Title: A leopard ate a chimpanzee: The first evidence from East Africa

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Introduction

Primates may have suffered predation pressures throughout their evolutionary history. Hominoids have been sympatric with large carnivores since the early Miocene in Africa (Werdelin and Peigné, 2010), and it is thought that predation pressure by large carnivores has played a significant role in their evolution (Hart and Sussman, 2005). For example, carnivore predation on *Proconsul* has been inferred from site R114 ("Pot-hole") on Rusinga Island, Kenya, where the partial skeleton of *P. heseloni* KNM-RU 2036 was recovered (Walker and Shipman, 2005).

In addition to fossil evidence, data on predation on living primates is also important for reconstructing the predation pressure on our human ancestors. Among potential nonhuman predators of living African apes, leopards (*Panthera pardus*) and lions (*Panthera leo*) have been known to actually prey upon apes. There has been only one report of lion predation on apes (Tsukahara, 1993). Lions are usually allopatric with apes because they are absent from tropical rainforests (Nowell and Jackson, 1996) where the majority of apes live. On the other hand, because leopards occur in most parts of sub-Saharan Africa (*ibid.*), they may be more likely than lions to prey upon apes. There has been limited information on leopard predation on apes, and all data have come from West and Central Africa (Table 1). Moreover, despite long-term research on

chimpanzees (*Pan troglodytes schweinfurthii*) at several sites in East Africa, no instances of leopard predation have been reported. This is probably because of the recent extirpation of leopards from most of the research sites. According to personal communications from experienced field researchers, there has been no evidence of the presence of leopards for a decade or more at the research sites of Gombe (Wilson ML) in Tanzania, and Kalinzu (Hashimoto C), Kibale (Struhsaker T, Mitani JC, and Mills DR), and Budongo (Newton-Fisher NE) in Uganda. The only exception is Mahale in Tanzania where leopards have lived sympatrically with chimpanzees, without evidence of predation by the former on the latter (Nishida 2012). There have been several reports of encounters between leopards and chimpanzees from Tanzania including Mahale (reviewed in Pierce, 2009). Responses of chimpanzees to leopards varied from emitting loud, fearful calls, vigilance, and acting in a threatening manner (e.g., Pierce, 2009); stalking a leopard that had called in the distance (Mitani JC, personal communication); to surrounding a den and killing a cub (Hiraiwa-Hasegawa et al., 1986).

Boesch (2009) asserted that *all* well-studied East African chimpanzee populations face little or no predation pressure. Although he recognized the presence of leopards at Mahale, he insisted that leopards were rare there, so that predation was negligible. During a systematic survey of leopard scats, we found the first evidence of

55 the consumption of an eastern chimpanzee at Mahale. Here, we report the details of this
56 evidence.
57
58 **Methods**
59 We collected leopard scats in the Mahale Mountains National Park, Tanzania (Nishida,
60 2012) for 41 days in June–August 2012. Although other large carnivores (lions, hunting
61 dogs, and hyenas) are reported to inhabit the park, no direct or indirect evidence of the
62 former 2 species has been observed in the study area for more than 2 decades (also, no
63 domestic dogs have been confirmed in the area). Hyena scats were observed in 2005
64 and 2008 but were distinguishable from those of leopards by its very whitish appearance
65 and finer digestion of bones. Thus, it is unlikely that we misidentified leopard scats with
66 those of other species. We walked observation trails within the home range of the
67 habituated M group chimpanzees (387 min/day on average). When a scat was found, we
68 recorded its location with GPS and carried it back to our camp. After being dried and
69 weighed, we inspected its contents for hair, bones, and skin. To confirm whether the
70 contents were of chimpanzees, we conducted morphological investigations and DNA
71 analysis. Taxonomic identification was based on previous work on comparative primate
72 postcranial morphology (Ward et al., 1995; Nakatsukasa et al., 2003). DNA was

73 extracted from a small bone using a TBONE EX KIT (DNA Chip Research Inc., Japan)
74 and a 331-base pair segment of the mitochondrial hypervariable control region (Inoue et
75 al., 2011) was analyzed. We also examined the XY homologous gene amelogenin for
76 sex identification and 8 microsatellite loci for individual identification (Inoue et al.,
77 2008).
78
79 **Results**
80 We collected 142 leopard scats, among which one contained the right and left patellae,
81 the distal end of a manual proximal phalanx, and an intact manual intermediate phalanx
82 of a chimpanzee (Fig. 1). The patellae are morphologically similar and almost identical
83 in size. The completely fused proximal epiphysis of the intermediate phalanx,
84 morphology of the ligamentous insertion on the patella and modestly developed flexor
85 sheath ridges on the phalanges suggest these bones belonged to an adult (not old), and
86 probably a female based on general size and robusticity criteria. The distal part is
87 chewed off and trabeculae are exposed dorsally in both patellae (Fig. 1 a, b). The break
88 surface is mediolaterally long and gently concave. The dorsal (= posterior) break edge is
89 more proximal than in the ventral (= anterior) break edge, which approximates the
90 original distal border. The missing part includes the whole attachment area of the

91 patellar ligament. The cut surface suggests that the leopard filled its mouth with the
92 distal part of the quadriceps femoris muscles and the patella and tried to cut off the
93 mouth infill from the remaining carcass. Probably, the patella (and the ligament) was
94 not fully turned over, and the leopard's carnassials could not reach the patellar ligament
95 but only the ligament attachment area. The right patella also has a bite mark on the
96 lateral rim (Fig. 1 b). There is no gnaw mark on the intermediate phalanx (Fig. 1 c).
97 Along the proximal epiphysis of the intermediate phalanx, the cortex is damaged,
98 probably caused by the acid (or acidotic erosion and physical stress). The break on the
99 proximal phalanx is a common fracture pattern.

100 The scat was found on June 18, 2012, at the beginning of the dry season. It was
101 not very fresh but estimated to be no older than 4 months from its appearance and the
102 extent of preceding rainfalls (the main factor in scat decay). The location (Fig. 2) is
103 within the M group's home range and is used exclusively by the group (Nakamura et al.,
104 2013). We had seen and heard evidence of leopards (foot prints, roars, etc.) on 10
105 different days within the preceding month. On June 13, a field assistant had observed a
106 leopard and night guards said they frequently observed leopards around that time.

107 Five M group chimpanzees that had disappeared within the preceding 4
108 months were potential candidates for the victim. DNA profiles of these candidates or of

109 their mothers were available (Table 2). Analyses of DNA extracted from a phalanx of
110 the victim (hereafter “Bone2012”) reconfirmed that Bone2012 was actually a female
111 chimpanzee. Her mitochondrial haplotype was B, a common haplotype in the M group
112 (Inoue et al., 2011), but among candidates, only a male AG had this haplotype.
113 Microsatellite analyses also showed that two candidates (CA and TZ) had different
114 alleles from Bone 2012 at 5 or more loci. Mothers of 3 other candidates (AG, ME, and
115 TZ09) did not share alleles with Bone2012 at 2 loci. Therefore, we conclude that
116 Bone2012 was not an individual from the M group.
117
118 **Discussion**
119 We confirmed that a leopard ate an adult female chimpanzee at Mahale. This is the first
120 evidence of leopard consumption of eastern chimpanzees (*P. t. schweinfurthii*), which
121 adds another subspecies to the list of apes consumed by leopards.
122 The scat was found within the M group’s home range but the victim was not
123 from the group. Because the home range of a different chimpanzee group reaches to
124 approximately 1 km north of the scat location, a small distance compared to known
125 leopard range sizes (Jenny, 1996), the leopard may have eaten a chimpanzee of that
126 group, then moved into the M group’s home range and defecated. Alternatively, it may

have eaten an unknown female right after her emigration from her natal group to the M group. If the leopard actually *killed* the victim, this means that a leopard can prey on a full adult female chimpanzee. Female chimpanzees are smaller in body size, less aggressive, and less gregarious than males, and thus could be more prone to predation. The predation risk would be even higher when females transfer alone between unit-groups. Thus, we might need to take such potential risk from female transfer into account when discussing how a female-dispersal social structure, like that of chimpanzees, could have evolved.

Contrary to the assumption of Boesch (2009) that no eastern chimpanzee research sites have as many leopards as in the Taï forest, we found comparable, or even greater, numbers of scats per day than at Taï or Lopé (Table 1). Nevertheless, we have to be cautious about direct comparisons because research efforts might differ. Evidence of leopards was quite frequent during the study period. On the basis of the 1–2 leopard sightings per year at Taï (Boesch and Boesch-Achermann, 2000, Table A.2), we cannot conclude that leopards are rarer in Mahale than in Taï.

Because leopards sometimes do scavenge (Bailey, 1993), we cannot determine from scat evidence alone whether the leopard killed the chimpanzee or scavenged a corpse. However, observations of 3 seriously injured M group chimpanzees may suggest

occasional leopard attacks on chimpanzees. In 2009, one male chimpanzee had a much deeper wound than usually caused by fights among male conspecifics. Further, in 2011, a mother-infant pair was found injured and the mother had 3 long, parallel scars from the head to the back, seemingly caused by claws. Because researchers had thought that leopards did not eat chimpanzees at Mahale (Nishida, 2012), they had assumed that all serious injuries came from intraspecific fights. Now, because there has been confirmed leopard consumption of a chimpanzee, we should also consider attacks by leopards as a possible cause of injury or death for Mahale chimpanzees. Again, if the victim was actually killed by a leopard, this means that predation pressure has been underestimated for more than 40 years at Mahale or, alternatively, that leopards have recently shifted their diet to include chimpanzees. If the former is the case, this might imply a wider underestimation of predation pressures on primates in general. Because predation events are rarely observable but can still be significant to primates' behavioral and social evolution, we might need to acquire a better picture of carnivore-primate relationships with long-term data. The ecology and behavior of Mahale leopards have yet to be studied. Because information on predation pressure on living apes is still too scarce to be used to infer the predation pressure on fossil hominins, we may need to investigate further the ecology and behavior of leopards that are currently sympatric with apes.

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230

231 **Table 1** Reported leopard predation/consumption of African apes

Study site (Country)	Species/subspecies	Evidence of predation		Source
		Leopard scats[1]	Indirect evidence	
Taï (Côte d'Ivoire)	*Pan troglodytes verus*	0/215 (15 months) 1/200 (1 year)	Three deaths possibly by leopards	Hoppe-Dominik, 1984 Boesch 1991; 2009, Zuberbühler and Jenny, 2002
Dzanga-Sangha (Central African Republic)	*Gorilla gorilla gorilla*	Yes[2]	N/A	Fay et al., 1995
Lopé (Gabon)	*G. g. gorilla* *P. t. troglodytes*	6/196 (8 years) 4/196 (8 years)	N/A	Henschel et al., 2005
Petit Loango (Gabon)	*P. t. troglodytes*	N/A	Leopard scats and footprints near chimpanzee corpse	Furuichi, 2000
Lui Kotal (Democratic Republic of Congo)	*P. paniscus*	Yes[2]	N/A	D'Amour et al., 2006

232 [1] The figures indicate the number of scats containing ape bones/the total number of scats collected. The duration of fecal collection is shown in parentheses.
233 [2] No mention of the number of scats.

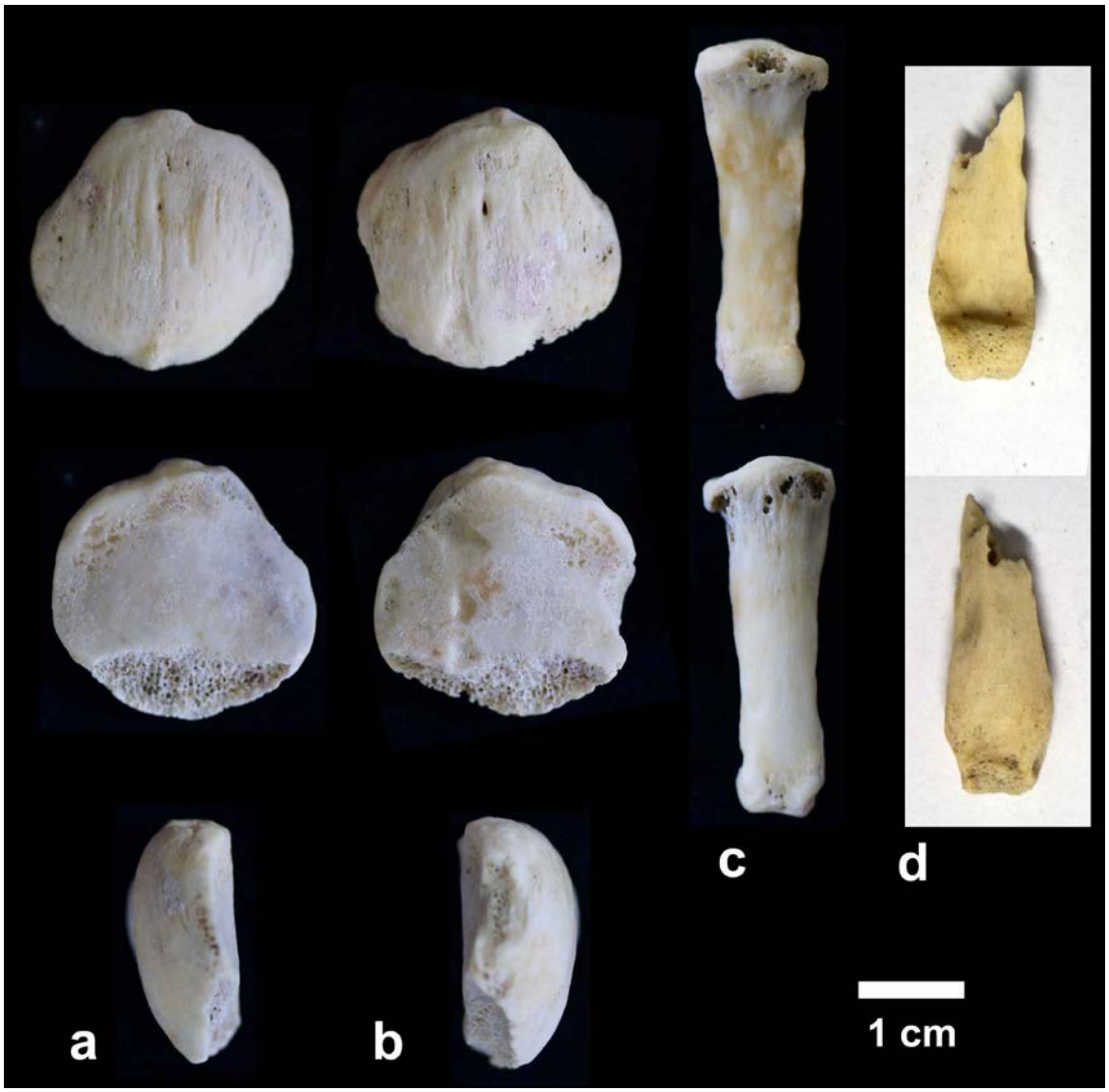
Table 2 DNA profile of the chimpanzee bone found in a leopard scat in comparison with those of M group chimpanzees that disappeared in 2012

Names of chimpanzees	**Age (years)**	**Sex**	**Mitochondrial haplotype[1]**	**Microsatellite loci[1]**							
				D9s910	**D11s2002**	**D2s1329**	**D12s66**	**D2s1326**	**D5s1470**	**D7s2204**	**D7s817**
Bone2012	adult?	F	B	104/104	148/148	178/202		182/218	190/190	245/249	116/116
Candidates											
CA	52[3]	F	C	104/110	148/156	182/198	158/182	182/186		249/253	112/124
TZ	30[3]	F	A	104/110	148/148	178/198	154/154	202/206	186/190	245/249	144/148
AG[2]	7	M	B	104/104	148/148	178/182	150/182	150/182	194/194	245/253	148/152
ME[2]	10	F	C	104/113	148/148	186/198	182/182	182/182	186/190	249/249	148/152
TZ09[2]	2	F	A	104/110	148/148	178/198	154/154	202/206	186/190	245/249	144/148

[1]Mitochondorial haplotype and microsatellite genotypes of the candidates are described in Inoue et al. (2011) and Inoue et al. (2008), respectively.
[2]DNA data from their mothers are shown because their own DNA is not available. A mother shares a mitochondrial haplotype and at least one allele at all loci with offspring.
[3]Estimated age
Underlined data show mismatches with Bone 2012.

242 **Figure 1**

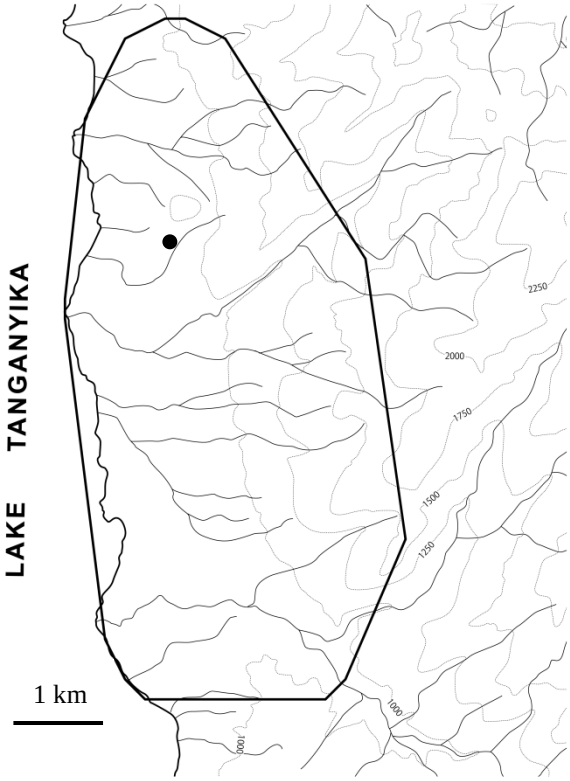
243



244

245

246 **Figure 2**



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248

249 **Figure Legends**

250 **Figure 1.** Recovered chimpanzee bones. a, b: left and right patellae, respectively (from
251 top to bottom: anterior, posterior, and lateral views). c: middle phalanx (top: palmar
252 view). d: distal fragment of a proximal phalanx (top: palmar view).

253

254 **Figure 2.** The location where the leopard scat with chimpanzee bones was found (black
255 dot) in relation to the home range of the M group chimpanzees (a polygon).