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A chimpanzee Mega-Culture? Exploring behavioral continuity in *Pan troglodytes schweinfurthii* across northern DR Congo

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Reactions of Chimpanzees to Humans in Relation to Their Distance from Roads and Villages

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Abstract

We compared the reactions to humans of Eastern chimpanzees (*Pan troglodytes schweinfurthii*) living in proximity to and at a distance from roads and settlements in the northern Democratic Republic of the Congo (DRC). We found that chimpanzees at a distance from the road were more likely to show curious or neutral reactions to us and were less likely to flee than those living closer to roads. In addition, contact durations with chimpanzees living in more remote forests lasted significantly longer. The implication is that with increasing distance from roads, chimpanzees have in the recent past had fewer negative encounters with humans.

Introduction

The chimpanzee (*Pan troglodytes*), one of our two closest living relatives, is currently disappearing across much of its range (Butynski, 2001; Walsh et al., 2003; Campbell et al., 2008). Over the past century, human hunting and habitat disturbance have, in combination with other threats such as ebola, reduced the species to perhaps one fifth of its former abundance. In many places where chimpanzees survive today, their populations have become fragmented by human activities such as logging and agriculture. The apes are frequently hunted by humans, both for subsistence and as a part of the expanding bushmeat trade (Peterson, 2003; Chapter 6); thus chimpanzees in proximity to villages and roads quickly learn to fear *Homo sapiens*. When researchers first made contact with chimpanzee populations at study sites such as Lopé (Tutin & Fernandez, 1991), Kibale (Johns, 1996), and Gombe (Goodall, 1986), the apes, instead of ignoring or showing curiosity towards the humans, would usually leave the area immediately. Such behavior is typical of free-living apes across the continent (Morgan and Sanz, 2003), and makes detailed scientific analysis of their behavior only possible after habituation: the acceptance by wild animals of a human observer as a neutral element in their environment (Tutin & Fernandez, 1991).

In areas remote from humans, researchers may encounter chimpanzees that do not flee, and instead remain in the area and observe them, often with curiosity (Itani & Suzuki, 1967). Morgan & Sanz (2003) encountered such chimpanzees, described as naïve by Fay (cited in Morgan & Sanz, 2003), in the Goualougo Triangle in The People's Republic of Congo. This region seems to have remained completely isolated from humans for centuries due to its swampy, inaccessible terrain.

Thurston Hicks (TH) observed a similar phenomenon in chimpanzees (*P. t. troglodytes*) of the Ngotto Forest, Central African Republic (Hicks et al., 2009), approximately 10 km south of the village of Grima. Upon becoming aware of the researchers, the Ngotto chimpanzees, unlike the more timid gorillas inhabiting these

forests, would sometimes remain in the area for hours, in large parties, peering at and displaying at the observers.

In our effort to study a population of chimpanzees (*P. t. schweinfurthii*) inhabiting the forests surrounding the town of Bili, the northern DRC, we initially tried to work with a group living within 15 km of the nearest human villages, Baday and Pangali, at the Camp Louis field station (Chapter 1; Ammann, 2001; Young, 2004). Since 1998, local Azande trackers working for conservationist Karl Ammann made sporadic attempts to supply the chimpanzees with sugar cane in order to observe them, but the apes remained elusive. Shelly Williams and her team managed to observe the apes in 2002 and 2003, and a team led by TH in 2004 made contact on numerous occasions, but the chimpanzees consistently reacted to the appearance of the researchers by fleeing. The adult males in particular would react with panic, sometimes leaping 15 m to the ground upon seeing the observers. Local Azande claimed that the apes had been hunted until the advent of a community conservation project in 2002, thus explaining their fear of humans. After 6 months of intensive efforts, we abandoned attempts at habituation in January 2005.

A near-pristine forest, called Gangu, is located to the west of Camp Louis, where according to local field assistant Ligada Faustin, the resident chimpanzees had the habit of fearlessly approaching humans, even on the ground. In order to investigate this population, we undertook a 5-month transect project, from March to July 2005, cutting and following three parallel 55-km transects west from the road into the Gangu Forest (Chapter 4). The chimpanzees in this forest indeed became progressively more naïve as we moved further from the road. Nest counts showed that they lived at an increased density as well.

Eventually, during the 2006-2007 field season, the Gangu field camp was established in this remote area, and efforts were made to habituate the naïve chimpanzees. Due to Congolese political instability, we were only able to spend 2 months with the apes. During the time that the research team was unable to work at Gangu, we conducted further ape surveys over an approximately 7000-km² region, and chimpanzees were contacted on several occasions.

After the Bili area was overrun by illegal gold miners in June 2007, we conducted a 13-month survey of chimpanzee populations across a large area approximately 200 km S of Bili, in forests near the towns of Leguga, Aketi, Buta, and Bambesa. Apparently, this population of chimpanzees is distributed continuously across a large area, as they were found to possess more or less the same material culture as those at Bili (Chapter 5), implying a continuous population until recent times. During this 13.5-month period, we contacted chimpanzees on an four occasions, always within 10 km of villages. In addition, we encountered a large number of chimpanzees and orphans for sale, indicating a developing bushmeat trade for the species in these forests (Chapter 6).

The goal of this study was to compare the behavior of chimpanzees living close to human villages and roads with those living in more remote forests. Two hypotheses were tested: 1. chimpanzees living in remote areas show more curious and less fearful behaviors towards humans, and 2. contacts with humans in remote forests last longer than in areas closer to roads and villages. Furthermore, the behavior of the Bili apes is compared to other chimpanzee study sites in which habituation has been attempted.

Materials and Methods

The study area

The main study area of the Bili ape research project encompasses an approximately 475 km² region of the forests and savannas west of Baday, a small village 25 km north-northwest of Bili (Chapter 1, Figure 5). The complex mosaic habitat consists of seasonally-burned savanna, savanna-woodland, regenerating forest, and gallery forest. In some areas, savanna and woodland are replaced by large tracts of undisturbed tropical moist forest. Camp Louis is located at 4°21'72"N, 24°56'72"E, and Camp Gangu is approximately 30 km to the west-southwest, at 4°19'34"N, 24°41'53"E. Both of these camps are located within the Bili-Uéré Hunting Reserve. Bili is the largest town near these field camps, with several thousand people living there and in the smaller villages along the road. West of Baday, human use of the region, other than the yearly burning of most of the savannas and some shifting cultivation close to the village, is minimal. Beginning roughly at the confluence of the Bo and Gangu Rivers lies a very large area of near-pristine primary forest centered around the Gangu. West of this area there is almost no human presence whatsoever, but elephants and chimpanzees are numerous. Human presence at Gangu is limited to brief visits by small groups of Azande fisher-folk in the dry season, who dam up small creeks and dig aestivating fish out of their burrows.

In 2006, we conducted surveys of a large area, stretching from the forests of Lebo just south of the Uele River to Zapay in the north (Chapter 1, Table 1; Appendix I). Chimpanzees were found throughout the area, and even within 4 km of large towns such as Bili, Lebo, and Zapay. As described in Chapters 1 and 3, in the majority of these areas we found more traces of hunting activities such as snares and cartridges in the forests, and we observed a greater quantity of bushmeat than at Bili.

From October 2007 to November 2008, we conducted a survey of the forests south of the Uele River, using the same methodology as at Bili (see Appendix I for GPS coordinates of the forest area surveyed and the number of days spent at each). This area was nearly devoid of savannas and more evenly-forested than to the north of the Uele. Chimpanzee nests were found throughout the region, even within 13 km of the large commercial center of Buta (Chapter 4, Figure 5). Unfortunately, so were chimpanzee orphans and bushmeat (Chapter 6), indicating heavy hunting of the species in the nearby forests.

For the purposes of this paper, I have divided the forests into two regions: one within 25 km of a main road or village, and the other outside of this distance. In practice, this means that only the Gangu Forest falls into the >25 km category, while all of the other forests, including the Camp Louis region, are in the <25 km category. Over the first year of study, I focused on Camp Louis and its surrounding forests and savannas; thus we will present this region as a subset of the <25 km category.

Methods

During the two field seasons at Bili, we attempted to locate and contact chimpanzees, with the eventual goal of habituating them for research. A contact is defined as having taken place any time the chimpanzees were aware of our presence. For several years preceding the current study, Ammann's team had been planting sugar cane in the Camp Louis area to attract the apes, but had had little success in achieving regular encounters (Hicks, pers. obs.; Young, 2004). From August 2004 to January 2005, we made intensive efforts to encounter and habituate the chimpanzees. We had no problem finding the chimpanzees; however, the apes continued to flee us.

Due to our fears for the safety of the chimpanzees in the Camp Louis area, the habituation efforts were abandoned in January of 2005.

In 2005, TH conducted a line transect survey in order to estimate the density of chimpanzees in the area, and also to investigate the claims of naïve chimpanzees to the west. Three 50-55 km transects were cut and followed into the Gangu Forest (with sections of the 160 km of transects left uncut and marked only with flagging tape – that was later removed – to discourage poachers from using them). Although counting chimpanzee nests along the transects was our priority, we did not pass up on making contact with the resident apes. In 2006, we established a new base camp at Gangu, where over a period of 2 months we managed to make numerous contacts.

A potential contact day includes any day in which TH or field assistant Jeroen Swinkels (JS) was in chimpanzee-inhabited forests and prepared to make a contact (whether actively searching for chimpanzees or at camp listening for them). If both teams were out searching for chimpanzees, this was counted as 2 days with the potential for a contact.

Upon hearing chimpanzee vocalizations, we would seek out the chimpanzees and attempt to make contact with them. One to three Azande trackers would accompany the researchers to help locate the apes. We also conducted stake-outs of fruiting trees favored by the chimpanzees. Including contacts made by the local field assistants without TH or JS, 102 contacts were made over the three field seasons, but this paper will only analyze those made by TH ($n = 72$) and JS ($n = 3$). Of these, 58.5% were achieved by following chimpanzee vocalizations and tree drums to their source and 24.5% by staking out fruiting trees; 17% were opportunistic encounters.

The local field assistants always wore red hats in order to help the apes distinguish them from potential poachers, but during contacts they were instructed to hide or to sit down and be inconspicuous. If possible, the researcher would position himself in an open spot no closer than 20 m from the chimpanzees (and usually up to 50 m back), and then make clucking and humming sounds while pretending to eat leaves. The researcher would remain seated unless he needed to be upright in order to film the chimpanzees. Occasionally the researcher and /or trackers would move around the tree in order to better observe all of the chimpanzees, but an effort was made to remain in one place.

We collected data on the chimpanzees' behavior in field notebooks, and were usually able to film the contacts as well (which later enabled us to more fully reconstruct the details). The data recorded included forest density (open, medium, or dense: i.e. visibility 0-1.9 m, 2-5 m, or >5 m), party-size, age and sex of the chimpanzees, contact duration for each individual present, whether the apes were on the ground or in trees, height in the trees, distance from the observer, and all individual reactions to our presence. A contact with a particular individual was assumed to have ended after the last visual or nearby auditory evidence of that individual was recorded.

The following individual behavioral patterns were observed (categories were adapted from Tutin & Fernandez, 1991). In parentheses following the definitions are the code numbers that we have paired with the categories.

- *Curiosity*: includes two or more of the following elements: staring, head-swaying, moving to obtain a clearer view of the observer, slapping tree trunk, and clapping hands (1).
- *Aggressive approach*: rapid noisy approach in the trees, either direct or oblique, towards the observer (2).

- *Aggressive display*: leaping about and shaking branches towards the observer without approaching (2.5).
- *Soft vocalizations*: hoo or whimper (3).
- *Loud vocalizations*: wraaghs, waas, or screams (4).
- *Ignore*: no discernible response shown; after glancing or staring at the observer, the individual continues with previous activity, or just sits and relaxes (5).
- *Ambiguous approach*: approaching the observer without signs of curiosity, in the process of fleeing (5.5).
- *Hide*: either moving behind vegetation (sometimes hiding the whole body, but often only the face), or pulling vegetation in front of face or body to form a screen (6).
- *Stealthy retreat*: slow, cautious, and almost silent descent from tree or avoidance on the ground (7).
- *Flee*: rapid jumping or sliding out of a tree or running at speed along the ground causing much noise (8).

In addition to these individual behaviors, following Morgan & Sanz (2003), group contacts (i.e. contacts considering the reaction of the group as a whole) were classified on a scale from ‘naïve’ to ‘immediate departure’. This was achieved by using the first reaction of the majority (> than half) of the chimpanzees during the contact. Again, in parentheses following the definitions below are the numbers I have paired with the categories. For some of the analyses, these contact types have been further divided into ‘naïve’ (the first three categories) vs. ‘immediate departure.’

- *Naïve*: After initial response, the majority of the chimpanzees present show continued curiosity toward human observers (as indicated by exhibiting the curious behaviors described above). After a period of intense interest, the chimpanzees may return to previous activities while monitoring human observers (for example, chimpanzees may build a day nest and then watch human observers while resting) (1).
- *Ignore*: Throughout the contact, chimpanzees show no discernible interest in observers. After noticing arrival of observers, chimpanzees continue with previous activities (or sit and relax) (2).
- *Nervous*: Chimpanzees retreat from observers by moving higher in the canopy or hiding behind vegetation. Chimpanzees alternate attention between monitoring observers and other chimpanzees in the party. Other indications of nervousness include pilo-erection, self-scratching and loose stool (3).
- *Immediate departure*: Chimpanzees immediately depart after becoming aware of human presence. Same as flee and stealthy retreat category for individual response (4).

For seven of the 73 contacts, there was no majority reaction; in these cases, in order to classify the contact, the chimpanzees’ reactions were split halfway between two categories (in four cases, for example, half of the chimpanzees fled immediately, and half stayed but were nervous). In such cases we awarded 0.5 representations to the two competing contact types: in the four cases used in the example above, categories 3 and 4 would each get 0.5 representations instead of one. This enabled us to determine the percentages of contact reaction types. However, in order to conduct

statistical analyses and also to construct the map shown in Figure 3, I used a different approach. To simplify the problematic cases described above, I scored as the contact reaction-type the number halfway between the two original tied reaction-type numbers. In four contacts, therefore, the chimpanzees' reactions were split between category 4 (immediate departure) and category 3 (nervous): the resulting category for these contacts was thus 3.5. Contact reactions of 3.5 were counted in the 'immediate departure' category. In the single case where the contact reaction was 1.5 (half of the individuals were curious and half ignored the observer) this was counted as an 'ignore'. In the two cases where 'nervous' (3) and 'curious' (1) were tied, they were treated as 'ignore' (2).

In addition to recording the first reaction of the individual chimpanzees during encounters, we continued to gather data on all of the reactions made by each chimpanzee for the duration of the contact. This we present in the results as 'total reactions per contact to the observer'.

Only a rough estimation of party sizes could be made, due to the low visibility in the forest and the timidity of the chimpanzees closer to the villages. Data on the age/sex composition of the parties we encountered is not presented in this paper, because for many individuals (especially in the non-Gangu forests) it was not possible to be sure of the age or sex. In cases where it was possible to determine the age and sex of individual chimpanzees, we used the age/sex classes of Goodall (1986). Infants still clinging to their mothers were not included in any of the analyses in this paper.

In the forests we surveyed to the south of the Uele River, less effort was put into following and making contact with the chimpanzees and more into studying their nests and tools. However, when we were able to make contact with them (by homing in on their morning calls or staking out fruit trees), we continued to gather data on their reactions.

Statistical analyses

All statistical analyses were carried out with R (version 2.9.0; R Development Core Team, 2009). A Mann-Whitney U test was used to compare contact duration in the Gangu Forest vs. non-Gangu forests. In addition, contact reaction type in the different forest regions was analyzed using the Pearson's χ^2 test. The same test was used to see if forest density or party-size affected the apes' behavior. We followed Morgan and Sanz (2003) in reporting individual contact durations and reactions without statistical analysis, due to the problem of non-independence of samples.

Two of the 75 contacts were excluded from all statistical comparisons except for those of contact rates per region, and party-size. One (in the Lingo Forest) was excluded due to procedural errors in the contact, and the other due to its location far to the south in the heavily-disturbed forest of Yoko, at the epicenter of the bushmeat trade (Chapter 6)

Results

Chimpanzee reactions to human presence

Over the 32 months spent in the northern DRC study region, there were 528.5 days when the potential existed for a contact with chimpanzees (Appendix I). We spent a total of 1,538.5 min either in direct observation (386.5 min) or in contact (1,152 min), with the Bili-Uele chimpanzees. Of this time, 748.7 min were in the Gangu Forest (148 min of observation and 600.7 min of contact time), and 790 min were in the non-Gangu regions (238.6 and 551.4 min, respectively), the latter

including 40 min of contact time south of the Uele River. Of the 47 non-Gangu contacts, 74.5% occurred in the wet season (considered here as the period between 1 April and 22 November), while 46.4% of the 28 Gangu Forest contacts occurred in the wet season.

Three (4 %) of our contacts were ended by the researchers. In addition, in four contacts in the Camp Louis area and one at Gangu, the chimpanzees appeared to already be leaving the area when the contact was initiated.

We achieved an average of 0.33 contacts per day in the Gangu Forest, compared with 0.11 in the forests closer to humans (including Camp Louis), and 0.15 considering only Camp Louis, which is close to the road. Comparing the Gangu and Camp Louis Forests, and omitting the days we spent working on transects (when contacts were not a priority), we reached an average of 0.46 contacts per day at Gangu Forest (2006-2007 field season) vs. 0.25 per day at Camp Louis ($\chi^2 = 2.95$, $df = 1$, $p = 0.09$) (for Camp Louis, we are considering here only the 130.5 day period between August 2004 and January 2005, the period of intensive habituation efforts prior to the transect study). During the final 24 working-day visit to Camp Gangu in January 2007 (when we had achieved a better knowledge of the area), the contact rate increased to 0.63 contacts per day, which was 2.5 times the contact rate at Camp Louis, a significant difference ($\chi^2 = 4.85$, $df = 1$, $p = 0.03$).

During the 2007-2008 field season, and during a visit to Lebo in September 2006, we spent 113 days in chimpanzee-inhabited forests to the south of the Uele River. During this time, we only managed to make contact with chimpanzees on five occasions, a contact rate of 0.04 per day spent in the forest. It should be mentioned that during this period our focus was not on habituation of the chimpanzees and we were not making as much of an effort to contact them. Nevertheless, we took advantage of every opportunity to do so and sometimes staked out fruit trees.

Based on the varying composition of parties we encountered within the same area (from one to nine individuals) (Hicks, unpublished data), it is likely that the Bili apes have a fission-fusion social system, as has been described in other chimpanzee populations (Itani & Suzuki, 1967; Nishida, 1968; Goodall, 1986; Boesch & Boesch-Achermann, 2000). Party-size averaged (mean \pm SEM) 3.1 ± 0.21 individuals per contact ($n = 75$). There was little difference between average party-size in the Gangu (3.09 ± 0.4 ; $n = 28$) and non-Gangu (3.04 ± 0.24 ; $n = 47$) forests.

Contact duration by forest region

First we consider group, not individual, contacts with chimpanzees (this includes 'groups' made up of only one chimpanzee). The average duration of the 73 group contacts made was (mean \pm SEM) 15.24 ± 3.28 min (median = 1.8). The average contact duration at Gangu was 21.45 ± 6.6 min (median = 3.6; $n = 28$) vs. 11.38 ± 3.28 min (median = 1.6; $n = 45$) for the non-Gangu forests. As predicted, Gangu contacts lasted longer than non-Gangu contacts, but the difference was not significant (two-tailed Mann-Whitney U test: $z = 0.97$, $p = 0.33$). However, when only arboreal contacts were considered (Gangu: 26.02 ± 7.73 ; $n = 23$; non-Gangu: 12.38 ± 3.89 ; $n = 38$) Gangu contacts lasted significantly longer (two-tailed Mann-Whitney U test: $z = 1.964$, $p = 0.049$). Even the Gangu contacts had a considerably shorter average duration than contacts at the Goualougo study (101.0 ± 6.44 ; $n = 218$) (Morgan & Sanz, 2003), as well as the Ngotto Forest (42.2 ± 8.45 ; $n = 8$) (Hicks et al., 2009).

Individual contact duration by age/sex category

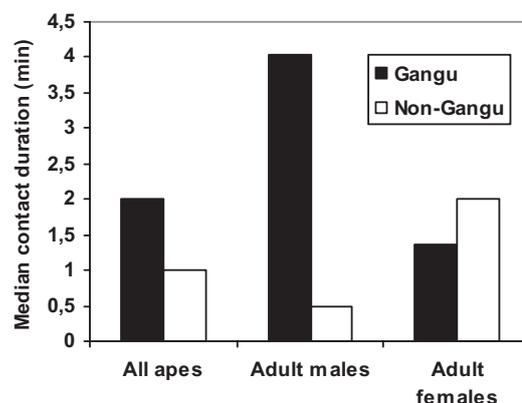
The average duration of all contacts with individual chimpanzees was (mean \pm SEM) 8.4 ± 1.44 min (median = 1; $n = 196$) (Table I). Because the data was not normally distributed, the medians are included as well). Contacts with adult female chimpanzees lasted an average of 11.5 ± 3.8 min (median = 1.5; $n = 39$), vs. 5.42 min (median = 0.6 min; $n = 35$) for contacts with adult males. Contacts with immature individuals of both sexes lasted an average of 18.1 ± 5.3 min (median = 3.5; $n = 39$).

Table I. Individual chimpanzee contact duration by age/sex class and forest region (these are the raw data for Figures 1 & 2). n = sample size.

Category	n	Avg. duration	Median duration	SEM
All chimpanzees	196	8.42	1	1.44
Chimpanzees Gangu	75	10.52	2	2.74
Chimpanzees non-Gangu	121	7.11	1	1.59
All adult males	35	5.42	0.6	2.04
Adult males Gangu	18	9.90	4.05	3.71
Adult males non-Gangu	17	0.67	0.5	0.26
All adult females	39	11.52	1.5	3.82
Adult females Gangu	16	6.00	1.37	4.23
Adult females non-Gangu	23	15.35	2	5.71

Contacts with individual Gangu chimpanzees lasted on average 10.52 ± 2.7 min vs. 7.11 ± 1.59 min for non-Gangu individual contacts (medians = 2 vs. 1 min) (Figures 1 & 2). Interestingly, contacts with individual males lasted notably longer at Gangu (9.9 ± 3.71 min) than at non-Gangu locations (0.67 ± 0.26 min) (medians = 4.1 vs. 0.5 min). Non-Gangu males almost always fled the contact site immediately. Unexpectedly, adult females showed the opposite pattern (6 ± 4.23 min average duration at Gangu vs. $15.4 \text{ min} \pm 5.71$ at non-Gangu locations) (median = 1.37 vs. 2 min).

Individuals identified as juvenile females ($n = 6$) showed particularly long contact durations independent of forest region. We were unable to identify the sex of



the remaining juveniles.

Figure 1. Chimpanzee individual reactions by forest region. Median duration (min) of contacts with individual chimpanzees by age/sex class and forest region. Because the data does not approach a normal distribution, median duration instead of average duration was used to construct the figure.

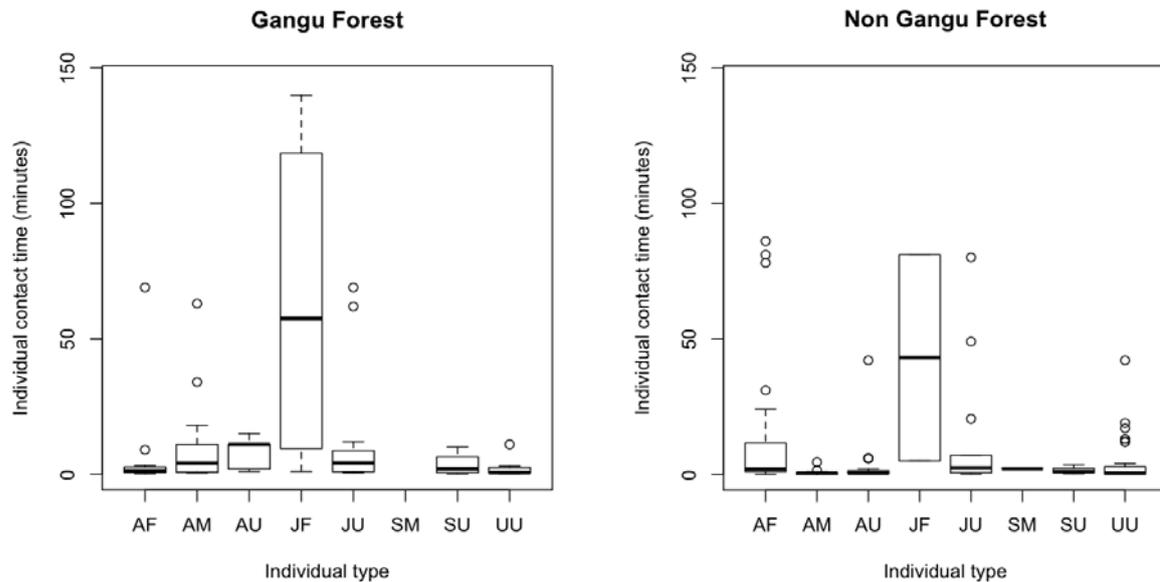


Figure 2. Box-plots of the individual contact durations (min) by age/sex class (AF = adult females, AM = adult males, AU = adults unknown, JF = juvenile females, JU = juveniles unknown, SM = sub-adult males, SU = sub-adults unknown, UU = unknown). A box-plot depicts sample minimum, lower quartile (Q1), median (Q2), upper quartile (Q3), sample maximum, and outliers.

Individual first reactions to observers

The majority of first reactions of chimpanzees to observers (53.6%) were retreats, with the apes either fleeing immediately (within a minute) or retreating stealthily (Table II). The other half of first reactions (46.4%) involved chimpanzees remaining in the same place, and 17.9% of all first reactions were curious ones. The first reactions of the chimpanzees clearly differed between Gangu and non-Gangu chimpanzees (Table II). At Gangu, 34.7% of first reactions were of curiosity, while in non-Gangu forests only 7.4 were. The pattern was nearly the opposite for the category of ‘flee’: at Gangu, this was the first response in 14.7% of encounters, while in non-Gangu forests, it

Table II. First reactions of chimpanzees to contacts, all forests ($n = 196$), Gangu Forest ($n = 75$) and non-Gangu forests ($n = 121$). Numbers in parentheses refer to the contact category codes defined in the text.

Reaction type	Allforests	% of first reactions	
		Gangu	Non-Gangu
Curious (1)	17.9	34.7	7.4
Aggressive approach (2)	0.5	0	0.8
Soft vocalizations (3)	0	0	0
Loud vocalizations (4)	4.1	2.7	5
Ignore (5)	5.1	6.7	4.1
Hide (6)	18.9	20	18.2
Stealthy retreat (7)	24	21.3	25.6
Flee (8)	29.6	14.7	38.8
Fearless reactions (1 - 5 combined)	27.5	44	17.3
Fearful reactions (7 and 8 combined)	53.6	36	64.4

made up 38.8% of first reactions. Fearless (i.e., non-flight and non-hide) first encounters in Gangu accounted for 44% of reactions, while in non-Gangu forests the figure was 17.3% (the ‘hide’ category, an intermediate reaction, accounted for 20 and 18.2 % of reactions, in Gangu and non-Gangu forests, respectively).

The first reactions to observers by age/sex category of chimpanzee are presented in Appendix II. Juveniles and sub-adults were the most likely to show a curious response, and the least likely to flee or retreat stealthily. Adult males were more likely to flee than any other age/sex class (almost always their reaction in the non-Gangu Forests), but they were also more likely to show curiosity than adult females (only in the Gangu Forest). More generally, in the Gangu Forest the first reaction was fearful (flee or stealthy retreat) in 36% of encounters, while in non-Gangu forests the figure was 64.4% (Table II).

Adult males in the Gangu Forest were more likely to show curious reactions (38.9%) to the observers than were adult females (25%) (Appendix II). However, they were also more likely to flee immediately than adult females (22.2% vs. 0). Adult females most often reacted with a stealthy retreat in the Gangu (43.8%). Juveniles and sub-adults were most likely to show curiosity (50 – 81.8%).

In non-Gangu forests, curiosity as a first reaction was very rare in any category except for sub-adults (75%). A large majority (88.2%) of adult male first reactions involved immediate flight or stealthy retreat. For adult females, departure accounted for 43.5% of first reactions.

Total reactions per contact to observers

In addition to the first reactions of individual chimpanzees to observers, we looked at the total reactions to observers per contact (Table III). In 42.7% of Gangu contacts, curiosity was shown by the chimpanzees, compared to only 11.6% in non-Gangu forest contacts.

Fearful reactions (stealthy retreat and immediate flight) were shown to a nearly equal degree in the majority of contacts of Gangu and non-Gangu, but fearless reactions were twice as common at Gangu (70.7 %) than in non-Gangu forests (34.7%).

Table III. Total reactions (%) made by chimpanzees to contacts in Gangu ($n = 75$) and non-Gangu ($n = 121$) forests. The table shows in what percentage of contacts each behavior category appeared, allowing multiple behaviors to be scored for each contact. Numbers in parentheses refer to the contact category codes defined in the text.

Reaction type	All forests	% contacts	
		Gangu	Non-Gangu
Curious (1)	23.5	42.7	11.6
Aggressive approach (2)	0.5	0	0.8
Aggressive display (2.5)	2	4	0.8
Soft vocalizations (3)	0.5	0	0.8
Loud vocalizations (4)	12.3	12	12.4
Ignore (5)	8.2	12	5.8
Ambiguous approach (5.5)	1.5	0	2.5
Hide (6)	25.5	28	23.1
Stealthy retreat (7)	55.1	70.7	45.5
Flee (8)	37.8	22.7	47.1
Fearless reactions (1 - 5.5 combined)	48.5	70.7	34.7
Fearful reactions (7 and 8 combined)	92.9	93.4	92.6

Juvenile and sub-adult apes were much more likely to show curious reactions to the observers than adults (Appendix III). Adult males were more likely to flee immediately than any other age/sex category (51.4%). Most non-adult male chimpanzees would eventually end the contact with a stealthy retreat

Looking only at the reactions of adult males, a clear difference exists between the Gangu and non-Gangu forests (Appendix III). Adult males showed curiosity in 50 and 11.8% of encounters in Gangu and non-Gangu forests, respectively. The same difference (although not as extreme) can be seen in the other age/sex categories, except for the sub-adults. In the non-Gangu areas, chimpanzees of all age/sex categories, with the exception of adult females, were more likely to flee or retreat stealthily than in the Gangu Forest.

Contact reaction types

There was a clear dichotomy in the reactions of chimpanzees between Gangu and the eastern forests (Figure 3). The Gangu chimpanzees had over six times the number of naïve contacts as non-Gangu chimpanzees (33.9 vs. 4.4%) (Table IV; Figure 4). This difference was significant (Fisher's exact test: $p = 0.01$; $n = 73$). For all non-flight contacts (categories 1 - 3), Gangu had 53.6 vs. only 24.4% for the non-Gangu forests, also a significant difference ($\chi^2 = 7.3594$, $df = 1$, $p = 0.01$; $n = 73$). We have included Morgan & Sanz's (2003) findings in the figure for comparison (see Discussion).

We investigated whether forest type had an effect on contact reaction type. No significant difference was found between contact reaction types in open, mixed, or dense forest, either when considering naïve vs. non-naïve reactions (Fisher's exact test: $p = 1$; $n = 71$) or immediate-departure vs. non-immediate departure reactions (Fisher's exact test: $p = 0.49$; $n = 71$) (16.7% of the six open-forest contacts, 13.6% of the 44 mixed-forest contacts, and 14.3% of the dense-forest contacts were naïve; 50.0% of the six open-forest contacts, 65.9% of the 44 mixed-forest contacts, and 76.2% of the 21 dense-forest contacts were immediate departure).

We investigated party-size as a possible factor influencing contact reaction type. For this analysis, we separated 'immediate departure' from the other three contact reaction types, 'naïve', 'ignore' and 'nervous'. Sixty-four percent of the 73 contacts were with chimpanzees in small parties (three individuals or less), and 36% in large parties (four individuals or more, with a maximum of nine); 23% of the

Table IV. Chimpanzee contact types by forest region (%). Data are entire contacts categorized as naïve, ignore, nervous, or fearful (based on the majority of reactions shown by the chimpanzees). For the seven contacts in which the chimpanzees reacted in equal numbers with two different behaviors, the two categories of behavior each received a score of 0.5. Contact types are from Morgan and Sanz (2003).

Contact type	Bili - S. Uele, all forests, $n = 73\%$	Gangu Forest, $n = 28\%$	Non-Gangu forests, $n = 45\%$	Goualougo Triangle (adapted from Morgan and Sanz 2003), $n = 218\%$
Naïve (1)	15.8	33.9	4.4	69
Ignore (2)	6.2	8.9	4.4	8
Nervous (3)	12.3	10.7	15.6	11
Immediate departure(<1 minute) (4)	64.4	46.4	75.6	11
All non-flight contact types (Types 1-3)	35.6	53.6	24.4	88

contacts were with only one individual. There was no significant difference in contact reaction type between small and large parties ($n = 73$; $\chi^2 = 0.322$, $df = 1$, $p = 0.57$). The same was true for contacts with one individual vs. contacts with more than one ($n = 73$; $\chi^2 = 0.0028$, $df = 1$, $p = 0.96$).

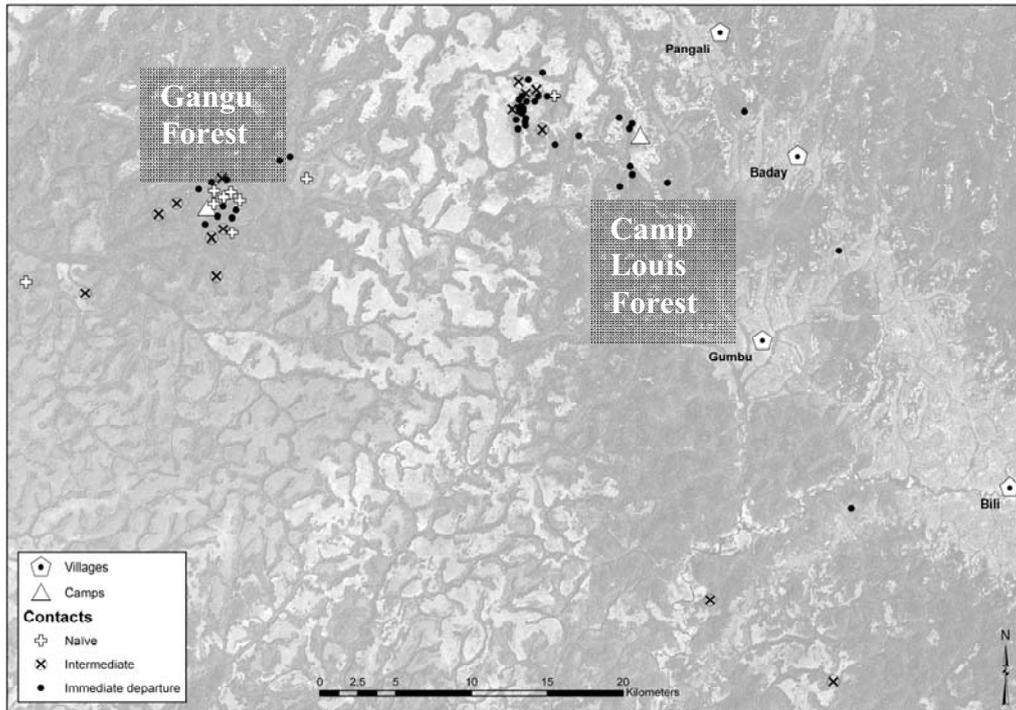


Figure 3. Contact reaction types across the study area. Contact reaction types were split into three categories: naïve (category 1), intermediate (1.5 – 3), and immediate departure (3.5- 4). The categories are defined in Materials and Methods. The Landsat ETM+ image files date from 2000 and were downloaded from GLCF at <http://glcf.umiacs.umd.edu>.

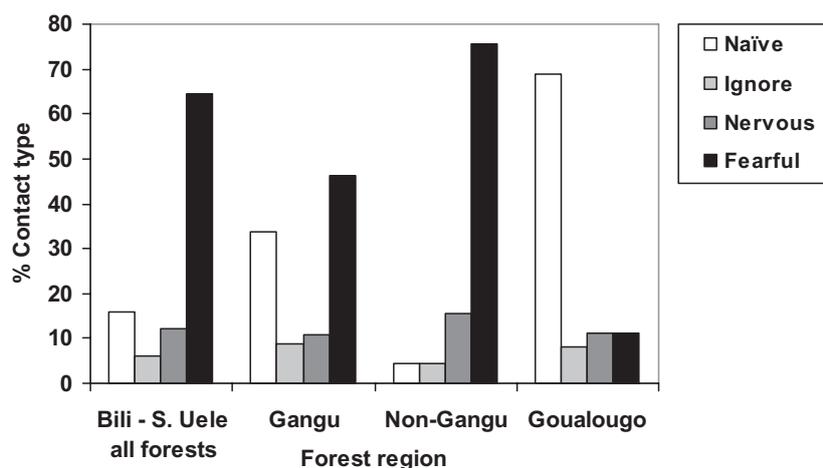


Figure 4. Chimpanzee contact types by forest region (%). The figure refers to contact types - not individual chimpanzee reactions, but entire contacts categorized as naïve (1), ignore (2), nervous (3), or fearful (4), based on the majority of reactions shown by the chimpanzees. See Appendix IV for the raw data. Contact types are from Morgan and Sanz (2003). Bili all forests = Gangu and non-Gangu forests. Goulougo data are from Morgan and Sanz (2003).

Table V. Comparison of individual reactions (%) among field sites (based on Table IV from Morgan and Sanz, 2003). The results from Kibale are originally from Johns (1996), those from Lopé are from Tutin and Fernandez (1991), and results from Goualougo are from Morgan and Sanz (2003). ‘n/a’ = researchers did not separate out particular behaviors from broader categories in their analyses.

Reaction type	LopéRese rve (<i>n</i> = 153)	Kibale Forest (<i>n</i> = 436)	Goua-lougo Triangle (<i>n</i> = 1131)	Bili, all Forests (<i>n</i> = 196)	Bili,Gangu Forest (<i>n</i> = 75)	Bili, non- Gangu forests (<i>n</i> = 121)
Curiosity	1	6.7	84	17.9	34.7	7.4
Ignore	3	25.8	4.95	5.1	6.7	4.1
Hide	5	6.9	7.6	18.9	20	18.2
Depart	74	35.6	3.45	53.6	36	64.4
Flight	39	25.5	1.41	29.6	14.7	38.8
Stealthy retreat	10	9.6	2.03	24	21.3	25.6
Approach/Await another	25	0.5	—	0	0	0
Charge (Aggressive display)	1	13.1	—	0.5	0	0.8
Loud vocalizations	8	7.10	n/a	4.1	2.7	5
Soft vocalizations	8	4.80	n/a	0	0	0

Cross-site comparisons

We have added our results to Morgan & Sanz’s (2003) cross-site comparison of first reactions of individual chimpanzees to observers between the Goualougo, Lopé and Kibale study sites (Table V). Overall, curious reactions were much more common at Bili than at Lopé or Kibale, but were not nearly as common as at Goualougo. Going by the curiosity measure, the Gangu Forest appears to lie about halfway between the ‘fearful’ condition of Lopé and Kibale and the completely naïve condition of Goualougo. Gangu, along with Kibale, also shows an intermediate frequency of ‘departure’ - much lower than at Lopé but much higher than at Goualougo. Interestingly, Kibale seems to stand out from the other populations with its large amount of aggression displayed at observers. The Bili chimpanzees were more likely to remain at the site and hide than any of the other populations.

Discussion

The purpose of this study was to test the hypothesis that chimpanzees living in remote forests would show less fear and more curiosity than those living closer to humans. Over the course of our stay at Bili we were able to compare the reactions of chimpanzees to observers in several neighboring forest regions. The majority of these regions (labeled ‘non-Gangu forests’, and including the region around Camp Louis) were less than 25 km from the nearest human roads and settlements, and were frequently visited by humans. The Gangu Forest, on the other hand, was much more isolated from humans (the nearest villages and roads were >25 km distant).

Our 2005 transect work showed over twice the density of chimpanzee nests in the Gangu Forest than in the area to the east near the roads, including Camp Louis (Chapter 4). The difference in ape density appears to be reflected in the increased number of contacts, as well as auditory observations (Chapter 3), although there were probably additional factors in play, such as the increase in our skill at finding the apes

by the time we reached Gangu. Nevertheless, by January 2007 we were averaging 0.63 contacts per day at Gangu, which is the same contact rate reported by Morgan & Sanz (2003) for the Goulougo study. If the Congolese political situation allows it, these chimpanzees would be ideal for habituation and further study.

The Bili chimpanzees living close to humans showed more fearful reactions than those living in the remote Gangu Forest. Contacts at Gangu lasted longer (although significantly so only when ground contacts were excluded from the analysis), and we had significantly more 'curious' reactions from the Gangu chimpanzees and fewer fearful ones.

Our data confirmed that the most fearful of the Bili chimpanzees were adult males living <25 km from the road, particularly in the Camp Louis region. These males typically fled immediately upon seeing us, often plunging 15 m or more to the ground. As expected, the duration of our contacts with these non-Gangu males was markedly shorter than contacts with adult males in the Gangu Forest. Female reactions, however, were more similar between the different study areas. We have no explanation for why the non-Gangu adult males showed such a panicked reaction; this pattern was not seen at Goulougo (Morgan & Sanz, 2003). At Kibale, however, the reaction was quite different: adult males were less likely than adult females to hide or flee and more likely to charge the human observer (we were never charged by a chimpanzee over the course of this study) (Johns, 1996). However, in both of those studies the chimpanzees were apparently further along in the habituation process than at Bili.

The several contacts that we had between 35 and 45 km from the road (the westernmost section of our transects) approached the naïve condition even more, with chimpanzees surrounding us in the trees and sometimes actively approaching us (films of these contacts, contrasted with fearful contacts closer to the road, are available at www.wasmoethwildlife.org/folder2004-2005). These chimpanzees, like those at Goulougo, seemed to be completely naïve, but unfortunately the small number of these contacts did not allow us to separate them out for comparison.

One factor that may have contributed to the difference in behavior between the Gangu and non-Gangu chimpanzees was the change in forest type between the two areas. In areas closer to the road, there was much seasonally-burnt savanna and savanna woodland, and the gallery forest in which the chimpanzees were most often found was very dense (this was probably due to past human disturbance: oil palm trees and other signs of past human cultivation were frequently observed in that area, but never at Gangu). In this habitat, it was harder for the researchers to get a clear view of the chimpanzees, and one can assume it was equally difficult for the chimpanzees to observe the researchers. This might have contributed to their more fearful reactions. However, even in dense vegetation at Gangu, the chimpanzees showed little fear. No significant difference was found between contact reaction types in the different forest types.

One factor was the same across forest regions: even at Gangu, the apes almost always fled immediately when we encountered them on the ground. This resembles the behavior of the chimpanzees of Goulougo, who were twice as likely to depart immediately when contacted on the ground (Morgan and Sanz, 2003), and also at Kibale (Johns, 1996), although some chimpanzees at the latter site also charged during terrestrial encounters. We observed a few exceptions: as described below, an adult male from Gangu approached us terrestrially to a distance of 8 m; during another contact, two Gangu juveniles climbed off the ground into a low-hanging tree to watch us while the adults fled. Finally, an adult male we encountered on the ground

close to the main road peered at us for approximately half a minute before stealthily retreating.

It should be pointed out that over the several years of intermittent research prior to TH's arrival at Bili in 2004, Shelly Williams' team as well as trackers hired by Karl Ammann occasionally attempted to observe or contact chimpanzees in the Camp Louis area. It cannot be ruled out that these earlier contacts might have been responsible for 'spooking' the chimpanzees in the region. Upon his arrival, TH found that one tracker in particular would attempt to rush to the base of the contact tree to point out the chimpanzees, and another tracker showed film of himself directing aggressive noises towards a female chimpanzee in a tree. Although we quickly put a stop to this and instructed the trackers in proper contact etiquette, this does raise the possibility that the Camp Louis chimpanzees may have been frightened in the past not by poachers but by the project trackers. It is unlikely, though, that this explains the extraordinary panic shown by the Camp Louis chimpanzees towards humans, in particular by the adult males. From her accounts to the press, it appears that Williams made only two contacts with Camp Louis chimpanzees, and that she did nothing to scare them. I have been able to confirm only five contacts made by Ammann's trackers. These contacts were sporadic and occurred across a large geographical area. In a contact filmed by Ligada Faustin in early 2004, this tracker can be seen to be standing at an appropriate distance from the tree and making little noise. In addition, the Gangu community of chimpanzees did not appear to show increasing fear as our contact rate with them increased, and they almost never reacted with the panic of the Camp Louis population. Finally, chimpanzees encountered close to roads on our surveys, far from the Camp Louis and Camp Gangu regions, also showed more fearful than naïve behaviors. The trackers asserted that people from the town of Gumbu had hunted chimpanzees in the Camp Louis area just prior to the arrival of Ammann and the conservation project; thus it is likely that the apes had been frightened by hunters, not researchers.

Our findings place the reactions of the Bili chimpanzees between the completely naïve behavior of the chimpanzees of the Goualougo Triangle (a site which has apparently never been visited by humans due to its inaccessibility) and the fearful behavior of the chimpanzees of Lopé and Kibale (these latter two sites were not as remote and isolated from humans as Gangu and Goualougo). Of the study sites sampled, the behavior of the chimpanzees we encountered in the remote Gangu Forest comes the closest to matching the naïve behavior of the Goualougo chimpanzees. The one occasion over the course of this study in which a chimpanzee intentionally approached us on the ground occurred within 1 km of Camp Gangu. This chimpanzee, a large adult male, initiated the contact with us (the author and three trackers) by walking purposefully towards us from about 30 m away to within 8 m of where we were sitting on the ground. He then climbed above our heads into a low sapling, and after watching us for about a minute, descended and moved slowly off into the undergrowth. In the same forest, we often observed juveniles continuing to feed as they watched us, and in several cases, young chimpanzees approached us in the canopy to within 15 m). One lone juvenile followed us for over 100 m through the forest. Such behavior almost never occurred in the non-Gangu forests, although it was common at Goualougo.

It is unlikely that the constellation of features encountered in the Gangu Forest – naïve chimpanzees, abundant elephants, and an almost total lack of human presence – was a coincidence. Such pristine areas are becoming increasingly rare in Africa, however, and their protection should be considered of paramount importance. It is our

hope that this study can be used to mobilize the DRC government to enforce the protected status of the Bili area, which was invaded by gold miners in June 2007. In addition, it may encourage researchers to seek out, study, and protect the remaining areas of untouched African wilderness before they are discovered and exploited by less-enlightened interests.

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References

- Ammann K. 2001. What happened to *Gorilla gorilla uellensis*? In *All Apes Great and Small*, Eds. Galdikas B. M. F, Briggs N. E, Sheeran L. K, Shapiro G. L, Goodall J. New York: Kluwer Academic/Plenum Publishers. Pp. 275-282.
- Boesch C. & Boesch-Achermann H. 2000. *The Chimpanzees of the Tai Forest: Behavioral Ecology and Evolution*. Oxford: Oxford University Press. 316 pp.
- Butynski T. M. 2001. Africa's Great Apes. In *Great Apes and Humans: The Ethics of Coexistence*, Eds. Beck B. B., Stoinski T. S, Hutchins M, Maple T. L, Norton B, Rowan A, Stevens E, & Arluke A. Smithsonian Institution Press: Washington, DC. Pp. 3-56.
- Campbell G, Kuehl H, Kouamé P, & Boesch C. 2008. Alarming decline of West African Chimpanzees in Côte d'Ivoire. *Current Biology* 18: R903-R904.
- Goodall J. 1986. *The Chimpanzees of Gombe: Patterns of Behaviour*. Belknap Press: Cambridge, MA. 674 pp.
- Groves C. 2005. Geographic variation within Eastern Chimpanzees (*Pan troglodytes schweinfurthii* Giglioli, 1872). *Australasian Primatology* 17: 19-46.
- Hicks T, Fouts R, & Fouts D. 2009. A survey of chimpanzees (*Pan troglodytes troglodytes*) and gorillas (*Gorilla gorilla gorilla*) in the selectively-logged Ngotto Forest, Central African Republic. *Journal of Applied Animal Welfare* 12: 165-188.
- Itani J. & Suzuki A. 1967. The social unit of chimpanzees. *Primates* 8: 355-381.
- Johns B. G. 1996. Responses of chimpanzees to habituation and tourism in the Kibale Forest, Uganda. *Biological Conservation* 78: 257-262.
- Morgan D. & Sanz C. 2003. Naïve encounters with chimpanzees in the Goulougo Triangle, Republic of Congo. *International Journal of Primatology* 24: 369-381.
- Nishida T. 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates* 9: 167-224.
- Peterson D. (2003). *Eating Apes*. Berkeley and Los Angeles: The University of California Press. 333 pp.
- Tutin C. E. G. & Fernandez M. 1991. Responses of wild chimpanzees and gorillas to the arrival of primatologists: Behaviour observed during habituation. In *Primate Responses to Environmental Change*, Ed. Box H. O. Chapman and Hall. Pp. 187-197.
- Walsh P, Abernathy K, Bermejo M, Beyers R, De Wachter P, Akou M, Huijbregts B, Mambounga D, Toham A, Kilbourn A, Lahm S, Latour S, Maisels F, Mbina C, Mihindou Y, Obaing S, Effa E, Starkey M, Telfer P, Thibault M, Tutin C, White L, & Wilkie D. 2003. Catastrophic ape decline in western equatorial Africa. *Nature* 422: 611-614.
- Young, E. 2004. The beast with no name. *New Scientist* 2468 October 9: 33-35.

Appendices

Appendix I. Dates and geographical location of chimpanzee surveys and days spent in each forest region, and chimpanzee contact-rate per forest region. For the columns ‘numbers of surveys’ and ‘kms walked by TH’, only surveys conducted by TH are included.

Location	Survey period	Surveyor	GPS coordinates	No. days in forest	No. contacts	Chimpanzee contacts per day in forest ($n = 75$)	No. surveys by TH	Km walked by TH
Camp Louis Forest 2004-2005	August 2004 – July 2005, August 2006 – February 2007	TH (2004-2005) TH / JS (2006-2007)	4°21’72” N, 24°56’72”E	262.5 (237 first season, 25.5 second season)	38 (Period 1: $n = 38$) (Period 2: $n = 0$)	0.15 (Period 1: 0.16) (Period 2: 0)	167 (plus transects)	12340.94 ¹
Gangu Forest	March – June 2005, August 2006 – February 2007	TH (2005, 2006) TH / JS (2007)	4°19’34”N, 24°41’53”E	85 (37.5 first season, 47.5 second season)	28 (Period 1: $n = 6$) (Period 2: $n = 22$)	0.33 (Period 1: 0.16) (Period 2: 0.46)	96 (plus transects)	326.99 ²
Zapay Forest	December 2006	TH	4°57’01”N, 25°06’31”E	9	1	0.11	13	49.43
Gbangadi	December 2006	JS	4°43’40”N, 24°46’60”E	6	0	0	na	na
S Bili Forest	July 2006 – November 2006	TH / JS	4°02’42”N, 25°02’11”E	48	3	0.06	24	88
Nawege and N Uele (Zaza) Forests	September 2006 (Nawege) August 2008 (Zaza)	TH / JS (Nawege) TH (Zaza)	3°37’14”N, 25°22’55”E 3°28’11”N, 25°10’73”E (Zaza)	5	0	0	4	9.14
Lebo	September 2006, August 2008	TH / JS (2006) TH (2008)	3°24’43”N, 25°20’65”E	24	1	0.42	12	31.03
Lingo	November 2008	TH	3°24’83”N, 23°30’11”E	9	1	0.11	8	38.5
Zongia	November 2008	TH	3°35’06”N, 23°45’75”E	8	0	0	8	35.7
Mbange E	January 2009	TH	3°13’73”N, 24°10’25”E	15	0	0	16	80.93
Mbange W	January – February 2008	TH	3°09’30”N, 24°02’88”E	9	0	0	11	45.48
Leguga	March 2008	TH	3°21’38” N, 24°57’84”E	14	2	0.14	18	48.52
Bambesa (Bongenge)	April 2008	TH	3°13’70”N, 25°51’16”E	10	0	0	11	46.5
Bambesa (Malembobi)	April – May 2008	TH	3°25’72”N, 25°47’91”E	3	0	0	6	18.49
Aketi (Akuma)	June 2008	TH	2°29’36”N, 23°56’93”E	4	0	0	8	23.47

Appendix I – Continued

Location	Survey period	Surveyor	GPS coordinates	No. days in forest	No. contacts	Chimpanzee contacts per day in forest ($n = 75$)	No. surveys by TH	Km walked by TH
Buta	September 2008	TH	2°48'82"N, 24°44'69"E	3	0	0	7	25.6
Ngume	September – October 2008	TH	2°45'83"N, 25°20'15"E	8	0	0	8	39.38
Aketi (Yoko)	November 2008	TH	2°36'43"N, 23°34'98"E	6	1	0.17	3	1.04
All forests N of the Uele River	2005-2008	TH (2004-2005, 2008)		415.5	70	0.17	304	1704.5
All forests S of the Uele River	2006-2008	TH / JS (2006-2007)		113	5	0.04	116	434.64
All non-Gangu forests	2004-2008	TH (2004-2008)		443.5	47	0.11	324	1823.55
All forests	2004-2008	TH (2004-2008) TH / JS (2006-2007)		528.5	75	0.14	420	2139.4

¹ Includes 99 km of transects.

² Includes 61 km of transects.

Appendix II. First reaction to observers (%) by category of apes ($n = 196$). 1 = curious, 2 = aggressive approach, 2.5 = aggressive display, 3 = soft vocalizations, 4 = loud vocalizations, 5 = ignore, 5.5 = ambiguous approach, 6 = hide, 7 = stealthy retreat, and 8 = flee. Plain text = All Bili Forests ($n = 196$), **Bold text = Gangu Forest ($n = 75$)**, *Italicized text = non-Gangu forests ($n = 121$)*.

Category	Adult males n = 35 n = 18 <i>n = 17</i>	Adult females n = 39 n = 16 <i>n = 23</i>	Adult unknown n = 35 n = 7 <i>n = 28</i>	Juvenile females n = 6 n = 4 <i>n = 2</i>	Juveniles unknown n = 25 n = 11 <i>n = 14</i>	Sub-adults unknown n = 8 n = 4 <i>n = 4</i>	Unidentified n = 48 n = 15 <i>n = 33</i>
1	25.7 38.9 <i>11.8</i>	15.4 25 <i>8.7</i>	9.1 42.9 <i>0</i>	16.7 25 <i>0</i>	44 81.8 <i>14.3</i>	62.5 50 <i>75</i>	0
2	0	0	0	0	4 0 <i>7.1</i>	0	0
2.5	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0
4	0	2.6 0 <i>4.4</i>	5.7 0 <i>7.1</i>	16.7 25 <i>0</i>	4 0 <i>7.1</i>	0	6.3 6.7 <i>6.1</i>
5	2.9 5.5 <i>0</i>	12.8 12.5 <i>13</i>	2.9 14.3 <i>0</i>	33.3 75 <i>50</i>	0	0	2.1 0 <i>3</i>
5.5	0	0	0	0	0	0	0
6	17.1 33.3 <i>0</i>	25.6 18.8 <i>3</i>	8.6 14.3 <i>7.1</i>	0	16 0 <i>28.6</i>	25 25 <i>25</i>	25 26.7 <i>24.2</i>
7	11.4 0 <i>23.5</i>	38.5 43.8 <i>34.8</i>	40 28.6 <i>42.9</i>	33.3 25 <i>50</i>	20 18.1 <i>21.4</i>	12.5 25 <i>0</i>	12.5 20 <i>9.1</i>
8	42.9 22.2 <i>64.7</i>	5.1 0 <i>8.7</i>	34.3 0 <i>42.9</i>	0	12 0 <i>21.4</i>	0	54.2 46.7 <i>57.6</i>

Appendix III. Total reactions per contact (%) by category of apes, $n = 196$. This appendix indicates the percentage of contacts per age/sex category in which each behavioral category was shown. 1 = curious, 2 = aggressive approach, 2.5 = aggressive display, 3 = soft vocalizations, 4 = loud vocalizations, 5 = ignore, 5.5 = ambiguous approach, 6 = hide, 7 = stealthy retreat, and 8 = flee. Plain text = All Bili Forests ($n = 196$), **Bold text = Gangu Forest ($n = 75$)**, *Italicized text = non-Gangu forests ($n = 121$)*.

Category	Adult males <i>n</i> = 35	Adult females <i>n</i> = 39	Adult unknown <i>n</i> = 35	Juvenile females <i>n</i> = 6	Juveniles unknown <i>n</i> = 25	Sub-adults unknown <i>n</i> = 8	Unidentified <i>n</i> = 48
	<i>n</i> = 18	<i>n</i> = 16	<i>n</i> = 7	<i>n</i> = 4	<i>n</i> = 11	<i>n</i> = 4	<i>n</i> = 15
	<i>n</i> = 17	<i>n</i> = 23	<i>n</i> = 28	<i>n</i> = 2	<i>n</i> = 14	<i>n</i> = 4	<i>n</i> = 33
1	31.4 50 <i>11.8</i>	25.6 31.3 <i>21.7</i>	8.6 42.9 <i>0</i>	66.7 75 <i>50</i>	52 81.8 <i>28.6</i>	75 75 <i>75</i>	0
2	0	0	0	0	4 0 <i>7.1</i>	0	0
2.5	2.9 5.6 <i>0</i>	0	0	16.7 25 <i>0</i>	8 36.4 <i>7.1</i>	0	0
3	0	2.6 0 <i>4.3</i>	0	0	0	0	0
4	2.9 5.6 <i>0</i>	15.4 6.3 <i>21.7</i>	5.7 0 <i>7.1</i>	83.3 75 <i>100</i>	28 27.3 <i>28.6</i>	0	6.25 6.7 <i>6.1</i>
5	5.7 11.1 <i>0</i>	15.4 18.8 <i>17.4</i>	2.9 14.3 <i>0</i>	33.3 25 <i>50</i>	8 18.2 <i>0</i>	0	2.1 0 <i>3</i>
5.5	0	7.7 0 <i>8.7</i>	0	0	8 0 <i>14.3</i>	0	0
6	17.1 33.3 <i>0</i>	38.5 31.3 <i>43.5</i>	20 57.1 <i>10.7</i>	16.7 0 <i>50</i>	24 9.1 <i>35.7</i>	37.5 25 <i>50</i>	25 26.7 <i>24.2</i>
7	45.7 55.6 <i>35.3</i>	66.7 87.5 <i>52.2</i>	57.1 85.7 <i>50</i>	83.3 75 <i>100</i>	72 90.9 <i>57.1</i>	100 100 <i>100</i>	33.3 40 <i>30.3</i>
8	51.4 38.9 <i>64.7</i>	23.1 6.3 <i>34.8</i>	42.9 14.3 <i>50</i>	0	12 0 <i>21.4</i>	0	60.4 53.3 <i>63.6</i>