



Intragroup Lethal Aggression in West African Chimpanzees (*Pan troglodytes verus*): Inferred Killing of a Former Alpha Male at Fongoli, Senegal

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Abstract Lethal coalitionary aggression is of significant interest to primatologists and anthropologists given its pervasiveness in human, but not nonhuman, animal societies. Chimpanzees (*Pan troglodytes*) provide the largest sample of recorded lethal coalitionary aggression in nonhuman primates, and most long-term chimpanzee study sites have recorded coalitionary killing of conspecifics. We report an inferred lethal attack by resident males on a former alpha male chimpanzee (*P. t. verus*) at Fongoli in Senegal. We describe the male's presence in the

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community, his overthrow, social peripheralization for >5 yr, and his attempt to rejoin the group as well as circumstances surrounding his death. We report attacks by multiple chimpanzees on his dead body, most frequently by a young adult male and an older female. The latter also cannibalized the body. Coalitionary killing is rare among West African chimpanzees compared to the East African chimpanzee (*P. t. schweinfurthii*). This pattern may relate to differences in population densities, research effort, and subspecies differences in biology and behavior.

Keywords Chimpanzee · Lethal aggression · *Pan troglodytes verus* · Senegal

Introduction

Coalitionary killing among adults has been reported in several nonhuman primate species but is rare (Wilson *et al.* 2014; Wrangham and Peterson 1996). It is most common in chimpanzees (*Pan troglodytes*), one of the most intensively studied wild primates. Lethal aggression in and between chimpanzee communities has been reported at almost every long-term research site where these apes have been studied for more than a decade (Wilson *et al.* 2014). A recent summary of lethal events at 18 chimpanzee and 6 bonobo (*Pan paniscus*) study sites representing 518 observer years of records found that intracommunity killing of weaned individuals was rare, with only 9 observed and inferred cases reported for a total 426 observation years (Wilson *et al.* 2014). The analyses did not support the hypothesis that anthropogenic disturbance caused lethal aggression in chimpanzees (Wilson *et al.* 2014). Instead, the authors concluded that an evolutionary adaptive explanation better fit the pattern of lethal aggression recorded in chimpanzees because indicators of competition intensity, such as the number of adult males within a community and population density, were the best predictors of lethal events (Wilson *et al.* 2014). Further patterns in the data include the following: 1) Most lethal aggression of weaned individuals involves adult males as both the victims and attackers. 2) Most lethal events involve attacks on individuals from neighboring chimpanzee communities. 3) The behavior is less common in the West African chimpanzee subspecies (*P. t. verus*) and the bonobo (*P. paniscus*) compared to other *Pan* taxa (Wilson *et al.* 2014, Fig. 1).

Here, we add to the database on lethal coalitionary aggression in providing an account of what appeared to be a lethal attack on a peripheral, former alpha male at the Fongoli savanna chimpanzee study site in Senegal (Foudouko). We place our case in the context of his group. We describe 1) the victim's social status, including his rise to and fall from alpha position, his peripheralization, and his attempts to reestablish himself in the male social group; 2) circumstances surrounding his death; 3) the treatment of his dead body by other community members; and 4) events that occurred in the Fongoli chimpanzee community immediately after his death. Finally, we 5) provide information on the different

alpha males thus far recorded at Fongoli, in addition to brief descriptions of their fall from alpha status, for comparison with Foudouko.

Methods

Study Site

The Fongoli study site, under the auspices of the Fongoli Savanna Chimpanzee Project (FSCP), is located within the Kedougou Department in southeastern Senegal (12°40'N, 12°13'W). The Fongoli study site is the hottest, driest and most vegetatively open site where chimpanzees are habituated to the presence of observers. The extensive dry season lasts for >7 mo (November–May), with rainfall averaging <1000 mm annually. The site is a woodland–savanna, which includes open (tall and short) grassland, woodland, bamboo woodland, and small patches of gallery forest, in addition to *ca.* 5% anthropogenically disturbed areas such as fields, artisanal gold mines, and villages (Bogart and Pruetz 2011; Pruetz 2006). The majority of the chimpanzees' home range is composed of woodland, while forest accounts for <3% of the area (Bogart and Pruetz 2011; Pruetz 2006). Temperatures exceed 40 °C at the end of the dry season, and all but a few water sources dry up by the late dry season.

Study Subjects

Observers began study of the Fongoli chimpanzee community in April 2001, and habituation took *ca.* 4 yr. We began systematic all-day follows of focal adult male subjects in early 2005 after habituation had proceeded to the point at which individual males tolerated the presence of observers and could be followed from night nest to night nest.

Community size between 2005 and 2013, when Foudouko was killed, ranged between 31 and 35 individuals. We defined age–sex classes as follows: infants, age ≤4 yr; juveniles, 4–7 yr; adolescents, >7 and <15 yr (males) or until a female gave birth; and adults as males >15 yr (Baldwin 1979). We refer to males known or estimated to be between 15 and 20 yr of age as young adult. During the study, the number of adult males ranged between 10 and 12. The number of adult females ranged between 7 and 8. The adult male/female sex ratio ranged between 1.4 and 1.7. Previous mitochondrial DNA analyses of individuals of juvenile age or older provide the matrilineal relatedness of all of the males and most of the females (excluding two females that had recently immigrated into the Fongoli community) of adult age at the time of Foudouko's death (Stewart 2011).

We ranked adult males in the dominance hierarchy based on pant-grunt records (pant-grunts are made by subordinate individuals to dominant individuals) and noted when rank changes occurred. Where a pair of adult males never pant-grunted to one another, we scored them as tying for rank.

During the early years of the project, observers did not collect all-occurrence data on focal subject social behavior, but we recorded any changes in the hierarchy as defined by observed pant-grunt records that did not coincide with the existing hierarchy.

Data Collection

Observers maintained a minimum distance of 10 m from most chimpanzees but, in the early years of the project, we followed mid-ranking adult male DF at a distance of 15–20 m when he was in small parties (<5 individuals) or when alone because of his relative timidity. Observers did not identify all adult females of the Fongoli community until January 2006.

Systematic behavioral data collection at Fongoli consists of all-day follows of focal adult males, with instantaneous sampling of general activity and location via a Global Positioning System (GPS) at 5-min intervals. We attempted to collect systematic behavioral data on adult male focal subjects ≥ 20 days per month, although seasonal factors such as river flooding result in some degree of monthly variation in data collection. We sampled rare but important behavioral events, such as contact aggression, copulations, hunts and meat sharing, and reactions to humans or predators opportunistically for all individuals. Operational definitions of chimpanzee behavior follow Nishida *et al.* (1999).

Data Collection and Analyses Specific to Foudouko

After March 2008, when Foudouko disappeared for almost 9 mo, we took detailed notes on his behavior whenever we encountered him. We recorded his reaction to observers and his social interactions and grouping with other individuals. Following the discovery of his body on June 15, 2013, three observers took detailed notes on how other community individuals reacted to his body over the course of 3.5 h, with two observers collecting data simultaneously (see Tables I, II and III). In addition, one observer took *ca.* 18 min of video as individuals interacted with Foudouko's body (Electronic Supplementary Material [ESM] Tables SI–SX, corresponding to Video Clips 1–10). We transcribed records from video clips (ESM Video Clips 1–10) and combined these with detailed observations taken by three different researchers (ESM Tables SI–SX) to provide a chronological account of the Fongoli chimpanzees' treatment of Foudouko's body after his death (see Table II). To assess the frequency with which observers saw Foudouko before and after his disappearance in early 2008, we compared days of data collection where he was seen and not seen from January 2006 to December 2007 and January 2008 to June 2013 ($N=90$ mo) (Fig. 1).

Ethical Note

We conducted all research reported here with permission and in accordance with guidelines set forth by the Department of Forestry in the Republic of Senegal

Table 1 Days Foudouko (FO) was observed following his peripheralization, including the individuals he was with and a description of their activity, Fongoli study site, Senegal^a

Date	Individuals ^b observed with FO and female swelling score in () ^c	Brief description of observations
12/15/2008	am: MM; af: NN (?), NI (0); im: NE, TV	Observers (KBO, DK) saw FO in this small party after not having seen him since March. Given his nervousness and the heat, observers left this party.
04/11/2009	am: MM; af: TI (1)	As MM and TI approached FO, TI appeared very excited, walked bipedal, and frequently turned to and grimaced at MM for reassurance. FO did not pant-grunt as MM and TI arrived. TI pant-grunted to FO. FO immediately began walking away quickly, followed by MM. They traversed a ravine and arrived at the opposite plateau, then turned and ran back down and up the original side. MM followed FO quickly but did not appear as nervous as FO, who periodically stood bipedal, looking back at observers. MM began stopping under shady areas before getting up and running after FO. Observers stopped following the party because of the heat and MM's apparent fatigue.
6/3/2010	am: DV	FO approached DV at the end of the day at Sakoto ravine and panted silently to DV. DV left the rest of the party to travel with FO; DV was excited, piloerect, and displaying silently as he followed FO. The rest of the party nested at Sakoto. The observer (JDP) did not see DV or FO return after losing them in woodland within minutes of their moving south, away from Sakoto.
6/19/2012	am: DV, JM, KL, BI, BN, MI, LT, SI, MM	See text for detailed description. Apparent chase of FO by KL, BI, BN, MI, and LT. The observer (JDP) saw FO following a chase by other males, and JDP followed FO for 15 min, as he moved parallel and <i>ca.</i> 500 m from the chimpanzee group's nest site.
7/9/2012		The observer saw FO at Saro 1 woodland area. The chimpanzee party on July 10 behaved nervously as if FO was in the vicinity of Tukantaba ravine.
8/4/2012	am: MM, LP, BO, JM, DF	MM and FO joined other adult males, arriving at 1721. They approached others brusquely and piloerect, with MM directly behind FO. FO approached to within <i>ca.</i> 10 m before he saw the observer (JDP), then dashed away. MM initially retreated with FO. LP was piloerect as FO and MM approached. BO had started down tree quietly, and all males appeared to have followed FO and MM. JDP found the party again at 17:35 h,

Table I (continued)

Date	Individuals ^b observed with FO and female swelling score in (°)	Brief description of observations
		<100 m away, near the head of the ravine. FO left as JDP unknowingly approached to <20 m from him in a vine tangle. MM followed FO downstream again. BO pant-hooted from woodland away from the ravine, and FO whimpered. FO and MM left but returned to the stream area. Party built nests here, and LP and FO seemed to build nests just downstream from others but out of sight of observer.
12/27/2012		Observer (MS) thought he might have seen FO at 17:58 h.
1/2/2013		Observer (MS) could not find chimpanzees but thought he saw FO at 17:46 h.
1/3/2013	am: DV, MM, KL, SI, BN; af: EV (3), LL (0), LU (0); im: LO, LT, LX, LN	08:47 h: FO traveled with DV, MM, KL, and EV; at 08:56 h, FO, DV, KL, MM, and EV moved into a burned woodland area; the observer (MS) noted that he did not want to bother the group given FO's timidity at 09:05 h, so it was not easy to see them as they followed FO. At 09:25 h, DV, MM, and FO moved along slowly and tried to conceal themselves from MS. Adult female LL, her infant son LO, adult female LU and her adolescent son LX, juvenile daughter SK, and infant daughter LN were also nearby. At 17:20 h, MS noted that FO was with the party. At 18:18 h, MS saw FO with LL in burned woodland. FO watched MS from ca. 70 m for ca. 7 min. At 18:19 h, FO traveled with LL (and LO), EV, DV, MM, KL, SI, and BN, who then appeared to nest at Maragoundi. FO ranged with this party without signs of agonism.
2/20/2013	am: MM, DV	At 07:04 h, MM and FO arrived. At 07:09 h, MM and FO moved to the Petit Kerouani ravine. At 07:12 h, FO approached the observer to within 50 m, where he ate fruit. At 10:45 h, DV and MM directed their attention toward FO, but did not approach. FO appeared to try to appeal to them to follow him, but they did not.
2/21/2013	am: MM; af: LL (2.5)	At 18:07 h, FO approached to within 40 m of the observer (JDP), looked at her, and then pant-grunted to DV. At 18:08 h, DV groomed FO. At 18:17 h, FO copulated with LL, and LL then groomed FO.
2/26/2013	am: MM; af: NI (0), NN (1); im: TV, NN	The observer (JDP) found MM at 07:00 h, and FO followed him across a long plateau after MM repeatedly pant-hooted, looked in the direction of the ravine, and appeared to wait for FO. FO favored either his hand or foot.

Table I (continued)

Date	Individuals ^b observed with FO and female swelling score in () ^c	Brief description of observations
3/29/2013	am: KL, DV; im: LX	The two males fused with the party of females and their offspring at 07:55 h. The party moved and fed until 09:05 h, when MM and FO moved ahead of the party and out of sight of JDP. At 13:47 h, the observer saw FO near the streambed. KL and LX could see FO. KL followed FO, while LX ran to pant-grunt to DV. The observer heard FO vocalize. KL returned to the group at 13:58 h. No sign of FO at 14:21 h.
4/4/2013	am: BO, LT, JM; af: LL (3)	At 08:02 h, FO left the termite mound and walked through burned woodland/bamboo habitat 45 m from observers. The observer heard multiple warning <i>wraaa</i> 's, possibly directed at FO. At 08:16 h, others <i>wraaa</i> at FO. As they walked, individuals seemed to direct their attention at FO.
4/11/2013	am: DV, MM, DF, LP, BN, SI, BO, LT, MI; af: EV (3), NN (2?), NA (1), NI (0.5), FA (0.5), LL (0.5); im: DW, LX, LO, VN, VC, TV, LN, SK, PI, SO, AM	FO groomed party members. FO appeared reluctant to leave estrous female EV.
5/4/2013	am: MM, KL	Adult males observed with FO at 06:50 h.
6/15/2013	am: DV, MM, KL, BO, JM, LT, BN, BI, DF, SI, MI, LP; af: FA (1), TM (3), LU (0), EV (1), LL (1), NA (0), NI (0), NN (1); im: LX, DW, SO, SK, TV, VN, LN, CY, VC, LO	Death of FO. See text and supplementary information (Tables S1–SX and Video Clips 1–10) for details.

^a Operational definitions of chimpanzee behavior follow Nishida *et al.* (1999)

^b af = adult males; af = adult females; im = immature chimpanzees

^c See Methods for details of scoring estrus. (0) = anestrus; (3) = peak estrus

and the IACUC guidelines of Iowa State University. All research on chimpanzees was strictly observational.

Results

Foudouko's Place in the Fongoli Community

We identified Foudouko as a sexually mature late adolescent or young adult male in 2003. We identified Foudouko as alpha male from early 2005, when adult males were habituated for nest-to-nest follows, until late 2007. He did not pant-grunt to any other adult males, and all other adult males pant-grunted to him. We estimated that Foudouko was likely in his late teens when he became an alpha male.

In 2006 and 2007, Foudouko was present in parties on 63.4% of observation days ($N = 426$ days) (Fig. 1). He lost alpha rank at the end of September 2007, at around the

Table II Observations of the Fongoli chimpanzee community interacting with or reacting to Foudouko (FO)'s corpse, Fongoli study site, Senegal^a

Time	Notes
06:19:27	All males, including adolescent male LX, subadult female EV, and a juvenile arrived at the body of the dead chimpanzee in a heightened state, with piloerections and giving warning vocalizations. They exhibited reassurance behaviors, including grabbing one another's testes and inserting their fingers in the mouths of other chimpanzees. (Observer MS speculates whether FO tried to approach estrus female TM during the night; TM arrived at the end of the group, with beta male MM.)
06:25:42	The group ceased their warning (<i>waaa</i>) vocalizations.
07:24:52	Group charged FO's body. Adult male LT, in a running display, hit subordinate adult male BI and continued his display.
07:25:11	Chimpanzees again grabbed FO's testicles, while others held his fingers in their mouths.
07:27:56	LT again displayed, chasing adult male BN and hitting adult female FA.
07:29:08	MM displayed, running while dragging FO's body, pulling on his arms.
07:29:56	MM left FO, and the observer was able to see that FO was motionless.
07:30:59	Adult male SI, FA, EV, adolescent female SO, and infant female VN (daughter of FA) approached and smelled FO.
07:33:04	TM aggressively rushed up to FO and smelled his body.
07:34:08	TM's infant son CY touched FO with his hands and smelled them.
07:34:26	Adult male KL displayed and jumped onto FO with both his feet, also slapping FO's body.
07:35:06	KL grabbed and pulled FO's foot, and hit FO with his right hand as FO was lying on his back on the ground.
07:37:38	CY was the only chimpanzee near FO. He moved around the body and smelled FO's head and his feet.
07:43:08	LT displayed, kicking FO with one foot on his chest.
07:47:44	Adolescent male LX opened FO's mouth.
07:48:52	Adult female LL smelled FO, but she prevented her infant son LO from touching FO.
07:50:58	The observer (MS) noted that FO had many wounds on his feet and his arms.
07:52:24	The observer (MS) approached FO, but MM became nervous and the observer halted. The observer returned to camp to notify others.
08:50	FA termite fished <40 m from FO's body. NN smelled ground nearby, where FO had been dragged. BN displayed and hit FO.
08:51	BN exhibited fear grin. LP pant-hooted. SI exhibited fear grin.
08:53	LP smelled FO, and DW approached and smelled FO (ESM Video Clip 1).
08:54	DV smelled FO's body. BO waved flies from FO's foot. LX smelled FO, moved hand, smelled FO's belly, and waved flies from FO's head. BN sat <2 m away from FO, and SI groomed BN. BN exhibited multiple, small, fresh wounds. FO had a gash on his right forearm and on his right thigh (ESM Video Clips 2–4).
08:56	LP lightly bit FO's body while piloerect, pulled at FO's hand, and shook a branch. BO and SI were piloerect, exhibited fear grins, and reassured each other via touching.
08:58	NI smelled FO but ascended the tree as BO arrived. BO exhibited fear grins and reassured NI. NI approached and touched FO's face.
09:00	BN pressed face to leg of body. Meanwhile DV fed on new leaves.
09:05	BN sat next to FO's legs, and SI groomed BN. LX arrived and inspected face and lightly touched FO; BN had fresh wound. Gash visible on FO's right forearm.
09:10	BN and SI were piloerect (Nishida <i>et al.</i> 1999) as they walked away. LU remained and looked at FO. SK arrived and sniffed FO's body. SK took FO's finger in her hand and picked it up as if to get FO's attention.

Table II (continued)

Time	Notes
09:13	FA walked slowly to <i>ca.</i> 1 m of FO, stopped, and stared. VN arrived at FA's side. FA touched FO's eyes, swatted flies from his torso, touched toes, stood over body, swatted flies from around FO's face, moved branch off of torso, and picked up penis to groom beneath. FA sniffed and manipulated penis, put penis in mouth. Large gash visible on FO's right ribcage.
09:16	NA and SO arrived and pulled at FO's leg. FA picked up FO's legs. NA pulled FO by legs. NA and FA focused on FO's feet.
09:17	LU arrived and pulled at FO's arms. FA put mouth to FO's lips; FA picked up FO's head in her hands.
09:19	Other individuals left; FA remained and pulled at FO's body by pulling his head.
09:20	FA pulled at FO's body and flipped it over, bit testicles and then inner thigh very hard, apparently trying to break through skin.
09:21	DW arrived piloerect and FA reassured DW, who displayed bipedal; TM also here.
09:22	TM groomed her own hand after touching FO's bleeding torso. DW inspected.
09:23	FA bit FO's neck skin and began cannibalizing meat there.
09:24	FA bit FO's torso, took piece in hand, and ate from there; TM appeared interested but was not seen to eat.
09:26	FA continued to take bites of FO, including one from his neck. TM arrived; LU and DW were <1 m from FO; SO <5 m from FO; FA bit FO's right thigh; DW bit FO's elbow gently. FA turned FO over, found piece of flesh and ate; FO appeared to have major wound on back; FA stuck finger in FO's anus, which was slashed open, apparently with canine teeth.
09:27	FA put finger in FO's anus and extracted fecal material; all chimps heard something and moved up into trees; DW was piloerect and pulled at FO's arm, and then pulled at FO's body and hit torso three times.
09:28	DW displayed, pulled, and slapped FO. FA pulled FO by arm, tried to bite off penis several times. DW displayed, slapped, and pulled FO. VN cried to her mother FA periodically, as if afraid. DW slapped FO and left. MM displayed (nonvocal) up to FO and then inspected TM's swelling. FA continued to examine FO. MM displayed over FO, dragged his body <i>ca.</i> 3 m, and then looked at him. FA followed. MM examined FO, then left. DW hit and dragged FO twice. FA left as KL arrived.
09:29	DW piloerect, pulled at FO's arm and hit body once; MM arrived piloerect at the body but then moved up the tree just behind it and inspected TM's swelling. TM pant-grunted submissively to MM.
09:30	FA moved FO's leg. VN ate bamboo shoots <1 m away from FO; MM sat at base of tree next to FO, shook branch.
09:31	MM displayed (nonvocal) and pulled FO's body <i>ca.</i> 5 m until he stopped abruptly, perhaps because he got blood on his hand.
09:32	FA sniffed FO's face.
09:33	DW piloerect, pulled, then hit FO three times. DW pulled FO, hit twice more, and flipped the body over. FA also pulled FO. KL displayed up (FA pant grunted to KL) and shook the branch but stopped short. MI was piloerect, behind KL. LX followed behind.
09:34	KL, piloerect, threw rock at FO. KL then hit FO three times; MI, piloerect, screamed after KL hits FO.
09:35	BN, KL, DW, and LL all crowded around FO's body; KL hit and slapped FO and threw a rock at the body. MI screamed and SI arrived, screaming. KL examined the body, and then groomed it. BN, LL, and LX approached. BN displayed (vocal), hit the body twice, and dragged FO as MI screamed, avoided this, and stood bipedal; KL then hit the body. SI screamed to KL; LX approached, then touched and examined FO's mouth. BN leaf clipped and then displayed (vocal) as MI also approached to examine FO. SI charged at MI and received reassurance from BN, who then continued a vocal display, stopping only as MM approached, piloerect. MM displayed (silent) over FO and stamped on his belly.

Table II (continued)

Time	Notes
09:37	LX sniffed FO's mouth, flipped open lips, sniffed wounds, and moved away.
09:38	MI exhibited bipedal sway displayed with piloerection. SI moved up and screamed submissively to him. MI moved away; BN leaf clipped <i>ca.</i> 1 m from body but avoided MM, who displayed up to the body, pulled at FO's leg, jumped on top of the body three times, hit him once, and then moved on.
09:39	LX sniffed FO's body; avoided BN, who displayed (vocal) throwing rock past body.
09:40	LX returned to examine FO and bit/licked neck wound. BN displayed (vocal) and attacked FO, including throwing a rock. BI arrived but stopped short of the body, <i>ca.</i> 1 m away, with piloerection, and he sat and swayed. Others left.
09:41	NN arrived to inspect FO. BI stood bipedal and NN screamed. BI reassured NN, and they both moved to sniff the body.
09:42	NN and BI examined FO. TM returned to the body with her juvenile son CY. NN vocalized and examined FO's face. TM smelled the body, looked in FO's mouth, and pulled back his lips. CY picked up and tossed FO's arm. TM left as BI started display, and LL approached and pant-grunted to BI. BI inspected LL's swelling.
09:43	CY sniffed and played with FO's left arm. LL descended the tree. BI started display. LL pant-grunted, and BI displayed toward her, then sat down; TM touched FO's body and quickly moved away afterward.
09:44	BI started to shake a branch after leaf clipping a moment before looking directly at FO. BI was then distracted by a swollen female (LL?). BI inspected her swelling.
09:45	LL groomed FO's left leg. BI watched closely from overhead.
09:46	LL approached and examined FO (LL left infant son LO 1 m away). BI also examined FO. LL looked under the testes, sniffed the penis, and bit FO lightly. LL appeared to be about to take a bite but left as BN arrived (piloerect) and groomed with BI, who had approached bipedally and swayed at BN (and LL). BN and BI groomed <i>ca.</i> 0.5 m from FO's arm.
09:51	NI approached the body, and her infant son VC inspected FO's face.
09:52	BI approached FO and waved flies from him. BI examined the gash in FO's left leg and groomed him. NI approached FO, and VC examined FO's face. NI retrieved VC as BI began agonistic sway. TV arrived. BI began display, and then waved flies away from FO. NI and VC examined FO's face. VC put a finger in FO's mouth. NI and VC left as BI swayed agonistically.
09:53	BN groomed BI; BI swatted flies away; NI arrived and sniffed FO's face until BI started bipedal display with piloerection; NI moved away quickly.
09:54	BI and BN swayed agonistically, both piloerect. BN provided reassurance to BI via testicular cupping.
09:55	BI and BN both became piloerect again. BN displayed (vocal) directly up to FO, sniffed the body, backed away, and groomed self, <i>ca.</i> 1 m away.
09:56	BN approached FO, vocalized, and examined the body. BN left at 09:57 h.
09:59	BN started a vocal display with leaf clip, shook a branch, and pulled FO's leg. MI arrived and BN left. LT also arrived. MI sat 1 m from FO and examined the body. LT and BN left as a motorcycle passed on a nearby trail.
10:01	LT returned, piloerect. MI examined a cut in FO's left big toe and looked under the testes. LT pulled on FO's penis and smelled. LT gave warning vocalizations directed at a large wound on FO's right foot, which MI pulled apart. FA arrived to reassure LT (held his fingers in her mouth) at 10:03 h. The body was dragged ≤ 15 m based on marks in dirt.
10:03	MI left as FA arrived to reassure LT. TM, KL, FA, and LT examined FO's foot, followed by DW, LX, MM, and BO.
10:04	BO and MI approached LX. LX <i>wraaa</i> 'd and screamed, sending all chimpanzees arboreal, and all screamed/ <i>wraaa</i> 'd and avoided display (of MM?).

Table II (continued)

Time	Notes
10:05	JM threw a rock at FO. DF arrived. JM displayed and threw a rock at FO. NN screamed and fled. LP fled. BO bit FO, pulled, and slipped, which caused JM to <i>waaa</i> . BO attacked FO again, as did LX. LT screamed. TM and CY left. KL arrived and touched, examined FO's foot, and then left.
10:08	BO cried. LX bit FO's hand. LP arrived to examine FO. MM arrived to examine FO's foot. BO bit and pulled FO several times but appeared to get frightened. BI pulled FO's leg. DV charged BO away from FO's body. NN approached to <2 m and <i>waaa</i> 'd at FO's body.
10:10	BI examined FO's anus and appeared to remove something. FA and LT <i>waaa</i> 'd in nearby tree.
10:11	FA approached FO to 1 m and examined him, as did BI. FA pulled at flesh with her mouth. NN <i>waaa</i> 'd 3 m away.
10:12	BO and BN (with piloerection) were back at the body. FA took a small bite where BO bit FO and moved away as BN examined FO. FA examined FO's left foot. DW examined the body. BI examined (sniffs) FO's body, then shook a branch with piloerection. DW inspected FO's wounds.
10:13	FA left the area as BI aggressively swayed in display. BI hit FO's body with a stick four or five times, then examined FO's foot. BI, DW, NN, and FA examined FO. BI bit FO's left foot and right thigh. DW dragged the body. MM was also at the body, with FA, BN, and DW. BI bit FO's foot and ankle, and all individuals nearby fled as FO's body jerks. (See Video Clip 7). BN, BO, and BI pulled and bit FO's body. BO continued to bite and slap FO and pulled on his own foot in excitement. MI arrived to watch. BO broke FO's right leg backward at the knee. He bit and slapped FO. DW examined FO's teeth.
10:14	BO bit FO's neck, which startled all the others. FA inspected FO. BN pulled and bit the body. BO and BI bit the neck and pulled at pieces back and forth. LT <i>waaa</i> 'd in the background.
10:16	BO bit and hit FO. BI did the same and then moved away. BI may have had been eating piece of flesh.
10:17	BO hit FO's torso 12 times with both hands, paused, and hit him five times again. BO's had hair/flesh hanging from mouth.
10:18	BO hit and bit FO. MI watched closely. BO broke FO's knee/leg, bit knee/leg, and hit again.
10:19	BO hit FO's body three times. MI inspected FO's body. NN approached, and BO reassured her while also giving a fear grin.
10:20	CY examined FO's body. BO reassured NN, who arrived and examined body. MI was <1 m from body. Many flies were around the body, but there were few when observers arrived at 08:50 h.
10:21	BN returned to <2 m of the body. MI pulled body. BO slapped body. BN hit and pulled body. BO bit an arm and pulled the body. NN followed, crying. LX, TM, and MI were <1 m away from body. MI pulled FO and BO followed the body, biting it. LX slapped FO twice. MI pulled body >10 m, biting neck and pulling FO by chin with his teeth. SK examined the body.
10:22	EV hit the body. JM and LT arrived to sniff where FO's body was and then moved on.
10:25	LU and LX approached the body. LX hit FO's leg. MI continued pulling the body. LX followed and hit the body. LX hit FO's leg. MI continued pulling the body, and LX followed and hit FO. LT arrived and examined the body. LP was 2 m away. MI pulled the body <i>ca.</i> 7 m farther. Most individuals watched him. TM and LX approached. CY examined the body, along with LP. MI continued pulling FO's body another 10 m. JM followed and threw a rock at the body. DW was near LX.
10:27	MI moved away, manipulating something in mouth.
10:28	DV arrived, and others left. TM arrived and examined FO's face. DV examined FO's foot. TM groomed FO's body.
10:29	CY examined FO's face. DV examined wounds at the back of FO's neck, then left. NI left with something in her mouth.
10:30	TM dragged FO's body by arm <i>ca.</i> 5 m. DV returned and examined body with TM (moved leg and sniffed hand) and waved flies off body (most individuals did this at some point).

Table II (continued)

Time	Notes
10:32	DV sat 2 m away from the body. TM examined the body and then bit an arm. She left at 10:33 h, as DV approached EV with piloerection. EV avoided DV. DV moved to eat bamboo shoots <i>ca.</i> 15 m away.
10:33	DW (with piloerection) pulled FO's body <i>ca.</i> 2 m, slapped body, flipped it over, and left.
10:34	NI arrived and examined FO's body. EV was 4 m away. EV sniffed the rocks FO was pulled over. TV arrived and examined the body. NI smelled a bloody twig from the neck area, licked pieces of vegetation, and appeared to put a piece in her mouth, perhaps along with piece of flesh.
10:35	EV smelled FO's neck. TM smelled bloody grass.
10:36	NI touched FO's fingers. TV smelled FO's neck. TM arrived, smelled FO's neck, and then reassured NI via hand out.
10:37	CY arrived to examine FO. BI arrived in (nonvocal) display, causing NI, EV, and TM to leave the body. NI mouthed bloody leaves, picked up pieces, and put in her mouth. She then wiped a piece off with her hand, found a piece of FO's hair, put it in her mouth, and then moved away. BI continued display up to TM, but she ignored him.
10:39	BI solicited TM for copulation. BI sniffed FO's body and swatted at flies.
10:41	BI left, followed EV, after she sniffed a bloody rock. Only TM remained, in the tree above.
10:42	DW examined FO's body, became piloerect, and then left.
10:44	DW examined the rock where the body was dragged.
10:45	DW displayed with piloerection and dragged FO <i>ca.</i> 1 m, slapped the body twice, and left. TM sat in a tree with CY. BI sat here also.
10:46	Most individuals <i>waaa'd</i> at a passing vehicle en route to artisanal mine. The observer approached and asked the vehicle to continue.
10:54	TM descended a tree, along with CY, to examine FO. She moved off at 10:56 h with BI, who waited <i>ca.</i> 10 m away.
10:58	DW moved off after others, as the party moved back east toward Sakoto (night nest area) and Saro 2 area SE.
11:17	Observer EGW collected blood samples, and we buried FO <i>ca.</i> 15 m SW of the spot where chimpanzees left him.

^a Operational definition of behaviors follow Nishida *et al.* (1999)

same time the beta male and Foudouko's frequent coalitionary partner, MM, was severely injured (suffering a broken or dislocated hip or femur). We did not see MM with the other males in the community for *ca.* 6 weeks after this (October 19–December 3, 2007), and he was very frail when he returned, submitting to almost all adult males of the community, including a very aged male; females also ignored his displays.

The last day on which we collected focal observation data on Foudouko was March 27, 2008, and he disappeared at the end of March 2008. On one of the last days on which we saw Foudouko, observer D. Kante estimated that most or all of the community's adult males chased him from one of the only permanent dry season water sources. We next saw Foudouko in December 2008, when K. Boyer Ontl and D. Kante found him with MM and two adult females (NI, NN) and their offspring (NE, TV), 263 days after he had disappeared. Foudouko was no longer tolerant of observers in that he repeatedly moved rapidly away from them and researchers abandoned their attempt to follow his party given the dry season heat stress.

Table III Observed postmortem attacks on Foudouko (FO)'s body that resulted in visible wounds or included attacking the body with tools at Fongoli study site, Senegal^a

Time period	Description of actor(s) and attacks
07:24–07:49	LT displayed at FO's body and hit the corpse with rock.
07:50–08:53	Observer one (MS) saw FO clearly at 07:50 h and noted multiple minor wounds on feet and arms. MS left to alert others at camp, and 1 h passed (07:52–08:53 h) during which no observers were with chimpanzees. Observers two (JDP) and three (EGW) arrived at 08:53 h and noted minor ^b gashes on right (R) forearm, R thigh, R ribcage, left (L) big toe, L leg; major ^c wound on R foot, on back; anus ripped open.
08:54–09:30	FA (adult female) bit testes and R inner thigh. NA (adult female) possibly bit inner thigh. NA appeared to bite R foot. FA bit through neck skin and ate a small ^d piece of flesh. FA bit the torso and ate a small piece of flesh. FA bit the neck and ate a small piece of flesh. FA bit R thigh. DW (adolescent male) bit elbow gingerly. FA retrieved a piece of flesh and ate. FA appeared to try to bite off the penis several times.
09:31–10:00	KL (adult male) hit the body with a rock. LX (adolescent male) bit/licked neck wounds. BN (adult male) hit the body with rock. LL (adult female) bit the body lightly.
10:01–10:28	JM (adult male) threw a rock at the body. BO (adult male) bit the body. LX bit a hand. BO bit the body several times. FA pulled pieces of flesh with mouth. FA took flesh from the body. BI (adult male) hit the body with a stick four or five times. BI bit the foot and ankle extensively, tearing at flesh. BN (adult male) bit the body. BI bit the body. BO bit the body. BO broke FO's leg/knee backwards. BO bit the body. BO bit the neck extensively. BN pulled and bit the body. BO bit the neck and pulled at pieces of flesh. (BO bit the neck a total of six times.) BI bit the neck and pulled at pieces of flesh (R side). BO bit the body. BI bit the body; appeared to eat a piece of flesh. BO bit the body. BO broke FO's knee/leg. BO bit the body. BO bit an arm and continued biting. MI (adult male) bit the neck, pulled the body by the chin with teeth (later left with flesh? in mouth). JM (adult male) threw a rock at the body. TM (adult female) bit an arm (she ate a piece of flesh two different times, once from foot).

^aOperational definition of behaviors follow Nishida *et al.* (1999)

^bMinor wounds were considered those that appeared somewhat superficial, e.g., <10 cm in length, <5 cm deep

^cMajor wounds were considered deep and/or relatively long compared to wounds typical of Fongoli males, e.g., >5 cm deep and/or >10 cm long; genital wounds are considered major wounds regardless of length or depth

^dAll pieces of flesh consumed appeared small to observers, *ca.* 5 cm in length or smaller

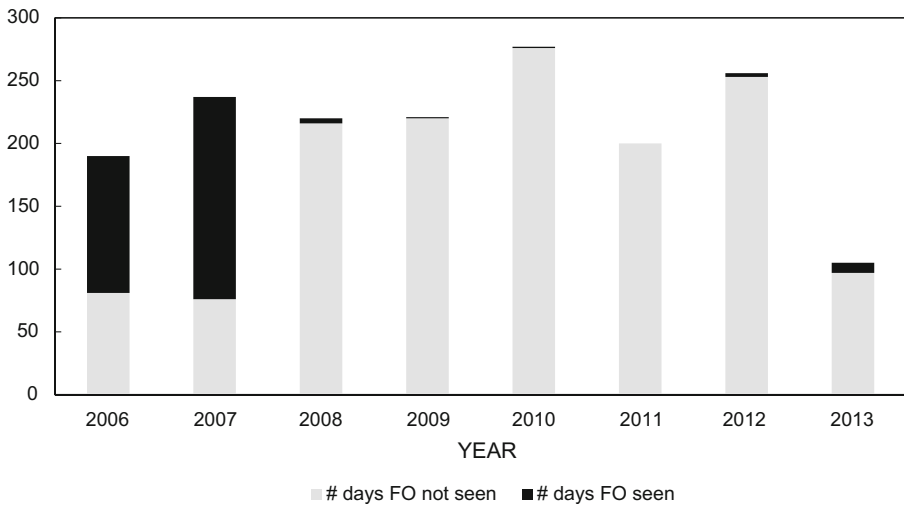


Fig. 1 Data collection days on which Foudouko was seen or not seen in the Fongoli chimpanzee study 2006–2013: Foudouko was the alpha male until late 2007. Fongoli study site, Senegal.

Observers saw Foudouko once or twice per year with other chimpanzees in 2008, 2009, and 2010 but did not see him in 2011. In 2012 and 2013, Foudouko appeared to be slowly integrating back into the adult male social group. We saw him in small parties with several adult males and with the whole community on one occasion, but he was mainly associated with MM, who had regained beta male status (Table I). Although most males were aggressive toward Foudouko, alpha male DV and MM (maternal siblings, based on mtDNA analyses: Stewart 2011) affiliated with him and were not aggressive toward him as were other adult males; they did not participate when other males chased Foudouko. For example, on June 3, 2010, J. D. Pruetz witnessed Foudouko arriving at Sakoto ravine late in the day. Foudouko approached adult male DV and quietly pant-grunted to him. Afterwards, both males disappeared into the woodland. The next day, after the adult males had moved southeast, adolescent male LT alarm called, which resulted in the males returning rapidly and chasing something unseen >1.5 km south. We have not seen Fongoli chimpanzees chase predators (spotted hyenas [*Crocuta crocuta*], leopards [*Panthera pardus*]) or prey for such distances (Pruetz and Boyer-Ontl, in prep.), nor were the alarm calls of prey species, e.g., *Papio papio*, heard. We have never encountered extra-community males in the Fongoli home range. The alarm calls given by LT sounded different to observers from calls given in response to snakes and potential predators (Pruetz and Boyer-Ontl, in prep.). These factors led observers to speculate that the males were chasing Foudouko. In 2013, Foudouko quietly approached a party and directed his gaze at MM, who left to travel with Foudouko and disappeared for 1 week.

In late 2012 and in 2013, Foudouko spent more time in proximity to the social group of males, and continued to display nervousness around researchers, hiding or moving away. For instance, on February 26, 2013, K. Boyer Ontl followed a small party containing Foudouko, MM, NI, NN, TV (NI's juvenile daughter), and VC (NI's infant son) for most of the day (Table I). Foudouko stayed >75 m from the observer on an open grassland plateau when she first encountered the party at dawn, and although he tolerated her at closer distances, e.g., 20 m, later in the day, most of the time he

positioned himself behind a tree or a tall tuft of grass. On several occasions, the behavior of Fongoli males suggested that Foudouko was in the vicinity, but observers did not see him. These encounters were almost always in the southwestern portion of the Fongoli chimpanzees' range, near the core area used during the rainy season especially and in the vicinity of the Fongoli research camp. Once, J. D. Pruettz witnessed the adult males of the Fongoli group engage in what appeared to be an aggressive chase. Only alpha male DV and beta male MM refrained from taking chase. The observer then saw Foudouko as she was returning to camp at dusk, and she followed him for 15 min from a distance, undetected. He moved parallel to the other chimpanzees' location at a nesting site at Maragoundi ravine (Fig. 2). He frequently climbed trees and gazed in the direction of the social group but disappeared on detecting the observer.

Circumstances Surrounding Foudouko's Death in 2013

We last saw Foudouko alive on May 5, 2013 when we observed him in the company of adult males MM and KL. During the days before his death, observers suspected that Foudouko was in the vicinity on several occasions. For example, on June 12, 2013, J. D. Pruettz followed the entire Fongoli community, excluding Foudouko, to Maragoundi ravine. At 19:30 h, after a chimpanzee screamed west of the nesting party, the males left their nests and ran in that direction. The observer followed adult male KL who stopped short of what sounded like an aggressive encounter, and they met adult male BI returning from the area. She then found adult males BN, MI, and LT returning from the area, followed by adult male SI returning from an area nearby moments later. Beta male MM was nearby, although he did not appear to have been involved in the confrontation. MM then disappeared until 18:00 h the following day. On June 14, 2013, two researchers (DK and LB) reported a similar incident in which all the adult males raced in a certain direction as if giving chase to another chimpanzee.

Foudouko likely approached the chimpanzee group during the night of the June 14/15 after they had nested at Sakoto ravine. Fongoli village is *ca.* 1 km from Sakoto and during the early morning of June 15 observers heard vocalizations (pant-hoots, screams) between 02:00 and 03:00 h. They were atypical compared to the pant-hoots often heard from camp when chimpanzees nested at Sakoto in that they were very loud, extensive, and their placement indicated that some individuals had left their nesting area and had moved south. Calls indicated that individuals were rapidly moving on the ground and involved in extensive agonism. Alpha male DV's pant-hoot, for example, indicated he was somewhere between the nesting site and the location where Foudouko was discovered dead the next morning. Beginning with the rank of alpha male, the adult male dominance hierarchy at the time of Foudouko's death was 1) DV, 2) MM, 3) BO, 4) KL, 5) JM, 6) LP, 7) MI, 8) LT, 9) DF, 10) BI, 11) BN, 12) SI.

Treatment of Foudouko's Body After Death

On the morning of June 15, 2013, a research assistant (M. Sadiakho) arrived before dawn at the chimpanzees' nesting site. He returned to camp at *ca.* 08:00 h and reported that he had seen a dead chimpanzee, which he presumed to be Foudouko because all 12 other community males were present. He reported that most of the males had attacked Foudouko's body (Table II). At this time, two additional researchers (J. D. Pruettz, E. G.

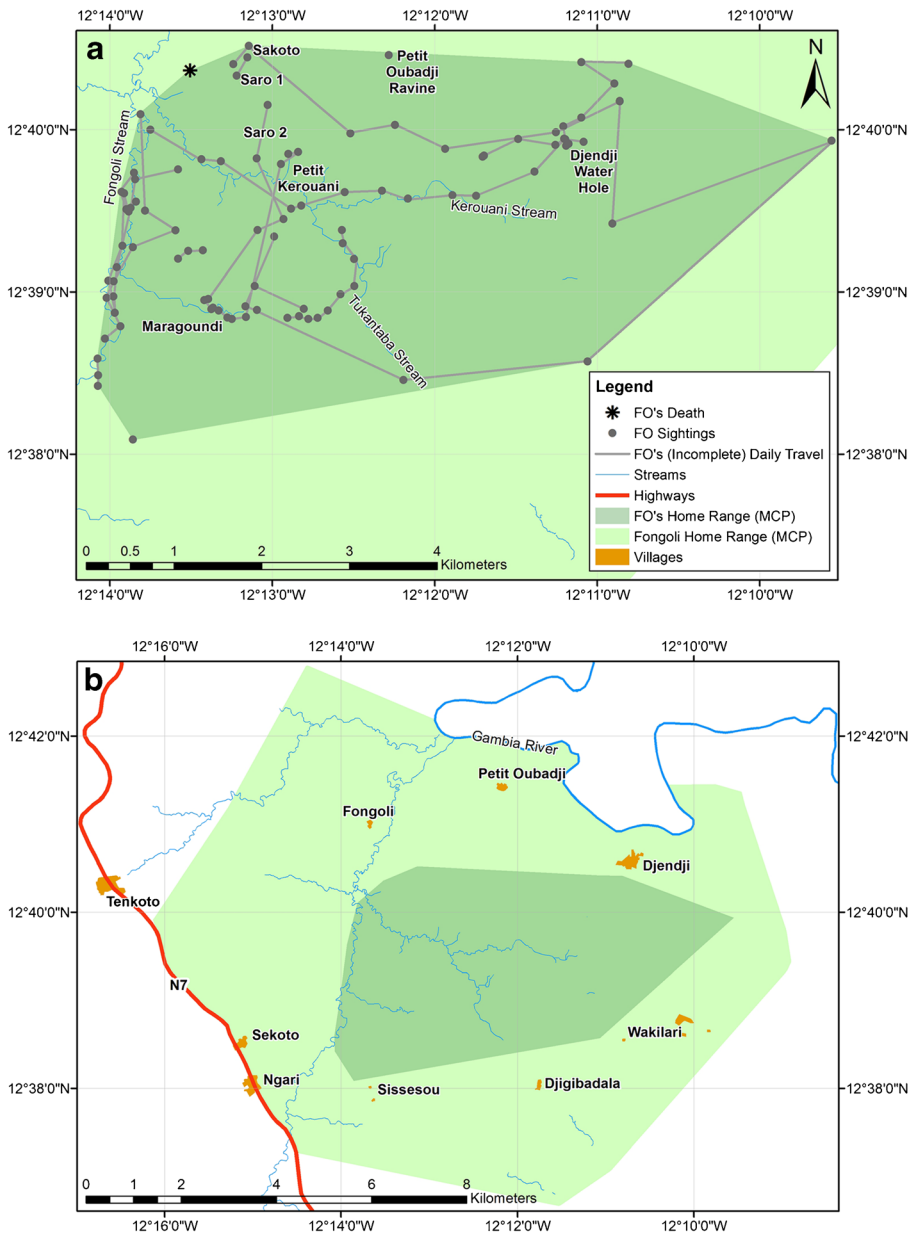


Fig. 2 Map (a) of locations where Foudouko was seen during his peripheralization and attempted reentry into the adult male Fongoli chimpanzee social group, relative to the home range area (b) of the entire social group. Fongoli study site, Senegal.

Wessling) left to observe the body (Table II). On arrival at the scene, one observer identified the dead chimpanzee as Foudouko. When J. D. Pruetz and E. G. Wessling arrived in the vicinity of the body, they saw adult female FA (alpha male DV's mother and presumably beta male MM's mother) termite fishing <40 m from Foudouko and other chimpanzees in the area. For the next 2 h, observers recorded the chimpanzees'

reactions to Foudouko's body, until the party departed (Table II). We observed fresh wounds on Foudouko's hands, feet, back, and anus, with most of the wounds on the neck, torso, and appendages (Figs. 3 and 4) being inflicted postmortem (Tables II and III). Given their locations and severity, none of the bite wounds would have been lethal, save for possibly a severe bite to the right foot (Fig. 5) that could have considerably hindered his movement and escape and that could have resulted in significant blood loss. This foot wound was the most severe wound seen on Foudouko's body when observers arrived at the scene. Chimpanzees may have inflicted this wound at or around the time of Foudouko's death. We observed few wounds on any other individuals recorded in the vicinity of Foudouko's body, i.e., potential attackers. Only older adult male BN exhibited fresh wounds, on his arm, and these appeared to be superficial. We approached Foudouko's body after the party left the area. We found little sign of rigor mortis when we left his body at 11:20 h, suggesting he died within the previous 24 h. We judged livor mortis as minimal given the extent to which his neck wound still bled on rupture during the postmortem attacks. However, because multiple chimpanzees turned over and dragged Foudouko's body, pooling patterns could have been interrupted. We found no extensive evidence of bleeding on the ground in the vicinity of Foudouko's body.

During observations of Foudouko's body, several young adult males beat his body and bit it repeatedly (Table III; Fig. 6), with young adult male BO most often attacking the body. Most group members, including several adult females, pulled on the body and smelled it intensely. Following BO, older adult female FA, mother of current alpha male DV and of adult male MM, attacked the body most frequently, and consumed more of it than any other chimpanzee. Neither of her sons attacked the body in similar fashion. These males had not behaved aggressively toward Foudouko earlier, and had engaged in affiliative behavior with him. MM displayed around the body several times, pulling Foudouko once and later stamping on him once. MM seemed to be attempting to rouse Foudouko, rather than trying to inflict injury, as his behavior was less aggressive than the other males' displays, e.g., adult males BN, KL, BI, MI, BO, LT, and JM and adolescent males LX and DW. Alpha male DV approached and smelled the body several times but did not display toward Foudouko or attempt to move him. Numerous females and their offspring approached and smelled the body. FA and a young adult female (TM) fed on different parts of the body but ingested only small pieces of flesh.

No attackers were matrilineally related to Foudouko (Stewart 2011). Two of the frequent attackers, young adult males BO and LT, were matrilineally related to one another (Stewart 2011). LT is the son of adult female LU, brother to adolescent male LX, and likely nephew of BO, as BO's mother WI (now deceased) was apparently LU's mother. BO, LT, LU, and LX attacked Foudouko's body. No other attackers were matrilineally related.

We buried Foudouko's body near where we discovered his corpse, under the supervision of the local authorities. His bones will be exhumed for examination in the future.

Events in the Community Immediately after Foudouko's Death

On June 16, 2013, an observer contacted the same chimpanzee party ($N = 29$ individuals) at dawn at their nesting site. At 06:05 h, almost all of the males and several



Fig. 3 Body of male chimpanzee Foudouko, 11:00 h, June 15, 2013. Fongoli study site, Senegal.

females (TM, EV) traveled silently and rapidly toward the site where they had left Foudouko's body. They began a pant-hoot chorus a few minutes after beginning travel, fell silent again, then reassured one another physically, e.g., touch fingers to mouth, hold genitals, embrace, as they traveled together, listening and looking toward the location where they left Foudouko's body. All of the males were present except BI, BN, and alpha male DV. Alpha male DV then arrived in a silent, charging display. The party continued traveling to Foudouko's burial site. Young adult male LT led the party, along with adolescent male DW and young adult males BO, MI, and JM. Young adult males JM and BO reassured one another by touching and embracing. DV and MM were further behind the party. All traveled silently and vigilantly. BN arrived at the rear of the party. At 06:35 h, the party neared the site where Foudouko's body was last seen, and multiple males smelled the ground.



Fig. 4 Close-up of male chimpanzee Foudouko's genital area with wounds inflicted after death. Fongoli study site, Senegal.



Fig. 5 Male chimpanzee Foudouko's fingers and toes with signs of bites. Fongoli study site, Senegal.

The party traveled quickly to the exact site where they last left Foudouko's body and smelled the ground intensely. They then moved *ca.* 15 m to where we buried Foudouko. They smelled the rocks around the burial site, including where we laid the body to prepare to lower it into the grave. After smelling other areas where the body had been dragged, the party left the site at 06:50 h and traveled back to Sakoto ravine, backtracking along the same route taken from the night nests to the burial site. The group gave alarm calls nervously and frequently in the direction of Foudouko's site, e.g., at 07:30, 08:41, 09:00, 09:20, and 12:40 h, despite having moved several hundred meters east. Third-ranked and young adult male BO hit beta male MM during a fight among the males at 09:25 h. MM and BI left the area, screaming. MM recruited his mother (based on behavioral indications and mtDNA analysis), adult female FA, who then helped recruit older



Fig. 6 Adult male chimpanzee Mike (MI) (*left*) and adolescent male LX (*right*) examine Foudouko's body. Fongoli study site, Senegal.

adult males DF, LP, and BN to retaliate against BO. BO also attacked (hit) fourth ranked male KL at 13:35 h after the party returned to Sakoto. Such an attack by BO, on MM especially, was unusual. The party, including all adult males, nested at Sakoto on June 16, 2013. On June 17, the party left Sakoto ravine in the morning and traveled north *ca.* 2 km to Petit Oubadji ravine, in the direction opposite of Foudouko's death site.

Alpha Males at Fongoli

Thus far at Fongoli, we have recorded four different alpha males in 11 yr of study following habituation for systematic data collection. The alpha male (YO) that rose from the third position in the hierarchy to take Foudouko's place disappeared in 2010, <1 yr after LP usurped him from the dominant position. YO held the alpha position for *ca.* 15 mo, while LP was alpha for just over 3 yr. Following LP's fall from alpha position in 2012, he was absent for a several weeks but then returned to range with community. LP dropped to the middle-lower end of the hierarchy, but he has since risen to middle ranking male. The ascendancy of young males into the dominance hierarchy ($N=12$ adult males) created an unstable hierarchy for several years. Only the highest and lowest ranks remained stable over a period of >2 yr at Fongoli (2013–2014), with the hierarchy stabilizing in early 2015. The current alpha male DV is the longest reigning alpha thus far, having usurped LP in March 2012.

Discussion

Our report of lethal coalitionary aggression in a community of wild, West African chimpanzees fits the general pattern among chimpanzees in which adult males are usually both attackers and victims (Wilson *et al.* 2014). However, most lethal coalitionary aggression in chimpanzees is between communities, rather than within communities as was the case here (Wilson *et al.* 2014). Foudouko's case is also only one of a few recorded for West African chimpanzees, a subspecies characterized, along with bonobos, as having relatively little lethal coalitionary aggression compared to the East African chimpanzee subspecies (Wilson *et al.* 2014).

The Fongoli chimpanzee community is more cohesive than other study groups, and the entire community often ranges together, especially during the early rainy season (Pruetz and Bertolani 2009). However, Foudouko was estranged from most members of his natal group for >5 yr, was rarely seen, and then only in the company of specific individuals until he began to attempt to rejoin the adult male social milieu. Chimpanzees are highly social, especially males, and living even a semisolitary life would have been exceptionally stressful, as has been shown in chimpanzees experiencing social isolation (Reimers *et al.* 2007). The peripheralization of an adult male is rarely reported in the literature (Nishida 2012). However, at Mahale, the former alpha male Ntologi was absent from M group for *ca.* 9 mo, ranging alone and some distance from the rest of the group save for occasional socializing with a male age-mate (Nishida 2012), similar to our observations of Foudouko and MM. Ntologi rejoined M group, along with

another adult male, Jilba, that had been similarly ostracized by the other males (Nishida 2012). Unlike Foudouko, Ntologi rose back up the ranks to alpha male in several months and retained the position for several years (Nishida 2012). However, like Foudouko, Ntologi was ultimately killed by community males. The M group chimpanzee community at Mahale decreased in number from 76 to 44 individuals over the course of the 5 yr that included Ntologi's return and rise to alpha, his fall from alpha status, his death, and the following year (Nishida 2012). Although only three corpses were recovered, Nishida (2012) surmised that an epidemic had likely caused such high mortality, as they never discovered a splinter group. Although researchers did not witness the attack on Ntologi that left him in a coma and ultimately killed him, Nishida (2012) speculated that a gang attack by the alpha male and other males in M group resulted in Ntologi's condition and was likely retaliation for the former alpha's 15 yr of domination. The same may be true for Foudouko's case at Fongoli, although our data on details of Foudouko's tenure as alpha is incomplete compared to that of later alphas.

The unstable male social hierarchy at Fongoli appears to be related to the relatively low number of adult females in this community. Of the 18 chimpanzee communities included in Wilson *et al.* (2014), Fongoli had the lowest chimpanzee density at 0.4 individuals per km² compared to the overall average of 3.6 individuals per km² ($N=18$ communities at 10 sites: Wilson *et al.* 2014) but the highest male to female sex ratio at 1.7 (Wilson *et al.* 2014, Extended Data Fig. 1a). The sex ratio of the communities for which we have evidence of intragroup lethal aggression of weaned individuals averaged 0.51 ($N=4$). With Fongoli included, the average was 0.75 ($N=5$). A sex ratio of 1.0 in *Ateles* has also been suggested as a contributing factor in lethal aggression among males (Campbell 2006; Valero *et al.* 2006).

The high level of male reproductive competition at Fongoli, along with a low population density and extremely low rate of intercommunity interactions (FSCP, *unpubl. data*) might explain the attack on Foudouko. This pattern supports the hypothesis that intracommunity aggression occurs when male–male social bonds relax as a consequence of low rates of intercommunity aggression and high rates of intracommunity competition (black-handed spider monkeys [*Ateles geoffroyi*], Barro Colorado Island, Panama: Campbell 2006; Yucatan, Mexico: Valero *et al.* 2006; East African chimpanzees [*Pan troglodytes schweinfurthii*], Ngogo, Uganda: Watts 2004) (see Table IV). Foudouko copulated with at least one receptive female and associated with another on two of the occasions he was with a mixed-sex party in 2013, several months before his death, indicating that he presented some degree of competition for other adult males in the community.

The skewed sex ratio at Fongoli may be due to human pressure. Local residents in the Kedougou region have noted that rare but opportunistic hunting of female chimpanzees has occurred in the area to obtain infants for the pet trade (P. Stirling, *pers. comm.*). One case of infant poaching has occurred at Fongoli since the project began in 2001 (Pruetz and Kante 2010), but given the slow life history of chimpanzees, even such a low rate could eventually reduce the number of reproductive females in a social group significantly. Moreover, the Fongoli group's home range is bordered on three sides by anthropogenic (a highway and the town of Kedougou) and natural (Gambia River) landscape features that could create movement challenges for potential female immigrants. Therefore, we cannot reject the hypothesis that anthropogenic disturbance

Table IV Intragroup lethal aggression, excluding infanticide, in nonhuman primates

Nonhuman primate species	Age-sex class of victim	Age-sex classes of attackers	Context of attack	Study site and reference
<i>Pan troglodytes</i>	Adult male	Likely adult males	Former alpha trying to reenter group	Fongoli, Senegal: This study
<i>P. t. schweinfurthii</i>	Adult male	Adult males	Increased male-male mating competition	Budongo, Uganda: Fawcett and Muhuzuma 2000
<i>P. t. schweinfurthii</i>	Adult male	Adult males	Low-ranking male ascending hierarchy	Ngogo, Uganda: Watts 2004
<i>P. t. schweinfurthii</i>	Adult male	Adult males	Former alpha male	Mahale, Tanzania: Nishida 1996
<i>P. t. schweinfurthii</i>	Adult male	Adult males	Alpha male	Mahale, Tanzania: Kaburu <i>et al.</i> 2013
<i>Macaca mulatta</i>	Adult male	Adult males	Concerted attack by four adult males	India: Lindburg 1971
<i>M. mulatta</i>	Adult male	Adult males	Inferred concerted attack by adult males	Cayo Santiago, Puerto Rico: Buhl <i>et al.</i> 2012
<i>Cebus imitator</i>	Adult male	Adult males	Alpha male (Ichabod, within-group)	Lomas Barbudal, Costa Rica: Gros-Louis <i>et al.</i> 2003; Perry 2008
<i>C. imitator</i>	Adult male	Adult males	Dominance struggle	La Suerte, Costa Rica: A. Campbell, cited in Perry 1998
<i>C. imitator</i>	Adult male	Adult males	Dominance struggle	Santa Rosa, Costa Rica: Fedigan <i>et al.</i> 1997; Rose 1998
<i>Cebus apella</i>	Adult male	Not observed	Alpha; during group takeover	Iguazu, Argentina: Scary and Tujaque 2012
<i>Brachyteles arachnoides</i>	Adult male	Six adult males, one adult female, two unidentified individuals	Mating competition; coalitional attack	Parque Estadual Carlos Botelho, Brazil: Talebi <i>et al.</i> 2009
<i>Ateles geoffroyi</i>	Subadult males	Adult males	Inferred death in two of three cases of observed coalitional attacks	Barro Colorado Island, Panama: Campbell 2006
<i>A. geoffroyi</i>	Young adult male	At least one adult male	Coalitional attack on victim	Otoch Ma'ax Yetel Kooh, Yucatan, Mexico: Valero <i>et al.</i> 2006

is a contributing factor of lethal aggression at Fongoli. However, this does not preclude the possibility that lethal intragroup aggression is also adaptive under such circumstances.

Treatment of Foudouko's Body After Death

Observers saw multiple adult males hit or bite Foudouko's body, including repeated and intense biting attacks by particular males, such as BO and BI. Several individuals consumed small pieces of flesh taken from his body. Adult females in particular cannibalized Foudouko's body, similar to reports in West African chimpanzees at Taí Forest, Ivory Coast (Boesch 2009). However, at Fongoli, females ate only small pieces of flesh, unlike a Taí female that ate the entire testes (Boesch 2009).

The wounding patterns on Foudouko's body were similar to those described in cases of lethal intergroup aggression (Muller 2002; Wrangham 1999). However, most of these wounds were made postmortem, including the trauma to the throat and most trauma to the genitals. Given the nature of these wounds, the video footage and descriptions of other lethal attacks by multiple males on lone males at other study sites (Watts 2004), and the patterns seen at Fongoli where multiple males have attacked a single individual (FSCP, *unpubl. data*; Marshack 2016), we suggest multiple individuals likely attacked Foudouko, which ultimately ended in his death during the night or early morning hours of June 15, 2013. On first encountering Foudouko's body, we recorded a wounding pattern similar to those reported in the case of wounds inflicted during lethal aggression directed at an incumbent alpha male at Mahale, Tanzania (Kaburu *et al.* 2013). The wounds we observed on Foudouko's hands, feet, and appendages suggest he was being held by some individuals, and it is likely that others were beating and stamping on him, as has been observed in East African chimpanzees (Watts 2004). He likely died of internal injuries. We also observed individuals using branches and rocks to attack Foudouko's dead body, although it was unclear whether these caused wounds. Kaburu *et al.* (2013) similarly reported that an attacking male used a branch to hold the victim's body down during a lethal coalitionary attack on the alpha. This is of interest given the focus on the use of weapons in reconstructing a hominin–human niche (Gintis *et al.* 2015; Phillips *et al.* 2014). Even though the weapons in the described cases could not be described as lethal weapons, they illustrate the use of tools as weapons during conspecific attacks.

Several studies have reported behaviors akin to caregiving or even mourning after the death of a conspecific social group member, especially kin (Boesch 2012; Buhl *et al.* 2012; Fiore 2013; King 2013). However, most of the reports in the literature on thanatology describe compassionate reactions to group members' deaths or dying (Fashing and Nguyen 2011). In our case, save for alpha male DV and a few individuals that did not approach Foudouko's body, almost all Fongoli chimpanzees behaved aggressively toward him. Similar behavior has been seen in rhesus monkeys (*Macaca mulatta*), in which adult males inferred to have killed another adult male also directed aggression at his dead body >20 times the baseline rate of aggression (Buhl *et al.* 2012). Adult female mandrills (*Mandrillus sphinx*) also directed coalitionary aggression at an incapacitated male (Setchell *et al.* 2006). A report of chimpanzees' reactions to a dead adolescent male at Chimfunshi Sanctuary in the Zambia notes that individual relationships affected the manner with which individuals reacted to their dead group member

(van Leeuwen *et al.* 2016). This seemed to be the case at Fongoli with MM in particular. Even though MM pulled and stamped on Foudouko's body at the end of his final display, all of his earlier displays involved vocalizations directed toward the body and, specifically, into Foudouko's face. The observer interpreted MM's behavior toward Foudouko as protective when he first approached the corpse early on the morning of June 15. The interpretation that MM's behavior was an attempt to rouse Foudouko coincides with that described for chimpanzees at Taí, Ivory Coast (Boesch 2012).

The chimpanzees' travel to the site of Foudouko's death the morning after he was killed is reminiscent of a report for bonobos at Lui Kotale, Democratic Republic of the Congo (Tokuyama *et al.* 2012). In that case, a large group traveled 1.8 km without feeding or foraging to a site where they had left a group member with a snare on his hand the previous night. The Fongoli chimpanzees exhibited nervous behavior for much of that morning, until the party had moved some distance from the site. Their direct and oriented travel in a nonfeeding context is notable given this chimpanzee community has not been observed to exhibit boundary patrolling behavior that is typical of chimpanzees elsewhere (Mitani and Watts 2005) despite the fact they have at least one other chimpanzee community bordering their home range.

Variation in Lethal Aggression Between Chimpanzee Subspecies

Chimpanzees contribute significantly to our understanding of lethal aggression in nonhuman mammals because this behavior is well documented, perhaps because this primate species is one of the best-studied wild animals in terms of observer-year effort (Wilson *et al.* 2014). Lethal aggression involving adults has been recorded in few other primates. It occurs in some Atelines (black-handed spider monkeys: Campbell 2006; muriquis [*Brachyteles arachnoides*]: Talebi *et al.* 2009), a taxon that is also characterized by high fission–fusion dynamics and female emigration from the natal group, as well as in *Cebus* that, unlike *Ateles* and *Pan*, exhibits male dispersal. At Lomas Barbudal in Costa Rica, the rate of observed and inferred lethal aggression among white-faced capuchins (*Cebus imitator*) over the course of 12 yr has been likened to that of the East African chimpanzee (Gros-Louis *et al.* 2003). Intergroup killing ($N = 2$) is more common than intragroup ($N = 1$) killing (Gros-Louis *et al.* 2003), but sample sizes are small.

Species and subspecies differences in lethal aggression appear to exist within the genus *Pan*. Records of observed, inferred or suspected lethal aggression are uncommon in West African chimpanzees compared to such data on the East African subspecies (Wilson *et al.* 2014), although the latter have been studied more intensively in terms of observation years and number of study sites. On average, lethal aggression in western chimpanzees occurs once every 5 yr when observed or inferred cases are considered, and if only observations are considered, once every 9 yr. Of the 58 total observed killings (infanticidal, intergroup, intragroup) reported for chimpanzees, 15 were of adults between groups, and only one involved the West African subspecies (Wilson *et al.* 2014). Statistically, there was no difference between lethal aggression in general in West African chimpanzees and bonobos, but East African chimpanzees had significantly higher rates of lethal aggression than bonobos (Wilson *et al.* 2014). Lethal aggression within a social group or community is rarer than intercommunity killing,

however, and small sample sizes preclude statistical testing of differences between species and subspecies. Nevertheless, of the nine recorded killings of weaned victims within a community (four observed, five inferred), only two are from Fongoli (Foudouko and adolescent male FR). Explanations for the differences in the recorded frequency of lethal coalitionary aggression between chimpanzee subspecies include possible variation in population densities, as well as the relative intensity of study of East African chimpanzees compared to other subspecies (Wilson *et al.* 2014).

The variable rates of lethal aggression in *Pan*, parsed along subspecies and species lines, suggest that genetic, cultural, or environmental mechanisms, or some combination of these factors, may explain the rarity of killing in western chimpanzees and bonobos. Although we cannot explicitly test these causal factors, it is intriguing that some studies recognize the western chimpanzee as the most genetically differentiated subspecies (Gonder *et al.* 2011), while others link *Pan troglodytes verus* more closely with the Nigerian subspecies (*P. t. ellioti*) than with East African (*P. t. schweinfurthii*) and Central African (*P. t. troglodytes*) chimpanzee subspecies (Prado-Martinez *et al.* 2013). Traits related to social cohesion and behavior also differ between the subspecies, such as larger party size and more frequent male–female cohesion during ranging (Boesch *et al.* 2008; Lehmann and Boesch 2005; Pruett and Bertolani 2009; Yamakoshi 2004), as well as biological differences such as the quicker resumption of swelling after parturition and extended female genital swelling (FSCP, *unpubl. data*; Stumpf 2007, Table 19.6) in West African chimpanzees. These similarities prevail across habitat types, supporting the hypothesis that variation in lethal aggression between chimpanzee subspecies may not be explained completely by environmental factors. Compared to East African chimpanzees, over evolutionary time, bonobos and western chimpanzees appear to have faced selective pressures under which lethal coalitionary aggression was less likely to provide fitness benefits for attackers, resulting in a decreased propensity toward such behavior.

Our contextualization of the ostracization, peripheralization, and subsequent death of a former alpha male chimpanzee at Fongoli adds to the database of lethal coalitionary aggression in chimpanzees. This case illustrates the potential complications of dichotomizing “natural” vs. “anthropogenic” explanations for the root causes of lethal coalitionary aggression and highlights the variation in lethal aggression between taxa of the genus *Pan*.

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