troglodytes*) inhabiting different regions across Africa display remarkable flexibility in their behaviors, in the domains of nest-construction (Koops, 2008; Chapter 5) and tool-use (Whiten et al., 2001), as well as in the structure of their social groups (Boesch & Boesch-Achermann, 2000). This same flexibility extends to their vocalizations, even to the extent that regional or community 'dialects' have been proposed (Mitani, 1992).

Unfortunately, just as we are beginning to document this rich behavioral diversity in our close evolutionary cousins, chimpanzee populations across Africa are coming under assault from a rapidly-proliferating commercial bushmeat industry (Walsh et al., 2003; Campbell et al., 2008; Chapter 6). Populations in northwest Africa and Gabon have been decimated by this trade along with habitat-destruction within the last 2 decades; in the species' Congo Basin stronghold (centered around the Democratic Republic of the Congo, hereafter abbreviated as DRC), the process seems to be only just gathering momentum (Chapter 6). Despite this recent wave of heightened persecution, chimpanzees in the DRC still survive in the heavily-degraded forests close to major human population centers such as Buta and Aketi, forests from which other large mammals such as okapis and elephants were extirpated decades ago (Chapter 4; Chapter 6). Little attention has been paid to the behavioral responses of chimpanzees to human predation. In some parts of Africa, as in the northern DRC, the apes' behavioral flexibility appears to have allowed them to survive in close proximity to *Homo sapiens*. Wilson et al., (2007) found that chimpanzees at Kanyawara, Uganda reduced their production of loud calls when crop-raiding, but not when entering border areas with other potentially dangerous chimpanzee communities. Similar changes in

behavior have been documented in other primate species: according to Van Roosmalen (2008: page 384), male spider monkeys (*Ateles paniscus*) in heavily-hunted areas of the Brazilian Amazon ceased making their species-typical long-calls. Likewise, Kavanagh (1980) showed that crop-raiding vervet monkeys (*Chlorocebus aethiops*) living in close proximity to humans in Cameroon had modified their intra-group vocalizations to include a higher proportion of softer '!kock' calls and a lower proportion of loud calls compared to savanna-living vervets who had little interaction with humans. They had also eliminated a vocal response given by savanna vervets specifically when encountering canids. Finally, these vervets had adopted more irregular ranging-patterns than their savanna-living con-specifics, and were thus harder for the researchers to locate.

Chimpanzees are also capable of suppressing their natural repertoire of vocalizations (Goodall, 1986). They do this in order to avoid having food stolen by con-specifics, in the context of male-female consortships in the danger zones at borders with neighboring communities, and during all-male patrols into the territories of rival communities.

The forests near Bili, DRC are characterized by low human population densities and are home to a large, apparently continuous population of chimpanzees (*Pan troglodytes schweinfurthii*). Although the apes are sometimes hunted, it appears that no large-scale commercial bushmeat trade has yet appeared in the area (Chapter 6). Between 2004 and 2007, Thurston Hicks (TH) spent a total of 18 months studying chimpanzees in this area, making regular contacts with the apes and recording their vocalizations and tree drums. In 2008, a 13.5-month survey was made of chimpanzee populations across a large area approximately 200 km south of Bili, in forests near the towns of Leguga, Aketi, Buta, and Bambesa. Interestingly, these chimpanzees were found to possess the same material culture as those at Bili (Chapter 5), implying that they form a continuous population, or have until recent times. Over the course of this survey, contact was made with the chimpanzees whenever possible (Chapter 2), and their vocalizations and tree drums were scored. As at Bili, TH also recorded all signs of human presence. The data we collected have allowed us to compare the behavior of chimpanzees living close to human villages and roads to that of those living in more remote forests. We hypothesize that the chimpanzees living in the pristine Gangu Forest should be more vocal than those living in other areas, particularly those areas with high human hunting pressure. We also hypothesize that chimpanzee sound-production in heavily-hunted forests should be more restricted to the early morning hours.

Methodology

The study area

The main study area of the 2004-2007 period of the Bili ape research project encompassed an approximately 475 km² area of the forests and savannas west of the small village of Baday (Chapter 1). Camp Louis was located at 4°21'72"N, 24°56'72"E, and Camp Gangu was located approximately 30 km to the west-southwest, at 4°19'34"N, 24°41'53"E. Gangu Forest remains nearly undisturbed by humans, and along with elephants, numerous species of non-human primates, and large carnivores, it is home to chimpanzees that show relatively little fear of humans (Chapters 1 and 2). The forest closer to the road (called here the Camp Louis Forest) also showed very little sign of human presence, but there was less wildlife and the chimpanzees almost always reacted to us with fear. The methodology of our 2004-2005 transect work and forest walks is described in Chapters 1 and 4.

In 2006, together with field assistant Jeroen Swinkels (JS), TH conducted 'path of least resistance'-style surveys across a large area, stretching from the forests of Lebo just south of the Uele River to Zapay on the border with the Central African Republic, with Bili lying approximately in the center, recording all evidence of chimpanzees, humans, and other

large mammals. Figure 4, Chapter 1 shows the survey regions we visited over the course of the study. From October 2007 to November 2008, TH conducted a survey of the forests south of the Uele River, using the same methodology as at Bili. Table I, Chapter 1 lists the GPS coordinates of the forest areas surveyed and the number of days spent and kilometers walked at each over the entire project. We divided the survey area into three main regions: the pristine Gangu Forest, the non-Gangu North Uele Forests, and the South Uele Forests (Chapter 1). The first two of these regions lie to the north of the Uele River: the pristine Gangu Forest lies >20 km from the nearest roads and villages, and the non-Gangu North-Uele forests were located <20 km from the roads. The third region surveyed, South Uele Forest, had a much higher human population density and all of it was within 20 km of roads and villages.

Chimpanzee vocalizations and tree-drums

Throughout our study, we attempted to locate chimpanzees in the forests and make contact with them. A potential contact day included any day in which TH was traveling or camping in chimpanzee-inhabited forests and it was possible to hear the apes, whether or not he was actively searching for them (Table I, Chapter 1 gives details on the potential contact days). In forests where chimpanzees were not heard or were heard rarely, TH confirmed their presence by the discovery of their night nests, feeding remains, and/or dung, and only forests in which recent chimpanzee presence was confirmed were included in this study. While in the forest, TH recorded all vocalizations and tree drums made by the apes throughout the day and night. Vocalizations were differentiated into 'pant-hoots' and 'other' (Goodall, 1986) (the latter were subdivided into 'screams', 'barks', 'rough calls' and 'grunts', but all of these categories were lumped together for analysis). Tree drums are staccato thumping sounds made by chimpanzees against buttresses. TH recorded the time and direction of all chimpanzee vocalizations and tree drums that he heard during the night (they frequently woke him up), as well as those heard by the field assistants. The latter were less-precisely documented; in cases where the assistants were not sure of the time of the vocalizations, they were omitted. It is likely that some of these nighttime vocalizations were missed due to sleep, but it is unlikely that there was any difference in the likelihood of missing them between the different study sites. Vocalizations made by chimpanzees during contacts in response to our presence (usually screams or alarm calls) were not included in the analysis. All recorded vocalizations were combined into one variable, 'Auditory events per hour'.

Over the first 3 months of the study (August to October 2004), although the durations of all auditory observation bouts were recorded, during bouts characterized by multiple chimpanzees vocalizing and / or tree drumming over an extended period of time, each separate pant-hoot and tree drum was not always reliably recorded. For this time period, we have estimated numbers of pant-hoots and tree drums based on the written notes and films made of the bouts. Following October 2004, all separate vocalizations within auditory bouts were systematically recorded.

Human presence

Over the course TH's 18 months at Bili and 13.5 months in the Aketi-Buta area, he walked a total of 2133 km through the forests (surveys conducted and data collected by JS or the Congolese field assistants were not considered in this analysis). Included in this total are repeat journeys along previously-walked routes, as long as these revisits did not occur on the same day. Systematic line transects made up 160 of the km walked in the Bili-Gangu region. In addition to documenting ape presence and signs of other large mammals, TH recorded all evidence of human presence (trails, fields, lean-tos, hunting camps, snares, cartridges, and encounters). The majority of routes that we followed in the South Uele and in some of the

North Uele forests were hunting or trapping trails, although occasionally we 'bushwhacked' or followed trails left by fisher-people. The trails that we followed in the Camp Louis area, however, were not obvious hunting trails, although according to our trackers they had been used by hunters prior to the installation of the conservation project in the region. For the most part we did not follow human trails at all in the Gangu Forest, precisely because, with one exception (a fisherman's trail that skirted the edge of the Gangu River), no such trails existed. Instead, we either cut transects, bushwhacked, or followed elephant trails.

In Table I, we define the categories of human evidence recorded by TH. We have omitted human trails (due to unreliable recording of this evidence-type) from the analysis.

Statistical analyses

All statistics analyses were carried out using the R (version 2.9.0; R Development Core Team, 2009). Comparisons between groups were done using Kruskal-Wallis non-parametric ANOVAs, and were followed when needed by post-hoc comparisons using kruskalmc from the pgirtmess package version 1.3.8. We ran a Principal Component Analysis (PCA) on the human evidence variables. The first two PCA axes summarizing the human evidence, which explained more than 50% of the variance, were used in a Spearman's Rank Correlation test to correlate human evidence with the chimpanzee auditory rates.

Table I. Type of human evidence, with definitions. The data is quantitative, and most items were counted individually, with the exception of 'villages', 'hunting camps', and 'camps', which often described conglomerations of dwellings.

Category of human evidence	Definition
I. Hunting Evidence	Direct evidence of human hunting. **1. Cartridges -** Spent red '00' cartridges. **2. Snares -** Traps set by hunter, often along snare trails. Snares came in three main forms: small string snares, small wire snares, and large 'bomb' wire snares up to 2.5 m in height. **3. Hunting camps -** Large campsites in forest clearings made by hunters; featuring smokestacks for smoking bushmeat and often stocked with snares. **4. Bushmeat** - Fresh or smoked carcasses of mammals encountered in the forest. **5. Hunting signs** - Hunting or snare trails, spears. **6. Batteries** - Probably used for night-hunting.
II. Mining	**7. Mining -** Evidence of mining activities: gold or diamond excavation and test pits, pans, shovels, and mining camps.
III. General Forest Use	Use of forest not specifically tied to mammal-hunting or mining. **8. Fishing signs** - Fishing nets, small fish smoke stacks, dams**.** **9. Bird-hunting signs** – Bird snares, plucked feathers. **10. Camps** – Temporary camps not specifically used for hunting, but for work in the fields or fishing. **11. Lean-tos** - Simple shelters built of saplings and herbs as a temporary shelter from the elements.
IV. General Human Presence	Refers to human presence in a forest area, usually tied to fishing or agriculture, but without direct use of the forest. **12. Artifacts** - Containers, tools. **13. Pets -** Dogs, chickens. **14. Signs** - General human sign. **15. Contacts** - Encounters with people. **16. Villages** - Semi-permanent dwelling-places. **17. Huts** - Durable mud or thatch houses, often associated with fields. **18. Fields** - Land cleared for agriculture, with crops such as manioc, bananas, and rice.

Results

Chimpanzee presence and sound frequencies in different forests

Chimpanzee nests were found throughout the region, in all forests that we surveyed, even within 13 km of the large commercial center of Buta (Figure 5, Chapter 4). In addition, to the south of the Uele River, our team encountered a large number of chimpanzee orphans and carcasses for sale, as compared to almost none being seen during our time at Bili, indicating a rapidly-accelerating bushmeat crisis for the species south of Uele (Chapter 6).

We compared mean chimpanzee sounds per hour across the 12 forest regions (Figure 1; the raw data are presented in Appendix I). The five forests with the lowest rates of sound-production were to the south of the Uele River. Three of the four regions with the highest rates of sound-production were to the north of the Uele River. Figure 2 gives a breakdown of the different sound-types made by the chimpanzees per main forest region as well as for the entire region.

Chimpanzee auditory frequencies between the three main survey regions

Figure 3 shows the average number of chimpanzee sounds heard per hour for each hour across the three main survey regions. The average number of chimpanzee sounds differed significantly between these three regions (Kruskal-Wallis chi-squared = 195.9, df = 2, $p < 0.001$). Subsequent post-hoc testing showed a significant difference between Gangu and the non-Gangu North Uele forests (critical value = 294.9, observed value = 417.8, $p < 0.001$), and also between Gangu and the South Uele forests (critical value =350.5, observed value = 504.0, $p < 0.001$), but not between non-Gangu North Uele and South Uele (critical value = 269.0, observed value = 86.2, p = ns).

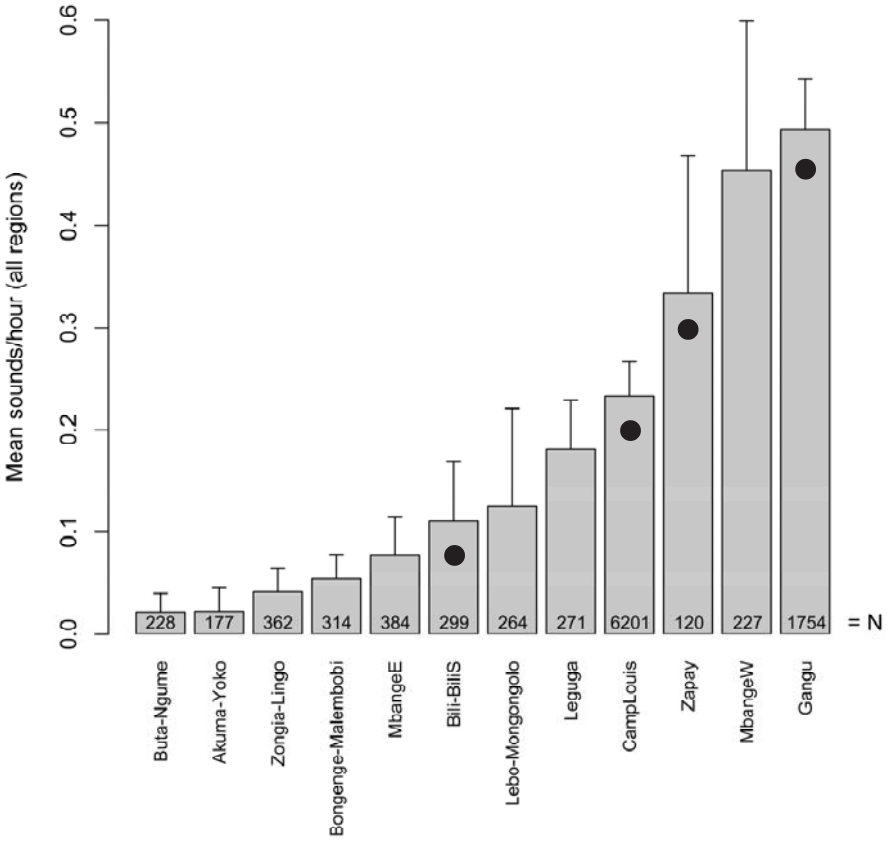


Figure 1. Mean (+ SEM) number of chimpanzee sounds (including pant hoots, tree drums, and other sounds) per hour across the 12 survey regions. Numbers of observation hours per region are given at the base of the bars. North Uele sites are indicated with black dots.

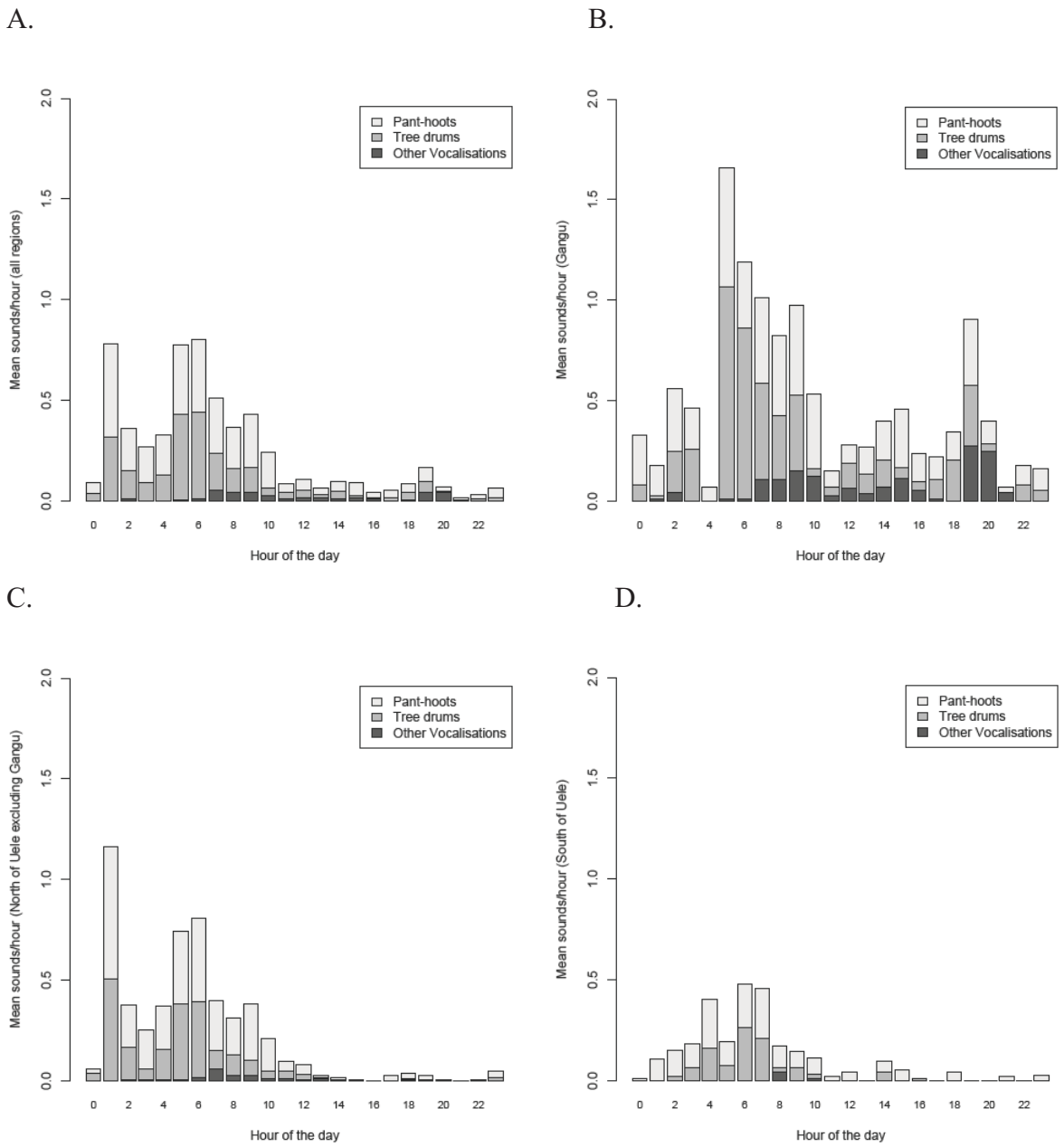


Figure 2. Mean sounds per hour made by chimpanzees combined across the three main survey regions: (A) All regions pooled. (B) Mean sound-types per hour, Gangu. (C) Mean sound-types per hour, north of the Uele excluding Gangu. (D) Mean sound-types per hour, South Uele.

Chimpanzee sound-production across the day

Next, we looked at differences between chimpanzee sounds made during individual hours across the three main study regions (Figure 4). Gangu chimpanzees, in addition to producing the highest rate of vocalizations and tree drums, were also more vocal throughout the day. Sound production for each hour was compared across the three main regions (Appendix II). During the night (23:00-5:00 hours) no statistical significant differences were found (Kruskal-Wallis tests, p = ns for all 6 hours). However with the exception of 11:00-12:00 and 18:00-19:00 all other hours showed a significant difference between regions at the $p < 0.05$ level. When we adjusted for multiple comparisons using a Bonferroni correction, the overall pattern proved to be robust, and only at 13:00, 18:00, and 21:00 hours significance was lost.

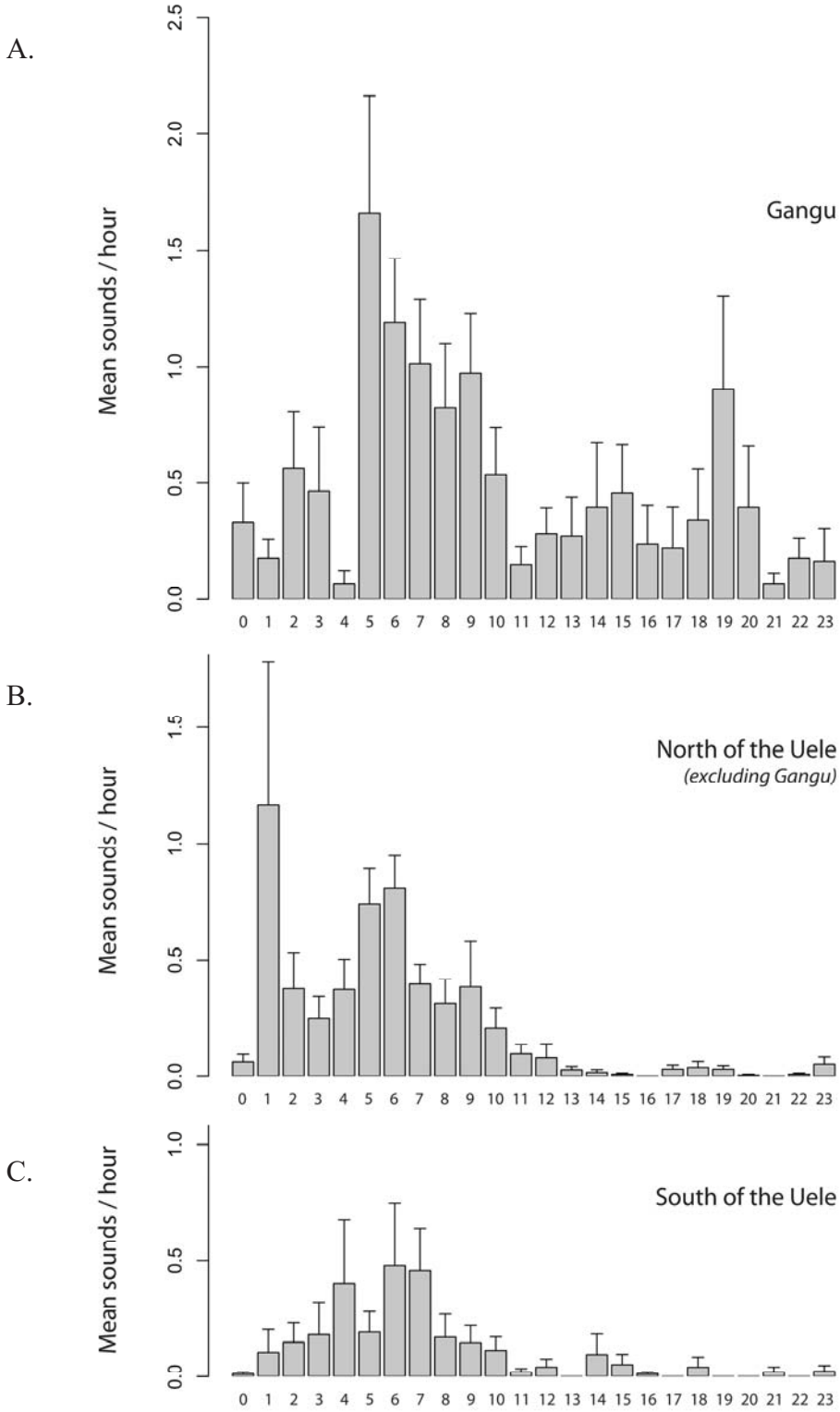


Figure 3. Mean (+ SEM) number of chimpanzee sounds recorded across the day in (A) Gangu, (B) north of the Uele, excluding Gangu, and (C) south of the Uele.

Human evidence

Major differences existed between the surveyed regions in the amount of human evidence encountered (Figures 5 & 6). In Figure 5a we show the encounter rate for all recorded human

evidence by survey region, ordered according to the level of chimpanzee sound production from Figure 1; Figure 5b includes only the hunting evidence found in the same regions. See appendices III and IV for more detailed information on human evidence encountered in the 12 different forest regions. Appendix IV focuses specifically on the hunting evidence.

With the exception of Bili South, all North Uele study regions had low encounter rates for human evidence. The lowest levels were found in the Gangu and Camp Louis Forests. We therefore compared the evidence of encounter rates in these regions with that in the other northern and the southern forests**,** and found a significant difference (Kruskal-Wallis chi-squared = 209.0, df = 2, $p <$ 0.001) Post-hoc testing showed that all three groups differed significantly from one another at $p =$ 0.001 (Gangu / Camp Louis vs other North Uele forests: critical value = 107.0, observed value is 206.2; Gangu/Camp Louis vs South Uele Forests critical value = 90.2, observed value = 341.6; Other North Uele forests vs South Uele Forests critical value = 72.4, observed value = 135.4). Gangu's actual human presence was in reality much lower than even that of Camp Louis; human evidence was found only at Gangu's eastern edge, which inflated the total (see notes, Appendix III). The sites with the highest levels of human presence and hunting were all to the south of the Uele. Mbange West in particular had high levels of human disturbance.

A

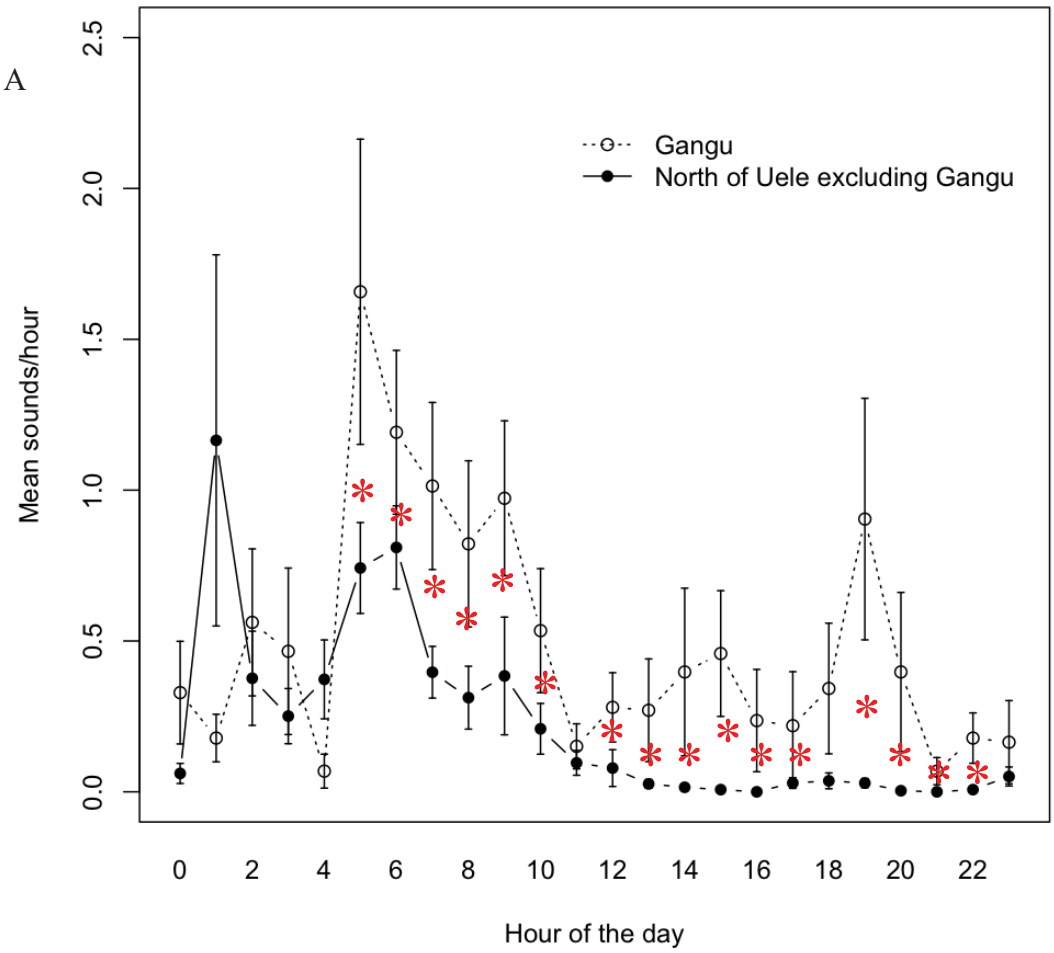
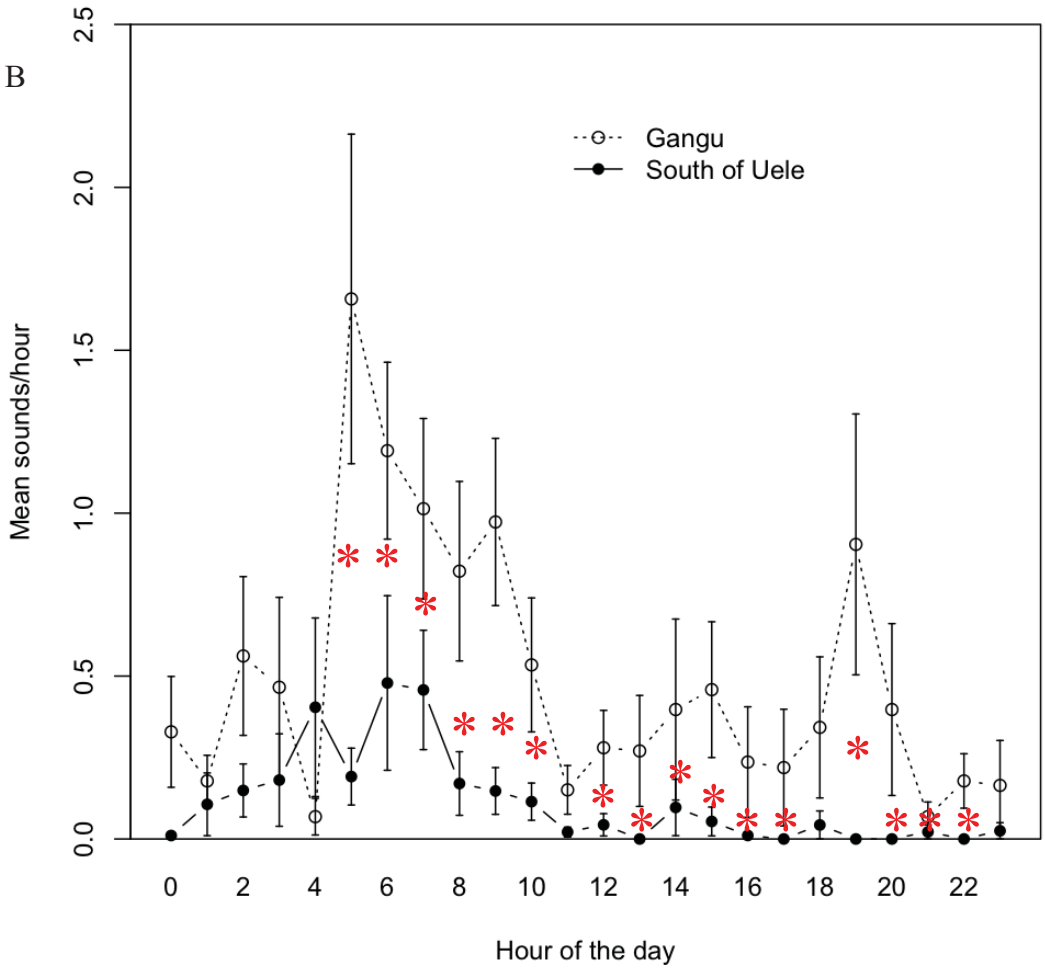


Figure 4. Comparisons of chimpanzee sounds by time of day between (A) Gangu and the other North Uele forests, and (B) Gangu and the South Uele forests. For visual clarity the three groups are presented in two pair-wise plots, but the asterisks in the figure indicate significant differences (p< 0.05) in the nonparametric Kruskal-Wallis ANOVA over all three groups.



To investigate the structure of the human evidence data, we ran a Principal Component Analysis (PCA). The first axis of the PCA (Figure 7; Appendix V) explained 31 % of the variation, and appears to be related to the amount of human hunting disturbance, ranging from non-hunting related indicators towards the right (lean-tos, pets, fields, huts, etc.) to direct indicators of hunting (snares, bushmeat, hunting camps etc.) on to the left (Eigen value = 2.38). The second axis explained an additional 21% of the variation and represents other human activities, with high positive loadings for mere human presence as indicated by villages, fields, and huts and high negative loadings for forest-related activities such as bird-hunting and mining (Eigen value = 1.97).

On these two axes, the Gangu Forest lies far to the right, characterized by a minimum level of human disturbance and hunting (PC1), and very few other signs of human presence (PC2). In contrast, Mbange West, Mbange East, and Buta-Ngume (all South Uele forests) lie towards the left and are characterized by high levels of both hunting-related evidence (PC1) and other indicators of human presence and forest use (PC2).

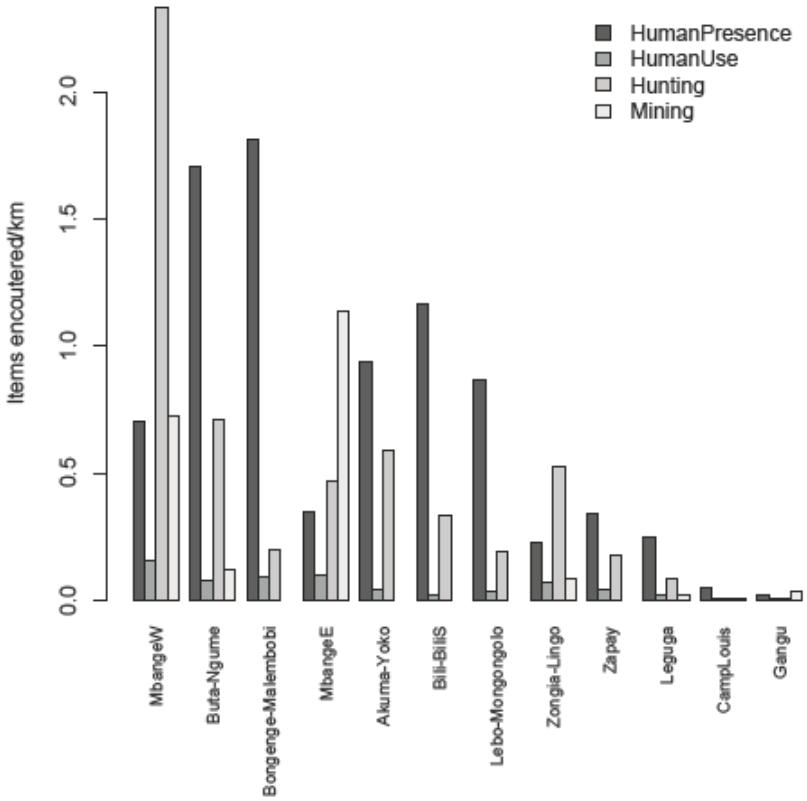


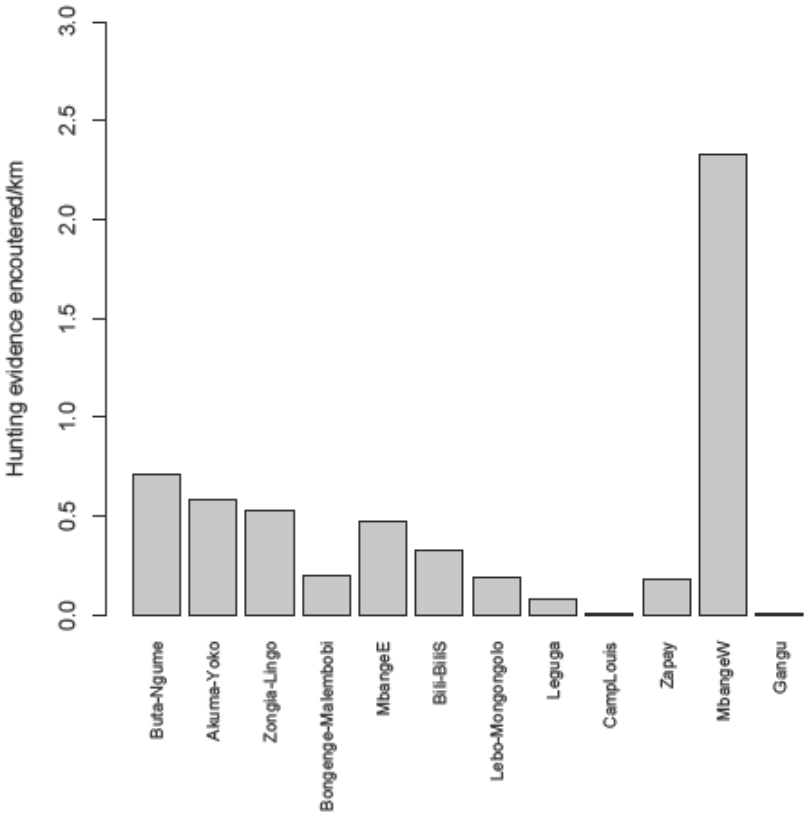
Figure 5. Human evidence types across the different study regions.

To investigate the relationship between human evidence and chimpanzee sound-production, we performed a Spearman rank correlation test between the first two PCA axes and chimpanzee sound production. The scatter-plot in Figure 8 compares the human evidence summarized by PC1 ("human hunting disturbance") found across the different forest regions surveyed and the number of chimpanzee sounds recorded per hour. Mbange West, the point shown in the top left of Figure 6, is a severe outlier, with high levels of human evidence and chimpanzee sounds, and was therefore not included in the final statistical analysis.

When the data-point for the outlier Mbange West was kept in the dataset, no significant correlation could be found (S = 174, $p = 0.11$, rho = 0.39). However, when Mbange West was excluded, human hunting-disturbance as summarized by PC1 did correlate significantly with sound (S = 64, $p = 0.009$, rho = 0.71). In contrast to the effect of PC1, the correlation with PC2 (human presence and forest use) was not significant, even with Mbange West excluded (S = 254, $p = 0.68$, rho = -0.16). This indicates that human hunting had a marked influence on rates of chimpanzee sound-production, but not more neutral human presence.

The structure of the Mbange West Forest was strikingly different from nearly all of the other forests we surveyed, except for small sections of the Akuma-Yoko Forest and Buta Forests. Throughout the Mbange West region, scattered patches of old-growth riverine forest were separated by enormous, thickly-tangled herb patches made up of *Megaphrynium*, *Haumania* and other towering herb species, with very few but tall trees (Figure 9). These herb patches extended for several kilometers, and were completely impenetrable. The only way we could travel through them was by following snare trails hacked out by local trappers.

A



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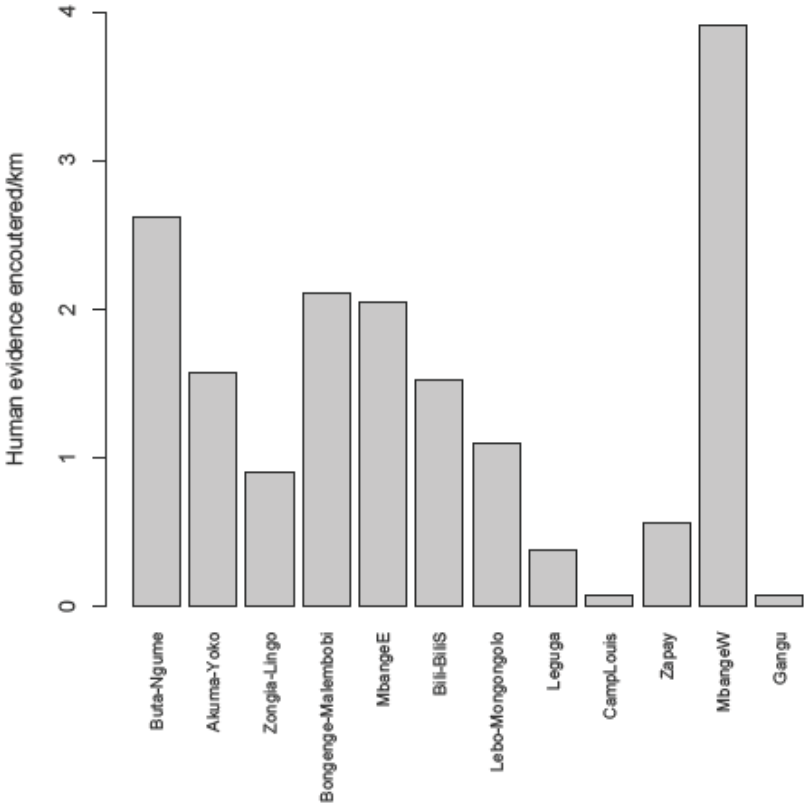

Figure 6. Human evidence encountered across the 12 study regions, A. total evidence, and B. only hunting evidence.

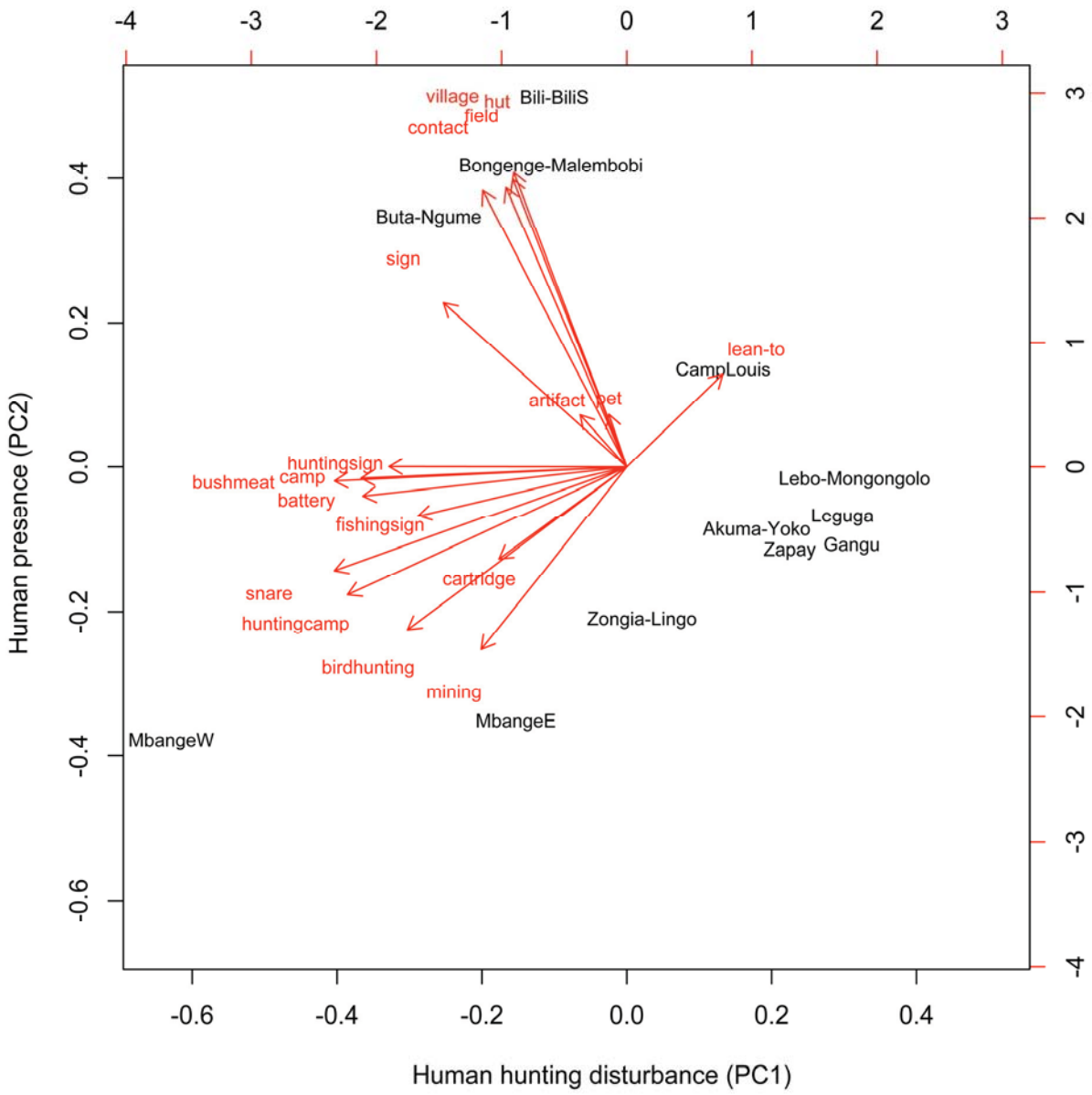

Figure 7. A Principal Component Analysis (PCA) of human evidence across the study regions. *Comparison between human evidence encounter rates and chimpanzee sound rate*

Clearly, however, the chimpanzees were able to follow hidden routes through them: in the early mornings, we would hear the apes pant-hooting from nearby; when we would rush in their direction to attempt a contact, we would lose them when they entered the thick wall of vines and herbs. We would hear the apes pant-hooting from within the herb patch throughout the day, but were never able to find them. We found travel signs of the apes in this forest. Despite the extremely high incidence of hunting and snaring at Mbange West, humans were apparently limited to traveling through the herb forest on pre-cut snare trails.

Although at Mbange West we heard the chimpanzees pant-hooting from within this dense forest-type and found feeding remains, we encountered no nest sites. This may be because we were obligated to follow human trapping trails through this nearly-impenetrable herb forest, trails that we can assume the chimpanzees would have avoided. In the Akuma Forest 70 km south-southwest, we found a similar kind of dense herb forest as the one that predominated at Mbange West, although at Akuma it made up a much smaller proportion of

the total forest. Later we found small patches of this forest-type in the Buta Forest to the east of Akuma. At Akuma and Buta we found abundant feeding remains of the chimpanzees in this forest-type, as well as nest sites and even a ground nest at Akuma (Figure 10).

Across the Likati River from Mbange West, in the Mbange East Forest, the chimpanzees had extremely low rates of vocalizations. This correlated well with the high level of human disturbance; the main difference from Mbange West was the absence of the herb-dominant forest-type.

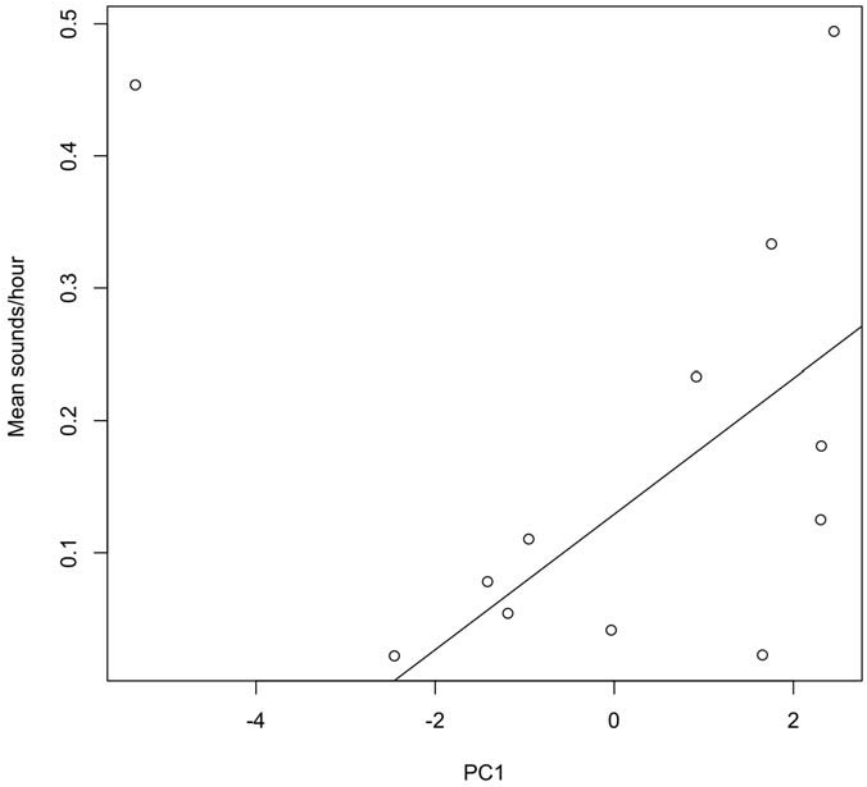

Figure 8. Scatter-plot of human hunting disturbance (PCI) found across the different forest regions surveyed (summarized by the first PCA axis largely representing hunting evidence) and the number of chimpanzee sounds recorded per hour. The least-square regression line was calculated excluding the outlier Mbange West, visible in the upper left corner of the plot.

Discussion

Chimpanzees across our study area in the northern DRC reacted in a consistent manner to human disturbance. The more human signs we encountered in a region, the fewer long-distance chimpanzee vocalizations or tree drums we heard throughout the day. In heavily-hunted areas the chimpanzees limited their sound-production to the early mornings.

At Gombe, Tanzania, Wrangham (1975) recorded the calls of chimpanzees habituated to humans between the hours of 5:00 and 20:00. The apes vocalized most often in the morning between 7:00 and 9:00 hours. There was then a gradual decline in their rate of calls across the day, but with no abrupt drop-off as was seen for the chimpanzees of our study except for those at Gangu. Wilson et al. (2007) documented a similar pattern to that seen in Gombe in the Kanyawara chimpanzees (the exception being when Kanyawara chimpanzees visited croplands, at which time rates of morning vocalizations declined to match the low

a. b.

Figure 9. a. Impenetrable herb forest at Mbange West (we were forced to travel on human-cut snare trails). b. Massive herb patch in the Akuma Forest. It would be very difficult to sneak up on chimpanzees in this kind of forest, as the massive *Megaphrynium* herbs are noisy to walk through.

Figure 10. A ground nest in the impenetrable herb tangle of the Akuma Forest.

levels typical of the rest of the day). The call-rates at Gombe and (non-cropland) Kanyawara resembled those at Gangu, but lacked Gangu's early-evening peak. It is the steep decline in sound-production immediately following the early morning hours shown by the non-Gangu North Uele as well as the South Uele chimpanzees in this study that requires an explanation.

The reduction of sound-production rates by chimpanzees in forests heavily-hunted by humans, as well as the tendency of the apes to limit their sound-production to the night and earliest morning hours, is likely a response to hunting pressure. Local hunters told us that their preferred hunting technique was to home in on chimpanzees at their night nests or feeding trees, from where they had heard the apes pant-hooting in the early morning. The hunters can stealthily surround a tree-full of feeding chimpanzees and silently knock them out of the trees one-by-one with poison arrows (Chapter 6). It is probable that in heavily-hunted areas, chimpanzees have learned to vacate their night nests early in the morning to avoid being ambushed by humans. Throughout the day, the chimpanzees manage to suppress their species-typical noisy social calls and tree drums to avoid giving human hunters cues to their presence. This would explain why we had almost no success in finding and contacting chimpanzees in the South Uele Forest, even when during night hours we heard their nearby pant-hoots and left camp in the early morning hours to find them. Unlike in the North Uele forests, we would nearly always find freshly-vacated nests but no sign of the chimpanzees themselves. In addition, we rarely heard South Uele apes vocalizing at fruit trees.

In our data set, the forests of Mbange West emerged as a clear outlier. As in many other forests in the South Uele region, signs of human mining were present there. We encountered several successful monkey-hunters in this forest and in the nearby village, and we found more snares than in any other forest surveyed. Strangely, however, the chimpanzees in this forest vocalized frequently, almost as frequently as at Gangu, and did not limit their vocalizations to the early morning. Just 10 km east across the road, at Mbange East, the evidence of hunting and snaring, although higher than at most other forest regions (an agile mangabey was shot out of a tree above our heads, and we encountered several large traps set for okapis), was lower than at Mbange West. As in other South Uele forests, but unlike at Mbange West, we almost never heard the chimpanzees, although we found their nests and feeding remains all around us. How can we explain this discrepancy?

A likely explanation is that the chimpanzees of Mbange West are uniquely-protected from humans by the dense herb 'seas' in which they live, and they feel confident enough in this forest-type to vocalize with the same frequency and pattern as do those at Gangu. For this reason, for our second series of analyses we excluded Mbange West, leading to a significant correlation between human signs and rates of chimpanzee vocalizations.

A potential bias in our study relates to the fact that in some forest areas, particularly to the south of the Uele, we were more likely to travel on human hunting trails than in other regions such as Gangu. This may have lead to an inflated encounter rate with human signs, particularly hunting signs, in the southern forests. This bias in methodology was unavoidable, for the obvious reason that at Gangu, there were no hunting trails, nor almost any other human signs, and there were very few at Camp Louis. We did use some ex-hunting / fishing trails at Camp Louis, but we found minimal evidence of hunting on them. The very lack of usable hunting trails at Camp Louis and Gangu (we usually had to cut our own) provides strong evidence that the higher rates of human sign in the south was not an artifact. Nevertheless, because we were following hunting trails in some forests but not at Gangu and Camp Louis, some bias in our detection of human signs can be expected.

Two additional potential complicating factors should be considered. In many of the regions we surveyed south of the Uele, the forests had been heavily-disturbed by humans and often partially converted to plantations. Perhaps there were simply fewer desirable food sources for the chimpanzees to pant-hoot about (as can be seen in Appendix VI, Chapter 4,

the small number of fruit species observed in the chimpanzees' diet south of the Uele raises this possibility). However, previous research with other chimpanzee populations points away from pant-hooting being tied directly to richness or quality of food resources; the behavior instead seems to be integral part of chimpanzee social life, serving an important function in the spacing of individuals within the group (Mitani & Nishida, 1993). Indeed, we had a difficult time locating and making contact with the South Uele chimpanzees even when feeding remains showed that they had been feeding at large fruiting trees. Another possibility that cannot be ruled out is that chimpanzees in areas with heavy human hunting pressure may live in lower population densities or travel singly to avoid human predation, giving them less opportunity to communicate with other apes. This is unlikely, however, as the average number of nests per site was nearly identical to the north and south of the Uele, whether or not ground nests were included (see Table III, Chapter 4).

A difference in chimpanzee density between the North Uele and the South Uele forests is also unlikely to explain our findings. As Chapter 4 makes clear, the encounter rate of chimpanzee nests was similar on both sides of the river. In fact, based on the amount of forest cover (Figure 5, Chapter 4), we might predict higher densities of chimpanzees in the South Uele region, and thus we would expect to hear more vocalizations. We found numerous chimpanzee nests, fresh traces, and artifacts in all of the South Uele forests in which we camped.

In areas such as the Buta and Yoko Forests, which were near cities and crisscrossed with fields and human paths, chimpanzees were still abundant although very quiet. These forests were empty of other large fauna, such as okapis, buffalos, and elephants, which were still present in the less-heavily-trafficked forests nearby (Chapter 1). Near cities, in the same forests in which chimpanzees were still common, we found no trace of these large mammals, and according to the locals they had been extirpated decades ago. Chimpanzees may be, in certain contexts, the only medium-to-large-sized mammal able to survive frequent contact with human hunters and agriculturists. Unfortunately, changes in the past 15 years make it unlikely that even they will long survive the new poaching onslaught (Chapter 6). We found chimpanzee nests within 13 km of Buta, the human commercial, population, and bushmeat center in the area (Chapter 4), as well as near other large population centers. However, local Buta agriculturalists, long-term residents of the area, claimed to us that the apes had lived much closer to Buta only 15 years ago, until that time to within 7 km of the city. They explained that since then the chimpanzees had been exterminated from or chased out of the newly-cut mosaic of fields and forest, mostly by waves of immigrants, who often hunted the apes with packs of dogs. The likelihood is that this expanding radius of chimpanzee-free forests will increase steadily in size, at least around roads, towns, and mines.

Vocalizations are an important part of chimpanzee social life. Clark and Wrangham (1994) proposed that 'arrival' pant-hoots serve to signify the status of adult chimpanzees. Marler and Hobbett (1975) found that they could discriminate between the calls made by different individual chimpanzees based on variations in frequency and temporal structure; undoubtedly, chimpanzees can do the same. Chimpanzees may also use pant-hoots to regulate spacing between group members and to express differences in rank (Mitani & Nishida, 1993), and also to differentiate between the members of different communities (Mitani et al., 1992). Boesch (1991) proposed that in a community of Taï Forest chimpanzees, tree drums conveyed symbolic information aiding in the coordination of travel between different parties. If the chimpanzees in the northern DRC are being forced by human disturbance to reduce their rate of vocalizations and tree drums, it would follow that this could have a disrupting effect on their social system. This could lead to the impoverishment of their traditions (van Schaik, 2002), as we will discuss in Chapter 5.

Chimpanzees show human-like flexibility in a number of basic behaviors, and thus it is not surprising that they are capable of adapting their vocalizations and other behaviors to incursions by *H. sapiens* into their habitats. In this chapter, we have presented evidence that chimpanzees inhabiting areas heavily-hunted by humans have reacted by significantly reducing their rate of vocalizations and tree-drums, and also limiting these to the early morning hours. This is a fine example of behavioral adaption in our evolutionary cousins, but it is uncertain whether or not it will be sufficient to counter the new wave of bushmeat hunting by immigrants that are now invading the area (Chapter 6).

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Appendices

Appendix I. Comparison of frequencies of chimpanzee auditory traits (pant-hoots, tree drum, and other sounds) across the 12 forest regions. The first four forest regions were north of the Uele River, and the following eight were south.

Forest region	Hours in forest	No. pant-hoots	Pant-hoots per hour	No. tree drums	Tree drums per hour	No. other sounds	Other sounds per hour	No. total sounds	Total sounds per hour
Camp Louis	6201	827	0.13	569	0.09	50	0.01	1446	0.23
Gangu	1754	394	0.23	362	0.21	111	0.06	867	0.49
Bili-Bili S	299	28	0.09	3	0.01	2	0.01	33	0.11
Zapay	120	30	0.25	7	0.06	3	0.03	40	0.33
Bongenge - Malembobi	314	10	0.03	7	0.02	0	0	17	0.05
Leguga	271	29	0.11	15	0.06	5	0.02	49	0.18
Lebo - Mongongolo	264	18	0.07	15	0.06	0	0	33	0.13
Zongia - Lingo	362	8	0.02	7	0.02	0	0	15	0.04
Mbange E	384	20	0.05	10	0.03	0	0	30	0.08
Mbange W	227	69	0.30	34	0.15	0	0	103	0.45
Buta - Ngume	228	3	0.01	2	0.01	0	0	5	0.02
Akuma - Yoko	177	4	0.02	0	0	0	0	4	0.02
All forests north of Uele River	8374	1279	0.15	941	0.11	166	0.02	2386	0.29
All forests south of Uele River	1956	161	0.08	90	0.05	5	0.01	256	0.13
All forests	10330	1440	0.14	1031	0.10	171	0.02	2642	0.26

Appendix II. Results of Kruskal-Wallis nonparametric ANOVAs for chimpanzee sounds per hour made during individual hours across the three main study regions (Figure 3). Significant differences at the $p = 0.05$ (uncorrected) and $p = 0.002$ (after Bonferroni correction) level are indicated by bold print. A loss of significance from the uncorrected Kruskal-Wallis test is indicated by bold, red print.

Hour	p	χ^2
0	0.1518	3.7699
1	0.2109	3.1131
2	0.4055	1.8055
3	0.3165	2.3008
4	0.4585	1.5596
5	**0.0001**	18.2948
6	**0.0000**	24.2343
7	**0.0016**	12.9369
8	**0.0002**	16.8859
9	**0.0000**	37.3630
10	**0.0001**	18.9643
11	0.2400	2.8535
12	**0.0018**	12.7012
13	**0.0056**	10.3657
14	**0.0001**	18.0797
15	**0.0000**	23.7517
16	**0.0000**	20.6432
17	**0.0116**	8.9159
18	0.0709	5.2923
19	**0.0000**	27.5696
20	**0.0006**	14.8469
21	**0.0044**	10.8495
22	**0.0004**	15.8436
23	0.4000	1.8215

Appendix III. Human evidence (hunting and mining signs, in addition to evidence of human use of forests such as fishing and clearing for fields, and neutral signs of presence) found per km walked in the forest, across the 12 study regions.

Forest region	Km walked	No. hunting signs	Avg. no. hunting signs / km	No. mining signs	Avg. no. mining signs / km	No. signs of human forest-use	Avg. no. signs of human forest use / km
Camp Louis	1230.6	9	0.01	6[1]	0.01	6	0.01
Gangu	327.4	3	0.01	11[1]	0.03	2	0.01
Bili-Bili S	88	29	0.33	0	0	2	0.02
Zapay	50	9	0.18	0	0	2	0.04
Bongenge - Malembobi	65	13	0.20	0	0	6	0.09
Leguga	49	4	0.08	1	0.02	1	0.02
Lebo - Mongongolo	31	6	0.19	0	0	1	0.03
Zongia - Lingo	74	39	0.53	6	0.08	5	0.07
Mbange E	81	38	0.47	92	1.14	8	0.10
Mbange W	46	106	2.33	33	0.73	7	0.15
Buta - Ngume	65	46	0.71	8	0.12	5	0.08
Akuma - Yoko	26	15	0.59	0	0	1	0.04
All N Forests	1696	50	0.03	17	0.01	12	0.01
All S Forests	437	267	0.61	140	0.52	34	0.08
All Forests	2133	317	0.15	157	0.07	46	0.02

Forest region	No. signs of presence	Avg. no.signs ofpresence / km	Total no. signs	Avg . no. signs / km
Camp Louis	63	0.05	84	0.07
Gangu	6	0.02	22[2]	0.07
Bili-Bili S	102	1.16	133	1.51
Zapay	17	0.34	28	0.56
Bongenge - Malembobi	118	1.82	137	2.11
Leguga	12	0.25	18	0.37
Lebo - Mongongolo	27	0.87	34	1.10
Zongia - Lingo	17	0.23	67	1.72
Mbange E	28	0.35	166	2.05
Mbange W	32	0.70	178	1.68
Buta - Ngume	111	1.71	170	2.62
Akuma - Yoko	24	0.94	40	1.54
All N Forests	188	0.11	267	0.16
All S Forests	369	0.84	810	1.85
All Forests	557	0.26	1077	0.51

[1] Three of the mines in the Gangu Forest and all of the mines in the Camp Louis Forest were decades old.

[2] At Gangu, 15 of the 22 items of human evidence (68%), including all of the mines, were found within 5 km of the east edge of the Gangu Forest, between the west bank of the Bo River and the savanna. No human evidence was found further than 10 km west of the Gangu Forest's east boundary; thus the Gangu Forest proper can be considered virtually untouched by humans.

Appendix IV. Hunting evidence found per km walked in the forest, across study regions.

Forest region	Km walked	No. cartridges	Avg. no. cartridges / km	No. snares	Avg. no. snares / km	No. hunting camps	Avg. no. hunting camps / km	No. other hunting signs	Avg. no. other hunting signs / km	No. total hunting signs	Avg no. hunting signs / km
Camp Louis	1230.6	0	0	1	0.001	6	0.01	2	0.001	9	0.01
Gangu	327.4	0	0	0	0	2	0.01	1	0.003	3	0.01
Bili-Bili S	88	9	0.10	7	0.08	4	0.05	9	0.10	29	0.33
Zapay	50	1	0.02	5	0.10	3	0.06	0	0	9	0.18
Bongenge-Malembobi	65	0	0	2	0.03	3	0.05	8	0.12	13	0.20
Leguga	49	0	0	2	0.04	1	0.02	1	0.02	4	0.08
Lebo - Mongongolo	31	0	0	2	0.07	2	0.07	2	0.07	6	0.19
Zongia - Lingo	74	24	0.32	4	0.05	7	0.09	4	0.05	39	0.53
Mbange E	81	9	0.11	14	0.17	7	0.09	8	0.10	38	0.47
Mbange W	46	8	0.18	70	1.54	10	0.22	18	0.40	106	2.30
Buta - Ngume	65	3	0.05	32	0.49	5	0.08	6	0.09	46	0.71
Akuma - Yoko	26	1	0.04	11	0.43	3	0.05	0	0	15	0.58
All N Forests	1696	10	0.01	13	0.01	15	0.01	0	0	38	0.02
All S Forests	437	45	0.10	150	0.34	38	0.09	47	0.11	280	0.64
All Forests	2133	55	0.03	163	0.08	53	0.03	47	0.02	318	0.15

Appendix V. Factor-loadings from the PCA analysis of the 18 human evidence items across the different study regions. For PC1, the lower the item's number in the series, the more likely it correlates with low frequencies of chimpanzee sounds. Loadings near 0 indicate that the evidence-type does not contribute to that particular axis, negatively or positively.

Evidence type	Factor loading PC1	Evidence type	Factor loading PC2
Lean-to	0.11627902	Village	0.43254065
Pet	-0.02165588	Hut	0.4226454
Artifact	-0.05646834	Field	0.41044499
Village	-0.13688522	Contact	0.40611163
Hut	-0.1380519	Sign	0.24158883
Field	-0.14625452	Lean-to	0.13642942
Cartridge	-0.15489359	Pet	0.07737847
Contact	-0.17441905	Artifact	0.0765755
Mining	-0.17635752	Hunting sign	0.00053498
Sign	-0.22206161	Camp	-0.0162684
Fishing sign	-0.25323691	Bushmeat	-0.0202007
Bird hunting	-0.26564099	Battery	-0.0422102
Hunting sign	-0.28795454	Fishing sign	-0.07152
Battery	-0.31983792	Cartridge	-0.1345631
Camp	-0.32182162	Snare	-0.1516323
Hunting camp	-0.33834701	Hunting camp	-0.1870454
Bushmeat	-0.3540457	Bird hunting	-0.238409
Snare	-0.35426473	Mining	-0.2675146