

# Hominid–Carnivore Coevolution and Invasion of the Predatory Guild

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Coevolution is defined as reciprocal selective pressures that operate to make the evolution of one taxon partially dependent on the evolution another. This process often involves multiple species exploiting shared limiting resources. In classic coevolutionary models, populations of sympatric species are seen to diverge in one or more morphological, ecological, or behavioral traits to effect more even partitioning of resources and reduce levels of interspecific competition. Character displacement and resource partitioning are thought to be central not only to how species coexist on limited resources, but also to how species invade new resource niches. Hominid invasion of the predatory guild at least 2 my ago would have brought them into contact with a range of new selective pressures including competition with a number of large-bodied predators. This study explores resource partitioning between hominids and other Plio-Pleistocene large-bodied predators through analyses of predator food transport strategies. The anatomical content (head/limb MNE) of hominid transported faunal assemblages at Bed I Olduvai and FxJj 50 (Koobi Fora), when compared to modern predator control cases, suggests that Plio-Pleistocene hominids practiced food transport strategies intermediate between those of top predators such as wolves and those of confrontational scavengers such as spotted hyenas. Plio-Pleistocene hominid food transport strategies do not resemble those of nonconfrontational scavengers such as brown and striped hyenas. The highly regular patterns differentiating bone assemblages accumulated by top predators, hominids, and confrontational and nonconfrontational scavengers suggest that hominid invasion of the predatory guild involved resource partitioning potentially based on some form of character displacement. © 1998 Academic Press

## INTRODUCTION

Numerous taphonomic and archaeological studies over the past two decades have led to a recognition of wide-spread and long-term associations between hominids and other large-bodied predators in past ecological communities. Indeed, throughout the course of hominid evolution there appears to have been a consistent overlap both in the use of space and in the foraging strategies employed by hominids and large-bodied predators (Clutton-Brock 1996; Stiner 1991a,b, 1994). Such hominid–carnivore associations are apparent in Plio-Pleistocene eastern and southern Africa (Binford 1981, 1984, 1985; Blumenshine 1987, 1995; Brain 1969, 1981; Bunn and Ezzo 1993; Bunn et al. 1980;

Lewis 1997; Oliver 1994; Potts 1982, 1988, 1991; Rose and Marshall 1996; Turner 1990; Walker 1984), Early Pleistocene western Asia and Europe (Bosinski 1995; Tchernov 1992; Turner 1992), and throughout the Old World during Middle and Late Pleistocene times (Germonpre and Lbova 1996; Goebel 1994; Han and Xu 1985; Huang et al. 1995; Olsen and Miller-Antonio 1992; Stiner 1991a,b, 1994).

The persistence of hominid–carnivore associations through space and time raises the possibility that coevolutionary pressures have dramatically affected the course of both hominid and carnivore evolution. Coevolution is defined as reciprocal selective pressures which operate to make the evolution of one taxon partially dependent upon the evolution of another

(Begon et al. 1990). Coevolution can involve multiple species, irrespective of taxonomic position. However, coevolution most frequently occurs among members of a feeding guild; classically defined as groups of species that utilize the same class of resources in similar ways (Jaksic 1981; Root 1967). The mechanisms underlying coevolution within a feeding guild revolve around interspecific competition for shared limited resources. The evolution of divergent behavioral, ecological, or morphological traits, to accomplish more even partitioning of resources among guild members are common coevolutionary outcomes.

Archaeological traces of Plio-Pleistocene hominid behavior suggest that hominids joined the predatory guild at least 2 my ago (Blumenschine 1987; Foley 1984; Lewis 1997; Turner 1990, 1992). As newcomers to the Plio-Pleistocene predatory guild, hominids would have been subject to an array of new selective pressures, including competition with large-bodied predators for meat and marrow resources (see Blumenschine et al. 1994). The nature and intensity of hominid-carnivore competitive interactions is suggested by patterns of carnivore and hominid damage on ungulate bones (Blumenschine 1995; Oliver 1994), ungulate skeletal element profiles (Binford 1981; Blumenschine and Marean 1993; Brantingham 1998; Marean et al. 1992; Potts 1983, 1988), and species diversity profiles (Binford 1981; Blumenschine 1987; Bunn and Ezzo 1993). The combined evidence implicates coevolutionary selective pressures as a major force in the evolution of the hominids (e.g., Shipman and Walker 1989; Walker 1984). Indeed, hominid-carnivore coevolution may have been integral to the evolution of a variety of unique human traits such as lithic technology (Blumenschine 1987), large brains (Aiello and Wheeler 1995), and complex social and foraging group organization (Binford 1981, 1984;

Brantingham 1998; Isaac 1978, 1983; Potts 1988, 1991; Rose and Marshall 1996; Shipman and Walker 1989).

This study addresses several questions: What types of coevolutionary relationships (if any) existed between Plio-Pleistocene hominids and large-bodied predators? Which predators were most likely involved? Did interspecific competition over prey animals lead to resource partitioning among Plio-Pleistocene predators? If resource partitioning is apparent, was it founded on some form of behavioral, ecological, or morphological character displacement? Many of these questions are implicit in recent studies of the structure of hominid scavenging opportunities (Blumenschine 1987; Blumenschine and Cavallo 1992; Cavallo and Blumenschine 1989; Lewis 1997; Potts 1988) and more generally underlie studies of Plio-Pleistocene hominid competitive efficiency (Binford 1981; Blumenschine 1995; Blumenschine et al. 1994; Bunn and Ezzo 1993; Rose and Marshall 1996). Here I focus on food transport behaviors in analyzing hominid-carnivore coevolutionary relationships. Food transport behavior is only one of several possible dimensions of hominid and predator foraging adaptations relevant to the study of hominid-carnivore coevolution (see Potts 1994). Food transport behavior is a logical starting point for several reasons. First, extensive habitual food transport is a key behavior distinguishing large-bodied predators from nonhuman primates (Potts 1991; Rose and Marshall 1996; Stiner 1994). Second, food transport is thought to be a primary behavioral mechanism for reducing levels of interspecific competition (Begon et al. 1990; Krebs and Davies 1993; Potts 1991; Stiner 1994; Vander Wall 1990). Thus, food transport may be expected to have played a critical role not only in hominid predatory adaptations but also in structuring potential hominid-carnivore coevolutionary relationships.

Plio-Pleistocene faunal assemblages from Bed I Olduvai Gorge (1.8–1.75 my) and Koobi Fora (1.9–1.5 my) comprise the early hominid sample used in this study (see Bunn 1982, 1986; Bunn et al. 1980; Leakey 1971; Potts 1982, 1988). Ethological data on modern predators are taken from a variety of sources (e.g., Kruuk 1972; Hoffer and East 1993; Mills 1989 1990; Schaller 1972). The comparative zooarchaeological data on predator bone transport are taken from Stiner (1994). Stiner's (1994: 249) measures of the anatomical content (head/limb MNE) and anatomical completeness (total MNE/MNI) of transported bone assemblages form the core of the analyses presented. These measures appear to differentiate predator faunal transport strategies. I also draw on some classical models of niche spacing (MacArthur 1972; MacArthur and Levins 1967; May 1974) to help characterize these data in terms of interspecific competition, resource partitioning and character displacement.

#### COMPETITION, CHARACTER DISPLACEMENT, AND RESOURCE PARTITIONING

Any discussion of hominid-carnivore coevolution necessarily involves a consideration of interspecific competition, character displacement, and resource partitioning. These processes are thought by many ecologists to be integral to the way that ecological communities are assembled and evolve through both space and time (Begon et al. 1990; Dayan and Simberloff 1996). The seminal paper by Brown and Wilson (1956) on competitive character displacement began with the observation that populations of closely related species differed more in sympatry than they did in allopatry. Character displacement is thought to occur where two

... closely related species have overlapping ranges. In the parts of the ranges where one species occurs alone, the populations of that species are similar to the other species and may even be difficult to distinguish from it. In the area of overlap, where the two species occur together, the populations are more divergent and easily distinguished, i.e., they 'displace' one another in one or more characters. The characters involved can be morphological, ecological, behavioral, or physiological; they are assumed to be genetically based. (Brown and Wilson 1956: 49)

Brown and Wilson (1956) surmised that selective divergence to minimize competition over a limited resource was the most likely explanation for these observed patterns.

The original definition of coevolutionary character displacement has been modified in several ways since the publication of the Brown and Wilson initial study. First, models of interspecific competition, character displacement, and resource partitioning have moved beyond a strict consideration of closely related species to consider the effects of these processes among distantly related taxa (e.g., Schluter 1986). The ideas of Brown and Wilson (1956) also have been extended to include resource partitioning and character displacement among multiple taxa, rather than just species pairs (e.g., Dayan and Simberloff 1996). This broader conception is known as "community-wide character displacement" (Dayan et al. 1990; Strong et al. 1979). Many examples of community-wide character displacement point toward coordinated divergence in feeding apparatus (e.g., tooth, jaw morphology) or body sizes (e.g., Dayan and Simberloff 1996; Dayan et al. 1989, 1990; Schluter 1994). Other examples document divergence in behavioral or ecological characters such as activity times or habitat preferences (e.g., Hickey et al. 1996; Ilse and Hellgren 1995). The result in all of these cases appears to be greater differentiation in the sizes or types of food re-

sources captured and consumed by competitors.

Models of competition-driven character displacement and resource partitioning have not been accepted without criticism. First, field studies and experiments demonstrating unequivocally both the occurrence and the effects of interspecific competition are few in number (Roughgarden 1983; Simberloff 1983; but see Schluter 1994; Schoener 1983). Second, changes in specific morphological (or behavioral) traits have been difficult to link to patterns of resource partitioning (Bernardo et al. 1995; Van Valkenburgh and Wayne 1994; but see Dayan and Simberloff 1996; Lewis 1997; Spencer 1995). Finally, it has been difficult to model and explain the mechanisms for inheriting behaviorally based resource partitioning (Arthur 1987).

These criticisms make it clear that we need to be cautious about extending the role of interspecific competition and character displacement too far (Connell 1980; Vrba 1992). It is questionable, for example, whether interspecific competition can be a primary mechanism in macroevolutionary events including speciation and extinction (e.g., Walker 1984). Additional experimental and field research is needed before such claims can be made. At the same time, interspecific competition, character displacement, and resource partitioning do appear to play important roles in the assembly of ecological communities, especially the behavioral and ecological organization of feeding guilds.

A number of studies have focused on interspecific competition, character displacement, and resource partitioning within predatory guilds. Studies of morphological character displacement include tracking divergent canine morphology among the small cats, canids, and mustellids of Israel (Dayan et al. 1990; Dayan and Simberloff 1996) and body size relationships among the North American mustellids (Dayan et al.

1989) and Neotropical cats (Kiltie 1984; see also Biknevičius and Van Valkenburgh 1996; Dayan et al. 1991; Gittleman 1985; Lewis 1997; Rozenzweig 1966; Van Valkenburgh 1985, 1988, 1996). Fewer studies have addressed behavioral or ecological character displacement among predators, though recent research on the effects of interspecific competition on group size and territorial defense may qualify (Grant et al. 1992; Wrangham et al. 1993; see also Van Valkenburgh and Wayne 1994). Issues of interspecific competition and resource partitioning are often implicit in studies of carnivore ethology (e.g., Creel and Creel 1995; Hoffer and East 1993; Kruuk 1972; Mills 1989, 1990; Schaller 1972). However, it has been difficult to operationalize explicit studies of these coevolutionary processes, perhaps because of the long generation times and the complexity of carnivore behavior.

Despite widespread interest in hominid-carnivore interactions, the range and importance of coevolutionary connections between these predators remains to be established. Questions of coevolutionary character displacement and resource partitioning between hominids and predators have been addressed explicitly in only a few studies (e.g., Walker 1984). Yet, these issues form the subtext in numerous others (Binford 1981, 1984, 1985; Blumenschine 1986a,b, 1987, 1995; Blumenschine and Cavallo 1992; Blumenschine et al. 1994; Blumenschine and Marean 1993; Brantingham 1998; Bunn and Ezzo 1993; Cavallo and Blumenschine 1989; Lewis 1997; Marean et al. 1992; Marean and Ehrhardt 1995; Potts 1983, 1988, 1991; Rose and Marshall 1996; Shipman and Walker 1989; Stiner 1991a, 1994). Below I present an explicit archaeological model of resource partitioning. The model may be used to infer levels of interspecific competition and in some cases the nature and intensity of competitive character displacement.

## AN ARCHAEOLOGICAL MODEL FOR RESOURCE PARTITIONING

Many formal models of resource partitioning are, at this stage, difficult for archaeologists to apply (e.g., Tillman 1982; Turelli 1981); numerous complicating assumptions about carrying capacities, predator and prey population densities, habitat structures, and the like would have to be made in order to faithfully apply these models to the archaeological record. The alternative is to turn to relatively simple models (e.g., MacArthur 1972; MacArthur and Levins 1967; May 1974) to begin to delineate potential coevolutionary relationships between early hominids and large-bodied predators. These models have their own weaknesses, but in general are well suited to the types of data available to archaeologists.

MacArthur and Levins (1967) and others have developed a series of relatively simple mathematical functions to describe how groups of species utilize a given resource (Fig. 1) (MacArthur 1972; May 1974). The models assume that the resource being utilized is unidimensional and distributed continuously (see Lyman 1994b). It is assumed also that each species has its own realized niche along the resource axis and that the species consume resources principally within those niche spaces. For analytical purposes, I use the term niche to refer to the relationship between an organism and a unidimensional resource. Thus, an organism's overall adaptation will be composed of many such niches. The efficiency of resource consumption is assumed to be highest at the center of the niche and less efficient toward the edges. The distribution of consumption efficiencies is what is described by the resource utilization function (RUF).

The MacArthur and Levins (1967) model suggests that the intensity of interspecific competition over a shared resource is proportional to the degree of

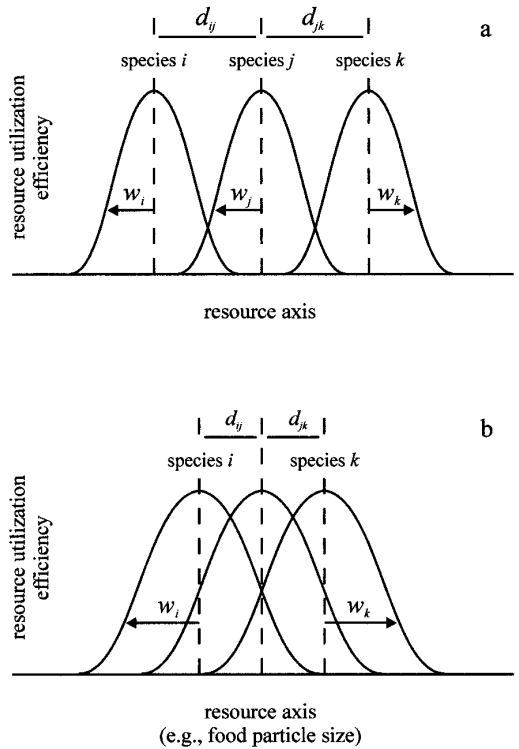


FIG. 1. (a,b) General graphical model of niche spacing and resource partitioning. Each curve represents the resource utilization function of a species along a unidimensional resource axis. After Begon et al. (1990: 271).

overlap in RUFs. The degree of RUF overlap is given by the formula

$$\alpha_{ij} = C_{ij}^{-d_{ij}^2/2(w_i^2 + w_j^2)}, \quad (1)$$

where  $\alpha_{ij}$  is the competition coefficient for species  $i$  on species  $j$ ,  $C_{ij}$  is a normalizing constant such as the base of a natural logarithm ( $e$ ),  $d$  is the distance between the means of the resource utilization functions, and  $w_i$  and  $w_j$  are the standard deviations (MacArthur and Levins 1967; May 1974). Thus,  $\alpha_{ij}$  is small and levels of interspecific competition are expected to be low when the curves are separated by a considerable degree (i.e.,  $d/[w_i \times w_j]^{1/2} \gg 1$ ) (Fig. 1a). In contrast,  $\alpha_{ij}$  approaches unity and levels of competition are expected to

be high with increasing overlap in the curves (i.e.,  $d/[w_i \times w_j]^{1/2} < 1$ ) (Fig. 1b). Importantly, the degree of overlap in this single resource dimension does not necessarily indicate the dynamics of interspecific interactions involving other resource dimensions. For example, the relative frequencies of prime-aged red deer in a comparative sample of Upper Paleolithic cave sites and hyena dens (e.g., Stiner 1991b) might define two RUFs describing the general utilization patterns of those prey by humans and hyenas. Similar frequencies of prime-aged animals in both hominid and hyena sites indicate overlapping utilization patterns. In turn, overlapping utilization patterns imply more frequent and more violent competitive encounters over prime-aged animals. However, inferred levels of interspecific competition over prime-aged red deer do not necessarily reflect the nature or intensity of competition over juvenile fallow deer, denning space, or any other shared resource.

MacArthur and Levins (1967) also suggested that there was a limit to the amount of RUF overlap that could be tolerated by two or more species (see also May 1974). Beyond this limit, competitive exclusion was likely to occur. This critical tolerance point has come to be known as the *limiting similarity* and is mathematically derived as  $\alpha_{ij} > .544$  (MacArthur and Levins 1967). In other words, coexistence of competitors was thought to be impossible if levels of competition went above this level. Similarly, invasion of a niche was thought to be impossible if the resulting niche positions produced competition coefficients above this tolerance point. In this case, species already established along the resource axis could prevent others from invading the niche.

Most ecologists no longer talk about a "universal" limit to similarity (Tillman 1982; Begon et al. 1990). Rather, it would appear that limits to similarity are system

specific and involve a fair degree of flexibility in how niche positions can be modified to deal with changing community and environmental characteristics. Ecologists now speak of an "optimal similarity" between species exploiting the same class of resource. Thus, the conditions leading to competitive exclusion of either established species or would-be invaders are quite narrow.

Yet, at some level competitive interactions do impact fitness, and to avoid these selective pressures species evolve towards an optimal similarity (or optimal dissimilarity). This optimal similarity should be reflected not only in the divergence of particular behavioral, ecological, or morphological traits, but also in the even partitioning of resources among competitors.

#### PREDATOR FOOD TRANSPORT

Food transport is central to many mammalian predatory adaptations (Ewer 1973; Kruuk 1972; Mills 1989, 1990; Stiner 1994). From the perspective of the individual forager, food may be transported to (1) monopolize the food source, (2) gain a processing advantage, (3) provision dependents, (4) share with other capable foragers, and (5) improve upon one's choice in mates (Stiner 1994:221; see also Bunn et al. 1988; Kelly 1995; O'Connell et al. 1990; O'Connell and Hawkes 1988). The first two "goals" of food transport play important roles in reducing feeding competition with both conspecifics and other predatory animals. Transporting animal tissues, to be cached for later consumption (Brain 1981; Mills 1990; Vander Wall 1990) or for immediate, unimpeded consumption, may effectively prevent other animals from gaining access to those resources. For this reason, transport of animal tissues may be a principal mechanism for partitioning a limited resource among various predators. The latter "goals" of food transport also influence intra- and inter-

specific competition, but serve complex social functions as well.

Complex food packages such as medium-sized ungulate carcasses can be divided up in numerous ways for transport (Bunn et al. 1988; Metcalfe and Barlow 1992). A variety of factors such as the condition of the animal when encountered, the distance from storage, processing, or consumption locations, the number of individuals present, and the possession of technology/morphology for processing certain types of tissues all may influence the final form in which animal tissues are transported (Binford 1978, 1981, 1984; Blumenshine 1986a,b, 1987; Blumenshine and Cavallo 1992; Brantingham 1998; Bunn et al. 1988; Lupo 1993; Lyman 1994a; Metcalfe and Jones 1988; O'Connell et al. 1990; O'Connell and Hawkes 1988; Perkins and Daly 1968; Potts 1988, 1991; Selvaggio 1994; Stiner 1994; Van Valkenburgh 1996). Character displacement operating in any one of these arenas could facilitate resource partitioning. For example, displacement of behavioral (e.g., Binford 1980; Hoffer and East 1993; Lieberman and Shea 1994) or morphological (e.g., Alexander 1991; Lewis 1997; Van Valkenburgh 1985) traits relating to foraging mobility or group size could effectively partition the timing of carcass access among predators (Brantingham 1998; Rose and Marshall 1996; Shipman and Walker 1989). Different carcass access times determine not only whether complete or partial carcasses are encountered, but also consumption sequences, the types of competition encountered at carcasses, and what skeletal elements are available for transport (see Blumenshine 1986a,b; Brantingham 1998; Potts 1983).

While the complex interactions of these factors are often difficult to tease apart for individual archaeological cases, comparisons of multiple bone assemblages may point to some consistent differences in the bone transport behaviors of different

large predators. In this regard, Stiner (1991a, 1994) has developed a log-log regression model that appears to separate predatory food transport strategies into a few broad groups. Stiner's model compares the anatomical content to anatomical completeness of carcasses represented in transported faunal assemblages. The behavioral correlates for the regression model come from actualistic and wildlife studies of modern carnivores (Stiner 1991a, 1994). Anatomical content refers to the types of skeletal elements transported from an encounter site, and here is measured as the ratio of the minimum number of head and horn elements to the minimum number of limb elements above the feet (head/limb MNE) (Stiner 1994; for a definition of these zooarchaeological counting units see Lyman 1994a); the ratio of head to limb elements in a complete carcass is 0.3. Anatomical completeness refers to the proportion of a complete carcass transported away from an encounter site and is measured as the ratio of the total minimum number of elements to the minimum number of individuals (tMNE/MNI) (Stiner 1994); the ratio of tMNE to MNI in a complete carcass is 106.

The regression highlights a range of food transport strategies practiced by modern and Pleistocene predators (Fig. 2) (Stiner 1994: 250–270). In general, the regression reveals a significant pattern of increasing frequency of head elements in transported assemblages as body part completeness in the same assemblages decreases ( $r = -0.70$ ,  $p \ll .001$ ). Transported faunas dominated by head elements appear to characterize the strategies of brown and striped hyena. In contrast, more complete carcass transport tends to characterize the strategies of wolves. However, since many of the bone assemblages come from contexts where the predators are not sympatric, I regard the observed patterns as generalized niches for predators engaging in different

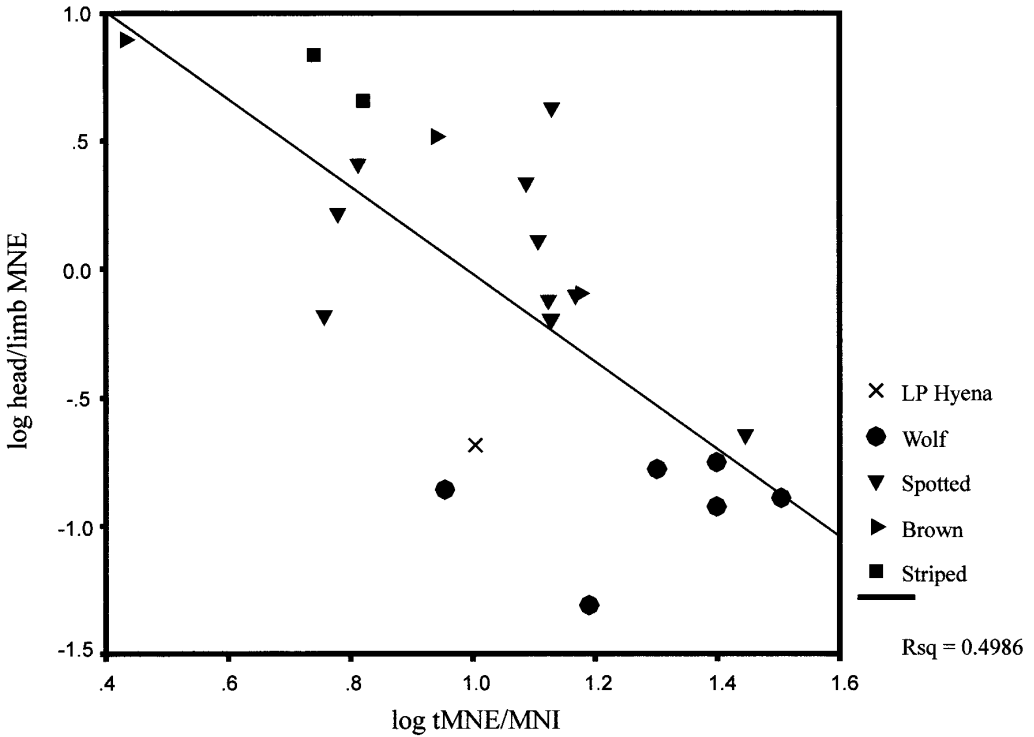


FIG. 2. Stiner's (1994) log-log regression of anatomical content (head/limb MNE) by anatomical completeness (tMNE/MNI) for several modern and Late Pleistocene predator control cases. LP hyena refers to the site FLKNN-2, which is attributed Plio-Pleistocene hyenas.

bone transport strategies (see Stiner 1994). These food transport niches are behaviorally rather than taxonomically defined. Three generalized niches are apparent: those of top predators, those of confrontational scavengers, and those of nonconfrontational scavengers. Top predators such as wolves are primarily hunters and concentrate on acquiring, transporting, and consuming bone-exterior tissues, including flesh and organs, and some bones as well; top predators will occasionally scavenge as well as break bones to gain access to bone-interior tissues such as marrow and head contents (see Binford 1981; Haynes 1982, 1983a,b). For the most part, bone assemblages accumulated by top predators are characterized by more complete carcasses and an emphasis on

meat-bearing skeletal elements (Binford 1981; Marean and Ehrhardt 1995).

Confrontational scavengers such as spotted hyenas concentrate on actively scavenging carcasses early in their resource lives to gain access to bone-interior tissues (see Blumenschine 1986a, 1987; Bunn and Ezzo 1993; Hoffer and East 1993; Mills 1990). Some confrontational scavengers also may actively hunt (Kruuk 1972; Mills 1990). Bone assemblages accumulated by confrontational scavengers are characterized by less complete carcasses and a predominance of skeletal elements bearing the greatest amounts of bone-interior tissues such as the larger limb bones and heads.

Nonconfrontational scavengers such as brown and striped hyenas rarely hunt



prey larger than or even similar in body size to themselves (Brain 1981; Mills 1990). Rather, nonconfrontational scavengers concentrate on opportunistically acquiring abandoned carcass parts from medium-sized herbivores for remaining bone-interior tissues and bone grease. Bone assemblages accumulated by nonconfrontational scavengers are characterized as very incomplete carcasses and a predominance of elements such as heads that tend to remain at carcasses after ravaging by other large-bodied predators (Potts 1983; Stiner 1991a, 1994; see also Blumenschine 1986a,b; Blumenschine and Cavallo 1992).

The reasons for this consistent pattern stem from the ecological parameters discussed above, but among these, the condition of the carcass when encountered and the nutritional status of both predator and prey appear to be particularly important: While head elements are often among the last elements to remain at a carcass ravaged by a succession of carnivores (Blumenschine 1986; Potts 1983), they also contain tissues that are rich in fats and carbohydrates throughout the year (Stiner 1991a, 1994; Speth 1987; Speth and Spielmann 1983). As a consequence, food transport strategies emphasizing head elements can be very attractive under a variety of circumstances.

It also is possible that the observed relationships between anatomical completeness and anatomical content may be related to the bone-crunching abilities of the different predators (see Blumenschine and Marean 1993; Marean et al. 1992). In this case, the more complete carcasses (high tMNE/MNI) seen in wolf accumulated assemblages may reflect less ability to destroy skeletal elements. In contrast, the less complete carcasses (lower tMNE/MNI) found in spotted hyena accumulations may reflect a greater ability to access bone-interior tissues and a propensity for destroying certain skeletal elements

through gnawing. If true, and assuming that complete carcasses were initially present in all of the assemblages, the general trend seen in the regression of increasing frequencies of head elements at the same time as carcass completeness decreases would be a taphonomic effect reflecting the degree of predepositional carnivore ravaging. The primary implication would be that the regression does not distinguish between different predator food transport strategies.

It is unlikely, however, that bone-crunching fully explains the observed patterns in Fig. 2. Indeed, it is not clear that the bone-crunching abilities of wolves (Binford 1981; Haynes 1982, 1983a,b), spotted hyenas (Blumenschine 1986; Blumenschine and Marean 1993; Lam 1992; Marean et al. 1992; Sutcliffe 1970), and brown and striped hyenas (Brain 1981; Ewer 1973; Mills 1990) differ to such a degree as to allow differentiation of these taxa within the regression; wolves are very efficient bone modifiers under certain circumstances; spotted, brown and striped hyenas have very similar dental and jaw morphologies and tend to modify bones in similar ways (see Biknevicius and Van Valkenburgh 1996; Brain 1981; Ewer 1973; Van Valkenburgh 1996). Thus, if the regression was merely tracking bone-crunching ability I would expect to see less of a spread between the predators. Since this is not the case either visually or statistically (Stiner 1994: 262–263), I favor the interpretation that the observed patterns are the result of different predatory bone transport strategies.

Each of the axes of the regression may be presented as unidimensional RUFs. Presenting the data in this way may help clarify the general shapes and positions of different predatory bone transport niches. Here I focus on anatomical content (log head/limb MNE). Figures 3a–3c present histograms for the anatomical content of assemblages collected by brown and

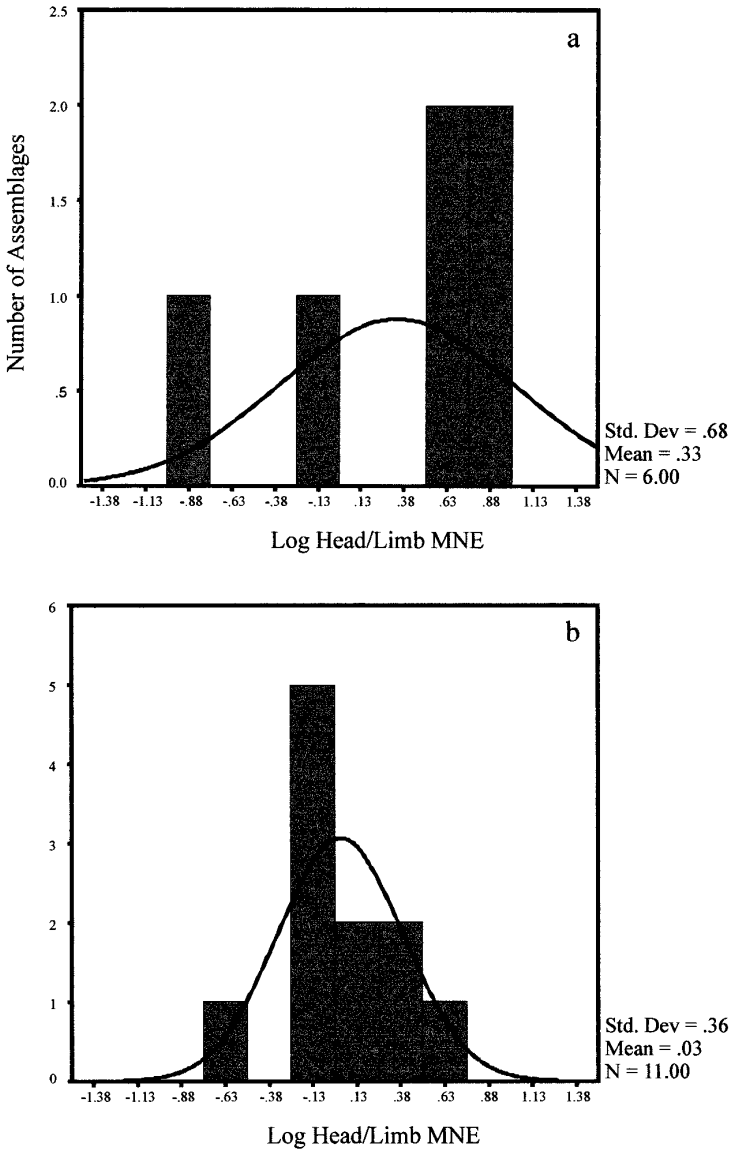


FIG. 3. (a-d) Resource transport functions for (a) brown and striped hyenas, (b) spotted hyenas, (c) wolves, and (d) Plio-Pleistocene hominids. Curves to the left of  $-0.52$  are limb/heavy relative to a complete carcass, whereas curves to the right are head heavy. Bed I Olduvai and Koobi Fora data are from Potts (1988) and Bunn (1982, 1986). Remaining data are from Stiner (1994).

striped hyenas, spotted hyenas, and wolves. Brown and striped hyenas are combined in this analysis to increase sample size. From a behavioral standpoint, this combination is acceptable because both species are nonconfrontational scav-

engers of similar body size, employ similar foraging tactics, and prefer primarily open habitats (Brain 1981; Gittleman 1985; Lewis 1997; Mills 1990). The RUFs illustrate the tendency for brown and striped hyenas, spotted hyenas, and wolves to

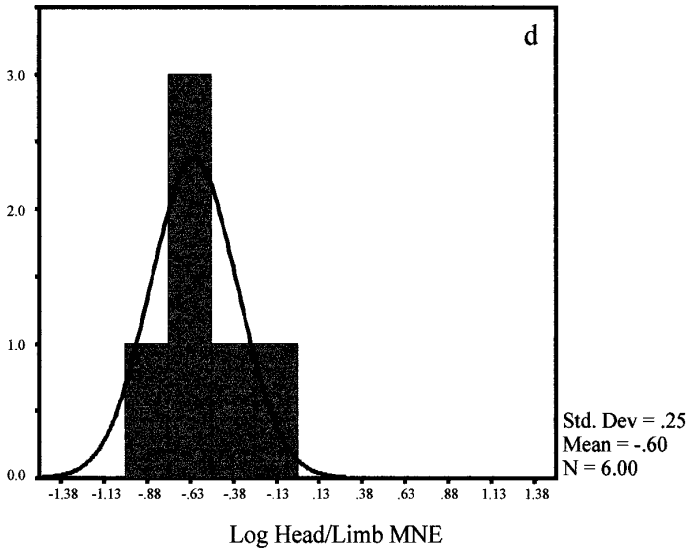
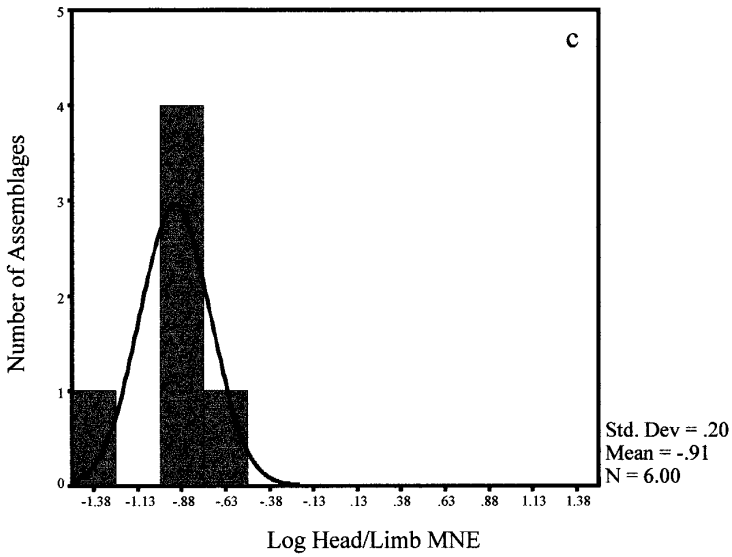


FIG. 3—Continued

transport somewhat different ranges of skeletal parts. The mean ratio of log head/limb MNE for brown and striped hyenas is 0.33 (extremely head heavy), while for spotted hyenas it is 0.03 (moderately head heavy) and wolves  $-0.91$  (extremely limb heavy). A series of pair-wise  $t$  tests indicate that these differences are statistically significant (brown/striped by spotted  $t =$

$2.6$ ,  $p < 0.05$ ; brown/striped by wolf  $t = 7.584$ ,  $p \ll 0.001$ ; spotted by wolf  $t = 6.962$ ,  $p \ll 0.001$ ).

Figures 4a–4b are based on the same data presented in Fig. 3, but focus on normalized RUFs generated from the data. The RUFs give a visual impression of the degrees to which generalized food transport niches overlap, and may indicate lev-

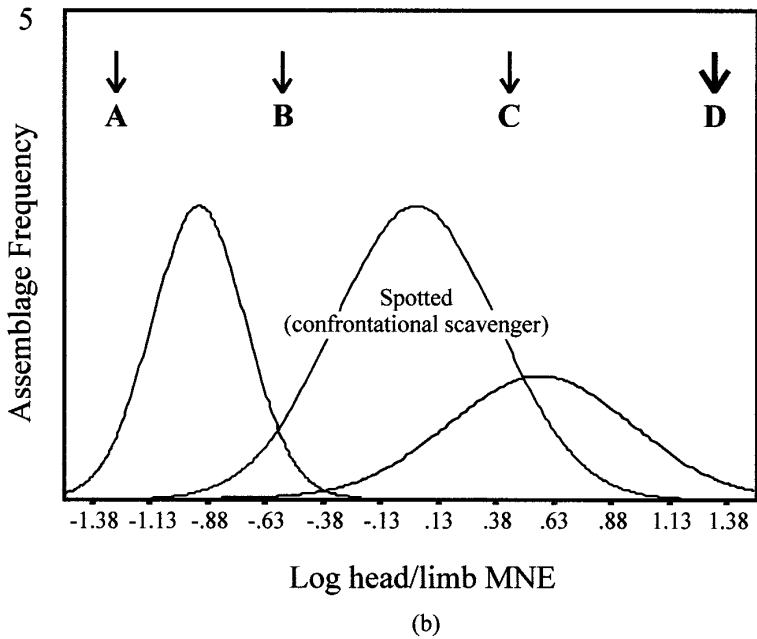
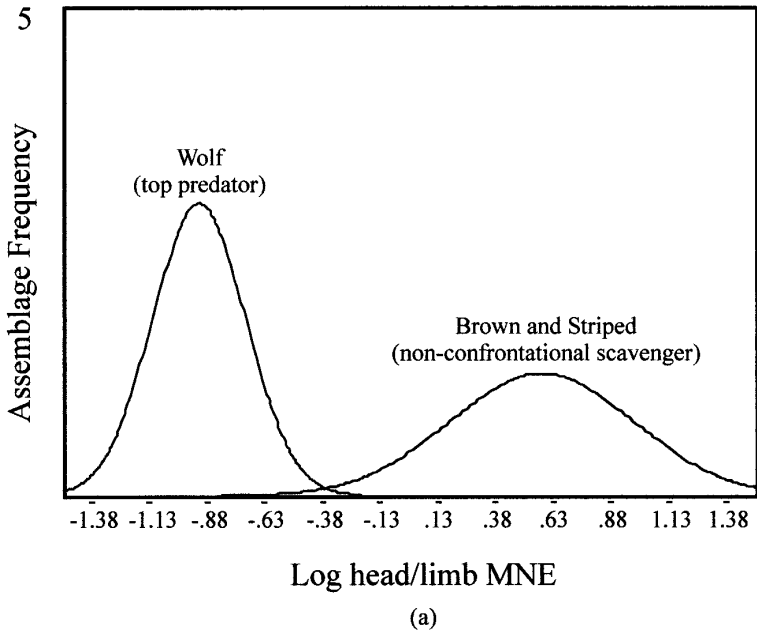


FIG. 4. (a,b) Resource transport functions for three large-bodied predators. Letters A, B, C, and D identify possible locations where hominids could invade the resource axis.

els of competition for certain skeletal elements. For example, the range of overlap in resource transport strategies between

spotted (confrontational scavenger) and brown and striped hyenas (nonconfrontational scavengers) suggests potentially

TABLE 1  
Competition Coefficients ( $\alpha$ ) Calculated for Four  
Different Predators' Food Transport Behaviors<sup>a</sup>

	B/S	S	W	LP
B/S	1.00			
S	0.60	1.00		
W	0.004	0.07	1.00	
LP	0.05	0.36	0.63	1.00

<sup>a</sup> Formula for calculating  $\alpha$  as in Eq. (1). Means and standard deviations for log head/limb MNE as in Figs. 3a–3d. B/S, brown and striped hyenas; SPT, spotted hyenas; W, wolf; LP, Lower Paleolithic hominid.

high levels of interspecific competition. Mills (1990: 260–265) observed numerous interactions between brown and spotted hyenas at both hunted and scavenged carcasses, leading her to conclude that spotted hyenas are generally dominant in these contexts. In a number of cases, however, brown hyenas were able to successfully defend carcasses from spotted hyenas. While resource defense generally is not a characteristic strategy of risk-averse, nonconfrontational scavengers such as brown and striped hyenas, direct (and violent) encounters with confrontational scavengers are predicted by the degree of overlap in spotted and brown and striped hyena RUFs. The degree of overlap in the skeletal elements transported by wolves (top predator) and spotted hyenas is considerably less. There is very little overlap in the skeletal elements transported by wolves and brown and striped hyenas. These data point to moderate levels of interspecific competition between top predators and confrontational scavengers, and very low levels of competition between top predators and nonconfrontational scavengers. Competition coefficients calculated using the formula given in (1.0) reinforce the visual interpretations of Fig. 4a (Table 1).

Figures 4a–4b and Table 1 also provide analytical boundaries for developing ex-

pectations about the nature of coevolutionary relationships between hominids and other large-bodied predators. Four analytical possibilities for hominid invasion of the bone transport niche are suggested (labeled A, B, C, and D in Fig. 4b). Positions A and D represent extreme strategies: Early hominid invasion at point A would be identified by assemblages consisting almost exclusively of limb elements. Such hypothetical bone assemblages would suggest that hominids had consistent access to both the meat and marrow associated with those elements. Invasion at point C would be identified by assemblages consisting almost exclusively of head elements, and would suggest that hominids had consistent access to head contents but infrequent access to the meat and marrow resources associated with limb elements. The attraction to invading the predatory niche at either of these two points is that such strategies would be bounded by competing predators only from one side. Invasion at point D, for example, would entail exploitative competition (Schoener 1983) primarily with predators practicing an nonconfrontational scavenging strategy. Competitive interactions with top predators and confrontational scavengers would be less important. In contrast, invasion at either point B or C would potentially involve contending with predatory bone transport strategies on both sides. Invasion at point B, for example, could involve interference competition (Schoener 1983) with both top predators and confrontational scavengers.

To begin to delineate which of these analytical possibilities may apply to Plio-Pleistocene hominid invasion of the food transport niche, I first return to Stiner's (1991a, 1994) log–log regression model to examine the location of several Plio-Pleistocene sites with respect to the predators discussed above. Following this analysis I focus on a more detailed comparisons of

hominid and predator resource transport functions.

### PLIO-PLEISTOCENE HOMINID FOOD TRANSPORT

Faunal assemblages from several East African Plio-Pleistocene sites are discussed below. Data from the Olduvai Bed I sites derive primarily from Potts (1988; but also Potts 1982; Bunn 1982, 1986). The Olduvai Bed I sites under consideration include DK, FLKNN-3, FLK North 6, FLK "Zinjanthropus," and FLKN 1-2. FLKNN-2 is also included and is attributed to Pleistocene hyenas. FxJ 50 is a Plio-Pleistocene site from Koobi Fora (Bunn 1982; Bunn et al. 1980). The taphonomy and formation processes of these sites have been studied in depth by a number of researchers with the conclusion that hominids were the primary agents of bone accumulation (Leakey 1971; Oliver 1994; Petraglia and Potts 1994; Potts 1982, 1988; Shipman 1986).

Skeletal element profiles for medium-sized herbivores at the Bed I sites and FxJ 50 have been interpreted by some researchers as representing selective bone transport by hominids (Bunn 1982; Bunn and Kroll 1986; Isaac 1978, 1983; Potts 1983, 1988, 1991; Rose and Marshall 1996). However, the recognition of hominid bone transport behavior is potentially complicated by an array of pre- and postdepositional taphonomic processes that may produce overlapping archaeological signatures. Density-mediated postdepositional bone attrition may substantially bias skeletal element profiles (see Lyman 1994). Potentially more problematic than decomposition in the African cases is the effect of predepositional carnivore ravaging of bones abandoned by hominids (Blumenschine and Marean 1993; Marean et al. 1992).

Several lines of evidence suggest that postdepositional bone attrition has not se-

riously biased Olduvai Bed I assemblages. First, bone-surface weathering studies indicate that most of the Olduvai Bed I assemblages were buried relatively rapidly and were in good condition at the time of burial (Potts 1988: 48-56; see also Behrensmeyer 1978, 1993; Behrensmeyer and Boaz 1980; Fisher 1995; Tuross et al. 1989). Second, good bone preservation is favored in calcium carbonate-saturated depositional environments such as occur in Bed I (Cerling and Hay 1986; Hay 1976; Hay and Reeder 1978; see Retallack 1984; Weiner et al. 1993). Calcium carbonate concentrations in Olduvai Bed I deposits are extremely high; calcium ( $\text{Ca}^{2+}$ ) makes up as much as much as 26.5 wt% (percentage by weight) of the deposits at FLKN and 4.6 wt% at FLKNN (Denys et al. 1996). Third, Bed I lake-margin sediments evidence a hyperalkaline, reducing depositional environment, a context ideal for bone preservation. Fourth, the persistence of lake-bottom euhedral calcite crystals (Cerling and Hay 1986; Hay 1976) in the lake-margin deposits suggests that calcium carbonate saturation has not altered substantially over time and is not a product of recent movement of carbonates through the deposits (see Weiner et al. 1993). Finally, the formation of pure calcite (presumably derived from the sediments) within the osteons and pores of many Bed I bones illustrates that bone minerals are very well preserved (Williams and Marlow 1987). Taken together, the speed of burial and depositional environment suggest that postdepositional bone attrition has not seriously impacted the composition of the bone assemblages.

Several researchers have suggested that hyena ravaging has destroyed many of the bones originally present at the Bed I sites (Blumenschine 1995; Blumenschine and Marean 1993; Marean et al. 1992). Experimental provisioning of captive and wild hyenas has demonstrated that carnivore gnawing preferentially destroys verte-

brae, ribs, and limb-bone epiphyses. Destruction of these low-density elements makes it difficult to distinguish ravaged death-site assemblages from transported bone assemblages, since both are characterized by a predominance of head and limb elements. While it is clear that some degree of hyena ravaging has occurred at the Bed I sites, several questions may be raised about the magnitude of this bias. In particular, the ecological and energetic basis for extensive ravaging of bone assemblages previously collected and processed by hominids is unclear. It is questionable, for example, whether large-bodied social predators such as spotted hyenas would gain sufficient energetic return from ravaging and ingesting bone fragments previously abandoned by hominid foragers. To extract sufficient energetic return hyenas would have to spend a significant amount of time at the site, which seems unlikely given the elevated risks of predation from remaining in one place for a long period of time. Alternatively, hyenas would have to make numerous trips of short-duration to the site, which would seem to be a poor investment of time and energy for low-utility resources. The degree of hyena ravaging suggested for the Olduvai sites is more consistent with bone-crunching at den sites (e.g., Brain 1981; Lam 1992), where the risks of predation are lower and time and distance constraints are not an issue. However, there is currently no evidence that any of the Bed I sites were associated with hyena dens (compare with Potts 1989). Ravaging may have yielded sufficient nutritional return if hyenas used interference tactics to pilfer relatively fresh bones from hominid foragers. Yet, studies of hominid cut and percussion marks on bones continue to suggest that hominids were the primary agents of bone accumulation at the Olduvai Bed I sites and that hyenas gained access to the bones only after hominids abandoned the sites (Blu-

menschine 1995; Oliver 1994). As a consequence, I argue that selective transport of skeletal elements over short distances (Brantingham 1998; see also Lupo 1993; O'Connell 1997) is the overriding pattern seen in the Olduvai Bed I bone assemblages.

As a means of further discerning the potential bone transport strategies employed by Plio-Pleistocene hominids Fig. 5 overlays data on anatomical content (head/limb MNE) and anatomical completeness (tMNE/MNI) of medium bovids from six Plio-Pleistocene sites on Stiner's (1994: 261) log-log regression for modern and Late Pleistocene predators (Table 2). The introduction of these data does not substantially reduce the strength of the relationship ( $r = 0.62$ ,  $t = -4.01$ ,  $p \leq 0.001$ ). Examining the Plio-Pleistocene sites in relation to the predator control cases suggests some interesting similarities and differences with the bone transport strategies discussed above. First, the Plio-Pleistocene cases occupy the lower center of the scatter, falling neither with the non-confrontational scavengers to the upper left, nor with the top predators to the lower right. The food transport strategies of the Plio-Pleistocene hominids are most similar to those of confrontational scavengers (e.g., spotted hyenas) in their central position. However, in contrast to confrontational scavengers the Plio-Pleistocene sites fall below the regression line, indicating that they are relatively limb-heavy (lower head/limb MNE) (see also Bunn and Ezzo 1993; Bunn and Kroll 1986; Potts 1983, 1988). The Plio-Pleistocene sites share this feature with assemblages collected by top predators (e.g., wolf), though the latter tend to be represented by more complete carcasses (higher tMNE/MNI).

Plio-Pleistocene hominid resource transport functions are presented in Figs. 3d and 6. The position and shape of the hominid curve is very suggestive of the ecological relationships between early

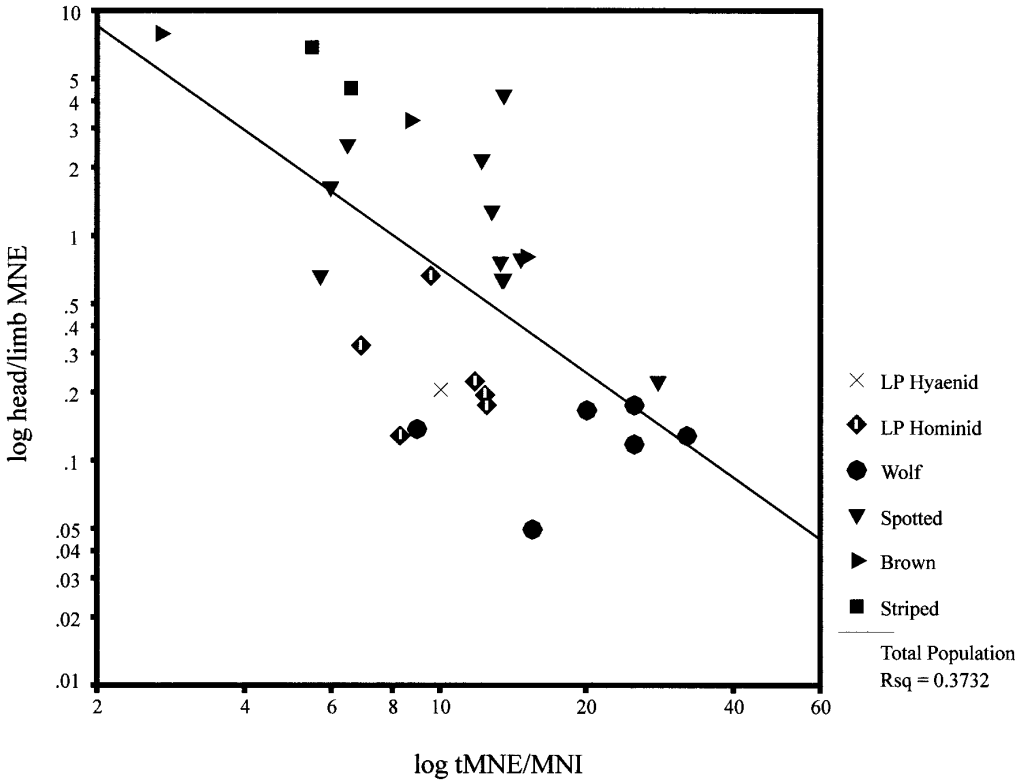


FIG. 5. Log-log regression of anatomical content (head/limb MNE) by anatomical completeness (tMNE/MNI) for Plio-Pleistocene hominids and other large bodied predators. Bed I Olduvai and Koobi Fora data are from Potts (1988) and Bunn (1982, 1986). Remaining data are from Stiner (1994).

hominids and large-bodied predators (Fig. 6). Interestingly, early hominid resource transport strategies do not fall at either of the extremes of the resource axis

(positions A and D in Fig. 4d). Moreover, the early hominid strategies do not fall between those identified with confrontational and nonconfrontational scavengers

TABLE 2  
Frequencies of Medium-Sized Bovid Head and Limb Elements, Total MNE and MNI at Olduvai Bed I Sites and FxJj 50<sup>a</sup>

Site	Head MNE	Limb MNE	tMNE	MNI	Head/limb MNE	tMNE/MNI
DK	22	67	125	18	0.33	6.9
FLKNN-3	17	25	115	12	0.68	9.6
Zinj	11	63	125	10	0.18	12.5
FLK North 6	6	26	59	5	0.23	11.8
FLKN 1-2	35	178	297	24	0.20	12.4
FxJj 50	4	30	50	6	0.13	8.3

<sup>a</sup> MNE estimates for FLKN 1-2 and FxJj 50 include size 3-4 bovids (Bunn 1982, 1986). Remaining data are for size 3 bovids (Potts 1988).



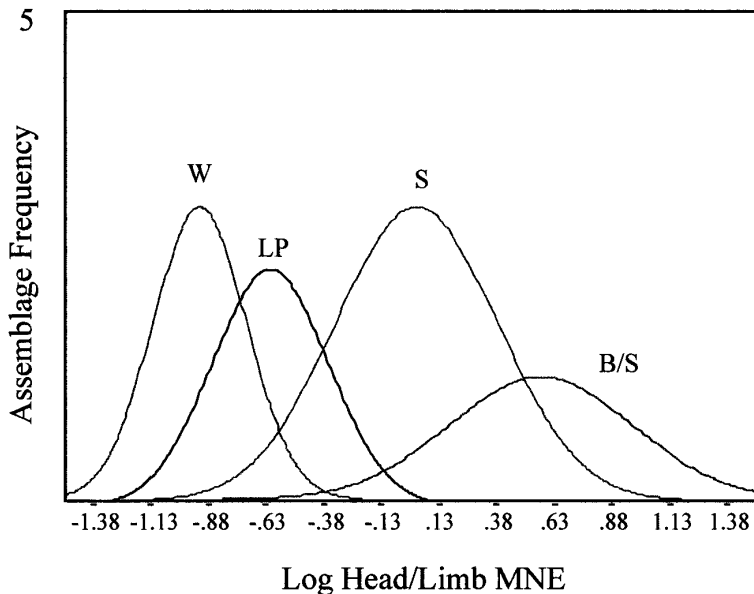


FIG. 6. Resource transport functions for Plio-Pleistocene hominids (LP), wolves (W), spotted hyenas (S), and brown and striped hyenas (B/S).

(corresponding to position C in Fig. 4d). The location of the hominid curve between transport strategies employed by top predators and confrontational scavengers suggests a niche position somewhat closer to the top predator pattern. However, a series of pairwise  $t$  tests indicate that the position of hominid cases is significantly different from that of the other predators (hominid-wolf  $t = -2.356$ ,  $p < 0.05$ ; hominid-spotted  $t = 4.265$ ,  $p < 0.001$ ; hominid-brown/striped  $t = 5.728$ ,  $p < 0.001$ ). This result argues against directly equating early hominid resource transport strategies with those top predators, confrontational scavengers, or nonconfrontational scavengers.

Figure 6 also gives the impression of tight niche packing; the full range head/limb proportions (limb dominated; balanced head-limb; head dominated) are represented. Tight niche packing may be expected to lead to fairly high levels of competition for resources. Table 1 presents competition coefficients calculated

for Lower Paleolithic hominids and the other large-bodied predators under consideration. What is not immediately apparent in either Fig. 6 or Table 1 is the remarkable regularity in spacing of the resource transport functions. Figure 7 presents the same data in an errorbar plot, and clearly highlights this feature of the RUFs.

## DISCUSSION AND CONCLUSION

Of the several analytical alternatives identified for the positioning of early hominids within the predatory food transport niche it would appear that hominids capitalized on (or created) a space between top predators and confrontational scavengers. This niche position leads to tight, but fairly even niche spacing. The available evidence suggests that levels of interspecific competition would have been high, but probably not sufficient to force competitive exclusion of one or more predators (*cf.* Walker 1984).

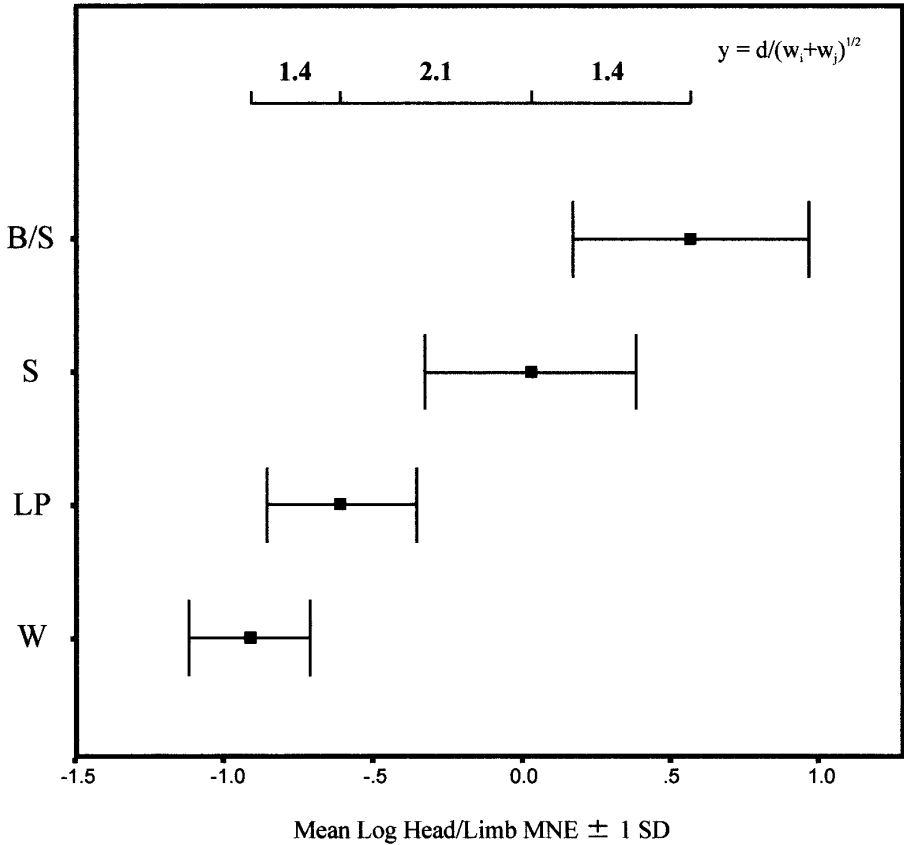


FIG. 7. Niche spacing shown as an error bar plot of the mean log head/limb MNE and one standard deviation. An equation showing the degree of spacing also is presented. Labels are the same as in Fig. 6. Variables are given in Eq. (1).

The comparison of large-bodied predator and Plio-Pleistocene hominid bone assemblages suggests that some form of resource partitioning was integral to hominid and other predatory bone transport strategies. The degree to which the strategies of top predators, early hominids, and confrontational and nonconfrontational scavengers separate out is quite remarkable and suggests that some level of "optimal similarity" was achieved with the appearance of Plio-Pleistocene hominids in the predatory guild.

The apparent resource partitioning represents a logical and complimentary way of dividing up medium ungulate carcasses (Fig. 8): (1) the organs and bone-exterior

fleshy tissues of fresh carcasses; (2) the full compliment of bone-interior tissues associated with head and limb elements; (3) head contents; and (4) marrow of the larger limb bones. The latter two packages represent a partitioning of the bone-interior tissues (see Blumenshine 1986a,b; Hill 1979; Potts 1983). In strategic terms, top predators appear to be associated with package 1, which reflects their specialized adaptation for hunting. Confrontational scavengers are associated with package 2 and employ both interference strategies for acquiring carcasses and actively defend those resources once captured. Non-confrontational scavengers are associated with package 3 and, in contrast to confron-

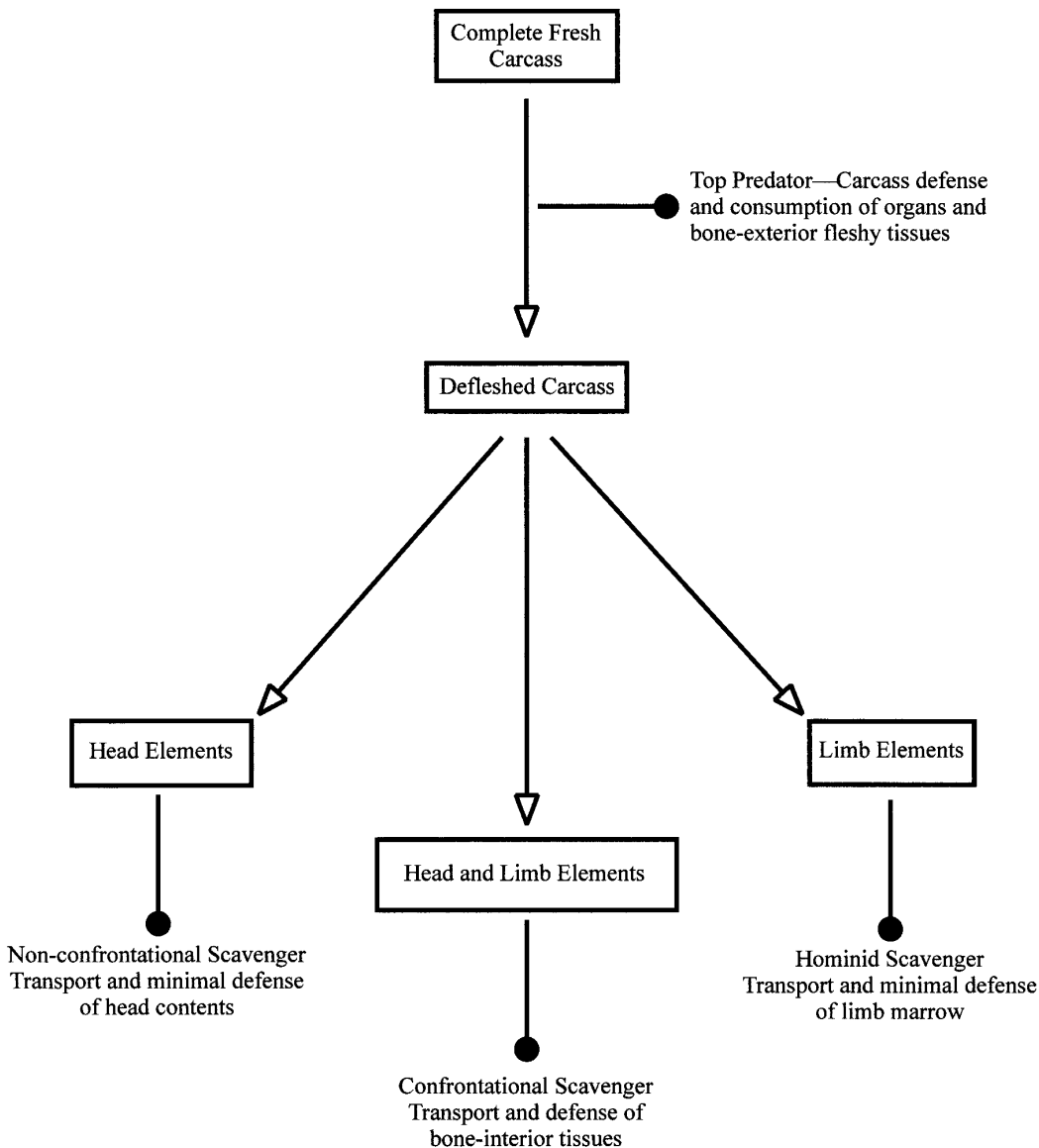


FIG. 8. Flow diagram representing the partitioning of a medium-sized ungulate carcass into four complimentary packages.

tational scavengers, invest little in active interference strategies and resource defense. Finally, Plio-Pleistocene hominids appear to be associated with package 4. This association may suggest that hominids invested little in defending ungulate carcasses from other predators. Rather, hominids may have invested more in

gaining access to freshly abandoned kills, quickly disarticulating defleshed limb elements, and removing those elements to processing locations where the pressures from predation and competition were lower (see Potts 1988, 1991). Thus, hominids may have employed the active search patterns of confrontational scavengers

(e.g., Hoffer and East 1993), but also the risk-adverse responses of nonconfrontational scavengers.

The validity of this interpretation of hominid-carnivore resource partitioning is dependent upon knowing that Plio-Pleistocene predators were comparable to the control cases discussed here. Numerous top predators, confrontational scavengers, and nonconfrontational scavengers are represented in the East African Plio-Pleistocene predatory guild (Ewer 1973; Blumenschine 1987; Lewis 1997; Turner 1990). In open habitats potential top predators include the lion (*Panthera leo*), the hunting hyena (*Chasmaporthetes*), and possibly *Homotherium* (Lewis 1997). The wild hunting dog (*Lycaon pictus*) also may have functioned as top predator in some open habitat contexts, depending upon the effectiveness of social pack hunting (Creel and Creel 1995; Fuller and Kat 1993). In closed habitats, true and false saber-toothed cats (*Dinofelis*, *Megantereon*, *Homotherium*) as well as leopards (*Panthera pardus*) may have been the principal top predators (Blumenschine 1987; Cavallo and Blumenschine 1989; Lewis 1997; Marean and Ehrhardt 1995). The role of confrontational scavenger likely was filled by Plio-Pleistocene spotted hyenas (*Crocuta crocuta*) (Blumenschine 1987, 1995; Lewis 1997; Turner 1990), whereas the principal nonconfrontational scavenger may have been Plio-Pleistocene representatives of brown (*Hyaena brunnea*) and striped hyenas (*H. hyaena*).

It also is important to recognize that the bone transport behaviors of these Plio-Pleistocene predators may have differed significantly from the control cases discussed here (see Lewis 1997). In particular, many of the suggested Plio-Pleistocene top predators are unlike modern wolves in that they did not apparently engage in extensive food transport. Possible exceptions are the wild hunting dog (*L. pictus*), the hunting hyena (*Chasmaporthetes*), and

the sabertooth cat (*Homotherium*). The behavior of these Plio-Pleistocene predators remains poorly understood, however (but see Lewis 1997; Marean and Ehrhardt 1995). Other modern species such as lions and leopards perhaps would be better analogs for Plio-Pleistocene top predators in East Africa. However, we currently lack bone assemblages collected by these modern predators. In contrast, the food transport behaviors of Plio-Pleistocene confrontational and nonconfrontational scavengers more likely resembled those of their Late Pleistocene and modern counterparts. However, the fact that the Bed I hyena accumulation, FLKNN-2, falls within the Plio-Pleistocene hominid range of food transport strategies gives some reason for caution (see Fig. 5).

The absence of a Plio-Pleistocene top predator engaging in extensive bone transport may suggest that there was a relatively open bone transport niche "bordering" the top predator strategy discussed here. I emphasize that such a niche probably was not equivalent to that of top predators because top predators would have monopolized the majority of fresh kills, with or without extensive food transport (see Fig. 8). Indeed, the fact that hominids did not invade the resource transport axis at point A (Fig. 4d) suggests that there was little "ecological space" for hominids as a bone-transporting top predator. Recent analyses of the composition of the East African Plio-Pleistocene predatory guild suggest that there was a much greater diversity of top predators than at present (Lewis 1997; Turner 1990), though niche saturation may have been similar to that seen today (Blumenschine 1987). This greater diversity of top predators may explain why Plio-Pleistocene hominids apparently did not hunt on a regular basis, but rather concentrated foraging efforts on scavenging and transporting fresh limb elements.

The lack of evidence for early hominid

invasion of the bone transport niche at point D also argues against interpretations that Plio-Pleistocene hominids were exclusively marginal scavengers (e.g., Binford 1981, 1984, 1985). Indeed, the Olduvai and Koobi Fora assemblages suggest that Plio-Pleistocene hominids employed resource transport strategies quite dissimilar to those employed by nonconfrontational scavengers such as brown and striped hyenas. Similarly, there may have been little "ecological space" between strategies employed by confrontational and nonconfrontational scavengers. The tight packing at this end of the resource axis may reflect the broad similarity in Plio-Pleistocene hyenid dental and jaw morphologies (see Biknevicius and Van Valkenburgh 1996; Brain 1981; Ewer 1973; Van Valkenburgh 1988, 1996).

While these interpretations do not resolve precisely how faunal resources were obtained, they may suggest that early hominids capitalized on an ecological "gap" within Plio-Pleistocene predatory food transport strategies. The alternative, of course, is that the observed partitioning of hominid and predator bone transport strategies was based on some form of behavioral, ecological or morphological character displacement. Indeed, the structure of hominid-carnivore resource partitioning may serve as a guide for the nature and potential magnitude of coevolutionary character displacement. Positions A and D in Fig. 4b, for example, represent extreme predatory adaptations. Hominid invasion at either of these points would have required major behavioral, ecological, or morphological innovations to compete successfully with established predators in these positions (see Shipman and Walker 1989). Craniodental and limb adaptations of top predators are extremely specialized for prey capture, transport, and processing (Biknevicius and Van Valkenburgh 1996; Lewis 1997; Van Valkenburgh 1996). Nonconfronta-

tional scavengers have similarly specialized adaptations for very high mobility search patterns, solitary foraging, and bone-crunching (see Mills 1990). Yet, current assessments of Plio-Pleistocene hominid functional morphology, technological organization, and behavioral ecology do not identify radical innovations matching these predatory adaptations in either form or function (but see Brantingham *in press*).

In contrast, niche positions more to the center of the resource axis require neither the specialized killing and grappling adaptations of top predators for bringing down live animals nor the solitary, high mobility adaptations of nonconfrontational scavengers for finding dispersed low-quality resources. Rather, occupation of more central niche positions hinges on interference strategies for acquiring resources and efficient resource processing adaptations. Hominid group foraging may have satisfied the first requirement in some contexts (Brantingham 1998; Rose and Marshall 1996). The availability of simple technologies such as hammer stones may have satisfied the second. In contrast to the complex craniodental adaptations of many predators, hammer stones represent an extremely energy efficient and rapid means of accessing bone-interior tissues. Indeed, hominids may have been able to break a major cost barrier associated with becoming a predator by means of this simple behavioral adaptation.

In this context, it is not unreasonable to view the origins and development of the earliest stone technologies as a form of coevolutionary character displacement; technological behaviors are an essential part of the hominid feeding adaptation and would have been subject to many of the same selective pressures that constrain predator feeding adaptations (see Dayan and Simberloff 1996). In particular, coevolutionary selective pressures may

have favored those technological behaviors that accomplished greater resource partitioning among sympatric predators. Increases in the efficiency by which stone raw materials and faunal resources were brought together, for example, may qualify as forms of character displacement if they can be demonstrated to have facilitated resource partitioning. Coevolutionary selective pressures may have favored continuous transport of flakes, hammer stones, or raw materials over greater distances or at much greater frequencies to ensure that appropriate processing equipment was available when relatively fresh carcasses were encountered (Torrence 1983, 1989; Toth 1982). The exploitation of stone caches also may have developed under similar selective pressures (Potts 1988, 1991).

The archaeological test for this scenario, as in all putative cases of character displacement, would be to examine the nature of hominid and predator food transport strategies in conjunction with hominid technological organization (Nelson 1991) in areas (or periods) where hominids are sympatric with specific predators and those where they are not. Tests of such hypotheses will require samples from a variety of regions where the composition of predator guilds are known to vary (e.g., Tchernov 1992; Turner 1990, 1992; Lewis 1997). It thus would be possible to compare resource partitioning in guilds composed of three, four, or five predators and with different mixtures of top predators, confrontational scavengers, and nonconfrontational scavengers. The prediction is that the extent of character displacement (e.g., technological organization) and resource partitioning should be greater in areas of sympatry.

Delineating the patterns and processes of hominid-carnivore resource partitioning and competitive character displacement in a given region and time frame will depend upon comparing contemporane-

ous bone assemblages accumulated by both hominids and predators. Any number of the known Plio-Pleistocene predators from East Africa could have engaged in resource transport strategies similar to those discussed here. Without comparative data for these predators, the conclusions presented here regarding hominid-carnivore coevolution should be taken as hypotheses to be tested in future research.

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