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
the consumption of an eastern chimpanzee at Mahale. Here, we report the details of this evidence.

Methods

We collected leopard scats in the Mahale Mountains National Park, Tanzania (Nishida, 2012) for 41 days in June–August 2012. Although other large carnivores (lions, hunting dogs, and hyenas) are reported to inhabit the park, no direct or indirect evidence of the former 2 species has been observed in the study area for more than 2 decades (also, no domestic dogs have been confirmed in the area). Hyena scats were observed in 2005 and 2008 but were distinguishable from those of leopards by its very whitish appearance and finer digestion of bones. Thus, it is unlikely that we misidentified leopard scats with those of other species. We walked observation trails within the home range of the habituated M group chimpanzees (387 min/day on average). When a scat was found, we recorded its location with GPS and carried it back to our camp. After being dried and weighed, we inspected its contents for hair, bones, and skin. To confirm whether the contents were of chimpanzees, we conducted morphological investigations and DNA analysis. Taxonomic identification was based on previous work on comparative primate postcranial morphology (Ward et al., 1995; Nakatsukasa et al., 2003). DNA was
extracted from a small bone using a TBONE EX KIT (DNA Chip Research Inc., Japan) and a 331-base pair segment of the mitochondrial hypervariable control region (Inoue et al., 2011) was analyzed. We also examined the XY homologous gene amelogenin for sex identification and 8 microsatellite loci for individual identification (Inoue et al., 2008).

Results

We collected 142 leopard scats, among which one contained the right and left patellae, the distal end of a manual proximal phalanx, and an intact manual intermediate phalanx of a chimpanzee (Fig. 1). The patellae are morphologically similar and almost identical in size. The completely fused proximal epiphysis of the intermediate phalanx, morphology of the ligamentous insertion on the patella and modestly developed flexor sheath ridges on the phalanges suggest these bones belonged to an adult (not old), and probably a female based on general size and robusticity criteria. The distal part is chewed off and trabeculae are exposed dorsally in both patellae (Fig. 1 a, b). The break surface is mediolaterally long and gently concave. The dorsal (= posterior) break edge is more proximal than in the ventral (= anterior) break edge, which approximates the original distal border. The missing part includes the whole attachment area of the
patellar ligament. The cut surface suggests that the leopard filled its mouth with the
distal part of the quadriceps femoris muscles and the patella and tried to cut off the
mouth infill from the remaining carcass. Probably, the patella (and the ligament) was
not fully turned over, and the leopard’s carnassials could not reach the patellar ligament
but only the ligament attachment area. The right patella also has a bite mark on the
lateral rim (Fig. 1 b). There is no gnaw mark on the intermediate phalanx (Fig. 1 c).
Along the proximal epiphysis of the intermediate phalanx, the cortex is damaged,
probably caused by the acid (or acidotic erosion and physical stress). The break on the
proximal phalanx is a common fracture pattern.

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

Five M group chimpanzees that had disappeared within the preceding 4
months were potential candidates for the victim. DNA profiles of these candidates or of
their mothers were available (Table 2). Analyses of DNA extracted from a phalanx of the victim (hereafter “Bone2012”) reconfirmed that Bone2012 was actually a female chimpanzee. Her mitochondrial haplotype was B, a common haplotype in the M group (Inoue et al., 2011), but among candidates, only a male AG had this haplotype. Microsatellite analyses also showed that two candidates (CA and TZ) had different alleles from Bone 2012 at 5 or more loci. Mothers of 3 other candidates (AG, ME, and TZ09) did not share alleles with Bone2012 at 2 loci. Therefore, we conclude that Bone2012 was not an individual from the M group.

Discussion

We confirmed that a leopard ate an adult female chimpanzee at Mahale. This is the first evidence of leopard consumption of eastern chimpanzees (P. t. schweinfurthii), which adds another subspecies to the list of apes consumed by leopards. The scat was found within the M group’s home range but the victim was not from the group. Because the home range of a different chimpanzee group reaches to approximately 1 km north of the scat location, a small distance compared to known leopard range sizes (Jenny, 1996), the leopard may have eaten a chimpanzee of that 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.
Acknowledgements

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References


Table 1  Reported leopard predation/consumption of African apes

<table>
<thead>
<tr>
<th>Study site (Country)</th>
<th>Species/subspecies</th>
<th>Evidence of predation</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taï (Côte d’Ivoire)</td>
<td>Pan troglodytes verus</td>
<td>Leopard scats¹</td>
<td>Hoppe-Dominik, 1984</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0/215 (15 months)</td>
<td>Boesch 1991; 2009,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1/200 (1 year)</td>
<td>Zuberbühler and Jenny, 2002</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Indirect evidence</td>
<td>Three deaths possibly by leopards</td>
</tr>
<tr>
<td>Taï (Côte d’Ivoire)</td>
<td>Pan troglodytes verus</td>
<td>N/A</td>
<td>Henschel et al., 2005</td>
</tr>
<tr>
<td>Dzanga-Sangha (Central African Republic)</td>
<td>Gorilla gorilla gorilla</td>
<td>Yes²</td>
<td>Fay et al., 1995</td>
</tr>
<tr>
<td>Lopé (Gabon)</td>
<td>G. g. gorilla</td>
<td>Leopard scats²</td>
<td>Henschel et al., 2005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6/196 (8 years)</td>
<td></td>
</tr>
<tr>
<td>Lopé (Gabon)</td>
<td>P. t. troglodytes</td>
<td>N/A</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>4/196 (8 years)</td>
<td></td>
</tr>
<tr>
<td>Petit Loango (Gabon)</td>
<td>P. t. troglodytes</td>
<td>N/A</td>
<td>Furuichi, 2000</td>
</tr>
<tr>
<td>Lui Kotal (Democratic Republic of Congo)</td>
<td>P. paniscus</td>
<td>Yes²</td>
<td>D’Amour et al., 2006</td>
</tr>
</tbody>
</table>

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.
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

<table>
<thead>
<tr>
<th>Names of chimpanzees</th>
<th>Age (years)</th>
<th>Sex</th>
<th>Mitochondrial haplotype</th>
<th>Microsatellite loci&lt;sup&gt;1&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>CA</td>
<td>52&lt;sup&gt;3&lt;/sup&gt;</td>
<td>F</td>
<td>C</td>
<td>104/110  148/156  182/198  154/154  186/190  144/148</td>
</tr>
<tr>
<td>TZ</td>
<td>30&lt;sup&gt;3&lt;/sup&gt;</td>
<td>F</td>
<td>A</td>
<td>104/110  148/148  178/198  150/182  202/206  245/249  148/152</td>
</tr>
<tr>
<td>AG&lt;sup&gt;2&lt;/sup&gt;</td>
<td>7</td>
<td>M</td>
<td>B</td>
<td>104/104  148/148  178/182  150/182  186/190  148/152</td>
</tr>
<tr>
<td>ME&lt;sup&gt;2&lt;/sup&gt;</td>
<td>10</td>
<td>F</td>
<td>C</td>
<td>104/113  148/148  186/198  182/182  202/206  148/152</td>
</tr>
<tr>
<td>TZ09&lt;sup&gt;2&lt;/sup&gt;</td>
<td>2</td>
<td>F</td>
<td>A</td>
<td>104/110  148/148  178/198  154/154  202/206  144/148</td>
</tr>
</tbody>
</table>

<sup>1</sup>Mitochondrial haplotype and microsatellite genotypes of the candidates are described in Inoue et al. (2011) and Inoue et al. (2008), respectively.

<sup>2</sup>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.

<sup>3</sup>Estimated age

<sup>4</sup>Underlined data show mismatches with Bone 2012.
Figure 1
Figure 2
Figure Legends

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

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