

# Hunting and Scavenging by Early Humans: The State of the Debate

Manuel Domínguez-Rodrigo<sup>1</sup>

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*During the last 25 years, there has been a shift towards the belief that early humans were scavengers instead of hunters. This revisionist interpretation has brought a reconciliation with the Darwinian paradigm of gradual progressive evolution that has traditionally guided (and very often, misled) an important part of anthropological thinking. However, empirical support for the scavenging hypothesis is still lacking. Recent data based on bone surface modifications from archaeological faunas suggest, in contrast, that hominids were primary agents of carcass exploitation. Meat seems to have been an important part of Plio-Pleistocene hominid diets. Passive scavenging scenarios show that this kind of opportunistic strategy cannot afford significant meat yields. Therefore, the hunting hypothesis has not yet been disproved. This makes the hunting-and-scavenging issue more controversial than before, and calls for a revision of the current interpretive frameworks and ideas about early human behavior.*

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## INTRODUCTION

Darwin's (1871) *Descent of Man and Selection in Relation to Sex* set the basis for an academic paradigm that has remained unchallenged in evolutionary studies until recently; that is, hominization began when our ancestors abandoned trees, adopted a bipedal gait, and used their free hands to make and use tools. It has been argued that in the dawn of culture, these tools became essential for the purpose of hunting and carcass processing. Meat, obtained by hunting, became the most stimulating element in hominid

<sup>1</sup>Departamento de Prehistoria, Facultad de Geografía e Historia, Universidad Complutense, Ciudad Universitaria s/n, 28040 Madrid, Spain; e-mail: mdr00008@teleline.es.

adaptation to savannas by triggering their intelligence, ultimately reflected in the progressive increase of brain size. In this interpretation, Darwin (1871) also considered that through evolution, men had become superior in mental endowment to women. This paradigm thrived in traditionally male-dominated academic circles, with a twofold sociobiological projection: human aggressiveness and gender differences emerged together as part of the same evolutionary process.

Darwin's idea of hunting among early hominids was an explicit hypothesis derived from a widespread belief among other contemporary naturalists that stone tools and bones from old deposits in caves probably reflected past human predatory activities (Boucher de Perthes, 1849). The preservation bias in Paleolithic archaeological sites (basically, only stone tools and bones have survived) helped these ideas to be widely accepted, and led the academic establishment to adopt the hunting paradigm for over a century (Binford, 1981, 1985, 1988a,b; Gamble, 1986, 1999; Kuper, 1994).

The hunting hypothesis and its sociobiological implication (the inevitability of aggressive behaviors), together with the social version of the Darwinian idea of the survival of the fittest, may have had an important contribution, outside academic circles, for contemporary colonial policies of exploitation of underdeveloped countries, as well as, indirectly, for warfare (Dennell, 1990; Farber, 1994; Hammond, 1980; Roszak, 1995). Several outstanding academic figures in the beginning of the twentieth century (such as Smith, Morton, Keith, and others) not only based some of the most important human evolutionary achievements on the acquisition of a hunting behavior by hominids in a very remote time period, but also justified present human behaviors based on that perspective (Bowler, 1986; Kuper, 1994; Lewin, 1987). Therefore, hunting became the most diagnostic behavioral trait to distinguish what was human from what was not. Not surprisingly, when Dart discovered the first remains of hominids in South Africa (*A. africanus*), at a time when the academic trend situated the origins of humans in Asia, his strongest argument to claim that *A. africanus* was the missing link between apes and humans was the behavior he reconstructed for this hominid species: hunting had been its way of life. The rejection of the hominid discoveries (the remains were thought to belong to a juvenile ape fossil rather than a hominid) led Dart to strengthen his arguments that he had discovered a hunting creature. He was convinced that the hominids had used tools. His evidence consisted of the broken animal limb bones, jaws and antlers found with the hominid fossils in several cave deposits (Dart, 1959, 1964). Dart named this tool set the "osteodontokeratic culture" and claimed that it had constituted the weaponry with which bloodthirsty australopithecines killed other animals and their own kind. These ideas were further exaggerated and popularized in Ardrey's (1961) *African Genesis* and (1976) *The Hunting Hypothesis*,

where he depicted these early hominids as killer apes, whose progression in murdering marked the early stages of hominid evolution, leaving an aggressive instinct in modern humans as a reminiscent feature of those times.

In the second half of the twentieth century, the hunting hypothesis was widely supported, not only by popular books, but also by several researchers to explain the origin of bipedalism (Fisher, 1982; Hewes, 1961; Lancaster, 1978) or to interpret early human adaptation to savannas and the earliest archaeological record (Washburn, 1950; see an extensive revision prior to the 1970s in Haraway, 1989). Apparent confirmation of the hunting hypothesis came with Lee and De Vore's (1968) *Man the Hunter*, as a result of a conference held in Chicago in 1966, in which ethnographic, and to a much less extent, archaeological evidence were combined to demonstrate that predation had always been a part of human societies. Modern analogues showed that hunting was an efficient way of adapting to different environments, and that a hunter-gatherer way of life was so stress-free that the abandonment of such an adaptive strategy should be explained in terms of extreme environmental situations and not cultural progression, as formerly thought. It was proposed that, "[O]ur intellect, interests, emotions and basic social life, all are evolutionary products of the hunting adaptation" (Washburn and Lancaster, 1968, p. 293). This conference also served to revive the old Darwinian idea that hunting was a male activity, and therefore, that men had shaped human evolution, despite the acknowledgment that gathering, mainly a female activity, was more important in terms of food contribution to hunter-gatherers' diets.

Supplemental evidence for the importance of hunting came from the study of apes (Goodall, 1963; McGrew *et al.*, 1978; Morris and Goodall, 1977; Suzuki, 1971, 1975; Teleki, 1973). Goodall (1986) demonstrated that chimpanzees were efficient hunters in the wild. This modified the hunting paradigm in a significant way: the progressive complexity of hunting strategies had shaped human evolution, instead of its radical emergence with hominids. Hominids had evolved from hunting small mammals, as do chimpanzees, to hunting almost every kind of animal (because of an increasing dependence on meat), as observed in modern human populations (Isaac, 1978, 1983, 1984). Goodall's studies were also used to claim hunting as a male activity, since female chimpanzees rarely participated in it.

In the early 1980s, the publication of Brain's (1981) *The Hunters or the Hunted?* and Binford's (1981) *Bones: Ancient Men and Modern Myths*, coinciding with a revisionist period parallel to important social and political changes (international conflicts and peaceful philosophies that bloomed during the 1970s) (Anderson, 1996; Farber, 1994; Jedick, 1998; Burner, 1998), helped initiate the undermining of the hunting hypothesis. Brain's revision of the Southern African cave deposits (Brain, 1981) showed that the bone

clusters found with hominids were the result of the action of carnivores. The bone tools claimed by Dart were the by-product of carnivores' consumption of carcasses, and hominids seemed even to have been preyed upon by some of the carnivores involved. Brain's taphonomic research cautioned against preconceived assumptions about the meaning of bone accumulations. During the 1970s, he was not the only one to caution that the association of stone tools and bones did not necessarily support the hunting hypothesis. Isaac (1978, 1983) was aware of this problem, and modified the traditional paradigm: hunting was no longer the most important element in the emergence of human behavior, but cooperative behavioral strategies, provided it could be shown that archaeological accumulations were primarily the result of hominid activities. Isaac's "home-base/food-sharing" model hinged upon the idea that establishing places as foci of activity and cooperating in bringing food to them (whether hunted or scavenged) were the key factors in modeling the emergence of early human behavior (Isaac, 1978). This behavior was structured around sexual division of labor: males obtaining animal proteins, and females gathering plants.

Despite Isaac's different approach, the hunting hypothesis was still widely accepted in other academic circles. Brain's studies had only served to shift the importance of hunting to explain the earliest archaeological record from early australopithecines to early *Homo* Leakey (1971). Additionally, during the 1980s, the discussion about the hunting paradigm and the new scavenging alternative took place only in the English-speaking academia. Most European traditions were still strongly influenced by the hunting hypothesis.

In 1981, Binford challenged the modern hominid behavior inferred in Isaac's model as well as other assumptions stemming from the hunting hypothesis. He claimed that hominids may not have been responsible for the bone accumulations at early sites, and depicted these ancestors as the most marginal scavengers in Plio-Pleistocene savannas. To evaluate this "marginal scavenger" or "obligate scavenger" model, Binford (1981) paid special attention to skeletal part profile analyses. He compared several carnivore dens and some modern hunter-gatherers' bone refuse at camps to preliminary faunal lists from Olduvai sites, and he concluded that carnivores rather than hominids were mainly responsible for early site formation. This led Isaac (1983) to revise his model and transform it into the "central-place foraging" model, using among other things, Bunn's zooarchaeological data (Bunn, 1981, 1982) on skeletal part representation and cut-marked bones from Olduvai and Koobi Fora archaeofaunas. In this model, hominids were still the principal agents in site formation, but the socioeconomic implications of the "home-base" model were eliminated. Hominids were simply gathering together at

certain loci to consume food, and food sharing and a sexual division of labor need not be implicit.

That was the onset of a debate that is still alive. Following this trend of “dehumanizing” hominids, the “stone cache” model of Potts (1982, 1988) was based on an optimal energy approach. Potts claimed that hominids would have created several refuge places where they would have stored stones with the intention of carrying carcasses to such spots, to avoid competition with carnivores. This model did not necessarily imply more premeditation than that observed in apes, or a more cooperative social organization. Regarding the hunting–scavenging issue, Potts (1982, 1988) argued that both strategies were equally used, although only access to fleshed carcasses would explain the strong hominid–carnivore competition he documented for Olduvai sites.

As a response to the male-biased interpretation of human evolution advocated by the “Man the Hunter” conference, several researchers also engaged in an attack of the hunting paradigm, because it had been used to perpetuate female marginalization in modern society (Tanner and Zihlman, 1976). This feminist critique of the hunting paradigm was part of a wider critical framework against what was called “androcentrism” in anthropology (Hays-Gilpin and Whitley, 1998). Following the “pendulum” effect, feminist revisionists produced “Woman the Gatherer” (Dahlberg, 1981) models to counter the traditional “Man the Hunter” paradigm.

During most of this debate, the empirical support for some of the scavenging scenarios proposed (Binford, 1981, 1985, 1988a,b; Shipman, 1983, 1986; Shipman and Phillips, 1976; Shipman and Rose, 1983; Stiner, 1990, 1991, 1994) was ambiguous, insufficient, or simply incorrect in the light of more recent studies (Bunn, 1991; Bunn and Ezzo, 1993; Bunn and Kroll, 1986; Blumenschine, 1988, 1995; Capaldo, 1995, 1997; Domínguez-Rodrigo, 1997a,b, 1999b; Jaubert and Brugal, 1990; Lyman, 1984, 1985, 1995; Marean, 1998; Marean *et al.*, 1992; Marean and Kim, 1998; Oliver, 1994; Potts, 1988; Rose and Marshall, 1996; Tappen, 1992, 1995). In this discussion, *ideas* have traditionally been more important than *data*. It was during the late 1980s and early 1990s that a more empirical approach allowed a more reliable understanding of the ecology of scavenging (Blumenschine, 1986; Bunn *et al.*, 1991; Domínguez-Rodrigo, 1996; Tappen, 1992) and the development of testing frameworks that were applied to the archaeological record.

Unfortunately, in spite of several years of actualistic studies on carnivore behavior, there was still a widespread belief among some zooarchaeologists that secondary scavenging from middle- and small-sized carcasses at carnivore kills can yield abundant meat (Auguste, 1991, 1995; Bar Yosef, 1989, 1994; Binford, 1985, 1988a; Blumenschine and Peters, 1998; Brugal,

1992; Brugal *et al.*, 1997; Stiner, 1991, 1994). Modern studies on predators show otherwise (Blumenschine, 1986; Domínguez-Rodrigo, 1999a). A lack of understanding of scavenging processes and the type of food they can afford indirectly lent support to behavioral reconstructions that may owe more to modern social trends than to actual data. After the Second World War, the Korean War, and the Vietnam War, the blooming of pacifist philosophies in the United States turned against the preconceived and untested ideas that humans were aggressive by nature (Farber, 1994; Roszak, 1995). There was a revival of Rousseau's ideal that humans were essentially good and peaceful (Anderson, 1996; Hoffman, 1998; Jedick, 1998). This may have had some repercussion in the behavioral models about early hominids that emerged in the 1970s and the 1980s. Some would believe (Domínguez-Rodrigo, 1994a) that the "make love, not war" slogan (Hoffman, 1998) may be in the background of the "sexual contract" models proposed to account for australopithecine behavior (Fisher, 1982; Lovejoy, 1981). Such philosophies, blended with the awareness of the site formation problem, could have promoted ideas of hominids engaged in peaceful behaviors, like scavenging carcass scraps scattered all over the savanna, as in the "marginal scavenger" model proposed by Binford (1981). Hominids were suddenly turned from the blood-thirsty and gruesome hunters described by Ardrey (1961, 1976), based on Dart's interpretations about *Australopithecus africanus* (Dart, 1959, 1964), into peaceful creatures roaming the landscape for food. The importance of social trends and their relationship to science has been widely treated by several researchers. As an excellent example, Donna Haraway (1989) has shown how primatology in the United States evolved parallel to social movements. She explores the consequences for primatology of the social relations of race, sex, and class in the construction of scientific knowledge, and argues:

For example, perhaps most primatologists in the field in the first decades after World War II failed to appreciate the interrelationship of people, land, and animals in Africa and Asia are at least partly due to the positions of the researchers within systems of racism and imperialism. Many sought "pure" nature, unspoiled by contact with people; and so they sought untouched pieces, analogous to the "natives" once sought by colonial anthropologists. . . . Wage labour, sexual and reproductive appropriation, and racial hegemony are structured aspects of the human social world. There is no doubt that they affect knowledge systematically. (Haraway, 1989, p. 7)

Haraway gives numerous examples of the effect of the "political agenda" of the researchers in their own research and views. Following this line of thought, Stanford (1998) has also recently acknowledged that modern interpretations of bonobo–chimpanzee differences are reflections of modern human male–female differences. He claims that

[T]he paradigm formation may itself be subject to social influences, because research biases lead one to collect some types of data rather than others. . . . Contextual biases

may emerge from the circumstances in which the research is done. They represent the situating ideas and interpretations of evidence in terms of the perspective the researcher brings to the research. (Stanford, 1998, p. 406)

This perspective is provided by the social context in which the researcher is inserted.

Currently, there is a diversity of opinions regarding early hominid behavior. There is a widespread belief in academia that scavenging was the main strategy used by hominids 2 Ma (million years ago) to obtain carcasses (Lewin, 1984). Some researchers, however, believe it is time to resurrect part of the old hunting paradigm (Bunn, 1995, 1996; Clark, 1996; Domínguez-Rodrigo, 1997a,b; Stanford, 1999; Tappen, 1995). Some still adhere to some of the most problematic implications of the old hypothesis. For example, Stanford (1999, p. 41) acknowledges that “[T]he reality of male predominance as hunters and of women as gatherers is not in dispute,” thereby assuming the gender dichotomy inherent to the Darwinian paradigm. He goes as far as to suggest the following.

[O]nly a biological interpretation of the relationship of meat to male dominance can fully address the root of patriarchal societies. This is not to say that meat eating is the central feature of all male-dominated societies. It can, however, be a defining trait of gender relations in some societies, such as those in which men hunt for a living while women gather. This brings us back to Man the Hunter. The idea that meat eating may have been a catalyst in human behavioral evolution fell in disfavor due to the backlash against Man the Hunter. The model was pilloried to the extent that it became a forbidden term, one that labeled its adherents as male-biased chauvinists, consciously or unconsciously ignorant of the role of women in human evolution. . . . Whether the actual role of females in early human prehistory fits our modern Western gender-balanced sensibilities is an entirely different question. While women may collect most hunter-gatherer protein, we should not ignore the fact that men are able to use meat for their own selfish and manipulative political ends. (Stanford, 1999, p. 211)

Despite the academic tendency among several Old World archaeologists to support scavenging by early hominids (Lewin, 1984), there is a recent revival of the “Man the Hunter” analogical model (Lee and Daly, 1999). However, our ideas about early hominid behavior still depend more on our paradigms than on unambiguous data-supported arguments. Today, while hunting and scavenging are still in dispute as early humans’ basic subsistence behavior, it is time for an academic revision of the subject. This paper deals with the strength of the evidence (or lack thereof) we have so far to support both types of hypotheses.

This work will present the hunting-scavenging discussion following its historical development. The first phase of the debate was based on skeletal part profile analyses. During this time, analogical frameworks were underdeveloped and interpretations were made by using data to support untested assumptions or by comparing data to unrelated analogies. The main assumption

made in most interpretations based on skeletal part profiles was that there was a typical human bone-accumulation pattern that could be archaeologically identified. These interpretations did not take into account the profound bias introduced by carnivore postravaging, responsible for the deletion of key anatomical elements that prevents archaeologists from reconstructing what originally was transported to sites by hominids. After the main characteristics of this phase are shown, the second phase of the debate is introduced. The switch from skeletal part analyses by some researchers to the study of bone surface modifications marked the onset of a new period of debate that was accompanied by the development of a variety of experimental and analogical frameworks. This leads us to the apex of the current debate, where researchers are trying to solve the contradictions among the analyses of tooth marks, percussion marks, and cut marks.

Currently, the main interpretive positions are the following:

1. Hominids hunted.
2. Hominids used confrontational scavenging to have access to fleshed carcasses.
3. Hominids scavenged carcasses that were undisturbed by carnivores.
4. Hominids passively scavenged defleshed carcasses at carnivores' kills.
5. Hominids used a combination of these four strategies.

Options 1, 2, and 3 would require primary (or early) access to fleshed carcasses, whereas Option 4 means secondary access to defleshed carcasses. The archaeological criteria used to support all these options varied historically, as can be observed in the following sections.

## THE "SKELETAL PART PROFILE" PHASE OF THE DEBATE

After more than two decades, the meaning of early African archaeological sites is still controversial. Most Africanists would now agree that some sites were created by hominids repeatedly carrying animal carcasses and stones to particular places in the landscape (Blumenschine, 1988, 1991, 1995; Blumenschine *et al.*, 1994; Blumenschine and Bunn, 1987; Blumenschine and Marean, 1993; Bunn, 1982, 1983, 1991; Bunn and Ezzo, 1993; Bunn and Kroll, 1986; Capaldo, 1995, 1997; Cavallo, 1997; Domínguez-Rodrigo, 1994a; Isaac, 1983; Oliver, 1994; Potts, 1982, 1988; Rose and Marshall, 1996; Schick and Toth, 1993; Selvaggio, 1994). This is one of the most important achievements of taphonomic studies of Plio-Pleistocene archaeological sites. However, the function of these sites (Blumenschine *et al.*, 1994; Domínguez-Rodrigo, 1994a; Isaac, 1978, 1983; Oliver, 1994; Potts, 1982, 1988; Rose and Marshall, 1996; Schick and Toth, 1993; Stanley, 1992) as well as the kind of hominid involvement with carcasses (Blumenschine, 1991, 1995; Blumenschine and Madrigal, 1993; Bunn and Ezzo, 1993; Bunn and Kroll, 1986;



Capaldo, 1995, 1997; Cavallo, 1997; Domínguez-Rodrigo, 1997a; Selvaggio, 1994) remain in dispute. Both issues are partly dependent on a central question that emerges from the long standing hunting-versus-scavenging debate: the extent of meat eating by early humans. Significant meat eating would support early access to carcasses and a food surplus that would enhance food sharing and cooperative behaviors as defined in Isaac's models (Isaac, 1978, 1983). Sites, thus, could be seen as social loci showing the beginnings of the basic structure of human behavior as observed in modern hunter-gatherer base camps. If, instead, carcasses yielded little food, as in passive scavenging scenarios, the amount of meat in early hominid diets would have been unimportant (Blumenshine, 1986). Low-yielding carcasses would not have promoted food sharing and cooperative behaviors similar to those in our species today.

The basis for this discussion was the analyses of skeletal part profiles at early sites. Skeletal part frequencies and taxonomic identification have long been zooarchaeologists' principal methods. Although other types of analyses—bone breakage patterns and bone surface modifications (tooth marks, cut marks)—have been incorporated to the study of archaeological sites, zooarchaeologists have mainly been concerned with the development of methods for quantifying the various anatomical parts and individuals represented in fossil bone assemblages (Binford, 1978, 1981, 1988a; Bunn, 1982; Bunn and Kroll, 1986, 1988; Grayson, 1984; Stiner, 1991). Identification of the damage undergone by these parts from perimortem and postmortem processes (butchery, dismembering, marrow extraction, burning, carnivore gnawing, trampling, weathering, and so on) has been a secondary analytical procedure, with the aim of reinforcing inferences drawn from the other primary types of analyses.

When skeletal part profiles are used to evaluate hominid behavior at archaeological sites, irrespective of their geographical location and age, there is always controversy. For instance, the interpretations of Binford (1981, 1984) and Binford and Ho (1985) of hominid participation in site formation at Zhoukoudian, Olduvai, or Klasies River Mouth have been contested, respectively, by the alternative explanations of Bunn and Kroll (1986) and Klein (1982a,b). The discussion of hominid behavior at African Plio-Pleistocene sites is a clear example of this situation. The debate, focused mainly on the skeletal part representation, led some researchers to suggest, as we have seen, that hominids were marginal scavengers (Binford, 1981, 1984, 1985, 1988a,b; Shipman, 1986), whereas others pictured them as successful hunters/scavengers (aiming at flesh rather than at marrow, when processing carcasses) (Bunn, 1981, 1982, 1983; Bunn and Kroll, 1986; Isaac, 1983, 1984). More recently, and on the basis of the same skeletal part profiles, some researchers suggest that hominids were transporting high-yielding meat sections from carcasses (Bunn and Ezzo, 1993; Potts, 1988), whereas

others argue that they were selecting high-yielding marrow bones that were already defleshed (Blumenschine, 1991, 1995; Blumenschine and Marean, 1993), or that hominids were opportunistic scavengers conditioned by processing costs (considered as risk factors) rather than calorie yields alone (Lupo, 1998). Throughout this debate, the identification of bone damage was used as a secondary argument by most of the researchers involved. Binford (1981, 1985, 1988a) used the evidence of tooth marks on fossil bones to support the hypothesis that carnivores were the main consumers of carcasses; Bunn (1981, 1982, 1983, 1991) and Oliver (1994) used the percentages and anatomical distribution of cut marks also found on some of these bones to claim that hominids were processing fleshed carcasses; Blumenschine (1988) and Potts (1982, 1988) used, in different ways, both types of marks to reconstruct the sequence of intervention of both agents (hominids and carnivores) in site formation. Blumenschine (1995) also used them to support the hypothesis that hominids were scavenging carcasses from felid kills, from which they removed the scraps of flesh and exploited their marrow contents.

This secondary use of bone damage as a taphonomic indicator of hominid and carnivore interaction at bone assemblages is responsible for the lack of development of the analytical procedures by which the study of bone surface modifications really could be diagnostic of hominid and carnivore interactions (Blumenschine, 1988). Researchers have often reported percentages of cut marks and tooth marks without differentiating their anatomical occurrence and without relating these percentages to a model in which their distribution would be meaningful in terms of supporting primary or secondary access by hominids to carcass resources.

The very controversies surrounding interpretations of hominid behavior based mainly on analyses of skeletal part profiles are a proof of their limited value (given the current analytical procedures) and of their excessive use in zooarchaeological studies. The reasons are discussed below.

### **Modern Humans as an Analogy for Hominids**

Skeletal part profiles are based on the assumption that there are diagnostic patterns in the ways that modern humans and other agents transport and accumulate bones. Actualistic ethnoarchaeological studies on differential transport of carcasses by humans have been carried out (Binford, 1978, 1981; Bunn *et al.*, 1988, 1991; O'Connell *et al.*, 1988, 1990, 1992) in order to create an analogy that can be applied to the archaeological record. Some of these studies have constituted, and still do in many academic circles, the basis for many taphonomists' analytical and interpretive procedures, based on the claim of White (1952) and Perkins and Daly (1968) that humans

preferentially transport certain anatomical units (such as limbs) from carcasses (the so-called “Schlepp effect”). In application, long bones are usually seen as the result of transport processes, whereas axial bones are assumed to be better represented at kill sites (Binford, 1981; Bunn, 1982, 1991; Bunn *et al.*, 1988, 1991; Bunn and Kroll, 1986).

However, there are important pitfalls in such simplistic analogical frameworks. Many factors determine the transport and accumulation of carcasses by humans. They include the cost of transport, conditioned by the distance between the carcass and the base camp; the number of individuals who participate in the transport; the time of day; and the size of the animal (Metcalf, 1989; Metcalf and Barlow, 1992; O’Connell *et al.*, 1988, 1990). Another factor that must be taken into account is the initial strategy concerning the preparation of the animals to be transported. Some human groups disarticulate carcasses where they obtain them and prepare them for transport, by discarding some bones on the spot (O’Connell *et al.*, 1992), whereas others do not (Domínguez-Rodrigo and Martí Lezana, 1996). Other circumstances that will affect the way that carcasses are accumulated are the cultural variations among different ethnic groups and their preferences for anatomical sections (O’Connell *et al.*, 1990, 1992) and the web of social interactions that will determine the way carcasses are shared, either within the group (same nuclear family, among several families, and so on) or outside the group (Marshall, 1994). Some of these behaviors will not show a clear archaeological signature (Bartram *et al.*, 1991; Garget and Hayden, 1991; Marshall, 1994). We should also consider humans as agents prone to distort their own bone accumulations, when they clean some areas of debris and garbage (O’Connell *et al.*, 1991).

However, one of the main objections that can be made about the use of skeletal part profiles for zooarchaeological purposes is that there is not a unique pattern of bone accumulation by modern humans. The way that the Nunamiut transport carcasses (Binford, 1978, 1981) is not the same as those exhibited, for instance, by the Hadza (O’Connell *et al.*, 1990) or the Kua (Bartram, 1993). Among the Hadza themselves, there is a wide variation in the parts that they select to be transported to base camps. Studies on carcass transportation by the Hadza show that the “Whitean” proposition—also developed in the Perkins and Daly model—that hunters preferentially transport appendicular rather than axial anatomical sections from kill sites, is wrong (Monahan, 1998; O’Connell *et al.*, 1990). When dealing with wildebeest and hartebeest carcasses, the Hadza seem to preferentially transport vertebrae, pelves, and ribs, followed by the head, scapulae, and limbs. For impala, the transport pattern is similar. For elands, the Hadza prefer to transport vertebrae and pelves followed (in order) by head, ribs, and limbs. Curiously, for buffalo (in spite of its similar size to the eland), limb bones are

most likely to be removed and axial bones are the least likely. With zebras, a high proportion of axial elements is transported; as is also the case with warthogs (O'Connell *et al.*, 1990).

Very often, Hadza foraging groups prepare carcasses prior to their transport by stripping meat from all the long bones, which are then cracked open in order to eat the marrow and afterwards are abandoned at or near the kill site (O'Connell *et al.*, 1992). Transport, thus, is mainly of axial and cranial elements (O'Connell *et al.*, 1992). On other occasions, with some species, the Hadza just separate the lower legs from carcasses and the metapodials and phalanges are either abandoned or consumed at or near the kill site, while the remaining limbs are transported to base camps (O'Connell *et al.*, 1992). That is, in some instances, meat from limbs is transported once it has been stripped from long bones, which are abandoned at kill sites, also referred to as "snack sites" (Bunn *et al.*, 1991). On other occasions, limb bones are also transported. In these cases, lower leg bones, usually considered diagnostically transported, are abandoned at kill sites.

Overall, the studies of O'Connell *et al.* (1990, 1991, 1992) show not only that the appendicular preference by humans has been exaggerated by ethnoarchaeological models—contra Binford (1978, 1981) and Bunn *et al.* (1988, 1991)—but also that carcass transport is highly patterned among Hadza, and that it varies among different carcass sizes and, even in the same size group, among different species. If a single human group shows variation in the patterns of carcass transport, it is not surprising that such difference becomes more important when comparing several human groups (Bartram, 1993; Domínguez-Rodrigo and Marti Lezana, 1996). The most important aspect of these studies is that they show that there is not a particular "human pattern" of bone transport and accumulation.

### **Sites as the Result of Multiple-Patterned Processes**

Another major objection that could be advanced against the analyses of skeletal part representation is that most of the models developed so far have been based on the differential transport of anatomical parts by humans from kill sites to base camps, and not on what is left after the consumption. Bone assemblages at sites are the result of dynamic processes of selection and destruction, which result in a distortion of the initial bone accumulations made by humans. They are the result of humans making decisions at kill sites, transporting selected bones, modifying and destroying part of these bones at camps due to consumption, abandonment, as well as the intervention of other agencies, physical (such as flowing water) and/or biological (such as carnivore postravaging). Thus, it is methodologically incorrect to

use data drawn from the initial stage of this process as a reference to be compared with the end product.

Comparisons should be among comparable units. Since we recognize that sites are palimpsests—the result of the intervention of several agents—single-patterned models (carnivore dens vs. human transport of carcasses, and so on) are not appropriate analogies for interpreting archaeological bone assemblages. This led some researchers to suggest that such a reference come from multiple-patterned models (Blumenschine, 1988, 1995; Blumenschine and Marean, 1993; Capaldo, 1995; Marean *et al.*, 1992; Selvaggio, 1994).

Given that hominids and carnivores (in particular, hyaenas) were involved in the formation of Plio-Pleistocene sites, as suggested by the presence of both cut marks and tooth marks on archaeological faunal assemblages (Bunn, 1981, 1982, 1983; Potts and Shipman, 1981), experiments carried out to test the effect of carnivore postravaging on bone accumulations made by humans led to the following two conclusions (Blumenschine and Marean, 1993; Capaldo, 1995; Marean *et al.*, 1992).

1. Axial bones (ribs, vertebrae, and pelves) and certain long bone epiphyses are preferentially deleted from assemblages, followed by the small compact limb bones. This creates an artificial profile, dominated by limb and cranial elements.
2. Epiphyseal fragments of limb bones are more likely to be deleted from assemblages than midshaft specimens.

Studies of bone density have demonstrated that the parts of the skeleton composed of cancellous tissue are prone to destruction or can be removed from their original site of accumulation by several processes, including flowing water, weathering, carnivore ravaging, etc. This is because they are less dense than other bone sections and usually contain significant amounts of grease (Lam *et al.*, 1998; Lyman, 1994). This adds a further dimension to the discussion of the utility of skeletal part profiles, because in sites where some of these processes, especially carnivore ravaging, were operating, the distortion of the anatomical patterns of carcasses is such that we are not able to discern whether hominids were selectively transporting certain skeletal units (e.g., limbs) or complete carcasses. Zooarchaeological explanations of both types of behavior can be used to support different strategies of carcass exploitation by humans. This ambiguity dominated the hunting–scavenging debate in the 1980s, when many researchers did not understand the mechanism of scavenging and how to recognize it in archaeofaunas.

Furthermore, the head–distal limb pattern is often an artifact of a particular type of analysis employed by many zooarchaeologists, which relies more on epiphyseal representation than on shaft fragments for element identification (Bartram and Marean, 1999; Marean and Frey, 1997). For this reason,

the analysis of skeletal parts is of limited use until new identification methods (such as analyses of diaphyseal fragments) have led to more accurate identification of element representations than the traditional approach. Recently, Rogers and Broughton (2001) have argued that this ambiguity disappears if a new theoretical statistical method is applied. However, they acknowledge that “[T]here are grounds for scepticism about all our empirical results because they rest on unsupported assumptions about transport and attrition” (Rogers and Broughton, 2001, p. 771). As an example, the measure of the intensity of attrition Rogers and Broughton use is incorrect because it is strictly theoretical (degrees of bone deletion without taking into account how bones are *qualitatively* deleted by attritional agents) and it is also contradicted by the studies of carnivore behavior (Blumenschine and Marean, 1993; Capaldo, 1995). Until attrition is correctly modelled, they cannot rule out equifinality. Recently, Lupo (2001) has clearly shown how large assemblages of bones, representing amalgamations of many butchery events, are poor reflections of observed transport and discard patterns.

## SCAVENGING AND ITS TESTING SCENARIOS

### What Can Be Scavenged From Carnivores?

Despite earlier efforts (Binford, 1981, 1985, 1988a; Shipman, 1983, 1986; Shipman and Rose, 1983, 1984), the basis of the current ideas about passive scavenging by early humans lies in the work of Blumenschine (1986, 1988, 1989, 1991, 1995) on the ecology of hominid-oriented opportunistic behaviors in savannas, the taphonomic indicators of trophic dynamics and food resource availability, carnivore behavior, and indicators of multiple-part processes on carcasses. Based on middle- and small-sized animals, which make up the bulk of Plio-Pleistocene archaeofaunas, Blumenschine’s studies showed that scavenging from carnivores is feasible only at felid kills (hyaenids and canids consume carcasses more thoroughly), and that secondary access to such carcasses barely yields any meat at all. Scavenging from leopard kills is the only exception (Cavallo and Blumenschine, 1989), provided access to the prey occurs before its total consumption (see discussion in Conclusions below). Otherwise, only long bone marrow and the braincase contents are available after felids consume their prey (Blumenschine, 1986). Blumenschine also showed how scavenging these resources was subject to certain ecological conditions: carcasses could be obtained in riparian habitats and mostly during the dry season. One carcass at a time does not produce enough food to be shared by a group of hominids, so this strategy would not enhance the food distribution and cooperative behaviors documented in our species.

Neither Blumenschine (1986) nor Domínguez-Rodrigo (1994b) have suggested that cooperative behaviors would have been necessary to exploit defleshed carcasses at carnivore kills.

Tappen's contribution to the ecology of scavenging documents some variation of carcass availability in time (year round instead of seasonal) and habitat (open floodplain instead of riparian forest) in wet savannas (Tappen, 1992, 1995), compared to the semiarid and dry savannas and steppes studied by Blumenschine (1986) and Domínguez-Rodrigo (1996). However, there are no differences among all these ecosystems in what is available for scavenging from carcasses.

Thus, one of the main ideas that actualistic studies of carnivores and of landscape taphonomy should convey is that this type of scavenging does not provide any significant amount of meat to secondary consumers. It is therefore surprising that some archaeologists still insist that scavenging at carnivore kills could have enabled our ancestors to obtain high meat yields or that scavenging at hyaenid dens could have afforded hominids any food at all (Auguste, 1991, 1995; Bar Yosef, 1989, 1994; Binford, 1988a; Brugal *et al.*, 1997; Fossé, 1995, 1996; Stiner, 1991, 1994). Scavenging can be a strategy for obtaining meat from small- and middle-sized carcasses only if it is confrontational (O'Connell *et al.*, 1988, 1990, 1992) or, more rarely, after certain catastrophic events (Capaldo and Peters, 1995) (see Conclusions below).

The differentiation of early and secondary access to animal resources through the analyses of skeletal part profiles (Binford, 1978, 1981, 1988a,b; Brain, 1981; Bunn, 1982; Bunn and Kroll, 1986, 1988; Grayson, 1984; Stiner, 1991, 1994) did not fully consider the bias in bone preservation produced by carnivores. Most Plio-Pleistocene sites are palimpsests in which we can document the intervention of both hominid and scavenging carnivores (Binford, 1981; Blumenschine, 1988, 1995). Recent studies of carnivores in African savannas and in captivity show that secondary access by carnivores to human-made bone accumulations results in the deletion of cancellous bones, as noted above (Marean *et al.*, 1992; Capaldo, 1995). Thus, it is very difficult to reconstruct all the original skeletal elements accumulated by hominids prior to carnivore intervention. Given the inefficacy of skeletal part analyses, a few years ago some researchers turned to a more reliable criterion: the study of bone surface marks. Recently, anatomical reconstructions based on diaphyseal fragments have led to skeletal part profiles that are not so profoundly biased by carnivore intervention at sites (Bunn and Kroll, 1986; Marean, 1998; Marean and Kim, 1998).

Experiments carried out by Blumenschine (1988, 1995), Selvaggio (1994), and Capaldo (1995, 1997) showed that study of long bone sections allowed the differentiation of bone modification processes by humans and by carnivores, and their order of intervention. On the basis of these experiments,

these authors suggested a three-stage consumption sequence, wherein felids initially defleshed carcasses, hominids demarrowed long bones and consumed the brain, and hyaenids processed the greasy bones. Within a few years of these studies being done, new research suggests that we need to reconsider the validity of this three-stage sequence to explain early human consumption of meat.

### **How to Test the Passive Scavenging Hypothesis: The Study of Bone Surface Marks**

Bones processed by humans and carnivores show surface modifications in the form of tooth marks, percussion marks, and butchery marks. Different methods have been created to reliably distinguish most of them (Blumenschine, 1988; Blumenschine *et al.*, 1996; Blumenschine and Selvaggio, 1989; Bunn, 1981; Capaldo and Blumenschine, 1994; Fisher, 1995; Potts and Shipman, 1981; Shipman, 1983; Shipman *et al.*, 1984; Shipman and Rose, 1983).

Tooth marks on bones are the result of carnivores extracting meat, marrow, and grease. Therefore, the occurrence of tooth marks on each anatomical element is directly linked to the resource available at the moment the carnivore had access (Selvaggio, 1994). Blumenschine (1988) also observed that the percentage of tooth marks on long bone sections varies according to the order of access. A carnivore with primary access leaves a high percentage of tooth marks on the midshaft sections (usually >75% of sections), caused by either only defleshing (felids) or defleshing and/or demarrowing (hyaenids and canids). Secondary access by carnivores to defleshed and demarrowed bones, as in the case of human-processed carcasses, results in a very low number of midshaft specimens bearing tooth marks (mean between 5 and 15%), because these bone sections do not contain any food (Blumenschine, 1988; Capaldo, 1995, 1997) (Fig. 1).

Primary and secondary access to bones processed by humans yield similar results in tooth marking on long bone epiphyseal and near-epiphyseal sections, since they retain grease both before and after being processed by humans. Therefore, tooth-mark frequencies on long bone midshaft sections have become one of the main indicators of the kind of interaction between hominids and carnivores (Blumenschine, 1995; Capaldo, 1995, 1997).

Hominids processing bones leave two different kinds of traces: percussion marks and butchery marks (that is, cut marks). Percussion marks can be differentiated from tooth marks (Blumenschine and Selvaggio, 1988) and are the result of human demarrowing of long bones. They are very useful not only as indicators of a particular type of carcass exploitation by hominids, but

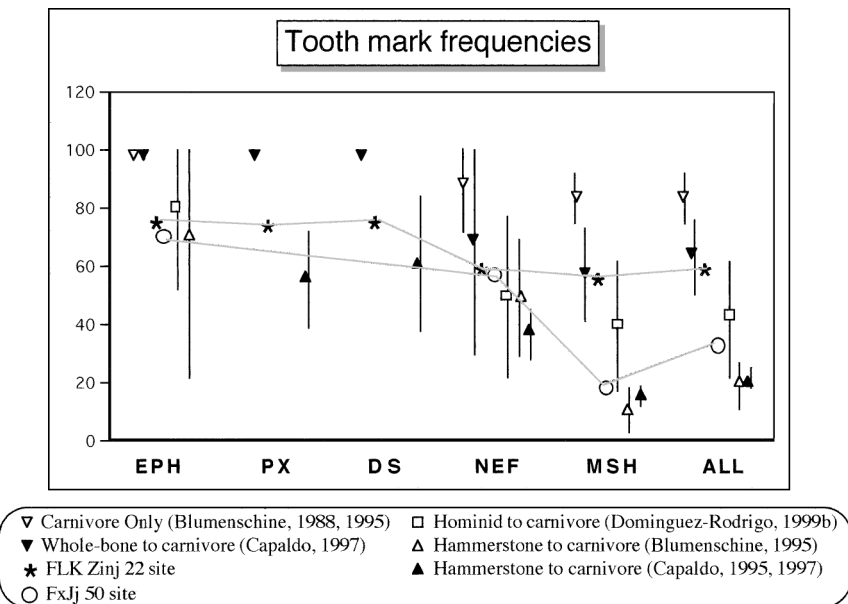


also as a control framework for different experiments on tooth marks subject to equifinality (Capaldo, 1995, 1997; Domínguez-Rodrigo, 1999b) (Fig. 2).

Butchery marks are diverse in morphology. Cut marks include long striations, usually parallel to one another, with internal striae. They are produced by the contact of sharp-edged stone tools on bones. On long bones, their occurrence depends on the activity performed by humans. When defleshing, cut marks appear on midshaft and near-epiphyseal sections (Domínguez-Rodrigo, 1997a,b). Dismembering leaves cut marks on the epiphyseal and near-epiphyseal sections (Binford, 1981). The removal of small scraps of flesh and the periostium from bones can be done by scraping rather than cutting. This leaves scrape marks that are shallow, multilineally patterned, and different from cut marks. In some cases, due to the difficulty of cutting through the tendons for disarticulation, unifacial or bifacial choppers, handaxes, or cleavers could be used instead of flakes. This results in deep chopping marks, which are less frequent than cut marks in the archaeological record. Reliable methods of evaluation and the interpretation of cut-mark distribution on bones can help reconstruct hominid involvement with carcasses (flesh and marrow exploitation or only marrow exploitation) and, therefore, their order of intervention (Domínguez-Rodrigo, 1997a, 1999b).

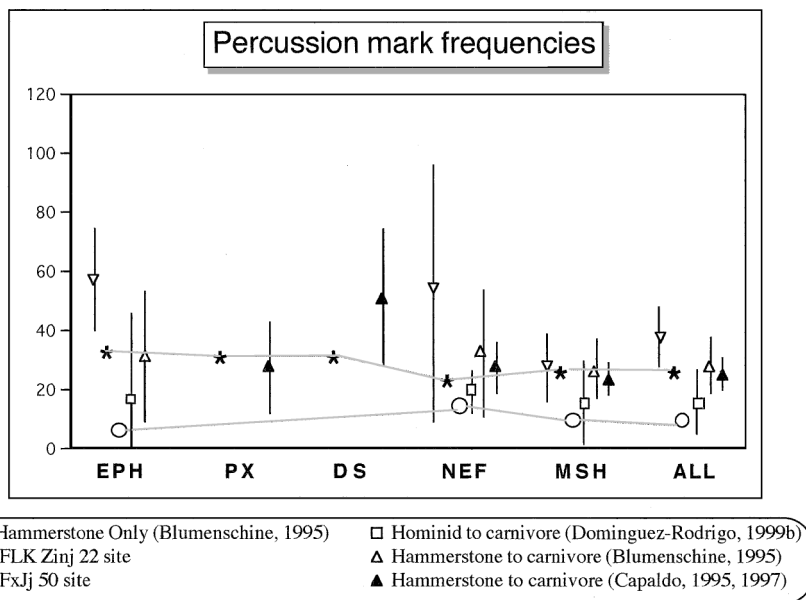
### **Application to the Archaeological Record**

The refinement of these actualistic experiments in the early 1990s has permitted their application to some early archaeological sites (Blumenschine, 1995; Capaldo, 1995, 1997; Domínguez-Rodrigo, 1997a,b, 1999b; Selvaggio, 1994). Initially, only the FLK 22 *Zinjanthropus* site from Olduvai Gorge (Tanzania) was studied, because of the amount of fauna and the well-preserved bone surfaces (Blumenschine, 1995). Blumenschine (1995), Capaldo (1995, 1997), and Selvaggio (1994) concluded that the archaeofauna from FLK Zinj was the result of hominids scavenging carcasses that had been largely defleshed by felids, transporting them in to be demarrowed, and other scavengers (namely, hyaenas), subsequently modifying the assemblages by removing bones and bone sections containing grease. The three-part sequence was supported by the percentages of tooth marks and percussion marks and their distribution according to long bone section. The frequency of tooth marks on epiphyseal and near-epiphyseal specimens was similar in experimental scenarios dealing with both primary and secondary access by carnivores to remains. This means that scavengers, probably hyaenas, very likely played a major role in modifying and destroying these bone sections after hominids had processed and discarded them. However, the high percentage of tooth marks on the midshaft sections of long bones could not



**Fig. 1.** Tooth-mark percentages on different bone sections from the FLK 22 and FxJj50 sites and from the experiments reproducing primary access to carcasses by carnivores (carnivore-only model) and primary access to carcasses by hominids (whole-bone-to-carnivore, hominid-to-carnivore and hammerstone-to-carnivore models). Percentages are shown in a 95% CI analysis, with the mean and its range of variation calculated using the  $t$  distribution, where  $t \cdot 0.025$  is the critical value of  $t$  with  $n - 1$  degrees of freedom. EPH, epiphysis; PX, proximal epiphysis; DS, distal epiphysis; NEF, near-epiphysis; MSH, midshaft.

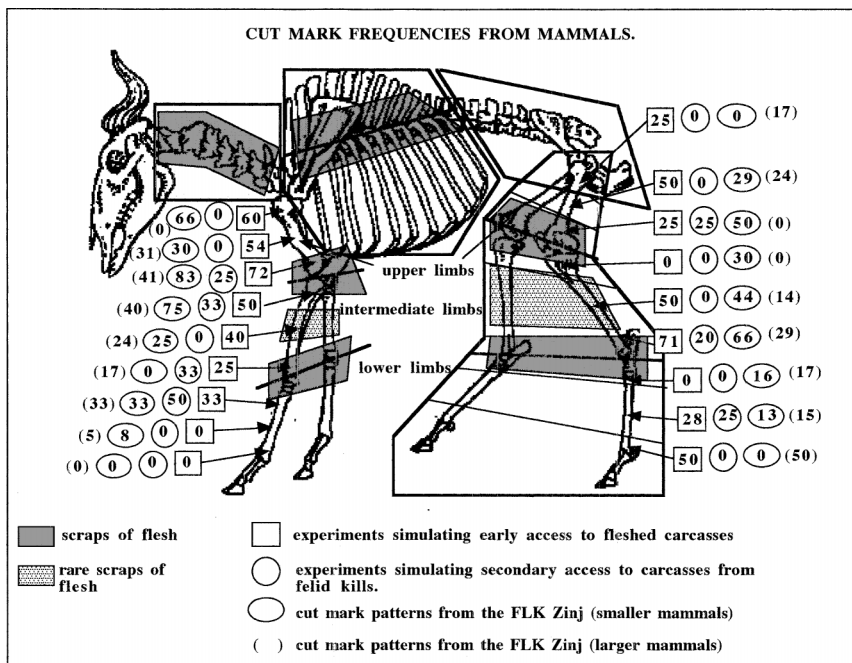
simply be explained by a secondary access of carnivores to the bones accumulated by hominids. The frequency of tooth marks on midshaft sections was significantly high and close to the percentages obtained in experiments in which carnivores have primary access to bone marrow (whole-bone-to-carnivore or carnivore-to-hominid models) (Blumenschine, 1988, 1995; Selvaggio, 1994; Capaldo, 1995, 1997) (Fig. 1). This could be explained if strictly flesh-eating carnivores, that is, felids, had defleshed the carcasses before hominids had had access to them. Hominids then would have mainly removed the marrow from long bones. This is reflected in the percentage of bone specimens bearing percussion marks, similar to the frequency obtained in experiments in which humans demarrow bones before carnivore intervention (Fig. 2). Hyaenids and other scavengers would then have consumed and modified elements and bone sections containing grease, skewing and biasing the original pattern of bones accumulated by hominids. They would have removed epiphyseal sections from long limb bones, the axial



**Fig. 2.** Percussion-mark percentages on different bone sections from the FLK 22 and FxJj50 sites and from the experiments simulating marrow extraction by hominids. Percentages are shown in a 95% CI analysis, with the mean and its range of variation calculated using the  $t$  distribution, where  $t \cdot 0.025$  is the critical value of  $t$  with  $n - 1$  degrees of freedom. EPH, epiphysis; PX, proximal epiphysis; DS, distal epiphysis; NEF, near-epiphysis; MSH, midshaft.

skeleton (including scapulae and pelves), and the compact limb bones (carpals, tarsals, phalanges), assuming that hominids had brought in these elements (Blumenschine, 1988, 1995; Blumenschine and Marean, 1993; Capaldo, 1995, 1997; Marean *et al.*, 1992).

The presence of cut marks on a significant number of specimens from FLK Zinj has not been considered important (Fig. 3), because of the ambiguity in their meaning and equifinality. Cut marks on bones could be the result of either hominids manipulating fully fleshed carcasses (Bunn and Kroll, 1986) or the removal of the marginal scraps of flesh that commonly survive carnivores' consumption of carcasses (Blumenschine, 1991, 1995). Binford (1986) suggested that some cut marks on fossil bones from the FLK Zinj site could reflect meat removal from desiccated carcasses. Lupo (1994) argues that the same bone section can be cut marked when dealing with carcasses stiffened by rigor mortis. According to Blumenschine (1995) and Capaldo (1995), the lack of experimentally and observationally controlled frameworks that compare these processes and the distribution of cut marks they produce, make this kind of bone surface modification of limited value



**Fig. 3.** Cut-mark percentages from the FLK 22 Zinj site and from experiments reproducing primary and secondary access by hominids to carcasses. Data were drawn from Domínguez-Rodrigo (1997a,b). The mean for secondary-access experiments was obtained only from defleshed carcasses in the study carried out in Masai Mara (Domínguez-Rodrigo, 1997b). The skeleton shows the distribution of scraps of flesh found at carnivores' kills (Domínguez-Rodrigo, 1999a).

to build inferences from the archaeological record. In addition, different processes generating the same end products make such results useless for inferential purposes, since they cannot be used to differentiate a unique and unambiguous process (Capaldo, 1995)—a phenomenon known as equifinality (Gifford-Gonzalez, 1991).

Capaldo (1995, 1997, 1998) claims that percentages and distributions of cut marks are indistinguishable in experimental scenarios reproducing early access (defleshing of carcasses) or secondary access (removal of flesh scraps from carnivore kills) to carcasses. The range of variation of both experimental samples overlap. Cut marks, thus, would be subject to equifinality (Capaldo, 1995, 1997, 1988). By excluding cut marks and solely relying on the frequency of tooth marks on limb bone midshaft sections, Blumenshine (1995) and Capaldo (1995) conclude that hominids were passive scavengers, as defined in their three-part model. This model was first subjected to experimentation and testing by Selvaggio (1994).

## ON THE UTILITY OF CUT-MARK ANALYSES TO INFER HOMINID EXPLOITATION OF CARCASSES

Blumenschine's pioneering study on the ecology of scavenging (Blumenschine, 1986) showed how passive scavenging could only be feasible at felid kills, because these carnivores deflesh carcasses but leave marrow-bearing bones unbroken most of the time. This strategy would have provided little or no flesh to hominids (see Fig. 4). In order to test if cut marks could result as the action of removing scraps of flesh at felid kills, it was necessary to further refine the observations initially made by Blumenschine (1986) about the diversity of products available for consumption to a passive scavenger. This required the study of the distribution of flesh scraps, with the aim of determining if there was a systematic occurrence of such scraps, and if so, how this could affect the global distribution of the resulting cut marks after their removal. A second step would be to experiment on fleshed and defleshed carcasses and compare results. With this kind of research, the first objection concerning the use of cut marks, that is, ambiguity in interpretation due to the lack of referential frameworks, could be refuted. Equifinality could also be tested and ruled out if the results in both sets of experiments did not overlap.

I carried out such research (Domínguez-Rodrigo, 1999a) on middle-sized carcasses, as these make up most of the carcass sizes represented in



**Fig. 4.** Carcass of a middle-sized animal after having been consumed by lions.

Plio-Pleistocene archaeofaunas. It was also focused on felids in African savannas, since this was the type of ecosystem and the carnivore species available during the formation of African Plio-Pleistocene sites. Of all the modern African felids, lions are the only predators with a middle-sized prey range. Even though Plio-Pleistocene savannas were not the same as modern ones, given the difference in humidity, temperature, vegetation, and trophic dynamics (carnivore and herbivore diversity), the overall ecological structure is similar to current African savannas (Domínguez-Rodrigo, 1994a, 2001). For this reason, the use of modern carnivores, with the same morphofunctional skills in carcass processing as Plio-Pleistocene carnivores is the best proxy we can use to replicate flesh availability to hominids from Plio-Pleistocene carnivore kills. A study of carcasses at modern lion kills documented a patterned distribution of flesh scraps after prey were defleshed, which is useful to evaluate to what extent hominids might have been scavenging in the past (Domínguez-Rodrigo, 1999a) (Fig. 3). If hominids were scavenging, we would expect the bones they processed to be cut-marked in the sections where modern carnivores leave flesh scraps.

Lions process the flesh of carcasses very thoroughly, leaving few edible flesh remains. The cranium is the only anatomical element in which flesh exists after lions abandon their kills; the remainder of the skeleton is defleshed. Metapodials are also left intact in most instances. Thus, the occurrence of scraps of meat on bones is not common. When documented, they were more frequent in the neck, and scarcer in the rest of the skeleton. They appeared unevenly on some bones, and were fairly small in size (Domínguez-Rodrigo, 1999a).

The differential distribution pattern observed on limbs can be seen in Fig. 3. Almost 90% of the scraps on limb bones occurred on the proximal/distal sections. On upper limb bones, almost all the scraps occurred on their distal portions. No midshafts of any upper limb bone retained any meat (Domínguez-Rodrigo, 1999a).

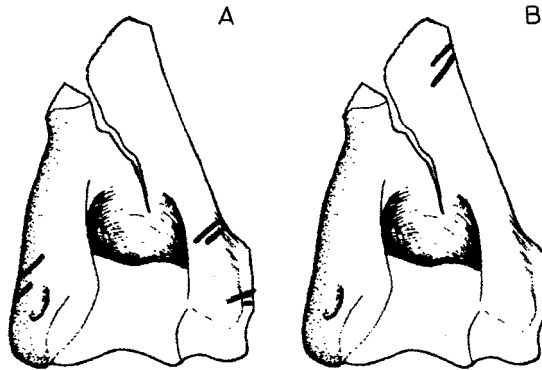
It is interesting to contrast the availability of flesh scraps in carcasses fed upon by lions to those defleshed by humans. The more thorough defleshing by lions when compared to humans may be due to their different ways of processing carcasses. Lions pull the flesh from their prey, tearing whole muscle masses from them. Thus, bones are defleshed more completely and the scraps remaining are more likely to occur on the ends of bones where the muscles are attached. In contrast, humans usually butcher carcasses by cutting through the flesh, so that muscle masses are not removed from bones as complete units. This could account for the usually common presence of scraps of flesh on bone midshafts and vertebrae in carcasses butchered by humans.

One of the most remarkable facts in this study was the observation that most of the carcasses found in riparian woodlands barely exhibited any scraps of flesh at all. All the flesh scraps observed were from carcasses in open plains. This may be due to the greater amount of time that lions spend consuming their prey in riparian woodland (from several hours to even days), compared to the short time span (1–3 h) of consumption in open plains, because of competition with other carnivores.

These results called for an appropriate analytical method on cut marks that could test different hypotheses, taking into account this differential anatomical location of scraps of flesh. Cut marks found on elements where flesh scraps are nonexistent at carnivore kills should reflect human activities not linked with passive scavenging. Cut marks on the mid-section or distal section of ribs or on midshaft sections from long bones, especially upper limb bones (humeri and femora), would indicate meat removal from fleshed carcasses rather than the removal of scraps from felid kills.

It then became clear that Blumenschine's, Capaldo's, and Selvaggio's methodology was not suitable for the study of cut marks, because the analyses of bone sections *per se* could never test, for instance, Bunn and Kroll's hypothesis that cut marks are related to the amount of flesh extracted from bones (Bunn and Kroll, 1986). Flesh is anatomically distributed in a differential way according to bone element, and analyses of cut marks *per* bone section can never relate the amount of meat removed to the distribution and percentages of the resulting cut marks. For instance, two completely different behaviors may mimic each other when analyzed through Blumenschine, Selvaggio, and Capaldo's approach. The removal of skin and periosteum from lower limb bones of carnivore-defleshed carcasses may leave an abundance of cut marks on all the lower-limb sections (epiphyses, near-epiphyses, and midshaft fragments). The total percentage and sectional distribution of cut marks per carcass will be similar to the case in which hominids processed fully fleshed upper limb bones and discarded the lower limb elements. The way to differentiate these two scenarios is by quantifying the cut marks by bone type (axial, upper limb, lower limb, and so on) as well as by bone section. This is important because flesh masses are differentially distributed according to the type of element, and the small scraps of flesh that might survive carnivore consumption also show a typical pattern of anatomical distribution according to bone type and bone section as we have seen (Fig. 3). This makes an excellent reference to interpret the anatomical distribution of marks on bones from archaeological sites.

Blumenschine, Selvaggio and Capaldo's methodology is problematic not only because it does not consider differential distribution of flesh, but also because of their definition of bone sections. They consider a bone specimen



**Fig. 5.** Different locations of cut marks on the same bone specimen and their different behavioral meaning: A, disarticulation; B, defleshing. These behaviors are masked when classifying the marks according to bone section type (epiphyseal, near-epiphyseal or midshaft fragments) instead of by the actual location of the marks (epiphysis versus midshaft).

that has a fragment of epiphysis with a section of the near-epiphysis and midshaft to be an “epiphyseal specimen.” Cut marks on the midshaft section of such fragments lead to classification as a cut-marked “epiphyseal fragment,” giving the incorrect impression that the cut mark is situated on the epiphysis itself (Fig. 5). The high survival of epiphyseal fragments attached to shaft sections and the high percentage of marks on these large specimens will result in a relatively high number of “epiphyseal fragments” showing marks. Thus, the actual distribution of marks according to bone section is not properly represented. This is of real consequence when evaluating different models of hominid carcass acquisition and processing behavior. For instance, the availability of scraps of flesh from midshaft sections of limb bones first consumed by lions has been shown to be rather limited (see above). The classification of cut marks on the midshaft of a specimen conserving part of the epiphysis as a cut-marked epiphyseal fragment would have quite different implications than would its classification as a cut-marked midshaft fragment. I have argued for a more precise classification of cut-mark location that does not lump together midshafts and epiphyses (Domínguez-Rodrigo, 1997a,b).

Thus, the reason for equifinality in Capaldo’s and Selvaggio’s studies is strictly methodological. By considering anatomical element as well as bone section, the possibility of equifinality can be excluded. Such research has been conducted for some years in East African savannas (Domínguez-Rodrigo, 1997a,b). Fully fleshed carcasses from natural deaths and human settlements and defleshed carcasses from felid kills were processed with



stone tools and the resulting distribution of cut marks was compared. It was found that primary and secondary access by hominids to carcasses can be differentiated by analysing cut-mark patterns (for a complete statistical data set see Domínguez-Rodrigo, 1997a, 1999a). Cut marks on fleshed carcasses showed the following results:

1. A significant percentage of cut-marked bones with respect to NISP.
2. Differential occurrence of cut marks by element. The meatiest elements (upper limb bones) have the most cut marks. These are followed by intermediate limb bones, and finally lower limb bones.
3. Differential distribution of cut marks according to bone section. In the preravaged human-made accumulations the mean figure of cut-marked midshaft specimens (with respect to the total number of all cut-marked fragments) is about 43%. In postravaged assemblages, it becomes higher than 50%. This is due to the disappearance of some proximal/distal ends due to density-mediated factors. Therefore, midshafts are the most abundant cut-marked specimens in bone assemblages that have completed the two-part process (hominid–carnivore).

In contrast, the situation with secondary access to carcasses from felid kills is significantly different. The results drawn from these experiments are as follows.

1. A lower total percentage of cut-marked bones with respect to NISP.
2. Differential occurrence of cut marks by element: In contrast to experiments reproducing early access by hominids, the meatiest limb elements (humerus and femur) have the fewest cut marks. Intermediate limb bones are also low-ranked, and metapodials are the highest ranked elements (>60%).
3. Differential distribution of cut marks according to bone section: In highly flesh-depleted carcasses, with the exception of metapodials, no upper or intermediate limb bone exhibits any cut mark on the midshafts, so that proximal/distal ends, not midshafts, exhibit the highest occurrence of cut marks (mean >80%, except metapodials).

Thus, there seems to be a clear relationship between the quantity of meat and cut-mark representation (Domínguez-Rodrigo, 1997a,b; Marshall, 1986). In a recent discussion about the meaning of cut marks on the fossil bones from FLK Zinj, Selvaggio (1998) and Capaldo (1998) engaged in arguments about cut-mark studies that ignore both these data (Domínguez-Rodrigo, 1997a,b) and other European studies of this kind (Blasco Sancho, 1995; Perez-Ripoll, 1992; Pumarejo and Cabrera, 1992; Martinez, 1998), focusing strictly in their own methodology and results. When the method

outlined above is applied to cut-mark data from the FLK Zinj site, a clear picture of the order of intervention of hominids in carcass processing is obtained.

This would support Bunn and Kroll's claim that cut-mark percentages are related to the amounts of flesh extracted (Bunn and Kroll, 1986). They indicate that 62% of the cut marks on all the cut-marked specimens from smaller animals and 40% of the cut-marked bones from larger animals are from meaty limb bones. Furthermore, as many as 73% of the cut-marked specimens from meaty limbs of smaller animals and 59% of the cut-marked specimens from meaty limbs of larger animals appear on midshafts.

With respect to the cut-mark patterns according to bone type, my own data drawn from FLK Zinj show a clear differential distribution: upper and intermediate limb bones make up most of the cut-marked specimens (88%), versus metapodials (12%). Proportionately (according to NISP), upper limbs show a greater representation of cut-marked specimens (40%) than do intermediate limb bones (30%) (Domínguez-Rodrigo, 1997a). This result is similar to the experiments simulating early access to fleshed carcasses. Cut-mark percentages and distribution in upper/intermediate limb bones (especially in humerus and femur) cannot be accounted for in terms of secondary access to carcasses. Although marrow extraction could also be reflected in cut marks on lower limb bones—as skinning is necessary (Blumenschine, 1986)—it would barely leave any marks on the other bones, and surely almost none on upper limb bones and their shafts.

These studies are further supported by Oliver's revision of the FLK Zinj archaeofauna (Oliver, 1994). Upper limb bones are highly cut-marked, followed by intermediate limb bones and, lastly, metapodials. This pattern is completely different from that obtained from secondary access to defleshed carcasses, and matches my experiments reproducing early access to complete carcasses.

If the similarity between my experimental results and the data generated by the analyses by Bunn and Kroll (1986) and Oliver (1994) of the FLK Zinj bone remains is valid, Plio-Pleistocene hominids were processing carcasses that had substantial amounts of meat. Blumenschine's hypothesis that Olduvai hominids were focusing on marrow extraction from bones already defleshed by carnivores and that the cut marks on the fossil bones reflect the removal of the scraps of flesh (Blumenschine, 1986, 1991) is not supported by this study on cut marks (Domínguez-Rodrigo, 1997a,b, 1999b) (Fig. 3). The cut-mark pattern obtained at the FLK Zinj site contradicts the information drawn from tooth marks on midshaft sections from the same long limb bone specimens. Obviously, none of the experimental models is correct if there are contradictions in the data from each kind of bone surface mark.

## TOOTH MARKS AND MULTIPLE-PART MODELS

Experiments on tooth marks by Blumenschine, Capaldo, and Selvaggio have been carried out making the following implicit assumptions: hominids exploited carcasses thoroughly (that is, they defleshed and/or demarrowed bones completely), and tooth marks are derived solely from the action of carnivore defleshing (e.g., felids) and breaking open bones for marrow and grease (hyaenids and canids). These assumptions exclude other potential tooth marking agents, such as hominids (Pickering and Wallis, 1997) or baboons (Domínguez-Rodrigo, 1999b), and the possibility that carcass exploitation by hominids had not been as thorough as modelled in these experiments. These two factors, especially the latter, can be crucial in giving tooth-mark frequencies different from those documented in most two-part experiments. Experimental studies on captive baboons in the Barcelona zoo (Spain) and wild baboons in Tsavo and Galana (Kenya) have shown that baboons may leave frequent marks on both fleshed and defleshed bones, which mimic the percentages and distributions of tooth marks made by carnivores on human-made bone accumulations (Domínguez-Rodrigo, 1999b). However, even if we exclude primates as a significant source of tooth marks on bones from Plio-Pleistocene archaeofaunas, the interaction between hominids and carnivores has only once been experimentally reproduced without contradictions.

Most actualistic experiments by Blumenschine, Capaldo, and Selvaggio on tooth marks fail to explain two important facts. First, tooth-mark percentages on midshaft specimens at the FLK Zinj site fall outside the range of variation of experiments modelling primary and secondary access to bones by humans, in which hominid–carnivore interaction is replicated. Second, there is a significant presence of complete bones (9–10% of the total MNE) (Potts, 1988) in most Olduvai Bed I sites, including the FLK Zinj site. That is contradictory to a marrow-based scavenging theory.

The abandonment of complete bones by hominids could only have been possible if the food yields from carcasses were enough, such that hominids did not have to exploit them thoroughly, that is, if they had been fleshed (Cavallo, 1997; Domínguez-Rodrigo, 1997a). We are dealing again with equifinality. Bones at these early sites could also represent other processes. Animals could have independently died on the spot where hominids had accumulated remains. The Zinj site, as most Plio-Pleistocene sites in Olduvai and elsewhere (especially in Peninj, or Koobi Fora, Gona, Omo, Lokalalei) was located in a habitat where animals could have been dying anyway. All of these localities are riparian/alluvial environments by rivers and lakes. If natural death would have been responsible for bone accumulation at these sites, why are these complete bones not found in such a relative

abundance anywhere else but at the Olduvai sites? Were animals not dying naturally in the alluvial plains of Peninj, Koobi Fora, Gona, or West Turkana? Furthermore, are bones retrieved through the current landscape project in Olduvai also complete in similar percentages? That would initially support this possibility. The Blumenschine and Masao (1995) report to the National Science Foundation shows some preliminary data in which bone fragment figures are shown and not a single claim about complete bones is made. Were animals thus dying only in the areas where hominids were accumulating debris? Also, complete bones have been found in other archaeological areas in Koobi Fora (not in archaeological sites with high concentrations of remains as in Olduvai) bearing cut marks, which clearly indicate that hominids were defleshing those bones but not demarrowing them (Bunn, 1994).

In addition, researchers tend to overemphasize the use of modern hunter-gatherer analogical models to explain early hominid behavior. Early hominids may have been exploiting carcasses in a different way, especially if their foraging groups were not as large as those of modern hunter-gatherer populations. Even modern humans do not always completely exploit the carcasses they consume and leave some marrow-containing bones intact. This is especially true in small foraging groups (Domínguez-Rodrigo and Marti Lezana, 1996). As Bunn and Ezzo (1993) have shown, fatty tissue is abundant in viscerae and around muscle tissues. Hominids could have obtained enough fat (actually more than from just the bone marrow) by primary access to fully fleshed carcasses. I have had the chance of working with the Mwalangulu in Kenya and the Masai in Peninj (Tanzania) and have witnessed how they abandon some marrow bones intact. I broke the bones and confirmed that the marrow was in optimal condition. Furthermore, modern hunter-gatherers are restricted to marginal environments. Thus, they maximize energy intake from carcass processing. Hominids may have enjoyed a different ecological situation (as paleoecology indicates) and their diet could have been quite different from modern hunter-gatherers (as some preliminary isotopic data suggest), making them focus more on meat and less on fat from carcasses than modern hunter-gatherers do, since fat may have been present in a large variety of nuts they may have collected. Besides, almost 50% of the bones abandoned completely by hominids are metapodials, where breakage takes more than five seconds and the marrow content is the least of all the long limb bones. Perhaps this is also why bone-collecting carnivores such as hyaenas accumulate long limb bones in their dens but rarely do they break open the metapodials. All these arguments are further supported by the fact that complete bones are frequent in Iron Age sites, showing that carcass exploitation was not thorough (Domínguez-Rodrigo, 2002, in press).

Therefore, the presence of several complete limb bones at sites could constitute one of the most important arguments against the passive scavenging hypothesis. Capaldo (1995) has convincingly shown that even in riparian habitats, hyaenas destroy all the greasy and marrow-containing bones. The facts that almost 10% of long bones at the early Olduvai sites are complete (Potts, 1988) and that hyaena postravaging has been documented there (Blumenschine, 1988; Blumenschine and Marean, 1993) suggest that the original number of complete bones could have been significantly higher (Capaldo, 1995). Potts (1988, p. 343) observes that several bone specimens at Olduvai sites exhibit "patterns of breakage attributable to carnivores," which would not be expected if hominids had broken open all the bones. Capaldo (1995, p. 298) further claims that "the low incidence of long bone flakes relative to other shaft fragments from FLK 22 suggests that (some) long bones were intact when modified by carnivores."

If hominids were aiming at marrow rather than flesh, because that is what they would have found on bones from medium-sized carcasses at felid kills (Blumenschine, 1986, 1991), it would not be expected that they had abandoned such a high number of complete limb bones. This suggests that they were exploiting carcasses not for marrow, but for flesh and marrow. This is further supported by another important fact: the number of axial bones (expressed both in MNE and NISP) is high in most Olduvai sites. For instance, in FLK Zinj, there are more than 800 axial bone remains (the most abundant bone type after limb bones), making up 30% of the whole bone assemblage. Axial-bone representation at early sites (both in MNE and NISP) varies from 20 to >40% (for instance, FLKN6) (see Capaldo, 1995). Capaldo's (1995) experiments demonstrate that axial bones at simulated sites are almost completely consumed by hyaenas with a mean of 5% of survival. They have been shown to be preferentially deleted by these carnivores (Marean *et al.*, 1992). Their high survivorship at Olduvai sites indicates their greater number before hyaena ravaging took place and also that hominids were transporting complete carcasses or sections of axial skeletons (devoid of marrow but with plenty of flesh). As Capaldo (1995, p. 350) acknowledges, "A flesh surplus might help to explain the presence of so many axial elements, pelves and scapulae at FLK 22; that is, why would hominids transport these items to the site if they were defleshed?" A further proof is the abundance of cut marks on scapulae, pelves, and ribs (Bunn and Kroll, 1986). Capaldo (1995, p. 315) further argues that his data "initially suggest that hominids may have removed moderate to large amounts of flesh from long bones."

There is another source of evidence that hominids might have abandoned some bones without extracting their marrow contents: the percentage of tooth marks on midshaft fragments at the FLK Zinj site. Blumenschine

(1988) and Selvaggio (1994) have experimentally demonstrated that the defleshing of long bones from medium-sized carcasses by carnivores is usually reflected in an average of 80% tooth-marked midshaft fragments. The percentage is similar in processes in which carnivores deflesh and demarrow bones, and those in which they simply deflesh carcasses and bones are broken by humans to extract the marrow (Blumenschine, 1988; Capaldo, 1995, 1997; Selvaggio, 1994). The percentage of tooth marks on such bone sections at the FLK Zinj site (57%) is outside the 95% confidence interval of these experiments, in which carnivores were primary agents of carcass defleshing, and those in which human defleshing and demarrowing of all the bones was followed by carnivore postravaging (Blumenschine, 1988; Capaldo, 1995). The only model that fits this percentage of tooth marks is the "whole-bone to carnivore" scenario, in which bones defleshed by humans were demarrowed by carnivores (Capaldo, 1995), although this model shows some contradictions when percussion marks are taken into account. Capaldo (1995, 1997) gives the bone size distributions in the specimens from Zinj and those from experimental scenarios where carnivores are primary and secondary bone modifiers. There is a similar percentage of all the specimen sizes in these experimental assemblages and the FLK Zinj, with the exception of the smallest (<3 cm) and the largest specimens (>10 cm). According to this, "the low incidence of long bone flakes relative to other shaft fragments from the FLK 22 suggests that long bones were intact when modified by carnivores" (Capaldo, 1995, p. 298). If post-depositional bone fragmentation had distorted tooth mark frequencies, this would be shown in the percentages of smaller fragments being higher than those documented in experimental assemblages. However, the percentage of small-sized fragments at the FLK Zinj is lower. Furthermore, if carnivores were the only cause of the post-depositional fragmentation of bones, as Capaldo suggests for some of the bone sample at the FLK Zinj, tooth mark percentages would be higher, since carnivores leave tooth marks on most of the bones they break (Blumenschine, 1988, 1995).

Based on this fact, and on Potts's suggestion that several of the bones at Olduvai sites were broken by carnivores, because of the damage patterns observed on them, as well as on Capaldo's analysis of flake sizes, which indicates the same process, I tried to experimentally reproduce such a scenario (Domínguez-Rodrigo, 1999b). I assumed that food yields from largely fleshed carcasses might have led to the abandonment of several marrow-bearing intact bones by hominids. This fact and the carnivore ravaging undergone by such bone accumulations might account for the particular percentage and distribution of the tooth marks found on bone surfaces at the FLK 22 Zinj site in Olduvai Gorge and the preservation of an important number of complete elements. Such a model should be considered as a mixture of "whole-bone to carnivore" and "hammerstone to carnivore"

experimental scenarios, using the terminology of Blumenschine (1988) and Capaldo (1995).

The results obtained in this study were surprising. Blumenschine (1995, p. 33) initially observed that

[T]he rate of tooth marking at FLK Zinjanthropus is substantially lower than that in the carnivore only sample for all size and portion categories for which adequate samples are present. Midshaft fragments are solely responsible for the overall higher rate of tooth marking at FLK Zinjanthropus compared to that in the hammerstone-to-carnivore sample; otherwise, epiphyseal and near-epiphyseal fragments at FLK Zinjanthropus are tooth marked at a rate predicted by the hominid-to-carnivore sample.

In no experimental study made by Blumenschine (1988, 1995) or Capaldo (1995) simulating early human access to carcasses did they observe such a high rate of tooth-marked midshaft bones as in the FLK Zinj site.

In my study on partially demarrowed carcasses, I obtained a particular pattern of tooth marks according to bone section (Domínguez-Rodrigo, 1999b). The mean of tooth-marked epiphyseal specimens is similar to that obtained in other hominid-to-carnivore experiments (Blumenschine, 1988, 1995; Capaldo, 1995). This is also true for near-epiphyseal fragments. However, the most important result of this study is that the percentage of tooth-marked midshaft specimens is very similar to that observed in the FLK Zinj sample (Fig. 1). The latter falls within the range of variation of the former. In no other hominid-to-carnivore experiment (modelling early human defleshing and demarrowing of bones) had the FLK Zinj sample been observed to fall within such ranges of variation. Only in the whole-bone-to-carnivore model did Capaldo (1995) obtain a similar percentage of tooth-marked midshaft fragments, but in this case, the lack of percussion marks invalidates the model as a useful heuristic approach to interpreting the FLK Zinj site.

The representation of midshaft fragments according to their size was similar to that obtained in other experimental studies and at FLK Zinj (Blumenschine, 1988, 1995; Capaldo, 1995). Thus, bias due to bone size representation is not a factor. Even the mean percentage of tooth-marked bones (irrespective of their section) is similar to that reported for the FLK Zinj bone sample.

This pattern, strikingly similar to that documented in FLK Zinj, suggests that carnivore activity at the site must not have been restricted to the ravaging of demarrowed bones broken by hominids. This should not be so surprising if we seriously consider the diagnostic framework for the three-part carnivore-to-hominid-to-carnivore hypothesis. In assemblages first modified by carnivores (Selvaggio, 1994) or only modified by carnivores (Blumenschine, 1988), the percentage of tooth-marked bones is much higher than that observed at FLK Zinj. If hominids had secondary access to such bone

assemblages, we should expect the tooth marking percentages made by primary carnivores and those made by secondary scavengers (after the intervention of hominids) to be significantly higher than those shown at FLK Zinj.

On the other hand, only one sixth of the complete limb bones used for this study survived carnivore consumption. This suggests, as Capaldo (1995) claims, that the original number of complete bones at FLK Zinj must have been significantly higher than that documented: about 10% of the total MNE of limb bones identified (Bunn, 1982; Potts, 1982, 1988). The tooth marks or cut marks on these complete bones still have to be carefully analyzed. However, some of the bones reveal a significant number of modifications actually made by archaeologists during excavation. This circumstance and the fact that some of them have been coated with glue prevent us from obtaining clear identifications. On the other hand, tooth marks do not necessarily indicate primary exploitation by carnivores. They could also have been made by small scavengers—such as jackals (personal observation)—that were unable to break the bones. In a brief analysis of some complete elements from other Olduvai sites, I documented no clear mark that could be attributed to carnivores, which would exclude them as primary carcass consumers. Further analyses of these complete specimens is necessary.

The fact that hominids may not have broken all the bones they accumulated is reflected in several other sites (such as FLK North 6, FxJJ 3 HAS, Gahi 5), in which complete bones from large carcasses exhibit cut marks but were not demarrowed (Bunn, 1994).

This work shows that tooth-mark abundance on midshaft sections from long bones is also subject to equifinality. A high frequency of tooth marks can be obtained in both experiments modelling primary access by carnivores and those modelling access by hominids to carcasses that are abandoned with some marrow-containing bones intact. Percussion marks are not valid for differentiating between these two opposite processes, as they were to refute the whole-bone-to-carnivore experimental model. Does this mean that since tooth marks are subject to equifinality, they should not be used to make behavioral inferences? The answer is negative; here, another association of marks is needed to rule out equifinality. Tooth marks and cut marks considered together should be enough to differentiate between processes resulting in the same tooth-mark patterns. Cut-mark analyses at the FLK Zinj suggest primary access by hominids to fleshed carcasses. This may have yielded enough food for hominids, allowing them to discard some complete marrow-bearing bones. Carnivore ravaging of the resulting bone assemblage to extract the grease and marrow may have led to the intermediate proportion of tooth marks on midshaft sections from long bones.



## ANALYSIS OF BONE SURFACE MODIFICATIONS FROM THE FxJj50 SITE: INCREASING THE FOSSIL SAMPLE

One of the problems in the reconstruction of behavioral patterns from the archaeological record is that these experimental scenarios have only been applied to one Plio-Pleistocene site (FLK Zinj). Therefore, we do not know the range of variation of bone surface modifications in other archaeofaunas.

In 1996, I conducted a study of the bones from the FxJj50 site. This important archaeological locality is situated in the Karari scarpment, East of Lake Turkana (Kenya). It was preserved in a fine-grained layer at the base of the Okote Tuff Complex, dating to more than 1.5 Ma. The bone assemblage consists of more than 2000 specimens, of which only 35% are identifiable. The analysis of surface marks was carried out on 271 limb bone specimens that could be identified to mammal size (Sizes 1–4). One reason for excluding larger mammals (like the many specimens of hippopotamus) and for lumping all these sizes together was that previous actualistic research on human and carnivore interaction had been restricted to animals of Sizes 1–4 (Blumenschine, 1988; Capaldo, 1995; Domínguez-Rodrigo, 1997a,b, 1999a,b; Selvaggio, 1994). Another reason was that the difference of resource availability prior to and after carnivore modification of carcasses is very marked in animals of these sizes and, therefore, more easily tested (Blumenschine, 1986). Since most of the models on the order of intervention of hominids and carnivores have been developed from experiments with limb bones (Blumenschine, 1988; Domínguez-Rodrigo, 1997a,b, 1999b; Selvaggio, 1994), I focused on the same anatomical elements in my analysis of FxJj50.

According to Bunn *et al.* (1980), bone preservation at this site is relatively good compared to any other Karari site; however, it is much worse than in the archaeofaunas from Olduvai, rendering the study more difficult, since marks can often be mistaken. A significant portion of the assemblage is composed of bones with a leached and crumbly surface, showing loss of external cortical layers in varied degrees. It is probable that most of the original modifications made by humans and carnivores on these bones have disappeared along with their cortical surfaces. An analysis of bone surface modification is only reliable if carried out on specimens showing better preservation. For this reason, 145 out of the 271 limb bone specimens belonging to Size 1–4 animals were discarded, due to bad surface preservation. The remaining 126 (i.e., 46%) were analyzed following the criteria outlined by Blumenschine (1988, 1995), Blumenschine and Selvaggio (1989), Blumenschine *et al.* (1996), and Domínguez-Rodrigo (1997). For identification of marks, 20× lenses were used under a strong (60 W) direct light.

Tooth marks were the most difficult to identify because of the surface pitting, so only those cases in which a *confident* identification could be made

were counted as tooth marks. Bad preservation has very likely affected the correct identification of several inconspicuous marks. Cut marks were classified following the criteria defined by Domínguez-Rodrigo (1997a): bone section and bone type were differentiated when possible. Limb bones were divided into upper (humerus and femur), intermediate (radius-ulna, tibia), and lower (metapodials) elements to include as many specimens as possible. Since shafts make up most of the sample, the number of specimens identified was larger when dividing limbs into three groups, instead of into separate elements. This was particularly evident in upper limb bones; in some cases, differentiation between femora and humeri from small shaft fragments was very difficult, but they could be confidently ascribed to upper limb bones since their sections were clearly different from intermediate and lower limb bones. Shaft shape and thickness have proved to be reliable indicators for anatomical identification. This method permitted inclusion of most of the specimens with marks.

The results of the study are shown in Table I. The incidence of percussion marks is substantially lower than in the hominid-to-carnivore experiments, both in all long bone fragments and when divided into bone sections (Fig. 2). Midshafts are marked at a lower rate than in Blumenschine's experiments. However, near-epiphyseal and epiphyseal specimens are marked at frequencies that fall within the range of variation of those experiments. The difference in number may be explained by different bone-breaking techniques and preservation factors (Domínguez-Rodrigo, 1999b).

The global tooth-mark frequency (35%) is slightly higher than in hominid-to-carnivore scenarios (Mean = 19%), although much closer to these than to carnivore-only models (Mean >80%) (Blumenschine, 1988). Percentages on epiphyseal (70%) and near-epiphyseal (58%) fragments are practically identical to those obtained in hominid-to-carnivore experiments.

**Table I.** Frequencies of Cut Marks, Percussion Marks, and Tooth Marks on Different Bone Sections From the Sample Analysed at the FxJ50 Site

	Epiphysis	Near-epiphysis	Midshaft	Total
Tooth marks	12/17 (70.5)	18/31 (58)	15/78 (19.2)	45/126 (35.7)
Cut marks	3/17 (17.6)	4/31 (12.9)	9/78 (11.5)	16/126 (12.6)
Percussion marks	1/17 (5.8)	4/31 (12.9)	7/78 (8.9)	12/126 (9.5)
	ULB	ILB	LLB	
Cut marks	5/25 (20)	5/28 (17.8)	2/23 (8.7)	12/75 (16)
	Shaft	Prox. end	Dist. end	
Cut-marked Bones	5	5	2	12

*Note.* Percentages for cut marks are also shown according to bone type. ULB, upper limb bone; ILB, intermediate limb bone; LLB, lower limb bone.

Midshaft specimens bearing tooth marks (Mean = 19%) are similar to hominid-to-carnivore models: Mean = 10% (Blumenschine, 1988, 1995) and 15% (Capaldo, 1995) (Fig. 1). This percentage of tooth marks contrasts with those obtained in carnivore-only experiments (Mean >80%). Therefore, tooth marks are indicative of early access to carcasses by hominids, and the subsequent modification of bones by scavengers. The tooth-mark frequencies at FxJj50 are incompatible with three- and two-part models in which carnivores are primary agents of carcass consumption. The abundance of tooth marks at this site is also incompatible with two-part models in which hominids have primary access to carcasses but do not fully exploit them (Domínguez-Rodrigo, 1999b) (Fig. 1). Tooth mark abundance in such models is significantly higher both lumping all the specimens together and, especially, on midshaft fragments. This could account for the lack of complete bones at the FxJj50, in contrast with the Olduvai sites, where they occur in significant numbers and have different tooth marking patterns (Fig. 1). This may indicate, as Potts (1996) suggested, that hominid behavior was not as uniform during the Plio-Pleistocene as previously thought, but highly variable.

Cut marks on the bones from FxJj50 constitute 12% of the assemblage analyzed. This percentage is much higher than that reported by Bunn *et al.* (1980) because they included most identifiable specimens regardless of their surface preservation. This taphonomic bias obviously affects the low amount of cut marks initially reported at the site. The cut-mark percentage presented here is based exclusively on the portion of the sample with relatively good surface preservation and only on long limb bones. (A few cut marks were also observed on other anatomical elements, like ribs, that are not taken into consideration here.)

The distribution of cut marks on the FxJj50 limb bones can be seen in Table I. Most cut marks occur on midshafts and on upper and intermediate elements: When taking into consideration bone type plus bone section, midshafts from upper limb bones are the most cut-marked (Table I; Fig. 4). Given the fact that midshafts (in general) and upper limb bones are practically devoid of even scraps of flesh at carnivore kills, the cut-mark pattern from the FxJj50 is indicative of flesh exploitation, and therefore, early access to carcasses by hominids. This is in accordance with the data drawn from the analysis of tooth marks. Secondary intervention of carnivores would explain the scarcity of epiphyseal specimens and the predominance of shaft fragments in the limb bone assemblage (Bunn *et al.*, 1980).

These results are in accordance with other studies. The analysis made by Monahan (1996) on Olduvai Bed II faunas also shows that upper limb bones are highly ranked among the cut-marked bones in some of the sites, further suggesting that hominids were primary agents in carcass exploitation.

## HUNTING AND SCAVENGING AS SEEN FROM THE PERSPECTIVE OF BEHAVIORAL ECOLOGY AND PRIMATOLOGY

The different types of hominids that existed in the deep past are extinct species that, physically and behaviorally, have no modern counterparts. Therefore, their ways of life can only be reconstructed by using dialectic analogues (not descriptive analogies) to reconstruct behavioral patterns from the limits imposed by the criteria of natural selection (Tooby and De Vore, 1987). This is what gives meaning to behavioral ecology (Foley, 1987), which provides a referential framework for the selective requirements that hominids had to overcome and to incorporate into their adaptive patterns (Domínguez-Rodrigo, 1994a).

The extent of meat consumption and its importance in the diets of early hominids are particularly relevant in this regard and can also be approached from a behavioral ecology standpoint. Meat seems to be important in ape diets according to their physiology and their ecological niche. Thus, while orangutans and gorillas are mostly vegetarians, meat consumption has been observed with a relative frequency in chimpanzees (Boesch, 1994a,b; Boesch and Boesch, 1989; Busse, 1976; Goodall, 1963, 1986; Huffman and Kalunde, 1993; McGrew *et al.*, 1978, 1979; Nishida *et al.*, 1979; Stanford, 1999; Stanford *et al.*, 1994; Suzuki, 1971, 1975; Teleki, 1973; Wrangham and Riss, 1990; Uehara *et al.*, 1992). Meat eating in orangutans is very occasional (Sugardjito and Nurhuda, 1981). Both orangutans and gorillas eat insects on a regular basis. Some authors claim that meat eating in these apes is a matter of energetic cost of capture versus energetic return, as they are not well adapted to hunting (Yamagiwa *et al.*, 1996). According to several studies, savanna chimpanzees hunt more often than those apes whose habitat is the dense tropical forest (Boesch, 1994b; Boesch and Boesch, 1989; McGrew, 1992; McGrew *et al.*, 1979; Nishida *et al.*, 1979; Stanford, 1999; Stanford *et al.*, 1994; Wrangham and Riss, 1990). This is also documented for other primates in similar environments: another important predatory species, the savanna baboons, are precisely adapted to open-vegetation areas (Altmann and Altmann, 1970; Strum, 1975, 1981, 1983).

Chimpanzees obtain most of the meat they eat by hunting (Boesch, 1994b; Boesch and Boesch, 1989; Goodall, 1986; Huffman and Kalunde, 1993; Stanford, 1999; Stanford *et al.*, 1994; Teleki, 1973; Uehara *et al.*, 1992; Wrangham and Riss, 1990) and only occasionally have been observed to pirate a fresh kill from baboons (Morris and Goodall, 1977). However, new observations have further confirmed that chimpanzees do scavenge from time to time and that those groups reported to scavenge do not live in areas as dense as a tropical forest (Hasewaga *et al.*, 1983). This subsistence behavior

is also reported among savanna baboons (Strum and Mitchell, 1987). Chimpanzees usually hunt and scavenge lightweight animals (<10 kg). This may be explained because larger animals are less frequent in woody areas and more difficult to process without tools. According to Goodall (1986), a chimpanzee group composed of 40 individuals may hunt as many as 20 or more prey in less than a year. This rate is even higher and markedly seasonal in more recent studies (Stanford *et al.*, 1994; Wrangham and Riss, 1990). Nevertheless, it seems to vary from one region to another. The rate of meat eating among the various populations of chimpanzees (measured by analysis of feces) shows that the groups living in savanna ecosystems eat more meat than groups that live in dense tropical forests (Boesch, 1994a,b; Boesch and Boesch, 1989; Goodall, 1986; Huffman and Kalunde, 1993; McGrew, 1992; Stanford, 1999; Stanford *et al.*, 1994; Uehara *et al.*, 1992; Wrangham and Riss, 1990). On the basis of these observations, it could be assumed that early hominids were also “frequent” meat eaters because both of their close resemblance with these apes in physiology, and because of being adapted to more open areas than are extant savanna chimpanzees (Foley, 1987; Stanford *et al.*, 1994; Uehara *et al.*, 1992).

It is, thus, not surprising that recent isotopic analyses on bones of *Australopithecus* have yielded a high level of C4, suggestive of consumption of meat (Sillen, 1992; Sponheim and Lee-Thorp, 1999), although the consumption of some plant tubers (such as *Cyperus*) could also display a C4 synthetic pathway. If that may have been the case with *Australopithecus*, the higher energetic requirements of early *Homo* (due to the development of a larger brain) must have further promoted behaviors that led to a significant amount of energy (and very likely, protein) in the diet (Aiello and Wheeler, 1995). Regular reliance on meat would imply hunting rather than scavenging, since opportunistic strategies of obtaining carcasses are temporarily and qualitatively limited (Blumenschine, 1986). We do not know how important meat was in early hominid diets, but, for meat to have been an important element, it must have been obtained and consumed on a regular basis. Research in this regard is advancing by stages. The first stage is to ascertain whether meat was part of early hominid diets, and if so, whether it was obtained through hunting or scavenging. The second stage would be to devise an analytical approach that would enable archaeologists to evaluate the frequency of meat consumption by Plio-Pleistocene hominids.

If the earliest members of our genus were responsible for the accumulation of the carcasses that appear at early sites, another element to consider is the reason for transporting so many bones to places that are supposed to have been used as common social loci. This can also be relevant for the hunting and scavenging discussion.

According to Blumenshine *et al.* (1994), hominids were transporting carcasses from open areas, in which competition is usually high, to closed-vegetation riparian zones, where they processed them with the aid of stone tools. The difference between this model and the “central-place foraging” model proposed by Isaac (1983) lies in the type of product consumed by hominids. In the “central-place foraging” model, hominids were assumed to have carried fleshed carcasses to sites, which yielded enough food to be shared by several individuals, whereas in the “refuge” model, hominids are thought to have transported mainly defleshed bones with high marrow yields. Despite these differences, both models converge on the idea that Plio-Pleistocene sites were relatively safe spots where bone transportation, processing, and consumption took place. Some authors (Binford, 1981; Blumenshine, 1991; Potts, 1988) believe that hominid behavior at these early sites can be accounted for in ethological terms, with hominid behavioral patterns falling within the behavioral patterns of extant apes. From an archaeological perspective, the problem is whether hominids could have generated the bone and artifact concentrations that appear at sites while maintaining a “socioeconomic structure” similar to that observed in other primates.

One of the main features of primates is that most of them live and forage in groups (Aldrich-Blake, 1970; Alexander, 1974; Bradbury, 1980; Clutton-Brock and Harvey, 1977; Crook and Gartlan, 1966; Di Fiore and Randall, 1994; Domínguez-Rodrigo, 1994a; Dunbar, 1988; Gartlan, 1968; Lee, 1983; Pulliam and Caraco, 1984; Rowen and Olson, 1983; Seyfarth *et al.*, 1978; Struhsaker, 1969; Terbourgh and Janson, 1986; van Hooft and van Schaik, 1992; van Schaik, 1983; van Schaik and van Hooft, 1983; Wrangham, 1979, 1980, 1983, 1987). Group foraging enhances the adaptation of individuals by improving their foraging efficiency, resource defense, and protection against predators (Dunbar, 1988; van Schaik and van Hooft, 1983). Kummer (1971) pointed out that primate societies are essentially “group solutions” to ecological problems. Therefore, it is not surprising to observe that grouping patterns among primates show a relation with particular ecological variables—as attempts to respond to the demands of trophic pressure (Clutton-Brock and Harvey, 1977; Dunbar, 1988; Foley, 1987; Lee, 1983; van Schaik, 1983; Wrangham, 1979, 1980).

It has been observed that group cohesion is remarkably strong in species adapted to environments in which the risk of predation is high (Alexander, 1974; Dunbar, 1988; Gartlan, 1968; van Hooft and van Schaik, 1992; Lee, 1983; van Schaik, 1983; Terbourgh and Janson, 1986; Wrangham, 1979, 1987). This characteristic becomes particularly marked among the primates adapted to savanna ecosystems (Dunbar, 1988). Savanna primates always act more cohesively than forest primates, especially those whose ecological

niche includes larger open-habitat areas, such as baboons (*P. cynocephalus*, *P. hamadryas*, *P. ursinus*, *P. papio*) and geladas (*T. gelada*). The trend toward a greater cohesion in primates seems, thus, to be related more to ecological criteria than to phylogenetic factors (van Schaik, 1983; van Schaik and van Hooft, 1983). Dunbar (1988) acknowledges that predation risks promote the formation of large groups and that the optimum group size is habitat-specific. He points out that “[T]he value of grouping as an anti-predator strategy will depend closely on both the local density of predators and the availability of safe refuges” (p. 132).

Therefore, according to the pattern commonly observed in living primates, the adaptation of hominids to the East African Plio-Pleistocene savannas should have further promoted social behaviors in which group foraging was a key adaptive feature (Clutton-Brock and Harvey, 1977, Domínguez-Rodrigo, 1994a). The behavioral models proposed to account for the East African Plio-Pleistocene archaeological sites, with the exception of Isaac’s “home base” model (Isaac, 1978), have not explicitly stated the social repercussion of the subsistential behaviors they try to reconstruct. However, all of them support the idea that hominids responsible for the early archaeological record were foraging and moving across the landscape in groups (Foley, 1987).

Some researchers, following the “early access to carcasses” or “hunting” hypothesis, suggest that hominids were already showing a “human” behavioral pattern, in which food was transported to particular places where it was collectively consumed (Bunn, 1982; Bunn and Ezzo, 1993; Bunn and Kroll, 1986; Isaac, 1978, 1983; Oliver, 1994). Others, defenders of the “scavenging” hypothesis, suggest that such a food-sharing attitude probably did not exist, because meat was scavenged and, therefore, not very likely to have yielded more than enough for one individual (Binford, 1981; Blumenschine, 1986, 1991). Some suggest that the social organization of hominids would have been more apelike and that food transport must have been influenced by ecological pressures (such as competition) rather than by social stimuli (Binford, 1981; Blumenschine *et al.*, 1994; Potts, 1982, 1988).

In a recent study of food availability and social stress among captive and wild baboons, we tested some of the assumptions stemming from the “scavenging” hypothesis (Domínguez-Rodrigo *et al.*, 1998). We combined three aspects of hominid behavior central to this hypothesis: group foraging, primate social structure, and food type and availability. We showed that marrow scavenging and the repeated use of specific places in certain habitats (riparian woodland) may be inconsistent with a group foraging strategy, because they could have led to social stress. Most of our experiments showed that stress within a group generated by food scarcity frequently turns into physical aggression. A similar study, when carried out in the wild in Tsavo

East National Park (Kenya), showed that social stress generated through these behaviors rarely turned into aggression, due to individuals escaping from the location where food was disposed. As a consequence, food remains were dispersed and not concentrated as they are at early Plio-Pleistocene archaeological sites. Ethological studies indicate that group adaptive patterns in living primates have important costs. As Dunbar (1988, p. 132) remarks, “[T]here are two kinds (of costs): those that are due to competition for access to limited food or other essential resources, and those that are due to living in close proximity to other individuals.” Following the results of our study, we believe that the scarcity of scavenged food and its transport by hominids to places of communal use (archaeological sites) might have generated social stress, that could have turned into regular intragroup aggressive behaviors, had hominids behaved as extant apes. We suggested that food transported to such sites must have been high-yielding to avoid such social stress (Domínguez-Rodrigo, 1997a; Domínguez-Rodrigo *et al.*, 1998).

The “refuge” model proposed by Blumenschine suggests that hominids might have transported carcasses to particular loci in the closed riparian habitats to avoid carnivore competition (Blumenschine, 1991; Blumenschine *et al.*, 1994). Hominids would, thus, have behaved as do most carnivores. However, carnivores behaving in this way do not generate significant bone accumulations. Tappen (1992) documented one single place where remains of five carcasses were accumulated in a modern savanna by carnivores. She did not witness the carnivores accumulating the assemblage and did find cut-marked specimens in it. She admits that the assemblage may have been made by poachers and that the spot attracted both humans and carnivores. Besides, the total surface “accumulation” amounts to an MNE of 13. In contrast, MNEs at archaeological sites at Olduvai are counted in the hundreds. Cavallo (1997) showed that leopards could accumulate a few carcasses (usually no more than three versus almost 50 carcasses at the FLK Zinj site) on the same tree but bones were not preserved because of hyaena consumption once they fall to the ground. Likewise, nobody has documented accumulations of middle-sized carcasses in the open air because lions can afford to process them at or near the kill sites, given their position in trophic dynamics.

There are three kinds of strategies adopted by carnivores to cope with competition: consumption of the prey in situ, short-distance transport of the prey depending on initial location, and systematic transport of carcass remains to the same spot (Domínguez-Rodrigo, 1994b). The first of these strategies tends to maximize the energy investment. It is a strategy adopted by carnivores according to their position in the trophic chain, determined by



body size and group size. Predators like the lion can afford to eat their prey on the spot, because they are gregarious and they are the largest of savanna predators (Schaller, 1972). Most carnivores in the intermediate or lower ranges of that trophic chain eat their prey on the spot only if the landscape does not allow them to move the prey to a sheltered place. Cheetahs will preferentially move their prey to high grass patches or behind bushes (Brain, 1981). Leopards will transport their prey to trees (Brain, 1981). Among group carnivores, like hyaenas or wild dogs, prey are initially disarticulated on the spot, and then some anatomical sections are dispersed around the kill site. These behaviors do not generate bone clusters from several individuals because they usually take place around the kill site, and transport rarely exceeds 250 m. Even in those cases in which more than one individual is transported to the same place (as some leopards do because of the scarcity of appropriate trees), prey rarely exceed three in number (Cavallo, 1997). Bone accumulations observed at hyaena or leopard dens result from feeding and from predators seeking refuge to reduce competition. In such cases, carnivores temporarily engage in a systematic transport of carcasses that involves a high energetic cost and a much higher risk of losing the prey to competitors than does the usual behavior of short-distance carcass transport (for a further analysis on carnivore behavior and refuge spots, see Domínguez-Rodrigo, 1994b).

Had hominids behaved like the rest of carnivores, moving carcasses to refuge locations, they would have been expected to do so in a different place each time, depending on where carcasses were obtained. Repeated transport to the same place can be better explained if “refuge seeking” was not the main or only reason for bone transport. From a carnivore point of view, it would make more sense if they transported bones or carcasses with feeding purposes as well.

Food brought to or obtained in social areas tends to be dispersed instead of concentrated as it is in archaeological sites, especially if it is scarce and if it is not shared (Domínguez-Rodrigo *et al.*, 1998). That is why nonhuman primates as well as carnivores do not generate significant debris. In the case of carnivores, that only happens when food is transported to dens or lairs to be shared.

Some researchers view archaeological sites as the result of accidental reoccupations of the same spots by hominids, like the spatial redundancy in nesting and sleeping site behavior observed in chimpanzees (Sept, 1992). Several species exhibit spatial redundancy in certain places. Two clear examples are predators in landscapes permitting “serial predation” as well as those which return daily to their lairs. However, repeated use of some spots is not the same thing as the accumulation of debris there. Archaeologists are

challenged to seek the answer not only to a spatially redundant behavior, but to a bone-plus-artifact accumulating behavior. Sept's studies (Sept, 1992) do not contribute substantially to the last issue.

Could hominids have produced the material accumulations observed at early sites if they maintained socioeconomic behavior the same as or similar to that of chimpanzees? Concerning tool use and transport, it should be emphasized that although chimpanzees have been reported to produce small clusters of stones, there are qualitative and quantitative differences between these and the bone and artifact clusters at archaeological sites. Chimpanzees sometimes carry tools to places where they need them for feeding purposes, but they have never been seen to carry stones to places with stones already there. This might be because chimpanzees use and transport tools only when they need them; that is, it is *ad hoc* and not premeditated. The reuse of such tools only occurs when chimpanzees forage in the same area every season or year (Boesch and Boesch, 1981). Stones thus accumulated are very few in number, and what we observe in early sites is different. Hominids were accumulating important amounts of stones in certain places (Potts, 1982, 1988). The co-occurrence of several raw material types seems to indicate that hominids carried stones to those places repeatedly, as if they considered them important. The transport of raw materials up to 8–10 km from their source contrasts with the transport behavior of chimpanzees, which have occasionally been observed to carry tools as far as 500 m (Boesch and Boesch, 1981). A further proof of the importance of stone transport is the differential treatment by hominids of raw materials: some were fully exploited and rarely discarded, being transported from one site to the next (Toth, 1982, 1987).

With respect to feeding habits, nonhuman primates do not transport food to predetermined places to be processed and eaten, but consume it where they find it. The rare food remains at sleeping sites (Sept, 1992) are due to the consumption of foods that are found in or near the trees where chimpanzees make nests. No food is imported to sleeping sites from distant places. Chimpanzees, like other primates, do not transport food to predetermined spots simply because their subsistence behavior does not require it. If hominids had retained the same behavior, they would never have produced dense bone patches. Even if bone or carcass transport had been necessary to avoid competition, bone clusters would not have been generated. (See above for similar observation regarding hominids and carnivores in the critique to the "refuge" model.) In contrast, early sites show that hominids regularly carried carcasses to them, which were processed with the aid of stone tools. Some animals carried in are species that were probably not obtained nearby. This may be indicative of social and subsistence behavior different from that reported among chimpanzees (*contra* Sept, 1992).

## CONCLUSIONS

Most of the traditional interpretations about scavenging by Plio-Pleistocene hominids have been based either on untested assumptions or when testable hypotheses were provided, they were subject to equifinality. The use and abuse of skeletal part frequencies is probably the clearest example of this. The best indicators of hominid–carnivore interactions rest on the analyses of bone surface modifications, which have allowed us for the first time to test the scavenging hypothesis (Blumenschine, 1995; Capaldo, 1995; Domínguez-Rodrigo, 1997a; Selvaggio, 1994). Despite initial interpretations, these studies do not support the scavenging hypothesis. Bone surface modifications (cut marks, percussion marks, and tooth marks) and the state of element preservation (complete versus fragmented bones) at FLK Zinj at Olduvai and FxJj50 at Koobi Fora are best explained by two-part models (hominid-to-carnivore) (Domínguez-Rodrigo, 1999b).

Upper limb bones and shafts from carcasses at both sites are the most often cut-marked appendicular sections, indicating early access by hominids to fleshed carcasses, because they are utterly devoid of flesh at carnivore kills. This is further supported by the incidence of cut marks on axial elements, especially on ribs (Bunn and Kroll, 1986; Capaldo, 1995), which are also indicative of primary access since they are defleshed after carnivores' initial consumption.

Tooth marks and midshafts from long limb bones vary between the FLK Zinj site and the FxJj50 site. Tooth-mark percentages on midshaft specimens at FLK Zinj are between the hammerstone-to-carnivore model and the carnivore-only model, based on the assumption of thorough exploitation of carcasses by hominids (Blumenschine, 1988, 1995). However, a hominid-to-carnivore model, assuming that marrow was not fully exploited, has provided the only experimental scenario in which tooth marks and percussion marks were reproduced to percentages similar to those observed at FLK Zinj (Domínguez-Rodrigo, 1999b). This model is the first one to explain both the pattern of bone surface modifications (tooth marks, cut marks, and percussion marks) as well as the survival of complete elements. Tooth marks on the midshaft specimens from the FxJj50 site are similar in percentage and distribution to those observed in the hammerstone-to-carnivore model of Blumenschine (1988, 1995) and Capaldo (1995, 1997), in which carcasses were fully exploited. No complete elements must have, therefore, been abandoned by hominids at this site prior to carnivore postravaging of bones.

Access by hominids to fleshed carcasses, as seems to be indicated by these data, is contradictory to passive scavenging from carnivore kills. Only the scavenging of small mammals from tree-stored leopard kills would allow hominids to have access to significant amounts of flesh by using opportunistic

strategies (Cavallo and Blumenschine, 1989). In that case, we would expect a high representation of animals belonging to small-sized species (10–100 kg.) or equally small infants/juveniles from medium-sized species. Most of the individuals documented so far at early sites are medium-sized, with a significant representation of both adults and subadults (Bunn, 1982), thus excluding hominid scavenging of leopard kills. Furthermore, the model for that scenario would require a low incidence of tooth marks on long bone midshaft sections, since cut marks in fossil fauna indicate access to fleshed carcasses (see above). Cavallo (1997) has documented that tooth marks on carcasses consumed by leopards can be as high as 90% of all the specimens. (Tooth-mark percentages on the earliest stages of prey consumption by leopards are unknown.) At present, the hypothesis of scavenging from leopard kills has been neither modelled nor tested. Leopards often leave their prey in trees for hours after having initially consumed part of it (Cavallo, 1997), which would allow scavengers access provided they can climb trees. Nonetheless, leopards have been documented to preferentially process the upper limbs of carcasses in the first stage of consumption (Cavallo, 1997). This fact necessitates a methodological approach that would be effective in testing access to partially fleshed carcasses after the leopard's initial consumption. In this case, tooth marks should be analyzed not only according to bone section (Blumenschine, 1995; Capaldo, 1995), but also by the type of element (Selvaggio, 1994). Selvaggio documents a pattern of tooth marks per bone type that seems to be related to the extraction of meat by carnivores. Midshaft sections from upper limb bones initially defleshed by carnivores are as highly tooth-marked (Selvaggio, 1994) as those documented in carnivore-only experiments (Blumenschine, 1995; Capaldo, 1995), regardless of the kind of element. This would suggest that initial consumption of small carcasses by leopards would leave a differential distribution of tooth-marked midshaft specimens: a high percentage on upper limb bones, and a low to absent percentage in intermediate and lower limb bones. Likewise, cut-marked midshafts from upper limb bones should be scarce if the flesh has initially been removed by leopards. As was observed above, neither of these situations have been documented at early sites.

In the current state of our knowledge, the most parsimonious explanation is that hominids obtained fleshed carcasses before other carnivores had access to them. The range of possibilities include hunting and confrontational or primary scavenging from mass deaths.

Capaldo and Peters (1995) have documented that natural deaths from mass drownings can yield abundant meat for scavengers. However, this type of event is infrequent and located only in certain geographic areas where mass migrations occur. Future studies on seasonality, like those carried out in the Upper Pleistocene of the Near East (Lieberman, 1993) could help to

shed more light on the formation of the bone assemblages at early sites and test this possibility. Confrontational scavenging, as advocated by Bunn and Kroll (1986) and Bunn and Ezzo (1993), implies that hominids confronted big Plio-Pleistocene felids; in my opinion, this behavior may have been too risky and costly for hominids (Treves and Naughton-Treves, 1999), especially given that African felids were bigger and more diverse in the Plio-Pleistocene savannas than today (Domínguez-Rodrigo, 1994a). However, this strategy could have enabled hominids to obtain meat as often as through hunting.

Data from the archaeofaunas at Olduvai and Koobi Fora suggest that hominids had primary access to fleshed carcasses. The strategies they used to obtain these carcasses are still unknown and difficult to test. The (still-untested) scavenging hypothesis has been assumed by several researchers as the most likely explanation for carcass acquisition by early hominids (Lewin, 1984), and even landscape modeling has been made on this basis (Blumenschine and Peters, 1998; Peters and Blumenschine, 1995). In the current stage of research, the hunting hypothesis cannot be ruled out, and it seems that its heuristic power is greater than that of the passive scavenging scenarios outlined so far. Perhaps we are not far from the threshold of another scientific revolution toward interpretations in which hominids are considered to have been more actively involved in obtaining carcasses.

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