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Published in:
American Journal of Primatology

DOI:
[10.1002/ajp.22023](https://doi.org/10.1002/ajp.22023)

[Link to publication](#)

Citation for published version (APA):
Hicks, T. C., Roessingh, P., & Menken, S. B. J. (2012). Reactions of Bili-Uele chimpanzees to humans in relation to their distance from roads and villages. *American Journal of Primatology*, 74(8), 721-733.
<https://doi.org/10.1002/ajp.22023>

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RESEARCH ARTICLE

Reactions of Bili-Uele Chimpanzees to Humans in Relation to Their Distance From Roads and Villages

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In order to assess the impact of human activities on chimpanzee behavior, we compared reactions to humans of Eastern chimpanzees (*Pan troglodytes schweinfurthii*) living in proximity to and at a distance from roads and settlements in the Bili-Uele landscape in Northern Democratic Republic of the Congo (DRC). We found that chimpanzees in the remote Gangu Forest 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, arboreal contact durations with Gangu chimpanzees lasted significantly longer than elsewhere. The most likely explanation for this phenomenon is that with increasing distance from roads, chimpanzees have in the recent past had fewer negative encounters with humans, and thus never learned to fear them. The discovery of this population of “naïve chimpanzees” presents us with an important research and conservation opportunity that may result in the installation of a long-term research site and increased protection of the population. *Am. J. Primatol.* 74:721–733, 2012. © 2012 Wiley Periodicals, Inc.

Key words: *Pan troglodytes schweinfurthii*; Bili-Uele landscape; Gangu Forest; naïve chimpanzees; behavior

INTRODUCTION

The relationship between humans and our primate cousins is complex, ranging from relatively benign (*Macaca fascicularis* in Bali [Fuentes, 2010]), to a mixture of mutual aggression and tolerance (*Pan troglodytes* in Uganda and *Macaca fuscata* in Japan [Hill & Webber, 2010]), to antagonistic (*Papio anubis* in Uganda [Hill & Webber, 2010]), and sometimes involves human hunting of non-human primates for bushmeat and in retaliation for crop-raiding [*Pongo pygmaeus*: Meijaard et al., 2011; *Pongo abelii*: Campbell-Smith et al., 2010; *P. troglodytes*: Hicks et al., 2010; *Gorilla gorilla gorilla*: Hennessey & Rogers, 2008]. As more forest is cleared and settlements are established in previously untouched wilderness, humans and nonhuman primates are increasingly coming into regular contact with one another [Fuentes & Hockings, 2010]. The conservation of nonhuman primates requires an understanding of the dynamics of the human–nonhuman primate interface, which is the subject of the pioneering field of ethnoprimateology [Fuentes & Hockings, 2010; Fuentes & Wolfe, 2002; Sponset, 1997]. A number of ethnoprimateological studies have focused on human cultural views of nonhuman primates [e.g. Fuentes & Hockings, 2010; Hill & Webber, 2010]. Also important to understand, however, is the impact of humans on nonhuman primate behavior. A few studies have addressed this topic. Van Roosmalen [2008, p. 384] reported that male

spider monkeys (*Ateles paniscus*) in heavily hunted areas of the Brazilian Amazon ceased making their species-typical long calls. Likewise, Kavanagh [1980] documented changes in the behavior of crop-raiding vervet monkeys (*Chlorocebus aethiops*) living in close proximity to humans compared to those who encountered humans more rarely. Nevertheless, opportunities to compare the behavior of nonhuman primates who encounter humans regularly with conspecifics who do not are rare. The current study provides a comparison of the behavior of naïve Eastern chimpanzees (*Pan troglodytes schweinfurthii*) living in remote forests to conspecifics who have come into regular contact with humans, and thus contributes to our understanding of the effects of repeated contacts with humans on nonhuman primate behavior.

Additional Supporting Information may be found in the online version of this article.

Contract grant sponsor: Wasmoeht Wildlife Foundation; Contract grant sponsor: Lucie Burgers Foundation; Contract grant sponsor: The Max Planck Institute for Evolutionary Anthropology; Contract grant sponsor: The International Primate Protection League.

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Received 9 September 2011; revised 27 January 2012; revision accepted 5 February 2012

DOI 10.1002/ajp.22023

Published online 1 May 2012 in Wiley Online Library (wileyonlinelibrary.com).

The chimpanzee (*P. troglodytes*), one of our two closest living relatives, is currently disappearing across much of its range. Over the past century, human hunting and habitat disturbance have, in combination with other threats such as ebola, reduced the species to a small fraction of its former abundance [Campbell et al., 2008; Goodall, 1996; Walsh et al., 2003]. 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 [Hicks et al., 2010; Peterson, 2003]. Chimpanzees living in proximity to roads and villages who have presumably come into contact with hunters learn quickly to fear *Homo sapiens*, as has been documented at Lopé [Tutin & Fernandez, 1991], Kibale [Johns, 1996], Gombe [Goodall, 1986], Tai South Group Forest [Bertolani & Boesch, 2008], and Ugalla (where chimpanzees fled immediately in 13 of 14 contacts, emitting warning barks prior to fleeing in half of the cases [D.L. Moore, unpublished data, from her July 2009 to March 2010 survey]). When researchers first made contact with these chimpanzee populations, the apes would usually leave the area immediately, probably an indication of previous negative encounters with humans. Such behavior is now typical of free-living apes across the continent [Morgan & Sanz, 2003].

Chimpanzee/human interactions, however, can be more complex. At the sites of Bulindi in Uganda and Bossou in Guinea, chimpanzees live in close proximity to humans and raid their crops, but are protected from hunting by the traditional beliefs of the local population. These chimpanzees rarely flee from researchers and villagers and are likely to ignore or behave aggressively toward them [Bulindi: McLennan & Hill, 2010; Bossou: Hockings, 2009]. Although the Bossou chimpanzees have been habituated to the presence of researchers for decades, which has likely contributed to their lack of fear of humans, their close proximity to villages and their sacred status in local tradition predates the research [Yamakoshi, 2011]. According to Kortlandt [1986], prior to habituation, they were not shy around humans and easy to observe.

Nigerian chimpanzees (*P. t. ellioti*) in the human-disturbed forests of Gashaka Gumti, who have been protected for some time from hunting by Islamic tradition, showed tolerant behavior (as opposed to nervous behavior or flight) in 59% of 68 contacts with researchers [Sommer et al., 2004], but appeared to flee more often when encountered off of a familiar village path [A. Fowler, pers. comm., June 16, 2011]. These chimpanzees live approximately 10.5 km from a village of about 600 people, in rugged terrain, which may have isolated them to some degree from humans.

In areas remote from human settlements, researchers may encounter chimpanzees who do not flee, but instead ignore them or react with curiosity [Itani & Suzuki, 1967]. Encounters with such chimpanzees were documented in the Goulougo Triangle in The People's Republic of Congo by Morgan and Sanz [2003] and Fay [1993] described them as "naïve." This area seems to have been completely isolated from humans for centuries due to its swampy, inaccessible terrain. Hicks et al. [2009] observed a similar phenomenon of curious chimpanzees (*P. t. troglodytes*) in the Ngotto Forest, Central African Republic, approximately 10 km south of the village of Grima.

The forests and savanna woodlands surrounding the town of Bili, Northern Democratic Republic of the Congo (DRC), are inhabited by a large population of Eastern chimpanzees (*P. t. schweinfurthii*) [Hicks, 2010]. Attempts to study them at Camp Louis, a field camp in the Bili region, were thwarted as the chimpanzees almost always fled the scene immediately. Local Azande field assistants claimed that the apes had been hunted until the advent of a community conservation project in 2002, thus explaining their fear of humans.

A near-pristine forest, called Gangu, has its eastern border 15 km to the west of Camp Louis. According to Ligada Faustin, a local field assistant familiar with the area, the chimpanzees there showed little fear of humans. In order to study the population density and behavior of these chimpanzees, we set up a base camp in the Gangu Forest and began to make regular contacts with the apes [Hicks, 2010]. In addition, we recorded the behavior of chimpanzees encountered at other localities across the Bili-Uele landscape.

The reaction of chimpanzees to humans appears to be affected by their proximity to roads and villages and their probability of encountering humans. We investigated this phenomenon by comparing several areas in the Bili-Uele landscape that differed in their distance to roads and villages. Two main hypotheses were tested: (1) chimpanzees living in remote areas show more curious and less fearful behaviors toward humans. (2) Contacts with chimpanzees in remote forests last longer than in areas closer to roads and villages. In order to investigate whether these predictions also hold for other populations of chimpanzees, we compared the behavior of the Bili apes to that of chimpanzees at other study sites.

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. The

complex mosaic habitat consists of seasonally burned savanna, savanna woodland, disturbed and regenerating forest, gallery forest, and tropical moist forest. Our two study camps, Camp Gangu and Camp Louis, were located within the Bili-Uéré Hunting Reserve (Table S1) [Hicks, 2010]. Bili is the closest large settlement to these field camps, with several thousand people living there and in the smaller villages along the road. Human use of the region northwest of Bili, other than the yearly burning of most of the savannas and some shifting cultivation close to the village, is minimal. Located roughly at the confluence of the Bo and Gangu Rivers is a very large area of near-pristine primary forest called Gangu, characterized by an abundance of elephants and chimpanzees and minimal human presence, measured by encounter rates of human signs such as artifacts, cartridges, hunting camps, and fields (Table S2) [Hicks, 2010].

In 2006, we conducted surveys of a large area outside of the Camp Louis-Gangu site, extending from the forests of Lebo just south of the Uele River to Zapay in the north (Table S1). Chimpanzees were found throughout the area, and even within 4 km of large settlements such as Bili, Lebo, and Zapay. In the majority of these forest localities, we found an increased encounter rate of human signs, including snares and cartridges (Table S2), indicating heavier hunting pressure than at Gangu-Camp Louis [Hicks, 2010].

From October 2007 to November 2008, we conducted a survey of the forests south of the Uele River (Table S1) (we refer to the entire area of our surveys, encompassing both sides of the Uele River, as the Bili-Uele landscape). This area was nearly devoid of savannas and more evenly forested than to the north of the Uele. We found chimpanzee nests throughout the region, even within 13 km of the large commercial center of Buta; we also documented 42 chimpanzee orphans and 33 carcasses, evidence that a large number of chimpanzees are being killed in this region [Hicks et al., 2010].

For the purposes of this article, we divided the forests into two categories: those located >20 km from a main road or village (the Gangu Forest), and those located <20 km (all other localities). We decided upon this approach due to the dramatic increase in elephant evidence and the decrease in human evidence that occurred 20 km from the road in the Gangu Forest (Table S2) [Hicks, 2010].

Data Collection Protocol

Our main priority throughout our time in the field was to locate and contact chimpanzees (see below for our definition of contact). The researcher and one to three Azande trackers would follow chimpanzee vocalizations heard from the camp or on trails to find the apes. We also conducted stakeouts of fruiting trees favored by the chimpanzees. In addition to

making contact with the chimpanzees, we recorded all signs of the apes and other large mammals. TH systematically recorded all evidence of human presence, such as fields, lean-tos, hunting camps, snares, cartridges, and encounters (Table S2) [see Hicks, 2010; Hicks et al., submitted for categories of human evidence and further methodological details]. Cartridges were collected to avoid counting them again during repeat passes. In 2005, we conducted chimpanzee nest surveys along three 50–55 km line transects from the Bili road through the Gangu Forest [Hicks, 2010]. In 2006, we established a new base camp in the Gangu Forest, where over a period of 2 months we managed to make 22 contacts.

A contact is defined as having taken place any time the chimpanzees were aware of our presence. Contacts with groups and individuals were considered to have ended the last time we heard or saw the chimpanzees within 50 m of us. A potential contact day includes any day in which TH or fellow researcher Jeroen Swinkels (JS) were in chimpanzee-inhabited forests and prepared to make a contact (whether actively searching for chimpanzees or in camp listening for them). If both teams were out searching for chimpanzees, this was counted as 2 days with the potential for a contact.

In order to calculate contact rate per region and party size, we analyzed 75 (TH = 72, JS = 3) contacts made over the 32 months spent in the field; for all other statistical comparisons, we limited our analyses to 73 contacts (we excluded two from the South Uele due to procedural and methodological problems with those contacts). Of the 75 contacts, 58.5% were achieved by following chimpanzee vocalizations and tree drumming to their source and 24.5% by staking out fruiting trees; the remaining 17% were opportunistic encounters.

The local field assistants wore red hats in order to help the apes distinguish them from potential poachers. During contacts, the assistants were instructed to hide or (if spotted by the chimpanzees) sit down. 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 from them), 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 the chimpanzees, but an effort was made to remain in one place.

We collected ad libitum data on the chimpanzees' behavior, and were usually able to film the contacts as well. The data recorded included forest density (open, medium, or dense: i.e. visibility 0–1.9, 2–5, or >5 m), party size, age, and sex of the chimpanzees [following the categories defined by Goodall, 1986, and excluding infants clinging to their mothers], contact duration for each individual present, whether

the apes were on the ground or in trees, their height in the trees, their distance from the observer, and all of the reactions of each individual to our presence.

We observed the following ten behavioral patterns for individual chimpanzees [categories adapted from Tutin & Fernandez, 1991]. In parentheses are the code numbers, we attributed to each category.

- (1) *Curiosity*: includes two or more of the following elements: staring, head-swaying, moving to obtain a clearer view of the observer, and approaching the observer.
- (2) *Aggressive approach*: rapid noisy approach in the trees, either direct or oblique, toward the observer, accompanied by threat gestures and barks.
- (3) *Aggressive display*: leaping about and shaking branches toward the observer without approaching.
- (4) *Soft vocalizations*: hoo or whimper.
- (5) *Loud vocalizations*: wraags, waas, or screams.
- (6) *Ignore*: no discernible response shown; after glancing or staring at the observer, the individual continues with previous activity, or just sits and relaxes.
- (7) *Ambiguous approach*: approaching the observer rapidly while attempting to flee, when the observer stands beneath the primary arboreal pathway.
- (8) *Hide*: either moving behind vegetation or pulling vegetation in front of face or body to form a screen.
- (9) *Stealthy retreat*: slow, cautious, and almost silent descent from tree or avoidance on the ground.
- (10) *Flee*: rapid jumping or sliding out of a tree or running at speed along the ground causing much noise. Stealthy retreat and flee have for some analyses been combined into a meta-category, “immediate departure” (vs. “non-flight”).

In addition to these individual behaviors, following Morgan and Sanz [2003], group contacts (i.e. contacts considering the reaction of the group as a whole) were classified on a scale from “naïve” (1) to “immediate departure” (4) using the first reaction of the majority (i.e. more than half) of the chimpanzees during the contact. For some of the analyses, these contact types have been divided into “non-flight” (the first three categories listed below) versus “immediate departure.”

- (1) *Naïve*: After initial response, the majority of the chimpanzees 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. At Bulindi, a similar category,

“monitor,” is used [McLennan & Hill, 2010], involving visual scanning but not necessarily involving the same levels of curiosity.

- (2) *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).
- (3) *Nervous*: Chimpanzees retreat from observers by moving higher in the canopy or hiding behind vegetation, and monitor observers and other chimpanzees in the party. Other indications of nervousness include pilo-erection, self-scratching, and loose stool.
- (4) *Immediate departure*: Chimpanzees immediately depart after becoming aware of human presence. Same as the combined “flee” and “stealthy retreat” categories for individual response (termed “immediate departure” by Morgan & Sanz, 2003).

McLennan and Hill [2010], in describing the behavior of the Bulindi chimpanzees, also include the group contact category “Intimidate,” characterized by continuous or repeated outbursts of threatening behavior by visible and/or nonvisible apes usually accompanied by loud group vocalizations and/or buttress drumming, continuing until researchers or chimpanzees depart the encounter site. Includes the subcategories “Mobbing” (the chimpanzees in a party reduce the distance to researchers to display and/or thrash the vegetation), and “Silent, aggressive pursuit of retreating researchers by chimpanzees.” None of the contacts in our study were of this type.

For seven of the 73 contacts, there was no majority reaction; in those cases, in order to classify the contact, we split the chimpanzees’ reactions halfway between two categories (e.g. in four cases 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, that is categories 3 and 4 in the example above. For statistical analyses, a different approach was required: for the four contacts in which the chimpanzees’ reactions were split evenly between the categories “immediate departure” and “nervous,” we scored them in the “immediate departure” category. In the single case where half of the individuals were curious and half ignored the observer, we scored the contact as “ignore.” In the two cases where “nervous” and “curious” were tied, they were scored as belonging to the category intermediate between these two, “ignore.”

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

The methods used to collect the noninvasive observational field data were in compliance with

animal care regulations and with the requirements and guidelines of the Institut Congolais pour la Conservation de la Nature (ICCN), and with the legal requirements of the DRC, as well as to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

Statistical Analyses

All statistical analyses were carried out using the program R [R Development Core Team, 2011]. We used a one-tailed Mann–Whitney *U*-test to compare contact durations of arboreal contacts in the Gangu Forest versus non-Gangu Forests. We used Pearson's chi-square test to compare contact rates between the different forest regions, human evidence encounter rates between forest regions, and the effects of party size on group contact types. In order to compare the percentages of different group contact types between regions, and the effects of forest type on this, we divided the region into three sections: Gangu East (within 5 km west of the forest's east edge), Gangu Central (between 5 and 10 km west of the forest's east edge), and Gangu West (>10 km west of the forest's east edge), and used Fisher's exact test. We followed Morgan and Sanz [2003] in reporting individual contact durations and reactions without statistical analysis, due to the problem of nonindependence of samples (i.e. we could not rule out that we did not encounter some of the same individual chimpanzees on multiple occasions). To investigate the relationship between human evidence counts and percentages of immediate departures across study regions, we conducted a Spearman's rank correlation coefficient test.

RESULTS

Observation Time and Contact Rates

Over the 32 months we spent in Northern DRC, there were 528.5 days when the potential existed for a contact with chimpanzees (Table S1). We compared our contact rates with chimpanzees in different forests and during different study periods (Table I). In the Gangu Forest, we spent 748.7 min with the chimpanzees (600.7 min in contact and another 148 min of direct observation), versus 790 min in non-Gangu Forests (551.4 min of contact time and 238.6 min of direct observation; 40 min of this was contact time south of the Uele River). A total of 54.6% of Gangu and 25.5% of non-Gangu contacts took place during the dry season (November 22 through March 31).

Comparing only the periods when we were not walking transects and were actively seeking out the chimpanzees, contact rates were higher at Gangu (2006–2007) than at Camp Louis (August 2004 through January 2005), but not significantly so

TABLE I. Numbers of Contacts Per Day in the Forest Compared Across Different Study Periods and Locations

Region and period	No. days in field	No. contacts	Avg. no. contacts/day
Gangu total (2005–2007)	85.0	28	0.33
Gangu (2006–2007) ^a	47.5	22	0.46
Gangu (January 2007) ^b	24.0	15	0.63
Non-Gangu Forests (2004–2008)	443.5	47	0.11
Camp Louis total (2004–2007)	262.5	38	0.15
Camp Louis (August 4 to January 5) ^c	130.5	32	0.25
South Uele Forests ^d (2006–2008)	113.0	5	0.04
Total days in forest (2004–2008)	528.5	75	0.14

^aThis period excludes the 2005 season, when our focus was more on transect work than making contact with the chimpanzees.

^bThis period covers our final visit to Gangu, in which we had achieved a better knowledge of the region and were focused entirely on making contacts with the chimpanzees (as opposed to walking transects or camp-building).

^cThis was the period of intensive habituation efforts prior to the transect study.

^dAlthough our focus was not as much on habituation during this period, we still attempted to follow chimpanzee vocalizations to contact the apes, and we sometimes staked out fruit trees.

($\chi^2 = 2.95$, $df = 1$, $P = 0.09$). During the final 24 working day visit to Camp Gangu in January 2007 (when we had achieved a level of knowledge of the area comparable to that at Camp Louis, and were able to focus our efforts exclusively on making contact with the chimpanzees), the contact rate increased to 0.63 contacts per day, which was 2.5 times the contact rate at Camp Louis, a significant difference ($\chi^2 = 4.85$, $df = 1$, $P = 0.03$). Contact rates were extremely low south of the Uele.

Group Composition and Party Size

Based on the varying composition of parties we encountered within the same area (from one to nine individuals), it is likely that the Bili apes have a fission–fusion social system, as has been described for other chimpanzee populations [Goodall, 1986; Itani & Suzuki, 1967; Nishida, 1968]. Party size averaged $3.1 \pm SE 0.21$ individuals per contact ($N = 75$). The average party sizes in the Gangu ($3.09 \pm SE 0.4$, $N = 28$) and non-Gangu ($3.04 \pm SE 0.24$, $N = 47$) Forests did not differ significantly.

Individual Contact Duration by Region and Sex

The median contact time with individual chimpanzees at Gangu was 2 min (mean = $10.5 \pm SE$

TABLE II. Individual Chimpanzee Contact Duration by Age/Sex Class and Forest Region

Category	<i>N</i>	Avg. (minutes)	Median (minutes)	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
Immature individuals	39	18.10	3.5	5.30

Raw Data for Tables S3 and S4.

2.7 min, $N = 75$), while that in the non-Gangu Forests was 1 min (mean = $7.1 \pm SE 1.6$, $N = 121$) (Tables II, S3 and S4). Contacts with adult females (mean = $11.5 \pm SE 3.82$ min, $N = 39$) lasted on average twice as long as those with adult males (mean = 5.4 ± 2.0 min, $N = 35$). Interestingly, contacts with individual males lasted notably longer at Gangu (mean = $9.9 \pm SE 3.7$ min, $N = 18$) than at non-Gangu locations (mean = $0.67 \pm SE 0.26$ min, $N = 17$). Non-Gangu males almost always fled the contact site immediately. Unexpectedly, adult females showed the opposite pattern between regions. Contacts with immature individuals of both sexes lasted an average of $18.1 \pm SE 5.3$ min (median = 3.5, $N = 39$; Table S3). Juvenile females showed particularly long contact durations independent of forest region (mean = $57 \pm SE 23.4$ min, median = 49.5, $N = 6$). We were unable to identify the sex of the remaining juveniles.

Individual First Reactions to Observers

The majority of first reactions of individual chimpanzees to observers were retreats, with the apes either fleeing immediately (within 1 min) or retreating stealthily (Table III). The first reactions of the chimpanzees clearly differed between Gangu and non-Gangu, with the Gangu chimpanzees nearly five times more likely to show curious reactions and almost twice less likely to flee than in other forests. First encounters in which the chimpanzees neither fled nor hid accounted for nearly half of the reactions at Gangu, while in non-Gangu Forests, the percentage was much lower.

Considering first reactions to observers by age/sex category (Table S5), juveniles and subadults were the most likely to show a curious response, and

the least likely to depart. Adult males were more likely to flee than any other age/sex class (almost always their reaction in the non-Gangu Forests), but in the Gangu Forest, they were also more likely to show curiosity than adult females.

Adult males in the Gangu Forest were more likely to show curious reactions (38.9%) to the observers than were adult females (25%). 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 at Gangu (43.8%). Juveniles (25% in the case of females and 81.8% in the case of unidentified individuals) and subadults (50%) were most likely to show curiosity

In non-Gangu Forests, curiosity as a first reaction was very rare in any category except for subadults (75%). A majority of adult male and nearly half of adult female first reactions involved immediate flight or stealthy retreat (88.2% and 43.6%, respectively).

Total Individual Reactions to Observers Per Contact

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, the chimpanzees displayed curiosity, compared to only 11.6% in non-Gangu Forest contacts.

Although immediate departure reactions (stealthy retreat and flight) were shown to a nearly equal degree in the majority of contacts of Gangu and non-Gangu, the pattern was otherwise similar to that found for first reactions. Nonflight reactions were nearly twice as common at Gangu (98.7%) than in non-Gangu Forests (57.8%).

For first reactions and total reactions of chimpanzees to observers, we also calculated for each response category the relative frequency of that response at Gangu and elsewhere; (Gangu minus non-Gangu) divided by (Gangu plus non-Gangu). This index ranges from +1 (exclusively observed at Gangu) to -1 (never observed at Gangu), and shows high levels of curiosity and other nonflight reactions and low levels of flight (Gangu at Fig. 1). Although more common at Gangu than elsewhere, aggression was rare, and appeared only as a secondary reaction.

Juvenile and subadult apes were much more likely to show curious reactions to the observers than adults (Table S6). Adult males were more likely to flee immediately than any other age/sex category (51.4%). Most chimpanzees that were not adult males would eventually end the contact with a stealthy retreat.

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,

TABLE III. Reactions of Chimpanzees to Contacts in the Gangu ($N = 75$) and non-Gangu Forests ($N = 121$), and in All Forests ($N = 196$)

Reaction type	Percentage of first reactions/Percentage of total reactions		
	Gangu	Non-Gangu	All forests
Curious (1)	34.7/42.7	7.4/11.6	17.9/23.5
Aggressive approach (2)	0	0.8/0.8	0.5/0.5
Aggressive display (3)	0/4.0	0/0.8	0/2.0
Soft vocalizations (4)	0	0/0.8	0/0.5
Loud vocalizations (5)	2.7/12.0	5.0/12.4	4.1/12.3
Ignore (6)	6.7/12.0	4.1/5.8	5.1/8.2
Ambiguous approach (7)	0	0/2.5	0/1.5
Hide (8)	20.0/28.0	18.2/23.1	18.9/25.5
Stealthy retreat (9)	21.3/70.7	25.6/45.5	24.0/55.1
Flee (10)	14.7/22.7	38.8/47.1	29.6/37.8
Non-flight reactions (1–8 combined)	64.0/98.7	35.5/57.8	46.5/74
Immediate departure reactions (9 and 10 combined)	36.0/93.4	64.4/92.6	53.6/92.9

The first number in each column represents the first reaction; the second represents total reactions. Note that more than one reaction was possible per contact, therefore total reactions do not equal 100%.

except for the subadults. 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.

Contact Duration by Forest Region

We now consider group contacts with chimpanzees (including “groups” made up of only one chimpanzee). The average duration of the 73 group contacts was $15.24 \pm \text{SE } 3.28$ min with a median of 1.8 [Gangu: $21.45 \pm \text{SE } 6.6$ (median = 3.6, $N = 28$); non-Gangu: $11.38 \pm \text{SE } 3.28$ (median = 1.6, $N = 45$) (Table S3)].

Previous research at Goulougo [Morgan & Sanz, 2003] and Kibale [Johns, 1996] showed that chimpanzees encountered on the ground were twice as likely to flee as those encountered in the trees. We found the same to be the case in our study (terrestrial contacts: mean duration = $3.64 \pm \text{SE } 1.58$ min, median = 0.75, $N = 12$; arboreal contacts: mean duration = $17.53 \pm \text{SE } 3.84$ min, median = 3.5, $N = 61$; one-tailed Mann–Whitney U -test: $W = 252.5$, $P = 0.046$; Table S3). Due to the low sample size of terrestrial contacts, especially at Gangu ($N = 5$), and the greater difficulty of determining when contacts had ended there (departures on the ground were less visible and less noisy than ones in the trees), we omitted those contacts from our analysis. The mean duration of arboreal contacts at Gangu was $26.02 \pm \text{SE } 7.74$ min (median = 11 min, $N = 23$), versus $12.38 \pm \text{SE } 3.89$ min (median = 1.3 min, $N = 38$) for the non-Gangu Forests, a significant difference (one-tailed Mann–Whitney U -test: $W = 305$, $P = 0.025$).

Contact Reaction Types

When considering group instead of individual contacts, there was a clear difference between the re-

actions of Gangu chimpanzees and those living in the forests closer to the roads (Figs. 2 and 3). The Gangu chimpanzees had over seven times the number of naïve contacts as non-Gangu chimpanzees (33.9% vs. 4.4% of contacts), a significant difference (Fisher’s exact test: $P = 0.01$, $N = 73$; Table S7). For all non-flight contacts (group response categories 1–3), the percentage for Gangu was 53.6 versus 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 in Figure 3 Morgan and Sanz’s [2003] findings from Goulougo and McLennan and Hill’s [2010] findings from Bulindi for comparison.

Our two westernmost contacts were with what appeared to be fully naïve chimpanzees; several of the apes approached us and examined us with curiosity, in a similar manner to the behavior typically shown by the Goulougo chimpanzees. Films of these contacts, contrasted with other Gangu contacts and “immediate departure” contacts closer to the road, are available at <http://www.wasmoethwildlife.org/folder2004-2005> and www.wasmoethwildlife.org/folder2006-2007.

Human Evidence, Forest Regions, and Contact Reaction Types

In the Gangu Forest, we encountered very few signs of human presence, 0.07 items per kilometer walked (Table S2). This was only one-tenth the average encounter rate of human signs in all other forests (0.71), a significant difference ($\chi^2 = 160.97$, $df = 1$, $P \leq 0.001$, $N = 1,072$). No cartridges or snares were found in the Gangu Forest. Although the Gangu and Camp Louis Forests did not differ significantly in their low human evidence encounter rates ($\chi^2 = 1.2304$, $df = 1$, $P = 0.267$, $N = 105$), 15 of the 22 items of Gangu Forest human evidence (68%), including

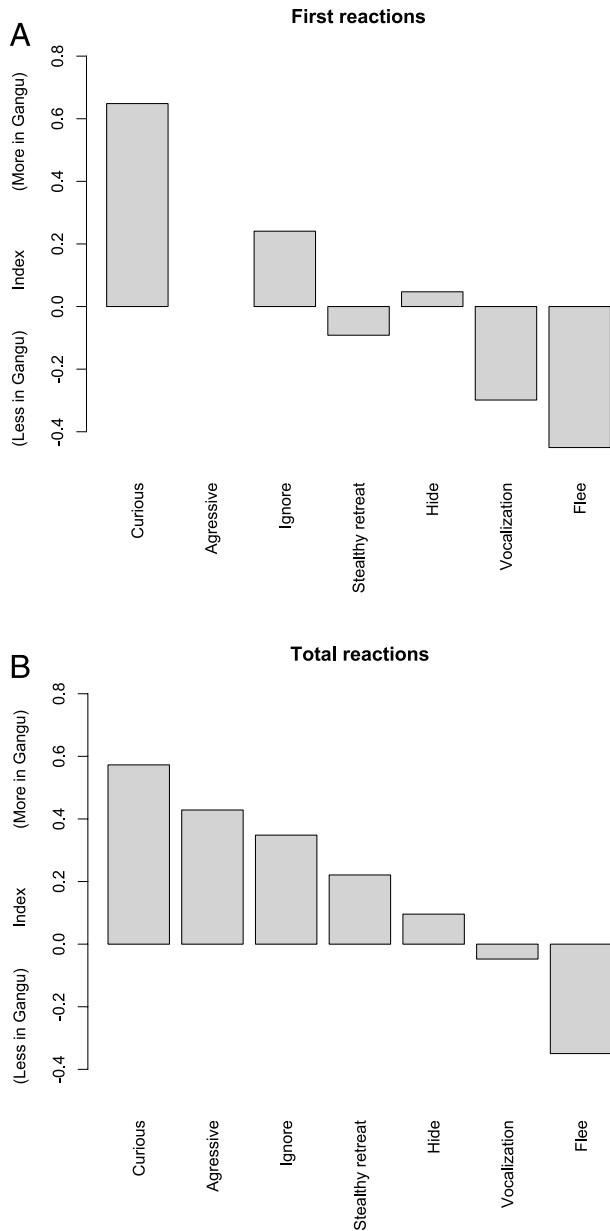


Fig. 1. Index showing relative frequency of (A) first reactions and (B) total reactions of individual chimpanzees to observers, compared between Gangu and non-Gangu Forests: (Gangu minus non-Gangu) divided by (Gangu plus non-Gangu). The index ranges from +1 (exclusively observed at Gangu) to -1 (never observed at Gangu).

all of the abandoned gold pits, were found within 5 km of the east edge of the forest, between the west bank of the Bo River and the savanna [Hicks, 2010]. We walked 79 km in the Gangu Forest between 10 and 20 km west of its eastern edge and found not a single item of human evidence; thus, the Gangu Forest interior can be considered virtually untouched by humans. Because human presence decreased drastically in an east-west gradient in the Gangu Forest (i.e. with increasing distance from the road), with no human evidence found in the far west, we divided

the region into three sections (Table S8): Gangu East (within 5 km west of the forest's east edge), Gangu Central (between 5 and 10 km west of the east edge), and Gangu West (>10 km west of the east edge). The human evidence counts per kilometer walked differed significantly in this east-west gradient with no human evidence found in the far west (Fisher's exact test: $P = 0.002$, $N = 105$).

Because human evidence encounter rates differed between forest regions in the Camp Louis-Gangu region, we analyzed whether percentage of immediate departure contacts increased depending on the amount of human evidence encountered per kilometer walked (Fig. 4 and Table S8). We found a significant difference in contact types per region, with fewer immediate departure contacts in the west (Fisher's exact test: $P < 0.001$, $N = 73$; Fig. 2; Table S8). The same result was found for the percentage of naïve contacts (Fisher's exact test: $P = 0.01$, $N = 73$). The Spearman's rank correlation coefficient ρ between items of human evidence per kilometer and percentage of immediate departure contacts was 0.8. Although the correlation was not significant and showed only a trend ($S = 2$, $P = 0.17$, $N = 4$), we must be cautious with this result due to the low sample size.

Influence of Forest Type and Party Size

We investigated whether forest type had an effect on contact (group) reaction type. No significant difference was found between contact reaction types in open, mixed, or dense forest, either when considering naïve (category 1) versus nonnaïve (categories 2–4) reactions (Fisher's exact test: $P = 1$, $N = 71$) or immediate departure versus nonflight 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). This was contrary to the situation at Bulindi, where chimpanzees were more likely to charge observers in dense forest and forest clearings [McLennan & Hill, 2010].

We also 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 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 contacts were with only one individual. There was no significant difference in contact reaction types between small and large parties ($\chi^2 = 0.322$, $df = 1$, $P = 0.57$, $N = 73$), nor for contacts with one individual versus >1 ($\chi^2 = 0.0028$, $df = 1$, $P = 0.96$, $N = 73$).

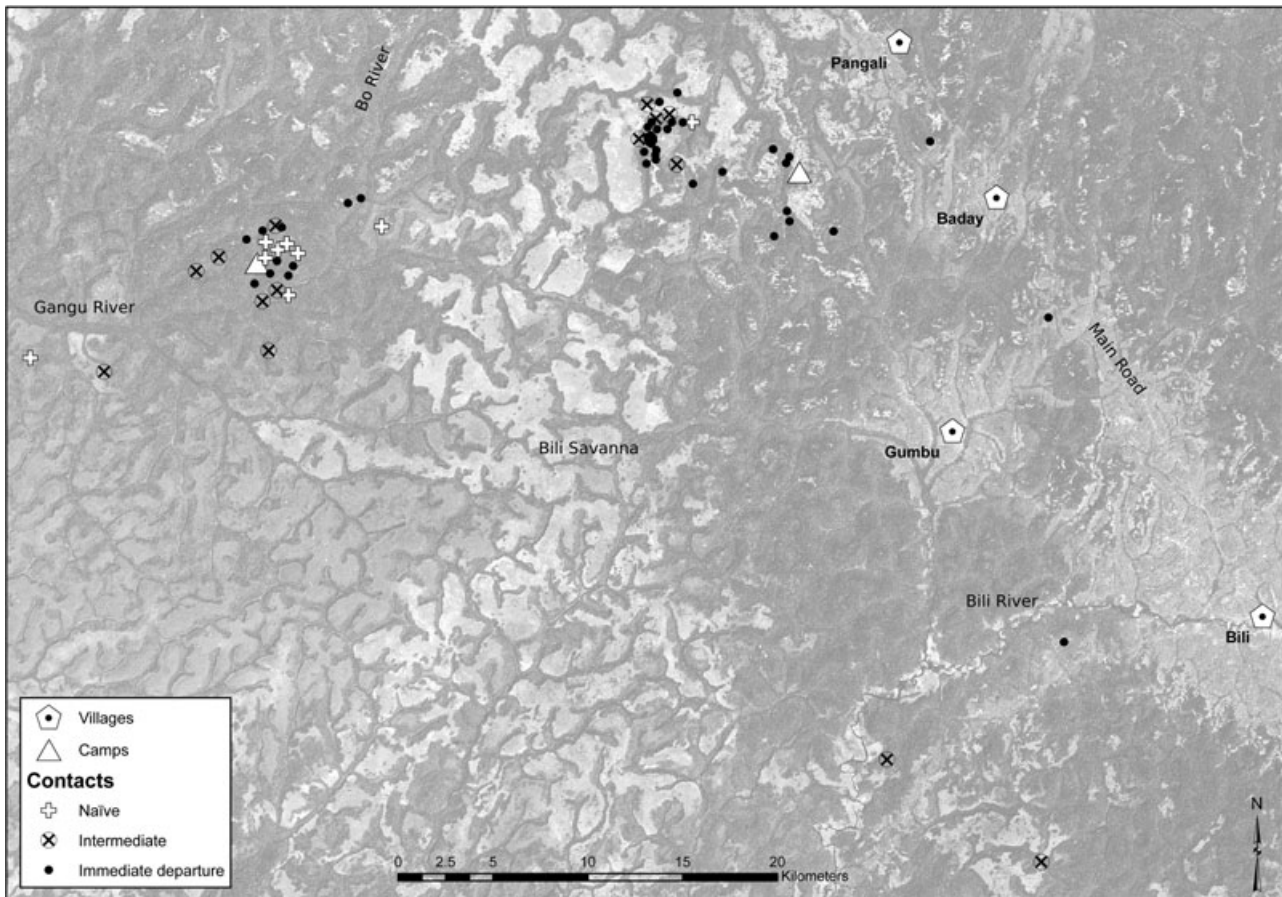


Fig. 2. Contact reaction types across the study area, based on the majority of chimpanzee reactions per contact. Contact reaction types were split into three categories: naïve, intermediate (consisting of ignore and nervous), and immediate departure. The Landsat ETM+ image files used to construct the map date from 2000 and were downloaded from GLCF at <http://glcf.umiacs.umd.edu>. Only the core study area is shown on the map; the Zapay and South Uele survey areas fall outside of the area represented (see maps in Hicks [2010]). Courtesy of Guido van Reenen and Sipko Hensen (University of Amsterdam).

Cross-Site Comparisons

We have added our results and those from Bulindi [McLennan & Hill, 2010] to Morgan and Sanz's [2003] cross-site comparison of first reactions of individual chimpanzees to observers between the Goulougo, Lopé, and Kibale study sites (Table IV). Overall, curious reactions were much more common at Bili than at Lopé or Kibale, but were not nearly as common as at Goulougo. 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 Goulougo. Gangu, along with Kibale, also shows an intermediate frequency of "departure" contacts—much lower than at Lopé but higher than at Goulougo. Bulindi chimpanzees rarely fled humans, either ignoring them or displaying elevated levels of monitoring and aggression toward them. McLennan and Hill [2010] stress, however, that the "monitor" behavior shown at such high levels by the Bulindi chimpanzees did not represent a naïve condition, as these chimpanzees were not isolated and had

regularly encountered humans in the recent past. Interestingly, Kibale and Bulindi stand out from the other populations with high levels of aggression displayed at observers. The Bili chimpanzees were more likely to remain at the site but hide than any of the other populations.

DISCUSSION

In this study, we tested the hypothesis that chimpanzees living in remote forests would be less likely to flee and show more curiosity toward observers than those living closer to humans. To do this, we compared the reactions of chimpanzees in the remote Gangu Forest with those living in forests closer to roads and settlements.

The results of our 2005 transect work demonstrated that the encounter rate for chimpanzee nests in the Gangu Forest was more than twice that of the Camp Louis area abutting the road [Hicks, 2010; Hicks et al., in preparation]. This difference in ape

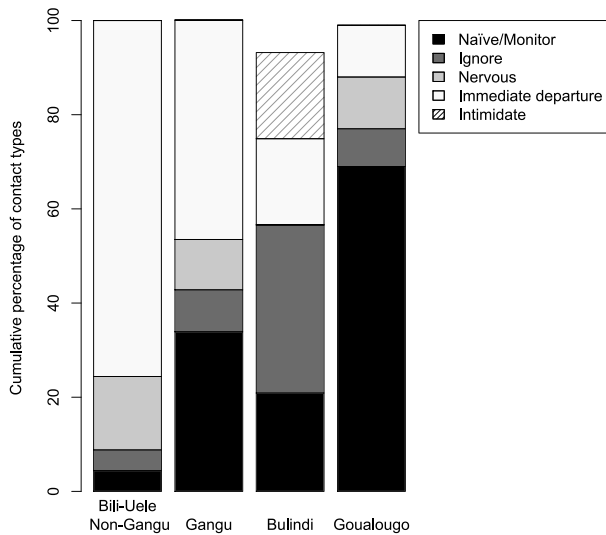


Fig. 3. Chimpanzee group contact types by forest region (cumulative percentage), based on the majority of reactions shown by the chimpanzees. At Bulindi 7% of the contacts were reported as “Undetermined” and are not plotted here. ‘Intimidate’ has been added based on the presence of this behavior at Bulindi. “Monitor” applies only to Bulindi, and probably represents a less-curious reaction than “naïve.” Goulougo: Morgan and Sanz [2003]; Bulindi: McLennan and Hill [2010]. See Table S7 for the raw data.

density appears to have been reflected in the increased number of contacts, as well as auditory observations, at Gangu [Hicks, 2010], although there may have been additional factors at 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 identical to the contact rate reported by Morgan and Sanz [2003] at Goulougo.

As predicted, arboreal contacts lasted significantly longer at Gangu than elsewhere, and the Gangu chimpanzees showed significantly more “curious” reactions and were less likely to flee. The chimpanzees most likely to flee were adult males living <20 km from the road, particularly in the Camp Louis region. These males almost always fled immediately upon seeing us, sometimes 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; males did not flee more than females at Goulougo [Morgan & Sanz, 2003]. At Kibale, the pattern was quite different: adult males were less likely than adult females to hide or flee and more likely to charge the human observer [Johns, 1996]. At Bulindi, adult males behaved aggressively toward researchers in 12.2% of first responses, while adult females never did, and

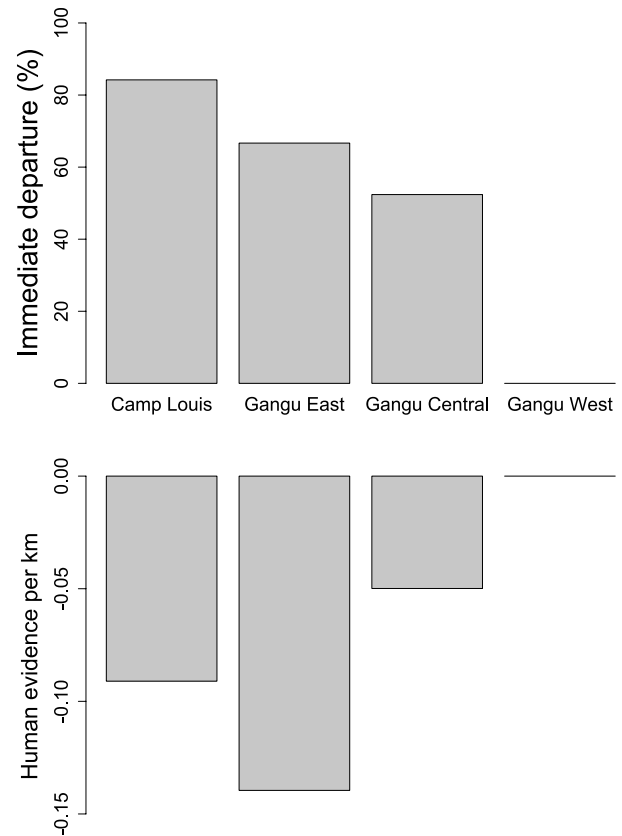


Fig. 4. A comparison of percentages of immediate departure contacts with chimpanzees and human evidence encountered per kilometer walked in four regions of the Camp Louis-Gangu region.

adult males were also less likely to retreat [McLennan & Hill, 2010].

Interactions between humans and chimpanzees appear to be quite flexible: at Bulindi and Bossou, where chimpanzees live in close association with people, but where the people do not kill them for cultural reasons, the chimpanzees have become accustomed to humans and rarely flee, but instead either ignore, monitor, and/or behave aggressively toward them [Hockings, 2009; McLennan & Hill, 2010]. Over the course of the study at Bili-Uele, we were never charged by a chimpanzee, and heard no reports of chimpanzees attacking villagers, despite some reports of crop-raiding by the apes.

On the face of it, the reactions of the Bulindi and Bossou chimpanzees to humans contradict our hypothesis that chimpanzees living closer to roads and settlements should react more fearfully to humans. Two possible and nonmutually exclusive explanations for the relative fearlessness of those chimpanzees compared to other populations living near roads and villages are as follows:

- (1) The Bulindi and Bossou chimpanzees, unlike those at Bili and elsewhere, are restricted to tiny

TABLE IV. Comparison of Individual Reactions (%) Among Field Sites

Reaction type	Lopé Reserve (<i>N</i> = 153)%	Kibale Forest (<i>N</i> = 436)%	Bulindi (<i>N</i> = 334)%	Goulougo 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) ^a (or monitoring)	1.0	6.7	32.9	84.0	17.9	34.7	7.4
Ignore (6)	3.0	25.8	49.1	5.0	5.1	6.7	4.1
Hide (8)	5.0	6.9	1.2	7.6	18.9	20.0	18.2
Depart (7, 9, 10)	74.0	35.6	10.0	3.5	53.6	36.0	64.4
Flight (10)	39.0	25.5	1.2	1.4	29.6	14.7	38.8
Stealthy retreat (9)	10.0	9.6	9.0	2.0	24.0	21.3	25.6
Approach/Await another (7)	25.0	0.5	n/a	n/a	0	0	0
Charge (aggressive display) (2–3) ^a	1.0	13.1	6.7	0	0.5	0	0.8
Loud vocalizations (5)	8.0	7.1	n/a	n/a	4.1	2.7	5.0
Soft vocalizations (4)	8.0	4.8	n/a	n/a	0	0	0

n/a = Behaviors were not separated out from broader categories. Kibale reactions based on Johns [1996]; Lope based on Tutin and Fernandez [1991]; Bulindi based on McLennan and Hill [2010]; Goulougo based on Morgan & Sanz [2003].

^aAt Bulindi, the equivalent category to curiosity is “monitoring,” although McLennan and Hill [2010] stress that it is a less curious response than at Goulougo.

^bAt Bulindi, the equivalent category to “charge/aggressive display” is “threaten.”

remnants of forests in the midst of a sea of cultivation, and thus have nowhere to flee. In addition, their dependence on human cultivars may force them into interacting with humans, which they would normally avoid.

- (2) The Bulindi and Bossou chimpanzees are protected from killing (but not harassment) by local taboos. The chimpanzees at these sites appear to be on more “equal footing” during encounters with humans than they are in areas where humans hunt them, and thus more likely to risk confrontation.

One factor that might have contributed to the difference in behavior between the Gangu and non-Gangu chimpanzees is a difference in forest type between the two areas. Near the road there was much seasonally burnt savanna, savanna woodland, and dense regenerating gallery forest. In this habitat, visibility was limited for the researchers and presumably for the chimpanzees, possibly contributing 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 (with two exceptions at Gangu: an adult male approached us terrestrially to within 8 m, where he climbed 2 m up into a sapling and sat observing us; on another occasion, two juveniles climbed into a tree 3 m above the ground to watch us

after the adults fled). The same was the case at Goulougo [Morgan & Sanz, 2003] and Kibale [Johns, 1996], where the chimpanzees were twice as likely to depart immediately when contacted on the ground, although at Kibale, some chimpanzees also charged during terrestrial encounters. At Bulindi [McLennan & Hill, 2010], arboreal chimpanzees were more likely to ignore the researchers, whereas when encountered on the ground, they were more likely to show the behaviors monitor, threaten, or retreat.

The possibility that the fearful behavior shown by the Camp Louis chimpanzees might have been caused by previous encounters in the early 2000s with the research teams of Shelly Williams and Karl Ammann is addressed in Hicks [2010]. We consider it unlikely that the small number of contacts with these teams would have led to the chimpanzees reacting with such uniformly fearful behavior when meeting humans, and chimpanzees in other localities near roads not previously visited by researchers showed the same fearful reaction. According to our local field assistants, it was past hunting of the Camp Louis chimpanzees by the villagers of Gumbu that led to their panicked reactions.

In many regions inhabited by chimpanzees where we also found high encounter rates of human evidence, we failed to encounter the apes because their calling rates were so low (Table S1) [Hicks, 2010; Hicks et al., in preparation]. Because we were unable to achieve contacts in these forests to include in our analyses, it is likely that we are underestimating the effect that proximity to humans and human hunting has on chimpanzee behavior.

In order to investigate whether or not chimpanzee behavior correlated with encounter rate of human evidence, we compared four forest regions in the Camp Louis-Gangu region on an east-west gradient. Although we found that both human encounter rate and percentage of immediate departure contact types decreased significantly with increasing distance from the road (and percentage of naïve contacts increased), we found only a trend in the relationship between these two factors, which is likely explained by the small number of survey regions.

Our findings place the reactions of the Bili chimpanzees between the completely naïve behavior of the chimpanzees of the Goulougo Triangle (a site which was in the past inaccessible to humans) and the fearful behavior shown by the chimpanzees at more accessible sites such as Lopé and Kibale. Of the study sites sampled, the behavior of the chimpanzees we encountered in the Gangu Forest was the closest to matching the naïve behavior of the Goulougo chimpanzees. On the other hand, even the Gangu contacts had a considerably shorter average duration than contacts at Goulougo ($101.0 \pm \text{SE } 6.44$ min, $N = 218$) [Morgan & Sanz, 2003], Ngotto ($42.2 \pm \text{SE } 8.45$ min, $N = 8$) [Hicks et al., 2009], and Bulindi ($50 \pm \text{SE } 5.78$ min, $N = 115$) [McLennan & Hill, 2010]. The average Gangu contact duration was most similar to that of Gashaka ($27 \pm \text{SE } 4$ min, $N = 88$) [Sommer et al., 2004].

Our results provide additional evidence that chimpanzees adapt their behavior to frequent negative encounters with humans as do other primate species [spider monkeys: Van Roosmalen, 2008; vervet monkeys: Kavanagh, 1980; western lowland gorillas: Hicks et al., 2009]. In addition to the behaviors documented in this article, we found evidence that the Bili-Uele chimpanzees reduce their call rates in areas where they regularly encounter humans [Hicks, 2010; Hicks et al., in preparation]. The relationship between humans and chimpanzees in our study region can be contrasted with other patterns of primate/human interactions, in areas where primates are protected to some degree from persecution by human cultural tolerance: although sometimes killed in retaliation for crop-raiding, Japanese macaques are partially protected by cultural taboos against killing them, and thus often show a lack of fear around humans and even aggression toward them, particularly where they are provisioned [Hill & Webber, 2010; Knight, 2003]. In Bali, temple macaques (*M. fascicularis*) interact on a daily basis with humans with little conflict [Fuentes, 2010].

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

there are ideal subjects for research, as they are easy to locate and observe. It is our hope that this study can be used to mobilize the government of DRC to enforce the protected status of the Bili area, which was invaded by gold miners in June 2007 [Hicks et al., 2010]. In addition, we hope to encourage researchers to seek out, study, and protect the remaining areas of untouched African wilderness before they are discovered and exploited by more destructive interests.

ACKNOWLEDGMENTS

We thank the Ministre de l'Environnement of the DRC for granting us permission to work in the country, and Chief Zelesi Yakisi for inviting us to set up a field site in his collectivity. Jeroen Swinkels, Ligada Faustin, Laura Darby, Adam Singh, Jan van Hooft, Karl Ammann, Richard Wrangham, Jan Sevink, Kisangola Polycarpe, and Vincent Nijman each made invaluable contributions to the research project. The map in Figure 2 was made with Guido van Reenen and Sipko Hensen at the University of Amsterdam GIS lab. Andrew Fowler, Deborah Moore, Cyril Grueter, and Nicole Seiler provided useful comments on the manuscript. Some of the results of this article were originally published as Chapter 2 of Hicks [2010].

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