PRIMATE ANTI-PREDATOR STRATEGIES

EDITED BY

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DEVELOPMENTS IN PRIMATOLOGY: PROGRESS AND PROSPECTS

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Adrian Treves and Paul Palmqvist

Introduction

Several hominin genera evolved to use savanna and woodland habitats across Pliocene Africa. This radiation into novel niches for apes occurred despite a daunting array of carnivores (Mammalia, Carnivora) between 6.0 and 1.8 Ma (Figure 17.1). Many of these carnivores would have preyed on hominins if given the opportunity. In this paper we ask what the behavioral adaptations were that permitted hominins to survive and spread, despite this potentially higher risk of predation in ancient Africa.

When considering hominin anti-predator behavior, many scholars looked first to material culture, such as fire or weaponry (Kortlandt, 1980; Brain, 1981). However, the idea that deterrent fire or weaponry freed early hominins from threats posed by predators is unsatisfying for several reasons. First, the modern carnivores now roaming Africa are survivors of humanity's repeated and systematic campaigns to eradicate problem animals, trade in skins, and so on. (McDougal, 1987; Treves & Naughton-Treves, 1999), whereas Pliocene carnivores would not have had a history of conflict with armed hominins. Second, thousands of modern humans fell prey to leopards (*Panthera pardus*), lions (*P. leo*) and tigers (*P. tigris*) in the twentieth century despite their sophisticated weapons and fire (Turnbull-Kemp, 1967; McDougal, 1987; Treves & Naughton-Treves, 1999; Peterhans & Gnoske, 2001). Although, thorn branches, stone tools, fire brands, pointed sticks, or bones could potentially help to repel carnivores from their kills (Kortlandt, 1980; Bunn & Ezzo, 1993; Treves & Naughton-Treves, 1999), such weaponry seems wholly inadequate for personal defense when large carnivores achieve surprise, attack in a pack, or are accustomed to overcoming heavier prey defended by horns, hooves, or canines. Therefore, we assert that weaponry by itself does not nullify the risk posed by predators. Moreover, controlled use of fire and stone tool technology appear late in the archaeological record relative to the evolution of
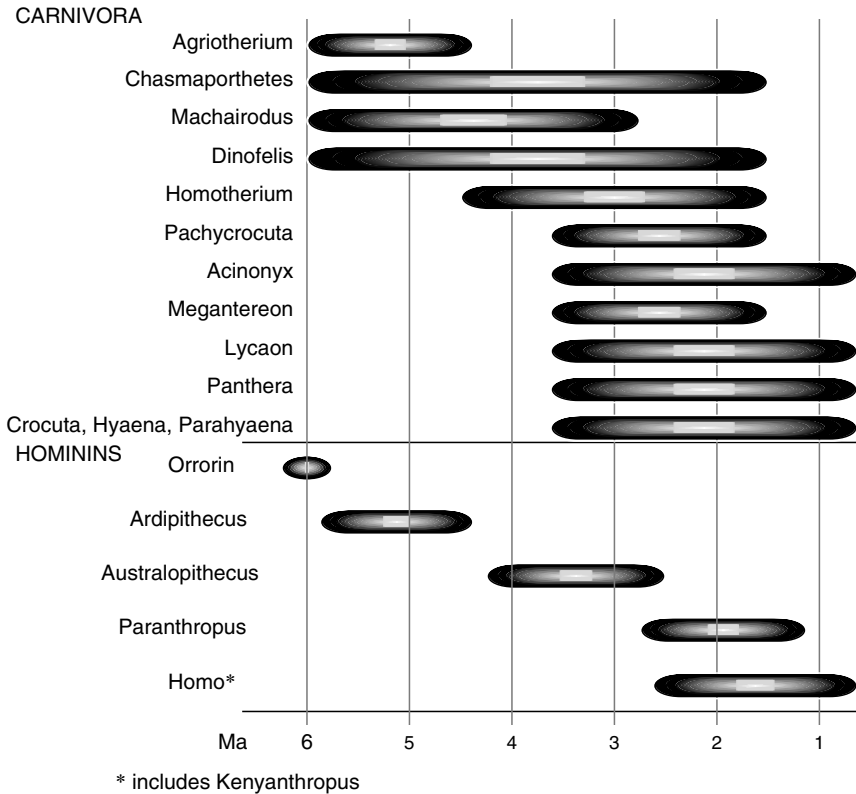
FIGURE 17.1. Time spans of paleopredator and hominin genera in Africa.

semi-terrestrial hominins in Pliocene Africa (Bellomo, 1994; Brain, 1994; Wolde-Gabriel et al., 1994; Brunet et al., 1997; Leakey et al., 1998; Haile-Selassie, 2001). Hominin anti-predator behavior remains a key puzzle of our human ancestry.

In the next section of this chapter we review African large carnivore ecology and hunting behavior in extant taxa and that reconstructed for Plio-Pleistocene forms ("paleopredators" hereafter). Following this, we review the anti-predator behavior of hominins by analogy with monkeys and apes; this analogy is parsimonious because of the observed cross-taxonomic consistency of their behavioral responses to predators. Vigilance behavior in relation to social organization is particularly informative. Finally, we integrate the two reviews to reconstruct the range of anti-predator behaviors open to hominins.

African Large Carnivores, Past and Present

Africa has long contained diverse carnivore communities (Figure 17.1). Carnivores have repeatedly radiated into various niches, including specializations for

predation, active or passive scavenging, open-country or forested habitats, and small or large ungulate prey (Table 17.1).

Following Sunquist & Sunquist (1989) we define a "large carnivore" as any species with average individual or group body mass >34 kg (e.g., *Hyaena hyaena* or *Lycaon pictus*, respectively). Subsequent reference to large/small prey relate to the carnivore under discussion.

Large carnivore diversity was greater in Africa's past than it is today (Figure 17.1). Between 6 and 3.6 Ma there were five genera of large carnivores without extant analogues (the long-legged ursid *Agriotherium*, the large coursing hyaenid *Chasmaporthetes*, and the saber-toothed felids Homotherium, *Machairodus* and *Dinofelis*). Then, from the mid-Pliocene (3.6 Ma), the archaic genera were joined by one large canid (*Lycaon lycaonoides*) (Martínez-Navarro & Rook, 2003), three new large felid genera (*Acinonyx, Megantereon* and *Panthera*), and four new genera of hyaenids (*Crocuta, Pachycrocuta, Hyaena,* and *Parahyaena*). At some sites, 8–10 species appear to have been coeval and broadly sympatric (Barry, 1987; Turner & Anton, 1997)(Figure 17.1). Niche separation under such conditions is not yet clear.

As the Pleistocene wore on (1.8 Ma onward) the archaic carnivores went extinct in Africa, partly as a result of a global carnivore guild turnover and species replacement (Figure 17.1). The African faunal turnover coincided with a decrease in woodland relative to grassland, more herd-living grazing ungulates, and fewer solitary or small-group-living large herbivores like giraffids, rather than from competition between the modern carnivore guild and archaic forms (Hendey, 1980; Turner, 1990; Werdelin & Turner, 1996; Turner & Anton, 1998).

Coexistence of hominins and carnivores is insufficient by itself to conclude that hominins evolved effective anti-predator defenses against such paleopredators. Coexistence would have had little selective impact if (a) carnivores did not kill Pliocene hominins regularly, or (b) if such predation were random with respect to hominin traits. Thus, in the following sections we assess whether paleopredators killed hominins regularly, and if so, were there consistent patterns of hominin-carnivore interactions that might have produced directional selection among hominins.

Habitat Selection

Carnivores generally go where prey are most abundant, but many will establish and defend territories year-round. Except for the leopard, all the extant African large carnivores are most abundant in open savannas and savanna-woodlands (variable mixtures of trees, grassland, and bushland where visibility is less than 100 m on average), coincident with highest ungulate densities (Table 17.1). Nevertheless, several carnivores can breed successfully within very arid regions or dense forest (Leakey et al., 1999; Bailey, 1993). The leopard is the greatest habitat generalist today, breeding from rainforest to desert, albeit preferring habitat with vegetation cover.

TABLE 17.1. African large carnivores, present and reconstructed.

| Genus | Mass, kg | Brief description or common name | Predominant Hunting Behavior | | | |
			Activity	Grouping	Attack	Habitat*
Acinonyx	ca. 50	cheetah	diurnal	solitary	stalking-coursing	open>woodland
Agriotherium	600–700	faster, more carnivorous than extant ursines	both?	solitary	opportunistic-coursing	woodland>open
Chasmaporthetes	50–70	long-legged hyena, felinoid teeth	both?	pack	coursing	open>woodland
Crocuta	ca. 60	spotted hyena	both	pack	coursing	open>woodland
Dinofelis	70–100	more powerful, less arboreal than leopard	both?	solitary	stalking	woodland>open
Homotherium	150–230	scimitar-toothed machairodont	both?	pack?	stalking-coursing	open>woodland
Hyaena, Parahyaena, Pliocrocuta	35–40	striped, brown, and Pliocene hyena	both?	solitary	opportunistic	all
Lycaon	25–40	African wild dog (L. pictus) or Pliocene form (L. lycanoides)	both	pack	coursing	open>woodland
Machairodus	130–230	scimitar-toothed machairodont	both?	pack?	stalking	open>woodland
Megantereon	80–110	dirk-toothed machairodont	both?	solitary	stalking	woodland>open
Pachycrocuta	100–130	giant hyena, robust bone-cracking teeth	both?	pack	opportunistic-coursing	all
Panthera leo	ca. 170	lion	both	pack	stalking	open>woodland
P. pardus	ca. 55	leopard	both	solitary	stalking	all

*Predominant habitat associations, e.g., "open>woodland" indicates less tree cover than grass cover.

Sources: Anyonge, 1993, 1996; Arribas & Palmqvist, 1999; Bailey, 1993; Barry, 1987; Berta, 1981; Boaz et al., 1979; Brain, 1981, 1994; Busse, 1980; Caro, 1987, 1989a,b; Cooke, 1991; Fanshawe & FitzGibbon, 1993; Ferretti, 1999; FitzGibbon, 1990a,b; Geraads, 1997; Hendey, 1974, 1980; Holekamp et al., 1997; Hunt, 1996; Keyser, 1991; Leakey, 1999; Lewis, 1997; Marean, 1989; Martin, 1989; Martínez-Navarro and Palmqvist, 1995, 1996; Miller & Carranza, 1996; Mills, 1989; Palmqvist, 2002; Palmqvist & Arribas, 2001; Palmqvist et al., 1996, 1999; Petter et al., 1994; Rook, 1994; Schaller, 1972; Taylor, 1989; Turnbull-Kemp, 1967; Turner & Anton, 1996, 1997, 1998; Turner, 1990, 1997; Werdelin, 1994.

As far as micro-site selection for hunting, only the leopard is known to hunt arboreal prey within 10–15 m of the ground. Leopards also kill in caves, cliff sides and houses (Simons, 1966; Turnbull-Kemp, 1967).

Among extinct carnivores, habitat use varied (Table 17.1). *Agriotherium* and machairodonts *Dinofelis* and *Megantereon* are believed to have selected more forested habitats based on their postcranial morphology, typical of stalking, ambush hunters. The latter two genera show relatively more robust forelimbs than hindlimbs. A comparative study of the postcrania in modern and Plio-Pleistocene carnivores shows *Dinofelis* resembles pantherine felids craniodentally, and its postcrania resembling modern prey-grappling lions, tigers, and leopards (Marean, 1989; Anyonge, 1996; Lewis, 1997). The postcrania of *Megantereon* reveal tree-caching and long-distance dragging capabilities, as in modern leopards and jaguars (*Panthera onca*) (Lewis, 1997; de Ruiter & Berger, 2000). *Homotherium* and *Machairodus* postcrania suggest cursorial tendencies in more open habitats, given their comparatively higher values for both brachial and crural indexes (Table 17.1). *Chasmaporthetes* and *Lycaon* have been associated with open-country habitats as well—although it should be noted that *Lycaon* today can hunt quite successfully in dense shrub land (Creel & Creel, 1995). The giant hyena *Pachycrocuta* was associated with more open habitats, particularly where medium to large ungulate carcasses were left by machairodont felids (Arribas & Palmqvist, 1998) (Table 17.1).

Associations of fossil hominins with remains of *Chasmaporthetes*, *Dinofelis*, *Homotherium*, *Machairodus*, Megantereon, and *Pachycrocuta* indicate sympatry in the period 6.0–1.8 Ma in habitats reconstructed as a mixture of woodlands and open country (Cooke, 1991; Keyser, 1991; Brain, 1994; Brantingham, 1998; Dominguez-Rodrigo & Pickering, 2003; Palmqvist et al., 2005). At a finer level, felid and hyaenid activity was considerable in and around the same caves with hominin remains (Brain, 1981, 1994; Turner, 1990). Deep caves would therefore have been dangerous resting sites (for vivid examples, see Simons, 1966; Brain, 1981). However, there seems to be evidence that hominins went voluntarily to caves used by paleopredators. For example, the presence of Plio-Pleistocene stone tools in South African caves without evidence of their manufacture (Brain, 1981) suggests that hominins came to some of these sites voluntarily (carrying tools) most likely, or, less likely, that predators transported their carcasses without losing the tools (e.g., in a portable container that neither fossilized nor dropped off the carcass when dragged).

The extant carnivores hunt by day and night, but seem to do so most often or most successfully between 19.00 and 07.00 with the exception of the diurnal cheetah (Table 17.1). There is some indication that carnivores hunt less by day when humans pose a threat to them (Turnbull-Kemp, 1967; van Schaik & Griffiths, 1996), a benefit hominins would not have enjoyed in the Pliocene for the reasons mentioned before. Moreover, observations of predation reveal that carnivores kill primates in the day as well as at night (reviews in Treves, 1999a; Boinski et al., 2000). Thus, hominins could not have escaped predation simply by diurnality.

In addition to some level of diurnal risk, hominins may have faced nocturnal threat at sleeping trees and caves, as do large primates today (Simons, 1966; Busse, 1980; Brain, 1994). Hominins might have preferentially selected smaller trees over larger ones and narrow or fragile ledges in caves rather than solid supports for sleeping sites. These microsites would provide earlier warning of nocturnal intrusion and impede the rapid approach of a predator such as *Agriotherium* in the early Pliocene and leopards or *Dinofelis* thereafter. In sum, hominins could not have escaped predation by using different habitats than large carnivores nor could they have done so by using them at different times of day, although such tactics may well have lessened their exposure to paleopredators.

Hunting Tactics

Stalking (ambush) predators rely on surprise or stealthy approach, followed by brief, high-speed pursuit (Taylor, 1989; Fanshawe & Fitzgibbon, 1993; Fitzgibbon & Lazarus, 1995). Their attacks are often aborted or fail when prey detect the predator in ambush or early in its approach. Hence, for stalking predators, the most vulnerable prey are the unwary, whether they are healthy adults, the young, or the old and infirm.

All the felids use ambush (stalking) to pounce or sprint after prey. They can accelerate rapidly but tire quickly. Among the extinct forms, *Dinofelis*, *Machairodus*, and *Megantereon* probably conformed to the felid pattern of stalking their prey using ambush, while *Acinonyx* and *Homotherium* show a mix of ambush and pursuit (coursing) adaptations with elongated and slender distal limbs suited to longer chases at higher speeds (Table 17.1). Since the Pliocene, *Acinonyx* has been specialized for longer chases, albeit still under 1 km.

In contrast to stalkers, coursing (pursuit) predators such as *Lycaon* and *Crocuta* often approach prey with little or no stealth; rather, they openly survey moving prey for weaknesses and chase their targets for distances often >1 km (Table 17.1). Because most prey detect the overt approach of coursing predators before they begin a chase, prey vigilance is reduced in importance relative to rapid, agile, sustained flight or escape into refuge. Therefore, the most vulnerable prey are those nearest the predators, those far from refuge, or those that flee slowly (e.g., the aged or infirm). Both extinct *Lycaon* and *Chasmaporthetes* were probably pack-hunting coursers as well, simply on the grounds of morphology and relatedness to their modern relatives, described above (Table 17.1).

Pachycrocuta was substantially larger and probably slower than the spotted hyena *Crocuta*, judging from its shorter distal limb segments and more robust postcrania. Although these features do not preclude coursing, taphonomic analyses suggest reliance on scavenging behavior for this extinct hyena (Palmqvist et al., 1996) (Table 17.1).

Third, opportunistic hunters such as extant ursine bears and *Hyaena* rarely pursue rapidly fleeing prey and typically attack prey opportunistically by random search using generalized locomotion (Table 17.1). Prey typically avoid such predators by detecting them first and seeking appropriate refuge, but data are scant on prey vulnerability. Some opportunistic predators can pursue into refuges.

We assume that *Agriotherium* was such a predator, although its long limbs raise the possibility that it might have sprinted for short distances (Table 17.1). There is no evidence currently available on the feeding behavior of *Agriotherium*, but it is worth mentioning that the similarly proportioned short-faced bear *Arctodus*, the largest Pleistocene carnivore of North America, included more flesh in its diet than brown bears according to biogeochemical ($^{13}\delta C$, $-^{15}\delta N$) analyses of bone collagen (Bocherens et al., 1995; Matheus, 1995).

Finally, there is a long-standing and fascinating debate over the benefits of group living in carnivores; it revolves around whether pack hunters have higher hunting success than solitary predators, can hunt larger prey, retain their kills for longer time against scavengers, avoid predation better themselves, or defend their territories more effectively. Of course, these are not mutually exclusive functions, but researchers have found one benefit accruing under one set of conditions and not another, only to be contradicted by studies from other sites (for selected examples, see Packer et al., 1990; Fanshawe & Fitzgibbon, 1993; Fuller & Kat, 1993; Creel & Creel 1995; Holekamp et al., 1997). The flexibility of large carnivore grouping—fission-fusion sociality—permits individuals to respond to short-term changes in prey abundance and ease of capture by joining or leaving aggregations. For this reason we echo Turner & Anton (1997), who warn that one consider as full a range of carnivore behaviors as possible. In short, hominins would on occasion have encountered both solitary paleopredators and aggregations of them whatever the taxon. But would some taxa regularly form groups that might have posed an added risk to hominins?

Modern *Crocuta* and *Panthera leo* sometimes hunt in packs, while *Lycaon* virtually always does so. Other extant carnivores hunt in pairs, trios, or larger groups more rarely (Table 17.1). The extinct canids and hyaenids probably hunted in groups a majority of the time, judging from their extant relatives. *Pachycrocuta* may be a borderline case: Although excavations of den sites suggested solitary foraging (Palmqvist & Arribas, 2001), the possibility remains that groups of *Pachycrocuta* foraged together while only individuals (mothers?) returned to the dens to provision young. The large brains with more developed optical lobes than olfactory lobes of *Homotherium* and *Machairodus* may reflect pack-hunting behavior, in contrast to the smaller-brained, more olfactory *Megantereon* (Martin, 1989; Palmqvist et al., 2003). *Agriotherium* and *Dinofelis* are both reconstructed as solitary given the behavior of ursine bears and leopards, respectively. *Chasmaporthetes* is still too poorly known, although its phylogeny and anatomy suggest open-country coursing, and therefore pack hunting (Table 17.1).

From the perspective of prey, pack hunting usually increases the risk for prey, the number of prey killed per hunt, and the size of prey taken (see reference to pack hunting above). Prey defenses seem the same whether animals are hunted by packs or by single predators, but further study would be valuable.

In sum, coursing paleopredators would have placed a premium on refuge use by hominins when in open country, while the more numerous opportunistic and stalking predator genera (Figure 17.1, Table 17.1) using more forested or bush habitats would demand vigilance by hominins.

Prey Selection

Carnivores sometimes select their prey before the start of the hunt, but more typically they hunt any prey they encounter (Kruuk, 1972; Holekamp et al., 1997). This opportunism tends to protect primates, which usually occur at lower densities than medium to large ungulates. Nevertheless, primates appear regularly in the scat of carnivores and in observed predation (Brain, 1981; Bailey, 1993; Treves, 1999a). Predation on primates varies with conditions. For example, when leopards face competition from larger carnivores they increase their exploitation of monkeys (Seidensticker, 1983). Individual prey preferences vary within the same species by individual, age-sex class, habitat, season, etc. Over short periods, individual carnivores or even packs are known to specialize on a single type of prey to the exclusion of others. Indeed, reports of leopards specializing on primates are not uncommon (Brain, 1981; Hoppe-Dominik, 1984; Boesch, 1991). There are thousands of records of wild carnivore attacks on modern humans (Corbett, 1954; Turnbull-Kemp, 1967; McDougal, 1987; Sanyal, 1987; Peterhans & Gnoske, 2001). For example, colonial archives reveal at least 393 Ugandan men, women, and children were killed or injured by lions, leopards, and spotted hyenas in the last century. This grim toll would surely have been elevated without modern weaponry and coordinated campaigns to extirpate leopards and lions (Treves & Naughton-Treves, 1999). It was once thought that primarily the infirm or inexperienced carnivores would approach human settlements or attack humans, but systematic study leads us to reject this idea (Turnbull-Kemp, 1967; Linnell et al., 1999; Treves and Naughton-Treves, 1999; Peterhans & Gnoske, 2001).

The size of potential prey is also a consideration for most carnivores. Body mass of hominins has been estimated repeatedly (see reviews in Mathers & Henneberg, 1996; Hens et al., 2000). We follow McHenry (1992), using estimates based on regressions of hindlimb joint proportions to identify a *range* of body sizes that describes adults of both sexes for all hominin species between 6.0 and 1.8 Ma—rather than a *mean* for a particular species at a particular time. His upper and lower bounds span 29–52 kg for *Australopithecus, Paranthropus*, and Pliocene *Homo* (McHenry, 1992, 1994). Leopard-sized and larger carnivores routinely kill prey weighing over 52 kg (Palmqvist et al., 1996). As noted above, leopards are capable of killing adult modern humans and transporting much larger prey to caches. Because adult baboons such as *Parapapio jonesi* (mass 30–40 kg: Brain, 1981; Delson et al., 2000) fell prey to paleopredators it would not be parsimonious to suggest that adult hominins were immune, resistant, or avoided by large carnivores thanks to their size.

Fossil Anatomy, Isotope Frequencies, and Composition of Bone Assemblages

Several lines of evidence hint at the prey preferences of archaic predators and therefore the likelihood they regularly hunted hominins: (a) craniodental and postcranial morphology of carnivores plus bone assemblages bearing traces of

carnivore foraging yield insights into dietary and hunting behavior; and (b) bone and enamel isotope measurements from fossils provide insights into diet. Below we briefly summarize a general consensus emerging from recent reviews.

(a) The saber-tooths *Homotherium*, *Machairodus*, and *Megantereon* were hyper-carnivores (>70% of their diet was meat) that could deflesh a carcass quickly, but rarely broke bones to access marrow; they would probably not have commonly transported meat to protect kills (Brain, 1981; Brantingham, 1998). Despite specialization for large ungulate killing, the saber-tooth felids would rarely have hunted hominins, yet hominins would still face danger if they encountered machairodonts at close quarters; the opportunism of large carnivores must always be kept in mind.

Equally carnivorous but more likely to focus on smaller prey and transport meat were the leopards and *Dinofelis*. At half a dozen southern African cave sites dated between 3.0 and 1.0 Ma, paleontologists have found fossil *Dinofelis* or leopards alongside fossils of many ungulates, at least 140 australopithecine hominins, and at least 324 baboons (Brain, 1981, 1994). Many of the large primate remains show characteristic patterns of damage by large felids and hyaenids (Brain, 1981; Keyser, 1991; Berger & Tobias, 1994; Turner, 1997; de Ruiter & Berger, 2000). Taphonomic evidence suggests that carnivores brought hominin remains to their dens. Some have proposed that leopards or *Dinofelis* specialized on large baboons and australopithecines, judging from the unusually high proportions of large primate fossils (Brain, 1981; Cooke, 1991).

Pliocene *Acinonyx* is reconstructed as a larger form (100 kg) than modern cheetahs, but still a specialist on small to medium-sized ungulates (Table 17.1). There is no evidence that hominins regularly fell prey to cheetahs given the size, specialized hunting behavior and timidity of the latter (e.g., Baeninger et al., 1977). The wolf-sized (45 kg) *Lycaon* of Pliocene Africa are reconstructed as hyper-carnivores—like extant *Lycaon* and wolves (*Canis lupus*)—that defleshed carcasses and, when undisturbed, cracked bones (Table 17.1). Their prey preferences were presumably the same as their extant relatives, i.e., medium to large ungulates (Rook, 1994; Palmqvist et al., 1999, 2003). Because healthy (non-rabid) wolves have sporadically killed modern humans in Eurasia, particularly women and children, in spates of encounters (Rajpurohit, 1998; Linnell & Bjerke, 2002), the paleoocanids may have posed a sporadic threat to hominins as well.

The habits of *Agriotherium* have not been reconstructed in detail, although its dentition suggests it was more carnivorous than ursids today (Hendey, 1980; Petter et al., 1994; Miller & Carranza, 1996; Geraads, 1997). Modern grizzlies (*Ursus arctos*) are confrontational scavengers that steal kills from hyper-carnivorous wolves (Smith et al., 2003). *Agriotherium* seems capable of the same behavior, therefore, opportunistic but not regular attacks on hominins seem most likely; the frequency of such encounters would rise when hominins use the same foraging areas as bears, as is sometimes seen today (Rajpurohit & Krausman, 2000).

Pliocene hyenas appear very similar to today's striped and brown hyenas, taxa that are predominantly passive, non-confrontational scavengers (Table 17.1). They would probably not have posed a common threat to hominins. *Crocuta* have killed

modern humans (Treves & Naughton-Treves, 1999), so the large paleohyenas presumably posed some threat to hominins, especially around carcasses. However there are no fossil assemblages of hyaenid prey or isotope data to support the idea that hyenas routinely killed hominins.

(b) Tooth enamel and bone C and N isotope measurements shed light on fossil carnivore diets. For example, carnivores eating mainly grazing animals that fed on C4 plants (tropical grasses) will have higher ratios of ^{13}C to ^{12}C in the hydroxyapatite and collagen of their tooth enamel and bones, respectively, than did carnivores who are mainly browsing animals that fed on C3 plants (trees, shrubs, forbs and tubers—plants that discriminate strongly against the heavy isotope of C). Lee-Thorp and colleagues (2000) showed South African paleopredators could be distinguished by their bone and enamel isotope ratios ($^{13}\delta$C). In their Pleistocene sample, lions ate the highest proportion of grazers, *Crocuta* was intermediate, while leopards ate more browsers and omnivores like baboons and hominins (Lee-Thorp et al., 1994; Sillen & Lee-Thorp, 1994; Spoonheimer & Lee-Thorp, 1999). Palmqvist et al. (2003) found the long-legged, ambush/coursing saber-tooth *Homotherium* and the coursing *Lycaon lycaonoides* (formerly *Canis falconeri*) of Venta Micena, Spain, had elevated heavy-nitrogen levels indicating a diet dominated by grazers, such as adult *Equus* and juvenile *Mammuthus*. By contrast, the short-legged *Megantereon,* comparatively depleted in ^{15}N, ambushed browsing ungulates such as megacerine deer in Spain's ancient forested habitats. Finally, *Pachycrocuta* shows intermediate ^{15}N values at this site, suggest it scavenged the prey of all the paleopredators described above (Palmqvist et al., 2003).

Leopard predation on robust australopithecines has been ruled unlikely based on tooth enamel carbon isotopes, as the $^{13}\delta$C values of *Paranthropus* and *P. pardus* are similar. However, the isotopic enrichment between *Paranthropus* and *Dinofelis* agrees with that expected of prey and predator (Lee-Thorp et al., 1994; 2000). These finds are strong indication that hominins were regularly hunted.

Competition Between Carnivores and Hominins

Hominins may have competed directly with some paleopredators over prey or carcasses. After defleshing by hyper-carnivores, carcasses retained long bone marrow, epiphyseal grease, brains, and other axial elements accessible to bone-cracking scavengers. But were hominins usually the primary predators? the confrontational scavengers? or passive, non-confrontational scavengers? Despite years of debate and re-analyses of bone assemblages, experts disagree about which Plio-Pleistocene hominin competed with which carnivore and in what manner (Bunn & Ezzo, 1993; Blumenschine, 1995; Capaldo, 1997; Brantingham, 1998; Selvaggio, 1998; Arribas & Palmqvist, 1999; Dominguez-Rodrigo & Pickering, 2003; Palmqvist et al., 2005).

In the earliest period, prior to 3.6 Ma, there were no *Crocuta* or *Pachycrocuta*—confrontational scavengers—but *Agriotherium* and perhaps *Chasmaporthetes* may have stolen kills from *Machairodus,* a primary predator. *Dinofelis* may have been

a primary predator and occasional confrontational scavenger when an opponent was smaller. Without the availability of close analogues for the archaic genera and scant taphonomic evidence, it is premature for us to speculate what role the earliest hominins may have played in scavenging. We have more evidence for predation or scavenging by hominins during the carnivore-rich late Pliocene (3.6–1.8 Ma) of Africa.

Hominin attempts to defend or steal a carcass could have increased the risk of attack by several carnivores approaching from many sides and using stealth. Although twentieth century humans have chased single large carnivores from the latter's kills using little or no weaponry, these carnivores had ample reason to fear humans, as mentioned previously (Sunquist & Sunquist, 1989; Treves & Naughton-Treves, 1999). Pliocene hominins engaging in confrontational scavenging would have had to overcome several obstacles to success. First, stealing a kill from paleopredators would have demanded very frequent vigilance and repeated, effective threats: The displaced carnivores would probably have remained nearby while newcomers continued to arrive. A scavenging hominin would have had to process a carcass and defend it while maintaining high levels of vigilance— mutually incompatible activities for a single individual (Treves, 2000). Many of these obstacles suggest the need for cohesive, coordinated group activity. Second, effective deterrent threats might have required weapons. Whatever weaponry used would have had to deter large carnivores with a habit of killing horned ungulates or primates with canines. Yet, missiles would be difficult to retrieve after use and hand-held weaponry would reduce the efficiency of butchery. Third, the optimal scavenging party size depends on per capita meat yield, which will increase with carcass size (Creel & Creel, 1995), but large carcasses are usually better defended and more attractive to multiple scavengers for longer periods.

All the complicating factors mentioned would reduce the time available for butchery or increase the risk to individual butchers (Brantingham, 1998; Lupo, 1998; Monahan, 1998). Coordination of activity among hominins would help but would require trust and practice. Then, assuming success, meat transport would require safe refuges from scavengers pursuing the encumbered hominins. At the moment, confrontational scavenging of the sort envisioned above appears an unlikely route to regular meat acquisition, hence we side more with authors who envision hominins as primary predators or as scavengers of unattended fresh carcasses who fled when challenged, rather than confrontational scavengers (Brantingham, 1998; Dominguez-Rodrigo & Pickering, 2003).

Anti-Predator Behavior and Hominin Reconstruction

We divide anti-predator behavior into two discrete strategies that correspond to different stages in a predator encounter. In the first stage we place all behavioral tactics displayed in the absence of predators, behaviors aimed at reducing the likelihood of encounter. The primary tactics of stage one are inconspicuousness, avoidance of dangerous locations, and vigilance oriented to early detection of a predator. The second stage begins when predators are encountered. The

corresponding anti-predator behaviors will reflect the immediacy of the threat, although the exact steps and sequence will vary with the type of predator, type of primate prey, cost-benefit ratio of prey responses, and with the physical context (Ydenberg & Dill, 1986; Lima, 1993; Treves, 2002). The primary tactics in stage two are monitoring of predators, escape, deterrence, and hiding among other targets (selfish herd). Each tactic has requirements that make the tactic useful in some situations but not in others. Because anti-predator behavior has been studied for decades we refer the reader to more general reviews (Edmunds, 1974; Klump & Shalter, 1984; Cheney & Seyfarth, 1990; Lima, 1990; Goodman et al., 1993; Treves, 1999a; Boinski et al., 2000; Miller & Treves, 2006), but we cite primary sources for anti-predator behavior of living hominoids.

In the Absence of Predators

Primates reduce the likelihood of encounter with predators by avoiding dangerous areas, behaving inconspicuously, or surveying their physical surroundings for danger. Avoidance of known dangerous areas is probably universal among primates, but the role of learned versus innate avoidance is unclear. As a result, we know little about how primates respond to changes in predator communities or changes in their encounters with carnivores—issues of importance when we consider hominin-carnivore interactions. Inconspicuousness depends on small group size or coordination of activities among associates. The larger a group, the more sounds, smells, and other signs that may be detectable to predators.

Apes often rely on inconspicuousness and avoidance of risky areas, especially after they encounter a predator. For example, chimpanzees (*Pan troglodytes*) in Senegal were more silent than usual when they were crossing broad grassland, ostensibly to avoid detection by the abundant large carnivores (Tutin et al., 1981). Lowland gorillas (*Gorilla gorilla*) moved quickly and quietly after encountering a leopard (Fay et al., 1995). Aché hunter-gatherers (*Homo sapiens*) moved camp to avoid a jaguar (Hill & Hurtado, 1995), and Indian villagers stayed in their settlements after tigers and leopards attacked some villagers who had gone into the forest (Corbett, 1954). Early hominins would likely have avoided areas such as dark caves, treeless habitat, high grass, and rocky outcrops, at least until these areas had been thoroughly surveyed for danger. It would seem conspicuous behaviors (tool-making, loud display, mating, play, etc.) would have been most safely performed high in trees or on rock ledges. However, hominin tool making appears to have occurred at lacustrine and riverine edges (Bunn & Ezzo 1993; Capaldo 1997; Dominguez-Rodrigo & Pickering, 2003; Palmqvist et al., 2005); the risk at such sites remains to be determined.

Surveillance of surroundings also seems universal among primates. Visual and auditory monitoring may forewarn primates of impending encounters with predators and help the primates respond appropriately. Vigilance reduces uncertainty about a given location but uncertainty resurfaces after individuals leave an area or otherwise interrupt monitoring, hence vigilance must be continuously renewed.

Vision is particularly useful in providing precise information about predator type, location, and movement. Auditory vigilance can complement visual monitoring, especially in visually obstructed microsites.

Non-primates who keep their heads down suffer higher predation rates than those who survey their environment (FitzGibbon, 1989). Equivalent data are not yet available for wild primates, but they do spend more time scanning their surroundings when risk is elevated (Treves, 2000). We have little quantitative data on vigilance in apes or humans, but the few data resemble those of monkeys (Wirtz & Wawra, 1986; Setiawan et al., 1996; Treves, 1997; Watts, 1998). Locational features, such as the density of foliage and associates, will modify the effectiveness of visual vigilance and, presumably, auditory vigilance as well (e.g., running water or noises produced by non-predators). Visual obstructions were associated with less time spent vigilant in two studies (Hill & Cowlishaw, 2002; Treves, 2002). Therefore, hominins using Pliocene African savanna-woodlands might have invested more in visual vigilance than those in closed, forested habitats. We discuss vigilance further below as it is intricately tied to social organization.

After Predator Encounter

Once potential prey animals have been detected by a predator, their particular anti-predator response will depend on their detecting the predator in turn and on its hunting tactics. At one extreme predators may remain undetected throughout the attack sequence. Nocturnal predation tends toward this extreme (Busse, 1980; Peetz et al., 1992; Wright, 1998), as does predation with complete surprise (Chapman, 1986; Peres, 1990). Attack by complete surprise followed by death leaves prey with only one recourse: to practice safety in numbers. We discuss aggregation further in "Trade-Offs Between Anti-Predator Aggregation and Vigilance" below.

If a predator is detected before it kills its prey, primates display several effective anti-predator tactics. Many individuals will produce alarm calls to warn associates some protect themselves without warning others. When primates have detected a predator they may produce predator warnings to deter further approach by that predator (Zuberbühler, 2000). Mobbing calls are used to attract attention to a predator or intimidate it. Chimpanzees and humans give alarm and mobbing calls (Corbett, 1954; Goodall, 1986; Hiraiwa-Hasegawa et al., 1986; Boesch, 1991; Tsukahara, 1993). Hominins would presumably have done the same.

In addition, all primates escape. We have found no convincing descriptions of primates using the "confusion effect" (i.e., escape not in a direct line to refuge, but in coordinated, evasive action confusing to the observer), to avoid predation, the kind of effect that is seen in some fish or open-country herds of ungulates (Edmunds, 1974). Moreover, primates virtually always flee to refuge rather than try to outdistance their attackers. Refuges for terrestrial primates include some trees and cliffs, while arboreal primate forms rapidly change levels. Humans and apes also commonly flee from predators and use refuges such as trees (Corbett, 1954; Boesch, 1991; Tsukahara, 1993; Hill & Hurtado, 1995). Presumably,

early hominins would have minimized forays away from refuge and maintained proximity to trees and cliff sides to improve their chances of escape from speedy predators.

More rarely, primates stand their ground to counterattack or mob predators. Of the two forms, mobbing appears to be less dangerous for the predator and is more common among primates much smaller than the predator. Mobbing involves two or more prey animals making repeated advances on a predator, usually while vocalizing and displaying in a conspicuous fashion. The predator is often distracted or repelled by persistent approaches. Adult males, acting alone or in small parties, are more likely to attack predators than other classes of individuals (Gautier-Hion & Tutin, 1988; Cowlishaw, 1994). Baboon counterattacks have been described most often. Sometimes adult male baboons coordinate a counterattack on a leopard or cheetah and may deliver serious injuries (Brain, 1981; Bailey, 1993; Cowlishaw, 1994), but at other times the males flee the scene (Smuts, 1985). The likelihood of counterattack by primates appears to depend on the size difference between predator and prey.

Silverback gorillas sometimes defend their groups from predators and hostile conspecifics by using intimidation displays. Chimpanzees have pursued and even killed cornered leopards (Boesch & Boesch, 1981; Hiraiwa-Hasegawa et al., 1986). Chimpanzees have attacked stuffed leopard models with sticks and stones (Kortlandt, 1980, 1989). However, healthy lioness-sized or larger carnivores may be too formidable, even for male apes in groups (Tsukahara, 1993). Counterattack with hand weapons may be an especially effective anti-predator tactic in some situations, but we have very little systematic evidence of this. It is doubtful that simple projectiles can deter coursing predators that do not abort pursuit easily or packs of carnivores emboldened by their own numbers. Moreover, a weapon does not provide protection if its wielder is surprised. Therefore, we doubt that hominins counterattacked carnivores in packs or lion-sized carnivores in the Pliocene.

Trade-Offs Between Anti-Predator Aggregation and Vigilance

Aggregation of individuals of one or more species has complex effects on predator detection. On the one hand, groups may detect predators earlier thanks to having many eyes and ears (Galton, 1871). Also, if associates warn each other in time, unwary individuals may remain safe (Bednekoff & Lima, 1998a,b). On the other hand, large groups may be more conspicuous to predators leading to higher rates of attack (Foster & Treherne, 1981; Fitzgibbon & Lazarus, 1995; Wright, 1998; Treves, 2000). Moreover, individuals in large groups may detect predators less quickly or reliably if larger groups contain more rivals and unfamiliar animals that must be monitored. For example, chimpanzee vigilance frequency was higher in large parties (Treves, 1997). Three solitary chimpanzees (an adult female and two juvenile females) averaged less of their time spent vigilant ($19.2 \pm 13.3\%$) than did nine chimpanzees observed in parties of 2–13 individuals who spent $46.5 \pm 26.3\%$ of their time vigilant. Most of this extra time was spent watching associates (50% of samples contained at least one glance at an associate); excluding this subset of samples the average time spent vigilant was $20.9 \pm 18.2\%$ in chimpanzee

parties. Time spent monitoring associates is a cost additional to competition between individuals in large chimpanzee parties (Goodall, 1986; Chapman et al., 1995). We doubt hominins organized themselves as did the forest chimpanzees described above because the risk of conspicuousness and the added costs of vigilance in large, competitive parties would have been prohibitive in the carnivore-rich terrestrial habits under consideration here.

Our conjecture leaves open the possibility that hominins formed quiet, cohesive groups with less distracting competition. If vigilance were coordinated in some fashion (i.e., outwardly directed mainly, or asynchronous: cf. Horrocks & Hunte, 1986; Koenig, 1995), having many eyes would be advantageous.

Many studies of birds and ungulates have shown decreases in individual vigilance in larger groups. This has been interpreted most often as the animals in groups relaxing their individual efforts at vigilance because wary associates will give warnings (Lima, 1995; Bednekoff & Lima, 1998a). Increasing vigilance with larger group size as described above for forest chimpanzees is rare among animals in general (Elgar, 1989; Treves, 2000). In two cases it has been associated with the attraction of multiple, solitary scavengers to a single carcass (Knight & Knight, 1986; Jones, 1998). Indeed, individual primates rarely if ever reduce vigilance with the absolute number of conspecific associates (Treves, 2000). More often, primates relax their vigilance when associates are positioned nearby, regardless of total group size (but see Hill & Cowlishaw, 2002; Cowlishaw et al., 2004 for recent refinements). Moreover, one sees the highest vigilance among dominant animals and mothers of neonates (Gould et al., 1997; Treves et al., 2001, 2003). In short, individual vigilance in primates is shaped strongly by inter-individual proximity and social relationships. Therefore, safety may depend on establishing familiarity, trust, and reciprocity with a few individuals who will warn others when a predator is detected.

Leaving aside predator detection and aggregation, prey in a group usually enjoy dilution of risk—the inverse relationship between group size (N) and per capita risk (Foster & Treherne, 1981). However, dilution of risk rarely follows a simple inverse relationship (1/N) for primate prey because individuals within groups vary in their vulnerability to predation (Treves, 2000). This would have held for hominin groups with mothers and young. Grouping may also generate predator confusion or enable more effective counterattack against predators.

In sum, the net protection afforded by large groups fluctuates in a delicate balance of costs and benefits that are contingent on many local factors. This makes it difficult to conclude that hominins would have formed large groups in response to the putative higher risk of predation in the Pliocene.

Social Organization Reconstructed for Hominins

We have virtually no evidence for the foraging group size of the earliest hominins. Reconstructions of social organization that try to account for phylogeny suggest hominins lived in societies similar to those of chimpanzees or bonobos (*Pan paniscus*) (Foley, 1987; Ghiglieri, 1989). Today, chimpanzees rarely form

parties exceeding 10 individuals (Chapman et al., 1994; Doran, 1997). Current evidence suggests that larger groups of apes are constrained by food availability (Chapman et al., 1995; Doran & McNeilage, 1998). However, the radiation of hominin taxa and extinction of several lineages cautions us against extrapolating uncritically from the social organization of living apes.

Consideration of the habitat rather than the phylogeny of the earliest hominins suggests the larger groups of savanna-woodland baboons (averaging 30–50 animals) may help us understand early hominin foraging groups in an open environment. Although habitat by itself does not ordain a certain group size, the foods available to the earliest hominins could have determined upper limits on aggregations. Bone and enamel isotope values from southern African fossils suggest that Plio-Pleistocene *Homo* and *Paranthropus* ate a higher-quality, more varied diet than either of two penecontemporaneous baboon species that focused on C3 plants (Lee-Thorp et al., 1994; Spoonheimer & Lee-Thorp, 1999). Given the larger body mass of hominins (see above) and this higher-quality diet, which presumably included variable amounts of animal proteins, average foraging group sizes exceeding 20 seem highly unlikely. However, we cannot reject this possibility yet.

Conclusions

Hominin ancestors of 6.0–1.8 Ma shared habitats with diverse genera of large carnivores that were opportunistic or with generalized predators that had no reason to fear hominins. In all likelihood, the hominins could not have avoided all encounters with these carnivores by virtue of diurnality, habitat selection, or body size. Nor could the hominins have deterred all attacks with weapons in this period. Given the existence of numerous ambush predators between 3.6–1.8 Ma, hominins would have experienced strong selection for efficient vigilance. Large parties of apes organized like those of chimpanzees are conspicuous and costly in terms of individual vigilance, competition for food and agonistic social interactions, hence we propose early hominin foraging parties would have adopted more cohesive and calmer social organization to maintain efficient vigilance and reduce conspicuousness to carnivores during diurnal foraging. Groups formed of trusted and familiar individuals often forage and travel with high levels of inter-individual proximity, experience minimal conflict, and coordinate vigilance more easily (Rasa, 1986, 1989; Koenig, 1994). For these reasons we rule out large (> 20) hominin groups and particularly large, multi-male groups—like those of many baboon populations—as probable ancestral, anti-predator tactics.

Considering the range of anti-predator behaviors among monkeys and apes has helped researchers define the most likely adaptations of early hominins. Hominins would generally have avoided predator encounter through vigilance, minimizing time spent in dangerous areas, and behavioral inconspicuousness. Forays into open country would have been limited in extent and duration by access to refuges, whereas hominins foraging within woodlands would have been constrained by the demands of efficient, unobstructed vigilance because of the

numerous ambush predators in Pliocene Africa. When close encounters occurred, the hominins would flee to refuge or counterattack. Counterattack would have been more likely by larger hominins against leopard-sized or smaller carnivores but virtually unknown against lioness-sized opponents in the period considered here. Hominins armed with weapons may have counterattacked more often, but we find no compelling evidence that material culture sheltered hominins from ambush and stalking predators before the advent of controlled fire. Frequent formation of foraging parties larger than 15–20 individuals seems unlikely given the dietary evidence presently available, although avoidance of nocturnal predation may have involved the formation of larger sleeping groups. Nevertheless, the essential nocturnal anti-predator adaptation was the use of trees or cliffs inaccessible to most large carnivores; this adaptation was important until the advent of controlled fire in the Pleistocene.

Modern humans may retain traces of some of the anti-predator adaptations of our ancestors. In particular, predictable behavioral responses and aversion to areas with dense vegetation or areas without suitable refuge (e.g., wide, open areas) should both be deeply embedded in human cognitive and perceptual abilities. These predictions are not trivial given that taxa differ based on selective pressures imposed by ancestral environments (Byers, 1997). Some animals perceive holes as refuges, while others perceive dense vegetation or open areas as avenues for escape (Lima, 1993). Experiments with sleeping sites, vigilance and group formation could test these ideas about ancestral human anti-predator adaptations; these would be analogous to the fruitful studies of brain and behavioral responses to strangers (reviewed in Treves & Pizzagalli, 2002).

In the following section, we consider some terrestrial mammalian taxa that live in environments with high predation pressure and display social organizations that share one or more of the following characteristics: inconspicuous, minimal internal conflict, or coordinated vigilance. For each we make predictions about the fossil record if one or more lineages of hominins had displayed such a social organization, and we make predictions about modern human behavior assuming we retain ancestral anti-predator adaptations.

Medium-Sized, Inconspicuous Groups

Individuals in groups of 10–15 animals can detect threats early and warn associates efficiently if distractions due to associates are few. For example, the Asian Hanuman langur (*Semnopithecus entellus*) forms large groups (averaging 29 members in 22 populations: Treves & Chapman, 1996), yet noisy, costly competition over resources seems to be muted by a combination of kinship bonds and even distribution of resources (Borries, 1993; Borries et al., 1994; Koenig, 1998). Male-male fighting is infrequent within groups because one male often monopolizes mates and evicts rivals. However, this calm evaporates when multiple males compete (Boggess, 1980; Borries, 2000). If modern humans retain traces of such a social organization, one should see higher vigilance among males watching for non-group rivals, and a significant increase in distractions and within-group vigilance

when male rivals co-reside in a group. Hominins displaying such a social organization between 6.0–1.8 Ma would show marked sexual dimorphism associated with polygynous mating. Their dentition might also reflect the use of evenly distributed, low-quality foods, such as foliage or grasses.

Small Groups with Male Protector

Small, inconspicuous groups with a protective individual occur among terrestrial primates (e.g., gorillas: Doran & McNeilage, 1998). One version would include females attracted to watchful males, where female-female rivalry would be strong because the male's protective sphere would not be infinitely divisible among many females. If modern humans retain traces of this social organization, one should see higher vigilance among males than females and the greatest increase in within-group vigilance when multiple females are present in a group. Among early hominins, one would expect strong sexual dimorphism with polygynous mating, but dentition would reflect a high-quality diet due to low group size.

Small, Cooperative Groups

Small groups within which individuals cooperate in anti-predator behavior can survive under heavy predation pressure. The use of coordinated vigilance or sentinel systems is particularly important in such conditions because one or two individuals survey the surroundings while the remainder of the group forages uninterrupted. Upon detection of a predator, the sentinel gives a visual or acoustic signal as an alarm and the group takes defensive action. Modern humans use sentinels, of course. Sentinel systems are also seen today in many cooperatively breeding species (Wickler, 1985; Savage et al., 1996), but also among less cooperative groups that must forage silently (Horrocks & Hunte, 1986). Of particular relevance may be the social mongooses Herpestidae found in African woodland-savannas. High levels of cooperation and reciprocity appear critical under heavy predation pressure (Rasa, 1986, 1989); pressure that leads to the retention of juveniles and sub-adults in their natal groups (NB: also a modern human trait). If modern humans show traces of this social organization, the sexes will be equally vigilant, and familiar associates may readily coordinate defensive behavior. Hominins using this system would show little sexual dimorphism and delayed maturation, as in modern humans. Dentition would reflect a high-quality diet due to low group size.

Solitary Foragers

This form of inconspicuous social organization is seen in orangutans among the living apes and has been interpreted as a response to food scarcity (Sugardjito et al., 1987), and perhaps to avoidance of threats posed by conspecifics rather than predators (Setiawan et al., 1996; Treves, 1998). Nevertheless, early hominins might have foraged alone and aggregated only at superabundant resources or at sleeping sites. If modern humans retain traces of such a social organization, one

should expect no coordination of vigilance within their groups and increases in vigilance with party size, particularly when reproductive females encounter non-father, adult males. Fossil hominins displaying such a system would presumably show extreme sexual size dimorphism (Rodman & Mitani, 1987) and evidence of high-quality diets.

Speculation about the behavior and social organization of ancient hominins is often dissatisfying because we will never be confident about the details. However, hominin anti-predator behavior demands further scrutiny. Enough data have accumulated to refine our hypotheses. We propose that the adaptive solution to the higher predation pressure of the end Miocene and Pliocene was a social adaptation that preceded any elaboration of material culture.

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