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Erratum

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ABSTRACT

This paper details the perilous world in which our ancestors evolved as a prey target for a significant number of carnivores. The first part details the predators that would have co-existed with ancient hominins in the highlighted geographic region and time and notable specimens that bear marks of having been the victims of carnivores. The second section shows how being hunted affected hominin behavioral and cognitive evolution. The final section discusses to what extent hominins may have been preferred prey for certain carnivores.

H*omo sapiens*, the only remaining hominin, is a breathtakingly self-centered species. Most are probably familiar with the popular image of a caveman wielding a spear to take down an animal several times larger than himself, and the more academic side of evolutionary study has provided a plethora of material discussing scavenging and hunting developments.

While meat consumption certainly has played a pivotal role in human evolutionary history, it is only one side of the coin. In relative terms, very rarely is the other side examined. Hominins evolved in a world where they were not only (ultimately) hunters but also hunted. Our ancestors were subject to many selection pressures, one of which was the presence of several terrestrial, aquatic, and aerial carnivores. This had a profound effect on behavioral and cognitive evolution.

This paper addresses three topics pertaining to Plio-Pleistocene predation on Eastern and South African hominins using available literature. The first section discusses the indications of carnivore activity on fossils, and describe the various taxa that posed a threat to ancient hominins. The second and primary aim is to determine what effect predator

presence had on hominin behavioral and cognitive evolution and any relevant adaptations. The third part consists of an analysis to determine what indications may exist that hominins were the preferred prey of any carnivore present in Eastern and South Africa during these time periods.

The parameters are as follows, the study focuses on hominin taxa present in East and South Africa between 5 million to 10,000 years ago. For the purposes of this analysis, East Africa is defined as the countries of Ethiopia, Kenya, Tanzania, and Uganda. South Africa refers to the country of the same name. References to outside regions will only be made with regards to the rest of Africa, or for the purposes of discussing modern analogues. Only confirmed hominin taxa (*Ardipithecus*, *Australopithecus*, *Paranthropus*, *Kenyanthropus*, *Homo*) are included.

Given that our ancestors evolved in an environment at the mercy of the elements, erosion, and a range of varying species, it is first necessary to specify how carnivory marks are distinguished on recovered remains. Developments in microscopy allowed for analysis to be conducted and a set of general criteria has been established to qualify marks on bones as predatory in origin. The canines of mammalian carnivores will produce sloping U-shaped puncture marks when viewed in cross-section. This analysis must be paired with contextual evidence from the site as microanalysis cannot confirm culprits alone. This is because other predators such as crocodiles may make tooth marks that closely resemble mammalian canines (Njau, 2012). Therefore, it is necessary to search for other evidence such as depositional clues: an ancient lacustrine environment, for example, will yield layers of siltstone and claystone, hence increasing the probability that any specimens with animal puncture marks were killed by a crocodile.

Extreme circumstances such as cases of cannibalism within the hominin fossil record are relatively rare and the known archaeological record only extends back to the Middle Pliocene site of Lomekwi 3, dated to 3.3 million years ago (Harmand, 2014). Still, it is crucial to distinguish carnivory marks from those of other sources. In contrast to carnivorous puncture marks, tool cut marks are V-shaped and tend to be elongated when viewed in cross-section. In addition, micro-striations can be seen within these marks. Though hammerstones produce a different shape in the form of a pit, they also contain these characteristic microstriations (Njau, 2012).

Evidence of carnivory from the Plio-Pleistocene can only be indirect, so there is a margin of error that complicates identification. Besides the previously stated fact that crocodiles and mammalian carnivores can make similar marks and hence complicate specific predator identification, other, more modern factors interfere as well. There are no formalized criteria or standardized methods for distinguishing carnivores and tool cut marks. Attempting to decipher the culprit of tooth marks through taphonomic context comes with controversy and lack of standardization as well (Njau, 2012). An example of this from a non-hominin case pertains to several fossil fragments found at Dikika, Ethiopia. Dated to 3.4 million years ago, these ungulate fossils (namely

a femur and rib) were claimed by McPherron et al. (2010) to feature stone tool cut marks due to the presence of microstriations and percussion marks. However, it has been pointed out that the marks appear on bones that would not typically be struck for marrow extraction. Furthermore, no tools were found at the site and indeed, there is a lack of widespread lithic technology from this period. Critics of the find contest that given the lack of tool evidence from the site, the marks on the bones are the result of taphonomic damage (Njau, 2012). Hence, the Dikika find remains unconvincing.

Before conducting an analysis of the effects of predation on hominins, it is important to first establish the carnivores that coexisted with them. Hominins evolved in an environment where they were subjected to threats from numerous predators. It is important to note that the temporal majority of hominin evolution occurred without tool and fire technology and certainly the kind that would be effective against large predators. While pointy sticks, bones, thorny branches, and other makeshift weapons could have been used in defense, it is unlikely they would have worked well. The fact that these carnivores would have been accustomed to hunting large, horned animals and often rely on surprise attacks coupled with the fact that humans are victims of predators even today with sophisticated weapons supports the assertion that primitive tools would have provided little protection (Treves & Palmqvist, 2007). Members of the mammalian order *Carnivora* were quite diversified by the Plio-Pleistocene although there is evidence of a decreasing trend in the biodiversity of large-bodied East African carnivorans after 3.6 million years ago (Lewis & Werdelin, 2007).

The big cats and related animals likely posed the greatest threat to ancient hominins, both from extinct and extant taxa. This is due both to their physical prowess, abundance, and longevity in regions where hominins were present.

The three most notable extinct genera of Felidae were *Homotherium*, *Dinofelis*, and *Megantereon*. *Homotherium* lived from approximately 4.35 to 1.4 million years ago and could be found throughout East Africa (Lewis & Werdelin, 2007). They are often called “scimitar-tooth cats” due to their steak-knife-like canines (Hart & Sussman, 2006). They were quite successful due to their adaptations for open environments such as elongated forelimbs and shortened forelimbs in comparison to other saber-tooths. Their ability to take down large prey and the fact that they may have traveled in groups means that hominins faced stiff competition if they encountered them in either a predator-prey or scavenging situation (Lewis & Werdelin, 2007).

Dinofelis was a long-lasting genus, found in the fossil record dating from 7.91 million until 900,000 years ago (Lewis & Werdelin, 2007). These cats were quite large; one genus, *Machairodus* stood around 1.2 meters high at the shoulder and had powerful, elongated, and serrated canines (Hart & Sussman, 2007). The various species of *Dinofelis* lived throughout East and South Africa (represented by *D. petteri*, *D. aronoki*, *D. piveteaui*, and *D. barlowi*) The largest species, *D. aronoki* lived from 3.18 to 1.6 million years ago in Ethiopia and Kenya. Contrary to *Homotherium*, *Dinofelis* lived in dense or mixed forest as can be seen in their more robust build; they possessed short

forelimbs and the smaller species, *D. petteri* and *D. piveteaui* had crouched postures more adapted for stalking and pouncing through underbrush. However, the success of the *Dinofelis* genus suggests that they may have lived in more than just thickly vegetated places, especially given that one area was usually inhabited by two *Dinofelis* species. It does not seem likely that they cached their prey in trees like modern leopards because their forelimbs appear to have lacked dexterity. Also, it has been observed in remains of North American *Dinofelis* species that the enlarged canines were quite prone to breakage, but this injury is totally absent from any African remains. Since dragging a carcass into high boughs would put a lot of stress on the canines, tree caching does not seem likely (Lewis & Werdelin, 2007). Furthermore, the long canines of sabertooths were not powerful enough to sever the spinal cord. Rather, the knife-like downwards stabbing inflicted by these felids was meant to trigger massive blood loss by ripping into soft tissue (Hart & Sussman, 2006).

Megantereon were present in East Africa and have been found at Aramis, South Turkwel, Koobi Fora, Kromdraai, and at the Shungura formation in Kenya. Their remains show that they were an extremely muscular felid and were comparable in front end morphology to a jaguar, although they were substantially more muscled. Their preferred habitat was probably the same as *Dinofelis* and they too were a stalking and ambush predator. As the smallest of the sabertooths, they were probably less of a threat to hominins than the larger genera and the latter may even have contended with them at scavenging sites (Lewis & Werdelin, 2007). Still, at around 91 kilograms, they were larger than modern leopards and may have been more adept at climbing trees thanks to powerful, large front paws (Hart & Sussman, 2006).

Big cats have most definitely been a threat to hominins throughout the course of history. Aside from numerous anecdotal cases in the modern era, there is evidence of this on a microbiological level; it was demonstrated that the bacteria *Helicobacter* was transmitted from ancient hominins to felids (Bassoti & Müller-Lissner, 2015). It is not a question of if, but who of the extant big cats targeted African hominins.

The modern big cats of Africa belong to the genus *Panthera* and the oldest definitive evidence of lions and leopards comes from Olduvai Bed I in Tanzania. With the caveat of limited fossil and taphonomic evidence, it seems these ancient lions and leopards displayed the same behavior as their modern counterparts. There is certainly evidence of leopards caching kills in trees due to similar cranial morphology between fossil and modern leopards, the high risk of kills being taken by other predators, and the numerous bone piles found in caves that may have fallen from tree-stowed carcasses (Lewis & Werdelin, 2007).

Since there is nothing to suggest behavioral differences between ancient and modern African pantherans, a reasonable assessment of risk to hominins can be inferred. Leopards in particular are known to be quite stealthy and have been known to grab infants off sleeping mothers with the latter being none the wiser. Furthermore, they frequently prey on the other great apes: chimpanzees, bonobos, and gorillas. Both

leopards and lions are able to hunt prey larger than themselves based on their tactic of biting in a way that severs the spinal cord. Of course, the latter can also hunt large prey due to its permanent presence in a social group (Hart & Sussman, 2007). Since there is not a question of if these species are capable of eating hominins, modern case studies of such will be presented in the third section of this paper.

As for cheetahs, they differ from the true big cats in a number of ways; their claws do not sheath, their prey is typically smaller than that of lions or leopards, and their bodies are developed for high speed in a completely terrestrial environment. There are few modern records of cheetahs preying on primates (Hart & Sussman, 2007). The cheetah fossil record is also limited. *Acinonyx* specimens have been found in Omo dating until about 2.5 million years ago and were also found at Koobi Fora. After the specimens from the later site, there is a significant time gap; no members of *Acinonyx* have been found that date from between then until the present. These early cheetahs differ significantly in morphology from the modern animal and their lack of abundance seems to suggest they were never a main competitor in the carnivoran East African guild (Lewis & Werdelin). Much like other taxa that will be discussed below, this lack of remains makes it difficult to infer how much of a threat cheetahs posed to ancient hominins.

The oldest Canid fossils in East Africa were recovered from Omo in Ethiopia and date to approximately 4-4.5 million years ago. However, the evidence for large canids does not become clear until about 3.5 million years ago (Lewis & Werdelin, 2007). Hominins were an easy prey item for African wild dogs (*Canis pictus*) if they chanced upon one; this animal hunts cooperatively by trailing and chasing down the prey in a pack and then attacking from behind. However, it has been shown through modern primate analogues that with the exception of sprint-capable monkeys (such as patas monkeys), most primates are the victims of individual dogs in chance encounters. The prey capture rate for African wild dogs is quite high at around fifty to seventy percent (Hart & Sussman 2006).

Patterns of presence of large canids vary throughout the Plio-Pleistocene. There seems to have been a lack of large canids from 2.7-2.4 million years ago. From 1.8-1.5 million years ago, the landscape was dominated by *Canis lycaonoides* (a possible ancestor of the African wild dog). A low yield of fossils makes it difficult to hypothesize the extent to which ancient canids may have impacted hominins. Furthermore, many extinct species may not have filled the same ecological role as modern species due to tooth morphology differences; notably, a lack of specialization in comparison to modern forms (Lewis & Werdelin, 2007). While a sparse fossil records hinders conclusions that can be drawn about the extent of canid predation on ancient hominins, given the size, speed, endurance, and cooperativeness of modern species, they may have been a formidable presence and a sheer lack of presence from the fossil record has erased the full extent of their threat.

Hyaenids first appeared around 17 million years ago and quickly adapted to be top carnivores within their ecosystems (Hart & Sussman, 2006). By the Pliocene, hyaenids were a worry to human ancestors. Remains from the genus *Chasmaporthetes* were found in Allia Bay, Marsabit County, Kenya and dated to 3.7-3.9 million years old. By 3.5 million years ago, the diversity of hyaenids in East Africa was substantial (Lewis & Werdelin, 2007). Given this fact, hominins present in the region would have faced a high risk of predation.

Over one hundred extinct species have been identified in the fossil record and the hyaenids seem to have taken two evolutionary directions. The first was a lineage developed for speed. *Chasmaporthetes* may have filled the long-distance hunting role seen in modern African wild dogs and seems to have had locomotor capabilities similar to cheetahs. *Euryboas* was present in South Africa and has been found in association with australopiths (Hart & Sussman, 2006).

The other evolutionary direction produced a more robust lineage that contains extant hyaenid members (Hart & Sussman, 2006). *Parahyaena howelli*, *Parahyaena brunnea* (the modern brown hyena), and *Hyaena hyaena* (the striped hyena that first appears at 1.9 million years ago) all possessed the bone-cracking abilities now seen in the two latter, extant forms mentioned (Lewis & Werdelin, 2007).

While much is still to be determined about the behavior of *Chasmaporthetes*, it seems that an individual hunter was not a great threat to even the most petite of early hominins, but if they did indeed fill the niche of modern African wild dogs and hunted in packs like that animal, they were far more dangerous (Lewis & Werdelin, 2007). Specimens belonging to the cave-dwelling *Pachycrocuta* have been found in Hadar, Ethiopia and date to 3.5 million years old, making them contemporaneous with *Australopithecus afarensis*. Furthermore, its weight of around two hundred kilograms (the largest hyena to ever live), huge and powerful jaws, and evidence from China of its hunting of woolly rhinoceros and giant elk, meant it could very easily have taken down an australopith. *Pachycrocuta* was present in much of East Africa during the Pliocene as evidenced not only by the Hadar fossils but also by specimens from South Turkwell, Kenya. They seem to have hunted in packs and brought pieces of their kill back to their dens where they could easily crack open the skull to ingest the fatty brain tissue (Hart & Sussman, 2006).

The need for East and South African Plio-Pleistocene hominins to live within close range of water presented another predatory risk. Crocodiles have not evolved much in the 200 million years they have existed and are still a well-known threat to modern *Homo sapiens* due to multiple documented attacks. Unfortunately, no direct evidence of crocodile predation on ancient hominins is known from the fossil record so their impact on ancient hominins can only be inferred from circumstantial evidence. Nile crocodiles have coexisted with hominins for a long time and can reach up to almost 6.5 meters in length. Sadly, the lack of studies identifying Nile crocodile stomach contents makes it difficult to determine how threatened ancient hominins were. The

only published study took place in the 1950s and indicated that humans are not preferred prey; only one percent of the stomach contents was identified as human (Hart & Sussman, 2006). However, it could be possible that the smaller size of ancient hominins such as *Australopiths* coupled with their lack of complex technology and protections (boats, spears, etc.) made them a more vulnerable target and hence, they may have made up a larger percentage of the diet. Intriguing as it is, there is no way to test this idea.

Nile crocodiles were not the only crocodilian with which ancient hominins contended. A crocodile called *Crocodylus thorbjarnarsoni* was discovered in the Lake Turkana Basin of Northern Kenya and reached up to 7.5 meters in length, making it the largest predator of that ecosystem. Hominin remains were also found in the deposits, making it very likely that they were a prey item (Brochu & Storrs, 2012).

As for other reptiles, again, the fossil record is quite poor concerning their association with ancient hominins. There is an apparent predator-prey relationship between snakes and mammals, though, as snakes began ecologically radiating at the same time as mammals. However, as with crocodiles, there is a lack of direct fossil evidence (Hart & Sussman, 2006). Thus, the degree to which early hominins fell prey to large snakes remains speculative.

Avian predation is not as prevalent as other carnivore activity due to the lack of abundance of predatory birds large enough to subdue a hominin. However, both modern records and fossil preservation yield cases of this activity. For instance, the crowned hawk-eagle is native to East Africa and with a 1.8-meter wingspan, their feet 19.05 centimeters wide, and claws up to 6.35 centimeters in length, they could have easily taken down small adult australopiths or their young. This eagle has been known to snatch at young children with the Zambian Department of Veterinary and Tsetse Control Services, noting a 1983 account of a crowned hawk-eagle attacking a seven-year-old, approximately twenty-kilogram boy on his way to school. The boy's uniform prevented the claw marks from fatally injuring him but he still sustained large gashes on his head, chest, and arms. It was noted that no nearby nest was present so this, coupled with the method of attack being consistent with hawk-eagle hunting behavior, made this very likely a predation attempt (Hart & Sussman, 2009).

The ability of large birds of prey to hunt primates of a similar size to early hominins is corroborated in other accounts. Skepticism behind the consistency of black eagles hunting baboons (seen an anomalous number of times in South Africa) was rebuked when documentation of a black eagle hunting hamadryas baboons in Eritrea four times in four days was published (Hart & Sussman, 2009). It should be noted that male hamadryas baboons may weigh between twenty to thirty kilograms and females ten to fifteen; males may reach a body length of eighty centimeters. Hence, it is feasible that large, carnivorous birds preyed on adult and young australopiths of a similar size.

In addition, the fossil record contains notable instances of avian predation. Most famously, the skull of the South African Taung child bears marks that heavily suggest she was the victim of a large eagle (Hart & Sussman, 2009). Thus, while birds of prey may in general have not had the diversity or size capable of taking down hominins with the same frequency and capability as terrestrial and aquatic carnivores, it is still apparent both from modern records and fossil traces that our ancestors at least occasionally fell prey to large avian predators.

The odds of a deceased animal being preserved as a fossil are incredibly low. Thus, it follows that the odds of an animal that was a victim of predation being preserved as a fossil with specific taphonomic marks needed to distinguish carnivory are even lower. Even if a felled hominin is not completely devoured by the carnivore that killed it, the exposure to scavengers and the elements, especially with the body in an already mangled state, will make it more than likely that the unfortunate hominin's remains will be lost to time. That stated, there exist a few uncovered fossils that display evidence of fatal predator injuries or scavenging activities.

Perhaps the most famous example of this, as noted above, is with the Taung child. This fossil consists of the skull of a female *Australopithecus africanus* juvenile dated to approximately 2 million years old. Though discovered in South Africa in 1925 by noted paleoanthropologist Raymond Dart, it was seventy years before Berger and Clarke proposed that the Taung child was the victim of a predator. This was put forth due to the presence of large gouge marks in the orbits of the skull that appeared to resemble damage from an eagle's talons. Comparisons with marks on the bones of monkeys killed by eagles in the Tai Forest, Ivory Coast revealed a high degree of similarity. In addition, there are punctures on the braincase and scratches in various places on the skull. An examination of Dart's notes pertaining to the skull's excavation ruled out the possibility that the scratches were produced during extraction from the encasing breccia (Berger & McGraw, 2007). As discussed in the section on avian predators, it is completely possible for crowned eagles to attack, maim, or kill young children so this, coupled with the trace marks on the fossil suggest the Taung child was a prey item for a large bird of prey.

Although not from the key African areas of analysis for this paper, a femoral diaphysis recovered from the Grotte à Hominidés near Casablanca, Morocco provides another rare, well-preserved example of human predation by carnivores. The shaft's isolation as a fossil and its condition make it difficult to determine to which species this individual belonged. However, *Homo rhodesiensis* was known to frequent the area so it is likely from this hominin. Dated to around 500,000 years old, fossil ThI94-UA28-7 features chew marks at both ends of the femoral shaft, specifically numerous punctures, scores, pits, and furrows. The marks are present on an area of thick cortical bone and five pits are greater than four millimeters in length and two millimeters in breadth, demonstrating that a large carnivore was responsible for these marks. The most likely candidate given its presence in the area during the Pleistocene and marks on the bone that correspond to its activities. Furthermore, the bone was found in a

cave, suggesting that hominins were often killed and cached in caves by various predators, most notably hyenas. There is not sufficient evidence to prove this individual was a victim of predation. Rather, they may have been dragged into the cave post-mortem and scavenged (Daujeard et al., 2016). Again, although ThI94-UA28-7 falls outside the regional zone of discussion, it is still a valuable specimen for the African hominin fossil record relating to predation.

Millions of years spent as a prey item caused hominin behavior and cognition to be altered significantly. This can be seen in the changes in brain structures as determined by reconstructions from endocasts and skulls as well as archaeological evidence for certain behaviors. Another key to understanding these changes is using modern analogues of extant great apes and their responses to predator threats. As discussed above in the profiled predators, leopards and lions hunt gorillas and chimpanzees respectively so there is pressure for these genera to develop strategies to deal with the risk.

Along with bonobos (*Pan paniscus*), the common chimpanzee (*Pan troglodytes*) is the closest extant relative of humans and thus serves as the best available analogue for how ancient hominins may have dealt with predator presence. Chimpanzees in the Taï Forest are at a high risk of predation by leopards, compared to chimpanzees in other African populations, such as the Gombe Stream chimpanzees of Tanzania. In the Taï Forest, leopard density may be as high as one per square kilometer and thus, resident chimpanzees have molded their behavior around the risk of predation; one study during a five-year period in the 1980s concluded that the actual mortality rate from leopard attacks on chimpanzees was relatively low, where only four were killed during the study time. However, the fact that chimpanzees took up numerous defenses indicates that it was the possible threat of predation rather than the actual rate of successful predation that caused changes in behavior (Boesch, 1991). This is an activity that is clearly observable in humans today; our chances of being mauled by a grizzly bear in a national park are quite low, yet we still take precautions like bringing bear spray. Observations of the Taï Forest chimpanzees revealed that individuals often utilized makeshift clubs and chased off leopards. These spontaneous weapons were not kept though; if they drove the leopard into a space too small for the chimpanzees to fit through, the latter would throw the club into the opening. It was also observed that there were more all-male bands in the Taï Forest population compared to the apes in the lower-risk Gombe Stream group. As male chimpanzees are known to display dramatic aggression, this configuration makes sense given the danger from leopards (Boesch, 1991).

Besides the genetic similarities chimpanzees and humans share, there are other similarities between the two species; one of the most notable is the presence of fission-fusion groups in both. In chimpanzees, females are the predominant sex to leave their natal group upon reaching maturity while in humans, where both sexes partake in this. It was suggested that this form of social behavior in chimpanzees may have been taken up in the distant evolutionary past as a response to predation (Boesch, 1991). While more evidence from the fossil record is needed, it may be possible that ancient

hominins adopted this group structure for the same reason, given the similar African environmental conditions in which the two evolved.

While greatly understudied in comparison to *P. troglodytes*, bonobos observed in this study had a lower risk of being hunted than many groups of chimpanzees. This could be explained by the fact that bonobos more often demonstrated sheltering in trees. While leopards are adept climbers, hiding in the canopy would give the cats fewer opportunities to spot and stalk the bonobos. This low risk of predation is borne out by the observation that, in contrast to common chimpanzees, female bonobos are the ones that tend to form same-sex groups (Boesch, 1991).

Gorillas are the other non-human African great ape and face many of the same dangers as chimpanzees, notably leopard attacks. A number of similarities and differences can be observed in how gorillas deal with predators. Like chimpanzees, they often show displays of aggressive defense and have even been known to partake in mobbing. One fact that differs gorillas from all other primates is that they do not take shelter in trees in an effort to escape carnivores (Isbell, 1994). This makes sense, given their massive size, coupled with their stocky build more suited to knuckle-walking.

While obviously only inferable in ancient hominins, predation may have been a factor behind the adoption of several behavior habits and tendencies in modern humans. One notable habit is selectivity of defecation areas. In modern society, this serves functions of hygiene and public decency, but in more primitive times, defecating in certain areas may have served as a way to mask the scent of feces from predators. Stalking carnivores often use olfactory cues as a means of tracking prey, so either hiding waste or defecating in an area far from the rest of the prey group would be at least somewhat effective in confusing potential predators (Bassotti & Müller-Lissner, 2015). This strategy can be observed in many species such as domestic cats (who are carnivores but can be prey for larger animals) as well as certain primates. Segregated areas for excretion are utilized for a number of reasons such as territory defense and demarcation and mate attraction, so it is not a stretch to think that hominins may have adopted selective areas for protection (Bassotti & Müller-Lissner, 2015).

As obligate bipeds, hominins are physiologically suited to fecal continence; the ano-rectal angle in bipeds is sharper and there are higher demands on the pelvic structure for support in upright stances. This serves in contrast to quadrupedal primates such as gorillas that have poor control of defecation due to the lack of demand for strength in the pelvis (Bassotti & Müller-Lissner, 2015).

With regards to technology, the factor of predation may have been an important impetus. The oldest evidence for fire control in South Africa comes from Swartkrans in early Pleistocene sediments. Analyses by Brain (1995) of fossils recovered from the area show that hominins were frequently the victims of predation by large felines. In Member I, the oldest layer, hominins make up 20.3% of the individual predatory victims found, and in Member 2, this percentage is only a little lower at 16.7%. However, in the youngest layer, Member 3, hominins represent only 5.1% of animals

killed. What is notable is that this layer formed after the first evidence of fire at the site; two hundred seventy non-primate bones in Member 3 show evidence of being heated to a temperature consistent with those found in the average campfire, suggesting that by this point, hominins learned to control fire.

Given this evidence, it appears that fire was first utilized not as a means of cooking food or for warmth, but rather as a protection against a carnivorous threat. With regards to the stages of fire control, fire-tending likely preceded fire-making as hominins appear to have grabbed naturally lit sticks and branches. Lightning-induced fire was probably common in the highveld environment of northeastern South Africa at the time, realizing that other animals avoided them. In addition to the thermal danger of fire, its illumination would unmask any nocturnal predators taking advantage of the nighttime darkness, thus adding credibility to the theory that fire was originally a deterrent (Brain, 1995).

The advent of hunting and the ability to cooperate to take down large game is seen as a triumph of human cognition. However, the development of cooperation amongst hominins (not just their congregation into social bands but also their ability to share labor and work together) more than likely came about first as a means to curb threats of predation and mount defensive attacks. It has already been discussed above that chimpanzees will often join together to chase off a leopard or other carnivore and this great ape analogue coupled with ecological and paleontological evidence implies that Plio-Pleistocene hominins may have developed cooperative ties at least in part for protection.

During the Plio-Pleistocene, East Africa had mostly converted into open grasslands and was home to *Homo ergaster*, the first hominin known to have completely lived on plains. In an environment where they coexisted with numerous solitary and social mammalian (and occasionally avian) carnivores, fight may have taken precedence over flight. As an animal that could not effectively outrun prey, whether by exhaustion or to a tree, a defensive attack may have been the only viable option. Group life allowed for two types of anti-predator defense to be exploited; heightened vigilance through surveillance by select group members or a mobbing defense by chasing off a directly threatening predator (Smith et al., 2012). While once again, most inferences about ancient hominin behavior can only be made indirectly through modern primates, appropriate analogues suggest many parallels in response to predators. A study of various primate responses to predators revealed that counter-attacks are observed in far greater frequency in terrestrial primates than in canopy-dwelling ones. Accompanying this trend is the fact that males tend to be the main participants and work together to drive off the predator (Willems & van Schaik, 2017). As *H. ergaster* was smaller and slower than the carnivores it encountered, a group effort was necessary.

Another correlation observed in the study was group size. Among studies of *Pan* and *Papio* (baboons), it was found that populations that live in the open tend to live in larger fission-fusion groups than do the ones in more closed, forested environments.

It should also be noted that both are known to counter-attack. It is logical that life on open savannahs could only have developed in full once cooperation, especially between males, was established across early *Homo*, so adaptation should be seen as a response to the rich variety of carnivorous taxa in East Africa. While it is impossible to know for certain how large *H. ergaster* groups were, neocortex analyses (based on correlations between the ratio of this structure and group size) imply a size of about one hundred ten. While this inference is highly debatable, given numbers seen in chimpanzees and the low energetic cost of bipedality compared to quadrupedalism (hence lower stress on resources), it appears that group numbers for *H. erectus* mirrored the upper limit seen in chimpanzees: around one hundred (Willems & van Schaik, 2017).

One more factor that is important to take into account is that by the time of *H. ergaster*, hominins had developed effective, if primitive weapons. Given this, it can be argued that their counter-attacks against predators were more effective than those seen in extant primates (Willems & van Schaik, 2017). Whatever the specifics of counter-attack were, it can reasonably be deduced that the development of cooperation within hominin groups came about for protection against predators and only later morphed into activities such as cooperative hunting.

During the course of Plio-Pleistocene human evolution, East Africa experienced tectonic and climatic changes that resulted in a thinning of forests and woodland. The result was a more open grassland environment with sparse tree cover. In this region, hominins were more vulnerable to predators with natural selection favoring an animal that could react to predatory threats on a more cognitive level.

While a number of factors likely play into the encephalization of hominins during the Plio-Pleistocene, predation risk certainly played a role in ancient hominins evolving the cognitive capacity required to perform the risk-mediating behaviors discussed previously. The main driving factor for this is that across the mammalian class, predators tend to show a preference for small-brained prey. Hence, there was a selective pressure for hominin individuals to possess greater cranial capacities; large brain size reduces the risk of becoming prey. While the mechanism for this association is not fully understood, it may be in part due to larger-brained prey's ability to devise more elaborate defense and escape plans (Shultz et al., 2012). This could in part explain why the australopiths ultimately went extinct; while large-brained, they did not undergo the same encephalization as the *Homo* genus and may not have been as effective in out-witting predators as the latter.

A cognitive ability that may have been favored due to the presence of predators was the ability to plan and predict. According to behaviorist John Endler, predation acts occur in six stages: encounter, detection, identification, approach, subjugation, and consumption. Across primates, species have defensive strategies that can stop the process at the "approach" stage. As discussed earlier, great apes such as chimpanzees respond defensively before the predator approaches. Preventing a carnivore's approach at the earliest possible time reduces both the odds of a successful hunt and the ex-

penditure of energy in defense (Hart & Sussman, 2011). On an open grassland, early detection and thwarting of predators was especially important given the inability of hominins to take shelter in trees.

Speech is a relatively new development in human evolution and is dependent on the presence and position of anatomical features. However, the use of communicative calls is well-established in primate populations. Most notably, vervet monkeys have distinct alarm calls for leopards, snakes, and eagles. Rhesus macaques and Japanese macaques also have predator-specific calls. Across primates in general, alarm calls are the most frequently observed defense strategy. Given this utilization of communicative sounds amongst primates, it is likely that the most primeval mutterings of language were used to warn others of a predator's presence. At later stages in evolution, vocal communication allowed hominins to plan defense strategies (Hart & Sussman, 2011).

As mentioned above, the development and communication of complex ideas is a recent phenomenon in human history. Even Neanderthals, with a cranial capacity exceeding that of modern humans, had a skull-base angle between *Homo sapiens* and chimpanzees. The high position of the larynx made their speech sounds limited in comparison to humans (with regards to vowel pronunciation range). *Homo erectus*, which lived until tens of thousands of years ago, had a skull base angle more similar to modern humans, meaning they were probably capable of pronouncing a greater range of sounds. The linguistics of such distant ancestors are still controversial so any ideas of articulate speech in ancient hominins are speculative (Hart & Sussman, 2011). Due to the murkiness of language development, it cannot be concluded with certainty that language evolved because of a need to communicate about predators. But given that other primates have warning calls specific to certain carnivores, the idea that language may have evolved from this base purpose cannot be discounted.

While the fossil record can provide only limited evidence of predation due to preservation biases and other taphonomic factors, modern analogues of human predation can be useful for determining the degree to which humans are preferred prey. While humans may not traditionally be the prey of certain animals, changes in ecological factors and other variables may make humans more susceptible to being hunted. Thus, modern accounts and case studies serve a useful purpose in determining what makes humans preferred prey.

Perhaps the most famous case of predation on humans in modern history is that of the Tsavo man-eating lions. Between March and December 1898, two males ravaged the area in which the Uganda Railway was constructing a line to the coast. Over this period, at least twenty-eight people were killed and devoured by the pair. At the time, this area of southeastern Kenya was covered in thick, nearly impenetrable thorns that would have aided the efforts of the lions to hide and ambush (Kerbis Peterhans & Gnoske, 2001). However, there are other ecological and physiological factors that help to explain why these two lions selected humans as their preferred prey.

At the time the attacks began, it was noted that several large ungulate species were not present in the Tsavo area, a phenomenon directly correlated to the elimination of elephants from the area, which allowed the thorny thickets to spring up. In addition, the 1890s saw anthropogenic activities introduce the rinderpest to Africa. This is a virus that infects bovines and other artiodactyls and at the time, it devastated the populations of wildebeest, buffalo, and other bovids that lions typically hunt. With their traditional preferred prey wiped out, lions would turn to one of the larger animals now present in the area: humans (Kerbis Peterhans & Gnoske, 2001).

Additionally, study of the skulls of the man-eaters indicates that both lions were missing the apical end of the lower left canines, injuries sustained earlier in life. The first man-eater shot (FMNH 23970) also displayed a severely damaged lower right canine with an exposed pulp cavity, also an antemortem injury (likely from a kick by a prey animal). Mal-occlusion meant that the mandible and incisors in particular were lopsided. This hindered the individual in his ability to hunt down preferred prey. The second man-eater killed (FMNH 23969) had a broken upper left carnassial (P4) and broken lower right canine, the latter of which was worn, indicating it was sustained many years before the lion was killed. It is doubtful, however, that the specific injuries to FMNH 23969 greatly affected his carnivorous behavior if at all. Further evidence for this lies in the fact that the lion with the greater dental injuries (FMNH 23970) was slain first and no human kills were reported by the still-living man-eater in the twenty days until the lion was killed. This makes it likely that FMNH 23970 was the primary man-eating culprit (Kerbis Peterhans & Gnoske, 2001). This assertion makes sense given the lion's dental trauma.

It should be noted however that despite the legends, these lions were not obligate man-eaters. Analysis of their teeth has revealed traces of warthog, eland, oryx, porcupine, zebra, and impala DNA, making it clear that they were still devouring other prey during their tenure as “man-eaters” (Kerbis Peterhans et al., 2001).

While it is clear from multiple ecological surveys that humans are not the preferred prey of lions under normal circumstances, ecological strain by anthropogenic activities and disease can drive large carnivores to seek out prey outside their typical preferences. In addition, the Tsavo lions were unique in their display of traumatic injuries so this case can lead one to conclude that weaker (or possibly older) individuals will target humans as the latter may be less risky to hunt than traditional prey; humans are both slower and lack the physical defenses seen on bovids. While the Tsavo case is certainly an isolated one, it provides insight as to what may turn otherwise occasional consumers of human flesh to a more amplified threat.

Man-eating can still be observed in many parts of the world. Although it is outside the geographical bounds of the ecological and direct evolutionary analysis of this paper, North America serves as an excellent example of a place that sees a fair number of humans as prey. Attacks on humans by large predators is increasing, and it is worth

observing what factors play into these attacks as they may be applicable to Africa and the rest of the world.

According to a 2017 study (Penteriani et al.), during the past sixty years, humans were killed in forty percent of attacks in North America, and these kills were attributable to felids (*Puma concolor*) and canids (*Canis lupus* and *Canis latrans*) as well as ursids (*Ursus arctos horribilis*, *Ursus americanus*, and *Ursus maritimus*). From these attacks, it was concluded that the most common victims were alone and were ten or under in age. Time of day also played a factor as ninety-four percent occurred during the day or evening. Of these attacks, fifty-three (fifty percent) were caused by the cougar, a large solitary cat similar to what ancient hominins encountered in Africa.

Humans are increasingly becoming preferred prey for these large carnivores in areas of North America. This is primarily due to growing encroachment onto the traditional territories of these carnivores, putting humans directly in a path to be hunted. Compounding this is relaxation of risk avoidance behavior; the fact that increasing integration into a technological world has made humans less knowledgeable on how to practically defend themselves against such attacks. Other factors that increase the numbers include leaving children unattended in high-risk areas (Penteriani et al., 2017).

Although it cannot be concluded yet that humans are preferred prey in these regions, a lack of vigilance shaped by decades of relatively predator-free living and coexistence with large carnivores are likely to influence an uptick in human casualties. Large carnivores do not randomly target (Penteriani et al., 2017). Therefore, if the human population increases in high-risk areas, predators will specifically target them more.

Finally, Northeast Africa provides an interesting case study. Hyenas are known to be both voracious scavengers and adept hunters, so it is no surprise that they target humans in highly anthropogenic areas. Given that spotted hyenas (*Crocuta crocuta*) are the apex predator in the arid region including Eritrea, Ethiopia, and Somalia, humans living there are more likely to be targeted as food (Gade, 2006). Hence, this region serves as an excellent case study for humans as preferred prey.

Surprisingly for an animal maligned in many cultures, hyenas are tolerated in anthropogenic environments within the countries mentioned above. They are seen as an efficient form of waste removal through their scavenging activities so allowed to wander into garbage dumps near human settlements. In addition, the presence of much armed conflict as well as disease and famine in this region has unfortunately provided opportunities for hyenas to devour human corpses. The allowance of hyenas for waste removal as well as the attraction of human remains has led to an increase in hyenas attacking livestock and killing people (Gade, 2006).

Given that humans and hyenas have co-existed in this region for centuries, it is likely that humans have developed coping mechanisms such as practicing a higher degree of risk avoidance behavior.

Looking into the fossil record, few assertions can be made. Due largely to preservation biases, it is difficult to draw conclusions as to whether and what ancient hominin species were preferred prey for various carnivores. However, South Africa with its fossil-rich caves offers some insight.

The Swartkrans site has yielded at least eighty-eight specimens of *Paranthropus robustus*, the most common prey item found there in association with leopards. The Drimolen site's remains tell the same story. The genus *Homo* is not represented in this context nearly as much, leading to the conclusion that it was better at defending itself against leopard attacks than the Australopiths (Kerbis Peterhans & Gnoske, 2001). In addition, *Paranthropus robustus* is thought to have been a habitat generalist, living both on open grasslands and in more vegetated areas. Analysis of fossil assemblages of this species with regards to abundance profile show it to be more similar to woodland-adapted taxa. Patterns of predation by carnivores are indicative of prey habitats so analysis of this type is useful for examining hunting preferences (de Ruiter et al., 2008). If *Au. robustus* frequented a woodland-like habitat, it makes sense for them to be targeted by leopards given the latter's tree-caching and climbing activities.

For certain, hunting has played a significant role in the evolution of humans. However, more scholarly study has been undertaken with humans being on the conducting end of the hunt rather than the receiving end. The ways in which the millions of years that bipedal hominins spent as prey (including after they began hunting) influenced their behavioral and cognitive evolution cannot be discounted. That primordial state still clearly resides in humans and it comes out whenever they watch a spine-chilling horror film or walk in the woods at dusk. In multiple ways, being the hunted rather than the hunter shaped who humans are mentally and, despite their largely modern technological existence, keeps them very much a part of the natural world.

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