Chapter 6
Predation on Hominins

6.1 Introduction

Early hominins lived with a greater number and a greater variety of predatory animals than exist in Africa today. Survival in these circumstances was a crucial aspect of early hominin evolution. Hominins were subject to ambush in relatively dense vegetation and pursuit in more open areas. Baboon analogies pertain to hominin susceptibility to various predators and potential responses to them. Carnivorans (mammals of the order Carnivora, as distinguished from carnivorous animals in general) must have presented the greatest danger to hominins. Particularly significant were leopards, their ancestors and relatives, and leopard-like saber-toothed felids. Baboon behavior suggests a variety of responses that would have been available to hominins, ranging from avoidance to counter-attacks.

Fossil evidence for predation on hominins is rare, which might seem to imply little danger, but observations of living baboons suggest that this is illusory. If the paleoanthropological record accurately reflects a low incidence of mortality from predation, it might be due to relatively effective countermeasures by the hominins. Baboon analogies suggest that this is the case.

6.2 Predators and Predation

Carnivorans are the greatest danger to extant baboons and this was probably true for early hominins as they evolved to an increasingly terrestrial way of life, and especially as they expanded into more open habitats (Willems and van Schaik 2017). The species that attack baboons all existed and/or had counterparts at various times during the era of early hominins (Lewis 2017).

G. E. King, *Baboon Perspectives on Early Human Ancestors*,
https://doi.org/10.1007/978-3-031-36769-4_6

Extant carnivorans display two basic modes of predatory attack (Hopley et al. 2023). One is ambush: the predator awaits its prey under some kind of cover. The other is pursuit (also called “coursing”). Pursuit implies a run that extends beyond the brief rush often made by an ambush hunter. A stalking phase may or may not be incorporated into either approach (Treves and Palmqvist 2007). Most carnivorans specialize, but some are skilled in both kinds of attack.

Inferences about the hunting behavior of prehistoric carnivorans can be made on the basis of morphology and comparative evidence. For instance, powerful forelegs suggest the grasping ability of an ambush hunter, while long legs indicate pursuit. Ambush hunters are most effective in woodland or in more open areas with large enough patches of cover (like modern leopards). Pursuit hunters are more effective in more open areas (like modern wild dogs). Jaws and teeth for crunching bone suggest scavenging rather than hunting; however, this signal is somewhat ambiguous because the extant spotted hyena is a specialized bone cruncher and also a formidable pack hunter (Kruuk 1972).

6.2.1 Potential Predators of Hominins

Early hominins lived among a variety of dangerous carnivorans (Table 6.1). Hominins seem to have originated during a time when modern carnivoran families, felids and hyaenids, became more common and replaced more archaic taxa (Lewis 2017). The earliest hominins (about 7 to 4 mya) shared their woodland habitats with saber-toothed cats (*Dinofelis* and *Machairodus*), both probably ambush hunters. The long-legged “hunting hyena” (*Chasmaporthetes*) might have been an ambush threat in woodland, but might also have attacked any hominin that wandered into the open. *Agriotherium*, a huge bear must have favored larger prey, but might have taken hominins in sudden woodland encounters and could have run them down in the open. With longer legs than extant bears, it was a faster runner. These and other ancient carnivorans are described in more detail in Table 6.2.

At neighboring sites in East Africa dating to more than 4 mya, *Australopithecus anamensis* thrived in mosaic environments; after 3.8 mya the hominins began to exploit grassland resources (Bobe et al. 2020). During this transitional period, danger from ambush predators presumably continued in woodland and arose more often near concentrations of trees and bushes in savannas. At the same time, hominins must have been exposed to more risk from pursuit hunters.

A host of carnivorans were added to the mix after 3.6 mya, including two more sabertooths, a giant hyena, and probable ancestors and/or close relatives of extant lions, leopards, cheetahs, and hyenas (Table 6.2). Many were “roughly the equivalent of modern species” (Lewis 2017: 35). The origin of taxa more like those in recent Africa, strengthens the argument for analogies with baboons. Meanwhile, the ancient saber-toothed genus *Dinofelis* and the “hunting hyena” *Chasmaporthetes* were still potential threats, as they persisted until about 1 mya.

Table 6.1 African large carnivores

Genus	Body mass in kg	Description	Habitat	Attack mode	Time Span
Machairodus	130–230	Saber-toothed cat	Open > woodland	Stalk/ambush	10 mya to 10 kya
Dinofelis	70–100 [150–230]	Saber-toothed cat	Woodland > open	Ambush/stalk	7 to 1 mya
Chasmaporthetes	50–70 [50–55]	Long-legged hyena	Open > woodland	Pursuit/pack	7 to 1 mya
Agriotherium	600–700	Fast-running bear	Woodland > open	Opportunist/ pursuit	6 to 3.6 mya
Megantereon	80–110 [40–65]	Saber-toothed cat	Woodland > open	Ambush/stalk	4(?) to 1mya
Homotherium	150–230 [115–345]	Saber-toothed cat	Open > woodland	Stalk/pursuit	4.2 to 1 mya
Pachycrocuta	100–130 [60, *n* = 1]	Giant hyena	All	Opportunist/ pursuit/pack	4(?) to 1 mya
Crocuta	~60 [40–65, *C. crocuta*]	Spotted hyena	Open > woodland	Pursuit/pack	4 mya to present
Hyaena	35–40 [35–45]	Striped hyena	All	Opportunist	4 mya to present
Parahyaena	35–40 [35–45]	Brown hyena	All	Opportunist	4.2 mya to present
Panthera leo	~170 [135–225]	Modern lion	Open > woodland	Stalking/brief pursuit	3.6(?) mya to present
Acinonyx	~50 [90, *n* = 1]	Fossil/ modern cheetah	Open > woodland	Stalking/long pursuit	3.6 mya to present
Panthera pardus	~55 [30–50]	Modern leopard	All	Stalking/ ambush	3.6(?) mya to present
Lycaon	25–40 [20–35]	Wild dog	Open > woodland	Pursuit/pack	2.4 mya to present

This table synthesizes information from Treves and Palmqvist (2007), Hopley et al. (2023), Bobe et al. (2020), Kuhn et al. (2016), and O'Regan and Reynolds (2009). Mass figures are from Treves and Palmqvist (2007); those in brackets are from South African species reconstructed by O'Regan and Reynolds (2009)

Paleoanthropological research can clarify some particular hominin–carnivore relationships, as shown by two examples from South Africa. Stable isotope research on fossils from one locality found that some potential predators had C_3 signatures similar to those of the hominins while others did not (Lee-Thorp et al. 2001). On this basis the strongest candidates for hominin predators were leopard, spotted hyena, and the saber-toothed *Megantereon.* The saber-toothed *Dinofelis* and the hyena *Chasmaporthetes*, having more mixed diets, were probably less likely to have attacked hominins. At another site, stratified remains of early *Homo* and leopards traced the relationship between the species across time in the context of cave

Table 6.2 Characteristics of some Plio-Pleistocene African carnivorans

Taxa	Time span	Limbs/body	Jaws/Teeth	Comments
Sabertooths				
Dinofelis	7–1 mya	Early and late species jaguar-sized; robust forelimbs for grappling (Hopley et al. 2023)	Moderate "sabers"—maybe slightly larger prey than jaguar (Anton n.d.)	Ambush
Megantereon	4–1 mya	Similar to leopard in body size but some closer to jaguar (Anton n.d.); short legs, very strong forelegs (Hopley et al. 2023)	Sabertooth features of neck and skull suggest killing larger prey than *Dinofelis* (Anton n.d.)	Ambush; less common than other sabertooths (Hopley et al. (2023)
Homotherium	4–1 mya	Short hind legs and back, poor for acceleration; moderate speed for longer distances; body size overlapped lions but lighter weight (Anton n.d.); long forelimbs with poor grasping ability (Werdelin and Lewis 2020)	Large incisors in arc like dogs and hyenas = greater role in grasping prey; possible pack hunter (Anton n.d.)	Short pursuit (maybe able to catch bipeds)
Other Felids				
Panthera cf. *pardus* (leopards)	3.6? mya to present	Fossil forms that were ancestors or close relatives of the extant leopard		Probably ambush
Panthera cf. *leo* (lions)	3.6? mya to present	Fossil forms that were ancestors or close relatives of the extant lion. Some larger		Probably emphasized prey larger than hominins
Acinonyx (cheetahs)		Fossil species larger than extant		Greater size might have allowed some predation on hominins
Hyaenids				
Chasmaporthetes	7–1 mya	"hunting hyena" with long legs		Pursuit
Parahyaena howelli	c. 4 mya		Generalized hyena without strong scavenging adaptations (Hopley et al. 2023; Werdelin and Lewis 2020)	Scavenging and pursuit (Hopley et al. 2023)
Pachycrocuta	4–1 mya	Giant hyena		

(continued)

Table 6.2 (continued)

Taxa	Time span	Limbs/body	Jaws/Teeth	Comments
Crocuta	2.5 mya–present		Earlier species not specialized for scavenging (Hopley et al. 2023)	Possible pursuit like extant species

References: Anton (n.d.), Hopley et al. (2023), Werdelin and Lewis (2020)

occupation (Pickering et al. 2008). The presence of leopards seemed to discourage hominin activity. It seems a reasonable speculation that the hominins still lacked the ability to drive the cats out of a desirable cave.

Some paleoanthropologists have argued that the relationship between hominins and their predators has been distorted by problems in excavation and interpretation. They maintained that the abundance and diversity of carnivores associated with hominins has been exaggerated because fossils from different time periods have been lumped together, forming a “palimpsest” (Hopley et al. 2023; O’Regan and Reynolds 2009). Others disagreed (e.g., Geraads and Daujeard 2011).

This is an important issue, but not a crucial one for the discussion presented here. Hominins during each time period lived with at least some of these carnivorans and were probably preyed upon by some of them. Furthermore, regardless of the number or taxonomic classification of coeval carnivoran taxa, hominins always faced the same two basic modes of attack: ambush and pursuit. The main shift in predator pressure probably came from increasing use of relatively open habitats by many hominin populations.

6.2.2 Baboon Predators

An abundance of large herbivores provided potential food for prehistoric carnivorans. This raises the question of whether or not predation on hominins was frequent enough to have a significant effect on hominin ecology and/or behavior (Treves and Palmqvist 2007). Contemporary Africa is broadly analogous to the Plio-Pleistocene situation in harboring a variety of large herbivores and large carnivorans, although the numbers and diversity of both are reduced (Willems and van Schaik 2017). The place of baboons in the modern biomes indicates that early hominins were subject to significant predation. All the large African carnivorans include baboons in their diets, even though they prefer other prey.

A survey of game reserves in southern and eastern Africa found that baboons had rarely been reported as prey, but the available data contained 97 instances of baboons killed by predators (Saayman 1971). Fieldwork by scientists began to add additional cases (Busse 1980; Stelzner and Strier 1981; Rhine et al. 1980). Synthesis of cases where a specific predator was identified or inferred provides the following distribution: leopard—78; lion—14; hyena—8. Cowlishaw (1994) obtained a comparable result in a survey of reports from across sub-Saharan Africa: leopards preyed on baboons at every site and lions in fewer localities, while hyenas of all species provided only a few cases.

Reports of baboons killed by leopards have continued to accumulate and provide more details (e.g., Bidner et al. 2018; Allan et al. 2021). Ordinarily, baboons are a relatively small part of the leopard diet (no more than 5% by biomass), but the rate increases under some circumstances. During a 5-month study of three female leopards in a montane region of South Africa, baboons equaled impala as the most frequent prey, each with 18 kills amounting to around 20% of the total biomass (Jooste et al. 2012).

Even where the percentages are low, baboons sometimes rank among the most frequent prey of leopards. Research in South Africa placed chacma baboons among the three most common animals in the leopard diet (along with bushbuck and duiker) (Williams et al. 2018). Another South African study also found baboons to be among the “main prey species” of leopards (Greyling et al. 2023).

Hyaenid predation on early hominins may have been somewhat higher than it is for extant baboons, because the hyenas were more diverse and numerous. However, the baboon evidence suggests that felids were always the most important in this regard. All early hominins lived with leopards, leopard ancestors or relatives, or leopard-like sabertooths such as *Megantereon* (Table 6.2).

Rowell (1966) suggested that baboon victims are “occasional young stragglers,” which seems to imply that predation has no significant behavioral or demographic effect on baboon groups. However, data from studies cited above tell a different story. Of 18 cases for which age/sex categories were reported, the baboons killed were 9 adult males, 5 adult females, and 4 immatures (Busse 1980; Stelzner and Strier 1981; Rhine et al. 1980; Saayman 1971). The survey by Cowlishaw (1994) also indicated that adult males were taken more frequently than females or young. Only in the unusual situation described by Jooste et al. (2012), where baboons were killed with the same frequency as impala, was there no sex difference among the victims.

It is possible that leopards prefer adult male baboons because they provide more meat than any other age-sex class. Other hypotheses were summed up by Cowlishaw (1994): (1) many adult males are peripheral and distant from nearest neighbors; (2) maturing and adult males go through solitary periods when transferring between groups; (3) leopards would prefer smaller baboons but usually find them in the center of a group.

Records of predation on baboons have been affected by two developments. First, hunting has greatly diminished carnivore populations in most parts of Africa. Second, probably because of hunting, the presence of human observers tends to result in avoidance by carnivores (Washburn et al. 1965). Consequently, data collected over the last 70 years likely represent the minimum of predation on baboons. Baboons probably faced greater danger from predators before that, and early hominins probably faced even greater danger.

6.2.3 Body Mass of Predators and Prey

Body mass is an important element in predator–prey relationships. One basic factor is the degree to which meat was essential to the predators. Studies of extant carnivores have established that species in which individual weight exceeds 21.5 kg are obligate meat eaters (Carbone et al. 1999; O'Regan and Reynolds 2009). That is, they must have a large quantity of meat on a regular basis to survive. All of the carnivores in Table 6.1 exceeded that threshold (Lewis 2017; O'Regan and Reynolds 2009).

This implies a readiness to exploit a variety of sources for meat. Some meat can come from scavenging, but this may set up intense and potentially dangerous competition among obligate carnivores. Even extant spotted hyenas, highly adapted for scavenging, are also very effective hunters (Kruuk 1972). Ungulates were undoubtedly the mainstay of the ancient carnivoran diet, but the need for meat might have led many to include early hominins (Treves and Palmqvist 2007).

The size of a predator relative to potential prey is important for two reasons. First, the predator must be large enough to take down the prey. Second, the predator must not be so large that the prey is not worth the effort (caloric expenditure) under ordinary circumstances. Application of this principle to hominin-baboon analogy requires an adjustment because early hominins were significantly larger than extant baboons (Chap. 2).

Median size of adult baboons, across all species, for adult males and females, is roughly 20 kg (range of about 10 to 30 kg, Fischer et al. 2019). Leopards and hyenas tend to be almost twice the size of baboons, and lions are about 7 to 11 times larger (cf. Table 6.1). These ratios provide the adjusted analogy for early hominins. According to recently applied data and techniques, the median body mass of early hominins, including earliest *Homo*, was about 42.5 kg (range of 25–60 kg, average ~43 kg, Ruff and Wood 2023). The relative sizes suggest that hominins might have been a small but regular part of the diet of many carnivores in the range of roughly 80–400 kg. This applies with varying degrees of probability to five of the extinct genera in Table 6.1

Several qualifications are in order. First, a powerful animal like a leopard can kill prey of its own weight, such as an extant human (Camaros et al. 2015), or greater, such as a gorilla (Fay et al. 1995). Therefore, even large adult male hominins were potential prey for early leopards or their close relatives, or sabertooths with similar capabilities. Extant leopards prefer prey in the range of 10–40 kg with the strongest preference at about 25 kg (Hayward et al. 2006), which suggests that female and young hominins may have been particularly at risk.

Second, even the smaller predators in Table 6.1 could have preyed on young hominins and might also have taken adult females. This is especially so if the females were much smaller than males as some interpretations of the fossils propose (Chap. 2). Extant cheetahs, for example, sometimes expand their prey base by killing juveniles of larger species (Annear et al. 2023). Extant cheetahs are not known to prey on baboons, but some of their prehistoric ancestors and relatives were larger.

Third, carnivores hunting in packs can bring down animals much larger than themselves. This is true of extant spotted hyenas and wild dogs, and may apply to fossil taxa such as the hyenas *Pachycrocuta* and *Chasmaporthetes*. Based on the behavior of extant hyenas, the hunting group might be a large pack or just two or three individuals. Smaller groups might profitably hunt smaller prey, such as hominins.

6.3 Defenses Against Carnivorans

The evidence for carnivorans that were contemporary with early hominins raises the question of how hominins survived this danger. Baboons demonstrate a number of different ways in which hominins might have coped.

6.3.1 Avoidance and Flight

Baboons can avoid predators by tactical movement during travel, such as staying away from dense vegetation that would provide cover for leopards (Altmann and Altmann 1970). Another avoidance tactic is to locate activities according to levels of danger (Hill and Weingrill 2007). A study of chacma baboons found that they spent more time feeding in low-risk relatively food-poor habitat than in a high-risk food-rich habitat; they also preferred the low-risk areas for other activities, including resting and grooming (Cowlishaw 1997a, b).

Baboons also keep predators at a distance by associating with certain other species. Buffalo and elephant intimidate predators (Fig. 6.1). Antelopes such as impala and bushbuck add to vigilance (Fig. 6.2), complementing baboon eyesight with their sense of smell; baboons respond to their warning barks (Washburn and DeVore 1961). Badenhorst (2018) inferred such behavior for early hominins, including *Australopithecus africanus*. He noted that the extinct *Gazella helmoedi* is thought to be a South African representative of the impala lineage that gave rise to one of the important “partners” of extant baboons.

Given warning, baboons are likely to flee. However, flight is complicated when the threat is “interior” rather than “exterior” (Itani 1967). That is, the predator seems to appear suddenly in the midst of a group. One reaction is rapid random motion that probably serves to confuse the predator. When a leopard jumped from bushes into the midst of a baboon group, the baboons responded with “a flurry of animals running in several directions” while uttering “a sudden barrage of loud, plosive vocalizations” (Altmann and Altmann 1970).

When baboons flee from danger, they seek shelter in trees or on cliffs. A study of wild baboons demonstrated the tactical relationship between refuges and behavioral

Fig. 6.1 Cape buffalo. Baboons associate with animals, such as buffalo and elephants, that intimidate predators. (Photo by Glenn King. Manyara, Tanzania)

Fig. 6.2 Baboons with an impala. The vision of the baboons and the olfactory sense of the antelopes complement each other in predator defense. (Photo by Glenn King. Tarangiri, Tanzania)

ecology. If refuges were readily available, a high-risk area was used more intensively. If refuges were scarce, the baboons adopted a time-minimizing strategy and left the area as soon as possible (Cowlishaw 1997a, b). As long as early hominins retained a significant degree of climbing ability (Chap. 2), they probably responded in similar ways.

However, reaching a refuge, even if close by, must have been more of a problem for hominins than for baboons. As bipeds, the hominins would not have the same speed as baboons. This might not have been a great issue in the woodland habitats of the earliest hominins, but that would have changed with increasing use of open areas (Willems and van Schaik 2017). Probably another factor was the declining arboreal abilities of hominins as they committed to a terrestrial way of life (Chap. 2). Here the defensive capabilities of baboons become an important analogy for early hominins.

6.3.2 Active Defense

Willems and van Schaik (2017) performed a literature survey and comparative analyses of primate "counter-attacks" against predators, covering 16 species of 13 genera. Of the 40 reports that they found, 60% pertained to either baboons or chimpanzees. The authors drew analogies to early *Homo*, but populations of later *Australopithecus* were also comparable in terms of increasingly diverse habitats, including savannas (Chap. 2). The general conclusions about primate counterattacks were:

1. They were more common than expected among terrestrial taxa in open habitats.
2. They were often unprovoked and proactive.
3. Males were four times more likely to be involved than females.
4. Males were 6.4 times more likely to jointly counterattack carnivorans compared with all other predators combined.
5. In 25% of the relevant reports (8 of 36), the predator was killed.

The contribution of baboons to these results is clear. Male baboons engage in active defense against predators (Fig. 6.3). Several adult male baboons can injure or kill a leopard and these are the usual odds in a daytime confrontation (Cowlishaw 1994; Cheney and Seyfarth 2007; Devore and Hall 1965). A single male can intimidate smaller carnivores, such as cheetahs (Baenninger et al. 1977; DeVore and Washburn 1963) and jackals (Altmann and Altmann 1970).

Counteraggression against leopards, the most frequent attackers, involves some risk. In one fight, for example, three males were injured (an adult, a subadult, and a juvenile). With regard to adaptive significance, males may be defending their offspring and/or actual or potential mating partners as well as themselves (Willems and van Schaik 2017). Because male baboons are individually dangerous and because they often cooperate (or at least synchronize their behavior), benefits of such behavior tend to outweigh the costs.

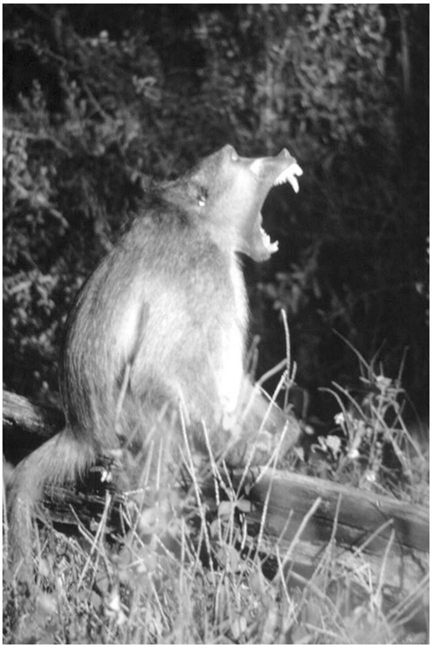

Fig. 6.3 A male chacma baboon displays the long canine teeth that may be used to defend himself and other members of his troop. (Photo by Curt Busse. Okavango, Botswana)

The survey by Cowlishaw (1994), which focused entirely on baboons, found that "retaliation occurred against a wide variety of predators and was almost always successful" (p. 300). This was based on a total of 15 encounters, 6 of them with leopards. In the course of these encounters four leopards and one defender were killed. More than one male was involved in at least five of nine events. In a single instance that involved a female defender, the predator was undeterred. In general leopards avoid baboons during the day (Hayward et al. 2006), although they attack refuges at night (see Sect. 6.5 below). This is particularly supported by "numerous studies" in South Africa (Jooste et al. 2012).

Baboons sometimes engage in "proactive" aggression against leopards. Kiffner et al. (2013) reported a female leopard with two cubs that were "mobbed" by a troop of forty baboons. During the interaction under discussion, "three adult male baboons persistently attacked the leopards" (Kiffner et al. 2013: 169). It was inferred that they killed a cub: during 30 min of observation after the interaction ended, only one cub was seen. This apparent result parallels the killing of a leopard cub by chimpanzees (Hiraiwa-Hasegawa et al. 1986), suggesting that early hominins might have had a similarly aggressive relationship with leopards and perhaps some of their felid predecessors.

Baboons are more intimidated by lions (Cowlishaw 1994), but sometimes respond aggressively (Altmann and Altmann 1970). In one incident a large chacma baboon troop used sustained and strenuous threats to coerce a lioness and cubs into vacating the baboons' travel path (Saayman 1971). Busse (1980) reported similar cases of "harassment." Baboons sometimes followed lions as far as several hundred meters until the carnivores moved away from the troop. Adult and subadult males performed this behavior more often than females.

6.3.3 The "Male Rampart"

Washburn and DeVore (1961) presented a model of baboon defense that some later authors referred to as the "male rampart." This melodramatic phrase obscures the nature and variation of the pattern, which simply involves one or more adult males taking a position between the group and potential or actual danger. Sometimes the "rampart" forms because males advance toward the threat. In other cases, it is the result of males retreating more slowly than other group members and then turning toward the predator (Altmann and Altmann 1970). Willems and van Schaik (2017), based on their comparative study, suggested that the so-called "rampart" hypothesis should be revived.

Rowell (1966) described such a deployment among olive baboons in a forest habitat. However, she emphasized that it occurred only when a minor cause of alarm elicited no response from adult males while others ran away. "A stronger stimulus produced precipitate flight, with the big males well to the front and the last animals usually the females carrying heavier babies" (p. 362). This vision of male terror titillated a number of writers, who neglected to ask what stimulus produced "precipitate flight." Although Rowell heard alarm calls associated with leopard and lion, "no other interactions with these predators were seen or deduced" (p.359). The cause of observed baboon flight was the approach of humans. Other baboon researchers have noted that baboons quickly learn to avoid humans, especially if any baboons are killed by them (Washburn and Hamburg 1965; Stolz and Saayman 1970).

Anderson (1986) included four baboon species in a general survey of primate responses to domestic dogs. Every baboon species displayed instances of aggression as well as flight. Males interposed themselves between their groups and the threat. Three species of baboons chased dogs and chacma baboons sometimes killed them. More recently, Zinner et al. (2000) saw comparable behavior in hamadryas baboons. Because they were crop raiders, the baboons risked being killed by humans or their dogs. Adult and subadult males effectively "shielded" other group members against dogs. They also preceded others into the dangerous areas of agricultural fields. The term "shield" is probably more appropriate than "rampart" for this behavior. A rampart is monolithic and static. Shields are portable and flexible in their use.

6.3.4 Use of Weapons

Active predator defense is one of those issues where different lines of evidence come together: in this case from baboons, chimpanzees, and paleoanthropology. Baboon and chimpanzee analogies indicate that early hominin males would have engaged in joint defense (Willems and van Schaik 2017). However, baboons and chimpanzees have long, sharp canine teeth; early hominin canines were reduced in size and more like incisors (Chap. 2). The hominins would probably have needed other weapons to defend themselves.

Chimpanzee evidence suggests that early hominins could have developed effective clubs and thrusting spears. In a field experiment, chimpanzees picked up branches that had been provided by researchers and used them to attack a moving mechanical leopard (Kortlandt 1980). In recent field research chimpanzees were observed killing galagos in tree holes with pointed branches, reminiscent of thrusting spears (Pruetz et al. 2015). Given upper body anatomy like chimpanzees, early hominins could have wielded such weapons to defend against predators. The uniquely hominin trait of bipedalism would have made it possible to carry such weapons continuously and use them at a moment's notice.

Stones are another possible weapon. For years there were sporadic and questionable accounts from diverse sources of chacma baboons defending themselves by throwing stones. Then primatologists reported that three troops in southern Africa dropped and threw stones at them from the tops of cliffs on numerous occasions (Hamilton et al. 1975). Escape movements and vocalizations indicated that the baboons regarded the humans as a threat. This report from southern Africa elicited accounts from other scientists about similar incidents in Kenya (Pickford 1975) and Sudan (Pettet 1975).

Treves and Palmqvist (2007) mentioned the use of stones, but expressed doubt that such "simple projectiles" could deter predators that are persistent in pursuit or "emboldened" by the numbers of a pack. This conclusion is implicitly connected with the authors' hypothesis that early hominins foraged in small groups of mutually trusting individuals that countered predation by maintaining a high level of vigilance. An alternative hypothesis emerges from the baboon model that they reject. A large group like a baboon troop might produce a barrage of stones sufficient to discourage many carnivores. Bipedal hominins could carry stones during group movement, especially adults who were not carrying young.

Again, chimpanzee analogy also comes into play. Chimpanzees demonstrate learned accuracy in throwing that might represent the potential of the LCA. Following on reports of individual differences in aimed throwing in wild and captive apes, Hopkins et al. (2012) studied chimpanzees to seek the neuroanatomical correlates of the behavior. They found that, in the brains of reliable throwers, the proportion of white matter to gray matter was significantly higher in the homologue of Broca's area and in the motor-hand area of the precentral gyrus. In addition, asymmetries in white matter within both brain regions were larger in the hemisphere contralateral to the chimpanzee's preferred throwing hand. The researchers suggested that a neural pattern like this could have provided the foundation for intense selection on increased motor skills associated with throwing in hominins.

To summarize the preceding argument: primate analogies lend themselves to a scenario in which early hominins combined (1) throwing ability evolved from a chimpanzee-like ancestor with (2) large baboon-like groups containing numerous males with baboon-like tendencies toward active defense against predators. Hopkins and colleagues also suggested a connection with the origins of speech and language, because of the involvement of a homologue for Broca's area. Speculation that the hominins in question had the rudiments of speech suggests that such communication might have helped to coordinate barrages of rocks.

6.4 Other Predators

Baboon analogies support sparse paleoanthropological evidence that early hominins faced dangers from air and water as well as land. Predation by raptors is almost certain; crocodiles and snakes are possibilities. The frequency of these events probably fell far short of attacks by leopards and other carnivorans.

6.4.1 Raptors

The skull of a juvenile *Australopithecus africanus* from Taung, South Africa, displays damage that is nearly identical to that which is inflicted on contemporary monkey skulls by the talons of eagles (Berger 2006). The fossil was the lone hominin found among the remains of mostly small animals like the assemblages formed by modern raptors (Berger and Clarke 1995). Though no additional cases have been discovered, there is no reason to think that the fate of the Taung child was unique. Damage to prehistoric monkey skulls also indicates attack by crowned eagles or similar raptors (Gilbert et al. 2009).

The Taung child is estimated to have weighed 10–12 kg. The African crowned eagle (*Stephanoaetus coronatus*) of today preys on mammals weighing up to 20 kg and prefers primates (specifically, mangabey monkeys). However, neither the crowned eagle nor any other raptor is known to have killed any primate weighing more than 13 kg (McGraw and Berger 2013). These data suggest immunity to attack by such raptors for most adult baboons and all adult hominins. However, juveniles like the Taung child, who move independently of their mothers, are and were vulnerable.

Baboon behavior toward raptors is comparable to their reactions to carnivorans. In two encounters with crowned eagles, olive baboons gave alarm calls that caused infants and juveniles to rush from trees and seek shelter under bushes or in close proximity to adults (Paciência et al. 2017). In both encounters adult male baboons took the lead in climbing trees and threatening the eagle, which withdrew. Similar behavior took place in encounters between hamadryas baboons and a different species of large eagle. In response to alarm calls, immatures rushed to adults while adult males threatened the eagle (Zinner et al. 2000; Zinner and Pelaez 1999).

6.4.2 Crocodiles

The lakes where hominins may have caught fish and gathered invertebrates were inhabited by crocodiles, enemies for which hominins would have had no active defense. *Australopithecus anamensis* at Kanapoi in Kenya lived near a lake containing at least three species of crocodiles. One of them, comparable to extant Nile crocodiles, was described as "gigantic" (Brochu 2020). Bones of early *Homo* from Olduvai Gorge seemed to display tooth marks characteristic of crocodiles and suggested that one or two individuals lost a leg in the encounters (Brochu et al. 2010). The researchers noted that the reptiles were common in lake and river basins throughout much of Africa and speculated that they were common predators on hominins.

Doubts have been raised about the crocodile interpretation of the skeletal evidence. Applying an alternative statistical method, McPherron et al. (2022) concluded that the original results are indistinguishable from a null model based on random data. On the other hand, baboon analogy supports the plausibility of crocodile predation on hominins. Interactions between the species were seen in the Okavango Delta of Botswana (Cheney and Seyfarth 2007). On three occasions a crocodile jumped out of shallow water to attack adult male baboons. Two of the baboons escaped injury, but the third was bitten on the face, arms, and a leg.

Baboons in this area become extremely vigilant when crossing water (Fig. 6.4) and anyone watching them "would have no doubt that they fear and despise these reptiles" (Cheney and Seyfarth 2007).These experienced observers had the impression that the baboons understood slightly different alarm calls that distinguished crocodiles from lions when they were near water. The bark for a mammalian predator set them running for trees while the (apparent) crocodile bark resulted in the baboons running a short distance from the water and then stopping to watch. It seems likely that early hominins behaved in similar ways in similar situations.

6.4.3 Snakes

Isbell (2009) argued that danger from snakes was an important factor in primate evolution. Headland and Greene (2011) presented evidence that this has been a continuing danger for hominins down to the present day. The former author emphasized vipers and the latter constrictors. There is a small amount of evidence for both from baboons. Isemonger (cited by Altmann and Altmann 1970) reported two

Fig. 6.4 A group of chacma baboons begin a water crossing in the Okavango swamp, where crocodiles are a danger. (Photo by Curt Busse. Okavango, Botswana)

python attacks on baboons (one successful) and an instance of baboons fighting a python at night. He also reported one case of a young baboon bitten by a puff-adder.

6.5 Sleeping Sites

Choice of sleeping sites is a prominent feature of primate adaptations. Multiple factors are involved (Markham et al. 2016), but safety from predators is probably the most frequently discussed in the literature. The probability of predation described above indicates that this was a major issue for hominins.

6.5.1 Sleeping Above the Ground

Early hominins, diurnal and using sight as their primary sense, were more vulnerable at night. As long as they retained some of their ancestral climbing ability, they probably used night refuges like those of baboons, i.e., trees or cliffs. An early study of Guinea baboons suggested that a regularly used sleeping tree was “a safe refuge from leopards” (Anderson and McGrew 1984). However, the data on actual predation might have been limited by the fact that the study concentrated on the transition from darkness before sunrise until the baboons had left the tree.

Fig. 6.5 A vervet monkey. This species and its close relatives are widely distributed in Africa, but are not able to use the full range of habitats exploited by baboons. (Photo by Curt Busse. Okavango, Botswana)

Isbell et al. (2018) used GPS to study collared leopards, baboons, and vervet monkeys (Fig. 6.5). They found that the two monkey species were equally vulnerable to leopards, but in very different ways. Vervets were vulnerable on the ground, but safe in trees at night because they are small enough to roost at the ends of flexible branches that leopards cannot negotiate. Baboons were vulnerable at night because they are too large to occupy terminal branches and/or hide in dense vegetation. During the day baboons were not attacked by leopards, presumably because of their active defense and propensity for counter-attacks. These results confirmed earlier reports of baboon defense during the day (e.g., DeVore and Washburn 1963) and vulnerability at night (e.g., Busse 1980).

Body size figures prominently in this comparison of baboons and hominins. Isbell et al. (2018) hypothesized that the size of early hominins, as with baboons discussed above, would have limited their ability to take refuge in trees at night but would have facilitated defense on the ground during the day. An additional factor that they mention is that baboons are within the range of prey size preferred by leopards (10–40 kg; cf. Hayward et al. 2006), as was true of early hominins. Vervets are much smaller at about 3–6 kg.

GPS data demonstrated the interest of leopards in baboons. Collared leopards remained near baboon-occupied sleeping sites longer than vacant ones (Bidner et al. 2018). Baboons were most often killed by leopards at or near their sleeping sites. This may be relevant to the observation on Guinea baboons that the first individual to leave the tree in the morning was usually an adult male (Anderson and McGrew 1984).

Bidner and colleagues found that leopards visited riverine sites more frequently than cliffside sites. They interpreted this to mean that leopard visits were often due to factors other than baboon presence; however, it seems possible that the leopards were aware that chances of success were greater where baboons slept in trees rather than on cliffs. Baboons tend to prefer cliffs to trees when both are available (Bidner et al. 2018; Hamilton 1982). Leopards are able to kill baboons on cliffs as well as in trees (Busse 1980); however, it seems possible that primates can more readily escape by using their grasping hands and feet to gain sections of the rock face that even the agile leopard cannot reach.

A recent study of climbing ability in humans may be relevant. Because our species is able to execute so many discrete activities, researchers often disagree on which were the movements most essential to the evolution of our species. Carroll (2021) elaborated on a recently introduced premise for analysis of this problem: the performance gap between female and male athletes narrows in sports, which most reflect movements with evolutionary significance. He investigated rock climbing and found that female climbers are some of the best in the world, a trend that is not found in any other major sport. Carroll's conclusion is that the exceptional ability of female rock climbers is evidence for the existence of sex-blind musculoskeletal adaptations to facilitate essential movements. Baboon evidence suggests that this was the use of cliffs to reduce the risk of predation.

Regulation of sleep patterns may be one more defense against predation. A study of olive baboons found that they lost sleep time when in less familiar locations, regardless of how long they had slept the prior night or how much they had physically exerted themselves the preceding day (Loftus et al. 2022). They also exhibited synchronized patterns of waking throughout the night, which suggests that maintaining sleep homeostasis is secondary to remaining vigilant.

6.5.2 Sleeping on the Ground

Starting with the premise of predation danger from leopards, indicated by their baboon studies, Isbell et al. (2018) raised the question of how hominins protected themselves at night when they eventually had to sleep on the ground. They made the novel suggestion that the hominins surrounded themselves with *bomas* constructed from thorny branches, like those that are still used in Africa today.

To the extent that a primate analogy might shed light on this hypothesis, it seems likely that chimpanzee nesting techniques would be more relevant than anything that might be seen in baboons. However, a complementary hypothesis can be constructed with the addition of baboon evidence. As described above, some baboons have been reported to throw and roll rocks down hills as a defensive measure. If early hominins chose hills or other high points for ground sleeping, they might have deterred predators with rocks. Chimpanzee-like upper body anatomy would have made accurate throwing possible and bipedalism would have made it possible to carry rocks to the sleeping ground to accumulate for the night. To extend the speculation one step further, the rocks might also have been used to reinforce or anchor the bomas.

Sleeping on the ground would presumably have entailed a need for a higher level of vigilance. Hominins might have been prepared for this by a baboon-like pattern of sleep. As noted above, baboons exhibited synchronized patterns of waking throughout the night, which suggests that maintaining sleep homeostasis is secondary to remaining vigilant when sleeping in risky habitats (Loftus et al. 2022).

6.6 Summary and Discussion

Early hominins lived among a greater number and variety of predatory animals than exist in Africa today. The greatest danger came from carnivorans (i.e., species of the order Carnivora, as opposed to meat-eating animals in general). These included modern species such as leopards and lions and, before them, their ancestors and close (extinct) relatives. Hominin environments also included species that have no close analogs today. One was a long-legged hyena that probably hunted rather than scavenged. Another was a giant bear with long legs, faster than any extant bear.

These predators were not all equally dangerous to early hominins. Distinguishing among them depends in large part on relative body mass. The predator must be large enough to subdue the prey, and the prey must be large enough to be worth the predator's expenditure of energy. A second consideration is the mode of attack, either ambush or pursuit. All things considered, including baboon analogy, the greatest enemies of early hominins were probably leopards, leopard ancestors and relatives, and those saber-toothed felids that were similar to leopards.

Baboon behaviors for dealing with carnivorans could have been used by early hominins. Tactical movement includes avoidance of possible ambush situations and adjustment of time spent in foraging areas to the degree of risk. Predators can be kept at a distance by associating with intimidating large herbivores, such as elephants and buffalo. Associations with certain antelopes multiplies vigilance.

When baboons flee from carnivorans, they seek refuge in trees or on cliff faces. Fossil evidence for retention of ancestral climbing ability suggests that this was an option for early hominins as well. However, bipedal hominins could not have reached such refuges as quickly as quadrupedal baboons do. This lends added importance to analogies from baboons regarding active defense ("counter-attack"). Early hominins, larger than baboons, might have confronted some of their predators. As in baboons and for the same reasons, males would have taken the primary role. First, they were larger than females and not primarily responsible for immatures. Second, they benefited from the behavior because they were defending actual or potential mates and actual or potential offspring. Third, the cost was relatively low because the behavior entailed joint action against a lone predator such as a leopard or less formidable predators such as cheetahs. Finally, the hominins might have begun using weapons at a very early point in their evolution. The main evidence for this comes from chimpanzees, but there are plausible reports of baboons using stones against perceived predators.

Evidence for prehistoric raptor attacks consists of talon punctures in the skull of one juvenile *Australopithecus* and in the skulls of a number of monkeys. Raptors sometimes attack baboons and other primates in the present, but apparently with little success against baboons. Baboons use some of the same tactics against raptors that they employ against mammalian carnivores.

No such tactics are effective against extant or prehistoric crocodiles. Early hominins were probably like baboons in using avoidance or extreme vigilance when near larger bodies of water. However, the danger was not ever-present, as it was in the case of carnivorans. Snakes occasionally attack primates for food in the case of constrictors and defense in the case of venomous snakes. It has been argued that snake attacks were an important factor in primate evolution. However, there are very few reports of baboons killed by snakes.

Predation is the main reason that baboons and other primates sleep in trees or on cliff faces. As noted above, retention of arboreal capabilities probably allowed early hominins to do the same thing. Primates prefer cliffs to trees where both are available. This may be due primarily to leopards, which are agile tree climbers and hunt baboons at night. Early hominins may have responded to the same danger in the same way. Even modern humans are quite capable of climbing trees, and proficiency in rock climbing is demonstrated by modern proponents of the sport with a minimal gap between men and women.

Eventually hominins began to spend nights on the ground, but perhaps later in their evolution than some researchers think. When they did, two baboon-like patterns may have helped to prepare them: group vigilance through sporadic waking of individuals, and the use of rocks for defense from heights.

References

Allan ATL, Bailey AL, Hill RA. Consistency in the flight and visual orientation distances of habituated chacma baboons after an observed leopard predation. Do flight initiation distance methods always measure perceived predation risk? Ecol Evol. 2021; https://doi.org/10.1002/ece3.8237.

Altmann SA, Altmann J. Baboon ecology: African field research. Chicago: University of Chicago Press; 1970.

Anderson JR. Encounters between domestic dogs and free-ranging non-human primates. App Anim Behav Sci. 1986;15(1):71–86. https://doi.org/10.1016/0168-1591(86)90024-9.

Anderson JR, McGrew WC. Guinea baboons *(Papio papio)* at a sleeping site. Am J Primatol. 1984;6:1–14.

Annear E, Minnie L, Andrew K, Kerley GIH. Can smaller predators expand their prey base through killing juveniles? The influence of prey demography and season on prey selection for cheetahs and lions. Oecologia. 2023;201(3):1–12. https://doi.org/10.1007/s00442-023-05335-8

Anton M. Behavior of *Homotherium* in the light of modern big cats. Die *Homotherium*-Funde von Schonigen. n.d.;9-23

Badenhorst S. Possible predator avoidance behaviour of hominins in South Africa. S Afr J Sci. 2018;114(7/8):Art. #a0274. https://doi.org/10.17159/sajs.2018/a0274.

Baenninger R, Estes RD, Baldwin S. Anti-predator behaviour of baboons and impalas toward a cheetah. Afr J Ecol. 1977;15(4):327–9. https://doi.org/10.1111/j.1365-2028.1977.tb00414.x.

Berger LR. Brief communication: predatory bird damage to the Taung type-skull of *Australopithecus africanus* Dart 1925. Am J Phys Anthropol. 2006;131(2):166–8. https://doi.org/10.1002/ajpa.20415.

Berger LR, Clarke R. Eagle involvement in accumulation of the Taung child fauna. J Hum Evol. 1995;29(3):275–99. https://doi.org/10.1006/jhev.1995.1060.

Bidner LR, Matsumoto-Oda A, Isbell LA. The role of sleeping sites in the predator-prey dynamics of leopards and olive baboons. Am J Primatol. 2018;80:e22932. https://doi.org/10.1002/ajp.22932.

Bobe R, Manthi FK, Ward CV, et al. The ecology of *Australopithecus anamensis* in the early Pliocene of Kanapoi, Kenya. J Hum Evol. 2020;140 https://doi.org/10.1016/j.jhevol.2019.102717.

Brochu CA. Pliocene crocodiles from Kanapoi, Turkana Basin, Kenya. J Hum Evol. 2020;140:102410. https://doi.org/10.1016/j.jhevol.2017.10.003.

Brochu CA, Njau J, Blumenschine RJ, Densmore LD. A new horned crocodile from the Plio-Pleistocene hominid Sites at Olduvai Gorge, Tanzania. PLoS One. 2010;5(2):e9333. https://doi.org/10.1371/journal.pone.0009333.

Busse C. Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve. Botswana Notes Records. 1980;12:15–21. www.botsoc.org.bw

Camarós E, Cueto M, Lorenzo C, Valentín, et al. Large carnivore attacks on hominins during the Pleistocene: a forensic approach with a Neanderthal example. Archeol Anthropol Sci. 2015; https://doi.org/10.1007/s12520-015-0248-1.

Carbone C, Mace GM, Roberts SC, Macdonald DW. Energetic constraints on the diet of terrestrial carnivores. Nature. 1999;402:286–8. https://doi.org/10.1038/46266.

Carroll C. Female excellence in rock climbing likely has an evolutionary origin. Curr Res Physiol (Journal Preproof). 2021; https://doi.org/10.1016/j.crphys.2021.01.004.

Cheney DL, Seyfarth RM. Baboon metaphysics: the evolution of a social mind. Chicago: University of Chicago Press; 2007.

Cowlishaw G. Vulnerability to predation in baboon populations. Behaviour. 1994;131:293–304. https://doi.org/10.1163/156853994X00488.

Cowlishaw G. Refuge use and predation risk in a desert baboon population. Anim Behav. 1997a;54:241–53.

Cowlishaw G. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Anim Behav. 1997b;53:667–86.

DeVore I, Washburn SL. Baboon ecology and human evolution. In: Howell FC, Bourliere F (eds) African ecology and human evolution. Aldine, Chicago; 1963. p. 335–367.

DeVore I, Hall KRL. Baboon social behavior. In: DeVore I, editor. Primate behavior, field studies of monkeys and apes. New York: Holt Rinehart Winston; 1965. p. 53–110.

Fay JM, Carroll R, KerbisPeterhans JC, Harris D. Leopard attack on and consumption of gorillas in the Central African Republic. J Hum Evol. 1995;29:93–9. https://doi.org/10.1006/jhev.1995.1048.

Fischer J, Higham JP, Alberts S, et al. The Natural History of Model Organisms: Insights into the evolution of social systems and species from baboon studies. eLife 2019;8:e50989

Geraads D, Daujeard C. Carnivore diversity in the African Plio-Pleistocene: a reply to O'Regan and Reynolds (2009). J Hum Evol. 2011;60:813–5. https://doi.org/10.1016/j.jhevol.2011.01.012.

Gilbert CC, McGraw WS, Delson E. Brief communication: Plio-Pleistocene eagle predation on fossil cercopithecids from the Humpata Plateau, southern Angola. Am J Phys Anthropol. 2009;139:421–9. https://doi.org/10.1002/ajpa.21004.

Greyling E, Comley J, Cherry MI, et al. Facilitation of a free-roaming apex predator in working lands: evaluating factors that influence leopard spatial dynamics and prey availability in a South African biodiversity hotspot. PeerJ. 2023;11:e14575. https://doi.org/10.7717/peerj.14575.

Hamilton WJ III. Baboon sleeping site preferences and relationships to primate grouping patterns. Am J Primatol. 1982;3(1–4):41–53. https://doi.org/10.1002/ajp.1350030104.

Hamilton WJ III, Buskirk RE, Buskirk WH. Defensive stoning by baboons. Nature. 1975;256:488–9. https://doi.org/10.1038/256488a0.

Hayward MW, Henschel P, O'Brien J, et al. Prey preferences of the leopard (*Panthera pardus*). J Zool. 2006;270(2):298–313. https://doi.org/10.1111/j.1469-7998.2006.00139.x.

Headland TN, Greene HW. Hunter-gatherers and other primates as prey, predators, and competitors of snakes. Proc Natl Acad Sci USA. 2011;108:20865-20866, E1470–4.

Hill RA, Weingrill T. Predation risk and habitat use in chacma baboons (*Papio hamadryas ursinus*). In: Gursky S, Nekaris KAI, editors. Primates and their predators. New York: Kluwer Academic; 2007. p. 339–54.

Hiraiwa-Hasegawa M, Byrne R, Takasaki H, Byrne JM. Aggression toward large carnivores by wild chimpanzees of Mahale Mountains National Park, Tanzania. Folia Primatol. 1986;47(1):8–13. https://doi.org/10.1159/000156259.

Hopkins WD, Russell JL, Schaeffer JA. The neural and cognitive correlates of aimed throwing in chimpanzees: a magnetic resonance image and behavioural study on a unique form of social tool use. Philos Trans R Soc B. 2012;367:37–47. https://doi.org/10.1098/rstb.2011.0195.

Hopley PJ, Cerling TE, Crete L, et al. Stable isotope analysis of carnivores from the Turkana Basin, Kenya: evidence for temporally-mixed fossil assemblages. Quatern Int. 2023;650:12–27. https://doi.org/10.1016/j.quaint.2022.04.004.

Isbell LA. The fruit, the tree, and the serpent: why we see so well. Cambridge MA: Harvard University Press; 2009.

Isbell LA, Bidner LR, Van Cleave EK, Matsumoto-Oda A. GPS-identified vulnerabilities of savannah-woodland primates to leopard predation and their implications for early hominins. J Hum Evol. 2018;118:1–13. https://doi.org/10.1016/j.jhevol.2018.02.003.

Itani J. Postscript by the editor. Primates. 1967;8:295–6. (cited by Altmann and Altmann 1970)

Jooste E, Pitman RT, van Hoven W, Swanepoel LH. Unusually high predation on chacma baboons *(Papio ursinus)* by female leopards *(Panthera pardus)* in the Waterberg Mountains, South Africa. Folia Primatol. 2012;83:353–60. https://doi.org/10.1159/000339644.

Kiffner C, Ndibalema V, Kioko J. Leopard (*Panthera pardus*) aggregation and interactions with Olive baboons (*Papio anubis*) in Serengeti National Park, Tanzania. Afr J Ecol. 2013;51:168–71.

Kortlandt A. How might early hominids have defended themselves against large predators and food competitors. J Hum Evol. 1980;9(2):79–112. https://doi.org/10.1016/0047-2484(80)90066-4.

Kruuk H. The spotted hyena, a study of predation and social behavior. Chicago: University of Chicago Press; 1972.

Kuhn BF, Hartstone-Rose A, Lacruz AIR, et al. The carnivore guild circa 1.98 million years: biodiversity and implications for the palaeoenvironment at Malapa, South Africa. Palaeobiol Palaeoenv. 2016; https://doi.org/10.1007/s12549-016-0245-0.

Lee-Thorp J, Thackeray F, van der Merwe J. The hunters and the hunted revisited. J Hum Evol. 2001;39(6):565–576. https://doi.org/10.1006/jhev.2000.0436

Lewis ME. Carnivore guilds and the impact of hominin dispersals. IN Boivin N, Crassard R, Petraglia M, editors. Human Dispersal and Species Movement From Prehistory to the Present. Cambridge University Press; 2017. p. 29–61. https://doi.org/10.1017/9781316686942.003.

Loftus JC, Harel R, Nunez CL, Crofoot MC. Ecological and social pressures interfere with homeostatic sleep regulation in the wild. eLife. 2022;11:e73695. https://doi.org/10.7554/eLife.73695.

Markham CA, Alberts SC, Altmann J. Haven for the night: sleeping site selection in a wild primate. Behav Ecol. 2016;27(1):29–35. https://doi.org/10.1093/beheco/arv118.

McGraw WS, Berger, LR. Raptors and primate evolution. Evol Anthropol. 2013;22(6):280–293. https://doi.org/10.1002/evan.21378.

McPherron SP, Archer W, Otarola-Castillo ER, et al. Machine learning, bootstrapping, null models, and why we are still not 100% sure which bone surface modifications were made by crocodiles. J Hum Evol. 2022;164:103071. https://doi.org/10.1016/j.jhevol.2021.103071.

O'Regan HR, Reynolds SC. An ecological assessment of the southern African carnivore guild; a case study from Member 4, Sterkfontein, South Africa. J Hum Evol. 2009;57:212–22. https://doi.org/10.1016/j.jhevol.2009.04.002.

Paciência FMD, Baluya D, Mbaryo P, et al. Olive baboons' (*Papio anubis*) response towards crowned eagles (*Stephanoaetus coronatus*) at Lake Manyara National Park. Primate Biol. 2017;4:101–6. www.primate-biol.net/4/101/2017/

Pettet A. Defensive stoning by baboons. Nature. 1975;256:549.

Pickering T, Egeland C, Dominguez-Rodrigo M, et al. Testing the "shift in the balance of power" hypothesis at Swartkrans, South Africa: Hominid cave use and subsistence behavior in the Early Pleistocene. J Anthropol Archaeol. 2008;27:30–45. https://doi.org/10.1016/j.jaa.2007.07.002.

Pickford M. Defensive stoning by baboons. Nature. 1975;256:549–50.

Pruetz JD, Bertolani P, Boyer Onto K, et al. New evidence on the tool-assisted hunting exhibited by chimpanzees (*Pan troglodytes verus*) in a savannah habitat at Fongoli, Sénégal. R Soc Open Sci. 2015;2 https://doi.org/10.1098/rsos.140507.

Rhine RJ, Norton GW, Roertgen WJ, Klein HD. The brief survival of free-ranging baboon infants (*Papio cynocephalus*) after separation from their mothers. Int J Primatol. 1980;1:401–409. https://doi.org/10.1007/BF02692282

Rowell T. Forest living baboons in Uganda. J Zool Lond. 1966;149:344–64.

Ruff CB, Wood BA. The estimation and evolution of hominin body mass. Evol Anthropol. 2023;32(4):223–237. https://doi.org/10.1002/evan.21988

Saayman GS. Baboon's responses to predators. Afr Wldlf. 1971;25:46-49.

Stelzner J, Strier K. Hyena predation on an adult male baboon. Mammalia. 1981;45:259–260.

Stolz LP, Saayman GS. Ecology and behavior of baboons in the northern Transvaal. Annals Transvaal Mus. 1970;26:99–143.

Treves A, Palmqvist P. Reconstructing Hominin interactions with mammalian carnivores (6.0–1.8 Ma). In: Gursky SL, Nekaris KAI, editors. Primate anti-predator strategies. Developments in primatology: progress and prospects. Boston: Springer; 2007. https://doi.org/10.1007/978-0-387-34810-0_17.

Washburn SL, DeVore I. The social life of baboons. Sci Am. 1961;204:62–71.

Washburn SL, Hamburg DA. The implications of primate research. In DeVore I (ed) Primate behavior: New York: Holt Rinehart Winston; 1965 p607-622.

Washburn SL, Jay PC, Lancaster JB. Field studies of Old World monkeys and apes. Science. 1965;150:1541–1547. https://doi.org/10.1126/science.150.3703.1541.

Werdelin L, Lewis ME. A contextual review of the Carnivora of Kanapoi. J Hum Evol. 2020;140:102334. https://doi.org/10.1016/j.jhevol.2017.05.001.

Willems EP, van Schaik CP. The social organization of *Homo ergaster*: inferences from anti-predator responses in extant primates. J Hum Evol. 2017;109:11–21. https://doi.org/10.1016/j.jhevol.2017.05.003.

Williams KS, Williams ST, Fitzgerald LE. Brown hyaena and leopard diets on private land in the Soutpansberg Mountains, South Africa. Afr J Ecol. 2018;2018:1–7. https://doi.org/10.1111/aje.12539.

Zinner D, Pelaez F, Berhane D. Anti-predator behavior of male hamadryas baboons *Papio hamadryas* in Eritrea. Afr Primates. 2000;4(1&2):54–8.

Zinner D, Pelaez F. Verreaux's eagles (*Aquila verreauxi*) as potential predators of Hamadryas baboons (*Papio hamadryas hamadryas*) in Eritrea. Am J Primatol. 1999;47:61–66. https://doi.org/10.1002/(SICI)1098-2345(1999)47:13.0.CO;2-K.