Baker, SA, Stewart, FA and Piel, AK

A case of suspected chimpanzee scavenging in the Issa Valley, Tanzania

http://researchonline.ljmu.ac.uk/id/eprint/22441/

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Baker, SA, Stewart, FA and Piel, AK (2023) A case of suspected chimpanzee scavenging in the Issa Valley, Tanzania. Primates, 65 (1). pp. 41-48. ISSN 0032-8332

A case of suspected chimpanzee scavenging in the Issa Valley, Tanzania

Sam A. Baker [1], Fiona A. Stewart [1,2], Alex K. Piel [1]

[1] University College London, UK

[2] Liverpool John Moores University, UK

[1] sam.baker.20@ucl.ac.uk (ORCID: 0000-0003-4613-8702)
[1,2] f.stewart@ucl.ac.uk
[1] a.piel@ucl.ac.uk

Abstract

Like humans, chimpanzees (*Pan troglodytes*) are well-known for their vertebrate and invertebrate hunting, but they rarely scavenge. In contrast, while hunting and meat consumption became increasingly important during the evolution of the genus *Homo*, scavenging meat and marrow from carcasses of large mammals was likely also an important component of their subsistence strategies. Here, we describe a confrontational scavenging interaction between an adult male chimpanzee from the Issa Valley and a crowned eagle (*Stephanoaetus coronatus*), which resulted in the chimpanzee capturing and consuming the carcass of a juvenile bushbuck (*Tragelaphus scriptus*). We describe the interaction and contextualise this with previous scavenging observations from chimpanzees.

Keywords

Meat-eating; Carcass theft; Inter-specific competition; Raptor; Hominin subsistence strategies; Hominin evolution

Acknowledgments

We thank the Tanzania Wildlife Research Institute (TAWIRI), Tanzania Commission for Science and Technology (COSTECH), and the Tanganyika District government for permission to conduct research at Issa. The UCSD/Salk Center generously provides long-term support for the research at Issa for Academic Research and Training in Anthropogeny (CARTA). We express our gratitude to Editor-in-Chief Masayuki Nakamichi for the opportunity to publish and to Drs. Michio Nakamura, David Watts, and Kazuhiko Hosaka for their valuable contributions to this manuscript.

Introduction

Despite rich comparisons between human and chimpanzee (*Pan troglodytes*) hunting techniques (Boesch and Boesch-Achermann 2000; Domínguez-Rodrigo and Pickering 2003), scavenging has been attributed almost exclusively to modern humans (Bunn 2001; Domínguez-Rodrigo et al. 2009) and early hominins (Thompson et al. 2019). Scavenging behaviour is broadly defined as the acquisition and consumption of organic tissue (e.g., meat, bone, etc.) from carcasses of vertebrates that were not killed by the scavenger.

Hominins are hypothesised to have begun consistently obtaining meat by scavenging in the Plio-Pleistocene (Shipman 1986; Blumenschine 1991; Blumenschine and Cavallo 1992), either passively (Blumenschine 1991; Blumenschine and Cavallo 1992; Pante et al. 2012) or confrontationally (O’Connell et al. 2002). A passive scavenging event involves the scavenger reaching a carcass following the departure of the original predator and was likely the basic pattern of scavenging for early hominins (Blumenschine 1991). A confrontational scavenging event is characterised by the scavenger displacing the original predator from the carcass and is inherently more risky for the scavenger.

Both types of scavenging behaviour also occur in wild chimpanzees (Morris and Goodall 1977; Goodall 1986; Watts 2008; Hosaka 2015; Hosaka and Ihobe 2015; Nakamura et al. 2019). Here, we follow the above definitions and separate confrontational scavenging into either power scavenging (Bunn 2001) or carcass theft (Watts 2008). Power scavenging involves the displacement of a species known to prey on chimpanzees, e.g., leopards (*Panthera pardus*) (Boesch 1991; Boesch 2009) and increases the chance of injury for both chimpanzees and the predator. Carcass theft involves the displacement of a species that does not prey on the scavenger (Watts 2008), e.g., raptors or medium-sized carnivores like civets (*Civettictis civetta*), caracals (*Caracal caracal*), and baboons (*Papio* spp.). The species displaced during confrontational scavenging is typically referred to as either the 'original predator' or 'confronted species', with the latter being more suitable when predation is difficult to infer.

In most cases, confrontational scavenging results in relatively early carcass access, whilst passive scavenging usually results in late access (Watts 2008). Both the risks and the expected payoffs are higher for confrontational scavenging as successful confrontational scavenging is more likely to lead to the acquisition of fleshed carcasses that yield greater caloric reward. Conversely, late access, usually via passive scavenging, typically results in the retrieval of a defleshed carcass and provides minimal caloric gain (Blumenschine 1991).

Significant archaeological evidence shows that by ~1.8-2 Myr ago, hominins were likely gaining regular access to fleshed carcasses of small and medium-sized bovids (Yravedra et al. 2020). However, disagreement persists concerning the point at which hominins gained access to carcasses. Blumenschine (1991) suggests that "maximisation of marrow (fat) yields, not flesh (protein) yields, was the criterion shaping decisions about carcass processing". That is, bone marrow via late access was likely the primary food source provided by scavenged carcasses. Others point to evidence for the existence of early access scavenging in hominins at *Homo erectus* deposits, such as Olduvai (FxJj 50) and Peninj sites in Tanzania (Blumenschine 1991; Domínguez-Rodrigo 2002), as well as from *Homo erectus* deposits in Gona, Ethiopia (Domínguez-Rodrigo et al. 2005). Pervasive across these sites are the high frequencies of cut marks, combined with low frequencies of carnivore tooth marks on upper-limb and pelvic bones from archaeofaunal remains of medium and large Bovidae species such as impala, gazelle, and wildebeest (Bunn et al. 1980) – indicative of hominin scavenging and modification (i.e., butchery).

Moreover, insufficient evidence exists of the projectile technology necessary for Plio-Pleistocene hominins to hunt prey of these sizes: Oldowan and early Acheulean technologies raise questions about their adequacy in this role (Stiner 2002). Domínguez-Rodrigo and Barba (2006) conclude that hominins ~1.75 Myr ago had systematic early access to carcasses and, if access was not facilitated by hunting, other strategies such as confrontational scavenging might have facilitated the capture of fleshed carcasses (O'Connell et al. 2002). Regardless of how the early versus late access debate is resolved, contemporary explanations for early access are hunting (Domínguez-Rodrigo et al. 2021) and confrontational scavenging (Ferraro et al. 2013).

Wild chimpanzee confrontational scavenging in the form of carcass theft described at Gombe, Tanzania, and Taï Forest, Ivory Coast (Table 1) may represent one potentially significant component of a subsistence model for a chimpanzee-human last common ancestor (LCA) or early hominins, and a precursor to increasingly complex and aggressive Plio-Pleistocene behaviour i.e., the 'home-base hypothesis' (Isaac 1971) and the 'hunting hypothesis' (Washburn and Lancaster 1968; Stanford and Bunn 2001). Now assume that an LCA lived in a tropical, deciduous woodland mosaic, with a mix of open (grassland) and closed (riparian forest) vegetation (reviewed in Andrews 2020), like the modern, open-habitats of some extant chimpanzees (Drummond-Clarke et al. 2022). In that case, we may expect similar subsistence strategies in the form of confrontational carcass thefts.

Chimpanzee scavenging

Wherever chimpanzees have been studied long-term, reports of meat-eating have followed, including a diverse vertebrate diet. Chimpanzees frequently hunt (Mitani and Watts 2001) and consume at least 51 mammal species (Watts in press), which include arboreal primates like red colobus monkeys (*Procolobus* spp.; Hobaiter et al. 2017) and bushbabies (*Galago senegalensis*; Pruetz and Bertolani 2007), as well as terrestrial mammalian species like bushpig (*Potamochoerus larvatus*) and bushbuck (*Tragelaphus scriptus*; Stanford 1996). Despite decades of long-term research at multiple communities across chimpanzee distribution (Nakamura et al. 2015; Boesch et al. 2019; Emery Thompson et al. 2020), less than two dozen observations of scavenging have been described, compared to thousands of successful hunting bouts.

We have limited data on the frequency with which different chimpanzee communities scavenge for food and how they react to finding carcasses. M-group (Mahale) chimpanzees have been observed scavenging some carcasses immediately upon possession (Nakamura et al. 2019) and have even deprived a leopard of access to a carcass (Nakamura et al. 2019). Equally, Mahale chimpanzees have also shown hesitation toward carcasses presumed to have been predated by a leopard (Hosaka et al. 2014). Mahale chimpanzees are analogous to their Ngogo (Uganda) and Gombe counterparts in that they occasionally demonstrate a reluctance to consume carcasses of prey and non-prey species (Nishida 1994; Nakamura et al. 2019). Reports from Ngogo describe a general curiosity toward carcasses (Watts 2008), while Gombe (Tanzania) chimpanzees sometimes ignore them entirely (Goodall 1986).

The differences in scavenging tendencies between communities are yet unknown; however, if variation exists in confrontational scavenging, it is likely a result of ecological differences, such as the density of sympatric predators (Nakamura et al. 2019). Chimpanzee encounters with predators are rarely observed directly. As a result, indirect accounts of confrontation are often inferred through (chimpanzee) vocalisations within the vicinity of the carcass or posthumously by predation marks, such as lacerations on the body and puncture wounds around the throat (Hiraiwa-Hasegawa et al. 1986; Nishida 1994). It is important to exercise caution when drawing conclusions about scavenging after the event. Leopards typically cache their prey for several days (Bailey 1993), so inferences alone are inadequate for determining whether confrontation occurred or if the carcass was passively scavenged whilst the leopard was away.

Only one first-hand account of confrontational scavenging by chimpanzees has been reported (Nakamura et al. 2019). It represents the only power scavenging observation beyond modern humans within the Primate order. The report describes Mahale M-group members depriving a leopard of a blue duiker (*Philantomba monticola*) carcass. Chimpanzee carcass theft has been documented 51 times, of which only seven (not including this observation) meet our criteria for Table 1 (see below).

Most (n=48) carcass thefts or ‘piracies’ from baboons have been reported from Gombe (in both Kasekela and Mitumba communities) (Gilby et al. 2017). However, we have only included accounts where both the predators and prey were identified, and their interaction was directly observed or reasonably inferred from the circumstances (e.g., via indirect observations and postmortem evidence). It is also compulsory that the carcass be consumed and not provided by researchers or previously hunted by chimpanzees and then abandoned. Consequently, we have cited only a small proportion (n=4) of detailed reports described in Morris and Goodall (1977) and Goodall (1986) in Table 1, summarising the remainder within the text above (Goodall 1986; Gilby et al.

2017). Similarly, we acknowledge three carcass thefts at Taï, reported by Boesch and Boesch-Achermann (2000), but have not included them in Table 1 due to the live status of the prey during the scavenging event, which contradicts our scavenging definition.

Here, we present the first observation of confrontational carcass theft in the Issa Valley (Figure 1) and contextualise it with previous descriptions from other communities. Our observation offers a second example of a chimpanzee-raptor confrontation but differs in an important way from the one reported at Taï over two decades ago (Boesch and Boesch-Achermann 2000). Issa chimpanzees (*Pan troglodytes schweinfurthii*) live in a savanna mosaic woodland and thus provide a more ecologically relevant model for hominin evolution (Drummond-Clarke et al. 2022).

Table 1 Published accounts of inferred and observed power scavenging and carcass theft across chimpanzee communities

Type	**Community**	**Scavenger age/sex**	**Scavenged species**	**Confronted species**	**Citation**
Power scavenging	M-group (Mahale, Tanzania)	adult female	blue duiker (*Philantomba monticola*)	leopard (*Panthera pardus*)	Nakamura et al. 2019
		–	red colobus (*Procolobus tephrosceles*)	leopard (*Panthera pardus*)	Hosaka 2015
Carcass theft		adult male	blue duiker	smaller-sized predator: e.g., civet or honey badger	Hosaka and Ihobe 2015
	Kasekela (Gombe, Tanzania)	adult male	bushbuck	olive baboon (*Papio anubis*)	Morris and Goodall 1977
		adult male	bushbuck	olive baboon (*Papio anubis*)	
		adult male	guinea fowl (*Meleagris numida*)	olive baboon (*Papio anubis*)	
		adult female	bushbuck	olive baboon (*Papio anubis*)	Goodall 1986
	Ngogo (Kibale, Uganda)	adult male	red duiker (*Cephalophus natalensis*)	olive baboon (*Papio anubis*)	David Watts, pers. comm., 22 Jan 2023
		adult male	blue duiker	olive baboon (*Papio anubis*)	

Note. Scavenging accounts were subject to the following criteria: accurate predator and prey identification, direct observation of interaction or reasonable inference based on circumstance, and the scavenging of a carcass not provided by researchers or previously hunted by chimpanzees and then abandoned

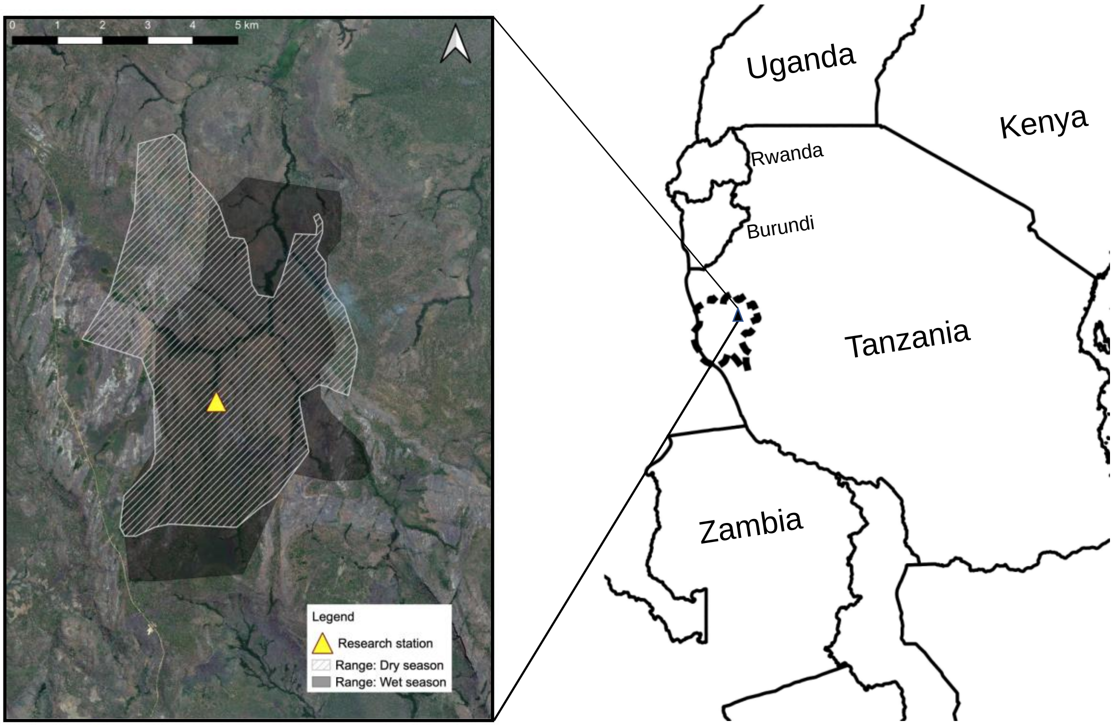

Figure 1 Issa community home ranges during the wet (shaded) and dry (lined) season from 2018-2020 are shown within the broader Greater Mahale Ecosystem (GME) (dotted outline)

Methods

Study site and subjects

The Issa Valley lies within the Tongwe West Forest Reserve, western Tanzania. Vegetation is characterised as a mosaic habitat of deciduous miombo woodland (dominated by *Brachysteria* and *Julbernardia*), interspersed with thin strips of riparian, evergreen forest (7% landcover), small patches of seasonally inundated grasslands, and rocky outcrops (Drummond-Clarke et al. 2022). Besides chimpanzees, the area hosts a rich diversity of small (D’Ammando et al. 2022) and medium-large (Piel et al. 2019) mammalian wildlife, including sympatric predators such as leopard, lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*), and wild dog (*Lycaon pictus*). Chimpanzees have preyed on various species, including blue duiker, bushbuck, and klipspringer (*Oreotragus oreotragus*) (Ramirez-Amaya et al. 2015; Moore et al. 2017; Piel and Stewart, unpublished data). The community have been habituated since 2018 and at the time of the observation, the community comprised 32 individuals (13 male and 12 female adults and subadults, along with seven dependent offspring) and ranged over at least 36km^2 (Giuliano et al. 2022).

Results

On 24 October 2021, S. Baker and a field assistant were following a party of nine chimpanzees, including five adult males (IM, SA, KI, BO, MA), one adult non-estrous female (BA), and three subadult males (DH, WI, MO). IM has been the highest-ranking male in the Issa community since 2018, followed by SA and KI. BO and MA are middle and low-ranking males, respectively. The party was crossing a riparian forest at 1345h when IM abruptly ran to the left out of the forest and into a (woodland) area of long grass. Researchers heard no vocalisations, and other party members continued travelling in the same direction as they were previously. In the moments immediately following, S. Baker observed a large raptor take flight from where IM now stood with the carcass (in mouth). Researchers were situated favourably as the bird took flight and confidently recalled its physical characteristics, identifying it as a mature crowned eagle (*Stephanoaetus coronatus*). Note: Observers did not detect laceration marks or puncture wounds on the carcass that indicated an attack by the raptor; IM was moving too quickly after he obtained the carcass, and once in the tree, the melee between group members shrouded the carcass from view. At this point, all the other chimpanzees in the party ran toward IM, who ran at speed to climb a nearby tree, and the others followed, except for MO, remaining near the base of the tree. Later, we confirmed that the carcass was a juvenile bushbuck (*Tragelaphus scriptus*), approximately 45 cm in head-body length. The bushbuck was lifeless when first observed but appeared intact and without deformation. Once in the tree (1350h), IM lost control of the carcass to an unidentified individual, and the five adult males (IM, SA, MA, BO, KI) began to compete for meat, accompanied by vocalisations (screams and hoots). KI procured a limb during the aggression, and the subadult male WI descended to the ground to retrieve a scrap that fell. Moments later (1353h), IM took back control of the carcass and was subject to intermittent begging behaviour (vocalisations and gestures – Gomes et al. 2019), primarily from males MA and SA and female BA for the following hour; only BA was allowed access to the meat. The remainder was entirely consumed by IM (Figure 2), who carried the carcass until 1530h. At that point, he dropped it, and WI retrieved and carried it for 60 minutes until 1630h when researchers lost contact with the party. In total, four individuals were observed to consume the meat, and only the skull remained (which researchers did not collect) when the party was last observed.

Figure 2 IM consumes the bushbuck carcass (credit: S. Baker/GMERC)

Discussion

With our description of a rare carcass theft at Issa, we contribute a new case of confrontational scavenging in chimpanzees from western Tanzania. This confrontation concerns the theft of a bushbuck carcass from a crowned eagle. Researchers were able to identify the confronted raptor species by its distinct physical characteristics: legs and flanks were blotched/ barred and closely spotted with black and white; underwing coverts had a bold chestnut colouration, spotted lightly with black; and primary underwing feathers were barred in black and white (Ferguson-Lees and Christie 2001). Although the moment of the theft was not directly observed, we can infer its occurrence due to the simultaneous flight of the crowned eagle from where chimpanzee IM was first observed holding the carcass. Due to the speed and direction in which IM travelled after scavenging, observers were unable to identify potential injuries on the carcass that alluded to predation by the raptor. Moreover, researchers detected no putrid odours after directly trailing IM and the carcass, suggesting that the bushbuck recently died.

Whilst possible, it is unlikely, that IM and the raptor converged on a live animal simultaneously. The chimpanzees were followed consistantly – across a semi-open woodland habitat – immediately preceding the point at which IM was observed with the carcass. Despite good visibility, no interaction was witnessed between the bushbuck and raptor, i.e., the raptor was not observed descending to the ground, nor were any vocalisations heard prior to researchers arriving at the scene. Therefore, it is most likely that the eagle had already preyed upon the bushbuck prior to the arrival of the chimpanzees when IM confronted and chased the eagle from the carcass.

It is plausible to assume that the crowned eagle captured and killed this bushbuck. The crowned eagle is a diurnal raptor (Nagy and Tökölyi 2014), a pursuit predator not recognised to scavenge prey (Potier et al. 2017). Crowned eagles are a known predator of (immature) bushbuck-sized antelope (Reeves and Boshoff 2016), a prey species of Issa (Piel and Stewart, unpublished data), Gombe (Newton-Fisher 2007), and Mahale (Hosaka et al. 2001; Hosaka et al. 2020) chimpanzees. Given these inferences, we may determine that the requirements of a confrontational carcass theft were met: (1) the carcass was fleshed and the tissue consumable, (2) the species likely previously in command of the carcass was a crowned eagle, a predator species non-threatening to chimpanzees, and (3) the dominant male chimpanzee (IM) likely chased the eagle off to gain access to the carcass. The event resulted in the complete consumption of the carcass, supporting the existence of confrontational scavenging in Issa chimpanzees, the first recorded at Issa since habituation was completed in 2018. Crucially, if we acknowledge that chimpanzees are capable of confrontational scavenging, then previously published ‘hunts’ may have been scavenging unseen by human observers who arrived after the event. Nakamura et al. (2019) contend that aggressive scavenging events could be underrepresented in the literature due to longstanding assumptions that chimpanzees hunt and do not scavenge.

We propose that the ecology of the area influences the frequency of these behaviours. For example, we see disproportionally higher densities of leopards at Mahale despite a relatively low density of medium-sized ungulates (Nakazawa 2020), allowing for greater exposure to fresh carcasses recognisable as food. Leopards are regularly encountered on remotely-triggered cameras at Issa (Piel and Stewart, unpublished data), but no density data have been reported.

Specific ecological conditions (predator-prey abundances) likely affected the confrontational scavenging behaviour of extant chimpanzees versus extinct hominins ~1.7 Myr ago. The differences in abundance and diversity of carcass and predator may have led to correspondingly higher frequencies of medium-to-large carcasses available for hominins (Van Valkenburgh 2001), increasing the opportunity and prevalence of confrontational scavenging.

Issa chimpanzees live in a predominantly open habitat, characterised by woodland and grasslands and one that resembles reconstructions of early hominin (e.g., *Ardipithecus*) paleohabitats (White et al. 2009). Chimpanzee dietary ecology, especially hunting, has long been used to inform our understanding of hominin evolution, namely how prey was attained and the complexity of group cooperation required to meet this goal (Stanford 1996; Sponheimer and Lee-Thorp 1999). In contemporary huntergatherer populations, scavenging can comprise up to 20% of meat intake during some periods of the year (Hadza: O'Connell et al. 1988).

Debate surrounds the method with which early hominins acquired large animal carcasses: the prevalence of confrontational scavenging (Pante et al. 2015; Thompson et al. 2019) compared to hunting (Domínguez-Rodrigo et al. 2021). Watts (2008) suggests confrontational scavenging provided a vital stepping-stone to hominin hunting – a transition that would propel humans from ‘marginal scavengers’, reliant on the ‘leftovers’ of carnivores (Shipman 1986), to successful hunter-scavengers proficient in aggressively securing fleshed carcasses from large predators (Bunn et al. 1986).

Additional accounts of confrontational scavenging in extant nonhuman primates, especially those in open-habitat communities, would expand behavioural insights into the ecological opportunities and limitations conceivably encountered by early hominins in similar habitats (O'Connell et al. 2002). The Issa Valley is particularly suited to provide a realistic (mosaic) woodland scavenging model of chimpanzees, as it is an analogous environment to which early hominins were adapted (Stanford and Bunn 2001).

Whether confrontational scavenging, as described at nearby Mahale and now at Issa, reflects a regional cultural tendency or an opportunistic strategy is unknown and cannot be better understood without numerous future observations. Furthermore, each new observation of scavenging by nonhuman primates helps us to understand the role of scavenging in extant species and, hopefully, in the future, the role of the local environment in predicting scavenging behaviour. Future research could use systematic statistical analyses of scavenging patterns across the *Pan* distribution to determine the role of habitat in influencing scavenging behaviour, especially in the context of human evolution. Due to the combination of abundant terrestrial mammalian wildlife, a diverse guild of large carnivores, and inter-specific spatial overlap at Issa, we predict similar scavenging observations in the future.

Declarations

All authors contributed to the study’s conception and design. SAB performed data collection. SAB wrote the first draft of the manuscript, and AKP and FAS commented on and edited subsequent versions. All authors read and approved the final manuscript. No funding was received to assist with the preparation of this manuscript. The authors have no relevant financial or non-financial interests to disclose.

References

Andrews P (2020) Last common ancestor of apes and humans: Morphology and environment. Folia Primatol 91:122-148. https://doi.org/10.1159/000501557

Bailey TN (1993) The African leopard: ecology and behavior of a solitary felid. Columbia University Press, Columbia

Blumenschine RJ (1991) Hominid carnivory and foraging strategies, and the socio-economic function of early archaeological sites. Philos Trans R Soc B 334:211-221. https://doi.org/10.1098/rstb.1991.0110

Blumenschine RJ, Cavallo JA (1992) Scavenging and human evolution. Sci Am 267:90-97. https://doi.org/10.1038/scientificamerican1092-90

Boesch C (1991) The effects of leopard predation on grouping patterns in forest chimpanzees. Behaviour 117:3-4. https://doi.org/10.1163/156853991X00544

Boesch C (2009) The real chimpanzee: sex strategies in the forest. Cambridge University Press, Cambridge

Boesch C, Boesch-Achermann H (2000) The chimpanzees of the Taï Forest: Behavioural ecology and evolution. Oxford University Press, Oxford

Boesch C, Wittig R, Crockford C, Vigilant L, Deschner T, Leendertz F (ed) (2019) The chimpanzees of the Taï Forest: 40 years of research. Cambridge University Press, Cambridge

Bunn HT (2001) Hunting, power scavenging, and butchering by Hadza foragers and by Plio-Pleistocene *Homo*. In: Stanford CB, Bunn HT (ed) Meat-eating and human evolution. Oxford University Press, Oxford, pp 199-218

Bunn HT, Isaac G, Kaufulu Z, Kroll EM, Schick K, Toth N, Behrensmeyer AK (1980) FxJj50: An Early Pleistocene site in northern Kenya. World Archaeol 12:109-136. https://doi.org/10.1080/00438243.1980.9979787

Bunn HT, Kroll EM, Ambrose SH, Behrensmeyer AK, Binford LR, Blumenschine RJ, Klein RG, McHenry HM, O'Brien CJ, Wymer JJ (1986) Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania [and comments and reply]. Curr Anthropol 27:431-452. http://www.jstor.org/stable/2742852

D'Ammando G, Caro T, Oelze VM, Phillips S, Sime P, Stewart FA, Piel AK (2022) Ecological drivers of habitat use by meso mammals in a miombo ecosystem in the Issa Valley, Tanzania. Front Ecol Evol 197. https://doi.org/10.3389/fevo.2022.773568

Domínguez-Rodrigo M (2002) Hunting and scavenging by early humans: the state of the debate. J World Prehist 16:1-54. https://www.jstor.org/stable/25801183

Domínguez-Rodrigo M, Baquedano E, Organista E, Cobo-Sánchez L, Mabulla A, Maskara V, ... González-Aguilera D (2021) Early Pleistocene faunivorous hominins were not kleptoparasitic, and this impacted the evolution of human anatomy and socio-ecology. Sci Rep 11:16135. https://doi.org/10.1038/s41598-021-94783-4

Domínguez-Rodrigo M, Barba R (2006) New estimates of tooth mark and percussion mark frequencies at the FLK Zinj site: the carnivore-hominid-carnivore hypothesis falsified. J Hum Evol 50:170-194. https://doi.org/10.1016/j.jhevol.2005.09.005

Domínguez-Rodrigo M, Mabulla A, Bunn HT, Barba R, Diez-Martín F, Egeland CP, ... Sánchez P (2009) Unraveling hominin behavior at another anthropogenic site from Olduvai Gorge (Tanzania): new archaeological and taphonomic research at BK, Upper Bed II. J Hum Evol 57:260-283. https://doi.org/10.1016/j.jhevol.2009.04.006

Domínguez-Rodrigo M, Pickering TR (2003) Early hominid hunting and scavenging: a zooarchaeological review. Evol Anthropol 12:275-282. https://doi.org/10.1002/evan.10119

Domínguez-Rodrigo M, Pickering TR, Semaw S, Rogers MJ (2005) Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the function of the world's oldest stone tools. J Hum Evol 48: 109-121. https://doi.org/10.1016/j.jhevol.2004.09.004

Drummond-Clarke RC, Kivell TL, Sarringhaus L, Stewart FA, Humle T, Piel AK (2022) Wild chimpanzee behavior suggests that a savanna-mosaic habitat did not support the emergence of hominin terrestrial bipedalism. Sci Adv 8: eadd9752. https://doi.org/10.1126/sciadv.add9752

Emery Thompson M, Muller MN, Machanda ZP, Otali E, Wrangham RW (2020) The Kibale Chimpanzee Project: Over thirty years of research, conservation, and change. Biol Conserv 252:108857. https://doi.org/10.1016/j.biocon.2020.108857

Ferguson-Lees J, Christie DA (2001) Raptors of the world. Christopher Helm, London, pp 248

Ferraro JV, Plummer TW, Pobiner BL, Oliver JS, Bishop LC, Braun DR, ... Potts R (2013) Earliest archaeological evidence of persistent hominin carnivory. PLoS One 8:e62174. https://doi.org/10.1371/journal.pone.0062174

Gilby IC, Machanda ZP, O'Malley RC, Murray CM, Lonsdorf EV, Walker K, ... Wrangham RW (2017) Predation by female chimpanzees: toward an understanding of sex differences in meat acquisition in the last common ancestor of *Pan* and *Homo*. J Hum Evol 110:82-94. https://doi.org/10.1016/j.jhevol.2017.06.015

Giuliano C, Stewart FA, Piel AK (2022) Chimpanzee (*Pan troglodytes schweinfurthii*) grouping patterns in an open and dry savanna landscape, Issa Valley, western Tanzania. J Hum Evol 163:103137. https://doi.org/10.1016/j.jhevol.2021.103137

Gomes C, Mundry R, Boesch C (2019) Why do the chimpanzees of the Taï forest share meat? The value of bartering, begging, and hunting. In: Crockford C, Vigilant L, Deschner, T, Leendertz F, Boesch C, Wittig R (ed) The chimpanzees of the Taï Forest: 40 years of research. Cambridge University Press, Cambridge, pp 316-338

Goodall J (1986) The chimpanzees of Gombe: Patterns of behavior. Harvard University Press, Cambridge

Hiraiwa-Hasegawa M, Byrne RW, Takasaki H, Byrne JME (1986) Aggression toward large carnivores by wild chimpanzees of Mahale Mountains National Park, Tanzania. Folia Primatol 47:8-13. https://doi.org/10.1159/000156259

Hobaiter C, Samuni L, Mullins C, Akankwasa WJ, Zuberbühler K (2017) Variation in hunting behaviour in neighbouring chimpanzee communities in the Budongo forest, Uganda. PLoS One 12:e0178065. https://doi.org/10.1371/journal.pone.0178065

Hosaka K (2015) Hunting and food sharing. In: Nakamura M, Hosaka K, Itoh N, Zamma K (ed) Mahale chimpanzees: 50 years of research. Cambridge University Press, Cambridge, pp 274-290

Hosaka K, Ihobe H (2015) Interspecific relationships. In: Nakamura M, Hosaka K, Itoh N, Zamma K (ed) Mahale chimpanzees: 50 years of research. Cambridge University Press, Cambridge, pp 213-224. https://doi.org/10.1017/CBO9781107280533

Hosaka K, Inoue E, Fujimoto M (2014) < Note > responses of wild chimpanzees to fresh carcasses of aardvark (*Orycteropus afer*) in Mahale. Pan Afr News 21:19-22. https://doi.org/10.5134/192912

Hosaka K, Nakamura M, Takahata Y (2020) Longitudinal changes in the targets of chimpanzee (*Pan troglodytes*) hunts at Mahale Mountains National Park: how and why did they begin to intensively hunt red colobus (*Piliocolobus rufomitratus*) in the 1980s?. Primates 61:391-401. https://doi.org/10.1007/s10329-020-00803-8

Hosaka K, Nishida T, Hamai M, Matsumoto-Oda A, Uehara S (2001) Predation of mammals by the chimpanzees of the Mahale Mountains, Tanzania. In: Galdikas BMF, Briggs NE, Sheeran, LK, Shapiro GL, Goodall J (ed) All apes great and small, Vol I: African apes. Kluwer Academic/Plenum, New York, pp 107-130

Isaac G (1971) The diet of early man: aspects of archaeological evidence from Lower and Middle Pleistocene sites in Africa. World Archaeol 2:278-299. http://www.jstor.org/stable/124119

Mitani JC, Watts DP (2001) Why do chimpanzees hunt and share meat?. Anim Behav 61:915-924. https://doi.org/10.1006/anbe.2000.1681

Moore J, Black J, Hernandez-Aguilar RA, Idani GI, Piel A, Stewart F (2017) Chimpanzee vertebrate consumption: savanna and forest chimpanzees compared. J Hum Evol 112:30-40. https://doi.org/10.1016/j.jhevol.2017.09.004

Morris K, Goodall J (1977) Competition for meat between chimpanzees and baboons of the Gombe National Park. Folia Primatol 28:109-121. https://doi.org/10.1159/000155801

Nagy J, Tökölyi J (2014) Phylogeny, historical biogeography and the evolution of migration in accipitrid birds of prey (Aves: Accipitriformes). Ornis Hung 22:15-35. https://doi.org/10.2478/orhu-2014-0008

Nakamura M, Hosaka K, Itoh N, Matsumoto T, Matsusaka T, Nakazawa N, … Nishie H (2019) Wild chimpanzees deprived a leopard of its kill: Implications for the origin of hominin confrontational scavenging. J Hum Evol 131:129-138. https://doi.org/10.1016/j.jhevol.2019.03.011

Nakamura M, Hosaka K, Itoh N, Zamma K (ed) (2015) Mahale chimpanzees: 50 years of research. Cambridge University Press, Cambridge

Nakazawa N (2020) Primates are an important food resource for leopards (*Panthera pardus*) in Mahale, Tanzania. Afr J Ecol 58:399-408. https://doi.org/10.1111/aje.1271

Newton-Fisher NE (2007) Chimpanzee hunting behavior. In: Henke W, Tattersall I (ed) Handbook of paleoanthropology. Springer-Verlag, New York, pp 1295-1320

Nishida T (1994) Review of recent findings on Mahale chimpanzees: Implications and future research directions. In: Wrangham, RW, McGrew WC, de Waal FBM, Heltne PG (ed) chimpanzee cultures. Harvard University Press, Cambridge, pp 373-396

O'Connell JF, Hawkes K, Jones NB (1988) Hadza scavenging: Implications for Plio/Pleistocene hominid subsistence. Curr Anthropol 29:356-363. https://doi.org/10.1086/203648

O'Connell JF, Hawkes K, Lupo KD, Blurton Jones N (2002) Male strategies and Plio-Pleistocene archaeology. J Hum Evol 43:831-872. https://doi.org/10.1006/jhev.2002.0604

Pante MC, Blumenschine RJ, Capaldo SD, Scott RS (2012) Validation of bone surface modification models for inferring fossil hominin and carnivore feeding interactions, with reapplication to FLK 22, Olduvai Gorge, Tanzania. J Hum Evol 63:395-407. https://doi.org/10.1016/j.jhevol.2011.09.002

Pante MC, Scott RS, Blumenschine RJ, Capaldo SD (2015) Revalidation of bone surface modification models for inferring fossil hominin and carnivore feeding interactions. Quat Int 355:164-168. https://doi.org/10.1016/j.quaint.2014.09.007

Piel AK, Bonnin N, Amaya SR, Wondra E, Stewart FA (2019) Chimpanzees and their mammalian sympatriates in the Issa Valley, Tanzania. Afr J Ecol 51:31-40. https://doi.org/10.1111/aje.12570

Potier S, Mitkus M, Bonadonna F, Duriez O, Isard PF, Dulaurent T, ... Kelber A (2017) Eye size, fovea, and foraging ecology in accipitriform raptors. Brain Behav Evol 90:232-242. https://doi.org/10.1159/000479783

Pruetz JD, Bertolani P (2007) Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. Curr Biol 17:412-417. https://doi.org/10.1016/j.cub.2006.12.042

Ramirez-Amaya S, McLester E, Stewart FA, Piel AK (2015) Savanna chimpanzees (*Pan troglodytes schweinfurthii*) consume and share blue duiker (*Philantomba monticola*) meat in the Issa Valley, Ugalla, western Tanzania. Pan Afr News 22:17-21. http://mahale.main.jp/PAN/22_2/22(2)_04.html

Reeves B, Boshoff AF (2016) Is diet adaptability a reason for the persistence of African crowned eagles *Stephanoaetus coronatus* in altered habitats?. Ostrich 87:29-36. https://doi.org/10.2989/00306525.2015.1108372

Shipman P (1986) Scavenging or hunting in early hominids: theoretical framework and tests. Am Anthropol 88:27-43. https://www.jstor.org/stable/679277

Sponheimer M, Lee-Thorp JA (1999) Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. Science 283:368-370. https://doi.org/10.1126/science.283.5400.368

Stanford CB (1996) The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of Pliocene hominids. Am Anthropol 98:96-113. http://www.jstor.org/stable/682956

Stanford CB, Bunn HT (2001) Meat-eating and human evolution. Oxford University Press, Oxford

Stiner MC (2002) Carnivory, coevolution, and the geographic spread of the genus *Homo*. J Archaeol Res 10:1-63. https://doi.org/10.1023/A:1014588307174

Thompson JC, Carvalho S, Marean CW, Alemseged Z (2019) Origins of the human predatory pattern: the transition to large-animal exploitation by early hominins. Curr Anthropol 60:1-23. https://doi.org/10.1086/701477

Van Valkenburgh B (2001) The dog-eat-dog world of carnivores: A review of past and present carnivore community dynamics. In: Stanford C, Bunn HT (ed) Meat-eating and human evolution. Oxford University Press, pp 101-121

Washburn SL, Lancaster C (1968) The evolution of hunting. In: Lee RB, DeVore I (ed) Man the hunter pp. Aldine, Chicago, pp 293-303

Watts DP (2008) Scavenging by chimpanzees at Ngogo and the relevance of chimpanzee scavenging to early hominin behavioral ecology. J Hum Evol 54:125-133. https://doi.org/10.1016/j.jhevol.2007.07.008

White TD, Ambrose SH, Suwa G, Su DF, DeGusta D, Bernor RL, … Vrba E (2009) Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*. Science 326:67-67. https://doi.org/10.1126/science.1175822

Yravedra J, Rubio-Jara S, Courtenay LA, Martos JA (2020) Mammal butchery by *Homo erectus* at the Lower Pleistocene acheulean site of Juma’s korongo 2 (JK2), bed III, Olduvai Gorge, Tanzania. Quat Sci Rev 249:106612. https://doi.org/10.1016/j.quascirev.2020.106612