



Fatal Chimpanzee Attack in Loango National Park, Gabon

Christophe Boesch · Josephine Head · Nikki Tagg ·
Mimi Arandjelovic · Linda Vigilant ·
Martha M. Robbins

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Abstract In some populations, chimpanzees engage in lethal aggression within and between social units. We report a fatal attack on an adult male chimpanzee at a new research site in Loango National Park, Gabon. We found a fresh corpse of an adult male chimpanzee only a few hundred meters from the research camp, after noting numerous vocalizations and chimpanzee movements the previous evening. Previous contacts with chimpanzees and fresh tracks in the area around the corpse suggest that 2 communities of chimpanzees range where the attack occurred and that members of the neighboring community killed the chimpanzee. To support the conclusion, we conducted genetic analysis for 13 Y-chromosome loci and 9 microsatellite loci of fecal samples from the dead individual, 5 possible attackers, and 2 members of the other community. Though we cannot exclude the possibility of an intracommunity killing, the combined observational and genetic evidence suggest an intercommunity attack. The case study adds to the growing evidence that intercommunity killings are a rare but widespread phenomenon among chimpanzees and not an artifact of human provisioning or habituation.

Keywords chimpanzees · fatal attack · gabon · intergroup conflict

Introduction

Chimpanzee social groups, or communities, throughout Africa are comprised of many adult males living with many adult females. Chimpanzees defend large territories and aggressively expel any male intruder while sometimes accepting female newcomers into a community (Boesch and Boesch-Achermann 2000). Lethal

C. Boesch (✉) · J. Head · N. Tagg · M. Arandjelovic · L. Vigilant · M. M. Robbins
Max Planck Institute for Evolutionary Anthropology, Leipzig O4103, Germany
e-mail: boesch@eva.mpg.de

aggression by chimpanzees occurs within and between social communities and has led to much discussion about its causes and function.

Goodall *et al.* (1979) observed conspecific killing of adults during territorial encounters in Gombe National Park, Tanzania, followed by more observations in the same population (Wilson *et al.* 2004). They also occurred in Mahale National Park, Tanzania (Nishida *et al.* 1985), and Kanyawara (Wilson and Wrangham 2003) and Ngogo (Watts *et al.* 2006) communities of the Kibale National Park, Uganda. However, no killing of adult males occurred among chimpanzees of the Tai National Park, Côte d'Ivoire (Boesch and Boesch-Achermann, 2000; Herlinger *et al.* 2001) during >16 yr of constant observations or among Budongo chimpanzees during 13 yr of study (Reynolds 2005). In addition to adults, infants comprised a large proportion of the victims of intercommunity killings (Goodall 1986; Muller and Mitani 2005; Nishida *et al.* 1985).

The first records of intracommunity killing of conspecifics among chimpanzees involved infants (Goodall *et al.* 1979; Hamai *et al.* 1992; Reynolds 2005; Suzuki 1971; Watts and Mitani 2000). More recently, researchers have documented 3 instances of intracommunity killings of adult males by group members (Budongo: Fawcett and Muhumuza 2000; Ngogo: Watts 2004; Mahale: Nishida 1996). Given the high level of cooperation among males of the same community for intercommunity defense, such killings seem puzzling. The killings may occur when lower-ranking males face high levels of mating competition (Fawcett and Muhumuza 2000) or when they are poorly integrated socially and pose a threat to higher-ranking males (Watts 2004).

Among chimpanzees, lethal aggression by male macrocoalitions may be a precursor of human warfare and therefore is important for our understanding of the origins of such activities in humans (Dennen 1995; Manson and Wrangham 1991; Wrangham and Peterson 1996). However, some authors argued that lethal aggression among chimpanzees is an artifact of food provisioning, as in Gombe and Mahale, or from the stress of human presence and observation, and that in reality intragroup interactions in chimpanzees are peaceful (Clark 2002; Power 1991). The argument is based on the absence of such killings in Tai chimpanzees and in early observations from Budongo forest (Reynolds and Reynolds 1965). More generally, the striking differences in the rate of lethal intercommunity attacks in different chimpanzee populations have raised the question of the generality of such violence within our nearest living relative.

We report an inferred lethal attack on a chimpanzee at a new study site within Loango National Park, Gabon. Because the attack involved unhabituated chimpanzees and occurred in the absence of any observer, we cannot rule out the possibility of an intracommunity attack. However, we combined indirect observations with genetic analysis of feces near the kill site to test our proposition that this was an intercommunity killing. In male philopatric species such as chimpanzees, males of one community should have more similar Y chromosome haplotypes than those of males of different communities (Erler *et al.* 2004; Eriksson *et al.* 2006). Such a lethal attack in unhabituated chimpanzees directly addresses the question of human influence on chimpanzee lethal violence and how widespread such violence may be.

Methods

Behavioral Observations

We started a new project in the central sector of Loango National Park, Gabon, in February 2005, with the aim to habituate chimpanzees and gorillas in this mixed habitat that includes tropical rain forest, coastal forest, swamps, and savanna. Two research teams, each comprising 1 researcher (Josephine Head and Nikki Tagg) and 1 field assistant, work in an area of *ca.* 20 km², bordered on the west by the Atlantic Ocean and on the east by a lagoon (Fig. 1). The research camp is situated on a strip of savanna at the western edge of the zone. At the time of the killing (August 2005),

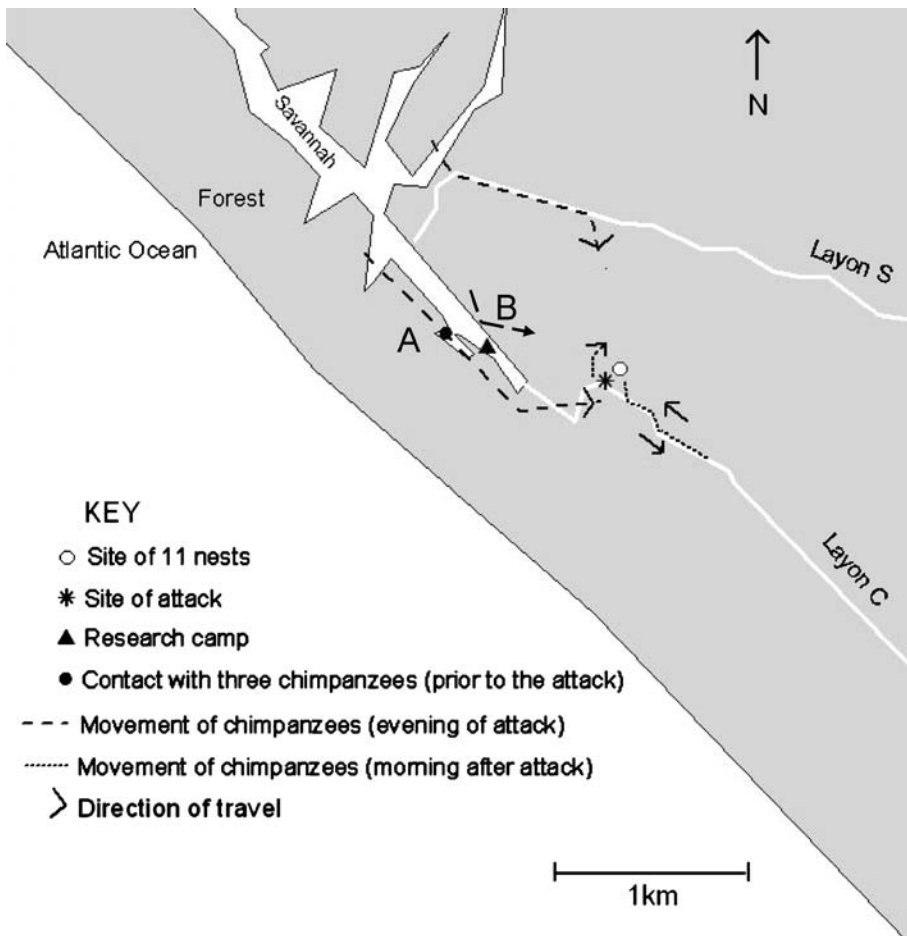


Fig. 1 Map of chimpanzee movements in relation to the scene of the chimpanzee attack.

all apes in the research area were unhabituated to human observers and had been contacted opportunistically only for short periods of time.

Initial contacts with the chimpanzees in the first 6 mo of the project ($n=112$) led us to believe that there may be 2 chimpanzee communities in the area. Chimpanzees in the northern portion of the site displayed fear responses such as alarm calling and fleeing us once spotted, whereas those contacted in the eastern and southern sector displayed much less fear; they rarely alarm called and showed regular curiosity toward us, and walked away from the contact site only after several min (average contact duration = 4.5 min). The suspected range of the northern community borders a small village within the park on the lagoon, which may account for the northern chimpanzees' fear of humans, whereas the southern-ranging naïve chimpanzees may never encounter people because their range appears to be bordered by large swamps to the north and west and there is no other sign of human disturbance. Researchers have more recently focused on the southern group. Preliminary observations suggested that the community comprises ≥ 50 chimpanzees because research teams have seen parties and fresh nest sites with as many as 30 individuals.

Genetic Analysis

To test whether 2 different communities were really present, we collected feces near and around the site of the attack, including a sample from the dead individual, in addition to fecal samples collected during routine observations as part of the overall study. Because we suspected that the attackers were from the northern community, we expected them to share a similar Y haplotype while those of the southern community and that of the dead individual would be distinctively different. We therefore collected 11 fecal samples for DNA analysis from the presumed attackers from night nests near the dead male. We had previously collected 17 fecal samples between February and June 2005 from the presumed southern range of the Loango study site. We first immersed fecal samples in ethanol for *ca.* 24 h and then dried and stored them on silica beads per Nsubuga *et al.* (2004).

We extracted 100-mg samples of dried feces via the Qiagen QIAamp DNA Stool kit per Nsubuga *et al.* (2004). We estimated the amount of amplifiable genomic DNA in the extracts via a quantitative polymerase chain reaction (PCR) assay (Morin *et al.* 2001). Arandjelovic and Vigilant genotyped all extracts at 13 Y-chromosome microsatellite loci, originally developed in humans but known to amplify in bonobos (Eriksson *et al.* 2006) and chimpanzees (Erler *et al.* 2004; H. Siedel and K. Langergraber, *pers. comm.*): DYS502, DYS510, DYS517, DYS520, DYS533, DYS562, DYS588, DYS612, DYS630, DYS469, and DYS632 (Erler *et al.*, 2004); DYS439 (Gusmão *et al.* 2002a); and DYS392 (Gusmão *et al.* 2002b). We assumed samples with >10 pg/ μ l of DNA that did not amplify at 3 Y-chromosome loci were female and did not consider them in further analyses.

If we obtained identical Y chromosome haplotypes from different samples, we then genotyped extracts from the samples at autosomal microsatellite loci known to be variable in chimpanzees to see if they were from the same or different individuals (D2s1326, D2s1329, D5s1470, D7s817, D7s2204, D9s910, D11s2002, D12s66, and vWF; Bradley *et al.* 2000; Lukas *et al.* 2005; Vigilant *et al.* 2001). To control for allelic dropout, we

performed multiple repetitions of each extract according to the guidelines in Morin *et al.* (2001). We considered samples to be from different individuals when they differed at 3 autosomal microsatellite loci (Eriksson *et al.* 2006).

We performed PCR amplifications for the Y-chromosome microsatellites per Eriksson *et al.* (2006; primer annealing temperatures and sequences are also contained therein). We performed PCR amplifications for the autosomal microsatellites per Bradley *et al.* (2000). In both cases, we used fluorescently labeled forward primers (HEX, 6-FAM, or NED) so that we could subsequently determine PCR fragment length via capillary electrophoresis (ABI310, Applied Biosystems) relative to an internal size standard (HD400) via Gene Mapper (Applied Biosystems).

Results

Sequence of Events

August 10, 2005 At 1718 h, we heard chimpanzee vocalizations *ca.* 500 m northwest of the camp. As we infrequently heard chimpanzee vocalizations north of the camp, we quickly advanced northwest to locate them, and at 1729 h, 400 m northwest of camp, made a very brief contact (<1 min) with 3 individuals on the ground that ran immediately and silently away to the southeast (point A in Fig. 1). We collected no information on their ages or sex.

At 1815 h a second party of 3 chimpanzees exited the savanna 200 m north of the camp, on the eastern side of the savannah, and after 2 min reentered the forest and continued southeast inside the forest belt (point B in Fig. 1). At the same time, we heard vocalizations again from the second party of chimpanzees to the southeast. We subsequently heard the 3 chimpanzees walking in the forest past the camp in a southeasterly direction and vocalizing twice.

From 1815 h to 1900 h, we heard vocalizations 300 m southeast of the camp, almost continuously, and sporadically after that until 2000 h (attack point in Fig. 1). Vocalizations included pant-hoots and screams, but were not remarkable in any way other than their duration. We noted no alarm call, such as waa-barks.

August 11, 2005 At 0545 h, we heard a short burst of pant-hoots from the camp coming from the same southeasterly location as the vocalizations from the previous night, and a research team advanced there soon after 0600 h to discover the corpse of an adult male chimpanzee, the attack victim. While there, the team contacted a group of chimpanzees that had apparently arrived to view the corpse. From 0600 to 0657 h, we saw a total of 9 chimpanzees, including ≥ 2 adult males and 1 adult female. No infant or juvenile was present. Over 20 min, each chimpanzee approached from the southeast and headed directly toward the corpse. On arrival, researchers saw 1 adult male chimpanzee resting ≤ 10 m of the corpse, he immediately ran away on noticing the observers. Another adult male advanced toward the corpse 2 min later, and sat by it for 1 min, before becoming aware of the researchers and running away. The other chimpanzees saw the researchers before arriving at the corpse and immediately ran away. All chimpanzees saw the researchers and departed silently in a northeast direction after the researchers tongue clacked to make their presence noticeable. We

believe that this group of chimpanzees was not from the southern zone, because their reaction to the presence of the researchers was more fearful than that of the southern chimpanzees.

Further investigations revealed fresh tracks of chimpanzees on the savanna over 1 km north of the attack site, heading south, suggesting that the 3 chimpanzees moving southeast had come down from the north (see point A in Fig. 1). To the east of the savanna, parallel to the movements of the 3 chimpanzees, there were additional tracks heading southeast and feces along the Layon S trail (Fig. 1). The feces were fresh and had been slightly affected by the rains during the night, indicating that they were deposited the previous afternoon. The tracks indicated ≥ 5 chimpanzees and were the same age as the feces. All tracks were oriented southward, clearly indicating the direction of travel. The chimpanzees probably moved silently and quickly because we heard no vocalization at the research camp from the north and found no feeding signs along the trail, into the southern zone of the research area. We heard chimpanzee vocalizations southeast of camp.

Additional investigation revealed >15 chimpanzee feces along Layon C (Fig. 1) near the attack site, continuing 500 m further to the southeast into the southern territory. The feces were fresh, certainly having been made early that morning. A chimpanzee nest site from the previous night, evidenced by the presence of fresh nests and feces, was <50 m northeast of the attack site. Extensive searching around the site of attack revealed no other nest or sign of chimpanzees in the area from that morning or the previous night. We propose that this was the nest site of the attacking chimpanzees because of the proximity to the attack site and number of nests. We had noted very few nest sites with such a large number of nests in the area. Combined, our observations suggest that the chimpanzees rose early (vocalizations heard at 0545 h) to advance further south into the southern zone, before returning to the corpse and then heading back north of the research area.

The Attack Victim

The dead chimpanzee was an adult male laying supine with his forelimbs and hind limbs spread. He had suffered multiple injuries on his exposed ventrum (Fig. 2). His testicles and penis and much of the skin from the groin and right thigh had been torn off, and both testicles were 20 m from the corpse. His throat was torn open, leaving a hole $\geq 15 \times 10$ cm. There were 7 large lacerations to the chest and stomach, exposing internal organs and several smaller puncture wounds. There were injuries on the back of the right thigh and both calves and on the insides of both forelimbs. There were also wounds on hands and feet, ears, right cheek, left eye, lips, and mouth, and the lower jawbone was completely exposed. The right eye was swollen closed.

Examinations of the site of attack suggested that the attack began 20 m from the location of the corpse. Many broken shrubs and much trampled vegetation and his testicles, small pieces of intestines, four chunks of flesh, and a clump of hair were within an area of ≤ 100 m² of the corpse. A path of flattened vegetation and trail of intestines linked the area to the corpse, suggesting that the victim had been dragged during the attack. The position of the corpse and the lack of any injury on his back suggest that he had been immobilized during the attack and had not moved since, presumably dying soon after receiving the massive injury to his throat.

Fig. 2 Fatally attacked chimpanzee. Note the severe injuries to the groin and torso.



Genetic Analysis

We analyzed 28 fecal samples, 7 of which yielded too little DNA for reliable genotyping. Of the remaining 21, 12 were from females and 9 from males. Although we genotyped 13 Y-chromosome microsatellite loci from each of the male extracts, only 3 are polymorphic (DYS533, **DYS612** and **DYS562**). The polymorphisms defined 1 haplotype in the attacker group and 2 haplotypes in the southern group. The dead male exhibited 1 haplotype of the southern group (Table 1).

According to autosomal microsatellite analysis, the attackers comprised 5 unique individuals, all of which shared the same Y-chromosome haplotype. The samples

Table 1 Loango chimpanzee Y-chromosome microsatellite haplotypes from the suspected attacker chimpanzees, the southern individuals, and the dead male

Haplotype		Polymorphic loci													
Identity/ Location	Hap ID	<i>n</i>	DYS 533	DYS 612	DYS 562	DYS 588	DYS 517	DYS 630	DYS 510	DYS 632	DYS 439	DYS 502	DYS 520	DYS 469	DYS 392
Attackers	A	5	196	186	178	155	207	157	235	142	227	221	246	203	124
Southern	B	1	196	189	174	155	207	157	235	142	227	221	246	203	124
Southern	C	1	192	189	174	155	207	157	235	142	227	221	246	203	124
Dead	C	1	192	189	174	155	207	157	235	142	227	221	246	203	124

Identity/location indicates supposed identity of the samples (attackers, individuals from the southern community, or the dead male). Hap ID indicates the arbitrary designation of the haplotype. *n* is the number of unique individuals sharing the haplotype, as revealed by microsatellite genotyping. The three polymorphic Y-chromosome loci are in bold and define the 3 observed Y haplotypes. Individual genotypes at a locus are given as fragment size.

from the southern community consisted of 2 individuals, each with a different Y-chromosome haplotype that did not match that of the attacker group. The dead male and the individual from the southern group with the identical Y-chromosome haplotype differed at 6 of 9 autosomal loci and so were not the same individual. However, the fact that they share a Y-chromosome haplotype indicates that they are related through the male lineage. Because chimpanzees are a male-philopatric species, we assume no Y-chromosome haplotype sharing across communities, and the dead male could have been from the southern community. However, because we were unable to identify all the males from the southern community we cannot be certain that the attacker Y-chromosome haplotype does not also occur in the southern community, and it remains possible, though unlikely when considering the behavioral data, that the attackers and the dead male were from the same community.

Discussion

Although we did not witness the chimpanzee attack, postmortem observations and genetic evidence underpin inferences on how the chimpanzee died and whether the attack was due to intercommunity or intracommunity aggression. The only individuals present in the research area capable of inflicting the wounds on the corpse are leopards and other chimpanzees. Leopards prey on chimpanzees and eat part of their victims (Boesch 1991). The chimpanzee's corpse was undisturbed and uneaten, which is inconsistent with a leopard attack, and no sign of leopards, e.g., tracks or feces, were in the area. Instead the injuries are consistent with a chimpanzee attack: removal of the genitalia, the large opening in the throat, and the presence of many small wounds on the body (Goodall *et al.* 1979; Wrangham and Peterson 1996; Watts *et al.* 2006).

The majority of fatal chimpanzee attacks in other populations involve the victim being an adult male or an infant (Goodall *et al.* 1979; Wilson and Wrangham 2003; Watts *et al.* 2006). Researchers have described only 1 killing of an adult female chimpanzee (Goodall *et al.* 1979). The Loango victim was an adult male, further adding to the likelihood that other chimpanzees conducted the attack. Further, a large group of chimpanzees was present at the site of attack from 1803 h the night of the attack until 0718 h the following morning. We can clearly infer from observations before and after the attack that late in the afternoon before the attack, ≥ 11 chimpanzees moved quickly and silently for ≥ 1 km in a southward direction.

The killing was most likely one of intercommunity aggression. The specific behavioral reactions toward observers of all individuals that came to look at the victim in the early morning on August 11 suggest they belonged to the northern community, which is compatible with the suggestion that they were coming toward camp from the north on the previous evening. We observed no sign of the southern community during the 2 d described herein, but some members reappeared 2 d later, moving northwest from farther southeast.

However, because we had begun this study only 6 mo before the attack and did not yet fully understand details of the chimpanzee home ranges, we cannot fully exclude the possibility of the attack being a result of intracommunity aggression. To test the scenario of intercommunity aggression, we genetically tested samples from

the attackers, the victim, and individuals that were very likely southern group members. The Y-chromosome results are compatible with intercommunity aggression, because the victim did not share a haplotype with 5 of the possible male attackers presumed to be from the northern community, but shared 1 haplotype with a member of the southern community. Because we did not sample all males from the 2 communities, alternative explanations are possible. However, behavioral observations, analysis of fresh tracks, and genetic sampling support a common scenario: the intercommunity killing of a southern male by males from the northern community.

We can draw 2 general conclusions: 1) wild chimpanzees may be very aggressive even in the absence of human observers, which can lead to conspecific killings, in contradiction to the suggestion of Clark (2002) and Power (1991) and 2) wild chimpanzees resort to intercommunity killing through most of their natural range, from groups in rather open habitat to ones in the dense forest, as well as groups that are artificially provisioned, ones under regular human observation, and ones not habituated to human presence. Therefore, the behavior may not be influenced by specific ecological conditions, but instead by typical sociological factors in societies like those of chimpanzees characterized by multimale fission-fusion society (Wrangham and Peterson 1996; Watts *et al.* 2006). This view is compatible with the idea of intergroup violence in chimpanzees as a precursor to human warfare.

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References

- Boesch, C. (1991). The effect of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*, 117:220–242.
- Boesch, C., and Boesch-Achermann, H. (2000). *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution*. Oxford University Press, Oxford.
- Bradley, B. J., Boesch, C., and Vigilant, L. (2000). Identification and redesign of human microsatellite markers for genotyping wild chimpanzee (*Pan troglodytes verus*) and gorilla (*Gorilla gorilla gorilla*) DNA from feces. *Conservation Genetics*, 1:289–292.
- Clark, M. (2002). *In Search of Human Nature*. Routledge, London.
- van der Dennen, J. (1995). *The Origin of War*. Origin Press, Groningen.
- Eriksson, J., Siedel, H., Lukas, D., Kayser, M., Erler, A., Hashimoto, C., Hohmann, G., Boesch, C., and Vigilant, L. (2006). Y-chromosome analysis confirms highly sex-biased dispersal and suggests a low male effective population size in bonobos (*Pan paniscus*). *Molecular Ecology*, 15:939–949.
- Erler, A., Stoneking, M., and Kayser, M. (2004). Development of Y-chromosomal microsatellite markers for nonhuman primates. *Molecular Ecology*, 13:2921–2930.
- Fawcett, K., & Muhumuza, G. (2000). Death of a wild chimpanzee community member: possible outcome of intense sexual competition. *American Journal of Primatology*, 51:243–247.
- Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. The Belknap Press of Harvard University Press, Cambridge, MA.
- Goodall, J., Bandura, A., Bergmann, E., Busse, C., Matam, H., Mpongo, E., Pierce, A., and Riss, D. (1979). Inter-community interactions in the chimpanzee populations of the Gombe National Park. In: Hamburg, D., and McCown, E. (eds.), *The Great Apes Benjamin/Cummings*. Menlo Park, CA, pp. 13–53.

- Gusmão, L., Gonzalez-Neira, A., Alves, C., Lareu, M., Costa, S., Amorim, A., & Carracedo, A. (2002a). Chimpanzee homologous of human Y specific STRs. A comparative study and a proposal for nomenclature. *Forensic Science International*, *126*:129–136.
- Gusmão, L., Gonzalez-Neira, A., Alves, C., Sanchez-Diz, P., Dauber, E. M., Amorim, A., & Carracedo, A. (2002b). Genetic diversity of Y-specific STRs in chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *57*, 21–29.
- Hamai, M., Nishida, T., Takasaki, H., & Turner, L. (1992). New records of within-group infanticide and cannibalism in wild chimpanzees. *Primates*, *33*:151–162.
- Herbinger, I., Boesch, C., & Rothe, H. (2001). Territory characteristics among three neighbouring chimpanzee communities in the Tai National Park, Ivory Coast. *International Journal of Primatology*, *32*:143–167.
- Lukas, D., Reynolds, V., Boesch, C., & Vigilant, L. (2005). To what extent does living in a group mean living with kin? *Molecular Ecology*, *14*:2181–2196.
- Manson, J., Wrangham, R. (1991). Intergroup aggression in chimpanzees and humans. *Current Anthropology*, *32*:369–390.
- Morin, P. A., Chambers, K. E., Boesch, C., & Vigilant, L. (2001). Quantitative PCR analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). *Molecular Ecology*, *10*:1835–1844.
- Nishida, T. (1996). The death of Ntologi, the unparalleled leader of M group. *Pan Africa News* 3:4.
- Nishida, T., Hiraiwa-Hasegawa, M., Hasegawa, T., & Takahata, Y. (1985). Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. *Zeitschrift für Tierpsychologie*, *67*:284–301.
- Nsubuga, A. M., Robbins, M. M., Roeder, A., Morin, P., Boesch, C., & Vigilant, L. (2004). Factors affecting the amount of genomic DNA extracted from ape feces and the identification of an improved sample storage method. *Molecular Ecology*, *13*:2089–2094.
- Power, M. (1991). *The Egalitarians: Human and Chimpanzee*. Cambridge University Press, Cambridge.
- Reynolds, V. (2005). *The Chimpanzees of the Budongo Forest: Ecology, Behaviour and Conservation*. Oxford University Press, Oxford.
- Reynolds, V., & Reynolds, F. (1965). Chimpanzees of the Budongo Forest. In: DeVore, I. (ed.), *Primate Behavior*. Holt, Rinehart and Winston, New York, pp. 368–424.
- Suzuki, A. (1971). Carnivory and cannibalism observed among forest-living chimpanzees. *Journal of the Anthropological Society Nippon*, *79*:30–48.
- Vigilant, L. (1999). An evaluation of techniques for the extraction and amplification of DNA from naturally shed hairs. *Biological Chemistry*, *380*:1329–1331.
- Vigilant, L., Hofreiter, M., Siedel, H., and Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences of the United States of America*, *98*:12890–12895.
- Watts, D. (2004). Intracommunity coalitionary killing of an adult male chimpanzee at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, *25*:507–521.
- Watts, D., and Mitani, J. (2000). Infanticide and cannibalism by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Primates*, *41*:357–365.
- Watts, D., Muller, M., Amsler, S., Mbabazi, G. & Mitani, J. (2006). Lethal intergroup aggression by chimpanzees in the Kibale National Park, Uganda. *American Journal of Primatology*, *68*:161–180.
- Wilson, M. L., Wallauer, W. R., & Pusey, A. E. (2004). Intergroup violence in chimpanzees: New cases from Gombe National Park, Tanzania. *International Journal of Primatology*, *25*:523–550.
- Wilson, M. L., & Wrangham, R. W. (2003). Intergroup relations in chimpanzees. *Annual Review of Anthropology*, *32*:363–392.
- Wrangham, R., & Peterson, D. (1996). *Demonic Males: Apes and the Origins of Human Violence*. Houghton Mifflin, Boston.