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Carnivoran paleoguilds of Africa: implications for hominid food procurement strategies

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Tool-using hominids, as carnivorous animals, would have been part of the various carnivore guilds present in Plio-Pleistocene Africa. Hominid dietary strategies must be understood within the larger context of carnivore behavior and ecology, as carnivorans could have affected the abilities of hominids to procure meat and/or marrow. The functional anatomy of extant and fossil carnivorans was examined to infer behaviors in fossil carnivorans that would have impacted on hominid dietary strategies in terms of carcass availability. Comparisons of guild structure were carried out to examine changes in carnivoran interactions and their implications for hominid behavior. Plio-Pleistocene carnivorans engaged in a wider range of behaviors than modern carnivorans. The sabertoothed felids *Dinofelis* and *Megantereon* probably did not provide much larger carcasses than modern species. Another sabertooth, *Homotherium* generated larger carcasses, but may have disarticulated and transported these carcasses. Fossil representatives of modern taxa may not have been equivalent ecologically within the carnivoran guild. Overall, hominids in eastern Africa probably had a greater range of scavenging opportunities than did those of southern Africa during the Plio-Pleistocene. Local and continent-wide extinction events in large-bodied carnivoran guilds from 1 to 2 Ma had a substantial effect on carcass availability and the risk to hominid scavengers. These structural changes in the carnivore guild may have provided an opportunity for hominids to widen their niche with respect to dietary behavior.

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Introduction

The past decade has seen a revolution in the focus of paleoanthropology as researchers have become interested in placing hominid evolution within the ecological context of surrounding paleocommunities (e.g., Andrews *et al.*, 1979; Van Couvering, 1980; Vrba, 1980, 1985, 1988; Blumenschine, 1986*a*,*b*, 1987, 1988; Kappelman, 1988; Potts, 1988*a*; Turner, 1988, 1989, 1992; Andrews, 1989; Marean, 1989; Behrensmeyer *et al.*, 1992; Turner & Wood, 1993). Within paleocommunities, carnivorans are particularly important to the study of hominid evolution because carnivorans potentially could have impacted on hominid dietary strategies in at least three ways: as potential predators of hominids, as competitors for meat and/or marrow, and as providers of carcasses for scavenging.

Historically, anthropologists have viewed carnivorans primarily as scavengers of hominid kills. For example, Dart's osteodontokeratic cultural model of hominid behavior envisioned predatory hominids defending their kills from large-bodied carnivorans (e.g., Dart, 1949, 1956). Hypotheses about the dynamics of the relationship between hominids and carnivorans were based upon the assumption that hominids were a dominant predator, if not the most dominant predator.

More recent research into the acquisition of animal resources has brought about a change in conceptualizing hominid dietary behavior. Based on the taphonomy and fauna of South African caves, Brain (1969, 1981) showed that early hominids were the prey and not the

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predators. Recognition of the importance of carnivorans in influencing hominid behavior has led to viewing early archaeological sites not necessarily as places representing the central social focus of a group (i.e., home base; e.g., Isaac, 1976, 1978), but alternatively as carcass-processing areas (e.g., Potts, 1984, 1988*a*). The timing of hominid *vs*. carnivoran access to carcasses is, however, a subject of much debate (e.g., Potts, 1984, 1988*a*,*b*; Binford, 1986; Bunn, 1986, 1991; Bunn & Kroll, 1986; Shipman, 1986*a*,*b*; Binford *et al*., 1988; Blumenschine, 1988; Bunn & Ezzo, 1993). Changing ideas about hominid dietary behavior coupled with paleocommunity research have led to viewing carnivorans not just as competitors and predators, but as species contributing to the structure of resources available to hominids (e.g., Blumenschine, 1986*a*,*b*, 1987; Marean, 1989; Sept, 1992).

Hominids, as carnivorous species, were part of the carnivore guilds of Plio-Pleistocene Africa. The term "carnivore" will be used here to denote any carnivorous species, while the term "carnivoran" will denote members of the Order Carnivora. A guild is a group of sympatric species that exploit the same class of resources in a similar way (Root, 1967; Stanley *et al*., 1983; Van Valkenburgh, 1985, 1988, 1989). Guild membership is based on significant overlaps in niche requirements without regard to taxonomic position (Root, 1967). The dietary strategies of hominids as carnivore guild members, therefore, must be understood within the larger context of carnivore behavior and ecology. Hominid behavior relating to the acquisition of animal resources would have been affected directly by behaviors of carnivorans as resource providers and/or competitors.

Debate still centers around whether hominids accumulated resources in a confrontational or passive manner, and over the relative importance of hunting *vs*. scavenging (e.g., Binford, 1981; Bunn, 1986, 1987, 1991; Sept, 1986; Blumenschine, 1986*a*,*b*, 1987, 1989; Bunn & Kroll, 1986; Potts, 1988*a*,*b*; Turner, 1988; Marean, 1989; Olsen, 1989; Speth, 1989; Bunn & Ezzo, 1993). This paper, however, is concerned primarily with investigating models of passive (non-confrontational) scavenging because carnivorans contribute directly to the distribution of carcasses across the landscape available for passive scavenging (Blumenschine, 1987).

Previous research on passive scavenging opportunities

Previous work on scavenging opportunities in modern habitats has shown possible avenues of behavior open to hominids. Schaller & Lowther (1969) found that in modern woodland–plains habitats there was enough scavengeable meat and incapacitated live prey during the dry season to sustain a hominid group. These researchers suggested that scavenging or hunting hominids might have specialized on the meat of large prey, a behavior that they felt may have brought hominids into competition with sabertoothed felids.

Actualistic studies conducted in Tanzania by Blumenschine (1986*a*,*b*, 1987) were devised to determine whether passive hominid scavenging opportunities could account, in part, for the composition of archaeological bone assemblages. Blumenschine (1987) demonstrated that the size of carcasses, the initial consumer species, the type of ecosystem, the season of year, and the type of habitat were all factors conditioning scavenging opportunities. Blumenschine (1987) noted that in the Serengeti and Ngorongoro Crater today, medium carcasses tend to retain marrow and head contents, while large carcasses retain both of these aspects, as well as flesh. In these two modern regions, spotted hyaenas tend to avoid riparian woodlands, making carcasses in this habitat better potential resources (Blumenschine, 1987). Based on the patterns of carcass consumption of lions and hyaenas, he hypothesized that there is an unoccupied

Table 1 Predictions about carnivoran behavior and guild structure relating to scavenging opportunities

Prediction	Resource provided to hominid scavenger	Source
Presence of closed habitat predator of large prey	Bone marrow, head contents, and perhaps some flesh protected from scavengers	Blumenschine, 1987
No closed habitat bone-crackers*	More resources remain on closed habitat carcasses	Blumenschine, 1987
Sabertoothed felids were closed habitat	Prey carcasses in closed habitats protected from scavengers	Marean, 1989
Sabertoothed felids were predators of large prey	Large prey carcasses: bone marrow, head contents, and some flesh	e.g., Schaller & Lowther, 1969; Gonyea, 1976*a,b*; Blumenschine, 1987; Marean, 1989
Homotherium was capable of transporting carcasses	Low amount of material for scavenging; restricted to within-bone nutrients	Marean & Ehrhardt, 1995
Low relative number of bone-cracking species within a guild	Greater amount of bone marrow and head contents in all habitats (if species number is related to relative abundance)	Blumenschine, 1987; Blumenschine *et al.*, 1994
Presence of tree-caching species	Near complete small prey	Cavallo & Blumenschine, 1989
Fossil and modern conspecifics exhibit similar behavior	Produce carcasses as in models based on modern species	Blumenschine, 1987, 1989; Turner, 1988*a*; Cavallo & Blumenschine, 1989
Scavenging opportunities greater in eastern Africa relative to southern in Plio/Pleistocene	Greater amount of bone marrow, head contents, and perhaps some flesh in eastern Africa relative to southern Africa	Turner, 1988*a*

*Bone cracking and bone crushing as defined by Werdelin (1989).

dry-season niche in riparian woodlands for scavengers capable of exploiting bone marrow and head contents from medium-sized carcasses.

A later actualistic study by Cavallo & Blumenschine (1989), attempting to provide explanations for the presence of small-bodied herbivores in archaeological assemblages, suggested that Plio-Pleistocene hominids could have scavenged these small herbivores from tree-stored leopard kills. These authors found that kills cached in trees persist for dramatically longer periods than do carcasses stored at ground level, are more predictably located, are less prone to seasonal fluctuations in abundance, and entail a low risk of predation for the scavengers due to the leopard's prolonged abandonment of cached kills.

These and other models of hominid dietary behavior created from actualistic studies were based on modern carnivorans in modern habitats. Many more carnivorans existed, however, in a single geographic area in Africa during the Plio-Pleistocene than do today (Turner, 1990). To ensure that the data used in these models is relevant ecologically for the more diverse African Plio-Pleistocene, behaviors of specific Plio-Pleistocene carnivorans must be identified. Assumptions and predictions in these models can be compared with behavioral data on fossil carnivorans to test whether these models are relevant for a given region and time period in Plio-Pleistocene carnivoran guilds. Some predictions about carnivoran behavior drawn from these models are presented in Table 1.

Fossil carnivorans can provide information about the ecological framework surrounding early hominids that affected scavenging opportunities. This study examines the functional morphology and guild structure of fossil carnivorans to assess behaviors that would have impacted on hominid dietary strategies in terms of carcass availability. Analyses of the structure of Plio-Pleistocene carnivoran guilds in eastern and southern Africa provide a multidimensional means of understanding carnivoran behavior and interactions and the potential role of hominids within carnivore guilds.

Behavioral components of guild structure

Behaviors impacting on hominid dietary strategies that can be predicted directly through functional anatomical analyses include locomotion, prey procurement, carcass transport and habitat preference (Lewis, 1995). These behaviors can be subdivided into categories based on the behaviors observed in extant species. A brief summary of these behaviors is provided in Table 2 to facilitate understanding of fossil carnivoran behavior, and because modern African species, or species that were very similar to modern species, are found in the African fossil record during the last 2 Ma.

Each of these behaviors in carnivorans is important for understanding the input of each species into the distribution of carcasses or portions of carcasses on the landscape and the nutrients remaining on those carcasses that might have been available for scavenging hominids. Understanding carcass transport and habitat preference is useful for predicting the portions of a carcass remaining after the initial predator has left and the likelihood of that carcass being easily discovered (Marean & Ehrhardt, 1995). Those carcasses that have had much of the heavily flesh-laden portions removed will have fewer available nutrients. Carcasses in open habitats are much more likely to be discovered than carcasses in mixed or closed habitats (Blumenschine, 1987).

Understanding the locomotion of a carnivoran aids in determining habitat and prey preferences, as well as inferring the ability of large-bodied carnivorans to carry prey into the trees. For example, despite indications of carcass-carrying capabilities in the postcranial skeleton, an extinct species would not be hypothesized to have cached carcasses in trees if the skeleton showed no indications of scansorial (climbing) or arboreal capabilities.

Prey preference, primarily in terms of size, can be inferred from the behaviors described in Table 2 and reflects the combination of body size, speed, prey procurement technique, and grouping behavior of the predator. Preferred prey size differs among large carnivorans, therefore examining prey size for a particular carnivoran is necessary for predicting the general size of carcasses left on the landscape. In general, carnivorans hunting in groups and larger solitary predators tend to take larger prey and smaller solitary predators tend to take smaller prey (Ewer, 1973; Mills, 1990; Caro, 1994). Solitary killers of large prey typically have some sort of lion-like adaptation, where the prehensility of the forelimb, coupled with anterior body strength, allows the predator to place and maintain a bite in spite of the thrashing of the prey. In extant taxa, species that exhibit group hunting behavior that involves several individuals contacting the prey usually are cursorial, and lack the ability to grapple with prey using the forelimb (e.g., wolves, hunting dogs, and hyaenas). These species rarely obtain prey substantially larger than themselves without the aid of other individuals because they lack the flexibility of movement in the limbs for grappling with prey. Therefore, the technique used to procure prey may be useful in inferring prey size and the possibility of grouping behavior during hunting.

Table 2 Definitions of behavioral categories that can be discriminated by postcranial morphology

Behavioral category	Definition	Species included in study*
Locomotor type		
Semi-arboreal	Spends large amount of time in the trees although may also travel on ground, may specialize on arboreal prey species	Clouded leopard
Scansorial	Capable of climbing, may store food in tree, specializes on terrestrial prey species	Jaguar, leopard
Long-distance running	Cursorial species capable of maintaining moderately fast speeds (up to 65 km/h) for quite some time	Wolf, hunting dog, spotted hyaena
High-speed sprinting	Cursorial species capable of running short distances at high speed (up to 110 km/h)	Cheetah
General cursorial	Cursorial species that are neither long-distance running, nor particularly fast	Black-backed jackal, brown hyaena, striped hyaena
Large-bodied generalists	Capable of climbing and running, but not specialists in either	Lion, tiger
Prey procurement type		
Prey grappling with suffocation or cervical bite	Prey is usually stalked or ambushed, grabbed with the manus/fore-claws, and a bite is placed to the back of the neck or to the throat or muzzle to asphyxiate prey	Clouded leopard, lion, jaguar, leopard, tiger
Knocking over with suffocation bite	Prey is pursued at high speed, tripped or knocked over, and a bite is placed to the throat or muzzle to asphyxiate prey	Cheetah
Abdomen/gonad biting	Prey is bitten repeatedly on the stomach, udder, anus, or gonads during pursuit by a group. Prey may be held orally by the muzzle and dies from physiological shock. This permits the capture of larger prey than would be predicted by body size	Wolf, hunting dog, spotted hyaena
Omnivory	Hunting is not the primary food source. Small prey may be grabbed with the teeth	Black-backed jackal, brown hyaena, striped hyaena
Carcass transport type		
Tree-caching	Carcasses are dragged up the trunk and laid in the crook of the tree or over a limb	Jaguar†, leopard
Carcass lifting	Relatively large carcasses or carcass pieces are lifted off of the ground and carried with normal locomotion	Spotted hyaena, striped hyaena, brown hyaena
Carcass dragging	Carcasses are dragged alongside the predator's body or between the legs	Lion, jaguar, leopard, tiger
Carrying a small piece	Relatively small carcasses/pieces are carried away	Wolf, black-backed jackal, hunting dog‡

Table 2 ***Continued***

Behavioral category	Definition	Species included in study*
None	Transport of small portions of a carcass is rarely observed	Cheetah, clouded leopard
Habitat preference§		
Open	Less than 20% canopy cover. Includes mainly grassland variants	Wolf, black-backed jackal, hunting dog, spotted hyaena, striped hyaena, brown hyaena, cheetah, lion
Mixed	Approximately 20% canopy cover. Includes moist savannas, riparian woodlands, and areas as the junction of open and closed habitats	Wolf, black-backed jackal, spotted hyaena, lion, jaguar, leopard, tiger
Closed	More than 20% canopy cover. Includes montane forests, lowland rain forests, and swamp forests	Wolf, clouded leopard, jaguar, leopard, tiger
Prey preference•		
Omnivorous	Diverse diet including fruits, insects, small vertebrates, and occasionally prey from lower limit of size class 1	Black-backed jackal, striped hyaena, brown hyaena
Size class 1‖	4–20 kg (e.g., arctic hare, springhare, dikdik, grysbok, steenbok)	Wolf, black-backed jackal,** hunting dog
Size class 2	20–80 kg (e.g., Thomson's and Grant's gazelles, springbok, puku, impala, topi, capybara, modern humans)	Eurasian wolf,** hunting dog,** cheetah, clouded leopard, jaguar, leopard
Size class 3	80–300 kg (e.g., hartebeest, wildebeest, gemsbok, caribou, tapir, sambar)	North American wolf,** spotted hyaena,** lion, tiger
Size class 4	300–950 kg (e.g., Cape buffalo, eland, juvenile elephant, gaur)	Rarely captured by extant carnivorans††
Size class 5	>1000 kg (e.g., giraffe, elephant, rhinoceros)	None

*Category assignments are based on the following references unless otherwise noted: (Hildebrand, 1961; Mitchell *et al.*, 1965; Estes & Goddard, 1967; Kruuk & Turner, 1967; Schaller, 1967, 1972; Eaton, 1970; Mech, 1970; Kruuk, 1972*a*,*b*; Ewer, 1973; Seidensticker, 1976; Elliot *et al.*, 1977; Kingdon, 1977; MacDonald, 1978; Mills, 1978, 1990; Owens & Owens, 1978; Rautenbach & Nel, 1978; Harrington, 1981; Sunquist, 1981; Bertram, 1982; Spoor & Belterman, 1986; Emmons, 1987; Rabinowitz *et al.*, 1987; Spoor & Badoux, 1989; Cavallo & Blumenschine, 1989; Fuller *et al.*, 1989; Le Roux & Skinner, 1989; Fuller & Kat, 1990; Kitchener, 1991; Hinde, 1992; Sheldon, 1992; Mills & Biggs, 1993; Stander & Albon, 1993; Caro, 1994; Scheel & Packer, 1995).

†This behavior is very uncommon in jaguars (Mondolfi & Hoogesteijn, 1986), although jaguars have also been observed dragging prey extremely long distances over rough terrain and even occasionally up rocky hills to caves (Schaller & Vasoncelos, 1978).

‡Hunting dogs also consume large quantities of meat and then regurgitate portions for pups and adult caretakers at the den (Scott, 1991).

§Although large carnivorans are not truly habitat specific, these characterizations represent habitats in which they often occur.

•Prey preference represents the average size of prey captured successfully by a solitary individual unless otherwise noted. Although different populations of the same carnivoran species may focus on different prey species due to predator body size or other ecological/environmental factors, placement reflects the largest average recorded.

‖Derived from antelope size classes delineated by Brain (1974).

**Placement represents average prey size when this species is hunting in groups.

††Occasionally a large group of hunting lionesses may capture prey in this range (Pienaar, 1969), but it is not the preferred body size for groups of lions overall. Solitary tigers have been noted to capture prey within this range (Seidensticker & McDougal, 1993). Tigers, however, are often 100–200 kg larger than the largest African lions.

Grouping behavior is not only important in predicting prey preference, but also in predicting the outcome of competitive interactions between two species of carnivorans at a carcass (Eaton, 1979). These interactions may be affected to some degree by variables such as the number of individuals present from each species, the level of hunger of these individuals, their previous experiences with other carnivorans and personality differences of individuals (Kruuk, 1972*b*). The two most important factors affecting the outcome of competitive interactions, however, are body size and grouping (Eaton 1979). Groups of lions are at the top of the African carnivoran hierarchy followed by groups of spotted hyaenas or hunting dogs. Solitary lions fall below these grouped carnivorans in the hierarchy (Eaton, 1979). In general, a group of spotted hyaenas can steal carcasses from solitary lions. A group of lions, however, can usually defend their kills from any other living African carnivoran. Solitary cheetahs, solitary hunting dogs, and solitary striped hyaenas are the lowest in the hierarchy of large-bodied carnivorans of sub-Saharan Africa.

Behaviors related to acquiring carcasses either through hunting or scavenging and behaviors related to transporting and utilizing carcasses provide insight into behavioral interactions within specific guilds and the state of carcasses distributed across the landscape. Understanding these behaviors in fossil carnivorans within a specific guild can provide indications of scavenging opportunities within that guild for early hominids.

Materials and methods

Materials

Twelve extant species were measured for comparison with the fossil taxa (see Table 2). Non-African species were included in the functional analyses to increase the diversity of behaviors examined. Fossil carnivoran specimens include material from Koobi Fora and Olduvai Gorge in eastern Africa, and Kromdraai, Sterkfontein, Swartkrans, and Bolt's Farm in southern Africa. Identifications of fossil material were made by personal observation and supplemented with museum catalogue identifications and reference to the literature (e.g., Hopwood, 1934; Ewer, 1954, 1955*a*,*b*,*c*, 1956*a*,*b*, 1967; Hendey, 1973; Petter, 1973; Leakey, 1976; Brain, 1981; Turner, 1986, 1987*a*,*b*, 1993; Cooke, 1991).

Measurements were chosen to reflect biomechanical ability with respect to the behaviors discussed above and included postcranial measurements and measurements of the nuchal region of the cranium. Linear measurements were taken to the nearest 0·01 mm using digital calipers. Articular surface measurements were made by tracing the curve between two defined points with a contour guide and then measuring the tracing.

Measurements of articular surface widths and depths establish the ability of each bone to rotate on its neighbor and/or the distribution of forces through the joint during loading (Taylor, 1974, 1989; Jenkins & Camazine, 1977; Godfrey *et al.*, 1995). Measurements of lever and load arms of flexors and extensors quantify biomechanical advantage in terms of strength and speed of muscle movement (Maynard Smith and Savage, 1956; Stern, 1974; Van Valkenburgh, 1985). Relative limb lengths were also measured, as highly cursorial species often elongate distal limb elements to increase stride length and angular velocity (Hildebrand, 1988). Limb lengths may also provide a very general picture of habitat preference in carnivorans (Gonyea, 1976*a*,*b*; Marean, 1989).

Procedures

Because most species are named and recognized from craniodental specimens, an alternative ecomorphological approach was taken to group specimens for analysis. Based on overall similarity in size and shape, fossil specimens were classed into morphotypes. As many morphotypes were based on associated partial skeletons, many previously unassigned postcranial specimens could be placed in morphotypes. Specimens found with craniodental material assigned by previous researchers to extant taxa usually were assigned to morphotypes bearing that name for clarity in this paper (e.g., Olduvai Gorge *Crocuta* morphotype). Use of a genus name within a morphotype, however, does not necessarily mean that this morphotype was behaviorally similar to that extant species within that genus. Specimens assigned to the same taxon from different sites or members were not grouped together unless the specimens were similar in both shape and size. Such a conservative method of grouping allows either the examination of differences in ecomorphological variables through time of presumably conspecific material or the recognition of differing morphology between morphotypes that might warrant changes in species or higher-level assignations.

Variables in extant taxa were examined for differences among species using analysis of variance (ANOVA) or Kruskal–Wallis tests. Appropriate unplanned pair-wise comparison tests were made if the null hypothesis of the equality of means was rejected. Significance was placed at the 95% confidence level for all analyses.

Two multivariate techniques, clustering and ordination, were performed to determine the degree of morphological similarity between morphotypes using the computer package NT-SYS (version 1.7, Rohlf *et al*., 1992). The unweighted pair-group method using arithmetic averages, or UPGMA, method of sequential, agglomerative, hierarchical, non-overlapping, or SAHN, cluster analysis was performed because it weights each species equally when computing the average dissimilarity of each species to a specific cluster. Cophenetic correlation coefficients measure the agreement between distance matrix values and those implied by the dendrogram. Coefficients greater than or equal to $|0{\cdot}8|$ indicate a good fit (Rohlf *et al*., 1992).

The ordination technique used, principal coordinates analysis (Gower, 1966), places species into a theoretically continuous sequence reflecting basic species properties through reduction to two, three, or n-dimensional space (Pimentel, 1979). Pearson product–moment correlations between variables and scores on the first n axes signify which variables were most important in determining placement of species along a given axis. A minimum spanning tree (MST) between taxa was also calculated for each matrix, and was used to determine whether distortion occurs in relationships viewed in reduced dimensions.

Analyses were performed on both raw data and functionally-based indices because indices describe shape and diminish the impact of differing body sizes on comparisons. Indices quantified either muscle leverages, shape, or limb proportions. Rank order correlation tests between index means and body weight from the literature were performed using Spearman's coefficient to discover whether differences among indices were correlated with differences in body size (Mosimann & James, 1979). No significant correlations were found between indices and body size in extant species; therefore, differences among species do not simply represent size-required modifications in skeletal design. Variables significantly separating extant taxa by behavior were included in analyses of fossil taxa.

Guild analyses were performed as a "taxon-free" (Damuth, 1992) method of comparing dietary opportunities between sites and regions. Several multivariate techniques were used to determine structural similarities among carnivoran guilds. Indices shown to differentiate between behavioral categories were plotted in bivariate and three-dimensional morphospace plots. These morphospace plots represent "ecomorphospace", where each axis represents a biological characteristic of the morphotype (Van Valkenburgh, 1994). Average Euclidean distances between pairs of guild members were calculated to examine structural differences in guilds as originally described by Van Valkenburgh (1985, 1988).

Overlap in taxa within ecomorphospace may represent competitive overlap in behavior (Van Valkenburgh, 1994). Three estimates of dispersion were calculated, therefore, to compare overlap within guilds. The average link in the MST connecting all guild members is a useful indicator of overall morphological similarity among guild members (Van Valkenburgh, 1985, 1988). Other estimates of dispersion include the average distance from the guild centroid to each species (DFC) and the average distance between any species and its nearest neighbor (NND). Both DFC and NND do not provide stable estimates of dispersion, and only DFC values can be compared statistically because the link lengths are independent (Van Valkenburgh, 1985). All three values, therefore, were calculated to provide an indication of dispersion. Pairwise comparisons of DFC values among guilds were carried out utilizing the Mann–Whitney U test.

Because most actualistic studies focus on eastern African fossil sites, the guilds of this region are the primary focus of this paper. The applicability of the models to specific sites at specific time periods will be examined. However, sites relatively close in time and space may contain different species due not only to ecological differences, but also to taphonomic bias. Therefore, a composite eastern African guild was compared with a composite southern African guild to determine general similarities in composition and dispersion between the two regions. The composition of these guilds will be discussed below. Specific southern African guilds will be dealt with in detail elsewhere.

Results

Behavior of some Plio-Pleistocene carnivoran taxa

At least 12 carnivoran genera are known from the African Plio-Pleistocene (Table 3). Of these 12, not all are found in both eastern and southern Africa. Some of the morphotypes of these genera will be presented here briefly to demonstrate the greater range of behaviors seen in carnivorans during the Plio-Pleistocene and to aid in understanding the discussion of these taxa in the analyses of guild structure. Specimens included in each morphotype are listed by body region in Table 4. Further analyses of these morphotypes, including specific characteristics, will be presented elsewhere (Lewis, 1995, 1997) and are merely summarized here.

Sabertoothed felids are particularly important to the study of hominid paleoecology because sabertooths have been hypothesized to be the providers of large carcasses for hominid scavenging (e.g., Blumenschine, 1987; Marean, 1989; Van Valkenburgh *et al.*, 1990). Three sabertoothed genera, *Dinofelis*, *Megantereon*, and *Homotherium* are known from both the eastern and southern African Plio-Pleistocene record. To test whether sabertoothed felids share an identifiable morphological pattern in their postcrania, morphotype of these three genera were analyzed with extant species using UPGMA. The result (Figure 1) demonstrates that there is not a shared morphological pattern in the postcrania among African sabertoothed species. This suggests that not only do sabertoothed morphotypes differ greatly in behavior from other species, but they also differ from each other. These differences mean that sabertoothed genera, species, or morphotypes must be considered individually in relationship to hominid behavior.

Dinofelis is often considered to be most closely related to living members of the genus *Panthera* and termed a “false sabertooth”, because it does not not have the fully-developed sabertooth masticatory apparatus (e.g., Walker, 1984; Marean, 1989). Other researchers (e.g.,

Table 3 Carnivoran morphotypes at some African Plio/Pleistocene sites

Taxon*	Morphotype	Taxon*	Morphotype
Recent Eastern Africa		Recent Southern Africa	
Canis mesomelas	Jackal	*Canis mesomelas*	Jackal
Lycaon pictus	Hunting dog	*Lycaon pictus*	Hunting dog
Acinonyx jubatus	Cheetah	*Acinonyx jubatus*	Cheetah
Panthera leo	Lion	*Panthera leo*	Lion
Panthera pardus	Leopard	*Panthera pardus*	Leopard
Crocuta crocuta	Spotted hyaena	*Crocuta crocuta*	Spotted hyaena
Hyaena hyaena	Striped hyaena	*Parahyaena hyaena*	Brown hyaena
Olduvai Gorge Bed I (1·9–1·7 mya)		Olduvai Gorge Bed II† (1·7–1·2 mya)	
Canis africanus	OG *Canis africanus*‡	*Canis africanus*	OG *Canis africanus*
Canis mesomelas	EA *Canis*	*Canis mesomelas*	EA *Canis*
Acinonyx jubatus	Cheetah§	cf. *Homotherium* sp.•	nm
Dinofelis sp.	KF *Dinofelis*	*Panthera leo*	OG *Panthera leo*
Panthera leo	OG *Panthera leo*	*Chasmaporthetes nitidula*‖	nm
Panthera pardus	OG *Panthera pardus*	*Crocuta* sp.	OG *Crocuta*
Megantereon sp.	KB *Megantereon***	*Hyaena hyaena*	*Hyaena hyaena*
Crocuta sp.	OG *Crocuta*		
Koobi Fora Okote Mb (1·62–1·39 mya)		Koobi Fora KBS Mb† (1·88–1·62 mya)	
Canis mesomelas	EA *Canis*	*Dinofelis barlowi*	KF *Dinofelis*
Dinofelis-barlowi	KF *Dinofelis*	*Homotherium* sp.	KF *Homotherium*
Homotherium sp.	KF *Homotherium*	*Crocuta crocuta*	Spotted hyaena
Megantereon sp.	KB *Megantereon*		
Panthera sp. A	KF *Panthera* A	Southern Composite††	
Panthera sp. B	KF *Panthera* B	*Canis atrox*‡	KA *Canis atrox*
Crocuta sp.	KF *Crocuta*	*Canis mesomelas*	SA *Canis*
Hyaena hyaena	Striped hyaena	*Canis terblanchei*‡§§	nm
		Lycaon pictus	Hunting dog
Eastern Composite••		*Acinonyx jubatus*	Cheetah
Canis africanus	OG *Canis africanus*	*Dinofelis barlowi*	BF *Dinofelis*
Canis mesomelas	EA *Canis*	*Dinofelis piveteaui*‖	KA *Dinofelis*
Acinonyx jubatus	Cheetah	*Homotherium* sp.**	KF *Homotherium*
Dinofelis sp.	KF *Dinofelis*	*Megantereon cultridens*‖	SA *Megantereon*
Homotherium sp.	KF *Homotherium*	*Megantereon gracile*	KB *Megantereon*
Megantereon sp.	KB *Megantereon*	*Panthera leo*	Lion
Panthera sp. A	KF *Panthera* A	*Panthera pardus*‖‖	Leopard
Panthera sp. B	KF *Panthera* B	*Chasmaporthetes nitidula*‖	nm
Panthera leo	OG*Panthera leo*	*C. silberbergi*‖	nm
Panthera pardus	OG *Panthera pardus*	*Crocuta crocuta*	Spotted hyaena
Chasmaporthetes nitidula‖	nm	*Pachycrocuta brevirostris*‖	nm
Crocuta crocuta	Spotted hyaena		
Hyaena hyaena	Striped hyaena	*Parahyaena brunnea*	Brown hyaena

*Taxon name given by previous researchers.

†This paleoguild contained too few morphotypes represented by postcrania to be analyzed.

‡Represented by few postcranial specimens and unlike any modern species.

§Morphotypes listed as a common name of a modern species had very little or no postcrania and fell within the range of that modern species in measurements of these elements.

•Possible presence of this genus is based on one fragmentary sabertooth canine (OLD 068/6158).

‖No postcranial material and unlike any modern species.

**Only one morphotype each of *Megantereon* and *Homotherium* from these sites is well represented by postcrania. The KB *Megantereon* and KF *Homotherium* morphotypes were substituted in the morphospace plots presented to provide a possible indication of where morphotypes of these genera might fall.

††Bolt's Farm, Kromdraai A, Sterkfontein 4, and Swartkrans Members 1 and 2.

§§These specimens have been referred to *Nyctereutes terblanchei* (Ficcarelli *et al.*, 1985). No *Nyctereutes*-like postcranial material has been found so far at sites included in this analysis.

••Olduvai Gorge Bed I and II and Koobi Fora Okote and KBS Members.

‖‖Fossil leopards vary in size in southern Africa, but do not differ morphologically from extant leopards.

Abbreviations: Mb, member; nm, not measured due to distortion or being represented only by dentition. Morphotypes: EA, eastern Africa; KF, Koobi Fora; KB, Kromdraai B; OG, Olduvai Gorge; KA, Kromdraai A; SA, southern Africa; BF, Bolt's Farm.

Table 4 Specimens included in fossil morphotypes

Morphotype	Specimens included
EA *Canis*	
Cranium	KNM-ER 3767
Forelimb elements	OLD 161; OLD 1220; OLD 1631; OLD 067/2605
Hindlimb elements	KNM-ER 1658; OLD 1028; OLD 1603; OLD 6251; OLD 61/7188; OLD 067/2602; OLD 067/2619; OLD 067/2621
KF *Dinofelis*	
Partial skeletons	KNM-ER 722 A-AJ; KNM-ER 3380 C-V; KNM-ER 4419 A-BG
Forelimb elements	KNM-ER 359; KNM-ER 364; KNM-ER 366; KNM-ER 1538; KNM-ER 3747; KNM-ER 6024 A-D; KNM-ER 6111
Hindlimb elements	KNM-ER 402; KNM-ER 893; KNM-ER 987; KNM-ER 3742
OG *Dinofelis*	
Forelimb elements	OLD 74-01; OLD 74-54; OLD 74-348
KF *Homotherium*	
Partial skeletons	KNM-ER 3093 A-AG; KNM-ER 3112 A-X
Forelimb elements	KNM-ER 696; KNM-ER 704; KNM-ER 791; KNM-ER 1546 A; KNM-ER 1580; KNM-ER 1721; KNM-ER 3113; KNM-ER 3743; KNM-ER 4456
Hindlimb elements	KNM-ER 894; KNM-ER 1665; KNM-ER 2012; KNM-ER 2092; KNM-ER 3096; KNM-ER 3738; KNM-ER 3744; KNM-ER 3750; KNM-ER 4979
KF *Panthera* A	
Partial skeleton	KNM-ER 2037 A-AA 1
KF *Panthera* B	
Forelimb elements	KNM-ER 700
Hindlimb elements	KNM-ER 693; KNM-ER 1815; KNM-ER 2013
KF *Crocuta*	
Cranium	KNM-ER 361
Partial skeletons	KNM-ER 721 A-AD; KNM-ER 712 A-W; KNM-ER 970 A-AS
Forelimb elements	KNM-ER 2008
Hindlimb elements	KNM-ER 695; KNM-ER 794; KNM-ER 872; KNM-ER 897 C,G; KNM-ER 953; KNM-ER 1184; KNM-ER 1539
OG *Crocuta*	
Forelimb elements	OLD 506, 1960; OLD 3020, 1960; OLD 2658, 1967; OLD 8397
Hindlimb elements	OLD 275, 1959; OLD 1032; OLD 7285; 1961
EA *Hyaena*	
Cranium	KNM-ER 3766
Cranium and partial skeleton	KNM-ER 1548 A-BC
Forelimb elements	KNM-ER 709; OLD 6140
Hindlimb elements	KNM-ER 1666 C; OLD 1565, 1963
SA *Canis*	
Forelimb elements	SK 195; SK 6373; SK 10591; SK 14017; SKX 496; SKX 753; SKX 855; SKX 2695; SKX 4585; SKX 9542; SKX 19531; SKX 21540; SKX 22448; SKX 29535; SKX 32140; SKX 33412; SKX 38147; SKX 47216
Hindlimb elements	SK 10760; SK 11173; SK 11597; SKX 677; SKX 1655; SKX 2691/2692; SKX 5864; SKX 9149; SKX 13422; SKX 13427; SKX 22964; SKX 38506; SKX 201128
BF *Dinofelis*	
Cranium	TM BF 1
Forelimb elements	UCMP 88765
Hindlimb elements	UCMP 69525/69526; UCMP 69527; UCMP 69528; UCMP 80286; UCMP 80288; UCMP 80309; UCMP 88749; UCMP 88753; UCMP 88772; UCMP 88776; UCMP 88787; UCMP 88777; UCMP 88780; UCMP 88781; UCMP 88783; UCMP 88784; UCMP 88786
KB *Megantereon*	
Partial skeleton	KB 5333 A-Z
Forelimb elements	KB 5356
Hindlimb elements	KB 5334 B; KB 5338; KB 5342; KB 5343; KB 5377; KB 5381; KB 5382

Abbreviations: KB, Kromdraai B; KNM-ER, Koobi Fora; OLD, Olduvai Gorge; SK and SKX, Swartkrans; TM BF, specimens from Bolt's Farm housed at the Transvaal Museum; UCMP, specimens from Bolt's Farm housed at the University of California Museum of Paleontology.

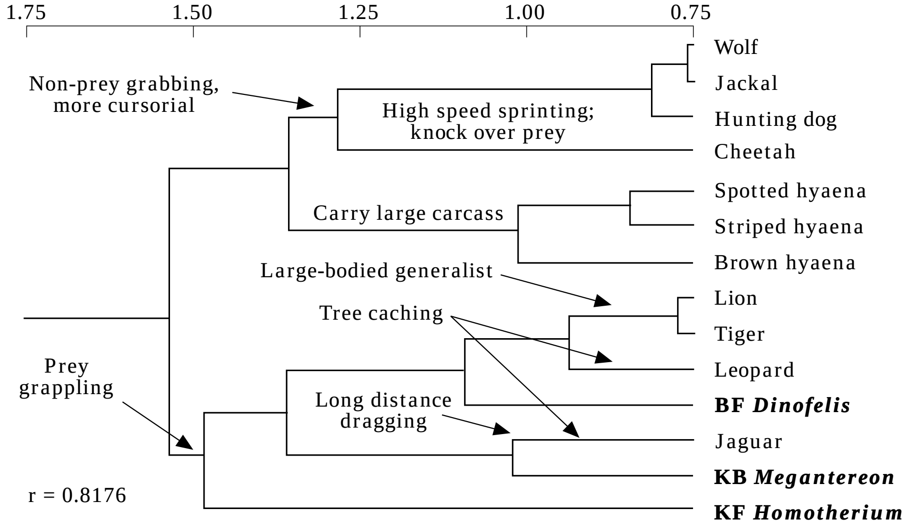


Figure 1. UPGMA dendrogram of postcranial indices in extant large-bodied carnivorans and three sabertoothed felid morphotypes: Bolt's Farm *Dinofelis barlowi*, Kromdraai B *Megantereon gracile*, and Koobi Fora *Homotherium*. Extant taxa separate into two groups: the cursorial canids, hyaenids, and cheetahs and the less cursorial pantherines. The cheetah does not fall with other felids. Hyaenids, which are most closely related to felids, fall with canids, suggesting that this dendrogram is reflecting primarily functional adaptations and not phylogeny. Note that *Dinofelis* is most similar to extant Asian and African prey-grappling felids. *Megantereon* is most similar in postcranial morphology to jaguars, representing possible closed habitat adaptations. *Homotherium* is unique among all prey grappling felid species. Abbreviations: BF, Bolt's Farm; KB, Kromdraai B, KF, Koobi Fora.

Berta & Galiano, 1983), however, have placed this genus in the sabertoothed subfamily Machairodontinae based on phylogenetic analyses.

The limb morphology of the Bolt's Farm *Dinofelis* morphotype, included in Figure 1, is more similar to modern prey-grappling lions, tigers, and leopards in terms of forelimb strength and rotatory ability than to other sabertooths. *Dinofelis* however, still has relatively more robust forelimbs than hindlimbs, a characteristic of sabertoothed felids. Specimens of this genus examined from Koobi Fora, although not as numerous, are very similar to those from Bolt's Farm. Both eastern and southern African specimens fall in size between African leopards and lions. The Bolt's Farm *Dinofelis* has been described as similar in many craniodental features to modern pantherine felids (Cooke, 1991), and may therefore, represent a machairodont that has converged on pantherines in craniodental, and to some degree, in postcranial anatomy.

Megantereon is most closely related to the American genus *Smilodon* (Berta & Galiano, 1983; Berta, 1987). *Smilodon* has been shown to be most similar in postcranial morphology to jaguars among extant taxa, although much larger in body size and more robust (Berta, 1987). The Kromdraai B *Megantereon* morphotype also shows an overall morphology most similar to that of extant jaguars (Figure 1). Characteristics of the KB *Megantereon* radius, in particular, are similar to that of the jaguar, suggesting similar abilities in using the forelimb to grapple with prey. Jaguars are also heavily muscled relative to other pantherines, as is *Megantereon*, and *Megantereon* probably fell between jaguars and leopards in body size. Other *Megantereon* morphotypes from Koobi Fora and Sterkfontein are not represented by enough postcranial material to be included in multivariate analyses of multiple skeletal elements, nor to determine whether more than one species exists.

Homotherium is unique in morphology among African felids past and present. The morphotype from Koobi Fora, shown in Figure 1, is the largest African sabertooth and shows several features of articular morphology and relative limb proportions indicating increased cursoriality relative to other sabertooths. The forelimb of this morphotype, however, still has rotatory abilities and has great strength in flexion and supination indicating potential prey grappling capabilities, although perhaps not to the extent of other sabertoothed felids. The limbs of the Koobi Fora *Homotherium* were longer than those of modern lions or tigers, yet the limbs do not indicate the heavy musculature relative to length common to other sabertooths, such as *Megantereon* or *Dinofelis*. In fact, *Homotherium* seems to have slightly less load-bearing capabilities relative to limb length than modern pantherines, suggesting that this felid had a radically different manner of interacting with prey.

Sabertoothed felids have been suggested to prefer primarily mixed or closed habitat due to their brachial index (Marean, 1989), which is the length of the radius divided by the length of the humerus multiplied by 100. In general primarily open habitat carnivorans, such as canids and the cheetah, have an index greater than 100, while mixed or closed habitat carnivorans fall below 100 (Figure 2). Both the Bolt's Farm and Koobi Fora *Dinofelis* morphotypes fall within the low end of the mixed/closed habitat range, as does the European form of *Megantereon cultridens*. A complete forelimb does not exist for African *Megantereon* morphotypes, however Turner (1987*b*) has suggested that the European and African forms are conspecific. The Koobi Fora *Homotherium* falls with more cursorial, open habitat species, unlike its congeners from Europe and North America.

In fact, European and North American species of *Homotherium*, like extant hyaenas, have longer forelimbs relative to hindlimbs in comparison with other taxa (Figure 3). Complete sets of limbs were not available for African morphotypes; therefore, lines representing the Bolt's Farm *Dinofelis* forelimb and the Koobi Fora *Homotherium* forelimb show potential placement for these morphotypes. Although the Kromdraai B *Megantereon* does not include a complete fore- or hindlimb, a complete femur and tibia of *Megantereon* (EFT 9846 C,D) from Elandsfontein, South Africa, indicate where, at least, this genus falls.

Most larger carnivorans have relatively longer hindlimbs. Within hyaenids, however, the shortened hindlimb relative to forelimb length has been suggested to be a compromise between normal locomotion and stability while carrying heavy loads (Spoor, 1985). *Homotherium*, at least, may have needed similar enhanced stability while capturing very large prey. Greater strength in flexing and supinating the forelimb along with (at least in non-African forms) the relatively shortened hindlimb suggest that, in general, sabertoothed felids may have been powerful prey grappling, ambush predators, and that some may have had a posture similar to that of a modern hyaena.

Other fossil felid morphotypes include a cheetah-like felid labeled "*Panthera* A" in the Kenya National Museums, and therefore, designated here as the Koobi Fora *Panthera* A morphotype. This morphotype includes two partial skeletons (KNM-ER 2037 and 3740), one of which, KNM-ER 3740, has an associated partial maxilla containing a premolar. This premolar is intermediate in size between lions and leopards (Werdelin, pers. comm.). Other more fragmentary dental and postcranial material labeled "Panthera A" in the Kenya National Museum may be a part of this morphotype, but was not included in this analysis. Some of the *Panthera* A material was originally mentioned briefly by Leakey (1976) as possibly belonging to "*Panthera crassidens*". Leakey noted that this material was similar morphologically to cheetahs, although she states that it is "clearly distinguishable" (1976: p. 307) from cheetahs. Turner (1984) has since demonstrated that "*P. crassidens*" is invalid

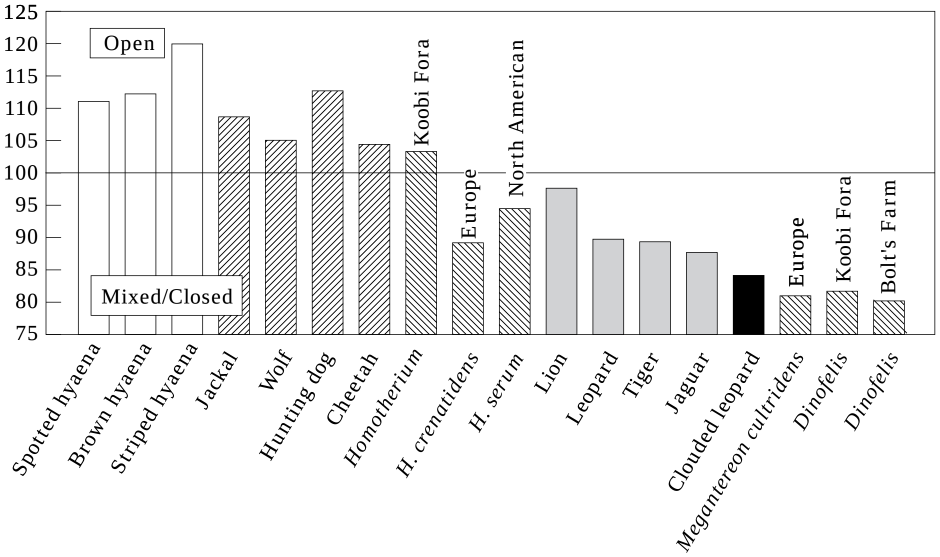


Figure 2. Brachial index in sabertoothed felids and extinct taxa. Although large-bodied carnivorans may frequent more than one habitat, the brachial index, in general, reflects primary habitat preferences. Species with brachial indices above 100 tend to prefer open habitats, while those with indices below 100 prefer mixed or closed habitats. Closed habitat species, such as the clouded leopards, have the lowest brachial index. *Homotherium* has the highest brachial index among sabertoothed felids and the Koobi Fora *Homotherium* probably was the most open habitat sabertoothed morphotype. Both *Dinofelis* and *Megantereon* morphotypes appear to have preferred more closed habitats. Data for the European and North American species were taken from the literature (Ballesio, 1963; Rawn-Schatzinger, 1992; Schaub, 1925). (□) Non-prey grappling; carcass carrying; (▨) cursorial; non-prey grappling; (▧) Sabertooth; (▩) prey grappling; drag carcass or tree caching; (■) Smaller bodied arboreal.

because the original description was based on a mixture of cheetah and leopard specimens from South Africa.

Among the *Panthera* A material, only KNM-ER 2037 was complete enough to use in multivariate analyses (Figure 4). *Panthera* A is very cursorial and does share many features with cheetahs including gracile tubular shafts of the long bones and a relatively deep but mediolaterally narrow patella. *Panthera* A, however, is much more robust than the extant cheetah. The associated dentition is *Panthera*-like, rather than *Acinonyx*-like, suggesting less hyper-flesh slicing than seen in the cheetah.

Although many fossil morphotypes assigned to modern taxa were not significantly different from their modern (presumed) conspecifics, several morphotyes differed in term of total morphological pattern. For example, fossil canids attributed previously to *Canis* from both eastern and southern Africa are more robust than modern jackals (Figure 5). Although most of this material has been placed in the modern species *Canis mesomelas*, these analyses show that the fossil material in both regions is unique, at least in terms of postcranial morphology and morphology of the nuchal region of the cranium.

Comparisons of specific carnivoran guilds

Although guild analyses were carried out on a variety of skeletal elements, only morphospace plots based on three ratios (biceps brachii leverage index, brachial index, and femoral midshaft shape index) will be presented here. Measurements and definitions of these indices are listed in

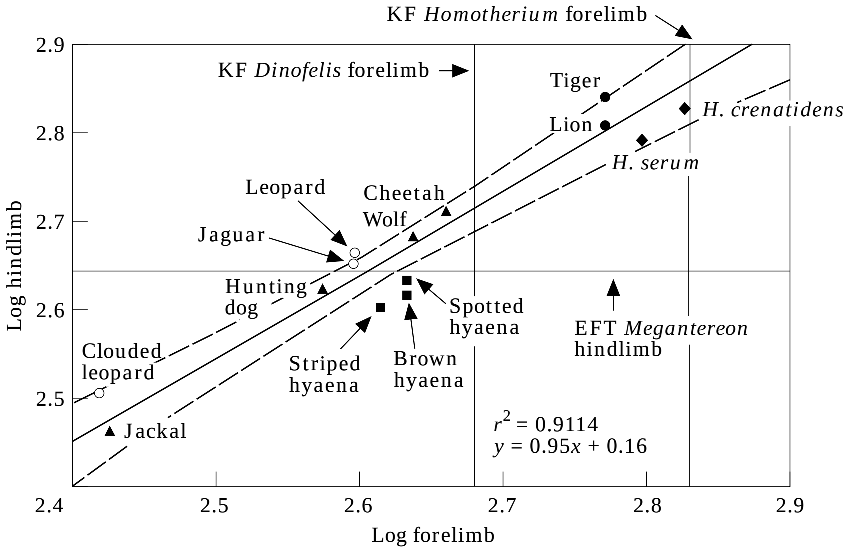


Figure 3. Log forelimb length *vs.* log hindlimb length. Light lines represent placement of species possessing only one complete limb. The heavy line is the regression line for extant taxa only ($y = 1{\cdot}1098x - 0{\cdot}2536$; $r^2 = 0{\cdot}8583$). Sabertoothed felids and hyaenids both have relatively longer forelimbs than hindlimbs. In hyaenids, relatively longer forelimbs may aid in shifting the center of gravity backwards while carrying heavy carcasses by mouth. The limbs are still proportioned in such a way, however, that relatively fast locomotion can occur. Sabertoothed felids may have needed similar body stability while grappling with large-bodied prey. A hyaenid-like posture for *Homotherium*, at least, does not necessarily diminish cursorial capabilities in this species. (●) Prey grappling, large-bodied generalist; (○) prey grappling, scansorial/arboreal; (▲) cursorial, no prey grappling or carcass carrying; (■) pursuit predator, carcass carrying; (◆) North American and European sabertoothed species.

Table 5, as are other indices included in the guild analyses, but not plotted. The biceps brachii leverage index measures the strength in flexing and supinating the forearm, a behavior crucial to prey grappling. The brachial index is a general indicator of habitat and cursorial indicators, as discussed above (Figure 2). Femoral midshaft shape indicates the loading capabilities of the hindlimb. Tubular femoral shafts (indices approaching 100%) are associated, in general, with cursoriality, while species with shafts that are wider mediolaterally than anteroposteriorally may indicate heavier loading of the hindlimbs during prey grappling with large prey or carrying carcasses.

Several groupings can be seen when all taxa and morphotypes are plotted in morphospace (Figure 6). Prey grappling species (felids minus cheetahs) are separated from non-prey grappling species (canids, hyaenids, and cheetahs) along the *x*-axis (BBL). The *y*-axis (BI), in general, separates more open habitat-adapted species from more mixed and closed-habitat species, as in Figure 2. Canids, hyaenids, cheetahs, and KF *Homotherium* have the highest scores, while clouded leopards and both *Dinofelis* morphotypes have the lowest. The *z*-axis (FMS) separates taxa with greater load-bearing ability in the limbs, either due to body size or carcass carrying ability, from more gracile taxa. KF *Homotherium* is unique among taxa examined in having an extremely wide femoral shaft. Both *Dinofelis* morphotyes, however, also have wide shafts in comparison with modern taxa. KB *Megantereon* falls with modern pantherine taxa along this axis. The lower values along the *x*- and *y*-axes place this morphotype on the edge of the modern pantherine region of morphospace.

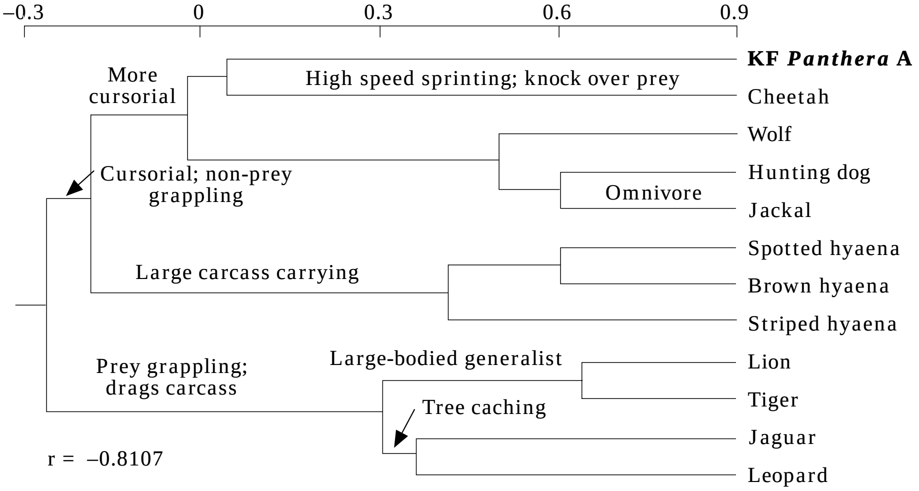


Figure 4. UPGMA dendrogram of postcranial characteristics in extant species and the Koobi Fora *Panthera* A morphotype. As in Figure 1, extant taxa are separated first by cursorial (canids, hyaenids, and cheetahs) *vs.* less cursorial (lions, tigers, leopards, and jaguars). Cheetahs and the *Panthera* A morphotype fall with the cursorial canids. This fossil morphotype is similar to cheetahs in relatively narrow articular surfaces and elongated limbs in comparison to other felids. The fossil morphotype, however, is much larger and more robust than the cheetah and has associated dentition that appears to be more *Panthera*-like. Abbreviations: KF, Koobi Fora.

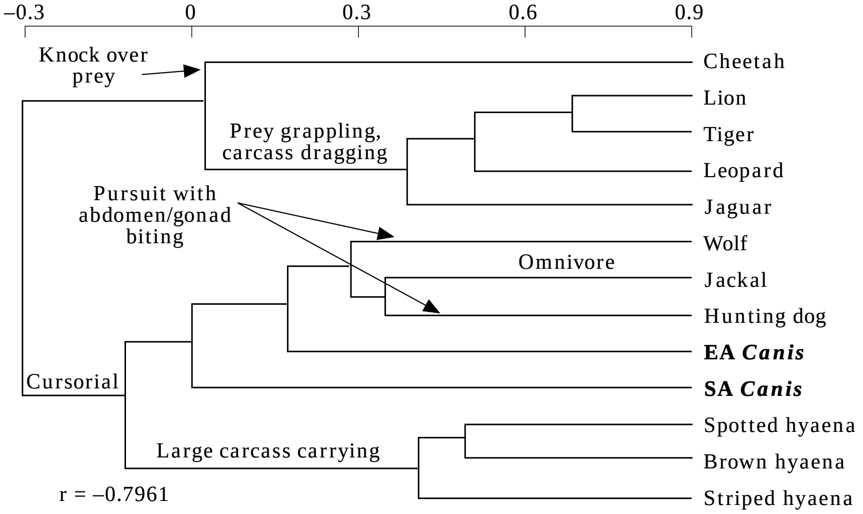


Figure 5. UPGMA dendrogram of postcranial characteristics in extant species and the eastern (EA) and southern (SA) African *Canis* morphotypes. The two fossil morphotypes contain material originally assigned to the modern black-backed jackal species, *C. mesomelas*, although they are more robust than the modern species. Neither morphotype, however, clusters with this extant species. The southern morphotype is least like modern taxa.

Although closely related carnivoran species often engage in similar behavior, several details suggest that phylogeny is not the predominant factor in the placement of taxa. For example, morphotypes belonging to the three sabertooth genera are separated. *Dinofelis*

Table 5 **Indices used in morphospace plots***

Species and Morphotypes	Biceps brachii leverage index (BBL)†	Brachial index (BI)‡	Femoral midshaft shape index (FMS)§
Cheetah	7·38	104·63	93·36
Wolf	11·83	105·17	94·88
Jackal	9·41	108·70	106·05
Spotted hyaena	8·99	111·11	113·07
Brown hyaena	7·55	112·37	114·91
Striped hyaena	7·26	120·01	110·74
Hunting dog	10·14	112·95	100·25
Lion	12·72	97·77	110·57
Jaguar	13·38	88·29	106·92
Leopard	11·49	90·09	107·13
Tiger	12·51	89·95	108·30
Clouded leopard	13·97	84·92	107·07
EA *Canis*	—	—	102·38
KF *Dinofelis*	15·29	82·09	119·23
BF *Dinofelis*	13·80	80·50	116·02
KB *Megantereon*	10·15	—	110·99
KF *Homotherium*	11·98	103·52	128·17
KF *Crocuta*	—	—	102·07
OG *Crocuta*	8·33	107·75	105·95

*Other indices included in the analyses of guild dispersion are: medial humeral trochlear lip height/humeral trochlear width; distal anteroposterior/biepicondylar humeral width; minimum/maximum radial head width; ulnar semilunar notch depth/width; superoinferior/anteroposterior femoral head width; medial astragalar lip height/astragalar trochlear width; astragalar neck length/astragalar length. All were multiplied by 100 and represent indices that are useful in inferring behavior (Lewis, 1995) and that are usually measureable in fossil specimens.

†Length from center of bicipital tuberosity to proximal end of radius/radial length × 100.

‡Radial length/humeral length × 100.

§Mediolateral/anteroposterior femoral midshaft width × 100.

All bone lengths are measured from articular surface to articular surface. — represents ratios that could not be obtained for these morphotypes. Abbreviations as in Table 3.

morphotypes are separated not only from other machairodonts, but also from the African pantherines, to whom they have also been suggested to be related. In addition, cheetahs fall towards the canids and hyaenids, although they have their own unique placement in morphospace related to their having less load bearing capabilities in the hindlimb, than do other taxa.

A few morphotypes did not possess all of the elements measured for the indices. If these morphotypes were assigned previously by other researchers to a modern species, and their morphology was not significantly distinct from that modern species, then data for the modern species were used in the graphical analysis presented below. This substitution allows a general picture of species packing within the guild to be studied, although this picture may differ slightly from the actual distribution within morphospace once more fossil specimens are recovered. These substitutions were not included in statistical analyses of morphospace. Not all morphotypes, however, had modern counterparts (e.g., *Chasmaporthetes* and *Panthera* A

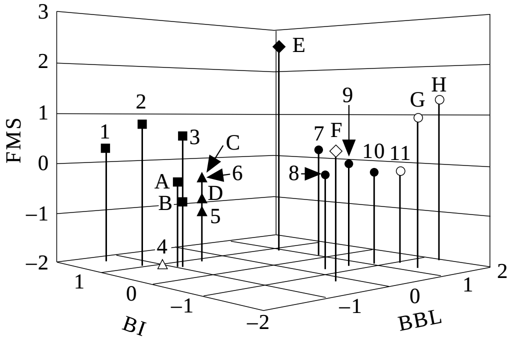


Figure 6. Morphospace plot of standardized ratios of brachia index (BI), biceps brachii leverage index (BBL), and femoral midshaft shape index (FMS) in all extant species and fossil morphotypes. The *x*-axis (BI) divides prey grappling (1–6, A–D) from non-prey grappling (7–11, E–H) morphotypes. The *y*-axis (BBL) divides morphotypes by habitat as seen in Figure 2. The *z*-axis (FMS) separates more cursorial morphotypes (negative numbers) from those with greater load-bearing ability in the hindlimb (positive numbers). Increased loading of the hindlimb may occur during prey grappling of large-bodied prey and carcass carying. Missing values for EA and SA *Canis* morphotypes were replaced by extant *C. mesomelas* values in the graph to reduce visual confusion. The brachial index for the European species of *Megantereon* (see Figure 2) was also used to plot KB *Megantereon*. None of these additions were included in any statistical analyses. Species and morphotypes are: 1. striped hyaena; 2. brown hyaena; 3. spotted hyaena; 4. cheetah; 5. hunting dog; 6. black-backed jackal; 7. lion; 8. leopard; 9. tiger; 10. jaguar; 11. clouded leopard; A. OG *Crocuta*; B. KF *Crocuta*; C. SA *Canis*; D. EA *Canis*; E. KF *Homotherium*; F. KB *Megantereon*; G. BF *Dinofelis*; H. KF *Dinofelis*. Abbreviations are as in Table 3.

Table 6 Estimates of dispersion of species in guild analyses

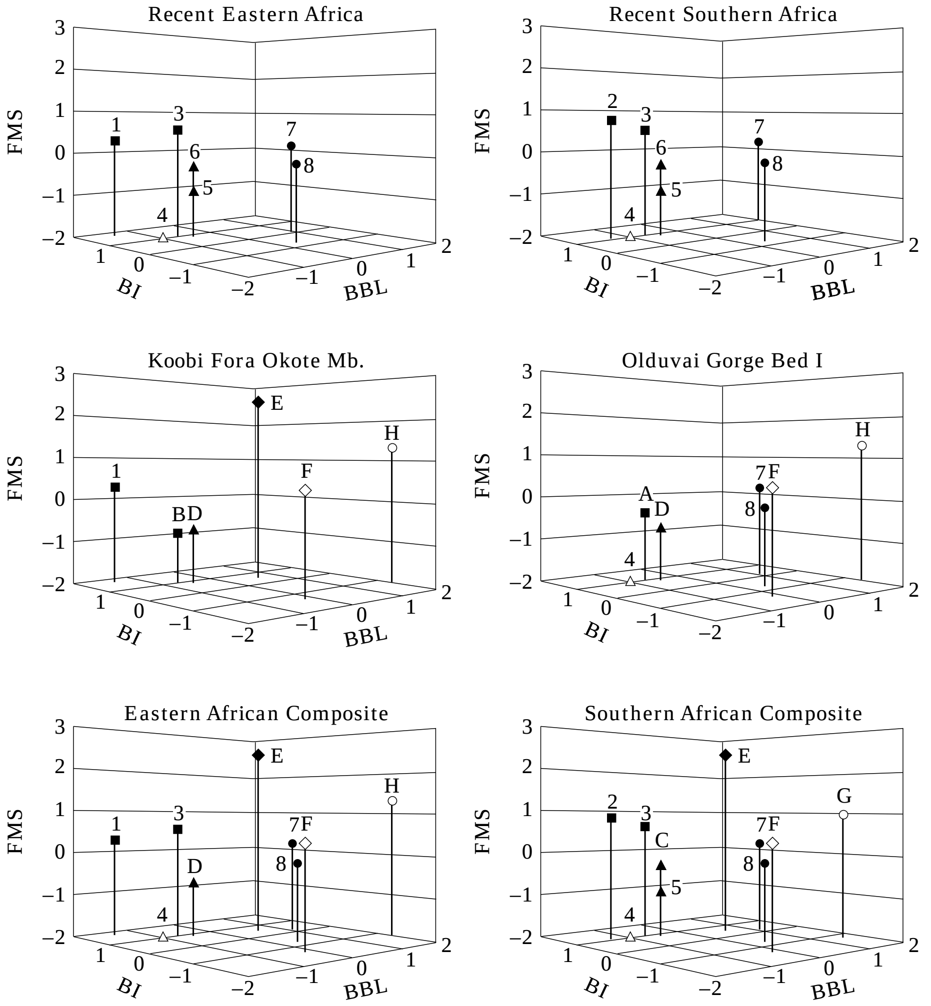
		Average					
Guild	*k*	MST	MST S.D.	NND	NND S.D.	DFC	DFC S.D.
Extant Eastern African	7	0·9437	0·1818	0·3621	0·1183	0·8655	0·1753
Extant Southern African	7	1·0158	0·1826	0·3812	0·1744	0·8436	0·1736
Koobi Fora Okote Mb	8	1·0456	0·1851	0·3911	0·2349	0·8286	0·2904
Olduvai Gorge Bed I	7	0·9110	0·2995	0·3556	0·2427	0·8955	0·2872
Eastern African Composite	11	0·8131	0·2033	0·3124	0·1927	0·9249	0·3716
Southern African Composite	10	0·9817	0·1843	0·3476	0·2502	0·7830	0·2800

Abbreviations: k, number of morphotypes included in guild analyses (see Table 3 for total number of morphotypes in each guild); MST, minimum spanning tree; NND, nearest neighbor distance; DFC, distance from guild centroids.

morphotypes). Species missing from the graphs or from the total analysis due to lack of postcranial material are noted below and in Table 3.

Although MST and NND values for each guild vary, none of the guilds were significantly different from one another in DFC values despite differences in guild composition (Table 6). This similarity in dispersion may change in the future with the inclusion of morphotypes currently represented only by craniodental material.

Comparison of the overall structure of recent eastern and southern African carnivoran guilds (Figure 7) shows that these guilds are very similar in dispersion estimates and species composition. The only difference in species composition between the two is the presence of brown hyaenas in the south and striped hyaenas in the east. Subtle differences in behavior between these two species, however, are reflected in the morphospace plot. Brown hyaenas are


Recent Eastern Africa

Recent Southern Africa

Koobi Fora Okote Mb.

Olduvai Gorge Bed I

Eastern African Composite

Southern African Composite

Figure 7. Morphospace plots of large-bodied carnivoran modern guilds and paleoguilds of Africa. Numbered morphotypes and symbols are as in Figure 6. Both modern guilds are relatively similar in representation of behavioral types and differ only in the presence of striped hyaenas in the eastern guild *vs.* brown hyaenas in the southern guild. Neither modern guild has taxa falling in the range of sabertoothed morphotypes. The Koobi Fora Okote paleoguild is missing the non-sabertoothed prey grappling morphotypes, while the Olduvai Gorge Bed I paleoguild has a lower diversity of felid morphotypes. The eastern and southern African composite paleoguilds (Table 3) have all behavioral groups represented, but differ in the forms of sabertoothed felids. The southern African composite paleoguild has a larger number of morphotypes represented only by dentition.

larger-bodied and more carnivorous than striped hyaenas. Neither extant guild has taxa falling in the regions occupied by sabertooth morphotypes.

When the paleoguild structure from Koobi Fora is examined (Figure 7), a marked difference from modern guilds is seen. Two morphotypes represented by postcrania, KF *Panthera* A and B, could not be plotted, yet were included in the statistical guild analyses. The Okote Member paleoguild, therefore, has only one more large-bodied species than the modern guild, yet the representation of behavioral types are quite different. The paleoguild has several, large prey-grappling sabertooths not found in modern guilds and the number of non-prey grappling species is lower. These three sabertooth morphotypes widen the region of ecomorphospace occupied by prey grappling species. In addition, the ecomorphology of the Koobi Fora *Crocuta* differs from the modern spotted hyaena and falls toward the canid region reflecting, in part, its less robust hindlimb. While *Panthera* A may have behaved similarly to a very robust, modern cheetah in terms of locomotion and prey capture technique, the only morphotype left that could possibly behave similarly to modern lions and leopards is *Panthera* B. Dental material of *Panthera* B (KNM-ER 874) may be that of a lion (Werdelin, pers. comm.), however, postcranial material shows some similarities to sabertoothed felids, as well as some unique features (Lewis, 1995) and probably does not belong with the dentition. In that case, lions or lion-like pantherines may have been present at Koobi Fora as previously noted (Leakey, 1976), although currently no evidence of leopards or leopard-like species have been found. This paleoguild, despite being not significantly different in the level of species packing from the modern eastern African guild as judged by DFC values, has taxa distributed in a different area of morphospace than the modern guilds. Because the KBS Member was represented by only three taxa (Table 3), guild studies for this member were not carried out.

In contrast to the Koobi Fora Okote paleoguild, Olduvai Gorge Bed I paleoguild is more similar to modern guilds in the behavioral types present and the morphotypes are packed more tightly. For example, the Bed I paleoguild has both lion and leopard morphotypes that are equivalent in ecomorphology to modern species (Figure 7). Except for the lack of *Homotherium*, all regions of ecomorphospace shown in Figure 6 are occupied, unlike the Koobi Fora Okote paleoguild. Two Bed I morphotypes, however, could not be included. The first, *Canis africanus*, is represented only by dentition and possibly one tibia (OLD/63 EF.HR 159). The morphology of the tibia suggests that this species, whether it is *C. africanus* or another species, may be an enlarged jackal-like form similar in morphology to modern black-backed jackals (Lewis, 1995).

The Olduvai Gorge Bed II paleoguild is even more similar to the modern guild in the appearance of the striped hyaena and the disappearance of *Dinofelis*. Bed II, however, also has the flesh-slicing hyaenid *Chasmaporthetes* (pers. obs.; Werdelin & Turner, 1996) for which no postcrania are known at this site. Studies of *Chasmaportehetes* from North America (Berta, 1981) suggest a more cursorial mode of locomotion than modern hyaenids. *Chasmaporthetes*, therefore, may have been played a role similar to that of a robust cheetah in the Bed II paleoguild. In addition, a fragmentary sabertooth canine (OLD 068/6158) may be *Homotherium* or another large machairodont. Bed II was not included in guild analyses due to the low number of morphotypes with postcrania.

Comparisons of composite paleoguilds

The portions of Olduvai Gorge and Koobi Fora examined are relatively similar in age and are relatively close to one another geographically. Although different taxa are listed at each site, the possibility of taphonomic bias cannot be discounted. In addition, southern African sites have been difficult to date, and often represent a different period of time from those in eastern Africa. Creating composite guilds for both southern and eastern Africa, therefore, provides a means of assessing general differences between the guilds from these regions from approximately 1·0–2·0 mya (Table 3 and Figure 7) and between these composite paleoguilds and the modern carnivoran guilds. Each member of Kromdraai, Sterkfontein, and Swartkrans was examined separately (Lewis, 1995) and will be presented elsewhere. As these sites, along with

Bolt's Farm, are in close geographical proximity, results will be presented here that summarize the Transvaal region carnivoran paleoguild for comparison with eastern Africa. This southern composite guild includes all specimens from Kromdraai A, Sterkfontein Member 4, Swartkrans Members 1 and 2, and Bolt's Farm.

Both composite guilds have a greater number of morphotypes than modern guilds and both have all regions of morphospace occupied that are filled in Figure 6. The eastern African paleoguild has the greatest number of morphotypes ($n=11$) included in the analyses and is the least closely packed of any guild examined, as evidenced by MST and NND values. Of 13 total morphotypes in the eastern paleoguild, only two, *C. africanus* and *Chasmaporthetes*, could not be analyzed statistically.

The southern African paleoguild, however has a greater number of total morphotypes ($n=17$), only ten of which could be included in the analyses. The southern paleoguild has morphotypes that are similar in morphology to the two morphotypes not included in the eastern paleoguild analyses, as evidenced by dental material, as well as several other canid, hyaenid, and sabertooth morphotypes that could not be included in the morphospace plots due to lack of sufficient postcranial material.

Both composite paleoguilds exhibit a greater diversity of behavior in felids due primarily to the presence of sabertoothed felids. Sabertoothed felids behaved differently from modern felids and from one another as evidenced by both their placement in the morphospace plots and by functional analyses. Eastern and southern African *Dinofelis* morphotypes also differ somewhat in their placement within ecomorphospace, implying possible subtle behavioral differences between congeners. The three sabertoothed genera, however, differ greatly in position within ecomorphospace reflecting at least differences in habitat use and prey preferences (in terms of body size), if not in other aspects of ecology.

A similar increased behavioral diversity among hyaenids in the paleoguilds in comparison with extant African guilds is also apparent when the dental record is examined. Two species of the flesh-slicing *Chasmaporthetes* occur in paleoguilds in southern Africa and one in eastern Africa, although not represented by postcranial material in either region. In addition, *Pachycrocuta*, the robust, hyper-bone-cracking hyaenid, is found only in the southern paleoguild and is also represented only by craniodental material.

Discussion

Behaviors inferred from postcranial and craniodental morphology can be compared with predictions about carnivoran behavior based on actualistic studies and other studies of scavenging opportunities. Below is a discussion of several specific groups of carnivorans and the implications of their morphology for hominid scavenging opportunities.

Sabertoothed felids

Models drawn from Blumenschine (1987) and Marean (1989) predict that sabertoothed felids were predators of large prey and inhabited closed habitats (Table 1). Ecomorphological analyses demonstrate that sabertoothed felids probably captured larger prey than their non-sabertoothed relatives. *Homotherium*, in particular, due to its large size and robusticity could have captured the largest prey, and thus, provided the largest carcasses, but probably did not prefer closed habitats. *Dinofelis* and *Megantereon* probably frequented more closed habitats, but were also probably capable of capturing larger prey than modern felids. The remains of carcasses generated by the latter two sabertooths, however, would have provided, at the very least, bone marrow and head contents due to the inability of sabertooths to crack anything but the smallest bones (Ewer, 1967, 1973; Van Valkenburgh *et al.*, 1990).

Marean & Ehrhardt (1995) have suggested that *Homotherium* was adept at carcass disarticulation and body-part transport based on analyses of tooth marks and body-part representations at a den site in Friesenhahn Cave in Texas. They have extrapolated this behavior to African *Homotherium*, suggesting that *Homotherium* would only have provided scavenging hominids with moderate amounts of scavengeable material. The large body size and powerful limbs of African *Homotherium* are not inconsistent with this suggestion of body-part transport. Therefore, despite the larger body size of prey preferred by *Homotherium*, as inferred from *Homotherium* body size and limb morphology, members of this genus may not have left large amounts of food for hominid or other scavengers.

The postcranial morphology indicates that the Koobi Fora *Homotherium* was relatively cursorial for a sabertooth, with distally elongate limbs and a slight reduction in prey grappling abilities. This morphology implies a fundamentally different means of capturing prey from modern felids. Perhaps *Homotherium* was pack hunting cooperatively to some degree. Such a behavior has been suggested tentatively for North American *Homotherium* by Marean & Ehrhardt (1995) as a means of penetrating the shield formed by adult proboscideans around juveniles. Pack hunting or grouping behavior would mean that there would be even less of a chance of meaty resources being left on a carcass. The presence of a pack of *Homotherium* individuals would also make the possibility of confrontational scavenging from this species even more difficult. Grouping behavior in *Homotherium*, however, has been dismissed by Rawn-Schatzinger (1992) based on the suggestions that denning behavior does not favor large groups in felids and that *Homotherium* does not show healed fractures, which would indicate caretaking by others in the group. Marean & Ehrhardt point out, however, that large groups of hyaenids and canids may use relatively circumscribed dens and that neither lions nor hyaenas tend to injured companions, yet they do hunt in groups. Although social behavior is difficult to infer with any certainty in fossil species, the postcranial morphology, in combination with the size and grouping behavior of their preferred prey (e.g., juvenile proboscideans) could be evidence of *Homotherium* hunting in pairs or groups. At the least, the postcranial morphology of the Koobi Fora *Homotherium* suggests that prey were interacting with prey species in a manner unlike any modern species.

Tree-caching species

Tree-caching species, such as modern leopards, have also been included within the models as a possible source of size class 1 and 2 bovids (Cavallo & Blumenschine, 1989; Table 1). Although fossil leopards may have engaged in this behavior in the past, no leopards, nor any leopard-sized, prey-grappling felid, are recorded, however, during KBS and Okote Member times at Koobi Fora. This lack, however, may be a taphonomic artefact, because fossil leopards have been found at Olduvai Gorge.

Megantereon and *Dinofelis*, therefore, are the only other possible tree-caching taxa, given their postcranial morphology. The rotatory capabilities and strength in the forelimb of these genera suggest scansorial capabilities, however, this morphology could also be associated with grappling of prey that was relatively large for the predator's body size in a closed habitat. Several other morphological factors must also be considered.

For example, the possession of saber teeth may have made dragging a carcass into a tree difficult if not impossible without risk of damaging the enlarged canines. Studies of canine strength in extant and extinct carnivorans, have shown that sabertoothed felids with an elongated, recurved, and flattened canine shape, as possessed by *Megantereon*, would have been more susceptible to breakage from oblique or mediolaterally directed forces than those of modern felids (Van Valkenburgh & Ruff, 1987). The canines, therefore, would be at risk while transporting carcasses, as the shifting of an unevenly distributed load carried in the mouth could incur such forces.

Dinofelis, the other possible scansorial sabertooth, was not included in Van Valkenburgh & Ruff's (1987) study of canine strength. This genus has relatively short, straight canines for a sabertoothed felid (Hemmer, 1965; Kurtén, 1972) and may have been able to withstand greater mediolateral bending. African specimens of this genus are, however, larger overall and more robust than modern leopards. Despite possessing features related to the potential for scansorial behavior, body size may have been a limiting factor on scansorial ability, and thus, tree-caching behavior, regardless of canine strength.

Tree-caching behavior has been suggested to be an effective means of protecting kills from terrestrial scavengers (e.g., Cavallo & Blumenschine, 1989). As most felids are capable of tree climbing, albeit with some difficulty, even lions have been known to scavenge cached carcasses occasionally, but with difficulty (Kruuk & Turner, 1967; Pienaar, 1969). Apparently, however, this does not happen with enough frequency to make the energy expended in caching carcasses cost ineffective. It is unlikely that such a behavior would be practiced, however, if there were large numbers of scansorial individuals, hominids or otherwise, with the strength and agility necessary to steal cached carcasses on a regular basis. Brain (1981) has demonstrated that some of the fossil cave sites of southern Africa may have accumulated below leopard feeding trees growing out of cave openings and that leopards may have preyed upon early hominids. Several factors, therefore, suggest that caching was a viable means for Plio-Pleistocene leopards to retain their kills: (1) Brain's taphonomic evidence of leopard caching from southern Africa, (2) the lack of more than one leopard-like species at any site, (3) similarities in modern and fossil leopard postcrania, and (4) the possible increase in the chances of losing a carcass on the ground due to the greater number of terrestrial species higher in the carnivoran hierarchy than leopards.

Cavallo & Blumenschine (1989) have suggested that scavenging from these cached carcasses could have been part of a mixed arboreal–terrestrial scavenging strategy in contrast to the mixed, terrestrial hunting–scavenging strategy suggested by previous researchers. The question then is what impact would hominid scavengers have had on leopard behavior? Would regular scavenging by hominids have caused leopards in the past to be more diligent than modern leopards in guarding carcasses? An increase in diligence by leopards would have resulted in an increased risk of predation to hominids. Could regular, successful scavenging by hominids through time make caching behavior by leopards not worth the energy expended? If one assumes that leopards maintained this behavior through time, then either leopards were successfully defending or hiding their carcasses from hominids for at least a large enough portion of the time for caching to still be cost-effective, or hominids were not attempting to scavenge from cached kills on a regular basis. Given possible feedback in leopard behavior, hominid scavenging from cached carcasses may not account for all of the size class 1 and 2 bovids found at archaeological sites. This suggestion, however, does not negate the potential importance of arboreal scavenging opportunities to early hominids.

Bone-cracking species

Although research presented here cannot address bone-cracking abilities in specific taxa, bone-cracking, as defined by Werdelin (1989), is an important component of the remains of a carcass left on the landscape and must be addressed. Models drawn from Blumenschine and colleagues (Blumenschine, 1987; Blumenschine *et al.*, 1994) suggest that there should be relatively few bone-cracking species within a guild to maximize carcass remains left for scavenging (Table 1). A wide diversity of bone-cracking morphotypes existed in southern Africa during the Plio-Pleistocene (Werdelin & Solounias, 1991; Werdelin & Turner, 1996), while bone-cracking morphotypes at Koobi Fora and Olduvai Gorge have been assigned to modern species. Eastern African hyaenids at these sites, therefore, probably were not able to access the contents of bones larger than those accessed by modern hyaenids. This difference in behavioral diversity represents a fundamental difference in guild partitioning between the two regions. Although the greater diversity of a certain type of carnivoran during the Plio-Pleistocene does not imply a greater relative abundance of these morphotypes, eastern Africa lacked, at least by the period of time discussed in this paper, the hyper-bone-cracking *Pachycrocuta* of southern Africa. *Pachycrocuta* could have accessed the head contents and marrow cavities of larger skeletal material than modern hyaenids, leaving fewer remains for scavengers.

Combining data on the postcrania of known bone-cracking species with work by previous researchers on their dentition, aids in understanding the paleoecology of fossil representatives of these species. Unfortunately, among African fossil taxa assumed to be bone-cracking (species of *Crocuta*, *Hyaena*, *Pachycrocuta*, and *Parahyaena*), the one genus not represented by living species, *Pachycrocuta*, has no identifiable postcranial material at the sites and time period in question. Examination of the postcranial remains, however, of the other taxa yields some interesting results.

Although the majority of specimens are similar to their modern congeners, skeletons of *Crocuta* from Koobi Fora show many similarities to brown hyaenas in their hindlimbs (Lewis, 1995) The hindlimb of modern brown hyaenas and these fossil spotted hyaenas are similar due to the lack of robusticity in the fossil spotted hyaenas hindlimb relative to the forelimb. This difference must be explored further because it suggests either a difference in overall biomechanical ability in these fossil that may have affected the carcass carrying ability of the fossil morphotype.

Models also predict that bone-cracking species should not prefer closed habitats (Table 1). Although no bone-cracking species were found with features indicating a preference for closed habitats, modern spotted hyaenas in both eastern and southern Africa have been observed scavenging in riparian woodlands (Bearder, 1977; Bunn *et al.*, 1988; O'Connell & Hawkes, 1988). Riparian woodlands and more closed habitats might, therefore, not have represented a habitat with a large reduction in competition from hyaenids for scavengeable resources as originally modeled by Blumenschine (1987, 1989).

Guild comparisons

Although this study contains extant and fossil morphotypes that are much more closely related in terms of phylogeny and temporal and geographic distribution than those in previous studies of large-bodied carnivoran guilds (e.g., Van Valkenburgh, 1985, 1988), differences in guild structure across both time and space are apparent. Analyses of the paleoguilds demonstrate not only a greater diversity of behaviors, but also several fundamentally different ways of partitioning guilds in the Plio-Pleistocene.

The carnivoran paleoguild from Olduvai Gorge Bed I conforms most closely to the models. This paleoguild has flesh-slicing cheetahs and sabertooths, as well as two omnivorous canids. Leopards, lions, and spotted hyaenas similar to their modern conspecifics also occur. The two sabertooths, however, do differ in behavior. Both morphotypes may have preferred more mixed or closed habitats. *Dinofelis* may even have had the capabilities to access carcasses cached in trees by leopards. Neither sabertooth morphotype probably could have provided the large carcasses that a sabertooth such as *Homotherium* may have provided. The largest carcasses, therefore, within this guild may have been only slightly larger than those produced by modern lions.

The Olduvai Gorge Bed II carnivoran paleoguild may have had a large sabertooth morphotype, the specific behaviors of which are unknown. If this dental morphotype is *Homotherium* and similar to the Koobi Fora *Homotherium* (a reasonable assumption given geographical and temporal proximity of the two sites), then this morphotype may have behaved as discussed for the Koobi Fora *Homotherium*. This guild also had at least two omnivorous canid morphotypes and a lion similar to the modern lion. Two of the hyaenid morphotypes were probably similar to modern eastern African hyaenids. A third hyaenid, *Chasmaporthetes*, was a flesh-slicing species, the postcranial anatomy of which is unknown. Studies of *Chasmaporthetes* in North America (Berta, 1981) suggest that this species, at least, was robust and cursorial. The Bed II morphotype, therefore, may have provided carcasses within the range of those provided by modern carnivorans or, if this morphotype was a pack hunter, may have produced larger carcasses with only the flesh removed.

The Koobi Fora Okote carnivoran paleoguild differs from both of the Olduvai paleoguilds in having three and maybe four sabertoothed morphotypes. Behavioral differences among sabertooths have been discussed above. *Panthera* A might be modeled as behaving similarly in terms of prey acquisition to a robust version of the modern cheetah. This guild, therefore, had four or five flesh-slicing morphotypes and at least one omnivorous canid morphotype. The one hyaenid species, assigned to *Crocuta* due to dental characters, differs from modern *Crocuta* in postcranial features and is slightly less robust (Lewis, 1995). The dentition of this morphotype, however, had the bone-cracking capabilities of modern spotted hyaenas.

Due to taphonomic effects, the Koobi Fora and Olduvai Gorge paleoguilds may present only a part of the overall structure of the carnivoran paleoguild in this region. For example, the Koobi Fora Okote paleoguild lacks leopard morphotypes, although a leopard morphotype is found at Olduvai Gorge. Perhaps, therefore, it is most useful to examine the composite paleoguilds when attempting to reconstruct scavenging opportunities.

Examination of the composite paleoguilds of eastern and southern Africa show not only a greater number of species, but species behaving unlike modern species. Sabertoothed felids probably occurred throughout different habitats, each with its own preferred prey body size. Even congeners of modern species may not have been completely "equivalent" ecologically to extant species. The overall greater number of carnivoran species in both regions mirrored the larger number of prey species.

The southern African composite paleoguild is even less like modern guilds than the eastern paleoguild due to the diversity of prey grappling felids, flesh-slicing hyaenids, and large, bone-cracking hyaenids. Although an in depth discussion of southern African paleoguilds will be provided elsewhere, it should be noted that differences in the behavior of south African sabertoothed felids and bone-cracking hyaenids may have affected the distribution of carcasses on the landscape. These differences must be considered before applying models based on eastern Africa to southern Africa.

In contrast, the composition and morphospace distribution of modern guilds probably has been structured by the cumulative affects of the expansion of hominids and environmental changes affecting habitats and the numbers of prey species. Many of the larger prey species, and all of the largest predators from the Plio-Pleistocene, have disappeared. Surviving species may have expanded their niches to a small degree, resulting in small changes in predator body size or robusticity. The paleoguilds examined, therefore, represent a time period during which substantial restructuring was occurring as hominids, presumably, entered the carnivore guild and other groups, such as the sabertoothed felids and larger hyaenids, went extinct (Walker, 1984).

When just the postcranial evidence is examined, the overall body size and strength seen in *Homotherium* and *Dinofelis* suggest that these species may have been at or near the top of the carnivoran hierarchy. If *Homotherium* was pack hunting or exhibiting any form of grouping behavior, then members of this genus were probably at the top of the hierarchy in eastern Africa. Although postcrania are unknown for *Pachycrocuta* at the sites examined in southern Africa, members of this genus may have represented the greatest threat of competition to *Homotherium*. In addition, slight differences in the robusticity and body size of fossil representatives of modern species might mean differences in placement in the hierachy relative to one another.

These paleoguilds, therefore, appear to have been more complete ecologically than modern guilds. Larger, predatory carnivorans existed, such as *Homotherium*, that may have been predominantly flesh-eating and specializing on larger prey than modern species, and *Pachycrocuta*, that could crack open much larger bones than modern hyaenas. Other flesh-slicing carnivorans more similar in body size to modern species, filled out the guild, generating a wide variety of carcass sizes in a variety of habitats.

Through time however, the larger bone-cracking species disappeared, first in eastern Africa, and then in southern Africa. Next, the larger of the more specialized flesh-slicing species, such as the sabertoothed felids and *Chasmaporthetes* disappeared. Larger carnivoran species that survived seem to be, for the most part, highly adaptable in terms of prey preference, carcass utilization, and habitat use. Changes in morphology and body size in some of these species through time may reflect a redistribution of species within the guild in response to ecological gaps created by the extinction of the largest species.

Hominid behavior and evolution

In general, fewer scavenging opportunities available to hominids may have existed in the past than previously thought. Although the greater behavioral diversity of carnivorans does not necessarily imply a greater relative abundance, the greater number of species and the larger region of morphospace utilized suggests the possibility of a greater number of competitive encounters. The greater number of large-bodied species in both more open (e.g., *Homotherium* and possibly *Chasmaporthetes*) and more closed habitats (e.g., *Dinofelis* and *Megantereon*) suggests that unless early hominids were near the top of the carnivore hierarchy, confrontational scavenging would have been very difficult. Opportunistic scavenging would also have been slightly more limited. Previous research (Marean & Ehrhardt, 1995) has suggested that *Homotherium* transported body parts back to a den. The present research has demonstrated that *Dinofelis* and *Megantereon* probably did not generate carcasses much larger than modern carnivorans and, despite the potential for scansorial ability, probably did not cache their carcasses. In addition, hominid scavenging from tree-stored leopard kills may have been lucrative and at the lower levels of risk indicated by Cavallo & Blumenschine

(1989) only if practiced at low enough frequency to prevent leopards from becoming overly diligent.

Different ecological and/or evolutionary pressures were operating on hominids in eastern and southern Africa in the past with respect to dietary behavior. Although confrontational scavenging would have been risky in both regions, the lack of bone-cracking ability in sabertooths would mean that at least bone marrow and head contents might remain for passive scavenging even if a particular sabertoothed species exhibited grouping behavior at carcasses. Hominids would have had a better chance in eastern Africa than in southern Africa of acquiring these resources, as eastern Africa lacked the large-bone cracking *Pachycrocuta*. *Pachycrocuta* was probably the dominant bone-cracking carnivoran and capable of accessing the contents of much larger bones than modern hyaenids. This difference in guild composition suggest that it may have been easier for scavenging behavior to have arisen first in eastern African hominids.

If one reasons that changes in the guild structure of carnivorans impacted upon hominids in terms of restructuring hominid access to prey or to carcasses, then it follows that changes in hominid morphology may be reflecting changes in carnivoran behavior and/or overall changes in the structure of carnivore guilds once hominids entered the guild. This suggestion was well articulated by Walker (1984) in his analyses of the impact of hominids on the paleoecology of the carnivore guild. Hominids have been considered the cause of various extinctions, including that of sabertooth cats (e.g., Ewer, 1967), however, the extinction of sabertoothed cats and other large-bodied taxa may have provided the catalyst for human evolution as suggested by Turner (1988). The decline of the large-bodied carnivorans and the eventual appearance of our species may reflect a chain reaction, an important part of which was the extinction of the sabertooth cats in Africa. With the extinction of the sabertoothed species in eastern Africa and the reduction of closed habitats, hominids may have moved from passive scavenging, low in the hierarchy, to become a dominant group predator. The extinction of sabertoothed species and hyper-bone-cracking species opened a variety of behavioral avenues to hominids. Walker (1984) has suggested that hominids were already exhibiting grouping behavior when they entered the carnivore guild. If so, this would have aided their chances in competitive encounters. The need to maintain or increase their place in the carnivore hierarchy would have favored not only grouping behavior, but increases in body size and advances in tool technology.

Summary and conclusions

The purpose of this research was to investigate resources available to scavenging hominids and how those resources were affected not only by individual carnivoran species, but also by the interrelationships among members of the surrounding carnivoran paleoguilds. Current hominid dietary models based on actualistic studies (e.g., Blumenschine, 1987, 1988, 1989) provide the best fit in terms of modeling carnivoran dietary behavior for Olduvai Gorge, for which they were originally devised, and eastern Africa in general. Modifications of models made here include (1) the suggestion of a greater number of competitive interactions among carnivorans due not only to the greater number of species, but also to the more densely filled ecomorphospace during the Plio-Pleistocene, particularly in southern Africa, (2) a demonstration of behavioral differences among sabertoothed felids and between fossil genera and their extant congeners, (3) a morphologically-based confirmation of the ability of *Homotherium* to provide larger carcasses than modern felids, although with the caveats suggested by Marean & Ehrhardt (1995), (4) a decrease in the significance of carcasses provided by *Dinofelis* and *Megantereon* due to the size of carcasses and the probability that they were not cached, and (5) the suggestion that scavenging from carcasses cached by leopards must have been conducted at a low enough frequency to prevent changes in leopard caching behavior.

In all, the changes in carnivoran guilds from the Plio-Pleistocene to the present most likely represent a substantial shift in the nature of carnivoran interactions and the procurement and utilization of carcasses. As part of the carnivore guilds during the last 2 Ma, hominids would have been affected dramatically by these changes whether they were a primary instigator of changes in guild structure by contributing to the extinction of various species, or were passive opportunists widening their niche breadth with the disappearance of sabertoothed felids and the larger-bodied hyaenids. Whatever the cause of these changes in guild stucture (e.g., environmental, competition-based, or some combination of the two), hominids not only survived the changes, but also underwent substantial modifications themselves in terms of anatomy, tool technology, and, presumably, social behavior, that led to a shift in their position within and eventual dominance of the hierarchy of the carnivore guilds of Africa.

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