4. Patterns of change in the Plio-Pleistocene carnivorans of eastern Africa

Implications for hominin evolution

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Abstract

This paper uses changes in origination and extinction rates and species richness of eastern African carnivorans through time to discuss issues related to the evolution of hominin behavior. To address the question of which taxa were most likely to have had competitive interactions with hominins, modern carnivorans were sorted into size classes based on shifts in behavior, ecology, and body mass. Four size classes were created, among which the two largest (21.5–100 kg and >100 kg) include those taxa whose behavior is most relevant to the evolution of hominin dietary behavior. Fossil taxa were then assigned to these size classes. A summary of the temporal range and reconstructed behavior and ecology of fossil members of the two largest size classes is presented. We discuss the relevance of each taxon to reconstructing hominin behavior and suggest that hominins must have evolved not only successful anti-predator strategies, but also successful strategies to avoid kleptoparasitism before carcass-based resources could become an important part of the diet. Although hominins were unlikely to have been top predators upon first entrance into the carnivore guild, effective anti-predator/anti-kleptoparasitism strategies in combination with the eventual evolution of active hunting would have increased the rank of hominin species within the guild. While the appearance of stone tools at 2.6 Ma has no apparent effect upon carnivorans, the appearance of *Homo ergaster* after 1.8 Ma may have been at least partly responsible for the decrease in the carnivoran origination rate and the increase in the extinction rate at this time. The behavior of *H. ergaster*, climate change, and concomitant changes in prey species richness may have caused carnivoran species richness to drop precipitously after 1.5 Ma. In this situation, even effective kleptoparasitism by *H. ergaster* may have been enough to drive local populations of carnivorans that overlapped with hominins in dietary resources to extinction. Possibly as a result, the modern guild, which evolved within the last few hundred thousand years, is composed primarily of generalists. Although the impact of *H. sapiens* on the carnivoran guild cannot be assessed due to a lack of carnivoran fossils from this time period, one might not consider the modern carnivore guild to be complete until the appearance of our species approximately 200,000 years ago.

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Introduction

Paleoanthropologists have long been interested in the transitions in diet and diet-related behavior that occurred during hominin evolution. Early work in this area envisioned hominins as top predators from whom other carnivores scavenged (e.g., Dart, 1949, 1956). Later research on the taphonomy and fauna found in South African caves suggested that early hominins were the prey and not the predators (Brain, 1969, 1981). While most researchers have accepted the hypothesis that vertebrate carcasses played an increasingly larger role in African hominin diet through time, debate over the nature of access to those carcasses and the amount of competition involved has continued for several decades (e.g., Isaac, 1971, 1978; Binford, 1981, 1986; Potts, 1984, 1988a, b; Bunn, 1986, 1991; Bunn and Kroll, 1986; Shipman, 1986a, b; Binford et al., 1988; Blumenschine, 1988, 1989, 1991; Turner, 1988; Cavallo and Blumenschine, 1989; Bunn and Ezzo, 1993; Blumenschine et al., 1994; Domínguez-Rodrigo, 1999, 2001; Treves and Naughton-Treves, 1999; Van Valkenburgh, 2001; Domínguez-Rodrigo and Pickering, 2003).

In any case, hominins, at some point, became members of the carnivore guild. As hominins became increasingly aggressive in their scavenging and/or hunting behavior, their ecological relationships with members of the order Carnivora are likely to have changed. Carnivorans, therefore, were not just potential competitors and predators, but also contributors to the structure of resources available to hominins (e.g., Schaller and Lowther, 1969; Walker, 1984; Blumenschine, 1986a,b, 1987; Turner, 1988, 1992; Cavallo and Blumenschine, 1989; Marean, 1989; Sept, 1992; Lewis, 1995b, 1997; Marean and Ehrhardt, 1995; Brantingham, 1998; Domínguez-Rodrigo, 1999; Van Valkenburgh, 2001). As such, factors affecting the partitioning of the guild by carnivorans are relevant to the study of human evolution.

How, then, do hominins fit into the carnivore guilds of Plio-Pleistocene Africa? In other words, what niche space was available to hominin species and how did that space change through time? How might the behavior of carnivoran species and hominin species have affected one another? Before we can answer these questions, we must explore the ecological framework surrounding hominins by reconstructing the behavior and ecology of extinct carnivorans and examining patterns in the evolution of this group in Africa (Turner, 1983, 1985, 1986, 1990, 1998; Walker, 1984; Lewis, 1995b, 1997).

The present paper uses data on carnivoran originations and extinctions and species richness from a previous paper (Werdelin and Lewis, 2005) in combination with data on changes in body size through time to address theoretical issues related to the evolution of hominin dietary strategies. Specific taxa of potential relevance to hominins are discussed. Our goal is to provide a summary of up-to-date information from our research on the changing nature of the carnivoran guild through time focusing on issues of relevance to hominin behavior and evolution.

The Importance of Carnivoran Body Size to Hominins

Many factors need to be considered to understand the complex ecological relationship between carnivorous taxa (e.g., Table 1). Part of the current study examines one of the most basic factors affecting niche partitioning of any type of guild: body size. Body size limits the choice of prey, such that larger predators capture prey with a wider range of body sizes (Gittleman, 1985). Body size is also an important determinant of interspecific rank at a carcass (Eaton, 1979; Van Valkenburgh, 2001). Sympatric carnivores that are similar in both morphology and

Table 1. Some factors affecting carnivore guild structure

Factor	Definition or example
Habitat preference	Amount of canopy cover, underbrush, water, etc.
Foraging time	Diurnal, nocturnal, crepuscular, etc.
Prey choice	Prey size
Hunting method	Ambush, pack hunting, etc.
Scavenging	Passive, aggressive, combination, etc.
Food transport	Ability to remove food items from view
Food caching	Ability to store food safely for future use
Food processing	Flesh only, bone-crushing, bone-cracking, etc.
Level of aggression	Intra- or interspecific levels of aggression
Grouping behavior	Solitary, pack hunting, solitary forager in a social group, etc.
Individual body size	Biomass of single individual
Group biomass	Biomass of foraging and/or social group

predatory behavior may reduce interspecific competition for food through differences in body size (Rosenzweig, 1966; Gittleman, 1985; Dayan and Simberloff, 1996), a pattern that has been recognized across various vertebrate taxa (e.g., Farlow and Pianka, 2002).

In carnivorous taxa, the fact that many species may hunt or at least eat in a group means that group or pack biomass must also be considered. Cooperative hunting specifically allows the capture of larger or faster prey than solitary hunting may allow (Kruuk, 1975; Packer and Ruttan, 1988), resulting in a larger prey carcass that may interest a greater range of scavengers. Grouping behavior, in general, allows larger carnivoran taxa, such as spotted hyenas (*Crocuta crocuta*) and African wild dogs (*Canis pictus*) to be more successful during interspecific competition, (e.g., at a carcass) such as that occurring over a carcass, than their body size alone would predict (Lamprecht, 1978; Eaton, 1979). Kleptoparasitism (food theft by other taxa) can still have a significant impact on groups or packs of carnivorans (e.g., Cooper, 1991; Gorman et al., 1998). For the above reasons, the potential for grouping behavior in extinct taxa must be addressed (e.g., Van Valkenburgh et al., 2003; Andersson, 2005), even though it may not be possible to positively identify specific types of grouping behavior or even grouping behavior in general in the fossil record.

Materials and Methods

The present study is part of a larger study on the evolution of African carnivorans within a global context. The material used herein consists of many hundreds of specimens of Carnivora found at Plio-Pleistocene sites in Ethiopia, Kenya, and Tanzania (Table 2).

Table 2. Localities included in the analyses

Country	Localities
Kenya	Allia Bay
	Eshoa Kakurongori
	Kanam East
	Kanapoi
	Koobi Fora
	Kosia
	Lainyamok
	Lothagam
	Nakoret
	Olorgesailie
	South Turkwel
	West Turkana (Nachukui Fm.)
Ethiopia	Aramis*
	Daka Mb., Bouri Fm.*
	Hadar
	Konso-Gardula*
	Omo
Tanzania	Laetoli
	Olduvai Gorge

*Data from three Ethiopian localities were taken from the literature (Asfaw et al., 1992; WoldeGabriel et al., 1994; de Heinzelin et al., 1999; Gilbert, 2003). Ages of included members can be found in Table 1 of Werdelin and Lewis (2005).

Nearly all of the specimens included have been studied and identified by the authors. As a result, identifications are based on a uniform view of morphology, taxonomy, and systematics, one in which craniodental and postcranial data have been treated equally. While we do not claim to be infallible in our identifications, we believe that our analyses provide a uniform baseline for understanding patterns of change in carnivoran evolution.

All named eastern African carnivoran species known during the last 4.5 million years are included in the study. Unnamed species have been included if they have been verified by us as being different from all other known species in the material. Specimens that cannot be definitively excluded from known taxa are counted as part of known taxa. As such, we provide a minimum estimate of the number of species within the data set. Further discussion of included taxa and evidence for the suggestion that sampling overall is relatively good throughout the time period investigated can be found in our larger study of species richness and turnover in Plio-Pleistocene carnivorans of eastern Africa (Werdelin and Lewis, 2005).

Data on the behavior, ecology, and body mass of extant African carnivorans were taken from the literature (Estes, 1991; Nowak, 1991; Kingdon, 1997; Sillero-Zubiri et al., 1997). While previous studies of body mass distributions within faunas have classified carnivorans into size classes, these studies have focused on dividing carnivorans into size classes of a predetermined width (e.g., 5-kg bins in Rodriguez et al., 2004) and/or have labeled carnivorans over 20 kg (Van Valkenburgh, 2001), 40 kg (Lambert and Holling, 1998), or 45 kg (Rodriguez et al., 2004) a large carnivore or large mammal. We wanted to see if there were any natural breaks in behaviors of relevance to hominins that might not be detected by equal bin widths in body size.

Extant taxa were sorted by body mass and the behavioral and ecological data on those taxa were examined for natural breaks in the data. In other words, we looked for changes in ecology and behavior as body size increases, with particular emphasis placed on shifts that might reflect changes in potential interactions with hominins. We identified general size classes of carnivorans based on maximum body mass such that the transition from one class to another represents a fundamental behavioral shift. While mean body mass might be a better method of assigning taxa to size classes, this information is not always available for extant taxa. Although we did examine the overall range in reported body mass for a given taxon in constructing our size classes, there were clear shifts in ecology and behavior that matched jumps in maximum body mass. While some taxa had body mass *ranges* that overlapped two categories, in all instances the *maximum* body mass fell with species most similar in behavior and ecology. Although males and females of sexually dimorphic species were considered separately during the construction of size classes, in no instance did males and females fall into separate categories. For this reason, sexes are not presented separately in this paper.

As the size classes are quite general, we did not calculate exact body masses for extinct taxa. Instead, specimens of extinct taxa were categorized based on their overall similarity in size and reconstructed behavior to extant taxa. While this study is not meant to represent the last word on the relationship between body size and behavior and ecology in carnivorans, these very general categories may prove of use in thinking about carnivoran behavior relative to hominins.

For the analyses of turnover in the carnivoran fossil record, each taxon was assigned a FAD and a LAD based on the oldest and youngest ages of the oldest and youngest sites from which it has been identified. The data were then binned into time intervals of equal length. While 500-Kyr bins are commonly used (e.g., Behrensmeyer et al., 1997), a shorter bin length (300 Kyr) provides finer grained analysis. Our previous work has demonstrated that the material was not sufficient for a shorter bin length than 300 Kyr even though we recognize that this may lump taxa together that did not actually overlap. As such, changes from bin to bin represent general changes, as bins are not equivalent to guilds. See Werdelin and Lewis (2005) for the stratigraphic ranges of all eastern African Carnivora taxa included in this study and further discussion of binning.

Results

BODY MASS OF EXTANT AFRICAN CARNIVORANS

Extant carnivoran taxa in Africa tend to fall into four groups based on maximum body mass, behavior, and potential relationship with hominins (Table 3). Although there is certainly overlap between groups, particularly among smaller species, the general categories hold up quite well. The characteristics of each group will be discussed in turn.

Carnivorans less than 10 kg (Size Class 1) exhibit the greatest diversity of behavior. While classification of this diverse group of taxa together might seem odd, this group is presumed to share the least potential to impact hominin behavior significantly. Members of this group today may occasionally raid human habitations, but are more easily intimidated by humans than their larger relatives. A recent study demonstrates that the carnivorans that have the highest chance of being killed by other carnivorans during interspecific encounters all belong to this group (Caro and Stoner,

Table 3. Size classes of extant eastern African Carnivora based on maximum body mass (kg)

Species	Family	Common name	Min. mass	Max. mass[1]
Size Class 1 (Max. mass < 10)				
Otocyon megalotis	Canidae	Bat-eared fox	3.0	5.3
Felis lybica	Felidae	Wild cat	3.0	8.0
Atilax paludinosus	Herpestidae	Marsh or water mongoose	2.2	5.0
Bdeogale crassicauda	Herpestidae	Bushy-tailed mongoose	1.3	2.1
Bdeogale nigripes	Herpestidae	Black-legged mongoose	2.0	3.5
Dologale dybowskii	Herpestidae	Savannah mongoose	0.3	0.4
Galerella sanguinea	Herpestidae	Slender mongoose	0.4	0.8
Helogale hirtula	Herpestidae	Somali dwarf mongoose	0.2	0.3
Helogale parvula	Herpestidae	Dwarf mongoose	0.2	0.4
Herpestes ichneumon	Herpestidae	Egyptian mongoose or Ichneumon	2.2	4.1
Ichneumia albicauda	Herpestidae	White-tailed mongoose	1.8	5.2
Mungos mungo	Herpestidae	Banded mongoose	1.5	2.3
Rhynchogale melleri	Herpestidae	Meller's mongoose	1.7	3.1
Ictonyx striatus	Mustelidae	Striped polecat or Zorilla	0.4	1.4
Lutra maculicollis	Mustelidae	African river or spot-necked otter	4.0	6.5
Poecilogale albinucha	Mustelidae	African striped weasel	0.2	0.4
Nandinia binotata	Nandiniidae	African palm civet	1.7	4.7
Genetta abyssinica	Viverridae	Ethiopian genet	1.3	2.0
Genetta genetta	Viverridae	Common genet	1.3	2.3
Genetta servalina	Viverridae	Servaline genet	1.0	2.0
Genetta tigrina	Viverridae	Blotched genet	1.2	3.2
Size Class 2 (Max. mass 10–21.5)				
Canis adustus	Canidae	Side-striped jackal	7.3	12.0
Canis aureus	Canidae	Golden jackal	6.0	15.0
Canis mesomelas	Canidae	Black-backed jackal	6.5	13.5
Canis simensis	Canidae	Ethiopian wolf	11.2	19.3
Caracal caracal	Felidae	Caracal	13.0	19.0

(*Continued*)

Table 3. Size classes of extant eastern African Carnivora based on maximum body mass (kg)—cont'd

Species	Family	Common name	Min. mass	Max. mass[1]
Leptailurus serval	Felidae	Serval	8.7	18.0
Profelis aurata	Felidae	African golden cat	5.3	16.0
Proteles cristatus	Hyaenidae	Aardwolf	8.0	14.0
Mellivora capensis	Mustelidae	Honey badger or Ratel	7.0	16.0
Civettictis civetta	Viverridae	African civet	7.0	20.0
Size Class 3 (Max. mass > 21.5–100)				
Canis pictus	Canidae	African wild dog	18.0	36.0
Acinonyx jubatus	Felidae	Cheetah	35.0	72.0
Panthera pardus	Felidae	Leopard	28.0	90.0
Crocuta crocuta	Hyaenidae	Spotted hyena	40.0	90.0
Hyaena hyaena	Hyaenidae	Striped hyena	25.0	55.0
Aonyx capensis	Mustelidae	African clawless otter	10.0	28.0[2]
Size Class 4 (Max mass > 100)				
Panthera leo	Felidae	Lion	120.0	250.0

[1] Body mass and biogeographical data were taken from the literature (Estes, 1991; Nowak, 1991; Kingdon, 1997; Sillero-Zubiri et al., 1997). As data on eastern African populations were not always available, ranges represent body mass ranges reported for African populations in general. Note that eastern African populations of some species may differ in body mass range (e.g., *C. pictus*) from populations in the rest of Africa as discussed in the text.

[2] While the largest African clawless otter is reported at 34 kg, individuals of this size are not common (Estes, 1991; Kingdon, 1997).

2003). Faunivorous members of this group capture prey that is too small to be a potential source for hominin scavenging. Even the smallest hominin adult was highly unlikely to be a prey item for members of this group. Today, carnivorans of this size worldwide are more likely to be killed by humans as pests (e.g., weasels in King, 1990) or for their pelts (e.g., raccoon dogs in Novikov, 1962) than pose a threat.

Size Class 2 carnivorans (10–21.5 kg) are also quite diverse in dietary behavior. Carbone et al. (1999) have shown that of the carnivorans worldwide weighing 21.5 kg or less, only 25% feed purely on vertebrates, 45% are omnivores, 10% are purely invertebrate feeders, and 19% are mixed vertebrate/invertebrate feeders. Most importantly, among those that consume vertebrates, prey size is still too small to be a useful scavenging resource (i.e., 45% or less of their body mass; Carbone et al., 1999). Today, members of this group, such as the various jackal species, tend to be of low rank in competitive interactions at carcasses. Highly aggressive species of this size, such as the honey badger (*Mellivora capensis*), might have been an annoying and dangerous species to encounter during foraging, particularly for any small band of hominins or solitary individuals. One would predict, however, that the potential for hominin death or serious injury at the hands of these carnivorans was less of a stressor than the potential for the same from larger carnivorans. As in the case of members of Size Class 1, most of these species are more likely to be killed by humans than actually cause the death of a human. As with the smallest size class, this group may have had less of an ecological impact on hominins than members of the two larger size classes.

Members of the third group of carnivorans (Size Class 3, >21.5–100 kg) exhibit behaviors that make them more likely than Size Class 1 or 2 carnivorans to have engaged in competitive and/or predatory encounters with hominins. Extant members are hypercarnivorous or primarily carnivorous and overlap to some degree in prey preference and other resource requirements. Terrestrial taxa in this size class prefer prey that is greater than 45% of their body mass (Carbone et al., 1999). This means that the preferred prey of Size Class 3 species would be large enough that individuals or groups might have competed with hominins for prey and/or engaged in interspecific competition at carcasses. Modern Size Class 3 species, however, do differ in behaviors associated with prey choice and procurement, carcass processing and transport, scavenging, and carcass defense (see Lewis, 1997 for a summary). Only one extant species in this class, the African clawless otter (*Aonyx capensis*), engages in behavior that is probably of little relevance to hominin evolution. We should note that all hominin species relevant to this discussion would be classified as Size Class 3.

Size Class 4 (>100 kg) today contains only the lion, *Panthera leo*. We have distinguished lions from other carnivorans due to their much larger maximum prey size (900 kg; Schaller, 1972) than other eastern African carnivorans (e.g., 300 kg for spotted hyenas; Schaller, 1972). While the most important components of the lion's diet in the Serengeti are the medium-sized (100–350 kg) wildebeest, zebra, and topi (Kruuk and Turner, 1967; Schaller, 1973), lions have also been known to prey upon elephant calves and young adult elephants (Pienaar, 1969). Lions are capable of bringing down prey in almost any habitat and are known to utilize all habitats within an area (Kruuk and Turner, 1967; Van Orsdol, 1982). Hunting success is affected by lioness group size, tactical strategy chosen by the group, prey species, and the interaction between time of the hunt and terrain (Stander and Albon, 1993). Presumably, not all extinct Size Class 4 taxa behaved like lions. However, the sheer size and robusticity of Class 4 species make them potential predators of hominins and potential competitors for prey and carcasses.

Among extant carnivorans, two Class 3 species (spotted hyenas and African wild dogs) engage in group hunting and thus are more dominant in interspecific competition than the body mass of the average individual would predict. Interestingly, the one living Class 4 species, the lion, also engages in social grouping, thus maintaining its dominance in interspecific competitions between groups. As one can debate whether group hunting Class 3 species should be considered as Class 4 species or even whether the two size classes merit distinction, the two groups were considered both together and separately in the analyses.

CHANGES IN DIVERSITY OF BODY MASSES THROUGH TIME

Our research indicates that both total species richness and mean standing richness across all known habitats of eastern African carnivorans reaches a peak roughly between 3.6 and 3.0 Ma (38 to 39 species) and then declines with a slight rise between 2.1 and 1.5 Ma (31 species) (see Figure 1). Unfortunately, intervals before 3.9 Ma are relatively undersampled, as are those between 0.9 Ma and the present. Nonetheless, a clear pattern can be seen during the well-sampled period between 3.9 and 0.9 Ma.

Studies of origination and extinction events in eastern Africa have indicated that there are two major peaks in the origination of new species: 3.9–3.6 Ma and 2.1–1.8 Ma (see Figure 2; also Figures 5 and 6 in Werdelin and Lewis, 2005). While these may both be sampling artifacts (the first due to poor sampling of the early Pliocene and the second due to the unique taxa found at Olduvai), it is interesting that there are absolutely no new species appearing between 3.0 and 2.4 Ma. There is a small peak in the extinction rate (3.3–3.0 Ma) that follows the first peak in origination rate. After that point, extinction rates are low and fairly constant until the extinction rate increases dramatically after 1.8 Ma. The greatest extinction rate then occurs between 1.5 and 1.2 Ma. Our data indicate that no turnover pulse occurs in carnivorans around 2.5 Ma.

One must ask whether these patterns are reflected across all carnivoran taxa. For example,

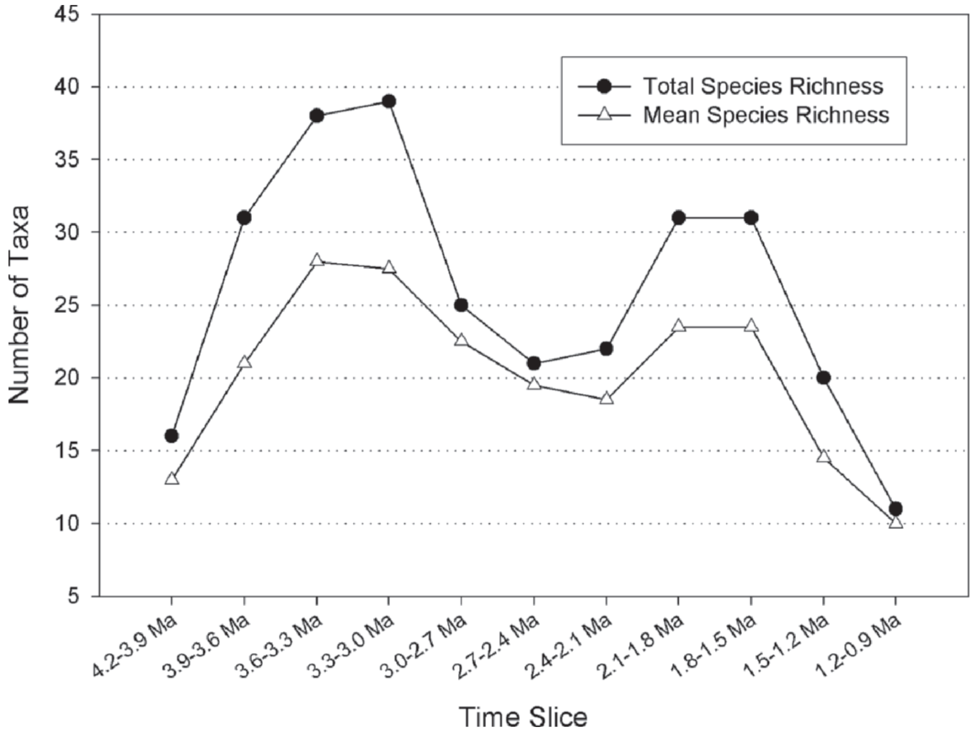

Figure 1. Species richness data for Plio-Pleistocene Carnivora of eastern Africa. Total richness and mean standing richness (MSR) are graphed in 300-Kyr bins from 4.2 to 0.9 Ma. As devised by Foote (2000), MSR = $(N_{bL} + 2N_{bt} + N_{Ft})/2$, where N_{bL} = # of taxa that originate before the bin interval, but go extinct within it, N_{bt} = # of taxa that originate before the interval and persist beyond it, and N_{Ft} = taxa that originate in the interval and persist beyond it. Intervals 4.2–3.6 Ma and 1.5–0.9 Ma are less well sampled than the intervening intervals. Peaks before 3 Ma (higher) and after 2 Ma (lower) are evident.

how are these patterns reflected in the number of taxa large enough to have impacted hominins? When species richness of just Size Classes 3 and 4 is examined (Figure 3), the pattern seen in overall species richness is repeated: high richness between 3.6 and 3.0 Ma, then a drop, and a smaller increase around 2.1–1.5 Ma. Most importantly, there were more species in both size classes in the past until around 1.2–0.9 Ma, during which time there were still at least two Size Class 4 species (*Panthera leo* and *Dinofelis piveteaui*). While today one Size Class 4 species occurs in eastern Africa (lions), in the past, there were up to eight known species. Granted, not all of them may have been significant to hominin dietary or predator avoidance strategies as discussed below. Due to the nature of the fossil record, there is always the possibility that there were even more species than we have detected thus far. However, such hypothetical species would most likely be close relatives of known species and thus not sympatric with them. This would mean an increase in beta- or gamma-diversity (as defined in Whittaker et al., 2001), but not the alpha-diversity that is critical for understanding the place of hominins in the carnivore guilds of the past.

Discussion

CARNIVORAN TAXA WITH POTENTIAL HOMININ IMPACT

To gain a full appreciation of the complexity of the changing ecological framework surrounding hominin evolution, one must take

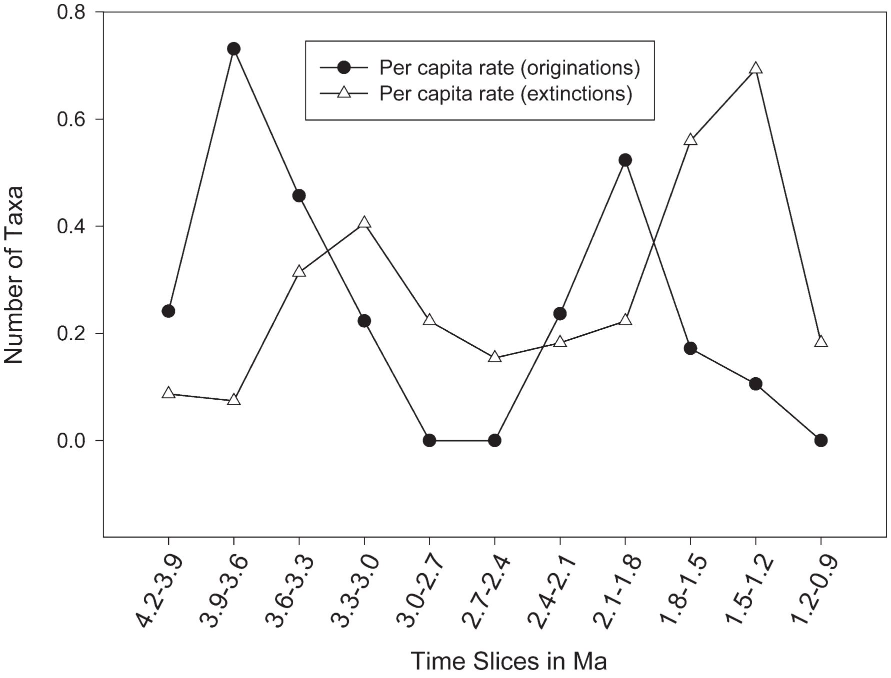

Figure 2. Per capita rates of origination and extinction for Plio-Pleistocene Carnivora of eastern Africa. Peaks in extinction follow peaks in origination, as one would expect. From 4.2 to 3.6 Ma and 1.5 to 0.9 Ma are less well sampled than the interval between them. Note the zero origination rate in the interval 3.0–2.4 Ma. No turnover pulse occurs in the 2.7–2.4 Ma interval. Per taxon rates show the same pattern as per capita rates (Werdelin and Lewis, 2005).

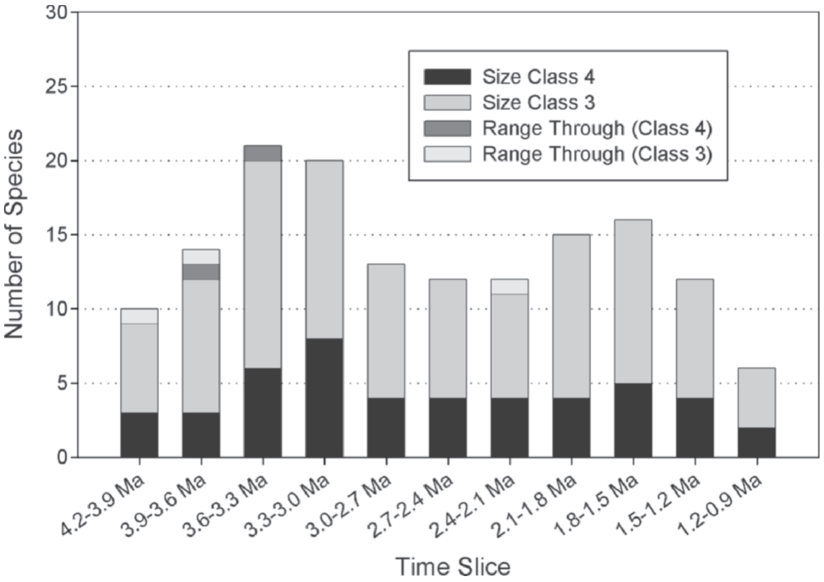

Figure 3. Changes in species richness of large-bodied carnivorans in Eastern Africa through time. These data represent minimum calculations of the number of taxa through time. Range through taxa are those that are not found during a particular time period, but are assumed to be present due to their presence in bins preceding and following a given bin. The highest overall species richness occurs between 3.6 and 3.0 Ma. A second smaller peak occurs during the 2.1–1.5 bins. The modern carnivoran fauna of eastern Africa is clearly reduced in species richness, particularly after 1.5 Ma.

an in-depth look at some of the taxa present in eastern Africa during this time period (see Table 4 for a list of Size Class 3 and 4 carnivorans present at key time periods). Unless otherwise stated, dates represent the time ranges that taxa occur in eastern Africa. In many cases, taxa may be found earlier or later in time at other localities outside of this region. Families and genera are presented in alphabetical order, for the most part, with some genera grouped by similarities in behavior and ecology or by systematic relationship. For more information on the evolution of specific African taxa or smaller members of the following families, please see Werdelin and Lewis (2005).

Canidae

Canis. Canids first appear in eastern Africa at approximately 4–4.5 Ma in the Omo (Fleagle and Brown, pers. comm.). The next oldest record occurs at Laetoli (*Nyctereutes* and cf. *Megacyon*) (Barry, 1987; Petter, 1987; Werdelin and Lewis, 2000, 2005), including the first Size Class 3 canid (cf. *Megacyon*). A third form at Laetoli has *Canis*-like features, but is smaller than the cf. *Megacyon* material (Barry, 1987; Werdelin and Lewis, 2005).

The oldest specimen of *Canis* is from South Turkwel and may have been part of a Eurasian migration of taxa into Africa at around 3.5 Ma (Werdelin and Lewis, 2000). The scant material found of this new species

Table 4. Size Class 3 and 4 Carnivorans present at key time periods

Family	3.6–3.3 Ma	2.7–2.4 Ma	1.8–1.5 Ma	Extant
Canidae	*Canis* sp. nov. A cf. *Megacyon* sp.		*Canis lycaonoides*[1]	*Canis pictus*
Felidae	cf. *Acinonyx* cf. *Panthera leo*[2] cf. *Panthera pardus*	cf. *Acinonyx* cf. *Panthera pardus*	cf. *Acinonyx* *Panthera leo* *Panthera pardus*	*Acinonyx jubatus* *Panthera leo* *Panthera pardus*
Felidae (st)	*Dinofelis petteri* *Homotherium* sp. *Megantereon ekidoit* cf. *Megantereon whitei*	*Dinofelis aronoki* *Dinofelis petteri* *Homotherium* sp. cf. *Megantereon whitei*	*Dinofelis aronoki* *Dinofelis piveteaui* *Dinofelis* sp. B *Homotherium* sp. cf. *Megantereon whitei*	
Hyaenidae	*Chasmaporthetes* cf. *nitidula* *Crocuta dietrichi* cf. *Crocuta ultra* *Crocuta* sp. nov. A cf. *Hyaena makapani* *Ikelohyaena abronia* *Pachycrocuta brevirostris* *Parahyaena howelli*	*Chasmaporthetes* cf. *nitidula* *Crocuta dietrichi* cf. *Crocuta ultra* *Crocuta* sp. nov. A cf. *Hyaena makapani*	*Chasmaporthetes* cf. *nitidula* *Crocuta dietrichi* *Crocuta ultra* *Hyaena hyaena*	*Crocuta crocuta* *Hyaena hyaena*
Mustelidae	*Enhydriodon – 4 species*	*Enhydriodon – 2 species*	*Enhydriodon – 1 species*	*Aonyx capensis*
Ursidae	*Ursinae* sp.			
Viverridae			*Pseudocivetta ingens* *Viverridae* sp. H	

st = sabertoothed felids.

[1] Formerly *Canis africanus*. See text for explanation.

[2] The attribution of the Laetoli specimens to cf. *Panthera leo* is extremely tentative. Note that no definite fossils of *Panthera leo* are known until Bed I at Olduvai Gorge. Due to the tentative attribution to *P. leo* at Laetoli, we have not scored *P. leo* as present as a range-through taxon between 3.3 and 2.1 Ma.

of *Canis* suggests that it may have been the same size as a medium-sized wolf, *C. lupus*. A fragmentary ulna from the Sidi Hakoma Member at Hadar may also belong to this species based on the size and age of the specimen, although no ulna has been found at South Turkwel to confirm this assignation. Other material at Hadar may belong to a slightly larger species of canid and two smaller species of *Canis*.

The modern species of African wild dog (subgenus *Lycaon*) is virtually unknown from eastern Africa with the earliest record occurring at Lainyamok (0.4 Ma). An earlier putative record from West Turkana (Harris et al., 1988) is an m1 trigonid that we consider indeterminate. The oldest known fossils of the extant species are from Hayonim Cave in Israel (Stiner et al., 2001). Material from South Africa suggests a relatively recent origin for African wild dogs (Lewis and Berger, 1998).

Other canid material that may be related to extant African wild dogs include *Canis africanus* from Bed II at Olduvai Gorge (Pohle, 1928; Ewer, 1965). Although the type specimen is missing, the remaining material is distinct morphologically from modern African wild dogs, but is probably part of the wild dog lineage. Martínez Navarro and Rook (2003) have synonymized *C. africanus* with *Xenocyon lycaonoides*, originally described from Gombaszög in Hungary (Kretzoi, 1938), and have suggested that this taxon is a plausible ancestor for the modern African wild dog. If this is true, leaving *Lycaon* with full generic status renders *Canis* paraphyletic. The paraphyly of *Canis* due to the nesting of *Lycaon* within *Canis* has been supported by recent systematic work on canids (Zrzavý and Řičánková, 2004). Pending revision of the genus *Canis*, we prefer to refer the wild dog lineage (e.g., *Lycaon*, *Xenocyon*) to *Canis*.

The evolution of larger canids in Africa is difficult to study due to a paucity of material. For the purposes of this paper, it is important to note that large canids were beginning around at about 3.5 Ma, although they may have been rare. Size Class 2 canids, such as jackals, are similar in age and rarity in the fossil record of eastern Africa. Although jackal-sized *Canis* has often been referred to *C. mesomelas* or said to be like this species (Petter, 1973; Leakey, 1976; Harris et al., 1988), we have found this material to be no more similar in morphology to this species than any other extant jackal species. Dental differences among these specimens indicate that they are likely to represent more than one species. The earliest material that may belong to *C. mesomelas* is from Lainyamok (Potts et al., 1988; Potts and Deino, 1995). Other Size Class 2 canids, such as *C. simensis*, the Ethiopian wolf, have no known fossil record. In fact, the Ethiopian wolf has been suggested to be a relict population descended from a Pleistocene migration of a wolf-like canid into the formerly larger Afro-Alpine ecosystem (Wayne and Gottelli, 1997).

Extant canine canids (e.g., wolves, jackals) tend to be fairly consistent in the relationship between morphology, behavior, and body size. Although there is not enough eastern African fossil material to test hypotheses about behavior, one might suggest that the larger species of *Canis* were not too different from either modern wolves or African wild dogs. However, none of the extinct taxa show the more hypercarnivorous dental adaptations of *C. pictus*. If so, modeling these taxa as African wild dogs or even wolves may not be completely appropriate, but may give at least an approximation of the level of interaction with hominins.

Wild dogs, like cheetahs, rarely engage in scavenging (Creel and Creel, 1995). Extant African wild dogs often lose carcasses to lions and spotted hyenas and are frequently the objects of predation by these species (Fanshawe and Fitzgibbon, 1993; Mills and Gorman, 1997; Creel, 2001). However, spotted hyenas are less successful in finding wild dog kills in more wooded habitats, as in the Selous Game Reserve (Creel and Creel, 1998). In short, if extinct large-bodied species of

Canis behaved similarly in the past, they may have been a potential source for scavengeable carcasses. However, the fact that the dentition of the fossil forms is not as specialized as that of extant wild dogs suggests that the fossil forms are not directly equivalent ecologically to the extant forms. For example, extant African wild dogs lack an entoconid on the lower carnassial and possess an anterior cusplet on P_4 (Tedford et al., 1995). These features may have evolved relatively recently to facilitate even more rapid consumption of flesh before lions and spotted hyenas could steal the carcass (Lewis and Berger, 1998). The Olduvai *Canis lycaonoides*, however, retains the entoconid on M_1 and lacks an anterior cusplet on P_4.

Of course, it is likely that in open habitats hominins would have been in competition with a number of different species at any carcasses generated. If hominins developed more effective strategies at locating large canid kills rapidly in more wooded habitats than other extinct, large-bodied carnivorans and could displace the canids and defend the carcass, then these kills may have been a useful resource.

Felidae

Acinonyx. The modern cheetah, *A. jubatus*, is a Size Class 3 predator adapted for short bursts of high-speed pursuit predation followed by quick consumption of the fleshy portions of carcasses. In interspecific encounters, cheetahs are of low rank and likely to be chased away from their kills, even when in coalitions (Caro, 1994). Cheetahs live at low densities and tend to be rare where the biomass of lions and spotted hyenas is high (Laurenson, 1995). Scavenging behavior in cheetahs is rare, but has been observed (e.g., Pienaar, 1969; Caro, 1994).

Unfortunately, there are few specimens of *Acinonyx* in the fossil record. A few specimens attributable to this genus first appear at Laetoli and occur infrequently, but consistently, in the Omo until about 2.5 Ma. *Acinonyx* is also known from the KBS and Okote Members at Koobi Fora and possibly earlier. These specimens clearly belong to *Acinonyx*, but are larger and morphologically distinct from the modern species. In fact, after its appearance in the Okote Member, *Acinonyx* is not found again until the present day. One can hypothesize that *Acinonyx* is present at very low levels from 3.8 Ma until the present. We consider the alternate hypothesis, that *Acinonyx* only recolonized the region fairly recently, to be less likely, but neither hypothesis can be disproved at this point. In any case, *Acinonyx* may never have been a significant competitor in the large-bodied carnivoran hierarchy of eastern Africa.

Dinofelis. Sabertoothed felids (subfamily Machairodontinae) in the eastern African Plio-Pleistocene include representative of three different tribes: the Metailurini (e.g., *Dinofelis*), the Homotherini (e.g., *Homotherium*), and the Smilodontini (e.g., *Megantereon*). Representatives of these tribes are quite different in morphology and presumably behavior.

The long-lived genus *Dinofelis* is found in eastern Africa from a maximum of 7.91 Ma (Lothagam) until possibly as recently as 0.9 Ma (Werdelin and Lewis, 2001b; Werdelin, 2003b). During this time interval *Dinofelis* was represented by at least five different species, many of whose ranges overlap temporally. Although an in-depth analysis and revision of this genus has been provided elsewhere (Werdelin and Lewis, 2001b), we will summarize briefly the adaptations of various species and discuss their relevance to hominin evolution.

After its occurrence at Lothagam, *Dinofelis* increases in size with the appearance of *D. petteri* (4.23–2.33 Ma). The largest eastern African form, *D. aronoki*, appears by 3.18 Ma and is found at localities in Ethiopia and Kenya until approximately 1.6 Ma (Nakoret) (Werdelin and Lewis, 2001b). *D. aronoki* may have been a little more cursorial than other members of this genus, given its reconstructed posture. Material from Bed I and II at Olduvai

Gorge indicates a unique form of *Dinofelis* (*Dinofelis* sp. B of Werdelin and Lewis, 2001b) that had extremely short, powerful forelimbs. This form has not been found elsewhere and is only known from three specimens.

A more recent species, *D. piveteaui*, was smaller than *D. aronoki* and had a more crouched posture, similar to *Megantereon. D. piveteaui* represents the most machairodont species of *Dinofelis* known (i.e., most flattened upper canines, reduced anterior premolars, and elongated carnassials). Although *D. piveteaui* was originally described from Southern Africa (Ewer, 1955), it is also known from Koobi Fora (Okote Mb.), Konso-Gardula, and Kanam East. If the 0.9 Ma date for Kanam East is correct (Ditchfield et al., 1999), then this would be the youngest sabertoothed felid in all of Africa.

One may note that for most of the temporal span addressed in this paper, there were two species of *Dinofelis* living at any given time in eastern Africa, although not necessarily at the same location. One species tended to be relatively larger (e.g., *D. aronoki*) and one tended to be a little smaller with a more crouched posture (e.g., *D. petteri* or *D. piveteaui*). Both types of species would have been of significance to hominins and may have preferred prey similar in size to the prey of lions.

Previous studies have demonstrated the morphological similarity between the South African species *D. barlowi* and *Panthera* (Lewis, 1995b, 1997). Despite sharing the enlarged forelimb relative to hindlimb with the genus *Megantereon* and other sabertooths, postcranial material of *Dinofelis* has been shown to be somewhat more similar to extant lions, tigers, and leopards than they are to *Megantereon* (Lewis, 1997). However, eastern African forms do not converge on modern *Panthera* in craniodental or postcranial morphology to the degree seen in *D. barlowi*.

Dinofelis has been suggested to have preferred dense forest (Marean, 1989) or mixed/closed habitats (Lewis, 1997). Habitat preference does not mean that a species is limited to that area, particularly as narrow categorizations of habitat preference cannot be made from carnivoran postcranial morphology (Van Valkenburgh, 1987; Taylor, 1989). Large, extant carnivorans in Africa may be found in a variety of habitats despite what their postcranial morphology might predict (e.g., lions, leopards, spotted hyenas; see review in Van Valkenburgh, 2001). Of course, it is possible that the ability of extant carnivorans to inhabit a variety of habitats successfully is a key component of the suite of adaptations that ensured their survival to the present. Yet while some species of *Dinofelis* may have preferred more open habitats (e.g., *D. aronoki*) or more closed habitats (e.g., *Dinofelis* sp. B from Olduvai Gorge), the somewhat more *Panthera*-like morphology of many species (relative to other sabertooths) suggests that species of *Dinofelis* may have ranged through a wide variety of habitats.

Suggestions that *Dinofelis* inhabited more mixed/closed habitats mean that their ability to cache carcasses in trees should be addressed. Such behavior has been rejected as being within the suite of activities open to the South African species *D. barlowi* (Lewis, 1995b, 1997). We concur with this assessment for eastern African species of *Dinofelis*, as well. Considerations of body mass aside, the smaller species certainly have the forelimb dexterity and strength to climb effectively, but possess the most machairodont canines. Tree-caching a shifting carcass would have been a risky behavior with high potential for damage to the canines. Unlike in North American taxa (Van Valkenburgh and Hertel, 1993), there is no known evidence of canine breakage in *Dinofelis*. The larger species, *D. aronoki*, had relatively less machairodont canines, but also had less rotatory ability in the forelimb. Thus, all species of *Dinofelis* appear unlikely candidates for tree-caching behavior, although they may have stolen carcasses from tree-caching leopards.

We should note that *Dinofelis* is better represented in the fossil record of eastern Africa than any of the other sabertooth taxa and yet there is no evidence of tooth breakage in *Dinofelis*. Van Valkenburgh (1988) has demonstrated that tooth breakage is associated with heavy carcass utilization and bone-eating. Based on an analogy to North American *Smilodon*, which has a large amount of tooth breakage, and the fact that modern big cats use their tongues as files to rasp flesh off bones, Van Valkenburgh (2001) has suggested that African sabertooths were probably quite capable of dismembering the carcass and engaging in bone-cracking. While this may certainly have been true, there is as yet no evidence to support the hypothesis that *Dinofelis*, or any other African sabertooth, had carcass-rendering behaviors similar to *Smilodon*. Of all of the sabertooths found in Africa during this time, some species of *Dinofelis* (e.g., *D. aronoki* or the South African *D. barlowi*) are certainly the best candidates for this behavior based on their craniodental and/or postcranial morphology. However, while some species of *Dinofelis* may converge to a small degree with *Panthera*, none of the eastern African sabertooths converges on *Smilodon* in craniodental or postcranial morphology.

Homotherium. *Homotherium* is present in eastern Africa from 4.35 to 1.4 Ma at a wide variety of sites. The earliest records are from Kanapoi and the Lonyumun Mb. of Koobi Fora and the most recent records are from the Okote Mb. of Koobi Fora. Previous studies have indicated that *Homotherium* was more cursorial than other sabertooths and had elongated forelimbs and relatively shortened hindlimbs (Ballesio, 1963; Beaumont, 1975; Kurtén and Anderson, 1980; Martin, 1980; Rawn-Schatzinger, 1992; Lewis, 1995b, 1996, 1997, 2001; Anyonge, 1996; Antón and Galobart, 1999). Cursorial adaptations such as the relatively (for a sabertooth) more distally elongate forelimbs and the reduction in supinatory ability of *Homotherium* are suggestive of adaptations to more open habitats (Martin, 1980; Lewis, 1995b, 1997). However, they probably were not limited to open habitats. The slight reduction in supinatory ability suggests that members of this taxon interacted with prey in a fundamentally different manner from other sabertooths or *Panthera*. In addition, this reduction, in combination with the large body size indicates little to no scansorial ability (Lewis, 1995b, 1997, 2001). However, morphological and taphonomic studies have suggested that *Homotherium* could capture prey somewhat larger than those captured by a lion (Lewis, 1995b, 1997; Marean and Ehrhardt, 1995). If African species transported portions of carcasses, as has been suggested for North American *H. serum* (Marean and Ehrhardt, 1995), or lived in groups (Turner and Antón, 1997), then there may have been very little left for hominin scavengers. In any case, challenging this taxon was probably a very risky behavior for early (pre 2 Ma) hominins.

Megantereon. The smilodontin sabertooth genus *Megantereon* has been reported from Aramis (ca. 4.4 Ma; WoldeGabriel et al., 1994), although this material has not yet been described. Other than the Aramis material, the oldest material is from South Turkwel and has been referred to the new species *M. ekidoit* (Werdelin and Lewis, 2000; cf. Palmqvist, 2002; Werdelin and Lewis, 2002 for a discussion of this taxon). A second species, *M. whitei* is known from the Okote Mb. of Koobi Fora. Unfortunately, other specimens of *Megantereon* from eastern Africa (e.g., Shungura Fm. Mbs. B–G) are isolated teeth, making taxonomic identifications and behavioral reconstructions impossible. Of the three sabertooth genera in eastern Africa at this time, *Megantereon* is the most poorly represented in terms of both numbers of specimens and localities at which it is found. This genus is not found in eastern Africa after about 1.4 Ma.

Members of this genus have been shown to have extreme strength in the forelimb (Lewis, 1995a, b, 1997; Martínez-Navarro and

Palmqvist, 1996). Specimens from Kromdraai, South Africa possess a limb morphology that is more similar to that of extant jaguars than to any of the modern African taxa or other African sabertooths, although they were much more heavily muscled than jaguars (Lewis, 1995a, b, 1997). As a result, African and European *Megantereon* have been identified as potential providers of large carcasses for hominins (Lewis, 1995b, 1997; Martínez-Navarro and Palmqvist, 1996; Arribas and Palmqvist, 1999).

Like *Dinofelis*, *Megantereon* has been suggested to inhabit dense forest (Marean, 1989) or mixed/closed habitats (Lewis, 1997) based on data from European specimens. The same caveats for reconstructing habitat preferences for carnivorans that were mentioned for *Dinofelis* certainly apply to *Megantereon*. While their crouched posture is indicative of an ambush predator and their size and limb morphology suggest an ability to climb trees (Lewis, 1995a, b, 1997), this does not mean that they were tied to specific habitats. Their forelimb morphology may reflect prey grappling more than scansorial ability (Lewis, 1997). Despite being the smallest of the sabertooths at this time period, if members of this genus did climb trees, they would have been more likely to steal cached carcasses than to cache carcasses for the same reasons discussed for *Dinofelis*.

Panthera. The earliest specimens attributable to *Panthera* are from Laetoli and represent two species: a lion-like one and one referred to *P*. cf. *pardus* (Barry, 1987; Turner, 1990). Unfortunately, the lion-like material is not diagnostic at the species level, although we have left it as *P*. cf. *leo* (see Werdelin and Lewis, 2005 for a discussion of the attribution of these specimens). The first definite appearance of lions is at Olduvai, Bed I, leaving a large gap between Laetoli and Olduvai.

The Laetoli leopard material is better preserved and complete. Leopards and leopard-like *Panthera* are overall more common than lions or lion-like specimens. Once again, however, the first definite leopard is from Olduvai, Bed I. From Bed I to the present, the record of lions and leopards in eastern Africa is reasonably continuous.

Several lines of evidence suggest that Plio-Pleistocene leopards cached carcasses (Lewis, 1997): (1) accumulations of bones in caves that may have fallen from leopard feeding trees (Brain, 1981), (2) similarities in modern and fossil leopard postcrania, and (3) the high probability of losing a carcass on the ground due to the great number of terrestrial carnivores higher in the carnivoran hierarchy than leopards. However, if hominins began to scavenge from these cached carcasses, leopards would probably have become more diligent in guarding their carcasses (Lewis, 1997). Even though *Dinofelis* and/or *Megantereon* may not have been the best climbers, hominins may also have had to compete with them for these carcasses (Van Valkenburgh, 2001).

At present, nothing exists to suggest behaviors outside of the range of modern *Panthera* in Africa for any of these taxa although neither of the modern taxa is well represented in the eastern African fossil record.

Hyaenidae

Chasmaporthetes. *Chasmaporthetes*, like *Acinonyx*, is a Size Class 3 carnivore with adaptations for hypercarnivory. The oldest specimen of *Chasmaporthetes* in eastern Africa is from Allia Bay (ca. 3.9–3.7 Ma). *C. nitidula* is known from diagnostic material from Hadar and Olduvai Gorge (Bed I). Although *C. silberbergi* has been reported from Laetoli (Turner, 1990), we are not convinced of this species attribution (see Werdelin and Lewis, 2005).

Chasmaporthetes, often called the “hunting hyena,” has been reconstructed as being similar to cheetahs in locomotor behavior (Brain, 1981). However, our preliminary analyses of postcranial material from Hadar indicate that the eastern African species may not be quite like Eurasian or North American forms in its locomotor capabilities. Postcranial material is unknown from other eastern African localities. The dentition of eastern Africa *Chasmaporthetes*, however, is highly adapted for flesh-slicing, as has been found in material from other continents (Galiano and Frailey, 1977; Berta, 1981; Kurtén and Werdelin, 1988; Werdelin et al., 1994). While our analyses of the Hadar specimens are not complete, we can state that *Chasmaporthetes* in eastern Africa cannot be considered directly equivalent to *Acinonyx* in any behavior except for flesh-slicing ability. More likely, *Chasmaporthetes* filled a more large-bodied *Canis*-like niche, including the long-distance running seen in the African wild dog, *Canis pictus*. This hypothesis, however, is still being tested.

With respect to hominin behavior, single individuals of *Acinonyx* and *Chasmaporthetes* probably posed little threat to a group of hominins, even in the smallest, earliest species. If *Chasmaporthetes* fulfilled a more *C. pictus*-like niche and hunted in packs, the risk from predation and interspecific encounters at carcasses would have been increased. Given the lack of *Chasmaporthetes* specimens and the evolutionary distance between this taxon and modern hyenas, hypotheses of grouping behavior in *Chasmaporthetes* remain purely speculative at this point.

Hyaena, Ikelohyaena, and Parahyaena. Specialized, bone-cracking hyenas are absent from the Miocene and earliest Pliocene of Africa (Werdelin and Turner, 1996; Turner, 1999). The earliest species in this category is *Parahyaena howelli* from Kanapoi and Laetoli (Barry, 1987; Werdelin and Solounias, 1996; Werdelin, 2003a; Werdelin and Lewis, 2005), an early relative of the living brown hyena. Although the current distribution of the modern species, *P. brunnea*, is limited to southern and southwestern Africa, this species is known from middle Pleistocene of Kenya (Werdelin and Barthelme, 1997).

Parahyaena howelli differs from the modern form in both craniodental and postcranial morphology (Werdelin, 2003a). As the early form is less derived than the modern form, they cannot be considered directly equivalent in behavior or ecology, although they are certainly similar. However, on a very general level, both taxa share bone-cracking teeth in combination with gracile (for a hyaenid) postcrania. As such, the behavior of the earliest *Parahyaena* may not have been too dissimilar from the modern form, particularly with respect to behaviors that may have impacted on hominins.

The earliest close relative of the modern striped hyena found in eastern Africa is *Ikelohyaena abronia*. This species has been found at Laetoli and possibly at Lothagam and Hadar (Sidi Hakoma Mb.). The oldest specimens of *Hyaena* found in eastern Africa occur at Koobi Fora (Lokochot Mb.). The earliest species of *Hyaena*, *H. makapani*, is smaller and more gracile than the living species. This species differs from *Ikelohyaena abronia* primarily in the loss of m2 and M2. Neither *I. abronia* nor *H. makapani* have the adaptations for bone-cracking seen in the modern striped hyena, *H. hyaena*. This fact, in combination with their gracile postcrania and smaller body size, suggests that they overlapped ecologically with hominins to a much lesser degree than *H. hyaena*. The living striped hyena, *Hyaena hyaena*, appears at about 1.9 Ma and is found from that time period to the present day.

Modern striped and brown hyenas are solitary foragers with a very omnivorous diet. While fecal analyses of brown hyenas indicate a large quantity of large mammal remains (Owens and Owens, 1978), behavioral studies indicate that in both brown and striped hyenas, only a little over a third of food items eaten were mammalian (Kruuk, 1976; Mills, 1978, 1982). Wild fruits, insects, bird eggs, and small reptiles and birds comprise the rest of the diet. Mammals consumed by striped hyenas (e.g., hyraxes, rodents, ground-living birds, hares, and ibex) (MacDonald, 1978) tend to be much smaller than the prey of brown hyenas (e.g., wildebeest, gemsbok, springbok, steenbok, and small canids) (Mills, 1982). Under natural conditions, mammalian remains fed upon by striped hyenas do not provide a meal for more than one individual (Mills, 1978). On the other hand, studies indicate that the vast majority of vertebrate consumption by brown hyenas results from scavenging, not hunting (Mills, 1978, 1982; Rautenbach and Nel, 1978).

Striped and brown hyenas probably evolved bone-cracking as a means of maximizing yield from scavenged carcasses. If the extinct form of *Parahyaena* behaved much like the modern form, it is possible that competition with early hominins may have contributed to its extinction in eastern Africa. A greater reliance on small prey, fruits, and insects may have permitted the modern striped hyena to survive while the ancestors of the modern brown hyena eventually disappeared from eastern Africa. Today brown hyenas are restricted to the South West Arid Zone and drier parts of the southern savannahs in the Southern African Subregion (Hofer and Mills, 1998). The disappearance of *Hyaena* in southern Africa suggests that there is more going on than competition with early hominins.

Pachycrocuta and Crocuta. The evolution of *Pachycrocuta* and *Crocuta* in Africa is quite complex. One can see from Table 4 that the number of hyaenids was much greater in the past than today. A brief discussion of our current understanding of *Crocuta* and *Pachycrocuta* evolution can be found elsewhere (Lewis and Werdelin, 1997, 2000; Werdelin, 1999; Werdelin and Lewis, 2005), although analyses of the evolution of *Crocuta* are still being completed.

Although our current understanding of the evolution of these taxa is more complex than in the past, we must reiterate that one cannot simply use modern spotted hyena behavior as a model for all *Crocuta* or *Pachycrocuta* species in the past. The bone-cracking dentition and postcranial adaptations for heavy carcass lifting evolved at different points within the evolution of *Crocuta* (Lewis and Werdelin, 1997, 2000). The early species *C. dietrichi*, for example, was small and probably more similar in behavior to modern brown hyenas. Even *C. ultra*, which is similar in craniodental morphology to *C. crocuta*, lacks the postcranial adaptations of the modern species. Unfortunately, modern spotted hyenas, *C. crocuta*, are unknown from the fossil record of eastern Africa. Although postcranial material is not known for all extinct members of the genus *Crocuta*, our current research suggests that the suite of adaptations that define spotted hyenas today developed only within the last one million years. Based on analyses of material from Eurasia and Africa, Turner and Antón (1995) have suggested that *Pachycrocuta brevirostris* was a group-living species that behaved somewhat similarly to modern spotted hyenas, but was less cursorial due to differences in body proportions. Unfortunately, there are few specimens of *Pachycrocuta* in eastern Africa.

While no single species (with the possible exception of the poorly known *Pachycrocuta*) may have encompassed the wide range of behaviors seen in extant spotted hyenas (bone-cracking, group hunting, confrontational scavenging, heavy carcass lifting, and transport behavior, etc.), eastern African hyaenids as a group probably covered all of these behaviors. Given the diversity of all hyaenids around 3.5 Ma, it is hard to imagine any salvageable carcasses present on the landscape at that time remaining available for a passive scavenger unless the hyaenid species were relatively rare and/or solitary at that time. *Crocuta*, as a genus, is a relatively much more common component of fossil assemblages in eastern Africa than *Pachycrocuta*. Although this could be due to differences in habitat usage or some other taphonomic bias, it is certainly possible that *Pachycrocuta* was not abundant in eastern

Africa despite being morphologically, and presumably ecologically, distinct from species of *Crocuta*.

Mustelidae

The only Size Class 3 and 4 mustelids found in eastern Africa during the Pliocene and Pleistocene belong to extinct members of the Enhydrini, or sea otters. (Extinct relatives of the modern African clawless otter, *Aonyx capensis*, were smaller than the modern form.) The genus *Enhydriodon* first appears in the Upper Miocene and then radiates extensively in the Pliocene (Werdelin and Lewis, 2005). Members of this genus are known from the Omo, Hadar, Koobi Fora, and other localities. The last appearance is at Nakoret, possibly around 1.6 Ma. While the early forms are within the size range of modern otters, some of the last forms have limb bones the size of *Homotherium* or even modern ursids. Like modern sea otters, the teeth of this species are durophagous and show an increase in size matching that of the postcranial elements.

The relevance of *Enhydriodon* to hominin evolution is unknown. If this genus maintained its aquatic lifestyle as it grew larger, then it was not truly part of the terrestrial carnivoran guild. However, we are currently testing whether differences between the early and later forms are due to differences in body size and/or locomotor adaptations. The morphologies of the different taxa are certainly distinct. A brief discussion of this genus can be found elsewhere (Werdelin and Lewis, 2005).

Ursidae

Although ursids were found in historic times in the Atlas Mountains of northern Africa (Nowak, 1991), the first report of this family in the Plio-Pleistocene of eastern Africa was from Aramis with the identification of *Agriotherium* (WoldeGabriel et al., 1994). This genus is also known from southern Africa (e.g., Hendey, 1980). Since the discovery at Aramis, material from the modern subfamily Ursinae has also been reported from eastern Africa (Werdelin and Lewis, 2005). At least one species is known from Hadar (Denen Dora and Kada Hadar Mbs.), Koobi Fora (Tulu Bor Mb.), and possibly West Turkana (Lomekwi Mb.). As analyses of this material are still underway, it is too early to comment on possible behaviors of these taxa and their significance to hominins.

Viverridae

Viverrids have an intriguing, albeit limited, fossil record in eastern Africa. At least two species of viverrids were large enough to warrant a Size Class 3 designation: *Pseudocivetta ingens* and a new species. *P. ingens* was first described from Olduvai, Bed I (Petter, 1967, 1973), but is now known from Koobi Fora (Upper Burgi and KBS Mbs.), the Shungura Fm. (Mbs. E + F and G), and Olduvai, Bed II. The second species is from the KBS Mb. at Koobi Fora and is somewhat similar to an enlarged *Civettictis*. The fossil record of smaller viverrids is described in more detail elsewhere (Werdelin and Lewis, 2005).

Both of the larger viverrids are within the lowest range of Size Class 3 and were not hypercarnivores. As the Koobi Fora viverrid is known from a single complete skull with dentition (KNM-ER 5339), little can currently be said about this species except that it was less hypercarnivorous than *Civettictis civetta*. As such, these taxa may have had little impact on hominins.

INTERSPECIFIC COMPETITION AND THE EVOLUTION OF HOMININS

Studies have shown that some larger-bodied carnivoran species, such as lions and spotted hyenas, attain high densities where prey species are abundant (Van Orsdol et al., 1985; Stander, 1991). However, not all large-bodied carnivorans are affected positively by increases in diversity or abundance of potential prey species. African wild dog populations have declined, sometimes to the point of local extinction, when prey density was high, yet increased when prey density was moderate to low (Creel and Creel, 1998). Creel (2001) has hypothesized that an increase in prey abundance may reduce interspecific competition for live prey while increasing interspecific interference competition at carcasses. Creel argues that when there is asymmetry in size or fighting ability among competitors, engaging in kleptoparasitism (food theft) results in a higher net benefit for the stronger competitor than hunting live prey even when prey is abundant. Linnell and Strand (2000) have suggested that interference intraguild interactions may result in one species avoiding a specific habitat to reduce encounters with a more dominant carnivore. Predators may also avoid specific activity periods (e.g., night) when more dominant carnivores are foraging (Van Valkenburgh, 2001). Such avoidance behavior could have a severe impact on foraging efficiency. Interference competition involves more than just kleptoparasitism, as interspecific killing is common among carnivorans (Van Valkenburgh, 1985; Palomares and Caro, 1999; see Van Valkenburgh, 2001 for a detailed review of interference competition among predators in various habitats around the world). Thus, lower ranking carnivores, such as wild dogs or cheetahs, are better off when prey densities are at low or moderate levels so that densities of higher ranking carnivores, such as lions and spotted hyenas, remain low (Laurenson, 1995; Linnell and Strand, 2000; Creel, 2001).

While researchers may disagree over the amount of opportunistic or confrontational hunting and scavenging that early hominins engaged in, most would probably agree that when hominins first entered the carnivore guild, they were not top predators. Hominins lack the natural equipment (e.g., claws and sharp teeth) of other predators and would have had difficulty dominating even similarly sized carnivorans in one-on-one encounters (Shipman and Walker, 1989; Van Valkenburgh, 2001). As such, resources from carcasses were less likely to be important to hominins as they entered the carnivore guild due to potential damaging affects from kleptoparasitism by higher ranking, large-bodied predators. We hypothesize that in a predator and prey species-rich environment, individual hominin species could only survive if, in addition to predator avoidance strategies, they either had a primarily non-carnivorous diet and thus did not participate in the carnivore guild (e.g., *Paranthropus*), or if they evolved effective strategies to resist kleptoparasitism. In other words, the ancestors of *Homo sapiens*, whether they were hunting or functioning as kleptoparasites themselves, had to evolve strategies to reduce kleptoparasitism from higher ranking carnivorans before they could increase their dependence on carcasses as a resource.

Studies have suggested that animals are the preferred source of energy for modern hunter-gatherers (e.g., Cordain et al., 2002), even though it may not always be a reliable source (O'Connell et al., 2002). At some point, therefore, hominins did evolve effective strategies to resist kleptoparasitism. Predator avoidance and kleptoparasite resistance strategies, in combination with the evolution of behavior that increased the success of active hunting, would have led to an eventual reversal in the relative dominance of hominins and carnivorans. When hominins had evolved to this point, we predict that carnivorans utilizing the same food resources as hominins would be of lower rank than hominins. As seen in the impact of high densities of modern spotted hyenas on wild dog populations, any concomitant increases in the density of hominins with the previously described behaviors may have pushed local carnivoran populations to extinction.

When might these strategies have evolved? First, we must consider the patterns of turnover in eastern Africa. When mammals in general are considered, the number of species in the Turkana

Basin and the amount of turnover increases between 3.0 and 1.8 Ma (Behrensmeyer et al., 1997). Our study, however, has shown that after the high peak of 3.3 Ma, turnover is reduced in carnivorans during this period and that species richness decreases only to rise briefly to reach a second, lower peak between 2.1 and 1.8 Ma (Werdelin and Lewis, 2005). We have suggested elsewhere (Werdelin and Lewis, 2005) that the increase in originations and overall high species richness of carnivorans at 3.3 Ma is due to adaptive radiations in hyaenids, felids, and mustelids in combination with migrations of taxa (e.g., *Canis* and *Megantereon* from the north and *Hyaena* from the south) occurring after the Mio-Pliocene extinction event in Africa.

How might the pattern seen in carnivorans relate to hominins? The drop in numbers of carnivoran species precedes the appearance of stone tools at 2.6 Ma, yet presumably occurs while the species richness (and possibly abundance) of prey is increasing. The presence of stone tools at 2.6 Ma (Semaw et al., 2003) probably signals a shift in dietary behavior in hominins, yet that behavior does not appear to have impacted carnivorans directly. Whether the appearance of tool-using hominins was relevant to the decline in carnivoran species richness after 2.4 Ma is as yet impossible to test with our data set. However, the carnivoran origination rate increased briefly again after the appearance of stone tools. Could competitive interference initiated by changes in hominin behavior be part of what was driving speciation events during this time? Competition with hominins could be part of what prevented carnivorans from reattaining their previous level of species richness, even though overall species richness in mammals was increasing during this time.

One thing is clear from our data: carnivoran origination rate drops and extinction rate increases after 1.8 Ma. In addition, a precipitous drop in carnivoran species richness is apparent after 1.5 Ma. These changes coincide with the earliest appearance of *Homo ergaster* (Feibel et al., 1989; Wood, 1991; Wood and Richmond, 2000) and a drop in overall species richness in eastern Africa (Behrensmeyer et al., 1997). We hypothesize that the changes in carnivorans are due to the appearance of new dietary strategies and behaviors in *H. ergaster* in combination with an increase in open habitats and concomitant decline in prey species richness occurring at the end of the Pliocene (Behrensmeyer et al., 1997). However, assuming that the drop in carnivoran species richness was due in part to *H. ergaster*, this decrease should not be seen as a confirmation of *H. ergaster* as active hunters. Van Valkenburgh (2001) has provided a compelling argument based on interference competition for why species of *Homo* functioning as a kleptoparasites must have engaged in confrontational scavenging. As seen in the complex web of interactions among extant African carnivorans, effective kleptoparasitism can negatively impact populations of species of lower interspecific rank. We suggest that effective confrontational scavenging by *H. ergaster* may have been enough to push some members of the carnivore guild to local extinction.

WHEN DID THE MODERN GUILD EVOLVE?

Does the drop after the 1.8–1.5 Ma interval represent the final reduction to the low number of large-bodied carnivorans seen today? The fact that sabertoothed felids such as *Megantereon* and *Homotherium* persist until after 1.5 Ma suggests that the modern guild structure had not yet appeared. In fact, the last sabertooth found in eastern Africa, *D. piveteaui*, is found at Kanam East, approximately 0.9 Ma. Unfortunately, the absolute number of taxa present at any time after 0.9 Ma is difficult to assess due to the low number of fossil localities with carnivorans dated later than this time.

Only three Size Class 3 and 4 carnivorans in the modern guild have a definite fossil record in eastern Africa: lions, leopards, and striped hyenas. Although small carnivorans have not been the focus of this paper, the same pattern occurs in those taxa (Werdelin and Lewis, 2005). Fossil evidence from South Africa and Israel suggests a relatively recent origin for wild dogs (Lewis and Berger, 1998; Stiner et al., 2001). The fossil record of *Crocuta* also indicates a recent origin for the modern species. In short, the modern guild appeared less than one million years ago and possibly relatively recently.

We have hypothesized that specialist carnivorans (e.g., sabertooths and giant otters) were more likely to become extinct than generalists during the last three million years and that the last one million years of carnivore evolution in Africa has been the age of the generalist (Werdelin and Lewis, 2001a, 2005; Peters et al., in press). A similar pattern has been shown for carnivorans in the North American Pleistocene (Van Valkenburgh and Hertel, 1998; Wang et al., 2004). The recent origin of many of the modern species may reflect environmental pressures (including those placed on them by hominins) driving the evolution of larger niche spaces (Lewis, 1995b). In any case, the few specialists that remain (e.g., cheetahs, wild dogs) are relatively low ranking and in danger of extinction.

Similar suggestions have been made for hominins. Environmental fluctuation and a subsequent decoupling of Pleistocene hominins from adaptation to one specific habitat is an important component of Potts's variability selection hypothesis (Potts, 1998). When considering the origins of the modern carnivore guild, one might not consider the modern eastern African carnivore guild complete until the appearance of the supreme generalist species, *Homo sapiens*.

Conclusion

Carnivorans reached their maximum species richness in eastern Africa approximately 3.3 Ma. Although we cannot accurately assess the numbers of Size Class 1 taxa or even those of Size Class 2, the two largest size classes (Size Classes 3 and 4) included a much larger group of species than today, with a much broader range of adaptations. The greater taxonomic diversity of large-bodied carnivorans in the past suggests a more complex structuring of niche space within carnivoran guilds. As a result, interspecific competition was probably greater in the past, although the appearance of a taxon in the fossil record does not indicate the abundance of that taxon.

Turner (1988) has stated that the extinction of the large-bodied taxa provided a catalyst for hominin evolution, a view echoed elsewhere (Lewis, 1995b). As more recent finds have extended the known temporal range of some large-bodied taxa (e.g., *Dinofelis*), we modify Turner's hypothesis to state that the decline in carnivoran species richness after 3.0 Ma provided niche space for hominins to enter the carnivore guild. At that point, hominins were of relatively low rank within the guild hierarchy. Support for this low ranking comes from the lack of impact that the appearance of stone tools in the fossil record has on species richness of carnivorans, even when just the large-bodied taxa are considered. This lack of impact may be due in part to the relatively localized behavior of early toolmakers (i.e., hominin populations may have been geographically restricted and/or the use or non-use of tools may have varied among populations as described by McGrew, 2004, for modern chimpanzees). In fact, the decrease in carnivoran species richness begins after 3.0 Ma, but well before 2.6 Ma, suggesting that hominins were not responsible for this decline. In any case, early hominins, such as *Ardipithecus*, *Australopithecus*, and even *Homo habilis* were more likely to be prey than competitors with the Size Class 3 and 4 carnivorans. If carcass-based resources were to become a relied-upon food source, hominins needed to evolve effective anti-predator/anti-kleptoparasitism strategies. These strategies, in combination with the eventual evolution of active hunting, would

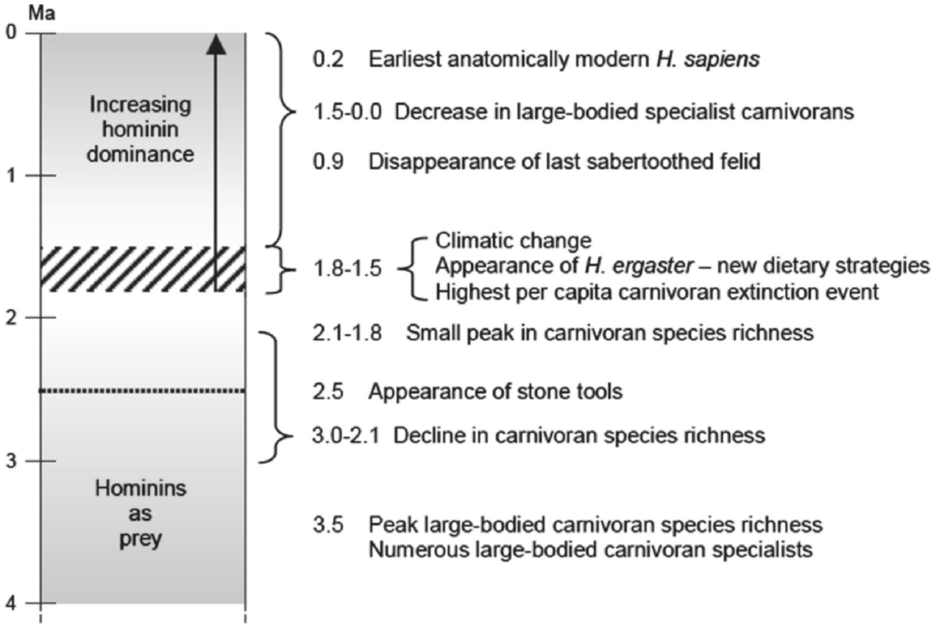

Figure 4. Key events in carnivoran and hominin evolution. Key events in the evolution of the two groups are presented side-by-side for comparison. Note that the appearance of stone tools has little effect on carnivoran species richness. After 1.5 Ma, hominins become increasingly dominant on the landscape and carnivorans decrease in species richness.

have increased the rank of hominin species within the guild (Figure 4).

The decline to the present depauperate group of carnivoran taxa began after 1.8 Ma and may be directly related to the appearance of new patterns of environmental use and dietary behavior by large-brained hominins (e.g., *Homo ergaster*) in combination with environmental change that began at the end of the Pliocene. While active hunting by hominins would have had an effect on carnivorans targeting the same prey species, active hunting is not the only means by which the carnivore guild could have been destabilized. Kleptoparasitism by high ranking carnivores has been shown to drive populations of lower ranking taxa to local extinction (Linnell and Strand, 2000; Creel, 2001). Effective kleptoparasitic strategies (i.e., confrontational scavenging) by *H. ergaster* could have had the same impact on some carnivoran taxa, although it is probably not a sufficient explanation for the extinction of all the species that become extinct during the early Pleistocene.

The question of when the modern guild first appears is difficult to answer at present due to the paucity of fossil sites known in eastern Africa from after 0.9 Ma. While a few taxa appeared quite early (e.g., lions, leopards, and striped hyenas), the rest of the large-bodied carnivorans probably appeared fairly recently. This lack of data also means that the impact of *Homo sapiens* on the carnivore guild during the last 0.2 million years cannot be assessed at present.

Finally, we must reiterate that with a few exceptions (e.g., *Panthera* and *Hyaena hyaena*), there is no morphological evidence that genera present today were morphologically (and presumably behaviorally) equivalent to their extinct congeners. While studying the present provides key insights into interpreting past behavior, any inferences drawn from studies of modern animals and environments must be treated as hypotheses and tested in the fossil record. For example, if the extant taxa were not present, were there any taxa that could have behaved in the hypothesized manner? This paper set out to address what carnivoran taxa were present in the past and provide a summary of our current understanding of behaviors relevant to the reconstructing the ever-changing ecological framework surrounding hominin evolution. While our understanding of these taxa is still incomplete, we believe that our continued analyses can only shed more light on the factors that drove a mammal from a primarily non-carnivorous order to become the dominant predator not only in eastern Africa, but across the world.

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