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Original Article

Impact of Humans on Long-Distance Communication Behaviour of Eastern Chimpanzees (*Pan troglodytes schweinfurthii)* in the Northern Democratic Republic of the Congo

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Abstract

We systematically recorded all long-distance chimpanzee vocalizations and tree drums over a 26-month study period in 13 forest regions in the Democratic Republic of the Congo. We found that the frequency of chimpanzee vocalizations and tree drums was considerably higher in the remote Gangu Forest than in other forest regions closer to human settlements and roads. We present evidence indicating that chimpanzees may reduce their levels of vocalizations in areas characterized by high levels of human hunting. The chimpanzees appear to have the behavioural flexibility necessary to modify their behaviour in areas where humans are a major threat. We discuss the possible consequences of this reduction in vocalization rate on the social system of the chimpanzees.

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Introduction

Chimpanzees *(Pan troglodytes)* inhabiting different regions across Africa display remarkable flexibility in their behaviours, in the domains of nest construction [Koops et al., 2007; Hicks, 2010], tool use [Whiten et al., 2001], and even in the basic structure of their social groups [Boesch and Boesch-Achermann, 2000]. This same flexibility extends to their vocalizations, even to the extent that regional or community 'dialects' have been proposed [Mitani et al., 1992]. Unfortunately, just as we are beginning to document this rich behavioural diversity in our close evolutionary cousins, chimpanzee populations across Africa are coming under assault from a rapidly proliferating

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commercial bushmeat industry [Walsh et al., 2003; Campbell et al., 2008]. Within the past 2 decades, populations in northwest Africa and Gabon have been decimated by this trade coupled with habitat destruction; in the species' Congo Basin stronghold (particularly in the Democratic Republic of the Congo, hereafter abbreviated as DRC), the process seems to be only just gathering momentum [Hicks et al., 2010].

Despite this recent wave of heightened persecution, chimpanzees in the DRC still survive in the heavily degraded forests close to major human population centres such as Buta and Aketi, forests from which other large mammals such as okapis *(Okapia johnstoni)* and elephants *(Loxodonta cyclotis)* were extirpated decades ago [Hicks, 2010]. Little attention has been paid to the behavioural responses that chimpanzees may adopt when confronted with human predation. Field research has shown that chimpanzees are capable of suppressing their natural repertoire of vocalizations [Goodall, 1986]. They do this in the context of male-female consortships in the danger zones at borders with neighbouring communities, during all-male patrols into the territories of rival communities, and in order to avoid having food stolen by conspecifics. The goal of the current study is to investigate how chimpanzees might alter their vocalizations when regularly encountering potentially dangerous humans. This research will add more data to the growing field of ethnoprimatology [Sponsel, 1997; Fuentes and Wolfe, 2002], with its focus on the complex relationships between humans and our primate relatives. It promises to enrich our understanding of the relationship between chimpanzees and humans in areas where the two species coexist, potentially crucial information for our efforts to mitigate conflict between the two species. In addition, it will benefit survey work in areas where chimpanzees are being hunted: just because chimpanzees are rarely heard does not have to mean that they are not present.

In some parts of Africa, as in the northern DRC, the apes' behavioural flexibility has 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. Chimpanzees living in close association with humans at Bossou, Guinea, reduced their pant-hoot vocalizations by about one half when crop-raiding, with females, who are more timid than males, showing the greatest reduction in vocalizations [Hockings, 2009]. Similar changes in vocalization behaviour have been documented in other primate species: spider monkeys *(Ateles paniscus)* reduce their call rate in regions where they are heavily hunted [Van Roosmalen, 2008], and vervet monkeys *(Chlorocebus aethiops)* [Kavanaugh, 1980] are more quiet when raiding crops.

The forests and savanna-woodlands near Bili, DRC, are characterized by low human population densities and are home to a large, apparently continuous population of chimpanzees *(Pan troglodytes schweinfurthii)* [Hicks, 2010]. Although the apes are sometimes hunted, there is no evidence that a large-scale commercial bushmeat trade has yet appeared in the area [Hicks et al., 2010]. Between 2004 and 2007, Thurston Cleveland Hicks (T.C.H.) spent a total of 18 months studying chimpanzees in this area, and in 2007, he conducted a 13.5-month survey of chimpanzee populations across a large area approximately 200 km south of Bili, in forests near the towns of Leguga, Aketi, Buta and Bambesa. Over the course of these surveys, we scored all vocalizations and tree drums; in addition, we recorded all signs of human presence and activity. This includes indicators of hunting in the region such as cartridges and

snares, which allow us to evaluate the effects of hunting pressure on chimpanzee sound production. The data we collected have allowed us to compare the behaviour of chimpanzees living in areas with different levels of human influence. In this study, we focus on vocalizations and tree drums; it might be expected that sound production will be most reduced in areas with higher encounter rates of indicators of human presence in general. More specifically we hypothesize that the chimpanzees living in areas with fewer indicators of hunting, in particular in the pristine Gangu Forest where there were almost no signs of hunting, should be more vocal than those living in areas with higher encounter rates of indicators of hunting pressure.

Methodology

The Study Area

Between 2004 and 2007, the main study area of the Bili ape research project encompassed an approximately 475 km² area of the forests and savannas northwest of the town of Bili [Hicks, 2010] (fig. 1). We worked out of two main research camps: Camp Louis (4°21′72′′ N, 24°56′72′′ E) and, approximately 30 km to the west-southwest, Camp Gangu (4°19′34′′ N, 24°41′53′′ E). The 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 [Hicks, 2010; Hicks et al., 2012]. The forest/savanna zone closer to the road (called from here on the Camp Louis Forest) also had very little sign of human presence, but the wildlife was less abundant and the chimpanzees almost always reacted to us with fear [Hicks et al., 2012].

Between 2004 and 2007, T.C.H. conducted 'path of least resistance' recce-style surveys in 4 localities across a large area north of the Uele River (online suppl. table 1; for all online suppl. material, see www.karger.com/doi/10.1159/350650) (recces: non-systematic exploratory reconnaissance walks across the landscape, usually following human or elephant trails, and searching for apes and signs of their presence such as dung, tree and ground nests, and feeding remains). From October 2007 to October 2008 (and in one brief visit to Lebo in 2006), T.C.H. carried out a survey of 9 forest regions south of the Uele River, using the same recce methodology as at Bili (online suppl. table 1) [Hicks, 2010]. In addition, in 2005 T.C.H. conducted 160 km of line transect surveys through the Camp Louis and Gangu regions. On both the recce and transect walks, we recorded all signs of chimpanzees, humans and other large mammals [Hicks, 2010].

The surveys were conducted in 13 forest regions to the north and south of the Uele River (fig. 1). Due to their proximity to one another and similar levels of human hunting pressure, several nearby forest regions were combined with one another: Zongia-Lingo, Buta-Ngume, and the forests just south of Bili. The Gangu Forest lies more than 20 km from the nearest roads and villages, while all other forests were located less than 20 km from the roads. The climate in the region is described in Hicks [2010]. We consider the dry season as representing the period between December and March, when the average monthly rainfall summed to <100 mm at 5 different weather stations across the region (Tukpwo, Bili, Aketi, and, with the exception of March, Buta and Bambesa) (online suppl. fig. 1–3).

Chimpanzee Vocalizations and Tree Drums

Throughout our study, we attempted to locate chimpanzees in the forests and observe them [Hicks et al., 2012]. In addition to our encounters with the chimpanzees, we confirmed their presence by the discovery of their night nests, feeding remains, and/or dung. Only forests in which recent chimpanzee presence was confirmed were included in this study [Hicks, 2010] (online suppl. table 1). While in the forest, T.C.H. systematically recorded all vocalizations and tree drums made by the apes throughout the day (05:00 to 22:00 h). Night sounds (data are presented in Hicks [2010]) were excluded from the analysis due to the likelihood that some were missed due to sleep. Vocalizations were differentiated into 'pant-hoots' and 'other vocalizations' (i.e. screams,
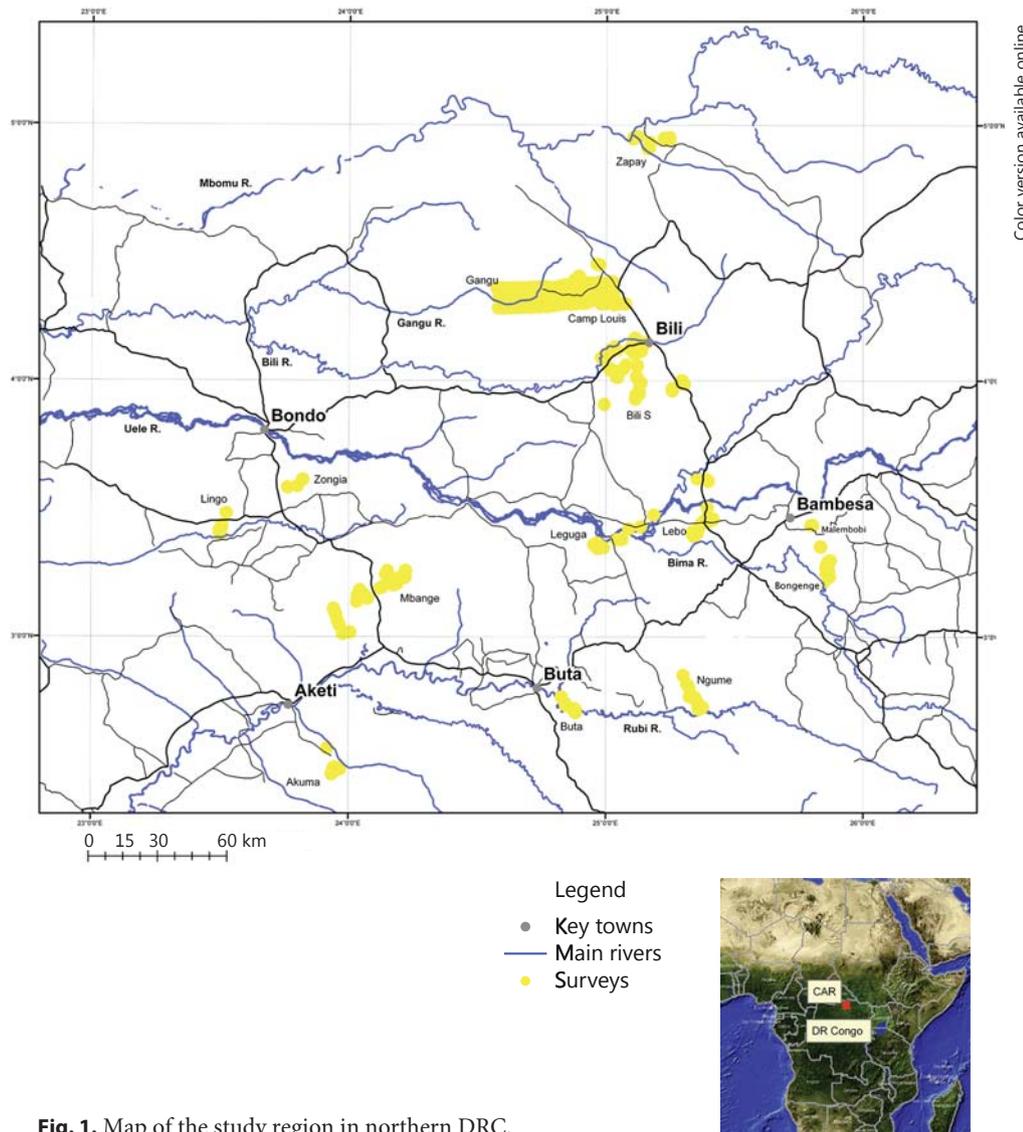
Fig. 1. Map of the study region in northern DRC.

barks, etc.) [Goodall, 1986]. Tree drums are staccato thumping sounds made by chimpanzees against buttresses. Because we did not want to confound our results with the reactions of the chimpanzees to our presence, vocalizations made by chimpanzees during contacts which we judged to be in response to our presence (screams, barks and alarm calls) were not included in the analysis. These were generally alarm calls (screams and wraah barks) emitted by the chimpanzees after having caught sight of us. All recorded vocalizations and tree drums were combined into one variable, 'auditory events per hour'. Unlike the findings in Hicks [2010], the first 3 months of data taken at Camp Louis (August through October) were discarded from this analysis because vocalizations were recorded only in bouts, but not as separate calls.

Table 1. Types of human evidence, with definitions

Category of human evidence	Definition
(I) Hunting evidence	Direct evidence of human hunting *(1) Cartridges:* spent red '00' cartridges *(2) Snares:* traps set by hunters, 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:* possibly 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, pets *(13) Signs:* general human sign *(14) Contacts:* encounters with people *(15) Villages:* semi-permanent dwelling places *(16) Huts:* durable mud or thatch houses, often associated with fields *(17) Fields:* land cleared for agriculture, with crops such as manioc, bananas, and rice

The data are quantitative, and most items were counted individually, with the exception of 'villages', 'hunting camps', and 'camps', which sometimes described conglomerations of dwellings. Human trails were not reliably recorded and so have been excluded from this list.

Human Presence

Human population densities to the south of the Uele River averaged between 2 and 3 times higher than to the north [Hicks, 2010]. Over the course of T.C.H.'s 14 months of surveys at Bili and 12 months in the Aketi-Buta area, he walked a total of 1,810.2 km through the forests (online suppl. table 1). In addition to documenting ape presence and signs of other large mammals, he recorded all evidence of human presence, such as fields, lean-tos, hunting camps, snares, cartridges and encounters (table 1) [Hicks, 2010]. Repeat journeys along previously walked routes were included in this total, as long as these revisits did not occur on the same day. To ensure that all items of chimpanzee and human evidence were counted only once, we took detailed data, including GPS way points and photographs, of each item, and we collected all spent cartridges. 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 in the Gangu Forest, with its near-complete absence of human trails, we sometimes 'bushwhacked' or followed trails made by elephants.

Chimpanzee Presence and Density

Clearly we can expect rates of chimpanzee sound production to be tied to chimpanzee densities: in areas with more chimpanzees, we would expect more sounds. In all of the areas surveyed in the current study, we confirmed the presence of chimpanzees [Hicks, 2010], but comparing their densities between the regions is complicated [Plumptre, 2000; Devos et al., 2008]. Nest encounter rates are frequently used to estimate ape population densities [Kuehl et al., 2008]. These estimations are fraught with difficulty however, due to differences in nest decay and production rates between sites and environmental differences. The majority of the data presented here come from recces. Our limited field time did not allow us to systematically rewalk the transects to determine the rate of appearance of new nests. These data would be needed to confidently estimate population densities. Lacking these data, we use nest encounter rates as an offset variable. Including the nest counts as an offset provides a correction for the amount of 'opportunity' there was to hear chimpanzee sounds due to differences in chimpanzee population densities in each of the 13 forests we visited. Although limited, we feel this technique is justified because we used the same recce methodology throughout the study, and true population density data are not available. As chimpanzees often shift their range within their overall territory [Goodall, 1986], it is possible that, although the apes occurred in a particular region, they were not nesting near our survey camps at the times we visited. Therefore, we ran two separate analyses, one using all nests as a proxy for ape density, and another limiting ourselves to fresh nests only (fresh nests still have green leaves and retain their structure, and are often accompanied by faeces or urine; see Hicks [2010]).

Statistical Analyses

We conducted 3 analyses. In the first we investigated the differences in hourly vocalization rates as a function of the time of day and the region in which the observations were made. The second analysis was a principal component analysis (PCA) of signs of human presence, characterizing the human impact in each region. Finally, we constructed a model in which we related overall sound production per region to the results from the analysis of human impact.

Chimpanzee sound production was analyzed with a generalized linear model using a negative binomial error distribution and log link function [Venables and Ripley, 2002]. The response variable was the auditory event count in each of the 6,553 h of observation. Regional differences in chimpanzee densities were corrected by incorporating an offset variable derived from chimpanzee nest density in the model as described below. Predictor variables were the region in which the data were collected (13 regions; fig. 1) and the time of day (modelled as sine and cosine of the hour converted to radians). A binary factor indicating if the sound was observed in the wet or the dry season was included since sound production might vary over the seasons (a suggestion of such variation was found by Sommer et al. [2004] for Gashaka chimpanzees that tended to make fewer sounds in rainier months). To correct for the effect of chimpanzee population size on sound production, we used two different estimates for chimpanzee density (fresh nests per kilometre and all nests per kilometre), both being log-transformed before entering them as offset into the model. Correction for autocorrelation of the observations was done by explicitly incorporating an autocorrelation term in the model, as was done in Fürtbauer et al. [2011]. The effect of each predictor variable was evaluated by comparing the fit of a full model incorporating all variables to a model that excluded the variable to test. The significance of the log likelihood ratio of the two models was evaluated using a χ^2 test. This method of evaluation (forced entry) prevents possible problems associated with stepwise model fitting [Mundry and Nunn, 2009]. We also used a likelihood ratio test comparing the fit of the full model with that of the null model comprising only the offset, the season correction, and the autocorrelation term. Post hoc comparisons of the number of auditory events between different regions were performed using simultaneous inference [Hothorn et al., 2008].

In order to make the highly correlated signs of human presence amenable to analysis, we first ran a PCA on the evidence counts. We used singular value decomposition of the centred data matrix scaled to unit variance, containing counts for 17 types of evidence (table 1) in 13 regions (table 2; fig. 1).

The first two PCA axes (see Results section) were incorporated as explanatory variables into a generalized linear model to investigate the detailed relationship between chimpanzee auditory

Table 2. Summary of the time spent in each forest region, the kilometres walked, and the major results of our surveys

Region	Hours	Kilometres walked	Chim-panzee sounds	Sounds/h	Percent time in wet season	Nests n	Fresh nests n	Nests/km	Fresh nests/km	Hu-man items n	Hu-man items/km	PC1	PC2
Akuma	75	23.47	0	0	1	23	3	0.98	0.13	36	1.53	−1.44	−0.68
Bili South	208	87.64	15	0.07	1	51	21	0.58	0.24	133	1.52	1.11	4.13
Bongenge	170	46.5	10	0.06	1	211	47	4.54	1.01	70	1.51	0.08	0.31
Buta-Ngume	167	64.98	1	0.01	1	58	5	0.89	0.08	170	2.62	2.65	3.33
Camp Louis	3,276	911.72	558	0.17	0.54	386	117	0.42	0.13	83	0.09	−1.07	0.22
Gangu	1,243	327.4	725	0.58	0.77	505	183	1.54	0.56	22	0.07	−2.17	−0.99
Lebo	187	31.03	8	0.04	1	131	29	4.22	0.94	34	1.10	−2.01	−0.04
Leguga	194	48.52	41	0.21	0	114	37	2.35	0.76	18	0.37	−2.08	−0.59
Malembobi	53	18.49	0	0	1	7	1	0.38	0.05	67	3.62	−1.75	1.25
Mbange East	272	80.93	28	0.10	0	92	4	1.14	0.05	166	2.05	1.85	−2.51
Mbange West	159	45.48	68	0.43	0	70	3	1.54	0.07	178	3.91	5.89	−1.89
Zapay	92	49.93	24	0.26	0	128	39	2.56	0.78	28	0.56	−1.41	−0.69
Zongia-Lingo	257	74.2	14	0.06	1	71	12	0.96	0.16	67	0.90	0.36	−1.84
North Uele total	4,819	1,376.69	1,322	0.27	0.58	1,020	360	0.74	0.26	266	0.19	–	–
South Uele total	1,534	433.6	170	0.11	0.59	777	141	1.79	0.33	806	1.86	–	–

Region names in italics are South Uele sites.

production levels in the 13 regions and the type of human evidence present. In this model the response variable was the sum of all hourly auditory event counts in each region. In addition to the two principal components, the fraction of observations in the wet season was included to correct for possible variation in sound production in different seasons [Sommer et al., 2004]. Log-transformed offset variables for the number of hours in the field and chimpanzee population density (approximated by nest counts as described above) were included to account for sampling effort and regional population differences. Mbange West, a severe outlier due to the unusual structure of the forest in this region (see Results and Discussion for more information), was removed from the analysis. This region showed both high levels of human evidence and chimpanzee sounds. In models with this data point included, we found no correlation between sound production and human evidence. With Mbange West excluded, the total sample size for the final analysis was 12 regions. For this analysis we also conducted a likelihood ratio test comparing the fit of the full model with that of the null model comprising only the offset terms and the season correction. All statistical analyses were carried out using R, version 2.13.1 [R Development Core Team, 2011].

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 centre of Buta (table 2) [Hicks, 2010]. No significant difference was found in the average number of nests per site north and south of the Uele, neither for all nest sites (2.29 ± 2.40 SD nests per site in the north vs. 2.34 ± 2.65 SD in the south, n = 693 and 393 sites, respectively; Wilcoxon rank sum test with continuity correction: W = 138,224, p = 0.65) nor for only those nest sites with tree nests (2.37 ± 2.51 SD nests per site in the north vs. 2.37 ± 2.66 SD in the south, n = 620 and 371 sites, respectively; W = 118,020, p = 0.4546).

Table 3. Likelihood ratio tests for explanatory variables in a generalized linear model with log link function and negative binomial error distribution, estimating the effect on sound production by chimpanzees as a function of the region where the data were collected and the time of the day of the auditory event

	2 · log lik.	d.f.	LR stat.	Probability
Full model	−4,226.12	6,350		
Null model	−4,692.83	6,336		
Comparison		14	466.71	<0.001
Region	−4,390.86	12	164.74	<0.001
Daytime	−4,575.19	2	349.07	<0.001

Log lik. = Log likelihood; LR stat. = likelihood ratio statistic.

The fit of this model was also compared to a null model containing only the offset, the autocorrelation, and the season terms. To evaluate the effect of a variable in the model, the full model was compared to a model that excluded one variable and the significance of the effect was tested using a χ^2 test. Region and time of day both had significant effects on sound production.

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 very few being seen during our time at Bili (42 orphans to the south vs. only 2 to the north; 34 bushmeat carcasses to the south vs. only 1 to the north), indicating a rapidly accelerating bushmeat crisis for the species south of Uele [Hicks et al., 2010].

We found significant differences in chimpanzee auditory events per hour across the 13 forest regions for region and the time of the day, when using fresh nest count as a proxy for chimpanzee population density (table 3; online suppl. table 3). Figure 2 shows the distribution of chimpanzee sounds limited to the hours when they were producing sounds. A likelihood ratio test comparing the full model to a null model showed that including region and time of day significantly improved the fit of the model (LR = 466.7, d.f. = 2, χ^2 test p < 0.001). Using all nests as a proxy for chimpanzee density – data not shown – gave the same results. Subsequent post hoc testing identified the regions that differed in chimpanzee sound production (online suppl. table 3). The 6 forests with the lowest rates of sound production were to the south of the Uele River. Four of the 5 regions with the highest rates of sound production were to the north of the Uele River. Gangu Forest chimpanzees, in addition to producing the highest rate of vocalizations and tree drums, were most vocal at dawn and dusk (fig. 3a). Elsewhere sound production showed a single peak in the morning (fig. 3b).

Human Evidence

Encounter rates with evidence of human presence differed greatly between the 13 forest regions surveyed (fig. 4, see online suppl. table 4 for detailed information, online suppl. table 5 for the hunting evidence only and online table 6 for factor loadings). 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 [Hicks et al., 2012]. The sites with the highest levels of human presence
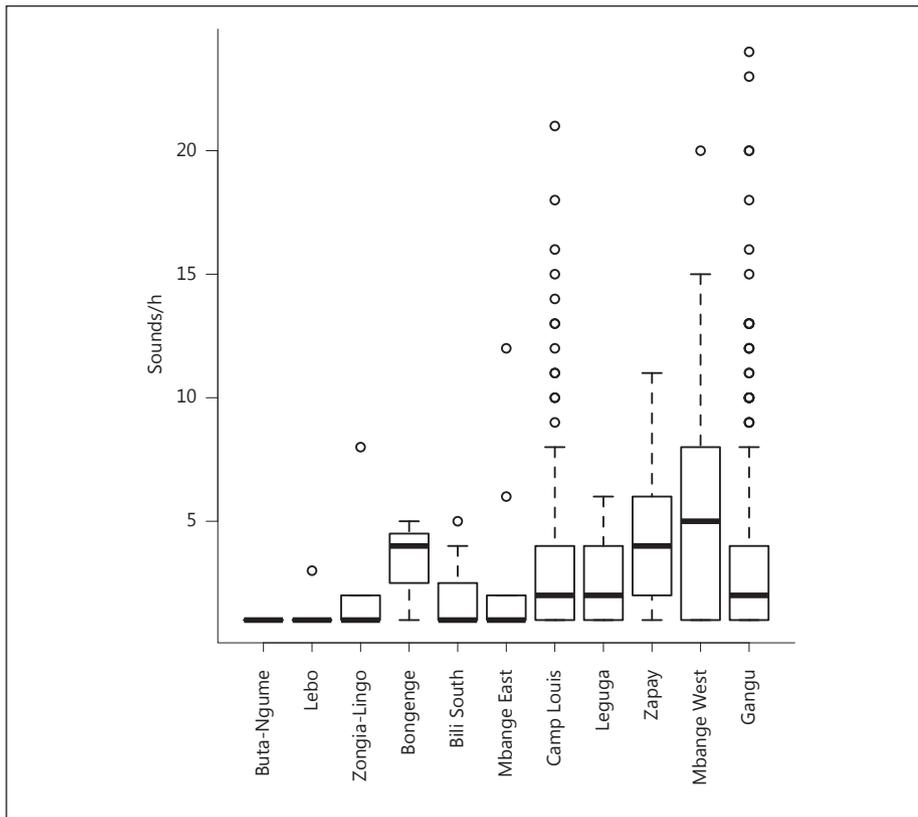
Fig. 2. Box plot of the number of chimpanzee sounds (including pant-hoots, tree drums and other sounds) per hour across the 13 survey regions. Hours with zero sounds were excluded from this figure (but not from the analysis), and therefore the 2 regions without any sounds heard (Akuma and Malembobi) are not shown in the plot.

and hunting were all to the south of the Uele. Mbange West in particular had high levels of human disturbance.

The difference in the evidence for human presence between the regions was also evident in the PCA (fig. 5). The first axis of the PCA, PC1, explained 33% of the variation, and appeared to be related to the amount of human hunting disturbance, ranging from low values for non-hunting-related indicators (lean-tos, human artifacts, fields, huts, etc.) to high values for direct indicators of hunting (snares, bushmeat, hunting camps, etc.; eigenvalue = 2.38). The second axis, PC2, explained an additional 22% of the variation and represented 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 (eigenvalue = 1.94). On the first 2 principal component axes, Gangu Forest lay far to the left, characterized by a minimum level of human disturbance and hunting (PC1), and very few other signs of human presence (a PC2 value near zero). In contrast, Mbange
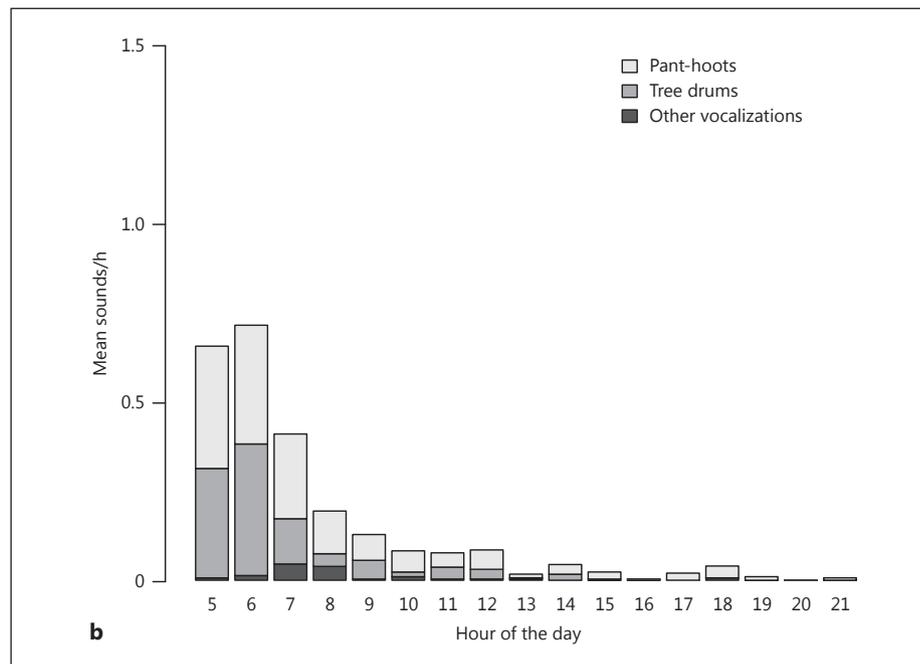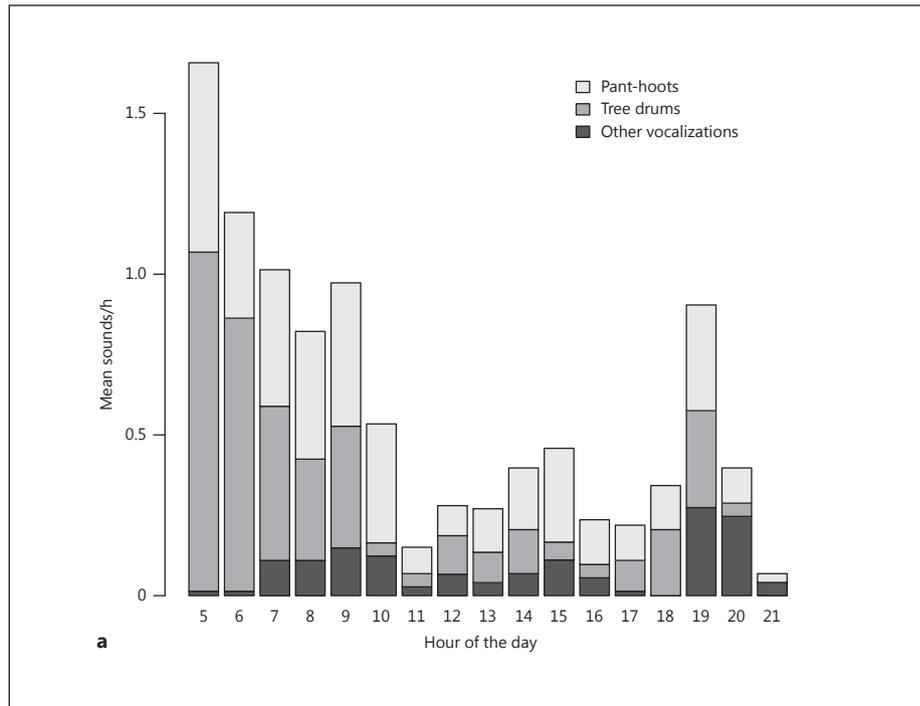
Fig. 3. Types of sound produced per hour by chimpanzees in Gangu (**a**), and all regions except Gangu (**b**) and their distribution over the course of the day.
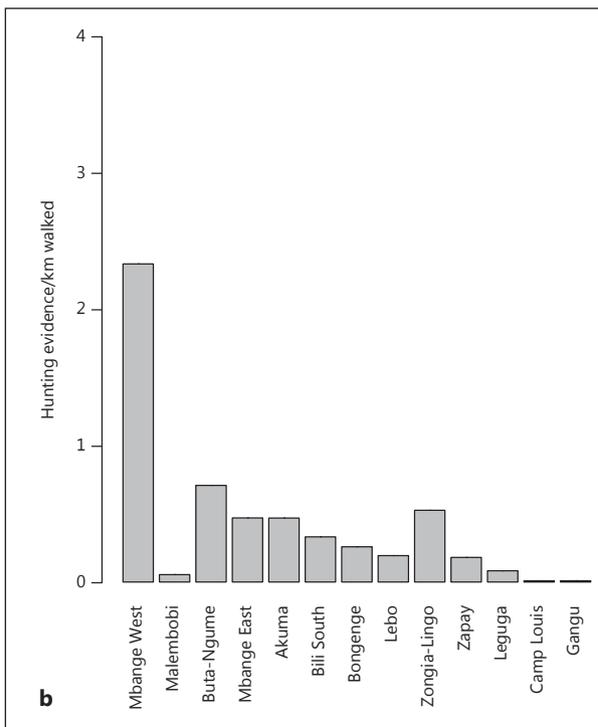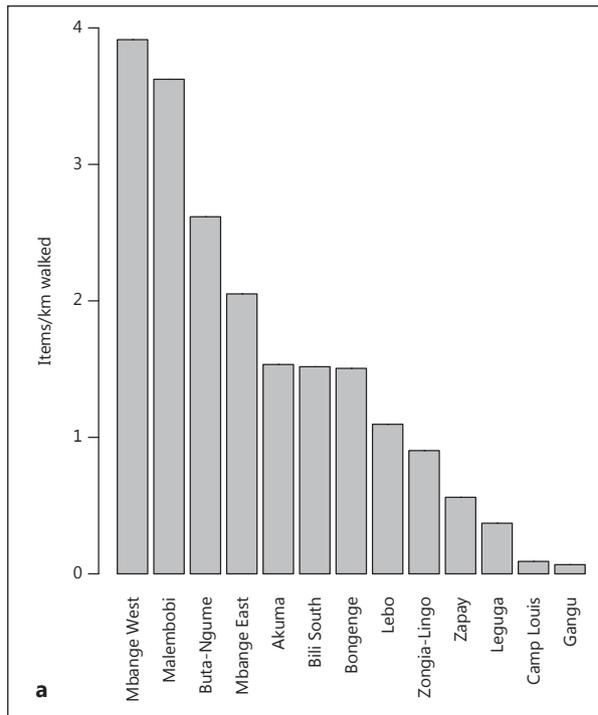
Hicks/Roessingh/Menken

Fig. 4. Human evidence encountered across the 13 study regions: total evidence (**a**), and hunting evidence only (**b**).
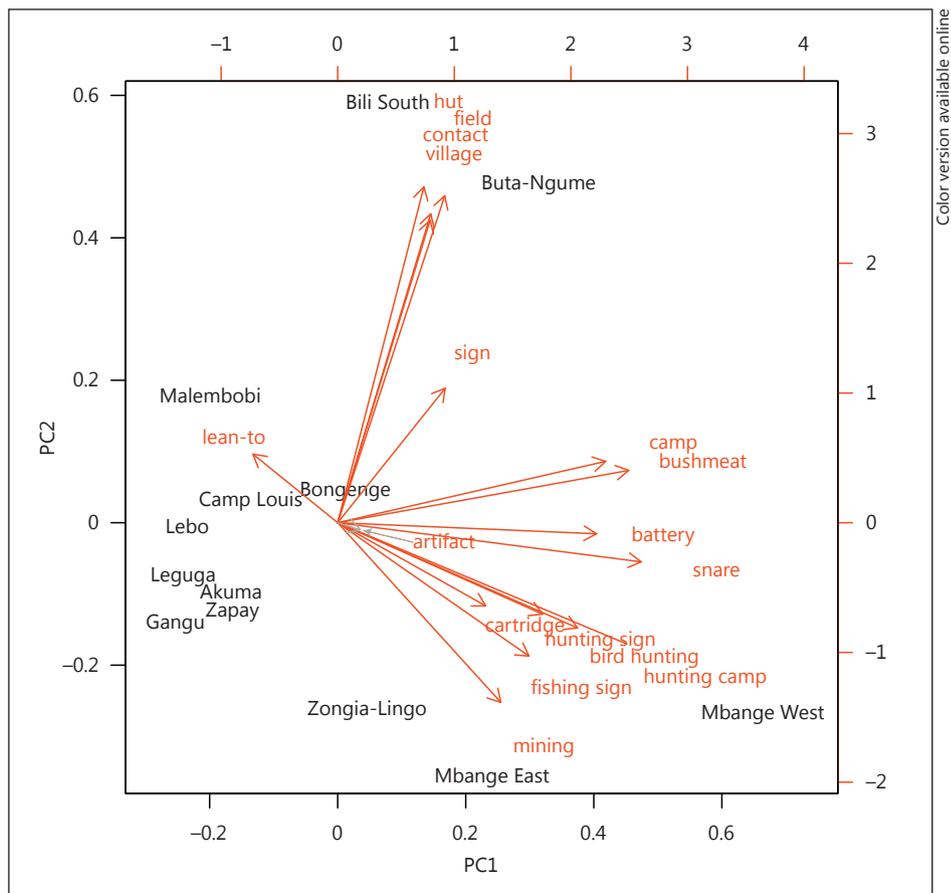
Fig. 5. Biplot [Gabriel, 1971] showing the first 2 principal components for both the 13 regions in which evidence of human presence was collected (bottom and left axis, scaled by the singular values of the matrix) and the 17 types of human evidence (top and right axis).

West, Mbange East and Buta-Ngume (all South Uele forests) lay more towards the right on PC1 (higher hunting pressure) and were characterized by high levels of other indicators of human presence and forest use (PC2).

Comparison between Human Evidence Encounter Rates and Chimpanzee Sound Rate

When we used nests of all ages as an offset term, hunting evidence as summarized by PC1 was found to be negatively correlated with sound production (coefficient for PC1 = –0.35, z = 11.7, p < 0.001; table 4a and fig. 6a). The Mbange West Forest emerged as a severe outlier (see fig. 6c and explanations below) and was therefore not included in this and subsequent analyses. A likelihood ratio test showed that a model including PC1 and PC2 as explanatory variables had a significantly better fit than the null model (LR = 194.9, d.f. = 2, χ^2 test p < 0.001). When, however, only fresh nests were used

Fig. 6. Scatter plots of human hunting disturbance (summarized by the first PCA axis largely representing hunting evidence) found across the different forest regions surveyed and the number of chimpanzee sounds recorded per hour. **a** Corrected for chimpanzee density using all nests. **b** Corrected for chimpanzee density using fresh nests only.
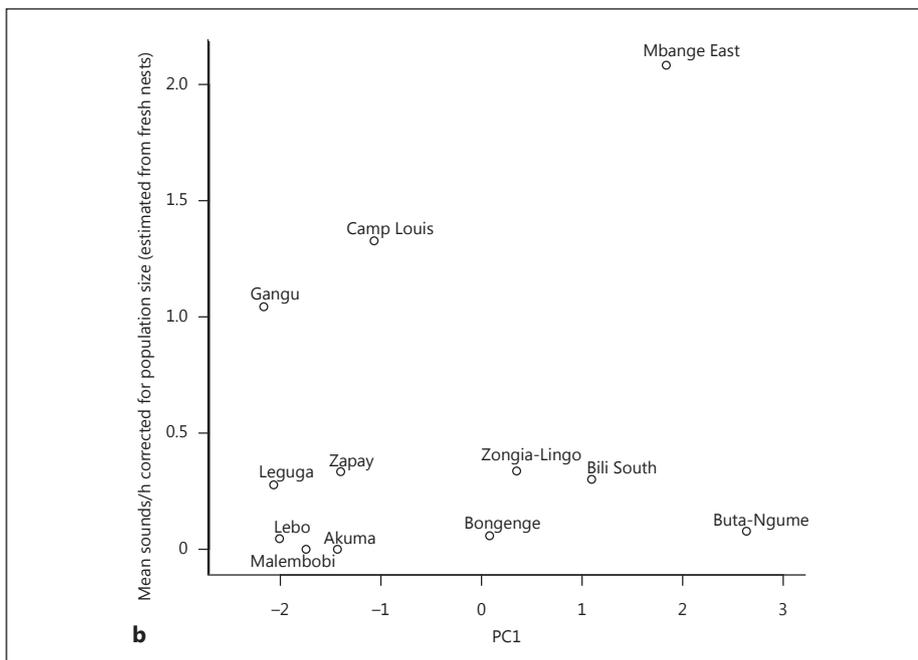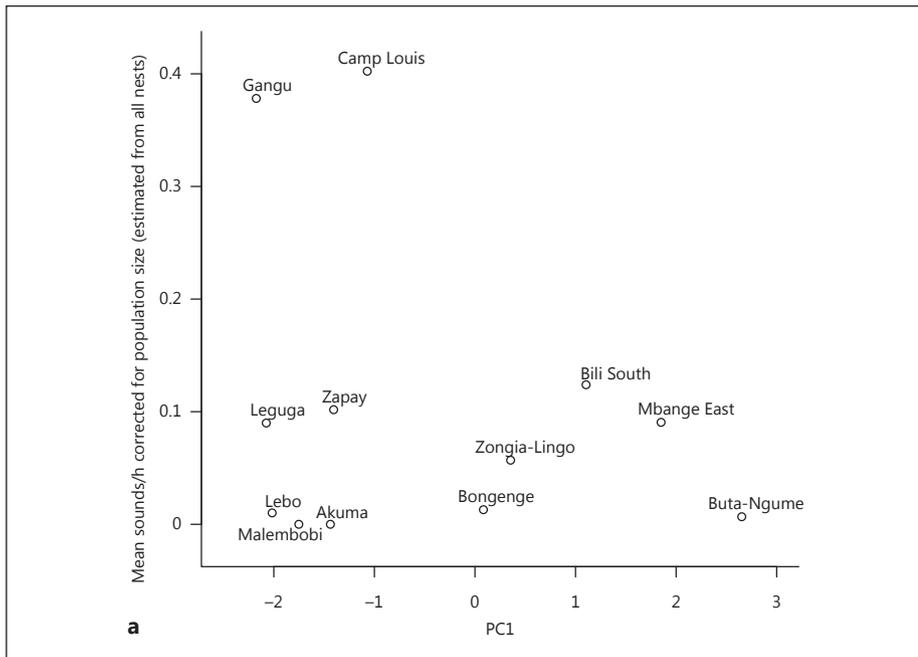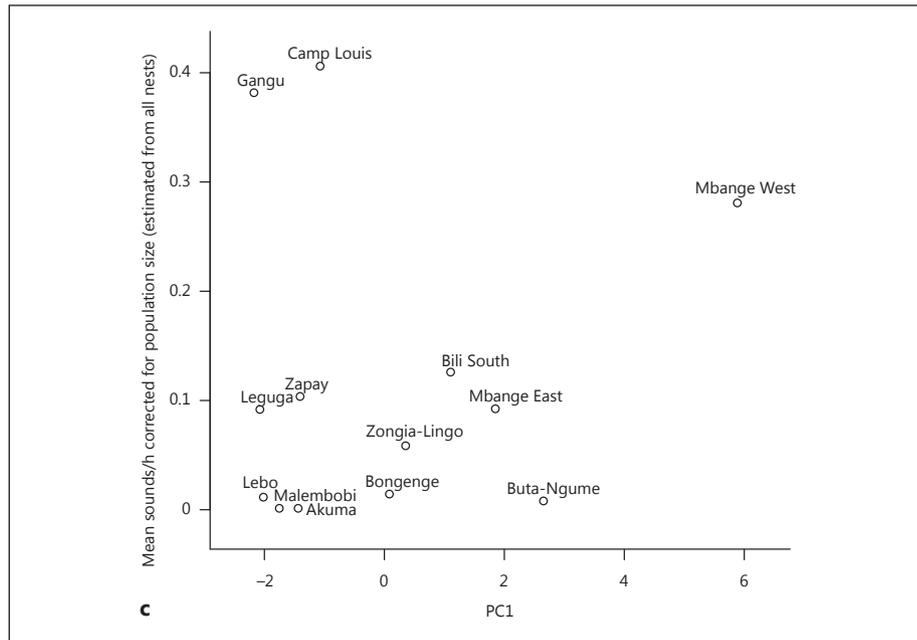
Fig. 6. Scatter plots of human hunting disturbance (summarized by the first PCA axis largely representing hunting evidence) found across the different forest regions surveyed and the number of chimpanzee sounds recorded per hour. The outlier Mbange West (a special region with large tracts of impenetrable forest) was not included in the analysis, but the position of this region is presented in **c**.

to estimate population density, the significant correlation was lost (coefficient for PC1 = 0.04, z = 0.21, p = 0.83), and the model was not better than a null model without these variables (LR = 0.35, d.f. = 2, χ^2 test p = 0.84; see table 4b and fig. 6b). As we explain in the statistics section and in the discussion, estimating chimpanzee density in the wild is difficult, and it is not obvious whether all nests should be used as our proxy or fresh nests only. It should also be noted that due to the small data set (only 12 sites analyzed), and the differing results depending on which correction factor we used for chimpanzee density, the above results for the correlation between human evidence and auditory events should be interpreted with care.

In contrast to the effect of PC1, which showed a significant negative correlation with chimpanzee vocalizations in the analysis in which the count of 'all nests' was used to construct the offset term for population density, the correlation with PC2 (interpreted to represent human presence and forest use, see the section on human presence above) was not significant in either of the two analyses (table 4). This indicates that human hunting may have an influence on rates of chimpanzee sound production, but not the mere presence of humans.

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 Forest and Buta Forests (<10 vs. >75% in Mbange West). Throughout the Mbange West region, scattered patches of old-growth riverine forest were separated by enormous, thickly

Fig. 7. Impenetrable herb forest at Mbange West, through which we were forced to travel on human-cut snare trails.

tangled herb patches made up of *Megaphrynium*, *Haumania* and other towering herb species, with very few, but tall, trees (fig. 7). These impenetrable herb patches extended for several kilometres, and could only be accessed following snare trails which had been hacked out by local trappers (presumably the trappers themselves were limited to using these trails). Clearly, however, the chimpanzees were able to follow hidden routes through them: in the early mornings, we would hear them pant-hooting from nearby; when we rushed in their direction to attempt a contact, we would lose them when they entered the thick wall of vines and herbs. We would then hear the apes pant-hooting from within the herb patch throughout the day. Although we were never able to locate them, we found feeding remains and travel signs of the apes in this forest (we also found abundant chimpanzee feeding remains in the Buta and Akuma herb forests and a ground nest at Akuma).

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. The measure for human disturbance at Gangu was likely overly inflated by ratings from its eastern edge, the only place where signs of humans were found [Hicks et al., 2012]. Excluding this eastern edge, Gangu's human presence was much lower than even that of Camp Louis.

Table 4. Results of two generalized linear models estimating chimpanzee sound production per region

a All chimpanzee nests

	2 · log lik.	d.f.	LR stat.	Probability
Full model	−967.39	8		
Null model	−1,162.32	10		
Comparison		2	194.93	<0.001
PC1	−1,148.61	1	181.23	<0.001
PC2	−967.61	1	0.22	0.640

b Only fresh chimpanzee nests

	2 · log lik.	d.f.	LR stat.	Probability
Full model	−99.55	8		
Null model	−99.91	10		
Comparison		2	0.35	0.839
PC1	−99.59681	1	0.04	0.837
PC2	−99.90591	1	0.35	0.553

Log lik. = Log likelihood; LR stat. = likelihood ratio statistic.

The models included the first two principal components of a PCA of evidence for human activity as explanatory variables. We used a negative binomial error distribution and a log link function. A variable with the percentage of observations in the wet season was included to correct for possible season effects. Chimpanzee population density and number of hours in the field per region were taken into account by incorporating offset variables for the number of observation hours and the total number of nests observed per region [either all nests (**a**) or only fresh nests (**b**)]. The fit of the models was also compared to a null model containing only the offsets and the season term. The significance of individual predictor variables was evaluated using a likelihood ratio test comparing the full model to a model with/without the tested variable. In **a**, the count of the chimpanzee nests per kilometre walked in the region was used as a proxy for population density. PC1 (representing hunting evidence) had a significant negative effect on sound production. The effect of PC2 (representing other use of the forest) was not significant. In **b**, only fresh chimpanzee nests were used to estimate density. Using this offset, none of the evaluated factors had a significant effect on sound production.

Discussion

Chimpanzee reactions to humans and other predators vary across sites, ranging from mobbing leopards [Boesch, 2009] and humans [McLennan and Hill, 2010], to showing curiosity towards humans [Hicks et al., 2012; Morgan and Sanz, 2003] or fleeing from them [Hicks et al., 2012]. Several factors (detailed in Hicks et al. [2012]) may determine the kind of reactions the apes have to humans, such as whether or not the local humans hunt chimpanzees and the degree to which humans and chimpanzees are forced to come into contact. Our study highlights a strategy used by chimpanzees in areas where they are heavily hunted: they appear to become cryptic, which

may make it more difficult for hunters to locate them. In our surveys of forests in northern DRC, chimpanzees consistently reduced their rate of sound production in areas with high human impact. In areas of low human impact, such as the Gangu Forest, chimpanzees often had higher rates of sound production, although this was not the case in all such forests. When we used chimpanzee nests as a corrective variable for population size, we found that the more human signs we encountered in a region, the fewer long-distance chimpanzee sounds we heard throughout the day, although this correlation disappeared when we used fresh nests only (table 4). In heavily hunted areas the chimpanzees limited their sound production to the early mornings, whereas in the remote Gangu Forest sound production continued across the day, with a large peak in the morning and a smaller peak in the early evening (fig. 3). Season did not make a significant contribution to sound production in the data set.

As noted above, the results for the relation between chimpanzee auditory events and signs of human presence as summarized by the PCA should be interpreted with due care. Although the PCA results show a logical and easily interpretable pattern, the results are based on only 17 types of evidence from 13 regions, and it is not clear how robust they actually are. To model the effects of human evidence on chimpanzee sounds, we subsequently estimated the effect of 4 variables based on only 12 data points. In addition, our results are critically dependent on the size of the chimpanzee populations we sampled, which will obviously influence the level of sound production in a region. Lacking true population estimates, we corrected for this effect by including nest counts as an offset variable in our models. Our nest encounter rates are relatively high compared to other DRC sites, probably due to the fact that we were actively searching for signs of chimpanzee presence. Nest counts also varied considerably between regions (table 2), and it is likely that population size did as well, making the correction for chimpanzee density essential. It is not clear however whether the count of all nests or the much smaller sample of fresh nests is the better estimator for population density. Although our results suggest an effect of human presence and of hunting-related signs in particular, we currently have insufficient evidence to draw these conclusions with confidence.

At Gombe, Tanzania, Wrangham [1975] recorded the calls of chimpanzees habituated to humans between the hours of 05:00 and 20:00. The apes vocalized most often in the morning between 07:00 and 09:00 h. 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, when their call rates were low throughout the day). Call rates at Gombe and (non-cropland) Kanyawara resembled those at Gangu, but had a less pronounced early evening peak. This small peak was found in the Kanyawara core zone, but was not observed in the periphery or cropland. An early-evening peak was also seen in the chimpanzees of Gashaka, Nigeria; in fact, the pattern of acoustic signals made by chimpanzees at this site [fig. 6 in Sommer et al., 2004] fits almost exactly that documented at Gangu. The Gashaka chimpanzees have been protected from hunting at least in recent years by the Islamic faith of the local people. It is the steep decline in sound production immediately following the early morning hours shown by the non-Gangu chimpanzees in this study that requires an explanation.

We documented a 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. Although we as yet have no conclusive evidence, 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 earliest morning hours, is likely a response to hunting pressure. This phenomenon has been documented in spider monkeys [Van Roosmalen, 2008]. Other populations of chimpanzees [Wilson et al., 2007; Hockings, 2009] and vervet monkeys [Kavanaugh, 1980] became more quiet when crop-raiding, a potentially dangerous activity in which they risked being attacked by humans.

Local hunters told us that their preferred hunting technique was to home in on chimpanzees in the early morning by following their pant-hoots to their night nests or feeding trees. The hunters can then stealthily surround a tree-full of feeding chimpanzees and silently knock them out of the trees one-by-one with poison arrows [Hicks et al., 2010], or shoot them with guns (this was never confirmed by personal observation, although we once encountered monkey hunters shooting agile mangabeys out of a tree after silently stalking them). 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 non-Gangu chimpanzees may 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 most of the South Uele forests, even when during night hours we heard their nearby pant-hoots and left camp in the early morning hours to find them [Hicks et al., 2012]. 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 chimpanzees 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 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 enough, 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 greater than in 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 not nearly as common as 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. A likely explanation for these observations is that the chimpanzees of Mbange West are uniquely protected from humans by the impenetrable tangle of herbs in which they live, and are able to vocalize in this forest type with the same frequency and pattern as do those at Gangu without exposing themselves to significant danger. It would be extremely difficult to sneak up on chimpanzees in this kind of forest; any approach of the trails would be telegraphed by the rustle of the abundant massive *Megaphrynium* herbs. This is an additional indication that it is not human/chimpanzee range overlap per se that leads to diminished chimpanzee sound production, but rather active hunting. Given that active hunting was apparently impractical at Mbange West, we excluded this region from our analyses

as an outlier. Our findings may also help explain why the chimpanzees of Gashaka, Nigeria, which have frequent encounters with humans, display a similarly high rate of sound production rates to that of the isolated Gangu chimpanzees; they are offered a degree of protection from hunting by the Muslim faith of the local villagers [Sommer et al., 2004].

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 led 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 (the few ex-hunting/fishing trails which we followed at Camp Louis had minimal evidence of recent 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 encounter rate of human signs in most South Uele forests 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.

Three additional potentially 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 available for the chimpanzees to pant-hoot about (the food list in Hicks [2010] may indicate an increased reliance on herbs and fewer fruits eaten by the southern chimpanzees, although our evidence is too fragmentary to draw any conclusions). However, previous research on other chimpanzee populations indicates that although pant-hooting is often associated with arrival in fruiting trees, it serves additional social functions as well, including status and the spacing of individuals within the group [Mitani and Nishida, 1993; Clark and Wrangham, 1994]. Indeed, we had a difficult time locating and making contact with the chimpanzees in most South Uele forests even when food 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, which may have an impact on their calling rates with other apes. This is unlikely, however, as there was no significant difference in the average number of nests per site to the north and south of the Uele.

In forests near cities such as Buta and Akuma, which were crisscrossed with fields and human paths, chimpanzees were still abundant but were 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 [Hicks, 2010]; 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 (for examples in Bossou, Guinea, see Hockings [2009], for Bulindi, Uganda, McLennan and Hill [2010]). Unfortunately, changes in the past 15 years in northern DRC make it unlikely that even they will long survive the new poaching onslaught [Hicks et al., 2010]. We found chimpanzee nests within 13 km of Buta, the human population, commercial and bushmeat centre in the area [Hicks et al., 2010], as well as near other large population centres – at first sight encouraging news. However, local agriculturalists, long-term residents of the area,

claimed to us that until 15 years ago, chimpanzees had lived within 7 km of Buta, but had since disappeared from the newly cut mosaic of fields and forest, hunted out by immigrants who pursued the apes with packs of dogs. Active searches by T.C.H. and our field assistants failed to find any trace of chimpanzees within 13 km of Buta. This expanding radius of chimpanzee-free forests will almost certainly increase in size, at least around the rapidly proliferating 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; it is likely that chimpanzees can do the same. Chimpanzees may also use pant-hoots to regulate spacing between group members and to express differences in rank [Mitani and Nishida, 1993], and also to differentiate between the members of neighbouring 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, and likely lead to the impoverishment of their traditions [van Schaik, 2002].

It is interesting as well to observe the variation in call rates between different regions: Gangu and Gashaka have strong secondary peaks in sound production in the early evening. In Kanyawara this evening peak was much smaller and limited to the core zone. No early evening peaks were found at Gombe or in the non-Gangu forests of our study. Are evening calls something that all chimpanzee populations would engage in if they could 'get away with it', but some groups are forced to suppress them due to risk from humans? Or are there other factors shaping call patterns in the different populations? This should be a fruitful line of inquiry for future research.

Chimpanzees show human-like flexibility in a number of basic behaviours [Whiten et al., 2001], and thus it is not surprising that they are capable of adapting their vocalizations and other behaviours to incursions by *H. sapiens* into their habitats. In this study, we have presented evidence that chimpanzees inhabiting areas heavily hunted by humans appear to react by strongly reducing their rate of vocalizations and tree drums, and also by limiting these to the early morning hours. This is a fine example of behavioural adaption in our evolutionary cousins, but it will unlikely be sufficient to counter the new wave of bushmeat hunting by immigrants who are now invading the area.

Conclusion

In summary, we found that the pattern of sound production differed between chimpanzees living in remote areas with little hunting pressure from those in areas with higher levels of hunting: in the less hunted areas, the chimpanzees called more frequently across the day, with peaks in calls at sun-up and sun-down, whereas in areas with higher hunting pressure they showed a sharp decline in vocalizations. This pattern was particularly strong in the isolated Gangu Forest, >20 km from the nearest road. Human presence per se did not appear to be the driving factor in chimpanzee

long-call reduction, but specifically hunting pressure. An interesting exception to the rule was Mbange West, which was characterized by high hunting pressure together with high rates of chimpanzee sound production. This is likely due to the uniquely dense and impenetrable nature of this forest, which seems to afford the chimpanzees some degree of protection from humans. This finding supports the idea that when chimpanzees are safe from hunting, they are able to engage in their full repertoire of vocalizations and tree drums.

Acknowledgments

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