1	Title:	Death of the alpha: within-community lethal violence among
2		chimpanzees of the Mahale Mountains National Park <sup>1</sup>
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## Abstract

Chimpanzees (*Pan troglodytes*) are capable of extreme violence. As with humans, wild chimpanzees engage in inter-group, sometimes lethal, aggression, which offers to the winners an opportunity to enlarge their territory, increase their food availability and potentially attract more mates. In contrast, within-community lethal violence among adult males is rare and, to date, only four cases (three observed and one inferred) have been recorded despite decades of observation. In consequence, the reasons for lethal violence between community members remain unclear. This paucity of observations may be due to the importance of male-male coalitions during inter-community encounters. Cooperation between males is also a key factor for the defense or advancement of social rank within the group. While the previous reported cases of within-community killing involved low ranked males, here we provide the first report of the killing of an incumbent alpha male by a coalition of adult males from the same community. We also report the first observed case of use of objects (a stone and a branch) by chimpanzees as weapons to main and kill a conspecific, which potentially increases our understanding of the origins of weapon-use in humans.

## Introduction

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Chimpanzees (Pan troglodytes) are capable of extreme violence. Adult males pursue an aggressive, collective, territoriality that contests inter-community dominance and secures access to food resources (Crofoot and Wrangham 2010; Mitani, Watts, and Amsler 2010; Wilson, Wallauer, and Pusey 2004). Isolated individuals in the periphery of their home range risk becoming victims of violent, potentially lethal, assaults by coalitional gangs of aggressors (typically adult males) from neighbouring communities. When lethal violence occurs, deep bite wounds and broken limbs are common, as are some more specific injuries: traumatic damage to the throat, removal of some or all of the genitalia, and disfiguring of the face (Wrangham 2006). There are now multiple reports from across the species' geographic range of such violence (Newton-Fisher and Emery Thompson forthcoming). In contrast, lethal violence among adult male chimpanzees of the same community is very rare, and remains poorly understood (Newton-Fisher and Emery Thompson forthcoming). Within communities, males depend upon one another during inter-community encounters to mitigate threats posed by males from other communities (Wrangham 1999). Furthermore, cooperation between males within communities may be important for the defence or advancement of social rank (de Waal 1982; Nishida and Hosaka 1996), and high social rank carries important advantages for reproductive success (Boesch et al. 2006; Newton-Fisher et al. 2010; Wroblewski et al. 2009). Nevertheless, within-community coalitional (or gang) attacks have been reported from both the wild and captivity (de Waal 1986; Fawcett and Muhumuza 2000; Goodall 1992; Mjungu 2010; Nishida 1996; Nishida and Hosaka 1996; Nishida

et al. 1995; Terio et al. 2011; Watts 2004), although only five cases of lethal violence between adult males of the same community of wild chimpanzees have been documented despite decades of detailed observation (*Sonso* community: Fawcett and Muhumuza 2000; *Kasakela* community: Goodall 1992; *Mitumba* community: Mjungu 2010; Terio et al. 2011; *Mahale M-group*: Nishida 1996, 2011; *Ngogo* community: Watts 2004). Of these, one was inferred from circumstantial evidence while three were observed directly. In both the *Sonso* and *Ngogo* communities, the victim was a low ranking, young adult male, while in Mahale's *M-group* and in Gombe's *Mitumba* community, the victim was a deposed alpha male who was certainly (*M-group*) or probably (*Mitumba*) low ranking at the time of the attack.

Here we provide the first report of lethal violence among wild chimpanzees in which the victim was the incumbent alpha male and the first in which chimpanzee aggressors used weapons (a stone and a branch), a finding that has important implications for understanding of the abilities and proclivities of our hominine ancestors.

## **Materials and Methods**

The Mahale Mountains National Park is a 1,613 km² reserve located on the eastern shore of lake Tanganyika (06° 15' S; 29° 55' E) in Tanzania, East Africa (Nakamura 2012; Nishida 1990, 2011). This National Park is characterized by a diversity of habitats, including semi-evergreen forest, montane savannah and bamboo woodland (Nakamura 2012; Nishida and Uehara 1981). Here, the chimpanzee community known as *M-group* has been studied intensively since 1975 (Nakamura 2012; Nishida 1990, 2011). At the time of the events reported here, group composition

was 10 adult males ( $\geq$ 16 years), 5 adolescent males (9-15 years), 2 juvenile males (5-8 years), 4 infant males (0-4), 20 adult females ( $\geq$ 14 years), 10 adolescent females (7-13 years), 5 juvenile females (3-6 years), 6 infant females (0-2 years).

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As part of a broader study, aggressive interactions and grooming behaviours were collected by SSKK from 8 adult males through long-day focal sessions (Altmann 1974) between February and November 2011, giving a total of 397 hours of observation.. Additionally, every 15 minutes, information on the identity of the adult male partners within 10 m of the focal animal was recorded. Cases of between-male aggression were also sampled ad libitum in order to calculate hierarchy linearity and stability but these data were not used to estimate aggression rates. Male rank order was determined using Elo-ratings derived from directed aggression (Albers and de Vries 2001; Neumann et al. 2011) using R (v2.14) functions provided by Christof Neumann (Neumann et al. 2011 & pers comm). Rank (in)stability was assessed using the index S presented by Neumann et al. (2011) and implemented in the same R functions. Values of S range between 0 and  $2/\max(Ni)$  where Ni is the total number of individuals present in consecutive days. Neumann et al. (2011) suggest S typically ranges from 0 (stable) to 0.5 (unstable). Hierarchy linearity was calculated using MatMan (ver. 1.1: de Vries, Netto and Hanegraaf 1993) through a matrix of the outcome of all aggressive interactions (from both focal and ad libitum sampling). In order to understand whether *PM* associated preferably with some male

partners, we used the *Dyadic association index* (DAI), which is calculated as follows:

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$$DAIab = \frac{\#ab}{\#a + \#b + \#ab}$$

Where #ab is the number of scan samples in which individual a was seen in association (<10m) with individual b, #a is the number of scan samples in which

individual a was not associated with b and #b is the number of scan samples in which b was not associated with a (Nishida, 1968).

To investigate whether the alpha male adjusted his social interactions with other adult males prior to his death, we used the Wilcoxon test to compare rates of grooming and aggression of the months comprised between February-July 2011 with those of the period August-September 2011.

Females were deemed cycling if they were seen with a sexual swelling during the

study period, and their reproductive status was assessed using a 3-point scale based on the swelling size: I=no swelling; II= medium size; III=maximum swelling (Hasegawa and Hiraiwa-Hasegawa, 1983).

The events reported here were witnessed by an experienced tourist guide Mwiga M. Kaimbe (MMK), and the tourist chimpanzee trackers Matthias Nelson (MN) and Hussein J. Mavumila (HJM). These witnesses each had between 5 and 10 years of experience with the chimpanzees of this community, and were able to identify the group members individually. SSKK and SI interviewed each witness independently within a week of the events and we have compiled their accounts. In addition, we independently viewed a portion of these events on video taken by MMK (the later part of the attack was not filmed).

## Results

# **Background information**

*PM* (*Pimu*, '*Pim*' in Nishida, 2011; Inaba, 2009), alpha male of the M-group since 2007, after displacing *Alofu* (*AL*: Inaba, 2009), was killed by a coalition of four adult males, from his own community on 2nd of October 2011. In addition to *AL* who had

been alpha male between 2003 and 2007 (Nishida 2011), in the group there were two former alpha males: Fanana~(FN) who held the alpha status between 1997 and 2003, and Kalunde~(DE) who was alpha male twice in the past, in 1991 and in 1996-1997 (table 1: Nishida 2011).

A total of 150 directed aggressive interactions were collected between February and November 2011: 77 aggression before PM's death and 72 after. In the two months prior to PM's death, the adult male hierarchy was stable (stability index S=0.04, where 0.00= stable), and the analysis of data on male-male aggressive interactions collected between May and September 2011 revealed a linear hierarchy ( $h_1=0.54$ ; Kr=0.42; DC=0.97; p=0.05). Table 1 shows the rank order of the male hierarchy prior to the killing of PM.

ID	Rank order	Years as alpha male	<b>Age in 2011</b>
PM	1	2007-2011	23
PR	2	-	20
AL	3	2003-2007	29
FN	4	1997-2003	33
OR	5	-	20
DE	6	1991, 1996-1997	48
CT	7	-	26
DW	8	-	23
BB	9	-	30
XM	10	-	16

Table 1. Rank order and age of the adult males of the M-group in the period when *PM* was killed.

A total of 103 grooming interactions between *PM* and the other males and 1405 scan samples were recorded. From these data it emerged that exchanged grooming bouts and associated more frequently with three males: *Bonobo* (*BB*), *AL*, and *DE* (Table 2)

ID PARTNER	Rate of grooming exchanged (min./hr observation)	DAI
AL	1.79	48.17
BB	1.33	59.19
DW	12.07	0.46
OR	42.13	1.16
DE	54.18	1.54
XM	0.17	4.02
FN	0.45	25.08
PR	8.02	0.43

Table 2. Frequency of grooming exchanged and association index (DAI) between *PM* and the other male partners.

Grooming between PM and the other males was not significantly different in these two months than in the preceding months (February-July: Wilcoxon: z = -1.690; N = 8; p = 0.091) and PM did not significantly increase the frequency of aggression directed to the other males when comparing the two periods (z = -1.859; N = 8; p = 0.063).

*PM*'s death was preceded by a vicious fight between himself and the beta male *PR (Primus)*, which appears to have precipitated the attack.

# The first fight

At around 10:00am, *PM* was in close association with two other adult males, *PR* and low-ranking *CT* (*Carter*), part of a large party that was spread out with the other males some distance away. Of the 10 adult males in *M-group*, only one, the 10<sup>th</sup> ranked *XM* (*Christmas*), was not in the party. At 10:10, and again at 10:17, *PM* charged at *PR* who, in both occasions, gave pant-grunt vocalisations (the stereotypical vocalisation acknowledging subordinate status in chimpanzees; Nishida et al. 1999) to *PM* and ran from him. At 10:44, *PM* and *PR* started grooming. They were joined at 10:46 by *VR* (*Vera*), an adult female with a new-born baby. *PM* started to groom her, while *PR* continued to groom *PM*.

At 10:49, a second adult female (cycling but not swollen at that moment), *EF* (*Effie*) approached the grooming cluster. At 10:51, during the grooming session *PM* attacked *PR*, by biting his left hand. *PR* reacted by biting *PM* on his face. The two males (*PM*, *PR*) started fighting – rolling, grappling with, and biting at one another – while *VR* and *EF* tried to pull back *PR* and *PM*, respectively. During this fight, *EF* bit *PM*, which gave the opportunity to *PR* to bite *PM* on the back. As a result of the fight, both *PM* and *PR* received injuries that were obvious in the aftermath: *PM* had a big cut to the right side of his head and his left hand, while *PR* had a similarly severe cut on his left hand.

The fight lasted at least 35 seconds, after which, according to the witnesses, PR broke away from PM and ran away towards the area where the other adult males were located and loudly screamed for support from them. MN observed PR climbing a tree near to four adult males: AL, OR (Orion), DE (Kalunde), and DW (Darwin),. A little farther away was the  $4^{th}$  ranked male FN. Once in the tree, PR was approached by the low ( $9^{th}$ ) ranking adult male, BB (Bonobo). Three of these males had each held

alpha status in the past: DE (1991, 1996-1997), FN (1997-2003), AL (2003-2007) (Nishida 2011). After PR climbed the tree, AL and DE charged at PM, and were followed by BB and OR.

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# Coalitional lethal violence

By 11.00, PR had already left the party, and the gang attack on PM from the other four males (AL, DE, OR, and BB) was underway. PM tried to run away, but soon these four males surrounded him. DW and FN followed and attempted to support the alpha male PM by directing threats to those attacking him, although to little effect. At 11:09, DE was seen extending his arm towards AL, behaviour in chimpanzees that is commonly associated with a request for support (Nishida et al. 1999). Apparently in response, AL pushed DW and FN away, providing DE and the other two males, OR and BB, with the opportunity to hit PM. Soon after this, FN departed but DW continued, intermittently, to try to help PM, in particular by attacking DE. Despite DW's efforts, the other males kept charging at and beating PM. Throughout, the attackers remained pilo-erect and in a highly excited, aroused state. PM was periodically struck and bitten. MN observed AL breaking a big piece of branch and using it to hold PM's body down. AL was seen grabbing PM's hand and biting it. DE was also seen grabbing PM's hand, and dragging him. Moreover, apparently in order to prevent PM from running away, the males bit his feet. PM may also have been seriously injured in his right arm, since he failed to sit up and could only lean on his left arm (Fig. 1). Ca. 45 min. after the start of the gang attack, an adult female (cycling but not

swollen at that moment), NK (Nkombo), who was in a nearby tree along with CT, was

heard screaming. Then, *NK* and *CT* came down and bit *OR*, apparently in order to prevent him from hitting *PM*. Soon after, however, *AL* charged at them and they fled: *NK* returning to the tree, probably wounded, while *CT* left the party.

HJM described how, at around 12:45, during a lull in the aggression and with *PM* severely incapacitated, bleeding, beaten and unable to flee, *AL* performed repeated undirected charging displays (a behaviour that male chimpanzees use to exhibit their dominant position: Goodall 1986) for *ca.* 15 minutes. Afterwards, *OR*, *BB*, *DE* and *AL* approached *PM*, who pant-grunted to *AL*. The four males attacked *PM* again. It was at this time that MN saw *DE* striking *PM* on the back of the head with a large stone held with both hands. Subsequently, *PM* tried to stand but he fell down. This was the final attack, and *PM* was dead by 13:25.

# Post-mortem inspection and causes of death

An examination of the wounds on PM's body by SSKK & SI confirmed the witnesses' account: there was a big hole on the nose and forehead (Fig. 2) caused by bites; the hands and feet were full of wounds: on the heels, there were deep cuts (Fig. 3a), the right index finger was almost severed (Fig. 3b) and on the left hand there was a large gash, which might have come from the initial conflict with PR, going from the wrist up to the palm. Furthermore, there were many lacerations on the mouth, on the back (especially on the lower back, around the anus) and on the testicles. In contrast, the attackers suffered few wounds: in addition to PR's injury to his left hand sustained in the first fight, AL had a cut on the back of his left knee.

## Discussion

We report the first observation of coalitional, intra-community, lethal violence in chimpanzees in which the victim was an incumbent alpha male. We also provide the first report of weapon-use in intra-specific violence in chimpanzees, with the use of a large stone to deliver what may well have been the killing blow.

This coalitional attack, if not the lethal violence, is probably best explained as an opportunistic challenge for social dominance by AL, who was alpha male before being displaced by PM. The fight between alpha male PM and beta male PR, which resulted in obvious wounds for both, may have created a situation that the third-ranked AL was able to exploit. This view is supported by the lack of any clear indication that PM's position as alpha male was under imminent threat prior to the attack.

PM did, however, direct more aggression towards PR (0.21/hr) than any other male (average rate: 0.06/hr) suggesting that PR, as beta male, represented a threat to which PM had to respond. Intriguingly, three weeks before his death PM was forced to seek refuge in a tree in the face of coalitional aggression by DW and PR that was apparently in provoked by screams from the fully swollen adult female LD (Linda), whom PM was harassing (sensu Clutton-Brock and Packer 1995).

The fight between *PR* and *PM* reported here could be regarded as an attempt by *PR* to seize alpha rank: from the result, they seemed fairly well matched; while *PR* fled and we ascribed the 'win' to *PM*, it was not convincing. *PR* had not, however, shown any prior indication of intent to challenge for alpha male, as has sometimes been seen in this community (withholding pant-grunts, or increasing grooming interactions before launching an attack: Inaba 2009), so his aggression may simply have been retaliation to the violent attack by *PM*, rather than an explicit challenge for

social rank. After the fight, PR was not seen in the company of other chimpanzees for almost a week, and may have been fearful of further aggression from PM if he was unaware of the subsequent coalitional violence. His narrow loss to PM, along with the costly nature of the fight to both participants, seems to have created an opportunity that AL exploited. Following the attack, although the hierarchy was thrown into a period of instability (for the month following, stability index S = 0.14), AL seized alpha status and held this after PR's return.

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DE, slayer of PM and AL's coalition partner in the attack, was in his late 40's (~48 yrs) at the time of these observations. He has a long 'political' history in Mgroup. He was twice alpha male himself, displacing NT (Ntologi) in 1991 and replacing NS (Nsaba) who disappeared in 1996 (Nishida 1996, 2011). DE has repeatedly shown 'allegiance fickleness', both in challenging and supporting the current alpha male, through which he has been able to maintain a higher status for himself in the community than would otherwise be the case (Nishida 2011). While it may be no more than coincidence, when DE was alpha male he led two vicious, but non-lethal, coalitional attacks on the adult male JI (Jilba) and attempted to mount a similar attack on the deposed NT, although this failed as NT escaped (Nishida 2011). In the months prior to PM's death, DE had been exchanging 73% of his grooming with the three top-ranking males (PM, PR, AL) which was significantly higher than the grooming exchanged with the other males (Mann-Whitney: U = 21;  $N_1 = 3$ ;  $N_1 =$ 6; p = 0.014), while PM was DE's main supporter against the other males (Kaburu unpublished data). Given DE's history, however, it is no surprise that he involved himself with the attack on PM and supported AL against his erstwhile ally.

As with other accounts of within-community lethal violence, the attack on *PM* by four adult males resembles inter-community attacks, notably in the intensity of the violence and the use of overwhelming force. The Imbalance of Power hypothesis (Bygott 1979; Manson and Wrangham 1991; Wrangham 1999) posits that with sufficient numbers, which in chimpanzees seems to be four attackers to a single victim (Newton-Fisher and Emery Thompson in press), costs to attackers are very low and they are able to engage in intense violence with little risk to themselves. Lethal violence in inter-community aggression is thought to yield benefits by slowly reducing the relative coalitional power of neighbouring groups, thus increasing the probability of winning future encounters (Boone 1991; Wrangham 1999, 2006), which is turn may allow territorial expansion (Crofoot and Wrangham 2010; Mitani, Watts and Amsler 2010).

The benefits of lethal violence within communities are less clear. Males in the same community are rivals for reproductive opportunities, so tolerance for rivals should be conditional on the fitness benefits that coalitional partners confer. When threats from neighbouring communities are low, as may be the case at present for *M*-group chimpanzees (although the disappearance of 15 individuals in 1995/6 remains unexplained: Nishida 2011), there may be less constraint on the use of violence in within-community aggression and the loss of an individual male may not be particularly costly to those who remain.

In the incident we report here, the four attackers were able to exert intense and ultimately lethal aggression despite the presence of allies for the victim. At least initially, *PM* received support from two males, one of whom was a previous alpha male and still outranked three of the attackers. Unlike in confrontations between

communities, the interests of males involved in within-community contests may rarely coalesce entirely and defenders have to balance the benefits they might gain from allying with a victim against the risk of becoming a new target for an aggressive coalition's violence: a coalition of at least four adult males may therefore be a difficult force to stop in such situations. It may be that the absolute size of the attacking coalition is more important than the ratio of attackers to victim(s).

The escalation of violence beyond that necessary for *AL* to defeat *PM* remains difficult to explain. The attackers, in particular *DE*, seemed intent on ensuring his death: *PM* had pant-grunted to *AL*, thus acknowledging that he had lost, and he may have died from his injuries in any event. Although some other accounts of lethal violence suggest planning, or 'revenge' (e.g. the previous case from Mahale, the death of *NT*: Nishida 2011), it may simply be that the pressures and fitness consequences of aggressive territoriality have resulted in male chimpanzees being adapted to exploit lethal violence whenever individual interests coalesce and they are able to achieve the necessary imbalance of power. To facilitate this, they may possess a psychological threshold related to the level of violence performed or the degree of wounding in the victim, beyond which they cannot control the intensity of their aggressive behaviour regardless of the behaviour of their victim (Watts 2004).

This episode also raises interesting questions regarding the evolution of weapon-use in human conflicts. To date, there is little evidence regarding when hominines started employing simple objects, such as stones and branches, as weapons to kill or maim conspecifics although anatomical evidence suggests that the ability to handle objects for throwing and clubbing might have evolved early (Young 2003). While chimpanzees will incorporate objects into displays of dominance (Goodall

1986; McGrew 1992), and have been reported to use spear-like sticks for extractive hunting of small mammals (Nakamura and Itoh 2008; Pruetz and Bertonali 2007), they typically rely on their sharp teeth to inflict wounds in violence against other chimpanzees (Wilson, Wallauer, and Pusey 2004; Wrangham 1999, 2006). The use of a branch and a stone in the killing of *PM* demonstrate that chimpanzees have at least rudimentary ability to use objects as weapons, although further observations are needed to clarify to what extent this observation represents more than the idiosyncratic behaviour of a particular adult male.

Nevertheless, the case reported raises the possibility that the use of objects as weapons may be a shared trait for chimpanzees and humans, perhaps linked to a general tendency to engage in lethal violence. Early hominines, with smaller and less effective canines than extant chimpanzees, might have used similar weapons to a greater extent than heretofore realised. If these hominines were also engaged in lethal coalitional aggression, then the usefulness of weapons in such contexts may have driven the development of deliberate crafting of such tools.

# 357 Figure legends 358 Fig. 1 PM (right hand side) is sitting, leaning on his left arm, surrounded by 5 males. 359 Individuals facing the cameras are AL (on the left) and DE (on the right). Males 360 turning with backs to the camera are from left to right: BB, OR and DW (Photo by 361 Jennifer Scott). 362 363 Fig. 2 PM severely injured in his face: He displays a big hole on the front and cut on 364 the right hand side of the face (Photo by Jennifer Scott). 365 366 Fig. 3 PM received a high number of injuries, among which, (a) his heels were bitten 367 in order to prevent him from running away and (b) his right index finger was almost cut off (Photo by Stefano Kaburu). 368 369

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# Footnotes

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