HOMININ-CARNIVORE INTERACTIONS: EVIDENCE FROM MODERN CARNIVORE BONE MODIFICATION AND EARLY PLEISTOCENE ARCHAEOFAUNAS (KOOBI FORA, KENYA; OLDUVAI GORGE, TANZANIA)

by

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ABSTRACT OF THE DISSERTATION

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Interactions between Oldowan hominins and larger carnivores likely shaped important aspects of hominin adaptation including morphology, foraging patterns, habitat preferences, and social behavior. Hypotheses of Oldowan hominin carcass procurement strategies include scavenging large muscle masses, flesh scraps and/or bone marrow from larger felid kills. Efforts to evaluate these hypotheses are hindered by a current inability to recognize zooarchaeologically the specific carnivore taxa with which hominins interacted. This dissertation helps redress this limitation by documenting and quantifying taxon-specific traces of modern African carnivore consumption of Thomson's gazelle through buffalo-sized prey carcasses, including gross bone damage patterns, the incidence and patterning of tooth marking, and tooth mark measurements. Integrating these taphonomic traces facilitates the construction of hypotheses concerning the

involvement of particular carnivores with Oldowan hominins. These results are applied to four Plio-Pleistocene archaeofaunas from East Africa to test hypotheses of hominin-carnivore interaction and document hominin carcass procurement strategies.

Oldowan hominin carcass foraging strategies were variable. New studies of three site-scale archaeofaunal assemblages from Koobi Fora, Kenya (FwJj14A, FwJj14B, and GaJi14) document hominin extraction of meat and marrow from several prey carcasses at each site, probably with little involvement from carnivores, which seems to have been restricted to off-site limb epiphyseal destruction by hyaenids following hominin butchery. The precise carcass resource procurement method (hunting, power scavenging, passive scavenging) is indecipherable, but it is likely that hominins were acquiring considerable quantities of meat and marrow. The lack of *bona fide* stone tools at these sites is surprising, despite apparent on-site hominin butchery, and may relate to raw material scarcity.

In contrast, analyses of a landscape-scale sample from lowermost Bed II, Olduvai Gorge, suggests involvement of a variety of carnivores with comparatively less hominin activity. Carnivore activity does not seem to have varied though time during lowermost Bed II, but it does appear to have varied over space in accordance with current predictions of vegetation regimes in different geographic locales. A model of diagnosing carnivores from bone damage and tooth mark patterns, using methodology derived from my modern studies, is applied to carcass parts from individual prey animals found in Beds I and II.

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Introduction: Research Issues and Objectives, Theoretical Perspectives

Oldowan Hominin Carnivory: Background

Understanding the nature of early hominin carnivory broadly overlaps with questions regarding the nature of the earliest hominin technology (Harris and Capaldo, 1993; Semaw *et al.,* 1997; Roche *et al.,* 1999), the varied and fluctuating environmental and ecological settings conditioning early hominin foraging patterns (Clark and Kurashina, 1979; Rogers *et al.,* 1994; Potts, 1998; Plummer *et al.,* 1999; Bobe *et al.,* 2002), and the contribution of dietary adaptation to the process of hominin morphological change and speciation (Aiello and Wheeler, 1995; Wood and Collard, 1999). The earliest archaeological evidence of hominin carnivory includes unmistakable evidence for at least a partial focus of tool-assisted consumption of wildebeest-sized mammals at 2.5-2.6 Ma (de Henzelin *et al.,* 1999; Domínguez-Rodrigo *et al.,* 2005). This diet was probably substantially different than that proposed for earlier Pliocene hominins, who presumably focused on plants and small animals (<10 kg), as do chimpanzees (Stanford, 1996; Mitani and Watts, 2001). This fundamental shift does not simply represent a change in diet, but also changes in biology and behavior, such as cranial and post-cranial morphology, growth and development patterns, locomotion, habitat preferences, activity patterns, population size and structure, social behavior, predator avoidance, technology, and cognitive capabilities. Foley (2001:316-317) lists over thirty expected evolutionary and ecological consequences of increased carnivory in hominins. Specifically, this adaptive shift consequently may have forced increased and novel interactions between hominins and carnivores, including competition for these carcasses potentially leading to resource

partitioning and character displacement (Brantingham, 1998; Stiner, 1991a, 1991b), and enhanced predation risk from sympatric carnivores (Van Valkenburgh, 2001).

Arguments about Oldowan hominin carcass acquisition modes have persisted for decades, mainly under the rubric of the 'hunting versus scavenging' debate (Binford, 1981; Brain, 1981; Bunn, 1981, 1982, 1983, 1986, 2000; Bunn and Kroll, 1986; Shipman, 1986; Blumenschine, 1986a, 1987, 1995; Potts, 1988; Blumenschine and Cavallo, 1992; Bunn and Ezzo, 1993; Lupo, 1994; Oliver, 1994; Capaldo, 1997; Domínguez-Rodrigo, 1997, 2002; Selvaggio, 1998; Domínguez-Rodrigo *et al.*, 2002). A fairly current summary was published a few years ago (Domínguez-Rodrigo 2002; see also Plummer, 2004), and the debate will not be reiterated here. Recently developed analytical methods for deciphering the timing of access of hominins and carnivores to larger mammal prey foods include models combining skeletal part profile and bone surface modification data (Oliver, 1994; Blumenschine, 1995; Monahan, 1996; Capaldo, 1997; Selvaggio, 1998; Bunn, 2001; Domínguez-Rodrigo *et al.,* 2002). These data may offer indications of primary versus secondary carcass access by early hominins, or relative amounts of meat and/or marrow consumed by early hominins, but they still do not provide information about specific carnivores with which hominins interacted during carcass procurement and consumption.

This first step – identifying the involvement of particular carnivore taxa with carcasses also accessed by hominins – is crucial to the evaluation of competing hypotheses regarding hominin-carnivore interactions during the Oldowan (Selvaggio and Wilder, 2001). Differentiating taphonomic signatures of hominins scavenging from (1) large, social, terrestrial felids (e.g. lions) versus (2) large, solitary, terrestrial felids (e.g.

some sabertoothed felids) versus (3) smaller, solitary, arboreal felids (e.g. leopards), or even water-cached hyaena kills, is currently nearly impossible. These types of scavenging by hominins are hypothesized, and scales and characteristics of these scavenging opportunities have been partially documented via actualistic studies (Blumenschine, 1986a, 1986b, 1987; Turner, 1988, 1992; Cavallo and Blumenschine, 1989; Marean, 1989; Selvaggio, 1994a, 1998; Marean and Ehrhardt, 1995; Tappen, 1995; Arribas and Palmqvist, 1999; Domínguez-Rodrigo, 1999, 2001).

Early hominin interactions with the carnivore paleoguild likely shaped important aspects of hominin adaptation such as foraging patterns, habitat preferences, and social behavior. The different hominin-carnivore interactions outlined above have diverse implications for Oldowan hominin morphology, behavior, and ecology. Our understanding of these interactions, however, is hindered by a current inability to recognize zooarchaeologically the specific carnivore taxa with whom hominins interacted. The aims of this dissertation, therefore, are twofold:

1. To further our ability to identify as specifically as possible the carnivore taxa involved with archaeofaunas, based on quantifiable taphonomic variables. This work builds on a series of previous studies of taxon specificity in modern carnivore gross bone damage and tooth marking patterns (see below).
2. To apply the above diagnostic signature criteria (cf. Binford, 1981) to Oldowan archaeofaunas from Koobi Fora and Olduvai Gorge, elucidating the hominin-carnivore interactions at sites from these locales during the Oldowan and Developed Oldowan (here, 1.85-1.5 Ma). The goal of this analysis is to test hypotheses of contrasting competitive contexts in particular landscape contexts,

which predict taphonomic traces of carnivore suites dominated by felids or hyaenids (Blumenschine and Peters, 1998; Blumenschine *et al.,* 2002; Blumenschine *et al.,* 2006). This research aims to enlarge the number of Oldowan archaeofaunas for which hominin-carnivore interactions over prey carcasses is hypothesized in order to move away from the current interpretation of Oldowan hominin carnivory which is based largely on studies of the FLK *Zinjanthropus* site from Bed I, Olduvai, as suggested by Monahan (1996), Domínguez-Rodrigo (2002), and Plummer (2004).

Taphonomic Test Criteria of Early Hominin Carnivory: Analytical Parameters

Skeletal element and element portion profiles were the first measure used to evaluate hominin carnivory, beginning with Dart's (e.g. 1949) description of the osteodontokeratic culture, and Brain's (1967, 1969) critique of it. These profiles remain standard albeit untested measures used to assess modes of carcass procurement and agents of bone assemblage accumulation (e.g., Binford, 1981, 1984; Potts, 1983; Blumenschine, 1986b; Bunn, 1986; Bunn and Kroll, 1986; Stiner, 1991a; Monahan, 1996; Brantingham, 1998; Marean, 1998). However, sometimes the unwarranted assumption that hominins acquired the inventory of skeletal parts present in an assemblage in a fully fleshed condition is made. For example, Bunn (1986) argues for an abundance of "meaty" limb bones at Plio-Pleistocene sites on the basis of long bone representation, but it has been shown that these same skeletal part profiles correlate strongly with the marrow yields of the elements, not their meat yields (Blumenschine and Madrigal, 1993). Marshall and Pilgrim (1991) obtained similar results on Kenyan

Pastoral Neolithic bone assemblages. More importantly, Marean and others (e.g., Turner, 1989; Marean *et al.,* 1992; Marean, 1998; Marean and Kim, 1998; Bartram and Marean, 1999) have thoroughly demonstrated that skeletal part profiles attributed to preferential transport by hominins from complete carcasses (e.g., the schlepp effect), or to hominin access to partially consumed, scavengeable carcasses, are mimicked by density-dependent survivorship of bones heavily modified by carnivores (*contra* Stiner, 2002).

Vrba's (1975, 1980) early use of age (mortality) profiles to assess the agent and/or accumulation mode of some of the South African australopithecine cave deposits initiated the use of such profiles to evaluate carcass procurement by hominins (e.g. Klein, 1982, 1989; Lyman, 1987; Stiner, 1990, 1991a). Some problems with using mortality profiles to infer accumulation mode include the inaccuracy of estimating animal age, variability in living age structures of prey, and seasonal shifts in prey population distributions (Lubinski, 2000), as well as various behavioral and ecological factors conditioning transport decisions (Pickering, 2002) and taphonomic factors biasing age profiles. As with skeletal part profiles, these interpretations assume that the distinctive age profiles associated with catastrophic and attritional death will be maintained throughout the taphonomic history of an assemblage. Systematic work should be conducted on the manner and degree to which carnivore modification, differential transport and preservation, and other taphonomic processes can alter animal age profiles in bone assemblages (Marean, 1995).

Bone surface modifications are currently the most useful way to link consumers to assemblages of fossil bones (e.g. Domínguez-Rodrigo, 2002). For the Oldowan, Bunn (1981) and Potts and Shipman (1981) were the first to unambiguously establish a role for

hominins in modifying bone assemblages at Plio-Pleistocene archaeological sites when they described the distinctive morphology of stone tool cut marks and carnivore tooth marks on fossils from Koobi Fora and Olduvai Gorge. Percussion marks inflicted by hammerstone and anvil breakage of bone, an additional unambiguous trace of hominin activity for which the extracted tissues (marrow and other edible tissues within bones) are distinct from those associated with cut marks (mainly skin, muscle and tendon), was soon recognized (Blumenschine and Selvaggio, 1988). Subsequently, results of carnivore modification of experimentally butchered bone has shown that the incidence and anatomical distribution of percussion marks and carnivore tooth marks is sensitive to the timing of hominin and carnivore access to carcasses, and the carcass tissues consumed by each (Blumenschine, 1988; Blumenschine and Marean, 1993; Selvaggio, 1994a; Capaldo, 1998). These experimental models of marks on bone surfaces have thus far been applied to only a handful of Oldowan (Lupo, 1994; Oliver, 1994; Blumenschine, 1995; Monahan, 1996; Capaldo, 1997; Domínguez-Rodrigo, 1997, 2002; Selvaggio, 1998; Domínguez-Rodrigo *et al.,* 2002) and Middle Stone Age/Middle Paleolithic archaeofaunas (Marean, 1998; Marean and Kim, 1998). However, the results show the ability of surface modification models to unambiguously disentangle the timing of hominin and carnivore access to carcasses, a key methodological step in assessing the place of hominins in a carnivore paleoguild.

Studies of bone surface modifications, especially together with skeletal part and age profiles, will prove useful in breaking the interpretive equifinalities associated with the use of these profiles alone. For example, before skeletal part or age profiles are attributed to the carcass procurement or transport activities of hominins, even moderate

frequencies of tooth-marked bone in an assemblage should alert faunal analysts to investigate the role of carnivore modification in shaping these profiles. As advocated by Domínguez-Rodrigo (1997, 2002), further refining classifications of bone portions and particularly locations of modifications on those bone portions will allow a more precise standardization of bone surface modification data and lead to more accurate behavioral interpretations based on such surface mark location data. For these reasons, I focus mainly on bone surface modification data when analyzing the series of archaeofaunas in this dissertation.

Taxon Specificity in Carnivore Taphonomic Traces

The extent of damage inflicted to bones by feeding carnivores corresponds to the degree to which each taxon reduces the inventory of edible tissues available for subsequent consumers of a carcass. Therefore, different carnivores provide different opportunities and constraints on carcass acquisition by hominins. These have been modeled for modern East African carnivores (Blumenschine, 1986a, 1987; Cavallo and Blumenschine, 1989; Domínguez-Rodrigo, 1999), and some extinct carnivores (Turner, 1988, 1992; Marean, 1989; Marean and Ehrhardt, 1995; Lewis, 1997; Arribas and Palmqvist, 1999). Learning taxon-specific patterns of carnivore damage to bones will permit zooarchaeologists to identify the carnivores with which hominins interacted, directly or indirectly, over carcass food resources. For example, the complementary scavenging opportunities posited for Oldowan hominins from lion kills (Blumenschine, 1986a, 1987; Domínguez-Rodrigo, 1999) and tree-stored leopard kills (Cavallo and Blumenschine, 1989; Blumenschine and Cavallo, 1992) would be distinguishable in

fossil assemblages if the gross bone damage and tooth marking patterns inflicted by lions and leopards on different sized prey could be distinguished.

More specific and comprehensive identifications of fossil bone modifiers among a suite of fossil carnivores are likely to be possible only if zooarchaeologists can recognize both taxon-specific gross bone damage and tooth marking patterns. Here, gross bone damage refers to refers to any degree of gnawing, fragmentation, and fracture, excluding tooth marks. Different families, genera, and even species of mammalian carnivores can be expected on the basis of their differning jaw strengths, bone crushing capabilities, and tissue specializations (meat versus bone) to produce different types of gross bone damage and destruction on carcasses of the same size. For mammalian carnivores, few such comparative gross bone damage studies have been published. This has been demonstrated for some North American (Miller, 1969; Haynes, 1980, 1983), and South and East African (Richardson, 1980; Brain, 1981; Domínguez-Rodrigo, 1999; Pobiner and Blumenschine, 2002, 2003) carnivores, but only at a very general level. A unique pattern of bone damage has also been posited for Pleistocene *Homotherium* in North America (Marean and Ehrhardt, 1995). Work by Andrews (1991; Andrews and Nesbit-Evans 1983) provides examples of taxon-specific damage to bones of very small prey inflicted by small mammalian carnivores and predatory birds. The most systematic study published to date compares damage patterns inflicted by four taxa of east African carnivores (cheetah, leopard, lion, spotted hyaena) modifying Thomson's gazelle and wildebeest-sized prey (Pobiner and Blumenschine, 2003). This dissertation builds and expands on that study.

Modern carnivores are not homogeneous in their feeding behaviors; therefore, recognizable taphonomic differences in the traces of these feeding behaviors are expected. Previous research specifically comparing bone modification by different carnivore taxa is descriptive, noting mainly qualitative differences (Miller, 1969; Brain, 1980, 1981; Haynes, 1980, 1981a, 1982, 1983; Richardson, 1980). Furthermore, few studies of taxon-specific mammalian tooth marking have been published. Two of these document or model taxon-specific carnivore tooth marking on avian prey (Pasitschniak-Arts and Messier, 1995; Lyver, 2000), and one compares bite mark patterns made by different carnviores on prey flesh, rather than bone (Murmann *et al*., 2006). Three other studies describe taxon-specific tooth mark frequency and/or morphology by modern carnivores on mammalian prey from a comparative perspective (Haynes, 1983: spotted hyaena, wolf, bear, lion, tiger, jaguar; Fiorillo, 1991: coyote, fox; Monahan, 1999: African wild dog, spotted hyaena; Selvaggio and Wilder, 2001: spotted hyaena, cheetah, leopard, lion, jackal), and three studies describe tooth marking by a single carnivore taxon (Sobbe, 1990: Tasmanian devil; Andrews and Fernandez-Jalvo, 1997: fox; d'Errico and Villa, 1997: spotted hyaena; Domínguez-Rodrigo, 1999: lion). Most recently, Domínguez-Rodrigo and Piqueras (2003) documented differences in tooth mark measurements, specifically tooth pit length and width, for a variety of carnivores (hyaena, jackal, bear, dog, lion) and baboons on the basis of body size, but not taxon. These results have only been applied to two Early Pleistocene archaeofaunas, FLK *Zinjanthropus* and Swartkrans Member 3 (Selvaggio and Wilder 2001; Pickering *et al.,* 2004). These studies have not fully succeeded in outlining unique features of gross bone damage and tooth marking by specific carnivore taxa. Currently, only for the family Crocodylia have

unique features of bone damage and tooth marks been well described based on neotaphonomic studies, and have these features been found in the fossil record (Njau and Blumenschine, 2006).

Identification of taxon-specific gross bone damage and tooth marking has also been initiated for members of other modern taxa, including crocodiles (Njau and Blumenschine, 2006), great white sharks (Ames and Morejohn, 1980), and chimpanzees (Pickering and Wallis, 1997; Plummer and Stanford, 2000; Pobiner *et al.,* in review). Excluding research on swallowed and/or digested bones, tooth marks of extinct taxa on prey have been attributed to fossil mammals (Haynes, 1980; Farlow *et al.,* 1986; Fiorillo, 1988; Sobbe, 1990; Armour-Chelu and Viranta, 2000; Marean and Ehrhardt, 1995), rodents (Collinson and Hooker, 2000), dinosaurs (Matthew, 1908; Carpenter, 1988; Currie and Jacobsen, 1995; Erickson and Olsen, 1996; Hungerbühler, 1998; Naish, 1999), broad-nosed crocodilians (Meyer, 1994; Joyce, 2000), and sharks (Deméré and Cerutti, 1982; Martin and Rothschild, 1989; Schwimmer *et al.,* 1997; Neumann, 2000).

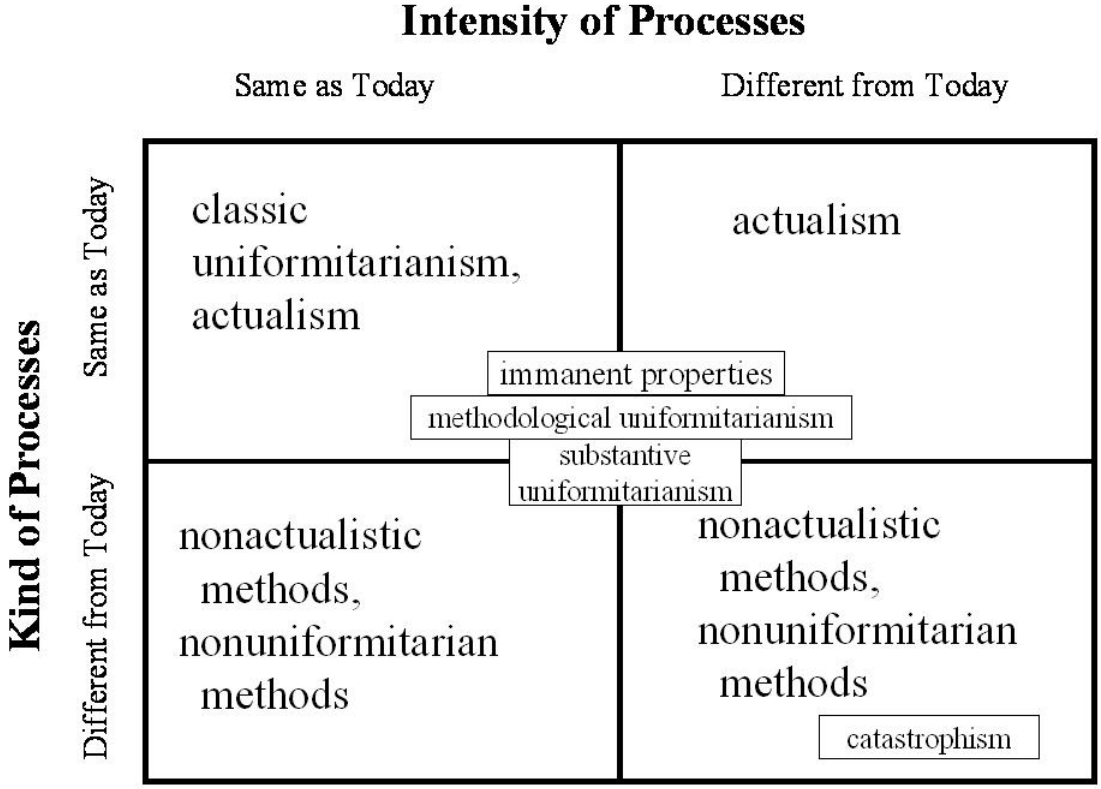
Conceptual Framework

A conceptual framework paleoanthropologists concerned with past human behavior works within includes elements of uniformitarianism, actualism, analogy, and middle-range research. Any historical science relies on uniformitarianism as a theoretical basis allowing actualism to construct relational analogies; middle-range theory establishes causal linkages between behavioral and other processes and diagnostic traces discernible in the archaeological record.

Charles Lyell outlined two major forms of uniformitarianism: 1) a testable theory or hypothesis and 2) an analytical procedure or assumption. The former, labeled substantive uniformitarianism, suggests that rates of change have been uniform through time and that change has generally been of a gradual versus catastrophic nature. This part of uniformitarianism is considered false, stifling to hypothesis formation (Gould, 1965), and untestable (Kitts, 1977). The latter, methodological uniformitarianism, is a procedural principle that asserts spatial and temporal invariance of natural laws and processes; therefore, past results may be ascribed to causes still in operation. This principle allows for the inference to be made that when similar products (i.e., bone damage) are seen in both modern and ancient settings, and we can observe the modern processes (i.e., chewing by a particular carnivore) that is responsible for the product, then we can infer that the same or similar process (i.e., chewing by that carnivore) was occurring in the past and is responsible for the ancient bone damage (see Figure 1.1).

Actualism is the method by which we ascribe modern products to modern processes. Actualism is based specifically in methodological uniformitarianism and asserts spatial and temporal invariance of natural laws concerning mechanical, chemical, and physical (but not behavioral) processes (Lyman, 1994). However, it does allow for different intensities of the same process to occur at different time. Actualism is defined as "the methodology of inferring the nature of past events by analogy with processes observable and in action at the present" (Rudwick, 1976: 110). The application of actualism in the fields of paleontology or taphonomy is often called actuopaleontology or neotaphonomy. Actuopaleontology and neotaphonomy are arguably one and the same; or, actuopaleontology is the employment of neotaphonomic data to the fossil record.

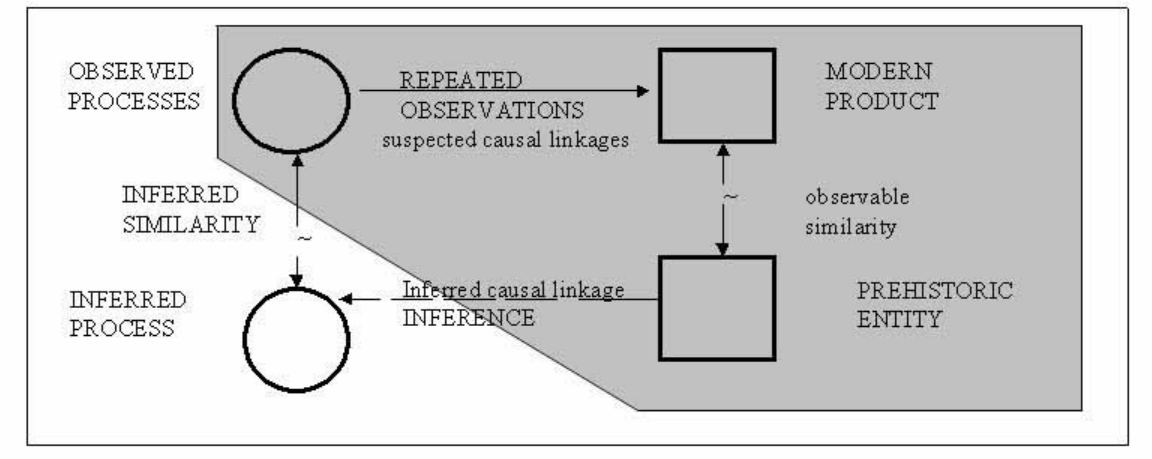
Figure 1.1. A model of uniformitarianism (adapted from Lyman, 1994:50, Figure 3.1). "Intersection of the different kinds and intensities of historic (taphonomic) processes defining uniformitarianism, actualism, and catastrophism as paradigms for explaining the past. Substantive uniformitarianism can encompass all four categories; methodological uniformitarianism and immanent properties assume processes of the same kind and either the same or different intensity as observed today."



Neotaphonomy, as defined by Hill (1978:88), "involves relevant experimentation or observations on the condition of modern vertebrate remains in various closely defined environments" which are designed to test taphonomic conjectures and to suggest consequences for paleoecological interpretation not visible in the fossil record, such as the absence of a taxon or the structure and composition of a paleocommunity (Lyman, 1994). Johnson (1985) describes neotaphonomic analogs as being based on direct observation of cause and effect, and measured with naturalistic or experimental data. The first major section of this dissertation, including Chapters 2, 3 and 4, are all part of a neotaphonomic study of carnivore bone modification.

The goal of actualism is to establish causal relationships between processes and products through the observation of present processes and traces (Marean, 1995). Actualism seeks to define diagnostic criteria in order to make this attribution; "if and only if" situations, or “if X, and only X, then Y” in which we can firmly attribute material residues (Y) to a single known taphonomic history or event (X) and eliminate equifinality (different events producing the same result or trace) (see Figure 1.2). For example, actualism is required and unquestioned in identification of a fossil as a femur, because the necessary and sufficient causal relation between the genetic controls and ontogenetic processes that result in the formation of the femur (Gifford, 1981). However, actualism does not purport that the fossil animal to which the femur belongs necessarily has the same behavior and ecology of a living analog; this "transferred ecology" falsely assumes that ecological relationships and community structure and interactions are directly transferable to the past (Lawrence, 1971; Gifford, 1981). Actualism is necessarily bound

Figure 1.2. A model of relational or analogical reasoning (adapted from Gifford-Gonzalez, 1989:44, Figure 1). The gray area is where observations are made in the present, or where actualistic research takes place. The inferred similarity on the left can be viewed as one or more uniformitarian assumptions.



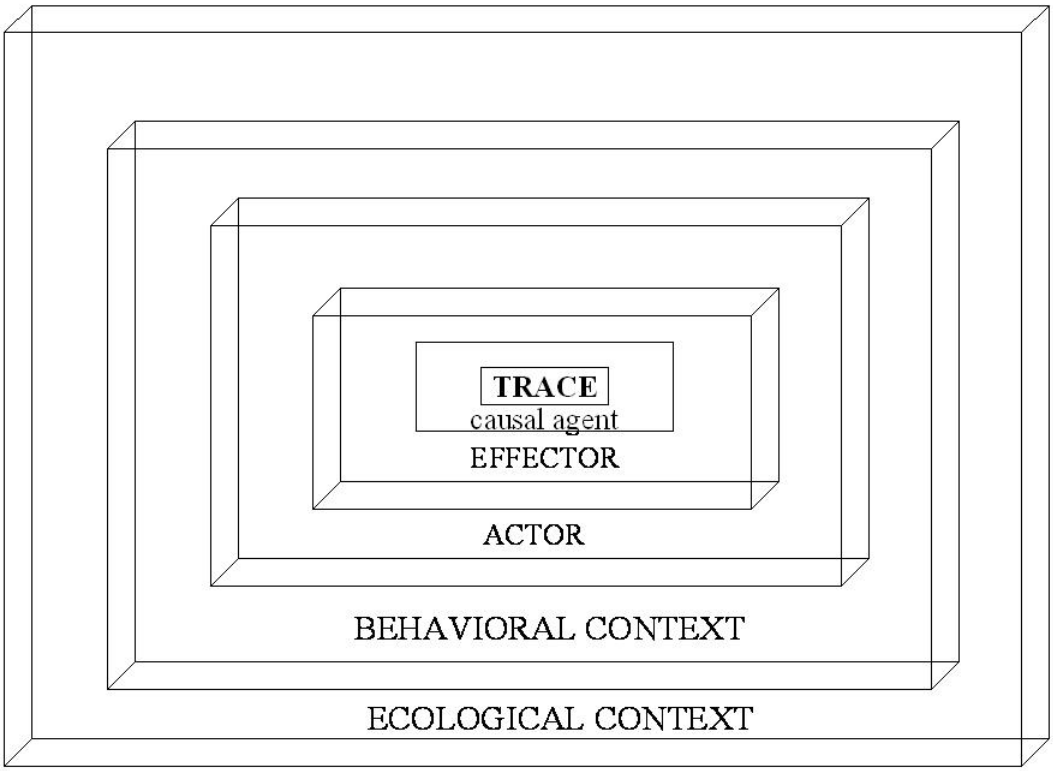
to the uniformitarian approach, and actualistic studies result in generalizations about the relations between processes and patterns which become our tools for interpreting the meaning of patterns in the fossil record (Marean, 1995).

Actualism necessarily relies on analogy and inference, which serve to make concepts and relationships in a novel field of inquiry more knowable by likening them to something more familiar. The two types of analogies used in science are formal analogy and relational analogy. In the former, two objects that share some properties known or visible for both implies that they share other properties known or visible only for one, while the latter involve a necessary relation between various aspects of the analogy; the associated attributes are thought to be causally related to the inferred properties. The most explicit framework for understanding taphonomic traces and building higher levels of inference comes from Gifford-Gonzalez (1991). She identifies six analytical categories within a nested system for which relational analogies can be used to distinguish the causal agency of the identified traces (Figure 1.3). In the first section of this dissertation, I am attempting to make linkages from the trace (e.g., a carnivore tooth mark) to the actor (e.g., a particular species of carnivore).

Middle-range theory was introduced to archaeology by Binford (1981). Middle-range theory stresses the establishment of a necessary and causal relation that is constant and unique between a particular process and its result; in other words, a diagnostic physical trace of an agent. Middle-range research is the search for immanent properties, the building of "a strong theoretically informed bridge between properties of the contemporary archaeological record and characteristics of the dynamic past" (Binford,

1981: 26). Middle-range research is necessarily conducted in the present as this is where the causal relationships between the processes and products can be observed.

Figure 1.3. A nested hierarchy of inference (adapted from Gifford-Gonzalez, 1991:229, Figure 2). "A nested system of analytical categories linking a trace, its immediate causal agent, the effector of the causal conditions, the actor setting the cause in motion, and behavioral and ecological contexts".



Gifford (1981) has outlined a procedure to establish that visible effects (traces) are diagnostic of particular cases (actions or events). First, observe dynamic interactions linking postmortem organic remains and processes that operate on them at the scale of the individual skeletal element. Next, establish the nature of cause-effect relations. Eliminate equifinalities until you have a diagnostic signature criterion. Then, establish the expected range of variation in the diagnostic signature criterion. Finally, test possible cause-effect relations and suspected diagnostic criteria with further observations, changing the scale of

investigations to the level of the fossil assemblage and predicting the structure of assemblages produced by the action of the specified processes.

Marean (1995) criticizes the comparative method, in which explanatory models are drawn from studies of fossil traces in which the relation between actor and trace has not been observed. He offers the example of arriving at inferred linkages between trace and actor from comparing five bone assemblages that allegedly accumulated in hyaena dens excavated in the last 30 years, with the goal of developing methods to recognize the accumulations of hyaenas versus humans, the approach of Cruz-Uribe (1991). The linkage between the trace and the actor is inferred: no one actually observed the hyaenas accumulating the bones. Potential inferential problems with this include the possibility of other actors (leopards, jackals) contributing to the assemblage and removal of bones by other processes. Regardless, this inference becomes the bridging argument used to identify fossil assemblages as hyaena dens. Klein and Cruz-Uribe (1984) advocate comparison between fossil assemblages only; but with such comparative studies, the analytical link between causal agent and trace (or actor and trace) is missing, and the bridging arguments rely on circumstantial evidence. I agree that this is not a source for secure archaeological inference and that archaeology cannot afford to have methods developed from circumstantial evidence. “Only if predictions pass this test of actualistic evaluation should they be employed in analysis of fossil material…the gravest problem in actualistic research is assuming that a given process is a necessary and sufficient cause of an observable attribute when no such relation has actually been established” (Gifford, 1981: 394).

Marean (1995: 66) prescribes an ideal three-step research structure combining uniformitarian principles, actualism, and middle range research. First, comparative studies should be used to establish hypotheses about linkages between actor and trace. Second, a naturalistic study is designed and implemented to test the validity of the hypothesis. Third, experimental studies are undertaken to further refine understanding of the linkages between actor and trace. In this way, the result is a robust bridging argument than can be used effectively in archaeological interpretation. This is similar to the argument used by Kay and Cartmill (1974) when using the functional morphology of modern species as models for that of fossi taxa; function is analagous to an actor (or more appropriately, behavior), and the functional morphology is analogous to the trace.

Scope of Dissertation and Sample Characteristics

This dissertation was undertaken in two main phases. The first phase involved studying samples of bones modified by different African carnivores under naturalistic and experimental conditions, and attempting to identify unique features of bone modification and tooth mark patterns by these carnivores to different sized prey. Recent research (Pobiner and Blumenschine, 2003) established indisputable, qualitative differences in the degree of gross bone damage and destruction by lions, leopards, cheetahs and spotted hyaenas to prey carcasses of varying sizes. I extended this research to include additional carnivores (jackals) and document taxon-specific gross bone damage and destruction and patterns of tooth mark densities, distributions, and two-dimensional measuements (length, width, and depth) for all of these carnivores. My gross bone damage and destruction analyses are restricted to forelimb and hindlimb bones, but

data were collected on all skeletal elements. Tooth mark measurement data were collected on all skeletal elements.

My total sample size includes 59 different carcasses or carcass parts from prey animals ranging in size from Thomson's gazelle to eland modified by lions, leopards, cheetahs, jackals, and spotted hyaenas under both captive and free-ranging conditions (see Chapters 2, 3, and 4). The samples from free-ranging carnivores were collected at Sweetwaters Game Reserve, now called Ol Pejeta Conservancy, and those from captive carnivores were collected at the Nairobi Animal Orphanage, both in Kenya. More details on these setting are in Chapter 2. A total of 1556 bone specimens were collected: 1195 from Sweetwaters Game Reserve, and 361 from the Nairobi Animal Orphanage. Over 6,000 tooth marks were generated in the entire sample, including tooth pits, punctures, scores, and furrows (Binford, 1981). Only 700 of these were measured and included in the present analyses.

Chapter 2 discusses the taxon specificity of flesh availability of carcasses and carcass parts modified by different modern African carnivores, and compares these to previous studies of scavengeable vertebrate resources for early hominins. Chapter 3 documents and quantifies taxon-specific carnivore gross bone damage and destruction patterns, and Chapter 4 does the same for tooth mark frequency, distribution, and morphology. Chapter 5 reviews the taxonomy, ecology, and behavior of Plio-Pleistocene carnivores, as bridges between modern carnivore bone modification and studies of archaeofaunas.

The second phase of this dissertation involved studying several previously unpublished archaeofaunas with evidence of both hominin and carnivore involvement

from the Okote Member, Koobi Fora, Kenya (~1.5 Myr), and middle-upper Bed I and lowermost Bed II, Olduvai Gorge, Tanzania (~1.84 – 1.70 Myr). The sample from Koobi Fora consists of three large site-scale archaeofaunas (FwJj14A, FwJj14B, and GaJi14), from the Koobi Fora and Ileret Ridges, and comprises a total of 5945 faunal specimens with no *bona fide* stone tools. This was the first comprehensive zooarchaeological and taphonomic analyses of these sites, which were excavated under the auspices of the Koobi Fora Field School from 1998-2004 (see Chapter 6). These three sites were accumulated in shallow, low energy fluvial settings that consisted of a mix of marshy and more open environments. The large number of cut- and percussion-marked bones from a variety of prey sizes and taxa at these three sites speak to fairly intensive hominin butchery and processing of both meat and marrow at these sites. The paucity of carnivore tooth marks suggests that hominins were not regularly scavenging from largely defleshed felid kills, but they still may have been scavenging from carnivore kills which were not fully defleshed, such as those of sabertoothed felids, or lions in lower competition settings (this study). The low proportion of limb epiphyses, however, also suggests that hominin butchery activities were followed by off-site hyaenid bone destruction during grease consumption. The lack of stone tools at these sites, where butchery activities presumably took place, is surprising.

The sample from Olduvai Gorge consists of 2196 specimens (1518 of which were analyzed taphonomically) selected from landscape-scale excavations in Bed I (1.84-1.79 Ma, Blumenschine *et al*., 2003) and lowermost Bed II (1.75-1.70 Ma, Manega 1993) by the Olduvai Landscape Paleoanthropology Research Project (OLAPP). Data collection on the fossil samples included standard zooarchaeological variables as well as data on

carnivore gross bone damage (see Appendix 5). I investigated three questions with these samples. First, does the intensity of carnivore activity vary through time during lowermost Bed II? I found this was not the case: the proportion of bones with carnivore gnawing damage and tooth marks did not change through time with what is currently hypothesized to be a change in landscape geomorphology. However, the epiphysis to shaft ratio decreased substantially, suggesting that the relative abundance of bone-crunching carnivores may have increased after this landscape change. Second, does carnivore activity vary geographically in lowermost Bed II? If so, is this variation predicted by hypothesized vegetation distribution? The carnivore tooth marks from this sample did not include any "diagnosable" to a particular carnivore taxon, as they were all relatively small, but the gross bone damage data seem to provisionally support this idea. Third, can the consumption of individual prey animals in the landscape assemblage be identified from carnivore-specific gross bone damage and tooth marking? Specific consumer(s), including a variety of carnivores and hominins, could be hypothesized for 17 individual prey carcasses or carcass parts from Beds I and II. This is an independent application of a novel type of taphonomic analysis conducted initially by R. Blumenschine and J. Njau on the same assemblage (unpublished data).

Chapter 6 reports on the results from the analyses of the assemblages from Koobi Fora, and Chapter 7 discusses those from Olduvai Gorge. Chapter 8 summarizes the major findings of each chapter of this dissertation, refines the fossil traces of hypothesized scavenging opportunities afforded to early hominins by different carnivores in light of new evidence presented here, and outlines future research related to these issues that I hope to undertake.

Chapter Two
Scavengeable Flesh Available from Modern Carnivore Kills

The samples described in this chapter also pertain to chapters three and four.

Sweetwaters Game Reserve

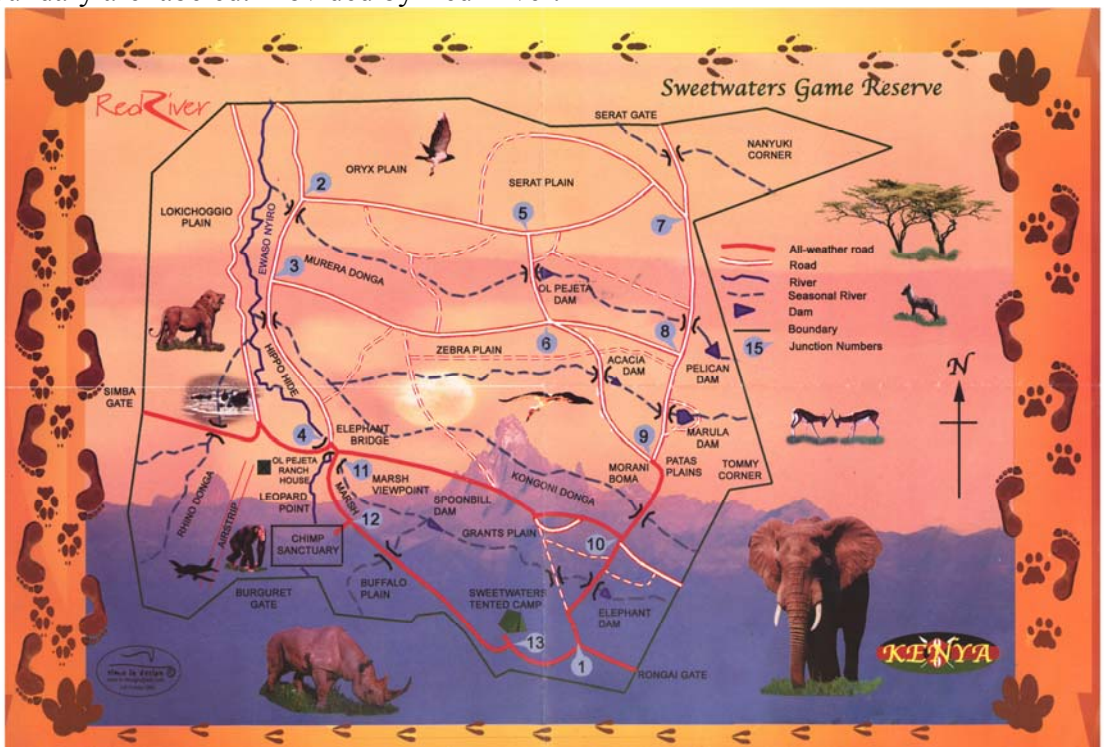
Site Description

The study of naturalistic carnivore bone modification was conducted from September 2002 – March 2003 on Sweetwaters Game Reserve (hereafter SGR), a 97km^2 fenced game reserve which is the eastern section of the 460km^2 Ol Pejeta cattle ranch. SGR is 257 kilometers north of Nairobi and 20 kilometers east of Nanyuki, in the Laikipia District of Kenya, to the west of Mount Kenya (Figures 2.1 and 2.2). It is situated on the equator and is located at approximately 36" 51' East. The average altitude is 1810 meters. SGR is a private game reserve, and during my study it was owned by Lonrho Hotels East Africa, a company which owns several hotels and safari clubs in Kenya. Lonrho owned and managed the two on-site hotels at SGR, Sweetwaters Tented Camp and Ol Pejeta Ranch House.

SGR vegetation can be described as a mosaic of grassland, woodland, scrub woodland and riverine woodland (Gatimu, 2005). Over 26 species of woody plants are present, but the vegetation is dominated by *Acacia drepanolobium* (~40%), the whistling thorn acacia; *Euclea divinorum* (~30%), a large bush (Figure 2.3); and *Psaidia punctulata* (~10%). *Acacia xanthophloea*, the yellow fever tree, dominates the riverine areas (Figure 2.3). Other shrubs or bushes include *Scutia myrtina, Olea africana*, *Rhamnus staddo,* and *Maerua tryphylla*. *Themeda triadra* and *Spolobolus* sp. are the two main grasses.

Figure 2.1. Map of Kenya with the location of Sweetwaters Game Reserve marked by a red star, near Mount Kenya. Copyright http://www.blissites.com/kenya/map.html

Figure 2.2. Map of Sweetwaters Game Reserve, designed primarily for tourists. Roads, rivers (perennial and seasonal), dams, landmarks, dongas, plains, and the reserve boundary are labeled. Provided by Red River.



The mean annual rainfall at SGR is 800mm, with a bimodal rainfall pattern; rain mainly falls during March-May (the "long" rains) and November-December (the "short" rains). Table 2.1 lists the monthly rainfall data collected at three stations on the reserve in 2002 and 2003. The terrain is fairly flat, but consists of three main east-west minor plateaus with short open grass ("plains"), and bushy valleys ("dongas"). The Ewaso Ngiro River, which is a permanent river, flows south through the eastern section of SGR. There are six seasonal streams which flow intermittently, and six man-made dams which provide drinking water to game during the dry seasons.

Figure 2.3. Photographs of typical vegetation at Sweetwaters Game Reserve. (A) *Euclea divinorum* bush. (B) Close up of *Euclea divinorum* leaves. (C) *Acacia xanthophloea* trees along the Ewaso Nyiro River. (D) A typical Sweetwaters mixed *Euclea divinorum/Acacia drepanolobium* landscape.

(A)

(B)

(C)

(D)

Table 2.1. Rainfall data in millimeters from three data collection points on Sweetwaters Game Reserve in 2002-2003, which covers the time during which I conducted this research. Courtesy of Sweetwaters Game Reserve general manager, Richard Vigne.

		Rongai Gate	Serat Gate	Research Centre
2002	January	49	40	75
	February	0	0	0
	March	103	80	124
	April	146	215	165
	May	166	89	111
	June	17	60	27
	July	14	33	15
	August	15	21	5
	September	1	9	12
	October	96	117	104
	November	68	66	52
	December	271	58	95
	TOTALS	**945**	**787**	**782**
2003	January	26	2	0
	February	2	22	0
	March	112	22	63
	April	166	222	192
	May	188	110	159
	June	81	44	60
	July	26	42	16
	August	329	239	112
	September	0	8	16
	October	117	0	51
	November	133	0	199
	December	116	7	86
	TOTALS	**1195**	**608**	**954**

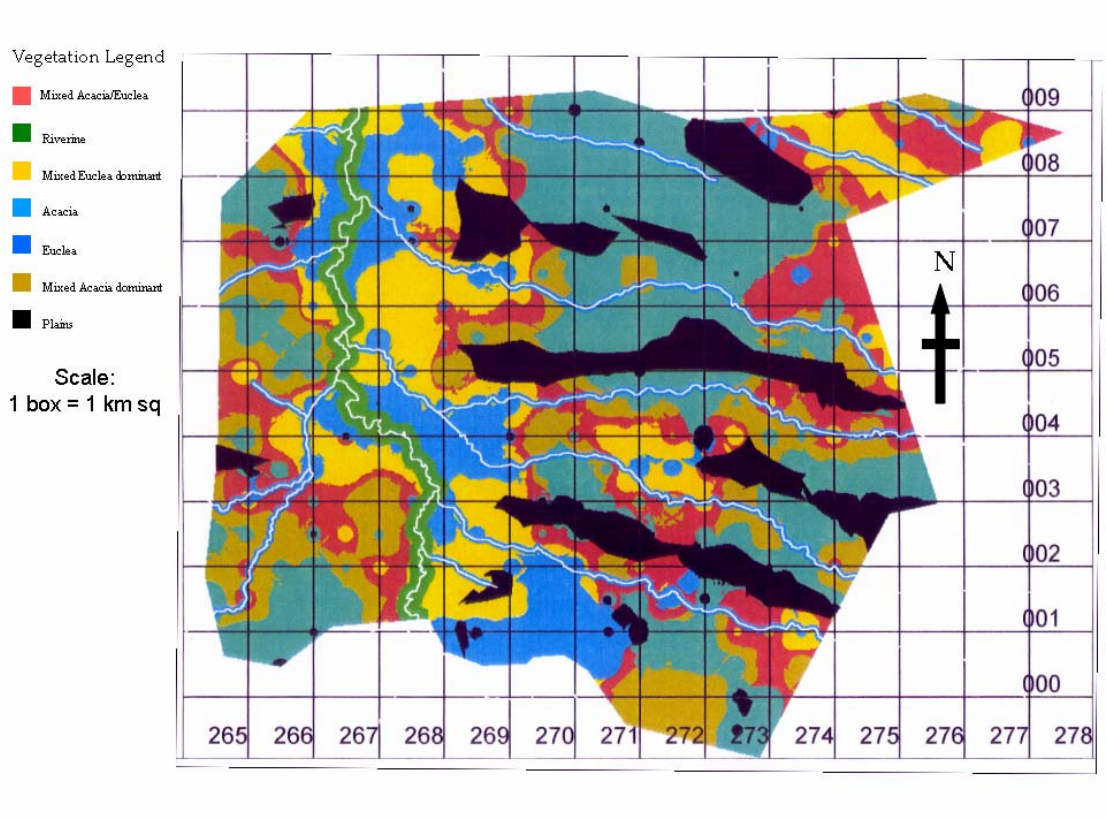
SGR was established in 1989 for tourism, mainly as a sanctuary for black rhino translocated from other sites in Kenya. While SGR was stocked with black rhinos, all of the other animals present were either originally on the land or have come onto it since it was enclosed. Sweetwaters is a private game reserve, and therefore does not fall under the jurisdiction of the Kenya Wildlife Service. However, because it is a black rhino reserve, it has strong links to the Kenya Wildlife Service which has particular guidelines

that such reserves must follow. These procedures include close monitoring of every rhino found within the reserve (the current rhino population is approximately 37 individuals). This monitoring is conducted by 4-8 teams of 2 armed guards each ("rhino patrols"), who are trained to recognize the individual rhinos by features such as ear notches. These rhino patrols survey different sections of the reserve every morning for about 5-6 hours, until the rhinos generally bed down for the hottest part of the day. These patrols were helpful in discovering some kills which were included in my sample, which is why I describe their activities here. Within SGR, straddling the Ewaso Nyiro, is a 200 acre fenced chimpanzee colony associated with the Jane Goodall institute. This facility mainly houses orphaned and abused chimps, and its aim is to house the chimps in a place where they can be introduced to social groups, rehabilitated, and taught to fend for themselves in an area similar to their natural living conditions.

An Earthwatch project, "Kenya's Black Rhino", has conducted intensive vegetation sampling and game count censuses since 1999. This project was established to address habitat issues pertinent to the conservation and management of the reserve's black rhinos and black rhino breeding locales in general. Earthwatch teams are generally on-site at SGR for a total of about 10 weeks during the two main dry seasons. Dr. Alan Birkett, an Honorary Research Fellow at Manchester Metropolitan University (MMU) and the PI of the Earthwatch project during my time at SGR, kindly provided me with a GIS vegetation map (Figure 2.4) and game count data (Figure 2.5), obtained through transects done by Earthwatch volunteers from 1996 and 1999-2001, to give me an idea of what prey the carnivores at SGR might encounter. The MMU GIS mapping used map datum ARC 1960, while my GPS was set to map datum WGS 84; to convert my sample

locations to ARC 1960 so I could plot them on the MMU map, I decreased the easting by 94 meters, and increased the northing by 300 meters.

Figure 2.4. GIS habitat map of Sweetwaters Game Reserve. The map datum used is Arc 1960. The habitats were designated via ground truthing. Courtesy of Dr. Alan Birkett, Manchester Metropolitan University.

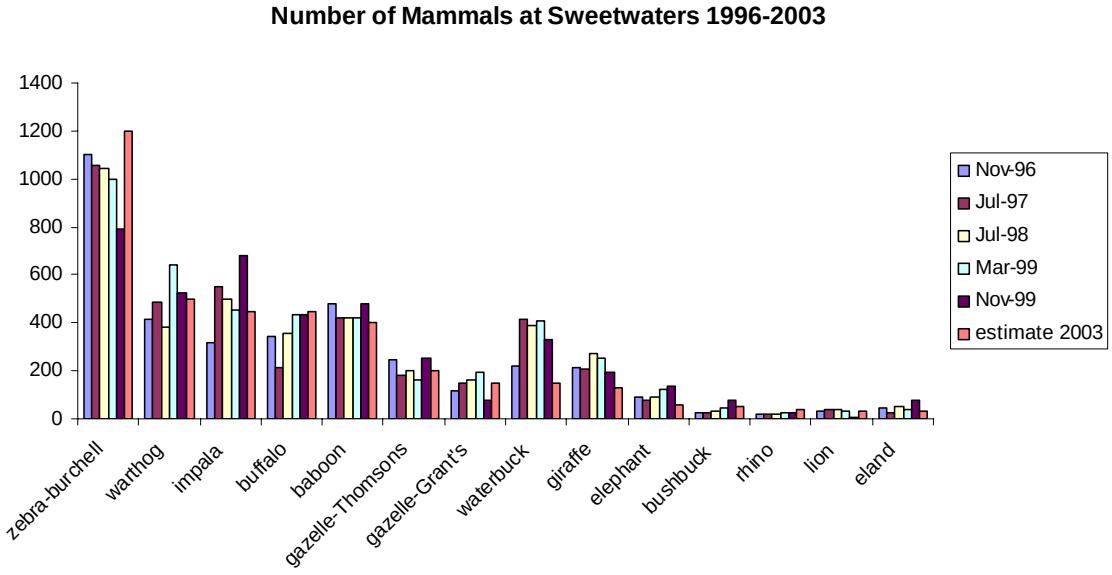


The mammal community is strongly dominated by Burchell's zebra, followed by warthog, impala, buffalo, and baboon. The composition of the entire mammal community is shown in Figure 2.5, the data for which come from Earthwatch's ground censuses in 1996 and 1999.

The predator community is strongly dominated by lions. Up to an estimated 43 lions were on Sweetwaters in 2002-2003, which is an extremely high density, close to that in Ngorongoro Crater and Nairobi National Park (Watkins, 2000). Lions were seen individually as well as in groups, ranging up to 12 feeding on a kill at any one time; their

pride structure seemed fairly fluid. Pride identity, composition, and general location/range are outlined in Table 2.2.

Figure 2.5. Sweetwaters mammal census data from 1996 through 2003. Data collected through ground counts and estimates. Courtesy of Dr. Alan Birkett, Manchester Metropolitan University and Richard Vigne, General Manager, Ol Pejeta Conservancy. Mammals with less than 30 individuals counted or estimated in 2003 are not included in this chart. These include: Grevy's zebra, oryx, hartebeest, steenbuck, hippo, jackal, suni, ostrich, otter, cheetah, duiker, Bohor reedbuck, patas monkey, striped hyaena, coypu, serval, white-tailed mongoose, bushbaby, leopard, and Cape hare (although there are estimated to be at least 300 Cape hare on the reserve).



There are 2 known resident leopards at SGR. Cheetah have not been seen on the reserve since about 1997, and the conventional wisdom is that either the lion density is too high to allow co-existence with cheetah, or the reserve area is too small, or both. Spotted hyaenas occur in low numbers; no more than 9 or 10 were seen at any one time. It is believed that at least some of the spotted hyaenas that are seen on SGR are residents on Ol Pejeta Ranch. Several of the spotted hyaenas that were using a large den there were poisoned in the past few years, drastically reducing the local spotted hyaena population. Striped hyaenas occur, but their numbers are difficult to estimate. There were at least three in 2002, a mother and two large cubs, which were ear-notched by Aaron Wagner

Table 2.2. Group structure and generalized location of Sweetwaters lions in early 2004. Lion prides or groups were named after the place on the reserve they were most commonly sighted. Provided in part by Felix Patton, PhD Candidate, Manchester Metropolitan University, who identified the individual lions based on spot patterns and individual markings. Collared lions are denoted with an asterisk (*).

GROUP NAME (After main location)	**COMPOSITION**	**NUMBER (AS OF 3/2003)**	**NAMES**	**TOTAL**
AIRSTRIP	Females SA Males	3 1	Ally, Amy, Ann Abel	4
CONSERVATION CENTRE	Females SA Males Cubs	1 2 2	Carrie Chas, Chic 1, 2	5
TENTED CAMP	Females Male SA Males Cub	1 1 1 1	Tiff Titus Tom Tina	4
OL PEJETA DAM	Females Male SA Males	2 1 6	Poppy, Pasha BanBan* Pete, Paul, Phil, Pat, Pip, Percy	9
OL PEJETA DAM 2	Female Cubs	1 3	Petra 1, 2, 3	4
MARULA DAM	Females Cubs - male Cubs - female	2 2 1	Jess*, Jules Jack, James Joan	5
ZEBRA PLAIN	Females SA Males	1 3	Zoe Zak, Zeb, Zulu	4
GRANTS PLAIN	Females SA Male	2 1	Gayle, Ginny Gregg	3
ROAMING	Females SA Male	1 2	Ribble (Unnamed)	3
OTHERS	Males	2	Minus, Sting	2
TOTAL ALL	Females Males SA Males Cubs - male Cubs - female Cubs - unsexed	**14** **4** **16** **2** **1** **6**		**43**

during his dissertation fieldwork (Ecology, Montana State University). Jackals are fairly common, but again, their numbers are difficult to estimate. Wild dogs had been extirpated, but were seen on SGR in 2004 for the first time in about 30 years. It is presumed that other smaller felids are present, but I did not see any. Considering that I spent a lot of time doing night drives with spotlights, the failure to see any small felids

likely indicates very low numbers, if not complete absence. It is possible that this is due to the presence of domestic dogs, which live in some of the staff quarters on SGR.

I first established contact with the general manager of SGR and Ol Pejeta Ranch, Richard Vigne, by email in April 2002, and in person in June 2002. He agreed to allow me to conduct my research project at Sweetwaters. He said I would be assigned an assistant (Tongoria) to help me with my activities as needed. The other personnel with whom I most often interacted, and who were all extremely helpful, included James Koskei, the former SGR Head Warden; Nathan Gichohi, SGR Assistant Warden, in charge of research activities; Dixon Kariuki, Head of Security at SGR; and James Lobenyoi, who was in charge of the Sweetwaters Research Center, where I lived. The research center was a converted horse stable situated a few hundred meters from the reserve headquarters, and along with 2 rondavels built more recently, has room to house 14 people. It is generally inhabited by 10 Earthwatch volunteers while their program is in session, and by one or two longer-term researchers such as me. I also liaised with Felix Patton, a PhD candidate in conservation biology at Manchester Metropolitan University, who was studying (in part) potential predation pressure by lions on black rhino calves, and therefore had an interest in the reserve's lion populations.

I began my research at SGR in mid-September 2002, and was on site through the end of March 2003, for a total of 129 days. The specific dates I was on site are listed in Table 2.3. I had an additional three days (June 18-20) with my advisor, Rob Blumenschine, during the Koobi Fora Field School in 2003, which I mention here because one of my samples was found during this time. My accommodation at SRG was the Sweetwaters Research Center. This location, just adjacent to the main SGR office,

gave me full access to the reserve, including night drives (between dusk and midnight), early morning (from 5:30 am onwards), and driving on and off the main roads. However, off-road driving was kept to a minimum and generally occurred only if I was following a predator that I thought was engaged in a hunt, due to the frequency of encountering aardvark holes which had the potential to cause serious damage to my vehicle.

Table 2.2. Dates on site at Sweetwaters Game Reserve. The main research season was from mid-September to end March 2002. Also listed is the total number of dry or wet days, defined by the absence or presence of rainfall, for each on-site period.

Dates	Total Days	Dry Days	Wet Days
September 11-14	4	4	0
September 17-30	14	14	0
October 1-15	15	0	15
November 1-8	8	0	8
November 13-30	18	2	16
Dec 1-5	6	6	0
Dec 13-21	9	0	9
Dec 24-27	4	0	4
Jan 16-24	9	0	9
Jan 27-31	5	5	0
Feb 4-21	18	18	0
Feb 25-26	2	2	0
March 10-16	7	7	0
March 20-22	3	3	0
March 24-30	7	0	7
TOTAL	**129**	**61**	**68**

Methods of Finding Carcasses

Initially, I was planning on finding carcasses using the following methods:

1. Looking for circling vultures.
2. Scanning appropriate trees for tree-stored leopard kills.
3. Utilizing SGR's radio telemetry equipment to track the two radio-collared lions on the reserve.

4. Liaising with Sweetwaters Tented Camp (STC) night game drive vehicles via radio contact.
5. Liaising with the rhino patrol via radios.
6. Chance encounters with feeding carnivores while on drives around SGR.

Each of these methods, along with an assessment of its relative effectiveness, will be described in more detail below.

1. Looking for circling vultures.

I initially hoped this would be the most productive carcass finding technique, following the procedures in Blumenschine (1986), but in fact it turned out to be the least productive. Ol Pejeta Ranch maintains an active slaughterhouse at which it slaughters its domestic cows, sheep and goats for meat as well as wild animals for meat and skins (before game utilization was discontinued in Kenya), which attracted all of the vultures in the general area. While the vultures would occasionally roost on SGR, there were only a few times I actually saw vultures scavenging from a lion kill, and I never saw them circling. No samples were obtained using this method.

2. Scanning appropriate trees for tree-stored leopard kills.

In the early 1990's, 5 leopards were released onto SGR. However, none of them were fitted with tracking devices, and when I arrived on-site the management estimated only 1 or 2 leopards were currently living on the reserve. I asked the rhino patrols if they knew of any trees that the leopards may have regularly utilized for stashing their kills, but they did not. I soon learned that STC regularly bought sheep from Ol Pejeta Ranch and put them up as bait in one particular tree which the night game drive vehicles stopped at every night and used spotlights to check for the leopard. While the leopard was seen only

occasionally, the bait was always eaten after a few days. Unfortunately, the bait was normally dragged down from the tree by the leopard, who possibly was avoiding being spotlighted by the STC night game drive vehicles, as well as avoiding competition with lions and hyaenas, which were both seen underneath the tree on different occasions. I liaised with SGR staff in order to more securely fasten the sheep to the tree (Figure 2.6), and did manage to obtain four leopard-only samples this way (SWT 012, 028, 030, 031), two of which (SWT 028, 030) were unfortunately scavenged by other carnivores (probably jackals) during the cleaning process. These leopard samples were sheep or goats, and originated as skinned half-carcasses, divided down the midline, without crania.

Figure 2.6. Photograph of leopard bait in tree. Parts of goats or sheep, usually hindlimbs, are routinely tied to a tree at Sweetwaters to attract leopards for tourist viewing. This photograph was taken on January 19, 2003.

3. Radio-tracking lions.

Two radio-collared lions lived on SGR while I was doing my study, which were collared by the Laikipia Predator Project prior to my arrival on site: the single resident adult male, nicknamed “BanBan”, and an adult female, nicknamed “Jess” (Figure 2.7). I

spent many hours driving around trying to locate these animals using the telemetry equipment that the Laikipia Predator Project had lent SGR, but with the undulating hill-and-valley topography, the radio tracking receiver was useful only at very close range. While I did find the collared lions a few times, I did not obtain any samples this way.

Figure 2.7. Photographs of the two SGR lions with collars during my study. These lions were collared by the Laikipia Predator Project, and I was able to use their tracking equipment, lent to Sweetwaters Game Reserve, to follow these lions. The male is named "BanBan" (first two photos) and female is named "Jess" (last two photos).

4. Coordinating with STC's night game drive vehicles.

STC regularly has clients go out on night drives for two two-hour blocks, from 7-9 and 9-11 pm, as well as early morning drives, from 6-8 am. This occurs at the clients' request, and did not happen every day or night, but most days and nights during the dry seasons there was at least one game drive vehicle out. I bought a hand-held VHF hand-held in Nairobi, was given permission by the SGR management to have it programmed

with their frequencies. Nathan Gichohi issued me radio name “Bravo”, which is how I was known to SGR and STC staff when we communicated by radio. The STC night game drive vehicles always brought bright (million candle power) spotlights on their night game drives, and occasionally found lions feeding on kills, especially on the plains. The vehicles would then radio me, I would drive out to their location (as they described it over the radio), and observe consumption. I would then normally drive back out to the location, which I had recorded precisely using a handheld Magellan GPS, just before or at sunrise to collect the bones and look for traces of other carnivores. The management preferred that I not observe kills from midnight until about six am. I obtained 5 samples using this method (SWT 006, 007, 008, 013, 037).

5. Coordinating with rhino patrol/SGR security.

As described above, the four rhino patrols are made up of two armed guards (with radios) which go on foot to different parts of the game reserve every day to look for black rhinos. With the cooperation of Dixon Kariuki, who oversees the rhino patrol operations, these patrols would radio me if they found any carcasses, whether they were still being consumed or not. I obtained four kills using this method (SWT 014, 024, 032, 033). Dixon himself also alerted me to a few samples located on the security rounds he conducted daily on motorcycle. I obtained six samples using this method (SWT 010, 016, 017, 021, 035, 036, 038).

6. Chance encounters.

I spent the first several days of my time at SGR driving around the reserve, familiarizing myself with the roads and terrain, but also looking for kills. I would normally leave for a circuit around the reserve twice or three times a day: once just before

or after dawn to return in the late morning; once in the late afternoon, to return by around sundown; and once in the evening, to return by about 11 pm. I quickly learned this was an extravagant use of time and fuel. I ceased making these drives on a daily or regular basis after about 1-2 months. I had to stick to the roads most of the time, as driving off-road was a fairly dangerous activity due to the large numbers of aardvark holes and warthog burrows hidden beneath the grass. As I could not safely drive off-road, my visibility was limited to what I could see from the main roads. Additionally, parts of the reserve became inaccessible during the rainy season due to impassable roads. I obtained two samples through chance encounters (SWT 002, 015).

7. Other methods.

Four samples were obtained when they were discovered by Earthwatch volunteers conducting walking game count transects (SWT 011, 025, 026, 027). I was also alerted to a few samples by people visiting and/or conducting other research on the reserve who happened upon them, either on foot or in a vehicle (SWT 003, 004, 005, 029, 034). I was twice alerted to kills by SGR staff, as it was made nearby to their posts (SWT 001, 023). Three samples were obtained when animals died on the ranch and I was able to use them for hyaena bait (SWT 018, 019, 020). Once, I used a sheep as bait just adjacent to a jackal den (SWT 022).

Procedures at Carcasses and Data Collected

Carcass consumption was observed whenever possible. At night, this was aided by a million power 12V powered spotlight, and I often used a red filter over the spotlight to minimize intrusion in the feeding episode. I also conducted longitudinal observations of carcass consumption when possible, though this was not a main focus of my

dissertation research. These consisted of taking notes while watching carcass consumption, sometimes aided by binoculars, but I was usually close enough so binoculars were not necessary. When carcasses were fed on by multiple lions, which normally occurred, I found it difficult to write down all of the feeding behaviors occurring simultaneously and in most instances instead used digital still and video photography for recording feeding behavior. Unfortunately, this was much more difficult in the dark, and often meant I was focusing on one or a few individuals while missing the feeding behaviors of other individuals on different parts of the carcass. I was able to get extremely close to the lions during carcass consumption; since the reserve operates as a tourist facility and houses many staff within its borders, the predators seemed fairly comfortable with close proximity of vehicles.

I never saw a complete carcass consumption episode from start to finish. This was mainly due to the management's policy that vehicles not drive around or sit on the reserve roads between midnight and sunrise without prior notification of security personnel, which is when the majority of carcass consumption occurred. Therefore, in many instances, I am only inferring that the sole consumer taxon of a carcass was lion. However, I am confident in this inference for the following reasons:

1. Lions are the vast majority of all the carnivores on the reserve. The spotted hyaena density on the reserve is very low. Jackal density is slightly higher, but still low.
2. When I went to pick up each carcass, my assistant and I always checked for spotted hyaena footprints, as well as other signs of spotted hyaena involvement

such as disarticulation and dragging of the carcass from its original kill or discovery spot.

3. The carcasses which had been consumed by spotted hyaenas, either as the initial or secondary consumer, exhibited characteristic disarticulation and scattering patterns which were different from those I either knew or inferred were fed on solely by lions.

When carcass consumption episodes occurred at night, or at another time when I could not stay on site, I went out at the earliest possible time the next day to retrieve the carcass.

When it was clear that the consumers were finished and no longer in the area, determined by having no visual or auditory evidence of them for at least 1 hour, kill site documentation began. Appendix 1 is my carcass retrieval site data sheet which lists all of the information collected at carcass retrieval sites. Appendix 2 my spreadsheet with the data collected at carcass retrieval sites, minus the flesh availability data, which is discussed in the next section. In contrast to Domínguez-Rodrigo (1999), gross bone damage data was not collected on site, because it could not be systematically observed in the vast majority of carcasses due to adhering skin and flesh. Only after bones were cleaned was gross bone damage data collected. Once this documentation was finished, the carcass was collected and put into the back of my Land Cruiser. While every effort was made to recover all bones and bone fragments, it is likely that some small fragments were not recovered, especially in tall grass habitats. The characteristics of the 38 kills I observed are detailed in Table 2.4, and summarized by predator taxon, NISP:MNE recovered, and prey size and age in Tables 2.5 and 2.6.

Prey size follows Bunn (1982), where the body weights of an individual in each size class, in pounds, are: 1 (<50); 2 (50-250); 3A (250-500); 3B (500-750); 4 (750-2000); 5 (2000-6000); 6 (>6000). Throughout this dissertation, prey size is absolute size, as opposed to animal size; for instance, a newborn zebra is prey size 1, not prey size 3.

Table 2.4. Details of carcasses observed and bone samples obtained from Sweetwaters Game Reserve. Samples were numbered SWT001-SWT038 in the order in which they were observed and collected. Primary carnivore consumer refers to the carnivore taxon which fed on the carcass either first or solely. Secondary carnivore consumer is listed only for those samples for which it is applicable. In two of these three instances (SWT 015, SWT 017) the kill was deliberately collected and transported elsewhere to leave as bait for hyaenas; in the third instance (SWT 036) there was evidence of hyaena involvement once the carcass had been abandoned for several days following primary lion consumption. SWT010 is possibly a cheetah kill, though there was no direct evidence for the consumer at the kill site, and cheetahs have not been sighted on the reserve in the past few years. Prey age is relative age: categories are A = adult (epiphyses fused), J = juvenile (epiphyses unfused), and F = fetus. Prey size follows Bunn (1982). Jackals are black-backed jackals, and hyaenas are spotted hyaenas.

ID Number	Primary Carnivore Consumer	# Primary Consumers	Secondary Carnivore Consumer (if applicable)	Prey Taxon	Prey Age	Prey Size	NISP:MNE recovered
SWT001	Lion	7		Zebra	A	3	79:73
SWT002	Lion	10		Hare	A	1	0:0
SWT003	Lion	8		Thomson's gazelle	J	1	23:16
SWT004	Lion	8		Grant's gazelle	J	2	14:13
SWT005	Lion	9		Warthog	A	2	0:0
SWT006	Lion	8		Zebra	A	3	123:123
SWT007	Lion	7		Zebra	A	3	153:153
SWT008	Lion	7		Zebra	F	2	27:6
SWT009	Lion	5		Grant's gazelle	J	1	26:23
SWT010	Cheetah?	1?		Thomson's gazelle	A	1	99:94
SWT011	Hyaena	1?		Zebra	A	3	52:51
SWT012	Leopard	1		Domestic sheep	J	1	18:18
SWT013	Lion	2		Warthog	A	2	56:55
SWT014	Lion	3		Zebra	A	3	135:130
SWT015	Lion	3	Hyaena	Zebra	A	3	33:32
SWT016	Lion	>1	Hyaena	Zebra	F	1	56:27
SWT017	Lion	>1	Hyaena	Zebra	A	3	52:52
SWT018	Hyaena	unknown		Domestic cow	J	2	0:0
SWT019	Hyaena	unknown		Domestic sheep	A	1	0:0
SWT020	Hyaena	unknown		Domestic	J	2	0:0

				goat			
SWT021	Lion	12		Zebra	J	3	44:44
SWT022	Jackal	unknown		Domestic sheep	A	1	71:64
SWT023	Lion	unknown		Impala	A	2	0:0
SWT024	Lion	5?		Zebra	A	3	61:61
SWT025	Lion	3		Zebra	A	3	0:0
SWT026	Lion	3		Zebra	F	1	0:0
SWT027	Lion	4		Grant's gazelle	J	1	24:7
SWT028	Leopard	1		Domestic cow	J	2	12:12
SWT029	Lion	5		Zebra	A	3	0:0
SWT030	Leopard	1		Domestic sheep	A	1	0:0
SWT031	Leopard	1		Domestic sheep	J	1	3:3
SWT032	Lion	5		Zebra	A	3	0:0
SWT033	Lion	10		Eland	A	4	74:74
SWT034	Lion	10		Zebra	J	2	18:15
SWT035	Hyaena	unknown		Thomson's gazelle	A	1	0:0
SWT036	Lion	4	Hyaena	Zebra	A	3	25:25
SWT037	Lion	1		Hare	A	1	0:0
SWT038	Lion	1 or 2		Warthog	J	2	16:8

Table 2.5. NISP and MNE of predator taxon/prey size samples from Sweetwaters Game Reserve. Relevant samples are abbreviated by the final digit(s) of their ID number. An asterisk (*) indicates carcasses with no bones recovered.

Predator Taxon	**Prey Size**	**Total # of Samples**	**# of Samples with Bones Recovered**	**Total NISP Recovered**	**Total MNE Recovered**	**Relevant Samples**
Lion	3/4	10	7	669	658	1, 6, 7, 14, 21, 24, 25*, 29*, 32*, 33
	2	7	5	131	95	4, 5*, 8, 13, 23*, 34, 38
	1	7	4	129	73	2*, 3, 9, 16, 26*, 27, 37*
Lion-Spotted Hyaena	3	3	3	110	109	15, 17, 36
Spotted Hyaena	3	1	1	52	51	11
	2	2	0	0	0	18*, 20*
	1	2	0	0	0	19*, 35*
Leopard	2	1	1	6	6	28
	1	3	2	6	6	12, 30*, 31
Cheetah	1	1	1	21	21	10
Jackal	1	1	1	71	64	22
TOTAL		38	25	1195	1083	

Table 2.6. Size and age of predator taxon/prey size samples from Sweetwaters Game Reserve. Size and age characteristics of samples are listed. Only samples for which bones were recovered are included.

Predator Taxon	**Prey Size**	**Prey Age**	**# of Samples with Bones Recovered**	**Relevant Samples**
Lion	3/4	A	6	1, 6, 7, 14, 24, 33
		J	1	21
	2	A	1	13
		J	3	4, 34, 38
		F	1	8
	1	J	3	3, 9, 27
		F	1	16
Lion-Spotted Hyaena	3	A	3	15, 17, 36
Spotted Hyaena	3	A	1	11
Leopard	2	J	1	28
	1	J	2	12, 31
Cheetah	1	A	1	10
Jackal	1	A	1	22
TOTAL			25	

Bone Cleaning Procedures

Soon after my arrival at SGR I hired the son of one of the reserve staff, Peter, who was living on the reserve, to assist me in cleaning and processing carcasses. The procedure we followed is outlined below.

Peter and I set up a carcass processing station behind the carpenter's work shed, just next to the research center. This consisted of a low pressure gas bottle connected to a stove, a circle of stones above a charcoal pit we used as a second boiling station, a series of large plastic buckets in which to store the bones during cleaning (especially when more than one carcass was being processed at a time), some plastic sheeting on which to lay the bones while they were drying, several metal pots, toothpicks and longer wooden skewers used for cleaning bones, and Omo (a local laundry detergent).

I normally obtained a carcass with some skin and flesh still remaining, and put it into the back of my Land Cruiser to drive it to the processing station. Peter then disarticulated the carcass and removed any remaining flesh and skin with the toothpicks and wooden skewers and his fingernails, or very carefully with a knife, under strict

instruction not to let the knife touch bone and produce any cut marks. Disarticulation sometimes, but not always, occurred at this point. He then put the carcass into one or several metal pots and placed it over either the gas burner or the charcoal pit with a small amount of Omo (for degreasing) to be boiled for a few hours. He then removed the carcass from the pot, with further disarticulation and flesh or skin removal occurring at this point, if appropriate. This procedure was repeated until all of the adhering flesh and/or skin was removed. The bones of the carcass were then laid out on plastic sheets to dry in the sun. The bones were then stored in the plastic buckets until I could label them.

I labeled the samples with "SWT" numbers because when I initially arrived at Sweetwaters, I was using SWT as an abbreviation for the reserve. Later, I began using "SGR" as an abbreviation for Sweetwaters Game Reserve, following the protocol used by other researchers there. I labeled the bones with blue colored fine point Sharpie permanent marker, following this convention: carcass number–bone number (e.g. SWT001-15). Some of the bones were still greasy, as I did not drill holes in them prior to boiling; these were further boiled and degreased when they arrived at Rutgers University in April 2005. When the carcasses had been labeled, they were stored in the attic of the SGR main office in cardboard boxes. I drove the samples to Nairobi in October 2004, put them into 6 large metal trunks, and shipped them back to the US via DHL Danzas Air and Ocean (K) Limited, the sea freight shipping branch of DHL. They arrived in the US in March 2005.

Using Sweetwaters as a Modern Analog: Drawbacks and Benefits

While SGR is a game reserve, it is not as "natural" or "pristine" as many of the national parks and reserves in East Africa where similar naturalistic observations of

carnivore consumption or consumption residues have been conducted (e.g. Blumenschine, 1986a; Tappen, 1995; Selvaggio, 1994b; Capaldo, 1995; Domínguez-Rodrigo, 1999). It is a small reserve, and has a relatively high human population living both within and around it. Its predator community has been significantly altered by human intervention in the form of poisoning of the spotted hyaena population and presumed earlier extirpation of wild dogs. Its herbivore community is more closely monitored (by Earthwatch) and as a result has also been altered. For example, in 2001, half of the current SGR elephant population (56 individuals) was translocated to Meru National Park in an effort to reduce browsing competition with the resident black rhinos.

However, working in this reserve had several benefits. The lions are relatively comfortable with vehicles, making close observations of feeding possible. The monitoring of the herbivore community means that prey population numbers are known. The management is very amenable to and supportive of research, which enabled me to be involved in activities such as leopard baiting. This support and communication with the reserve staff led to the discovery of the majority of my carcass samples.

Sweetwaters seems to support an unusual predator community, with an extreme dominance by lions. While this community is not the result of natural ecological factors, there are some natural circumstances in which this could happen: for example, with a species-specific disease affecting only one carnivore species. This lion dominance, coupled with a fairly high prey biomass, seems to result in a low interspecific competition for larger mammal carcasses, especially for intra-bone resources. This will be explored further in the flesh availability discussion section.

Nairobi Animal Orphanage

NAO Pilot Study 2001

In November and December 2001, I conducted a short pilot study at the Kenya Wildlife Service (KWS) Nairobi Animal Orphanage (NAO), located at the Kenya Wildlife Service headquarters complex on Langata Road, 10 km south of Nairobi city center. The NAO was established in 1964 as a refuge for wild animals found abandoned, orphaned or injured throughout Kenya. The aims of the orphanage are to release the animals into the wild whenever possible, provide conservation education to Kenyans and visitors from all over the world. I initiated this study to (1) determine the feasibility of conducting a more extensive study, and (2) make contacts with the necessary officials at KWS in case I decided to do so. The main contact person at this point was Dr. Muthiu, who was in charge of the NAO. The carnivores that were housed at the NAO during the pilot as well as the more extensive study are listed in Table 2.7.

The main objectives of this study were to collect bone samples modified by one species of carnivore in a controlled setting. Additionally, I was occasionally able to film either part of or the entire feeding episode, with the aim of linking specific tooth marks on bones to specific carnivore jaw actions (e.g. Van Valkenburgh, 1996). However, I learned fairly quickly that this was difficult, as the carnivores seemed to use a variety of teeth and jaw actions during consumption activities.

I conducted the pilot study on November 20, 21, 27, 29, and December 4, 2001. On each of these days, I observed and sometimes videotaped consumption of a fully fleshed bone, bones, or bone portions by one or two carnivores in their cages. The carnivores are fed every day (except Monday) at 2pm, and this is when I conducted

Table 2.7. Details of carnivores at the Nairobi Animal Orphanage used for feeding experiments. Includes samples obtained in November/December 2001 and February 2004. NAO15 was recovered from an unknown cheetah individual. The jackals were black-backed jackals.

Species	**Name(s)**	**Age (when study was conducted)**	**Sex**	**Experiment Year(s)**	**ID Number(s)**
Cheetah	Sammy & Mailu	4 years	Males	2001	NAO1
Lion	Mathiu	9 years, 12 years	Male	2001, 2004	NAO2, NAO6, NAO19
Leopard	Loita	Juvenile†	Male	2001	NAO3
Jackal	Jack & Jill	Adults†	Male & female	2001, 2004	NAO4, NAO14, NAO21, NAO33
Serval	Ali	Sub-adult†	Male	2001, 2004	NAO5, NAO27
Cheetah	Mailu & Mara	7 years	Male & Female	2004	NAO9, NAO22, NAO34
Cheetah	Robbie	12 years	Male	2004	NAO7, NAO20, NAO31
Leopard	Langata	Adult†	Male	2004	NAO8, NAO18, NAO30
Cheetah	3 cubs, no names	Several weeks	unsure	2004	NAO10, NAO25, NAO29
Lion	Shaba	4 years	Male	2004	NAO11
Lion	Daudi	3 years	Male	2004	NAO12, NAO23
Lion	Charlie	Sub-adult†	Male	2004	NAO13, NAO28
Lion	George	Adult†	Male	2004	NAO16, NAO26, NAO32
Lion	Msichana & Mvulana	5 years	Male & Female	2004	NAO17, NAO24

†indicates that the exact age of the animal was unknown, and the relative age was listed here.

observations and videotaping. The following day, I would return to the NAO at 8am, when the carnivores were put into smaller inner cages so their larger outer cages could be were cleaned, and retrieve the bone samples. However, on one or two occasions I was able to either observe and/or record the entire consumption sequence, as the orphanage staff let me into the cage immediately after consumption to retrieve the bones (this was only possible with the cheetahs). Consumption was deemed finished once the animals left the bones alone and showed no further interest in them for 10 minutes or longer. The details of the carnivores observed and videotaped, and the samples obtained (NAO1-5), are listed in Table 2.8. The samples were numbered NAO 1-5, in the order in which they were obtained. All of the bones fed to the carnivores were from domestic cows.

Table 2.8. Characteristics of sample obtained from 2001 and 2004 studies at the Nairobi Animal Orphanage. Samples were always collected the morning after observations of feeding were made, except in the case of NAO10, when samples were collected immediately following feeding observation and videotaping. Where bones were initially articulated, this is indicated by a dash (–) between elements. Where bones were not initially articulated this is indicated by a comma (,) between elements. All ribs and vertebrae were articulated to each other. All bones are whole unless otherwise specified.

ID Number	Species	# of Consumers	Date Observed	Bones Collected	NISP:MNE recovered
NAO1	Jackal	2	11/20/01	Distal femur	2:2
NAO2	Serval	1	11/21/01	Scapula	4:1
NAO3	Leopard	1	11/27/01	Distal femur-patella	2:2
NAO4	Lion	2	11/29/01	Femur-tibia-patella-calcaneum-navicular-cuboid	33:7
NAO5	Cheetah	1	12/4/01	Ribs, scapula, cervical vertebrae	22:9
NAO6	Lion	1	2/14/04	Ribs, vertebrae, innominate	21:19
NAO7	Cheetah	1	2/14/04	Scapula-humerus-radio-ulna, tibia-tarsals	15:14
NAO8	Leopard	1	2/14/04	Vertebrae, sacrum, innominate	17:17
NAO9	Cheetah	2	2/14/04	Humerus-radio-ulna, carpals, sacrum, innominate	10:10
NAO10	Cheetah	3 (cubs)	2/14/04	2 scapulae	2:2
NAO11	Lion	1	2/14/04	7 ribs	12:12
NAO12	Lion	1	2/14/04	Femur-tibia	4:4
NAO13	Lion	1	2/14/04	Femur-tibia	6:6
NAO14	Jackal	2	2/14/04	Ribs, cervical vertebrae	18:15
NAO15	Cheetah	1	2/14/04	Scapula	1:1
NAO16	Lion	1	2/14/04	Innominate-femur-tibia-tarsals	10:9
NAO17	Lion	2	2/14/04	Ribs, vertebrae	34:34
NAO18	Leopard	1	2/22/04	Ribs, vertebrae	14:12
NAO19	Lion	1	2/22/04	Tibia-tarsals	4:4
NAO20	Cheetah	1	2/22/04	Humerus-radio-ulna-carpals	14:8
NAO21	Jackal	2	2/22/04	Scapula, innominate, proximal femur	7:3
NAO22	Cheetah	2	2/22/04	Humerus-radio-ulna-carpals	8:8
NAO23	Lion	1	2/22/04	Innominate	1:1
NAO24	Lion	2	2/22/04	Scapula-humerus-radio-ulna-carpals	8:8
NAO25	Cheetah	3 (cubs)	2/22/04	2 scapulae	4:2
NAO26	Lion	1	2/22/04	Innominate-femur-tibia-tarsals	9:7
NAO27	Serval	1	2/22/04	Whole chicken	n/a
NAO28	Lion	1	2/22/04	Humerus-radio-ulna-carpals	6:6
NAO29	Cheetah	3 (cubs)	2/28/04	Innominate-proximal femur	5:4
NAO30	Leopard	1	2/28/04	3 lumbar vertebrae-innominate-sacrum	7:7
NAO31	Cheetah	1	2/28/04	Humerus-radio-ulna-carpals	8:8
NAO32	Lion	1	2/28/04	Femur-tibia-tarsals	7:6
NAO33	Jackal	2	2/28/04	Scapula, 4 thoracic vertebrae	25:5
NAO34	Cheetah	2	2/28/04	Innominate-sacrum; scapular-humerus-radio-ulna-carpals	21:11

NOTE: The MNE:NISP figures are misleading because sometimes elements were broken by chopping for preparation to feed the carnivores.

I then brought the bone samples to the Osteology Division, National Museums of Kenya. Here, I employed two skilled technicians (both coincidentally named Ezekiel) who regularly macerate carcasses for use in their comparative collections to clean my bone samples. I strictly instructed the technicians to use only their fingernails and the wooden sticks I provided them to remove flesh and periosteum from the bones to avoid making metal cut marks, though some were present on the samples, likely both from the butcher in Nairobi as well as the KWS staff who prepare the meals for the carnivores. The technicians boiled the samples with a small amount of Omo, removed any remaining flesh, and air dried them in the Osteology Division laboratory. The samples were superficially examined after the pilot study, and then packed in boxed and shipped back to the US for analysis with the SGR samples.

NAO Study 2004

In February 2004, I conducted a more extensive study at the NAO, similar to the pilot study. The dates of this study were Feb 14, 21, and 28. The main contact person this time was Dr. Adeela Sayeeid, the veterinarian and KWS Animal Curator in charge of the orphanage. The same methods were utilized, except this time not every consumption episode was observed and/or videotaped. I learned that every 2 days, 280 kg of cow meat (on the bone) is delivered for use by the NAO (140 kg) and the Safari Walk (140 kg). During this study, I was able to have more input into what bones/body parts were fed to which animals as I assisted in the preparation process, which began at 1:30 every day (again, except Mondays). The cow meat was delivered in essentially “half-cow” packets, or articulated half-skeletons, with no skin. The orphanage staff used pangas (machetes), axes, and metal knives to divide them up into portions to be fed to the resident carnivores.

The Safari Walk is another exhibit at the KWS headquarters, where animals are kept in much larger enclosures than at the NAO. I obtained two samples (NAO8, NAO18) from the leopard in the safari walk, as the one that was now housed at the NAO was very old and had a problem with its teeth, and was therefore being fed deboned meat. Again, all of the animals were fed domestic adult cow bones except the serval, which was fed domestic chicken (sample NAO27). I recorded which bones or body parts were fed to each animal, and when I collected the bones, I recorded what parts still had flesh adhering (bulk or scraps) and what parts of the bones were gnawed to the point of destruction. The bones from this study were all photographed using a digital camera before cleaning by the same Osteology Division technicians as in 2001. The details of the sample from this and the previous study are outlined in Tables 2.7 and 2.9. While spotted hyaenas were initially used in the feeding experiments, the animal keepers said no bones remained after their feeding (they were always fed cow ribs), so they are not included in any discussions of these experiments from here on.

Table 2.9. Summary of predator-specific sample from the Nairobi Animal Orphanage. All prey bones were from adult cows, except NAO27, which was a whole chicken. Relevant samples are abbreviated by the final digit(s) of their ID number.

Predator Taxon	**Total # of Samples**	**Relevant Samples**
Lion	13	4, 6, 11, 12, 13, 16, 17, 19, 23, 24, 26, 28, 32
Leopard	4	3, 8, 18, 30
Cheetah	11	5, 7, 9, 10, 15, 20, 22, 25, 29, 31, 34
Serval	2	2, 27
Jackal	4	1, 14, 21, 33
TOTAL	**34**	

I initially inquired of Dr. Bagine (Head of Research, KWS) in my research proposal whether the carnivores could be fed wild game if I paid for the game myself. I was hoping to rule out any potential effects of using domesticated animals on bone thickness as well as include a larger variety of animal sizes in the study. Unfortunately,

this was right after consumption game utilization (culling) was temporarily banned in Kenya, so Dr. Bagine said this was not possible. I then inquired to Dr. Sayeeid whether the carnivores could be fed domestic goats or sheep, to get a larger prey sample size, especially size 1 and 2 prey. She said this wasn't possible either, as they had done taste aversion feedings with goats and sheep (using lithium) to discourage them from eating these animals if they were to be released into the wild again, that these feedings had "adverse affects", and that the animals would likely not eat goats or sheep.

Flesh Availability: Introduction and Methods

Flesh availability data were collected principally with the aim of documenting potential scavenging opportunities for early hominins. However, the importance of flesh available from carnivore kills for the zooarchaeological record is twofold. First, in a theoretical sense, this flesh is important in terms of nutritional yield to model scavenging opportunities for early hominins, which is considered here. Second, in a methodological sense, this flesh is important in terms of stone tool-assisted butchery, which leaves behind cut marks. The ease of butchery may be inversely related to the size of flesh packet adhering to the bone, and therefore removing small pieces of flesh remaining on a carcass ("scrap defleshing") may in fact result in a higher number of cut marks than removing large muscle masses ("bulk defleshing"); this will be discussed later. Specifically, it is the size (amount), distribution, and nutrient yield of these muscle masses and flesh scraps available for hominins which are the critical variables. Flesh "scrap", as a term, is subjective, and has a connotation of something that is not useful. I will follow the

convention in using the term scrap, though I argue that a term like morsel, with a connotation of desirability, would be more accurate in its use here.

Unfortunately, I did not collect systematic bone portion-specific flesh availability data, which would have allowed for a more accurate and specific link between flesh availability and carnivore gross bone damage by bone portion. Flesh availability data were collected on a bone-by-bone basis, recording whether the bones remaining after consumption retained: 1) bulk flesh 2) flesh scraps 3) no flesh. These categories were not mutually exclusive for individual bones (see below). Table 2.10 summarizes the samples from SGR and NAO for which flesh availability data was recorded.

Table 2.10. Samples for which flesh availability and gross bone damage and destruction data were recorded. SGR samples were normally complete or nearly complete carcasses, while NAO samples were carcass parts. See Tables 2.4 and 2.8 for further detail on these samples. Where SGR samples are listed both under lion and spotted hyaena, flesh availability data was collected first following lion consumption, and again following spotted hyaena consumption.

Predator Taxon	Prey Size	Total # Samples	Total # SGR Samples	SGR Sample Numbers	Total # NAO Samples	NAO Sample Numbers
Lion	3/4	16	9	1, 6, 7, 14, 15, 17, 21, 24, 33	7	19, 23, 24, 26, 28, 32, 33
	2	4	4	4, 13, 34, 38	0	n/a
	1	4	4	3, 9, 16, 27	0	n/a
Leopard	4	2	0	n/a	2	18, 30
	2	1	1	28	0	n/a
	1	2	2	12, 31	0	n/a
Cheetah	4	6	0	n/a	6	20, 22, 25, 29, 31, 34
	1	1	1	10	0	n/a
Hyaena	3/4	5	5	11, 15, 17, 34, 36	0	n/a
	2	1	1	19	0	n/a
	1	1	1	20	0	n/a
Jackal	4	1	0	n/a	1	21
	1	1	1	22	0	n/a

"Bulk flesh" presence was defined here as the majority of the major muscle masses still adhering to the bone; any bone retaining more flesh than could be described as "flesh scraps" (as described next), or over 10% of their original flesh mass, was

included in this category. Flesh scraps were defined following Domínguez-Rodrigo (1999:380): bones with only flesh scraps remaining had less than 10% of their original flesh mass present, including only small packets of flesh still adhering to the bone, approximately less than the size of a normal human's palm in area but larger than 2-3 cm and 150g. A flesh scrap was defined this way to try to distinguish those scraps which would be "worth scavenging" for hominins in a less subjective way. My definition of scraps, though vague, included very small pieces of meat (~10g) which theoretically could be pinched between the thumb and forefinger and sliced off the bone. I did not note "practical" absence of flesh scraps as did Domínguez-Rodrigo. See Figures 2.8-2.12 for photographs of bulk and scrap flesh remaining on bones.

To compare my carcass consumption sequence with that derived from Blumenschine's observations (1986a), I constructed an "inferred" carcass consumption sequence (ICCS). This ICCS is based on the percentage of bone elements recovered with bulk flesh still remaining. The higher the percentage, the later the bone is consumed in the sequence, resulting in a larger rank number. I compare my ICCS with a modified version of Blumenschine's (1986a:64) carcass consumption sequence of lions and hyaenas on medium sized adults by leaving out those elements of his sequence for which I did not collect data, e.g., viscera and within-bone nutrients (Table 2.11 and 2.12). Blumenschine included thoracic vertebrae in his "ribcage" category, and his "maxilla" category is a rough equivalent of my "cranium" category. Where more than one bone or carcass part was at the same place in the carcass consumption sequence, they were grouped together and given an average number; for example, in Table 2.11, the tibia and

cranium both retained bulk flesh 50% of the time, and they were ranked 4.5 for the inferred carcass consumption sequence.

Figure 2.8. Photographs illustrating bulk and scrap flesh remaining on different parts of the same zebra carcass (SWT 006). The first photo (a) illustrates bulk flesh still remaining on the lower ribcage (intercostally), thoracic vertebrae, and lumbar vertebrae. The second photo (b) illustrates flesh scraps still remaining on a section of the upper ribcage consisting of three thoracic vertebrae and the 6 ribs articulated to these vertebrae. The flesh scraps are indicated by the arrows, and are located on the intercostal portions of the ribs, especially the proximal rib portions (close to the vertebrae), as well as the vertebral centrae.

(a)

(b)

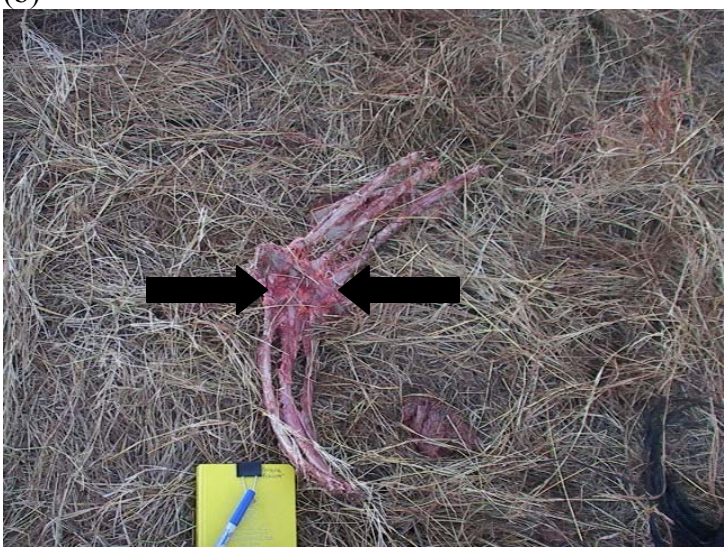


Figure 2.9. Photographs illustrating bulk and scrap flesh remaining on different parts of the same zebra carcass (SWT 007). The arrows indicate areas of bulk (a, first photo) and scrap (b, second photo) flesh The top photo illustrates bulk flesh still remaining on the right scapula, medial to the scapular spine, and flesh scraps remaining on the more cranial and caudal portions of the scapula. The bottom photo illustrates a few flesh scraps still remaining on part of the left scapula, notably on the lateral margin, more caudally, and in a few places on the skull, especially near the braincase and zygomatic.

(a)

(b)

Figure 2.10. Differential flesh distribution on size 3 and 4 bones from prey consumed by lions at SGR. A left femur of an eland (SWT033 – top left), with flesh scraps on the proximal end and a defleshed midshaft ; a right femur of a zebra (SWT014 – top right) with bulk flesh on the proximal and distal epiphyses and flesh scraps on the midshaft; a zebra ribcage (SWT014 – bottom left) with some bulk intercostal flesh, especially on the proximal ribs, and flesh scraps remaining on most of the distal ribs; and a zebra innominate (SWT006 – bottom right) with a defleshed center of the iliac blade, flesh scraps on the rest of the ilia (superior/anterior iliac blade) and packets of bulk flesh on the ischia and pubes.

Figure 2.11. Photograph illustrating bulk flesh remaining on two scapulae consumed by three cheetah cubs (NAO 25).

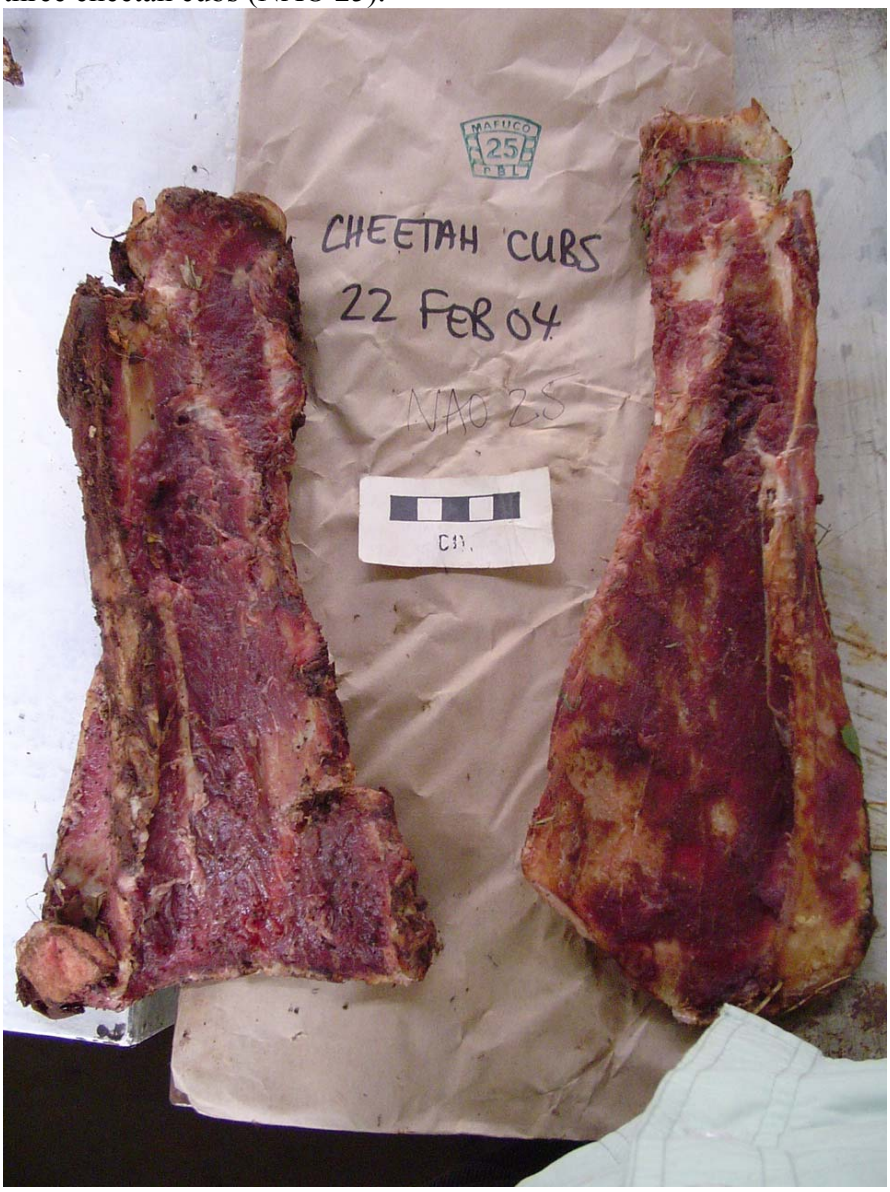


Figure 2.12. Photograph illustrating bulk flesh and flesh scraps fed on by a leopard. Bulk flesh remains on cervical vertebrae fed on by the leopard (NAO 18; top), and some flesh scraps remain on an innominate and lumbar vertebrae, specifically on the neural spine bases (indicated by the arrows), fed on by the same leopard in a different feeding episode (NAO 30; bottom).

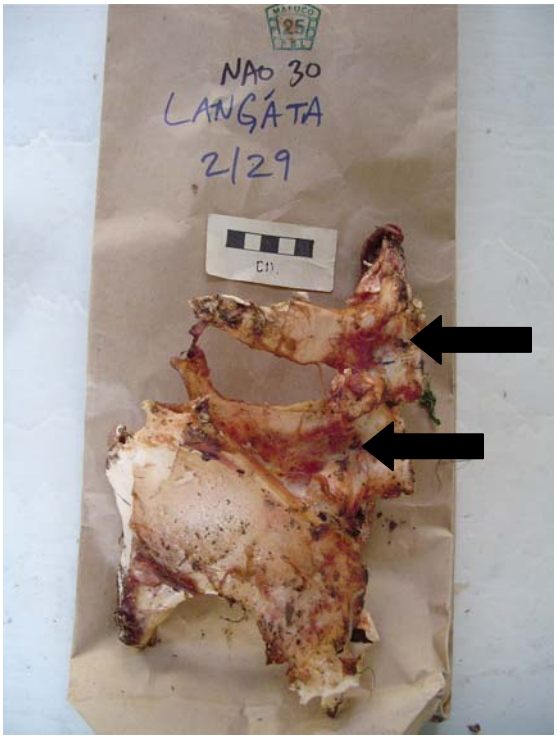


Table 2.11. Flesh availability in adult size 3 and 4 carcasses consumed by lions at SGR. ICCS is the "inferred" carcass consumption sequence. Carcass consumption sequence is inferred based on percentage of bones recovered with bulk flesh still remaining (see details in text). Comparability is made with a modified version of Blumenschine's (1986a:64) carcass consumption sequence of lions on medium sized adults by leaving out those elements of his sequence for which I did not collect data, e.g., viscera and within-bone nutrients. Blumenschine included thoracic vertebrae in his "ribcage" category, and his "maxilla" category is a rough equivalents of my "cranium" category. N is the total number of bones available for analysis from all appropriate carcasses. When there were no bones of an element available for analysis, this is indicated by a "0" in the N column and a blank cell in the other columns; when there were bones of an element available for analysis but none demonstrating a particular flesh availability level, this is indicated by a "0" and "0%" in the appropriate columns. The carcasses from which these data were extracted are listed in Table 2.6.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh	ICCS (Bulk)	Blumenschine's Modified CCS
Hindlimb	31	30	97%	13	42%	17	55%	1	3%		
Femur	15	15	100%	5	33%	10	67%	0	0%	1	2
Tibia	16	15	94%	8	50%	7	44%	1	6%	4.5	9
Forelimb	39	38	97%	27	69%	11	28%	1	3%		
Scapula	12	12	100%	8	67%	4	33%	0	0%	10	7
Humerus	13	12	92%	9	69%	3	23%	1	8%	11	6
Radio-ulna	14	14	100%	10	71%	4	29%	0	0%	12	10
Thorax	34	33	97%	18	53%	15	44%	1	3%		
Ribs	8	7	87%	5	63%	2	25%	1	13%	9	4.5
T. Vertebrae	7	7	100%	4	57%	3	43%	0	0%	6.5	4.5
L. Vertebrae	7	7	100%	3	43%	4	57%	0	0%	3	3
Innominate	8	8	100%	3	38%	5	63%	0	0%	2	1
Sacrum	4	4	100%	3	75%	1	25%	0	0%	13	
Head/Neck	25	22	88%	14	56%	8	32%	3	12%		
H/Mandible	10	8	80%	6	60%	2	20%	2	20%	8	11
Cranium	8	7	87%	4	50%	3	38%	1	13%	4.5	12
C. Vertebrae	7	7	100%	4	57%	3	43%	0	0%	6.5	8
TOTAL	**130**	**124**	**95%**	**72**	**56%**	**51**	**39%**	**6**	**5%**		

Often a single bone retained a combination of bulk flesh and flesh scraps remaining, or flesh scraps and no flesh remaining, and it was recorded as such, though the exact locations of the bulk or flesh scraps was not systematically recorded. For purposes of analyses aimed at documenting scavengeable resources for early hominins, I used the maximum flesh availability for each bone. Data from skeletal units (ribs, vertebrae) were recorded as a single data point, rather than from each rib or vertebra; any variability in

the sample was noted, and the most common level of flesh availability was recorded. These recording procedures were followed for all of the SGR samples, and those NAO samples for which this data was recorded (NAO 18-34).

Table 2.12. Flesh availability in size 4 carcasses parts consumed by lions at NAO. See Table 2.11 caption for more methodological details.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh
Hindlimb	5	5	100%	1	20%	4	80%	0	0%
Femur	2	2	100%	0	0%	2	100%	0	0%
Tibia	3	3	100%	1	33%	2	67%	0	0%
Forelimb	6	6	100%	2	33%	4	67%	0	0%
Scapula	2	2	100%	1	50%	1	50%	0	0%
Humerus	2	2	100%	0	0%	2	100%	0	0%
Radio-ulna	2	2	100%	1	50%	1	50%	0	0%
Thorax	3	2	67%	0	0%	2	67%	1	33%
Ribs	0								
T. Vertebrae	1	1	100%	0	0%	1	100%	0	0%
L. Vertebrae	0								
Innominate	2	1	50%	0	0%	1	50%	1	50%
Sacrum	0								
Head/Neck	0								
H/Mandible	0								
Cranium	0								
C. Vertebrae	0								
TOTAL	**14**	**13**	**86%**	**3**	**21%**	**10**	**71%**	**1**	**7%**

The parts into which I divide carcasses for analysis are the following: hindquarters (including femur and tibia); forequarters (including scapula, humerus, and radio-ulna); trunk (including thoracic, lumbar, and caudal vertebrae, innominate, sacrum, and ribs); and head/neck (including cranium, mandible/hemimandible, and cervical vertebrae). Carpals, tarsals, metacarpals, metatarsals, and phalanges are excluded from this analysis, as they possess negligible flesh (Blumenschine, 1986a). This grouping scheme was based on my carcass consumption observations and data in Hill (1989). It is modified from the scheme described by Blumenschine (1986a), who included the lumbar vertebrae and innominate with the hindquarters, and the cervical and thoracic vertebrae

and ribcage with the forequarters. I found it more anatomically realistic to include a trunk or thorax section, which accounts for most of these differences.

It is important to stratify the sample by prey carcass size, as I found that this is one of the most critical variables conditioning the capabilities of carnivore consumers to modify and destroy bones. I categorized prey animals into size classes following the conventions by Bunn (1982), using adult body weights: size 1 = <50 lbs; size 2 = 50-250 lbs; size 3 = 250-750 lbs; size 4 = 750 – 2000 lbs; size 5 = 2000 – 6000 lbs; size 6 = >6000 lbs. However, I categorized each prey animal according to an estimation of its actual body weight, not the average weight of an adult of that taxon. Therefore, I often classified juvenile animals into a lower size class than their adult counterparts. I made a simple age determination based solely on bone fusion; if all bones were fused, the animal was recorded as an adult, and if any bones were unfused, it was recorded as a juvenile or sub-adult. Fetal animals were those that were found with their mothers and were clearly unborn at the time of death (SWT 008, 016, 026). This led to some size categories including both adults and juveniles, especially size 1 and 2. While this method normalizes for absolute size, it does introduce some variation in terms of the nutritional yield of carcasses. Juvenile carcasses in general store and mobilize fat differently than adults (see Blumenschine, 1986a), and secondary sex characteristics, such as larger horns and neck flesh in males and pelvic and femur flesh in females, will be less developed. However, this difference is fairly small, and may be more troublesome when considering edible resources from marrow rather than flesh.

I report flesh availability data on a predator taxon/carcass size-specific basis, as well as a carcass part and bone-by-bone basis. I have found that these categories are the

most ecologically realistic for defining recognizable differences in carcass consumption patterning, which then results in differences in flesh availability, gross bone damage and destruction, and proportions of tooth-marked specimens. I maintain that initially analyzing samples at coarser levels may mask important ecological factors, as previous research has shown that carcass size is an important variable in carnivore bone modification, damage and destruction levels (Blumenschine, 1986a; Capaldo, 1998; Domínguez-Rodrigo, 1999; Selvaggio, 1994a). However, stratifying the sample by carcass size and predator taxon, while important, leads to s risk of reducing sample sizes to levels that do not support statistical analyses. Therefore, I do combine some samples when general patterns of flesh availability and gross bone damage and destruction levels emerge, such as carcasses of similar sizes (1 and 2) consumed by lions, or multiple carcasses consumed by a similar number of lions, to permit description of patterning in flesh availability as well as statistical analyses.

Flesh Availability: Results

Size 3/ 4 Prey

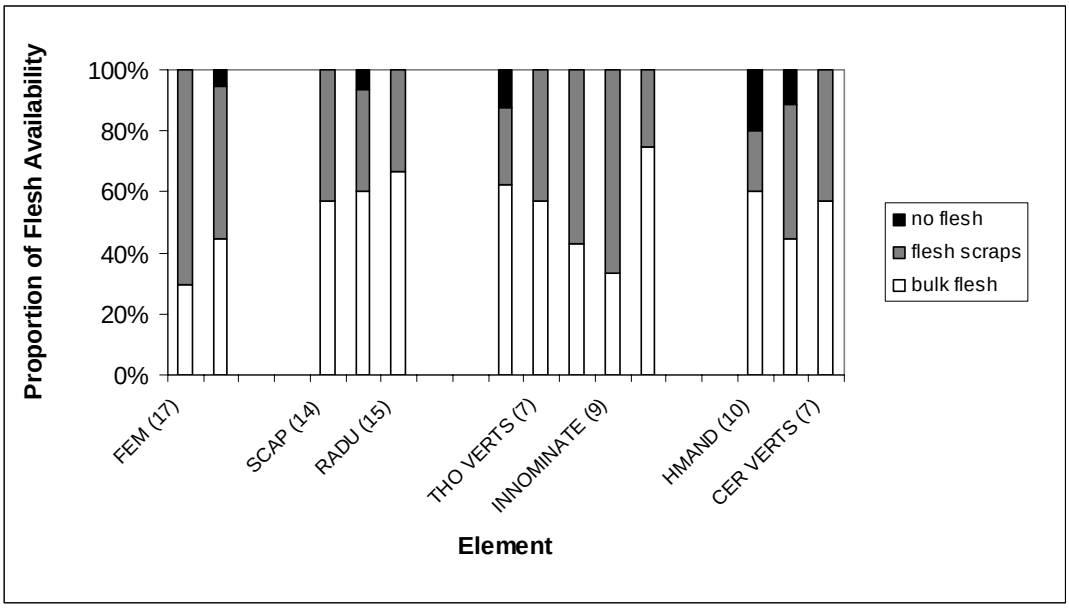
As indicated in Table 2.10, sample sizes were generally small, but were best for lions (N = 8 from SGR, N = 7 from NAO) and cheetah (N = 6 from NAO). Table 2.11 and Figures 2.8-2.14 present and illustrate the flesh availability on size 3 and 4 carcasses (from SGR) and carcass parts (from NAO). Size 3 and 4 carcasses are considered together because 1) the flesh availability pattern was consistent among them, and 2) I had only one size 4 carcass from SGR, which was generally consistent with the size 3 carcass flesh availability pattern.

1. Lion Consumption of Size 3 & 4 Carcasses and Carcass Parts

A. The SGR Sample

The carcass-wide distribution of flesh remaining after lion consumption of size 3 and 4 carcasses at SGR is illustrated in Table 2.11 and Figure 2.13. The vast majority of bones (95%) were abandoned with at least some scavengeable (bulk or scrap) flesh on size 3 and 4 lion-consumed carcasses. Over 50% of bones were abandoned with large muscle masses which would likely be a very attractive resource for a scavenging hominin. The distribution of flesh on the adult prey carcasses, represented as the ICCS, generally followed Blumenschine's (1986a:64) carcass consumption sequence of lions on medium sized adult prey carcasses (Table 2.11). Overall, the hindlimb is the first part to be consumed, followed by the thorax, then the head, and then the forelimb.

Figure 2.13. Carcass-wide distribution of flesh availability in size 3 and 4 carcasses consumed by lions at SGR. Bones are grouped by carcass part: hindquarters, forequarters, trunk, and head/neck. Metapodials and phalanges are not included, as they have negligible flesh available before consumption. Proportion of flesh availability refers to the percentage of the total sample of individual bones bearing either bulk flesh, flesh scraps, or no flesh. The number in parenthesis following the element names refers to the number of individual bones analyzed, from which the flesh availability data is derived. The total number of carcasses analyzed is 9; sample details are in Table 2.10.



I observed complete defleshing on only four individual bones/bone sets: the cranium, ribcage, and tibia from one carcass (SWT 024) and the hemimandibles from another (SWT033). SWT024 was an adult male zebra killed in late December (at the end of the short rainy season) and fed on by an unknown number of lions, though it is suspected that a group of 5 lions seen near the carcass were the ones that killed and ate it. SWT033 was an adult male eland killed in mid-March and fed on by 10 lions. It is unclear why these kills in particular should have been more defleshed than any others. It is possible that SWT033 could have been accessed by hyaenas, though there was no direct evidence that hyaenas had been there. I visited it several times over many hours while the lions were feeding, and then left it overnight, as they were not yet finished.

I did not systematically record the exact location of bulk and scrap flesh at a level of detail beyond individual skeletal elements of these samples. However, in some instances, I was able to determine the differential flesh distribution within elements from digital photographs taken at the kill site. The patterning I found from examining these photographs is described here. For limb bones, when there was a differential flesh distribution including flesh scraps and complete defleshing, the midshaft was most often defleshed and the proximal and distal epiphyses retained flesh scraps. In cases where the flesh differential included bulk and scrap flesh, the same patterning was evident, where the midshafts most often only flesh scraps left on them while the proximal and distal ends retained bulk flesh. When the innominate was partially defleshed, the iliac blades were almost always defleshed or retained only a few flesh scraps, and the superior iliac blades were gnawed; the ischia were usually partially defleshed and partially retained flesh scraps; and the pubis was often found with flesh scraps or even small packets of bulk

flesh. The lumbar vertebral bodies were often found with bulk flesh, or less often flesh scraps, remaining, while the lumbar vertebral spines were normally completely defleshed and well-gnawed or only retained a few small flesh scraps still remaining and were marginally gnawed. Ribs often had bulk flesh, but when only flesh scraps were retained they were usually on the proximal ends, or along the margins where bits of intercostal flesh were present, and the rest of the rib shafts were defleshed.

It is noteworthy nearly all of these carcasses were abandoned with skin remaining on the limb bones from the middle or distal tibia and radio-ulna through the distal limbs, probably because there is virtually no flesh worth extracting from these limb portions (e.g. Outram and Rowly-Conwy, 1998). In contrast to Domínguez-Rodrigo (1999:381), I did not find that "disarticulation and dismemberment are frequent" in lion kills. In fact, I observed very few instances of lions detaching and transporting a limb or any other carcass part of a size 3 or 4 prey animal. When such transport did occur, it was minimal (less than 20 meters). This difference could be due to lower competition at SGR.

B. The NAO Sample

The carcass-wide distribution of flesh retained after lion consumption of size 4 carcass parts from NAO is illustrated in Table 2.12 and Figure 2.14. There are slightly lower flesh availability levels in this sample compared with the sample from SGR; there are three bones (femur, lumbar vertebrae, innominate) which were devoid of bulk flesh. Possible reasons for this discrepancy will be offered in the discussion. However, while the sample size is small, the overall pattern of flesh availability from these NAO size 4 samples is generally similar to that seen in the SGR size 3 and 4 samples. The combined SGR and NAO flesh availability data is illustrated in Figure 2.15.

Figure 2.14. Carcass-wide distribution of flesh availability in size 4 carcass parts consumed by lions at NAO. The total number of feeding episodes is 7. See Table 2.8 for details on carcass parts presented to the lion(s) during each feeding episode. See Figure 2.13 caption for more details.

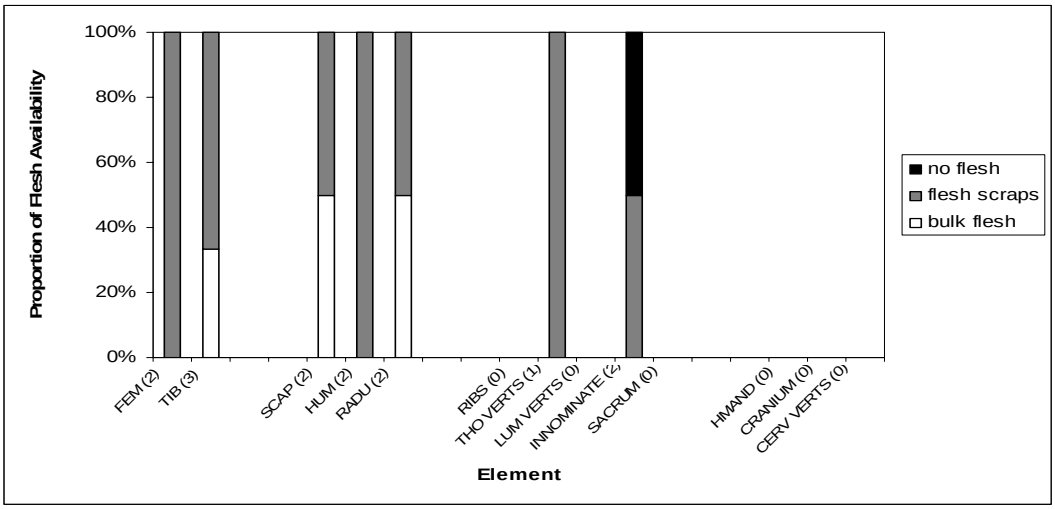
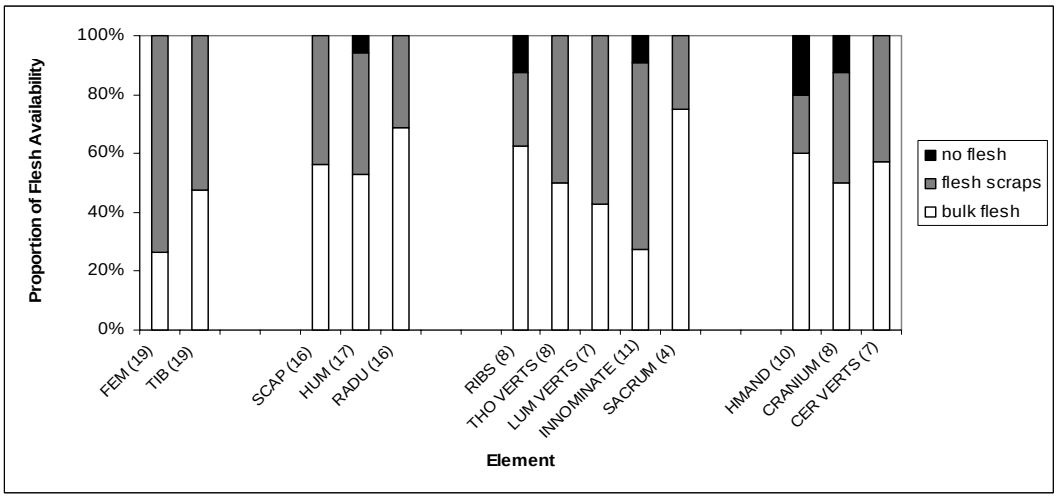


Figure 2.15. Carcass-wide distribution of flesh availability in size 3 and 4 carcasses and carcass parts consumed by lions at SGR and NAO. The total number of carcasses and carcass parts consumed is 15. See Figures 2.13 and 2.14 for further details.

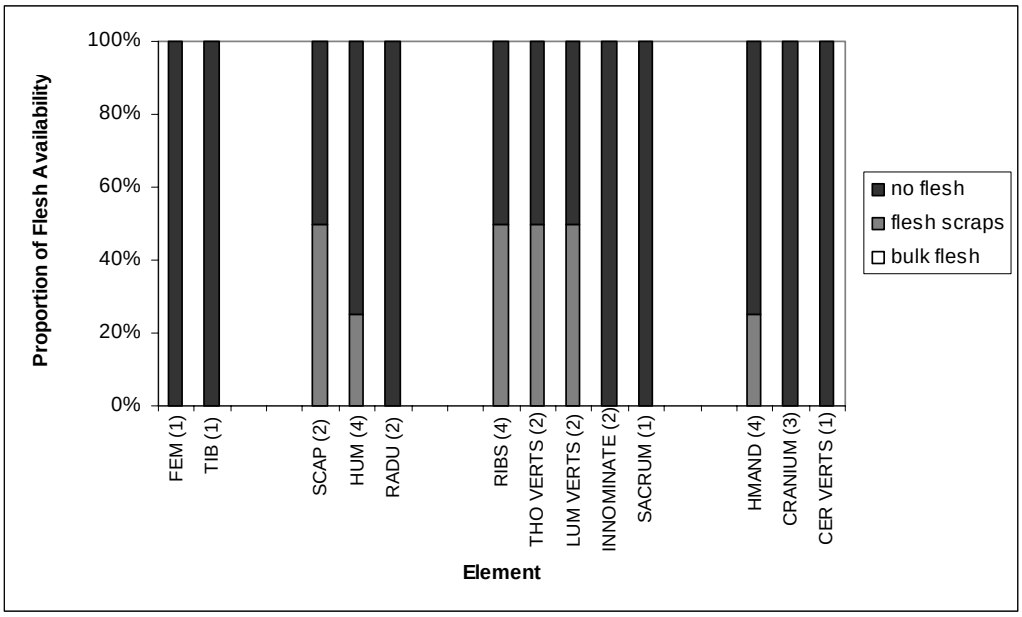


2. Hyaena Consumption of Size 3/4 Carcasses

The carcass-wide distribution of flesh remaining after hyaena consumption of size 3 and 4 prey animals is illustrated in Figure 2.16 and Table 2.13. In stark contrast to the lion-consumed samples from both SGR and NAO, none of the bones from the carcasses consumed by hyaenas had any bulk flesh left for a scavenger. Less than 30% of the bones

retained even flesh scraps; these included some forelimb bones (scapula, humerus), some bones from the trunk (ribs, thoracic and lumbar vertebrae), and the hemimandible. The majority of the bones, just over 70%, were found completely defleshed in all carcasses. These included the hindlimbs, the intermediate forelimb (radio-ulna), innominate and sacrum, cranium and cervical vertebrae.

Figure 2.16. Carcass-wide distribution of flesh availability in size 3 and 4 carcasses consumed by spotted hyaenas at SGR. The total number of carcasses is 5. See Table 2.4 for sample characteristics and Figure 2.13 caption for more details.



This result generally follows Blumenschine's (1986a) consumption sequence, as the femur and innominate are the first two bones to be defleshed. Additionally, limbs were often removed from the main carcass site, presumably for consumption under less intra-specific competitive conditions by the hyaenas (Kruuk, 1972). No flesh availability and gross bone damage and destruction data was collected on spotted hyaena samples from the NAO because there were no bone remains left after spotted hyaena consumption. They were always fed sections of cow ribcages.

Table 2.13. Flesh availability in size 3 and 4 carcasses consumed by spotted hyaenas at SGR. Comparability is made with a modified version of Blumenschine's (1986a:64) carcass consumption sequence of spotted hyaenas on medium sized adults.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh	ICCS (Scraps)	Blumenschine's Modified CCS
Hindlimb	2	0	0%	0	0%	0	0%	2	100%		
Femur	1	0	0%	0	0%	0	0%	1	100%	3.5	2
Tibia	1	0	0%	0	0%	0	0%	1	100%	3.5	6
Forelimb	8	3	38%	0	0%	3	38%	5	72%		
Scapula	2	1	50%	0	0%	1	50%	1	50%	11.5	8
Humerus	4	1	25%	0	0%	1	25%	3	75%	8.5	7
Radio-ulna	2	0	0%	0	0%	0	0%	2	100%	3.5	10
Thorax	11	4	36%	0	0%	4	36%	7	64%		
Ribs	4	2	50%	0	0%	2	50%	2	50%	11.5	4.5
T. Vertebrae	2	1	50%	0	0%	1	50%	1	50%	11.5	4.5
L. Vertebrae	2	1	50%	0	0%	1	50%	1	50%	11.5	3
Innominate	2	0	0%	0	0%	0	0%	2	100%	3.5	1
Sacrum	1	0	0%	0	0%	0	0%	1	100%	3.5	
Head/Neck	8	1	13%	0	0%	1	13%	7	87%		
H/Mandible	4	1	25%	0	0%	1	25%	3	75%	8.5	11
Cranium	3	0	0%	0	0%	0	0%	3	100%	3.5	12
C. Vertebrae	1	0	0%	0	0%	0	0%	1	100%	3.5	9
TOTAL	**29**	**8**	**28%**	**0**	**0%**	**8**	**28%**	**21**	**72%**		

3. Smaller Carnivore Consumption of Size 4 Carcass Parts (Leopards, Jackals, Cheetahs)

None of the smaller carnivores completely defleshed any of the bones from which they fed. The leopard left bulk flesh on the cervical vertebrae it fed from, but only flesh scraps on the innominate and lumbar vertebrae (Table 2.14). Both the scapula and innominate from which the jackals fed were nearly fully fleshed when they were retrieved (Table 2.15). The cheetah samples ranged from fully fleshed (36%) to those with only flesh scraps remaining (64%) (Table 2.16). It is possible that the age of the cheetahs was a factor in the flesh remaining on the bones; of the three scapulae, 2 that were fed on by cheetah cubs had bulk flesh remaining, while the one with only flesh scraps remaining was fed on by 2 adult cheetahs. However, when the cheetah cubs fed on an articulated innominate and a femur, they left only flesh scraps, similar to when the

Table 2.14. Flesh availability in size 4 carcass parts consumed by leopards at NAO. See Table 2.11 caption for more methodological details.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh
Hindlimb	0								
Femur	0								
Tibia	0								
Forelimb	0								
Scapula	0								
Humerus	0								
Radio-ulna	0								
Thorax	2	2	100%	0	0%	2	100%	0	0%
Ribs	0								
T. Vertebrae	0								
L. Vertebrae	1	1	100%	0	0%	1	100%	0	0%
Innominate	1	1	100%	0	0%	1	100%	0	0%
Sacrum	0								
Head/Neck	1	1	100%	1	100%	0	0%	0	0%
H/Mandible	0								
Cranium	0								
C. Vertebrae	1	1	100%	1	100%	0	0%	0	0%
TOTAL	**3**	**3**	**100%**	**1**	**33%**	**2**	**67%**	**0**	**0%**

Table 2.15. Flesh availability in size 4 carcass parts consumed by jackals at NAO. See Table 2.11 caption for more methodological details.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh
Hindlimb	0								
Femur	0								
Tibia	0								
Forelimb	1								
Scapula	1	1	100%	1	100%	0	0%	0	0%
Humerus	0								
Radio-ulna	0								
Thorax	1	1	100%	1	100%	0	0%	0	0%
Ribs	0								
T. Vertebrae	0								
L. Vertebrae	0								
Innominate	1	1	100%	1	100%	0	0%	0	0%
Sacrum	0								
Head/Neck	0								
H/Mandible	0								
Cranium	0								
C. Vertebrae	0								
TOTAL	**2**	**2**	**100%**	**2**	**100%**	**0**	**0%**	**0**	**0%**

same two adult cheetah fed on an articulated innominate, femur, tibia, and a scapula. Because of the small sample sizes, I do not compare these samples to Blumenschine's consumption sequence.

Table 2.16. Flesh availability in size 4 carcass parts consumed by cheetahs at NAO. See Table 2.11 caption for more methodological details.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh
Hindlimb	3	3	100%	0	0%	3	100%	0	0%
Femur	2	2	100%	0	0%	2	100%	0	0%
Tibia	1	1	100%	0	0%	1	100%	0	0%
Forelimb	9	9	100%	5	56%	4	44%	0	0%
Scapula	3	3	100%	2	67%	1	33%	0	0%
Humerus	3	3	100%	0	0%	3	100%	0	0%
Radio-ulna	3	3	100%	3	100%	0	0%	0	0%
Thorax	2	2	100%	0	0%	2	100%	0	0%
Ribs	0								
T. Vertebrae	0								
L. Vertebrae	0								
Innominate	2	2	100%	0	0%	2	100%	0	0%
Sacrum	0								
Head/Neck	0								
H/Mandible	0								
Cranium	0								
C. Vertebrae	0								
TOTAL	**14**	**14**	**100%**	**5**	**36%**	**9**	**64%**	**0**	**0%**

Size 1/2 Prey

Samples sizes are smaller for size 1 and 2 prey than for size 3 and 4 prey, and the sample consists entirely of carcasses from SGR. Again, the largest sample is for lions (N = 4 for each of size 1 and size 2); the other carnivore taxon-prey size samples are all only 1 or 2 carcasses or carcass parts. Size 1 and 2 carcasses are considered both separately and together, where appropriate.

1 .Lion Consumption of Size 1 & 2 Carcasses

The carcass-wide distribution of flesh retained after lions abandoned size 1 and 2 prey animals is illustrated in Tables 2.17-2.19 and Figures 2.17-2.19. On size 2 carcasses

consumed by lions, there was just a single bone (a cranium), representing 3% of the sample, retaining bulk flesh. However, half of the bones in the sample still retained flesh scraps, and 14 (47%) were completely defleshed. This is in strong contrast to the flesh distribution on lion size 3 and 4 kills, where all carcass parts usually retained bulk and scrap flesh remaining, and very few bones were completely defleshed. Overall, the hindlimb is the first part to be completely defleshed, followed by the head/neck, then the thorax, and then the forelimb. This is the same overall carcass part consumption sequence when spotted hyaenas consume size 3 and 4 carcasses.

Not a single bone from size 1 carcasses consumed by lions retained any bulk flesh. 4 bones (29%) retained flesh scraps, and the remainder (15 bones; 79%) were completely defleshed. This is an even stronger contrast than size 2 carcasses to the flesh distribution on lion size 3 and 4 kills, and is fairly similar to the flesh availability levels on size 3 carcasses consumed by spotted hyaenas. If size 1 and 2 lion-eaten carcasses are combined, the flesh availability patterns are generally similar to those seen when these two carcass sizes are separated. The combined results are show in Table 2.19 and Figure 2.19.

There is a cautionary note about this sample: 3 out of the 4 size 2 carcasses were juvenile. While the only adult carcass (SWT 013), which was a warthog, did retain relatively more flesh scraps than the other carcasses, as well as the only instance of a bone retaining bulk flesh (the cranium), there were other carcasses which also retained flesh scraps on the same bones as SWT013. Therefore, I think including these carcasses together as a single sample is justified. The size 1 sample age profile is also skewed: three of the four carcasses in this sample were from juveniles, and the last (SWT 016)

was fetal zebra which was in utero when it and its mother (SWT 017) were killed.

However, juveniles were not always significantly smaller than adults; some carcasses labeled juvenile were of similar size to adults, but exhibited some unfused bones.

Table 2.17. Flesh availability in size 2 carcasses consumed by lions at SGR. Comparability is made with a modified version of Blumenschine's (1986a:62) carcass consumption sequence of lions on small sized adults. See Table 2.11 caption for more methodological details.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh	ICCS (Bulk and Scraps)	Blumenschine's Modified CCS
Hindlimb	6	2	33%	0	0%	2	33%	4	67%		
Femur	2	0	0%	0	0%	0	0%	2	100%	1	2
Tibia	4	2	50%	0	0%	2	50%	2	50%	5.5	4
Forelimb	12	8	67%	0	0%	8	67%	4	33%		
Scapula	4	4	100 %	0	0%	4	100%	0	0%	9.5	5
Humerus	5	2	40%	0	0%	2	40%	3	60%	2.5	7
Radio-ulna	3	2	67%	0	0%	2	67%	1	33%	8	8
Thorax	5	3	60%	0	0%	3	60%	2	40%		
Ribs	2	0	0%	0	0%	1	50%	1	50%	5.5	6
T. Vertebrae	0										
L. Vertebrae	1	0	0%	0	0%	1	100%	0	0%	9.5	3
Innominate	2	0	0%	0	0%	1	50%	1	50%	5.5	1
Sacrum	0										
Head/Neck	7	3	43%	1	14%	2	29%	4	57%		
H/Mandible	5	2	40%	0	0%	2	40%	3	60%	2.5	9
Cranium	2	1	50%	1	50%	0	0%	1	50%	5.5	10
C. Vertebrae	0										
TOTAL	**30**	**16**	**53%**	**1**	**3%**	**15**	**50%**	**14**	**47%**		

Figure 2.17. Carcass-wide distribution of flesh availability in size 2 carcasses consumed by lions at SGR. The total number of carcasses is 4. See Table 2.4 for sample characteristics and Figure 2.13 caption for more details.

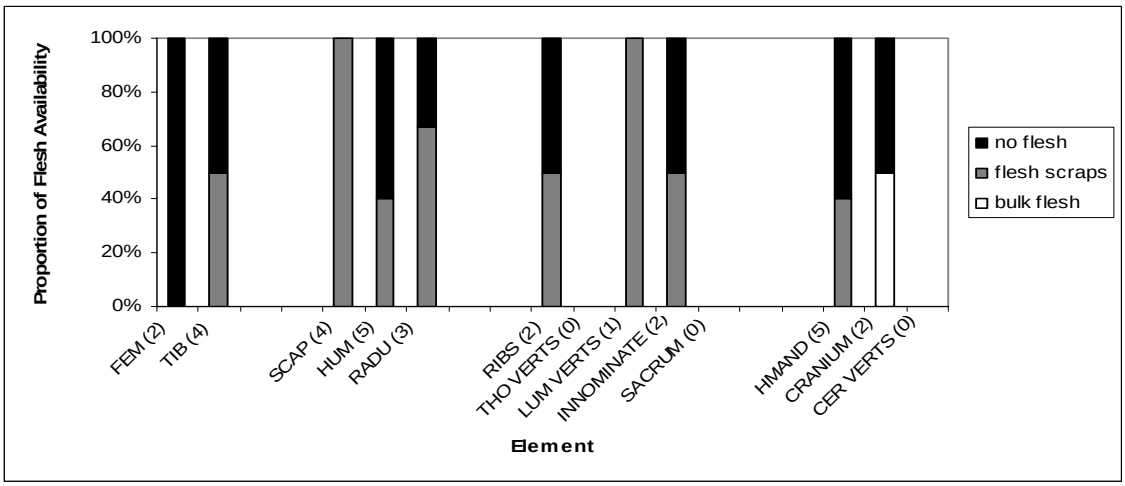


Table 2.18. Flesh availability in size 1 carcasses consumed by lions at SGR. Comparability is made with a modified version of Blumenschine's (1986a:62) carcass consumption sequence of lions on small sized adults. See Table 2.11 caption for more methodological details.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh	ICCS (Bulk and Scraps)	Blumenschine's Modified CCS
Hindlimb	4	1	25%	0	0%	1	25%	3	75%		
Femur	3	0	0%	0	0%	1	33%	2	67%	5.5	2
Tibia	1	0	0%	0	0%	0	0%	1	100%	2.5	3
Forelimb	6	2	33%	0	0%	2	33%	4	67%		
Scapula	1	0	0%	0	0%	0	0%	1	100%	2.5	4
Humerus	2	0	0%	0	0%	1	50%	1	50%	7.5	5
Radio-ulna	3	0	0%	0	0%	1	33%	1	67%	5.5	6
Thorax	2	1	50%	0	0%	1	50%	1	50%		
Ribs	0										
T. Vertebrae	0										
L. Vertebrae	0										
Innominate	2	1	50%	0	0%	1	50%	1	50%	7.5	1
Sacrum	0										
Head/Neck	7	0	0%	0	0%	0	0%	4	100%		
H/Mandible	4	0	0%	0	0%	0	0%	4	100%	2.5	7
Cranium	3	0	0%	0	0%	0	0%	3	100%	2.5	8
C. Vertebrae	0										
TOTAL	**19**	**0**	**0%**	**0**	**0%**	**4**	**21%**	**15**	**79%**		

Figure 2.18. Carcass-wide distribution of flesh availability in size 1 carcasses consumed by lions at SGR. The total number of carcasses is 4. See Table 2.4 for sample characteristics and Figure 2.13 caption for more details.

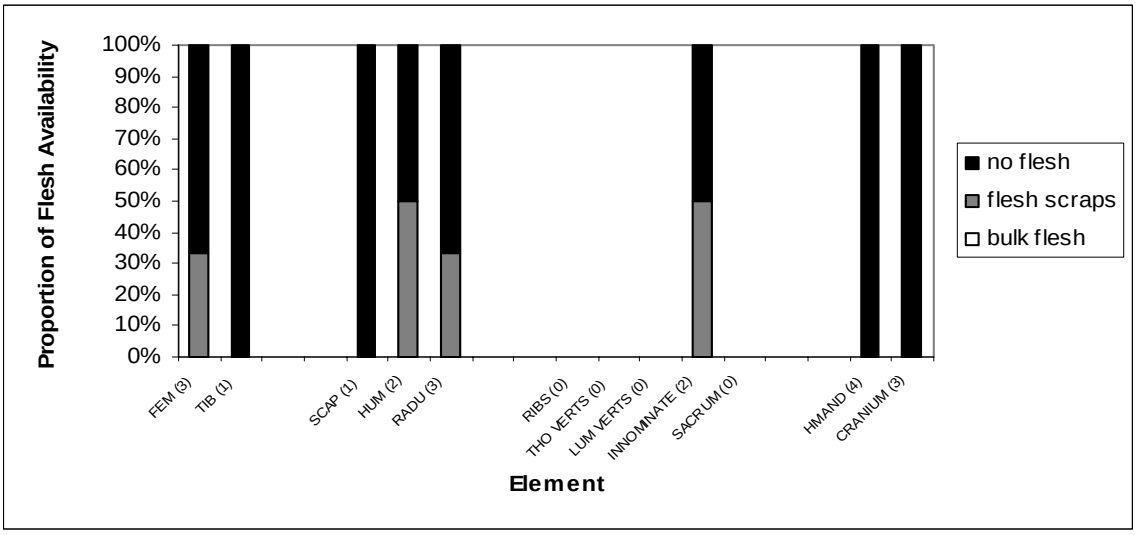
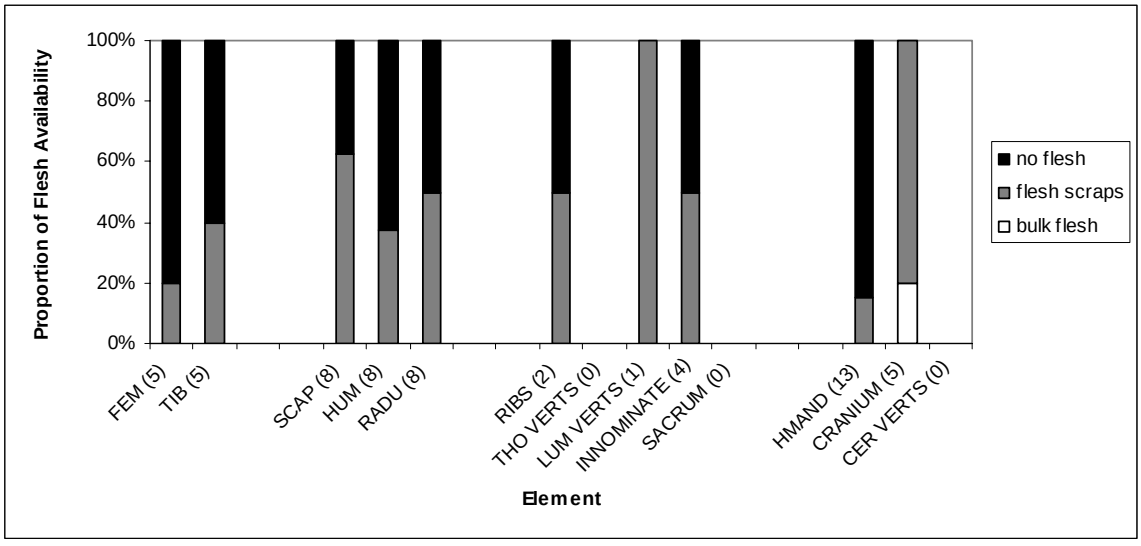


Table 2.19. Flesh availability in size 1 and 2 carcasses (combined) consumed by lions at SGR. Comparability is made with a modified version of Blumenschine's (1986a:62) carcass consumption sequence of lions on small sized adults. See Table 2.11 caption for more methodological details.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh	ICCS (Bulk and Scraps)	Blumenschine's Modified CCS
Hindlimb	10	3	30%	0	0%	3	33%	7	75%		
Femur	5	1	20%	0	0%	1	20%	4	80%	2	2
Tibia	5	2	40%	0	0%	2	40%	3	60%	4	4
Forelimb	24	12	50%	0	0%	12	50%	12	50%		
Scapula	8	5	63%	0	0%	5	63%	3	38%	8	5
Humerus	8	3	38%	0	0%	3	38%	5	63%	3	7
Radio-ulna	8	4	50%	0	0%	4	50%	4	50%	6	8
Thorax	7	4	57%	0	0%	4	57%	3	43%		
Ribs	2	1	50%	0	0%	1	50%	1	50%	6	6
T. Vertebrae	0										
L. Vertebrae	1	1	100%	0	0%	1	100%	0	0%	9	3
Innominate	4	2	50%	0	0%	2	50%	2	50%	6	1
Sacrum	0										
Head/Neck	18	7	39%	1	6%	6	33%	11	61%		
H/Mandible	13	2	15%	0	0%	2	15%	11	85%	1	9
Cranium	5	5	100%	1	20%	4	80%	0	0%	10	10
C. Vertebrae	0										
TOTAL	**59**	**26**	**44%**	**1**	**2%**	**25**	**42%**	**33**	**56%**		

Figure 2.19. Carcass-wide distribution of flesh availability in size 1 and 2 carcasses consumed by lions at SGR. The total number of carcasses is 8. See Table 2.4 for sample characteristics and Figure 2.13 caption for more details.



2. Hyaena Consumption of Size 1/2 Carcasses

Spotted hyaenas completely consumed all flesh, and virtually all bone, from the three size 1 and 2 carcasses which I left for them. These samples consisted of domestic sheep and cow (juveniles) whose hindlimbs were used for unrelated experiments (Pobiner and Braun, 2005). The entire front ends of the carcasses, from the thoracic vertebrae cranially, were left out on the SGR airstrip for hyaenas. The only bones remaining from these samples were a completely defleshed isolated palate and upper cranium (SWT 018), and part of a scapula (SWT 019); SWT 020 was completely consumed (or transported).

3. Leopard Consumption of Size 1/2 Carcasses

There were only 3 leopard-eaten size 1 and 2 samples available for analysis; one size 2 carcass (SWT 028; Table 2.20) and two size 1 carcasses (SWT 012, 031; Table 2.21). These samples were domestic sheep or goats that had been skinned, cut in half, and fixed to a tree for baiting a leopard which was then occasionally observed by the Sweetwaters Tented Camp night game drive vehicles. As mentioned in the methods sections, most of these bait carcasses were partially or wholly pulled off of the tree by the leopard; the bones available for analysis were only those which the leopard could not remove, normally those bones from the part of the hindlimb which was used to tie the bait to the tree. Because of the small sample sizes and skewed body part representation, I do not compare these samples to Blumenschine's consumption sequence.

The leopard defleshed the bones from the size 2 carcass fairly thoroughly, following the normal carcass consumption sequence in which the innominate and femur were completely defleshed and the tibia still had flesh scraps. The two size 1 carcasses

were less well defleshed; one was left with flesh scraps, while the other was left with bulk flesh.

Table 2.20. Flesh availability in the size 2 carcass consumed by a leopard at SGR. See Table 2.11 caption for more methodological details.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh	ICCS (Bulk and Scraps)
Hindlimb	2	1	50%	0	0%	1	50%	1	50%	
Femur	1	0	0%	0	0%	0	0%	1	100%	2.5
Tibia	1	1	100%	0	0%	1	100%	0	0%	1
Forelimb	0									
Scapula	0									
Humerus	0									
Radio-ulna	0									
Thorax	1	0	0%	0	0%	0	0%	1	100%	
Ribs	0									
T. Vertebrae	0									
L. Vertebrae	0									
Innominate	1	0	0%	0	0%	0	0%	1	100%	2.5
Sacrum	0									
Head/Neck	0									
H/Mandible	0									
Cranium	0									
C. Vertebrae	0									
TOTAL	**3**	**1**	**33%**	**0**	**0%**	**1**	**33%**	**2**	**67%**	

Table 2.21. Flesh availability in size 1 carcasses consumed by a leopard at SGR. See Table 2.11 caption for more methodological details.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh	ICCS (Bulk and Scraps)
Hindlimb	4	4	100%	2	50%	2	50%	0	0%	
Femur	2	2	100%	1	50%	1	50%	0	0%	3.5
Tibia	2	2	100%	1	50%	1	50%	0	0%	3.5
Forelimb	0									
Scapula	0									
Humerus	0									
Radio-ulna	0									
Thorax	2	2	100%	2	100%	0	0%	0	0%	
Ribs	0									
T. Vertebrae	0									
L. Vertebrae	1	1	100%	1	100%	0	0%	0	0%	1.5
Innominate	1	1	100%	1	100%	0	0%	0	0%	1.5
Sacrum	0									
Head/Neck	0									
H/Mandible	0									
Cranium	0									
C. Vertebrae	0									
TOTAL	**6**	**6**	**100%**	**4**	**67%**	**2**	**33%**	**0**	**0%**	

At first it would seem that combining these two samples, which exhibit quite different flesh availability patterns, is not justified. However, the actual size difference between the size 2 animal, a juvenile cow, and the size 1 animals, domestic goat and sheep, was fairly small. The combined sample is presented in Table 2.22.

Table 2.22. Flesh availability in size 1 and 2 carcasses (combined) consumed by a leopard at SGR. See Table 2.11 caption for more methodological details.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh	ICCS (Bulk and Scraps)
Hindlimb	6	4	67%	2	33%	2	33%	2	33%	
Femur	3	2	67%	1	33%	1	33%	1	33%	2.5
Tibia	3	2	67%	1	33%	1	33%	1	33%	2.5
Forelimb	0									
Scapula	0									
Humerus	0									
Radio-ulna	0									
Thorax	3	2	67%	2	67%	0	0%	1	33%	
Ribs	0									
T. Vertebrae	0									
L. Vertebrae	1	1	100%	1	100%	0	0%	0	0%	1
Innominate	2	1	50%	1	50%	0	0%	1	50%	4
Sacrum	0									
Head/Neck	0									
H/Mandible	0									
Cranium	0									
C. Vertebrae	0									
TOTAL	**9**	**6**	**67%**	**4**	**44%**	**2**	**22%**	**3**	**33%**	

4. Cheetah and Jackal Consumption of Size 1 Carcasses

There was one sample each from cheetah and jackal consumption of size 1 carcasses. However, the cheetah sample (SWT 010; Table 2.23) was only tentatively attributed to cheetah; as this predator taxon identification is uncertain and it is possible that this carcass was accessed by vultures, I will not discuss this sample further.

The single jackal sample (SWT 022) was a domestic sheep left just adjacent to a jackal den. There was no evidence that any other carnivore had fed from this carcass, and I am confident in attributing this sample to consumption only by jackals. The carcass was virtually complete upon retrieval, and the only bone which had been fed on until only

flesh scraps were present was one of the femora. The rest of the bones retained bulk flesh, with the ribs and the innominate also retaining flesh scraps in some areas (Table 2.24).

Table 2.23. Flesh availability in a size 1 carcass parts probably consumed by a cheetah at SGR. See Table 2.11 caption for more methodological details.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh
Hindlimb	4	4	100%	1	25%	3	75%	0	0%
Femur	2	2	100%	0	0%	2	100%	0	0%
Tibia	2	2	100%	1	50%	1	50%	0	0%
Forelimb	6	4	67%	0	0%	4	67%	0	0%
Scapula	2	0	0%	0	0%	0	0%	0	0%
Humerus	2	2	100%	0	0%	2	100%	0	0%
Radio-ulna	2	2	100%	0	0%	2	100%	0	0%
Thorax	5	5	100%	0	0%	5	100%	0	0%
Ribs	1	1	100%	0	0%	1	100%	0	0%
T. Vertebrae	1	1	100%	0	0%	1	100%	0	0%
L. Vertebrae	1	1	100%	0	0%	1	100%	0	0%
Innominate	1	1	100%	0	0%	1	100%	0	0%
Sacrum	1	1	100%	0	0%	1	100%	0	0%
Head/Neck	4	4	100%	0	0%	4	100%	0	0%
H/Mandible	2	2	100%	0	0%	2	100%	0	0%
Cranium	1	1	100%	0	0%	1	100%	0	0%
C. Vertebrae	1	1	100%	0	0%	1	100%	0	0%
TOTAL	**19**	**19**	**100%**	**1**	**5%**	**18**	**95%**	**0**	**0%**

Table 2.24. Flesh availability in a size 1 carcass consumed by jackals at SGR. See Table 2.11 caption for more methodological details.

	N	# of Bones with Any Flesh	% of Bones with Any Flesh	# of Bones with Bulk Flesh	% of Bones with Bulk Flesh	# of Bones with Flesh Scraps	% of Bones with Flesh Scraps	# of Bones with No Flesh	% of Bones with No Flesh
Hindlimb	4	4	100%	3	75%	1	25%	0	0%
Femur	2	2	100%	1	50%	1	50%	0	0%
Tibia	2	2	100%	2	100%	0	0%	0	0%
Forelimb	6	6	100%	6	100%	0	0%	0	0%
Scapula	2	2	100%	2	100%	0	0%	0	0%
Humerus	2	2	100%	2	100%	0	0%	0	0%
Radio-ulna	2	2	100%	2	100%	0	0%	0	0%
Thorax	5	5	100%	5	100%	0	0%	0	0%
Ribs	1	1	100%	1	100%	0	0%	0	0%
T. Vertebrae	1	1	100%	1	100%	0	0%	0	0%
L. Vertebrae	1	1	100%	1	100%	0	0%	0	0%
Innominate	1	1	100%	1	100%	0	0%	0	0%
Sacrum	1	1	100%	1	100%	0	0%	0	0%
Head/Neck	4	4	100%	4	100%	0	0%	0	0%
H/Mandible	2	2	100%	2	100%	0	0%	0	0%
Cranium	1	1	100%	1	100%	0	0%	0	0%
C. Vertebrae	1	1	100%	1	100%	0	0%	0	0%
TOTAL	**19**	**19**	**100%**	**18**	**95%**	**1**	**5%**	**0**	**0%**

Comparisons of Flesh Availability Across Different Sized Prey Carcasses Consumed by Different Carnivore Taxa

Pobiner and Blumenschine (2002, 2003) and Pobiner (2005) initially demonstrated that spotted hyaena gross bone damage and destruction patterns on size 3 upper hindquarters were analogous to that of lions on size 1 carcasses. While I will discuss gross bone damage and destruction data later, the data presented here argues that a similar scaled relationship can also be demonstrated for carcass-wide flesh availability patterns. Figure 2.16, which illustrates flesh availability in size 3 and 4 spotted hyaena-eaten carcasses, is very similar to Figure 2.18, which illustrates flesh availability in size 1 lion-eaten carcasses. The total proportion of bones retaining flesh scraps versus bones that were completely defleshed in the spotted hyaena-size 3 and 4 prey sample is 28%:72%; in the lion-size 1 and 2 sample it is 21:79%. The sample sizes are probably too small to warrant bone-by-bone or even carcass part-by-carcass part flesh availability comparisons; what is important is the overall general similarity in patterning of flesh consumption. However, general similarities can be seen in the relatively higher amount of flesh left on intermediate versus upper limb bones (radio-ulna and tibia versus humerus and femur).

I would have liked to extend Pobiner and Blumenschine's (2003) demonstration of similar damage and destruction patterns on size 3 upper hindquarters eaten by lions and size 1 upper hindquarters eaten by cheetahs to flesh availability data presented here. However, the single "cheetah" sample is not attributed to cheetah with complete confidence, and therefore is not suitable for comparison. We can instead compare the lion-size 3 and 4 sample (Figure 2.13, Table 2.11) to size 1 carcasses consumed by

leopards (Table 2.21). While this is a very small sample, again, there are overall similarities. The overall ratio of bones with bulk, scrap, and no flesh available in the lion-size 3 and 4 sample is 56%:39%:5%. In the leopard-size 1 sample, the ratio is fairly similar: 67%:33%:0%. Again, the leopard sample size is too small to warrant comparing the skeletal distributions of flesh.

Limb Flesh Distribution

A systematic differential flesh distribution pattern was expected between limbs in which there was more flesh retained on the intermediate limb bones (radio-ulna and tibia) that the upper limb bones (humerus and femur) (Figure 2.10, top left and top right). However, in the majority of the samples collected (including those from both SGR and NAO), this was surprisingly not the case (Table 2.25). 17 of the 28 (61%) humerus-radio-ulna pairs exhibited no differential flesh availability. Of the 11 (39%) of the upper limb pairs which did exhibit differential flesh availability, 9 of these (82%) exhibited less flesh on the upper limbs. 15 of the 25 (60%) femur-tibia pairs exhibited no differential flesh availability. Of the 10 (40%) of the lower limb pairs which did exhibit differential flesh availability, 6 of these (60%) exhibited less flesh on the upper limbs. A total of 30 limbs from the SGR sample, some of which were not coded in this analysis, exhibited a flesh distribution patterns in which approximately the distal third of the intermediate limb element (tibia or radio-ulna) technically retained bulk flesh due to their still having skin remaining on the limb from this area distally to the phalanges.

Within individual limbs, I expected that more flesh would be observed on proximal and distal portions than on midshaft portions. This was the case, but only for a

very small majority of the total SGR and NAO sample: 17 out of 33 limbs (52%). 10 of these limbs (30%) exhibited no intra-element flesh availability differential, and 6 of these limbs had more flesh on the midshaft versus on one or both of the epiphyseal portions. Importantly, all of the latter limbs were intermediate limbs (tibiae and radio-ulnae) from the NAO sample. The intra-bone distribution of flesh on upper limbs conforms more to the expected scenario where midshafts are relatively more defleshed than epiphyses.

Table 2.25. Differential inter-element limb flesh availability. Flesh availability was coded as bulk, scrap, or absent (see text for more details). Upper limbs are femur (F) and humerus (H); intermediate limbs are tibia (T) and radio-ulna (R). Each element pair within a single limb exhibiting the flesh distribution is listed under the appropriate column with the carcass number. Data were only collected on limb elements present, which explains the absence of some element pairs from some carcasses, which were deleted either by destruction/consumption or movement away from the main carcass area. This also explains why some sample numbers are listed twice in the same column: for instance, both femur-tibia pairs from SWT001 exhibited less flesh on the upper versus intermediate limbs. Total numbers of limb element pairs exhibiting each specific inter-element flesh availability state are listed in the bottom row.

Femur-Tibia			Humerus-Radio-ulna		
More Flesh on Upper Limb	Equal Flesh on Upper & Intermediate Limbs	Less Flesh on Upper Limbs	More Flesh on Upper Limb	Equal Flesh on Upper & Intermediate Limbs	Less Flesh on Upper Limbs
SWT009, NAO34	SWT006, SWT006, SWT007, SWT007, SWT010, SWT011, SWT012, SWT021, SWT021, SWT022, SWT022, SWT024, SWT031, SWT033, SWT033, SWT034, NAO32	SWT001, SWT001, SWT010, SWT014, SWT014, SWT017, SWT017 SWT028, NAO26	SWT007, SWT033, NAO20, NAO26	SWT006, SWT006, SWT009, SWT010, SWT010, SWT011, SWT011, SWT014, SWT014, SWT017, SWT017, SWT021 SWT022, SWT022, NAO28	SWT007, SWT024, SWT033, NAO22, NAO24, NAO31
2	**17**	**9**	**4**	**15**	**6**

The Relationship of Number of Carcass Consumers, Season, and Habitat to Flesh Availability

The most useful sample for relating number of carcass consumers to flesh availability is the SGR lion-size 3 and 4 sample, as it is the sample with the largest number of carcasses (Table 2.26). While at first there appears to be an inconsistent

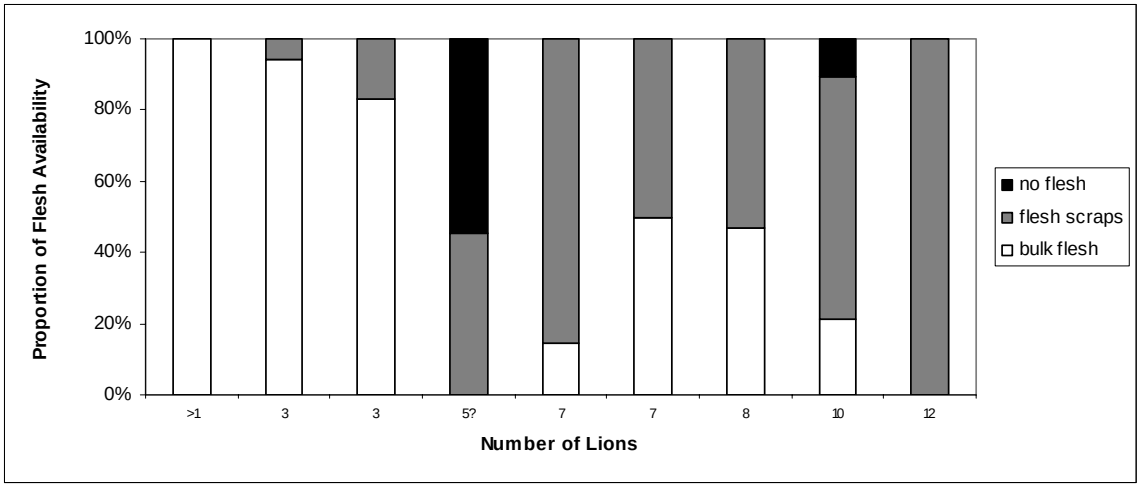
relationship between number of consumers and flesh availability in this sample (Figure 2.20a), we can stratify the sample into three levels of lion group sizes: from 1-3 lions, 7-8 lions, and 10-12 lions. It is at this analytical level that patterns begin to emerge (Figure 2.20b). The three carcasses fed on by 1-3 lions (SWT 014, 015, and 017) retain very high amounts of bulk flesh, on over 80% of all carcass parts. Only a few bones are even defleshed to where only flesh scraps are available. I will disregard the carcass fed on by (possibly) 5 lions, SWT 024, at present (see below). The remainder of the sample of carcasses fed on by 4-8 lions (SWT 001, 006, 007) show a much lower proportion of bulk versus scrap flesh than those fed on by smaller groups of lions. None of the bones from these carcasses are completely defleshed. The final sub-sample, those fed on by >9 lions,

Table 2.26. The relationship between flesh availability, habitat, consumption time, and number of feeding lions on size 3 and 4 carcasses from SGR. The first number in the third, fourth, and fifth columns is the total number of bones with bulk, scrap, or no flesh, and the second number is the percentage of the total sample from that carcass of bones with bulk, scrap, or no flesh. Time between initial sighting and retrieval refers to the number of hours between when the carcass was discovered and when I retrieved it.

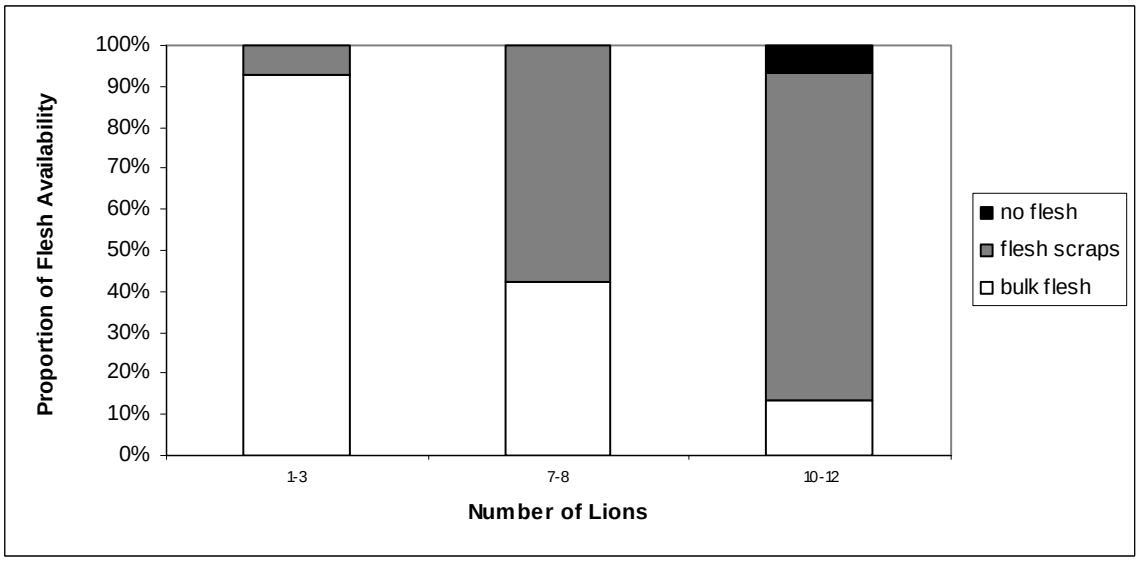
# of Lions	Carcass Number	Total # Bones	# /% Bones with Bulk Flesh	#/% Bones with Flesh Scraps	#/% Bones with No Flesh	Habitat	Time Between Initial Sighting and Retrieval
>1	SWT017	19	19 (100%)	0 (0%)	0 (0%)	open *Acacia* woodland	2.5 hours
3	SWT014	18	17 (94%)	1 (6%)	0 (0%)	open *Acacia* woodland	0.5 hours
3	SWT015	18	15 (83%)	3 (17%)	0 (0%)	open *Acacia* woodland	15 hours
5?	SWT024	11	0 (0%)	5 (45%)	6 (55%)	open *Acacia* woodland	1.25 hours
7	SWT001	7	1 (14%)	6 (86%)	0 (0%)	grassy clearing within *Acacia* woodland	10 hours
7	SWT007	16	8 (50%)	8 (50%)	0 (0%)	open plains	8 hours
8	SWT006	15	7 (47%)	8 (53%)	0 (0%)	open plains	9 hours
10	SWT033	19	4 (21%)	13 (68%)	2 (11%)	at edge of dam (man-made waterhole) in *Acacia* woodland	32 hours
12	SWT021	11	0 (0%)	11 (100%)	0 (0%)	open plains	21 hours

Figure 2.20. The relationship between number of lion consumers and flesh availability in size 3 and 4 carcasses at SGR. Top (a) illustrates each carcass individually, and bottom (b) groups number of lion consumers into three categories and excludes SWT024.

(a)



(b)



includes SWT 021 and 033. SWT 033, fed on by 10 lions, exhibits a bulk: scrap flesh availability pattern similar to those carcasses fed on by 4-8 lions, except that now, there are bones present that have been completely defleshed. SWT 021, a sub-adult zebra (a size 3 animal but with unfused epiphyses) fed on by 12 lions, was completely devoid of bulk flesh and only had scraps of flesh remaining after the lion feeding. Strangely, SWT

024, which was fed on by at least 5 lions (5 lions were seen in the near vicinity of the kill), had the least amount of flesh of any of the size 3 carcasses, with flesh scraps remaining on just less than half of the bones present, with the remainder of the bones having been completely defleshed. It is possible that a greater number of feeding lions had been present before my observation of the carcass, as I did not directly observe the five lions but was given this number by Nathan Gichohi, who said he had seen them in the area nearby. This kill is not included in the data used to construct Figure 2.20b.

Another way to stratify this sample is by season. SWT 001, 006, and 007 all occurred in mid-late September, at the end of the longer dry season. SWT 014, 015, and 017 all occurred in mid-October through early November, during the beginning of the short rains. SWT 021 occurred in early December, at the middle of the short rains. SWT 024 occurred in late December, at the end of the short rains. SWT 033 occurred in mid-March, at end of the shorter dry season. The two carcasses with no bulk flesh available, SWT 021 and 024, occurred during the middle and end of the short rains, respectively. It is possible that during this time, the distribution of herbivores (mainly zebras, the lions' principle prey), was more scattered due to a higher availability of water sources outside the troughs that provide water during the dry seasons. This could have led to decreased prey availability, which then could have led to more complete carcass exploitation. However, disentangling the effect of season from the effect of lion group size is difficult, as it seems that lion group size was fairly consistently higher in the wet season.

It is difficult to disentangle the effect of habitat from the effect of lion group size, for a few reasons (see Table 2.26). My lion-size 3 and 4 kills were either found in open *Acacia* woodland or open plains, but none were found in riparian woodland or *Euclea*

bushland. This was likely due to decreased visibility and vehicle navigability in the latter habitats. As well, all of the lion feeding episodes including large groups of lions occurred in open plains. Therefore, effects of habitat on flesh availability cannot be separated from effects of lion group size on flesh availability.

Flesh Availability: Discussion

Naturalistic Versus Captive Samples

Certain issues should be taken into consideration when using flesh availability and gross bone damage and destruction data from a captive setting such as NAO. Both the flesh consumption and gross bone damage and destruction data could be either anomalously high or anomalously low compared with that from naturalistic settings for several different reasons. For instance, low intra- and inter-specific competition leading to a longer period of time with a carcass part, as well as boredom, could cause anomalously high flesh consumption and gross bone damage. Alternatively, low intra- and inter-specific competition leading to earlier satiation, as well as regular access to food, could cause anomalously low flesh consumption and gross bone damage. The most appropriate data presented here to explore these possibilities are the size 3 and 4 carcasses or carcass parts eaten by lions from SGR and NAO. When a difference in flesh availability is present, carcass parts eaten by the NAO lions have slightly less bulk versus scrap flesh available than those from SGR, though none of the limb bones from NAO were completely defleshed (see Figs 2.10 and 2.11). This could be interpreted as supporting the argument that flesh consumption is higher in captive settings. However, I

think these differences are minor enough to warrant combining and comparing the two groups of samples.

Lion Samples: Flesh Availability, Potential Hominin Scavenging Opportunities, and Variability in Ecosystems

As previous researchers have found (Blumenschine, 1986a; Domínguez-Rodrigo, 1999), lion carcass processing and flesh consumption show fairly consistent patterning. However, the details of the patterning in flesh consumption I observed was somewhat different that that of Blumenschine (1986a) and especially Domínguez-Rodrigo (1999). I found relatively substantial overall flesh availability: 100% of my carcasses retained bones with bulk flesh on most carcass parts. Only 5% of individual bones were completely defleshed, and only 3% of limb bones were completely defleshed. I found a substantial amount of bulk flesh and flesh scraps left on both upper and intermediate limb bones of size 3 and 4 ungulates defleshed by lions. In fact, only 1 out of 31 size 3 and 4 upper limb bones was completely defleshed, and only 1 out of 33 size 3 and 4 intermediate limb bones was completely defleshed. In contrast, Domínguez-Rodrigo (1999) found that lions usually nearly completely deflesh carcasses. From his data (Domínguez-Rodrigo, 1999:381, Table 1), I calculated that he found bulk or flesh scraps on 18% of his carcasses, and practical or total absence of flesh on 81% of his carcasses. Similarly, Selvaggio (1994a) found that limbs of size 3 prey consumed by lions were abandoned with little or no flesh on humeri and femora, and only occasionally with small scraps of flesh near the distal epiphyses of the radio-ulnae and tibiae. In contrast, Blumenschine's (1986a:86-89) observations are more similar to mine: he found that lions completely defleshed medium sized adult carcasses just less than 30% of the time. There

could be several reasons for these differences, including: 1) a different definition of what constitutes bones being abandoned with “little flesh”/flesh “scraps”, or “nearly” or “completely” defleshed; 2) differing ecologies of the study areas.

Although he found higher levels of inter-specific competition levels for carcass resources in open plains (Domínguez-Rodrigo, 2001), Domínguez-Rodrigo found less flesh remaining on size 3 lion kills in the Maasai Mara located in riparian woodlands versus those located in open plains, which he attributes to the longer lion carcass processing time in riparian woodlands (1999). Blumenschine (1986a) found less flesh remaining on size 3 carnivore kills in the open plains of Serengeti and Ngorongoro, which he attributes to the relatively higher consumption completeness levels of these kills by hyaenas (sometimes following lion primary access). Additionally, hyaenas were the initial consumers on the majority of kills found in the open vegetation components ecosystems, while lion kills were most often found in the riparian woodlands. While I do not have strictly comparable data to these studies, as none of my kills were in riparian woodlands, my kills in open *Acacia* woodlands did retain more flesh than those in open plains, in apparent contrast to Domínguez-Rodrigo’s data. However, I do have data that may address his speculation on the underlying mechanism for this differential in flesh availability, whichare the amounts of time spent consuming carcasses. If I compare flesh availability on lion-size 3 and 4 carcasses and carcass parts from SGR versus NAO (Figures 2.12-2.14), in all cases, there is a slightly higher proportion of bulk: scrap flesh available on the SGR samples versus the NAO samples. The NAO samples were all carcass parts fed to one or two lions, consumed over a period of 18 hours. My SGR samples did not have a uniform distribution of time over which they were consumed, and

in nearly all instances I did not observe the complete consumption process from start to finish. Table 2.14 lists the number of hours between which the carcass was first discovered and the time I retrieved it. This is a very loose measure of consumption time, as sometimes the carcasses were initially discovered abandoned and other times they were discovered still being consumed. However, it is noteworthy that the carcasses with relatively low flesh availability were also all retrieved after at least 8 hours since their initial spotting, and in all of these instances, they were left overnight because the lions were still consuming the carcass when it was first discovered. Therefore, my data lends tentative support to Domínguez-Rodrigo's hypothesis, but does not address the link between habitat and length of consumption episode. Additionally, the number of lion consumers may play a role in this relationship.

Compared with lions, I found that hyaenas consumed the flesh from of size 3 carcasses to a much greater extent than lions, which is in accordance with previous studies (e.g. Blumenschine, 1986a; Selvaggio, 1994a). However, I did find some scavengeable resources in the form of flesh scraps on carcasses abandoned by hyaenas. This is most likely due to a lower inter- and intra-specific competition level in this ecosystem. As mentioned earlier, some spotted hyaena dens on the nearby ranch, where it is thought the spotted hyaenas at SGR live at least seasonally, were poisoned within the last few years. This drastically reduced their group sizes. Rarely are more than a dozen spotted hyaenas seen together, and normally they are seen individually or in small groups of 2 or 3 animals. Blumenschine (1986a) observed that hyaena consumption of size 3 carcasses is not constrained by obstruction to edible parts, as is that of lions, and they

consume carcasses of this size to an extent instead dependent upon feeding group size. My findings support this observation.

The differences I found in flesh availability on lion kills compared with these previous studies (Blumenschine, 1986a; Selvaggio 1994a; Domínguez-Rodrigo, 1999) is likely a result of a lower level of intra- and inter-specific competition at SGR compared other ecological settings (Serengeti, Ngorongoro, Maasai Mara). Overall, interspecific competition level seems to have a greater effect on flesh availability than intraspecific competition, as measured by the number of lions feeding on a carcass. While the predator community at SGR may be relatively "unnatural", there are several ecological scenarios in the past that could have produced a similar relative abundance of at least partially fleshed carcasses to what I found at SGR, making my observations of flesh availability relevant to the fossil record. These include:

1. Drought. Drought can result in a higher than normal abundance of fully fleshed herbivore carcasses (e.g. Capaldo and Peters, 1995).
2. Presence of sabertoothed felids. These carnivores, many of which are reconstructed to be solitary and as large as modern lions (Rawn-Schatzinger, 1992; Lewis, 1997), likely took large prey and consumed relatively less flesh and bone from those prey than modern lions (Marean, 1989). This ecological niche is partially filled in modern ecosystems by cheetahs, though they are smaller and take smaller prey, and live in more open environments than have been proposed for some of the sabertoothed felids (Gonyea, 1976; Marean, 1989; Lewis, 1997).

In a study of locomotor diversity among past and present predator guilds, VanValkenburgh (1985) found that of four recent guilds, the Serengeti was unusual in

having both the maximum species richness and closest species packing (as measured by degree morphological similarity). “In the Serengeti, the high predator diversity results from a partial filling of the gaps visible in the other guild plots (i.e., it is due to an apparent increased packing of species)” (Van Valkenburgh, 1988: 417). She suggests that some of this high predator diversity is the result of the richness and abundance of terrestrial herbivore prey (basically, high food availability) in the Serengeti. This in turn is likely the result of a high amount of savanna-woodland mosaic vegetation, as opposed to more closed woodland or forest vegetation, as the former tends to have greater herbivore carrying capacities. Therefore, the Serengeti’s carnivore community may be unusual, at least for extant communities. It is possible that in the past, especially in more wooded and forested places, carnivore niches were not as tightly packed, and carnivore communities were more likely to contain flesh-specialists such as sabertoothed felids which could have left larger, more partially fleshed carcasses than in most modern savannah modern environments. I argue that the Sweetwaters ecosystem may be a more useful model for these types of potential hominin scavenging opportunities than the modern Serengeti ecosystem. Certainly, it increases the range of variation in the modern ecosystems available to use to interpret the past.

Leopard, Cheetah, and Jackal Samples: Flesh Availability and Potential Hominin Scavenging Opportunities

Comparable data from other studies on flesh availability in tree-stored leopard kills is scarce. Selvaggio (1994a) found that incompletely consumed leopard kills had large quantities of flesh still available, and that kills that leopards had abandoned when they were completely consumed still retained marrow and occasional scraps of flesh.

Cavallo and Blumenschine (1989) describe a sub-adult size 1 tree-stored leopard kill in which most of the hindquarter flesh was consumed, but the anterior half of the carcass was complete; they describe another instance in which a similar carcass was cached in a tree for 18 hours before consumption. These observations, along with my data, suggest that tree-stored leopard kills go through stages of decreasing flesh availability. It is possible that my observations are of less value as they are less "natural", since the carcasses I observed were domestic animals tied to a tree to use as bait, but as they are in general agreement with previous studies, I am confident of their utility. It is also possible that the flesh consumption I observed is less than what would be expected under "normal" circumstances, because: 1) this tree is regularly baited, and the leopard may be more satiated, more often; or 2) the leopard regularly removes part of the bait for consumption elsewhere, and may be uncomfortable consuming the bait to the fullest extent possible at this tree due either to being observed by tourists or possible competition with lions and/or hyaenas, both of which I observed beneath the tree at different times. My data confirms that tree-stored leopard kills are indeed a potential scavenging opportunity for (at least partially) arboreal early hominins, provided they utilized them sparingly.

All of the jackal consumed samples had substantial flesh available; jackals did not reduce any of the muscle masses even to flesh scraps. This is likely either because of their small size relative to the amount of meat on the carcasses or carcass parts, or because as canids, their dentition is less adapted to flesh-slicing than that of felids (Van Valkenburgh, 1989). Therefore, kills of small canids such as jackals could be a very profitable scavenging opportunity for early hominins. However, jackals' natural

predation habits do not include hunting mammals larger than themselves; this likely limits them as potential providers of large quanitites of scavengeable foods.

Unfortunately, I only had one (uncertain) cheetah kill SGR from which to gather flesh availability data. However, I did have 6 NAO samples of cheetahs feeding on cow bones or carcass parts. I found that cheetahs never completely deflesh bones, even in my NAO samples, with no inter-specific competition, or any real limit on consumption time. I therefore envisage free-ranging cheetahs to consume even less flesh relative to these samples. This is supported by Blumenschine's (1986a) and Selvaggio's (1994a) observations; Selvaggio (1994a) noted that cheetah consumed carcasses were usually abandoned with large strips of flesh on both axial and appendicular elements. These are therefore another potential scavenging opportunity for early hominins, and may be useful as a model for flesh availability on sabertoothed felid kills (see more below), as they were also flesh specialists even among felids (Ewer, 1973).

Blumenschine (1986a) notes a similarity in completeness upon abandonment of cheetah kills of size 1 prey to lion kills of size 3 prey. He interprets this similarity to indicate that carcass size in relation to consumer size is a good predictor of flesh availability on abandonment by carnivores with similar extractive potentials. I note a similarity between leopard consumption of size 1 prey and lion consumption of size 3 prey, which supports this idea. Importantly, Blumenschine (1986a) suggests that the physical principles underlying the completeness of carcasses encountered by scavengers in modern settings will apply to the past. This could be extended to fossil taxa. It has been suggested that sabertoothed felids could have provided moderate (Marean and Ehrhardt, 1995) to significant (Blumenschine, 1987; Marean, 1989) amounts of

scavengeable flesh on large herbivore carcasses for a scavenging hominin. My data lend support to the idea that sabertoothed felids, some of which are reconstructed as solitary predators of either size 3 or size 4 herbivores in closed habitats (Marean, 1989; Lewis, 1997), could have provided beneficial scavenging opportunities for early hominins.

Flesh Availability: Inter- and Intra-Element Flesh Distribution and Potential Application to the Timing of Hominin Access to Carcasses

Regardless of predator taxon and prey size, if there was a differential distribution of flesh between limb bones, there was nearly always relatively more flesh on the intermediate limb bones (radio-ulna, tibia) than the upper limb bones (humerus, femur). This is in accordance with findings by both Blumenschine (1986a) and Domínguez-Rodrigo (1999), who note that carnivores tend to consumer upper limb bone flesh before intermediate limb bone flesh, and strengthens the argument that this is an ecological "rule". However, about 60% of upper-intermediate limb pairs, both femur-tibia and humerus-radio-ulna pairs, exhibited no differential flesh distribution: the flesh availability on both bones was about the same (they either exhibited bulk flesh or flesh scraps). Therefore, in the majority of cases, upper limb bones do not have relatively more flesh present on them than intermediate limb bones from the same carcass.

About half (52%) of limbs retained more flesh on proximal and distal portions than midshaft portions. Most of the limb bones which exhibited this pattern were upper limb bones (femur or humerus); all of the limb bones which had more flesh on the shafts or distal limb sections were intermediate limb bones (tibia or radio-ulna).

These unexpected results may be in part due to the presence of flesh on the distal portions of intermediate limb bones (tibia and radio-ulna), which often have skin left on

them from the distal shaft down through the phalanges. While about half (52%) of limbs retained more flesh on proximal and distal portions than midshaft portions, most of the limb bones which exhibited this pattern were upper limb bones (femur or humerus); all of the limb bones which had more flesh on the shafts or distal limb sections were intermediate limb bones (tibia or radio-ulna). This has consequences for models of hominin scavenging from carnivore kills. Domínguez-Rodrigo (1997) argues that the differential distribution of cut marks between and within limb elements may indicate the timing of hominin access to carcasses: a predominance of cut marks on midshafts of upper limb bones may indicate early hominin access to meat-bearing bones from which they removed fairly large amounts of flesh. This is based on the assumption of differential flesh distribution remaining on lion kills of size 3 and 4 prey, which I have shown at least in one ecosystem is not the predominant pattern. Therefore, this model may not be applicable to all ecological scenarios, and it may be best only applied to upper limb bones. Additionally, my measures of "bulk" and "scrap" flesh are very general, and are meant to be used more relatively than absolutely. It is possible, and even likely, that bones I coded as having equivalent amounts of flesh remaining on them in fact have substantially different absolute amounts of flesh available for a potential scavenger.

Quantifying Flesh Availability and Scavenging Opportunities

There are currently two main models of hominin scavenging from carnivore kills: confrontational and passive scavenging. Each of these models has, as underlying assumptions, a higher or lower relative amount of scavengeable material, respectively. Bunn's (2001) confrontational or power scavenging model assumes hominins would have access to a substantial amount of meat as well as within-bone nutrients. Modern Hadza

power scavengers can yield "essentially fresh, whole carcasses" (Bunn, 2001:201). Binford's (1981) passive scavenging model assumes hominins would have access to only occasional 'scraps' of flesh, and within-bone nutrients (marrow, brain), making this foraging mode hardly worth a hominin's time and effort. However, Blumenschine and Cavallo (1992) maintain that even within-bone nutrients are substantial enough to make passive scavenging worthwhile. It is useful here to take a closer look at the energetics of scavenging returns, in light of Domínguez-Rodrigo's (1999) definitions of bulk flesh and flesh scraps left by lions on carcasses.

Domínguez-Rodrigo (1999) uses the term 'fleshed' bone to refer to those bones that retain at least 10% of their original flesh mass. But how much flesh might this actually be? Using Blumenschine and Caro's (1986) and Outram and Rowly-Conwy's (1998) data, an average adult male wildebeest hindlimb flesh yield is approximately 8.68 kilograms, and that average zebra hindlimb flesh yield is approximately 22.5 kilograms (Table 2.26). In this example, a 'defleshed' wildebeest or zebra hindlimb could still yield up to almost 1 and over 2 kilograms of flesh, respectively, a substantial amount of meat that could possibly feed multiple hominin individuals. Additionally, this is only from one hindlimb. We can estimate the flesh yield of each carcass part of an adult wildebeest and zebra using the data from Blumenschine and Caro (1986) and Outram and Rowly-Conwy (1998) (see Table 2.27). Therefore, scavenging flesh even from 'defleshed' wildebeest or zebra carcasses could yield a maximum of 5.5 and 15.2 kilograms of meat, respectively, *even when within-bone nutrients are not considered*, which can be substantial (Blumenschine and Madrigal, 1993). Using an estimate of 4 calories per gram of flesh, this would yield 2,200 calories from a wildebeest carcass and 6,080 calories from a zebra

carcass, enough for the entire daily caloric requirements of at least one *Homo erectus/ ergaster* male, estimated to require approximately 2,090 - 2,290 calories per day (Leonard and Robertson, 1997; Aiello and Wells, 2002).

Table 2.27. Estimates of maximum flesh yield from a fully fleshed and defleshed adult male wildebeest, and from three domestic horses. Data from Blumenschine and Caro (1986:285, Appendix 2), and Outram and Rowley-Conwy (1998:840, Table 1). All weights are in kilograms.

Carcass Unit	Average Wildebeest Unit Flesh Weight	10% of Average Wildebeest Flesh Weight	Mean Horse Edible Meat Weight	10% of Mean Horse Edible Meat Weight
Forelimb[1]	6.74	0.7	14.00	1.4
Hindlimb[2]	8.68	0.9	22.50	2.3
Pelvis[3]	6.13	0.6	23.75	2.4
Lumbar[4]	4.10	0.4	10.00	1.0
Ribcage[5]	18.73	1.9	44.75	4.5
Neck[6]	7.38	0.7	23.75	2.4
Head[7]	2.13	0.2	11.25	1.2
Total	53.89	5.4	150.00	15.2

[1]Includes flesh from the scapula, humerus, radio-ulna, carpals, and metacarpal
[2]Includes flesh from the femur, tibia, tarsals, and metatarsal
[3]Includes flesh from the innominate and sacrum
[4]Includes flesh from the lumbar vertebrae
[5]Includes flesh from the sternum, ribs, and thoracic vertebrae
[6]Includes flesh from all cervical vertebrae
[7]Includes flesh from the skull, mandible, and tongue, as well as brain

As previously noted, Domínguez-Rodrigo (1999) uses the term ‘scrap’ to refer to a packet of flesh over 150 grams, slightly larger than the size of a “quarter pounder” hamburger. This may seem like a small amount of meat, but again, multiplying 150 grams by 4 calories per gram, this ‘scrap’ of meat yields 600 calories. Therefore, only four scraps of flesh on an entire carcass would theoretically exceed the total daily estimated caloric requirements of a *Homo erectus/ergaster* male. While these scenarios do not taking into account the nutritional consequences of a very high protein diet (Speth, 1989), they are meant to emphasize the significant amount of caloric resources available in even small amounts of scavengeable meat from mammal carcasses.

Flesh Availability: Conclusions

This study of flesh availability on carcasses and carcass parts eaten by free-ranging and captive carnivores demonstrates a significant amount of variability based mainly on carnivore taxon and prey size. On size 3 and 4 prey, lion, leopard, cheetah, and jackal consumption all leave considerable amount of flesh present on all skeletal elements. Specifically, 95% of the time, there is some flesh remaining when free-ranging lions consumed size 3 and 4 carcasses, and 56% of the time, this is in the form of bulk flesh, or large muscle masses. The other larger carnivores always leave some flesh remaining on these larger carcasses or carcass parts; in order of decreasing bulk versus scrap flesh availability, they are jackal (100%), cheetah (36%), and leopard (33%). In contrast, free-ranging spotted hyaenas fully deflesh bones of size 3 and 4 carcasses 72% of the time, and never leave any bulk flesh, only flesh scraps. Even size 2 carcasses consumed by felids offer some scavengeable resources for early hominins: 44% of the bones of size 1 and 2 carcasses consumed by lions had at least flesh scraps remaining, as did 67% of those consumed by leopards, and 100% of those consumed by cheetahs and jackals. Carnivore number, age, habitat, and season of kill may all influence flesh availability, especially in lion kills as documented here.

These results agree with previous studies that argue that scavenging from spotted hyaenas would not be profitable for early hominins (e.g. Blumenschine, 1986a); however, this study documents a much higher amount of scavengeable resources in the form of meat and marrow from size 3 and 4 lions kills than previous studies (Blumenschine, 1986a; Domínguez-Rodrigo, 1999). This may be simply a result of sampling a different ecosystem, with a lower level of competition than those previously sampled (the

Serengeti, Maasai Mara, and Tsavo). This, combined with a simple model calculating the actual amount in kilograms of scavengeable meat resources (Table 2.26), supports the hypotheses that scavenging from abandoned size 3 and 4 felid kills would have been a high-yield foraging strategy for early hominins even without considering within-bone nutrient yield (e.g. Blumenschine, 1986a).

This study sheds some doubt on the current ability of zooarchaeologists to recognize the timing of access of hominins to carcasses based solely on the inter- and intra-limb patterning of cut marks (e.g. Domínguez-Rodrigo, 1997; Nilssen, 2000). In butchery experiments simluating scavenging from lion kills, Domínguez-Rodrigo (1997) found that cut marks were least frequent on upper (versus intermediate or lower) limb bones and on the midshafts of limb bones, as these limb elements and portions were the most flesh-depleted after lion consumption (Domínguez-Rodrigo, 1999). He then hypothesizes that the presence of cut marks on upper or "meaty" limb elements, and especially midshafts of these meaty limb elements, is a zooarchaeological signal of hominin early access to carcasses. This builds on earlier work which tested similar hypotheses in the Oldowan archaeofaunal record (e.g. Bunn and Kroll, 1986). However, my results of flesh distribution on lion kills were different than those found by Domínguez-Rodrigo (1999). I found that lions hardly ever completely defleshed limb elements, and although they did normally preferentially deflesh upper versus intermediate or lower limb elements, this preference was weak. Therefore, the assumption upon which these models rest - that cut mark placement alone is indicative of the timing of hominin access to carcasses and can distinguish between hunting and scavenging - is tenuous. Here, identifying felid-specific bone damage and tooth marks are potentially informative.

Chapter Three
Carnivore Gross Bone Damage and Destruction

Introduction and Methods

Gross bone damage and destruction data were collected on the samples detailed in Chapter 2 with the following three goals:

1. Description and quantification of the specific gross bone damage levels inflicted on each skeletal element and portion of different sized ungulate prey by different carnivores. Presentation of carnivore taxon-specific patterns of skeletal element and portion gross bone damage and destruction.
2. Substantiation of the scaling relationship in gross bone damage and destruction with increasing carcass size and bone eating capabilities (Pobiner and Blumenschine, 2002, 2003), to facilitate modeling of hypothetical gross bone damage and destruction capabilities of extinct carnivores.
3. Exploring the relationship between flesh availability and gross bone damage patterns, in order to construct hypotheses regarding scavenging opportunities for early hominins based on damage and destruction levels seen in archaeofaunas. (This will be considered in Chapter 4, along with the relationship of these patterns to tooth mark data).

In this study, carnivore *gross bone damage* refers to any degree of gnawing, fragmentation, and fracture (excluding tooth marks, which will be defined and described in Chapter 4). Carnivore *fragmentation* of bone is defined as the creation of more than one bone from the original skeletal element through breakage as the result of the feeding process. Bone fragmentation can result in identifiable and/or unidentifiable skeletal

elements and portions. Carnivores generally fragment bones using static rather than dynamic loading (cf. Johnson, 1985; Lyman, 1994). Carnivore *bone destruction or deletion* results in the complete and total absence of a particular skeletal element or portion following carnivore feeding.

Gross bone damage and destruction data were collected after bone samples were cleaned, following details in Chapter 2. The samples for which gross bone damage and destruction data were recorded are listed in Table 3.1. Gross bone damage and destruction data were collected using the coding convention in Table 3.2. The specified gross bone damage and destruction levels were based on methods developed in Pobiner and Blumenschine (2003), as well as descriptions of gross bone damage and destruction mainly in Haynes (1981a, 1981b, 1983) and Brain (1981). In this dissertation, the gross bone damage categories are defined and expanded to a more specific, detailed, and *quantified* level for each bone and bone portion. These definitions were largely generated and modified during the collection of data on gross bone damage and destruction.

Table 3.1. Samples from SGR and NAO for which gross bone damage and destruction data were recorded. Hyaena is spotted hyaena.

Predator Taxon	Prey Size	Number of Samples	Relevant Samples
Lion	3 & 4	20	SWT001, SWT006, SWT007, SWT014, SWT021, SWT024, SWT033, NAO2, NAO6, NAO11, NAO12, NAO13, NAO16, NAO17, NAO19, NAO23, NAO24, NAO26, NAO28, NAO32
Hyaena	3 & 4	4	SWT011, SWT015, SWT0017, SWT036
Leopard	4	4	NAO3, NAO8, NAO18, NAO30
Cheetah	4	10	NAO1, NAO7, NAO9, NAO10, NAO15, NAO20, NAO22, NAO25, NAO29, NAO34
Jackal	4	4	NAO4, NAO14, NAO21, NAO33
Lion	1 & 2	9	SWT003, SWT004, SWT008, SWT009, SWT013, SWT0016, SWT027, SWT034, SWT038
Hyaena	1 & 2	3	SWT018, SWT019, SWT020
Leopard	1 & 2	3	SWT012, SWT028, SWT031
Cheetah	1	1	SWT010
Jackal	1	1	SWT022

Table 3.2. Coding convention for gross bone damage and destruction levels on specific bone portions. Only parts present at and collected from the kill site were coded. For bones with paired (right and left) or multiple (e.g. vertebrae, ribs) elements in a carcass, the gross bone damage level of each individual bone was recorded. Damage levels were recorded from 0-4, where damage level 0 = no visible damage, and damage level 1 = tooth marks only. Damage levels 2, 3, and 4 are specified below. These bone damage levels were adapted but expanded from those in Pobiner and Blumenschine (2003), which did not include a "tooth marks only" damage level. Abbreviations: PX = proximal, SH = shaft, DS = distal. Specific portion definitions are in footnotes.

	Damage Level 2	Damage Level 3	Damage Level 4
HINDQUARTER			
Greater Trochanter	superior margin gnawed	1/2 destroyed	destroyed to base
Femur Head	some cancellous bone exposed	partially destroyed	completely destroyed
Proximal Femur[1]	marginal gnawing	partially destroyed	completely destroyed to PX SH
Femur Shaft	gnawing on PX and DS ends of intact SH, missing epiphyses	SH partially fragmented	SH heavily fragmented/ destroyed
Distal Femur – Patellar Groove	marginally gnawed	partially destroyed	destroyed to DS SH
Distal Femur – Condyles	marginally gnawed	partially destroyed	destroyed to DS SH
Patella	marginally gnawed	partially destroyed	only fragments remain
Proximal Tibia	tibia crest gnawed	articular surfaces also gnawed	destroyed to PX SH
Tibia Shaft	gnawing on PX and DS ends of intact SH, missing epiphyses	SH partially fragmented	SH heavily fragmented/ destroyed
Distal Tibia	cancellous bone exposed on DS articular areas	destruction of some part of DS epiphysis	destroyed to DS SH
Iliac Blade	Crest gnawed	1/2 destroyed	destroyed to acetabulum
Posterior Innominate[2]	gnawing on caudal margin of pubis and/or ischial tuberosity	1/2 destroyed	completely destroyed
Pubic Region[3]	gnawing on cranial margin of pubic symphysis	destruction of some part of region	completely destroyed
Ischial/Pubic Base[4]	gnawing on margin of posterior projection of ischium	posterior projections of ischium 1/2 destroyed	destroyed to superior ischium
Acetabulum	margins gnawed	partially destroyed	only fragments remain
Sacrum	marginally gnawed	partially destroyed	only fragments remain (e.g. isolated vertebral bodies)
Lumbar Centra	light gnawing on margins of body	more significant gnawing, cancellous bone exposed	only fragments remain
Lumbar Processes[5]	neural spine and/or transverse processes up to 1/2 destroyed	neural spine and/or transverse processes 1/2 to almost completely destroyed	neural spine and/or transverse processes completely destroyed
FOREQUARTER			
Scapular Blade[6]	superior margin gnawed (and cartilage extension destroyed)	up to 1/2 of blade destroyed	blade including spine destroyed; only neck and glenoid remain
Scapular Glenoid[7]	marginally gnawed acromium	gnawing along margins of glenoid fossa	only fragments remaining
Proximal Humerus	gnawing on head +/or tubercles	at least one tubercle destroyed	head also destroyed
Humerus Shaft[8]	gnawing on PX and DS ends of intact SH, missing epiphyses	SH partially fragmented	SH heavily fragmented/destroyed
Distal Humerus	marginal gnawing on epiphysis	partial epiphyseal destruction	epiphysis completely destroyed
Olecranon Process (Ulna)	marginal gnawing with some cancellous bone exposed; articular area still intact	partial destruction	olecranon process completely destroyed
Proximal Radio-Ulna	marginal gnawing on/around articular surface	partial destruction	epiphysis completely destroyed
Radio-Ulna Shaft	gnawing on PX and DS ends of intact SH, missing epiphyses	SH partially fragmented	SH heavily fragmented/destroyed
Distal Radio-Ulna	marginal gnawing on/around articular surface	partial destruction	epiphysis completely destroyed
Ribs	less than 1/4 destroyed	up to only 1/4-1/3 remains (usually PX)	fragments only

Sternum	marginal gnawing on PX or DS end	heavy gnawing on all regions	fragments only
Thoracic Centra	marginal gnawing on inferior region of body	body significantly gnawed in various places	fragments only
Thoracic Neural Process[5]	modal spine with marginal gnawing on DS end	modal spine up to 2/3 destroyed	modal spine more than 2/3 destroyed
Cervical Centra	marginal gnawing on any part of centra	significant gnawing on any part of centra	fragments only
Cervical Processes	marginal gnawing on any projections/processes	significant gnawing on any projections/processes	fragments only
PODIALS			
Calcaneum	marginal gnawing on calcaneal tuber	calcaneal tuber partially destroyed	fragments only
Astragalus	marginal gnawing (small amount of cancellous bone exposed)	at least one articular surface destroyed/significant cancellous bone exposed	fragments only
Other Tarsals/Carpals[9]	marginal gnawing	partial destruction	fragments only
Proximal Metapodial	marginal gnawing	partial destruction	fragments only
Metapodial Shaft	gnawing on PX and DS ends of intact SH, missing epiphyses	partial destruction	fragments only
Distal Metapodial	marginal gnawing (small amount of cancellous bone exposed, esp. on DS condyles)	partially destroyed (e.g. one condyle), some articular area still present	completely destroyed up to near-epiphyses
Phalanges	marginal gnawing, esp. DS end	destruction of DS end	fragments only
HEAD			
Atlas/Axis Bodies	marginal gnawing (small amount of cancellous bone exposed)	partially destroyed	fragments only
Atlas/Axis Processes	marginal gnawing (small amount of cancellous bone exposed)	partially destroyed	fragments only
Face[10]	nasals less than 1/2 destroyed	nasals destroyed	orbits heavily gnawed or destroyed; nasals destroyed
Maxilla/Premaxilla	labial margin of premaxillae gnawed	premaxillae partially or completely destroyed, but maxilla still attached to cranium	isolated palate
Cranial Base[11]	small amount of spongy bone exposed +/or destruction of thinner bones (palatine, auditory bulla, styloid process)	occipital region partially destroyed	missing from skull
Upper Cranium[12]	small amount of spongy bone exposed +/or minimal destruction	isolated frontals	missing from skull
Mandible Gonial Angle	marginal gnawing only	marrow cavity accessed	missing from mandible
Mandible Ascending Ramus	less than 1/4 destroyed	1/4 to 3/4 destroyed	missing from mandible
Mandible Horizontal Ramus	gnawing on mandibular symphysis only (missing incisors/canines)	mandibular symphysis destroyed up to premolars and/or posterior margin gnawed	missing from mandible

[1] defined as all epiphyseal areas excluding greater trochanter and head
[2] defined as region posterior of iliac blade beginning at branch, including ischial tuberosity, to iliopubic ramus
[3] defined as pubis and pubic symphysis (t-shaped area)
[4] defined as all regions posterior of acetabulum and obturator foramen
[5] modal refers to the most common gnawing state
[6] includes the scapular spine
[7] includes the neck between the blade and articular surface, as well as the coracoid process
[8] on zebras, includes third trochanter
[9] includes fibula
[10] nasals through orbits (upper part of snout)
[11] occipital region
[12] from midline of eyes upwards

Gross bone damage levels were only recorded on skeletal elements present.

Elements which are presumed to have been present initially, but were destroyed during

consumption, were not recorded. This may lead to an impression of lower damage levels than are actually present. Often, with very small or very young animals consumed by a group of lions, only a few identifiable bone fragments, and many non-identifiable bone fragments, remained at the consumption site. For example, if seven lumbar vertebrae were initially present in the whole carcass, and only a single one with damage level 2 remained, damage level 2 was recorded as the data point for that element in that carcass, as opposed to one vertebrae exhibiting damage level 2 and six vertebrae exhibiting damage level 4 for an average damage level of 3.7. I chose this data collection method in order to maximize applicability of my results to the archaeological record. Only those elements present after carnivore consumption even have the potential for fossilization; therefore, I characterize only those elements present after consumption, not those elements initially present but then destroyed. While I believe that this method is the most accurate for characterizing gross bone damage patterns, it can underestimate the maximum possible gross bone damage to a bone portion.

I use paired bones (e.g. left and right femora) from a single carcass as two separate data points. It might be expected that carnivores feeding on a carcass would consume the same amount of flesh from, and therefore cause similar levels of gross bone damage to, these bone pairs. However, I found this was not the case. For example, for the 14 lion-damaged size 3 and 4 carcasses from SGR for which there are data for both the left and right portions of the femur, I find no instances where the gross bone damage levels in any of the right and left femur portions were the same. The same reasoning applies to ‘near-bone’ pairs or groups from single carcass parts (e.g. the femur and tibia, or scapula, humerus, and radio-ulna from the same carcass). In the same carcass sample,

out of four instances, not once are the gross bone damage and destruction levels of distal humeri the same as the olecranon process of the ulna.

It is most often the "usual" (modal and/or median) gross bone damage levels, and sometimes the maximum or minimum level, that a predator can inflict on a bone of a certain sized prey animal which are relevant to this study. Sometimes the modal gross bone damage is most appropriate to use, especially when the range of gross bone damage inflicted across carcasses is small. Other times, especially with a large range of gross bone damage across carcasses, the median gross bone damage level is more suitable. For these samples, there often is no modal gross bone damage, since each gross bone damage value occurs at a similar frequency. Additionally, in an archaeological collection, it is often difficult or impossible to confidently identify pairs or groups of bones from a single individual. Therefore, when trying to characterize gross bone damage and destruction patterns across individuals of a particular prey size, I argue that it is advantageous to use all available bones as individual data points. Both median and modal values for all bones and portions were determined using each individual bone as a data point (Table 3.3). These data are depicted in the figures here in radial diagrams made using the radar graph feature in Microsoft Excel.

Table 3.3. Minimum, median, modal, and maximum gross bone damage and destruction data for each bone portion from SGR. Data are presented on a predator taxon/carcass size basis. Minimum damage is the first number presented, median damage is the second number presented, modal damage is the third number presented, maximum damage is the fourth number presented, and the total number of bone or bone portions from which the data derives (not the number of carcasses) is the fifth number presented: minimum/ median/ mode/ maximum/ number of bones in the sample. Modal damage is not presented for cheetah and jackal, as there was only one sample for each; in these species, the third number is the maximum damage, and the fourth number is the number of bones or bone portions. When there is no mode (most common damage state), an "X" is entered in that place. Where no data was available, that cell is blank. This includes elements that were likely transported away from the kill site. On occasion, destruction level is inferred

when bone portions were not present; e.g. if a proximal femur with gnawing damage is present, but the femur shaft and distal femur of the same bone are absent, those portion are inferred to have been destroyed, and the data is presented in parentheses. Boldface numbers correspond to damage levels represented in Figures 3:15-3:18.

Predator Prey Size	Lion Size 3 & 4	Hyaena Size 3 & 4	Lion Size 1 & 2	Hyaena Size 1 & 2	Leopard Size 1 & 2	Cheetah Size 1	Jackal Size 1
HINDQUARTER							
Greater Trochanter	0/1.50/**0**/4/10	2/**3.00**/X/4/2	4/4.00/**4**/4/5		0/**1.67**/X/4/3	0/0/0/2	0/0/0/2
Femur Head	0/1.30/**1**/4/10	0/**0.50**/X/1/2	4/4.00/**4**/4/5		1/2.00/**1**/4/3	0/0/0/2	0/0/0/2
Proximal Femur	0/1.88/**1**/4/8	2/2.00/**2**/2/2	2/3.50/**4**/4/6		0/**1.67**/X/4/3	0/0/0/2	0/0.5/1/2
Femur Shaft	0/0.75/**1**/1/8	0/**0.50**/X/1/2	0/**2.00**/X/4/8		0/0.67/**1**/1/3	0/0/0/2	0/0/0/2
Distal Femur – Patellar Groove	1/2.44/**2**/4/9	2/**3.00**/X/4/2	4/4.00/**4**/4/5		1/1.33/**1**/2/3	0/0/0/2	0/0/0/2
Distal Femur – Condyles	0/**1.20**/X/2/10	0/**2.00**/X/4/2	4/4.00/**4**/4/5		0/1.33/**1**/2/3	0/1.00/2/2	0/0/0/2
Patella	2/**3.00**/X/4/2		4/4.00/**4**/4/1				0/0/0/2
Proximal Tibia	0/1.60/**2**/3/10	2/2.00/**2**/2/1	2/3.57/**4**/4/7		0/1.33/**2**/2/3		0/0/0/2
Tibia Shaft	0/**0.5**/X/1/6	(4/**4.00**/X/4/1)	0/1.43/**1**/3/7		0/0.33/**0**/1/3		0/0/0/2
Distal Tibia	0/0/**0**/0/5	(4/**4.00**/X/4/1)	0/1.00/**0**/4/5		0/0/**0**/0/3		0/0/0/2
Iliac Blade	2/2.29/**2**/3/7	2/2.00/**2**/2/2	2/2.83/**3**/4/6		0/0/**0**/0/2	1/1.50/2/2	2/2.00/2/2
Posterior Innominate	0/1.14/**1**/3/7	2/2.00/**2**/2/2	1/**2.40**/X/4/5		0/0/**0**/0/2	0/0/0/2	2/2.00/2/2
Pubic Region	0/1.00/**0**/3/7	0/0/**0**/0/2	1/2.80/**4**/4/5		0/**1.00**/X/2/2	0/0/0/2	0/0/0/2
Ischial/Pubic Base	1/2.22/**2**/3/9	0/**0.50**/X/1/2	2/3.60/**4**/4/5		2/2.00/**2**/2/2	0/0/0/2	0/0/0/2
Acetabulum	0/0.63/**1**/1/8	0/**0.50**/X/1/2	1/1.50/**1**/3/6		0/0/**0**/0/2	0/0/0/2	0/0/0/2
Sacrum	2/2.33/**2**/3/6	3/3.00/**3**/3/2			2/2.00/**2**/2/2	2/2.00/2/1	0/0/0/2
Lumbar Centra	0/1.36/**2**/2/32	0/1.60/**3**/3/10	0/0.25/**0**/1/4		0/0.25/**0**/1/4	0/0/0/0/6	0/0/0/0/7
Lumbar Processes	0/1.90/**2**/3/32	0/1.65/**0**/3/10	2/2.50/**2**/3/4		0/0.25/**0**/1/4	2/2.17/2/3/5	0/0.14/0/2/7
FOREQUARTER							
Scapular Blade	2/2.20/**2**/3/5	2/2.33/**2**/3/3	2/3.14/**3**/4/7	2/3.00/X/4/3		0/0/0/0/2	
Scapular Glenoid	0/0.71/**0**/3/7	1/1.67/**2**/2/3	1/**2.88**/X/4/8	4/4.00/4/4/3		1/1.00/1/1/2	
Proximal Humerus	2/2.50/**2**/4/4	2/3.33/**4**/4/3	2/3.57/**4**/4/7	4/4.00/4/4/3		0/0/0/2	
Humerus Shaft	0/1.25/**1**/4/4	1/2.33/**3**/3/3	0/2.00/**2**/4/8	4/4.00/4/4/3		0/0/0/2	
Distal Humerus	0/0.75/**0**/3/4	0/**1.67**/X/4/3	1/2.00/**2**/3/7	4/4.00/4/4/3		0/0.5/1/2	
Olecranon Process (Ulna)	0/2.20/**0**/4/5	4/4.00/**4**/4/2	2/**3.00**/X/4/5	4/4.00/4/4/3			
Proximal Radio-Ulna	0/0.60/**0**/2/5	4/4.00/**4**/4/2	1/**1.67**/X/4/6	4/4.00/4/4/3			
Radio-Ulna Shaft	0/0.86/**0**/3/5	3/3.00/**3**/3/2	0/**1.60**/X/3/5	4/4.00/4/4/3			
Distal Radio-Ulna	0/0.80/**0**/4/5	4/4.00/**4**/4/2	0/2.60/**4**/4/6	4/4.00/4/4/3			
Ribs	2/2.14/**2**/4/189	2/2.07/**2**/4/49	2/2.75/**3**/3/38	4/4.00/4/4/3		0/0.67/0/2/21	0/1.31/2/3/26
Thoracic Centra	0/1.37/**2**/3/88	0/2.29/**2**/4/13	0/0.20/**0**/1/5	4/4.00/4/4/3		0/0/0/0/12	0/0/0/0/12
Thoracic Neural Process	0/2.02/**2**/4/88	0/**1.29**/X/4/13	2/2.20/**2**/3/5	4/4.00/4/4/3		0/0.46/0/2/13	0/0/0/0/12
Cervical Centra	0/0.87/**0**/4/23	0/1.33/**0**/4/12	2/2.00/**2**/2/4	4/4.00/4/4/3		0/0/0/0/7	0/0/0/0/5
Cervical Processes	0/1.32/**0**/4/23	0/1.83/**2**/4/12	0/0/**0**/0/4	4/4.00/4/4/3		0/0.49/0/2/7	0/0/0/0/5
PODIALS							
Calcaneum	0/0.75/**0**/2/8	0/0/**0**/0/1	1/1.67/**2**/2/3		3/3.00/**3**/3/1	0/0/0/0/2	
Astragalus	0/0.17/**0**/1/6	0/0/**0**/0/1	0/2.00/**2**/4/4		1/**1.50**/X/2/2	0/0/0/0/2	
Other Tarsals	0/0/0/**0**/15	0/0/**0**/0/2	0/0/**0**/0/3		0/0/**0**/0/1	0/0/0/0/3	
Proximal Metatarsal	0/0.17/**0**/1/6		1/1.33/**1**/2/3		0/0/**0**/0/3	0/0/0/0/2	
Metatarsal Shaft	0/0.33/**0**/1/6		0/0.25/**0**/1/4		0/0/**0**/0/3	0/0/0/0/2	
Distal Metatarsal	0/0.17/**0**/1/6		1/3.25/**4**/4/4		0/0/**0**/0/3	0/0/0/0/2	
Posterior Phalanges	0/0.17/**0**/1/6		no data		0/0/**0**/0/2	0/0/0/0/6	
Carpals	0/0/**0**/0/41		1/**1.50**/X/2/2	4/4.00/4/4/3		0/0/0/0/16	
Proximal Metacarpal	0/0.20/**0**/1/5		1/2.25/**1**/4/4	4/4.00/4/4/3		0/0/0/0/2	
Metacarpal Shaft	0/0/**0**/0/5		0/**1.00**/X/3/5	4/4.00/4/4/3		0/0/0/0/2	
Distal Metacarpal	0/0.20/**0**/1/5		2/2.33/**2**/3/3	4/4.00/4/4/3		0/0/0/0/2	
Anterior Phalanges	0/0/**0**/0/3			4/4.00/4/4/3		0/0/0/06	
HEAD							
Atlas/Axis Bodies	0/0.5/**0**/2/10	0/0/**0**/0/4	0/0/**0**/0/2	4/4.00/4/3		0/0/0/0/2	0/0/0/0/2
Atlas/Axis Processes	1/1.88/**2**/2/10	0/**1.33**/X/2/4	2/2.00/**2**/2/2	4/4.00/4/3		1/1/1/1/2	0/0/0/0/2
Face	0/**1.00**/X/2/4	0/**1.00**/X/2/3	4/4.00/**4**/4/3	4/4.00/4/3		3/3.00/3/1	
Maxilla/Premaxilla	0/0.50/**0**/2/4	0/0.33/**0**/1/3	3/3.83/**4**/4/6	4/4.00/4/3		3/3.00/3/1	
Cranial Base	0/0.50/**2**/2/4	0/**1.00**/X/2/3	4/4.00/**4**/4/3	4/4.00/4/3		2/2.00/2/1	
Upper Cranium	0/0/**0**/0/4	0/0.67/**0**/2/3	4/4.00/**4**/4/3	4/4.00/4/		2/2.00/2/1	
Mandible Gonial Angle	0/0.40/**0**/2/5	0/2.00/**3**/3/4	0/2.88/**3**/4/8	4/4.00/4/3		0/0/0/2	
Mandible Ascending Ramus	0/1.40/**2**/2/5	2/2.75/**2**/4/3	2/3.57/**4**/4/7	4/4.00/4/3		0/0/0/2	
Mandible Horizontal Ramus	0/0.33/**0**/2/6	0/0.67/**0**/2/3	0/2.00/**3**/3/7	4/4.00/4/3		0/0/0/2	

In some instances, leopard-modified goat or sheep carcass parts from SGR were previously or subsequently butchered during the baiting procedure or removing the bait from the tree. The bones from these samples sometimes have cut marks on them, which were recorded, but excluded from analysis. On occasion, I could not confidently attribute some of the gross bone damage observed either to leopards or butchery. This was noted, and the damage was not included in this analysis. This applies specifically to SWT 012 and 031.

SWT037, a hare, was excluded from the lion-size 1 gross bone damage and destruction analysis. Its unusually small prey size compared with the rest of my sample (size 1a, Bunn, 1982) may have skewed the gross bone damage and destruction analysis results, which are from analysis of size 1b prey. My aim is to diagnose gross bone damage and destruction patterns as they relate to flesh availability on animals that hominids may have scavenged. I would conclude, then, that hominids would not have been able to scavenge animals hare-sized or smaller from lion-like carnivores, as they would have been completely destroyed during carnivore consumption.

Some of the NAO samples were completely unusable for gross bone damage/ fragmentation analyses, as they were fragmented during preparation for feeding to the carnivores. This preparation sometimes caused bone portions not normally or naturally accessible (e.g. midshafts of cow long bones) to be exposed and vulnerable to gross bone damage by the NAO carnivores. These samples are NAO 2, 23, and 25. Other NAO samples were only partially unusable for gross bone damage/ fragmentation analyses. For instance, NAO 1 was a distal femur and patella given to two jackals. This sample cannot be used to evaluate gross bone damage on the proximal femur, since it was not present to

begin with, but it can be used to evaluate gross bone damage to the distal femur. These samples are NAO 1, 3, 4, 5, 6, 7, 8, 9, 11, 14, 16, 17, 18, 19, 20, 21, 22, 24, 26, 29, 30, 33, and 34. Data on presence/absence of tooth marks could also be collected on some of these samples. NAO 10, 12, 13, 15, 28, 31, and 32 were completely usable for the gross bone damage and destruction analyses. NAO 27, a whole chicken, fed to and consumed completely by a serval, was completely excluded from this analysis. In a few instances in the NAO samples, destruction of the patella was inferred by destruction of both the distal femur and proximal tibia. Two additional concerns with these samples from captive animals are potential "boredom" destruction of bones for non-nutritive purposes, or "deprivation" destruction caused by underfeeding.

Results

Size 3/4 Carcasses

1. Lion Bone Damage (SGR and NAO)

A. The SGR Sample

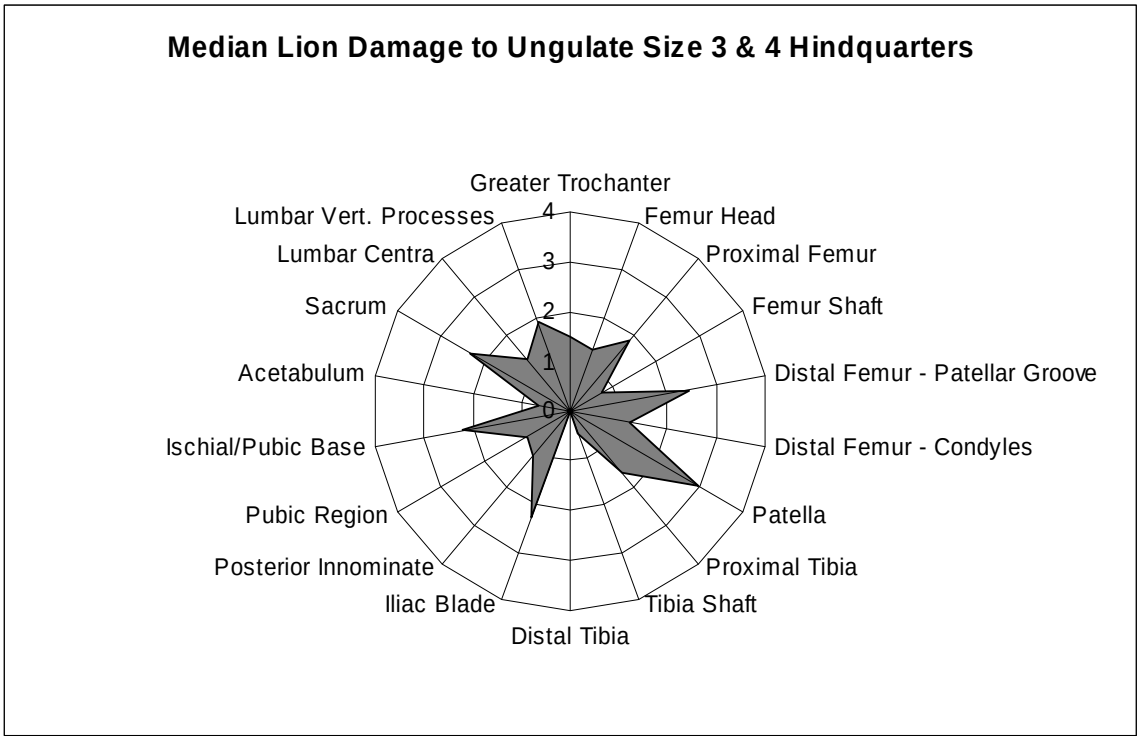
Hindquarters

Patterning in gross bone damage to specific bone portions is evident from Figures 3.1-3.3. Lions did not fragment size 3 and 4 adult femora; on these bones, gnawing damage to the epiphyseal portions (especially distal, but also proximal) is usually more intense than damage on the shafts, which are normally tooth-marked. The patella is normally heavily gnawed. The proximal tibia is normally minimally gnawed or tooth-marked, the tibia shaft is sometimes tooth-marked, and the distal tibia is undamaged. Of the different portions of the innominate, the iliac blade is usually the most intensely

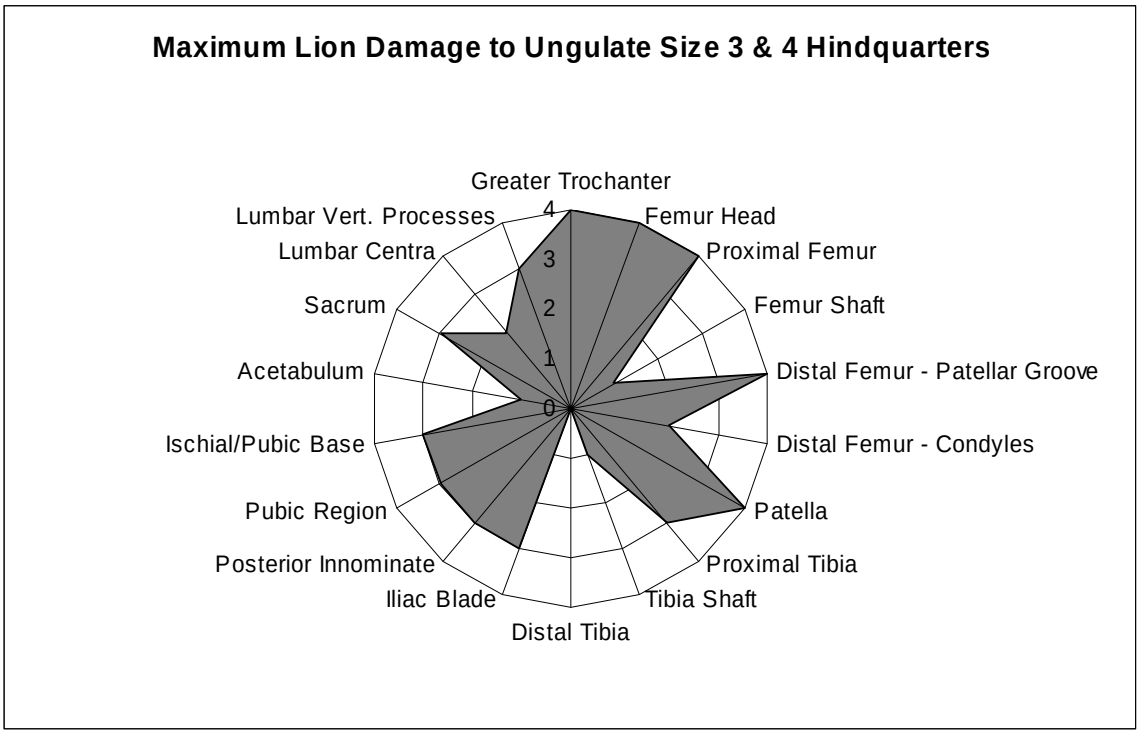
damaged, followed closely by the ischial/pubic base. The sacrum is also normally heavily gnawed. Conversely, the femur and tibia shafts normally only display tooth marking present, as does the acetabulum. Lumbar vertebral processes are normally marginally gnawed; centra are normally tooth-marked to marginally gnawed but usually less damaged than the processes. Lions are able to inflict more damage on juvenile than adult size 3 hindlimbs (Figure 3.3). Here, this is specifically evident on the femur head, proximal femur, distal femur condyles, and iliac blade of juvenile versus adult animals.

Figure 3.1. Damage and destruction diagrams for lion-damaged size 3 and 4 hindquarters from SGR. These diagrams illustrate the median (a, top) and maximum (b, bottom) damage levels inflicted by lions on these bone portions. Damage level definitions are listed in Table 3.2. Seven carcasses are included in the analysis. Not all carcasses provided data for every bone portion; the number of bones or bone portions from which the data are derived is presented in Table 3.1. Data are from Table 3.3.

(a)



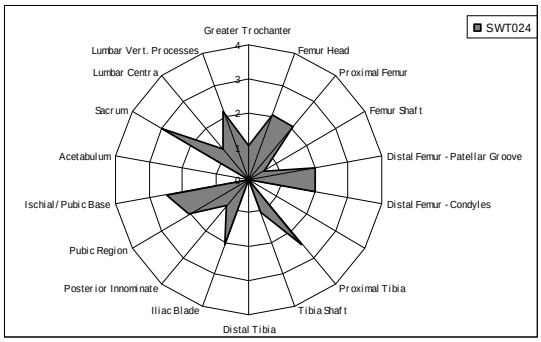
(b)

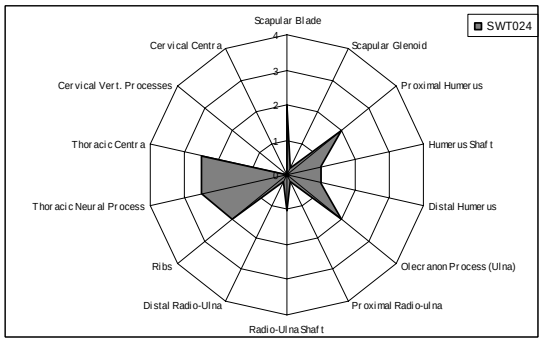


The number of lions feeding on a carcass does condition the maximum level of gross bone damage inflicted to hindquarter carcass parts to some degree (Figure 3.4). Some of the gross bone damage levels inflicted to these bone portions do not vary with lion group size (N = 6 portions: femur shaft, proximal tibia, iliac blade, acetabulum, lumbar centra, and lumbar vertebral processes). Of those portions that do very with lion group size (N = 11 portions), for six portions the gross bone damage level always increases with an increase in lion group size (greater trochanter, distal femur – patellar groove, patella, posterior innominate, pubic region, ischial/pubic base). However, for five portions the gross bone damage level actually decreases when the lion group size increases from 7-8 to 10-12 (femur head, proximal femur, distal femur – condyles, tibia shaft, sacrum).

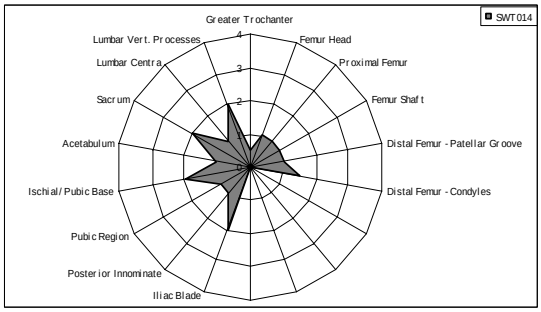
Figure 3.2. Damage and destruction radial diagrams for individual lion-damaged size 3 and 4 hindquarters and forequarters from SGR. These diagrams illustrate actual damage levels inflicted by lions on each of these individual bone portions. Damage level definitions are listed in Table 3.2, and the data are in Table 3.3. Damage levels are median levels when elements are paired (e.g. the right and left greater trochanter). When data were not available for a particular element or portion, that element or portion is not labeled (named) in the damage diagram. The diagrams are presented in order of increasing number of lion consumers on hindquarters (left) and forequarters (right) from top to bottom (from a to g); the data on consumer number is in Table 2.4.

(a, n lions = 1?)

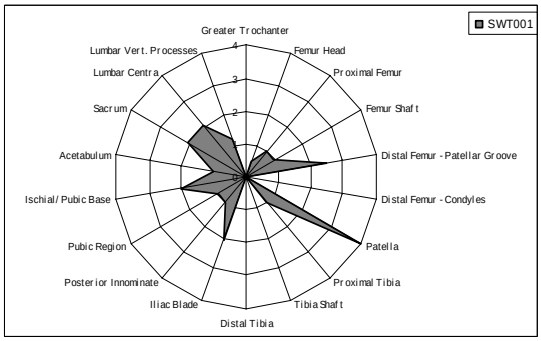




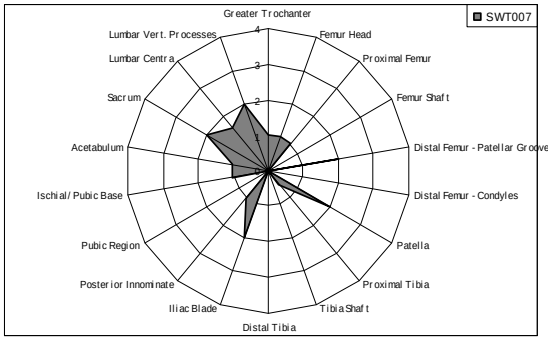
(b, n lions = 3)

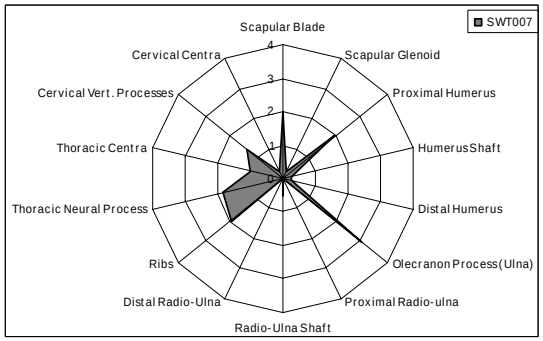


(c, n lions = 7)

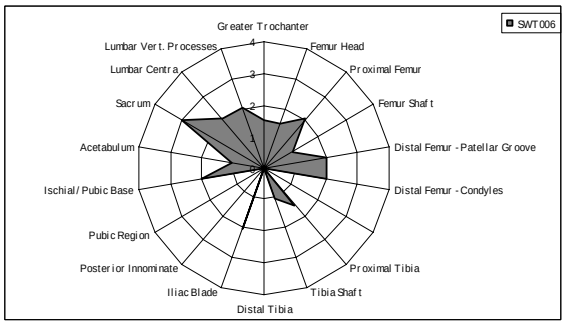


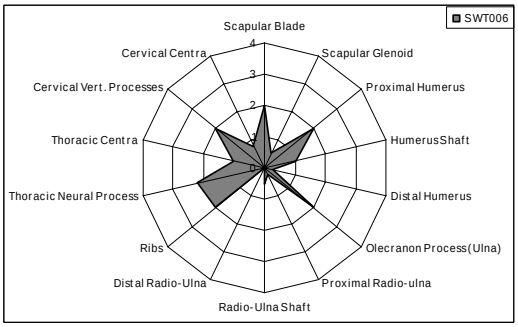
(d, n lions = 7)



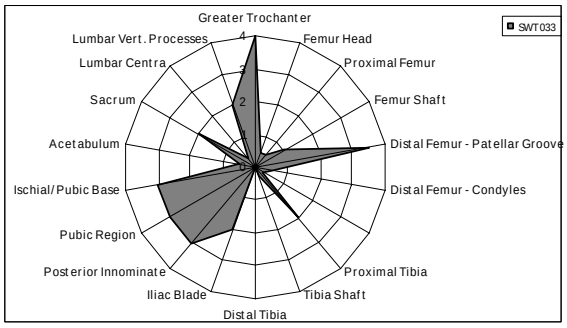


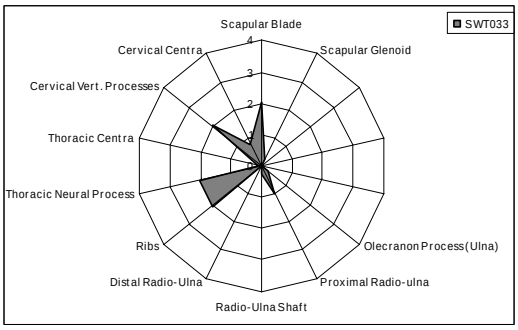
(e, n lions = 8)



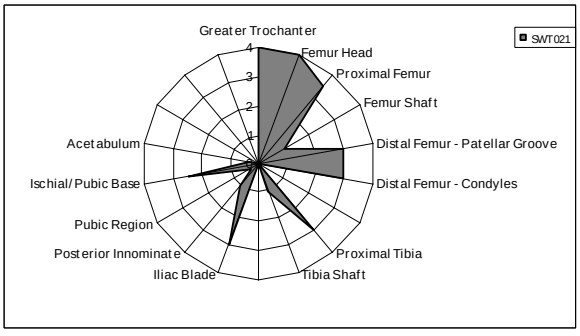


(f, n lions = 10)





(g, n lions = 12)



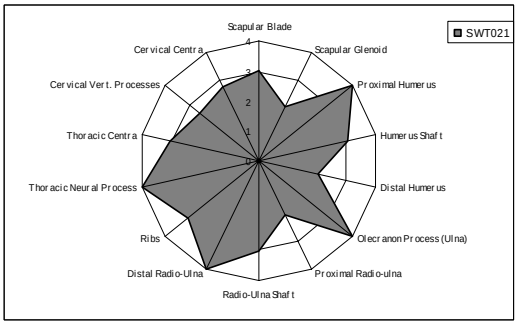
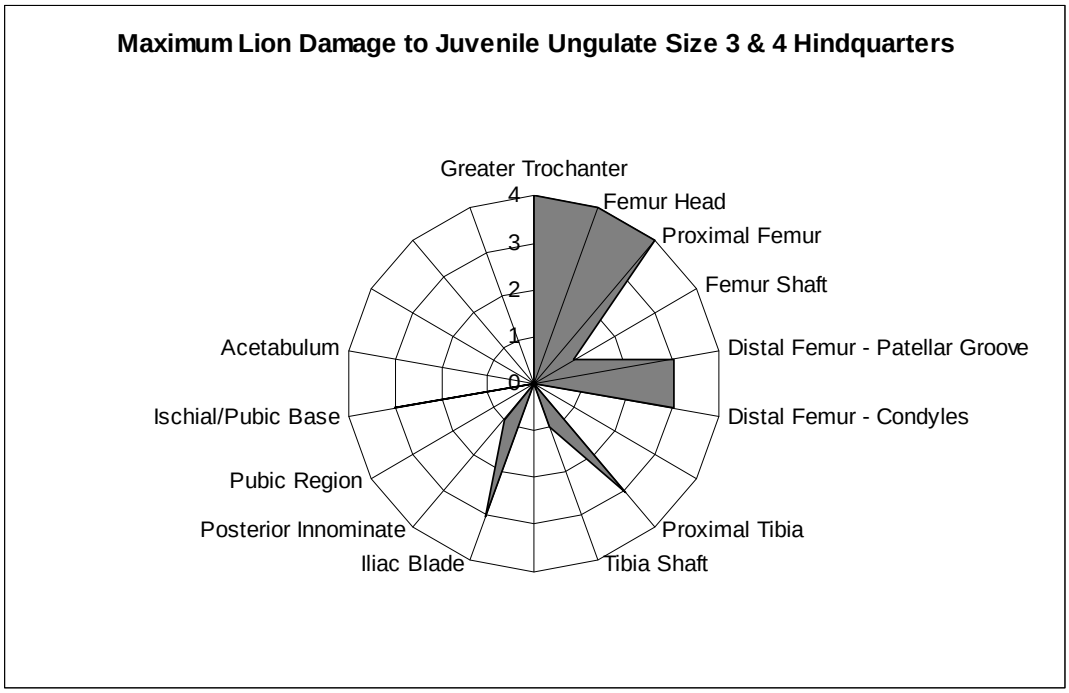


Figure 3.3. Damage and destruction diagrams for juvenile only and adult only lion-damaged size 3 and 4 hindquarters from SGR. These diagrams illustrate the maximum damage levels inflicted by lions on these bone portions. The data represented are in Tables 3.3 and 3.5. N is the number of samples represented. Damage level descriptions are listed in Table 3.2.

(a) juvenile only, N = 1



(b) adult only, N = 6

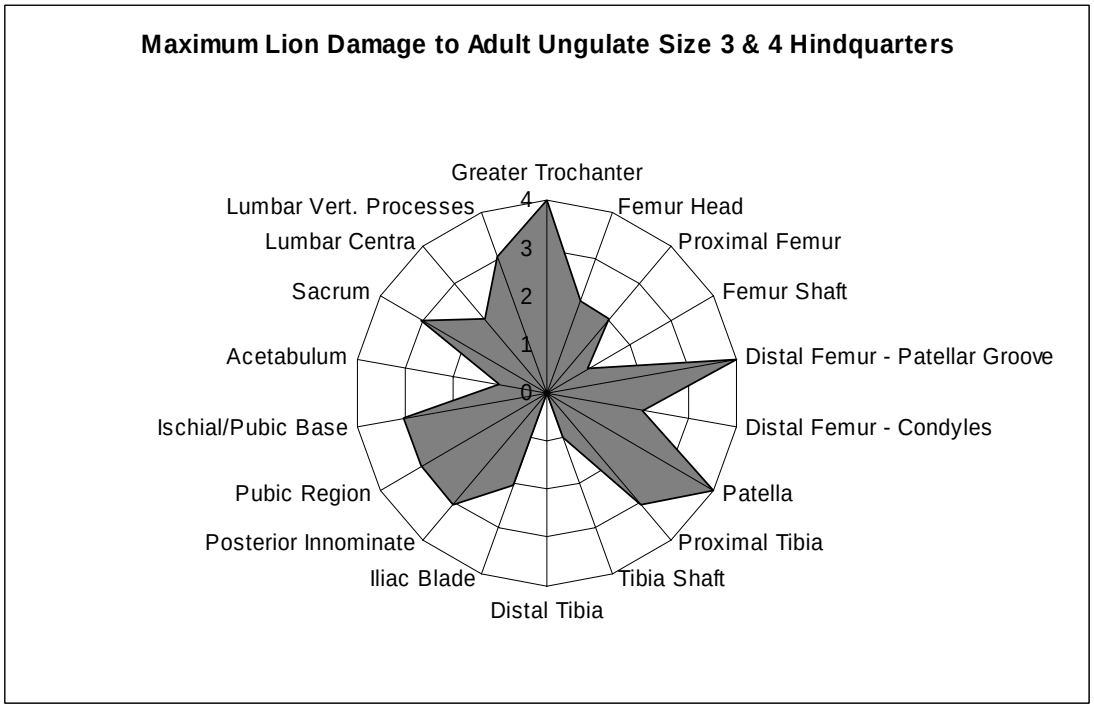
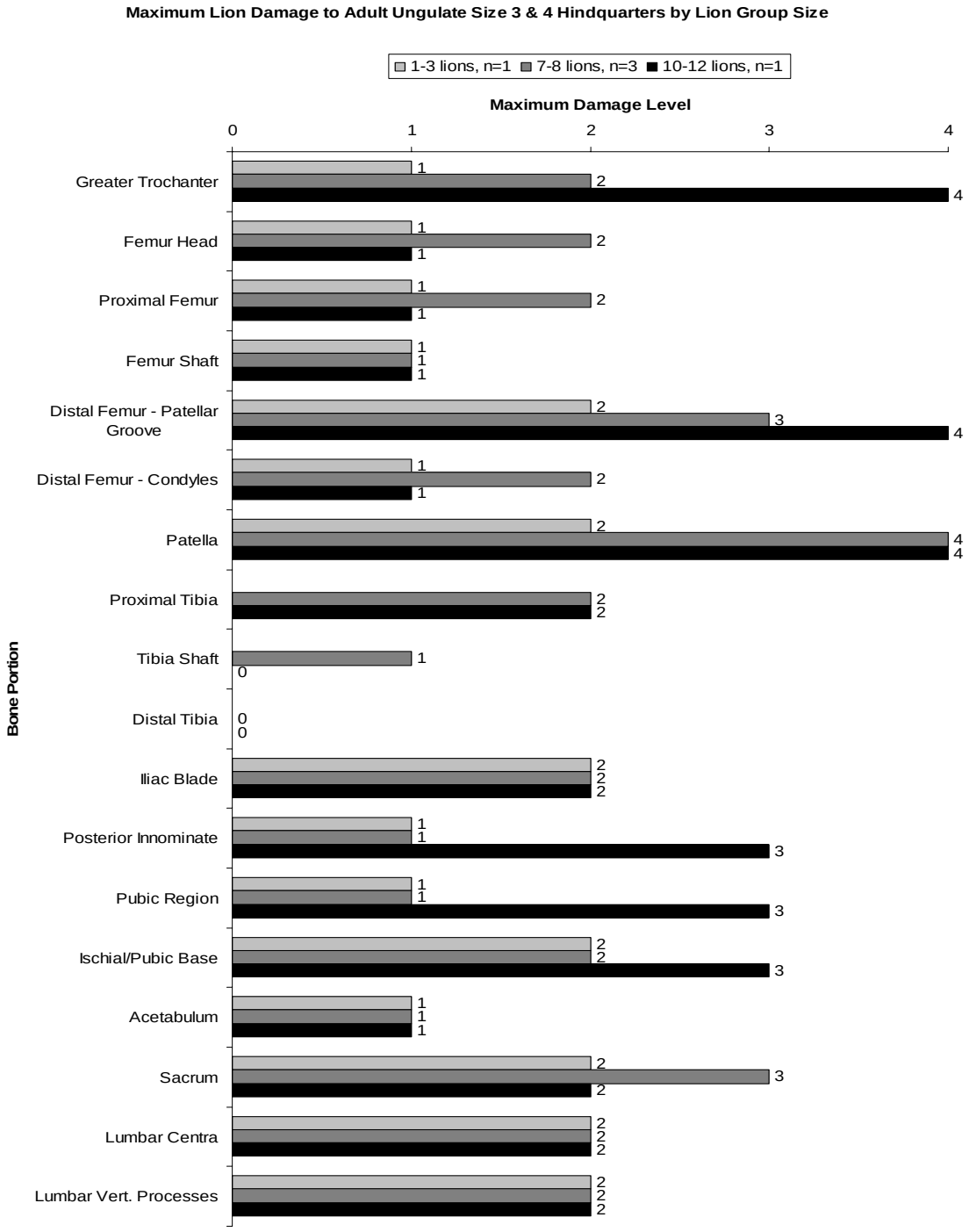


Figure 3.4. The relationship between number of lion consumers and maximum gross bone damage and destruction levels to hindquarters from adult size 3 and 4 carcasses at SGR. No data were available for the tibia from samples consumed by 1-3 lions. Damage level 4 is inferred for the patella for 10-12 lions; the patella was not recovered from these samples and is presumed to have been consumed. Where maximum damage level is not indicated, there are no bones of that skeletal element or portion in my sample. Damage level descriptions are listed in Table 3.2.



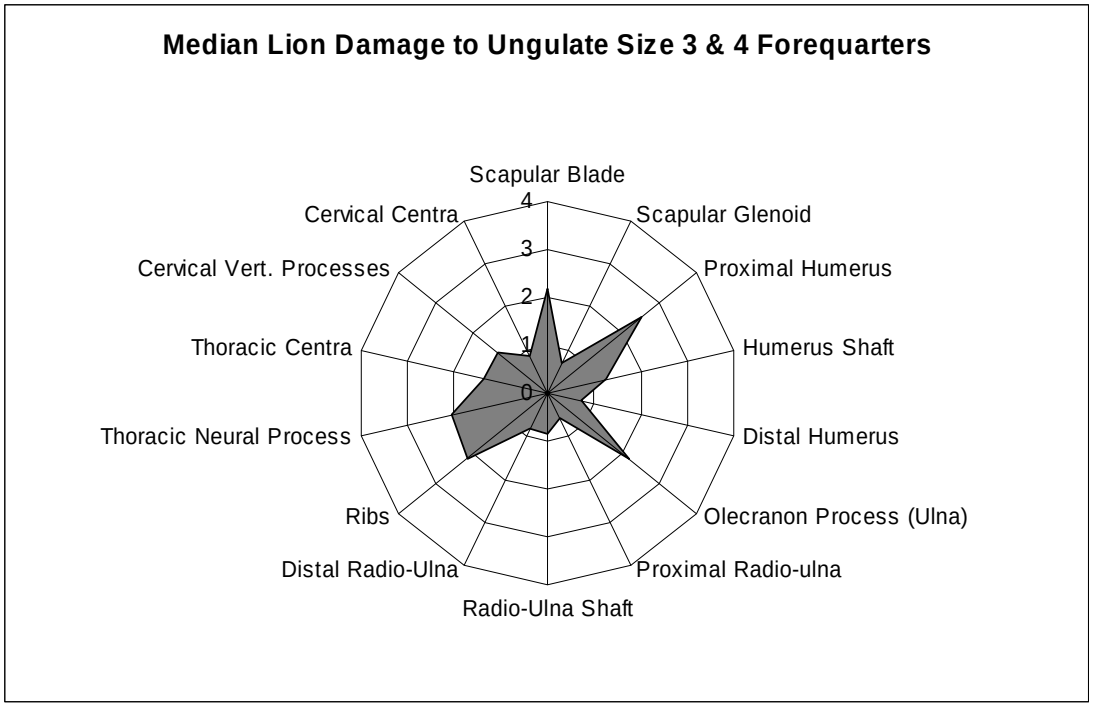
Forequarters

Patterning in gross bone damage to specific bone portions of size 3 and 4 ungulates is also evident in forelimbs (see Figures 3.5 and 3.6). The scapular blade is always minimally gnawed, and the scapular glenoid is always undamaged. Proximal humeri are always minimally gnawed; the humerus shaft is always tooth-marked, and the distal humerus is usually undamaged, or in one case, is tooth-marked. A similar pattern is observed in the radio-ulna. The olecranon process of the ulna is normally minimally to well gnawed, but the rest of the bone is either only tooth-marked or undamaged. Ribs from adult prey carcasses are all marginally gnawed except one, which is only tooth-marked. Ribs from the juvenile prey carcass are all significantly gnawed to fragmented. Thoracic vertebral processes range from undamaged to well gnawed for adults, and thoracic centra range from undamaged to marginally gnawed in adults, to well gnawed in the juvenile. Cervical vertebral processes range from undamaged to marginally gnawed in adults, to fragmented/destroyed in the juvenile. Cervical centra range from undamaged to fragmented/destroyed. Again, lions are able to inflict significantly more damage on juvenile than adult size 3 forelimbs (Figure 3.5), on all portions except the ribs and thoracic vertebral processes.

Initially, the number of lions does not seem to condition the maximum level of gross bone damage inflicted to forequarter carcass parts in any systematic way (Figure 3.7). For only one of the 11 bone portions (proximal radio-ulna) for which data on both lion group sizes 7-8 and 10-12 are available does the amount of gross bone damage actually increase between these group sizes. In five instances the gross bone damage value stays the same (scapular blade, distal radio-ulna, ribs, cervical centra and

Figure 3.5. Damage and destruction diagrams for lion-damaged size 3 and 4 forequarters from SGR. These diagrams illustrate the median (a) and maximum (b) damage levels inflicted by lions on these bone portions. See Figure 3.1 caption for more details. Damage level descriptions are listed in Table 3.2.

(a)



(b)

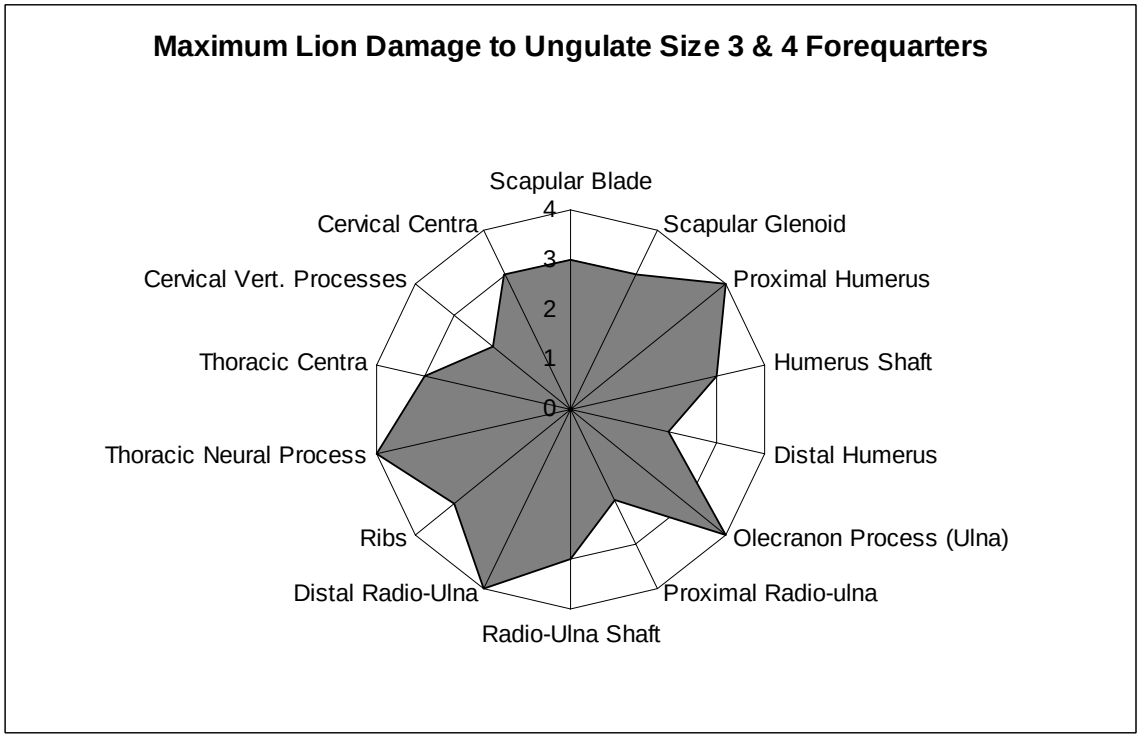
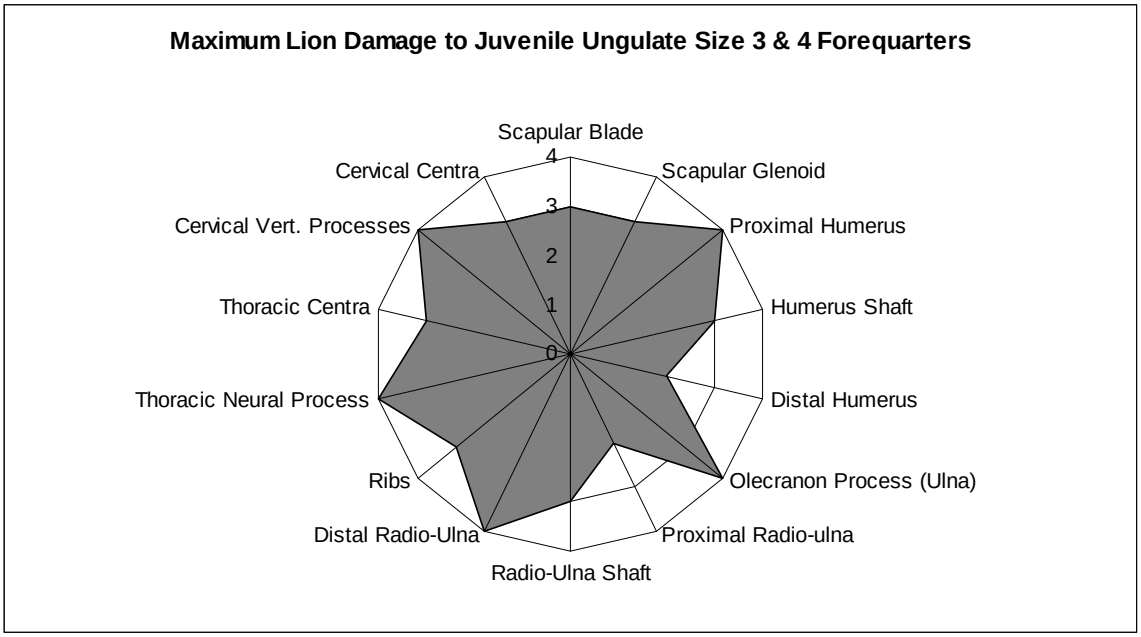


Figure 3.6. Damage and destruction diagrams for mixed adult/juvenile and adult only lion-damaged size 3 and 4 forequarters from SGR. These diagrams illustrate the maximum damage levels inflicted by lions on these bone portions. The dingle juvenile carcass is considered in the top diagram (a), and only adult carcasses are considered in the bottom diagram (b). The data are in Tables 3.3 and 3.5. Damage level descriptions are listed in Table 3.2.

(a)



(b)

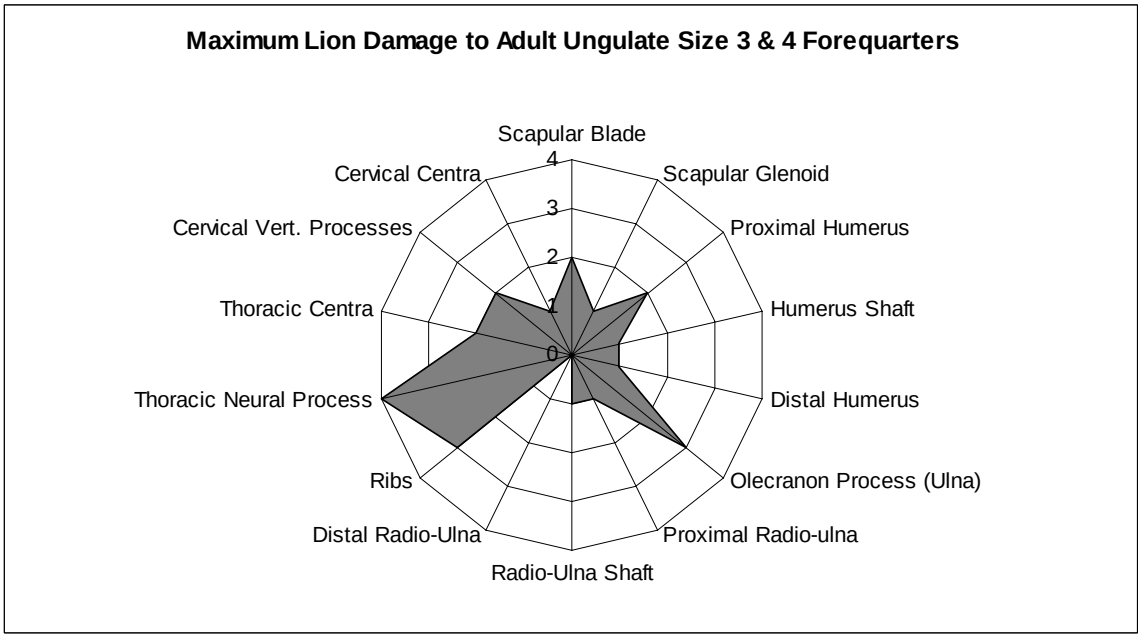
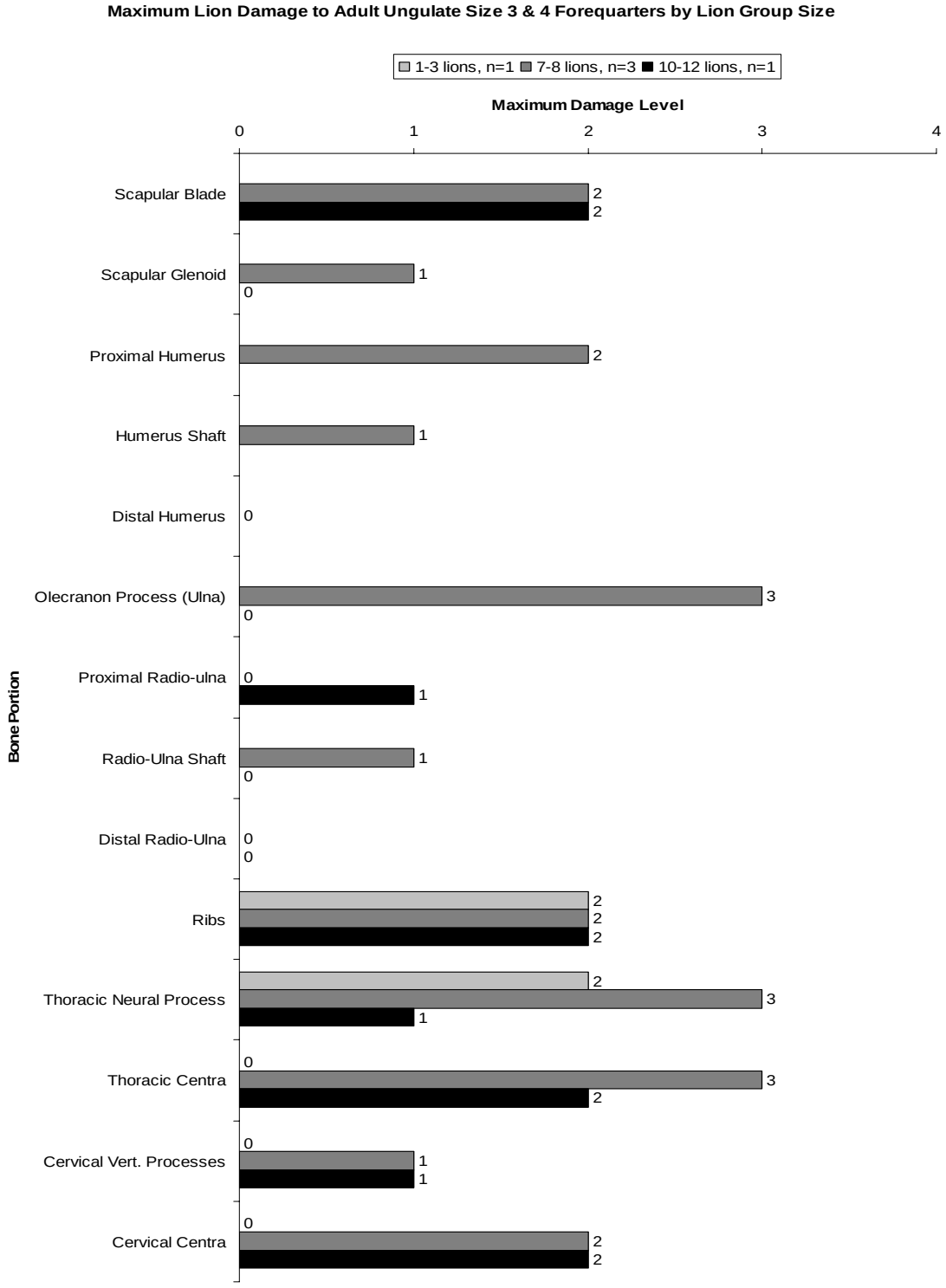


Figure 3.7. The relationship between number of lion consumers and maximum damage and destruction levels to forequarters from adult size 3 and 4 carcasses at SGR. Data for lion group size 1-3 were only available for the ribs and vertebrae. Data for lion group size 10-12 was unavailable for the humerus. See Figure 3.4 caption for more details. Damage level descriptions are listed in Table 3.2.



processes), and in five instances the gross bone damage value actually decreases (scapular glenoid, ulnar olecranon process, radio-ulna shaft, thoracic centra and processes). However, in four of the five forequarter bone portions for which data are available for both lion group sizes 1-3 and 7-8, which all happen to be vertebrae and ribs, the gross bone damage level increases with an increasing number of lions. My sample is likely too small to adequately explore the relationship between number of lions and gross bone damage levels in forelimb bone portions.

B. The NAO Sample

The NAO sample of gross bone damage and destruction done to size 4 carcass parts by captive lions is generally similar to the SGR sample of gross bone damage and destruction done to size 3 (mainly) and 4 carcasses by free-ranging lions (Tables 3.4 and 3.5). Sometimes the NAO and SGR damage level on the same bone portions are equivalent; on other bone portions, the NAO damage level is higher than the SGR damage level. Often these differences, when they do exist, are minimal and consist of the minimum or maximum levels of gross bone damage on a bone portion in the NAO sample being within one damage level of the same bone portion in the SGR sample. Beyond this, the striking differences, where the average and either minimum or maximum gross bone damage levels are differ by more than one gross bone damage level, are outlined below. The differences are mainly in the hindlimb, which exhibits higher gross bone damage and destruction levels at NAO than at SGR.

Femur: Damage levels are higher at NAO than SGR. Lions always destroy the greater trochanter at NAO, but rarely at SGR; most often it is not damaged. The femur head and

other parts of the proximal femur are on occasion destroyed at NAO, but never at SGR. The femur shaft could be heavily gnawed at NAO, but if damaged at SGR, is only tooth-marked. The distal condyles are sometimes destroyed at NAO, but never at SGR.

Tibia: The proximal end of the tibia is nearly always destroyed at NAO, but never destroyed at SGR. The tibia shaft is on occasion fragmented at NAO, but is never even marginally gnawed at SGR.

Innominate: The iliac blade is always heavily gnawed or destroyed at NAO, but is always minimally gnawed at SGR. The posterior innominate is always destroyed at NAO, but never at SGR. Damage to the pubic region at NAO ranges from 2-4, but from 0-3 at SHR.

Humerus: Lions sometimes heavily fragment or destroy the proximal humerus at NAO, but never at SGR.

Table 3.4. Minimum, median, modal, and maximum bone damage and destruction data for each bone portion from NAO. Data are presented on a predator taxon/carcass size basis. Minimum damage is the first number presented, median damage is the second number presented, modal damage is the third number presented, maximum damage is the fourth number presented, and the total number of bone or bone portions from which the data derives (not the number of carcasses) is the fifth number presented: minimum/ median/mode/maximum/number of bones in the sample. All samples are from adult cow, a size 4 ungulate. Where no data was available, "no data" is entered into the cell. This includes elements and portions that were not presented to these captive carnivores, sometimes due to the process of butchering the cow carcass into carcass parts for feeding. On occasion, destruction level is inferred when bone portions were not present, as specified in Figure 3.3 caption. Damage level descriptions are listed in Table 3.2.

Predator Prey Size	Lion	Leopard	Cheetah	Jackal
HINDQUARTER				
Greater Trochanter	4/4/4/4/4	no data	0/0/0/0/1	0/0/0/0/1
Femur Head	0/1.75/0/4/4	no data	0/0/0/0/1	0/0/0/0/1
Proximal Femur	0/2/X/4/4	no data	0/0/0/0/1	0/0/0/0/1
Femur Shaft	1/2.2/3/3/5	0/0/0/0/1	no data	0/0/0/0/2
Distal Femur – Patellar Groove	1/3.4/4/4/5	0/0/0/0/1	no data	0/0/0/0/1
Distal Femur – Condyles	1/3.2/4/4/5	0/0/0/0/1	no data	0/0/0/0/1
Patella	0/2.7/4/4/3	2/2/2/2/1	no data	0/0/0/0/1
Proximal Tibia	2/3.7/4/4/7	no data	0/0/0/0/1	no data
Tibia Shaft	0/1.4/1/3/7	no data	0/0/0/0/1	no data
Distal Tibia	0/0/0/0/7	no data	0/0/0/0/1	no data
Iliac Blade	3/3.5/X/4/2	2/2/2/2/2	0/1/X/2/2	no data
Posterior Innominate	4/4/4/4/2	no data	no data	no data
Pubic Region	2/3/X/4/2	no data	0/0/0/0/1	0/0/0/0/1

Ischial/Pubic Base	2/2.5/X/3/2	no data	0/0/0/0/1	0/0/0/0/1
Acetabulum	0/0.5/X/1/2	no data	0/0/0/0/1	0/0/0/0/1
Sacrum	no data	1/1/1/1/1	0/0/0/0/2	no data
Lumbar Centra	0/0.63/0/1/11	0/0/0/0/9	no data	no data
Lumbar Processes	0/0.78/0/3/11	0/1.55/2/4/9	no data	no data
FOREQUARTER				
Scapular Blade	no data	no data	0/1.29/2/2/6	0/0/0/0/2
Scapular Glenoid	no data	no data	0/0/0/0/5	0/0/0/0/2
Proximal Humerus	2/3/X/4/2	no data	0/2/X/4/6	no data
Humerus Shaft	0/0.5/X/1/2	no data	0/0.16/0/1/6	no data
Distal Humerus	0/0/0/0/2	no data	0/0.33/0/2/6	no data
Olecranon Process (Ulna)	0/1/X/2/2	no data	0/1.2/0/3/5	no data
Proximal Radio-Ulna	0/0/0/0/2	no data	0/0.2/0/1/5	no data
Radio-Ulna Shaft	0/0/0/0/2	no data	0/0/0/0/5	no data
Distal Radio-Ulna	0/0/0/0/2	no data	0/0/0/0/5	no data
Ribs	2/2/2/2/21	0/0/0/0/1	no data	0/0/0/0/1
Thoracic Centra	0/0.26/0/2/25	2/2/2/2/1	no data	0/0.25/0/1/25
Thoracic Neural Process	0/1.3/2/4/25	3/3/3/3/1	no data	0/1/2/2/25
Cervical Centra	0/0.4/0/2/5	0/0.17/0/1/6	no data	0/0/0/0/4
Cervical Processes	0/1/X/2/5	1/1/3/2/3/6	0/0/0/0/10	0/0/0/0/4
PODIALS				
Calcaneum	0/1/X/2/7	no data	0/0/0/0/1	no data
Astragalus	0/0/0/0/7	no data	0/0/0/0/1	no data
Other Tarsals	0/0/0/0/7	no data	0/0/0/0/1	no data
Proximal Metatarsal	no data	no data	no data	no data
Metatarsal Shaft	no data	no data	no data	no data
Distal Metatarsal	no data	no data	no data	no data
Posterior Phalanges	no data	no data	no data	no data
Carpals	0/0.25/0/1/10	no data	0/0/0/0/28	no data
Proximal Metacarpal	no data	no data	no data	no data
Metacarpal Shaft	no data	no data	no data	no data
Distal Metacarpal	no data	no data	no data	no data
Anterior Phalanges	no data	no data	no data	no data
HEAD				
Atlas/Axis Bodies	no data	0/0/0/0/1	no data	no data
Atlas/Axis Processes	no data	0/0/0/0/1	no data	no data
Face	no data	no data	no data	no data
Maxilla/Premaxilla	no data	no data	no data	no data
Cranial Base	no data	no data	no data	no data
Upper Cranium	no data	no data	no data	no data
Mandible Gonial Angle	no data	no data	no data	no data
Mandible Ascending Ramus	no data	no data	no data	no data
Mandible Horizontal Ramus	no data	no data	no data	no data

NOTE: The single serval sample, NAO 2, is not included in this table. It is a scapula to which no damage or destruction was inflicted by the serval.

Table 3.5. Minimum, median, and maximum bone damage and destruction data for each size 4 bone portion modified by lions from NAO, and from the *adult only* sample of size 3 and 4 modified by lions at SGR. Minimum damage is the first number presented, median damage is the second number presented, and maximum damage is the third number presented. See captions from Tables 3:3 and 3:4 for more details. Damage level descriptions are listed in Table 3.2.

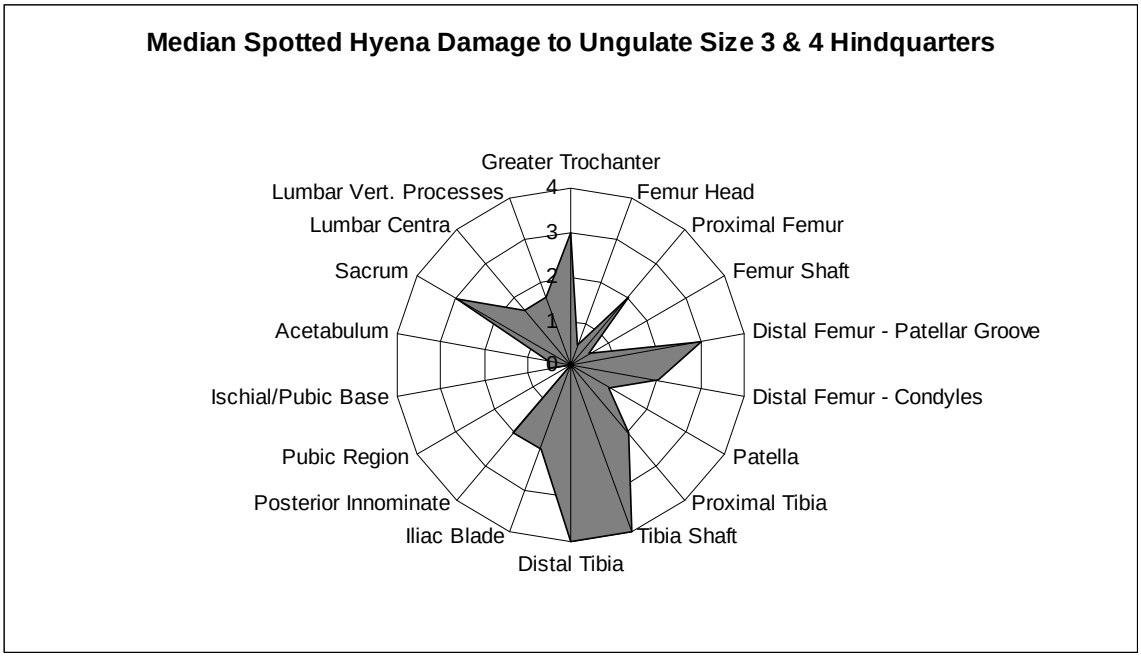
Sample	NAO	SGR (adult only)
HINDQUARTER		
Greater Trochanter	4/4/4	0/1.22/4
Femur Head	0/1.75/4	0/1.00/2
Proximal Femur	0/2/4	0/1.00/2
Femur Shaft	1/2.2/3	0/0.71/1
Distal Femur – Patellar Groove	1/3.4/4	1/2.38/4
Distal Femur – Condyles	1/3.2/4	0/1.00/2
Patella	0/2.7/4	2/3.00/4
Proximal Tibia	2/3.7/4	0/1.44/3
Tibia Shaft	0/1.4/3	0/0.40/1
Distal Tibia	0/0/0	0/0/0
Iliac Blade	3/3.5/4	2/2.00/2
Posterior Innominate	4/4/4	0/1.17/3
Pubic Region	2/3/4	0/1.17/3
Ischial/Pubic Base	2/2.5/3	1/2.14/3
Acetabulum	0/0.5/1	0/0.71/1
Sacrum	no data	2/2.33/3
Lumbar Centra	0/0.63/1	0/1.36/2
Lumbar Processes	0/0.78/3	0/1.90/3
FOREQUARTER		
Scapular Blade	no data	2/2.00/2
Scapular Glenoid	no data	0/0.20/1
Proximal Humerus	2/3/4	2/2.00/2
Humerus Shaft	0/0.5/1	0/0.67/1
Distal Humerus	0/0/0	0/0.33/1
Olecranon Process (Ulna)	0/1/2	0/1.75/3
Proximal Radio-Ulna	0/0/0	0/0.25/1
Radio-Ulna Shaft	0/0/0	0/0.50/1
Distal Radio-Ulna	0/0/0	0/0/0
Ribs	2/2/2	2/2/3
Thoracic Centra	0/0.26/2	0/1.10/2
Thoracic Neural Process	0/1.3/4	0/1.69/4
Cervical Centra	0/0.4/2	0/0.49/4
Cervical Processes	0/1/2	0/1.08/2
PODIALS		
Calcaneum	0/1/2	0/0.50/2
Astragalus	0/0/0	0/0/0
Other Tarsals	0/0/0	0/0/0
Proximal Metatarsal	no data	0/0.17/1
Metatarsal Shaft	no data	0/0/0
Distal Metatarsal	no data	0/0/0
Posterior Phalanges	no data	0/0/0
Carpals	0/0.25/0	0/0/0
Proximal Metacarpal	no data	0/0/0

Metacarpal Shaft	no data	0/0/0
Distal Metacarpal	no data	0/0/0
Anterior Phalanges	no data	0/0/0
HEAD		
Atlas/Axis Bodies	no data	0/0/0
Atlas/Axis Processes	no data	1/1.88/2
Face	no data	0/0.67/2
Maxilla/Premaxilla	no data	0/0/0
Cranial Base	no data	0/0.66/2
Upper Cranium	no data	0/0/0
Mandible Gonial Angle	no data	0/0.40/2
Mandible Ascending Ramus	no data	0/1.50/2
Mandible Horizontal Ramus	no data	0/0.33/2

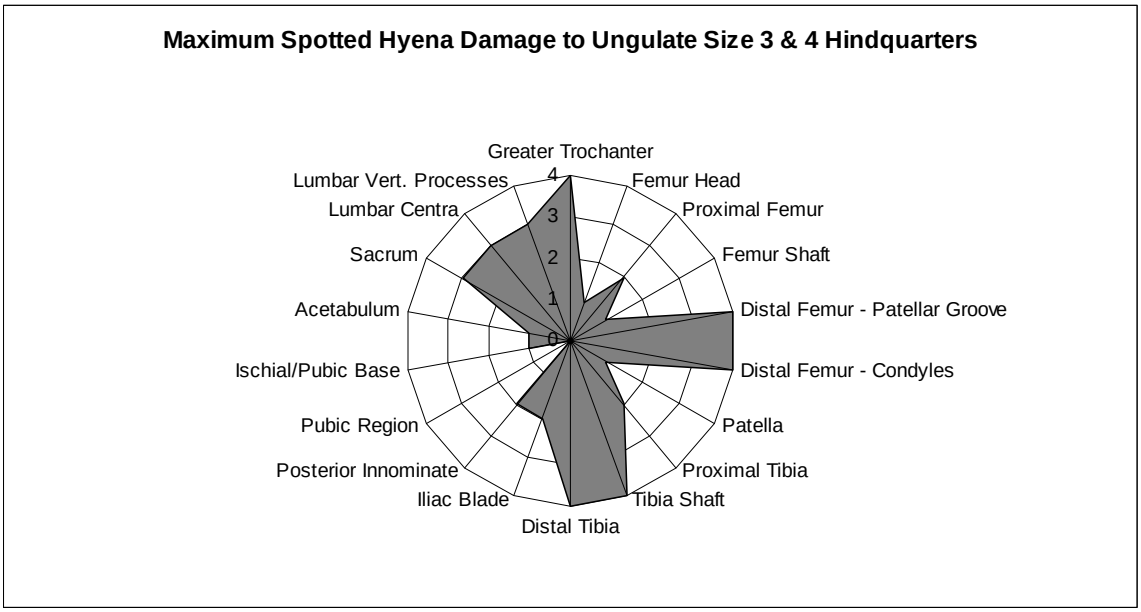
2. Spotted Hyaena Bone Damage (SGR)

Hyaenas generally inflict more damage to size 3 and 4 carcass parts than lions (Figures 3.1, 3.3, and 3.8). However, damage levels inflicted by spotted hyaenas at SWT

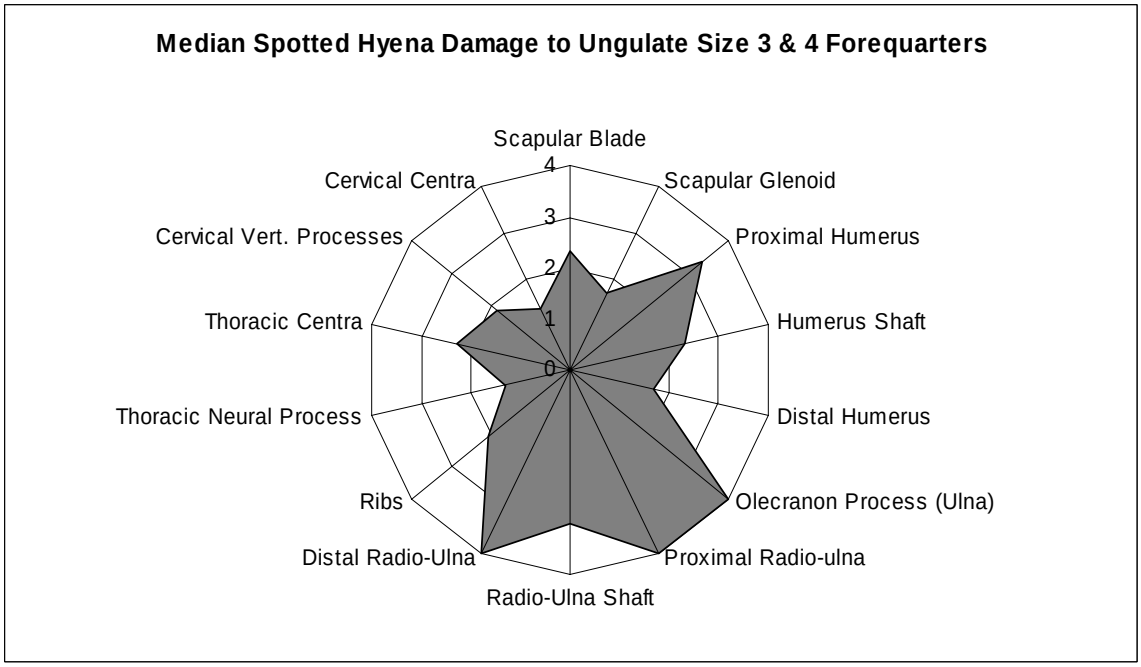
Figure 3.8. Damage and destruction diagrams for spotted hyaena-damaged size 3 and 4 hindquarters and forequarters from SGR. These diagrams illustrate the median (a, c) and maximum (b, d) damage levels inflicted by spotted hyaenas on bone portions from hindquarters (a, b) and forequarters (c, d). Damage level descriptions in Table 3.2.
(a)



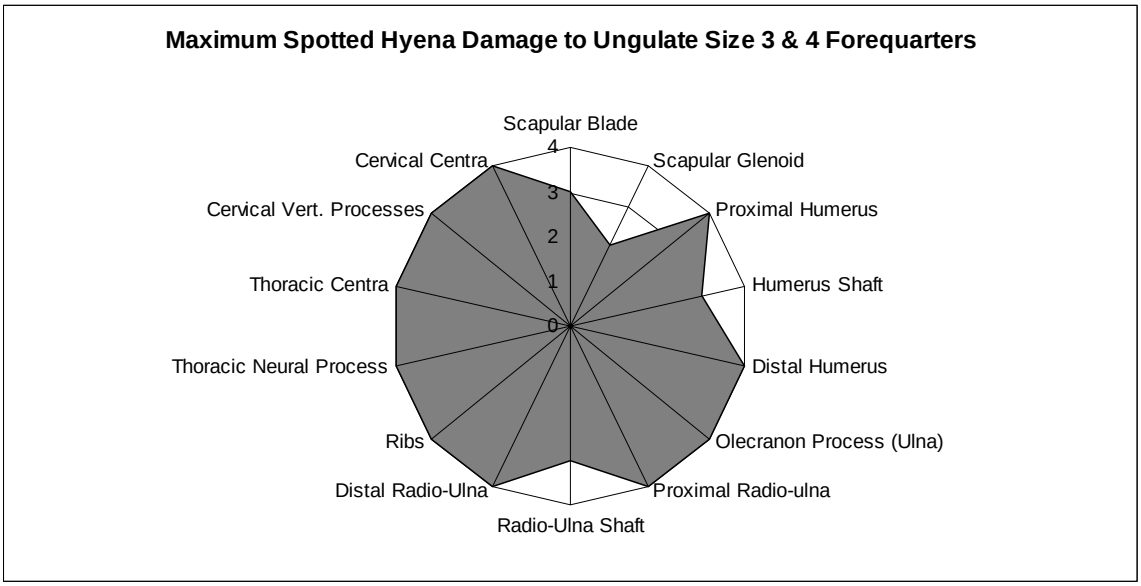
(b)


Maximum Spotted Hyena Damage to Ungulate Size 3 & 4 Hindquarters
Greater Trochanter
Femur Head
Proximal Femur
Femur Shaft
Distal Femur - Patellar Groove
Distal Femur - Condyles
Patella
Proximal Tibia
Tibia Shaft
Distal Tibia
Iliac Blade
Posterior Innominate
Pubic Region
Ischial/Pubic Base
Acetabulum
Sacrum
Lumbar Centra
Lumbar Vert. Processes
0
1
2
3
4

(c)


Median Spotted Hyena Damage to Ungulate Size 3 & 4 Forequarters
Scapular Blade
Scapular Glenoid
Proximal Humerus
Humerus Shaft
Distal Humerus
Olecranon Process (Ulna)
Proximal Radio-ulna
Radio-Ulna Shaft
Distal Radio-Ulna
Ribs
Thoracic Neural Process
Thoracic Centra
Cervical Vert. Processes
Cervical Centra
0
1
2
3
4

(d)



are much lower than that inflicted by spotted hyaenas in a comparable study in the Serengeti (Blumenschine, 1986a). My results likely underestimate the maximum gross bone damage of which spotted hyaenas are capable due to artificially low group size.

Hindquarters

The greater trochanter is the most damaged femur portion, from minimally gnawed to destroyed. The femur head is either unmodified or only tooth-marked, but the rest of the proximal femur is marginally gnawed. The femur shaft is either unmodified or only tooth-marked, while the distal femur ranges from unmodified to destroyed. In the single tibia sample, the proximal end is minimally damaged and the shaft is not damaged at all. The iliac blade and posterior innominate are always minimally gnawed, the ischial/pubic base and acetabulum are either undamaged or only tooth-marked, and the pubic region is undamaged. The sacrum is always heavily gnawed or fragmented.

Forequarters

For size 3 and 4 ungulates, hyaena-modified forequarters exhibited more gross bone damage overall than the hindquarters (Figure 3.8). The scapular blade is minimally to heavily gnawed; the scapular glenoid is minimally gnawed or only tooth-marked. The proximal humerus ranges from minimally gnawed to destroyed; the shaft ranges from tooth-marked to fragmented; and the distal humerus ranges from unmodified to destroyed. The radio-ulna exhibited more overall gross bone damage than the humerus in the single radio-ulna sample available: the proximal and distal radio-ulnae are destroyed, and the shaft is fragmented.

3. Leopard, Cheetah, and Jackal Bone Damage (NAO)

Captive leopards, cheetahs, and jackals do relatively minimal damage to size 4 carcass parts (Tables 3.3 and 3.4). The maximum damage a captive leopard inflicts is fragmenting one of nine lumbar vertebral processes. Heavy gnawing is inflicted on the single sample of thoracic vertebral (neural) processes and one each of the cervical and lumbar vertebral processes. Both patellae in the sample are marginally gnawed, as are both iliac blades, two lumbar vertebral processes, three of five cervical vertebral processes, and the single thoracic vertebral centrum. A sacrum, a cervical vertebral process, four of the six lumbar vertebral processes, and one out of six cervical centra exhibit only tooth marks. All other portions are undamaged.

Captive cheetahs do even less gross bone damage overall than leopards to size 4 carcass parts, though two of six proximal humeri are fragmented, and two of five ulnar olecranon processes are heavily gnawed. One of two iliac blades, two proximal humeri, one of six distal humeri, and three of six scapular blades are marginally gnawed. One

scapular blade, one of five radio-ulna shafts, and one of six humerus shafts are tooth-marked. All other portions are undamaged.

Captive jackals do the least gross bone damage of all of the captive carnivores in my sample. The only bones they damage are thoracic vertebrae: 5 of the 25 thoracic vertebral processes are marginally gnawed (though the other 20 were from parts of vertebrae for which damage could not be exclusively attributed to jackals, and not butchery), and one of the 25 centra of the same vertebrae is tooth-marked.

Size 1/2 Carcasses

1. Lion Bone Damage (SGR)

Size 1 and 2 samples are considered together since most of them are juvenile, and they exhibit generally similar gross bone damage and destruction patterns (Figures 3.9, 3.10, 3.11). As with size 3 and 4 prey, the hindlimbs of size 1 and 2 prey exhibit less overall gross bone damage than the forelimbs, and the upper limb bones exhibit more overall gross bone damage than the intermediate limb bones.

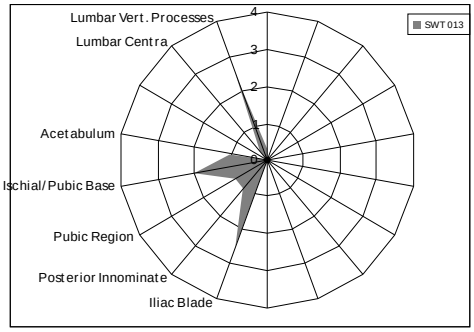
Hindquarters

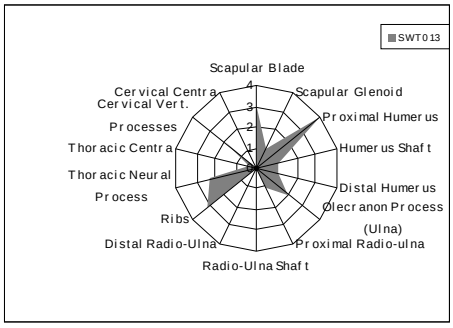
Lions always heavily fragment or completely destroy the proximal and distal ends of femora and patellae of size 1 and 2 prey. They normally, but not always, damage the femur shaft to some degree. The proximal tibia is always at least marginally gnawed, and usually heavily gnawed or fragmented. Damage on the distal tibia ranges from absent to severe. All parts of the innominate are always at least tooth-marked, and can be fragmented or destroyed. Lumbar centra are usually not damaged, or occasionally tooth-marked; lumbar vertebral processes are either marginally or heavily gnawed.

Figure 3.9. Damage and destruction diagrams for lion-damaged size 1 and 2 hindquarters and forequarters from SGR. The diagrams are in order of increasing number of lion consumers from top to bottom within each size class (Size 2: a to d; Size 1: e to h); the data on consumer number is in Table 2.4. See Figure 3.2 caption for more details.

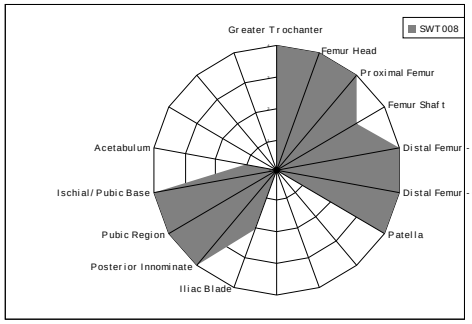
Size 2

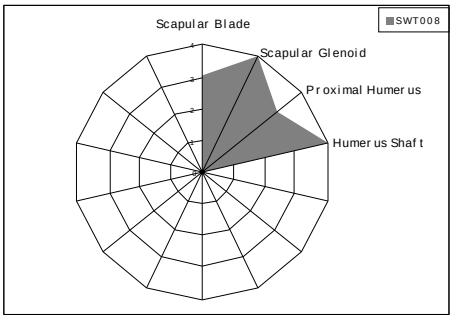
(a, n lions = 2)



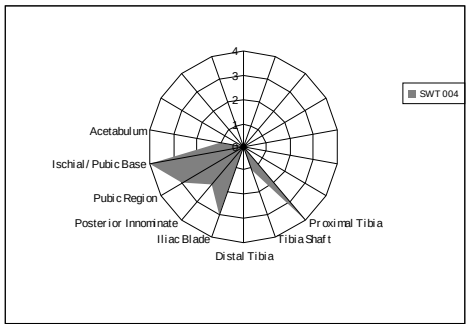


(b, n lions = 7)

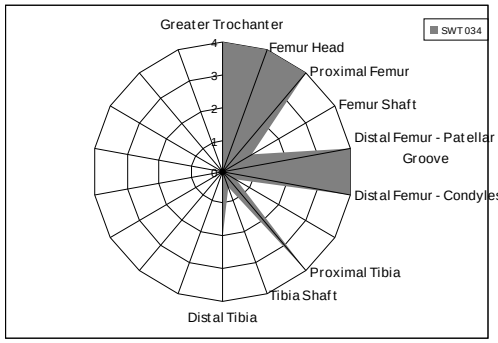


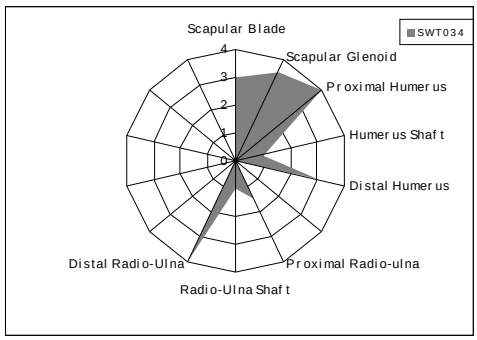


(c, n lions = 8)



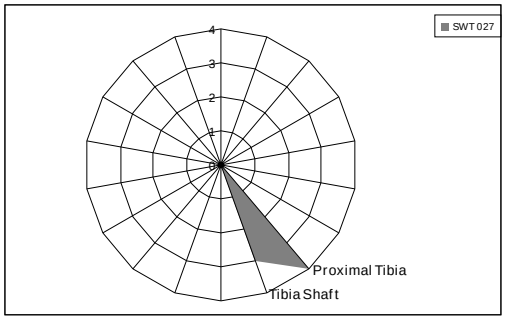
(d, n lions = 10)

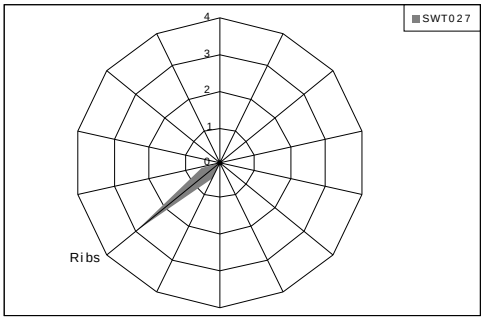




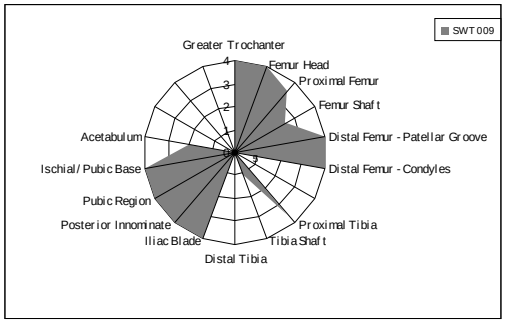
Size 1

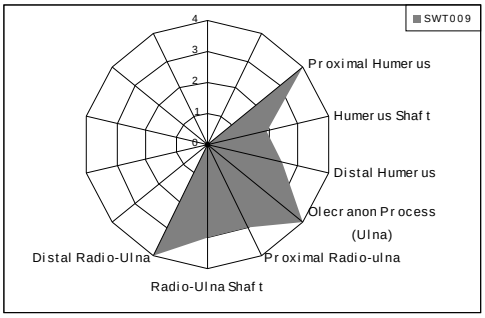
(e, n lions = 4)



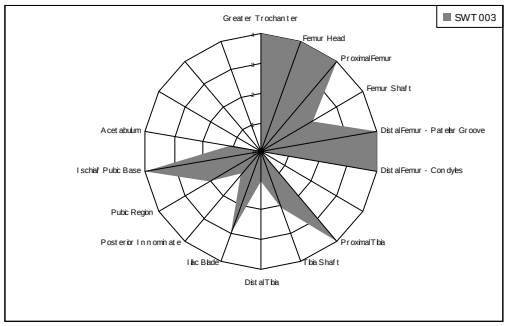


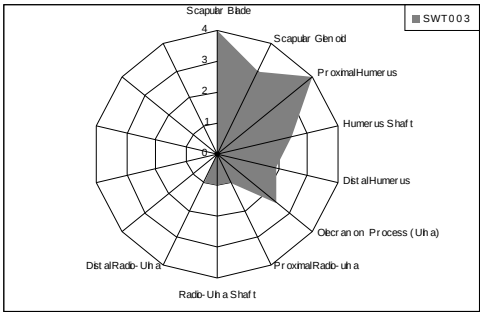
(f, n lions = 5)



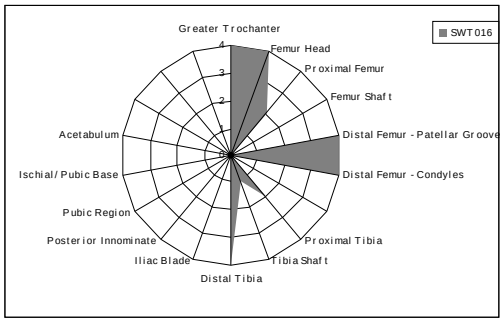


(g, n lions = 8)





(h, n lions = >1)



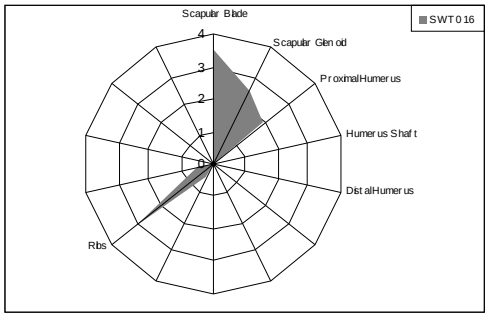
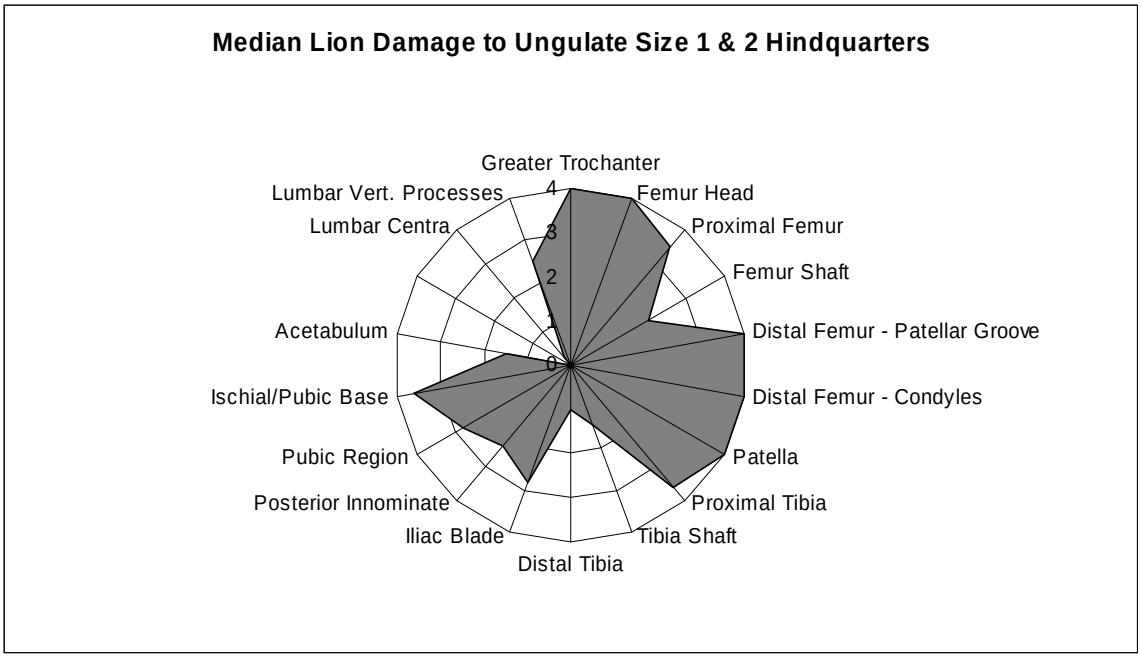


Figure 3.10. Damage and destruction diagrams for lion-damaged size 1 and 2 hindquarters from SGR. These diagrams illustrate the median (a, top) and maximum b. (bottom) damage levels inflicted by lions on these bone portions. Damage level descriptions are listed in Table 3.2.

(a)



(b)

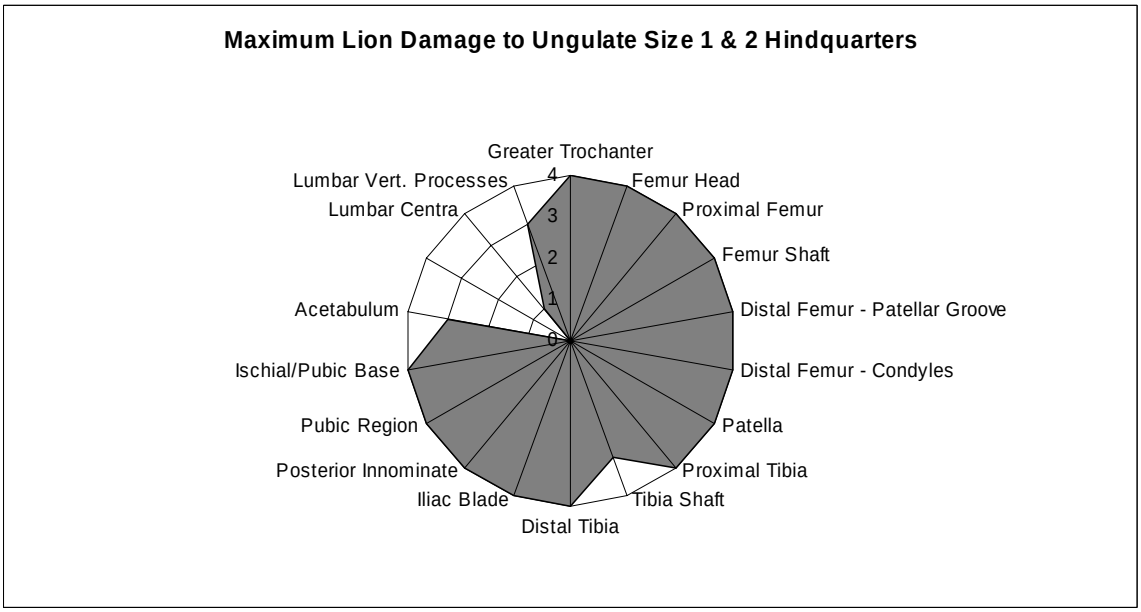
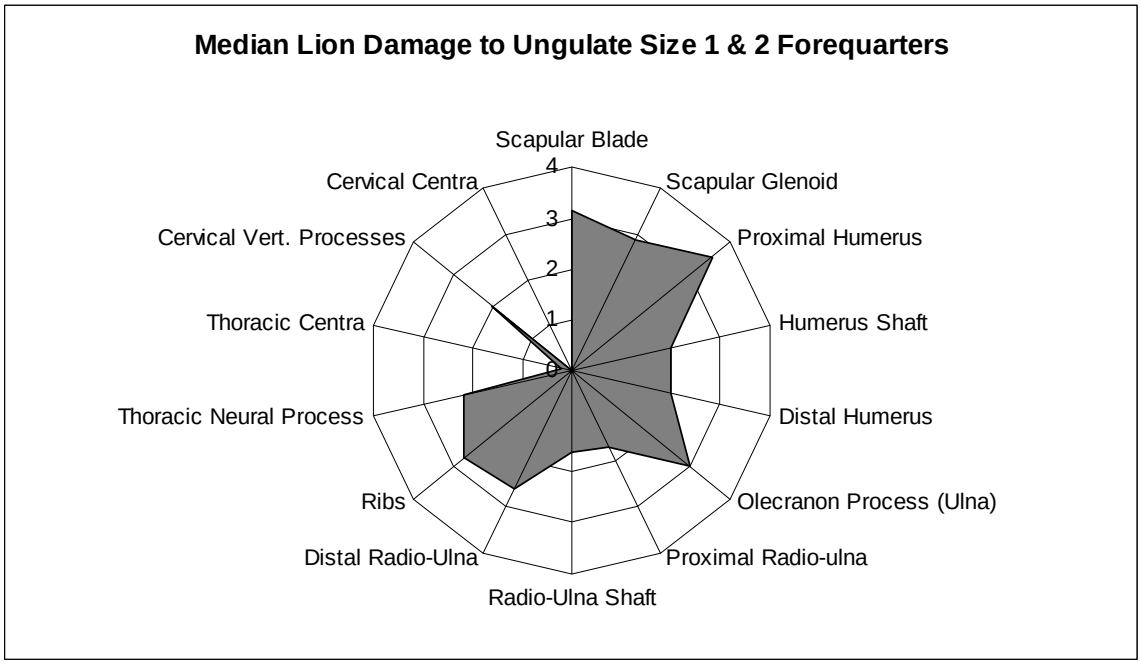
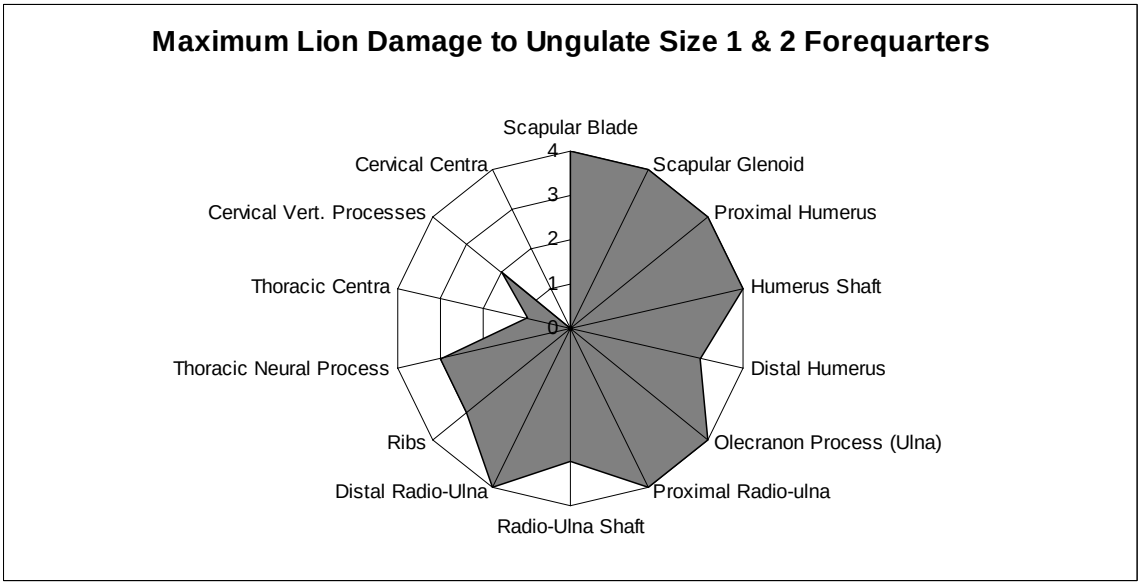


Figure 3.11. Damage and destruction diagrams for lion-damaged size 1 and 2 forequarters from SGR. These diagrams illustrate the median (a, top) and maximum (b, bottom) damage levels inflicted by lions on these bone portions. Damage level descriptions are listed in Table 3.2.

(a)



(b)



Forequarters

Lions heavily fragment or destroy scapular blades of size 1 and 2 prey, while scapular glenoids range from exhibiting only tooth marking to complete destruction. Proximal humeri are relatively more damaged (minimally to destroyed) than distal humeri (tooth-marked to heavily gnawed). Humerus shafts vary from undamaged to completely destroyed. The ulnar olecranon process is always at least minimally gnawed, while the remainder of the proximal radio-ulna is always at least tooth-marked. The distal radio-ulna ranges from undamaged to destroyed, and the radio-ulna shaft ranges from undamaged to heavily gnawed. Ribs are usually heavily gnawed and fragmented. Thoracic and cervical centra are normally undamaged or occasionally tooth-marked. Thoracic vertebral processes are usually marginally gnawed, and occasionally heavily gnawed, while cervical vertebral processes are marginally gnawed.

2. Spotted Hyaena Bone Damage (SGR)

There was virtually nothing left of the three size 1 and 2 carcass parts eaten by spotted hyaenas. These were articulated forelimbs and ribcages of domestic sheep and goats, essentially front ‘halves’, purposefully left out on the SGR airstrip to obtain spotted hyaena modification samples. The back ‘halves’ were used for unrelated butchery experiments (Pobiner and Braun, 2005). In one case (SWT020), the carcass was completely consumed or transported; in another (SWT018), only a completely defleshed isolated palate and upper cranium (two separate bones) were recovered; in another (SWT 019), part of one of the scapulae was recovered about 25 meters from the original site.

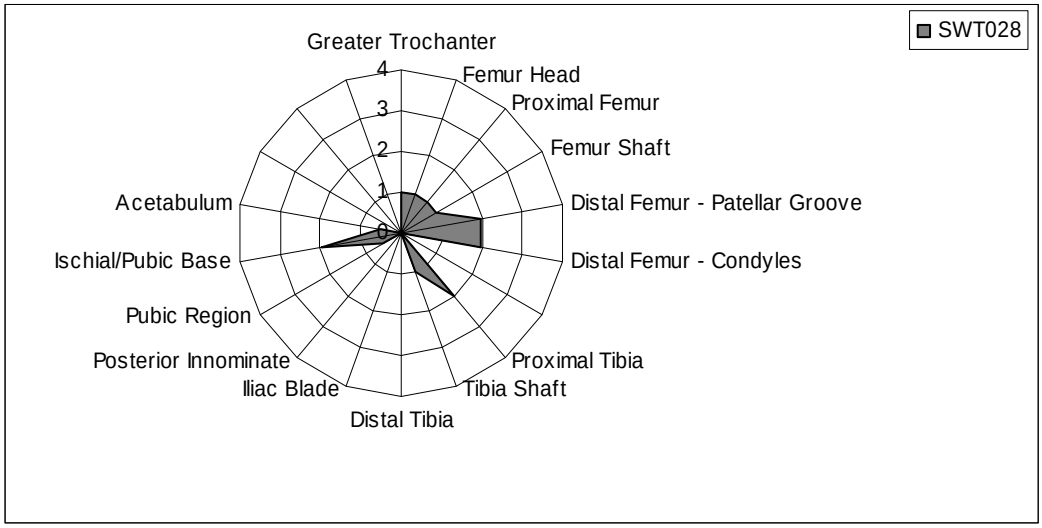
3. Leopard Bone Damage (SGR)

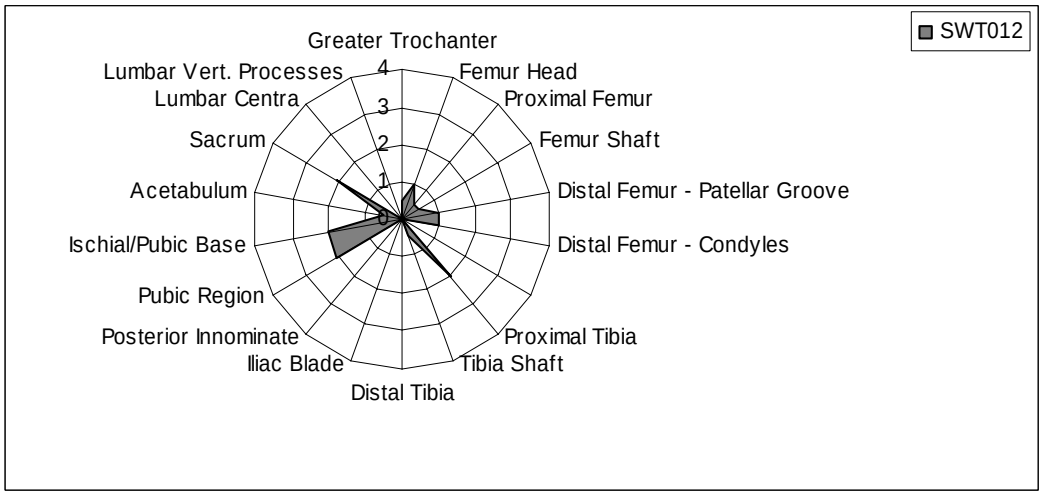
The three carcass parts in this sample were all hindlimbs of sub-adult domestic sheep or goats that were tied to a tree and left as bait for a resident leopard.

Hindquarters

Leopard gross bone damage to these size 1 and 2 hindquarters was fairly variable (Figures 3.12 and 3.13). This may be an effect of the small sample size, or the "bait" nature of the samples themselves. Damage to the proximal femur ranged from no damage to complete destruction. The femur shaft was either undamaged or tooth-marked. The distal femur was either tooth-marked or marginally gnawed. The proximal tibia ranged from undamaged to marginally gnawed. The tibia shafts were both either undamaged or only tooth-marked. The distal tibia was always undamaged. The pubic region ranged from undamaged to marginally gnawed, and the ischial/pubic base was the most damaged part of the innominate, with marginal gnawing always present. The rest of the innominate was undamaged. The sacrum was always marginally gnawed. The lumbar vertebral centra and processes were usually undamaged, and occasionally tooth-marked.

Figure 3.12. Damage and destruction diagrams for individual leopard-damaged size 1 and 2 hindquarters from SGR. See Figure 3.2 caption for more details. Damage level descriptions are listed in Table 3.2.





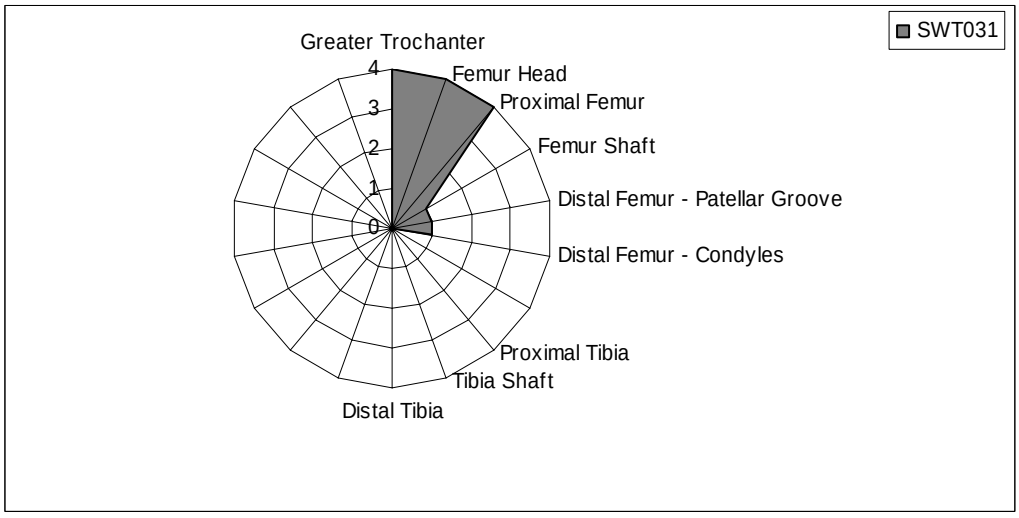
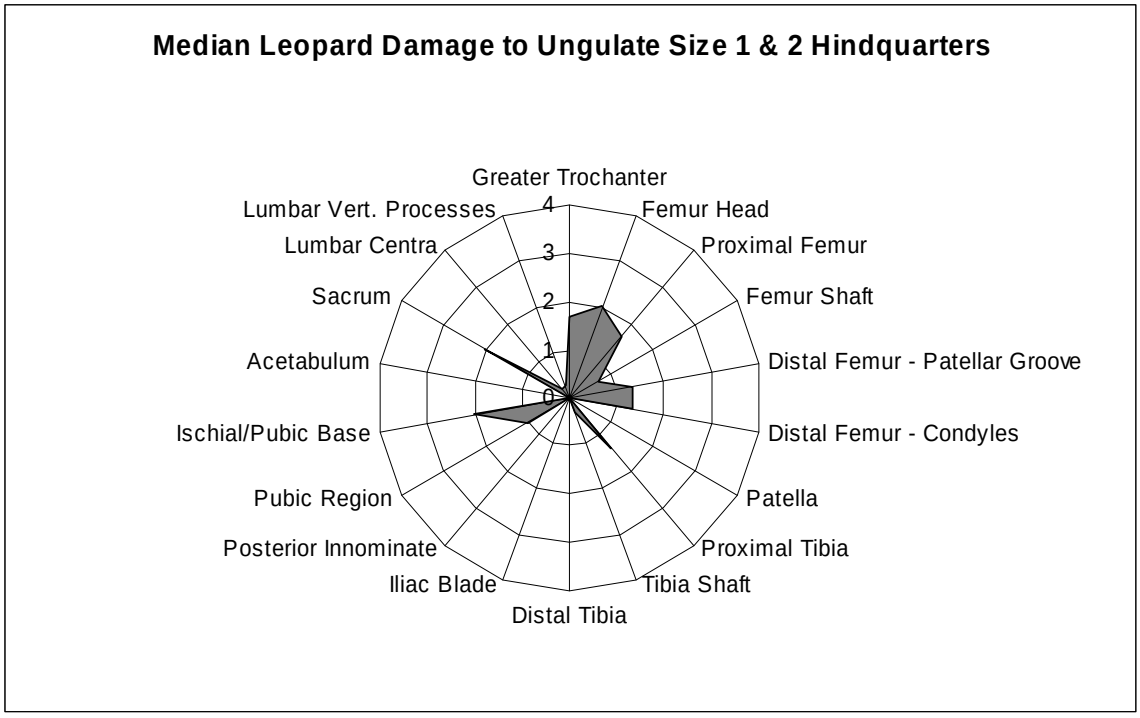
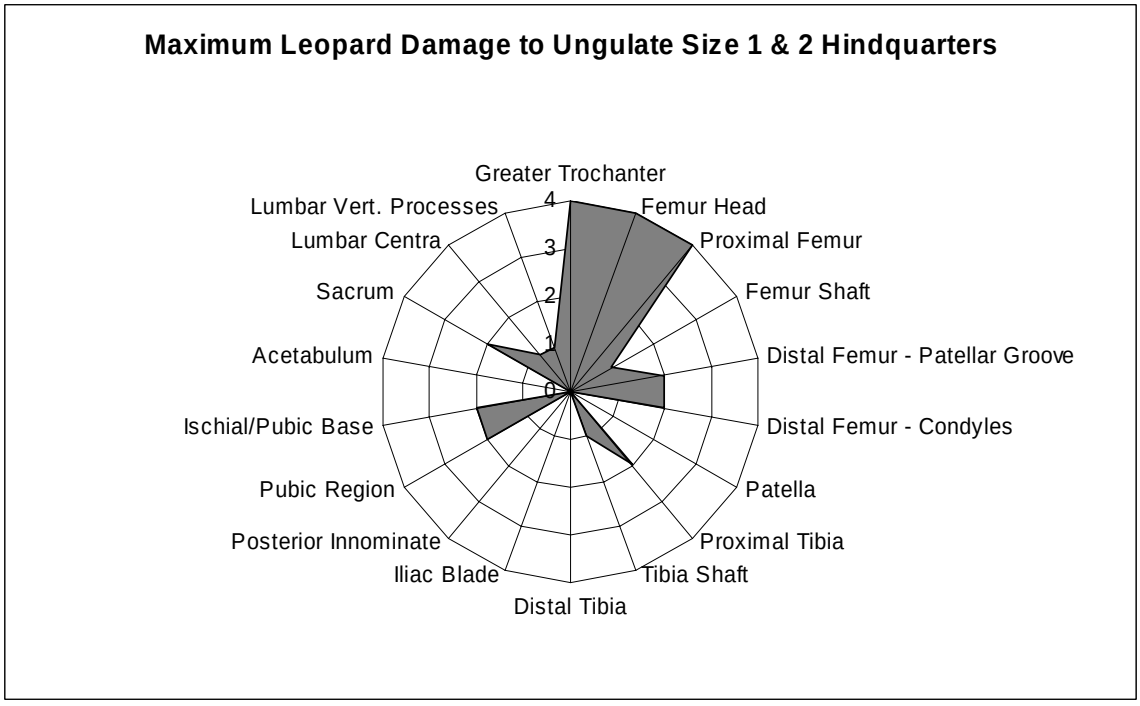


Figure 3.13. Damage and destruction diagrams for leopard-damaged size 1 and 2 hindquarters from SGR. These diagrams illustrate the median (a, top) and maximum (b, bottom) damage levels inflicted by leopards on these bone portions. Damage level descriptions are listed in Table 3.2.

(a)



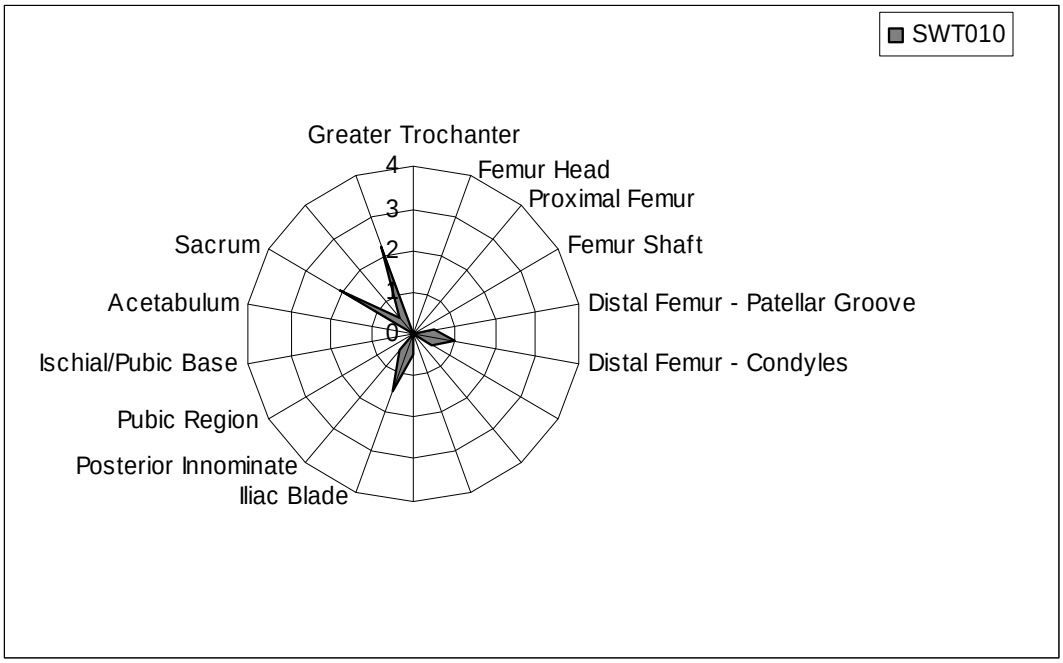
(b)



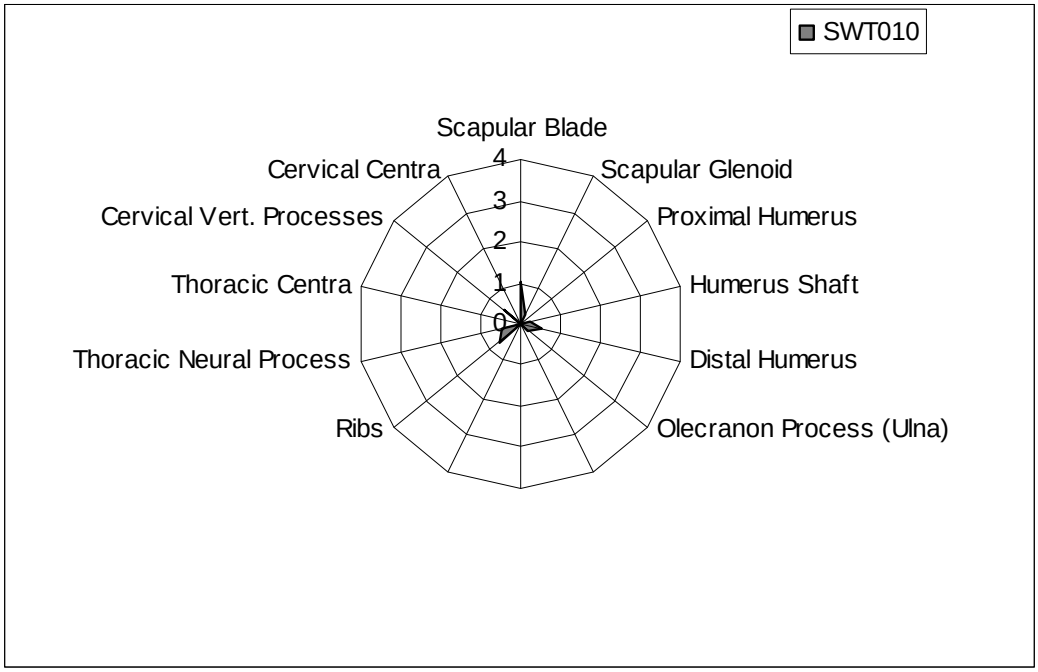
4. Cheetah and Jackal Bone Damage (SGR)

In this sample, cheetahs and jackals inflict minimal if any gross bone damage to all forelimb and hindlimb bones and bone portions of fully fleshed size 1 carcasses (Figure 3.14). The highest gross bone damage inflicted was heavy gnawing, by the cheetah, on a single lumbar vertebral process. Other than that, both the cheetah and jackal inflict the most gross bone damage (relatively), marginal gnawing, on the hindquarters to the iliac blade. The jackal also marginally gnawed the posterior innominate. The cheetah marginally gnawed one of the two distal femora, the sacrum, five of the six lumbar vertebral processes, seven of the twenty-one ribs, three of the thirteen thoracic vertebral processes, and one of the cervical vertebral processes. One of the two proximal femora is

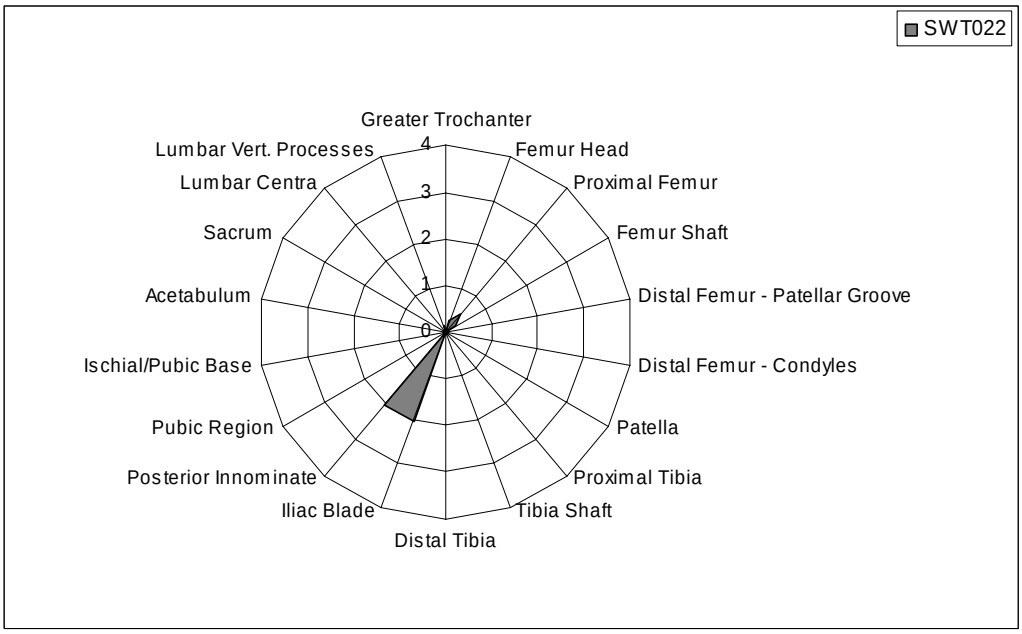
Figure 3.14. Damage and destruction diagrams for size 1 hindquarters and forequarters from SGR damaged by a cheetah and jackals. Cheetah: SWT010, a and b; jackals: SWT022, c. See Figure 3.2 caption for more details.
(a) cheetah, hindquarters



(b) cheetah, forequarters



(c) jackal, hindquarters



tooth-marked by the jackal, and one of the two iliac blades and one of the cervical vertebral processes are tooth-marked by the cheetah. Otherwise, all other bones and bone portions were undamaged.

Comparisons of Skeletal-Wide Damage and Destruction Patterns Across Different Sized Prey Carcasses Consumed by Different Carnivore Taxa

The most productive comparisons in my sample of skeletal-wide gross bone damage and destruction patterns by free-ranging carnivores are between hyaenas modifying size 3 and 4 prey (Figure 3.15) and lions modifying size 1 and 2 prey (Figure 3.16), and between lions modifying size 3 and 4 prey (Figure 3.17) and leopards modifying size 1 and 2 prey (Figure 3.18). I am not including gross bone damage and destruction data from NAO samples in this analysis because those carnivores were presented only carcass parts or even isolated skeletal elements, making skeletal-wide analyses inappropriate. Also, it is important to mention again that the hyaena group size at SGR is unnaturally small, and therefore the hyaena-modified size 3 and 4 samples likely exhibit unusually low gross bone damage and destruction levels.

Figures 3.15 – 3.18 show a pattern within the two carcass size groups (1/2, 3/4) of progressively greater bone destruction that corresponds to increasing body size and/or jaw strength of the carnivores under consideration (also see Pobiner and Blumenschine, 2003). Carnivores with increased bone destruction ability (spotted hyaenas versus lions, lions versus leopards) reduce and eventually destroy skeletal elements and skeletal element portions more intensely than do carnivores with lower relative bone-eating capabilities.

More specifically, the progression of element and portion destruction seen among lions modifying size 1 and 2 carcasses fairly closely matches that inflicted by spotted hyaenas modifying size 3 and 4 carcasses (Figures 3.15 and 3.16). In both sets of samples, heavy gnawing and destruction is focused in the limb epiphyses, some of the

Figure 3.15. Skeletal-wide bone damage and destruction patterns for spotted hyaena-modified size 3 and 4 ungulate prey from SGR. Damage and destruction level is either modal damage, or median damage when modal damage was nonexistent mathematically; these values are indicated in boldface in Table 3.3. The damage and destruction level was rounded up or down to the next whole number when applicable to facilitate shading. No damage (damage level 0) is indicated in white; tooth marking only (damage level 1) is indicated in light grey; marginal gnawing (damage level 2) is indicated in medium grey; heavy gnawing (damage level 3) is indicated in dark grey; and fragmentation and/or complete destruction (damage level 4) is indicated in black. Skeletal elements for which no data was collected are not displayed in the figure.

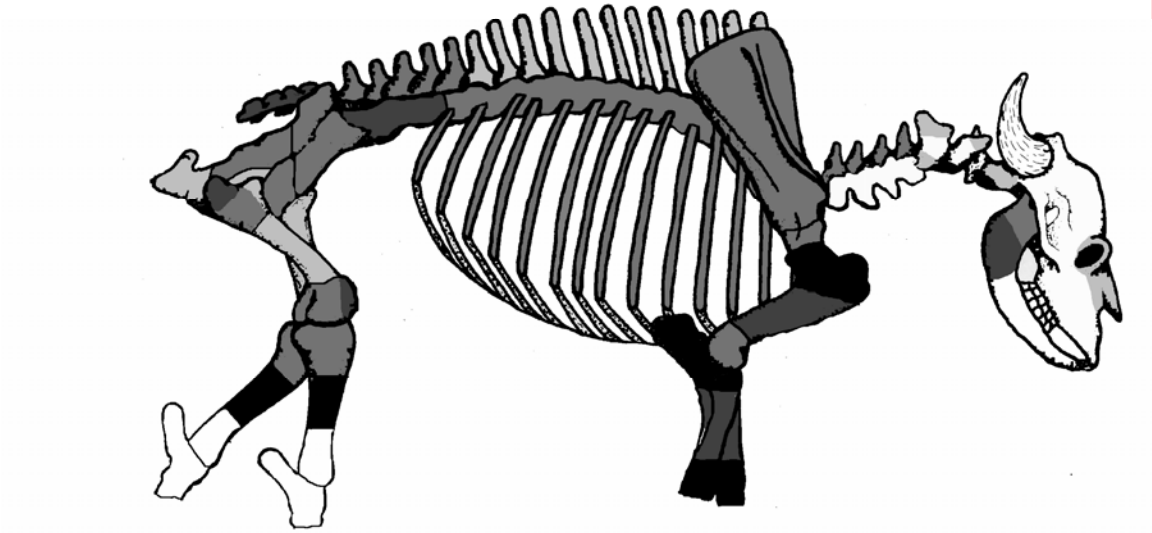


Figure 3.16. Skeletal-wide bone damage and destruction patterns for lion-modified size 1 and 2 ungulate prey from SGR. See Figure 3.13 caption for more details.

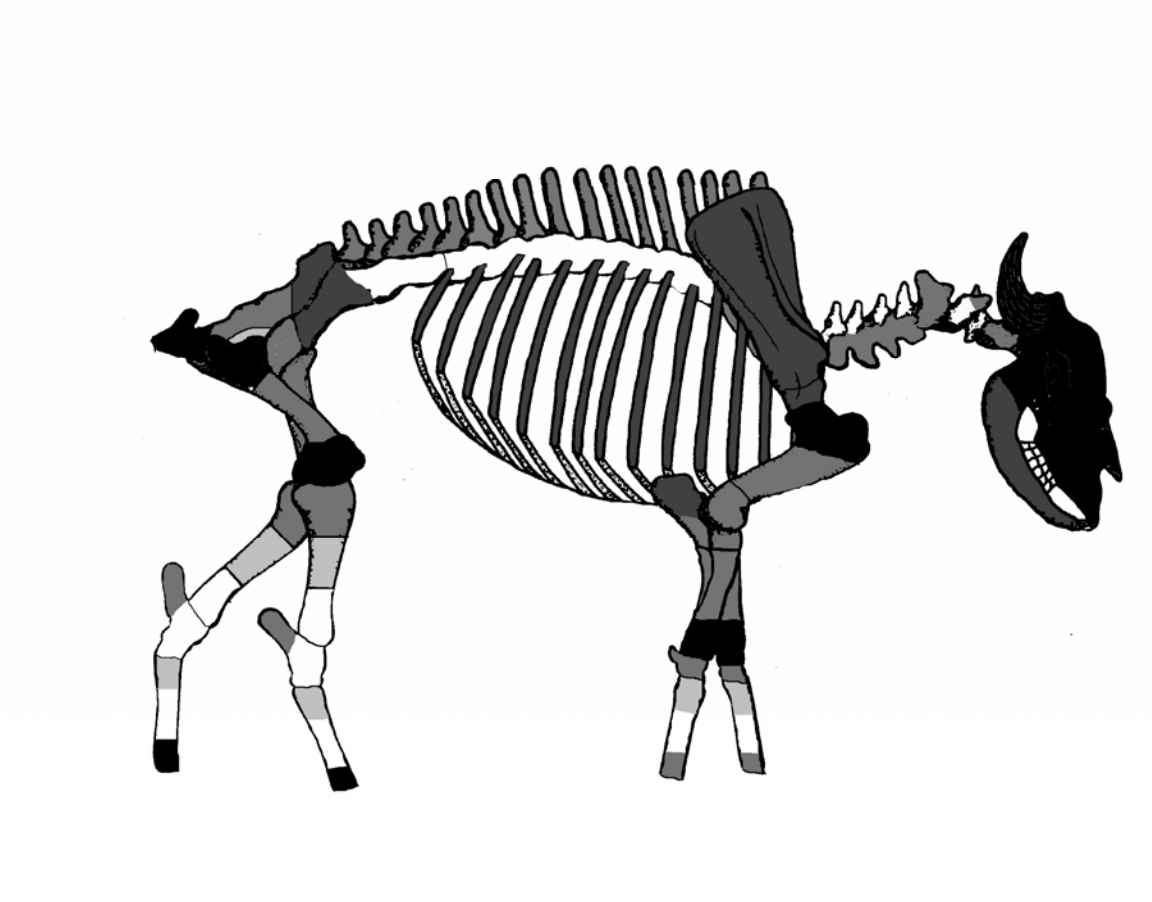


Figure 3.17. Skeletal-wide bone damage and destruction patterns for lion-modified size 3 and 4 ungulate prey from SGR. See Figure 3.13 caption for more details.

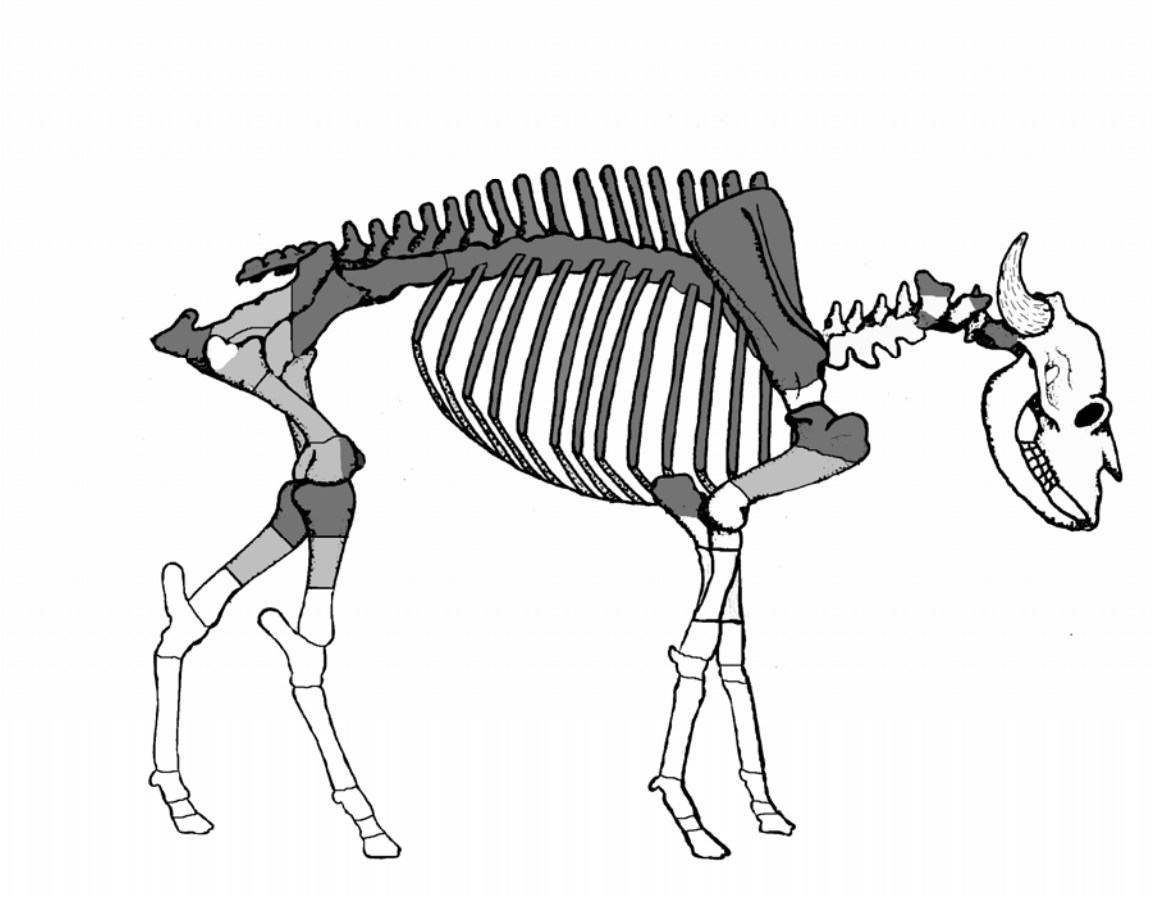
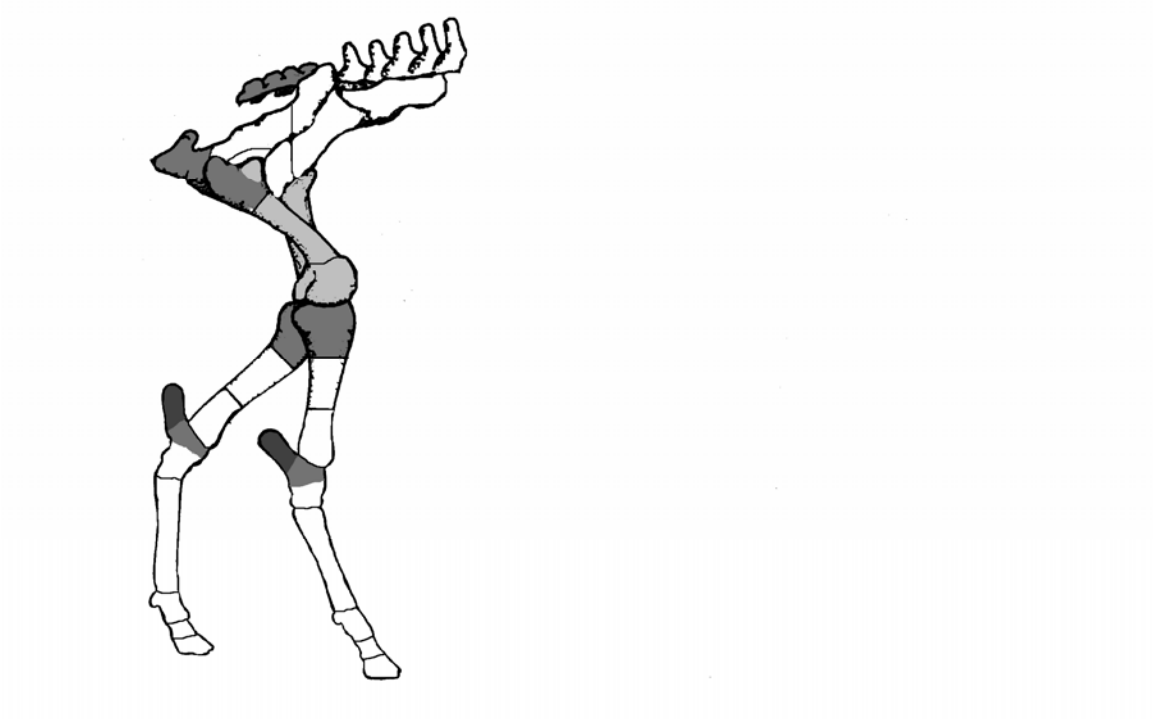


Figure 3.18. Skeletal-wide bone damage and destruction patterns for leopard-modified size 1 and 2 ungulate prey from SGR. See Figure 3.13 caption for more details.



limb shafts, and parts of the mandible. In the lion-modified samples, this also extends to the posterior parts of the innominate, most of the cranium, and the scapula. In both sets of samples as well, the radio-ulnae are destroyed, while the tibiae are unmodified. The low levels of damage by spotted hyaenas on the cranium and parts of the cervical vertebrae may result from the unusual spotted hyaena ecology at SGR. Captive and naturalistic studies of spotted hyaena bone modification both document higher levels of gross bone damage and destruction than seen here (e.g. Blumenschine, 1986a; Binford *et al*., 1988; Hill, 1989; Marean *et al*., 1991). The more minimal lion damage recorded on thoracic and lumbar vertebrae may be the result of my methodology, as I do not record the destruction of each individual vertebra.

Additionally, these patterned similarities extend to size 1 and 2 hindlimb carcass parts modified by leopards, and size 3 and 4 carcasses modified by lions (Figures 3.17 and 3.18). The two main differences in the data depicted by these figures are the higher levels of leopard damage to the calcaneum and other tarsals, which may be due to the nature of the samples (they were skinned, allowing access to the ankle joint), and the higher levels of lion damage to parts of the innominate and the lumbar vertebrae, which could be due to either leopard satiation after consuming flesh and within-bone nutrients from the distal limb elements, or to the leopard's physical discomfort, distress, or inaccessibility to these elements due to their particular position when they were tied to the tree. I observed both lions and spotted hyaenas lurking around the tree more than once, seemingly waiting for the leopard bait to fall, and this impending inter-specific competition may have caused the leopard to abandon the hindlimb without more fully consuming the flesh on the innominate and lumbar vertebrae.

These observations demonstrate that spotted hyaena damage and destruction of size 3 and 4 carcasses mirrors the location and intensity of damage inflicted by lions on size 1 and 2 carcasses, while lions damage the same bones to a similar extent on size 3 and 4 carcasses that leopards damage on size 1 and 2 carcasses. This was noted by Richardson (1980), and discussed in further detail by (Pobiner and Blumenschine, 2003:124): "This patterning suggests the existence of a simple mechanism underlying the degree of skeletal reduction inflicted by modern carnivores when extracting flesh and within-bone edible tissues: the increased bone size and strength of larger carcasses imposes greater mechanical constraints to nutrient extraction that can only be overcome by carnivores with greater jaw strength and dental adaptations to bone eating."

Discussion

Taxon-Specific Carnivore Gross Bone Damage and Destruction

There have been relatively few studies focusing specifically on carnivore gross bone damage and destruction to different skeletal elements and portions by larger African carnivores. Some studies report data on accumulation of prey bone remains in dens/lairs or scats (e.g. Simons, 1966; Henschel *et al.*, 1979; Skinner *et al.*, 1980; Andrews and Nesbit-Evans, 1983; Skinner and van Aarde, 1991; Skinner *et al.*, 1998; deRuiter and Berger, 2000; Pickering, 2001), or actual prey consumption amounts, methods or rates (e.g. Kruuk, 1972; Schaller, 1972; Bearder, 1977; Kingdon, 1977; Skinner *et al.*, 1980; Henschel and Tilson, 1988; Skinner and Smithers, 1990). Those studies that do focus on carnivore damage and destruction offer mainly qualitative, sometimes anecdotal descriptions of gross bone damage to a few skeletal elements or portions, or only report

deletion/destruction of bones and not systematic, *quantitative* patterning of damage and destruction (e.g. Brain, 1969, 1981; Miller, 1969; Sutcliffe, 1970; Shipman and Phillips-Conroy, 1977; Haynes, 1980, 1981a, 1983; Maguire *et al.*, 1980; Richardson, 1980; Kent, 1981; Bunn, 1983; Richardson *et al.*, 1986; Binford *et al.*, 1988; Hill, 1989; Milner and Smith, 1989; Cruz-Uribe, 1991; Marean and Spencer, 1991; Morey and Klippel, 1991; Lam, 1992; Marean *et al.*, 1992; Hudson, 1993; Phillips, 1993; Villa and Bartram, 1996; Arribas and Palmqvist, 1998; Domínguez-Rodrigo, 1999; Palmqvist and Arribas, 2001). Some of these studies are in less controlled modern or even fossil settings, where the agents of bone modification are assumed, but not securely known. These studies are important precedents, and can be useful in characterizing general patterns of carnivore bone modification. However, they are not as valuable for diagnosing taxon-specific carnivore damage in the fossil record as this more controlled study in which the carnivore consumer is known with a high degree of certainty.

There are a few reasons why the damage levels on some bone portions at NAO might be higher than SGR (see Tables 3.3 and 3.5). These reasons include, but are not limited to: the ability to access and/or do more damage to bone portions due to butchery for feeding preparation; carnivore boredom or object-centered play (Haynes, 1982); longer gnawing time, reflecting an overcompensation for relatively weaker jaws than their wild counterparts (Haynes, 1981a); and lower inter- and intra-specific competition, possibly leading to more time available for consumption and smaller amount of food available. These hypotheses are neither mutually exclusive nor testable with my sample. Number of carnivore consumers seems not to have been a factor, as the two samples in which two lions had access to the bones, NAO 17 and 24, did not have systematically

higher damage and destruction levels than other samples of similar bones and portions modified by a single lion. Haynes (1981a) argues that the major differences between gnawing by captive carnivores and their wild counterparts are differences in motivation (hunger, urge for exercise) and amount of soft tissue available on the bone; the latter pertains less to my study, as the captive carnivores were normally fed fully fleshed bones. Given these general similarities but potential differences between samples modified by free-ranging and captive carnivores, I focused mainly on the SGR sample in the analyses and ensuing discussion. The samples from NAO are best treated as an example of the maximum gross bone damage and destruction possible by particular carnivores on different sized prey.

The scaling in gross bone modification and destruction with increasing carcass size and bone-eating capabilities documented here suggests that general taxon-specific patterns of skeletal element and portion survival can be diagnosed for modern carnivore consumers on particular carcass sizes. These patterns are depicted in Figures 3.15 – 3.18. If the bone destruction capabilities of fossil carnivores can be specified, it should then be possible on the basis of fossil skeletal element and portion profiles to eliminate particular carnivore taxa from consideration as the last modifiers of bones from individual carcass size classes. This has important implications for identifying the carnivore species involved with a fossil assemblage. For clear examples: leopard (and most probably cheetah)-like felids and jackal-like canids, and lion-like felids, can be excluded as agents of fragmentation of limb shafts on size 1/2 and size 3/4 carcasses, respectively. Conversely, for size 3 and larger carcasses, large hyaenids are the only carnivores

capable of destroying long bone shafts, severely reducing and fragmenting the mandible, innominate and scapula.

Previous studies have shown that age of an animal at death, as well as size, can be a factor in the degree of gross bone damage by specific carnivores. For example, Richardson (1980) notes that unfused epiphyses of juvenile prey are easily chewed off by various carnivores. Figures 3.3 and 3.5 illustrate that lions inflict more damage to sub-adult versus adult bones of size 3 and 4 animals. Therefore, both size and age should be taken into account when assessing gross bone damage and destruction patterns, especially of carnivores modifying larger sized prey, and when trying to identify the carnivore responsible for damage to a particular bone element or portion. However, my sample size of juvenile carcasses of size 3 and 4 animals is insufficient to fully address this issue.

The number of lion consumers seems to have some effect on bone damage level (Figures 3.4 and 3.7). However, this effect is not strong enough to have predictive value regarding the absolute or even relative numbers of lions which had access to a carcass. It is possible that in reality this effect is strong, but that my lack of longitudinal observation of carcass consumption prevented me from collecting the data to demonstrate this. SWT 021, a zebra fed on by 12 lions (the largest group size in my sample), does have higher levels of damage on the hindquarters and forequarters than most of the other samples. Unfortunately, this sample was also a juvenile, which means I cannot discriminate between age and consumer number as the more important factor in the higher damage levels exhibited on this sample.

Ideally, gross bone damage and destruction level data could be related to remaining edible tissue data (relative amounts of flesh, marrow, and brains) in order to

identify if there is the predictive relationship of the former from the latter. If there is a predictive relationship between gross bone damage level and edible tissue remaining for particular bones or bone portions, then it might be possible to construct hypotheses about the amount of edible tissue available from a fossil bone based on the amount of carnivore damage that bone has sustained. This could then be extrapolated on a bone-by-bone basis to an archaeofaunal assemblage exhibiting carnivore and hominin damage, to characterize the amounts and types of edible resources scavenging hominins could have encountered. Ultimately, relative amounts and types of edible tissues available to hominins which influenced different archaeofaunal assemblages could be compared. Unfortunately, the edible tissue data I collected was on a coarser scale (skeletal element) than the gross bone damage and destruction data (skeletal element portion), and was not collected systematically. In the future, I plan to collect systematic data on both edible tissue availability and gross bone damage level by bone portion, to test the hypothesis that there is a relationship between these two variables.

As suggested by Lyman (1984), I document that a carcass size threshold is passed beyond which a carnivore ecomorph (size/chewing capabilities) is capable of destroying bones. It is assumed that density conditions bone durability and therefore determines the ability of a skeletal element or portion to withstand carnivore damage and destruction (Lyman, 1984, 1993; Klein, 1989; Marean, 1991; Marean *et al.*, 1992; Lam *et al.*, 1999; but see Richardson, 1980; Garvin, 1987, cited in Lyman, 1993; and Klippel *et al.*, 1987 for contradictory results; see Lyman, 1993 for a thorough discussion). Although most of my size 3/4 carnivore-modified prey samples are zebra, their bone density is generally similar to that of bovids and cervids (Lam *et al.*, 1999). Therefore, these results can be

applied to assemblages consisting of both artiodactyls and perissodactyls. In fact, in some bone portions, equid absolute density is slightly lower than in bovids, so the bone modification patterns outlined here may be slightly depressed when compared with size 3 and 4 bovids. As Lam *et al.* (1999) note, no published study has presented data in sufficient enough detail to detect any differential treatment of equid elements by carnivores, though they do occur in modern and fossil hyaena den assemblages (e.g. Hill, 1989; Klein *et al.*, 1991; Villa and Bartram, 1996).

Bone Damage and Bone Density

Two hypotheses now arise. 1) Lion damage to zebra bones is correlated with bone density. 2) Therefore, bone density is likely to be an underlying factor in differential intra-ecomorphotype carnivore damage and destruction patterns. I can test these hypotheses using intra-element bone density data from Lam *et al.* (1999) and the damage and destruction data presented here (Table 3.6, Figure 3.19). If the second hypothesis is supported, bone damage levels should decrease with bone density.

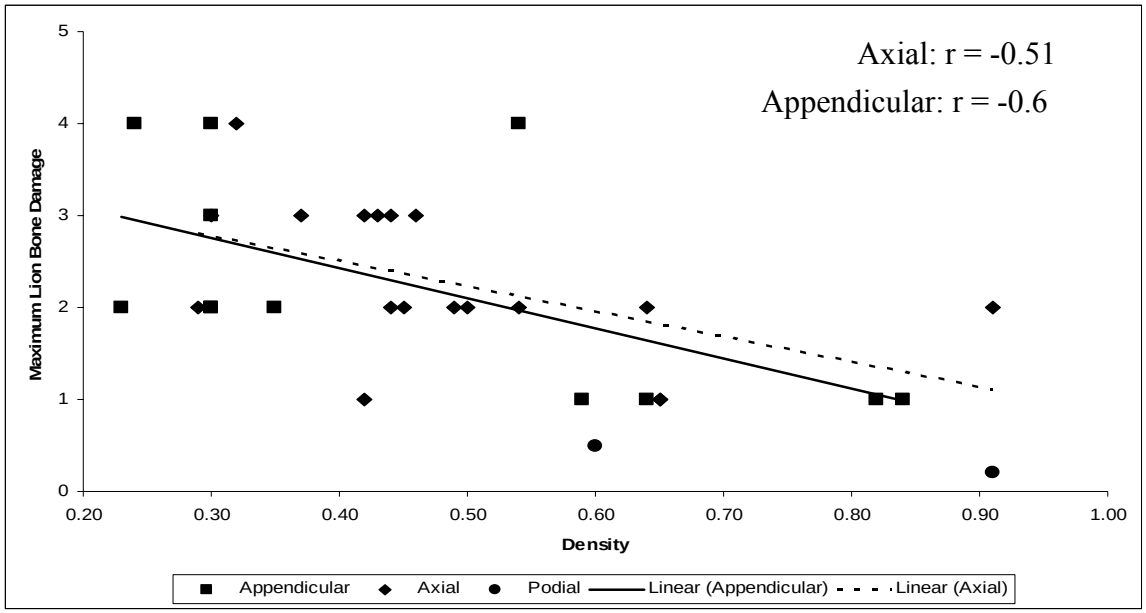
Table 3.6. A comparison of equid bone density data and lion bone damage and destruction patterns on adult equid bones. Bone density data are from Lam *et al.* (1999: 351-353, Table 1). Scan sites are from Lam *et al.* (1999: 348-349). Some of the scan sites are averaged to get a composite density for a particular skeletal element; this is indicated in the scan site(s) column by multiple scan sites separated by commas. The cranium and patella are excluded, as they were not analyzed by Lam *et al.* (1999). Median adult only lion damage level is derived exclusively from SGR, and was calculated following methods described in the text.

Equid Skeletal Element/Portion	Scan Site(s)	Mean Bone Density	Median Adult Only Lion Damage Level
HINDQUARTER			
Greater Trochanter	FE7	.24	0.88
Femur Head	FE1	.35	1.14
Proximal Femur	FE2	.30	1.40
Femur Shaft	FE4	.59	0.67
Distal Femur – Patellar Groove	FE6	.30	2.00
Distal Femur – Condyles	FE6	.30	1.14

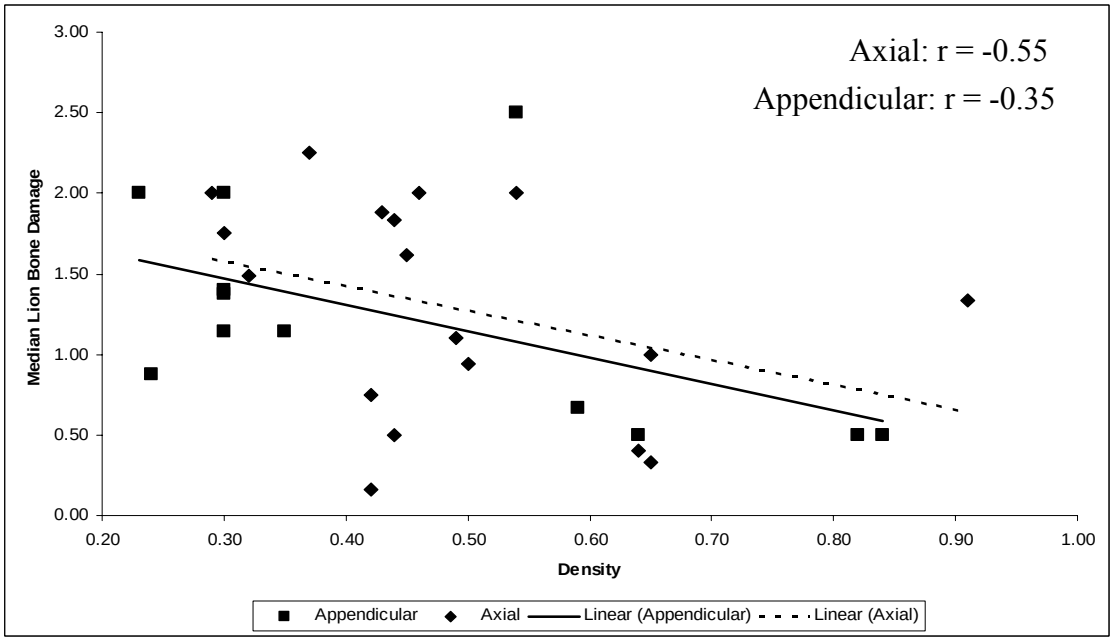
Proximal Tibia	TI1	.30	1.38
Tibia Shaft	TI3	.82	0.50
Distal Tibia	TI5	.45	0.00
Iliac Blade	IL1	.29	2.00
Posterior Innominate	PU2	.42	0.75
Pubic Region	PU1	.44	0.50
Ischial/Pubic Base	IS2	.30	1.75
Acetabulum	AC1	.65	1.00
Sacrum	SC1, SC2	.37	2.25
Lumbar Centra	LU1, LU2	.45	1.62
Lumbar Processes	LU3	.43	1.88
FOREQUARTER			
Scapular Blade	SP2, SP3, SP4, SP5	.54	2.00
Scapular Glenoid	SP1	.64	0.33
Proximal Humerus	HU1	.23	2.00
Humerus Shaft	HU3	.64	0.50
Distal Humerus	HU5	.36	0.00
Olecranon Process (Ulna)	UL1, UL2	.54	2.50
Proximal Radio-Ulna	RA1, RA2	.44	0.00
Radio-Ulna Shaft	RA3	.84	0.50
Distal Radio-Ulna	RA4, RA5	.43	0.00
Ribs	RI1, RI2, RI3, RI4, RI5, RI6	.46	2.00
Thoracic Centra	TH1	.32	1.10
Thoracic Neural Process	TH2	.49	1.49
Cervical Centra	CE1	.50	0.16
Cervical Processes	CE2	.42	0.94
PODIALS			
Calcaneum	CA1, CA2, CA3, CA4	.60	0.50
Astragalus	AS1, AS2	.66	0.00
Other Tarsals	Cuboid, Fibula, Navicular	.60	0.00
Proximal Metatarsal	MR1	.59	0.00
Metatarsal Shaft	MR3	.91	0.20
Distal Metatarsal	MR5, MR6	.59	0.00
Posterior Phalanges	P11, P12, P13, P21, P22, P23, P31	.62	0.00
Carpals	Cuneiform, Lunate, Magnum, Scaphoid, Unciform	.62	0.00
Proximal Metacarpal	MC1	.55	0.00
Metacarpal Shaft	MC3	.84	0.00
Distal Metacarpal	MC5, MC6	.58	0.00
Anterior Phalanges	P11, P12, P13, P21, P22, P23, P31	.62	0.00
HEAD			
Atlas/Axis Bodies	AT1, AX2	.44	1.83
Atlas/Axis Processes	AT2, AT3, AX1, AX3	.49	0.00
Mandible Gonial Angle	DN6	.64	0.40
Mandible Ascending Ramus	DN7, DN8	.91	1.33
Mandible Horizontal Ramus	DN1, DN2, DN3, DN4, DN5	.62	0.00

Figure 3.19. Relationship between zebra skeletal element/portion bone density and bone damage inflicted by free-ranging lions. Appendicular elements include upper and intermediate limb bones; axial elements include the innominate, scapulae, vertebrae, ribs, and mandibulae. Each data point is a bone element or portion as listed in Table 3.6. The distal tibia, distal radio-ulna, and podials are excluded, as lions do not usually damage these bones (except the calcaneum). All zebra are adult. Figure 3.19a represents maximum lion damage (only measured to whole numbers, explaining the more segmented appearance of these data), and Figure 3.19b represents median lion damage (calculated to two decimal places). Damage level descriptions are listed in Table 3.2.

(a)



(b)



The correlation between maximum bone damage and bone density is statistically significant ($r = -0.56$, $p = .001$). Additionally, the correlation between median bone damage and bone density is statistically significant ($r = -0.50$, $p < 0.01$). Therefore, the first hypothesis is supported; bone density is likely to be an underlying factor carnivore gross bone damage and destruction patterns. When bones are divided into skeletal groups (axial and appendicular), bone portion density is significantly correlated to maximum bone damage level in both groups (Figure 3.19a: $r = -0.51$, $p = 0.03$ – axial; $r = -0.60$, $p = 0.04$ - appendicular), but not to median bone damage level in either group (Figure 3.19b: $r = -.55$, $p = 0.07$ – axial; $r = -0.35$, $p = 0.15$ – appendicular).

Why does this relationship not hold up when bones are divided into skeletal groups? It is likely that there is a combination of structural, anatomical, behavioral, ecological, and energetic factors which complicate the relationship between bone density and median lion bone damage within skeletal groups. Bony projections such as the ulnar olecranon process and sacrum are likely accessed first during flesh consumption, irrespective of their relative density, potentially confounding this relationship. The amount and distribution of meat on the skeleton, which is what the flesh-specialist felids are presumably interested in, may condition bone damage levels. Perhaps the bones with smaller muscle masses are more likely to be damaged due to the higher likelihood of the lions hitting bone earlier during feeding; or, perhaps those with larger muscle masses are more attractive, causing them to sustain heavier damage during feeding. The number, age, and sex of lions could condition bone damage levels, as could inter- and intra-specific competition levels (e.g. Behrensmeyer and Pobiner, 2004), which may condition median bone damage levels more than maximum bone damage levels. When lion flesh

consumption is less complete it is likely that these above factors will work, either individually or in combination, to diminish the intensity of bone damage on particular bone portions independent of the density of those portions.

Energetically, it is possible that lions are in fact interested in the grease and/or bone marrow of zebra, though bone marrow is a less likely attraction since they cannot fragment zebra long bones. Zebra bone marrow yields are relatively much lower than those of equivalent sized bovids, due to their higher density of trabecular bone in their limb shafts (Blumenschine and Madrigal, 1993; Outram and Rowly-Conwy, 1998). Interestingly, the Hadza prefer the meat and bone marrow of zebra, believing the marrow is of high quality, even though there is less of it than similar sized bovids; they consistently bring their bones back to camp and reserve the marrow for children, and prefer their meat (O'Connell *et al.*, 1988; Bunn, 1993; Oliver, 1993). Differences in fat qualities are generally recognized by human consumers (Binford, 1978; Levine, 1998), and other contemporary people also prefer equid meat and marrow (Levine, 1998). The likely underlying nutritional mechanism for this preference is a relatively high proportion of essential fatty acids in equid tissues (Lam *et al.*, 1999).

Models of Fossil Carnivore Gross Bone Damage and Destruction

The results of this study allow modeling of relative gross bone damage and destruction capabilities of fossil carnivores, based on those capabilities for modern carnivores derived from two parameters of their fundamental feeding niche: tissue specialization (flesh versus bone), and bone destruction capabilities (minimal versus intense) following Pobiner and Blumenschine (2003). This will be explored further later in this dissertation. I will focus here on sabertoothed felids and their potential bone

modification capabilities, based on that of modern felids, especially cheetahs, as these two flesh-specialist felid groups may have similar bone modification capabilities.

Modern African cheetahs weight an average of 27 kgs. They live alone or in small groups of mothers and cubs, or sometimes 2-3 brothers. They prefer open habitats; and prey mainly on prey weighing < 60 kgs of size 2 and much less often size 3 prey, which are usually juveniles (Kruuk and Turner, 1967; Pienaar, 1969; Eaton, 1970; Schaller, 1972; Kingdon, 1977; Estes, 1993; Phillips, 1993). Few observations of cheetah bone modification have been made, and most are unsystematic. Kingdon (1977) says cheetahs do not eat skin or bones, but Skinner and Smithers (1990) and Phillips (1993) document consumption sequences for cheetah, and the former say that if the prey is very small, they might eat the skin and/or bones.

The only systematic observations of cheetah bone modification under controlled circumstances have been done by Brain (1981) and Phillips (1993). Brain (1981) compares the consumption and damage patterns of bovid and primate skeletons fed on temporarily captive cheetahs. He notes that the cheetahs did very little damage to the skeletons of the size 2 bovid carcasses provided as prey (sheep, bushbuck, springbok and impala), and observed that damage was restricted to the distal ribs, scapular blades, and vertebral processes. He observed similar levels of damage on skeletal remains of prey eaten by wild cheetahs. Phillips (1993), who also documented wild and captive cheetah consumption, found slightly higher gross bone damage levels in his samples than Brain (1981). He observed that wild cheetahs consume the entire skeleton, except the skull, of prey weighing <10 kg (adult steenbok or springbok fawns). They also consumed up to over 75% of the ribcage of an adult springbok, and partially consumed the thoracic neural

spines and the scapular spines. In his study, captive cheetahs partially consumed the ribs of all goat and sheep samples, and one cheetah fully consumed several vertebrae of one of the samples (Phillips, 1993). Pobiner and Blumenschine (2002, 2003) also document maximum levels of bone modification to bones from size 1 prey by wild cheetahs. They found that for hindquarters, cheetahs destroyed the greater trochanter of the femur, and the patella; they heavily gnawed lumbar vertebral processes, and marginally gnawed the distal femur, proximal tibia, iliac crest, posterior innominate, and sacrum (Pobiner and Blumenschine, 2003). For forequarters, cheetahs destroyed the ribs, sternum, and thoracic neural processes, heavily gnawed the scapular blade, and marginally gnawed the proximal humerus (Pobiner and Blumenschine, 2002).

Machairodontinae, the subfamily including the sabertoothed species, includes three tribes: the Smilodontini, including the American genus *Smilodon* as well as the "dirk-toothed" *Megantereon*; the Homotheriini, which includes *Machairodus, Amphimachairodus, Lokotunjailurus*, and the "scimitar-toothed" *Homotherium*; and the Metailurini, which includes *Adelphailurus, Metailurus*, and the "false sabertooth" *Dinofelis* (Antón and Turner, 1997). These different genera are grouped together here for purposes of simplicity; more specifics on their ecology and behavior are presented in the Chapter 5. In general, they are similar in body size to modern lions or tigers (Antón and Turner, 1997), though the African *Megantereon* is much smaller than the European form and is between modern lion and leopard body size (M. Lewis, pers. comm.). They likely live in more closed environments (Gonyea, 1976; Van Valkenburgh, 1987; Marean, 1989), though this is debated (Martin, 1989; Lewis, 1997; Lee-Thorpe *et al.*, 2000). While they actual method of killing is debated and was likely unique (Biknevicius *et al.*,

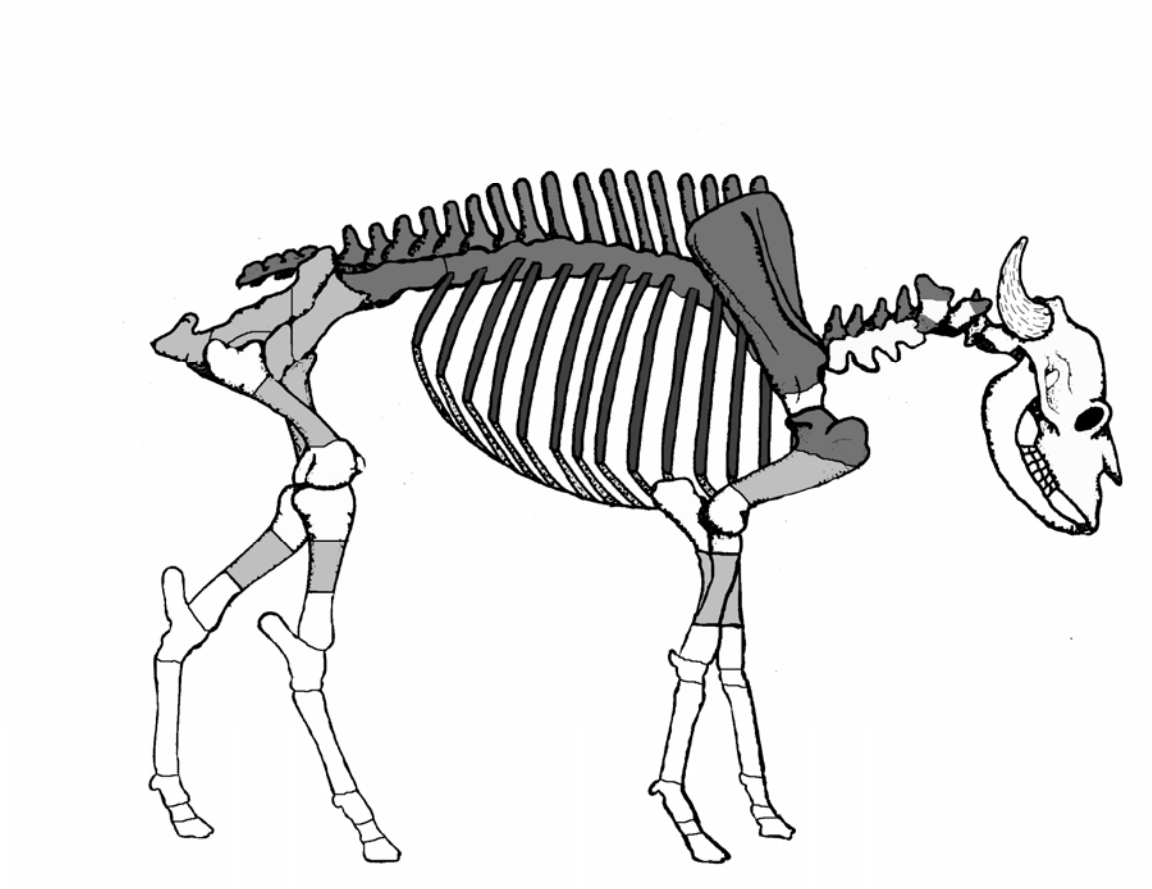
1996), they probably preyed on medium to large-sized ungulates, possibly specializing on juveniles very large ungulates (Matthew, 1910; Bohlin, 1940; Kurtén, 1952; Ewer, 1973; Akersten, 1985; Marean, 1989; Rawn-Schatzinger, 1992; Marean and Ehrhardt, 1995; Palmqvist *et al.*, 1996; Antón and Galobart, 1999) and generally taking prey of relatively larger size than their Felinae counterparts (Emerson and Radinsky, 1980). Their social structure is debated (cf. Marean, 1989; Lewis, 1997), with some researchers finding evidence for sociality, especially in "den" deposits (Gonyea, 1976; Marean and Ehrhardt, 1995). Conversely, Rawn-Schatzinger (1992) interprets *Homotherium serum* from Friesenhahn Cave in Texas to have been a solitary predator because: 1) modern felids that use dens tend to be solitary; 2) space limitations in dens do not favor large groups; and 3) the lack of healed fractures seen in the La Brea *Smilodon* suggests group hunting was not occurring. However, Marean and Ehrhardt (1995) counter that 1) most extant large cats are solitary and this criteria is not useful in evaluating relationships between sociality and denning; 2) large groups of spotted hyaenas or wolves sometimes use dens with small amounts of space; and 3) animals that live in groups such as hyaenas and lions do not tend to the needs of injured conspecifics. Whether sabertoothed felids were solitary or social may not have had a significant effect on the level of gross bone damage they inflicted, as number of consumers seems not to predictably affect gross bone damage levels in lion-modified samples (Figures 3.4 and 3.7), although number of lions does seem to affect the amount of edible tissue consumed (Figure 2.20, Blumenschine, 1986a).

A combination of a) previous studies on cheetah bone modification on size 1 and 2 carcasses (Brain, 1981; Phillips, 1993; Pobiner and Blumenschine, 2002, 2003) and my observations of captive cheetahs feeding on size 4 carcass parts; b) details of sabertooth

ecology and behavior (above paragraph), and c) observations of sabertoothed felid tooth mark frequencies (Marean and Ehrhardt, 1995), these can be used to model potential sabertoothed felid gross bone damage capabilities. This model is presented in Figure 3.20. This figure is similar to Figure 3.17, which documents lion damage to generally similar sized prey. Some researchers argue that sabertoothed cats had weaker bite forces than modern felids (e.g. Kurtén, 1952; Matthew, 1910) and may have avoided contact with bone during feeding to avoid breakage of their long, narrow canines (Akersten, 1985; Anyonge, 1996; Biknevicius and Van Valkenburgh, 1996; Bohlin, 1940; Emerson and Radinsky, 1980; Gonyea, 1976; Kurtén, 1952; Martin, 1980, 1989; Van Valkenburgh and Hertel, 1993; Van Valkenburgh and Ruff, 1987; Van Valkenburgh *et al.*, 1990) and therefore may have inflicted less gross bone damage than hypothesized here. Based on dental microwear evidence, Anyonge (1996) finds evidence for very low proportions of bone in the diet of *Smilodon* based on canines, and Van Valkenburgh and colleagues (1990) specifically assert that *Smilodon* probably consumed less bone than the cheetahs based on carnassials. Additional studies of purported sabertoothed felid accumulations would be useful, with detailed descriptions and quantifications of gross bone damage levels to all skeletal elements, as well as studies of sabertoothed felid cranial and dental functional morphology particularly oriented towards this research question.

Little work has been done investigating the systematics, let alone potential habitat preferences and predatory behavior, of larger Plio-Pleistocene canids mainly due to the paucity of fossil evidence (Lewis and Werdelin, in press). I hope to do experimental work with large canids (e.g. African wild dogs, *Lycaon/Canis pictus*, or wolves, *Canis lupus*) as a model for potential gross bone damage and destruction capabilities of the size 3

Figure 3.20. Hypothetical bone damage and destruction capabilities of sabertoothed felids on size 3 and 4 ungulates. This hypothetical gross bone damage is based on my observations of cheetah damage to size 4 carcass parts from NAO, Brain's (1981), Phillips' (1993), and Blumenschine's (in Pobiner and Blumenschine 2003) observations of captive and wild cheetah damage to entire skeletons of size 2 prey. Damage levels for Brain's and Phillips' samples were inferred based on their descriptions and photographs of damage to size 2 bovid prey by both captive and wild cheetahs (Brain, 1981:24-27; Phillips, 1993:488-490). Tooth marking distribution is based on Marean and Ehrhardt's (1995) documentation of tooth marking on Proboscidea (mammoth/mastodon) and *Homotherium serum* (sabertoothed felid) bones from Friesenhahn Cave in Texas, a Pleistocene den attributable to *Homotherium serum*. Those skeletal elements from Freisenhahn on which tooth marks were found in both taxa over 50% of the time are hypothesized here to exhibit tooth marks. As Marean and Ehrhardt (1995) did not specify on which bone portion they observed these tooth marks, tooth mark presence was indicated here for limb shafts only, and for the anterior and posterior parts of the innominate only, based on results of the current study of the distribution of tooth marks in samples of modern felid-modified carcasses.



canids found in the Plio-Pleistocene fossil record at locales with butchered bone, including *Canis africanus* from Bed II at Olduvai Gorge (Pohle, 1928; Ewer, 1965). However, Lewis and Werdelin (in press, a) note that *Canis africanus* is less dentally hypercarnivorous than the modern African wild dog. Therefore, it might be more appropriate to base a *C. africanus* gross bone damage capability model on a modern jackal, assuming the aforementioned scaling relationship exists, or a modern wolf. I plan to develop this model further in the future. Also, Lewis and Werdelin (in press, a) suggest that this lack of dental hypercarnivory indicates that *C. africanus* is likely to have provided less scavenging opportunities to early hominins than modern African wild dogs. However, they speculate that if hominins developed effective strategies for scavenging larger canid kills in more wooded habitats, where modern spotted hyaenas are less successful in finding them, they may have been a useful resource.

Conclusions

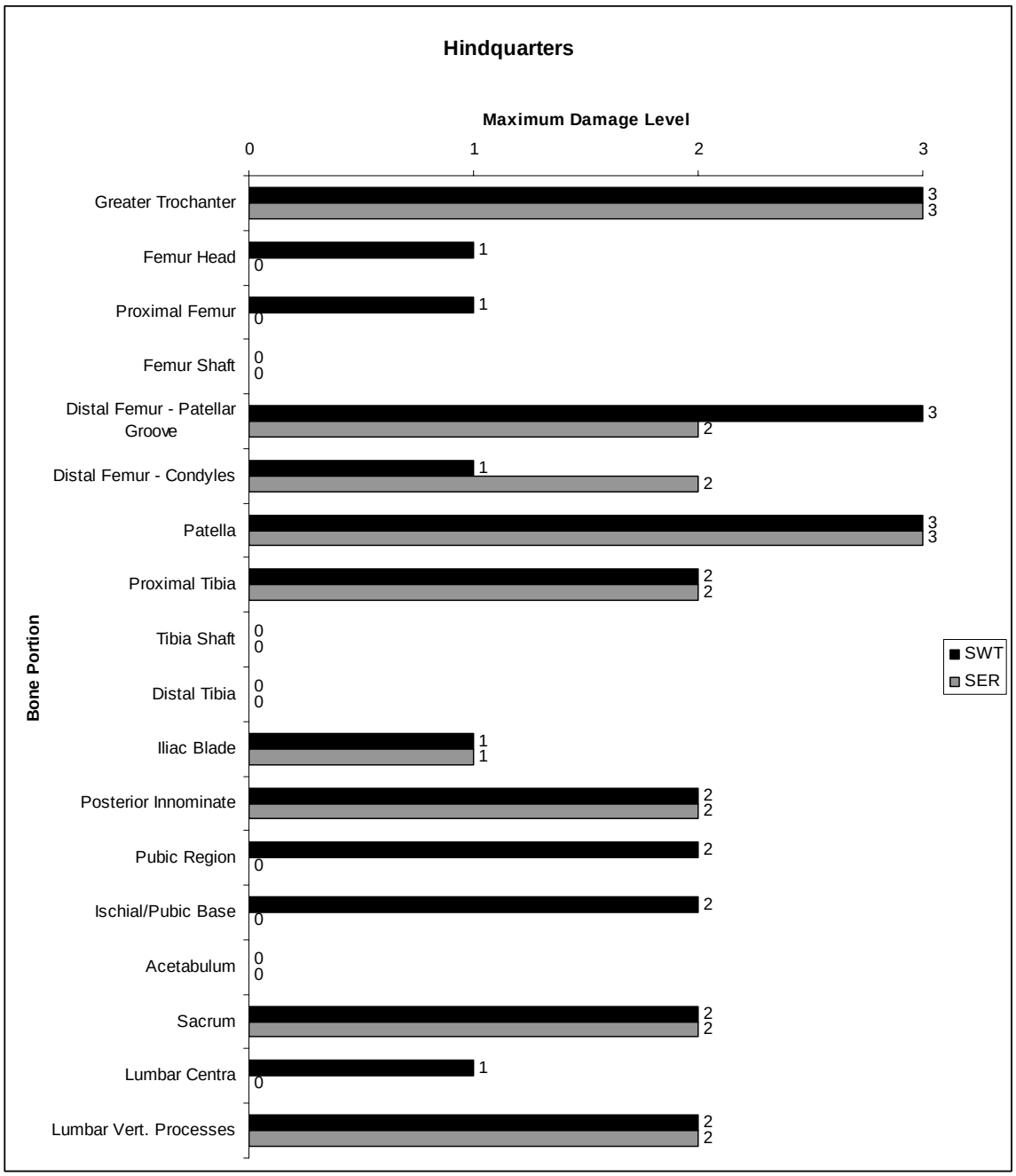
This study is original in its documentation and especially *quantification* of gross bone damage and destruction by larger African carnivores on different sized prey (though see Pobiner and Blumenschine, 2002, 2003 for precedents). In this study, I stress the need to document gross bone damage patterns on a skeletal element and prey size-specific basis, as these two variables most condition carnivore gross bone damage patterns. Carnivore gross bone damage on forelimbs is usually greater than on hindlimbs, and damage generally decreases from upper to intermediate to distal limb elements. Combining all limb elements, or even limb portions, together analytically may mask

important patterning which allows the identification of the carnivore taxon responsible for the damage to an individual bone or a bone assemblage.

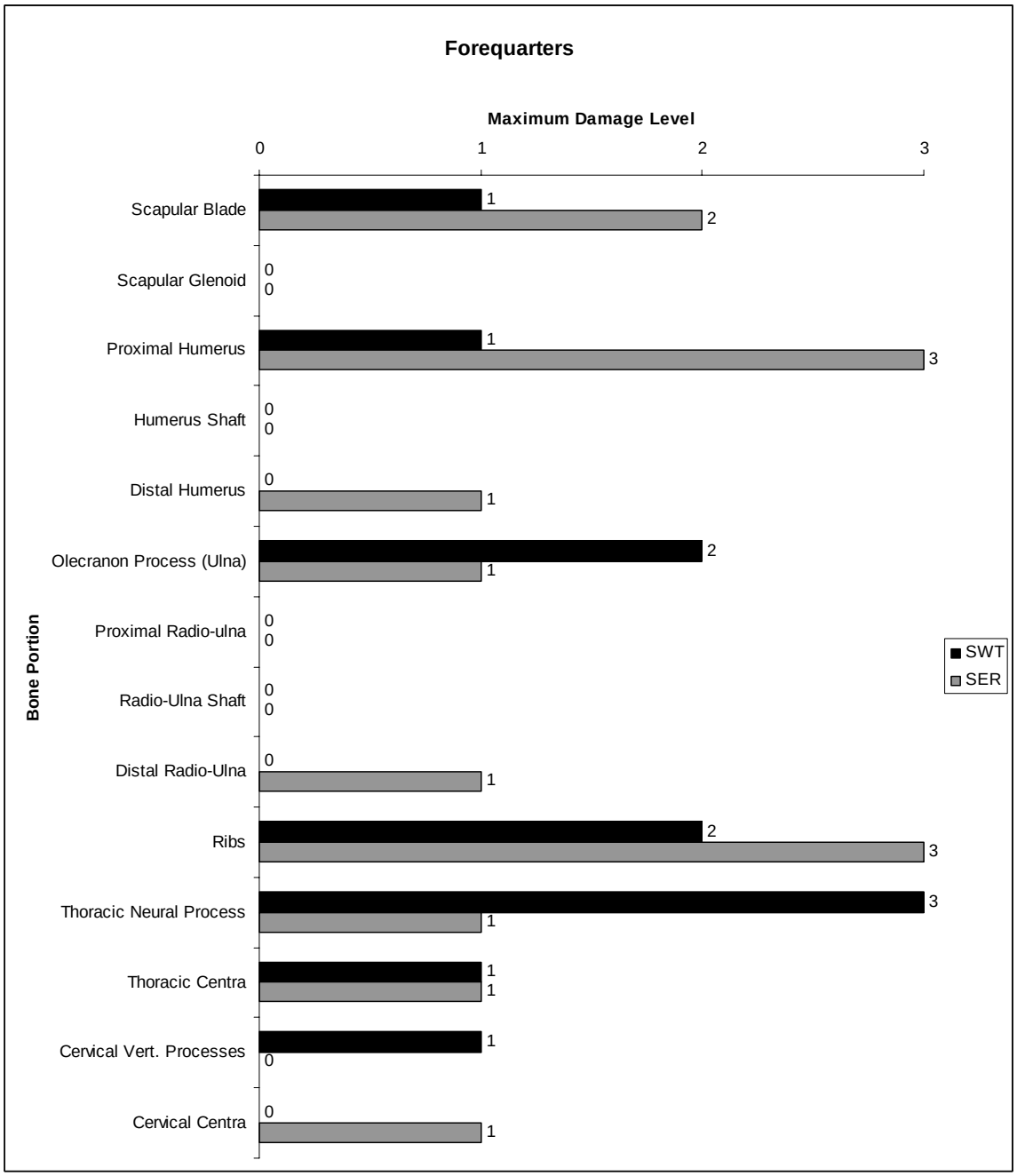
While the focus here has been on median or modal damage levels, the minimum and maximum levels are also important, as they document the *range of capabilities* of carnivores to modify bones of a specific prey size. This study was conducted in a single ecosystem, with particular ecological parameters, including high lion and low spotted hyaena population densities. Other ecosystems, and especially paleoecosystems, likely had differing carnivore densities as well as different species compositions, community structures, and niche packing (cf. Valkenburgh, 1985, 1988, 1989, 1999; Lewis, 1997; Werdelin and Lewis, 2005) leading to different levels of intra- and inter-specific competition. However, despite different ecological parameters, the damage levels found on lion-consumed size 3 and 4 prey at Sweetwaters are similar to that of the Serengeti ecosystem (Figure 3.21). This similarity exists despite the fact that the Sweetwaters samples were all zebra and one eland, which are larger than the wildebeest in the Serengeti sample, and strengthens the utility of the Sweetwaters sample as a model of lion damage capabilities. Still, in some cases, the minimum or maximum bone modification levels seen here may be more appropriate data to use. Additional research on bone modification especially by cheetahs, leopards, jackals, and other canids will help to improve our understanding of gross bone damage capabilities by modern and fossil carnivores. Also, a variety of factors besides carnivore taxon are likely responsible for gross bone damage patterns, including food availability, intra- and inter-specific competition over carcass resources, the amount of edible material within or adhering to a bone, and the social and ecological context of bone damage (Fisher, 1995).

Figure 3.21. Comparison of maximum bone damage levels to lion-damaged ungulate size 3 and 4 hindquarters and forequarters from the Sweetwaters and Serengeti Game Reserves. Unpublished Serengeti data from R. J. Blumenschine. For comparability to the Serengeti data, Sweetwaters data were recalculated, so damage levels are not the same as in previous analyses. Damage levels here are: 0 = unmodified or tooth-marked; 1 = minimally gnawed; 2 = heavily gnawed; 4 = fragmented or destroyed. SWT = Sweetwaters, SGR = Serengeti.

(a)



(b)


Forequarters
Maximum Damage Level
0
1
2
3
Bone Portion
Scapular Blade
Scapular Glenoid
Proximal Humerus
Humerus Shaft
Distal Humerus
Olecranon Process (Ulna)
Proximal Radio-ulna
Radio-Ulna Shaft
Distal Radio-Ulna
Ribs
Thoracic Neural Process
Thoracic Centra
Cervical Vert. Processes
Cervical Centra
SWT
SER

The predator taxon/prey size-specific bone modification patterns here attest to the scaling relationship of gross bone damage levels with increasing prey size and predator specialization on within-bone nutrients. The characterization of this relationship allows zooarchaeologists of identify the last carnivore to modify/fragment particular bones or bone portions. This identification can be extended to an assemblage-level scale, permitting the identification of the carnivores with which hominins interacted over carcass resources, especially in conjunction with tooth mark analyses (which will be presented in Chapter 4). Additionally, the scaling relationship means we can model potential bone modification capabilities of extinct carnivores if we know their body size/edible tissue specialization. This scaling relationship is at least partially dependent on bone density, which underscores again the need to examine particular bone elements and portions as separate data sets in zooarchaeological assemblages.

Chapter Four
Patterns in Carnivore Tooth Marks

Introduction

Modern and fossil bones that bear tooth marks can potentially provide insights into the ecology, behavior, and functional morphology of the predator taxa that produced them (Erickson and Olson, 1996). For example, they can reveal the identity of extinct carnivores, their killing and feeding behaviors, their prey preferences, the degree of competition for a particular carcass or assemblage of carcasses, and the biomechanical capabilities of their jaws and dentitions.

Bone is ingested by present day fishes and sharks, reptiles, birds, and mammals (Erickson and Olson, 1996), and utilization of bone from a carcass by mammals is a common phenomenon in modern terrestrial ecosystems (Fiorillo, 1991). I identified four main activities from a survey of the literature as causing tooth marking on modern and fossil bones:

1. Bone utilization by carnivores, herbivores, and birds as a nutritional source of calcium, potassium and phosphorous (Kruuk, 1972; Mundy and Ledger, 1976; Gauthier-Pilters and Dagg, 1981; Richardson *et al.*, 1986).
2. Bone utilization by carnivores as a nutritional source of bone marrow, grease, and fat (Haynes, 1980; Binford, 1981; Brain, 1981; Blumenschine and Marean, 1993).
3. Bone utilization by rodents for non-nutritive purposes, to wear down their continuously growing incisors (Brain, 1981; Farlow *et al.*, 1986).
4. Flesh utilization by a variety of taxa (including primates, carnivores, dinosaurs, and sharks), leaving incidental tooth marks as occasional by-products.

Such incidental tooth marks have been documented on invertebrate prey, usually on ammonites thought to have been preyed on by mosasaurs (Kaufmann and Kelsing, 1960; Saul, 1979; Mapes and Hansen, 1984; Hewitt and Westermann, 1990; Mapes *et al.*, 1995; Tsujita and Westermann, 1998). However, most of the paleontological literature on tooth marks refers to those purportedly made by extinct mammals (Williston and Moodie, 1917; Welles, 1943; Haynes, 1980; Farlow *et al.*, 1986; Fiorillo, 1988; Sobbe, 1990; Armour-Chelu and Viranta, 2000; Brand *et al.*, 2000; Collinson and Hooker, 2000); sharks (Applegate, 1965; Deméré and Cerutti, 1982; Martin and Rothschild, 1989; Cigala-Fulgosi, 1990; Everhart *et al.*, 1995; Mapes *et al.*, 1995; Schwimmer *et al.*, 1997; Neumann, 2000; Shimada and Everhart, 2004; Shimada and Hooks, 2004); fossil crocodilians (Meyer, 1994; Joyce, 2000; Njau and Blumenschine, 2006); and predatory dinosaurs (Beasley, 1907; Matthew, 1908; Dodson, 1971; Cruickshank, 1986; Carpenter, 1988; Rogers, 1990; Fiorillo, 1991; Rothschild and Tanke, 1992; Currie and Zhao, 1994; Currie and Jacobsen, 1995; Erickson and Olson, 1996; Erickson *et al*,. 1996; Harris, 1998; Naish, 1999). These reports are generally descriptive in nature, and largely assume the identity of the predator that inflicted the tooth marks, rather than demonstrate this identity.

Tooth marks produced by mammalian carnivores, especially bone-crunching hyaenas, have been recognized on bones from Plio-Pleistocene archaeological sites (Maguire *et al.*, 1980; Richardson, 1980; Binford, 1981; Bunn, 1981; Potts and Shipman, 1981; Shipman and Rose, 1983; Wilson, 1983; Milner and Smith, 1989; Cruz-Uribe, 1991; Morey and Klippel, 1991; Cruz-Uribe and Klein, 1994; Blumenschine, 1995; Andrews and Fernandez-Jalvo, 1997; Capaldo, 1997; Monahan, 1996; Marean, 1998;

Marean and Kim, 1998; Milo, 1998; Selvaggio, 1998; Marean *et al*., 2000). Recently, modern and fossil crocodile bone modification has been recognized and described (Njau and Blumenschine, 2006). As well, recent studies of captive and wild chimpanzee bone modification have been made in an effort to characterize primate bone modification and to distinguish primate from carnivore gross bone damage patterns (Pickering and Wallis, 1997; Plummer and Stanford, 2000; Tappen and Wrangham, 2000; Pobiner *et al.*, in review). However, again, most of these studies assume the identity of the carnivore that inflicted the tooth marks, usually naming spotted hyaenas or their ancestors as the culprits.

There are two main types of tooth mark data which have the potential to diagnose the specific carnivore taxa or ecomorphs which have modified zooarchaeological or paleontological assemblages: 1) the proportion and patterning of tooth marking across skeletal elements, and 2) tooth mark morphology. Both of these types of data require actualistic or modern process studies to set a baseline which is then used to interpret data from fossil assemblages (e.g. Blumenschine and Marean, 1993; Blumenschine, 1995). Tooth mark frequency and distribution data have mainly been used to reconstruct the timing of access of carnivores and hominins to Lower and Middle Paleolithic archaeofaunas (Selvaggio, 1994a, 1998; Blumenschine, 1995; Capaldo, 1997, 1998; Marean, 1998; Marean and Kim, 1998; Marean *et al.*, 2000; Egeland *et al.*, 2004). The utility of this type of data to identify the carnivore agent(s) involved with bone assemblages has yet to be investigated.

Normally, tooth marks found on fossil faunas are simply attributed to the most abundant carnivore in the assemblage, or a carnivore (or carnivores) that is assumed to

have the capability of inflicting the tooth marks and gross bone damage (see above). However, zooarchaeologists are increasingly embracing more quantitative methods of identifying the specific carnivore actor(s) that inflicted tooth marks on archaeofaunas, based on measurements of carnivore tooth pits (e.g. Andrews and Fernandez-Jalvo, 1997; Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Pickering *et al.*, 2004). This follows similar recent attempts by wildlife biologists (Pasitschniak-Arts and Messier, 1995; Lyver, 2000) to measure and compare distances between paired canine tooth marks with distances between canine teeth of the relevant mammalian predators for the purposes of identifying small mammal predators of birds and eggs. The zooarchaeological studies mentioned above have a different approach based on measurements of carnivore tooth pits, although Brain measured extant and extinct carnivore canine spacing (Brain, 1970) for his famous demonstration of a close match between spacing of a fossil leopard's canines (SK 349) with punctures on a juvenile australopithecine's parietal bones (SK 54) in an attempt at this direct "matching" approach (Brain, 1981:269). These tooth pit measurements are not usually compared directly to the sizes of modern or fossil carnivore teeth because the exact appropriate measurement location on a tooth of a carnivore taxon that may have created a pit is unclear, though this has been attempted with at least one archaeofaunal assemblage (Lyman, 1994:213). My study also used measurements of tooth pits in an attempt to identify the carnivore taxon responsible for the creation of those pits; this will be discussed in more detail in this chapter.

Mammalian carnivores generally produce tooth marks as a byproduct of flesh consumption and bone fracture for marrow consumption by employing static loading,

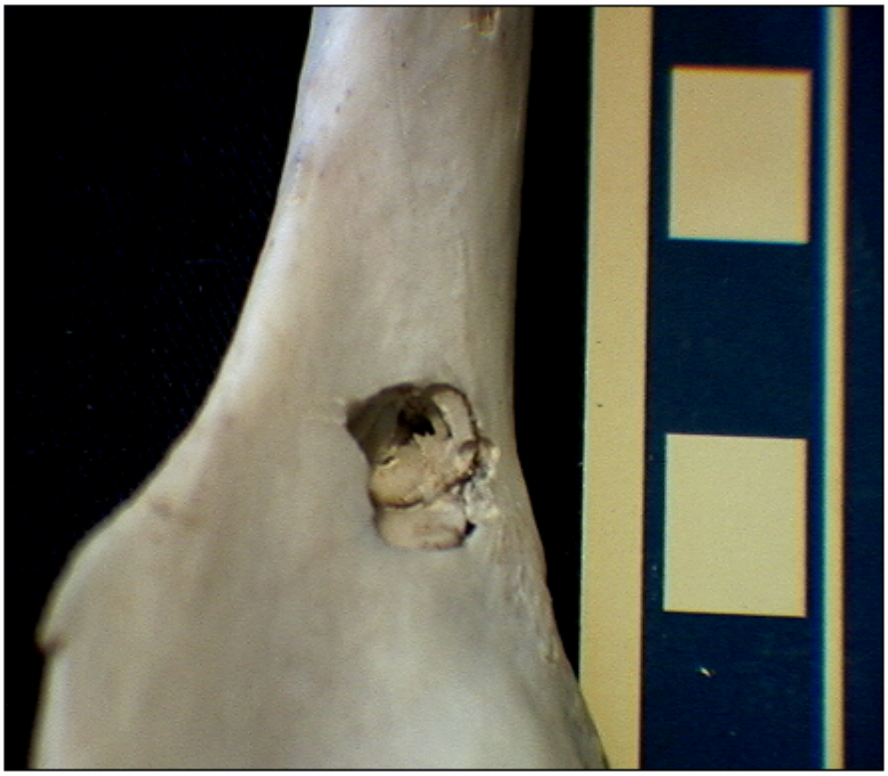
which is "a constant compressive pressure technique that generally employs an even distribution of force" (Fisher, 1995:192). Though they can be confused with other types of bone surface modifications (Haynes, 1981; Fisher, 1995), carnivore tooth marks as a class of bone surface modification are recognizable and differentiated from other types of bone surface modifications after study with experimental collections marked by known actors (Blumenschine *et al.*, 1996). Various definitions and descriptions of carnivore tooth marks have been offered (e.g. Binford, 1981; Haynes, 1981b:435-436; Lyman, 1994:206-212, and citations therein; Fisher, 1995:36-40; Blumenschine *et al.*, 1996:496). I use the following definitions and identification criteria:

1. Tooth *pits* and *punctures* are circular, oval or polygonal marks in plan form with bowl-shaped cross-sections, though crocodile tooth pits can be more angular (Njau and Blumenschine, 2006). They are the result of pressure on the bone surface from a tooth. The internal surfaces of these marks can appear crushed due to flakes of the outer wall of the bone (cortical bone) being pressed into the mark (punctures) or modification of the histological structure of the exposed bone (pits) (Figure 4.1). The key distinction between these marks is that punctures are large marks penetrating the full thickness of compact cortical bone (whether it is the thin compact bone overlying cancellous bone, or the thicker cortical bone of limb shafts, for example) while pits are shallower and smaller, not penetrating all layers of the cortical compact bone. Here, both tooth pits and punctures are defined as having a long axis no more than three times the length of the short axis; if the long axis is longer than this, the mark is classified as a tooth score.

2. Tooth *scores* and *furrows* are linear marks, variable in length, and U-shaped in cross-section, often with smooth bottoms (Figure 4.2). They result from a tooth dragging across

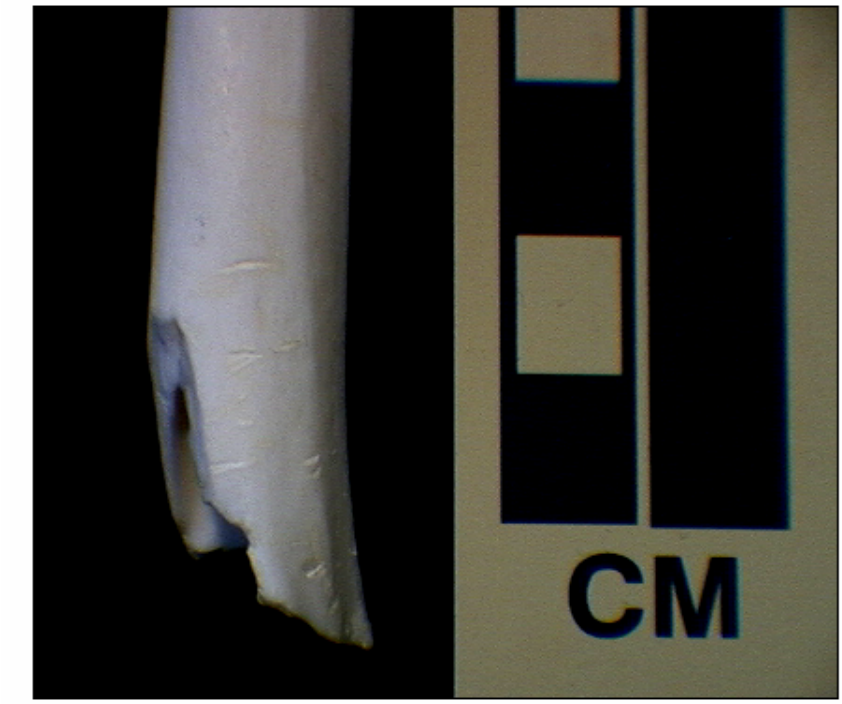
Figure 4.1. Photographs of a lion tooth puncture, tooth scores, and tooth pits on specimens from SGR. A conspicuous lion tooth puncture on a Thomson's gazelle innominate (SWT003-7, a), and less conspicuous lion tooth scores and pits on a Thomson's gazelle proximal metapodial (SWT003-11, b).

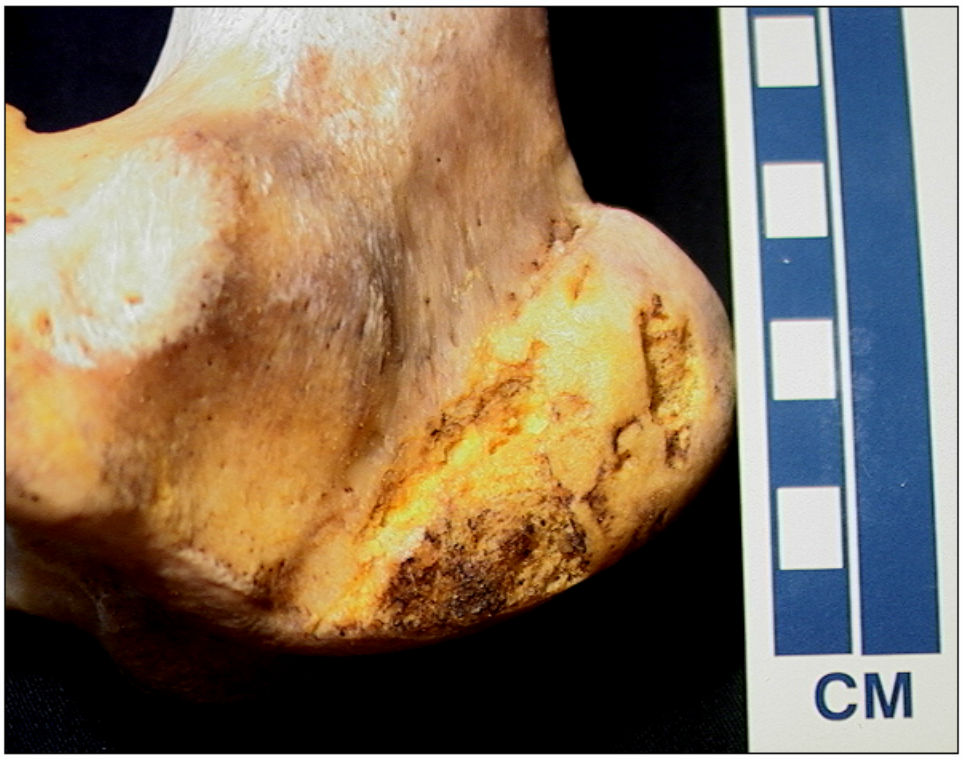
(a)



(b)

Figure 4.2. Photographs of lion tooth scores and furrows on specimens from SGR. Lion tooth scores on a Thomson's gazelle distal tibia (SWT003-24, top) and lion tooth furrows on a zebra distal femur (SWT001-77, bottom).





the surface of a bone. They are analogous in some ways to pits and punctures in that furrows penetrate compact bone and scores do not. They can have a variety of orientations on the bone, but are most often oriented roughly perpendicular or transverse to the long axis of long bones. Any of these tooth marks can occur in isolation or in clusters, possibly the result of a single tooth versus more than one tooth in the tooth row or a multi-cusped tooth creating the mark. Tooth scores are defined as being at least three times as long as they are wide (Selvaggio, 1994b). Tooth furrows are deeper, larger marks that penetrate through the cortical surface of a bone.

The teeth of modern carnivores are presumed to be specialized for different functions. In general, broad, low-cusped molars crack and grind; blade-like carnassials slice flesh and other soft tissues; pointed premolars pierce; and knife-like canines stab (Van Valkenburgh, 1996). Interfamilial differences in dental architecture and cranial and mandibular functional morphology will also affect feeding behavior. For example, felids emphasize the anterior teeth (incisors and canines) as opposed to the posterior teeth (premolars and molars). Even within felids, though, there are interspecific differences: cheetahs have well-developed premolars and carnassials at the expense of reduced canines, while lions have more massive canines and less well-developed anterior premolars. Spotted hyaenas have massive premolars with felid-like carnassials, and moderately developed canines. Wild dogs differ from hyaenas in having molars posterior to the carnassial and a four premolars that are not expanded mediolaterally. Some general predictions from these intra-family differences are that lions and spotted hyaenas will use their premolars for bone cracking, but that wild dogs will use their postcarnassial molars. This is supported by work on differential mandibular cortical thickness in these species,

where the mandibles of spotted hyaenas are buttressed beneath the premolars, but those of wild dogs are buttressed beneath the carcassials and molars (Biknevicius and Ruff, 1992). Carnassials are assumed to be the flesh-slicing teeth in all larger African carnivores (Van Valkenburgh, 1996).

In a study of free-ranging African carnivores (wild dog, spotted hyaena, lion, and cheetah), Van Valkenburgh (1996) found that these predictions were largely supported, and that the use of teeth was not random with respect to the type of food consumed. However, she found that there was not a perfect association between a particular type of tooth and its function, some generalities prevailed. Skin is normally cut by chewing with the carnassials in all species, with the felids also usually using the adjacent premolar. Wild dogs spread the function of skin-slicing fairly evenly among the different teeth. Incisors and canines are normally used by all four species both to separate subcutaneous tissue and muscle from the carcass and to feed on muscle, thought the cheetah used both anterior and posterior teeth for the latter. Bone cracking and consumption by lions was generally done with the premolars and carnassials, while hyaenas used premolars alone or sometimes in concert with the anterior part of the carnassial. Wild dogs used carnassials in combination with post-carnassial molars (as opposed to premolars) most often in muscle and bone consumption as well as bone cracking, which was done especially with post-carnassial molars. These differences could lead to predictions of different tooth mark morphologies created by these different species; for instance, tooth marks created by bone-cracking in lions and hyenas could be expected to be similar to each other, but different from those of wild dogs.

I used a digital video camera to film both wild and captive animals as they fed on fleshed bones in an attempt to link tooth morphology with tooth mark morphology, follwing on Van Valkenburgh's (1996) study, but I ran into similar problems as Shipman and Rose (1983). I could keep the animal's mouth in view and in focus, but could not isolate areas of the bone in which only one type of tooth (of the four: incisor, canine, premolar, and molar) was being used. Therefore, I can only analyze taxon-specific tooth marks in isolation of the feeding behavior or tooth morphology that created them. However, since the ultimate goal of this analysis is to apply the results to fossil assemblages affected by an unknown number and identity of carnivore taxa, this level of resolution is adequate.

Methods

Tooth Mark Frequency and Distribution

Every bone collected from NAO and SGR were examined under high incident, bright light with a 10X hand lens (see Chapter 2 for more methodological details). The following tooth mark data were recorded when a tooth mark was identified:

1. Tooth mark type (pit, puncture, score, furrow)
2. Number of each tooth mark type on each skeletal element and portion. Skeletal elements and portions are defined in Appendix 3. Tooth marks were recorded as being on the proximal or distal surface if they were within 2 centimeters of the actual articular surface, or as defined in Appendix 3. When tooth marks occurred in particularly dense patches (over ~15 marks in a 2cm^2 area), I often found it

difficult to replicate counts of individual tooth marks, and my counts are likely off by approximately +/- 10%.

3. Whether or not there was any tooth mark within approximately 2 cm of carnivore gross bone damage including a fractured or gnawed edge if carnivore gross bone damage was present on that element/portion

All skeletal elements and portions that did not display carnivore tooth marks were also recorded as such.

Both the presence/absence of tooth marks and the actual number of tooth marks on each skeletal element and portion were recorded. This insured the collection of both 'tooth mark-count' data (the actual number of tooth marks on particular elements and specimens), and 'fragment-count' data (the percentage of total specimens yielding at least one tooth mark) (see Abe *et al.*, 2002 for analogous cut mark recording methodology). As some of the samples consist largely of whole bones while others are mainly bone fragments, this seemed like the most appropriate tooth mark data collection method. The data analysis focuses on 'fragment-count' data, since this minimizes potential problems with tooth marks that may be difficult to count accurately. The 'tooth mark-count' data are presented in Appendix 4. Here, then, tooth mark frequency refers to the proportion of bone specimens of a particular sample (e.g., skeletal element) which exhibit at least one tooth mark, rather than the number of tooth marks on a particular bone specimen.

Tooth Mark Morphology

Where tooth mark identification was at all ambiguous, I did not identify the mark as a measurable tooth pit or puncture (for morphological analysis), even though the marks on these bones could not have been caused by any other agent aside from the occasional

recognizable cut mark resulting from preparation of the bones. The following were criteria or mark features which rendered tooth marks unsuitable for measurement:

1. Incipient: only partially crushed; for instance, only one side or wall of the mark is crushed upon inspection with a hand lens. N =32 marks at SGR, none at NAO.
2. Incomplete: one side of the mark is missing, usually on the edge of a bone. N = 14 marks at SGR, N = 3 marks at NAO.
3. Walls not crushed: on occasion, I noted smooth depressions with no crushing evident that likely would not be recognized on fossil bones as tooth pits., N = 12 marks at SGR, N = 2 marks at NAO.
4. Irregular outline: two bones from NAO exhibited a total of six tooth pits with an irregular outline such that I did not think they would be recognized on fossil bones.

I found it more difficult to identify tooth marks on bones of juvenile animals due to their friable surfaces.

I chose to use only linear (versus area) dimensions to distinguish morphology because the measurements required are simple and inexpensive to take as well as easily replicable. Tooth mark area measurements have been analyzed in the past (e.g. Selvaggio and Wilder, 2001), but these require digital image analysis, which is more time consuming and costly. I used 3M Express Vinyl Polysiloxane Impression Material to make tooth mark molds. I measured tooth mark molds with Mitutoyo digital calipers to the nearest hundredth of a centimeter. I chose to measure tooth mark molds rather than actual tooth marks for three main reasons: 1. Margins of tooth marks were sometimes easier to see on the molds than on the marks themselves. 2. Tooth mark molds can be

subsequently measured using a microscope in the future. 3. Tooth mark molds are a re-usable record of both modern and fossil tooth marks which can be analyzed at any time and place. 4. Tooth mark depth can be measured, and cross-sectional shape characterized.

Due to time constraints, I could not measure all of the tooth marks (the total number of tooth marks in my entire sample was nearly 6,000). I chose to measure the largest (longest) score, pit, and puncture on each bone. I measured length and width of tooth scores. Depth of many of the tooth scores was too small to be accurately measured. I measured length (maximum dimension), width (perpendicular to maximum dimension), and depth of tooth pits and punctures. Pit and puncture depth was measured after sectioning each mold with a razor blade at the point of maximum depth. I made two molds of each tooth mark so I could preserve a pristine copy even after sectioning molds for measuring pit and puncture depth for any future microscopic or digital imaging analyses. I measured a total of 328 scores, 198 pits, and 174 punctures. I did not measure furrows due to their relative scarcity. For the tooth mark morphology analyses, I combined the samples from NAO and SGR to increase the sample size of taxon-specific tooth marks. I also combined tooth pits and punctures in some analyses to increase sample size.

I analyzed tooth mark size using linear dimensions (length and width) for tooth scores and tooth pits and punctures, and I also analyzed tooth mark depth for pits and punctures. The focus of the analysis was to determine if different carnivore taxa create different sized tooth marks. However, I also wanted to explore whether prey size, skeletal element, and long bone portion might contribute to tooth mark size. Skeletal element groups were based on bone morphology, and included: 1. axial (cranium, mandible,

vertebra, rib, innominate, scapula); 2. appendicular (femur, tibia, metatarsal, humerus, radius, ulna, radio-ulna, metacarpal); and podial (carpals, tarsals, equid second and fourth metacarpal and metatarsal, suid metapodial, patella, phalange, sesamoid). Long bone portions were epiphysis, near epiphysis, and midshaft. I present descriptive statistics and box plots with 95% confidence intervals and total ranges displayed. I also ran an ANOVA on each data set (predator taxon, prey size, skeletal element group, and long bone portion) to determine if the tooth marks in these different groups were significantly different from each other. Statistical analyses and graphics were done using the program PAST (PAleontological STatistics) version 1.44 (Hammer *et al.*, 2001). Jackals did not create tooth scores in my sample, nor did they do so on long bone epiphyses in another actualistic sample (Domínguez-Rodrigo and Piqueras, 2003).

Tooth Mark Frequency and Distribution: Results

Nairobi Animal Orphanage

The proportion of total bones with tooth marks from the Nairobi Animal Orphanage was generally low (Table 4.1: lion 35%; leopard 19%; cheetah 13%; jackal 4%). Compared with similar sized carcasses from Sweetwaters Game Reserve, bones from carcass parts to which NAO lions had access were much less often tooth-marked (60% at SGR versus 35% at NAO). The reasons for this discrepancy are unclear, especially since damage levels at NAO were relatively higher than at SGR (see Chapter 3). Perhaps the lions at NAO were under lower intraspecific competition, leading to less complete defleshing. Alternatively, the higher representation of podials in the NAO sample, which tend not to be tooth-marked, depress the overall tooth mark proportion. It

Table 4.1. Number of specimens (NISP tooth-marked/total NISP) and proportion of tooth-marked specimens from the Nairobi Animal Orphanage. Abbreviations for skeletal elements are in Appendix 3. N = the number of carcass parts (samples) from which the data were collected. All carcass parts were from size 4 prey (cows). Blank cells indicate that no data on that skeletal part were collected.

	Predator Taxon			
Skeletal Part	Lion (N = 13)	Leopard	Cheetah	Jackal
N	13	4	11	4
MAND				
MAX				
CRAN				
RIB	(16/22) 72%	(0/2) 0%	(0/1) 0%	(0/3) 0%
VRT		(0/2) 0%		(0/3) 0%
C-1		(0/1) 0%	(0/1) 0%	(0/1) 0%
C-2				
CVRT	(2/8) 25%	(2/9) 22%	(3/16) 19%	(0/3) 0%
TVRT	(10/22) 45%	(1/2) 50%		(1/20) 5%
LVRT	(2/7) 29%	(3/8) 38%		(1/4) 25%
SACR		(1/2) 50%	(0/8) 0%	
CAUD		(0/3) 0%		
INN	(4/4) 100%		(1/7) 14%	(0/3) 0%
SCAP			(4/11) 36%	(0/6) 0%
Axial Bones (subtotal)	**(34/63) 54%**	**(7/29) 24%**	**(8/54) 15%**	**(2/43) 5%**
HUM	(3/3) 100%		(4/7) 57%	
FEM	(5/8) 63%	(0/1) 0%	(0/1) 0%	(0/2) 0%
RADU	(3/3) 100%		(2/6) 33%	
RAD				
ULN				
TIB	(5/7) 71%		(0/1) 0%	
MP				
MT				
MC				
LB	(1/1) 100%		(0/1) 0%	(0/1) 0%
Limb Bones (subtotal)	**(17/22) 77%**	**(0/1) 0%**	**(6/16) 38%**	**(0/3) 0%**
PAT	(0/1) 100%	(0/1) 0%		(0/1) 0%
FIB	(0/6) 0%		(0/1) 0%	
CARP	(1/15) 7%		(0/35) 0%	
TARS	(0/1) 0%			
CALC	(3/7) 43%		(0/1) 0%	

AST	(0/7) 0%		(0/1) 0%	
NAVC	(0/6) 0%		(0/1) 0%	
PHA				
PHA1				
PHA2				
PHA3				
SES	(0/1) 0%			
Compact Bones (subtotal)	**(4/44) 9%**	**(0/1) 0%**	**(0/39) 0%**	**(0/1) 0%**
NID	(3/29) 10%	(0/6) 0%	(0/11) 0%	(0/2) 0%
TOTAL	**(55/158) 35%**	**(7/37) 19%**	**(14/109) 13%**	**(2/49) 4%**

is also possible that bone portions which became tooth-marked during consumption were subsequently destroyed, leading to higher damage levels coupled with lower tooth mark frequencies. The possible relationship between gross bone damage, fragmentation, and the proportion of tooth-marked skeletal elements will be explored more fully later in this chapter. Regardless of the reason for the discrepancy, the main focus of the rest of the tooth mark frequency and location analyses will be on the data from SGR.

Sweetwaters Game Reserve

1. Carcass-Wide Tooth Mark Frequency and Location

The number or frequency of tooth-marked specimens (represented as % NISP tooth-marked for each skeletal element) varies widely both within and between predator/ prey size samples, from 0% to 100%. In the size 3/4 samples, axial bones are more frequently tooth-marked than limb bones, which are in turn more frequently tooth-marked than compact bones (Tables 4.2 and 4.3, Figure 4.3). Compact bone tooth marks were particularly scarce; the only size 3/4 compact bones that exhibited tooth marks were from the sub-adult zebra specimen fed on by 12 lions (SWT021); six of these exhibited higher than usual amounts of damage. Most of the lion-damaged bones without tooth marks

Table 4.2. Number of specimens (NISP tooth-marked/total NISP) and proportion of size 3 and 4 tooth-marked specimens bearing tooth marks from Sweetwaters Game Reserve. For equids, metapodials include only metacarpal and metatarsal III. See Table 4.1 caption for more details.

	Predator Taxon		
Skeletal Part	Lion	Lion-Spotted Hyaena	Spotted Hyaena
N	7	3	1
MAND**	(3/7) 43%	(0/2) 0%	(1/1) 100%
MAX			
CRAN*	(3/7) 43%	(1/2) 50%	(0/1) 0%
RIB	(166/192) 86%	(44/59) 75%	(12/21) 57%
VRT			
C-1	(5/5) 100%	(1/1) 100%	(0/1) 0%
C-2	(3/3) 100%	(0/1) 0%	(0/1) 0%
CVRT	(23/27) 85%	(1/5) 20%	(3/4) 75%
TVRT	(78/96) 81%	(3/8) 38%	(2/4) 50%
LVRT	(24/33) 72%	(1/6) 16%	(1/4) 25%
SACR	(5/6) 83%	(1/1) 100%	(1/1) 100%
CAUD			
INN	(9/9) 100%	(1/1) 100%	(0/2) 100%
SCAP	(11/12) 92%	(4/4) 100%	
Axial Bones (subtotal)	**(330/397) 83%**	**(57/90) 63%**	**(20/40) 50%**
HUM	(7/9) 78%	(3/4) 75%	
FEM	(14/14) 100%	(1/1) 100%	(2/2) 100%
RADU	(8/10) 80%	(2/2) 100%	
RAD			
ULN			
TIB	(10/13) 77%		(0/1) 0%
MP			
MT	(6/26) 23%		(0/3) 0%
MC	(3/22) 14%	(0/3) 0%	
LB			
Limb Bones (subtotal)	**(48/94) 51%**	**(6/10) 60%**	**(2/6) 33%**
PAT			
FIB			
CARP	(0/52) 0%	(0/7) 0%	
TARS	(0/16) 0%		(0/3) 0%
CALC	(2/12) 16%		(0/1) 0%

AST	(2/8) 25%			(0/1) 0%
NAVC	(0/4) 0%			
PHA				
PHA1	(2/17) 12%			
PHA2	(1/14) 7%	(0/1) 0%		
PHA3	(0/11) 0%	(0/1) 0%		
SES	(0/22) 0%			
Compact Bones (subtotal)	**(7/156) 4%**	**(0/9) 0%**		**(0/5) 0%**
NID		(1/1) 100%		
TOTAL	**(385/647) 60%**	**(63/109) 58%**		**(22/51) 43%**
NISP:MNE	(669:658) 1.02	(110:109) 1.01		(52:51) 1.02

* Includes hyoid

** Includes mandible and hemimandible fragments

Table 4.3. Number of specimens (NISP tooth-marked/total NISP) and proportion of size 1 and 2 specimens bearing tooth marks from Sweetwaters Game Reserve. See Table 4.1 and 4.2 captions for more details.

	Predator Taxon			
Skeletal Part	Lion	Leopard	Cheetah	Jackal
N	9	3	1	1
MAND**	(10/12) 83%		(0/2) 0%	
MAX				
CRAN*	(9/33) 27%		(1/1) 100%	
RIB	(22/41) 54%		(0/21) 100%	(6/27) 22%
VRT	(3/7) 43%			
C-1	(1/1) 100%		(1/1) 100%	
C-2	(1/1) 100%		(1/1) 100%	
CVRT	(0/5) 0%		(1/5) 20%	(0/7) 0%
TVRT	(6/6) 100%		(0/13) 0%	(0/13) 0%
LVRT	(4/4) 100%	(1/4) 25%	(0/6) 0%	(0/7) 0%
SACR	(1/1) 100%	(0/1) 0%	(1/2) 50%	(0/3) 0%
CAUD		(1/5) 20%		(1/1) 100%
INN	(8/8) 100%	(0/3) 0%	(1/2) 50%	(2/2) 100%
SCAP	(7/8) 88%		(2/2) 100%	
Axial Bones (subtotal)	**(72/127) 57%**	**(2/13) 15%**	**(8/56) 14%**	**(9/53) 17%**
HUM	(9/11) 81%		(0/2) 0%	

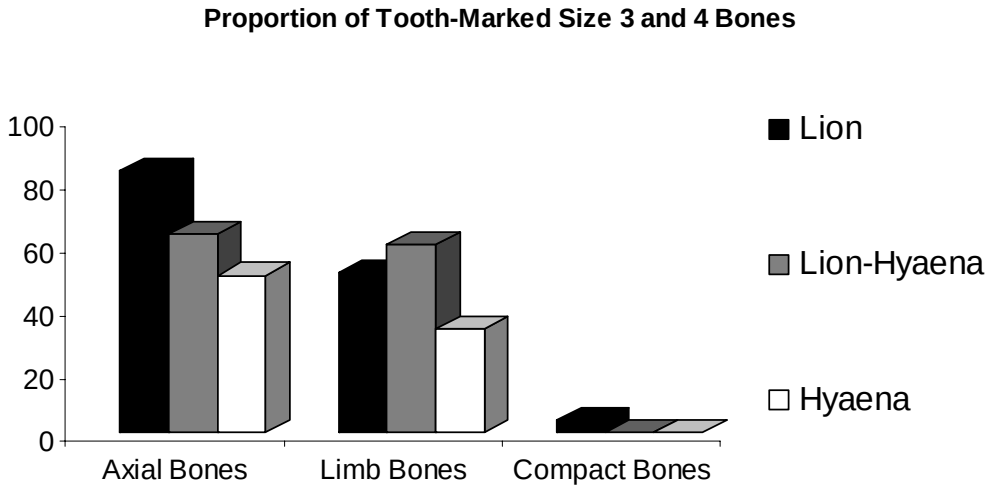
FEM	(12/13) 92%	(3/3) 100%	(1/2) 50%	(2/2) 100%
RADU	(3/3) 100%		(0/2) 0%	
RAD	(5/5) 100%			
ULN	(1/1) 100%			
TIB	(12/13) 92%	(1/4) 25%	(0/2) 0%	(0/2) 0%
MP				
MT	(6/6) 100%	(0/5) 0%	(0/2) 0%	
MC	(5/14) 36%		(0/2) 0%	
LB	(1/4) 25%			
Limb Bones (subtotal)	**(54/70) 77%**	**(4/12) 33%**	**(1/12) 8%**	**(2/4) 50%**
PAT				(0/1) 0%
FIB	(0/3) 0%			
CARP	(2/8) 25%		(0/7) 0%	
TARS	(0/3) 0%			
CALC	(3/3) 100%	(1/1) 100%	(0/2) 0%	
AST	(3/5) 60%	(2/2) 100%	(0/2) 0%	(0/1) 0%
NAVC	(0/3) 0%	(0/1) 0%	(0/2) 0%	
PHA				
PHA1		(0/2) 0%	(0/8) 0%	
PHA2		(0/2) 0%	(0/8) 0%	
PHA3	(0/2) 0%	(0/2) 0%	(0/8) 0%	
SES	(0/1) 0%			
Compact Bones (subtotal)	**(8/28) 29%**	**(3/10) 30%**	**(0/37) 0%**	**(0/2) 0%**
NID	(12/28) 43%			
TOTAL	**(146/253) 58%**	**(9/35) 26%**	**(9/105) 9%**	**(11/59) 18%**
NISP:MNE	(262:168) 1.56	(33:33) 1.00	(99:94) 1.05	(71:64) 1.11

* Includes hyoid
** Includes mandible and hemimandible fragments

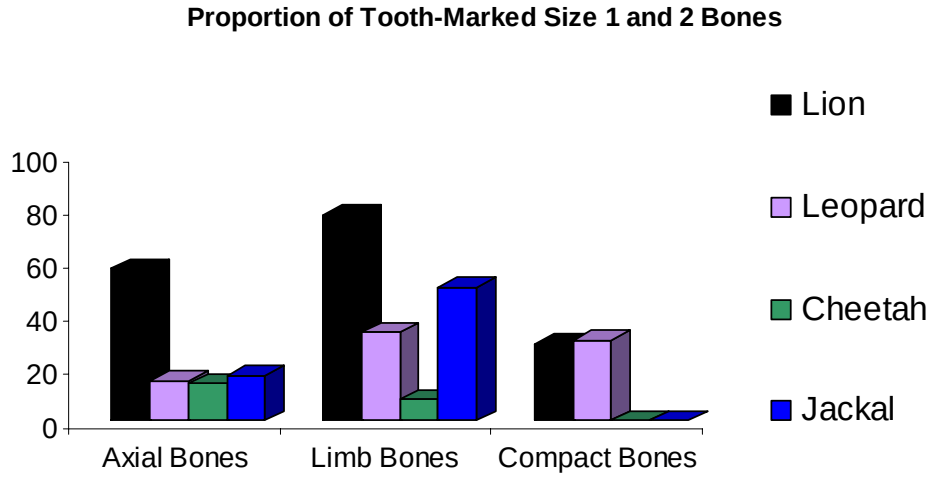
were from SWT014, a zebra fed on by three lions which may have consumed SWT013 (a warthog killed on the same day, less than two kilometers away). Upon retrieval of SWT014, I noted unusually high amounts of flesh remaining. Total proportions of bones with tooth marks among size 3 and 4 samples were similar; lion: 60%, lion followed by spotted hyaena: 58%, spotted hyaena: 43%.

Figure 4.3. Relative proportion of tooth-marked axial, limb, and compact bones. Sample is stratified by predator and prey size: size 3 and 4 prey (a), size 1 and 2 prey (b). Data are from Tables 4.1 – 4.3.

(a)



(b)



A different rank order of the proportion of tooth-marked skeletal elements among skeletal regions is found in size 1/2 samples (except for the cheetah-damaged sample, in which it is the same for large carcasses). Lion-, leopard-, and jackal-damaged size 1/2 limb bones are more frequently tooth-marked than axial bones. Lion- and leopard-damaged size 1/2 compact bones had relatively high proportions of tooth marks (29% and

30%, respectively), most likely due to the ability and tendency of lions and leopards to access these distal limb bones during more complete carcass part consumption. The only size 1/2 lion-damaged scapula, humerus, and femur fragments without tooth marks were from two fetal zebra specimens (SWT008, SWT016),which had friable surfaces, rendering tooth marks more difficult to identify. The total proportion of bones with tooth marks among these samples varies more widely than the size 3/4 samples: 58% for lion, 26% for leopard, 9% for cheetah and 18% for jackal.

2. Limb Bone Tooth Mark Frequency and Location

Upper limb bones (humerus and femur) are more frequently tooth-marked than intermediate limb bones (radius, ulna, tibia), which are more frequently tooth-marked than lower limb bones (metacarpal, metatarsal) in all samples from NAO and SGR (Tables 4.4, 4.5, and 4.6). The only exception is the lion-spotted hyaena sample, which has a very small intermediate limb bone sample (N = 2). Lower limb bone tooth marking was absent in most samples, and infrequent in the lion-damaged size 3/4 sample (13%); all lion tooth-marked size 3/4 metapodials except one were from the sub-adult zebra sample, SWT014. However, lower limb bone tooth marking was fairly prevalent on the lion/size 1/2 sample (43%), and would have been even higher (69%) had the undamaged warthog metapodials (SWT013) been excluded.

Table 4.4. Number of tooth-marked long bone specimens (NISP tooth-marked/total element and portion NISP) and proportion of tooth-marked long bone specimens by individual skeletal element and portion from the Nairobi Animal Orphanage. Portion definitions and abbreviations for skeletal elements are detailed in Appendix 3. RADU includes radio-ulna, radius, and ulna. Shafts (bottom row) includes PSH, MSH, and DSH; Epiphyses (penultimate row) includes PX and DS.

Tooth-marked	Predator Taxon/Carcass Size			
Limb Portion	Lion/4	Leopard/4	Cheetah/4	Jackal/4
HUM – PX	(0/2) 0%		(1/5) 20%	
HUM – PSH	(1/3) 33%		(2/6) 33%	
HUM – MSH	(0/3) 0%		(2/5) 40%	
HUM – DSH	(0/3) 0%		(1/6) 17%	
HUM – DS	(0/3) 0%		(0/6) 0%	
FEM – PX	(1/2) 50%			(0/1) 0%
FEM – PSH	(0/2) 0%			(0/1) 0%
FEM – MSH	(3/7) 46%	(0/1) 0%		(0/2) 0%
FEM – DSH	(5/5) 100%	(0/1) 0%		(0/1) 0%
FEM – DS	(3/3) 100%	(0/1) 0%		(0/1) 0%
ULB – PX	(1/4) 25%		(1/5) 20%	(0/1) 0%
ULB – PSH	(1/5) 20%		(2/6) 33%	(0/1) 0%
ULB – MSH	(3/10) 30%	(0/1) 0%	(2/5) 40%	(0/2) 0%
ULB – DSH	(5/8) 63%	(0/1) 0%	(1/6) 17%	(0/1) 0%
ULB – DS	(3/6) 50%	(0/1) 0%	(0/6) 0%	(0/1) 0%
ULB (subtotal)	**(13/35) 37%**	**(0/3) 0%**	**(6/28) 21%**	**(0/6) 0%**
RADU – PX	(1/3) 33%		(2/6) 33%	
RADU – PSH	(0/3) 0%		(1/6) 17%	
RADU – MSH	(0/3) 0%		(0/6) 0%	
RADU – DSH	(0/3) 0%		(0/6) 0%	
RADU – DS	(0/3) 0%		(0/6) 0%	
TIB – PX	(0/1) 0%			
TIB – PSH	(4/6) 67%			
TIB – MSH	(3/8) 38%			
TIB – DSH	(0.6) 0%			
TIB – DS	(0/6) 0%			
ILB – PX	(1/4) 25%		(2/6) 33%	
ILB – PSH	(4/9) 44%		(1/6) 17%	
ILB – MSH	(3/11) 27%		(0/6) 0%	
ILB – DSH	(0/9) 0%		(0/6) 0%	
ILB – DS	(0/9) 0%		(0/6) 0%	
ILB (subtotal)	**(8/42) 19%**		**(3/30) 10%**	
PX (all elements)	(2/8) 25%		(3/11) 27%	(0/1) 0%
PSH (all elements)	(5/14) 36%		(3/12) 25%	(0/1) 0%
MSH (all elements)	(6/21) 29%	(0/1) 0%	(2/11) 18%	(0/2) 0%
DSH (all elements)	(5/17) 29%	(0/1) 0%	(1/12) 8%	(0/1) 0%
DS (all elements)	(3/15) 20%	(0/1) 0%	(0/12) 0%	(0/1) 0%
Epiphyses (all elements)	(5/23) 22%	(0/1) 0%	(3/23) 13%	(0/2) 0%
Shafts (all elements)	(16/52) 31%	(0/2) 0%	(6/35) 17%	(0/4) 0%

Note: There were no lower limb bones in the NAO sample.

Table 4.5. Number of tooth-marked long bone specimens (NISP tooth-marked/total element and portion NISP) and proportion of tooth-marked size 3 and 4 long bone specimens by individual skeletal element and portion from SGR. For equids, metapodials include only metacarpal and metatarsal III. See Table 4.4 caption for more details.

	Predator Taxon		
Limb Portion	Lion	Lion-Spotted Hyaena	Spotted Hyaena
HUM – PX	(5/8) 63%	(1/1) 100%	
HUM – PSH	(7/9) 78%	(0/1) 0%	
HUM – MSH	(4/9) 44%	(3/4) 75%	
HUM – DSH	(3/9) 33%	(1/3) 33%	
HUM – DS	(5/10) 50%	(1/2) 50%	
FEM – PX	(12/12) 100%	(1/1) 100%	(1/2) 50%
FEM – PSH	(11/13) 85%	(0/1) 0%	(2/2) 100%
FEM – MSH	(9/14) 64%	(1/1) 100%	(1/2) 50%
FEM – DSH	(12/14) 86%		(1/1) 100%
FEM – DS	(13/14) 92%		(0/1) 50%
ULB – PX	(17/20) 85%	(2/2) 100%	(1/2) 50%
ULB – PSH	(18/22) 82%	(0/2) 0%	(2/2) 100%
ULB – MSH	(13/23) 57%	(4/5) 80%	(1/2) 50%
ULB – DSH	(16/23) 70%	(1/3) 33%	(1/1) 100%
ULB – DS	(18/24) 75%	(1/2) 50%	(0/1) 50%
ULB (subtotal)	**(82/112) 73%**	**(8/14) 57%**	**(5/8) 63%**
RADU – PX	(7/10) 70%		
RADU – PSH	(3/10) 30%		
RADU – MSH	(4/10) 40%	(2/2) 100%	
RADU – DSH	(3/10) 30%		
RADU – DS	(0/9) 0%		
TIB – PX	(2/13) 15%		(0/1) 0%
TIB – PSH	(9/13) 69%		(0/1) 0%
TIB – MSH	(3/13) 23%		(0/1) 0%
TIB – DSH	(1/13) 8%		(0/1) 0%
TIB – DS	(0/13) 0%		(0/1) 0%
ILB – PX	(9/23) 39%		(0/1) 0%
ILB – PSH	(12/23) 52%		(0/1) 0%
ILB – MSH	(7/23) 30%	(2/2) 100%	(0/1) 0%
ILB – DSH	(4/23) 17%		(0/1) 0%
ILB – DS	(0/22) 0%		(0/1) 0%
ILB (subtotal)	**(33/114) 29%**	**(2/2) 100%**	**(0/5) 0%**
MCM – PX	(1/8) 13%	(0/1) 0%	
MCM – PSH	(2/8) 25%	(0/1) 0%	
MCM – MSH	(0/8) 0%	(0/1) 0%	

MCM – DSH	(1/8) 13%	(0/1) 0%	
MCM – DS	(1/8) 13%	(0/1) 0%	
MTM – PX	(1/12) 10%		(0/1) 0%
MTM – PSH	(1/12) 10%		(0/1) 0%
MTM – MSH	(2/12) 20%		(0/1) 0%
MTM – DSH	(1/12) 10%		(0/1) 0%
MTM – DS	(2/12) 20%		(0/1) 0%
LLB – PX	(3/20) 10%	(0/1) 0%	(0/1) 0%
LLB – PSH	(3/20) 15%	(0/1) 0%	(0/1) 0%
LLB – MSH	(2/20) 10%	(0/1) 0%	(0/1) 0%
LLB – DSH	(2/20) 10%	(0/1) 0%	(0/1) 0%
LLB – DS	(3/20) 15%	(0/1) 0%	(0/1) 0%
LLB (subtotal)	**(11/85) 13%**	**(0/5) 0%**	**(0/5) 0%**
PX (all elements)	(29/63) 46%	(2/3) 66%	(1/4) 25%
PSH (all elements)	(33/65) 51%	(0/3) 0%	(2/4) 50%
MSH (all elements)	(22/66) 33%	(6/8) 75%	(1/4) 25%
DSH (all elements)	(22/66) 33%	(1/4) 25%	(1/3) 33%
DS (all elements)	(21/66) 32%	(1/3) 33%	(0/3) 0%
Epiphyses (all elements)	(50/129) 39%	(3/6) 50%	(1/7) 14%
Shafts (all elements)	(77/197) 39%	(7/15) 47%	(4/11) 36%

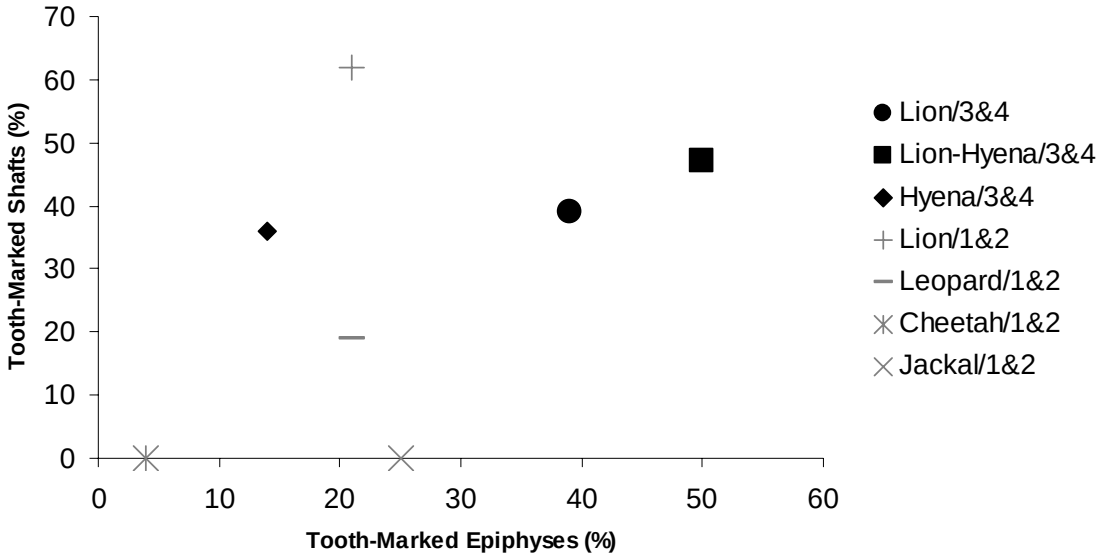
Table 4.6. Number of tooth-marked long bone specimens (NISP tooth-marked/total element/portion NISP) and proportion of tooth-marked size 1 and 2 long bone specimens by individual skeletal element and portion from the Sweetwaters Game Reserve. See Tables 4.4 and 4.5 caption for more details.

	Predator Taxon			
Limb Portion	Lion	Leopard	Cheetah	Jackal
HUM – PX	(1/1) 100%		(0/2) 0%	
HUM – PSH	(5/6) 83%		(0/2) 0%	
HUM – MSH	(2/3) 67%		(0/2) 0%	
HUM – DSH	(2/4) 50%		(0/2) 0%	
HUM – DS			(0/2) 0%	
FEM – PX		(1/2) 50%	(0/2) 0%	(1/2) 50%
FEM – PSH	(8/8) 100%	(1/3) 33%	(0/2) 0%	(0/2) 0%
FEM – MSH	(7/10) 70%	(1/3) 33%	(0/2) 0%	(0/2) 0%
FEM – DSH	(8/9) 89%	(2/3) 33%	(0/2) 0%	(0/2) 0%
FEM – DS	(1/1) 100%	(3/4) 75%	(1/2) 50%	(1/2) 50%
ULB – PX	(1/1) 100%	(1/2) 50%	(0/4) 0%	(1/2) 50%
ULB – PSH	(13/14) 93%	(1/3) 33%	(0/4) 0%	(0/2) 0%
ULB – MSH	(9/13) 69%	(1/3) 33%	(0/4) 0%	(0/2) 0%
ULB – DSH	(10/13) 77%	(2/3) 33%	(0/4) 0%	(0/2) 0%

ULB – DS	(1/1) 100%	(3/4) 75%	(1/4) 25%	(1/2) 50%
ULB (subtotal)	**(34/42) 81%**	**(8/15) 53%**	**(1/20) 5%**	**(2/10) 20%**
RADU – PX	(1/4) 25%		(0/2) 0%	
RADU – PSH	(4/4) 100%		(0/2) 0%	
RADU – MSH	(3/4) 75%		(0/2) 0%	
RADU – DSH	(2/3) 67%		(0/2) 0%	
RADU – DS	(0/2) 0%		(0/2) 0%	
TIB – PX		(0/3) 0%	(0/2) 0%	(0/2) 0%
TIB – PSH	(9/9) 100%	(1/3) 33%	(0/2) 0%	(0/2) 0%
TIB – MSH	(8/11) 73%	(0/3) 0%	(0/2) 0%	(0/2) 0%
TIB – DSH	(8/11) 73%	(1/3) 33%	(0/2) 0%	(0/2) 0%
TIB – DS	(1/6) 17%	(0/3) 0%	(0/2) 0%	(0/2) 0%
ILB – PX	(1/4) 25%	(0/3) 0%	(0/4) 0%	(0/2) 0%
ILB – PSH	(12/15) 80%	(1/3) 33%	(0/4) 0%	(0/2) 0%
ILB – MSH	(11/15) 73%	(0/3) 0%	(0/4) 0%	(0/2) 0%
ILB – DSH	(10/13) 77%	(1/3) 33%	(0/4) 0%	(0/2) 0%
ILB – DS	(1/8) 13%	(0/3) 0%	(0/4) 0%	(0/2) 0%
ILB (subtotal)	**(35/55) 64%**	**(2/15) 13%**	**(0/20) 0%**	**(0/10) 0%**
MCM – PX	(0/8) 0%		(0/2) 0%	
MCM – PSH	(4/9) 44%		(0/2) 0%	
MCM – MSH	(3/10) 30%		(0/2) 0%	
MCM – DSH	(5/10) 50%		(0/2) 0%	
MCM – DS	(2/7) 29%		(0/2) 0%	
MTM – PX	(1/4) 25%	(0/3) 0%	(0/2) 0%	
MTM – PSH	(5/6) 83%	(0/3) 0%	(0/2) 0%	
MTM – MSH	(2/5) 40%	(0/3) 0%	(0/2) 0%	
MTM – DSH	(6/7) 86%	(0/3) 0%	(0/2) 0%	
MTM – DS	(1/1) 100%	(0/4) 0%	(0/2) 0%	
LLB – PX	(1/12) 8%	(0/3) 0%	(0/4) 0%	
LLB – PSH	(9/15) 60%	(0/3) 0%	(0/4) 0%	
LLB – MSH	(5/15) 33%	(0/3) 0%	(0/4) 0%	
LLB – DSH	(11/17) 65%	(0/3) 0%	(0/4) 0%	
LLB – DS	(3/8) 38%	(0/4) 0%	(0/4) 0%	
LLB (subtotal)	**(29/67) 43%**	**(0/16) 0%**	**(0/20) 0%**	
PX (all elements)	(3/17) 18%	(1/8) 13%	(0/12) 0%	(1/4) 25%
PSH (all elements)	(24/44) 55%	(2/9) 22%	(0/12) 0%	(0/4) 0%
MSH (all elements)	(25/43) 58%	(1/9) 11%	(0/12) 0%	(0/4) 0%
DSH (all elements)	(31/43) 72%	(2/9) 22%	(0/12) 0%	(0/4) 0%
DS (all elements)	(4/17) 24%	(3/11) 27%	(1/12) 8%	(1/4) 25%
Epiphyses (all elements)	(7/34) 21%	(4/19) 21%	(1/24) 4%	(2/8) 25%
Shafts (all elements)	(80/130) 62%	(5/27) 19%	(0/36) 0%	(0/12) 0%

The relative proportion of tooth-marked long bone epiphyses and shafts among the SGR samples (Tables 4.5 and 4.6; Figure 4.4) covaries positively, but the relationship is weak ($r_s = 0.44$, $p = 0.33$). Spearmann's rank correlation coefficient was calculated both because of the low sample size and because it is the rank order of values, rather than the actual values, that I am examining. This statistic will be used several times in the analysis for the same reason. The hyaena-damaged size 3/4 and especially lion-damaged size 1/2 samples have a relatively high proportion of tooth-marked shafts relative to epiphyses. This is likely because tooth marking occurs during defleshing and fragmentation on these samples; in the other samples, fragmentation levels were much lower. Cheetahs and jackals did not tooth mark limb shafts, but that may be due to small sample sizes from these carnivore taxa.

Figure 4.4. Relationship between proportions of tooth-marked epiphyses and shafts in SGR samples. "Shafts" include proximal shafts, midshafts, and distal shafts. Size 3 and 4 prey samples are in black, and size 1 and 2 prey samples are in grey.



Tooth Mark Frequency and Distribution: Discussion

Size 3/4 Prey

The proportion and pattern of tooth-marked skeletal elements on its own is not useful in distinguishing between carnivore agents on size 3/4 ungulate bones. The main differences among these samples seem to stem from higher proportions of tooth-marked axial bones in the lion-only sample (83%) versus the lion-hyaena (63%) and hyaena-only sample (50%). As well, there are lower proportions of tooth-marked limb bones in the hyaena-only sample (33%) versus the lion-only sample (51%) and the lion-hyaena sample (60%), though the hyaena-only sample is small (6 limb bones). It has been suggested that carnivores (especially hyaenas) preferentially destroy less dense axial bones (Marean *et al.*, 1992), and this may be the explanation for this pattern. Hyaenas destroy or delete (via transport) tooth-marked axial bones, depressing what may have been an originally higher proportion of tooth-marked skeletal elements. Destruction most likely explains the lower proportion of tooth-marked vertebrae and mandibles, while transport is the most likely explanation for metacarpals and phalanges.

When the distribution and frequency of tooth marks on limbs is analyzed, there are no significant differences among the size 3/4 samples accessed by lions only and both lions and hyaenas: they both exhibit about the same proportion of tooth-marked limb shafts and epiphyses, though the actual percentages of tooth-marked epiphyseal specimens is higher (in both lions and hyaenas). Therefore, additional carnivore agents accessing a larger prey carcass do leave more tooth marks than a single agent, but only to a small degree. However, hyaenas acting alone create more tooth-marked shaft versus epiphyseal fragments. Presumably, this is due to the same bone density mechanism as

discussed above for axial bones, as well as a preference for the grease and nutrient rich limb bone ends (Binford, 1978; Lyman, 1985). This in agreement with previous studies which have found that carnivore ravaging preferentially deletes limb bone ends (Bunn and Kroll, 1986; Binford *et al.*, 1988; Blumenschine, 1988; Marean and Spencer, 1991; Marean *et al.*, 1992; Blumenschine and Marean, 1993).

Size 1/2 Prey

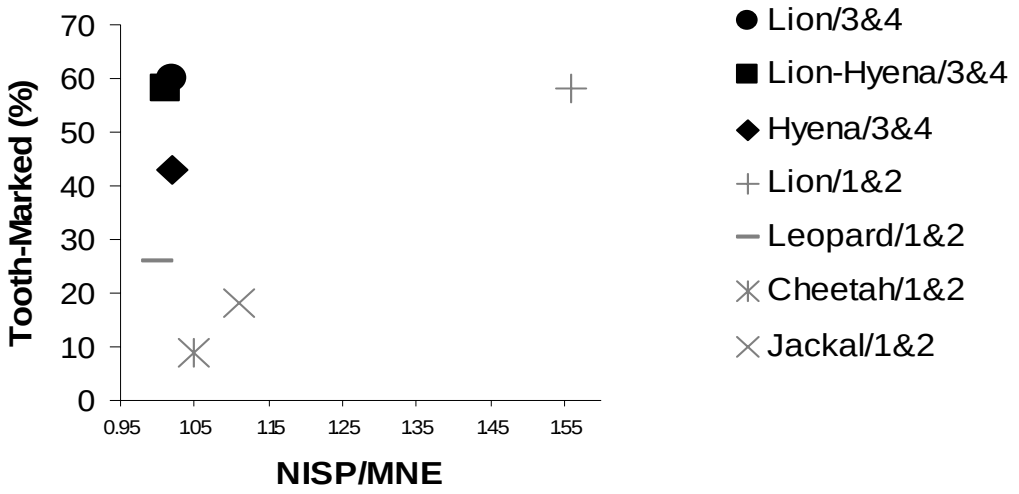
On size 1/2 ungulate bones, lions create tooth marks with a much higher overall frequency than other carnivores (58% for lions versus 26% or less for other carnivores). Lions tooth mark size 1/2 axial elements at a much higher frequency than other carnivores (57% versus 17% or less), and the same pattern holds for limb bones (77% versus 50% or less) and compact bones (29% versus 0% for other carnivores). The size 1/2 tooth-marked shaft to tooth-marked epiphysis ratio is much higher in lions (62%:21%) than in leopards (19%:21%); cheetahs and jackals did not leave any tooth marks on limb shafts.

Fragmentation and Tooth Marking

Is the higher frequency of tooth marking in lion- damaged size 1/2 prey versus other carnivores accessing prey of the same size due to fragmentation, which is relatively high in the lion sample? Is the creation of bone fragments through the action of chewing related to the proportion of bone specimens that preserve a record of that action (a tooth mark)? The weak relationship between fragmentation and tooth mark frequency in the entire SGR sample is suggests that the two are not related (Figure 4.5; $r_s = -0.15$, $p = 0.76$). Though the lion/size 1 and 2 sample, with the highest fragmentation index, has a relatively high proportions of tooth-marked bones (>50%), similar proportions are found

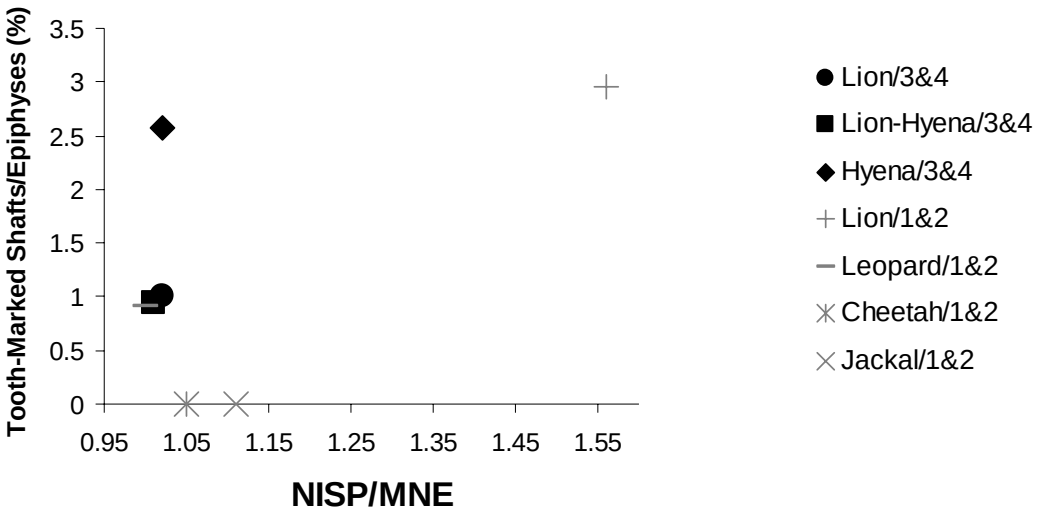
in lion/size 3 and 4 and lion-hyaena/size 3 and 4 samples, though they have low fragmentation ratios. When just the lion limb bone sample is considered, the relationship between fragmentation and tooth marking is still negative: 33% of limb bones (18/36) which have been fragmented (where the diaphysis was breached) are tooth-marked, while 47% of whole limbs bones (including those missing one or both epiphyses, but where the diaphysis was intact) are tooth-marked (73/154). This further supports the counterintuitive result that the relationship between fragmentation and tooth marking is not straightforward. One would expect that defleshing alone would produce fewer tooth-marked bones than defleshing *and* bone breakage, but this does not seem to be the case.

Figure 4.5. Relationship between fragmentation (represented by NISP/MNE) and tooth mark frequency from SGR samples. Size 3 and 4 prey samples are in black, and size 1 and 2 prey samples are in grey.



When comparing fragmentation to the proportion of tooth-marked shaft versus epiphyseal limb bones (Figure 4.6; $r_s = 0.11$, $p = 0.82$), though the relationship is weak, the hyaena/size 3 and 4 and lion/size 1 and 2 samples are clearly separated.

Figure 4.6. Relationship between fragmentation (represented by NISP/MNE) and the relative proportion of tooth-marked limb shafts versus epiphyses. Size 3 and 4 prey samples are in black, and size 1 and 2 prey samples are in grey.



Finally, the relationship between the extent of epiphyseal removal and the proportion of tooth-marked shaft fragments is negative and significant (Figure 4.7a; $r_s = -0.85$, $p = 0.01$), as has previously been shown (Blumenschine and Marean, 1993, Figure 16-5, reproduced here as Figure 4.7b). These two graphs are complementary: the carnivore-only samples of Blumenschine and Marean (1993) have higher proportions of tooth-marked shafts and lower epiphyseal/shaft ratios than any of my samples, falling in the upper left hand corner of the graph. These samples were nearly all size 2 or 3 mammals modified by spotted hyaenas, causing both high numbers of tooth marks on shafts during fragmentation of shafts for marrow consumption and fragmentation of epiphyses for grease consumption. The spotted hyaenas in my samples did not fragment bones to the same extent in Blumenschine and Marean's study (Blumenschine pers. comm., personal observation). The only sample in my study that comes close to theirs is

my lion-damaged size 1/2 prey sample, which is more extensively fragmented than my other samples.

Figure 4.7a. Relationship between the extent of epiphyseal deletion (represented by number epiphyses/shafts) and the proportion of tooth-marked shaft fragments. Data are from Tables 4.5 and 4.6.

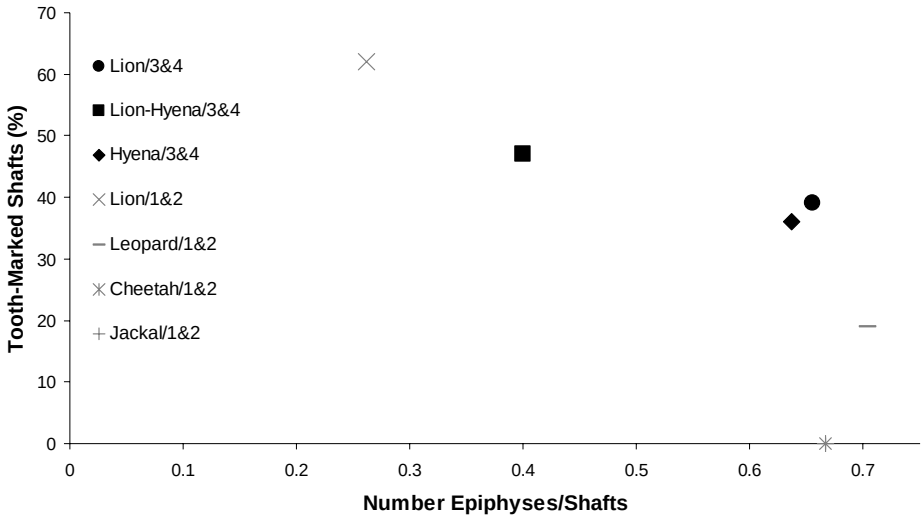


Figure 4.7b. Reproduced figure from Blumenschine and Marean (1993: 287, Figure 16-5). Relationship between the extent of epiphyseal deletion (represented by number epiphyses/shafts) and the proportion of tooth-marked shaft fragments in hammerstone only, carnivore only, and simulated site samples.

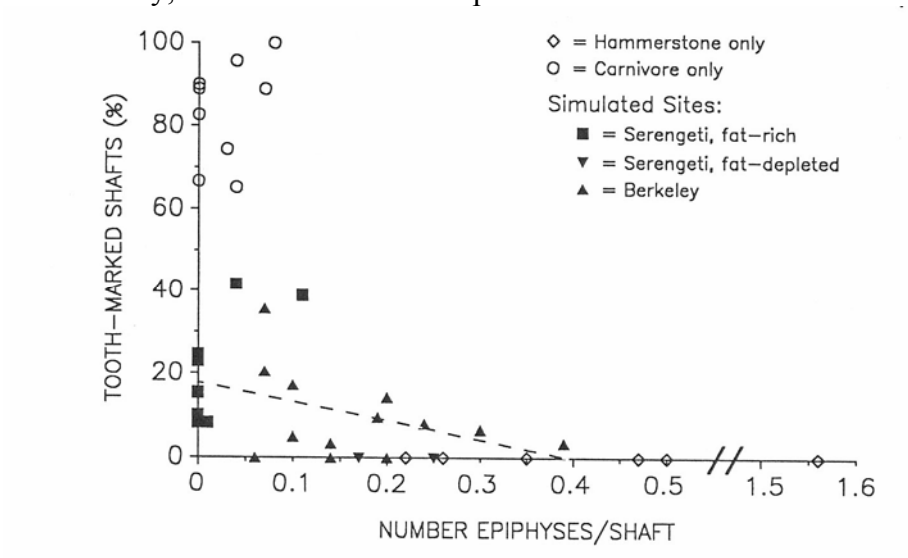
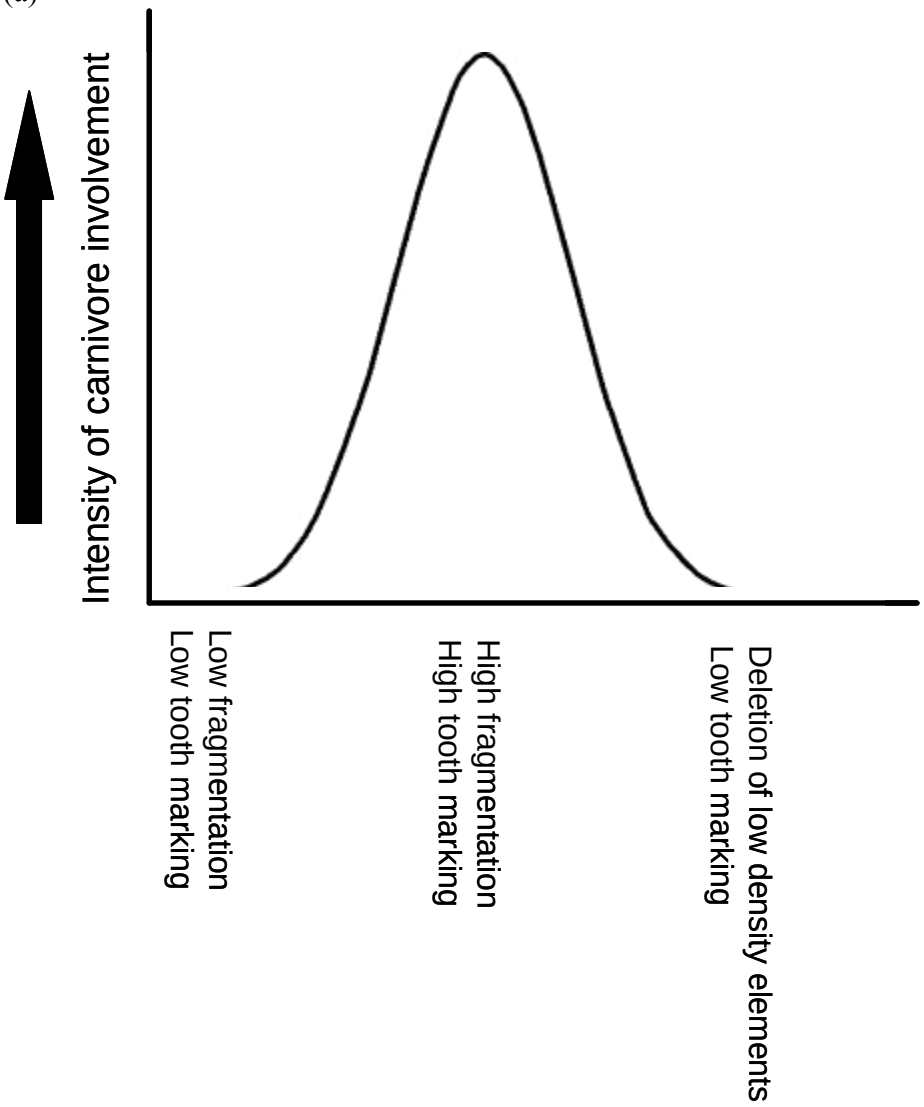
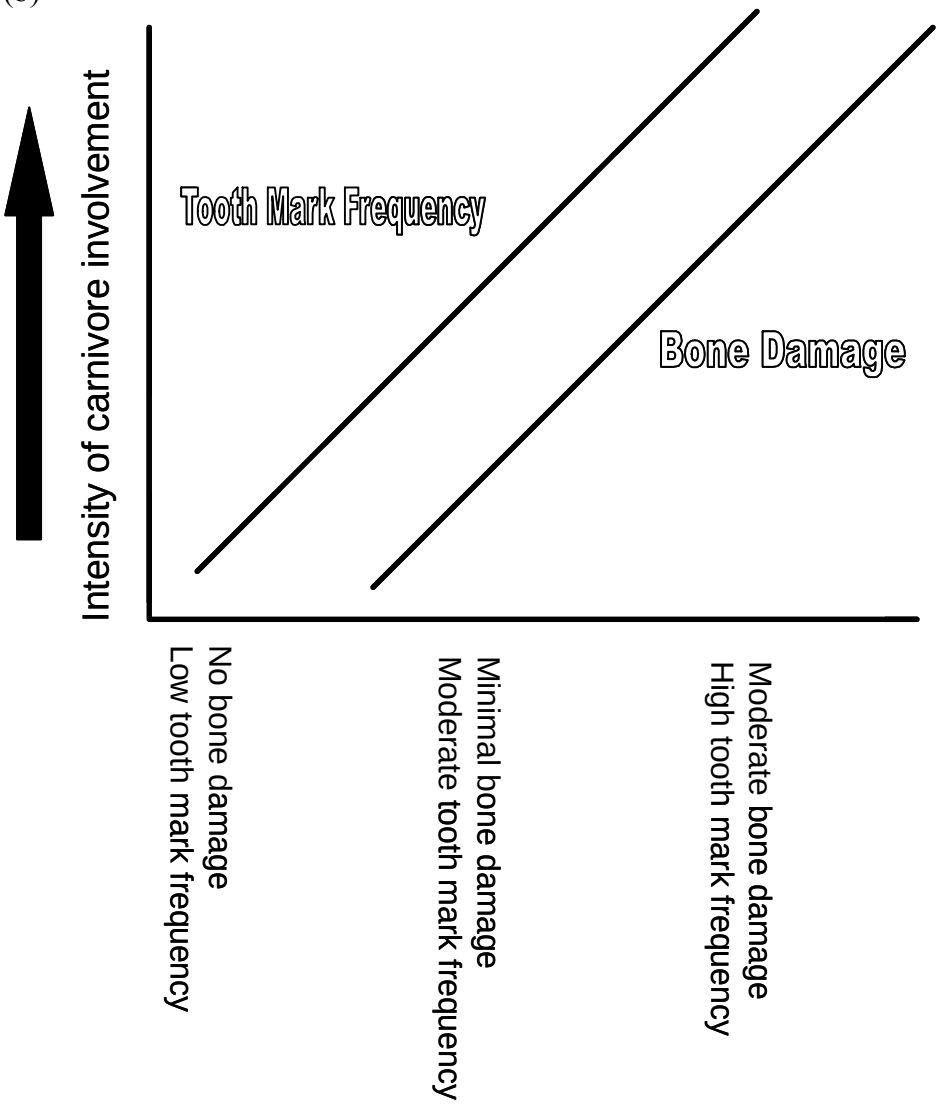


Figure 4.8. Hypothetical change in relationship between carnivore tooth mark frequency and skeletal element fragmentation/deletion as intensity of carnivore competition or involvement with a bone assemblage increases. (a) For carnivores capable of fragmenting bones of a particular prey size. (b) For carnivores incapable of fragmenting bones of a particular prey size.

(a)



(b)


Intensity of carnivore involvement
Tooth Mark Frequency
Bone Damage
No bone damage
Low tooth mark frequency
Minimal bone damage
Moderate tooth mark frequency
Moderate bone damage
High tooth mark frequency

Integrating Tooth Mark Frequency and Distribution, and Bone Damage Data

Evidence for carnivore involvement in a fossil assemblage consists of both tooth marks and gross bone damage (described in Chapter 3). The relationship between evidence of any carnivore damage and evidence of tooth marking is (necessarily) positive and nearly significant (Figure 4.9; $r_s = 0.74$, $p = 0.06$). In all of my samples of both captive and free ranging carnivores in which the number of carnivore-damaged bones was greater than three, the proportion of all carnivore-damaged bones that exhibited only tooth marks (0-25%) was much smaller than the proportion of carnivore-damaged bones exhibiting only diagnosable carnivore damage (16-68%) or a combination of both carnivore damage and tooth marking (17-78%) (Tables 4.7 and 4.8; Figure 4.10). There does not seem to be any relationship between fragmentation intensity and whether or not gross bone damage is accompanied by tooth marking. In fact, all of the captive carnivore samples and both of the free-ranging lion samples (size 1/2 and size 3/4) exhibit more damage associated with tooth marking than damage without accompanying tooth marks. The reasons for this are unclear, but may have to do with the time over which carcass consumption (and resulting bone damage) took place. The orphanage carnivores and the Sweetwaters lions are subject to relatively low interspecific competition compared with other Sweetwaters carnivores (e.g. they are the "dominant carnivores" in their cages or on the game reserve). Perhaps this low competition level leads to a more "relaxed" feeding experience in which these carnivores can feed more thoroughly, creating more tooth marks, though this does not seem to correlate to relatively thorough meat removal on the lion-eaten samples from Sweetwaters (Chapter 2). Alternatively, it may be related to the biomechanics of feeding itself.

Figure 4.9. Relationship between carnivore damage and tooth mark frequency at Sweetwaters Game Reserve.

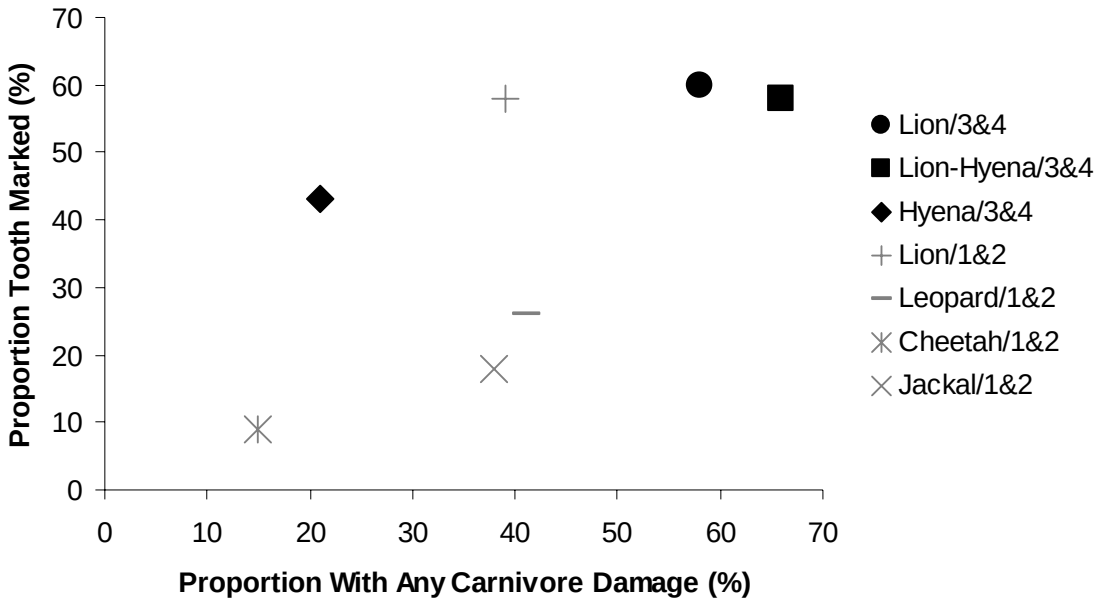


Table 4.7. Proportion of bones with evidence of carnivore damage from the Nairobi Animal Orphanage. All skeletal elements are included. The data in each cell are the following: number of skeletal elements/total number of skeletal elements in that predator taxon carcass size sample, in parentheses, and the calculated percentage. The second column, any carnivore damage, is the total percentage of bones displaying any type of diagnosable carnivore damage, including tooth marks, gnawing damage, or destruction of a portion of the element. In the last three columns, the specific type of carnivore damage is noted: tooth marks only, gross bone damage and/or destruction only, and both. Two proportions are given: first (top), the proportion of bones with that type of carnivore damage out of the entire sample; second (bottom), the proportion of bones with that type of carnivore damage out of the sample of carnivore damaged bones only.

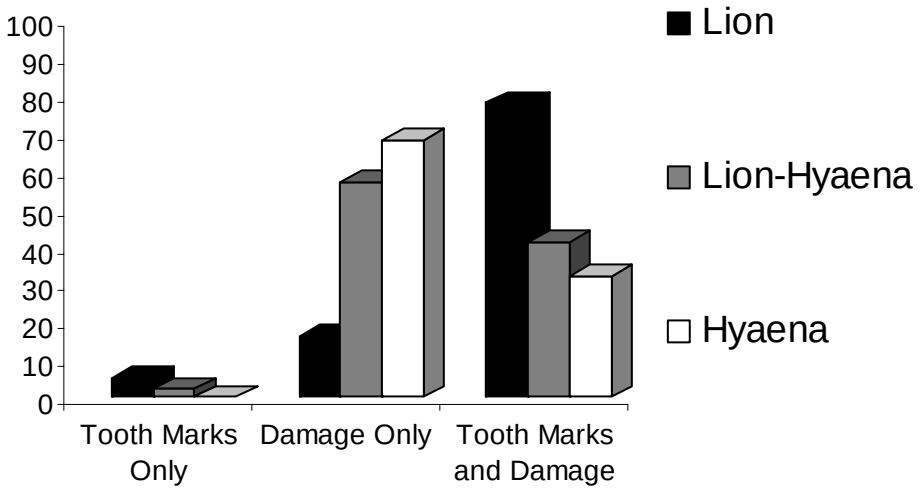
Predator Taxon/ Carcass Size	No Carnivore Damage	Any Carnivore Damage	Tooth Marks Only	Damage/ Destruction Only	Both Tooth Marks and Damage/ Destruction
Lion/4	(95/139) 68%	(44/139) 32%	(3/139) 2% (3/44) 7%	(17/139) 12% (17/44) 39%	(24/139) 17% (24/44) 55%
Leopard/4	(26/36) 72%	(10/36) 28%	(1/36) 3% (1/10) 10%	(4/36) 11% (4/10) 40%	(5/36) 14% (5/10) 50%
Cheetah/4	(91/112) 81%	(21/112) 19%	(2/112) 2% (2/21) 10%	(8/112) 7% (8/21) 38%	(11/112) 10% (11/21) 52%
Jackal/4	(47/49) 96%	(2/49) 4%	(1/49) 2% (1/2) 50%	(1/49) 2% (1/2) 50%	(0/49) 0% (0/49) 0%
Total	(259/336) 77%	(77/336) 23%	(7/336) 2% (7/77) 9%	(30/336) 9% (30/77) 39%	(40/336) 12% (40/77) 52%

Table 4.8. Proportion of bones with evidence of carnivore damage from Sweetwaters Game Reserve. Underneath predator taxon/carcass size is NISP:MNE, which is a measure of fragmentation. Hyaenas are exclusively spotted hyaenas. See Table 4.7 caption for more details.

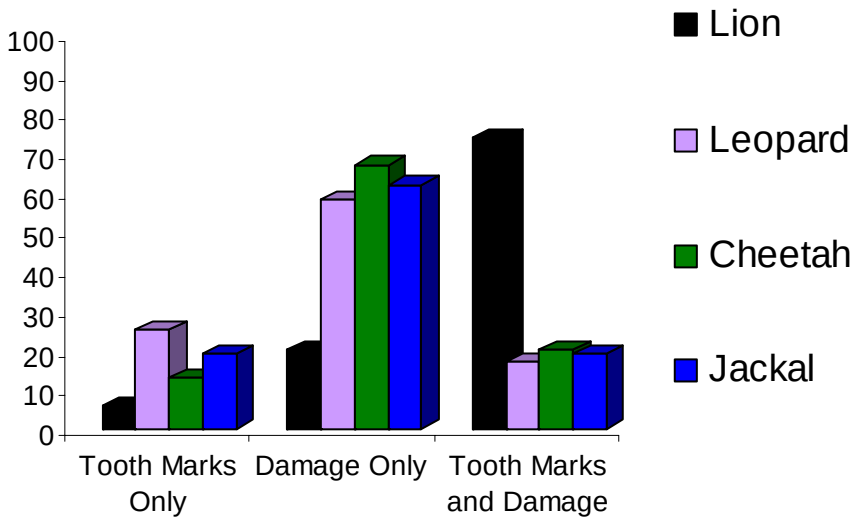
Predator Taxon/ Carcass Size NISP:MNE	No Carnivore Damage	Any Carnivore Damage	Tooth Marks Only	Damage/ Destruction Only	Both Tooth Marks and Damage/ Destruction
Lion/1-2 (262:168) 1.56	(100/165) 61%	(65/165) 39%	(4/165) 2% (4/65) 6%	(13/165) 8% (13/65) 20%	(48/165) 29% (48/65) 74%
Leopard/1-2 (33:33) 1.00	(17/29) 59%	(12/29) 41%	(3/29) 10% (3/12) 25%	(7/29) 24% (7/12) 58%	(2/29) 7% (2/12) 17%
Cheetah/1-2 (99:94) 1.05	(87/102) 85%	(15/102) 15%	(2/102) 2% (2/15) 13%	(10/102) 10% (10/15) 67%	(3/102) 3% (3/15) 20%
Jackal/1-2 (71:64) 1.11	(43/69) 62%	(26/69) 38%	(5/69) 7% (5/26) 19%	(16/69) 23% (16/26) 62%	(5/69) 7% (5/26) 19%
Lion/3-4 (669:658) 1.02	(238/573) 42%	(335/573) 58%	(18/573) 3% (18/335) 5%	(55/573) 10% (55/335) 16%	(262/573) 46% (262/335) 78%
Lion-Hyaena/3-4 (110:109) 1.01	(23/67) 34%	(44/67) 66%	(1/67) 1% (1/44) 2%	(25/67) 37% (25/44) 57%	(18/67) 27% (18/44) 41%
Hyaena/3-4 (52:51) 1.02	(8/39) 21%	(31/39) 79%	(0/39) 0% (0/31) 0%	(21/39) 54% (21/31) 68%	(10/39) 26% (10/31) 32%
Total	(516/1044) 49%	(528/1044) 51%	(33/1044) 3% (33/538) 6%	(147/1044) 14% (147/538) 27%	(348/1044) 33% (348/538) 65%

Figure 4.10. Relative proportion of carnivore-damaged bones from SGR exhibiting tooth marks only, feeding damage only, and both. Sample is stratified by predator and prey size: size 3 and 4 prey (a), size 1 and 2 prey (b).

(a)



(b)



77% of all bones from the captive carnivore samples and 49% of all bones from the free-ranging carnivore samples exhibited no evidence of carnivore damage (Tables 4.7 and 4.8). This underscores previous arguments that a lack of evidence for carnivore damage does not equal a lack of evidence for carnivore activity (Haynes, 1980, 1983; Kent, 1981; Fisher, 1995). Bones which did exhibit both tooth marks and feeding damage have tooth marks within 2 centimeters of that feeding damage over 70% of the time, and at least 94% of the time except in hyaenas (Table 4.9).

Table 4.9. NISP and proportion of bones from Sweetwaters Game Reserve with both tooth marks and gnawing damage on which tooth marks are found within 2 centimeters of gnawing damage. Limb bones include FEM, HUM, TIB, RADU, RAD, ULN, MTM, MCM.

Predator Taxon/ Carcass Size	Lion/ 1-2	Leopard/ 1-2	Cheetah/ 1-2	Jackal/ 1-2	Lion/ 3-4	Lion-Hyaena/ 3-4	Hyaena/ 3-4
All Bones	(115/121) 95%	(5/6) 83%	(3/4) 75%	(5/7) 71%	(183/203) 90%	(55/64) 86%	(17/22) 77%
Limb Bones	(45/46) 98%	(3/3) 100%	(1/1) 100%	n/a	(34/36) 94%	(6/6) 100%	(1/2) 50%

Tooth Mark Frequency and Distribution: Summary and Conclusions

Tooth marking varies between skeletal elements from 0-100% across different carnivore taxa/prey size samples from both naturalistic and captive settings (Tables 4.1, 4.2 and 4.3). The proportion of tooth-marked speicmens varies by prey size irrespective of carnivore agent of modification: the average tooth mark frequency for size 3/4 prey is 58% (range: 43-60%), and the average tooth mark frequency for size 1/2 prey is 39% (range: 9-58%). Tooth marks are not distributed in an even or patterned way across prey skeletal elements (Figure 4.4). Tooth mark frequency and location is generally less useful than gross bone damage patterning to differentiate between carnivore agents who may have modified bones of a particular sized prey. The main exception is lions modifying size 1 and 2 prey, who create significantly more tooth marks (58% across skeletal elements) than other taxa (<26%) (Table 4.3).

Both captive and free-ranging carnivores consistently tooth mark ungulate prey upper limb bones (humerus, femur) more frequently than intermediate limb bones (radius, ulna, tibia), which they in turn tooth mark more frequently than lower limb bones (metapodials) (Tables 4.4, 4.5 and 4.6). This relationship, which holds true in this sample except for in spotted hyaenas (which have a low sample size of intermediate limb bones), is likely due to the distribution of meat and marrow on ungulate carcasses (cf. Blumenschine, 1986a), which decreases from the upper limbs distally towards the lower limbs. These results are similar to an earlier study (Domínguez-Rodrigo, 1999) which found very little to no damage on lower limb bones of lion-eaten size 3/4 prey. There is no consistent relationship between frequency of tooth-marked limb epiphyses and shafts (Figure 4.4), though the carnivores capable of higher damage levels on a particular prey

size tended to have lower epiphyseal tooth mark frequencies on that prey size, possibly because some of the previously tooth-marked epiphyses were destroyed during consumption.

Fragmentation (measured by NISP/MNE) does not have a strong relationship to the proportion of tooth-marked specimens for all skeletal elements (Figure 4.5), but fragmentation by lions of size 1 and 2 prey and by spotted hyaenas of size 3 and 4 prey creates a higher proportion of tooth marks on limb shaft versus limb epiphyses, presumably due to destruction/deletion of epiphyseal limb portions (Figure 4.6). Therefore, relative proportion of limb shaft tooth marking can be related to carnivore *fragmentation*, but not overall carnivore *access or involvement*. The number of tooth-marked limb shafts is inversely related to the number of epiphyses/shafts (Figure 4.7a) across all carnivore samples. The relationship between the proportion of tooth-marked skeletal elements and intensity of carnivore involvement or competition varies depending on the capability of particular carnivore taxa to fragment and destroy bones of a particular prey size (Figure 4.8a, 4.8b).

My intra-limb bone tooth mark distribution results differed from those of Domínguez-Rodrigo (1999), who studied damage on lion-eaten carcasses in Maasai Mara, Kenya. He found "very few conspicuous tooth marks were observed on their shafts" (Domínguez-Rodrigo, 1999: 385), referring to upper limb bones. At Sweetwaters, 57% of size 3 and 4 prey upper limb bone midshafts had at least one tooth mark present, and if proximal and distal shafts are included, the proportion increases to 69% (Table 4.5). The proportion is even higher for size 1 and 2 prey: 69% of midshafts were tooth-marked, and 80% of all shafts were tooth-marked (Table 4.6). I suspect the discrepancy is

due to Domínguez-Rodrigo identifying only conspicuous tooth marks, on uncleaned specimens, in the field, and that lions do commonly make tooth marks on limb shafts during defleshing.

Tooth Mark Morphology: Results

Tooth Scores

Tooth score length and width are not statistically different among carnivore taxa (Tables 4.10, 4.14). However, tooth score length is significantly different between prey sizes, and tooth score width is significantly different between prey sizes, skeletal groups, and long bone portions (Table 4.14). Tooth scores on size 3/4 prey (95% CI: 7.43-8.57 mm) are longer than those on size 1/2 prey (95% CI: 5.46-6.94 mm), but the widths of tooth scores on bones of the two prey size groups are statistically indistinguishable (Table 4.11). Tooth scores on appendicular elements (95% CI: 7.41-9.05) are longer than on axial elements (95% CI: 6.43-7.57 mm) and podials (95% CI: 5.20-8.72), but tooth scores on podials are wider than those on axial and appendicular elements (Table 4.12). Tooth scores on epiphyses are longer (mean length: 11.19 mm) than those on near-epiphyses (mean length: 7.77 mm) and midshafts (mean length: 8.16 mm) (Table 4.13), following

Table 4.10. Descriptive statistics for length and width of tooth scores stratified by predator taxon. N = the number of tooth marks in the sample for a particular predator taxon. S.D. is standard deviation, and 95% CI is 95% confidence interval. All numbers are in millimeters and are rounded to two decimal places. Data illustrated in Figure 4.11a.

	Cheetah (N = 8)		Leopard (N = 8)		Lion (N = 304)		Spotted Hyaena (N = 7)	
	length	width	length	width	length	width	length	width
Min	2.21	0.59	4.02	0.45	1.32	0.26	4.04	0.25
Max	12.60	2.00	11.73	2.14	27.97	3.54	18.35	1.55
Mean	7.25	1.41	7.56	1.12	7.38	1.31	8.42	1.07
S.D.	3.55	0.60	2.89	0.56	4.27	0.54	5.58	0.42
95% CI	4.78-9.72	1.00-1.82	5.56-9.56	0.73-1.51	6.91-7.85	1.25-1.36	4.28-12.56	0.76-1.38

Table 4.11. Descriptive statistics for length and width of tooth scores stratified by prey size. N = the number of tooth scores in the sample for a particular prey size. See Table 4.10 caption for more details. Data illustrated in Figure 4.11b.

	Size 1 and 2 (N = 107)		Size 3 and 4 (N = 220)	
	length	width	length	width
Min	1.32	0.26	2.1	0.25
Max	27.97	2.73	22.89	3.54
Mean	6.20	1.34	8.00	1.28
S.D.	3.90	0.55	4.28	0.54
95% CI	5.46-6.94	1.24-1.43	7.43-8.57	1.20-1.36

Table 4.12. Descriptive statistics for length and width of tooth scores stratified by skeletal group (axial, appendicular, podial). N = the number of tooth scores in the sample for a particular skeletal group. See Table 4.10 caption for more details. Data are illustrated in Figure 4.11c.

	Axial (N = 205)		Appendicular (N = 108)		Podial (N = 15)	
	length	width	length	width	length	width
Min	1.52	0.26	1.64	0.25	1.32	0.52
Max	27.97	2.89	21.12	3.54	14.38	2.96
Mean	7.00	1.23	8.23	1.41	6.96	1.53
S.D.	4.15	0.50	4.39	0.56	3.50	0.72
95% CI	6.43-7.57	1.15-1.31	7.41-9.05	1.31-1.51	5.20-8.72	1.18-1.89

Table 4.13. Descriptive statistics for length and width of tooth scores stratified by long bone portion (epiphysis, near-epiphysis, midshaft). N = the number of tooth scores in the sample for a particular long bone portion. See Table 4.10 caption for more details. Data are illustrated in Figure 4.11d.

	Epiphysis (N = 12)		Near-Epiphysis (N = 74)		Midshaft (N = 22)	
	length	width	length	width	length	width
Min	3.08	0.81	1.64	0.25	2.21	0.34
Max	20.6	2.95	18.84	3.54	21.12	2.00
Mean	11.19	1.77	7.77	1.43	8.16	1.14
S.D.	5.07	0.67	3.83	0.56	5.29	0.40
95% CI	8.33-14.05	1.40-2.14	6.91-8.63	1.31-1.55	5.94-10.37	0.96-1.32

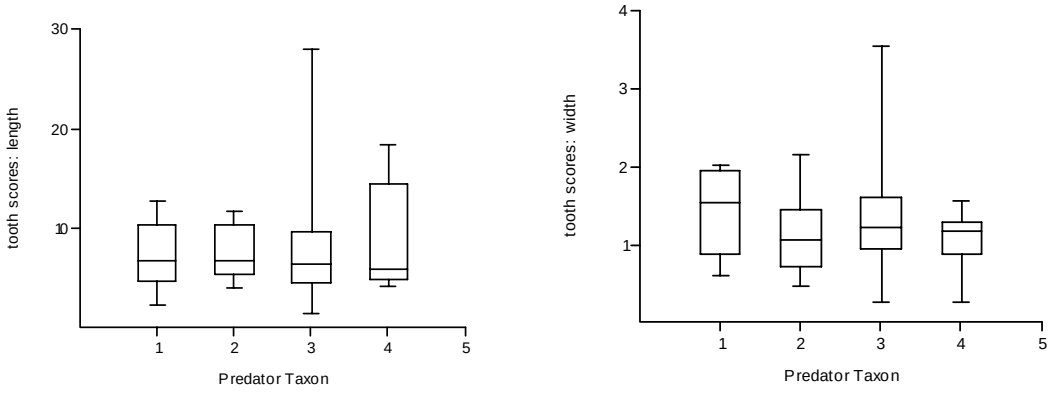
Table 4.14. ANOVA results for tooth score length and width reported in Tables 4.10 – 4.13. Significant results, where $p<0.05$, are shown in boldface. All numbers have been rounded to two decimal places.

Variable	Length		Width	
	F	p	F	p
Predator Taxon	0.14	0.93	0.85	0.47
Prey Size	13.46	**<0.01**	0.83	0.36
Skeletal Group	3.08	**0.04**	5.73	**<0.01**
Long Bone Portion	3.28	**0.04**	5.42	**0.01**

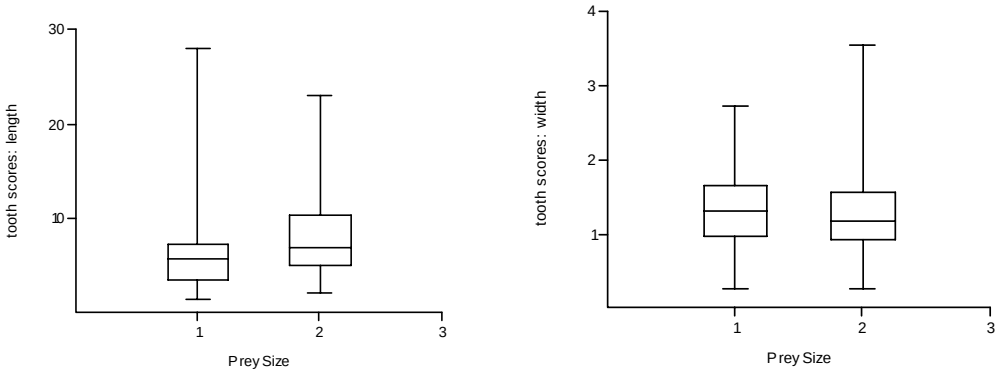
Domínguez-Rodrigo and Piqueras (2003). However, the ranges of tooth score sizes for all of these variables overlap highly (Figure 4.11).

Figure 4.11. Mean, standard deviation, and range of tooth score length (left) and width (right) measurements stratified by predator taxon (a), prey size (b), skeletal group (c), and long bone portion (d). For predator taxon, 1 = cheetah, 2 = leopard, 3 = lion, 4 = spotted hyaena. For prey size, 1 = size 1 and 2, 2 = size 3 and 4. For skeletal group, 1 = axial, 2 = appendicular, 3 = podial. For long bone portion, 1 = epiphysis, 2 = near-epiphysis, 3 = midshaft. All measurements are in millimeters. The boxes represent the 25-75 percent quartiles, the horizontal line inside the box is the median, and the whiskers are the minimal and maximal values.

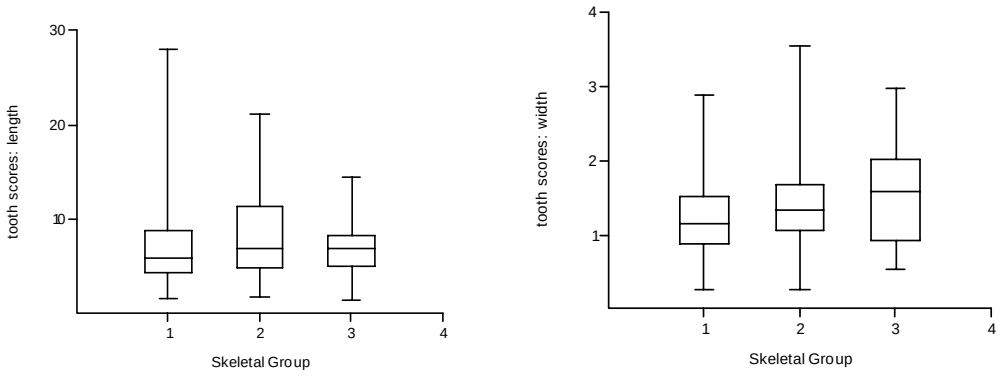
(a) Predator Taxon



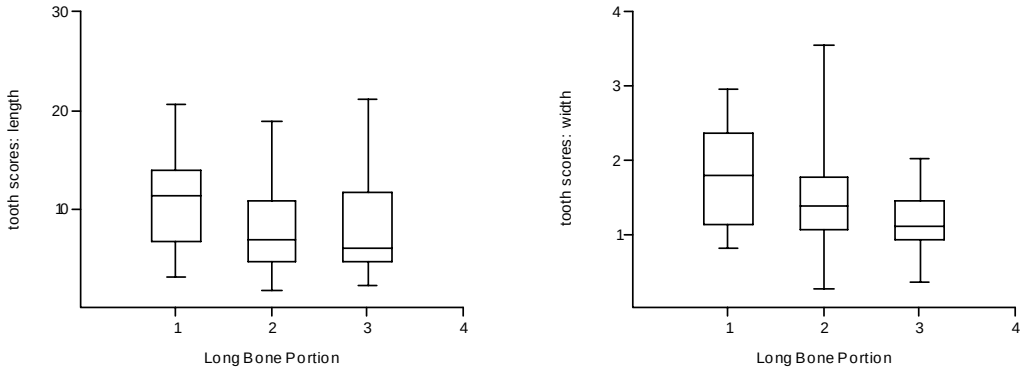
(b) Prey Size



(c) Skeletal Group



(d) Long Bone Portion



Tooth Pits and Punctures

Tooth pit and puncture length and width both differ significantly by carnivore taxa, but depth does not (Tables 4.15, 4.19). The mean length of tooth pits is largest in spotted hyaenas (5.78 mm), followed by lion (4.90 mm), leopard (3.51 mm), jackal (3.26 mm), and cheetah (3.25 mm). The mean width of tooth pits follows nearly the same rank order: spotted hyaenas (4.50 mm), lions (3.42 mm), leopards (2.54 mm), with cheetahs (2.15 mm) creating slightly wider pits than jackals (2.02 mm).

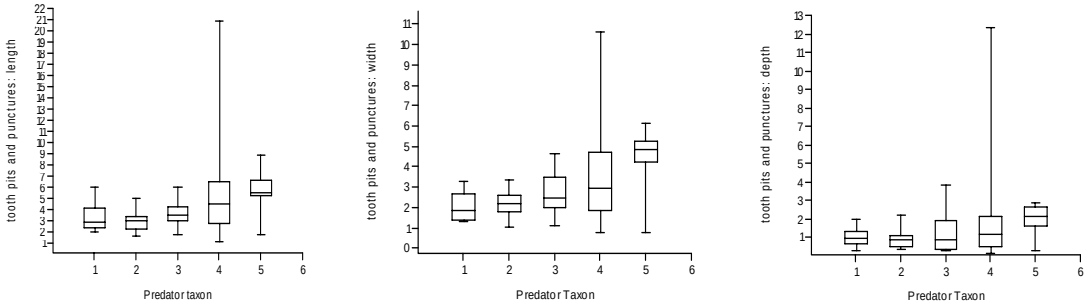
Table 4.15. Descriptive statistics for length, width, and depth of tooth pits and punctures stratified by predator taxon. N = the number of tooth pits and punctures in the sample for that particular predator taxon. L = length, W = width, D = depth. See Table 4.10 caption for more details. Data are illustrated in Figure 4.12a.

	Jackal (N = 10)			Cheetah (N = 11)			Leopard (N = 17)			Lion (N = 323)			Spotted Hyaena (N = 9)		
	L	W	D	L	W	D	L	W	D	L	W	D	L	W	D
Min	1.87	1.24	0.20	1.57	10.01	0.30	1.61	1.08	0.20	1.01	0.70	0.10	1.63	0.72	0.20
Max	5.85	3.25	1.96	4.92	3.3	2.16	5.89	4.58	3.78	20.88	10.62	12.32	8.79	6.08	2.83
Mean	3.26	2.02	0.95	2.85	2.15	0.88	3.51	2.54	1.17	4.90	3.43	1.52	5.78	4.50	1.91
S.D.	1.33	0.75	0.57	0.93	0.73	0.55	1.22	1.08	1.04	2.80	2.04	1.48	2.03	1.61	0.93
95% CI	2.40-4.12	1.55-2.49	0.60-1.30	2.30-3.40	1.72-2.58	0.57-1.19	2.94-4.08	2.03-3.05	0.68-1.66	4.59-5.21	3.21-3.64	1.36-1.68	4.45-7.11	3.44-5.56	1.30-2.51

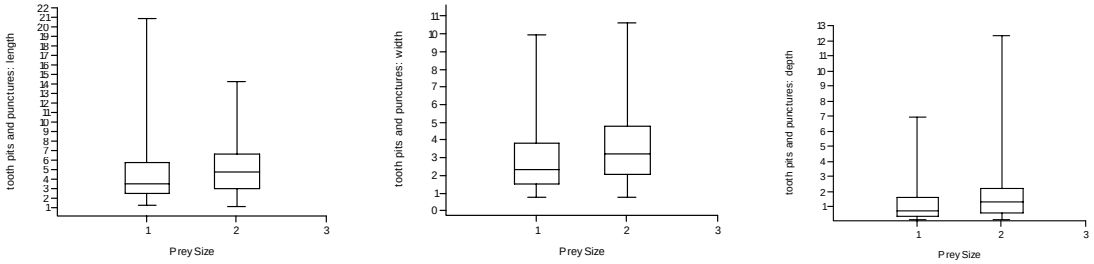
Importantly, the lengths and widths of the combined samples of tooth pits and punctures created by different carnivores only overlap on the lower end of their ranges (Figure 4.12). In other words, all carnivores create small tooth pits and punctures, but only lions and spotted hyaenas create large tooth pits and punctures.

Figure 4.12. Mean, standard deviation, and range of tooth pit and puncture length (left), width (center), and depth (right) measurements. For predator taxon, 1 = jackal, 2 = cheetah, 3 = leopard, 4 = lion, 5 = spotted hyaena. See Figure 4.11 caption for more details.

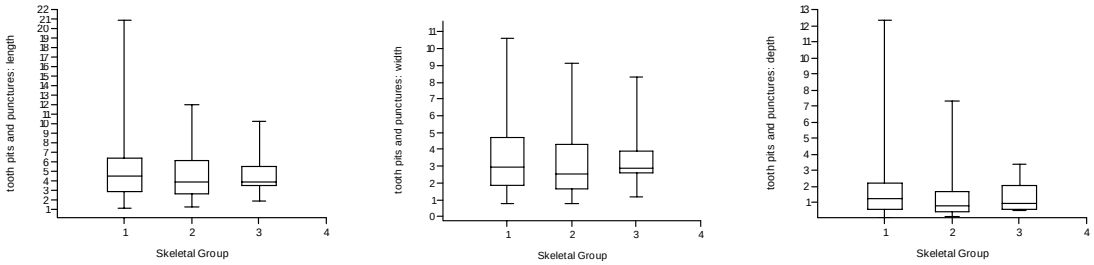
(a) Predator Taxon



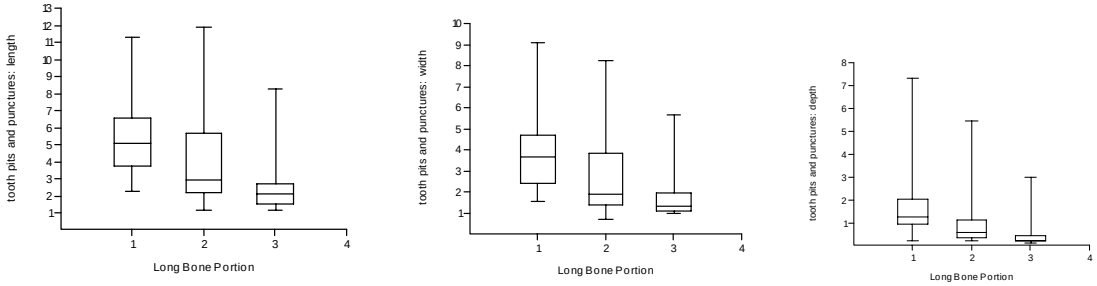
(b) Prey Size



(c) Skeletal Group



(d) Long Bone Portion



Lions have the widest range of linear measurements (1.01 – 20.88 mm length, 0.70 – 10.62 mm width, 0.10 -12.32 mm depth), but the 95% confidence intervals for spotted hyaena tooth marks have the largest values (4.45 - 7.11 mm length, 3.44 - 5.56 mm width, 1.30 – 2.51 mm depth). The wider ranges of measurements of lion tooth marks may be related to the much larger sample size of pits and punctures marks, which is an order of magnitude larger than the samples from other carnivores.

The width and depth of the combined samples of tooth pits and punctures on different sized prey are statistically distinguishable, where larger sized prey exhibit wider and deeper, but not longer, tooth pits and punctures (Tables 4.15, 4.19). Again, though, the ranges of these measurements overlap to a large degree (Table 4.16, Figure 4.12), where small prey exhibit smaller marks, and large prey exhibit smaller and larger marks. None of the linear measurements differ by skeletal group (Table 4.17).

Table 4.16. Descriptive statistics for length, width, and depth of tooth pits and punctures stratified by prey size. N = the number of tooth pits and punctures in the sample for that particular prey size. See Table 4.10 caption for more details. Data are illustrated in Figure 4.12b.

	Size 1 and 2 (N = 135)			Size 3 and 4 (N = 235)		
	length	width	depth	length	width	depth
Min	1.08	0.7	0.1	1.01	0.7	0.1
Max	20.88	9.88	6.9	14.17	10.62	12.32
Mean	4.46	3.00	1.24	4.96	3.53	1.61
S.D.	3.01	2.09	1.42	2.51	1.90	1.41
95% CI	3.95-4.97	2.65-3.35	1.00-1.48	4.65-5.27	3.29-3.77	1.43-1.79

Table 4.17. Descriptive statistics for length, width, and depth of tooth pits and punctures stratified by skeletal group (axial, appendicular, podial). N = the number of tooth pits and punctures in the sample for that particular skeletal group. See Table 4.10 caption for more details. Data are illustrated in Figure 4.12c.

	Axial (N = 242)			Appendicular (N = 110)			Podial (N = 18)		
	length	width	depth	length	width	depth	length	width	depth
Min	1.01	.07	0	1.08	.07	0.1	1.71	1.11	0.42
Max	20.88	10.62	12.32	11.90	9.09	7.31	10.24	8.28	3.36
Mean	4.87	3.42	1.60	4.53	3.13	1.24	4.65	3.40	1.31
S.D.	2.78	2.01	1.49	2.65	1.96	1.30	2.19	1.82	0.91
95% CI	4.52-5.22	3.39-3.45	1.40-1.80	4.04-5.02	2.76-3.50	1.00-1.48	3.63-5.67	2.56-4.24	0.90-1.72

Length, width, and depth of tooth pits and portions are significantly different among long bone portions (Tables 4.18, 4.19). Epiphyses exhibit the largest pits and punctures (95% confidence interval for length is 4.83 - 6.29 mm, width 3.33 - 4.47 mm, depth 1.27 - 2.13 mm) , followed by near epiphysis (length 3.44 - 4.81, width 2.31 - 3.33, depth 0.72 - 1.34), and then midshafts (length 1.38 - 3.96, width 0.97-2.69, depth 0.01-

1.07). This pattern holds even within a single taxon in my sample, lion, length and width (but not depth) of pits and punctures are larger on epiphyses, then near epiphyses, then midshafts (Tables 4.20, 4.21).

Table 4.18. Descriptive statistics for length, width, and depth of tooth pits and punctures stratified by long bone portion (epiphysis, near-epiphysis, midshaft). N = the number of tooth pits and punctures in the sample for that particular long bone portion. See Table 4.10 caption for more details. Data are illustrated in Figure 4.12d.

	Epiphysis (N = 42)			Near-Epiphysis (N = 57)			Midshaft (N = 10)		
	length	width	depth	length	width	depth	length	width	depth
N	42	42	42	57	57	57	10	10	10
Min	2.25	1.53	0.2	10.8	0.7	0.2	1.12	0.97	0.1
Max	11.32	9.09	7.31	11.9	8.24	5.45	8.23	5.65	2.95
Mean	5.56	3.90	1.70	4.13	2.82	1.03	2.67	1.83	0.54
S.D.	2.42	1.86	1.40	2.65	1.93	1.20	2.09	1.39	0.86
95% CI	4.83-6.29	3.33-4.47	1.27-2.13	3.44-4.81	2.31-3.33	0.72-1.34	1.38-3.96	0.97-2.69	0.01-1.07

Table 4.19. ANOVA results for tooth pit and puncture length, width and depth reported in Tables 4.15 -4.18. Significant results, where $p<0.05$, are shown in boldface. All numbers have been rounded to two decimal places.

Variable	Length		Width		Depth	
	F	p	F	p	F	p
Predator Taxon	3.68	**<0.01**	3.82	**<0.01**	1.29	0.27
Prey Size	3.58	0.06	6.19	**0.01**	5.95	**0.02**
Skeletal Group	0.58	0.56	0.81	0.45	2.59	0.07
Long Bone Portion	6.96	**<0.01**	6.80	**<0.01**	5.10	**<0.01**

Table 4.20. Descriptive statistics for length and width of tooth pits and punctures on different long bone portions created by lions only. N = the number of tooth pits and punctures in the sample for that particular long bone portion. See Table 4.10 caption for more details.

	Epiphysis (N = 36)			Near-Epiphysis (N = 53)			Midshaft (N = 10)		
	length	width	depth	length	width	depth	length	width	depth
Min	2.25	1.53	0.20	1.08	0.70	0.2	1.12	0.97	0.1
Max	11.32	9.09	7.31	11.9	8.24	5.45	8.23	5.65	2.95
Mean	5.82	4.13	1.80	4.23	2.89	1.06	2.67	1.83	0.54
Standard Error	0.42	0.32	0.25	0.37	0.27	0.27	0.66	0.44	0.27
Variance	6.28	3.69	2.18	7.40	3.89	1.50	4.36	1.93	0.74
SD	2.50	1.92	1.48	2.72	1.97	1.23	2.09	1.39	0.86
95% CI	5.00-6.64	3.50-4.76	1.31-2.29	3.50-4.96	2.36-3.42	0.53-1.60	1.38-3.96	0.97-2.69	0.01-1.07

Table 4.21. ANOVA results for lion only tooth pit and puncture length and width on different long bone portions, as reported in Table 4.20. Significant results, where $p<0.05$, are shown in boldface. All numbers have been rounded to two decimal places.

	F	p
Length	7.26	**<0.01**
Width	7.51	**<0.01**
Depth	5.34	0.06

When tooth pits and punctures are analyzed separately, it is clear that the statistical differences in the length and width of tooth pits and punctures created by different carnivore taxa are both being driven by tooth punctures, while the statistical differences in the length and width of tooth pits and punctures on different long bone portions are both being driven by tooth pits (Tables 4.22, 4.23; Figure 4.13). The depths of tooth pits are also statistically different by predator taxon (which was not the case when pits and punctures were combined), prey size, and long bone portion (Table 4.22). As statistical differences in tooth puncture length and width are caused *only* by predator taxon, and not by any other variable, measurements of individual tooth punctures are more useful for distinguishing which carnivore may have modified a bone than tooth pits (Table 4.24).

Table 4.22. ANOVA results for length, width and depth of tooth pits only. Significant results, where $p<0.05$, are shown in boldface. All numbers have been rounded to two decimal places.

Variable	Length		Width		Depth	
	F	p	F	p	F	p
Predator Taxon	0.55	0.65	0.76	0.52	2.78	**0.04**
Prey Size	0.29	0.59	2.34	0.13	11.51	**<0.01**
Skeletal Group	1.38	0.25	1.55	0.22	2.41	0.09
Long Bone Portion	3.95	**0.02**	4.93	**0.01**	7.83	**<0.01**

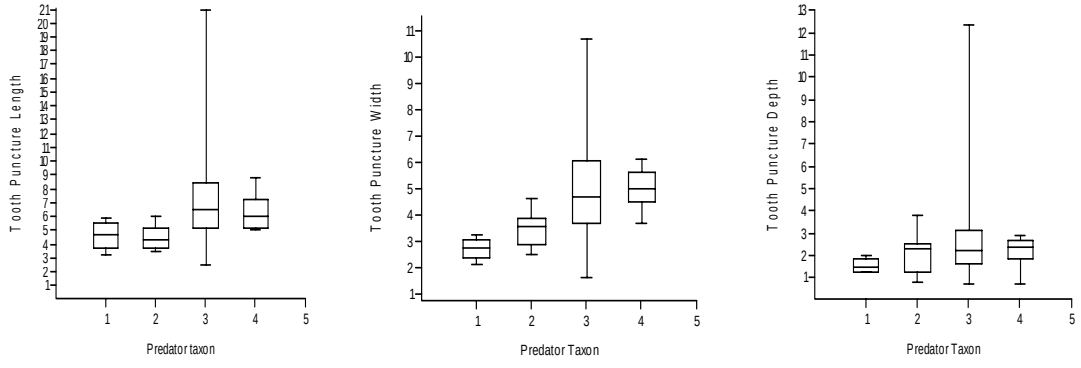
Table 4.23. ANOVA results for length, width and depth of tooth punctures only. Significant results, where $p<0.05$, are shown in boldface. All numbers have been rounded to two decimal places.

Variable	Length		Width		Depth	
	F	p	F	p	F	p
Predator Taxon	3.00	**0.03**	3.38	**0.02**	1.03	0.38
Prey Size	1.77	0.19	1.37	0.24	1.29	0.26
Skeletal Group	0.57	0.57	0.55	0.58	0.19	0.83
Long Bone Portion	0.98	0.33	2.60	0.12	1.54	0.22

Table 4.24. Descriptive statistics for length, width, and depth of tooth punctures only stratified by predator taxon. N = the number of tooth punctures in the sample for that particular predator taxon. L = length, W = width, D = depth. See Table 4.10 caption for more details. Data are illustrated in Figure 4.13.

	Jackal (N = 4)			Leopard (N = 6)			Lion (N = 154)			Spotted Hyaena (N = 8)		
	L	W	D	L	W	D	L	W	D	L	W	D
Min	3.17	2.11	1.18	3.36	2.5	0.76	2.44	1.64	0.7	5.03	3.68	0.68
Max	5.85	3.25	1.96	5.89	4.58	3.78	20.88	10.62	12.32	8.79	6.08	2.83
Mean	4.54	2.72	1.51	4.41	3.48	2.13	6.91	4.96	2.58	6.30	4.98	2.12
S.D.	1.18	0.48	0.35	0.94	0.74	1.07	2.63	1.83	1.53	1.39	0.82	0.72
95% CI	3.38-5.70	2.25-3.19	1.16-1.86	3.65-5.16	2.88-4.07	1.27-2.99	6.49-7.32	4.67-5.25	2.34-2.82	5.33-7.26	4.41-5.54	1.62-2.62

Figure 4.13. Mean, standard deviation, and range of tooth puncture length (left), width (center), and depth (right) measurements. For predator taxon, 1 = jackal, 2 = leopard, 3 = lion, 4 = spotted hyaena. Cheetahs are excluded from the comparison because they only created a single tooth pit. See Figure 4.11 caption for more details.



Tooth Mark Morphology: Discussion

Lenghts and widths of tooth scores are not easily distinguishable between carnivore taxa, prey size, skeletal group, or long bone portion due to their overlapping size ranges (Figure 4.11). This supports results of a previous study where tooth pit size was more useful than tooth score size for distinguishing between carnivores (Domínguez-Rodrigo and Piqueras, 2003). Tooth score length may distinguish between smaller and larger carnivores, as only lions and hyaenas create tooth scores longer than 13 millimeters, but most of the longer tooth scores were created by lions.

The length and width of punctures are statistically distinguishable among carnivore taxa (Table 4.19), *contra* the assertions of Domínguez-Rodrigo and Piqueras (2003). In an earlier study, Selvaggio and Wilder (2001) took digital measurements of the area of tooth pits made by different carnivores, and found that bone density (reflected in bone portion) strongly conditioned tooth pit area. They did not statistically test the hypothesis that different carnivores created different sized tooth pits, but were instead interested in testing (and supported) the hypothesis that multiple carnivores had inflicted tooth marks bones at FLK *Zinjanthropus* after finding a larger range of the area of tooth pits at this site than those created by modern African carnivores. Using tooth pit length and width measurements, Domínguez-Rodrigo and Piqueras (2003) determined that "tooth marks alone cannot confidently be used to identify specific carnivore taxa in bone assemblages" (Domínguez-Rodrigo and Piqueras, 2003: 1388). Instead, they identify three groups of tooth pit sizes (< 4mm; 4 – 6 mm; >6 mm) made by different groups of carnivore taxa (all carnivores but especially jackals, leopards and cheetahs; mainly

baboons, dogs and bears; mainly lions and hyaenas, respectively). Again, they did not directly statistically test whether tooth pit measurements differed among taxa.

All of the carnivore taxa in this study (except spotted hyaenas) can create small tooth pits and punctures (<6mm in length), but only the larger taxa (lion and spotted hyaena) can create large tooth pits and punctures (>6mm in length). While there are statistical differences in the lengths and widths among all of the carnivores that create tooth punctures when analyzed together, these differences break down when carnivores of similar size are compared (Table 4.25). Therefore, it is the size of the carnivore rather than the taxon which is most conservatively distinguishable using measurements of a single tooth mark. This is the same conclusion reached by Domínguez-Rodrigo and Piqueras (2003).

Table 4.25. T-test results for pairwise comparisons of length and width of tooth punctures created by smaller (jackals, leopards) and larger (lions, spotted hyaenas) carnivores. All numbers have been rounded to two decimal places.

Carnivore Taxa	Length		Width	
	t	p	t	p
Jackal versus Leopard	0.65	0.52	0.20	0.85
Lion versus Spotted Hyaena	-0.03	0.98	-1.78	0.11

Tooth scores and pits on different long bone portions are statistically distinguishable by length, width and depth (Tables 4.19, 4.22), though these measurements are still largely overlapping among long bone portions. This supports results of Selvaggio and Wilder (2001) and Domínguez-Rodrigo and Piqueras (2003), who both found larger tooth pit sizes on cancellous versus cortical bone, and their conclusion that tooth pit size is at least partially conditioned by bone density. This could be a confounding factor when trying to distinguish carnivore taxa or even carnivore size

from tooth mark size, and I agree with their recommendations that tooth marks on long bones should be analyzed using a methodology which stratifies them by portion.

Additional factors besides those investigated here (carnivore taxon, prey size, skeletal element group, and long bone portion) may affect tooth mark morphology and measurements. For instance, tooth cusp shape can vary with age and wear, and this could impact tooth mark morphology (Fisher, 1995).

My initial conclusions partially contradict those of two similar earlier studies (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003). Tooth mark morphology, measured in two dimensions, *can* statistically distinguish among carnivore taxa responsible for the creation of a group of tooth marks. However, since the ranges of tooth mark sizes overlap, it is identifying the carnivore taxon involved from a single tooth mark is problematic. On the other hand, tooth mark size can identify whether larger carnivores created at least some of the tooth marks in a fossil assemblage, since only larger carnivores can create larger tooth marks but all carnivores can create small tooth marks. Tooth pits and punctures above 6 mm long are only created by lions or spotted hyaenas, in accordance with Domínguez-Rodrigo and Piqueras (2003). Tooth pits and punctures above 4.6 mm wide are only created by lions or spotted hyaenas. This is similar to the result of Domínguez-Rodrigo and Piqueras (2003) who found that only lions and hyaenas create tooth pits over 4 mm wide. The results for tooth pit and puncture depth are similar the results for length and width, but only lions create tooth pits over 4 mm deep. Surprisingly, hyaena tooth pits and punctures in this sample are only slightly deeper than those of smaller carnivores.

I plan to pursue additional analyses to try to refine our ability to identify carnivore taxa by their tooth marks when I study the complete set of over 6000 tooth marks. For instance, ratios of some of the linear tooth mark measurements may be taxon-specific. Width of tooth marks may be directly proportional to depth on a taxon-specific basis, especially those of tooth punctures, and this may sort the taxa better than either measure alone. The same may apply to the length and width ratio of tooth scores.

Integrating Gross Bone Damage and Destruction and Tooth Mark Data

The most accurate way to deduce which carnivore or carnivores were involved in the modification of bones from a fossil assemblage is using combination of tooth mark frequency, location, and measurement data *with* gross bone damage and destruction location and intensity data (as suggested by Domínguez-Rodrigo and Piqueras, 2003), on a prey size-specific basis. For example, a size 3 ungulate humerus with large tooth pits (over 6mm length) on the distal epiphysis and marginal gnawing on the proximal epiphysis is likely to have been fed on by a lion. A size 1 bovid with marginal gnawing on the distal end small tooth pits and scores on the midshaft is likely to have been fed on by a leopard. The most conservative application of this is on a specimen-by-specimen basis. Prey taxa should first be stratified by size, and then each skeletal element and portion examined for gross bone damage patterns, tooth mark patterns, and tooth mark measurements. Then, particular patterning across an assemblage can be used to construct a hypothesis for the involvement of a particular carnivore or carnivores with the assemblage.

Summary data on gross bone damage level, tooth mark frequency, and tooth mark measurements on each skeletal element on a prey size-specific basis from the samples used in this dissertation are presented in Tables 4.26 and 4.27. These tables can be used as the basis for constructing hypotheses regarding the involvement of specific carnivore taxon with a bone assemblage. These hypotheses can be built using a flow chart type of organization. Figure 4.14 shows an outline of this flow chart, along with two hypothetical examples of its utilization. As is evident from this diagram, equifinalities are still present and even common when attempting a carnivore taxon diagnosis (Example 2). However, in some cases, fairly confident assessment of the involvement of a specific carnivore can be made (Example 1). Knowledge of the dental morphology of extinct carnivores can even facilitate hypotheses of the involvement of some of these carnivores with specific skeletal elements or portions. For example, the strong jaws and large bone-cracking premolars of *Pachycrocuta* might be expected to create more bone damage and larger tooth punctures than modern lions or hyenas, while the flesh specializations of sabertoothed felids might be expected to create less bone damage and smaller tooth marks than modern lions and leopards. More data will fill in the blank cells in Tables 4.26 and 4.27 and likely increase the ranges of variation of gross bone damage levels, and possibly tooth mark measurements.

Table 4.26. Carnivore-specific traces on skeletal elements and portions of size 1 and 2 prey. Definitions of specific portions are from Table 3:2. Gross bone damage level and tooth pit/puncture format is median (minimum – maximum). Gross bone damage level (but not tooth marking present) for spotted hyaenas includes data from both spotted hyaena only and lion-spotted hyaena samples. Tooth marking present format is number of specimens with tooth marks/total number of specimens (for example, 1/2 means tooth marks were present on one out of the two specimens, in NISP, not MNE). Data on tooth marking location on limbs was not collected in the same format (specific location) as damage level; tooth marking location was only recorded on a 5 part portion basis (PX, PSH, MSH, DSH, DS). Therefore, tooth marking presence or absence cannot be consistently evaluated for the femur greater trochanter and femur head; these cells are labeled n/a where necessary. More details on specific portions are in footnotes. Tooth marks recorded on proximal or distal shafts are included in shaft category. Tooth marks recorded on vertebral zygopophyses are included in vertebral processes category. For tooth pits and punctures, if there is only one sample, a range (minimum – maximum) is not given. If no tooth pits or punctures were measured from that category, the cell is blank. Metacarpals and metatarsals for zebras only include the "main" metapodial (MCIII and MTIII). Data from captive carnivore sample (NAO) are not included except for lions for stricter realism in predator taxon/prey size categories. Prey of all ages are included.

Skeletal Element/Portion	Gross Bone Damage Level	Tooth Marking Present	Tooth Pit/Puncture Length	Carnivore Taxon
HINDQUARTER				
Greater Trochanter	0 (0-0)	n/a		Jackal
	0 (0-0)	n/a		Cheetah
	1.67 (0-4)	n/a		Leopard
	4 (4-4)	n/a		Lion
Femur Head	0 (0-0)	n/a		Jackal
	0 (0-0)	n/a		Cheetah
	2 (1-4)	n/a		Leopard
	4 (4-4)	n/a		Lion
Proximal Femur	0.5 (0-1)	1/2	5.85	Jackal
	0 (0-0)	0/2		Cheetah
	1.67 (0-4)	1/3		Leopard
	3.5 (2-4)	0/1		Lion
Femur Shaft	0 (0-0)	0/2		Jackal
	0 (0-0)	0/2		Cheetah
	0.67 (0-1)	2/3	3.67	Leopard
	2 (0-4)	9/9	3.49 (1.12-8.62)	Lion
Distal Femur – Patellar Groove	0 (0-0)	0/2		Jackal
	0 (0-0)	0/2		Cheetah
	1.33 (1-2)	1/2[1]		Leopard
	4 (4-4)	0/0		Lion
Distal Femur – Condyles	0 (0-0)	0/2		Jackal
	1 (0-2)	1/2	3.08	Cheetah
	1.33 (0-2)	1/2[1]	3.66 (2.83-4.48)	Leopard

	4 (4-4)	0/0		Lion
Patella	0 (0-0)	0/1		Jackal
	No data	No data		Cheetah
	No data	No data		Leopard
	4 (4-4)	0/0		Lion
Proximal Tibia	0 (0-0)	0/2		Jackal
	0 (0-0)	0/2		Cheetah
	1.33 (0-2)	0/3		Leopard
	3.57 (2-4)	0/1		Lion
Tibia Shaft	0 (0-0)	0/2		Jackal
	0 (0-0)	0/2		Cheetah
	0.33 (0-1)	1/3	2.05	Leopard
	1.43 (0-1)	12/13	4.01 (1.73-9.7)	Lion
Distal Tibia	0 (0-0)	0/2		Jackal
	0 (0-0)	0/2		Cheetah
	0 (0-0)	0/3		Leopard
	1 (0-4)	1/6		Lion
Iliac Blade	2 (2-2)	1/2	5.12	Jackal
	1.5 (1-2)	1/2	1.60	Cheetah
	0 (0-0)	0/2		Leopard
	2.83 (2-4)	5/6	7.43 (2.63-13.47)	Lion
Posterior Innominate	2 (2-2)	2/2	2.74	Jackal
	0 (0-0)	0/2		Cheetah
	0 (0-0)	0/2		Leopard
	2.4 (1-4)	2/2		Lion
Pubic Region	0 (0-0)	0/2		Jackal
	0 (0-0)	0/2		Cheetah
	1 (0-2)	0/2		Leopard
	2.8 (1-4)	2/3[2]		Lion
Ischial/Pubic Base	0 (0-0)	0/2		Jackal
	0 (0-0)	0/2		Cheetah
	2 (2-2)	0/2		Leopard
	3.6 (2-4)	2/3[2]		Lion
Acetabulum	0 (0-0)	0/2		Jackal
	0 (0-0)	0/2		Cheetah
	0 (0-0)	0/2		Leopard
	1.5 (1-3)	6/7	5.44 (3.72-8.31)	Lion
Sacrum*	0 (0-0)	0/1	2.67	Jackal
	2 (2-2)	1/1	2.94	Cheetah
	2 (2-2)	0/1		Leopard
	No data	No data		Lion
Lumbar Centra	0 (0-0)	0/7		Jackal

	0 (0-0)	0/6		Cheetah
	0.25 (0-1)	1/4	1.61	Leopard
	1.6 (0-3)	2/4		Lion
Lumbar Processes	0.14 (0-2)	0/7		Jackal
	2.17 (2-3)	0/6		Cheetah
	0.25 (0-1)	0/4	5.89	Leopard
	1.65 (0-3)	3/4		Lion
FOREQUARTER				
Scapular Blade	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard
	3.14 (2-3)	5/7	20.88	Lion
Scapular Glenoid	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard
	2.88 (1-4)	3/5	6.37 (2.47-8.83)	Lion
Proximal Humerus	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard
	3.57 (2-4)	1/2	9.68	Lion
Humerus Shaft	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard
	2 (0-4)	9/10	4.46 (2.11-8.23)	Lion
Distal Humerus	No data	No data		Jackal
	0.5 (0-1)	1/2		Cheetah
	No data	No data		Leopard
	2 (1-3)	3/5		Lion
Olecranon Process (Ulna)	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard
	3 (2-4)	4/4	4.82 (4.79-4.85)	Lion
Proximal Radio-Ulna	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard
	1.67 (1-4)	5/8[3]		Lion
Radio-Ulna Shaft	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard
	1.6 (0-3)	9/9	4.37 (1.20-10.25)	Lion
Distal Radio-Ulna	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard

	2.6 (0-4)	0/2		Lion
Ribs	1.31 (0-3)	6/27	2.48 (1.87-3.17)	Jackal
	0.67 (0-2)	0/21		Cheetah
	No data	No data		Leopard
	2.75 (2-3)	22/43	3.63 (1.92-6.99)	Lion
Thoracic Centra	0 (0-0)	0/13		Jackal
	0 (0-0)	0/13		Cheetah
	No data	No data		Leopard
	0.2 (0-1)	2/3	3.82	Lion
Thoracic Neural Process	0 (0-0)	0/13		Jackal
	0.46 (0-2)	0/13		Cheetah
	No data	No data		Leopard
	2.2 (2-3)	6/6	4.45 (2.78-6.00)	Lion
Cervical Centra	0 (0-0)	0/6		Jackal
	0 (0-0)	0/5		Cheetah
	No data	No data		Leopard
	2 (2-2)	0/4		Lion
Cervical Processes	0 (0-0)	0/6		Jackal
	0.49 (0-2)	1/5	2.02 (1.57-2.47)	Cheetah
	No data	No data		Leopard
	0 (0-0)	0/5		Lion
PODIALS				
Calcaneum	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	3 (3-3)	1/1	4.37 (3.68-5.05)	Leopard
	1.67 (1-2)	3/3	5.39 (2.61-10.24)	Lion
Astragalus	0 (0-0)	0/1		Jackal
	0 (0-0)	0/2		Cheetah
	1.5 (1-2)	2/2	3.67 (3.36-3.98)	Leopard
	2 (0-4)	3/5	3.24 (2.95-3.52)	Lion
Other Tarsals	No data	No data		Jackal
	No data	No data		Cheetah
	0 (0-0)	0/1		Leopard
	0 (0-0)	0/3		Lion
Proximal Metatarsal	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	0 (0-0)	0/3		Leopard
	1.33 (1-2)	1/5		Lion
Metatarsal Shaft	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	0 (0-0)	0/3		Leopard
	0.25 (0-1)	6/6	3.26 (1.08-8.88)	Lion

Distal Metatarsal	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	0 (0-0)	0/4		Leopard
	3.25 (1-4)	1/2		Lion
Posterior Phalanges	No data	No data		Jackal
	No data	No data		Cheetah
	0 (0-0)	0/6		Leopard
	No data	No data		Lion
Carpals	No data	No data		Jackal
	0 (0-0)	0/7		Cheetah
	No data	No data		Leopard
	1.5 (1-2)	2/8		Lion
Proximal Metacarpal	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard
	2.25 (1-4)	0/8		Lion
Metacarpal Shaft	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard
	1 (0-3)	5/10	4.89 (1.24-11.90)	Lion
Distal Metacarpal	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard
	2.33 (2-3)	3/8		Lion
Anterior Phalanges	No data	No data		Jackal
	No data	No data		Cheetah
	No data	No data		Leopard
	No data	No data		Lion
HEAD				
Atlas/Axis Bodies	0 (0-0)	0/1		Jackal
	0 (0-0)	0/1		Cheetah
	No data			Leopard
	0 (0-0)	0/1		Lion
Atlas/Axis Processes	0 (0-0)	0/1		Jackal
	1 (1-1)	1/1		Cheetah
	No data	No data		Leopard
	2 (2-2)	0/1		Lion
Face	No data	No data		Jackal
	3 (3-3)	0/1		Cheetah
	No data	No data		Leopard
	4 (4-4)	0/0	4.27 (2.39-6.14)	Lion
Maxilla/Premaxilla	No data	No data		Jackal
	3 (3-3)	0/1		Cheetah

	No data	No data		Leopard
	3.83 (3-4)	2/6	7.24 (4.60-9.87)	Lion
Cranial Base	No data	No data		Jackal
	2 (2-2)	0/1		Cheetah
	No data	No data		Leopard
	4 (4-4)	0/0		Lion
Upper Cranium	No data	No data		Jackal
	2 (2-2)	0/1		Cheetah
	No data	No data		Leopard
	4 (4-4)	2/3	4.16	Lion
Mandible Gonial Angle	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard
	2.88 (0-4)	1/3		Lion
Mandible Ascending Ramus	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard
	3.57 (2-4)	1/2	4.56	Lion
Mandible Horizontal Ramus	No data	No data		Jackal
	0 (0-0)	0/2		Cheetah
	No data	No data		Leopard
	2 (0-3)	4/6	4.87 (1.92-9.44)	Lion

* Includes caudal vertebrae here
[1]Number of tooth-marked femur distal ends is used for both femur patellar groove and condyles.
[2]Number of tooth-marked pubes is used for both pubic region and ischial/pubic base.
[3]Number of tooth-marked proximal radio-ulnae, radii, and ulnae is used proximal radio-ulna.

Table 4.27. Carnivore-specific traces on skeletal elements and portions of size 3 and 4 prey. Hyaena refers to spotted hyaena. See Table 4.24 caption for more details.

Skeletal Element/Portion	Gross Bone Damage Level	Tooth Marking Present	Tooth Pit/Puncture Length	Carnivore Taxon
HINDQUARTER				
Greater Trochanter	1.5 (0-4)	n/a	7.63 (3.24-10.88)	Lion
	3 (2-4)	n/a		Hyaena
Femur Head	1.3 (0-4)	n/a	6.58 (2.25-10.96)	Lion
	0.5 (0-1)	n/a		Hyaena
Proximal Femur	1.88 (0-4)	12/12		Lion
	2 (2-2)	1/2		Hyaena
Femur Shaft	0.75 (0-1)	13/14	4.64 (2.42-6.86)	Lion
	0.5 (0-1)	1/2		Hyaena
Distal Femur – Patellar Groove	2.44 (1-4)	13/14[1]		Lion
	3 (2-4)	0/2[1]		Hyaena

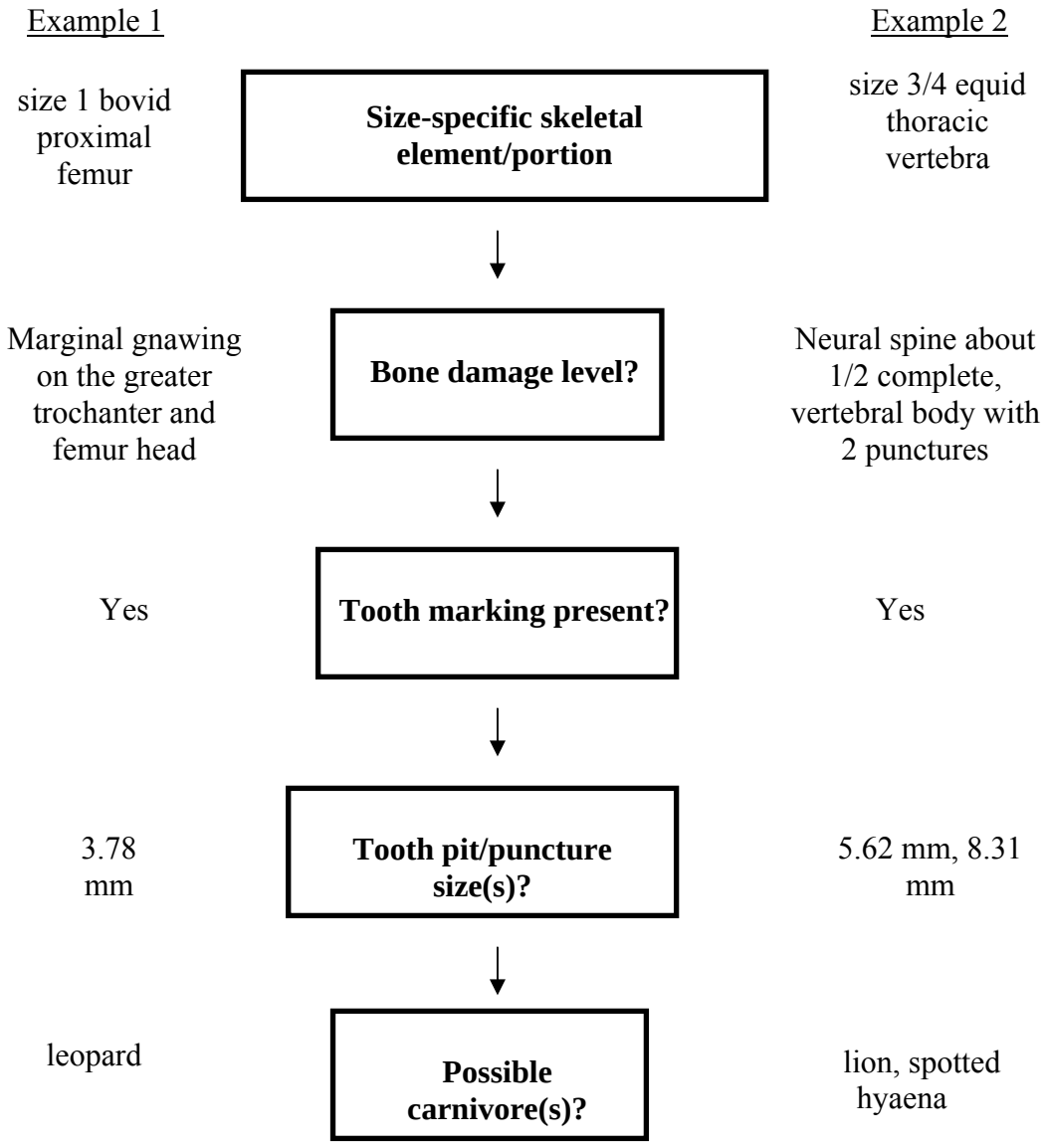
Distal Femur – Condyles	1.2 (0-2)	13/14[1]	5.82 (3.06-11.32)	Lion
	2 (0-4)	0/2[1]		Hyaena
Patella	3 (2-4)	0/2		Lion
	No data	No data		Hyaena
Proximal Tibia	1.6 (0-2)	2/11	6.04 (4.63-7.05)	Lion
	2 (2-2)	0/1		Hyaena
Tibia Shaft	0.5 (0-1)	9/12	2.44	Lion
	4 (4-4)	0/1		Hyaena
Distal Tibia	0 (0-0)	0/13		Lion
	4 (4-4)	0/1		Hyaena
Iliac Blade	2.29 (2-3)	9/9	7.19 (2.03-12.89)	Lion
	2 (2-2)	0/2		Hyaena
Posterior Innominate	1.14 (0-3)	8/9		Lion
	2 (2-2)	0/2		Hyaena
Pubic Region	1 (0-3)	5/8[2]	7.32	Lion
	0 (0-0)	0/2		Hyaena
Ischial/Pubic Base	2.22 (1-3)	5/8[2]	4.29 (1.61-5.94)	Lion
	0.5 (0-1)	0/2		Hyaena
Acetabulum	0.63 (0-1)	8/9		Lion
	0.5 (0-1)	0/2		Hyaena
Sacrum	2.33 (2-3)	5/7	4.28 (2.62-6.58)	Lion
	3 (3-3)	1/1	6.56	Hyaena
Lumbar Centra	1.36 (0-2)	8/33	6.72 (5.27-8.16)	Lion
	1.6 (0-3)	0/4		Hyaena
Lumbar Processes	1.9 (0-3)	22/33	5.39 (2.78-10.04)	Lion
	1.65 (0-3)	1/4	6.51	Hyaena
FOREQUARTER				
Scapular Blade	2.2 (2-3)	11/12	3.37 (1.62-6.45)	Lion
	2.33 (2-3)	0/0		Spotted Hyaena
Scapular Glenoid	0.71 (0-3)	0/12	4.97 (2.85-7.09)	Lion
	1.67 (1-2)	0/0		Hyaena
Proximal Humerus	2.5 (2-4)	5/8	6.22 (2.90-9.46)	Lion
	3.33 (2-4)	0/0		Hyaena
Humerus Shaft	1.25 (0-4)	6/8	8.75	Lion
	2.33 (1-3)	0/0		Hyaena
Distal Humerus	0.75 (0-3)	4/9	5.43	Lion

	1.67 (0-4)	0/0		Hyaena
Olecranon Process (Ulna)	2.2 (0-4)	n/a[4]	4.64 (2.44-6.47)	Lion
	4 (4-4)	0/0		Hyaena
Proximal Radio-Ulna	0.6 (0-2)	7/10[4]	7.71	Lion
	4 (4-4)	0/0		Hyaena
Radio-Ulna Shaft	0.86 (0-3)	7/10	2.79 (2.49-3.00)	Lion
	3 (3-3)	0/0		Hyaena
Distal Radio-Ulna	0.80 (0-4)	0/9		Lion
	4 (4-4)	0/0		Hyaena
Ribs	2.14 (2-4)	157/184	4.31 (1.01-11.81)	Lion
	2.07 (2-4)	12/21	3.51 (1.63-5.39)	Hyaena
Thoracic Centra	1.37 (0-3)	51/87	6.33 (2.10-14.17)	Lion
	2.29 (0-4)	1/4	7.78	Hyaena
Thoracic Neural Process	2.02 (0-4)	52/83	3.76 (1.53-11.19)	Lion
	1.29 (0-4)	2/4		Hyaena
Cervical Centra	0.87 (0-4)	12/21	5.71 (2.84-9.11)	Lion
	1.33 (0-4)	0/4		Hyaena
Cervical Processes	1.32 (0-4)	22/32	4.90 (2.09-9.99)	Lion
	1.83 (0-4)	3/4	6.03 (5.03-8.79)	Hyaena
PODIALS				
Calcaneum	0.75 (0-2)	2/12	6.11 (3.05-8.71)	Lion
	0 (0-0)	0/1		Hyaena
Astragalus	0.17 (0-1)	2/10	1.71	Lion
	0 (0-0)	0/1		Hyaena
Other Tarsals	0 (0-0)	0/20		Lion
	0 (0-0)	0/3		Hyaena
Proximal Metatarsal	0.17 (0-1)	1/12		Lion
	No data	No data		Hyaena
Metatarsal Shaft	0.33 (0-1)	3/12	1.97 (1.89-2.05)	Lion
	No data	No data		Hyaena
Distal Metatarsal	0.17 (0-1)	1/12	4.42	Lion
	No data	No data		Hyaena
Posterior Phalanges	0.17 (0-1)	3/42[3]	3.57	Lion
	No data	No data		Hyaena
Carpals	0 (0-0)	0/52		Lion
	No data	No data		Hyaena

Proximal Metacarpal	0.2 (0-1)	1/8		Lion
	No data	No data		Hyaena
Metacarpal Shaft	0 (0-0)	2/8		Lion
	No data	No data		Hyaena
Distal Metacarpal	0.2 (0-1)	1/8	3.50 (3.28-3.72)	Lion
	No data	No data		Hyaena
Anterior Phalanges	0 (0-0)	3/42[3]		Lion
	No data	No data		Hyaena
HEAD				
Atlas/Axis Bodies	0.5 (0-2)	2/6		Lion
	0 (0-0)	0/1		Hyaena
Atlas/Axis Processes	1.88 (1-2)	7/8		Lion
	1.33 (0-2)	0/1		Spotted Hyaena
Face	1 (0-2)	2/5	3.78	Lion
	1 (0-2)	0/1		Hyaena
Maxilla/Premaxilla	0.5 (0-2)	0/3		Lion
	0.33 (0-1)	0/1		Hyaena
Cranial Base	0.5 (0-2)	2/4	6.82	Lion
	1 (0-2)	0/1		Hyaena
Upper Cranium	0 (0-0)	0/3		Lion
	0.67 (0-2)	0/1		Hyaena
Mandible Gonial Angle	0.4 (0-2)	0/8		Lion
	2 (0-3)	0/2		Hyaena
Mandible Ascending Ramus	1.4 (0-2)	3/8	8.32 (6.94-9.69)	Lion
	2.75 (2-4)	0/2		Hyaena
Mandible Horizontal Ramus	0.33 (0-2)	0/8		Lion
	0.67 (0-2)	0/2		Hyaena

[1]Number of tooth-marked femur distal ends is used for both femur patellar groove and condyles.
[2]Number of tooth-marked pubes is used for both pubic region and ischial/pubic base.
[3]Phalanges were not identified as anterior or posterior, so the sum of all phalanges is used for both anterior and posterior phalanges.
[4]Tooth marks on olecranon processes were included in the count of tooth marks on proximal radio-ulnae.

Figure 4.14. Flow chart depicting organization of traces to investigate for carnivore taxon-specificity based on data in Tables 4.22 and 4.23.



Chapter Five
Carnivores of the Plio-Pleistocene: Taxonomy, Ecology and Behavior

While actualistic studies of modern African carnivores are useful for identifying potential carnivore taxa acting on modern bones, it is necessary to acknowledge the likelihood for archaeofaunas to have been modified by extinct carnivores. The African larger carnivore guild during the Plio-Pleistocene included a much larger diversity of taxa than the modern guild (Turner, 1990; Lewis, 1997). The next section will review the evolution, biogeography, behavior, and ecology of the three families of larger African carnivores most relevant to discussions of hominin-carnivore interactions: canids (*Canis, Lycaon*), felids (Felinae: *Panthera leo, Panthera pardus, Acinonyx jubatus*; Machairodontinae: *Megantereon, Machairodus, Amphimachariodus, Lokotunjailurus, Homotherium, Dinofelis)* and hyaenids (*Crocuta, Hyaena, Parahyaena, Chasmaporthetes, Pachycrocuta*). Taxonomic discussions are included only where relevant. Ursids are not considered, as they are not found in eastern or southern Africa at the time of early hominin carnivory (Werdelin and Lewis, 2005). Following this will be a discussion of carnivore guild evolution, and an ecological perspective on carnivore guild interactions and its applicability to early hominins.

Canidae

A radiation of African canids in Pliocene times is likely, as the three of five Pleistocene genera are exclusively Africa with records going well back into the Pleistocene (*Fennecus, Lycaon, Otocyon*) (Ewer, 1973). The earliest record of canids in Africa is material from a *Vulpes*-sized animal from the early Pliocene at Langebaanweg

(Hendey, 1974b; Werdelin and Lewis, 2000); the records of living *Vulpes* species are limited to the late Pleistocene. The next canid record is from Laetoli, at about 3.75-3.5 Ma (Barry, 1987); there may be multiple taxa present, including some not related to *Canis* (Werdelin and Lewis, 2000). The next canid record is from South Turkwel, at about 3.5-3.2 Ma, consisting of craniodental material attributed to *Canis* new species A (Werdelin and Lewis, 2000). The only other Pliocene canid material from Africa is an isolated upper canine from the Lonyamun Member of the Nachukui Formation at Lothagam (Werdelin, 2003).

Jackal (Canis sp.)

Jackals are the most abundant canids in the South African Plio-Pleistocene (Savage, 1978). The first fossil canid from eastern Africa is an unpublished specimen that probably comes from the Mursi Formation, Omo, at ~4.0-4.5 Ma (Werdelin and Lewis, 2005). The earliest defined *Canis* in East Africa is from South Turkwel at 3.5-3.2 Ma (Werdelin and Lewis, 2000). *C. mesomelas* goes back to the 3.1 Ma at Hadar (Boaz *et al.*, 1982), and is identified from the Kalochoro Member at West Turkana (Harris *et al.*, 1988) and the KBS Member in East Turkana (Leakey, 1976). In South Africa the earliest record is from Sterkfontein Member 4 (Turner, 1987a). *C. mesomelas* is the most common carnivore at Swartkrans (Ewer, 1956). The earliest material referable to the living *C. mesomelas* is from Lainyamok at 392-330 Ka (Potts *et al.*, 1988; Werdelin and Lewis, 2005). *C. adustus* is found only in the last Pleistocene of East Africa and Zimbabwe, with possible records in South Africa at Makapansgat Member 3 (Ewer, 1956) and Hopefield in the Middle Pleistocene (Savage, 1978). *C. aureus* fossil material is limited to North Africa, and the fennec has no fossil record south of the Sahara

(Savage, 1978). *C. terblanchei*, found at Kromdraai, Coopers and Elandsfontein, is described as a jackal about the same size as the living *C. adustus* with relatively small incisors (Broom, 1948; Ewer, 1956; Hendey, 1974b). We can therefore assume that by the time of the earliest Oldowan, fossil jackals were occupying a niche similar to the one inhabited by modern jackals.

Modern jackals have a wide habitat tolerance, but are absent from forests (Estes, 1993; Kingdon, 1977). Black-backed jackals (*C. mesomelas)* tend to be associated with closed woodland to more open terrain, golden jackals (*C. aureus*) with grasslands, and side-striped jackals with open woodland (Fuller *et al.*, 1989; Skinner and Smithers, 1990). Jackals are omnivorous and opportunistic, eat a wide variety of food, including fruits, groundnuts, berries, grass, eggs, insects and other invertebrates, small vertebrates, and small to medium sized mammals; of adult antelopes, dik-dik and Thomson's gazelle seems to be the upper limit of its killing capacity but it may tackle sick adults of larger species (Kingdon, 1977; Skinner and Smithers, 1990). Jackals are facultative opportunistic hunters, meaning that they hunt in groups opportunistically, usually when appropriate prey is available (Moehlman, 1987). In the Serengeti, black-backed and golden jackals systematically search near maternal herds of gazelles for concealed fawns which provide the bulk of their diet (Wyman, 1967; Estes, 1993). Jackals will readily scavenge from carcasses; while they normally live and hunt in pairs, as many as 20 or 30 jackals have occasionally been seen together on lion kills (Kingdon, 1977) or on seal carcasses on the Namibian coast (Skinner and Smithers, 1990).

Hunting dog (Lycaon pictus)

The oldest occurrences of *Lycaon* sp. indet. were thought to be a left lower canine identified by Hendey (1974a) from Swartkrans, and material from Kromdraai A, but this may be an incorrect identification (Turner, 1986b). Harris and colleagues (1988) refer to cf. *Lycaon* sp. from the Kalochoro Member of West Turkana (2.3-1.9 Ma), and Leakey (1976) mentions a mandibular fragment of *Lycaon* size at East Turkana, but no further details are available (Turner, 1990). One further possible occurrence in east Africa is a skull from Olduvai described by Pohle (1928) as *Canis africanus*; all of this earlier material may in fact be *Canis.* A large *L. pictus* recorded from Elandsfontein (Ewer and Singer, 1956) is then the earliest clear record of the genus in Africa, and in East Africa the earliest *Lycaon* is from Lainyamok (Potts *et al.*, 1988; Werdelin and Lewis, 2005). Hendey (1974a) implies that *Lycaon* arose from a wolf-like *Canis* ancestor early in the late Pliocene or early Pleistocene, and that *C. atrox* and *C. africanus* were early members of that lineage. *C. africanus* from Olduvai Bed II is probably older than *C. atrox* from Kromdraai A. Hendey (1974a) believes the large fossil canids of the African Pleistocene are all directly related to the living *L. pictus*, with *C. africanus* as the earliest member of the lineage followed by the Kromdraai A *C. atrox*, the Elandsfontein *L. pictus*, and then the late Pleistocene *L. pictus*, which was basically the same as the extant species. *Canis atrox* from Kromdraai A and *Canis africanus* from Olduvai Gorge are hence referred to the genus *Lycaon* by Hendey (1974a). Martínez-Navarro and Rook (2003) recommend that the Early to Early Middle Pleistocene forms of *Lycaon* be referred to the species *L. lycaonoides*, and the Middle-Late Pleistocene and extant African specimens be referred to *L. pictus*. *Lycaon* is distributed across Africa from Algeria to the Cape from middle Pleistocene times to the present (Savage 1978).

The evolution of the hunting dog lineage is characterized by the graduate transformation of the primitive large molars of the Late Pliocene *Lycaon* into the smaller hypercarnivorous teeth of the extant hunting dog (Martínez-Navarro and Rook, 2003). There are clear craniodental morphological adaptations that separate the four modern canids that regularly cooperatively hunt (wolf, wild dog, dhole, and bush dog) and the three of these (excluding the latter) that are documented to consume vertebrate prey much larger than themselves from other canids (Van Valkenburgh and Koepfli, 1993). These features indicates specialization for large bite forces at the canines and efficient meat slicing with the carnassials, which is consistent with expected adaptations for killing and consuming large ungulates (more so than hunting in large groups). The survival of a pathological *Lycaon* specimen from Venta Micena into old age suggests that the collaborative social behavior seen in extant *Lycaon pictus* was already developed in the Early Pleistocene (Palmqvist *et al.*, 1999). In sum, this evidence indicates that by Olduvai Bed II times, a large, social hunting canid which regularly consumed size 2 and 3 prey (*L. pictus* or *C. africanus*) was a member of the African carnivore paleoguild.

Modern African hunting dogs range through all types of savanna and bush (Estes, 1993), but they are mainly associated with open plains and open savanna woodland and their distribution coincides with that of their medium-sized gregarious ungulate prey (Kingdon, 1977; Skinner and Smithers, 1990). They avoid forest or woodland with thick underbrush or tall grass cover and montane forest, although they will use the adjacent montane grasslands. They are the most carnivorous canids, cooperatively hunting and consuming their prey, and they rarely scavenge (Kruuk, 1972; Mills and Biggs, 1993; Creel and Creel, 1995). They seldom come to the freshest of carcasses laid out to attract

predators and when they have been documented as scavenging, the prey was freshly killed (Skinner and Smithers, 1990). However, they have been recorded stealing kills from leopards, lions, and hyaenas (Creel and Creel, 1995). They are extremely sensitive to indirect competition with lions and interference competition with spotted hyaenas (Frame and Frame, 1981; Creel and Creel, 1995; Mills and Gorman, 1997; Gorman *et al.*, 1998). They do not often attack larger adult bovids or zebra adults as they do juveniles and will avoid bunched cattle, tending to go for solitary individuals. The prey is consumed within 30 minutes (Kingdon, 1977), and often all that is remaining from small prey (Thomson's gazelle) are vertebrae and some larger limb bones, the head, and parts of the skin and stomach cavity (Estes and Goddard, 1967; Skinner and Smithers, 1990).

Felidae

The felids are the most abundantly found carnivores in Africa (Savage, 1978), but lions and leopards become common only in the early Pleistocene (Ewer, 1973). The two subfamilies of felids relevant to this study are the Felinae and the Machairodontinae. Felines have conical upper canines, while machairodonts (sabertooths) have scimitar- or dirk-shaped upper canines (Biknevicius et al., 1996); this will be described in more detail below.

Felinae

Lion (Panthera leo)

Panthera goes back the Villafranchian in Europe and may be of African origin but it is pure speculation without a Pliocene record (Savage, 1978). Lions, *Panthera leo*, are fairly rare in east African deposits (Turner, 1990). The earliest record of the lion is at

Laetoli in Tanzania at about 3.5 Ma (Barry, 1987), and the next record is from Member G, Shungura at 2.3-1.9 Ma (Howell and Petter, 1976; Turner, 1986a). However, there are several records of "large felinae" from Omo Usno, Shungura C, D, and F (Howell and Petter, 1976), suggesting the presence of lion there from ~3.0 Ma (Turner, 1990). At East Turkana, the earliest records of *P. leo* is from the Okote Member at 1.6-1.4 Ma (Leakey, 1976), and the lion is known from Olduvai (Ewer, 1965; Petter, 1973). In South Africa, the earliest appearance is in Member 4 at Sterkfontein at about 2.8-2.4 Ma (Turner, 1986b, 1987a, 1990). Stable carbon isotope analysis of lion tooth enamel from Member 2, Swartkrans, indicates a definite preference for C_4-eating prey (Lee-Thorpe *et al.*, 2000). It spread into Europe after that at about 0.9 Ma (Turner, 1990).

In historic times, lions were found throughout Africa, Arabia, Greece, northern India, and southwest Asia; they are presently limited to sub-Saharan Africa with a small relict population in the Gir Forest Reserve of northern India (Antón and Turner, 1997). Lions live throughout Africa except in desert (e.g. the Kalahari in Botswana) and rainforest (e.g. West Africa and Zaire) as long as medium-sized and large herbivores are present (Estes, 1993; Kingdon ,1977). Savanna and plains habitats with good variety and biomass of ungulates carry up to 1 lion/3 mi^2; where prey density is very low, such as in *miombo* woodland or Sahel, there may be only 1 lion/50-100 mi^2 (Estes, 1993). Like other cats, lions are visual hunters, using a stalk and ambush technique, and predominantly nocturnal (Kingdon, 1977). Unusually for cats they are primarily social, and lionesses engage in communal hunts (Kingdon, 1977; Estes, 1993). Prides of up to 40 (but usually ~13-21) related females reside in a traditional home range/territory; males can form coalitions of up to 4 individuals to improve their reproductive chances (Estes,

1993). Home range size depends on prey density and ranges from 20-400 km^2. There is a strong negative correlation between home range size and the abundance of prey during the season of least abundance (Van Orsdol *et al.*, 1985). Lions tend to select the more vulnerable individuals of the most available species and while preferences sometimes develop in areas of prey abundance, the lion can generally be described as a catholic and opportunistic feeder (Kingdon, 1977). Lions will take small game, including rodents, birds, turtles, lizards, fish, ostrich eggs, termites, and fruit (Ewer, 1973; Kingdon, 1977; Estes, 1993). Their principal foods, however, are common ungulates from impala to wildebeest and zebra in size, between 50 and 300 kg (Skinner and Smithers, 1990; Estes, 1993). They will scavenge up to ¼ to ½ of their food, appropriating kills of primarily spotted hyaenas but also cheetah and leopard (Schaller, 1972; Ewer, 1973).

Leopard (Panthera pardus)

Panthera pardus, the leopard, is also first recorded from East Africa at Laetoli at about 3.5 Ma (Barry, 1987) and from South Africa at Sterkfontein Member 2 at about 3.4-3.0 Ma (Turner 1987a, 1990). *Panthera pardus* is also reported from Olduvai Bed I, Omo, and many later African sites (Savage, 1978). The largest sample of leopards is from Swartkrans from 1.8-0.75 Ma (Brain *et al*., 1988; Turner, 1993). Leopards have probably been taking their prey up into trees for the past few million years, as seen at Swartkrans (e.g. Brain, 1981; see below). A recent analysis of stable carbon isotope values of leopard teeth from Members 1 and 2, Swartkrans, yielded a wide range $\delta^{13}C$ values but does indicate that there was a shift in leopard dietary preferences to prey that ate a more C^4 (grassy) diet during later Swartkrans times, perhaps favoring the extinct antilopine

Antidorcas bondi (Lee-Thorpe *et al.*, 2000). *P. pardus* is first recorded in Europe at the same site as lions (Antón and Turner, 1997).

P. pardus currently has the largest range of the larger cats, living in Africa, the Near and Middle East, southern Asia, and the Malaysian archipelago (Antón and Turner, 1997). Leopards have a wide habitat tolerance and while they are generally associated with rocky kopjies, hills, mountain ranges and forest, they also occur in semi-desert (Skinner and Smithers, 1990). They are solitary animals, except during mating season or when a female is accompanied by juveniles. The size of the home range can widely from 40-400km^2 and probably depends on the availability of food (Schaller, 1972; Bothma and le Riche, 1986; Skinner and Smithers, 1990). Leopards tend to prey on small to medium sized mammals less than 70 kg in mass, but they are extremely adaptable and will take whatever is available in their home range including reptiles, birds, tortoises, and insects (Pienaar, 1969; Ewer, 1973; Le Roux and Skinner, 1989; Skinner and Smithers, 1990). Leopards will scavenge carcasses where they are available (Skinner and Smithers, 1990). Leopards are nocturnal stalkers and pouncers, and when they live in areas frequented by other predators, they store their food in tree branches, caves, or holes (Kingdon, 1977; Brain, 1981; Le Roux and Skinner, 1989; Skinner and Smithers, 1990). Leopards can lose prey to lions, hyaenas, jackals or vultures (Kruuk, 1972; Schaller, 1972; Kingdon, 1977).

Cheetah (Acinonyx jubatus)

The oldest record of the cheetah, *Acinonyx jubatus*, in Africa is from the Member 2 deposit of the Silberberg Grotto at Sterkfontein at about 3.4-3.0 Ma (Turner, 1987a, 1990). *Acinonyx* appears in the early Pleistocene at Laetoli and the Omo and in the later Pleistocene of east, south, and north Africa; the genus is recognized in the Villafranchian

of Europe and Asia (Antón and Turner, 1997; Lewis and Werdelin, in press). The scarcity of fossil cheetah specimens is not surprising considering cheetah's solitary nature and large territories.

Historically, cheetahs were found historically in Africa, Asia, and the Near East but they now confined to isolated populations in Africa (Savage, 1978; Antón and Turner, 1997). Modern cheetahs are widespread in sub-Saharan savannas and arid zones, wherever suitable prey occurs, though generally at very low density (Estes, 1993). Though they live in sparsely vegetated sub-desert and steppe, as they need bushes, grass, or other cover to get within sprinting range of prey and to hide from other predators; they do not occur in forest or woodland with a thick underbrush or tall grass cover (Estes, 1993; Skinner and Smithers, 1990). Cheetahs are the most diurnal living African felid (Ewer, 1973). Those that live on migratory game have huge home ranges, about 800 km^2, but much smaller home ranges (<100 km^2) are defended by resident males in areas of high prey density (Estes, 1993). While males are often found together, females never are; they live alone or with their cubs (Caro and Collins, 1986). Cheetahs are specialists on small to medium sized open plains prey such as gazelle; in wetter areas they concentrate on impala, kob, lechwe, and reedbuck (Estes, 1993). They also eat smaller antelope (oribi, duiker), calves and yearlings of all the larger antelopes, warthog, young zebra, some small game such as hares (Estes, 1993), aardvarks, porcupines, ostriches, ground birds such as bustards and guinea fowl (Pienaar, 1969). Prey above 60 lbs. is rarely killed (Schaller 1969, 1972; Eaton, 1970). Taking of carrion is very rare but it has been known to occur (Ewer, 1973; Pienaar, 1969). At times they can lose a high proportion of their prey to lions (Kingdon, 1977), but they do not scavenge other carnivore's kills.

Machairodontinae

The Machairodontinae include three tribes: the Smilodontini, the Homotheriini, and the Metailurini; the first two shared a more recent common ancestor and are therefore regarded as more closely related (Antón and Turner, 1997). The African Plio-Pleistocene machairodonts include *Megantereon* (Smilodontini), *Homotherium* (Homotheriini), and *Dinofelis* (Metailurini). Overall characteristics of sabertooths likely include specialization on large sized prey (Bohlin, 1940; Ewer, 1973; Marean, 1989) with rapid flesh consumption but inefficient bone processing (Marean, 1989). Based on a study of carnassial dental microwear of *Smilodon*, a North American taxon, sabertooths probably consumed less bone than cheetahs and may have avoided bone in order to protect its long canines from breakage (Bohlin, 1940; Kurtén, 1952; Emerson and Radinsky, 1980; Martin, 1980, 1989; Akersten, 1985; Van Valkenburgh and Ruff, 1987; Van Valkenburgh *et al.*, 1990).

However, detailed study of sabertooth postcranial ecomorphology indicates probable differences among the sabertooth genera (Lewis, 1995). In Africa, *Dinofelis* and *Megantereon* were probably mixed/closed habitat ambush predators, while African *Homotherium* was more even more cursorial and may have lived in more open habitats than their North American congeners, with more distally elongated forelimbs. Marean (1989) describes habitat partitioning among machairodonts as vertical, suggesting possible climbing capability in *Dinofelis*. Stable carbon isotope analyses of Swartkrans Member 1 sabertooths indicate that *Megantereon* preferred C_3 habitats while *Dinofelis* preferred more open, C_4 habitats (Lee-Thorpe *et al.*, 2000), though both of these

reconstructions are based on single specimens. These differences will be discussed in detail below.

Megantereon

Megantereon has been found in Eurasia, North America and Africa; the Eurasian and African specimens are most likely conspecific and all of the specimens might belong in one species, *M. cultridens* (Antón and Turner, 1997; Sardella, 1998). The origin of this species is uncertain as it is found in Eurasia and Africa by 3.0 Ma and in North America shortly afterwards; a primitive form, referable to *Megantereon* sp. from the latest Miocene in China, may suggest an Asian origin (Sardella, 1998). A recent discovery of *M. ekidoit* (a new species) from South Turkwel in Kenya at 3.6 to 3.2 Ma is the oldest *Megantereon* in Africa (Werdelin and Lewis, 2000), though an older specimen from Aramis has been attributed to *Megantereon* (WoldeGabriel *et al.*, 1994). The reported *Megantereon* from Laetoli (Barry, 1987) probably belongs to *Dinofelis* (Werdelin and Lewis, 2001). Other East African occurrences include material from the Usno Member at ~3.1 Ma (Turner, 1987b), possible specimens from Shungura Member B and later members of the Omo Formation (Howell and Petter, 1976). South African occurrences include material from Kromdraai, Swartkrans and Sterkfontein (Turner, 1986a). The latest appearances seems to be from the Okote Member in East Africa at about 1.5 Ma and Member 3 at Swartkrans in South Africa, close to 1.0 Ma (Vrba, 1981; Brain *et al.*, 1988; Turner 1990, 1993), although the *Megantereon* material from Elandsfontein may be as recent as Middle Pleistocene (Hendey, 1974b). The South African material is sometimes separated into three species, *M. whitei*, *M. gracile* and *M. eurydon*, but other

views lump all the material into *M. cultridens* (Turner, 1987b). See Lewis and Werdelin (in press, b) for a comprehensive review of *Megantereon* taxonomy.

Megantereon is 'dirk-toothed', with very elongated but much less flattened canines, either smooth or with very slight serrations (Ewer, 1973). The upper carnassials are less specialized, with a small inner lobe and the absence of the anterior accessory cusp. The European *Megantereon* was about the size of a large leopard, with especially massive forelimbs and claws the size of a lion (Antón and Turner, 1997). It was relatively short-limbed with bear-like, plantigrade hind feet, powerfully developed forelimbs, comparatively small brains with well-developed olfactory lobes (Martin, 1989; Palmqvist *et al.*, 1996; Lewis and Werdelin, in review). It was probably an ambush predator and solitary hunter. Body proportions suggest it was able to bring down and hold large prey. Post-cranial characteristics suggest it had similar abilities as the jaguar in using the forelimb to grapple with prey (Lewis, 1997), which would have been relatively large for its body size, as it was one of the smallest Plio-Pleistocene African machairodonts (Lewis and Werdelin, in review). The skull of *Megantereon* has well-developed infraorbital canals, implying that these cats had a well-developed cluster of nerves passing through it to their whiskers as do modern cats (Antón and Turner, 1997). Antón and Turner (1997) speculate on preferred prey at the late Pliocene (2.0 Ma) Spanish locality of La Puebla de Valverde, and based on the carnivore guild present, conclude that *Megantereon* was probably interested in the zebrine horse *Equus stenonis* and the deer *Croizetoceros ramosus*. Carbon isotope analysis of a single *Megantereon cultridens* specimen from Swartkrans Member 1 indicates preferences for C_3-eating prey (Lee-Thorpe *et al.*, 2000).

Lewis and Werdelin (in press, b) suggest that even passively scavenging hominins may have found "useful, but not bountiful" remains left behind from *Megantereon* carcasses.

Machairodus, Amphimachairodus, and *Lokotunjailurus*

These three taxa are all Mio-Pliocene in age, but they are included here as they have been found in occurrence with early hominins, though not of Oldowan age. *Machairodus aphanistus* is mainly a Eurasian and North African Upper Miocene species (Petter and Howell, 1987; Antón and Turner, 1997; Werdelin and Sardella, 2006). *Machairodus* appears in Africa from the late Miocene of the Middle Awash, Ethiopia (Haile-Selassie *et al.*, 2004) and Toros-Menalla, Chad (Vignaud *et al.*, 2002). In the Pliocene, it is identified from Sahabi (Howell, 1987), Langebaanweg (Hendey, 1974b), and Aïn Brimba (Petter and Howell, 1987). *Machairodus* is regarded as the ancestor of *Homotherium*. It was about the size of a lion and had elongated metapodials, pointing to a more terrestrial lifestyle than its ancestors (Antón and Turner, 1997). *Machairodus* sp. was reported from Olduvai Bed II (Cushing, 2002) but this is likely a misidentification, possibly of *Homotherium*, based on comparison to the published details of the skull from Aïn Brimba (Petter and Howell, 1987). The successor genus of *Machairodus* is *Amphimachairodus*; the youngest occurrence of this genus is at Langebaanweg, at 5.3-5.0 Ma (Werdelin and Sardella, 2006).

Specimens from the Upper Miocene at Lothagam previously identified as *Machairodus* are placed into *Lokotunjailurus emageritus* (Werdelin, 2003). This large felid has a strongly laterally compressed, serrated upper canine, an extremely large claw on the first digit of its forelimb paw, and a relatively slender appendicular skeleton, lacking extreme machairodont features. It resembles species referred to the genus

Machairodus, but differs in some dental characteristics that relate the Lothagam form to *Homotherium* and suggest it may be closer to *Homotherium* than any other machairodont (Werdelin, 2003). It may, then, be the evolutionary link between *Machairodus* and *Homotherium*, especially if some later *Machairodus* material is actually *L. emageritus*.

Homotherium

Homotherium is known from East Africa from Kanapoi and the Lonyamun Member of Koobi Fora by 4.1 Ma; Laetoli at 3.7 Ma; South Turkwel at 3.6-3.2 Ma; and Hadar at 3.4-3.2 Ma (Howell and Petter, 1976; Leakey, 1976; Barry, 1987; Petter and Howell, 1988; Werdelin and Lewis, 2000; Werdelin and Lewis, 2005). Early *Homotherium* in East Africa (referred to as *H. hadarensis* by Petter and Howell (1988)) is smaller than later representatives of the genus (Werdelin and Lewis, 2000). *Homotherium* is comparatively rare in the Transvaal caves (Turner, 1990), and includes material from Kromdraai A (Ewer, 1955), Makapansgat (initially misidentified as *Megantereon* – Collings *et al.*, 1976), Sterkfontein (Turner, 1987a), as well as from Bolt's Farm (Lewis, pers. comm.). The latest appearances of *Homotherium* in Africa are from Kromdraai A in South Africa and the Okote Member of East Turkana in East Africa, at ~1.4 Ma (Turner, 1990; Lewis and Werdelin, in press).

Homotherium is scimitar-toothed felid, having upper canines with wide, laterally compressed blades, not greatly elongated, and with serrated edges (Ewer, 1973). The upper carnassials are extremely specialized, with no inner lobe and with an extra anterior accessory cusp adding to the length of the cutting blade. *Homotherium latidens* were long-legged pursuit predators, with comparatively large brains and enlarged optic regions suggesting some degree of nocturnal predation (Martin, 1989; Rawn-Schatzinger, 1992;

Palmqvist *et al.*, 1996). The skeleton of *Homotherium* is large but comparatively slender with very elongated forelimbs, relatively small claws with reduced retraction, short lumbar vertebrae, and a short tail; this combination of features is unique and its lifestyle is clearly unknown (Antón and Turner, 1997; Lewis, 1997; Antón *et al.*, 2005). Lewis (1997) draws attention to articular morphology and relative limb proportions that indicate increased cursoriality relative to other sabertooths, as well as decreased limb musculature (indicating decreased load-bearing capabilities) relative to limb length found in other sabertooths. Lewis (1997, 2001a) also notes somewhat reduced supinatory, and presumably prey grappling abilities, in *Homotherium*. A *Homotherium* specimen from Koobi Fora has a brachial index more similar to cursorial, open habitat species than mixed or closed habitat species. The elongated neck and shortened lumbar region of *Homotherium* combined with elongated forelimbs and a high scapula probably resulted in a hyaena-like body shape (Antón and Turner, 1997; Lewis, 2001a). Reconstruction of a shortened calcaneum implies a reduction in leaping ability compared with modern cats, with little to no scansorial ability (Antón and Turner, 1997; Lewis, 2001a). The cheek teeth of *H. latidens* are very specialized for slicing, with anterior cheek teeth much reduced in size. Rawn-Schatzinger (1992) has reconstructed *Homotherium* as having similar body proportions as *Smilodon populator* together with reduced claw retraction, which she thinks suggests a sprinting ability. A pathological bony growth similar to those seen in *Smilodon* is also found on the humerus of *Homotherium latidens* from Senèze in France (Antón and Turner, 1997). This suggests that despite its supposed cursorial traits, *Homotherium* still brought down large prey with the force of its front forelimbs. Antón *et*

al. (2005) reconstruct *Homotherium* morphology as efficient for locomotion at moderate speeds, with less ability for jumping and sudden acceleration that pantherine cats.

Palmqvist and colleagues (1996) conclude that *Homotherium latidens* had hunting behavior similar to a modern lion on the basis of age profiles of prey. Lions preferentially kill juveniles of large species such as elephants; at Venta Micena in Spain, the proboscidean *Mammuthus meridionalis* is represented primarily by juveniles. This is similar to evidence from Freisenhahn Cave (Marean, 1989; Rawn-Schatzinger, 1992), in which *Homotherium serum* seems to have selected almost 100% juveniles of two *Mammuthus* species. Marean and Ehrhardt (1995) re-analyzed the Freisenhahn material and concluded that *H. serum* disarticulated skeletons of their preferred size 4 prey at the kill site and selectively transported body parts, including limb bones of high flesh yield (humerus, femur, and tibia) away from the kill to more favorable locations (dens/ woodlands). They suggest that this species may have possessed a social behavior and hunting strategy involving pairs or larger groups similar to lions, which could have allowed them to penetrate the protective shield of adult mammoths. This conclusion was also reached by Antón *et al*. (2005) based on reduction of the claws, which could have limited the ability of individuals to bring down large prey. Conversely, Rawn-Schatzinger (1992) reconstructs *Homotherium* as a solitary hunter based on the use of dens in extant felids primarily by solitary species, and the presence of whole prey individuals, presumably transported whole, at Freisenhahn Cave. Marean and Ehrhardt (1995) found tooth marking attributable to *Homotherium serum* to be common at Freisenhahn Cave: 54% of proboscidean bones have at least one tooth mark present, and bones that are most frequently tooth-marked are ribs, humerus, metacarpal, femur, astragalus, and metatarsal

(all at least 95% MNE preserving at least one tooth mark). *Homotherium* seems to have been able to capture prey larger than modern lions (Lewis, 1995, 1997; Marean and Ehrhardt, 1995) but if *Homotherium* in Africa transported portions of carcasses as suggested for the North American species, or lived in groups, they may have left relatively little in the way of scavengeable resources for early hominins (Lewis and Werdelin, in press).

Dinofelis

Dinofelis is found in all northern hemisphere continents and Africa, where it is most common, and where its evolution seems to have been centered (Werdelin and Lewis, 2001). In Africa, the earliest *Dinofelis* is recorded at Lothagam (*Dinofelis* sp., Werdelin and Lewis, 2001; Werdelin, 2003), and then Langebaanweg (Hendey, 1974b). The taxonomy of Langebaanweg material is unclear, but it has recently been assigned to *D.* cf. *diastemata* (Werdelin and Lewis, 2001). Slightly younger than this is a new species, *D. aronoki*, from the Upper Burgi (Koobi Fora) and may include material from the Middle Awash, Hadar, and Olduvai Gorge. East African material from ~4.0 Ma to 2.5 Ma (Kanapoi, Allia Bay, Siki Hakoma and Denen Dora – Hadar, Laetoli, Omo Shungura B, and Koobi Fora Tulu Bor) can be referred to another new species, *D. petteri*. *D. darti* is known only from Makapansgat. Other specimens older than 1.6 Ma from South Africa (e.g. Sterkfontein, Bolt's Farm) are generally referred to the large taxon *D. barlowi*, while those younger than 1.6 Ma from East and South Africa (e.g. Kromdraai A, Koobi Fora Okote Member, and Kanam East) are assigned to *D. piveteaui*. An exhaustive list of East and South African locales with *Dinofelis* remains is found in Werdelin and Lewis

(2001:151). The youngest specimen *D. piveteaui* is from Kanam East in East Africa, dated to ~1.0 Ma (Werdelin and Lewis, 2001).

Sabertooths of the tribe Metailurini, including *Dinofelis*, are often referred to as "false" sabertooths because their dental morphology falls to some extent between machairodontines and felines, with flattened but short canines (Antón and Turner, 1997). *Dinofelis* had retractile claws with a somewhat enlarged claw on the first digit, indicating a difference in the use of the forepaw from extant felids (Gonyea, 1976, Werdelin and Lewis, 2001). *Dinofelis* has a shorter tail than modern pantherine felids (Hendey, 1974b). *Dinofelis* is the most likely of the machairodonts to have a prey acquisition behavior similar to *Panthera*, as its upper canines are only slightly or not at all different from modern larger *Panthera* species (Werdelin and Lewis, 2001). Ecomorphology of both craniodental and postcranial material suggests a trend in *Dinofelis* (culminating in *D. barlowi*) converging on modern pantherine cats in morphology and behavior (Werdelin and Lewis, 2001). However, this trend is reversed in the youngest species, *D. piveteaui*, which has the most machairodont ecomorphology. In general, *Dinofelis* evolved from the robust, leopard-like form at Langebaanweg to a form more similar to modern lions or tigers in craniodental proportions as well as robusticity and proportions of the postcrania. Overall, the forelimb apparatus of *Dinofelis* is more similar to the forelimb of extant prey-grappling felids than other machairodonts, though it does resemble machairodonts in having more robust forelimbs than hindlimbs due to an increase in forelimb robusticity (Lewis, 1995, 1997; Werdelin and Lewis, 2001). This increased forelimb robusticity indicates that *Dinofelis* would have had great strength when grappling with prey, but would have lost some rotatory ability (Lewis, 1995; Werdelin and Lewis, 2001).

Different *Dinofelis* species had slightly different postcranial morphology, but in general *Dinofelis* has extremely shortened distal limbs elements compared to modern felids, suggesting they inhabited closed or mixed habitats, were not fast runners with less cursorial adaptations than modern lions, and were ambush predators (Werdelin and Lewis, 2001). However, stable carbon isotope analysis of a single *Dinofelis* specimen from Swartkrans indicates that it concentrated on C_4-eating prey (Lee-Thorpe *et al.*, 2000).

Hyaenidae

Although the modern hyaenid family is small, hyaenids are diverse and abundant in the fossil record with almost 100 species named (Werdelin and Solounias, 1991). Based on both fossil and molecular evidence, the hyaenids are presumed to have their origins at about 25 million years (Werdelin and Solounias, 1991), in the Viverridae (Savage, 1978). The oldest hyaenid fossils are about 17 million years old, from the late early Miocene site of Bézian (Werdelin, 1996a) and soon after from China (Werdelin and Solounias, 1991). However, hyaenids did not become numerous until the Pliocene (Ewer, 1978). The oldest hyaenids are placed in the genera *Protictitherium* and *Plioviverrops*, small, civet-like forms which may have had semi-retractile claws indicating at least a semi-arboreal niche (Werdelin, 1996b). These are followed in the lower middle Miocene by a series of 'dog-like' hyaenas. After the dog-like hyaenids there is a split into two major clades (Werdelin, 1996b). One clade continues the trends of larger size and more cursorial limb elements seen in the evolution of the dog-like hyaenids; this clade is composed of *Lycycaena*, *Hyaenictis*, and *Chasmaporthetes*, which can collectively be

described as cursorial hunting hyaenas. The second clade, which exhibits an increase in size and an emphasis on the bone-cracking versus shearing component of the dentition in most species, leads to the modern bone-cracking, scavenging hyaena. The characteristic feature of this group is the broadening of the premolars, especially the upper and lower P3, which are the main bone-cracking teeth in living hyaenas. Members of this clade, including the modern bone-crackers *Crocuta*, *Hyaena,* and *Parahyaena* and the Pleistocene hyper bone-cracker *Pachycrocuta*, become common only after the terminal Miocene extinction of the dog-like hyaenas and were absent in sub-Saharan Africa before ~4.0 Ma. The maximum hyaenid diversity in Africa is in the early Pleistocene with nine species, followed by three each in the middle and late Pleistocene (Savage, 1978).

The earliest hyaenid record in sub-Saharan Africa is of the genus *Protictitherium*, reported from the middle Miocene of Fort Ternan (Ewer, 1973; Schmidt-Kittler, 1987; Werdelin and Turner, 1996). *Ictitherium* is found in the late upper Miocene in the Samburu Hills and Lothagam (Werdelin and Turner, 1996). *Hyaenictitherium namaquensis* is found in the late upper Miocene/early Pliocene at Sahabi, Langebaanweg, Klein Zee, and Lothagam. *Hyaenictis hendeyi* is from the late upper Miocene/early Pliocene at Langebaanweg, and *Adcrocuta eximia* is from the lower Pliocene at Sahabi. *Ikelohyaena abronia*, the earliest close relative of the modern striped hyaena, is from the lower Pliocene at Langebaanweg, Laetoli, Hadar, and possibly Lothagam (Lewis and Werdelin, in press). The earliest *Chasmaporthetes* is from Allia Bay at 3.9-3.7 Ma (Werdelin and Lewis, 2005). The three species of *Chasmaporthetes, C. nitidula, C. silberbergi,* and *C. australis*, are found in the late upper Miocene through the Pleistocene at Langebaanweg, Swartkrans, Sterkfontein, Laetoli, Olduvai Gorge, and Hadar

(Werdelin and Lewis, 2005). *Pachycrocuta bellax* and *brevisrostris* are known from the upper Pliocene through the early Pleistocene at Makapansgat, Sterkfontein, Kromdraai A, and Hadar. The earliest bone-cracking hyaena is *Parahyaena howelli* from Kanapoi at 4.23-4.07 Ma, an early relative of the living brown hyaena (Werdelin and Lewis, 2005). *Hyaena makapani*, which is smaller than more gracile that the living striped hyaena with fewer adaptations to bone cracking, appears at about 3.5 Ma (Werdelin and Lewis, 2005).

The three living hyaena genera all originated in the Pliocene. *Crocuta* is found from the lower Pliocene through today, at Laetoli, Makapansgat, Chemeron, the Awash, Hadar, Shungura Member G, Kanam, Olorgesailie, Swartkrans Member 1, Makapansgat, Kromdraai A, Elandsfontein, Broken Hill, Buluwayo Waterworks, Beds I and II at Olduvai Gorge and the more recent Eyasi deposits in Tanzania, as well as in hundreds of Pleistocene cave sites throughout Europe and Asia either used as dens by or natural traps for the European subspecies, the cave hyaena (Ewer, 1967; Collings *et al.*, 1976; Werdelin and Solounias, 1991 and references therein; Lewis and Werdelin, 2000). *Hyaena hyaena* appears at about 1.9 ma (Werdelin and Lewis, 2005), and is found in the Usno and Shungura Member B, East and West Turkana, Kromdraai B, Makapansgat Member 3, Swartkrans Member 1, and Bed I at Olduvai Gorge (Petter, 1973; Howell and Petter, 1976; Leakey, 1976; Randall, 1981; Turner, 1986b, 1990; Werdelin and Solounias, 1991) and possibly Laetoli (Dietrich, 1942). The oldest specimen of the living brown hyaena, *Parahyaena brunnea*, is from the middle Pleistocene of Kenya (Werdelin and Barthelme, 1997; Werdelin and Lewis, 2005).

Spotted hyaena (*Crocuta*)

Crocuta became widespread as a single species in Africa but diversified into many species in Eurasia (Savage, 1978). Werdelin and Solounias (1991) suggest that the evolutionary relationships within this genus need to be restudied, and Turner (1990) would subsume all of the *Crocuta* specimens from Africa into *C. crocuta*. However, this review recognizes *Crocuta* sp., *C. dietrichi*, *C. ultra*, and *C. crocuta* as distinct species (cf. Lewis and Werdelin, 2000) and they will be discussed below.

Lewis and Werdelin (1997, 2000) summarized the patterns of evolution and ecology in the genus *Crocuta*, noting a three-stage evolutionary trend. Prior to 2.5 Ma, *Crocuta* is found in association with larger hyaenids and may have occupied an omnivorous ecological niche similar to that of modern *Hyaena*. Then, between 2.5 and 1.5 Ma, *Crocuta* dental anatomy suggests an expansion of the scavenging capabilities to that seen in the modern species, possibly due to a lack of sympatric hyaenid associations. Finally, after 1.5 Ma, a change in limb proportions and an increase in overall body size probably indicate an expansion into the more modern predatory *Crocuta* niche.

Lewis (2001b) specifically addresses the evolutionary history of *Crocuta*, detailing the ecology of the three known species. The first stage (*Crocuta* sp.), from 4.1-3.36 Ma and represented by material from West Turkana, was a very large animal with a relatively and absolutely large carnassial, a seemingly hypercarnivorous adaptation. From 3.7-1.6 Ma, *Crocuta dietrichi* (e.g. from Laetoli) was a small with gracile but heavily muscled post-crania and short, wide cheek teeth. It had longer limbs than modern *C. crocuta*, indicating a less sloped back and a more cursorial locomotion pattern. Its limb proportions were similar to a brown hyaena and it may have had a dog-like appearance in limb shape. The next stage, early *Crocuta ultra*, which was common in eastern and

southern Africa, was more robust than *Crocuta* sp. and *C. dietrichi* and had teeth more indicative of bone-cracking than flesh-slicing. It had a gluteal muscle orientation on the pelvis similar to modern *C. crocuta*, indicating a possible shift in its center of gravity, but its limb proportions were not quite like those of the modern species. It has a shorter tibia that *C. dietrichi*, and probably had not developed the modern spotted hyaena transport capabilities. Lewis (2001b) described the adaptive niche of this animal as "power scavenging". At 0.9 Ma, the late *Crocuta ultra* (e.g. from Olorgesailie) had a large body size, a short P2, a long P3, a short and narrow M1, and still did not have fully modern limb proportions; this species was on a different evolutionary trajectory than the modern *Crocuta crocuta*. The appearance of the modern *C. crocuta* is not well dated (~1 Ma, Lewis and Werdelin, 2000) but the earliest occurrence may be from Elandsfontein (South Africa). It has a smaller body than *C. ultra*, a long, narrow P4 and M1, modern postcranial and proportions; these changes indicate an increase in bone-cracking and flesh slicing (predatory behavior) and modern transport capabilities. A recent investigation of the stable carbon isotope value of a single tooth from Member 1, Makapansgat referred to *C. crocuta* yielded a $\delta^{13}C$ value of – 9.2, indicating that this taxa concentrated on prey which ate a mainly C_3 diet (Lee-Thorpe *et al.*, 2000). The suite of adaptations that define modern *Crocuta*, including bone-cracking, group hunting, confrontational scavenging, and heavy carcass lifting and transport behavior, developed only within the last million years (Lewis and Werdelin, 2000, in press).

Modern spotted hyaenas have a wide distribution on the African continent south of the Sahara, absent only from the desert areas of the Sahara and Namibia, central African forests, and most of South Africa. They are probably the most numerous of all of

the living African predators (Kingdon, 1977), though their distribution has shrunk considerably in historical times due to human influences (Skinner and Smithers, 1990). The two most important factors influencing and limiting spotted hyaenas are humans and lions, both which provide large quantities of waste but also compete for the same resource (Kingdon, 1977). Spotted hyaenas are predominantly nocturnal (e.g. Gasaway, 1991) but can also be active during the daylight hours (Skinner and Smithers, 1990). The spotted hyaena is a savanna species, associated with open plains, dry acacia bush, open woodlands, rocky country and semi-desert scrub (Kingdon, 1977; Skinner and Smithers, 1990). Their distribution is determined primarily by the availability of prey (Kingdon, 1977). Throughout their range, spotted hyaenas feed predominantly on medium or large ungulates and tend to prey on three or four dominant species. They are very adaptive and flexible in their diet and social structure, and can either live and hunt in groups of up to 50 to exploit large concentrations of prey, or forage singly on scattered small prey and carrion. Spotted hyaenas have also been recorded as taking a wide range of other prey besides ungulates including pangolins, hares, birds, fish, reptiles, tortoises, crabs, snails, termites and fruit (Kingdon, 1977; Skinner and Smithers, 1990). Modern spotted hyaenas do not always relying on scavenging; they killed over 70% of their own food in several study areas (Kruuk, 1966; Mills, 1990; Gasaway, 1991). Dens of breeding spotted hyaenas often accumulate bones, but bone caching is uncommon (Skinner and Smithers, 1990).

Striped hyaena (*Hyaena hyaena*)

Hyaena hyaena is known primarily from Africa from the Villafranchian to the recent (Werdelin and Solounias, 1991). The sample from Makapansgat is one of the

largest samples of a carnivore species known for the African Plio-Pleistocene (Turner, 1990). The age structure of the Makapansgat sample based on dental criteria suggests old age is commonly attained (Turner, 1988). No other studies of fossil striped hyaenas have been undertaken. The striped hyaena currently lives in the drier parts of northern and eastern Africa and also ranged in recent years through Arabia minor, Persia, southern USSR and a large part of India (Kingdon, 1977). In Africa, they extend as far west as Senegal and southwards through Egypt as far as Tanzania (Ewer, 1973).

Modern striped hyaenas prefer dry country, living in dry savanna, arid zones, and deserts (Estes, 1993). Striped hyaena diet can be described as focusing on scavenged mammal remains with a significant amount of insects and fruit (Kruuk, 1976). The small mammal component of the diet can include hares, bat-eared foxes, gazelle fawns, dik-diks, and birds (Estes, 1993). They establish communal dens at which bones accumulate, usually in stony or rocky areas, or sometimes in deep caves or burrows that they excavate themselves (Kingdon, 1977; Skinner *et al.*, 1980). Food caching in striped hyaenas is similar to that of brown hyaenas except that they tend to cache food near the den most of the time (Mills, 1978a). Striped hyaenas are reported to be strictly nocturnal but they may be more flexible in areas uninhabited by humans (Kingdon, 1977; Kruuk, 1976). Their social organization is similar to that of brown hyaenas, normally foraging on their own or in pairs; (Kingdon, 1977; Mills, 1978b). Home ranges vary from ~45-550 km^2 (Mills, 1978b).They are usually dominant over leopards and cheetahs, appropriating their kills, and smaller carnivores are ignored or treated as prey (Estes, 1993). They are dominated both ecologically and behaviorally by spotted hyaenas, surrendering food and running away when chased, and they give lions a wide berth.

Brown hyaena (*Parahyaena brunnea*)

Parahyaena brunnea, sometimes called *Hyaena brunnea*, is also found from about the Villafranchian to the recent and previously had a much greater range than it does at present (Werdelin and Solounias, 1991). The earliest occurrence is from Sterkfontein Member 4 at 2.8-2.4 Ma (Turner, 1987a). It has also been found in South Africa at Swartkrans (Ewer, 1955; Turner, 1993), Kromdraai A, and Elandsfontein (Ewer and Singer, 1956), Florisbad (Dreyer and Lyle, 1931), Mumbwa Caves (Clark, 1942); and in East Africa at Hadar, Omo (Usno Formation and Shungura Members C, E, F, and G) (Howell and Petter, 1976; Turner, 1990; Werdelin and Solounias, 1990). *P. brunnea* is also found at Laetoli, based on a single damaged upper carnassial (Pohle, 1928). In North Africa it appears at the base of the Middle Pleistocene and continues from there (Ewer, 1967). Klein (1986) has attributed a series of fossil dens in the south-western Cape of South Africa to *P. brunnea*.

Living brown hyaenas are found only south of the Zambezi River, except for a marginal extension of their distributional range into the arid southwest parts of Angola (Estes, 1993; Skinner and Smithers, 1990). Even in this area, their distributional range has shrunk in historical times and they are not commonly found South Africa except for the northernmost Transvaal and the Cape Province. They are particularly associated with the South West Arid Zone and the drier parts of the Southern Savannas (Skinner and Smithers, 1990). Cover in which to retreat is an essential requirement; they utilize bushes or holes in the ground, often near food supplies, for this purpose (Mills, 1987). They live in desert, semi-desert, open scrub, and open woodland savanna with a maximum annual rainfall of about 650 mm. In central Botswana they live in semi-desert scrub; in the

northern Transvaal, they prefer rocky, mountainous areas with bush cover; in Namibia, they occur in the Namib Desert, scavenging along beaches at night. Brown hyaenas are nocturnal, solitary foragers but most live in groups which occupy fixed territories and they will scavenge communally (Skinner and Smithers, 1990; Estes, 1993).Territories average ~300 km^2 (Mills, 1990). They are predominantly scavengers with a catholic, seasonally flexible diet, emphasizing mammals (Mills and Mills, 1978; Skinner and Smithers, 1990). Their diet also includes a wide range of small mammals, birds, reptiles, insects, marine organisms, eggs and fruit (Skinner, 1976; Skinner and Smithers, 1990; Estes, 1993). Several brown hyaenas can congregate at a carcass but unless there is a lot of meat present only one feeds at a time, and no more than three brown hyaenas feed together (Mills, 1990; Estes, 1993). Brown hyaenas carry food to provision their young at the den; some of these assemblages have been studied for information on their diet (Skinner, 1976; Mills and Mills, 1977, 1978; Skinner and van Aarde, 1991). Excess food is sometimes cached (Mills, 1990). Brown hyaenas keep clear of lions and hyaenas, and wild dogs will drive them off carcasses, but they easily appropriate the kills of cheetahs and have been known to steal from leopards (Owens and Owens, 1978; Skinner and Smithers, 1990). Their greatest competitors for food are black-backed jackals, which may trail them when foraging (Skinner and Smithers, 1990). In the Kalahari, both interference and exploitation competition with spotted hyaenas causes a decrease in brown hyaena population density (Mills, 1987).

Chasmaporthetes

Chasmaporthetes as a genus is characterized by a slender skeletal structure with cursorial, cheetah-like adaptations as stated above (Berta, 1981; Kurtén and Werdelin,

1988; Werdelin and Turner, 1996) and a dentition less robust than in the bone eaters *Crocuta* and *Hyaena* (Kurtén and Werdelin, 1988), suggesting an essentially flesh specializing adaptation. Tooth enamel structure of *Chasmaporthetes lunensis* from the late Pliocene of Italy is also consistent with the hypothesis that *Chasmaporthetes* was primarily a meat, not bone, eater (Ferretti, 1999). However, the relative position of the M_1 in the jaw is characteristically hyaenid, pointing to the importance of scavenging in the overall *Chasmaporthetes* ecology (Kurtén and Werdelin, 1988). An analysis of European *Chasmaporthetes* postcranial material suggests long limbs and a possible preference for relatively open habitats (Lewis, 1997). However, an analysis of the stable carbon isotope ratio in *Chasmaporthetes nitidula* tooth enamel from Member 1, Swartkrans, yielded $\delta^{13}C$ ratios of –6.8 to –7.1, suggesting either a diet including range of C_3 and C_4 eating herbivores or a concentration on mixed feeders (Lee-Thorpe *et al.*, 2000). This does not support the idea that this taxa preferred open habitats and could arguably speak to the importance of scavenging to *Chasmaporthetes*, albeit scavenging unlike any modern hyaena as it would not have been able to access bones in the same way (M. Lewis, pers. comm.).

Pachycrocuta

Pachycrocuta bellax is found in South Africa at Kromdraai A, Makapansgat Member 3, and Sterkfontein Members 4 and 5 and in East Africa in the Turkana Basin (Turner, 1990; Werdelin and Solounias, 1991; Werdelin, 1999). It is large, with a long lower carnassial. Turner (1987a, 1990) would allocate all *Pachycrocuta* material from Africa to *P. brevirostris* while other authors (e.g. Werdelin, 1999) suggest *P. bellax* is a result of local evolution within the African continent.

Toerien (1952) first referred material from Africa found at Makapansgat to *P. brevirostris* (originally *Crocuta brevirostris*), and later Randall (1981) assigned more Makapansgat specimens to this species. This taxon is known in Africa from 3.0 to 1.5 Ma from Makapansgat Member 3, Kromdraai A, Sterkfontein Members 4 and 5, Hadar (though see Werdelin, 1999 for disagreement), and West Turkana (Howell and Petter, 1979; Randall, 1981; Boaz *et al.*, 1982; Turner ,1986b, 1987a; Werdelin, 1999). Earlier material may be found at Lukeino and Chemeron but the dates and species allocation are both uncertain (Turner, 1990). Werdelin (1999) recently attributed some relatively small craniodental material from the Pliocene of East Africa, some of which had been designated *C. crocuta*, to *P. brevirostris*, and this may be the earliest occurrence of this species in Africa. He speculates that the genus migrated to Africa from Asia prior to 3.3 Ma (Werdelin, 1999). Postcranial remains (distal tibia, proximal and distal fibula) of cf. *Pachycrocuta* sp. are recently reported from South Turkwel, Kenya (Werdelin and Lewis, 2000) and it is possible that these belong to *P. brevirostris* as well. During this time, there seems to be a relatively small *Pachycrocuta* (the size of modern *Crocuta*), and a small species of *Crocuta* (M. Lewis, pers. comm.), which may contribute to the difficulties of allocating specimens to one genus or the other based solely on size.

Pachycrocuta brevirostris is the largest of the true hyaenas (Werdelin, 1999), with a body size probably similar to that of a modern lion but had relatively shorter distal limb elements (radius and especially tibia) than living taxa – body proportions seemingly more adapted for power and strength than for speed (Antón and Turner, 1997). The anatomical reconstructions are based mainly on material from Zhoukoudien, where at least 2000 specimens including an almost complete skeleton are present. It essentially

occupied the ecological niche played in the modern African carnivore guild by the spotted hyaena, but with a larger body and skull and therefore probably a greater ability to consume carcasses. *P. brevirostris* was unlikely to have been a solitary scavenger due to its large body size and shortened distal limb elements which would have made extensive locomotion needed to find undefended carcasses energetically costly. Comparisons with modern carnivores in terms of frequencies of different prey size classes killed and scavenged, as well as taphonomic study of Venta Micena in Spain, suggests that this hyaenid was a bone-cracking scavenger which fed largely on carcasses of ungulates preyed upon and partially consumed by flesh-eating carnivores such as sabertoothed felids and wild dogs, and transported these carcasses and carcass parts to dens (Palmqvist *et al.*, 1996; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001). Werdelin (1999) speculates that *Pachycrocuta brevirostris*, *Crocuta crocuta* and *Pliocrocuta perrieri* as "ecological vicars" for one another (from Asia, Africa, and Europe respectively), originating after the extinction at the end of the Miocene of the earlier bone-cracking hyaena *Adcrocuta eximia* and all subsequently dispersing into each other's original domains.

Plio-Pleistocene African Carnivore Paleoguilds and Potential Hominin Niche Space

A guild is traditionally defined a group of sympatric species that utilize the same resources in a similar way, and guild membership is based on significant overlaps in niche requirements without regard to taxonomy (Root, 1967). In reference to fossil taxa, the term 'carnivore paleoguild' is used here in reference to mammalian carnivorous species with overlapping temporal and spatial ranges, as it has been by others (e.g. Van

Valkenburgh, 1985, 1988, 1989, 1995; Turner, 1990; Lewis 1995, 1997; Brantingham, 1998). Here I am specifically referring to the feeding guild of carnivorous taxa which occur in the fossil records of eastern and southern African between ca. 3.0-1.0 Ma (see Werdelin and Lewis, 2005: 144, Figure 2, for a complete taxonomic list and stratigraphic ranges of East African Plio-Pleistocene carnivores). Guilds have been suggested as useful units for the analysis of coevolution as a response to competition for shared resources (Stanley *et al.,* 1983). Carnivore guilds are tightly constrained in ecological space, so changes to one part of the guild can affect its entirety (Dayan and Simberloff, 2005). Hominin competition, whether direct or indirect, with Plio-Pleistocene carnivores for shared limited resources (larger mammal carcasses) has been suggested as leading to coevolution in the form of competition-driven resource partitioning and character displacement (cf. Walker, 1984; Shipman and Walker, 1989; Turner, 1992; Lewis, 1995, 1997; Brantingham, 1998).

Figure 5.1, reproduced from Blumenschine and Pobiner (2003), provides the taxonomic composition of the modern and Plio-Pleistocene larger mammalian carnivore paleoguilds in East and South Africa. The composition of the paleoguild is inferred from time-stratigraphic associations of fossil carnivore taxa. The taxa are arrayed within a matrix that defines some basic aspects of each taxon's fundamental feeding niche, defined here by carcass sizes and edible tissue specialization (with corresponding bone modification potential). Individual carnivore taxa are located within the matrix for each carcass size group according to the maximum extent to which they are capable of destroying bone while extracting flesh and within-bone tissues. Hence, carnivores positioned further to the left in the matrix are those known or inferred on the basis of

functional morphology to be less capable bone destroyers, and correspondingly more regular providers of scavengeable food to secondary consumers from a wider array of carcass parts. These taxa are dominated by felids, particularly those species that are small relative to carcass size. Carnivores positioned toward the right of the matrix are dominated by hyaenids, reflecting the ability of these species to extract food within bone and to deprive consumers from other taxa of scavengeable food.

There was a significant shift in the global carnivore guild at the beginning of the Pliocene (Antón and Turner, 1997). The large cats of the earliest Pliocene were all machairodonts, largely flesh-specialists; the hyaenas had started to become specialized for bone crushing, obtaining a living from scavenging when necessary; and a second major morphotype occurred throughout the Pliocene in the form of *Chasmaporthetes*, the cursorial hunting hyaenas. The lion, the leopard, the cheetah, and the spotted hyaena all appear in the eastern and southern African fossil record at about 3.5 Ma. They do not replace the older carnivores, however; *Homotherium* and *Megantereon* persist until about 1.5 Ma in Africa, and *Dinofelis* until even later. Brown and striped hyaenas originated in Africa by about 3.0 Ma (Turner, 1990). There has been a major change in the Plio-Pleistocene African larger carnivore guild from about 5.0 Ma, when virtually none of the living species existed, through about 3.0 Ma, when most of the extant taxa were present alongside many archaic species, to 1.0 Ma, by which time only the modern species were left (Turner, 1990; Werdelin and Lewis, 2005).

Subsequent change in the African carnivore guild may have been related to changes in the prey species, which were likely related to climatic shifts at about 2.5 Ma with the spread of savannas (Turner, 1990; Turner and Antón, 1996; Antón and Turner,

Figure 5.1. Proposed fundamental feeding niches of Plio-Pleistocene and modern African larger mammalian carnivores (after Pobiner and Blumenschine, 2003). Fundamental feeding niche is defined here by carcass size-specific tissue specialization (flesh, marrow/head contents, grease) and degree of bone modification (none, minimal/ moderate, major). Carnivores are positioned at the maximum value along the two tissue and bone modification axes in accordance with reported or hypothesized grease extraction/bone modification capabilities. The positions should be seen as approximate and are based in part for fossil taxa on a combination of body size and dental morphology (c.f. Marean, 1989). The fossil taxa in this table are those with cranial remains identified by Turner (1990), Lewis (1995, 1997), and Marean (1989) as belonging to the Plio-Pleistocene African mammalian carnivore paleoguild at about the time of the archaeological evidence for the earliest hominid carnivory, which presently spans 2.5-1.8 million years ago. Where more than one species of a fossil genus have been reported (i.e. *Chasmaporthetes nitidula* and *silberbergi*), only the genus is listed. Prey is assumed to be adult; sub-adult prey is not considered. Fossil taxa are positioned at the bottom left of each cell, and are noted in boldface. Reconstructions of carnivore paleobiology were assembled from Antón and Turner (1997); Hendey (1974b); Kurtén and Werdelin (1988); Lewis (1995, 1997); Marean (1989); Marean and Ehrhardt (1995); Rawn-Schatzinger (1992); Turner (1987, 1990); Turner and Antón (1996), Werdelin (1999); Werdelin and Turner (1996) and references therein.

Carcass Size	**flesh <----------TISSUE SPECIALIZATION----------> bone** **minimal <----------BONE DESTRUCTION----------> intense**
1 & 2	*Acinonyx jubatus* *Panthera pardus* ***Panthera sp. A*** *Panthera leo* ***Homotherium*** *Lycaon pictus* ***Megantereon*** *(Para)Hyaena brunnea* ***Dinofelis*** *Crocuta crocuta* ***Panthera pardus*** *Panthera leo* ***Chasmaporthetes*** ***Canis sp.*** ***Crocuta ultra*** ***Pachycrocuta***
3 & 4	*Panthera leo* ***Homotherium*** *Lycaon pictus* ***Megantereon*** *(Para)Hyaena brunnea* ***Dinofelis*** *Crocuta crocuta* ***Panthera leo*** ***Chasmaporthetes*** ***Canis sp.*** ***Crocuta ultra*** ***Pachycrocuta***
5 & 6	*Panthera leo* ***Homotherium*** *(Para)Hyaena brunnea* ***Panthera leo*** *Crocuta crocuta* ***Canis sp.*** ***Crocuta ultra*** ***Pachycrocuta***

1997; Behrensmeyer *et al.,* 1997; Bobe *et al.*, 2002; Bobe and Behrensmeyer, 2004; but see Werdelin and Lewis, 2005). The rise of the modern African cursorial, grassland-adapted ungulate fauna occupying more open habitats, and the predators among the Felinae better adapted to hunting them, may have been a factor in the extinction of the machairodonts in Africa in the middle Pleistocene (Ewer, 1973). However, members of the two subfamilies coexisted for about 2.0 Ma before the sabertooths went extinct; competition was therefore probably not the straightforward mechanism for this extinction (Antón and Turner, 1997). Also, why *Homotherium* and *Chasmaporthetes*, with limb proportions suggesting an adaptation to running in open terrain, became extinct at a time when there are indications of a change to more open vegetation in Africa is unclear. Werdelin and Lewis (2005) see a different (but not mutually exclusive) pattern, where the species richness of carnivores in east Africa gradually declines after ~3.3 Ma. They attribute this trend to a gradual extinction of habitat and prey specialists and a survival of generalists, especially in the last million years.

Marean (1989) distinguishes two distinct large carnivore communities in the African Plio-Pleistocene: a mixed and open habitat community composed of the extant felids, *Crocuta*, and the cursorial *Chasmaporthetes*; and a closed habitat community dominated by the machairodonts and possibly the hyper bone-crusher *Pachycrocuta*. In a more detailed study of African carnivore paleoguilds, Lewis (1997) finds similarity in the overall structure of modern eastern and southern African carnivore guilds in dispersion estimates and species composition, with the main difference in species composition being the presence of brown hyaenas in the south and striped hyaenas in the east; neither guild has taxa falling into the morphospace regions occupied by sabertooths. The Koobi Fora

Okote Member (~1.5 Ma) paleoguild structure is markedly different from modern African carnivore guilds, with only one more large-bodied species that the modern guild, but a very different representation of behavioral types due to the presence of the three machairodonts. The Olduvai Bed I paleoguild (~1.8 Ma) is more similar to modern guilds in the behavioral types present and the tighter morphotype packing; the Bed II (~1.6 Ma) paleoguild is even more similar to the modern guild in species composition. The southern African carnivore paleoguild is even less like modern guilds than the eastern paleoguild.

The extinction of the sabertoothed felids corresponds with the shrinking of the hyaenid fauna to the few surviving species in association with modern felines, possibly because of the reduction in carcass supply with the demise of the former (Ewer, 1967; Antón and Turner, 1997). Numerous other authors have suggested that the extinctions of sabertooths and *Pachycrocuta* were ecologically related (e.g. Collings *et al.*, 1976; Turner, 1990; Turner and Antón, 1996), but recent analysis posits that the extinctions of the hyaenas are decoupled from those of the sabertooths (Werdelin and Lewis, 2005). Additionally, it appears that while both *Megantereon* and *Homotherium* went extinct more or less simultaneously at 1.4 Ma, *Dinofelis* may have become extinct later, at 0.9 Ma (Werdelin and Lewis, 2005).

Sabertoothed felids have also been hypothesized to have influenced hominin evolution (Ewer, 1967; Walker, 1984; Turner, 1988; Lewis, 1997). Hominin scavenging from sabertooth kills has been widely discussed (e.g. Blumenschine, 1987; Marean, 1989; Palmqvist *et al.*, 1996; Arribas and Palmqvist, 1999), including in other parts of this dissertation, and will not be reiterated here. The eastern and southern African ungulate fauna, to varying degrees at different times (based on carnivore to ungulate species

ratios), were likely able to provide large quantities of scavengeable food for early hominins (Turner, 1988). Given the diversity of large carnivores that existed in the African Plio-Pleistocene (Turner, 1990; Lewis, 1997), many potential niches existed in these paleoguilds for a partially carnivorous hominid.

How did encroachment on the carnivore paleoguild, which occurred by at least 2.5 Ma (de Heinzelin *et al.*, 1999, Domínguez-Rodrigo *et al.*, 2005), affect hominin paleobiology? Undoubtedly, hominins encountered novel predators and competitors once they began eating mammalian prey. Which carnivores may have preyed on early hominins? This is largely unknown. Lewis and Werdelin (in press, a) suggest that single individuals of *Acinonyx* and *Chasmaporthetes* probably posed little threat to early hominins, unless *Chasmaporthetes* was a pack hunter. However, *Homotherium* was probably a significant threat (Lewis and Werdelin, in press), and even solitary *Megantereon* (Lewis and Werdelin, in review) and *Dinofelis* may have been as well. Modern leopards attack large animals including gorillas (Fay *et al.*, 1995) and hunt primates in relationship to their abundance (Zuberbühler and Jenny, 2002), so they presumably would have preyed upon early hominins, especially those reconstructed to inhabit more closed environments and retain some arboreal capabilities. Lions are a significant threat to modern humans (e.g. Packer *et al.*, 2005), and presumably were an even greater threat to smaller early hominins. A survey of carnivore damage on early hominin fossils would help to elucidate direct predation on early hominins by particular carnivore taxa.

The definition of competition used here is: “a mutually negative interaction between two ore more species within the same guild or trophic level” (excluding mutual

predation) (Morin, 1999: 29-30). The two most common forms of competition are *interference competition*, which involved direct interactions between two species, and *exploitative competition*, operated indirectly by depletion of some shared resource (Morin, 1999). With which carnivores might early hominins have competed? Interspecific competition is expected to be relatively intense among large carnivores because prey represents a resource that is difficult to acquire, is patchily distributed, and is worth defending or stealing (Van Valkenburgh, 1995, 1999). Interspecific competition among modern African carnivores can take five forms (Van Valkenburgh, 1985; Creel *et al.*, 2001; Caro and Stoner, 2003): 1) avoidance at visual or olfactory contact; 2) active avoidance via shifts in habitat use (e.g. Linnell and Strand, 2000); 3) exploitative competition when sharing the geographic range, habitat, and diet; 4) food stealing, especially among species that live in more open habitats and kill and eat large carcasses that take time to consume; and 5) interspecific predation (e.g. Van Valkenburgh, 1985; Palomares and Caro, 1999). The total effect of interference competition involving an individual is likely to be a change in that individual's reproductive success; the sum effect of interference competition involving a particular species is likely to be a change in the size or structure of the population (Frame, 1986). In many modern ecosystems, interspecific interactions among sympatric predators play a primary role in their distribution and abundance (Van Valkenburgh, 1999). Interspecific competition, especially in the forms of exploitative competition and interspecific killing, is pervasive among modern African carnivores and likely has strong direct effects on population number and dynamics as well as indirect effects such as substantial changes in habitat preference, activity patterns, group size, and even in prey populations (Frame, 1986;

Palomares and Caro, 1999; Caro and Stoner, 2003). Potential interspecific competition is related in part to overlap in niche space, loosely here defined as activity pattern, habitat preference, and prey overlap. A table of ecology and behavior of Plio-Pleistocene carnivores, based on information presented in this chapter, and hominins is a first attempt at elucidating potential competition among these contemporaneous taxa (Table 5.1).

Lewis and Werdelin (in press, a) argue that hominins that participated in the carnivore paleoguild in the predator and prey species-rich environment that characterized the Plio-Pleistocene had to evolve effective strategies to resist kleptoparasitism before they could increase their dependence on carcasses as a significant resource. Once they evolve these strategies, they would have increased their rank in the paleoguild, and in concert with increase in density could have driven local carnivore populations to extinction. There was no apparent effect of the origination of carnivory at 2.5 Ma on the carnivore paleoguild, suggesting that hominin competition with carnivores for carcass resources did not immediately affect the carnivore paleoguild. However, the appearance of *Homo erectus/ergaster* after 1.8 Ma may have had an effect, as the number of carnivore extinctions increases and the number of originations decreases at this time. Consequently, carnivore species richness drops sharply after 1.5 Ma. The effect of kleptoparasitism by *Homo erectus/ergaster* coupled with changes in climate and prey species richness may have been enough to drive local populations of carnivores that competed with these early hominins for prey species to extinction. For example, if fossil *Parahyaena* behaved similarly to the modern form, it may have disappeared as a result of competition with early hominins. Theoretical work on intra-carnivore competition

suggests that density increase in a predator with superior exploitative-competition ability could cause a reduced carrying capacity in a competitor (Linnell and Strand, 2000).

Encroachment on the carnivore paleoguild may have also affected other aspects of hominin paleobiology which are likely not directly visible in the fossil record, such as population size. It has been speculated that pack living among some carnivores evolved in response to intraguild interactions (e.g., Eaton, 1979; Venkataraman, 1995). Lamprecht (1978) has proposed the hypothesis that competition promotes large foraging groups in predators which defend their kills against scavengers, but limits foraging group size in predators seeking to reduce competitive pressure by hunting and feeding inconspicuously. Group size in hominins may have been influenced by interspecific interactions with larger mammalian carnivores, and perhaps this influence increased with an increasing proportion of carnivory in the hominin diet. This could have initiated a feedback loop, where increases in population size continued to increase the rank of hominins among contemporaneous carnivores.

Table 5.1. Realized and hypothesized ecological niches of Plio-Pleistocene modern and fossil larger carnivores in the families Felidae, Hyaenidae, and Canidae that existed between ~2.5-1.5 Ma, including early Oldowan stone tool making hominins. Table structure loosely follows Bertram, 1979: 222-223. Order of carnivores from top to bottom is based on maximum adult body weight and hunting group size (sum of "carnivore body weight" in an average hunting group). For modern taxa, information is from Bertram (1979) and references therein except for *Hyaena* (information from Kingdon, 1977) and *Parahyaena* (information from Skinner and Smithers, 1990). For fossil taxa, cell entries are the sum of all available information on all species of that genus. Where specific information or a particular citation was used to fill in a cell, a reference is given. A question mark indicates a lack of information. Prey size is preferred prey size (prey sizes from Bunn, 1982), but does not include all prey sizes taken. *Hyaena makapani,* which is not considered here, is assumed to have similar adaptations to the modern striped hyaena (Lewis and Werdelin, in press). Fossil *Crocuta* species (*dietrichi* and *ultra*) are also not considered, although they likely had different adaptations that modern *Crocuta* (Lewis and Werdelin, in press). *Homo ergaster* refers to African *Homo ergaster* or *erectus* specimens between ~1.8-1.4 Ma only. Habitat preferences for *Homo* species are broad generalizations assumed from environmental reconstructions of archaeological sites rather than the fossils themselves, which are often described without any environmental setting information.

Species	Adult weight (kg)	Habitat preference	Hunting – time of day	Hunting Group Size	Hunting strategy	Prey Size	Caching/ Denning
Panthera leo	122-238	savanna, plains. miombo woodland	nocturnal	1-8	stalk with short sprint	3-4	no/no
Homotherium	120-240[1,2]	open habitats[6,8,9,10]	diurnal[1,9]	1[9], 1-8[17]	prey grappling, stalk and ambush but slightly cursorial[6,7,13,14], or pursuit[9]	3-4[1,17]	?/yes[9,17]
Pachycrocuta	120-240[3]	open habitats	?	groups[3]	*Crocuta*-like but more/exclusive scavenging[3,4,18]	3-4[3]	?/yes[3]
Crocuta crocuta	40-86	savanna, open woodlands	nocturnal	1-19	long distance pursuit	3-4	yes/yes
Megantereon	40-100[2,4]	mixed/closed habitat[6,9,11,12]	nocturnal*	1[1]	prey grappling, jaguar-like, ambush[1,6,9]	3-4[1,6,9]	?/?
Dinofelis	60-120[2,5]	mixed/closed habitat[6,11,12]	nocturnal*	1*	prey grappling, ambush[6]	3-4[6]	?/?
Panthera pardus	32-60	hilly/rocky/treed areas, semi-desert	nocturnal	1	stalk and pounce	2	yes/yes
Chasmaporthetes	>21.5[2]	Open[8,13,14] (?mixed[11]) habitats	diurnal**	?	fast sprint[13,14]**	?	?/?
Homo ergaster	56-66[7]	≈*H. habilis* and dry open savanna[15,16]	diurnal***	groups***	?	1-5[19]	?/?
Homo habilis	32-37[7]	wooded grassland, swampy floodplain, lake and river margins[15]	diurnal***	groups***	?	1-5(6)[20]	?/?
Lycaon pictus	17-36	open plains, miombo woodlands	crepuscular	9-40	long distance pursuit	2	yes/yes
Hyaena hyaena	37-55	dry country with rocky areas	nocturnal	1-2	short chase or stalk (mostly scavenge)	1-4	yes/yes
Parahyaena brunnea	28-50	semi/desert, open scrub, woodland savanna	nocturnal	1	short chase or stalk mostly scavenge)	1-4	yes/yes
Acinonyx jubatus	35-65	savanna, open woodland, sub-desert	diurnal	1-3	stalk, then fast sprint	1-2	no/no
Canis sp. (jackal)	7-15	desert, woodland savanna, open areas	crepuscular	1-2	direct pursuit	1	yes/yes

[1]Antón and Turner, 1997
[2]Lewis and Werdelin in press
[3]Turner and Antón, 1996
[4]Palmqvist *et al.*, 1996
[5]Werdelin and Lewis, 2001
[6]Lewis, 1997
[7]McHenry and Coffing, 2000
[8]Martin, 1989
[9]Palmqvist *et al.*, 2003
[10]Rawn-Schatzinger, 1992

[11]Lee-Thorpe *et al.*, 2000
[12]Marean, 1989
[13]Kurtén and Werdelin, 1988
[14]Berta, 1981
[15]Plummer, 2004
[16]Domínguez-Rodrigo *et al.*, 2001
[17]Marean and Ehrhardt, 1995
[18]Palmqvist and Arribas, 2001
[19] this study
[20]Blumenschine and Pobiner, 2006
*possibly nocturnal and solitary based on similarities to modern leopards
**possibly diurnal with a fast sprint hunting strategy based on similarities to modern cheetahs
***based on shared hominoid sociobiology and ecology

Chapter Six
Zooarchaeological and Taphonomic Analyses of Fauna from FwJj14A, FwJj14B, and GaJi14, Okote Member, Koobi Fora

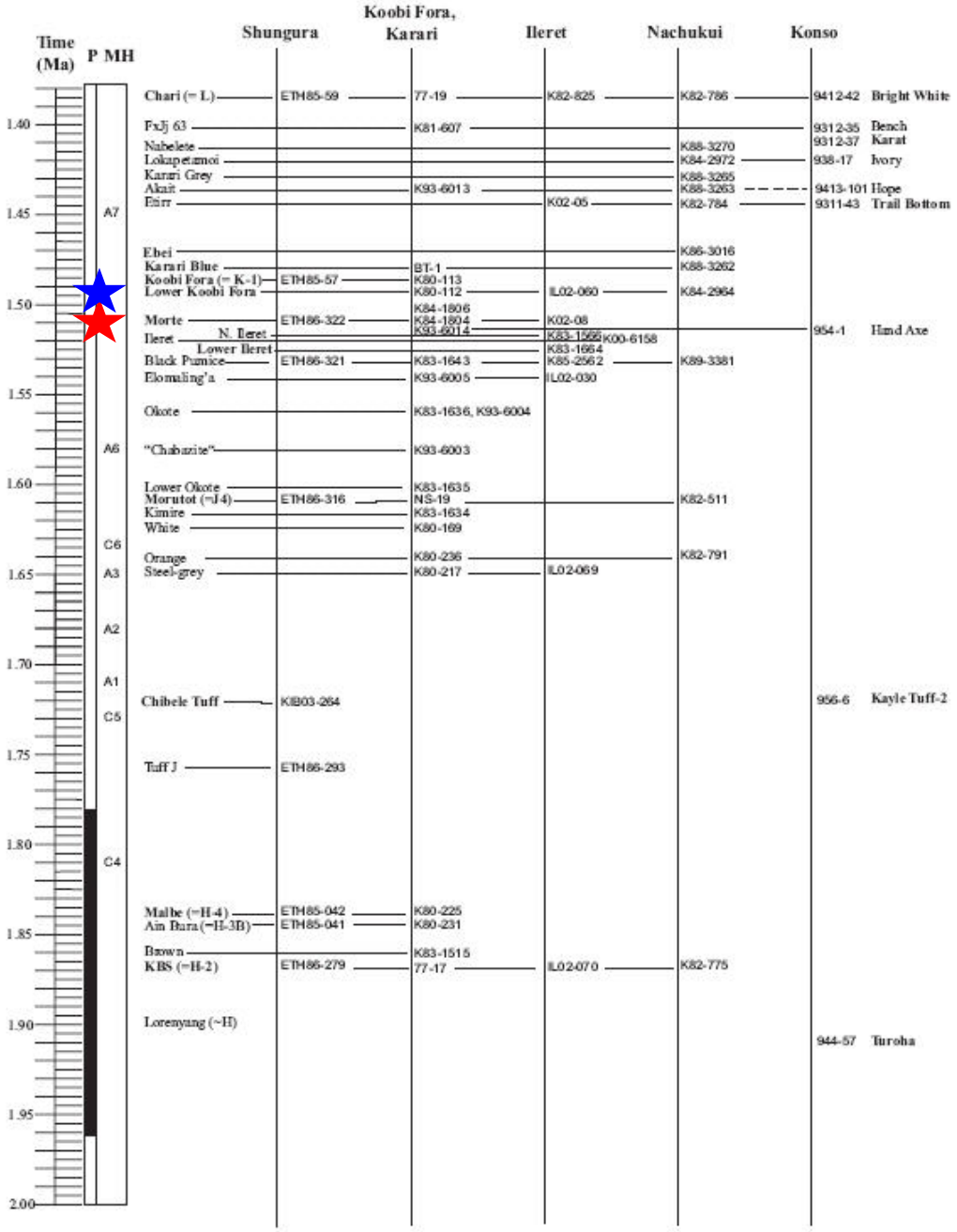
Introduction

During the past 40-plus years, the Koobi Fora region of northern Kenya has yielded a wealth of information about Plio-Pleistocene hominin body and trace fossils (stone tools and butchered bones), including their paleoenvironmental and temporal contexts. This chapter deals with the zooarchaeology and taphonomy of three sites from Koobi Fora: FwJj14A, FwJj14B, and GaJi14. The location of the Koobi Fora Formation region and sediments within the northern Turkana region, and of these sites within the Koobi Fora region, is shown in Figure 6.1. All of these sites lie stratigraphically within the Okote Member of the Koobi Fora Formation, which spans the time interval from ~1.65-1.39 Ma (Brown *et al.,* 2006; Figure 6.2). They yielded a predominance of bone remains, many of them bearing hominin-induced modification from butchery, and no *bona fide* stone tools. Therefore, they can be referred to as Isaac's site type D (Isaac and Crader, 1981).

These sites are named using SASES (Standardized African Site Enumeration System, Nelson 1971). Their KNM accession numbers in the Archaeology Division of the National Museums of Kenya are 4176 (FwJj14A and FwJj14B), and 4177 (GaJi14). They were excavated by the Koobi Fora Field School, a joint training and research program operated by Rutgers University and the National Museums of Kenya Archaeology Division, between 1997 and 2004. I was involved in directing the excavation at bone sites from 1998 through 2004. This chapter updates an initial publication on these sites (Rogers *et al.*, 2004).

Figure 6.1. Image of Lake Turkana with locations of Okote sites. From **www.globalgeografia.com/mondo/laghi.htm.** The approximate locations of FwJj14A and FwJj14B (top, red star, Ileret Ridge), and GaJi14 (bottom, blue star, Koobi Fora Ridge), are noted.

Figure 6.2. Chronological framework of the upper part of the Koobi Fora Formation. Reproduced from Brown *et al.*, 2006: 200 (Figure 8). The approximate temporal location of GaJi14 (blue star) and FwJj14A and FwJj14B (red star) are shown.



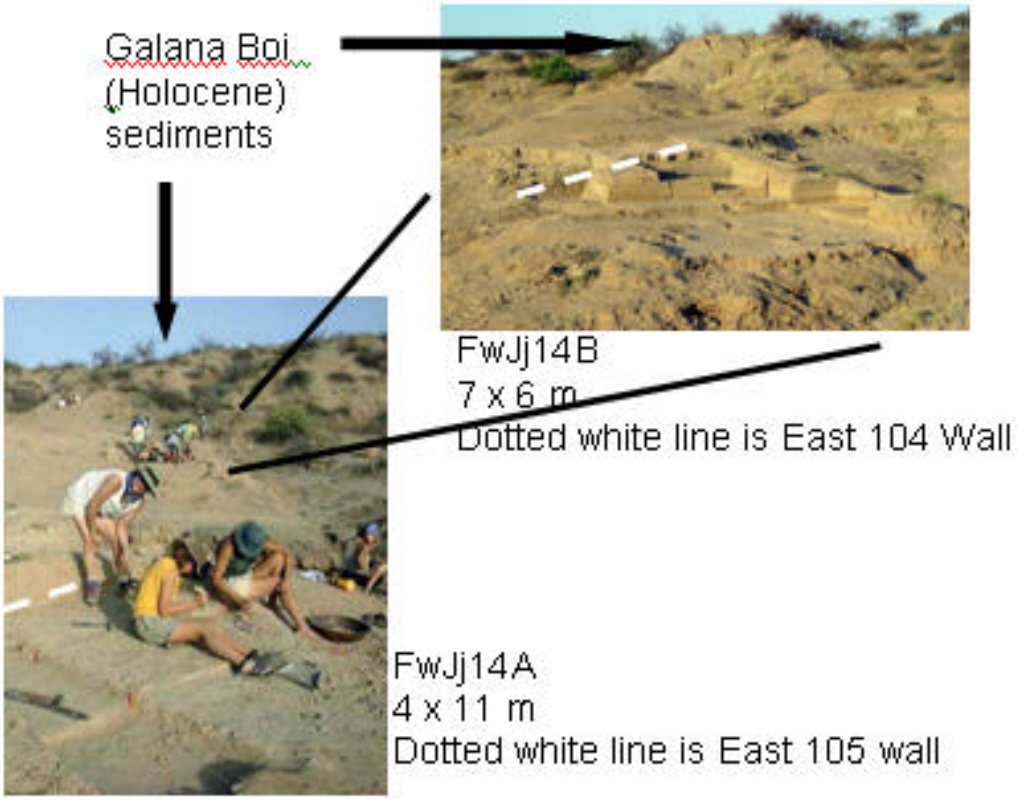
History of Research and Geological Setting

FwJj14A and FwJj14B

FwJj14A and FwJj14B are located in Area 1A, in the Ileret sub-region of Koobi Fora. The site was discovered in 1997 by Chris Monahan, who was then an instructor on the Koobi Fora Field School. He was conducting a surface survey in the area and found a dense concentration of hominin-modified bones, which were collected. In 1998, excavation of the site commenced, under the auspices of the Koobi Fora Field School. Excavation at the site continued through 2004, directed most often by myself but also at times by David Braun, Mzalendo Kibunjia, Steven Merritt, Chris Monahan, Michael Pante, and Michael Rogers. Excavation began in the part of the site later designated FwJj14A, and later we opened up a second excavation across a gully, FwJj14B. We initially believed that FwJj14B was at the same horizon as FwJj14A, but we now believe it is at a different time horizon, representing a different depositional setting and behavioral occurrence. A schematic map and photographs of the site are in Figure 6.3. Holocene sediments of the Galana Boi Formation outcrop nearby to FwJj14B, but the site is on an isolated small hill, and therefore I am confident that all of the finds are from the Okote Member.

Previous finds of cut-marked bones from the Okote Member from Area 1A have been reported by Bunn (1994: a hippo rib shaft and a size 1 antilopine tibia), as well as from Area 8A, near FwJj1 (a hippo humerus distal epiphysis plus shaft, a size 1 antilopine proximal metacarpal plus shaft, and a size 5 *Giraffa* metapodial shaft) and Area 5 (a hippo rib shaft and a size 1 antilopine proximal metacarpal plus shaft). These latter finds were all given the site designation FwJj0.

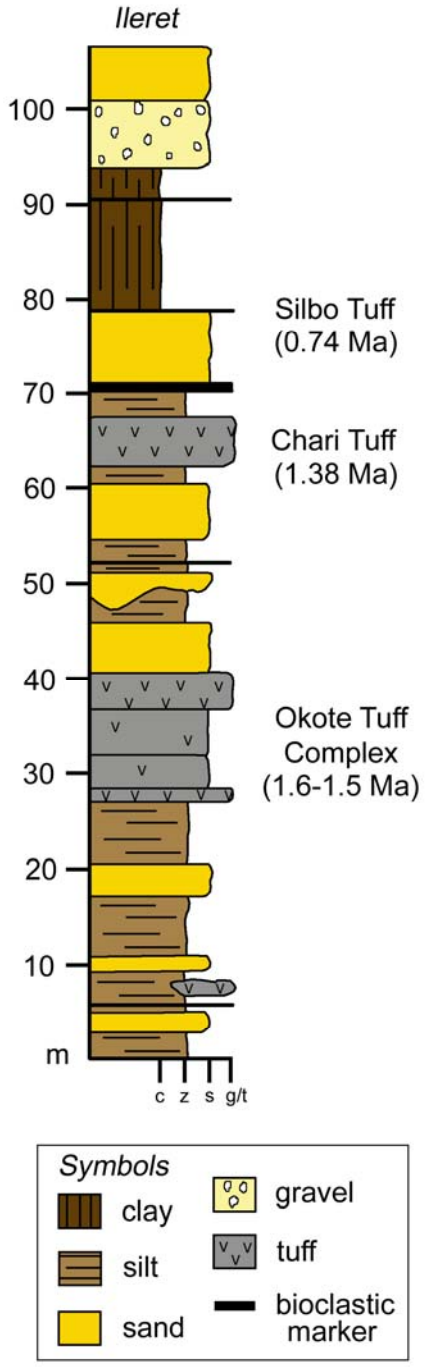
Figure 6.3. Photographs of excavations at FwJj14A and FwJj14B.



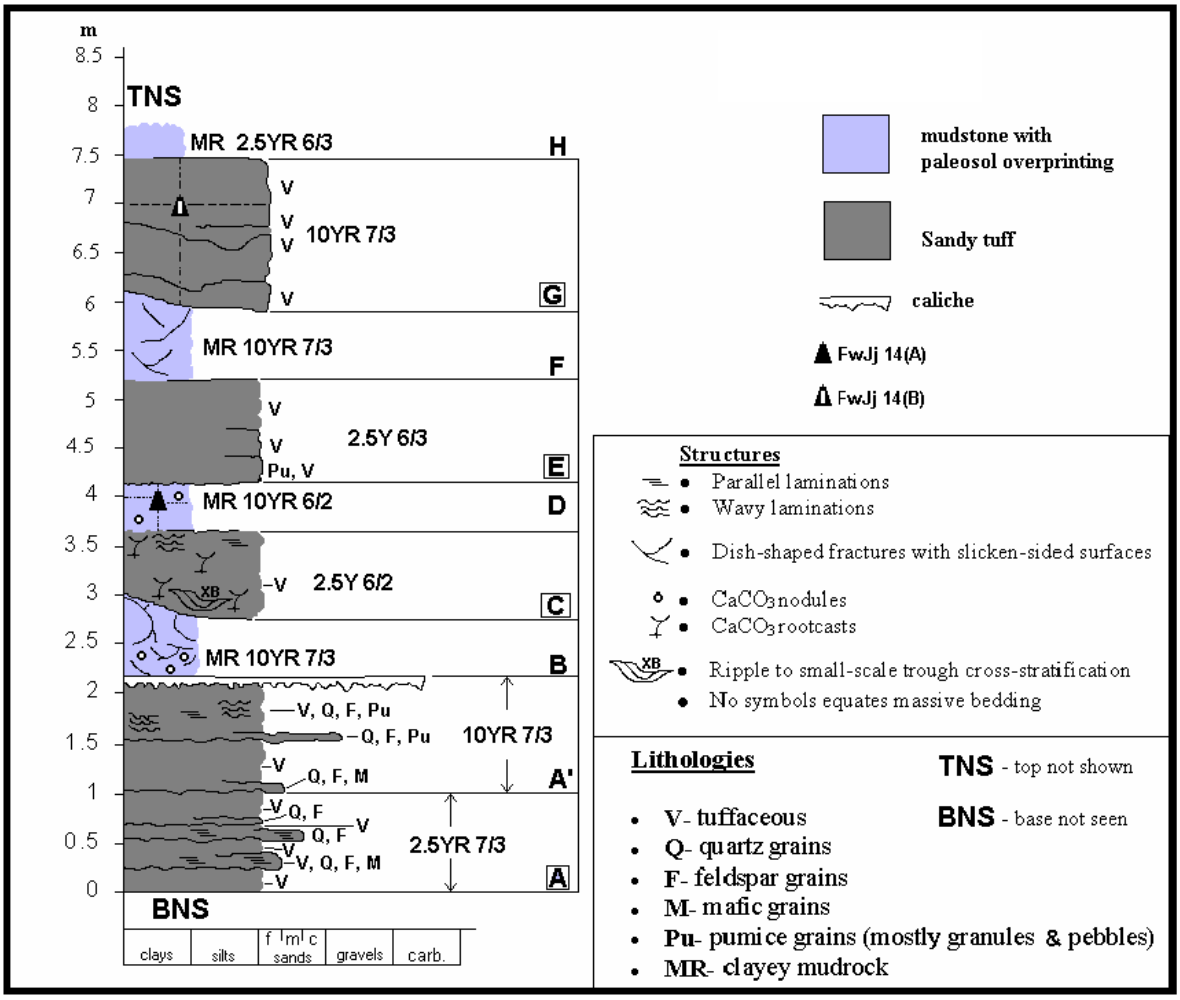
The local site stratigraphic section and interpretation of sedimentary units, courtesy of Christopher Lepre, are in Figure 6.4. The fauna at FwJj14 derive from sediments that form part of a widespread geologic horizon at Ileret known as the 'Lower/Middle Tuff Complex' (cf. Isaac and Behrensmeyer, 1997). Unit C in Figure 6.4 is interpreted as the Northern Ileret Tuff. FwJj14A and FwJj14B lie just above the Northern Ileret Tuff, which is dated to approximately 1.52 Ma (Brown *et al.,* 2006). FwJj14B lies about 3 meters higher in the section than FwJj14A; these two sites, therefore, represent hominin behavior at two different times, as well as in two different paleogeographic settings (Figures 6.4 and 6.5).

Figure 6.4. Composite stratigraphic section from Ileret and local stratigraphic section at FwJj14A and FwJj14B. Composite stratigraphic section (a) is after Brown and Feibel (1991) and courtesy of Rhonda Quinn. Local stratigraphic section (b) and interpretation (c) are courtesy of Chris Lepre (unpublished data). Unit C is interpreted as the Northern Ileret Tuff, and Units A and A' are interpreted as marking the base of the Lower/Middle Tuff Complex in Area 1A. FwJj14A is in unit D, and FwJj14B is in Unit G.

(a)



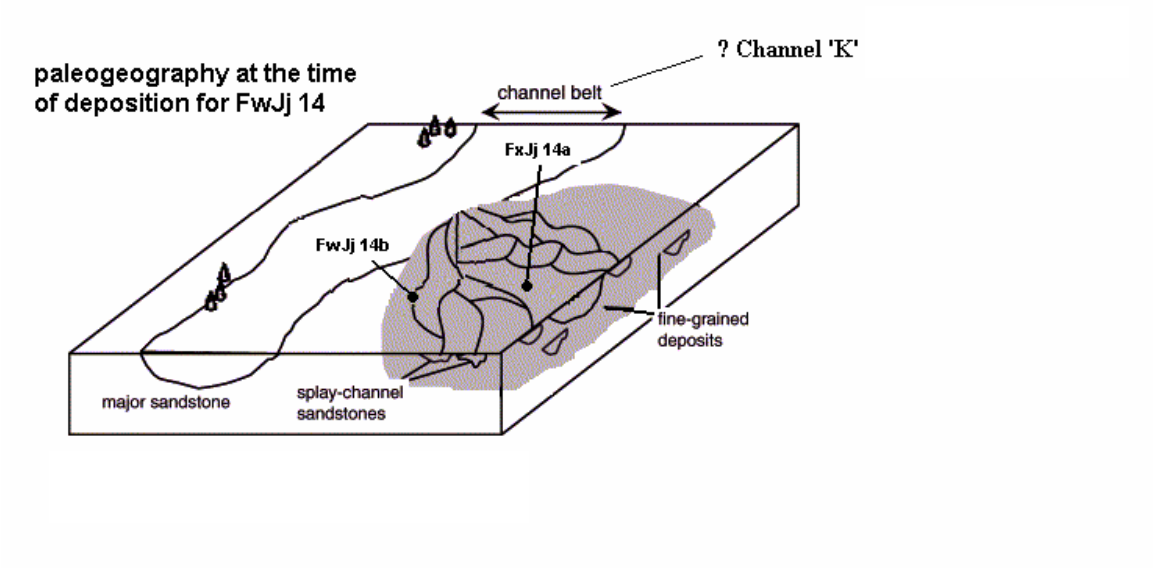
(b)


m
8.5
8
7.5
7
6.5
6
5.5
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
TNS
MR 2.5YR 6/3
H
V
V
V
10YR 7/3
V
G
MR 10YR 7/3
F
V
V
2.5Y 6/3
Pu, V
E
MR 10YR 6/2
D
XB
V
2.5Y 6/2
C
MR 10YR 7/3
B
V, Q, F, Pu
Q, F, Pu
10YR 7/3
V
Q, F, M
A'
V
Q, F
Q, F
V
V
V, Q, F, M
2.5YR 7/3
V
A
BNS
clays
silts
f
m
c
sands
gravels
carb.
mudstone with paleosol overprinting
Sandy tuff
caliche
FwJj 14(A)
FwJj 14(B)
Structures
Parallel laminations
Wavy laminations
Dish-shaped fractures with slicken-sided surfaces
CaCO3 nodules
CaCO3 rootcasts
XB
Ripple to small-scale trough cross-stratification
No symbols equates massive bedding
Lithologies
TNS - top not shown
BNS - base not seen
V- tuffaceous
Q- quartz grains
F- feldspar grains
M- mafic grains
Pu- pumice grains (mostly granules & pebbles)
MR- clayey mudrock

(c)

Unit and thickness (centimeters)	***Lithology and structure***	***Process***	***Interpretation***
(top not shown) H: 25	Medium bedded clayey mudstone; massive	Suspensionary sedimentation; channel in-filling and migration	overbank; *medial* to proximal floodplain
G: 125	massively bedded tuffaceous silty-sand; individual scour and fill defining the base of 3-4 sub-units; fines upward; diffuse to distinct upper contact	basal channel incision; minor cut-and-fill; in-filling and aggradation	broad shallow alluvial channels; proximal channel
F: 75	massive bed of clayey mudstone; slicken-sided fracture surfaces; erosive upper contact	overbank sedimentation; channel migration; episodic flooding followed by hiatus in sedimentation	*distal* to medial floodplain
E: 105	medium-sized beds of tuffaceous silty-sand; massive; upper contact is distinct to diffuse	planar bed flow of the upper/lower flow regime; overbank splay	*medial* to proximal floodplain
D: 40	medium bedded clayey mudstone; massive; sparse carbonate nodules (<5 cm); upper contact is sharp to slightly erosive	suspensionary sedimentation; channel in-filling and migration	overbank; *medial* to proximal floodplain
C: 65	thickly bedded tuff; moderate amount of trough-stratification that fines upward into ripple, wavy, and parallel laminations; moderate carbonate root-casts and sparse nodules; fines-upward from medium-/coarse-sand sized glass shards, quartz grains, and feldspar grains to fine-grained glass shards; upper contact is diffuse to distinct	basal channel incision; channel in-filling and aggradation	broad shallow alluvial channels; proximal channel
B: 55	massively bedded clayey mudstone; small (<5 cm) carbonate concretions; slicken-sided fracture surfaces; erosive upper-contact	suspensionary sedimentation and/or destruction of structure by pedogenesis; fluctuating water table from episodic flooding followed by pedogenesis	overbank of alluvial channels; *distal* to medial floodplain
A: 210 (base not seen)	very thinly bedded fine- to coarse-sand interspersed though-out medium bedded tuffaceous silty-sand; individual beds are massive with local laminations; within sandier units light and dark mineral grains are preserved as separate supra- and sub-adjacent micro-strata; pumice occurs locally; thin caliche caps unit; sharp upper contact	planar bed flow of the upper/lower flow regime; episodic local scouring; followed by a depositional hiatus	broad shallow alluvial channels, *proximal* to medial floodplain

Figure 6.5. Reconstruction of the paleogeographic settings of FwJj14A and FwJj14B. Courtesy of Christopher Lepre (unpublished data). Channel 'K' is from Isaac and Behrensmeyer, 1997.



Christopher Lepre's summary of the site paleogeographic setting (unpublished data) is summarized here (Figure 6.5). At FwJj14B, the fauna is from a thin irregular lens within a bed of hard tuffaceous silty-sand. At the northern margin of the site, the fossiliferous layer unconformably extends northward upon the margin of an ancient watercourse. If the fossiliferous layer is traced to the southern end of the exposure, it forms a part of a complex of river deposits that consist mainly of silts and sands. The fauna at FwJj14B accumulated on the lateral margin of a broad and shallow stream. The fossils were deposited on a substratum of clayey mud, and as the channel aggraded, they were covered with coarser sediment. At FwJj14A, the fauna was retrieved from a dense clayey mudstone that is well-indurated with calcium carbonate. This fauna accumulated on a paleolandscape that was adjacent to a watercourse and was subsequently covered by fine-grained sediment. This paleolandscape was most-likely a small flood-basin nestled within a system of channels. The depositional context of FwJj14A suggests that this site is relatively less-disturbed and perhaps accumulated *in situ*, although the small skeletal

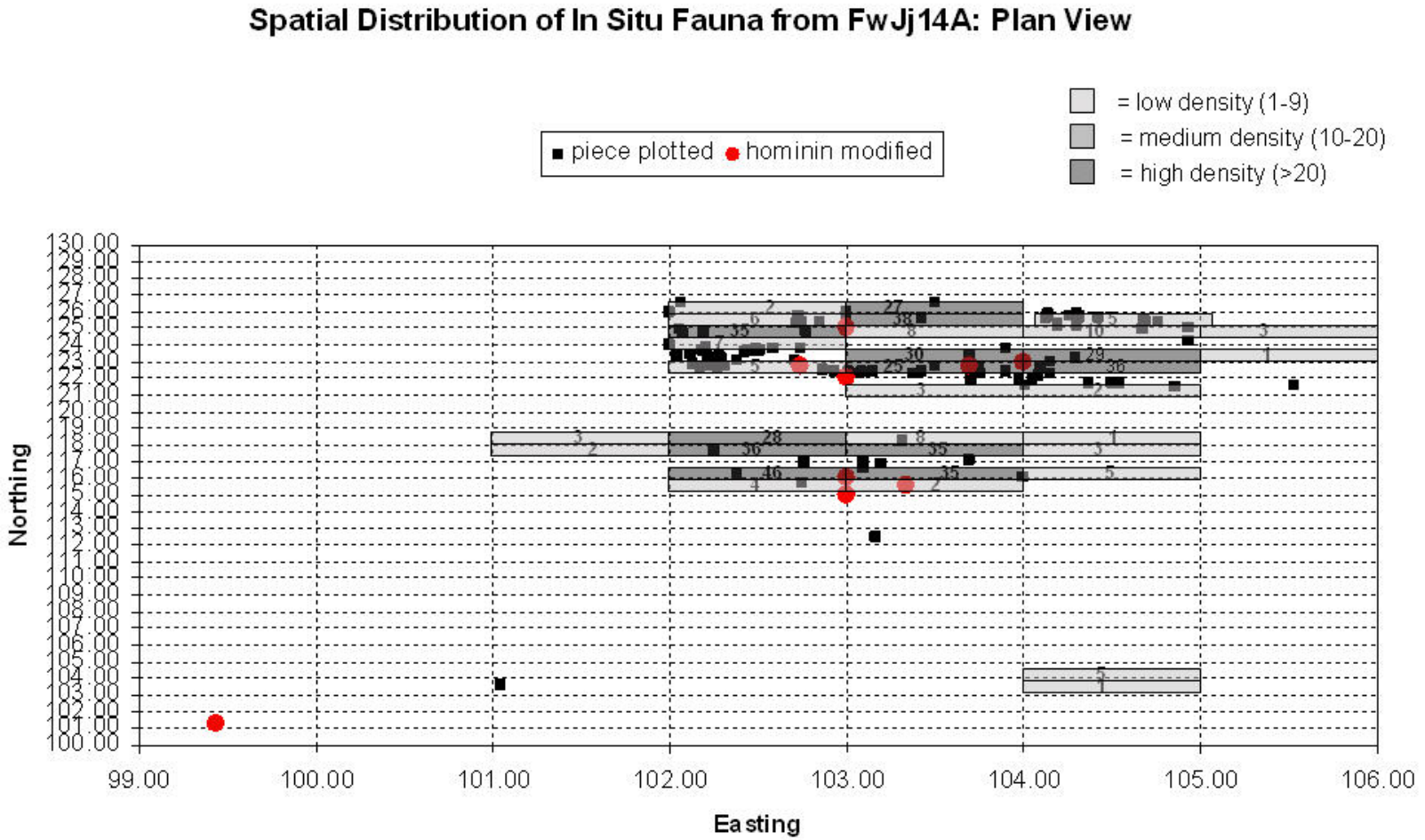
elements recovered from FwJj14B and their relative completeness suggest that they were not transported very far from their primary point of discard/accumulation.

Excavation at FwJj14A and FwJj14B proceeded in either 10 or 5 centimeter spits, depending on the density of bone encountered. In FwJj14A the bone was not concentrated horizontally or vertically (Figures 6.6a and 6.6b). Fauna derives from several square meters of horizontal area, and occurs over a 1.3 meter vertical dispersion. At FwJj14B, there seem to be two areas of denser bone concentrations both vertically and horizontally: one particularly rich area from 99 to 101 East, 100 to 104 North, and 99.90 to 100.10 meters below datum; and a second area from 103 to 104 East, 100 to 102 North, and 100.70 to 100.90 meters below datum (Figures 6.7a and 6.7b). The hominin-modified bones have a similar distribution to the non-modified bones. There was no preferred orientation or dip of excavated bones from FwJj14A or FwJj14B.

In 2004, surface survey during the Koobi Fora Field School in an area a few hundred meters from FwJj14A and FwJj14B by Chris Lepre, Michael Pante, Rhonda Quinn, and Hillary Sale yielded surface finds of hominin post-crania. This part of the site was since designated FwJj14East. I studied the associated fauna collected from the surface at FwJj14East in July and September 2004, and June 2005 with Stephen Merritt. This fauna includes at least one cut-marked specimen (a size 3 bovid proximal radius); these data will be presented in more detail elsewhere.

Figure 6.6. Spatial distribution of *in situ* finds at FwJj14A. NISP of fauna from "level bags" (either found while digging but in questionable spatial position or in screens, in 10 cm levels, within a 1 meter square area) are represented by numbers within each excavated square meter. NISP of this "level bag" fauna includes hominin modified bones (even though these are also plotted separately on this figure), but not non-modified piece-plotted bones. Piece-plotted or level-bag bones with hominin modifications (cut or percussion marks) are represented by red circles; other piece plotted bones are represented by black squares. Level bag bones with hominin modifications are placed in the southwest corner of the square from which they derive on the plan view figures, and in the most west and deepest point of the relevant square on the elevation figures. The plots show relative abundances by square and are not intended to be a detailed depiction of piece plotting. Note X and Y axes are unequal in the plan view illustrations, though they are equal in reality.

6.6a


Spatial Distribution of In Situ Fauna from FwJj14A: Plan View
piece plotted
hominin modified
= low density (1-9)
= medium density (10-20)
= high density (>20)
Northing
Easting
99.00
100.00
101.00
102.00
103.00
104.00
105.00
106.00

6.6b

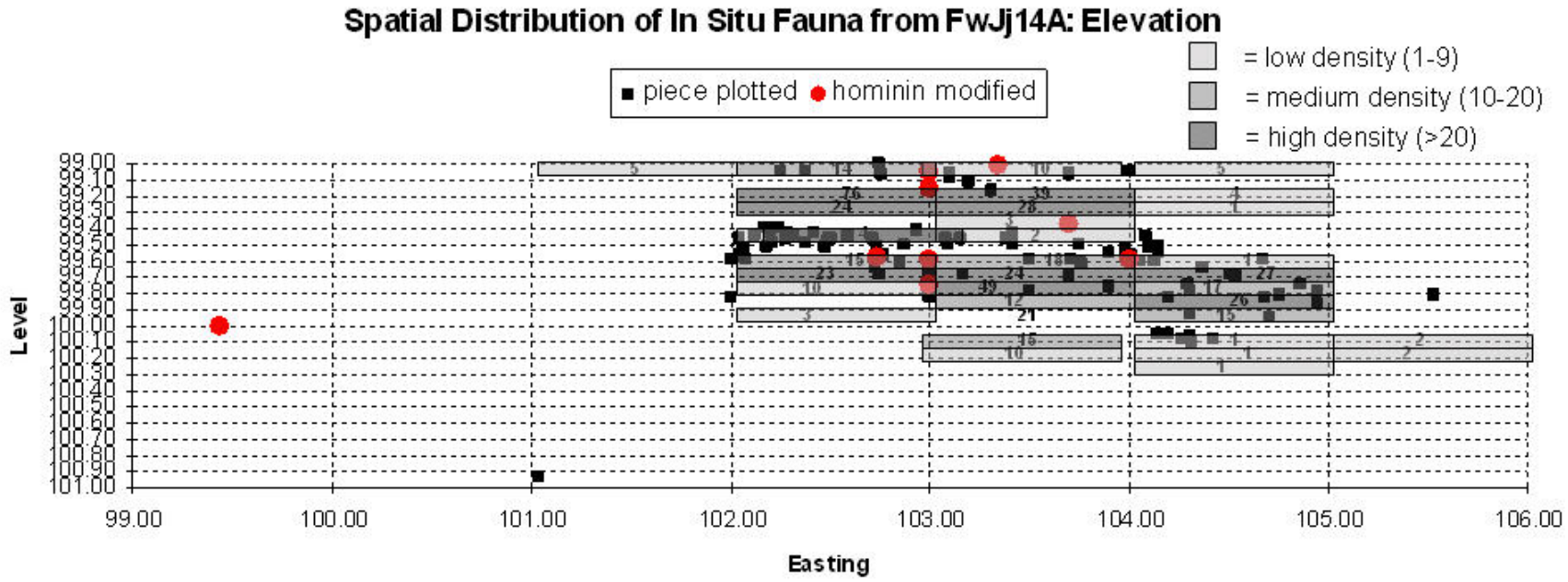
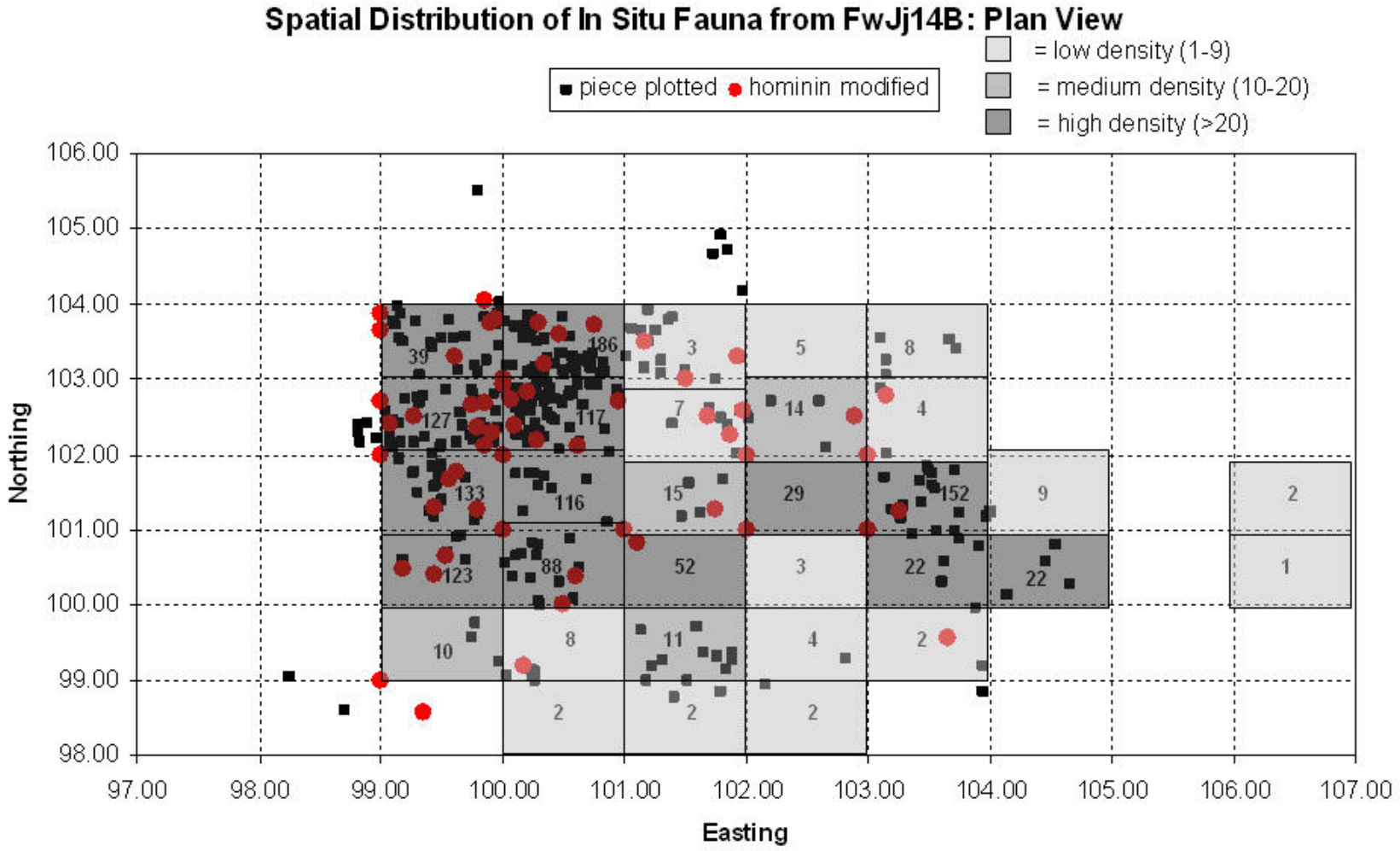
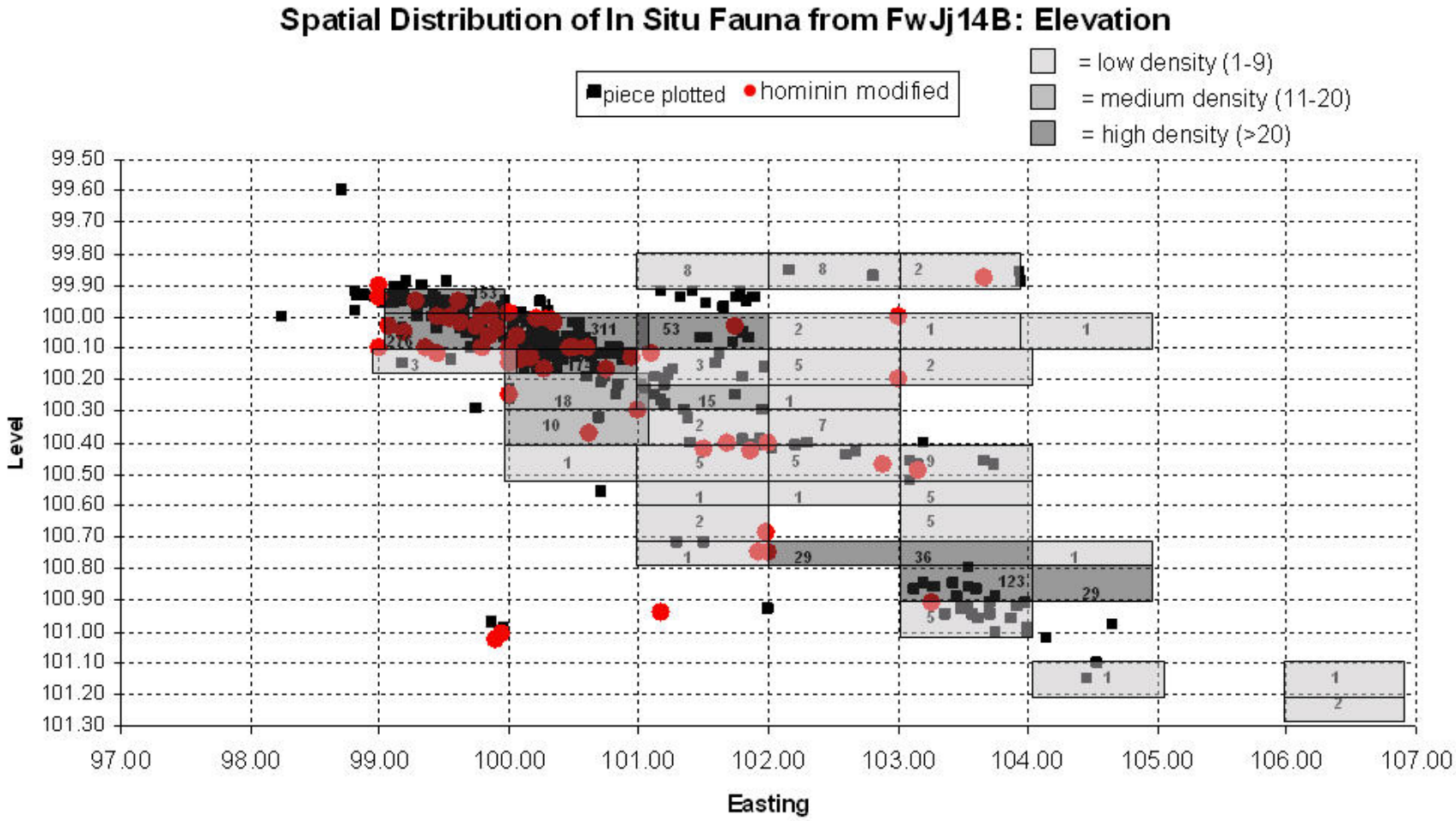

Spatial Distribution of In Situ Fauna from FwJj14A: Elevation
piece plotted
hominin modified
= low density (1-9)
= medium density (10-20)
= high density (>20)
Level
Easting
99.00
100.00
101.00
102.00
103.00
104.00
105.00
106.00

Figure 6.7. Spatial distribution of *in situ* finds at FwJj14A. See Figure 6.6 caption for more details.

6.7a



6.7b


Spatial Distribution of In Situ Fauna from FwJj14B: Elevation
piece plotted
hominin modified
= low density (1-9)
= medium density (11-20)
= high density (>20)
Level
Easting
99.50
99.60
99.70
99.80
99.90
100.00
100.10
100.20
100.30
100.40
100.50
100.60
100.70
100.80
100.90
101.00
101.10
101.20
101.30
97.00
98.00
99.00
100.00
101.00
102.00
103.00
104.00
105.00
106.00
107.00

GaJi14

GaJi14 is located in Area 103, in the Koobi Fora ridge region (Figure 6.1). It is within a few hundred meters of GaJi5, a site described by Henry Bunn in Volume 5 of the Koobi Fora monograph series (Bunn, 1994, 1997). GaJi5 consists of a surface collection of fauna, including 11 modified bones of at least 5 larger mammal carcasses (Table 6.1), found by Bunn and colleagues in 1979. However, none of the 35 *in situ* bones found in the $4m^2$ test excavation conducted later that year were cut-marked. Bunn also reports additional finds of cut-marked bones in 1984, in a cluster about 350m north of GaJi5 at the same horizon designated GaJi0, including isolated funds of a hippopotamus pelvis, atlas and tibia, and a suid tibia "at penecontemporaneous localities spaced kilometers apart within the Area 103 outcrops" (Bunn, 1994: 256). Excavations by Bunn and others with the Koobi Fora Field School in 1989, 1990, 1992, and 1993 yielded approximately 60 cut-marked and percussion-notched bones.

GaJi14 was discovered in 1997 by Christopher Monahan, who was an instructor on the Koobi Fora Field School at the time. He was conducting a surface survey near GaJi5 when he found a fairly dense concentration of hominin-modified bones. In 1998, an initial surface collection of hominin-modified bones was made. In 1999, excavation of the site commenced, under the auspices of the Koobi Fora Field School. Excavation at the site continued through 2004, directed mainly by myself along with Steven Merritt, Christopher Monahan, Michael Pante, and Michael Rogers. Excavation began initially in GaJj14A, and later Mike Rogers opened up a second excavation a few meters away, GaJi14B, which we believe to be in the same stratigraphic interval. A photograph and diagram of the site and the relationship between GaJi14A and GaJi14B are shown in

Figure 6.8. I treat GaJi14A and GaJi14B separately and together as a single site (GaJi14) in this chapter, depending on the analysis being conducted.

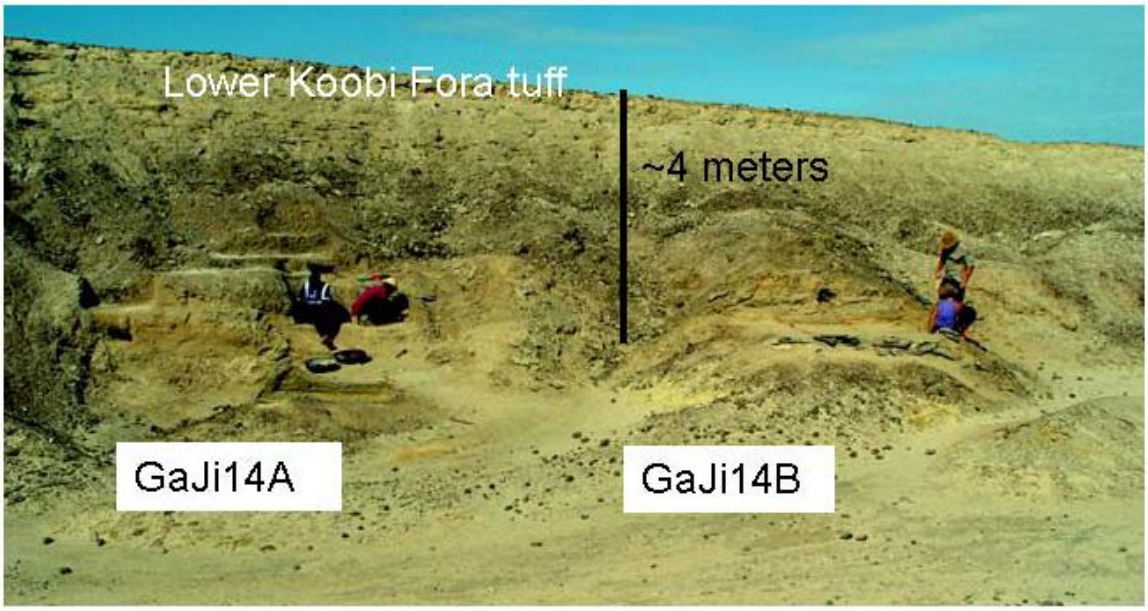
Table 6.1. Fauna with cut marks or percussion notches from GaJi5 and GaJi0. CM = cut marks; PN = percussion notch; PX = proximal; DS = distal; SH = shaft; EPI = epiphysis. Data from Bunn (1994: 258).

Site	Catalogue Number	Taxon	Size	Skeletal Element	CM/PN
GaJi5	1	Bovid	3A	Ilium	CM
GaJi5	70	Bovid	3	Rib, PX	CM
GaJi5	79	Mammal	3	Limb SH	CM
GaJi5	101	*Hippopotamus aethiopicus*	4/5*	Ulna SH	CM
GaJi5	103	*Giraffa*	5	Metatarsal SH	CM
GaJi5	104	*Giraffa*	5	Metatarsal SH	CM
GaJi5	121	Bovid	3A	Ischium	CM
GaJi5	153	Mammal	4	Rib SH	CM
GaJi5	184**	Suid	3A	Tibia, DS EPI + SH	CM
GaJi5	230	Bovid	3A	Mandible, articular condyle	CM
GaJi0	25	Hippo	4/5*	Pelvis 1/2, fragment	CM
GaJi0	26	Hippo	4/5*	Atlas vertebra, complete	CM
GaJi0	27	Hippo	4/5*	Tibia, complete	CM
GaJi0	28	Suid	3A	Tibia, DS EPI + SH	CM
GaJi0	29	Mammal	5	Rib SH	CM
GaJi0	30	Mammal	3	Femur SH	CM
GaJi0	31	*Hippopotamus aethiopicus*	4*	Humerus, DS EPI + SH	CM
GaJi0	32	*Hippopotamus aethiopicus*	4*	Radio-ulna, complete	CM
GaJi0	33	Bovidae	3B	Mandible, ramus fragment	CM
GaJi0	34	*Hippopotamus aethiopicus*	4*	Radio-ulna, PX EPI + SH	CM
GaJi0	37	Mammal	3/4	Humerus SH	CM
GaJi0	38	*Giraffa*	5	Metapodial SH	CM
GaJi0	39	Hippo	4/5*	Rib SH	CM
GaJi0	40	Hippo	4/5*	Rib SH	CM
GaJi0	41	Suid	3A	2nd Phalanx	CM
GaJi0	42	Bovid	2	Femur SH	PN
GaJi0	43	Bovid	3A	Humerus, PX EPI + SH	CM
GaJi0	44	Hippo	4/5*	Rib SH, PX	CM
GaJi0	45	Hippo	4/5*	Rib SH, PX	CM
GaJi0	46	Hippo	4/5*	Rib SH	CM
GaJi0	47	Giraffa	5	Metatarsal SH, PX 1/2	CM
GaJi0	48	Bovid	3A	Tibia SH	CM
GaJi0	49	Bovid	3A	Radius, complete	CM
GaJi0	50	Bovid	2	Tibia SH	CM
GaJi0	52	Mammal	5	Scapula blade	CM
GaJi0	56	Hippo	4/5*	Phalanx	CM
GaJi0	57	Equid	4*	Calcaneum	CM
GaJi0	58	Bovid	3A	Metapodial, DS EPI + SH frag	CM
GaJi0	59	Hippo	4/5*	Axis, complete	CM
GaJi0	60	Hippo	4/5*	Scapula	CM
GaJi0	61	Hippo	4/5*	Scapula	CM
GaJi0	62	Hippo	4/5*	Tibia, DS EPI + SH	CM

*assumed, though not listed by Bunn

** listed as specimen number 183 in Bunn 1997:442.

Figure 6.8. A photograph of GaJi14A and GaJi14B with information on the position of the excavations with respect to the Lower Koobi Fora tuff.



The Pleistocene sedimentary sequence of the Koobi Fora Ridge subregion (Area 103) is characterized by under 5 meters of siliciclastic sands, silts, and clays, capped by a half meter thick, fine-grained tuff (R. Quinn, pers. comm.; Figure 6.9a). The lowermost exposures of the sequence contain thin layers of alternating silts and coarse sands with parallel cross-bedding indicating small river channels and beach facies. The sequence fines upward to a dark clay layer, which was subaerially exposed evident by vertic soil structures and pedogenic carbonates. The paleosol is a poorly- to moderately developed vertisol, indicating a bimodal rainfall environment with a dry season of approximately four months (see Wynn, 2004). The paleosol is overlain by alternating silts and coarse sands, marking the return to small channels and lake shore environments. A portion of the Koobi Fora Tuff Complex, deposited in a low- to moderate- velocity channel setting, caps the sequence.

The lithology and facies associations at GaJi14 indicate lake shore environments with small, marginal channels and floodplains (R. Quinn, pers. comm.; Figure 6.9b). Paleogeographic reconstructions of the Koobi Fora Ridge illustrate the presence of a small, transgressing and regressing, precursor of Lake Turkana (Feibel, 1988, 1997; Brown and Feibel, 1991; Feibel *et al.*,. 1991). GaJi14 is preserved within small, shallow tributaries of the ancient lake.

Field identifications to the base of the Koobi Fora Tuff Complex (Bunn, 1997) dated between 1.61 and 1.49 Ma (McDougall and Brown, 2006) places the stratigraphic section in the upper KBS/lower Okote Member boundary (R. Quinn, pers. comm.). Cut-marked fauna is found in the lowermost portions of channel sands, stratigraphically four meters below the Koobi Fora Tuff Complex. GaJi14 is ~15 meters above the arenaceous bioclastic marker bed, designated as A6. Sedimentation rates of the upper KBS Member calculated from the Koobi Fora Ridge subregion (25 cm/kyr, Feibel, 1988) yields a scaled age for A6 of 1.62 Ma. Therefore, the age of GaJi14 is constrained by the youngest tuff of the complex, the Lower Koobi Fora Tuff, dated to 1.49 Ma and by A6, scaled to 1.62 Ma (suggested error: ± 0.05 Ma, after Feibel *et al.*, 1989). Using the above sedimentation rates and the age of the Lower Koobi Fora Tuff (if this is the tuff capping the site section), I will use 1.49 Ma as an approximate age for the site, though it may be older.

Figure 6.9a. Composite stratigraphic section for the Koobi Fora Ridge subregion. Courtesy of Rhonda Quinn, after Brown and Feibel (1991).

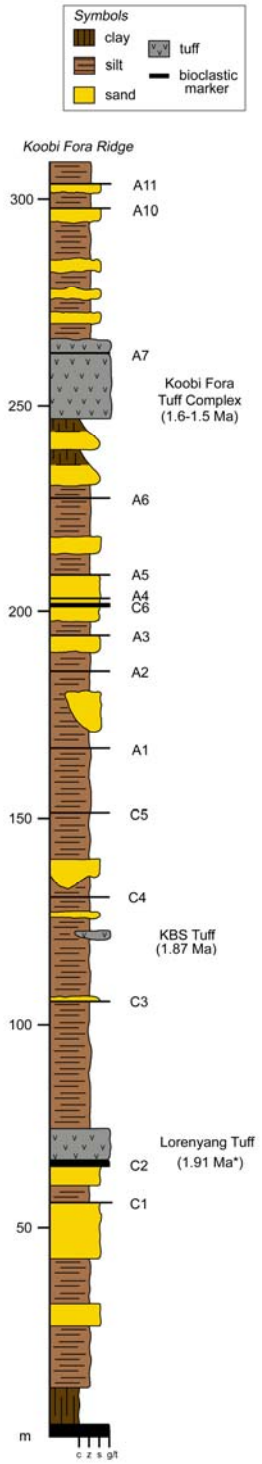
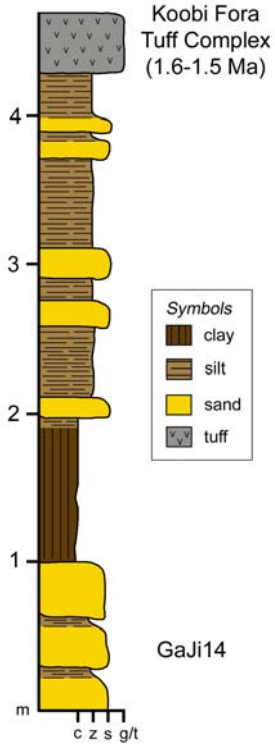


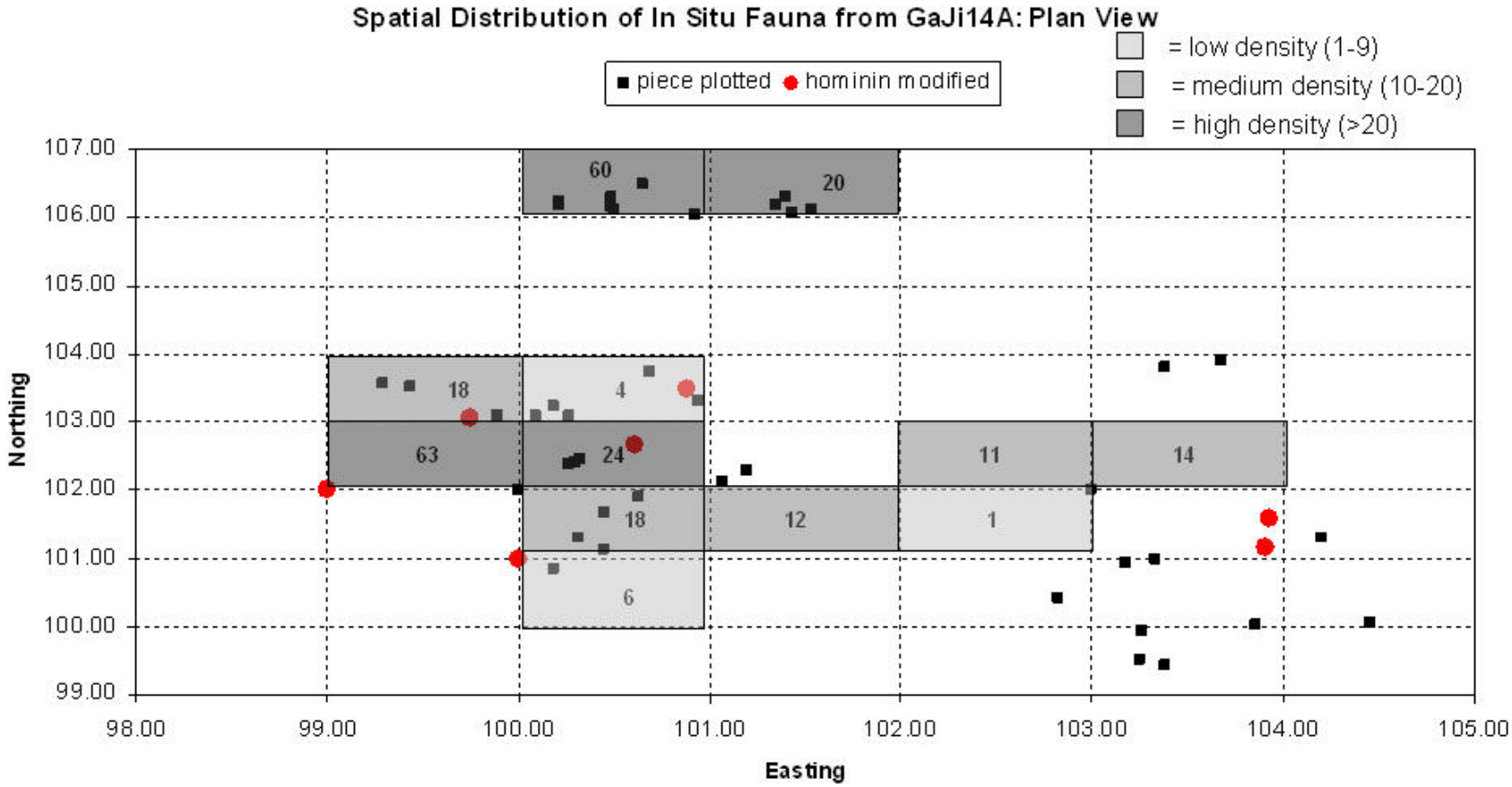
Figure 6.9b. Site stratigraphic section for GaJi14. Courtesy of Rhonda Quinn, unpublished data.



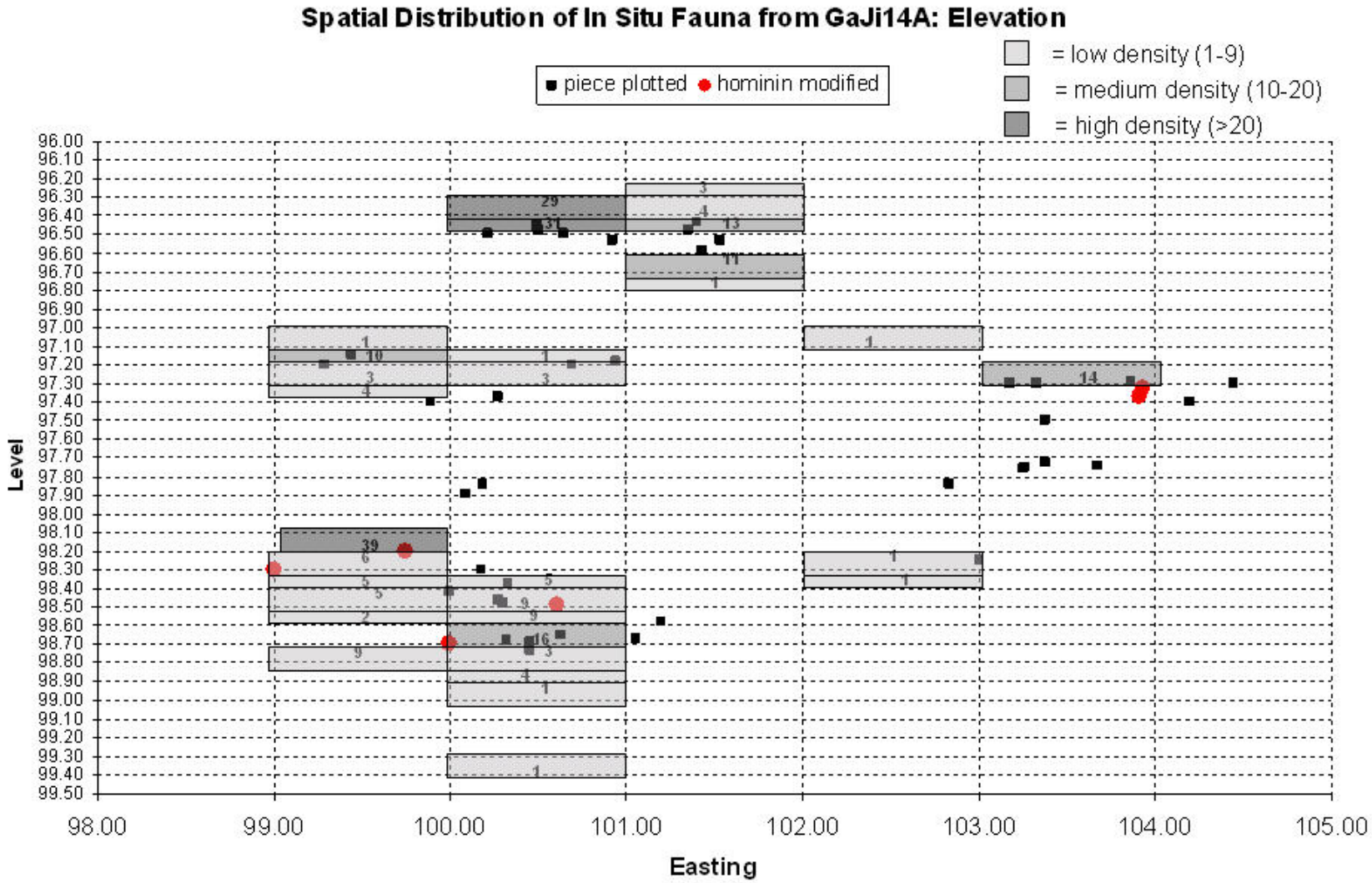
Excavation at GaJi14 proceeded in either 10 or 5 centimeter spits, depending on the density of bone encountered. GaJi14A has some pockets of denser bone accumulation horizontally, but vertically the bone is either moderately clumped or distributed randomly throughout almost two meters (Figure 6.10). In GaJi14B, the bone is densest horizontally from 102 to 103 East and 99 to 103 North. Vertically the bones are distributed through two meters but are concentrated in the highest 50 centimeters within the dense horizontal concentration. The cut-marked bones from GaJi14A are distributed (apparently) randomly horizontally but are in the lower part of the vertical distribution. At GaJi14B, the cut-marked bones are only in the top meter part of the vertical distribution.

Figure 6.10. Spatial distribution of *in situ* finds at GaJi14Aand GaJi14 B. See Figure 6.5 caption for more information.

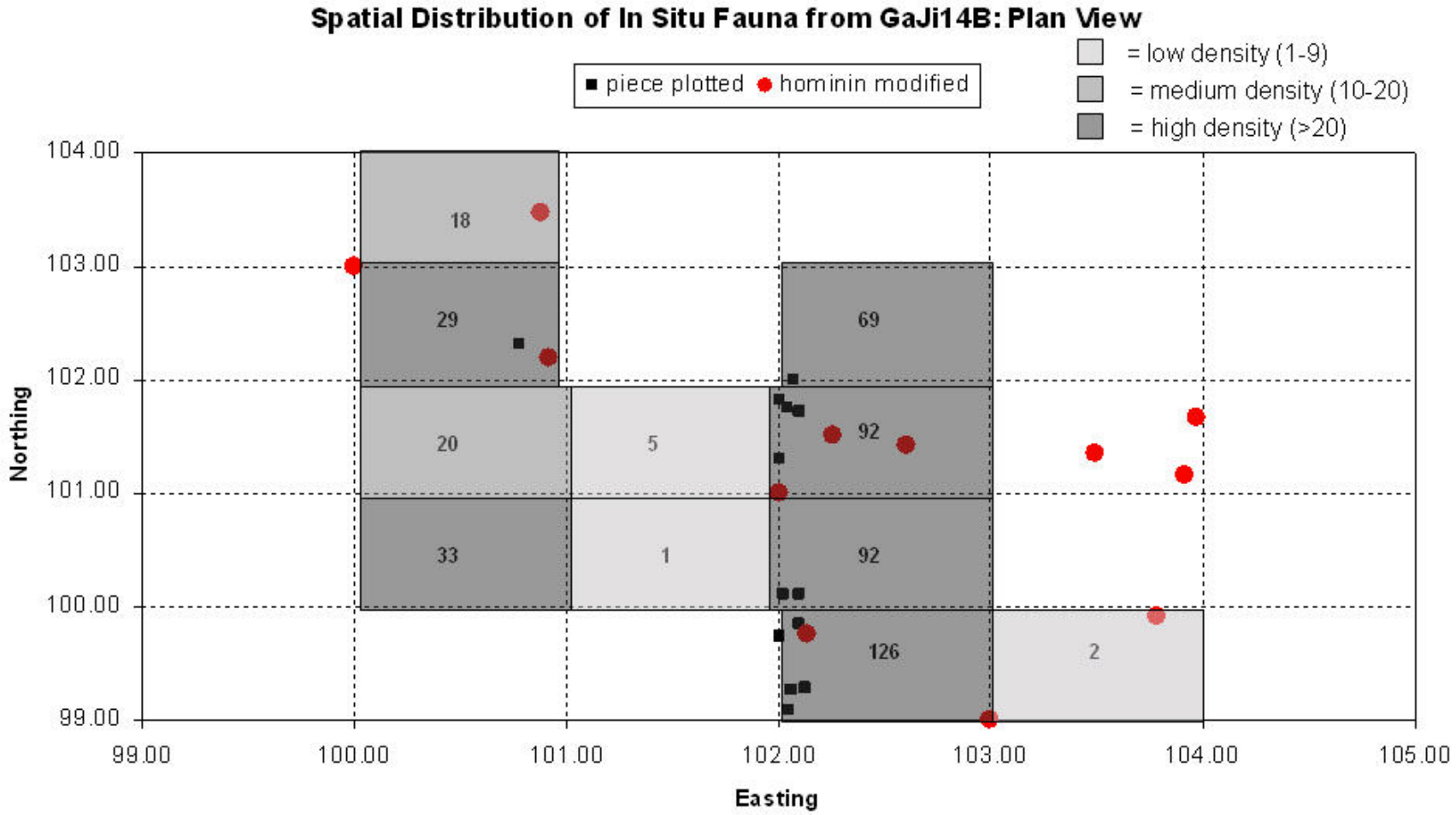
6.10a



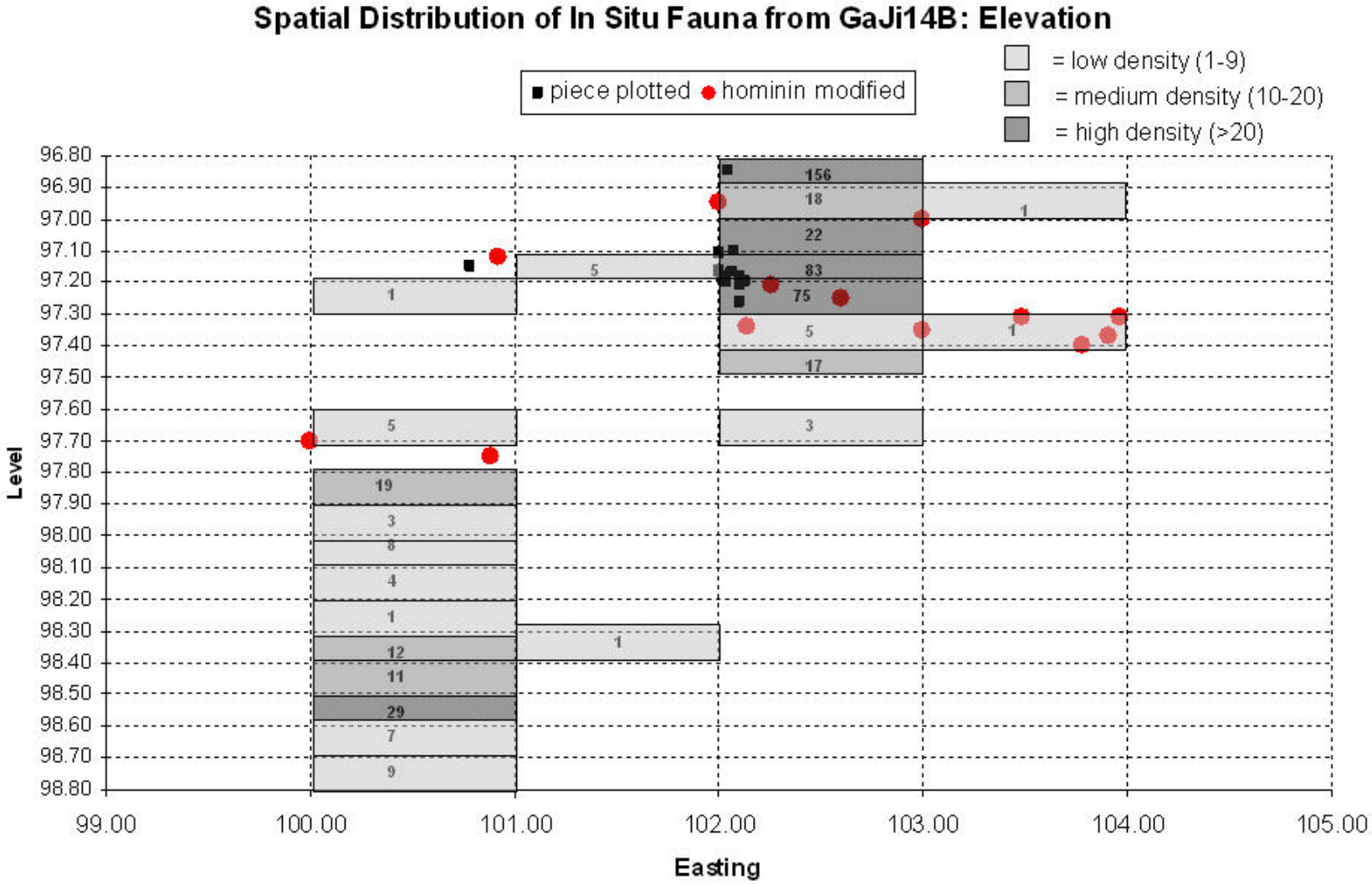
6.10b


Spatial Distribution of In Situ Fauna from GaJi14A: Elevation
piece plotted
hominin modified
= low density (1-9)
= medium density (10-20)
= high density (>20)
Level
Easting
96.00
96.10
96.20
96.30
96.40
96.50
96.60
96.70
96.80
96.90
97.00
97.10
97.20
97.30
97.40
97.50
97.60
97.70
97.80
97.90
98.00
98.10
98.20
98.30
98.40
98.50
98.60
98.70
98.80
98.90
99.00
99.10
99.20
99.30
99.40
99.50
98.00
99.00
100.00
101.00
102.00
103.00
104.00
105.00

6.10c


Spatial Distribution of In Situ Fauna from GaJi14B: Plan View
piece plotted
hominin modified
= low density (1-9)
= medium density (10-20)
= high density (>20)
18
29
69
20
5
92
33
1
92
126
2
Northing
Easting
104.00
103.00
102.00
101.00
100.00
99.00
99.00
100.00
101.00
102.00
103.00
104.00
105.00

6.10d


Spatial Distribution of In Situ Fauna from GaJi14B: Elevation
piece plotted
hominin modified
= low density (1-9)
= medium density (10-20)
= high density (>20)
Level
Easting
96.80
96.90
97.00
97.10
97.20
97.30
97.40
97.50
97.60
97.70
97.80
97.90
98.00
98.10
98.20
98.30
98.40
98.50
98.60
98.70
98.80
99.00
100.00
101.00
102.00
103.00
104.00
105.00
156
18
22
83
75
5
17
3
1
5
1
1
5
19
3
8
4
1
12
11
29
7
9
1

Methods and Sample

All materials excavated from FwJj14A, FwJj14B, and GaJi14 were brought back to the Archaeology Division, National Museums of Kenya for further study. This study was initially undertaken on a subset of the earlier excavated faunal assemblages by Christopher Monahan and Michael Rogers, who both kindly agreed to share copies of their notes and analyses with me so I could do a comprehensive study of all of the excavated fauna from 1999-2004 as part of my dissertation. The majority of the specimens were labeled with the site name and number, excluding those in level bags or those too small to write on. Labeling of the bones was done by various people during the period of excavation and analysis, including myself. I re-checked all taxonomic and taphonomic identifications. I bought wooden storage trays and plastic ziploc bags in Kenya for all the specimens and organized them in numerical order. However, during this study some specimens were separated into different trays for particular analyses. Many of the tooth specimens were pulled for isotope analysis by Rhonda Quinn. These specimens were put a tray labeled "Teeth" and include teeth from other sites at Koobi Fora. I put hominin and carnivore modified specimens were into four separate trays for photography and further analyses, one each for FwJj14A, FwJj14B, GaJi14A, and GaJi14B. These trays were left under the care of J. W. K. Harris when I was finished with them. I labeled these trays with the site designations and "modified specimens". Recently (in August 2006), a trunk of un-analyzed faunal material from at least one of these Okote sites that had been misplaced was found; I have not yet studied this material.

I analyzed each bone fragment separately, and entered data into a Microsoft Excel database I constructed. Data collected on each bone is outlined in Appendix 5. This

coding convention was similar to the one developed by Tom Plummer, Joe Ferraro, Jim Oliver and myself while we were analyzing the fauna from Kanjera South in 2004.

I made identifications of taxon, skeletal element, portion, segment, side, and size (following Brain, 1981 and Bunn, 1982) with the assistance of the comparative collection of modern fauna originally derived from the Osteology Division, and currently housed in the Archaeology Division. I identified specimens to as specific a mammal size class as possible, but sometimes I could only identify specimens to a size class bracket, such as size 2/3A or 3B/4, especially for long bone shaft fragments. Additionally, size class designations were not made on small level bag specimens. Specimens were identified to their actual size class for the individual specimen, rather than the size class assigned to adults of that species. For instance, I identified a juvenile hippo first phalanx (with cut marks) from GaJi14A as size 3/4 rather than size 5. Paul Watene, working in the Archaeology Division, often assisted me in making taxonomic and skeletal part identifications. On occasion, I brought particularly difficult specimens to identify to Ogeto Mwebi, head of the Osteology Division, for assistance, or to the Palaeontology Division for confirmation of identification of extinct taxa. Bones described as "unidentifiable" could not be assigned to a taxonomic level finer than Phylum Vertebrata. Identifiable bones were at least identifiable to Class (e.g. Mammalia), or a finer taxonomic level.

I identified bone and tooth specimens to skeletal part or element whenever possible. Sometimes I could only identify bones to axial or appendicular; additionally, sometimes long bones could only be identified to upper (humerus or femur), intermediate (radio-ulna or tibia), or lower (metapodial) long bone. I calculate MNE (Minimum

Number of Elements) where possible for all mammal skeletal elements. I made MNE calculations within each taxon by examining bone specimens on an individual basis and using the following criteria: mammal size class, overlap of homologous parts, and differences in individual size, age, and morphology. I then used MNE data to calculate MNI (Minimum Number of Individuals) for each taxon. I did not make MNI calculations for bovids above the tribe level. I only calculated bovid tribe MNIs using teeth and hyoids, as other bovid postcrania was generally too fragmentary to be identified to the tribe or species level.

I coded mammal long bone portions using two schemes. The first was Blumenschine's (1988) scheme (1=proximal, 2=distal, 3=near epiphyseal fragment, and 4=midshaft). The second was a scheme developed by Joe Ferraro and myself while discussing bone portion analyses on various occasions (A=proximal epiphysis, B=proximal near epiphysis, C=midshaft, D=distal near epiphysis, E=distal epiphysis). One can only choose one of Blumenschine's portion codes (1, 2, 3, or 4) following his scheme, which we found problematic, because many long bones contained more than one of these portions. In the Ferraro-Pobiner portion scheme, any or all codes could be used, depending upon which portions were actually present. For instance, a RAD A-C with a TM on C means that a bone is a radius with the proximal epiphysis through midshaft present, and a tooth mark located on the midshaft portion. I found this a simple and easy way to describe bone portion presence for visualization purposes, as well as describe more precisely the location of bone surface modifications. However, I coded using both schemes to maximize comparability with previous analyses.

I collected weathering stage data (Behrensmeyer, 1978) where appropriate. I only recorded weathering stage on fairly complete, adult specimens, where the surface preservation was good, as this was originally how the scheme was meant to be used (A. K. Behrensmeyer, *pers. comm.*). I measured maximum length and width of each bone specimen using digital calipers, and recorded these measurements to the nearest millimeter. When a bone specimen was broken into several pieces (with modern breaks), either I did not measure it or I measured the largest fragment. Either way, this was noted in the database. Also, bone specimens fully or mostly encased in calcium carbonate were not measured. Paul Watene measured many of the bones from the spit and screen bags.

I collected taphonomic data on bone surface 'readability' and modifications using a bright, high incident light and a 10X hand lens, as described in Blumenschine *et al.* (1996). Bone surface 'readability' refers to the ability to detect diagnostic morphology of surface modifications, which is dependent upon the extent and severity of surface degradation and alteration (Thompson, 2005). Bone surface degradation and alteration are caused by pre- and post-depositional processes including abrasion, diagenesis, and physical and chemical weathering. I coded bone surface readability in an index, following Monahan (1996, pers. comm.): 1=0-24%, 2=25-49%, 3=50-74%, 4=75-99%, 5=100% "readable". The index does not specify if the part of the bone surface is completely unreadable and part is pristine, perhaps resulting in a 3, or if the entire surface is slightly altered, which could also result in a 3. The reason(s) for any 'unreadability' was also recorded (see Appendix 5). I recorded bone surface 'readability' for cortical, fracture, and medullary surfaces where applicable, but only cortical surface 'readability' data are presented here. I did not record 'readability' for any bone surface exposed solely due to a

recent break. A few bone specimens could not be coded for cortical surface readability (N = 20 at FwJj14A, N = 3 at FwJj14B, N = 15 at GaJi14A, and N = 15 and GaJi14B); these specimens all had no original cortical surface remaining.

All non-tooth bone specimens were examined for surface modifications, and specimens often exhibited more than one type of surface modifications. These include cut marks (attributed to stone tools with high confidence), cut mark-like marks (those marks with some, but not all, of the diagnostic criteria for stone tool cut marks), tooth marks (attributed to carnivores with high confidence), tooth mark-like marks (those marks with some, but not all, of the diagnostic criteria for carnivore tooth marks), sedimentary abrasion, excavation/preparation (modern) marks, root etching, rodent gnawing, indeterminate marks, hammerstone pit or striae (attributed to hammerstones with high confidence), and hammerstone pit or striae-like marks (those marks with some, but not all, of the diagnostic criteria for hammerstone pits and striae) (see Appendix 5). Criteria for distinguishing marks are found in Lyman (1994) and White (1991) and references therein.

I recorded whether a major recent break was present on all faunal specimens except whole bones and teeth, except when the age of a break was ambiguous. I did not record minor (<10% estimated missing) recent breaks. I recorded the presence or absence of green breaks for long bones which preserved either a midshaft and/or a near epiphyseal portion. I also recoded relative circumference of long bones using a coding system where 1=<25% of the original circumference was present; 2=25-49%; 3=50-74%, 4=75-99%; 5=100%.

A total of 124 specimens from all of the sites (N = 10 from FwJj14A, N = 13 from FwJj14B, N = 14 from GaJi14A, and N = 87 from GaJi14B) were originally assigned numbers during excavation but are not included in any analyses, as they are not fossil vertebrate fauna. These are detailed in Table 6.2. Additionally, 71 bones which refit onto other specimens at modern breaks were not included in NISP counts (Table 6.3).

Table 6.2. Specimens from FwJj14A, FwJj14B, GaJi14A, and GaJi14B originally catalogued but excluded from analysis. Specimens found *in situ* (including those from level bags) are in boldface; those found on the surface are not. When multiple specimens from a single level bag were identified, the number of specimens is noted in parentheses following the specimen's number and letters designations.

Identification	Site	Specimen Number(s)
non-artifactual stone fragment	FwJj14A	2, 162, 164, 1467e, 1474, **2004**, 6117
possible crab claw	FwJj14A	634
possible fossilized fruit seed case	FwJj14A	1503
coprolite	FwJj14A	1636
non-artifactual stone fragment	FwJj14B	1240, 4005, **4109, 4142, 5020, 6068**, 6099b
dirt	FwJj14B	4021
pumice	FwJj14B	**4034, 4041, 6042, 6081, 6087**
non-artifactual stone fragment	GaJi14A	2, 72, **570, 1216**
shell	GaJi14A	19a, 19b, 22, 55, **1226c, 1230**
gastropod cast	GaJi14A	44, 46
calcium carbonate concretion	GaJi14A	58
bird bone, possibly modern	GaJi14A	61
non-artifactual stone fragment	GaJi14B	38
pumice	GaJi14B	**891**
bird bone, possibly modern	GaJi14B	**907**
gastropod shell or silicified operculum	GaJi14B	22q, 612, 617, 618, **809, 811, 863a-b (2), 864q-y (9), 879a-e (5), 881a-d (4), 882b-e (4), 883x and ab (2), 884j-r (9), 885h-l (5), 886a-k (11), 887l-t (8), 888r-x (8), and 889o-y (11)**

Analysis was generally done on the proportions of the total number of skeletal elements that had bone surface modifications (% modified), rather than the proportion of the total number of modifications on a certain skeletal element (% of modifications). This was done to address questions of preferential butchery of particular elements, to be able to compare the proportions of specific elements bones across sites, and to compare to experimental models.

Table 6.3. Number of refitting specimens with modern breaks from FwJj14A, FwJj14B, and GaJi14B not included in NISP counts. All surface specimens refit onto other surface specimens, and all *in situ* specimens refit onto other *in situ* specimens. No refits were found at GaJi14A.

Site	Number of Surface Specimens/ Number of In Situ Specimens
FwJj14A	65/0
FwJj14B	0/3
GaJi14B	1/2

Zooarchaeological and Taphonomic Analyses: Results

A total of 5945 bone specimens were analyzed from FwJj14A, FwJj14B, and GaJi14. The organization of the results is as follows:

1. FwJj14A and FwJj14B paleoenvironmental, zooarchaeological, and taphonomic analyses excluding hominin and carnivore bone modification;

2. the same analyses for GaJi14; and

3. Results pertaining to hominin and carnivore behavior, based on a variety of data.

FwJj14A and FwJj14B: Paleoenvironments, Zooarchaeology, and Taphonomy

The NISP from FwJj14A is 2170 and the NISP from FwJj14B is 1782. Their distribution in terms of surface, *in situ*, identifiable, non-identifiable bones and teeth are presented in Tables 6.4 and 6.5. The taxonomic lists from FwJj14A and FwJj14B are presented in Tables 6.6 and 6.7. Tables 6.8 and 6.9 list the MNI, with relevant elements and specimen numbers, for each mammalian taxon at FwJj14A and FwJj14B (respectively). There are a total of 14 individuals reconstructed at FwJj14A and 15 at FwJj14B. The majority of the individuals are from size classes 2 and 3 but also include a size 1 cercopithecoid (from FwJj14B), size 5 hippos (from both sites), and size 6 elephants (from both sites).

Table 6.4. Total number of *in situ* and surface specimens from FwJj14A and FwJj14B.

Site	NISP *In Situ* (Plotted/Level Bags)	NISP Surface	Total NISP
FwJj14A	516 (138/378)	1654	2170
FwJj14B	1584 (347/1237)	198	1782

Table 6.5. Distribution of the faunal samples from FwJj14A and FwJj14B into identifiable (ID) bones, non-identifiable (NID) bones, and teeth, found on the surface and *in situ*.

Site	Surface	Surface: NID Bones	Surface: ID Bones	Surface: Teeth	*In Situ*	*In Situ*: NID Bones	*In Situ*: ID Bones	*In Situ*: Teeth
FwJj14A	1654	701	661	292	516	386	97	33
FwJj14B	198	149	39	10	1584	1277	232	75

Table 6.6. Taxonomic list from FwJj14A.

Class	Order	Family	Tribe	Genus	Species
Reptilia	Crocodilia	Crocodylidae		*Crocodylus*	sp.
		Tomistomidae		*Euthecodon*	*brumpti*
	Testudines	Chelonia			
Osteichthyes	Siluriformes	Clariidae			
Mammalia	Artiodactlya	Bovidae	Aepycerotini		
			Alcelaphini		
			Alcelaphini	*Damaliscus/Connochaetes*	
			Hippotragini		
			Reduncini		
			Reduncini	*Kobus*	*kob*
		Elephantidae		*cf. *Elephas*	*recki*
		Hippopotamidae		*Hexaprotodon*	*protamphibius*
		Suidae			
	Perissodactlya	Equidae			
	Primates	Cercopithecidae		*Theropithecus*	*brumpti***
	Proboscidea				
	Rodentia	Thryonomyidae		*Thryonomys*	*swinderianus*

*The Elephantidae specimens, all fragmentary teeth, are likely *Elephas recki* based on faunal age estimates (Harris, 1983).

** The species designation of *Theropithecus brumpti* is made based on faunal age estimates, as this is the only species of *Theropithecus* found during this time interval.

Table 6.7. Taxonomic list from FwJj14B.

Class	Order	Family	Tribe	Genus	Species
Reptilia	Crocodilia	Crocodylidae		*Crocodylus*	sp.
		Tomistomidae		*Euthecodon*	*brumpti*
	Testudines	Chelonia			
Osteichthyes	Siluriformes	Clariidae			
Mammalia	Artiodactlya	Bovidae	Aepycerotini		
			Alcelaphini		
			Antilopini	*Gazella*	cf. *granti*
			Reduncini		
			Reduncini	*Kobus*	*kob*
		Elephantidae		*cf. *Elephas*	*recki*
		Hippopotamidae		*Hexaprotodon*	*protamphibius*
		Suidae			
	Perissodactlya	Equidae			
	Primates	Cercopithecidae		*Cercopithecus*	sp.
	Proboscidea				
	Rodentia	Thryonomyidae		*Thryonomys*	*swinderianus*

*The Elephantidae specimens, all fragmentary teeth, are likely *Elephas recki* based on faunal age estimates (Harris, 1983).

Table 6.8. MNI of taxonomically identifiable specimens at FwJj14A, with relevant elements and specimen numbers. See Appendix 3 for skeletal element abbreviations.

Taxon	Size	MNI	Elements/Specimen Numbers
Aepycerotini	2	1	HYO/650
Damaliscus/Connochaetes sp.	3A	2	RM^3/1060, RM^3/2064
cf. *Elephas recki*	6	1	Tooth fragments
Equidae	3/4	1	I_3/657
Hexaprotodon protamphibius	5	1	CVRT/1012-97, CVRT/1221
Kobus kob	3	1	RM^2/6112
Reduncini	3	3	RM_2/1104, RM_3/1137, RM_2/1273, RM_2/2042
Suidae	3A	1	ULN/301, PHA2/1236
Suidae	3	1	C-1/1111, TIB/1144, 1118, MC/6103, NAV/6168
Suidae (large)	3	1	TVRT/602, AST/1093, INN/1201
Theropithecus brumpti	2	1	Lower C (root)/657

Table 6.9. MNI of taxonomically identifiable specimens at FwJj14B, with relevant elements and specimen numbers. See Appendix 3 for skeletal element abbreviations.

Taxon	Size	MNI	Elements/Specimen Numbers
Aepycerotini	2	1	HYO/3094B
Alcelaphini	3	1	HYO/3124, HYO/5222
Alcelaphini (small)	2/3A	1	LM^2/5059
Cercopithecus sp.	1	1	HUM/5233
cf. *Elephas recki* (juvenile)	6	1	Tooth fragments
Gazella granti	2	1	RM_2/4066
Hippopotamidae (juvenile)	5	1	Tooth fragments, VRT/6001
Hippotragini	3B/4	1	HYO/3097
Kobus kob	3	1	LM_3/3034
Reduncini	3	3	RM_2/3043, RM_2/3044, RM_2/3046, LM_2/3140
Suidae 3A	3A	1	MAG/3055
Suidae (large)	3	1	MC/5220, CUN/3147c
Suidae	3B	1	MT/3132

A. Paleoenvironmental Reconstruction using Taxonomic Presence/Absence Data

The fauna from FwJj14A and FwJj14B includes both terrestrial and aquatic taxa (Tables 6.6, 6.7, 6.8, and 6.9). The taxa most useful in reconstructing the paleoenvironment more specifically are *Cercopithecus* sp., *Damaliscus/Connochaetes*, *Gazella* cf. *granti*, *Kobus kob*, the hippotragine bovid, *Hexaprotodon protamphibius*, *Theropithecus brumpti*, and *Thryonomys swinderianus*, based on morphology (Boissiere, 2005), tooth carbon isotopes (Cerling *et al.,* 2003), tooth microwear (Iwamoto, 1993; Teaford, 1993) and diet and habitat preferences of their extant counterparts (Estes, 1993; Kappelman *et al.,* 1997; Kingdon, 1997; Plummer and Bishop, 1994; Scott, 1979; Spencer, 1997).

Modern species of *Cercopithecus*, guenons, are highly arboreal tree-dwelling monkeys that live in a variety of forest niches (Estes, 1993). Extant *Damaliscus/ Connochaetes* (alcelaphine) species are grazers to hypergrazers (Cerling *et al.,* 2003), and tend to prefer open habitats (Scott, 1979) but are water dependent (Estes, 1993; Kingdon,

1997). Extant *Gazella granti* (Grant's gazelle) are classified as mixed feeders (Cerling *et al.,* 2003), preferring open environments (Scott, 1979) such as secondary grasslands (Spencer, 1997) and are water-independent (Estes, 1993). They usually live in high, well-drained areas during the rains and move to flat, grassy valleys during the dry seasons, and are fairly tolerant of bush and tall grass, as least seasonally (Kingdon, 1997). Extant *Kobus kob* (kob) are grazers to hypergrazers (Cerling *et al.,* 2003), preferring open habitats (Scott, 1979) with light cover (Kappelman *et al.,* 1997). Kobs are water-dependent and are tied to floodplain or edaphic grasslands, generally living in low-lying flats or green pastures in well-watered valleys; they concentrate on short pastures on higher parts of floodplains during rainy periods, and occupy green pasture areas bordering marshlands during dry periods (Estes, 1993; Kingdon, 1997; Spencer, 1997). However, they may depend more on cover than other open-habitat bovids (Plummer and Bishop, 1994). Living hippotragine bovids are grazers with molars adapted to grinding hard grasses (Kingdon, 1997). *Hexaprotodon protamphibius*, an extinct hippo, has recently been placed in a more "terrestrial grade" of hippos relative to other sister taxa, and can be interpreted as adapted to life near the water surface (Boissiere, 2005). Molar microwear study indicates *Theropithecus oswaldi* had a similar diet to the highly graminivorous modern gelada baboon but with a slightly leafier component to the diet, which suggests it lived in similar grassy habitats (Iwamoto, 1993; Teaford, 1993). *Thryonomys swinderianus*, the savannah cane rat, is water-dependent and feeds on coarse grasses in seasonally waterlogged valley-bottoms (Kingdon, 1997).

Taken as a whole, the fauna from FwJj14A indicate a paleoenvironment with a significant aquatic (fluvial and/or lacustrine) but relatively shallow-water component,

possibly an oxbow lake or a deltaic environment, indicated by the fish, hippo, and crocodiles, as well as the water-dependent alcelaphine, kob, and cane rat. This was accompanied by swampy areas, possibly in valleys, and also possibly undergoing seasonal flooding events. The fauna from FwJj14B is similar to that at FwJj14A, with the addition of 1) Grant's gazelle, indicating that the paleoenvironment must have also exhibited a more open, grassy component, preferred by this taxon as well as *Theropithecus brumpti* and the hippotragine bovid; and 2) an arboreal monkey (*Cercopithecus*), indicating a nearby gallery forest.

B. Description of Fauna, Site Formation Processes, and Non-Hominid or Carnivore Taphonomy

The assemblages from both FwJj14A and FwJj14B are relatively fragmentary, with a prevalence of mainly modern breaks, but also many green or spiral fractured limb bones. Table 6.10 details the breakage observed at FwJj14A and FwJj14B. As expected, surface bones generally have a higher incidence of modern breaks than those found *in situ*.

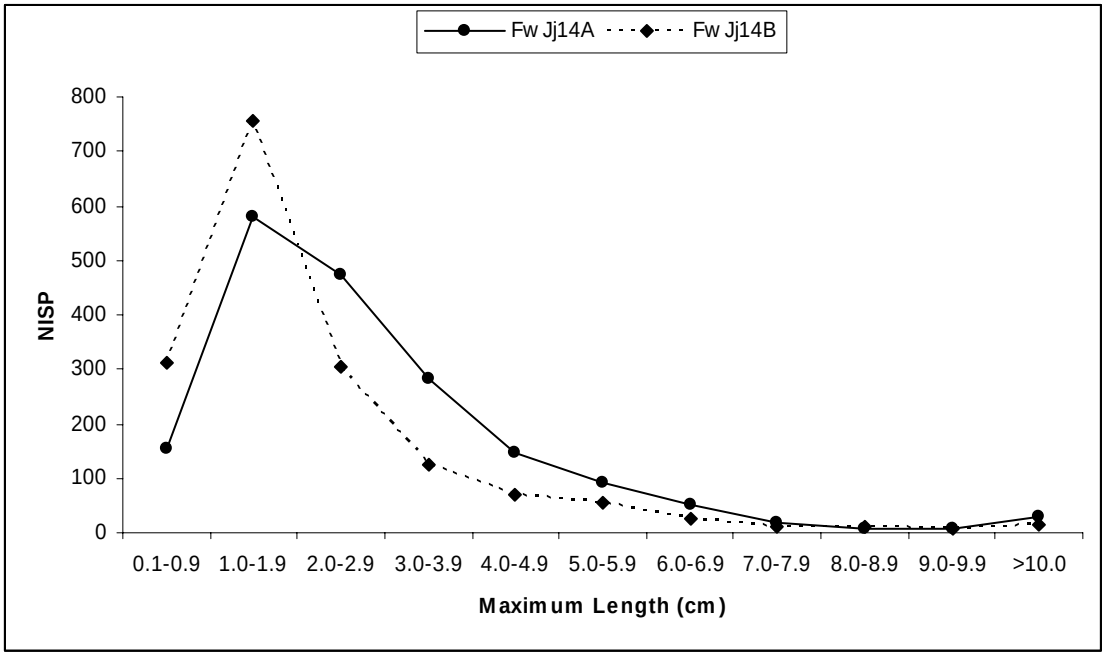
Table 6.10. Numbers of specimens with recent and green (spiral) fractures at FwJj14A and FwJj14B on limb and non-limb bones. Numbers refer to surface/*in situ*/total NISP.

		Recent Break Only	Green Break Only	Both	Neither
FwJj14A	Limb Bones	93/4/97	59/6/65	111/5/116	12/1/13
	Non-Limbs	878/121/999	n/a	n/a	3/362/365
FwJj14B	Limb Bones	3/6/9	9/54/63	3/26/29	0/7/7
	Non-Limbs	116/706/822	n/a	n/a	39/599/638

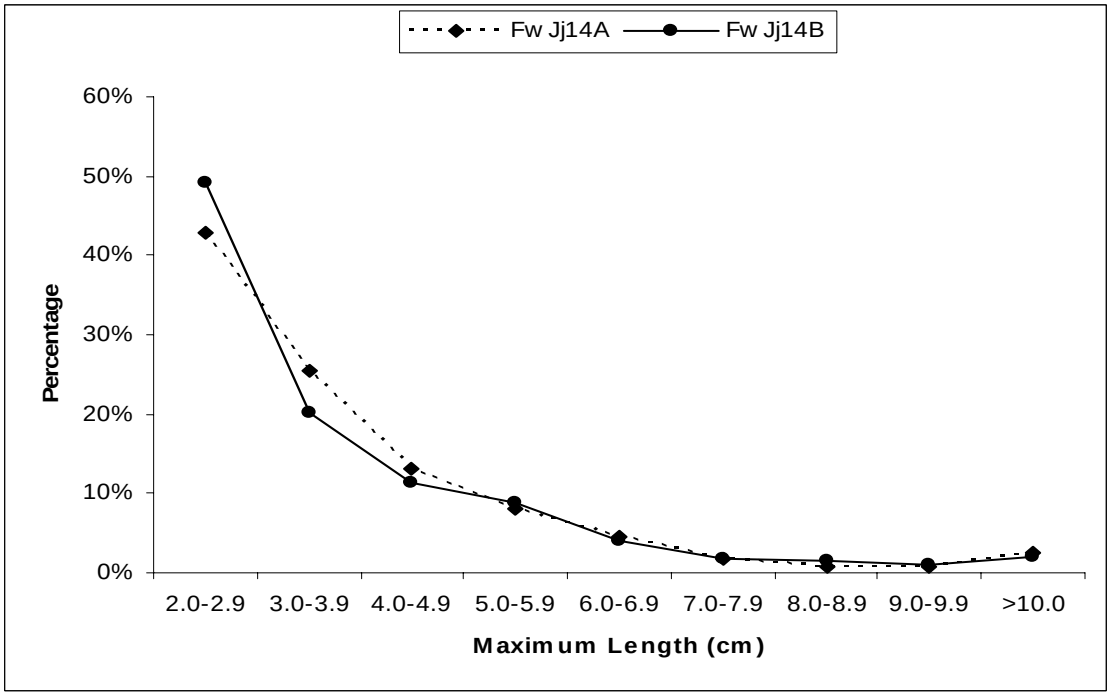
The specimen size profiles, based on length, are presented here in two formats (Figure 6.11). The first includes all specimens and displays the actual number of specimens that fall into each size range, and the second includes only those specimens

Figure 6.11. Size distribution of all bone specimens from FwJj14A and FwJj14B. Top figure (a) includes bones < 2mm in length, and bottom figure (b) includes only bones > 2mm in length. Abundance of small bones indicates lack of significant transport.

(a)



(b)



over 2.0 cm, as many zooarchaeological analyses do, and displays the percentage of total specimens that fall into that size range. The high numbers of small specimens indicate a lack of winnowing and significant transport.

Most of the bones from FwJj14A and FwJj14B could not be assigned weathering stages, as they were too incomplete (Table 6.11). However, of the thousands of bones for which a weathering stage was not formally coded, nearly all did not exhibit any signs of weathering, indicating a relatively rapid burial of these assemblages.

Table 6.11. Numbers of specimens from FwJj14A and FwJi14B in each weathering stage. Weathering stage is following Behrensmeyer, 1978.

Weathering Stage	FwJj14A (NISP)	FwJj14B (NISP)
0	124	29
1	25	10
2	6	2
3	1	0
Total	156	41

The vast majority of specimens from both FwJj14A and FwJj14B were between 76-99% "readable" (Table 6.12). The increasing numbers of surface modifications observed as surface readability increases suggests that surface readability likely affects the identification of bone surface modifications, as suggested by Monahan (1996) and Thompson (2005). Cut, percussion, and tooth marks will be discussed in more detail below.

Table 6.12. Surface readability and (CM), percussion (PM), and tooth marks (TM) on bone specimens at FwJj14A and FwJj14B.

	FwJj14A		FwJj14B	
Readability	N (%)	# CM/PM/TM	N (%)	# CM/PM/TM
0-25%	145 (8%)	1/0/0	26 (2%)	0/0/0
26-50%	125 (7%)	4/2/0	19 (1%)	0/0/0
51-75%	231 (13%)	5/1/1	89 (5%)	3/2/0
76-99%	1147 (63%)	107/9/2	1494 (91%)	61/9/0
100%	160 (9%)	15/7/2	22 (1%)	4/0/0
Total	**1808**	**132/19/5**	**1650**	**68/11/0**

A variety of surface modifications excluding cut, percussion, and tooth marks were identified on bones at FwJj14A and FwJj14B (Table 6.13). A small fraction of the faunal specimens exhibit sedimentary abrasion (3% from FwJj14A and 1% from FwJj14B), supporting the hypothesis that only minimal transport of the fauna has occurred. Most of the identifiable bones with sedimentary abrasion are long bone fragments (N = 38), followed by ribs (N = 5) and a maxilla fragment (N = 1). If these bones were broken before they were potentially fluvially transported, they would fall into Voorhies Group I (most easily transported); if they were all whole bones, then most would fall into Voorhies Group II (gradually transported) (Voorhies, 1969). Most of these specimens have recent breaks, but this is not indicative of a lack of ancient breakage.

Table 6.13. Numbers (NISP) of specimens with non-hominid or carnivore bone surface modifications from FwJj14A and FwJj14B.

Surface Mark Type	FwJj14A	FwJj14B
Cut Mark-like	115	24
Carnivore Tooth Mark-like	34	13
Sedimentary Abrasion	65	16
Excavation/Preparation	3	10
Root Etching	29	6
Rodent Gnawing	1	0
Indeterminate	68	25
Hammerstone Pit or Striae-Like	17	14
Total	**268**	**89**
No Surface Marks	767	1609

A smaller fraction of the faunal specimens exhibit root etching (1% from FwJj14A and less than 1% from FwJj14B), suggesting that the fauna generally did not come into contact with roots from plants on a land surface. In a modern study, root etching was most common under salt bushes on upper lake edges (Njau, 2000). This finding supports the idea of rapid burial. Only a single specimen, from FwJj14A, exhibits

rodent gnawing. Hominin and carnivore bone surface modifications will be discussed in more detail.

C. Zooarchaeological and Taphonomic Analyses

The majority of the specimens from FwJj14A (65%) and FwJj14B (84%) could not be identified to a specific mammal size class, mainly due to the highly comminuted nature of the assemblages. However, of those specimens that could be identified to size, size 2 and especially 3 mammals dominate the faunal assemblages at FwJj14A and FwJj14B (Figure 6.12, Table 6.14).

Figure 6.12. Frequency distribution of bone specimens identified to mammal size class from FwJj4A and FwJj14B. Mammal size classes were condensed from Table 6.12. Here, Size Class 1 includes 1 and 1/2; Size Class 2 includes 2 only; Size Class 3 includes 2/3A, 2/3, 3, 3/4, 3A, 3B, and 3B/4; Size Class 4 includes 4 and 4/5; Size Class 5 includes 5 a d 5/6. Using these divisions means that some of the specimens from Table 6.12 were not included in this figure, those that could not be identified to these size classes. This excluded proportion is 14.5% of the specimens originally identified to specimen size at FwJj14A, 11.5% of those at FwJj14B. Data from Table 6.14.

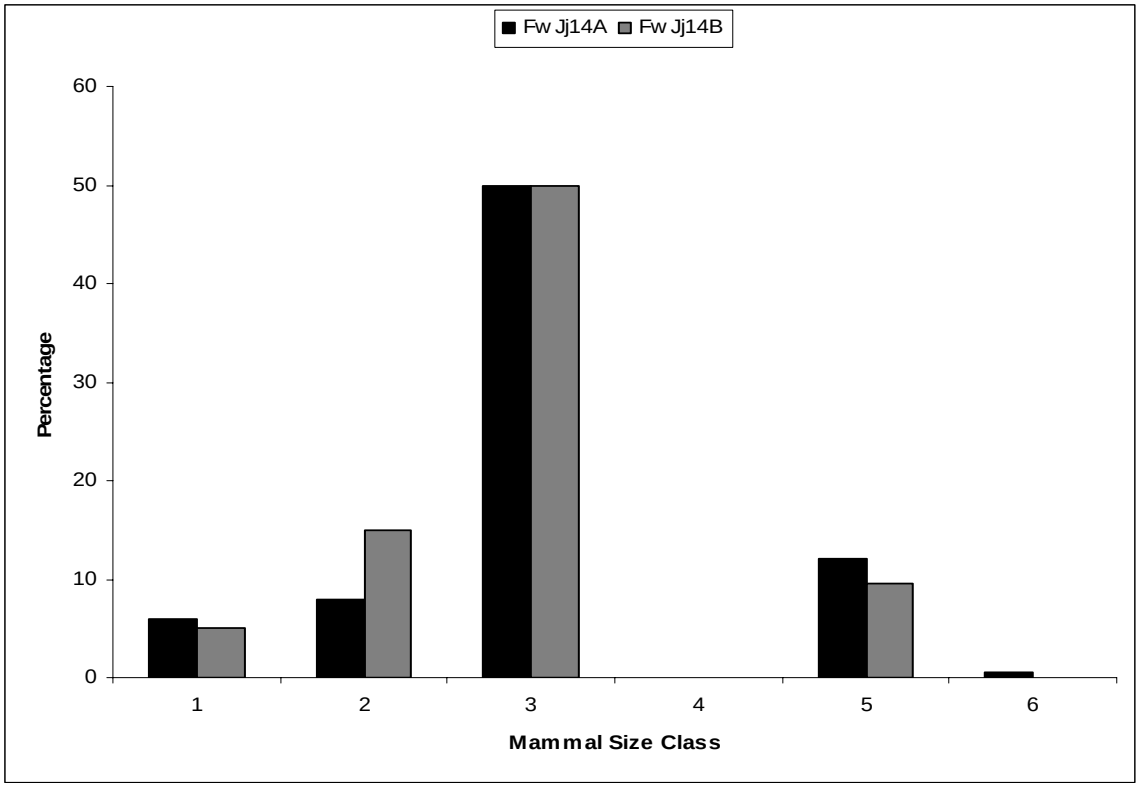


Table 6.14. Distribution of bone and tooth specimens from FwJj14A and FwJj14B into mammal size classes. Total NISP and percentage of NISP of those specimens identifiable to size class (following Bunn 1982) are given. Number and percentage of total NISP of specimens of indeterminate size are at the bottom of the table.

	FwJj14A		FwJj14B	
Mammal Size Class	NISP	% NISP	NISP	%NISP
1	14	2	5	2
1/2	29	4	9	3
2	56	8	34	11
2/3A	98	14	38	13
≥2	23	3	9	3
2/3	51	7	25	9
3	235	33	90	31
3/4	6	1	9	3
3A	27	4	14	5
3B	5	1	3	1
≤3	3	0.5	0	0
≥3	22	3	21	7
≥3A	2	0.5	0	0
≥3B	4	0.5	1	0
3B/4	20	3	4	1
4	1	0	0	0
4/5	1	0	0	0
≥4	24	3	6	2
5	75	11	25	9
5/6	7	1	2	0
6	4	0.5	1	0
TOTAL	**707**		**290**	
Indeterminate size	1320	65	1481	84

I did not construct age profiles because the assemblages consist of mostly fragmentary specimens. However, of the 61 mammalian bones and complete teeth from FwJj14A which could be identified to a relative age (sub-adult or adult) based on epiphyseal fusion or relative tooth size and features, 53 (87%) were adult and 8 (13%) were sub-adult. At FwJj14B, 7 of the 11 specimens for which age could confidently be identified were adult (64%), and 4 were sub-adult (36%).

I did not calculate MNE or MNI values for the non-mammal specimens, as most of these specimens included crocodile teeth, small pieces of fish crania or vertebrae, and turtle/tortoise plastron fragments. Non-mammals (N = 121) at FwJj14A and FwJj14B are listed in Table 6.15.

Table 6.15. NISP of non-mammal specimens from FwJj14A and FwJj14B.

Taxon	FwJj14A (NISP)	FwJj14 B (NISP)
Fish	71	0
Crocodile	28	4
Turtle/Tortoise	24	2
TOTAL	**121**	**6**

MNE and NISP data for bones from FwJj14A and FwJj14B identifiable to skeletal element and taxonomic level finer than mammal are presented in Table 6.16 and Figure 6.13. Excluding teeth and those specimens that could possibly conjoin with others (including specimens only identifiable to 'axial'; long bones and upper, intermediate, or lower long bones which could be the same elements as other bones identifiable to specific long bones; metapodials, which could be the same specimens as metacarpals or metatarsals), there are 129 elements from FwJj14A and 84 elements from FwJj14B. At both FwJj14A and FwJj14B, there are slightly more appendicular elements than axial elements, and compact bones are underrepresented (Figure 6.14). However, the rib MNE count is likely an underestimation (see Methods), so there may be a higher number of axial specimens at both sites. Excluding patellae, using either NISP or MNE, there are relatively similar numbers of forelimbs and hindlimbs at FwJj14A (Figure 6.15); using NISP there are slightly more hindlimbs, but using MNE there are slightly more forelimbs. However, at FwJj14B, forelimbs are dominant over hindlimbs using both NISP and MNE (Figure 6.15).

Table 6.16. NISP and MNE for each skeletal part from FwJj14A and FwJj14B. See Appendix 3 for skeletal element abbreviations.

	FwJj14A		FwJj14B	
Skeletal Part	NISP	MNE	NISP	MNE
TTH[1]	291	16	86	19
MAND	17	10	7	6
MAX	4	1	3	3
CRAN	21	1	17	1
HC	4	4	1	1
HYO	1	1	4	4
AX	1	1	0	0
CLAV	0	0	0	0
RIB[2]	107	3	52	4
VRT[3]	24	n/a	7	n/a
C-1	2	2	0	0
C-2	0	0	0	0
CVRT	14	9	1	1
TVRT	7	6	4	4
LVRT	5	4	2	2
SACR	0	0	1	1
CAUD	0	0	0	0
INN	14	13	6	5
SCAP	3	3	1	1
LB[3]	260	n/a	73	n/a
ULB	6	3	11	3
HUM	18	11	17	8
FEM	14	7	6	5
PAT	1	1	0	0
ILB	0	0	0	0
RADU	3	3	1	1
RAD	11	3	8	7
ULN	11	7	5	5
TIB	34	17	8	5
FIB	1	1	1	1
CARP	3	3	5	5
TARS	1	1	1	1
CALC	2	2	1	1
AST	5	5	0	0
NAVC	0	0	0	0
LLB (MP)	21	7	13	6
MT	3	3	6	6
MC	5	5	4	3
PHA	0	0	0	0
PHA1	1	1	3	3
PHA2	1	1	1	1
PHA3	0	0	1	1
SES	1	1	0	0

[1]Only complete teeth or a single "tooth" instance for each taxon were used to calculate tooth MNE, therefore this number is likely to be an underestimation.

[2] RIB MNE was calculated using those specimens with articular ends (heads) only, and is therefore likely an underestimation.

[3]LB refers to long bone shafts only, and VRT refers to a fragment of an unspecified vertebra; therefore MNEs were not calculated for these categories.

Figure 6.13. Skeletal part profile (based on Minimum Number of Elements) for FwJj14A and FwJj14B. CRAN includes MAND, MAX, HYO, and HC. The full names of skeletal elements for which abbreviations are used here are listed in Appendix 3. Data from Table 6.16.

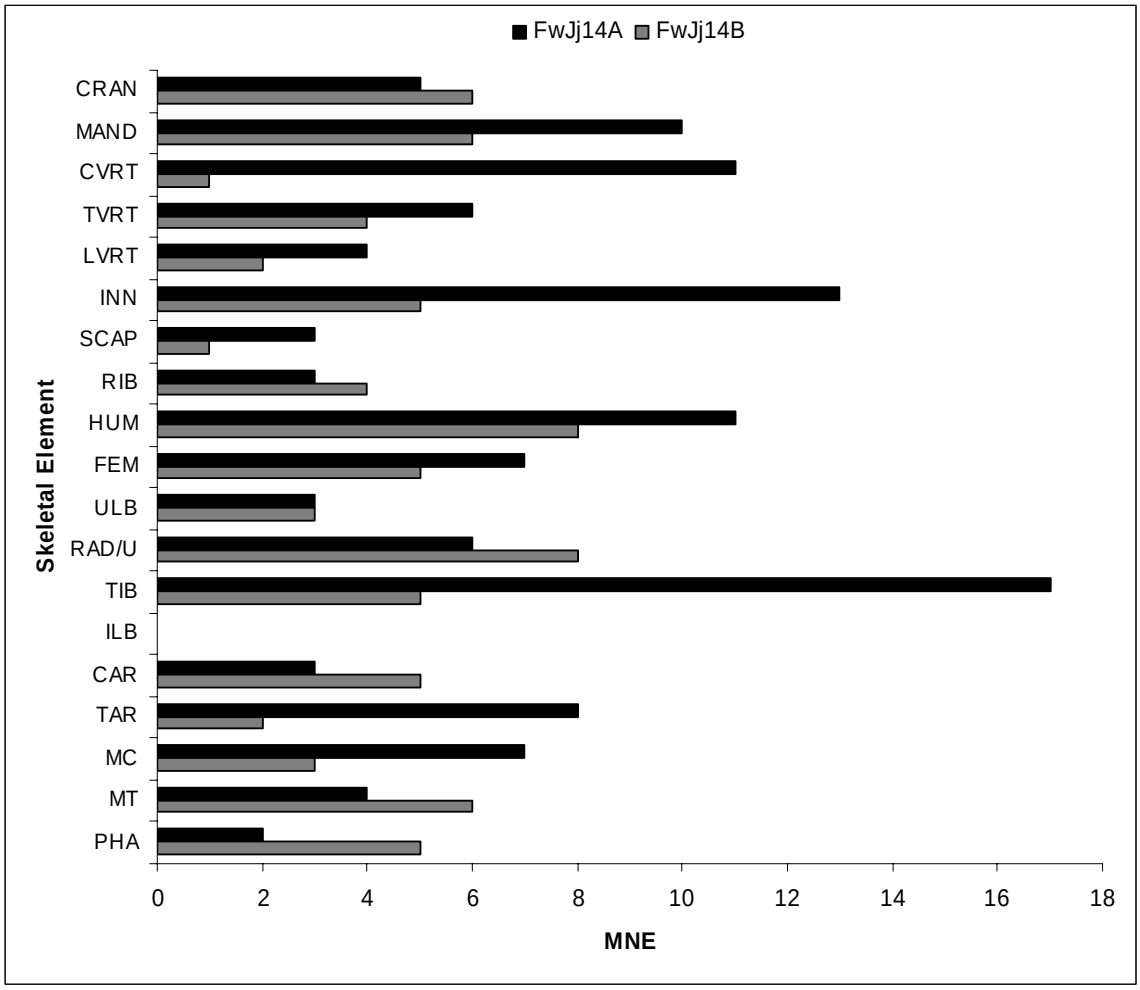


Figure 6.14. MNE at FwJj14A and FwJj14B stratified by skeletal element category: axial, appendicular, and compact. Appendicular elements include humerus, femur, radius/radio-ulna, tibia, metacarpal, metatarsal. Axial elements include cranium, mandible, horn core, hyoid, innominate, sacrum, scapula, rib, vertebra, clavicle. Compact bones include patella, fibula (ungulate), carpal, tarsal, sesamoid, phalanx. Data from Table 6.16.

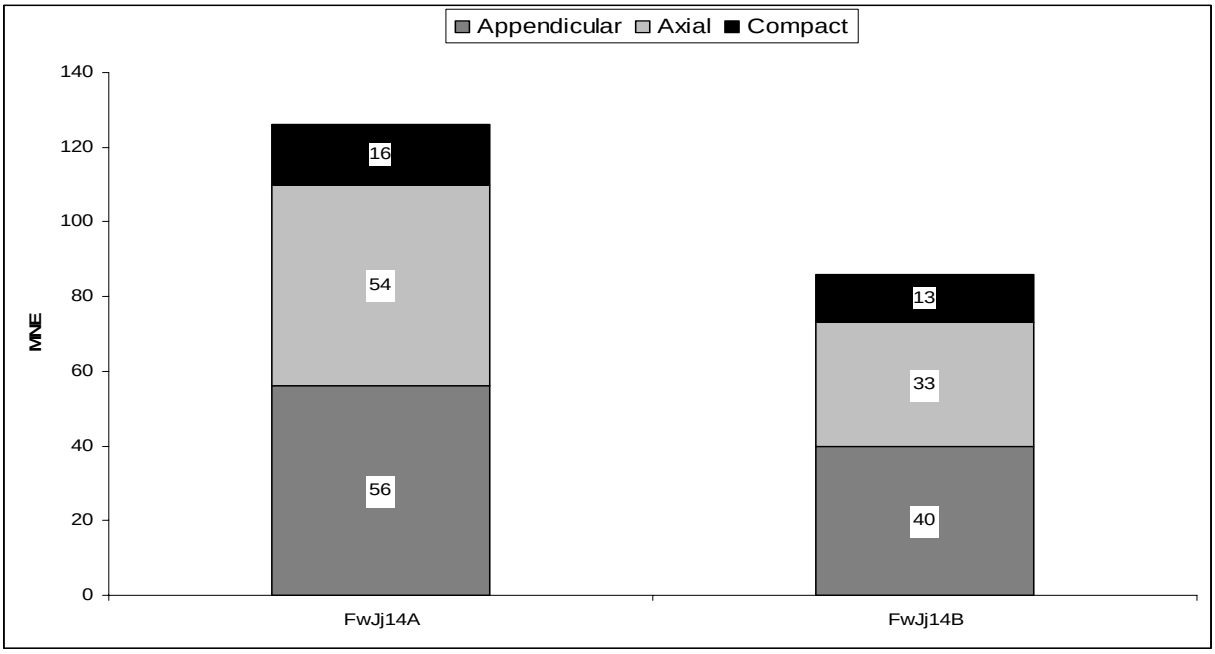
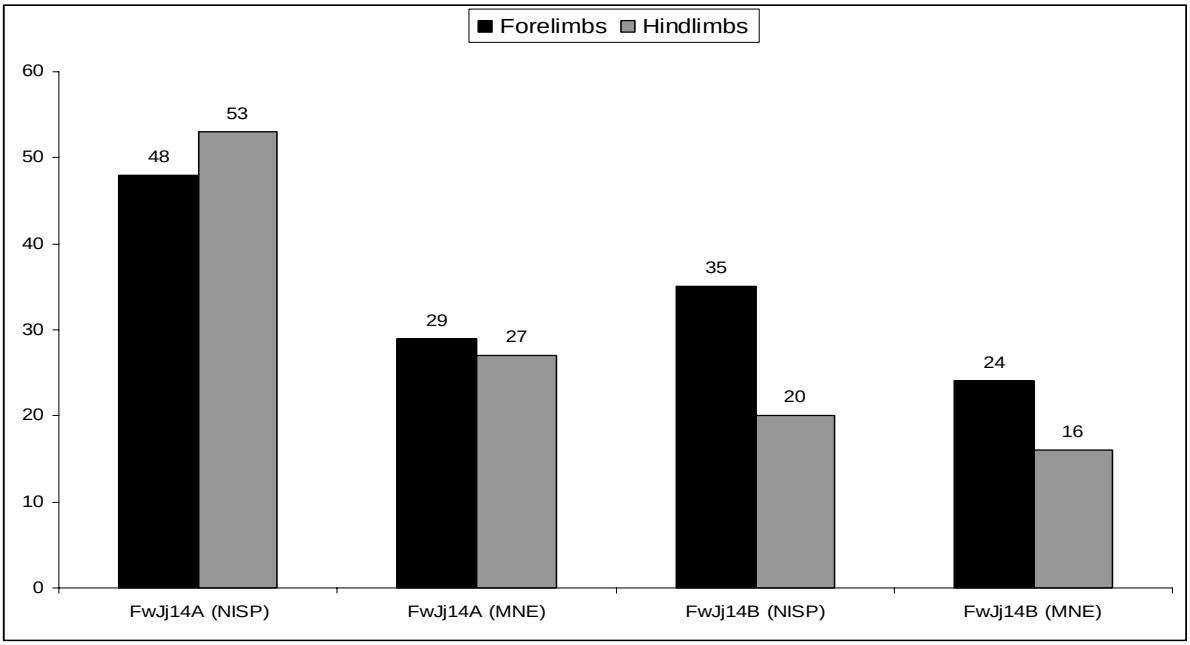


Figure 6.15. Comparison of forelimb and hindlimb NISP and MNE from FwJj14A and FwJj14B. Forelimb includes humerus, radius, ulna, radio-ulna, and metacarpal; hindlimb includes femur, tibia, and metatarsal. Counts are shown above each column. Data from Table 6.16.



Limb shafts vastly outnumber epiphyseal and near-epiphyseal specimens by an order of magnitude at both FwJj14A and FwJj14B (Table 6.17). Differential counts of limb categories (upper, intermediate, and lower) can vary based on whether NISP or MNE data are used (Figure 6.16). At FwJj14A, the order of relative abundance of limb categories is intermediate > upper >lower based both on NISP and MNE. At FwJj14B, using NISP, the order of relative abundance of limb categories is upper > lower > intermediate. However, when MNE is used, the order is upper = intermediate > lower.

Table 6.17. Limb portions and epiphysis: shaft ratios from FwJj14A and FwJj14B. These data are based on NISP counts of each limb portion, where refitting pieces were not counted as new bones. When condensing the mammal carcass sizes listed above into three size categories here (1 and 2, 3 and 4, and 5 and 6), bones originally identified as crossing over two size categories (e.g. size 2/3) were put into the larger size category (e.g., size 3). Bones which were only identifiable to a range of size classes (e.g. ≥ size 3) are classified as "unsized" here. Near epiphyseal portions were defined as having cancellous bone on the internal surface, while midshafts had no cancellous bone on the internal surface. Epiphyses were those areas that directly articulated with other limbs, or parts of the bones immediately adjacent to those. Limb portions were identified as specifically as possible on each specimen (see definitions in Blumenschine, 1988). The seven portion categories used here are CO=complete; EPI=proximal or distal epiphyseal end only; EPI+NEF=proximal or distal epiphysis with some near epiphyseal bone; EPI+NEF+MSH= proximal or distal epiphysis with some near epiphyseal and midshaft bone; SH=only midshaft; MSH+NEF=midshaft bone with some near epiphyseal (internally cancellous) bone; NEF=only near epiphyseal bone. When calculating the epiphysis: shaft (EPI: SH) ratio, MSH and MSH+NEF specimens were included in the shaft count, and all other specimens (except complete specimens) were included in the epiphysis count.

	FwJj14A					**FwJj14B**				
Mammal Size Class	1&2	3&4	5&6	unsized	total	1&2	3&4	5&6	unsized	total
CO	0	0	0	0	0	0	0	0	0	0
EPI	6	15	0	5	26	2	2	0	0	4
EPI+NEF	1	3	0	0	4	0	0	0	0	0
EPI+NEF+MSH	1	10	0	0	11	1	4	0	0	5
MSH	22	221	2	34	279	12	97	0	15	124
MSH+NEF	4	25	0	3	32	1	3	0	0	4
NEF	0	1	0	0	1	0	0	0	0	0
EPI:SH ratio	**0.3**	**0.12**	**0**	**0.14**	**0.14**	**0.23**	**0.06**	**0**	**0**	**0.07**

The long limb bone circumference data are remarkably similar from both sites, which are dominated by shaft splinters with less than 25% of the original circumferences preserved (Figure 6.17), attesting again to the highly comminuted nature of the bone assemblage, especially the long limb bones.

Figure 6.16. Limb bones from FwJj14A and FwJj14B stratified by limb bone category. Upper limb bones include humerus and femur; intermediate limb bones include radius, ulna, radio-ulna, and tibia; lower limb bones include metapodials, metacarpal, and metatarsal. NISP of each limb category includes those specimens identifiable only to upper, intermediate, or lower limb bones, as well as those specimens identifiable to a specific skeletal element. MNE of each limb category only includes those specimens identifiable to a specific skeletal element. Counts are shown above each column. Data from Table 6.16.

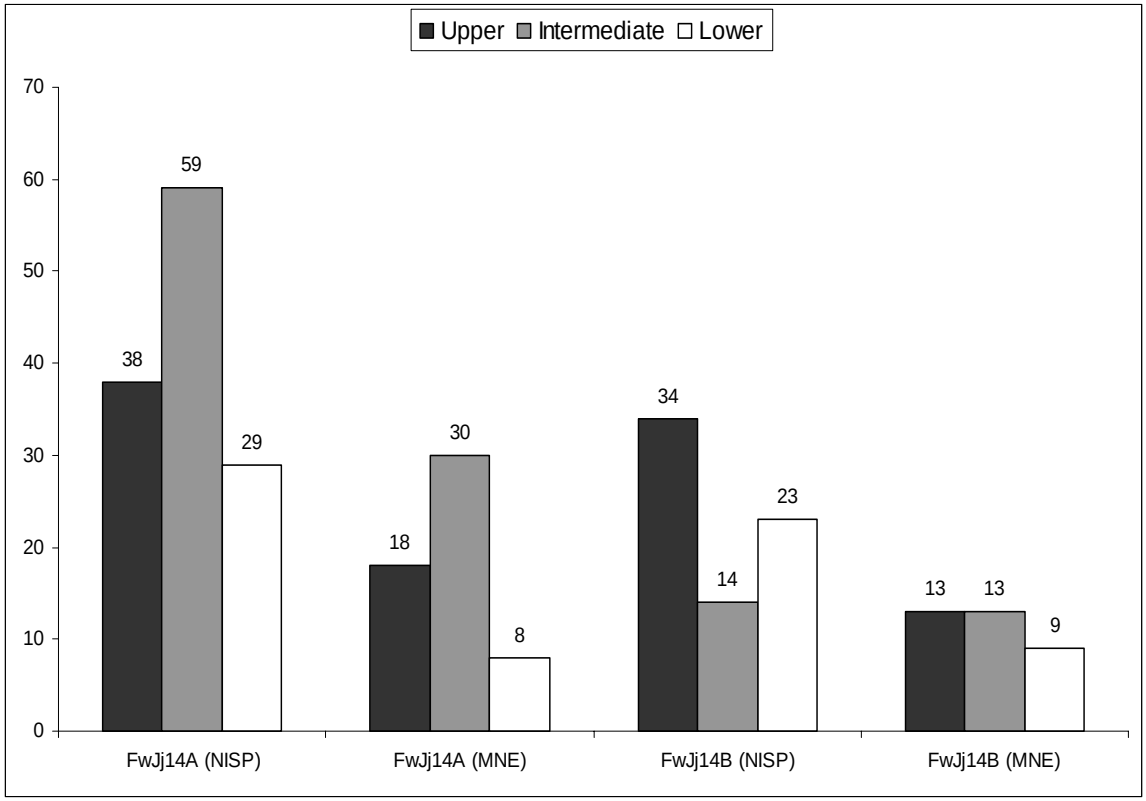
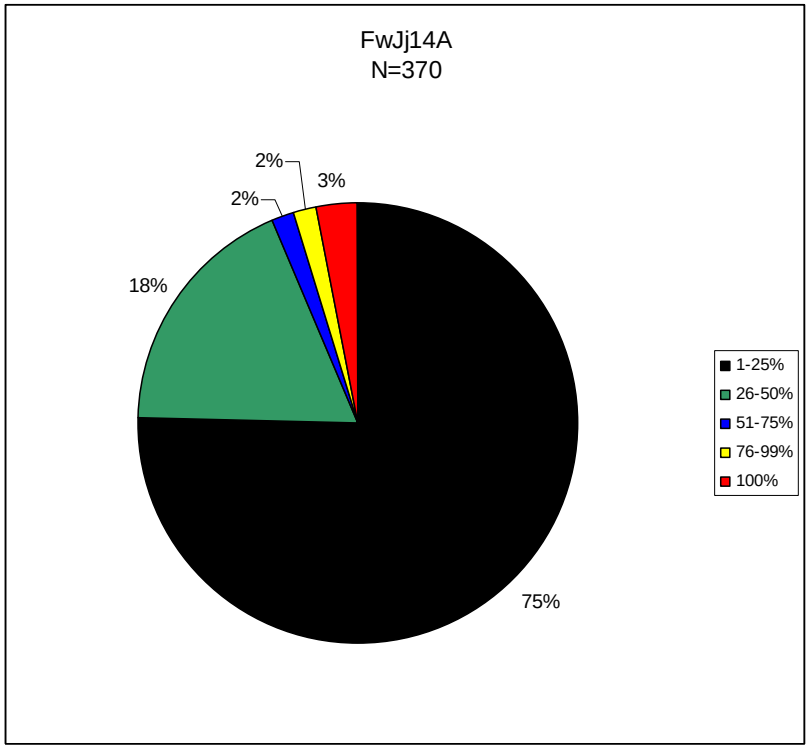
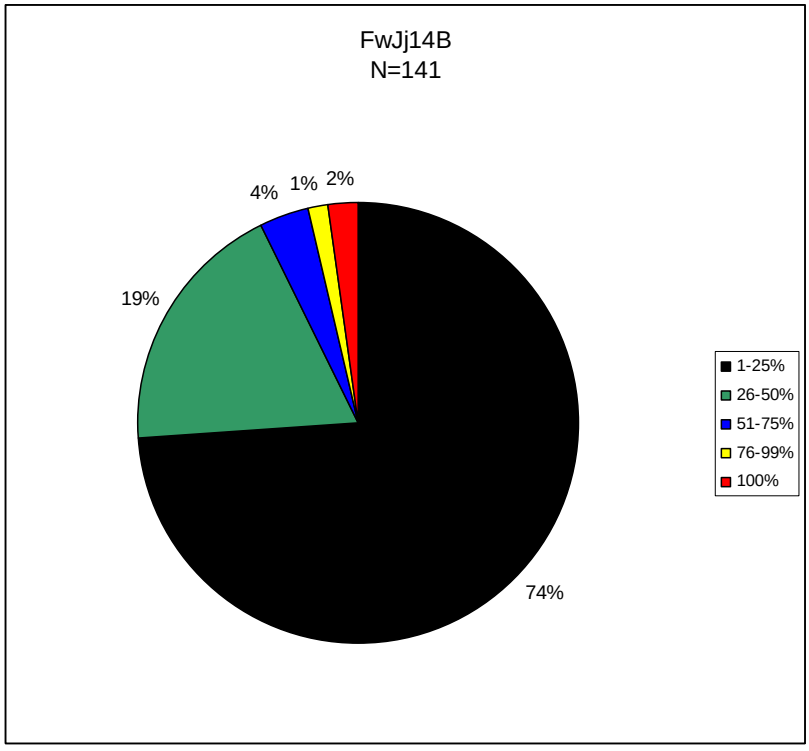


Figure 6.17. Long bone circumference distributions at FwJj14A and FwJj14B. Long bone circumferences were estimated visually. N refers to the total number of long bone specimens in the sample from each site.

(a)



(b)



GaJi14: Paleoenvironment, Zooarchaeology, and Taphonomy

The NISP from GaJi14 is 2087. The distribution of specimens in terms of surface, *in situ*, identifiable, non-identifiable bones and teeth is presented in Tables 6.18 and 6.19. The taxonomic list from GaJi14 is presented in Table 6.20. Table 6.21 lists the MNI, with relevant elements and specimen numbers, for each mammalian taxon at GaJi14A. There are a total of 20 individuals reconstructed at GaJi14. The majority of the individuals are from size classes 2 and 3 but also include a cane rat (size 1), size 5 hippos (including *Hexaprotodon protamphibius)*, a size 5 giraffe (*Giraffa jumae)*, and a size 5 rhino.

Table 6.18. Total number of *in situ* and surface specimens from GaJi14.

NISP In Situ (Plotted/Level Bags)	NISP Surface	Total NISP
1250 (360/892)	837	2087

Table 6.19. Distribution of the faunal sample from GaJi14 into identifiable bones, non-identifiable bones, and teeth, found on the surface and *in situ*.

Surface	Surface: NID Bones	Surface: ID Bones	Surface: Teeth	In Situ	In Situ: NID Bones	In Situ: ID Bones	In Situ: Teeth
736	398	292	46	1251	928	266	56

Table 6.20. Taxonomic list from GaJi14.

Class	Order	Family	Tribe	Genus	Species
Reptilia	Crocodilia	Crocodylidae		*Crocodylus*	sp.
		Tomistomidae		*Euthecodon*	*brumpti*
	Testudines	Chelonia			
	Squamata	Varanidae		cf. *Varanus*	*niloticus*
Osteichthyes	Siluriformes	Clariidae			
Mammalia	Artiodactlya	Bovidae	Alcelaphini	*Damaliscus/Connochaetes*	sp.
			Reduncini	cf. *Kobus*	*sigmoidalis*
			Reduncini		
			Tragelaphini	*Tragelaphus*	cf. *strepsiceros*
		Giraffidae		cf. *Giraffa*	*jumae*
		Hippopotamidae		cf. *Hexaprotodon*	*protamphibius*
		Hippopotamidae			
		Suidae		*Kolpochoerus*	*limnetes/olduvaiensis*
		Suidae			
	Carnivora	Felidae			
	Perissodactlya	Equidae		*Equus*	sp.
				Hipparion	sp.
		Rhinoceratidae			
	Primates	Cercopithecidae		cf. *Theropithecus*	*oswaldi*
	Rodentia	Thryonomyidae		*Thryonomys*	*swinderianus*

Table 6.21. MNI of taxonomically identifiable specimens at GaJi14, with relevant elements and specimen numbers. See Appendix 3 for skeletal element abbreviations.

Taxon/Size	Size	MNI	Elements/Specimen Numbers
Alcelaphini	3	1	LM^1/953
Connochaetes/Damaliscus	3	1	$LM^{1\&2}$*/219
Equus sp.	3/4	2	RM_2/230, RM_1/524, RM_2/525, M_3/1049, RM_3/1050, RP_3/1118, SCAP/534, LM_2**/791
Equus sp. (juvenile)	3A	1	LdP_2**/709
Felidae	2	1	FEM/560
Giraffa jumae	5	1	SEMIL/1060, SCAPH/526
Hippopotamidae (juvenile)	3/4	1	TTH/509, PHA1/7
Hippopotamidae	5	1	Tooth fragments, VRT/511, 575/FEM
Hexaprotodon protamphibius	5	1	MAXT/631, CVRT/587, MAND/588
Hipparion sp.	4	1	MTM/1, RP_3/234, RM_1/767, SCAP/504, MP/512, I/721
Kobus sigmoidalis	3	1	RM_2/1084
Kolpochoeres limnetes/olduvaiensis	3	1	LM_3/1048
Rhinoceratidae	5	1	MAND/774
Suidae	3	1	Tooth fragments, FEM/623, MAND/724, SCAP/1108
Suidae (juvenile)	2	1	566/dP2
Suidae (large)	3	1	TIB/1103
Theropithecus oswaldi	2	1	CLAV/1115
Thryonomys swinderianus	1	1	RI(upper)/805
Tragelaphus strepsiceros	3	1	$RP^{3\&4}$*/224

*tooth or teeth in maxilla
**tooth or teeth in mandible

A. Paleoenvironmental Reconstruction using Taxonomic Presence/Absence Data

The fauna from GaJi14 includes both terrestrial and aquatic taxa (Tables 6.20, 6.21). The taxa most useful in reconstructing the paleoenvironment more specifically are cf. *Varanus niloticus*, cf. *Kobus sigmoidalis*, cf. *Giraffa jumae*, *Kolpochoerus limnetes*, cf. *Theropithecus oswaldi*., *Damaliscus/Connochaetes* sp., *Tragelaphus* cf. *strepsiceros*, cf. *Hexaprotodon protamphibius*, *Theropithecus oswaldi*, and *Thryonomys swinderianus*. Paleoenvironmental reconstructions are based on morphology (Boissiere, 2005); tooth carbon isotopes (Cerling *et al.,* 2003; Sponheimer and Lee-Thorpe, 1999); molar

microwear (Iwamoto, 1993; Teaford, 1993) and diet and habitat preferences of their extant counterparts (Estes, 1993; Kingdon, 1997; Plummer and Bishop, 1994; Scott, 1979; Spencer, 1997).

Extant *Varanus niloticus*, the Nile monitor lizard, is found near riverine or lacustrine water sources throughout eastern Africa, except in high altitude areas and the drier parts of northern and eastern Kenya (Spawls *et al.,* 2002). Modern *Kobus* species are grazers (Cerling *et al.,* 1997), preferring edaphic grasslands (Spencer, 1997). Fossil ecomorphological analyses suggest that *Kobus sigmoidalis* was also an edaphic grassland inhabitant (Spencer, 1997). Tooth carbon isotope analysis suggests that South African *Giraffa jumae* was a browser of C_3 plants (Sponheimer and Lee-Thorpe, 1997). On the other hand, tooth carbon isotope analysis suggests that *Kolpochoerus limnetes* was a grazer of C_4 vegetation, likely with some degree of water dependency (Cerling *et al.,* 2003). Molar microwear study indicates *Theropithecus oswaldi* had a similar diet to the highly graminivorous modern gelada baboon but with a slightly leafier component to the diet, which suggests it lived in similar grassy habitats (Iwamoto, 1993; Teaford, 1993). Extant *Damaliscus/Connochaetes* (alcelaphine) species are grazers to hypergrazers (Cerling *et al.,* 2003); they tend to prefer open habitats (Scott, 1979), but are water dependent (Estes, 1993; Kingdon, 1997). Extant *Tragelaphus strepsiceros*, the greater kudu, is a browser to hyperbrowser (Cerling *et al.,* 2003), feeding on dicots in woodland habitats (Spencer, 1997). *Hexaprotodon protamphibius*, an extinct hippo, has recently been placed in a more "terrestrial grade" of hippos relative to other sister taxa, and can be interpreted as adapted to life near the water surface (Boissiere, 2005). *Thryonomys*

swinderianus, the savannah cane rat, is water-dependent and feeds on coarse grasses in seasonally waterlogged valley-bottoms (Kingdon, 1997).

Taken as a whole, the fauna from GaJi14 indicates a paleoenvironment with a significant aquatic (fluvial and/or lacustrine) but relatively shallow-water component, possibly an oxbow lake or a delta, indicated by the fish, hippo, and crocodiles, as well as the water-dependent alcelaphine, browsing suid, and cane rat. This was accompanied by swampy areas, possibly in valleys, and also possibly undergoing seasonal flooding events. *Kobus sigmoidalis* suggests edaphic grasslands. The greater kudu indicates a more wooded component to the vegetation, and the giant baboon indicates that there were also drier, open grassy areas nearby.

B. Description of Fauna, Site Formation Processes, and Non-Hominid or Carnivore Taphonomy

The assemblage from GaJi14 is relatively fragmentary, with a prevalence of mainly modern breaks, but also many green or spiral fractured limb bones. Table 6.22 details the breakage observed at GaJi14. Surface bones do not generally have a higher incidence of modern breaks than those found *in situ*, but this is due to the higher number of *in situ* specimens overall.

Table 6.22. Numbers of specimens with recent and green (spiral) fractures on limb and non-limb bones at GaJi14. Numbers refer to surface/*in situ*/total NISP.

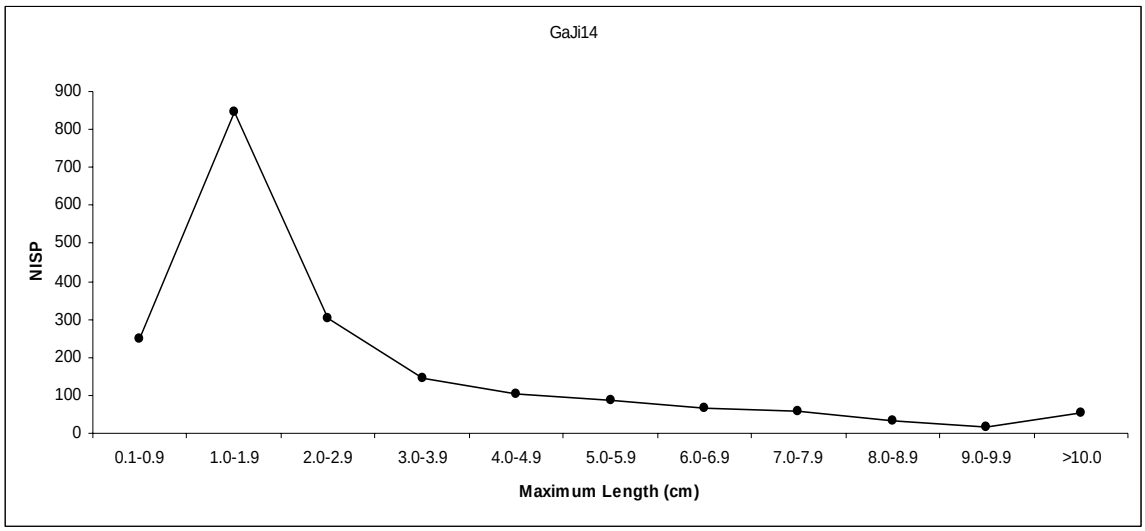
	Recent Break Only	Green Break Only	Both	Neither
Limb Bones	43/11/54	44/34/78	53/24/68	7/16/22
Non-Limbs	363/564/936			111/587/707

Specimen size profiles, based on length, are presented here in two formats (Figure 6.18). The first includes all specimens and displays the actual number of specimens that

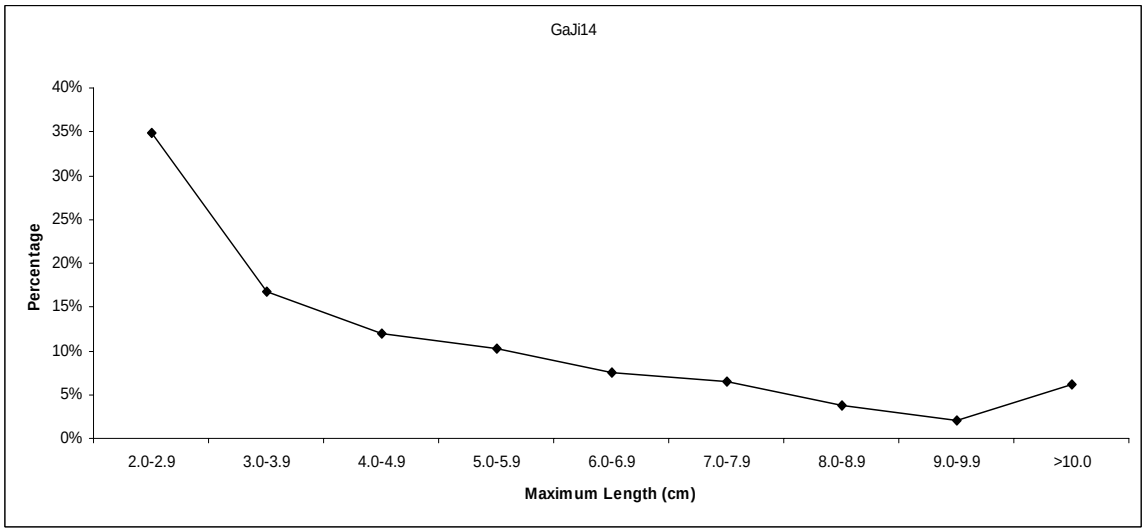
fall into each size range; the second includes only those specimens over 2.0 cm, as many zooarchaeological analyses do, and displays the percentage of total specimens that fall into that size range. The high numbers of small specimens indicate a lack of winnowing and significant transport.

Figure 6.18. Size distribution of all faunal specimens from GaJi14. Top figure (a) includes bones < 2mm in length, and bottom figure (b) includes only bones > 2mm in length. Abundance of small bones indicates lack of significant transport.

(a)



(b)



Most of the bones from GaJi14 could not be assigned a weathering stage, as they were too incomplete (Table 6.23). However, of the hundreds of bones for which a weathering stage was not formally coded, nearly all did not exhibit any signs of weathering, indicating a relatively rapid burial of these assemblages.

Table 6.23. Numbers of specimens from GaJi14 in each weathering stage. Weathering stage is following Behrensmeyer, 1978.

Weathering Stage	FwJj14 (NISP)
0	98
1	9
2	8
3	3
4	1
Total	139

The vast majority of specimens from both GaJi14 were between 76-99% "readable" (Table 6.24). The increasing numbers of surface modifications observed as surface readability increases suggests that surface readability likely affects the identification of bone surface modifications, as suggested by Monahan (1996) and Thompson (2005). Cut, percussion, and tooth marks will be discussed in more detail.

Table 6.24. Surface readability of bone specimens with cut (CM), percussion (PM), and tooth marks (TM) from GaJi14.

Readability	N (%)	# CM/PM/TM
0-25%	86 (4%)	0/0/0
26-50%	90 (5%)	0/0/0
51-75%	136 (7%)	13/4/0
76-99%	1598 (82%)	74/15/1
100%	42 (2%)	3/0/0
Total	**1952**	**90/19/1**

A variety of bone surface modifications excluding cut, percussion, and tooth marks were identified on bones at GaJi14 (Table 6.25). A small fraction of the faunal specimens exhibit sedimentary abrasion (2%), supporting the hypothesis that only

minimal transport of the fauna has occurred. Most of the identifiable bones with sedimentary abrasion are long bone fragments (N = 16), followed by ribs (N = 9), mandibles (N = 2), then a scapula and an innominate. If these bones were broken before they were potentially fluvially transported, they would fall into Voorhies Group I (most easily transported); if they were all whole bones, then most would fall into Voorhies Group II (gradually transported) (Voorhies, 1969). Most of these specimens have recent breaks, but this is not indicative of a lack of ancient breakage.

Table 6.25. Numbers of non-hominid or carnivore bone surface modifications from GaJi14.

Surface Mark Type	NISP
Cut Mark-like	58
Tooth Mark-like	22
Sedimentary Abrasion	43
Excavation/Preparation	7
Root Etching	21
Rodent Gnawing	0
Indeterminate	32
Hammerstone Pit or Striae-like	10
Total	**156**
No Surface Marks	1831

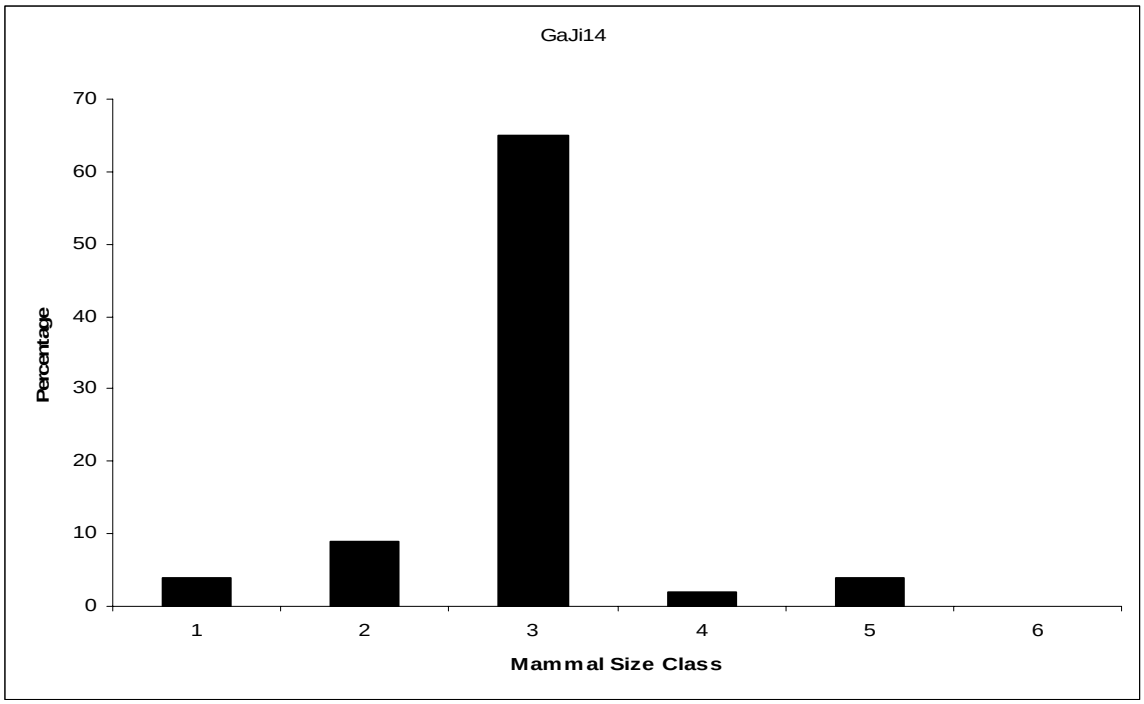
A smaller fraction of the faunal specimens exhibit root etching (1%), suggesting that the fauna generally did not come into contact with roots from plants on a land surface. In a modern study, root etching was most common under salt bushes on upper lake edges (Njau, 2000). This finding supports the idea of rapid burial. Hominin bone surface modifications are discussed below.

C. Zooarchaeological and Taphonomic Analyses

The majority of the specimens from GaJi14 (74%) could not be identified to a specific mammal size class, mainly due to the relatively highly comminuted nature of the

assemblages. However, of those specimens that could be identified to size, size 2 and especially 3 mammals dominate the faunal assemblages at GaJi14 (Figure 6.19, Table 6.26).

Figure 6.19. Frequency distribution of bone specimens identified to mammal size class from GaJi14A and GaJi14B. Mammal size classes were condensed from Table 6.24. Here, Size Class 1 includes 1, 1/2; Size Class 2 includes 2 only; Size Class 3 includes 2/3A, 2/3, 3, 3/4, 3A, 3B, and 3B/4; Size Class 4 includes 4, 4/5; Size Class 5 includes 5, 5/6. Using these divisions means that some of the specimens (those that could not be identified to these size classes) from Table 6.24 were not included in this figure. This excluded proportion is 16% of the specimens originally identified to specimen size at GaJi14. Data from Table 6.26.



Age profiles were not constructed because the assemblages consist of mostly fragmentary specimens. However, of the 44 mammalian bones and complete teeth from GaJi14 which could be identified to a relative age (sub-adult or adult) based on epiphyseal fusion or tooth size and features, 31 (70%) were adult and 13 (30%) were sub-adult. The number of adult specimens is likely vastly underestimated.

Table 6.26. Distribution of bone and tooth specimens from GaJi14 into mammal size classes. Total (N) and percentage of NISP of those specimens identifiable to size class are given. Number and percentage of total NISP of specimens of indeterminate size are at the bottom of the table.

Mammal Size Class	NISP	% NISP
1	5	1
1/2	15	3
2	44	9
2/3A	29	6
≥2	20	4
2/3	35	7
3	155	32
3/4	75	15
3A	14	3
3B	11	2
≤3	1	0.2
≥3	27	6
≥3A	0	0
≥3B	2	0.4
3B/4	14	3
4	11	2
4/5	1	0.2
≥4	11	2
5	18	4
5/6	1	0.2
6	0	0
TOTAL	**490**	
Indeterminate size	1371	74

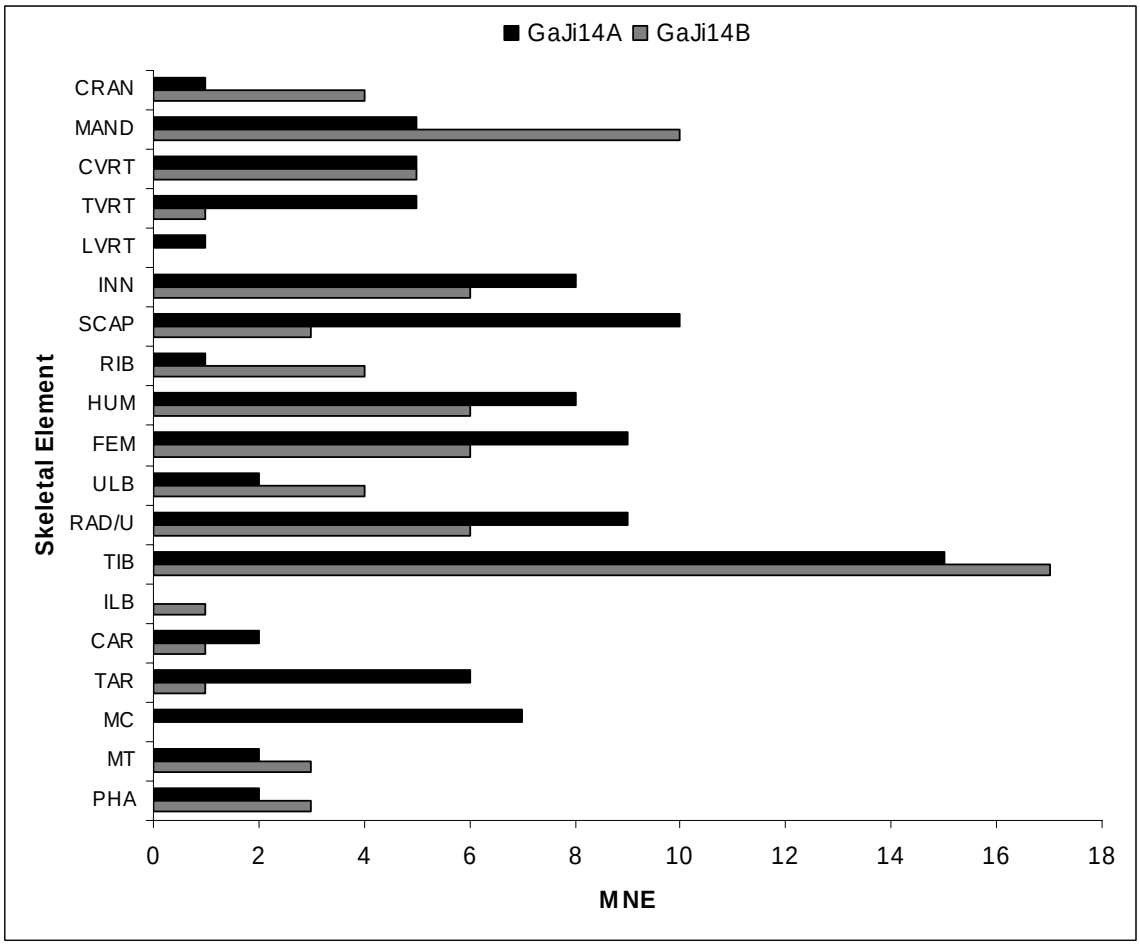
I did not calculate MNE or MNI for non-mammals, as most of these specimens included crocodile teeth, small pieces of fish crania or vertebrae, and turtle/tortoise plastron fragments. The NISP of non-mammals from GaJi14 (N = 224) is listed in Table 6.27.

Table 6.27. NISP of non-mammal specimens from GaJi14.

Taxon	NISP
Fish	183
Crocodile	29
Turtle/Tortoise	12
TOTAL	**224**

MNE and NISP data for bones from GaJi14A and GaJi14B identifiable to skeletal element and taxonomic level lower than mammal are presented in Table 6.26 and Figure 6.20. Initial analysis was conducted with the two assemblages separately, and post-hoc joining of these data sets is not possible without re-analysis of the actual specimens. Excluding teeth and those specimens identified to the MNE level that could possibly conjoin with others (including specimens only identifiable to 'axial'; long bones and upper, intermediate, or lower long bones which could be the same elements as other

Figure 6.20. Skeletal part profile (based on Minimum Number of Elements) for GaJi14A and GaJi14B. See Figure 6.13 caption for more details. As the initial analysis was done separating GaJi14A and GaJi14B, that is how the data are presented here. Data from Table 6.28.



bones identifiable to specific long bones; metapodials, which could be the same specimens as metacarpals or metatarsals), there are 108 elements from GaJi14A and 82 elements from GaJi14B. At both GaJi14A and GaJi14B, there are slightly more appendicular elements than axial elements, and compact bones are underrepresented (Figure 6.21). However, the rib MNE count is likely an underestimation (see Methods), so there may be a higher number of axial specimens at both sites. Excluding patellae, using either NISP or MNE, there are relatively similar numbers of forelimbs and hindlimbs at GaJi14A (Figure 6.22); using NISP there are slightly more hindlimbs, but using MNE there are slightly more forelimbs. At GaJi14B, though, forelimbs are dominant over hindlimbs using either NISP or MNE.

Figure 6.21. MNE at GaJi14A and GaJi14B stratified by skeletal element category: axial, appendicular, and compact. See Figure 6.14 caption for more details. As the initial analysis was done separating GaJi14A and GaJi14B, that is how the data are presented here. Data from Table 6.28.

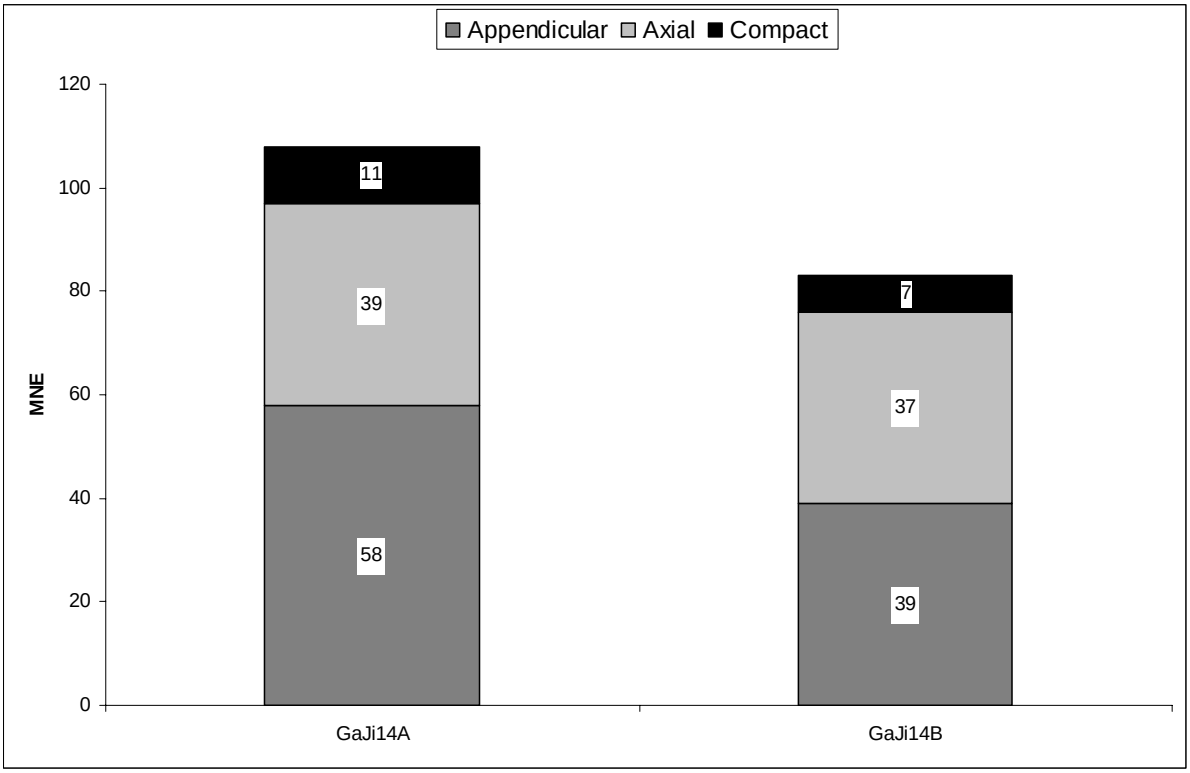
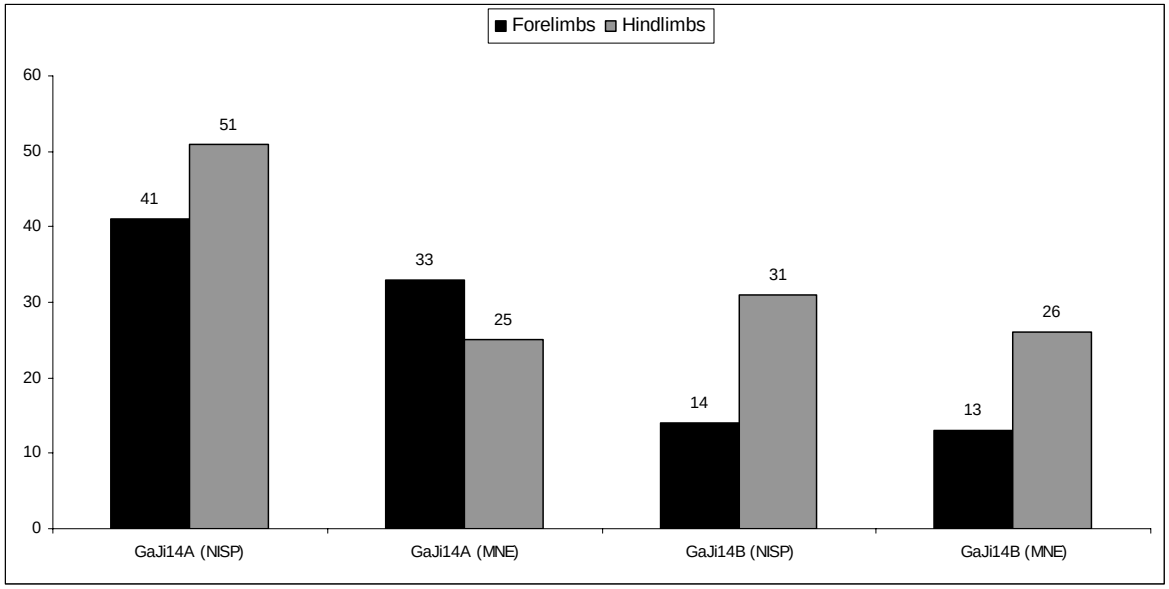


Figure 6.22. Comparison of forelimb and hindlimb NISP and MNE from GaJi14A and GaJi14B. See Figure 6.15 caption for more details. As the initial analysis was done separating GaJi14A and GaJi14B, that is how the data are presented here. Data from Table 6.28.



Limb shafts vastly outnumber epiphyseal and near-epiphyseal specimens by an order of magnitude at GaJi14A and GaJi14B (Tables 6.28, 6.29). Differential counts of limb categories (upper, intermediate, and lower) are the same both GaJi14A and GaJi14B regardless of whether NISP or MNE data are used (Figure 6.23). The order of relative abundance at both sites is intermediate>upper>lower. At both GaJi14, the long limb bone specimens are dominated by those with incomplete circumferences (Figure 6.24). This again attests to the highly comminuted nature of the bone assemblage, especially the long limb bones.

Table 6.28. NISP and MNE for each skeletal part from GaJi14A and GaJi14B. See Appendix 3 for definitions of skeletal element abbreviations. Since the initial analysis was done separating GaJi14A and GaJi14B, that is how the data are presented here.

	GaJi14A		GaJi14B	
Skeletal Part	NISP	MNE	NISP	MNE
TTH[1]	43	9	37	14
MAND	6	5	12	10
MAX	1	1	5	4
CRAN	2	1	5	3
HC	0	0	0	0
HYO	0	0	0	0
AX	0	0	1	1
CLAV	1	1	0	0
RIB[2]	58	1	44	4
VRT[3]	16	n/a	8	n/a
C-1	0	0	0	0
C-2	0	0	0	0
CVRT	6	5	5	5
TVRT	6	5	2	1
LVRT	1	1	0	0
SACR	0	0	0	0
CAUD	1	1	1	1
INN	8	8	6	6
SCAP	10	10	3	3
LB[3]	43	n/a	60	n/a
ULB	6	2	4	4
HUM	11	8	7	6
FEM	20	9	8	6
ILB	0	0	1	1
PAT	0	0	0	0
RADU	1	1	1	1
RAD	14	8	5	5
ULN	8	8	1	1
TIB	24	15	20	17
FIB	1	1	0	0
CARP	2	2	1	1
TARS	0	0	0	0
CALC	2	2	1	1
AST	3	3	0	0
NAVC	1	1	0	0
LLB (MP)	11	8	11	8
MT	2	2	3	3
MC	7	7	0	0
PHA	0	0	0	0
PHA1	2	2	3	2
PHA2	0	0	1	1
PHA3	0	0	0	0
SES	0	0	1	1

[1]Only complete teeth or a single "tooth" instance for each taxon were used to calculate tooth MNE, therefore this number is likely to be an underestimation.

[2] RIB MNE was calculated using those specimens with articular ends (heads) only, and is therefore likely an underestimation.

[3]LB refers to long bone shafts only, therefore MNE was not calculated for this category. VRT is also too vague a category to calculate an MNE.

Table 6.29. Analyses of limb portions and epiphysis: shaft ratios from GaJi14. See Table 6.17 caption for more details.

	GaJi14A				
Carcass Size	1&2	3&4	5&6	unsized	total
CO	0	1	0	0	1
EPI	3	5	1	0	9
EPI+NEF	0	7	1	0	8
EPI+NEF+SH	1	17	0	0	18
SH	16	139	0	7	162
SH+NEF	8	12	0	0	20
NEF	0	3	1	0	4
EPI:SH ratio	**0.14**	**0.17**	**2.0**	**0**	**0.17**

Figure 6.23. Limb bones from GaJi14A and GaJi14B stratified by limb bone category. See Figure 6.16 caption for more details. As the initial analysis was done separating GaJi14A and GaJi14B, that is how the data are presented here. Data from Table 6.28.

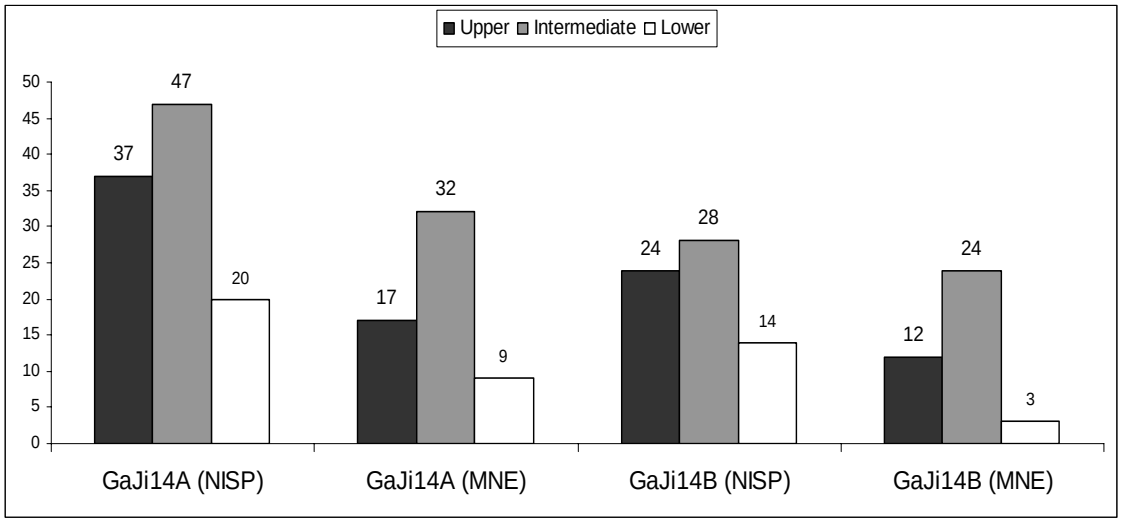
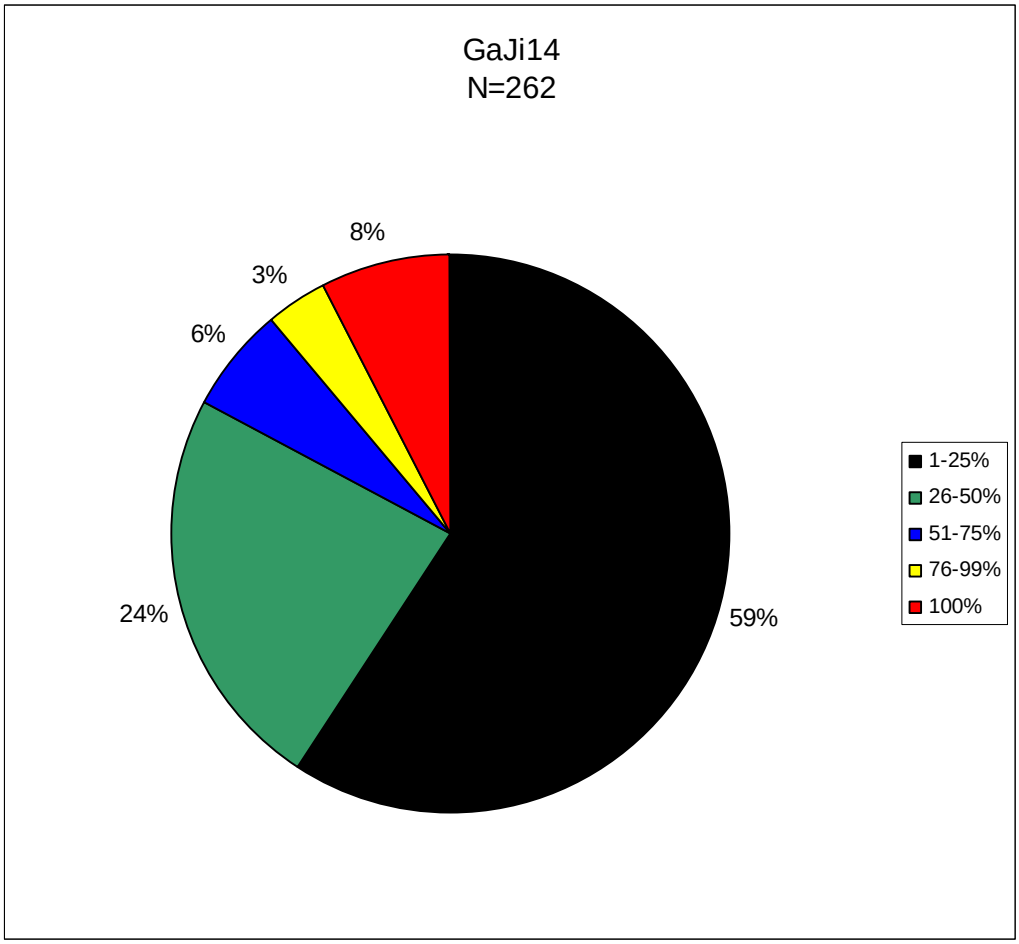


Figure 6.24. Long bone circumference distribution at GaJi14. See Figure 6.17 caption for more details.



Hominin and Carnivore Taphonomy: FwJj14A, FwJj14B, and GaJi14

One of the most remarkable taphonomic features of the archaeofaunas from FwJj14A, FwJj14B, and GaJi14 is the relatively high number of hominin-modified bones present at both of these sites. The detailed data collected on these specimens related to hominin and carnivore modification are presented in Appendices 6a-6d.

A total of 147 of the 1653 mammal bones (9%) from FwJj14A have hominin bone surface modifications. 140 of these have high bone surface readability (>75%; Table 6.12). 124 bones from FwJj14A are cut-marked only, 17 are percussion-marked only, and 2 are both cut and percussion-marked. From FwJj14B the number of hominin-modified

bones is 74/1713 (5%); 69 have high bone surface readability (Table 6.12). 63 are cut-marked only, 5 are percussion-marked only, and 5 are both cut- and percussion-marked. From GaJi14, 92 of 1659 mammal bones are hominin-modified (6%); 83 of these have high bone surface readability (Table 6.24). 86 are cut-marked only, 13 are percussion-marked only, and 4 are both cut and percussion-marked. Hominin-induced bone surface modifications (cut and percussion marks) are hereafter called "butchery marks" when referred to together. The butchery marks at these three sites are found on a variety of skeletal elements from different sized mammals (Tables 6.30, 6.31, 6.32).

Table 6.30. Skeletal distribution of butchery-marked mammal bones from FwJj14A by skeletal element and skeletal group. Numbers are NISP. Bones originally classified as 2/3 or 2/3A are placed into size category 3&4 here. Bones originally classified as ≤ or ≥ any size class are placed into the indeterminate (indet.) size category here. Cells contain: number of cut-marked (CM) or percussion-marked (PM) bones at FwJj14A&B/ total number of specimens in each category (percentage cut- or percussion-marked). Where cells are blank, no bones were found. The far right "Total" column refers to total number of hominin modified (HM) bones. This number can be lower than the total of modified bones in each row, as some bones exhibit both cut and percussion marks on the same specimen. Here, CVRT includes C-1 and C-2; CRAN includes MAX; RAD/U includes radius and radio-ulna; PHA includes PHA, PHA1, PHA2, PHA3. See Appendix 3 for skeletal abbreviations.

Skeletal Element	Size 1&2		Size 3&4		Size 5&6		Indet. Size		***Total***
	CM	PM	CM	PM	CM	PM	CM	PM	***HM***
Axial (Subtotal)	**3/29 (10%)**	**0/29 (0%)**	**15/88 (17%)**	**0/88 (0%)**	**2/5 (40%)**	**0/5 (0%)**	**4/88 (5%)**	**1/88 (1%)**	**25/210 (11%)**
MAND	0/2 (0%)	0/2 (0%)	2/7 (29%)	0/7 (0%)			1/8 (13%)	0/8 (0%)	**2/17 (12%)**
CRAN			1/3 (33%)	0/3 (0%)			0/13 (0%)	0/13 (0%)	**1/16 (6%)**
HYO	0/1 (0%)	0/1 (0%)							**0/1 (0%)**
RIB	1/18 (6%)	0/18 (0%)	3/45 (7%)	0/45 (0%)	0/2 (0%)	0/2 (0%)	3/42 (15%)	1/42 (2%)	**8/107 (7%)**
VRT	1/2 (50%)	0/2 (0%)	0/5 (0%)	0/5 (0%)	0/1 (0%)	0/1 (0%)	0/16 (0%)	0/16 (0%)	**1/24 (4%)**
CVRT	0/1 (0%)	0/1 (0%)	2/8 (25%)	0/8 (0%)	2/2 (100%)	0/2 (0%)	0/3 (0%)	0/3 (0%)	**4/14 (29%)**
TVRT	0/1 (0%)	0/1 (0%)	0/7 (0%)	0/7 (0%)					**0/8 (0%)**
LVRT			3/5 (60%)	0/5 (0%)					**3/5 (60%)**

SACR									**0/0 (0%)**
CAUD									**0/0 (0%)**
INN	1/3 (33%)	0/3 (0%)	4/8 (50%)	0/8 (50%)			0/4 (0%)	0/4 (0%)	**5/15 (33%)**
SCAP	0/1 (0%)	0/1 (0%)					0/2 (0%)	0/2 (0%)	**0/3 (0%)**
Appendicular (subtotal)	**4/33 (12%)**	**0/33 (0%)**	**52/298 (17%)**	**12/298 (4%)**	**0/4 (0%)**	**0/4 (0%)**	**3/50 (6%)**	**0/50 (0%)**	**69/385 (18%)**
LB	3/20 (15%)	0/20 (0%)	29/199 (15%)	8/199 (4%)	0/1 (0%)	0/1 (0%)	2/41 (5%)	0/41 (0%)	**42/261 (16%)**
ULB			1/5 (20%)	1/5 (20%)			0/1 (0%)	0/1 (0%)	**1/6 (16%)**
HUM	0/2 (0%)	0/2 (0%)	2/13 (15%)	1/13 (8%)	0/1 (0%)	0/1 (0%)	0/2 (0%)	0/2 (0%)	**3/18 (17%)**
FEM	1/3 (33%)	0/3 (0%)	2/7 (29%)	1/7 (14%)	0/2 (0%)	0/2 (0%)	0/1 (0%)	0/1 (0%)	**4/13 (31%)**
ILB									**0/0 (0%)**
RAD/U	0/1 (0%)	0/1 (0%)	4/12 (20%)	0/ (0%)			0/1 (0%)	0/1 (0%)	**4/14 (29%)**
ULN	0/1 (0%)	0/1 (0%)	4/8 (50%)	0/8 (0%)			0/1 (0%)	0/1 (0%)	**4/10 (40%)**
TIB	0/1 (0%)	0/1 (0%)	7/31 (23%)	1/31 (3%)			0/2 (0%)	0/2 (0%)	**7/34 (21%)**
LLB (MP)	0/4 (0%)	0/4 (0%)	1/16 (6%)	0/16 (0%)			1/1 (100%)	0/1 (0%)	**2/21 (10%)**
MT			1/3 (33%)	0/3 (0%)					**1/3 (33%)**
MC	0/1 (0%)	0/1 (0%)	1/4 (25%)	0/4 (0%)					**1/5 (20%)**
Compact (subtotal)	**0/6 (0%)**	**0/6 (0%)**	**2/10 (20%)**	**0/10 (0%)**	**0/0 (0%)**	**0/0 (0%)**	**0/0 (0%)**	**0/0 (0%)**	**2/16 (13%)**
PAT			1/1 (100%)	0/1 (0%)					**1/1 (100%)**
CARP	0/1 (0%)	0/1 (0%)	0/2 (0%)	0/2 (0%)					**0/3 (0%)**
TARS			0/1 (0%)	0/1 (0%)					**0/1 (0%)**
CALC	0/2 (0%)	0/2 (0%)							**0/2 (0%)**
AST	0/2 (0%)	0/2 (0%)	1/3 (33%)	0/3 (0%)					**1/5 (20%)**
NAVC									**0/0 (0%)**
PHA			0/3 (0%)	0/3 (0%)					**0/3 (0%)**
SES	0/1 (0%)	0/1 (0%)							**0/1 (0%)**
NID (subtotal)	**0/0 (0%)**	**0/0 (0%)**	**0/0 (0%)**	**0/0 (0%)**	**0/5 (0%)**	**0/5 (0%)**	**47/1053 (4%)**	**5/1053 (0.5%)**	**51/1058 (5%)**
Total (CM, PM)	**7/68 (10%)**	**0/68 (0%)**	**69/396 (17%)**	**12/396 (3%)**	**2/14 (14%)**	**0/14 (0%)**	**54/1191 (5%)**	**6/1191 (0.5%)**	

Total (all BM bones)	**7/68 (10%)**	**80/396 (20%)**	**2/14 (14%)**	**59/1191 (5%)**	**147/1653 (9%)**

Note: One fish bone from FwJj14A (1/71, 1% of all fish bones), a spine, is cut-marked.

Table 6.31. Skeletal distribution of butchery-marked mammal bones from FwJj14B by skeletal element and skeletal group. See Table 6.30 caption for more details.

Skeletal Element	Size 1&2		Size 3&4		Size 5&6		Indet. Size		***Total***
	CM	PM	CM	PM	CM	PM	CM	PM	***HM***
Axial (Subtotal)	**0/15 (0%)**	**0/15 (0%)**	**12/49 (21%)**	**0/49 (0%)**	**0/5 (0%)**	**0/5 (0%)**	**7/38 (17%)**	**1/38 (2%)**	**17/106 (16%)**
MAND	0/1 (0%)	0/1 (0%)	2/4 (50%)	0/4 (0%)			0/2 (0%)	0/2 (0%)	**2/7 (29%)**
CRAN			0/2 (0%)	0/2 (0%)	0/1 (0%)	0/1 (0%)	1/15 (6%)	0/15 (0%)	**1/18 (6%)**
HYO	0/1 (0%)	0/1 (0%)	3/3 (66%)	3/3 (0%)					**3/4 (75%)**
RIB	0/9 (0%)	0/9 (0%)	2/27 (7%)	0/27 (0%)	0/3 (0%)	0/3 (0%)	6/18 (33%)	1/18 (6%)	**8/57 (14%)**
VRT			0/3 (0%)	0/3 (0%)	0/1 (0%)	0/1 (0%)	0/2 (0%)	0/2 (0%)	**0/6 (0%)**
CVRT	0/1 (0%)	0/1 (0%)	2/8 (25%)	0/8 (0%)	2/2 (100%)	0/2 (0%)	0/1 (0%)	0/1 (0%)	**0/1 (0%)**
TVRT	0/1 (0%)	0/1 (0%)	2/3 (66%)	0/3 (0%)					**2/4 (50%)**
LVRT			0/2 (0%)	0/2 (0%)					**0/2 (0%)**
SACR	0/1 (0%)	0/1 (0%)							**0/1 (0%)**
CAUD									**0/0 (0%)**
INN			1/5 (20%)	0/5 (0%)					**1/5 (20%)**
SCAP	0/1 (0%)	0/1 (0%)							**0/1 (0%)**
Appendicular (subtotal)	**7/19 (37%)**	**2/19 (11%)**	**25/120 (21%)**	**6/120 (5%)**	**0/0 (0%)**	**0/0 (0%)**	**1/14 (7%)**	**0/14 (0%)**	**37/154 (24%)**
LB	2/7 (29%)	0/7 (0%)	9/56 (18%)	1/56 (2%)			1/10 (10%)	0/10 (10%)	**12/73 (16%)**
ULB			3/11 (27%)	0/11 (0%)					**3/11 (27%)**
HUM	1/3 (33%)	1/3 (33%)	2/12 (17%)	1/12 (8%)			0/2 (0%)	0/2 (0%)	**4/17 (24%)**
FEM	0/1 (0%)	1/1 (100%)	1/5 (20%)	1/5 (20%)					**2/6 (33%)**
ILB									**0/0 (0%)**
RAD/U	1/2 (50%)	0/2 (0%)	2/8 (20%)	0/8 (0%)					**3/10 (30%)**
ULN	2/2 (100%)	0/2 (0%)	1/3 (33%)	0/3 (0%)			0/1 (0%)	0/1 (0%)	**3/6 (50%)**
TIB			2/7 (29%)	1/7 (14%)			0/1 (0%)	0/1 (0%)	**2/8 (25%)**
LLB (MP)	0/2	0/2	1/10	1/10					**2/13**

	(0%)	(0%)	(10%)	(10%)					**(23%)**
MT			2/6 (33%)	0/6 (0%)					**2/6 (33%)**
MC	1/2 (50%)	0/2 (0%)	2/2 (100%)	1/2 (50%)					**3/4 (75%)**
Compact (subtotal)	**1/3 (33%)**	**0/3 (0%)**	**0/8 (0%)**	**0/8 (0%)**	**0/0 (0%)**	**0/0 (0%)**	**0/1 (0%)**	**0/1 (0%)**	**1/12 (8%)**
PAT									**0/0 (0%)**
CARP	1/2 (50%)	0/2 (0%)	0/2 (0%)	0/2 (0%)			0/1 (100%)	0/1 (0%)	**1/5 (20%)**
TARS			0/1 (0%)	0/1 (0%)					**0/1 (0%)**
CALC	0/1 (0%)	0/1 (0%)							**0/1 (0%)**
AST									**0/0 (0%)**
NAVC									**0/0 (0%)**
PHA			0/5 (0%)	0/5 (0%)					**0/5 (0%)**
SES									**0/0 (0%)**
NID (subtotal)			**1/1 (100%)**	**0/1 (0%)**	**0/1 (0%)**	**0/1 (0%)**	**17/1425 (1%)**	**1/1425 (<0.1%)**	**19/1427 (1%)**
Total (CM, PM)	**8/37 (24%)**	**2/37 (5%)**	**37/178 (21%)**	**6/178 (3%)**	**0/6 (25%)**	**0/6 (0%)**	**25/1478 (2%)**	**3/1478 (0.2%)**	
Total (all BM bones)		**9/37 (27%)**		**40/178 (22%)**		**0/6 (0%)**		**28/1478 (2%)**	**74/1713 (5%)**

Table 6.32. Skeletal distribution of butchery-marked mammal bones from GaJi14 by skeletal element and skeletal group. See Table 6.30 caption for more details.

Skeletal Element	Size 1&2		Size 3&4		Size 5&6		Indet. Size		***Total***
	CM	PM	CM	PM	CM	PM	CM	PM	***HM***
Axial (Subtotal)	**3/24 (13%)**	**0/24 (0%)**	**14/88 (16%)**	**0/88 (16%)**	**1/7 (14%)**	**0/7 (0%)**	**10/62 (16%)**	**0/62 (0%)**	**28/181 (15%)**
MAND	2/6 (33%)	0/6 (0%)	0/8 (0%)	0/8 (0%)	0/2 (0%)	0/2 (0%)	0/2 (0%)	0/2 (0%)	**2/18 (11%)**
CRAN	0/2 (0%)	0/2 (0%)	0/3 (0%)	0/3 (0%)	0/1 (0%)	0/1 (0%)	1/8 (13%)	0/8 (0%)	**1/34 (3%)**
HYO									**0/0 (0%)**
RIB	0/13 (0%)	0/13 (0%)	9/44 (20%)	0/44 (0%)	0/1 (0%)	0/1 (0%)	6/32 (19%)	0/32 (0%)	**15/90 (17%)**
VRT					0/1 (0%)	0/1 (0%)	0/9 (0%)	0/9 (0%)	**0/10 (0%)**
CVRT	0/1 (0%)	0/1 (0%)	0/7 (0%)	0/7 (0%)	0/1 (0%)	0/1 (0%)	0/2 (0%)	0/2 (0%)	**0/11 (0%)**
TVRT			1/6 (17%)	0/6 (0%)			1/2 (50%)	0/2 (0%)	**2/8 (25%)**
LVRT			0/1 (0%)	0/1 (0%)					**0/1 (0%)**

SACR									**(0/0) (0%)**
CAUD							0/2 (0%)	0/2 (0%)	**0/0 (0%)**
INN	1/2 (50%_	0/2 (0%)	2/9 (22%)	0/9 (0%)	1/1 (100%)	0/1 (0%)	0/2 (0%)	0/2 (0%)	**4/14 (29%)**
SCAP			2/10 (20%)	0/10 (0%)			2/3 (66%)	0/3 (0%)	**4/13 (31%)**
Appendicular (subtotal)	**5/25 (20%)**	**1/25 (4%)**	**38/232 (16%)**	**6/232 (3%)**	**0/2 (0%)**	**0/2 (0%)**	**4/21 (19%)**	**1/21 (5%)**	**49/280 (18%)**
LB	2/7 (29%)	0/7 (0%)	11/87 (13%)	1/87 (1%)			3/19 (16%)	1/19 (5%)	**16/113 (14%)**
ULB	0/2 (0%)	0/2 (0%)	3/8 (38%)	0/8 (0%)					**3/10 (30%)**
HUM	0/3 (0%)	1/3 (33%)	4/16 (25%)	1/16 (6%)					**6/19 (32%)**
FEM	0/2 (0%)	0/2 (0%)	3/24 (17%)	0/24 (0%)	0/1 (0%)	0/1 (0%)	1/1 (100%)	0/1 (0%)	**4/28 (14%)**
ILB			0/1 (0%)	0/1 (0%)					**0/1 (0%)**
RAD/U	1/2 (50%)	0/2 (0%)	2/19 (11%)	1/19 (5%)					**3/21 (14%)**
ULN	0/1 (0%)	0/1 (0%)	1/8 (13%)	0/8 (0%)					**1/9 (11%)**
TIB	1/5 (20%)	0/5 (0%)	5/37 (14%)	1/37 (3%)	0/1 (0%)	0/1 (0%)	0/1 (0%)	0/1 (0%)	**6/44 (14%)**
FIB*	1/1 (100%)	0/1 (0%)							**1/1 (100%)**
LLB (MP)	0/1 (0%)	0/1 (0%)	4/21 (19%)	2/21 (10%)					**4/22 (18%)**
MT	0/1 (0%)	0/1 (0%)	1/4 (25%)	0/4 (0%)					**1/5 (20%)**
MC			4/7 (57%)	0/7 (0%)					**4/7 (57%)**
Compact (subtotal)	**0/2 (0%)**	**0/2 (0%)**	**3/23 (13%)**	**0/23 (0%)**	**0/2 (0%)**	**0/2 (0%)**			**3/27 (11%)**
PAT									**0/0 (0%)**
CARP			0/1 (0%)	0/1 (0%)	0/2 (0%)	0/2 (0%)			**0/3 (0%)**
TARS									**0/0 (0%)**
CALC	0/1 (0%)	0/1 (0%)	1/2 (50%)	0/2 (0%)					**1/3 (33%)**
AST	0/1 (0%)	0/1 (0%)	0/2 (0%)	0/2 (0%)					**0/3 (0%)**
NAVC			1/1 (100%)	0/1 (0%)					**1/1 (100%)**
PHA			1/6 (17%)	0/6 (0%)					**1/6 (17%)**
SES			0/1 (0%)	0/1 (0%)					**0/1 (0%)**
NID (subtotal)			**1/4 (25%)**	**0/4 (0%)**			**11/1167 (1%)**	**3/1167 (0.3%)**	**15/1171 (1%)**

Total (CM, PM)	**7/51 (14%)**	**1/51 (2%)**	**57/347 (16%)**	**6/347 (2%)**	**1/11 (9%)**	**0/11 (0%)**	**25/1250 (2%)**	**4/1250 (0.3%)**	
Total (all BM bones)		**8/51 (16%)**		**59/347 (17%)**		**1/11 (9%)**		**29/1250 (2%)**	**92/1659 (6%)**

*This cut-marked fibula is a long bone, not a compact bone.
Note: Two fish bones are cut-marked, one spine and one NID bone, 2/176 or 1%.

The proportion of butchered bones in each size class category (size 1 and 2 - small, size 3 and 4 - medium, size 5 and 6 - large) is not statistically significant at any of the three sites (Table 6.33). However, this does not mean that different sized carcasses are being butchered in the same way. In both actualistic (Pobiner and Braun, 2005) and archaeological (Lyman, 1992; Milo, 1998) studies, larger carcasses display higher frequencies of cut-marked bones than smaller carcasses. It follows that if hominins were butchering small and medium mammals in the same manner, we might expect to find a higher frequency of cut marks on the medium size mammals. Since this is not the case at these Okote sites, where there are similar frequencies of cut marks on small and medium sized mammals, hominins at these sites may have been butchering medium sized mammals less intensively than small mammals.

Table 6.33. Results of chi-square analyses on the proportion of butchered bones in each size class category (size 1 and 2, size 3 and 4, size 5 and 6) from FwJj14A, FwJj14B, and GaJi14. P-values are rounded to two decimal places.

Site	chi-square	d.f.	p-value
FwJj14A	2.48	4	0.29
FwJj14B	1.64	4	0.44
GaJi14	0.63	4	0.73

The paucity of butchery marks on the largest mammals, size 5 and 6, is likely related to the paucity of bones from these animals in the assemblage. However, it is not known if this is due to a preference for hominins for small and medium size mammals, or a lower relative abundance of these larger mammals available to hominins for butchery.

Differences in cut mark frequencies could also relate to different raw materials being used to butcher different sized mammals (Dewbury and Russell, 2006), but as there are no stone tools from these sites, this hypothesis might be testable if micro-fragments of tools inside cut marks were found.

The proportion of butchery marks across skeletal groups (axial, appendicular, and compact) is also statistically similar at all three sites (Table 6.34). One interpretation of this result is that hominins had equivalent access to each of these skeletal groups (cf. Milo, 1998). However, since there is a higher number of axial versus appendicular and compact elements in an ungulate skeleton, this result could be interpreted as indicating that a higher proportion of butchery occurred on limb elements relative to axial elements. Alternatively, carnivores may have deleted (destroyed) some of these less dense axial elements. Capaldo (1995: 117-118), who used metal knives for butchery, found a higher proportion of butchery marks, including cut, scrape, and percussion marks, on bones in my axial category (his CRL, AXL, and APS categories: 42.8%) than long bones (37.1%) in his whole bone to carnivore sample, but not in his hammerstone to carnivore sample (29.6% of axial bones versus 31.7% of long bones were butchery-marked). Butchery marks on compact bones were not recorded in the former sample, but in the latter, they were much lower (3.0%). The results from the Okote sites could support a behavioral interpretation of defleshing and hammerstone breakage followed by carnivore activity,

Table 6.34. Results of chi-square analyses on the proportion of butchered bones in each skeletal group (axial, appendicular, and compact) from FwJj14A, FwJj14B, and GaJi14. P-values are rounded to two decimal places.

Site	chi-square	d.f.	p-value
FwJj14A	3.84	4	0.15
FwJj14B	3.58	4	0.17
GaJi14	0.91	4	0.63

with an overabundance of cut marks on podials, possibly resulting from disarticulation.

The primary consumer of mammal carcasses is assumed to extract nutrients from the meatiest, highest ranked elements first, or at higher proportions, than lower ranked elements. This is true for carnivores (Blumenschine, 1986a), and possibly for modern humans (Binford, 1978), though a multitude of variables conditions modern human butchery strategies. If hominins had early access to carcasses with large amounts of flesh on them, there are two predicted butchery patterns that might have occurred: complete consumption or unbiased butchery strategy, in which skeletal elements or groups are butchered in proportion to their availability; or a gourmet strategy, in which only the higher-yield elements or groups are more frequently butchered (cf. Binford, 1978). If hominins had late access to carcasses with flesh only remaining on the lower ranked elements, a predicted butchery pattern would include disproportionate amounts of cut marks on those lower ranked elements remaining after carnivore consumption (unless flesh scrap removal was occurring on higher ranked elements, obscuring the differential cut mark patterning).

Spearman's rank-order correlation coefficient on size 3 and 4 mammals indicates that there is no correlation between carnivore consumption of skeletal elements and butchery of these skeletal elements or carcass regions by hominins at any of the three sites (Table 6.35). If one assumes that butchery marks will be inflicted on all bones at uniform rates and densities, that subsequent fragmentation of defleshed parts did not differentially distribute butchery marks, and that skeletal parts were not differentially deleted from the assemblage after hominin feeding, this indicates that hominins were practicing an unbiased strategy; they were not butchering different skeletal elements or

carcass parts in the same rank order as carnivores consume those elements. It is therefore possible that hominin butchery strategies of size 3 and 4 mammals may have been based on variables other than relative proportion of meat and marrow extractable from particular skeletal elements, although we cannot know this until the above assumptions have been tested. Alternatively, hominins may have had late access to carcasses which still contained flesh scraps on them; this hypothesis will be explored further below. It is important to note that the data above are based on comparing MNE data for carnivore access to NISP data for cut marks here, which is the only available data on which to base the analysis. The relatively high proportion of cut marks on crania and mandibles, including hyoids, compared with their low rank may indicate either a higher encounter rate of heads, a higher preference for processing heads, a higher survival rate for heads, or more densely distributed cut marking on heads and more thorough fragmentation prior to or after fossilization (e.g., recent break rates). The sample size of size 1 and 2 mammal skeletal elements is too small for comparison.

There are a total of 28 percussion-marked specimens at FwJj14A (Table 6.30). Five of these are non-identifiable specimens, and the rest are limbs. Of the four percussion-marked limbs identifiable to skeletal element or limb class (upper, intermediate, or lower), three are upper limbs (75%) (Table 6.36). At FwJj14B, there are a total of 11 percussion-marked specimens (Table 6.31), 1 of which is a rib and 2 of which are non-identifiable. Of the seven percussion marks on identifiable limb specimens, 4 (57%) are upper limbs (Table 6.37). Assuming that hominins had access to all of the limbs found at FwJj14A and FwJj14B (which is an untested assumption), and that the frequency of percussion marking on bones is strongly and positively correlated

Table 6.35. The relationship between the order of carnivore access to skeletal elements of size 3 and 4 prey and the proportion of butchered specimens of those elements at FwJj14A, FwJj14B, and GaJi14, as measured by Spearman's rank-order correlation coefficient (r_s). Consumption sequence is following Blumenschine 1986a. Numbers in front of parentheses and consumption sequences numbers are ranks. Numbers in parentheses is NISP of cut-marked bones for that skeletal element or carcass region. For carcass regions: Upper Hindlimb includes innominate, femur, lumbar vertebra, and proximal tibia; Upper Forelimb includes thoracic vertebra, ribs, humerus, scapula, cervical vertebra, and proximal radio-ulna; Head includes cranium and mandible; Lower limb includes shaft and distal tibia, shaft and distal radio-ulna, and metapodials.

	Consumption Sequence	FwJj14A	FwJj14B	GaJi14
Skeletal Element				
Innominate	1	2 (33%)	7 (20%)	3 (29%)
Femur	2	3 (31%)	3 (33%)	6 (14%)
Lumbar Vertebra	3	1 (60%)	10 (0%)	10 (0%)
Thoracic Vertebra	4	10 (0%)	1 (50%)	4 (25%)
Ribs	4	8 (7%)	8 (14%)	5 (17%)
Humerus	5	6 (17%)	6 (24%)	1 (32%)
Scapula	6	10 (0%)	10 (0%)	2 (32%)
Cervical Vertebra	7	4 (24%)	10 (0%)	10 (0%)
Tibia	8	5 (21%)	5 (25%)	6 (14%)
Radio-Ulna	9	2 (33%)	2 (38%)	7 (13%)
Hemimandible	10	7 (13%)	4 (29%)	8 (11%)
Cranium	11	9 (6%)	9 (6%)	9 (3%)
(r_s)		0.298	0.007	0.353
p-value		0.347	0.983	0.259
Carcass Region				
Upper Hindlimb	1	1 (36%)	3 (18%)	1 (25%)
Upper Forelimb	2	3 (18%)	2 (23%)	3 (20%)
Head	3	4 (10%)	4 (17%)	4 (7%)
Lower Limbs	4	2 (21%)	1 (33%)	2 (22%)
(r_s)		0.4	0.4	0.4
p-value		0.6	0.6	0.6

With the frequency of hominins breaking these bones to access marrow (also an untested assumption), the dominance of percussion marking on upper limbs indicates that hominins preferentially hammerstone-broke these bones. This supports a hypothesis of access to these carcasses by hominins prior to bone-crunching carnivores, which tend to destroy upper limb bones for marrow before consuming lower limb bones (e.g.

Table 6.36. Distribution and percentage of percussion- and tooth-marked limb shafts from FwJj14A. Numbers in cells are: number of marked specimens/number of specimens in each category (percentage). See Figure 6.16 caption for distribution of limb bones into ULB, ILB, and LLB categories. LB refers to those specimens only identifiable as long bone shafts.

	Size 1 & 2	Size 3 & 4	Size 5 & 6	Size Indet	Total
Percussion-marked					
ULB	0/7 (0%)	3/3 (10%)	0/ (0%)	0/4 (0%)	3/24 (13%)
ILB	0/3 (0%)	1/54 (2%)	0/ (0%)	0/6 (0%)	1/63 (2%)
LLB	0/1 (0%)	0/16 (0%)	0/ (0%)	0/0 (0%)	0/17 (0%)
LB	0/20 (0%)	9/199 (5%)	0/ (0%)	1/39 (3%)	10/259 (4%)
Total	**0/31 (0%)**	**13/299 (4%)**	**0/ (0%)**	**1/49 (2%)**	**14/383 (4%)**
Tooth-marked					
ULB	0/7 (0%)	0/3 (0%)	0/0 (0%)	0/4 (0%)	0/24 (%)
ILB	0/3 (0%)	1/54 (2%)	0/0 (0%)	0/6 (0%)	1/63 (2%)
LLB	0/1 (0%)	0/16 (0%)	0/0 (0%)	0/0 (0%)	0/17 (0%)
LB	1/20 (5%)	2/199 (1%)	0/0 (0%)	0/39 (0%)	3/259 (1%)
Total	**1/31 (3%)**	**3/299 (1%)**	**0/0 (0%)**	**0/0 (0%)**	**4/383 (1%)**

Table 6.37. Distribution and percentage of percussion-marked limb shafts from FwJj14B. There were no tooth-marked specimens from FwJj14B. See Table 6.34 caption for more details.

	Size 1 & 2	Size 3 & 4	Size 5 & 6	Size Indet	Total
Percussion Marks					
ULB	2/5 (40%)	2/19 (11%)	0/0 (0%)	0/2 (0%)	4/26 (15%)
ILB	0/2 (0%)	1/19 (5%)	0/0 (0%)	0/1 (0%)	1/22 (5%)
LLB	0/5 (0%)	2/26 (8%)	0/0 (0%)	0/0 (0%)	2/31 (6%)
LB	0/7 (0%)	1/55 (2%)	0/0 (0%)	0/10 (0%)	1/72 (1%)
Total	**2/19 (11%)**	**6/119 (4%)**	**0/0 (0%)**	**0/13 (0%)**	**8/151 (5%)**

Table 6.38. Distribution and percentage of percussion-marked limb shafts from GaJi14. There were no tooth-marked limb specimens from GaJi14. See Table 6.36 caption for more details.

	Size 1 & 2	Size 3 & 4	Size 5 & 6	Total
Percussion Marks				
ULB	0/4 (0%)	0/43 (0%)	0/0 (0%)	0/47 (0%)
ILB	0/6 (0%)	3/51 (6%)	0/0 (0%)	3/57 (5%)
LLB	0/1 (0%)	1/28 (4%)	0/0 (0%)	1/29 (3%)
LB*	0/6 (0%)	1/65 (2%)	0/0 (0%)	1/71 (1%)
Total	**0/17 (0%)**	**5/187 (3%)**	**0/0 (0%)**	**5/204 (2%)**

Blumenschine, 1986a). While percussion mark frequencies indicate that hominins were not preferentially exploiting the highest yielding marrow bones, including the tibia and femur (Blumenschine and Madrigal, 1993), percussion mark sample sizes are likely too small to decipher any differences in inter-bone mark frequencies.

At GaJi14, a total of 8 bones are percussion-marked, 5 limbs and 3 non-identifiable specimens (Table 6.32). Here, however, there is a different pattern. None of the four percussion-marked limbs identifiable to skeletal element or limb class are upper limbs (Table 6.38). Here, then, hominins were apparently processing upper limb bones for marrow at a lower rate, if at all, than lower limb bones. The order of the relative amount of marrow in different ungulate limbs varies between taxa (Blumenschine and Madrigal, 1993), but the upper and intermediate limbs consistently contain more marrow than lower limbs. Unfortunately, the sample size of percussion-marked bone is too small for statistical analysis. Regardless, the presence of percussion marks on lower limb bones from FwJj14B and GaJi14 indicates that at these sites, hominins were breaking open less attractive bones in terms of marrow yields. Alternatively, hominins may be preferentially fragmenting lower limbs of juveniles, which contain more marrow than their upper limbs (Blumenschine and Madrigal, 1993). This is not due to a predominance of lower limbs at these sites; at FwJj14B, lower limbs make up 39% of the total limb NISP, and at GaJi14, they are 29%. However, at FwJj14A, only 13% of the total limb sample is lower limbs, which may account for the absence of percussion-marked limbs at this site.

The limb bones from all of the sites are usually fragmented. Assuming that a lack of carnivore tooth marks on all of the limb bones (except one) means that hominins were responsible for all limb bone breakage, rank order of fragmentation of long bones

(measured by NISP:MNE) can be compared with rank order of marrow wet weight to investigate if hominins preferentially fragmented long bones with the highest marrow yields (Table 6.39). This comparison shows that at FwJj14A, GaJi14A, and GaJi14B, hominins (*if* they were the agents of breakage) generally broke open limb bones according to their rank order of marrow yield.

Table 6.39. The relationship between the fragmentation of long bones at FwJj14A, FwJj14B, and GaJi14 and marrow wet weight of adult wildebeest long bones, as measured by Spearman's rank-order correlation coefficient (r_s). Rank Order is rank order of marrow wet weight. Wildebeest marrow wet weight rank was derived from data in Blumenschine and Madrigal (1993: 566). For the archaeological sites, the first number in the cell is the fragmentation rank order, followed by the NISP/MNE after the comma. The number in the parentheses is the actual NISP/actual MNE. r_s and p have been rounded to two decimal places.

		Fragmentation Rank Order, Value (NISP/MNE)			
Limb Bone	Rank Order	FwJj14A	FwJj14B	GaJi14A	GaJi14B
Tibia	1	1.5, 2.00 (34/17)	2, 1.60 (8/5)	2, 1.60 (24/15)	2, 1.18 (20/17)
Femur	2	1.5, 2.00 (14/7)	4, 1.20 (6/5)	1, 2.22 (20/9)	1, 1.30 (8/6)
Radius	3	3, 1.92 (25/13)	5, 1.08 (14/13)	4, 1.35 (23/17)	4.5, 1.00 (7.7)
Humerus	4	4, 1.63 (18/11)	1, 2.13 (17/8)	3, 1.38 (11/8)	3, 1.17 (7/6)
Metacarpal	5	5.5, 1.00 (5/5)	3, 1.30 (4/3)	5.5, 1.00 (7/7)	none present
Metatarsal	6	3.3, 1.00 (3/3)	6, 1.00 (6/6)	5.5, 1.00 (2/2)	4.5, 1.00 (3.3)
(r_s)		0.81	0.37	0.87	0.75
p-value		0.05	0.47	0.02	0.08

There are three tooth-marked specimens from FwJj14A, and none from FwJj14B. One tooth-marked specimen is a larger mammal (size 3B/4) long bone midshaft, with no butchery marks present. The other two tooth-marked specimens, a size 3 tibia midshaft (# 1024-97) and a size 3 long bone midshaft (# 1208), also have cut marks. On the tibia, the marks do not intersect or overlap, so a sequence of hominin and carnivore access cannot be determined directly from modifications (Figure 6.25). However, the fact that the bone has carnivore tooth marks in multiple places, near the edges of the bone in more than one place, leads to the conclusion that carnivores fragmented the bone. Whether this took

place before or after the hominins removed meat, leaving cut marks, is impossible to determine but it likely occurred afterward. On the long bone midshaft, however, the tooth mark is overlying the cut marks, demonstrating that the hominin butchery took place before the carnivores accessed the bone (Figure 6.26). The only tooth-marked specimen from GaJi14 is a size 3 bovid calcaneum, with tooth marks that could be attributed to crocodiles (cf. Njau and Blumenschine, 2006, Figure 6.27). This bone also has cut marks on it. The sequence of access of hominins and carnivores, or crocodiles, is ambiguous, though it is likely that post-crocodile hominin access was not a common occurrence.

Figure 6.25. Specimen number 1024-97 from FwJj14A, a cut- and tooth-marked size 3 bovid left tibia proximal shaft and midshaft. The photograph is of the lateral side, with the proximal end to the right, and the distal end to the left. The cut marks, on the top, are circled in blue, and the tooth mark, on the bottom, is circled in shown in red. Close up photos of the cut and tooth marks are on the right.

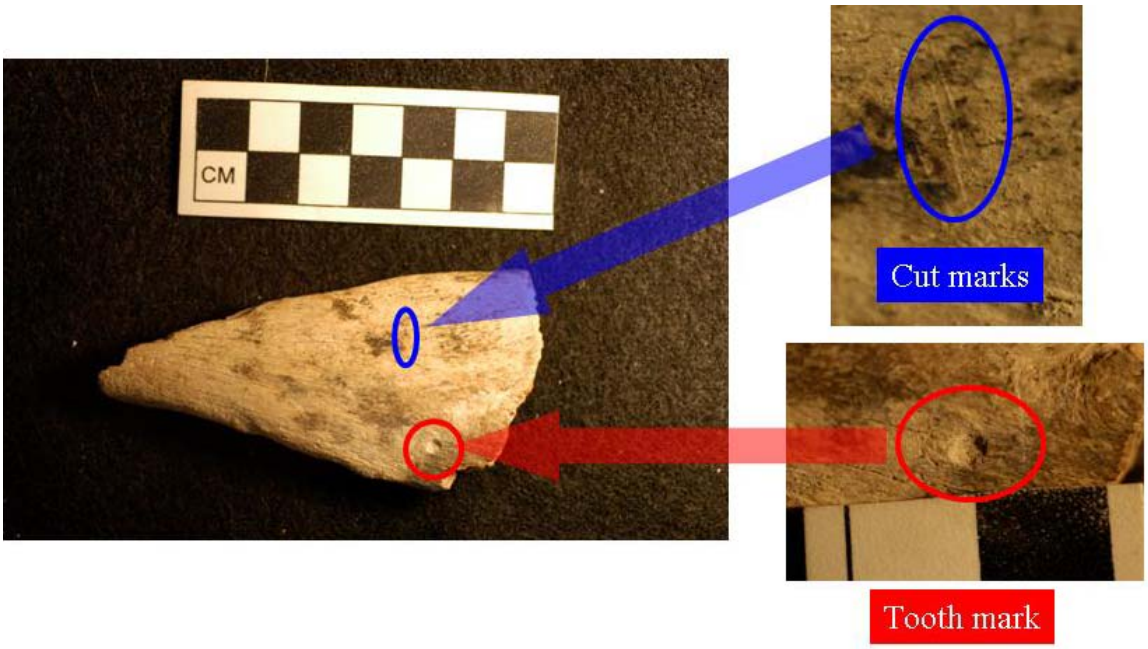


Figure 6.26. Specimen number 1208 from FwJj14A, a size 3 mammal long bone with a tooth mark overlying a cut mark. A close up photo, detailing the tooth mark overlying the cut mark, is on the bottom.

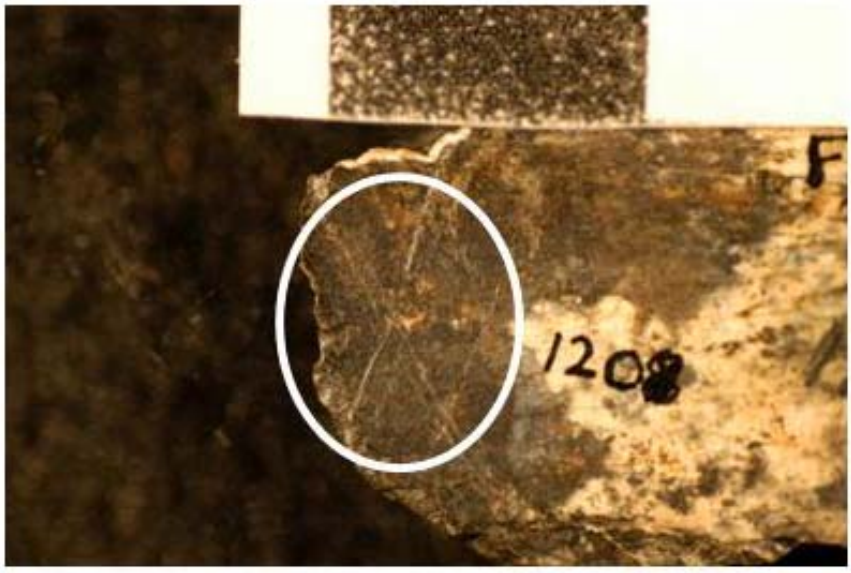
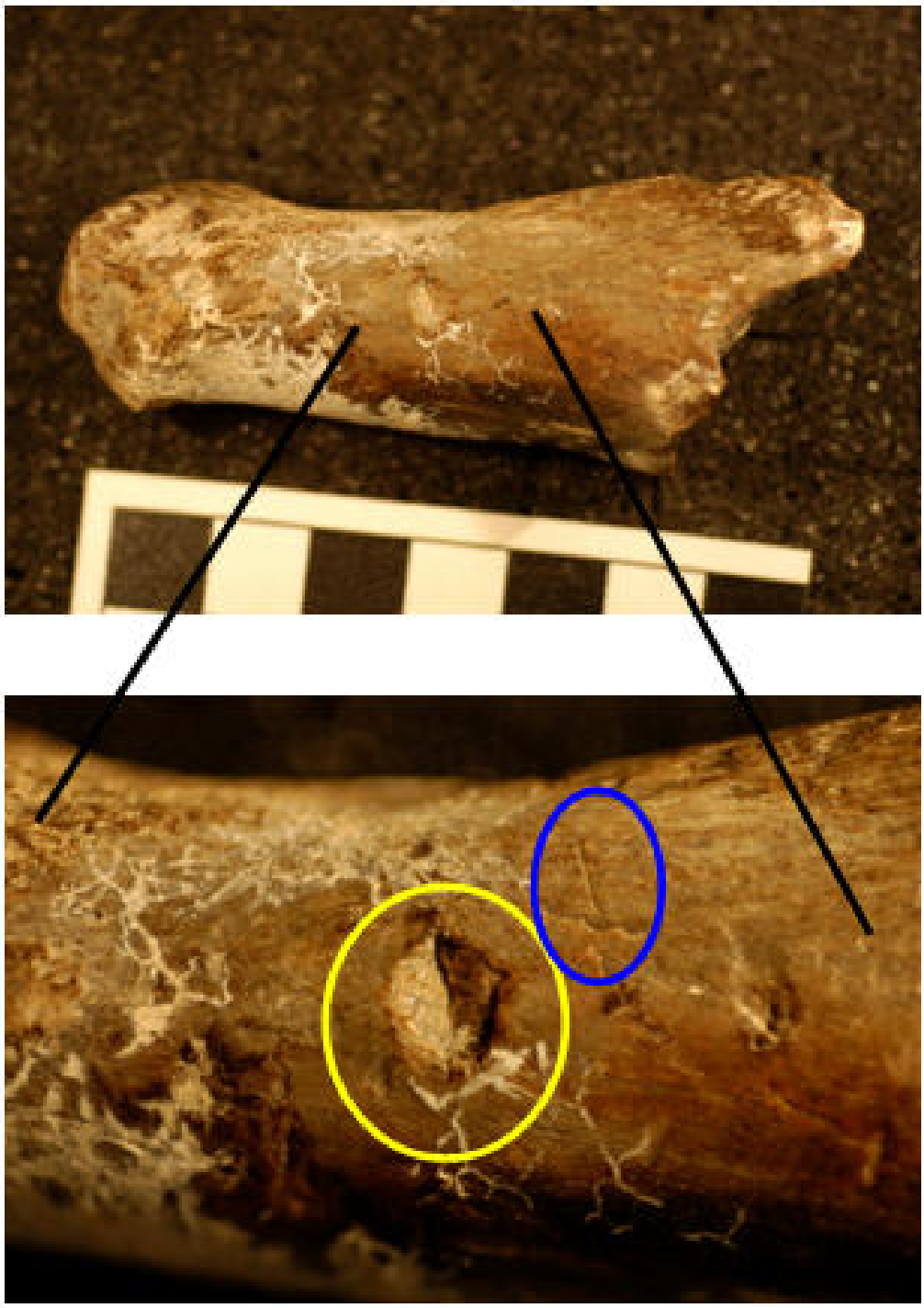


Figure 6.27. Specimen number 1034b from GaJi14A, a size 3 bovid left calcaneum with cut marks and possible crocodile tooth marks. Cut marks are circled in blue, and one of the tooth marks, possibly inflicted by a crocodile (cf. Njau and Blumenschine 2006), is circled in yellow. The bottom photograph is a close up of the cut and tooth marks.



The low frequency of carnivore tooth marks does not necessarily indicate a lack of carnivore activity at these three sites. However, it probably indicates that if carnivores accessed these carcasses, were not consuming bones on site. If carnivores were consuming limb epiphyses in the same place that hominins were butchering these carcasses, one would expect much higher frequencies of tooth-marked limbs, comparable to experimental models. In Selvaggio's (1998) carnivore to hominin scenario 66% of limb bone fragments were tooth-marked; in her carnivore to hominin to carnivore scenario, 56% of limb bones were tooth-marked. Capaldo (1998) found that 22% of appendicular long bones were tooth-marked in his hominin (hammerstone) to carnivore scenario, while 64% of appendicular long bones were tooth-marked in his whole bone to carnivore scenario. In Blumenschine's (1995) carnivore only scenario, 83% of limb bones were tooth-marked.

The following scenario may explain the low proportion of epiphyses and near-epiphyses, combined with the very low number of tooth-marked limbs (for example, 3/660 specimens, <1%, at FwJj14A): hominins processed carcasses and carcass parts for meat and marrow consumption, fragmenting the limbs. Subsequently, carnivores deleted greasy epiphyses from the assemblage by removing (transporting) them and consuming them off site. This may also apply to axial and compact elements, the latter of which are underrepresented at the sites. However, this is hard to evaluate without knowing how the un-marked limb bones were broken. While total MNIs were not calculated at any of the sites due to time constraints on refitting, knowing the proportion of animals at each site that were butchered by hominins would help in evaluating this scenario, and enable a more refined hypothesis of the relative contribution of hominins and other agents to the

accumulation of carcasses at these sites. Alternatively, *in situ* density-mediated attrition could be responsible for the virtual lack of complete limb epiphyses and relative paucity of epiphyseal fragments.

Limb shafts, as opposed to epiphyses and near-epiphyses, dominate the limb specimens from FwJj14A, FwJj14B, and GaJi14 (Table 6.40). The relative proportions of portions from all three sites are generally similar to that from carnivore-hominin-carnivore experimental scenarios, as well as from FLK *Zinjanthropus*. However, a carnivore-hominin-carnivore scenario can be ruled out due to the extremely low proportion or absence of tooth-marked bones at these sites. The relative proportions are also different from the hammerstone only experimental scenario, supporting the idea that while there is a low frequency or absence of tooth marks at these sites, the deletion of epiphyses and near-epiphyses indicates that carnivores were likely involved in the site

Table 6.40. Numbers of epiphyseal, near-epiphyseal, and limb shaft specimens from different experimental scenarios of hominin and carnivore access, FLK *Zinjanthropus*, FwJj14A, FwJj14B, and GaJi14.

Experimental Scenario	% Epiphyses	% Near-Epiphyses	% Midshafts
Hammerstone only[1]	27	4	69
Carnivore only[1]	3	22	75
Hammerstone to carnivore[1]	2	14	84
Whole bone to carnivore[2]	1	17	82
Hammerstone to carnivore[2]	6	19	76
Carnivore to hominin[3]	42	12	46
Carnivore to hominin to carnivore[3]	11	15	74
FLK *Zinjanthropus*[3]	15	23	62
FwJj14A*	9	8	83
FwJj14B*	7	8	85
GaJi14*	11	20	69

[1]Data from Blumenschine (1995)
[2]Data from Capaldo (1998)
[3]Data from Selvaggio (1998)
*For these assemblages, limb portions are not mutually exclusive; a limb bone can consist of more than one portion.

formation processes. Since the relative proportions of limb ends at the Okote sites (7-11%) are slightly higher than the proportions of limb ends from both the hammerstone to carnivore (6%) and whole bone to carnivore (1%) scenarios, it is possible that the carnivore destruction of limb ends, if it occurred, was slightly less intense than these particular experiments.

As mentioned above, the intra-element and carcass region cut mark patterning could be interpreted as late access to carcasses, forcing hominins to focus on low utility elements, coupled with scrap defleshing of higher ranked elements. Perhaps, then, hominins were butchering defleshed felid kills? Based on experimental scenarios, Domínguez-Rodrigo (2002, Domínguez-Rodrigo and Barba, 2006) propose that hominin butchery of fully fleshed carcasses versus defleshed felid kills can be distinguished based on three measures of cut mark frequencies:

1. Overall cut mark frequencies (NISP) over 15% versus less than 10%.
2. Cut mark frequencies decrease from upper to intermediate to lower limbs, versus increasing.
3. High frequencies of cut-marked limb midshafts (43-50% of total NISP), versus no cut marks on midshafts except for metapodials.

Evaluation of these criteria at the Okote sites is enigmatic. 1. The overall frequencies of cut marks on all specimens, and on *only identifiable* specimens, at FwJj14A, FwJj14B, and GaJi14 are 5% (*16%*), 6% (*19%*), and 9% (*16%*), respectively. Depending on whether Domínguez-Rodrigo and Barba (2006) include non-identifiable specimens, which is unclear, the interpretation changes from butchery of defleshed felid kills to butchery of fully fleshed carcasses at all three sites. When teeth, specimens with

recent breaks, and specimens < 2 cm in length are excluded for maximum comparability with experimental scenarios, these percentages are changed only slightly (11%, 9%, and 8%, in the same order as above). 2. Intermediate limbs are cut-marked more frequently than both upper and lower limbs at FwJj14A, but at FwJj14B the numbers of cut marks across limb classes are the same, and at GaJj14 lower limb bones are more frequently cut-marked than intermediate and upper limbs (Tables 6.41, 6.42, and 6.43). However, these differences are not statistically significant (Table 6.44). 3. The proportion of cut marks on limbs that are found on midshaft portions is very high, (88% at FwJj14A, 87% at FwJj14B, and 77% at GaJi14). However, this calculation does not take differential representation of limb portions into account. The proportion of midshafts out of the total number of limb specimens is also high at these sites (81% at FwJj14A, 83% at FwJj14B, and 68% at GaJi14), rendering the proportion of cut-marked specimens from each long bone portion statistically indistinguishable (Table 6.45). Therefore, these criteria do not help distinguish whether hominins butchered defleshed felid kills or fully fleshed carcasses. The taphonomic data relevant to answering this question are the tooth mark data, which do not support the scenario of hominins butchering felid kills. If this was the case, we would expect higher frequencies of tooth-marked limb midshafts (Blumenschine, 1995; Selvaggio, 1998).

Table 6.41. Cut mark distributions on long bone portions from FwJj14A. Individual cut marks could be counted on more than one portion. Numbers in cells are: number of cut-marked specimens/number of specimens in each category (percentage).

	Size 1 & 2	Size 3 & 4	Size 5 & 6	Indet Size	Total
HUM – PX	0/0 (0%)	0/3 (0%)	0/0 (0%)	0/1 (0%)	0/4 (0%)
HUM – PSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
HUM – MSH	0/1 (100%)	2/13 (15%)	1/1 (100%)	0/0 (0%)	3/15 (20%)
HUM – DSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)	0/1 (00%)
HUM – DS	0/1 (0%)	0/3 (0%)	0/0 (0%)	0/0 (0%)	0/4 (0%)
FEM – PX	0/2 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)	0/3 (0%)
FEM – PSH	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)

FEM – MSH	1/2 (50%)	2/7 (29%)	0/2 (0%)	0/0 (0%)	3/11 (27%)
FEM – DSH	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
FEM – DS	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)	0/1 (0%)
ULB – PX	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
ULB – PSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ULB – MSH	0/0 (0%)	1/5 (20%)	0/0 (0%)	0/0 (0%)	1/5 (20%)
ULB – DSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ULB – DS	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
RAD/U – PX	0/0 (0%)	0/0 (38%)	0/0 (0%)	0/1 (0%)	0/1 (0%)
RAD/U – PSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
RAD/U – MSH	0/1 (0%)	4/10 (40%)	0/0 (0%)	0/0 (0%)	4/11 (36%)
RAD/U – DSH	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
RAD/U – DS	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ULN – PX	0/1 (0%)	2/6 (33%)	0/0 (0%)	0/0 (0%)	2/7 (29%)
ULN – PSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ULN – MSH	0/0 (0%)	2/3 (66%)	0/0 (0%)	0/1 (0%)	2/4 (50%)
ULN – DSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ULN – DS	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
TIB – PX	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
TIB – PSH	0/0 (0%)	1/4 (25%)	0/0 (0%)	0/1 (0%)	1/5 (20%)
TIB – MSH	0/1 (0%)	7/26 (27%)	0/0 (0%)	0/3 (0%)	7/26 (29%)
TIB – DSH	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
TIB – DS	0/0 (0%)	0/4 (0%)	0/0 (0%)	0/0 (0%)	0/4 (0%)
ILB – PX	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ILB – PSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ILB – MSH	0/0 (0%)	0/0 (20%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ILB – DSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ILB – DS	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
MCM – PX	0/1 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/2 (0%)
MCM – PSH	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
MCM – MSH	0/0 (0%)	1/3 (33%)	0/0 (0%)	0/0 (0%)	1/3 (33%)
MCM – DSH	0/0 (0%)	0/2 (0%)	0/0 (0%)	0/0 (0%)	0/2 (0%)
MCM – DS	0/0 (0%)	0/2 (0%)	0/0 (0%)	0/0 (0%)	0/2 (0%)
MTM – PX	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
MTM – PSH	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
MTM – MSH	0/0 (0%)	0/3 (0%)	0/0 (0%)	0/0 (0%)	0/3 (0%)
MTM – DSH	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
MTM – DS	0/0 (0%)	1/1 (100%)	0/0 (0%)	0/0 (0%)	1/1 (100%)
LLB – PX	0/0 (0%)	0/7 (0%)	0/0 (0%)	0/0 (0%)	0/7 (0%)
LLB – PSH	0/0 (0%)	0/2 (0%)	0/0 (0%)	0/0 (0%)	0/2 (0%)
LLB – MSH	0/0 (0%)	2/12 (17%)	0/0 (0%)	0/1 (0%)	2/13 (15%)
LLB – DSH	0/0 (0%)	0/2 (0%)	0/0 (0%)	0/0 (0%)	0/2 (0%)
LLB – DS	0/2 (0%)	0/8 (0%)	0/0 (0%)	0/0 (0%)	0/8 (0%)
Total	**1/14 (7%)**	**24/125 (19%)**	**1/3 (33%)**	**0/10 (0%)**	**26/152 (17%)**
LB – EPI**	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/20(0%)
LB – NEF**	0/0 (0%)	0/16 (7%)	0/1 (0%)	0/6 (0%)	0/25 (6%)
LB – MSH**	3/20 (43%)	20/183 (11%)	0/0 (0%)	2/33 (6%)	25/236 (11%)
Total ULB CM	1/7 (14%)	5/30 (17%)	1/3 (33%)	0/4 (0%)	7/44 (16%)
Total ILB CM	0/3 (38%)	16/54 (30%)	0/0 (0%)	0/6 (0%)	16/63 (25%)
Total LLB CM	0/1 (0%)	2/16 (13%)	0/0 (0%)	0/0 (0%)	2/17 (12%)

Total EPI CM	0/7 (3%)	3/33 (9%)	0/0 (0%)	0/4 (0%)	3/44 (7%)
Total NEF CM	0/3 (0%)	1/31 (3%)	0/1 (0%)	0/2 (0%)	1/20 (5%)
Total MSH CM	1/5 (20%)	41/265 (15%)	1/3 (33%)	0/6 (0%)	43/279 (15%)

**Only identifiable to long bone, not to a specific skeletal element, or to upper, intermediate, or lower limb

Table 6.42. Cut mark distributions on long bone portions from FwJj14B. See Table 6.41 caption for more details.

	Size 1 & 2	Size 3 & 4	Size 5 & 6	Indet Size	Total
HUM – PX	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
HUM – PSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
HUM – MSH	1/2 (50%)	2/8 (50%)	0/0 (0%)	0/2 (0%)	3/12 (25%)
HUM – DSH	0/1 (0%)	1/1 (100%)	0/0 (0%)	0/0 (0%)	1/2 (50%)
HUM – DS	0/1 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/2 (0%)
FEM – PX	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
FEM – PSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
FEM – MSH	0/1 (0%)	1/5 (20%)	0/0 (0%)	0/0 (0%)	1/6 (17%)
FEM – DSH	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
FEM – DS	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ULB – PX	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ULB – PSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ULB – MSH	0/0 (0%)	3/11 (27%)	0/0 (0%)	0/0 (0%)	3/11 (27%)
ULB – DSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ULB – DS	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
RAD/U – PX	0/0 (0%)	1/2 (50%)	0/0 (0%)	0/0 (0%)	1/2 (50%)
RAD/U – PSH	0/0 (0%)	0/3 (0%)	0/0 (0%)	0/0 (0%)	0/3 (0%)
RAD/U – MSH	1/2 (50%)	1/7 (14%)	0/0 (0%)	0/0 (0%)	2/9 (22%)
RAD/U – DSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
RAD/U – DS	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ULN – PX	1/1 (100%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	1/1 (100%)
ULN – PSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ULN – MSH	1/1 (100%)	1/3 (33%)	0/0 (0%)	0/0 (0%)	2/4 (50%)
ULN – DSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ULN – DS	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
TIB – PX	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
TIB – PSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
TIB – MSH	0/0 (0%)	2/7 (29%)	0/1 (0%)	0/0 (0%)	2/8 (25%)
TIB – DSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
TIB – DS	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ILB – PX	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ILB – PSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ILB – MSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ILB – DSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
ILB – DS	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
MCM – PX	0/0 (0%)	1/1 (100%)	0/0 (0%)	0/0 (0%)	1/1 (100%)
MCM – PSH	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
MCM – MSH	1/1 (100%)	1/3 (33%)	0/0 (0%)	0/0 (0%)	2/4 (50%)
MCM – DSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
MCM – DS	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
MTM – PX	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
MTM – PSH	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
MTM – MSH	0/0 (0%)	2/6 (33%)	0/0 (0%)	0/0 (0%)	2/6 (33%)
MTM – DSH	0/0 (0%)	0/2 (0%)	0/0 (0%)	0/0 (0%)	0/2 (0%)
MTM – DS	0/0 (0%)	0/2 (0%)	0/0 (0%)	0/0 (0%)	0/2 (0%)

LLB – PX	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
LLB – PSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
LLB – MSH	0/1 (0%)	1/9 (0%)	0/0 (0%)	0/0 (0%)	1/10 (10%)
LLB – DSH	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/2 (0%)
LLB – DS	0/2 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/2 (0%)
Total	**5/14 (36%)**	**17/76 (22%)**	**0/0 (0%)**	**0/0 (0%)**	**22/90 (24%)**
LB – EPI*	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
LB – NEF*	0/0 (0%)	1/3 (33%)	0/0 (0%)	0/0 (0%)	1/3 (33%)
LB – MSH*	2/7 (29%)	10/52 (19%)	0/0 (0%)	1/10 (10%)	13/69 (19%)
Total ULB CM	1/5 (20%)	4/19 (21%)	0/0 (0%)	0/2 (0%)	5/26 (19%)
Total ILB CM	1/2 (50%)	4/19 (21%)	0/0 (0%)	0/1 (0%)	5/22 (23%)
Total LLB CM	1/5 (20%)	4/26 (15%)	0/0 (0%)	0/0 (0%)	5/31 (16%)
Total EPI CM	0/3 (0%)	2/8 (25%)	0/0 (0%)	0/0 (0%)	2/11 (18%)
Total NEF CM	0/2 (0%)	2/12 (16%)	0/0 (0%)	0/0 (0%)	2/14 (14%)
Total MSH CM	6/15 (40%)	19/97 (20%)	0/0 (0%)	1/12 (8%)	26/124 (21%)

**Only identifiable to long bone, not to a specific skeletal element, or to upper, intermediate, or lower limb

Table 6.43. Cut mark distributions on long bone portions from GaJi14. See Table 6.41 caption for more details.

	Size 1 & 2	Size 3 & 4	Size 5 & 6	Indet Size	Total
HUM – PX	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
HUM – PSH	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
HUM – MSH	0/2 (0%)	3/15 (20%)	0/0 (0%)	0/0 (0%)	3/17 (18%)
HUM – DSH	0/0 (0%)	1/8 (13%)	0/0 (0%)	0/0 (0%)	1/8 (13%)
HUM – DS	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
FEM – PX	0/1 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/2 (0%)
FEM – PSH	0/0 (0%)	0/2 (0%)	0/1 (0%)	0/0 (0%)	0/3 (0%)
FEM – MSH	0/1 (0%)	2/20 (10%)	0/0 (0%)	0/0 (0%)	2/21 (10%)
FEM – DSH	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
FEM – DS	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
RAD/U + ULN – PX	0/1 (0%)	1/7 (14%)	0/0 (0%)	0/0 (0%)	1/8 (13%)
RAD/U + ULN – PSH	0/0 (0%)	0/3 (0%)	0/0 (0%)	0/0 (0%)	0/3 (0%)
RAD/U + ULN – MSH	1/2 (50%)	2/18 (11%)	0/0 (0%)	0/0 (0%)	3/20 (15%)
RAD/U + ULN – DSH	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
RAD/U + ULN - DS	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)	0/0 (0%)
TIB – PX	0/2 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/3 (0%)
TIB – PSH	0/1 (0%)	2/10 (20%)	0/0 (0%)	0/0 (0%)	2/11 (18%)
TIB – MSH	2/4# (50%)	2/32 (6%)	0/0 (0%)	0/1 (0%)	4/37 (11%)
TIB – DSH	0/0 (0%)	0/7 (0%)	0/1 (0%)	0/0 (0%)	0/8 (0%)
TIB – DS	0/0 (0%)	0/5 (0%)	0/1 (0%)	0/0 (0%)	0/6 (0%)
MCM – PX	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
MCM – PSH	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
MCM – MSH	0/0 (0%)	2/7 (29%)	0/0 (0%)	0/0 (0%)	2/7 (29%)
MCM – DSH	0/0 (0%)	0/5 (0%)	0/0 (0%)	0/0 (0%)	0/5 (0%)
MCM – DS	0/0 (0%)	2/5 (40%)	0/0 (0%)	0/0 (0%)	2/5 (40%)
MTM – PX	0/0 (0%)	0/3 (0%)	0/0 (0%)	0/0 (0%)	0/3 (0%)
MTM – PSH	0/0 (0%)	0/3 (0%)	0/0 (0%)	0/0 (0%)	0/3 (0%)
MTM – MSH	0/0 (0%)	1/4 (25%)	0/0 (0%)	0/0 (0%)	1/4 (25%)
MTM – DSH	0/0 (0%)	1/2+ (50%)	0/0 (0%)	0/0 (0%)	1/2 (50%)
MTM – DS	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)

MP – PX	0/0 (0%)	0/2 (0%)	0/0 (0%)	0/0 (0%)	0/2 (0%)
MP – DS	0/0 (0%)	0/3 (0%)	0/0 (0%)	0/0 (0%)	0/3 (0%)
Total	**3/16 (19%)**	**19/170 (11%)**	**0/3 (0%)**	**0/1 (0%)**	**24/190 (13%)**
ULB – MSH*	0/1 (0%)	2/8 (25%)	0/0 (0%)	0/0 (0%)	2/9 (22%)
ILB – MSH*	0/0 (0%)	0/1 (0%)	0/0 (0%)	0/0 (0%)	0/1 (0%)
LLB – MSH*	0/1 (0%)	4/17 (24%)	0/0 (0%)	0/2 (0%)	4/20 (20%)
LB – EPI**	0/0 (0%)	0/2 (0%)	0/0 (0%)	0/0 (0%)	0/2 (0%)
LB – NEF**	0/2 (0%)	4/16 (25%)	0/0 (0%)	0/2 (0%)	4/20 (20%)
LB – MSH**	2/6 (33%)	13/65 (20%)	0/0 (0%)	1/8 (13%)	16/79 (20%)
Total ULB CM	0/6 (0%)	8/59 (14%)	0/1 (0%)	0/0 (0%)	6/57 (11%)
Total ILB CM	3/10 (30%)	7/85 (8%)	0/2 (0%)	0/1 (0%)	10/98 (10%)
Total LLB CM	2/6 (33%)	10/54 (19%)	0/0 (0%)	0/2 (0%)	12/62 (19%)
Total EPI CM	0/5 (0%)	3/31 (10%)	0/1 (0%)	0/0 (0%)	3/37 (8%)
Total NEF CM	0/3 (0%)	8/59 (14%)	0/2 (0%)	0/2 (0%)	8/66 (12%)
Total MSH CM	5/17 (29%)	31/187 (17%)	0/0 (0%)	1/11 (9%)	37/215 (17%)

#Includes one fibula midshaft

†Refers to specimens not identifiable to metacarpal or metatarsal

*Not identifiable to skeletal element but identifiable to upper, intermediate, or lower limb

**Only identifiable to long bone

+Includes one specimen identified to metapodial, arbitrarily classified here as a metatarsal to be able to include it in the analysis

Table 6.44. Results of chi-square analyses on the proportion of cut-marked specimens in each limb class from FwJj14A, FwJj14B, and GaJi14. See Figure 6.16 caption for grouping of limb bones into ULB, ILB, and LLB categories. Analyses were conducted on specimens from all body sizes, and then separately for size 3 and 4 specimens. The sample sizes of cut-marked specimens from size classes 1/2 and 5/6 were too small for this analysis. P-values are rounded to two decimal places.

Site	Size Class	chi-square	d.f.	p-value
FwJj14A	3/4	3.02	4	0.22
	All	2.31	4	0.32
FwJj14B	3/4	0.33	4	0.85
	All	0.37	4	0.83
GaJi14	3/4	3.23	4	0.20
	All	3.22	4	0.20

Table 6.45. Results of chi-square analyses on the proportion of cut-marked specimens in each long bone portion category from FwJj14A, FwJj14B, and GaJi14. Long bone portions are epiphysis, near-epiphysis, midshaft. See Table 6.44 caption for more details.

Site	Size Class	chi-square	d.f.		p-value
FwJj14A	3/4	4.18	4		0.12
	All	3.73	4		0.16
FwJj14B	3/4	0.21	4		0.90
	All	0.38	4		0.83
GaJi14	3/4	1.13	4		0.57
	All	2.61	4		0.27

Now that it is established that hominins were likely the primary carcass accumulators and modifiers at FwJj14, a closer look at the locations of cut marks on particular skeletal elements, and on particular taxa, to make more specific interpretations regarding butchery strategies and access to particular carcass resources, is warranted. Descriptions of cut marks here will focus on those from which behavioral interpretations can be made.

Cut Marks Across Skeletal Elements: Butchery Activities

Crania and Mandibles

The unusual findings of three cut-marked hyoids from size 3 bovids (two alcelaphines and a hippotragine, Figure 6.28) at FwJj14B underscore both the exceptional

Figure 6.28. Specimen number 3124 from FwJj14B, a cut-marked fragment of a size 3 alcelaphine hyoid.

preservation at the site as well as the ability of hominins to obtain and process the crania of the three bovids from which the hyoids derive. Cut marks on hyoids may relate to the

removal of the tongue for consumption (cf. Nilssen, 2000). Specimens 1112 from FwJj14A, a bovid size 3 left mandible (horizontal ramus), 5007 from FwJj14A, a bovid size 3 right mandible (gonial angle), and 5097 from FwJj14B, a bovid size 3A mandible, all have cut marks on the medial surface that may also be related to the removal of the tongue, or disarticulation (cf. de Henzelin *et al.,* 1999; Nilssen, 2000). Specimen 5214 from FwJj14B, a bovid size 2/3A right mandible, has cut marks on the inferior symphysis. One specimen at FwJj14A, a bovid size 3 cranium, has cut marks on the occipital that may be related to removal of the head (Figure 6.29; cf. Nilssen, 2000).

Figure 6.29. Cut-marked bovid size 3 occipital from FwJj14A, specimen number 1203a. A red circle indicates the locations of cut marks on the second, close up photograph (b). (a)

(b)

Ribs

There are several cut-marked rib specimens from these sites (seven from FwJj14A, eight from FwJj14B, 13 from GaJi14). Many of these are small fragments and the exact anatomical location of the cut marks (e.g. dorsal or ventral side) is difficult to determine (Figure 6.30), but there are cut marks on both dorsal and ventral surfaces of several rib specimens. The location of cut marks on rib dorsal surfaces demonstrates that hominins had access to the meatier parts of ribs.

Vertebrae

Cut marks are located in various areas of vertebrae, including the base of thoracic and lumbar neural spines (Figure 6.31), which may indicate filleting (cf. Nilssen, 2000), and cranial and caudal aspects of cervical vertebral bodies (Figure 6.32), which may indicate disarticulation (cf. Nilssen, 2000). Specimen 1111 from FwJj14A, a size 3A suid

C-1, has cut marks on a zygopophysis and near the cranial articulation; this may be related to disarticulation of the head (cf. Nilssen, 2000).

Figure 6.30. A cut-marked rib from Fw14A, specimen number 1205.

Figure 6.31. Specimen 1071 from GaJi14A, a cut-marked size ≥3 mammal thoracic neural spine. The red arrow indicates the location of the cut marks on the close up photograph (bottom), likely indicating filleting.

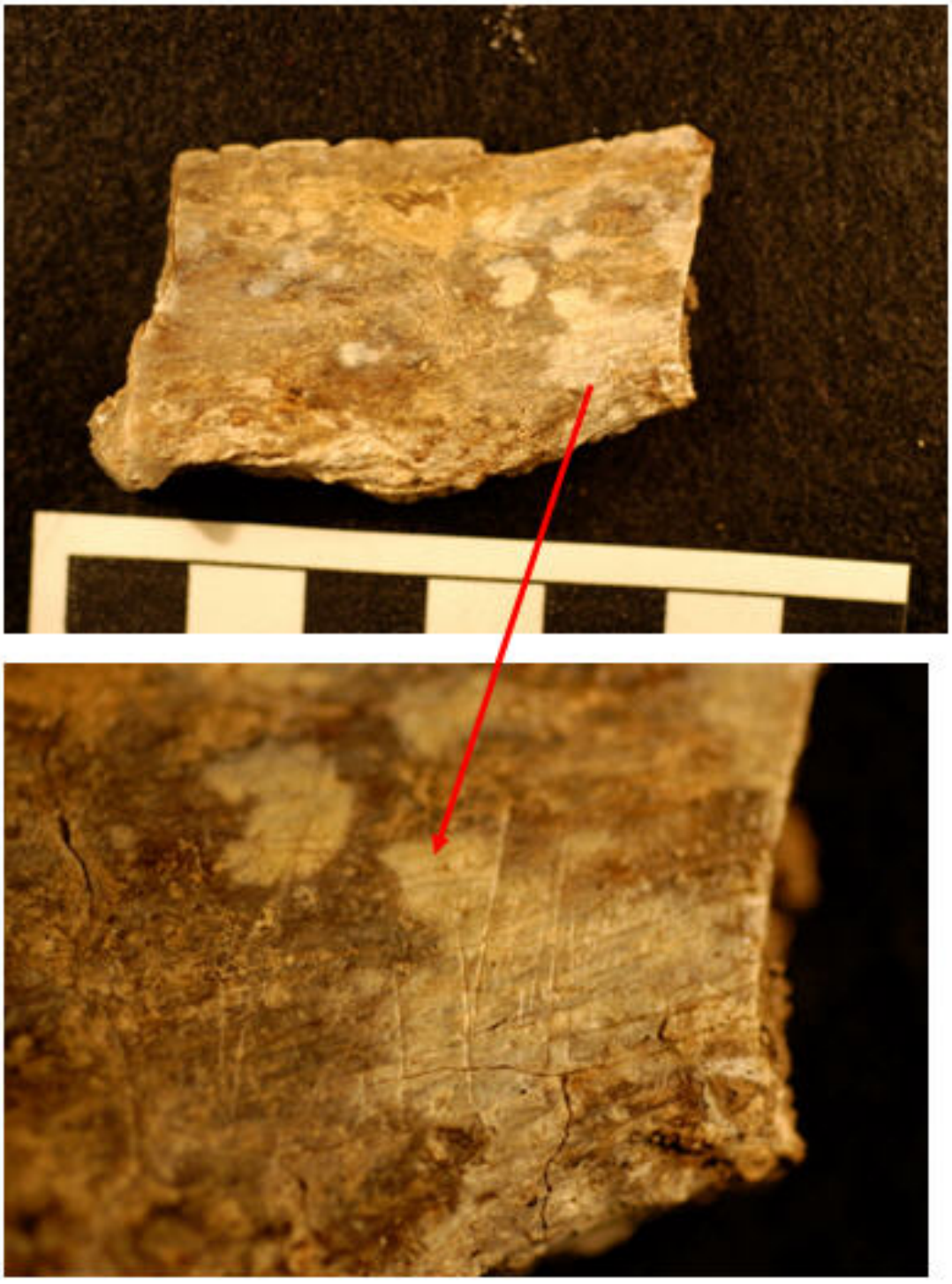
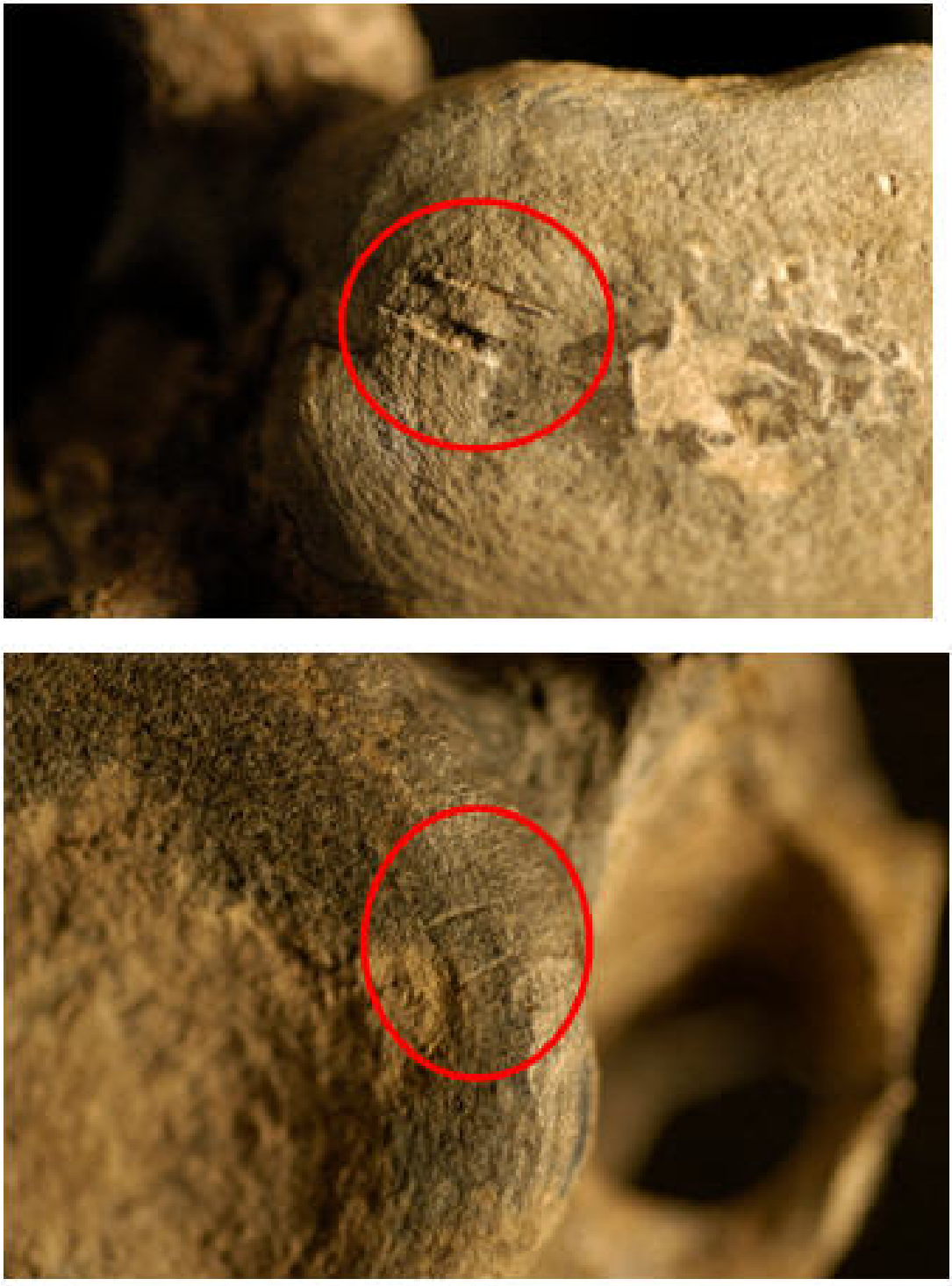


Figure 6.32. Close up photographs of cut marks on two hippo cervical vertebrae from FwJj14A, specimens 1012-97 (top) and 1221 (bottom). The red circles indicate the locations of the cut marks: on the cranial (1012-97) and caudal (1221) aspects of the vertebral bodies, likely indicating disarticulation of these cervical vertebrae. Cut marks on the top specimen are quite broad, and would be classified as chop marks.



Innominates

Cut marks on the medial ilia of three size 3 mammals from FwJj14A (specimens 102, 1014-97, and 1226) either indicate disarticulation of the innominate from the sacrum (in a juvenile) or filleting (cf. Nilssen, 2000). Cut marks on a size 3 suid innominate and a size 2/3 mammal innominate from FwJj14A, specimens 1201 and 12 respectively, indicate either disarticulation of the innominate from the femur, or filleting (cf. Nilssen, 2000). Cut marks on a size 3A bovid ischium from FwJj14B (specimen 3005) and a mammal size 5/6 ilium from GaJi14 (specimen 1090) likely indicate filleting (cf. Nilssen, 2000).

Scapulae

The only cut-marked scapulae from the Okote sites are from GaJi14. One of these, from a large mammal (specimen 1008, Figure 6.33), has cut marks likely indicating disarticulation of the scapula from the humerus (cf. Nilssen, 2000). The other three specimens, all from size 3 or larger animals, have cut marks indicating filleting (cf. Nilssen, 2000).

Carpals and Tarsals

Cut marks on a size 2 suid left magnum from FwJj14B (specimen 3055, Figure 6.34) likely indicates forefoot disarticulation (cf. Nilssen, 2000). Cut marks on a suid size 3A right astragalus from FwJj14A (specimen 1093) and a bovid size 3 right navicular-cuboid from GaJi14 (specimen 1119, Figure 6.34), indicate hindfoot disarticulation (cf. Nilssen, 2000). Cut marks on a bovid size 3 left calcaneum from GaJi14A (specimen 1034, Figure 6.27), probably indicates skinning (cf. Nilssen, 2000).

Figure 6.33. Cut-marked scapula of a large mammal (≥ size 3), specimen 1008 from GaJi14. Cut marks likely indicate disarticulation of the scapula from the humerus. A close up photograph of the cut-marked area is on the bottom.

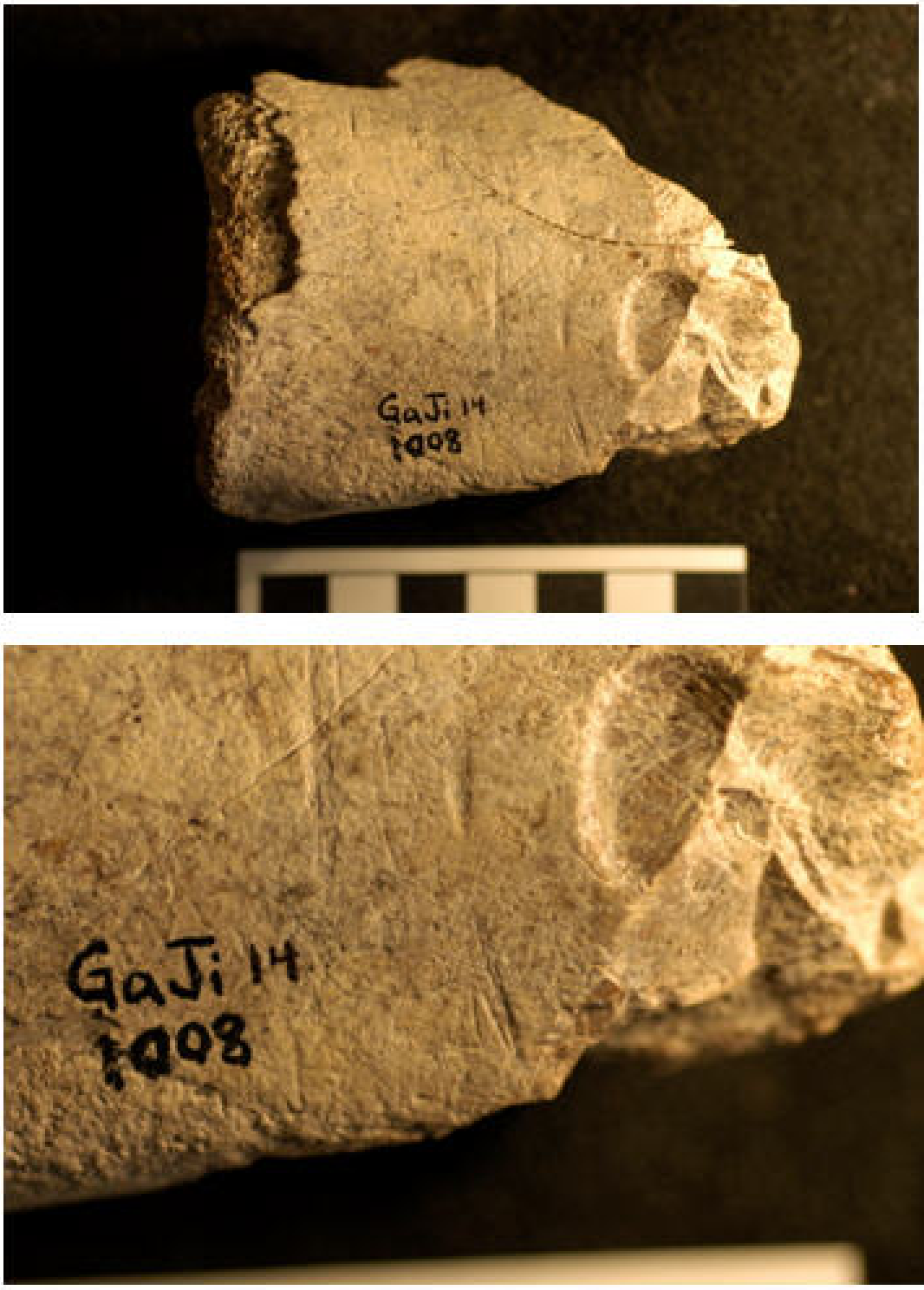
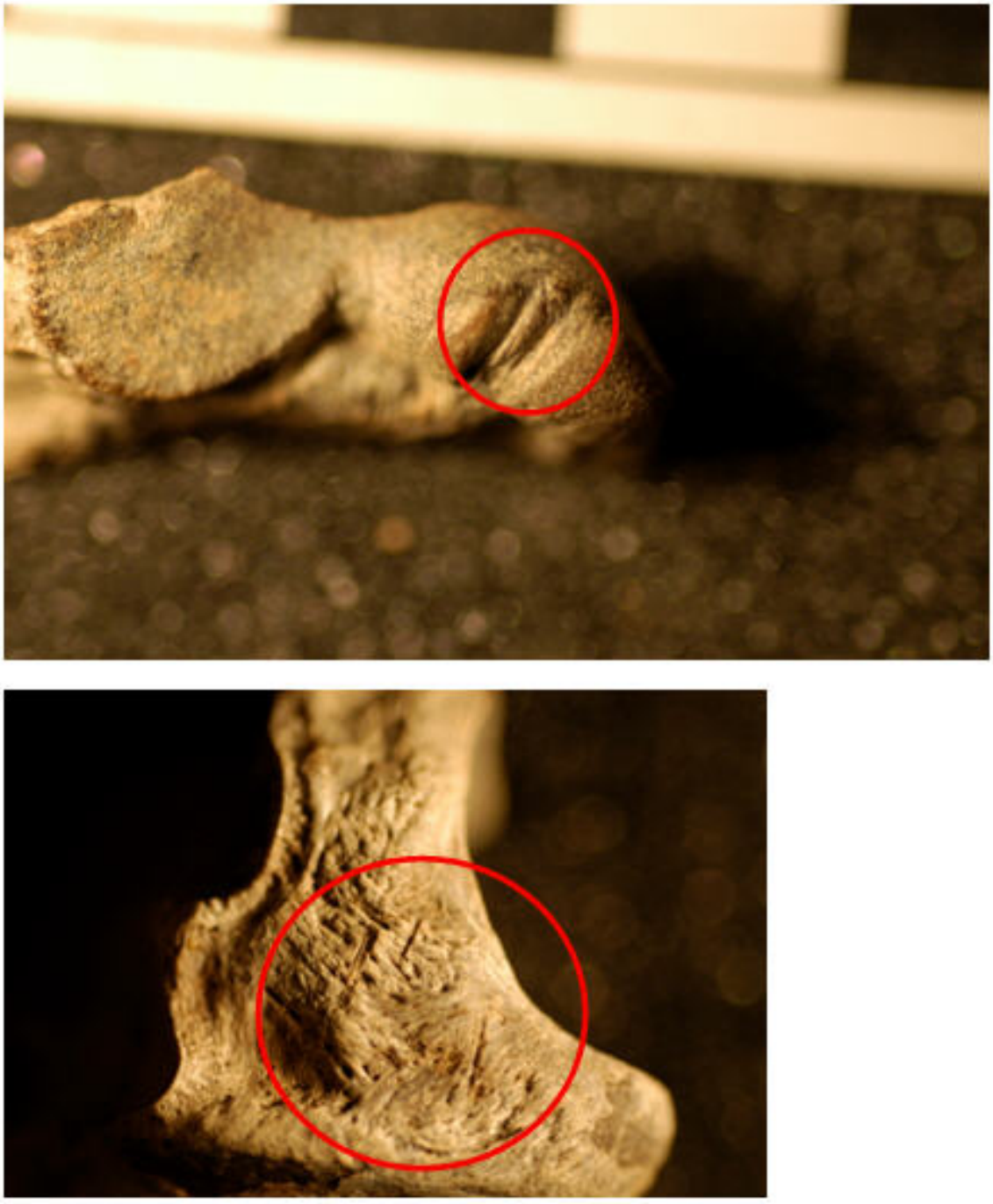


Figure 6.34. Close up of cut marks on a suid size 3A left magnum from FwJj14B, number 3055, and a bovid size 3 right navicular-cuboid from GaJi14A, number 1119. Cut marks are indicated by the red circles, and suggest forefoot (top) and hindfoot (bottom) disarticulation, respectively.

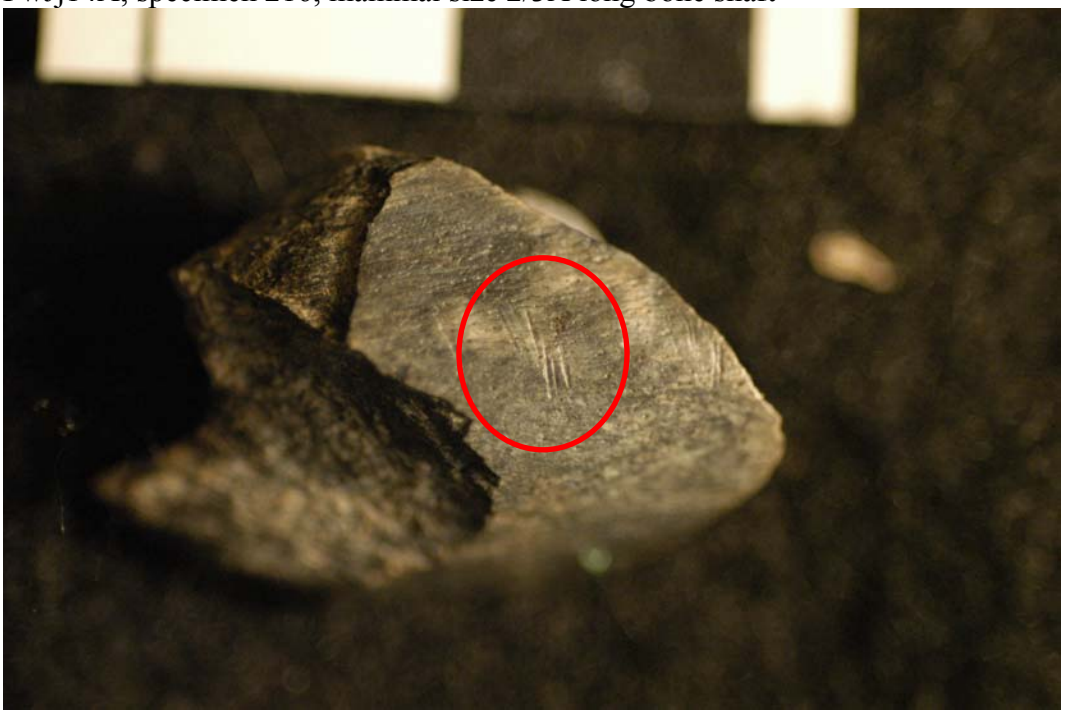


Limbs

Cut marks on limb midshafts of fossil ungulates have long been interpreted as evidence of defleshing (e.g. Bunn and Kroll, 1986). More recent experimental studies document that while this is still a valid interpretation, cut marks on limb epiphyses and near-epiphyses cannot strictly be interpreted as resulting from disarticulation (e.g. Nilssen, 2000; Pobiner and Braun, 2005). Dozens of specimens from the three Okote sites have cut marks predominantly on limb midshafts, indicating unambiguous access to flesh of a variety of sizes of mammals (size 1 through size 5, Tables 6.41, 6.42, and 6.43, Figure 6.35). Whether this flesh was in the form of scraps, or larger muscle masses, cannot be deciphered using current actualistic models. Cut marks on limb epiphyses are restricted to size 3 distal metapodials (condyles) or near-epiphyses, likely indicating disarticulation (personal observation, Figure 6.36), skinning or periosteum removal (Wilson, 1982; Figures 6.37, 6.38, 6.39); and size 2 or 3 posterior ulnae, either indicating skinning or filleting (cf. Nilssen, 2000). The only exception is a cut-marked size 3 bovid right proximal radius, with cut marks just below the medial/anterior side, just below the articular surface. These cut marks can be interpreted as filleting or disarticulation marks (cf. Nilssen, 2000). It is likely that the lack of cut marks on limb epiphyses is related to the lack of limb epiphyses in general at these sites, as noted previously.

Figure 6.35. Examples of long bone midshafts with cut marks from the three Okote sites. Cut marks are circled in red.

FwJj14A, specimen 216, mammal size 2/3A long bone shaft



FwJj14A, specimen 1016-97, a bovid size 3 radius midshaft

FwJj14A, specimen 1019-97, a bovid size 3A left femur midshaft

GaJi14, specimen 101, a size 3/4 ungulate right humerus

Figure 6.36. Cut marks on a size 3A bovid distal metatarsal condyle from FwJj14A (specimen 1007-97), and a size 3 suid left third metacarpal from FwJj14B (specimen 5220). These cut marks probably indicate disarticulation. Cut marks are circled in red.

Figure 6.37. FwJj14B, specimen 3035, a bovid size 3 metacarpal midshaft with cut marks and a percussion flake scar. Cut marks are on the posterior side, including scrape marks (circled in red) and a percussion flake scar is on the anterior side (posterior view – top, anterior close-up view – bottom).

Figure 6.38. Cut marks on a size 2/3A bovid metacarpal from FwJj14A (specimen 1003-97) from FwJj14A. Cut marks possibly indicate skinning or preparation for marrow extraction by removing periosteum. Close-up photo on bottom. Cut marks are circled in red.

Figure 6.39. A scrape mark at a green fracture edge of a size 3 bovid metatarsal from GaJi14A (specimen 6). This mark, indicated with a red circle, probably indicates periosteum removal in preparation for hammerstone breakage.

Twelve of the cut marks from each of the Ileret sites (FwJj14A and FwJj14B) and 5 of the cut marks from the Koobi Fora ridge site (GaJi14) are scrape marks (Figures 6.37, 6.38, 6.39), which can be interpreted as removal of periosteum in preparation for hammerstone breakage and marrow extraction. These marks were only found on intermediate and lower limb bones, as one would expect from the relatively thick periosteum on these bones.

In sum, the cut marks on limbs at the three Okote sites indicate defleshing of upper limbs, defleshing of intermediate limbs and disarticulation of radio-ulnae, and disarticulation, skinning, and periosteum removal on lower limbs. Whether defleshing was of bulk or scrap flesh is not discernible.

Cut Marks Across Taxa: Dietary Reconstructions

What can cut marks tell us about which animals were actually eaten by hominins at these Okote sites? Here, I will explore the dietary information available from the cut-marked fauna.

At FwJj14A, cut marks are present on specimens not identifiable to a higher taxonomic level than "mammal" ranging from size 1 to 4. At least six bovid individuals were butchered (a size 2/3A, a size 3A, and four size 3 individuals) as were two suids (a size 3A and two different size 2 individuals). At least one hippo was butchered. One fish was also cut-marked. A total of at least 10 individuals were butchered.

At FwJj14B, cut marks are present on mammals ranging from size 1 to 3. At least seven bovids were butchered: one size 2, one size 2/3A, one size 3A, three size 3, and one size 3B/4. Of the three size 3 bovids, two are alcelaphines, and one is a hippotragine (all identified based on hyoid morphology). Three suids were butchered, a size 3A, a size 3, and a size 3B. One *Cercopithecus* (size 1 monkey) was also butchered at FwJj14B (Figure 6.40). A total of at least 11 individuals were butchered.

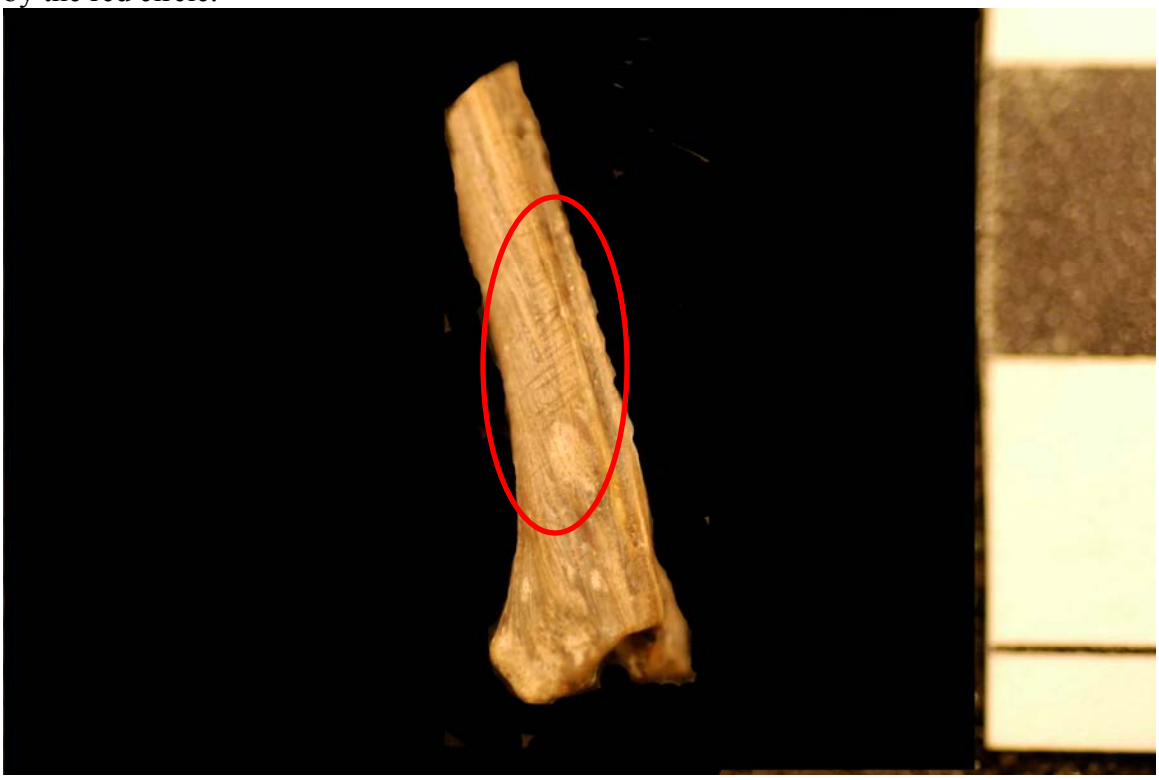
At GaJi14, cut marks are present on mammals ranging from size 1 to 5 or 6. Seven bovids were butchered: 2 size 2 (one mature, one immature), one size 2/3A, one size 3A, one size 3, one size 3B, and one size 3B/4. One suid size 2/3, one juvenile hippo (size 3/4), and a fish (Figure 6.41) were also butchered at GaJi14. A total of at least 10 individuals were butchered.

In sum, these three sites from the Okote Member at Koobi Fora show evidence for butchery of a total of 31 individuals, including 29 mammals and 2 fish. The individuals with butchery marks for which habitat preference can be assumed include aquatic taxa (hippo, fish), a monkey which presumably required tall trees (*Cercopithecus)*, water-

dependent alcelaphines, and the grass-eating hippotragine. This indicates that hominins acquired meat from animals in a variety of habitats: water edge, riverine forest, and open, grassy areas.

Figure 6.40. Cut marks on a *Cercopithecus* sp. humerus from FwJj14B, specimen 5233. Cut marks are indicated with a red circle.

Figure 6.41. Cut-marked fish spine from GaJi14B, specimen 637. Cut marks are indicated by the red circle.



Discussion

Whether hominins processed entire carcasses at kill/death sites, or disarticulated and transported carcass parts to butchery sites to be processed there, can only be hypothesized, given the relatively small sample sizes of identifiable specimens from these sites. However, based on inter- and intra-skeletal element cut and percussion mark distribution, the extremely low frequency or absence of carnivore tooth marks, and the low numbers of limb epiphyses (especially upper and intermediate limbs), a hypothesis of hominin foraging strategies at these three Okote Member sites can be presented.

Based on cut, percussion, and tooth mark frequencies and locations, hominins had access to flesh and marrow from the majority or all of the carcasses they butchered at

these sites. They probably disarticulated some elements or groups of elements for transport (crania, vertebrae, possibly innominates from femora and scapulae from humeri, forelimbs, and hindlimbs), but whether this disarticulation was indeed in preparation for transport or was part of on-site butchery activities is uncertain. Hominins conducted various butchery activities at these sites, including defleshing of ribs, vertebrae, innominates, scapulae, and limbs. Tongue removal was also practiced. Percussion marks and scrape marks indicate marrow access to all classes of limbs (upper, intermediate, and lower), though scrape marks only occur on intermediate and lower limbs. Evidence of skinning on metapodials is also present. If hominins were conducting butchery activities in a high risk setting, we would not expect to see butchery of bones that occur late in the butchery sequence (low ranked elements), or specific activities that require longer processing time or effort, such as disarticulation of vertebrae, removal of intercostal flesh, and skinning of metapodials in preparation for marrow extraction. Since we do see these behavioral traces, hominins were most likely conducting butchery activities in a low risk or low competition setting.

Based on limb bone portion representation, after hominins had extracted the meat and marrow from the limbs, bone-crunching carnivores (hyaenids) then destroyed the grease-rich limb epiphyses. It appears as if this destruction did not occur on site, as on-site limb epiphysis destruction would be expected to leave tooth-marked epiphyseal and near-epiphyseal fragments (Blumenschine and Marean, 1993). The hyaenids likely removed limb epiphyses before consuming them. This may indicate that even after hominins extracted the resources from these carcasses usable to them, their presence in the general vicinity of the site may have prevented hyaenids from processing the grease-

rich epiphyses on site. Alternatively, higher intra-specific hyaenid competition may have led to off-site versus on-site epiphyseal destruction (cf. Marean and Bertino, 1994). Hyaenid deletion of limb epiphyseal portions may have also removed evidence for disarticulation of limbs, in the form of cut marks, especially on upper limbs. The presence of cut marks on three out of four of the tooth-marked specimens from these sites indicates that carnivore activity was not independent of hominin carcass processing. Alternatively, the virtual lack of complete epiphyses and relative paucity of epiphyseal fragments may result from *in situ* density-mediated attrition rather than carnivore activity.

What conclusions can we draw about the frequency of hominin carcass access based on the evidence from these three sites? While the amount of time represented at each site is unknown, a total of 10-11 individual prey items, at minimum, were butchered at each site. Processing of metapodials for meat scraps and marrow, indicated by cut, scrape, and percussion marks, also probably indicates relatively thorough butchery and resource extraction. If hominins had access to large numbers of carcasses, one could assume that they would not process metapodials for meat and marrow. Therefore, it is likely that hominins had infrequent access to carcasses in the vicinity of these sites, which they thoroughly processed for all extractable resources prior to hyaenid deletion of limb epiphyses, probably as well as less dense axial elements such as ribs and vertebrae. The lack of correlation between rank of carnivore preference (based on meat yield) and rank of frequency of butchered skeletal elements or carcass parts might indicate that hominins were not preferentially butchering the meatier parts of carcasses. Alternatively, butchering the "meatiest" elements might leave fewer cut marks than those with smaller

muscles, or those with multiple attachment sites, which may require more cutting actions to remove. A more refined actualistic reference model is needed to break this equifinality.

A comparison of cut mark frequencies across carcass sizes, skeletal element groups, long bone portions, and limb classes among the three sites indicates general similarities in the butchery practices at these sites (Table 6.46). The difference between cut marks on limb classes is nearly significant, but this can probably be explained by variation in relative abundance of limbs in different classes at these sites. For example, the higher number of cut marks on intermediate limbs from FwJj14A (16/25, 64%) corresponds to a higher proportion of intermediate limbs found at this site (63/124, 51%). Whether this differential distribution of limb classes is due to differential transport of these limbs by hominins, or some other factor, is not known. We can then group these three sites together when discussing hominin butchery and foraging strategies, and compare the behavioral signal at these sites with other penecontemporaneous sites within the Koobi Fora basin and elsewhere.

Table 6.46. Results of chi-square analyses on cut marks on different carcass sizes, skeletal element groups, long bone portions, and limb classes across the three Okote member sites: FwJj14A, FwJj14B, and GaJi14. Carcass sizes are 1 and 2, 3 and 4; skeletal element groups are axial, appendicular, compact; long bone portions are epiphyses, near-epiphyses, midshafts; limb classes are upper, intermediate, lower. P-values are rounded to two decimal places.

Analytical Unit	chi-square	d.f.	p-value
Carcass Size	3.28	4	0.06
Skeletal Group	2.53	4	0.64
Long Bone Portion	6.51	4	0.16
Limb Class	9.45	4	0.05

During Okote Member times at Koobi Fora, stone tools were both abundant in the Karari region in fluvial contexts, but preservational context of bone is poor, rendering the surfaces bones from sites excavated on the Karari leached and chalky and difficult for

bone surface modification identifications (Bunn, 1994). In the Koobi Fora Ridge and Ileret regions, where these three sites are located, bone preservation is very good, hominin fossils are also abundant, but stone tools are rare in the fluvial and shallow, ephemeral lake margin settings (Bunn, 1994). There is a decrease in archaeological visibility of hominin activity traces as defined by sites with stone tools with an increase in distance to raw material. The Karari is situated at the confluence of the axial drainage system of the perennial ancestral Omo River and higher gradient, marginal streams that intermittently carried stone cobbles into the area from the eastern basin margins, so raw materials were locally and abundantly available in channel gravels. In contrast, the nearest raw materials to Ileret are 5 kilometers to the east, and on the Koobi Fora Ridge raw materials are 15 kilometers away, in channel gravels to the east or northeast (Bunn 1994). At these sites, then, hominins must have carried stone tools to carry out butchery activities, but did not discard them due to scarcity of suitable raw material. In fact, there are only two possible lithics found on the surface in Areas 101 and 103 (Koobi Fora ridge) after decades of surface surveys (Bunn, 1994). Bunn concludes, based on analyses of cut mark morphology, that the hominins on the Koobi Fora ridge and Ileret used large cutting tools, as opposed to flakes, for butchery. A test of this hypothesis is beyond the scope of this dissertation, but is worth pursuing in the future. It is surprising that with so much evidence for butchery there is no debris from flaking production, suggesting that Bunn is right.

While there are no stone tools found in association with the butchered bones from any of these three sites, there is an archaeological site within the same general time horizon, about 3-5 kilometers to the southeast, in area 8A (J. W. K. Harris, pers. comm.):

FwJj1. This is the only excavatable archaeological site with lithics and fauna that has been found in the Koobi Fora Formation in the Ileret region (Harris and Isaac, 1997), and it is found within a local cluser of hominin fossil finds (Isaac *et al.*, 1976). The material was concentrated entirely at the interface between a sandy mudstone and an overlying sand lens, which both form part of the infilling of a small channel, and it was likely discarded on a bar or bank feature in a low-lying floodplain. The nature of the artifact occurrence is interesting: only one core scraper and one hammerstone were found *in situ*, while the rest of the artifacts are flakes (detached pieces), including 40 groups of 111 refitting pieces out of a total of 432 lithics (Harris and Isaac, 1997; Isaac *et al.*, 1976). The artifacts are spatially concentrated, possibly indicating a single flaking event, or multiple flaking events within a short period of time. Harris and Isaac (1997) speculate that the paucity of cores in the assemblage may reflect the fact that the nearest contemporary raw material source is at least several miles away. The dominance of flakes could support Bunn's (1994) hypothesis that the cut marks at Ileret were made by large cutting tools, if these flakes were the byproduct of shaping these large cutting tools. Alternatively, the dominance of flakes could indicate that these were the desired products of stone knapping. Regardless, the incidence of what seems to be a place where hominins were knapping and discarding flakes speaks to the specialized nature of sites in Ileret at this time. The fauna has not been analyzed, and though bones are sparse, highly fragmented, and their surface preservation is somewhat eroded (Isaac *et al.*, 1976; Harris and Isaac, 1997; J. W. K. Harris, pers. comm.), it would be worth comparing these bones with the assemblages from FwJj14A and FwJj14B, and especially looking for butchery or carnivore marks. The fauna includes *Crocodylus* and *Euthecodon*, hippo, and primates

from the excavation (which were found in the same beds as the artifacts), and bovid, equid, hippo, crocodile, and *Clarias* (fish) from the surface (Harris and Isaac, 1997).

FxJj50, an Okote Member site from the Karari, was originally reported by Bunn *et al.* (1980) and has undergone recent reanalysis of bone surface modifications (Domínguez-Rodrigo, 2002). Inter-limb cut mark frequencies at FxJj50 and the three Okote sites are statistically similar ($\chi^2 = 11.18$, d.f. = 6, $p = 0.08$), but intra-limb cut marks frequencies are statistically different ($\chi^2 = 13.80$, d.f. = 6, $p = 0.03$). Adjusted residuals (cf. Grayson and Delpech, 2003), which are used to determine which values are driving the statistical difference, indicate that this difference is driven by: 1) the significantly lower proportion of cut-marked midshafts at FxJj50; 2) the significantly lower proportion of cut-marked near-epiphyses at FwJj14A; 3) the significantly higher proportion of cut-marked midshafts at FwJj14A; and 4) the significantly higher proportion of cut-marked near-epiphyses at FxJJ50 (Table 6.47). However, FxJj50 has relatively fewer limb midshafts than the Ileret and Koobi Fora Okote sites ($\chi^2 = 50.60$, d.f. = 4, $p < 0.001$; Table 6.48), which probably accounts for this difference. The relationship between the adjusted residuals of the cut-marked limb portions and the portion representation itself across sites is strongly positive and statistically significant (Pearson's $r = 0.90$, $p < 0.001$), indicating that cut-marked limb portion frequencies are not independent of limb portion frequencies. For example, though cut-marked midshafts from FxJj50 are underrepresented, midshafts are also underrepresented at FxJj50. Still, while Domínguez-Rodrigo (2002) interprets the cut mark distribution at FxJj50 to indicate access to meaty upper limbs by hominins, hominins at FxJj50 may have had relatively less access to meaty limb shafts than at the other Okote sites.

Table 6.47. Adjusted residuals, based on chi-square analyses, for cut marks by long bone portion across four Okote Member sites from Koobi Fora (FwJj14A, FwJj14B, GaJi14, FxJj50). EPI = epiphysis, NEF = near epiphysis, MSH = midshaft. NISP cut marked and adjusted residuals (AR) are given. Significant values of adjusted residuals, indicating which values are driving the significant difference ($\chi^2 = 13.20$, d.f. = 6, p = 0.04), are in bold. AR values are rounded to two decimal places.

	Site							
	FwJj14A		FwJj14B		GaJi14		FxJj50	
	NISP CM	AR	NISP CM	AR	NISP CM	AR	NISP CM	AR
EPI	3	-0.44	2	-0.26	3	-0.49	3	1.73
NEF	1	**-2.32**	2	-0.80	8	1.67	4	**1.98**
MSH	43	**2.15**	26	0.81	37	-0.98	9	**-2.77**

Table 6.48. Adjusted residuals, based on chi-square analyses, for long bone portions portions across four Okote Member sites from Koobi Fora (FwJj14A, FwJj14B, GaJi14, FxJj50). EPI = epiphysis, NEF = near epiphysis, MSH = midshaft. NISP for each bone portion and adjusted residuals (AR) are given. Significant values of adjusted residuals, indicating which values are driving the significant difference ($\chi^2 = 50.60$, d.f. = 4, $p < 0.001$), are in bold. AR values are rounded to two decimal places.

	Site							
	FwJj14A		FwJj14B		GaJi14		FxJj50	
	NISP CM/ Total NISP	AR	NISP CM/ Total NISP	AR	NISP CM/ Total NISP	AR	NISP CM/ Total NISP	AR
EPI	44	0.85	11	-1.77	37	0.01	17	0.69
NEF	20	**-5.48**	14	-1.76	66	**4.28**	31	**3.69**
MSH	279	**3.72**	124	**2.70**	215	**3.39**	78	**-3.44**

In addition to the possible difference in butchery mark frequencies between sites from the Karari, Koobi Fora, and Ileret regions, tooth marks are much more common at FxJj50 that at the Koobi Fora and Ileret sites. Whether this was due to regional-scale differences in carnivore abundance or hominin behavior is not known. The current carnivore presence/absence data from the Okote Member by region does not support the idea that there were more carnivores in the Karari region than the Ileret and Koobi Fora regions (Table 6.49). There are a higher number of carnivore species identified from the Koobi Fora Ridge region, and especially the Ileret Ridge region, compared with the Karari.

Bunn (1994) hypothesized, based on the available evidence at the time, that

Table 6.49. Carnivore taxa identified from the Okote Member at each of the three regions of Koobi Fora: Ileret, Karari, Koobi Fora. An "X" in cell indicates that that carnivore has been identified from that region and "(X)" indicates a tentative identification. A small viverrid or herpestid identified from Ileret and a viverrid identified from Koobi Fora are not included in the table. Data from L. Werdelin and M. Lewis, pers. comm..

Carnivore Taxon		Ileret	Karari	Koobi Fora
Mustelidae	cf. *Torolutra*	X		X
	Mellivora sp.	X		
Viverridae	*Genetta genetta*	X		
Hyaenidae	*Crocuta ultra*	X	X	X
	Hyaena sp.	X		
Felidae	*Dinofelis piveteaui*	X	X	X
	Megantereon whitei	X		(X)
	Homotherium sp.	X		
	Panthera leo	X		
	Acinonyx sp.			X

hominin daily mobility at Koobi Fora and Ileret only rarely involved the transport of carcass parts to central places or the recurrent use of such locations. The evidence from the three Okote sites analyzed here refutes this hypothesis. Bunn (1994) further suggests that if the only difference between the Koobi Fora/Ileret and Karari hominin behavioral patterns was the need to conserve raw materials, then more sites with repeated butchery events would be expected at Koobi Fora and Ileret. This is indeed the case, with the new evidence presented here. These sites can be interpreted as recurrently visited places where hominins transported and processed carcass parts of several animals. However, how much of the processing of carcass parts occurred before or after transport, the former of which might a higher level of predation risk, is still unknown.

Summary

This chapter reports on three new penecontemporaneous Early Stone Age archaeological sites from the Okote Member (~1.5 Ma) at Koobi Fora: FwJj14A,

FwJj14B, and GaJi14. These three sites are all relatively unique for the Oldowan, as they all consist solely of extremely well-preserved fauna, some of which displays hominin butchery marks, and lack stone tools. There are a total of 292 cut-marked and 27 percussion-marked bones from these three sites; 4 bones are tooth-marked. Cut marks occur on a variety of taxa of a total of 31 individuals (10 or 11 at each site) including an arboreal monkey (*Cercopithecus* sp.), fish, hippos, bovids, and suids.

FwJj14A and FwJj14B are located in Area 1A, in Ileret region. The fauna from both sites are found in sediments that form part of the 'Lower/Middle Tuff Complex'. The sites lies just above the Northern Ileret Tuff, dated at ~1.52 Ma (Brown *et al.,* 2006). At FwJj14A, the fauna was in a dense clayey mudstone well-indurated with calcium carbonate. This fauna accumulated adjacent to a watercourse that was subsequently covered by fine-grained sediment. This paleolandscape was most-likely a small flood basin nestled within a system of channels.

FwJj14B is within 30 meters of FwJj14A spatially, across a gully, and is situated 3m above FwJj14A stratigraphically. The fauna at FwJj14B accumulated on the lateral margin of a broad, shallow stream. The fossils here were deposited on a substratum of clayey mud, and as the channel aggraded, they were covered with coarser sediment.

GaJi14 is located in Area 103, in the Koobi Fora ridge region. The site lies about 4 meters below the Koobi Fora tuff, and is dated to at least ~1.49 Ma (Brown *et al.,* 2006) and possibly as old as 1.62 Ma. The fauna at GaJi14 accumulated within small, shallow tributaries of an ancient lake.

The low degree of weathering and lack of preferred orientation of the bones at the three sites supports a scenario of relatively rapid burial as well as lack of significant

fluvial transport. The presence of sedimentary abrasion on a small proportion of the bones, though, does indicate at least some fluvial activity at each site. The assemblages are highly comminuted, both due to ancient fracture, some of which was caused by hammerstone breakage, but some of which was due to modern breakage of fossils on the surface and *in situ*.

Based on the lack of articulating elements and evidence for whole or partial carcasses, the higher proportions of limbs than would be expected if whole carcasses were being butchered, and cut marks located on tarsals, carpals, and distal metapodials, as well as in particular areas of some elements (e.g. crania, innominates, scapulae, vertebrae, limb epiphyses) indicating disarticulation, it can be hypothesized that hominins disarticulated and presumably transported carcass parts to these locations for butchery activities. Cut marks on limb midshafts, scapulae, innominates, ribs and vertebrae indicates hominin defleshing, including cut marks on mandibles and hyoids indicating tongue removal. Scrape marks and percussion marks demonstrate that after removing meat, hominins also broke some of these bones open for marrow extraction.

The relatively high numbers of cut marks, presence of some but fewer percussion marks, and very low numbers of tooth marks (present at only one site, FwJj14A) indicates that hominins may have had early and mainly exclusive access to these carcasses during the first stage of the resource life of the carcasses. Even when the sample only includes long bone shaft fragments > 2 cm in length without recent breaks for maximum comparability with actualistic assemblages, percussion mark frequencies at all of the sites (3% at FwJj14A, 4% at FwJj14B, and 9% at GaJi14) are much lower than Blumenschine's hammerstone-only and hammerstone-to-carnivore experimental samples,

at 28% and 27% (Blumenschine, 1995). However, the low proportion of limb epiphyses does indicate that after hominin butchery took place, carnivores (hyaenids) probably removed and consumed these grease-rich limb portions. 3 of 4 tooth-marked elements are also cut-marked, indicating interdependence, not independence, of hominin and carnivore access. Alternatively, the low proportion of limb epiphyses may result from *in situ* density-mediated attrition. Based on individual specimens and overall patterns of cut, percussion, and tooth marking, hominins had access to meat and marrow from these carcasses and carcass parts. However, whether the cut marks are indicative of scrap or bulk defleshing is not known; an experimental model which clearly distinguishes these behaviors is still lacking (e.g. Pobiner and Braun, 2005). Experimental models of carcass procurement modes, based on cut and tooth marks frequencies, differentiating between hunting and high-yield scavenging (regardless of whether this scavenging involved early or late access by hominins to carcasses) are also still lacking.

Within and across these three sites, there are statistically similar proportions of cut marks (% NISP cut-marked) on bones from different carcass sizes (1 and 2, 3 and 4, 5 and 6); skeletal groups (axial, appendicular, compact); limb classes (upper, intermediate, lower); and limb portions (epiphysis, near-epiphysis, midshaft). Experimental and archaeological studies indicate that we might expect larger carcasses to be cut-marked at a higher frequency than smaller ones. As this is not the case at these sites, this result could be interpreted as relatively less exploitation of larger carcasses, but this interpretation is tenuous. The equivalency of proportion cut marking across skeletal elements and limb classes, along with the lack of relationship between % NISP cut-marked for each skeletal element and the relative utility of that element both lead to the

hypothesis that hominins were butchering the carcass parts that were available to them in an unbiased strategy, instead of butchering only the meatiest elements or only meaty upper limbs. This could indicate a low carcass encounter rate, assuming that carcasses or carcass parts were always butchered when encountered. Alternatively, this could indicate butchery in a low risk environment. There are high numbers of cut marks on limb midshafts at all three sites, but there are also high numbers of midshafts in the assemblages, so there are not statistically more cut marks on midshafts than other limb portions. However, the prevalence of cut marks primarily on midshafts does indicate a considerable amount of limb defleshing. Given this relatively intensive processing, which presumably required flake manufacture or at least resharpening, the lack of flakes or even flaking debris at the site is surprising.

Paleoenvironmental evidence indicates that hominins were conducting butchery activities in near shallow rivers with gallery forests (FwJj14B) swampy, seasonally flooded areas (FwJj14A and GaJi14), but also with more open, grassy components (FwJj14B). Butchered taxa include those preferring all of these different environments. The likelihood is that these three sites were each amenable to butchery activities by offering hominins particular resources, such as shade and water, but not stone raw material. The nearest raw material source to FwJj14A and FwJj14B is about 5 kilometers away, while the nearest raw material source to GaJi14 is about 15 kilometers away. The closest archaeological site in Ileret, FwJj1 (about 3-5 kilometers to the southeast) is dominated by flakes, many of which refit; this supports the notion that raw material distance may have influenced hominin behavior in this part of the Koobi Fora landscape. FxJj50, an Okote Member site from the Karari region of Koobi Fora, has significantly

less cut-marked limb shafts (though it also has many few limb shafts) and a much higher number of tooth-marked bones. Here, hominins seem to have relatively less access to meaty portions, and carnivores were more active, though whether carnivore and hominin activities were related is unclear.

Chapter Seven
Landscape-Scale Carnivore and Hominin Activity, Bed I and Lowermost Bed II, Olduvai Gorge

Introduction

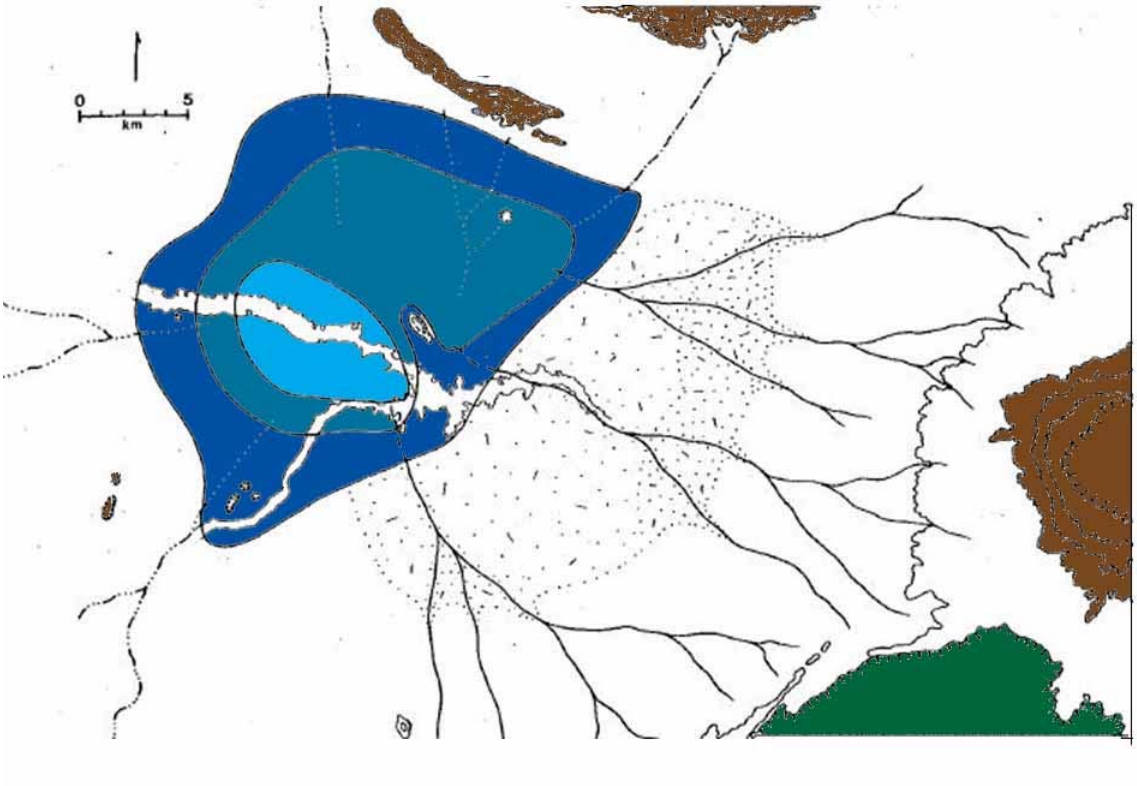
Olduvai Gorge: Setting and Brief History of Research, and Current Research Question

Olduvai Gorge is a ravine in the southeastern Serengeti Plain situated adjacent to the Rift Valley of northern Tanzania. The gorge consists of two branches: the Main Gorge, which begins at Lakes Masek and Ndutu and extends 46 km eastwards towards Olbalbal, and the Side Gorge, which originates in the uplands of Lemagrut Volcano to the south and joins the main gorge about 9 km west of Olbalbal (Cushing, 2002). It is surrounded by volcanic highlands to the south and east, and the Serengeti plains to the north and west (Figure 7.1).

Olduvai Gorge has a rich Plio-Pleistocene fossil, lithic, and hominin record preserve in its lacustrine and tuffaceous deposits which trace back to almost 2 million years (Figure 7.2). The paleontological significance of Olduvai was first recognized by Wilhelm Kattwinkel, a German entomologist, in 1911. Subsequently, geologist Hans Reck organized an expedition there in 1913, accompanied by a team including Louis Leakey. They divided the sedimentary deposits into five beds, numbered I-V from bottom to top. Louis and Mary Leakey continued to conduct research at Olduvai until the discovery of the FLK *Zinjanthropus* specimen by Mary in 1959 (Leakey, 1959) put it on the paleoanthropological map. Soon after that discovery, potassium-argon dating established the great antiquity of the *Zinj* level at 1.7-1.9 million years ago (Leakey *et al*., 1961). The Leakeys continued their research for at Olduvai for over another decade. The fossils, artifacts, and hominins they recovered have been the subject of intense

paleoanthropological research for decades, including that focused on reconstructing early hominin carnivory (e.g., Bunn and Kroll, 1986; Binford *et al*., 1988; Potts, 1988; Blumenschine, 1995; Monahan, 1996; Capaldo ,1997; Selvaggio, 1998).

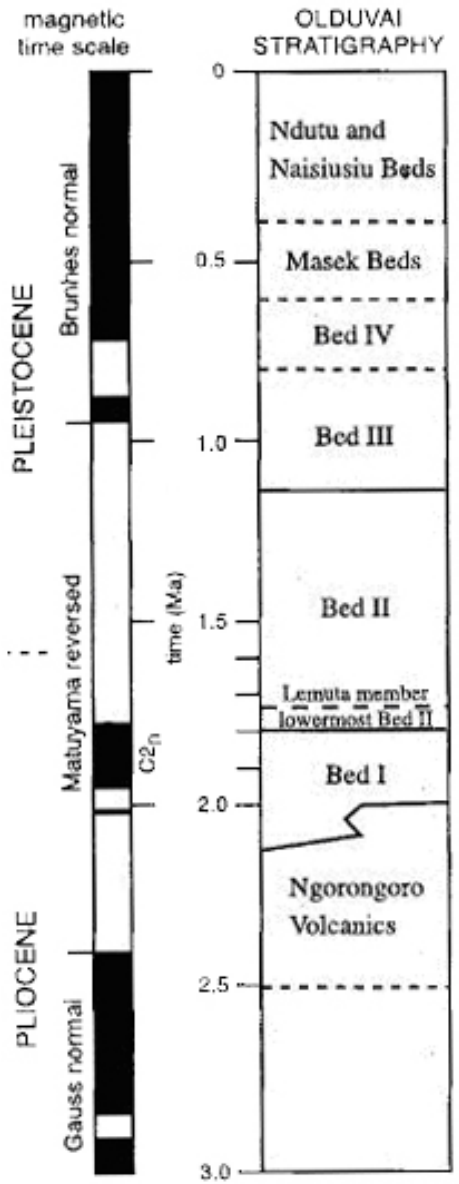
Figure 7.1. Location and paleogeography of Olduvai Gorge. After Peters and Blumenschine (1995: 327), based on Hay (1976) and several 1:50 000 scale topographic maps. From lightest to darkest, the blue is the perennial saline lake Olduvai, the intermittently dry portion of the lake, and the intermittently flooded lake margin. The brown are various hills and mountains. The green is Ngorongoro crater, and the black lines emanating from the lake are drainage lines.



Current fieldwork at Olduvai Gorge, conducted by the Olduvai Landscape Paleoanthropology Project (OLAPP), is focused on reconstructing hominin land use patterns during Bed I (1.84-1.79 Ma, Blumenschine *et al*., 2003; Walter *et al*., 1991; Tamrat *et al*.,1995) and lowermost Bed II, between Tuff IF and IIA or the Lemuta Member (1.75-1.70 Ma, Manega, 1993; Hay, 1996). This study includes a rich array of

geological, paleoenvironmental, paleoanthropological, archaeological, faunal, and taphonomic studies (e.g. Cushing, 2002; Blumenschine *et al*., 2003; Liutkus *et al*., 2005; Tactikos, 2005; Bamford *et al*., 2006; Njau and Blumenschine, 2006). This study is a part of the larger OLAPP research project, and was conducted under the direction of R. Blumenschine.

Figure 7.2. Chronostratigraphy of Olduvai Gorge with a paleomagnetic time scale. From Ashley and Driese, 2000: 1066.



Amy Cushing's dissertation (2002) on the fauna recovered from OLAPP's excavations between 1989 and 1997 provides much of the framework for this part of my dissertation. She used these landscape faunal assemblages to test predictions about hominin land use behaviors. She concluded that hominins in upper Bed I and lowermost Bed II times did not permanently inhabit the excavated areas, but instead may have used them seasonally or daily, as they did not offer year-round overnight refuges. This study will build on her work, as well as new fine-scale habitat reconstructions, asking specific questions of the carnivore traces in the faunal assemblages that are relevant to early hominin foraging patterns.

Specifically, this study investigates:

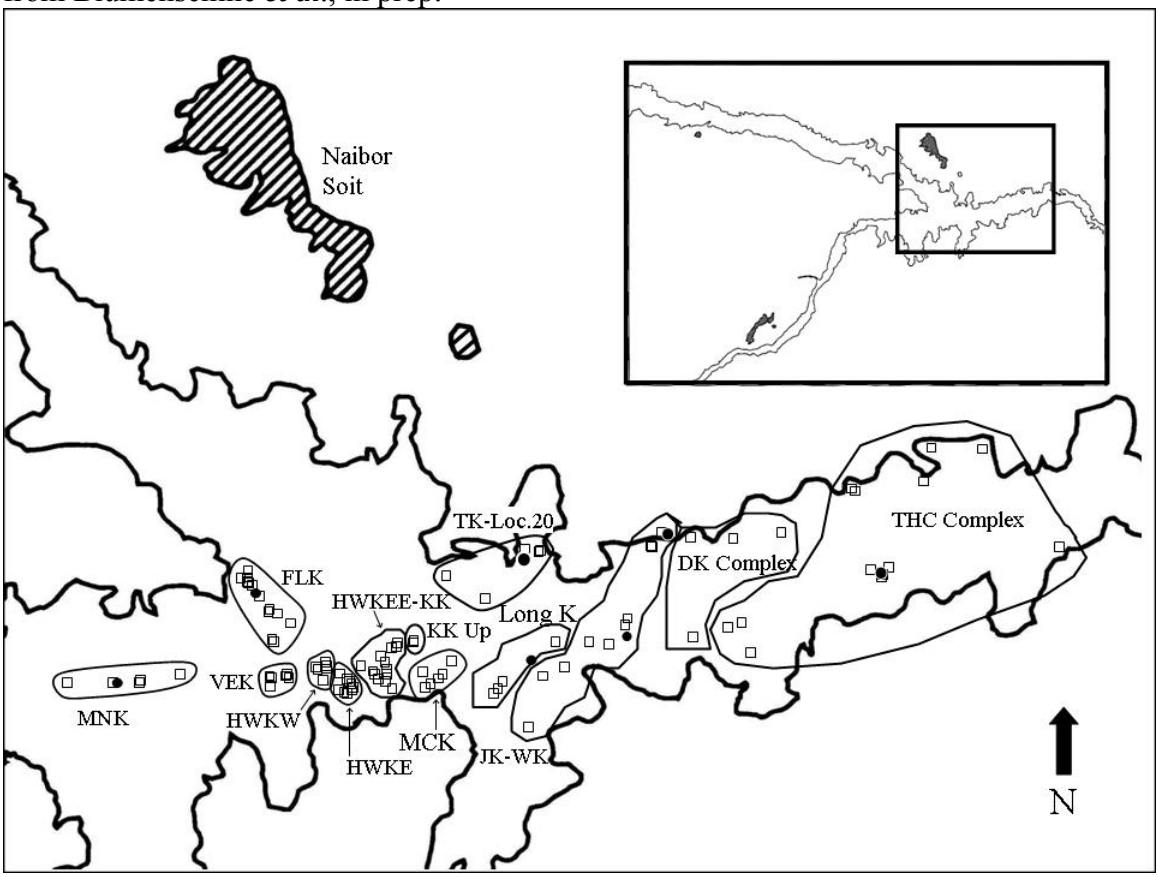
1. If, and how, the intensity of carnivore activity (measured by carnivore bone damage) varied through time during lowermost Bed II.
2. If there are differences in relative activties of particular carnivores in different parts of the landscape (geographic locales) during lowermost Bed II times, and if these differences are predicted by the hypothesized vegetation of these different geographic locales.
3. If carnivore gross bone damage and tooth marking can be used to identify carnivore-specific damage to particular prey individuals in landscape faunal assemblage.

Habitat Reconstructions and Predicted Carnivore Abundances

For this analysis, habitat reconstructions are at the scale of the geographic locale, currently used by the Olduvai Landscape Paleoanthropology (OLAPP) project. These geographic locales take several variables into account, including lithology and faulting,

and are defined by geographic proximity of trenches. A map of these geographic locales with constituent trenches, is shown in Figure 7.3. One of OLAPP's working, hypothetical reconstructions of the vegetation in each of these locales is sensitive to the synsedimentary faulting that compartmentalized the lowermost Bed II eastern basin (H. Stollhofen, unpublished).

Figure 7.3. Map of the geographic locales at Olduvai with trench groupings. Modified from Blumenschine *et al*., in prep.



One working hypothesis is that during lake regressions, this faulting may have at times created enough relief on the upthrown foot walls of the faults to support trees, while the downthrown hanging walls are more likely to have had open marshy terrain (R. Blumenschine, pers. comm.). Based on these two types of vegetation regimes, different relative carnivore abundances would be predicted. On the upthrown foot walls in a

wooded environment, the carnivore community would likely consist of lions, leopards, possibly spotted hyaenas, and an absence of cheetah. In contrast, on the downthrown hanging walls, the predicted carnivore community is dominated by cheetah and spotted hyaena, possibly with lions, but an absence of leopards. The current geomorphological reconstruction of the lowermost Bed II landscape posits FLK/VEK and TK-Loc 20 as high foot walls, HWKE and MCK as intermediate, and HWKEE-KK, Long K, and MNK as low hanging walls. JK-WK, DK, and THC are progressively increasing in altitude across the alluvial plain towards Mt. Olmoti to the east.

Methods and Materials

The entire sample I examined is comprised of 2196 faunal specimens. The sample was selected to maximize numbers of bones in each geographic locale for which taphonomic data were collected in the allotted data collection time frame. This meant that a random subset of bones from geographic locale was analysed, mainly focusing on long bones. Samples focused on lowermost Bed II, in order collect data on the largest possible landscape-scale sample, but included larger samples from individual trenches and levels from Bed I in order to test the utility of a novel data collection and analysis technique which uses individuals prey carcasses or carcass parts as the unit of analysis. This will be described in more detail below. The sub-sample on which taphonomic data are reported excludes teeth (N = 485), tortoise carapace (N = 102), bird (N = 62), fish (N = 17), micromammal, including rodent (N = 8), and crocodile (N = 4), for a total of 1518. The distribution among the geographic locales of specimens on which taphonomic data was collected is listed in Table 7.1.

Zooarchaeological data collected on each specimen includes the same data as were collected for the Koobi Fora faunal assemblages (see Appendix 6), but also included four columns for carnivore damage level (following Table 3.2) where applicable: proximal, shaft, distal (for long bones), and overall damage level (for non-long bone specimens) (Table 6.2). I measured tooth marks to the nearest hundredth of a centimeter using Mitutoyo digital calipers (Table 6.3). All specimens with carnivore tooth marks (NISP = 21) also displayed gross bone damage (NISP = 153).

Table 7.1. Distribution of Olduvai study sample on which taphonomic data were collected (NISP = 1171) by locale, trench, and level. Pre- or post-incision refers to the temporal location of the sample relative to valley incision that occurred during lowermost Bed II times. When the temporal position of the horizon that the sample is from is uncertain relative to the incision, the cell says "mixed". Samples from the Lower Augitic Sandstone, upper-middle Bed I, middle Bed II, and the Lemuta member are indicated in the cell with "n/a" footnotes.

Locale	Trench	Level	NISP	Pre or Post Incision
DK	52	14	11	Pre-
	73	13	1	Pre-
	74	3	1	Pre-
	75	3	1	Pre-
		5	1	Pre-
		6	1	Pre-
		7	1	Pre-
		8	3	Pre-
		9	4	Pre-
		10	1	Pre-
		11	1	Pre-
		12	7	Pre-
FLK	100	4	18	Pre-
		5	33	Pre-
HWKE	104.5	4	149	Pre-
	104.6	2	67	Post-
HWKEE-KK	25	6	2	Pre-
	26	2	1	Post-
	107	2	2	Post-
		3	3	Post-
	120	2	16	Pre-
		3	12	Pre-
		4	7	Pre-
JK-WK	46	4	11	Pre-
		12	8	Pre-
		13	2	Pre-
	81	1	24	Pre-
		4	1	Pre-

	84	1	17	Pre-
	86	1	18	Post-
		2	7	Post-
		4	2	Pre-
		9	2	Pre-
	98	5	31	Pre-
		7	6	Pre-
	125	1	1	n/a[1]
		6	10	Pre-
KK	119	3	1	Pre-
Loc. 64	57	3	204	n/a[2]
	57A	3	103	n/a[2]
	65	3&4	554	n/a[2]
Long K	51	2	4	Post-
		3	15	Post-
		4	6	Post-
		6	14	Pre-
		8	1	Pre-
MCK	50	5	5	Post-
MNK	19	1Z	2	Mixed
	101	3	2	Mixed
		4	2	Pre-
	102	1	1	Post-
		4	1	Post-
		7	1	Mixed
THC	56	2	2	Pre-
		7	11	Pre-
	78	4	1	Pre-
	79	4	2	Post-
	80	1	1	Post-
		5	6	Pre-
	85b	2	2	Post-
		4	1	Post-
		7	1	Post-
TK-Loc20	41	1	5	Pre-
		1B	10	Pre-
		4	9	Pre-
		8	10	Pre-
	42	3	1	n/a[3]
		4	1	n/a[3]
		5	5	n/a[3]
		9	1	n/a[3]
	123	1	15	n/a[4]
		2	2	n/a[4]
	124B	7	1	Pre-
	124C	5	1	Pre-
		6	4	Pre-
VEK	21	1	17	Post-
		2	10	Pre-

[1]from the Lower Augitic Sandstone
[2]from upper middle Bed I (between tuff IC and IF), on the western side of the lake
[3]from middle Bed II
[4]from the Lemuta Member

Table 7.2. Specimens from the Olduvai sample with carnivore gross bone damage. Specimens identified to "Vertebrate" are probable, but not definite, mammal specimens. NID is not identifiable to skeletal element and portion. Where carnivore tooth marks are not listed, none were present. Length, width, and depth of tooth marks are measured to the nearest hundredth of a centimeter. Carnivore damage levels for long bone portions are 1 = tooth marks only; 2 = marginal gnawing; 3 = heavy gnawing to fragmentation; 4 = destroyed. Description of overall damage level for all other skeletal elements is in Table 3.2. Skeletal element abbreviations are in Appendix 3.

							Carnivore Damage Level			
Locale	Trench	Level	Specimen #	Taxon	Size	Skeletal Element, Portion	PX	SH	DS	Overall
DK	75	8	18	Mammal	1	LB, MSH	4	3	4	
DK	75	9	22	Mammal	1	LB, MSH	4	3	4	
DK	52	14	2	Mammal	1/2	LB, MSH	4	3	4	
DK	52	14	4	Vertebrate	2/3	HUM, MSH	4	3	4	
DK	52	14	7	Vertebrate	indet	NID	4	3	4	
DK	52	14	3	Vertebrate	1	LB, MSH	4	3	4	
DK	52	14	5	Vertebrate	1	LB, MSH	4	3	4	
DK	52	14	6	Vertebrate	2	LB, MSH	4	3	4	
DK	73	13	1	Vertebrate	3/4	LB, MSH	4	3	4	
DK	75	6	16	Vertebrate	indet	LB, MSH	4	3	4	
DK	75	8	20	Vertebrate	indet	LB, EPI (unfused)	4	4	3	
DK	75	9	23	Bovidae	1	RAD, DSH – DS	4	4	3	
DK	75	10	25	Mammal	5	PHA	0	3	4	
DK	75	11	26	Vertebrate	1	LB, MSH	4	3	4	
DK	75	12	32	Mammal	1/2	LB, MSH	4	3	4	
DK	75	12	29	Vertebrate	indet	LB, MSH	4	3	4	
DK	75	12	30	Vertebrate	indet	LB, MSH	4	3	4	
DK	75	12	31	Vertebrate	indet	LB, MSH	4	3	4	
DK	75	12	33	Vertebrate	indet	LB, MSH	4	3	4	
FLK	100	4	169	*Kolpochoerus afarensis*	2	MAXT				4
FLK	100	4	173	Mammal	1	LB, MSH	4	3	4	
FLK	100	4	149	Mammal	3/4	LB, MSH	4	3	4	
FLK	100	4	168	Mammal	3/4	LB, MSH	4	3	4	
FLK	100	4	159	Mammal	2/3	RIB, SH				3
FLK	100	4	158	Mammal	1/2	RIB, SH				3
FLK	100	5	199	Mammal	1	FEM, DS	4	4	3	
FLK	100	5	194	Mammal	3A	FEM, MSH	4	3	4	
FLK	100	5	200	Mammal	2/3	LB, MSH	4	3	4	
FLK	100	5	196	Mammal	1	LB, MSH	4	3	4	
FLK	100	5	177	Mammal	1	LB, MSH	4	3	4	

FLK	100	5	195	Mammal	1	ULB, MSH	4	3	4	
FLK	100	5	176	Mammal	2/3	RIB, SH – DS				3
FLK	100	5	201	Mammal	indet	RIB, SH				3
FLK	100	5	202	Mammal	indet	RIB, SH				3
HWKE	104.5	4	784B	Bovidae	2/3A	FEM, PX – MSH				1
HWKE	104.5	4	784A	Bovidae	2/3A	FEM, MSH – DS				2
HWKE	104.5	4	696	Bovidae	3	FEM, MSH – DSH				1
HWKE	104.5	4	698	Bovidae	2/3A	MAND, HRAM				3
HWKE	104.5	4	653	Bovidae	2/3A	MC, CO				1
HWKE	104.5	4	821	Bovidae	1	THO, VT				1
HWKE	104.5	4	700	Suidae	2/3	RAD, PX – MSH				1
HWKE	104.6	2	5	Suidae	2	CER, VT				1
HWKE	104.6	2	8A	Bovidae	3A	FEM, DSH – DS				2
HWKE-KK	120	2	44	Vertebrate	1/2	LB, MSH	4	3	4	
HWKE-KK	120	2	46	Vertebrate	1/2	LB, MSH	4	3	4	
HWKE-KK	120	2	49	Vertebrate	1/2	LB, MSH	4	3	4	
HWKE-KK	120	2	51	Vertebrate	1/2	LB, MSH	4	3	4	
HWKE-KK	120	2	53	Vertebrate	1/2	LB, MSH	4	3	4	
HWKE-KK	120	2	56	Vertebrate	1/2	LB, MSH	4	3	4	
HWKE-KK	120	2	54	Vertebrate	1/2	LB, MSH	4	3	4	
JK-WK	98	5	31	Mammal	indet	LB, MSH	4	3	4	
JK-WK	98	5	20	Mammal	1/2	LB, NEF	4	3	4	
JK-WK	46	4	8	Mammal	1	FEM, MSH – DS	4	3	0	
JK-WK	46	4	2	Mammal	1	LB, MSH	4	3	4	
JK-WK	46	4	3	Mammal	1	LB, MSH	4	3	4	
JK-WK	46	4	9	Mammal	1	LB, MSH	4	3	4	
JK-WK	46	12	28	Mammal	1/2	LB, MSH	4	3	4	
JK-WK	86	1	3	Vertebrate	2/3	LB, MSH	4	3	4	
JK-WK	86	1	15	Vertebrate	1/2	LB, MSH	4	3	4	
JK-WK	86	1	21	Vertebrate	1/2	LB, MSH	4	3	4	
JK-WK	86	1	17	Vertebrate	1/2	LB, MSH	4	3	4	
JK-WK	125	6	13	Bovidae	3A	MP, DS	4	4	3	
Loc. 64	57	3	236	Bovidae	2	HUM, MSH – DS	4	3	1	
Loc. 64	57	3	802	Bovidae	3B	HUM, MSH	4	3	4	
Loc. 64	57	3	665	Bovidae	3A	RAD, PX – MSH	1	3	4	
Loc. 64	57	3	661	Bovidae	1	ULN, PX – MSH	3	3	4	
Loc. 64	57	3	780	Ungulate	5	RAD, PSH – MSH	4	3	4	
Loc. 64	57A	3	319	Bovidae	3A	RAD, PX – MSH	1	3	4	
Loc. 64	57	3	663	Bovidae	1	FEM, PX	3	4	4	

Loc. 64	57	3	575	Bovidae	2/3A	FEM, MSH – DSH	4	3	4	
Loc. 64	57	3	828	Bovidae	1	HUM, DS	4	4	3	
Loc. 64	57	3	664	Bovidae	2	HUM, DSH – DS	4	4	3	
Loc. 64	57	3	667	Bovidae	2/3A	HUM, DSH – DS	4	4	3	
Loc. 64	57	3	666	Bovidae	3A	HUM, MSH – DS	4	3	0	
Loc. 64	57	3	240	Bovidae	3A	HUM, MSH – DS	4	3	0	
Loc. 64	57	3	670	Bovidae	1	HUM, MSH – DSH	4	3	4	
Loc. 64	57	3	162	Bovidae	3A	MC, MS – DS	4	3	0	
Loc. 64	57	3	662	Bovidae	3A	MC, PX – MSH	3	3	4	
Loc. 64	57	3	269	Bovidae	2/3A	MP, DS	4	4	3	
Loc. 64	57	3	760	Bovidae	3A	MT, MSH – DS	4	3	0	
Loc. 64	57	3	763	Bovidae	3A	MT, MSH – DS	4	3	0	
Loc. 64	57	3	160	Bovidae	3B	MT, PX – MSH	0	3	4	
Loc. 64	57	3	158	Bovidae	3B	TIB, MSH – DS	4	3	0	
Loc. 64	57	3	155	Bovidae	1/2	ULN, MSH – DS	4	3	0	
Loc. 64	57	3	756	Bovidae	3B	ULN, PX – MSH	2	3	4	
Loc. 64	57	3	566	Equidae	3B/4	FEM, MSH	4	3	4	
Loc. 64	57	3	889	Equidae	3B/4	MC, PX – MSH	0	3	4	
Loc. 64	57	3	161	Equidae	3B/4	RAD, DSH – DS	4	3	0	
Loc. 64	57	3	786	Mammal	2	ULN, PX – MSH	2	3	4	
Loc. 64	57	3	301	Primate	2	HUM, MSH – DSH	4	0	4	
Loc. 64	57	3	697	Ungulate	2/3	LB, DS	4	4	3	
Loc. 64	57A	3	405	Bovidae	1	HUM, MSH – DSH	4	3	4	
Loc. 64	57A	3	171	Bovidae	2/3A	MC, PX – PSH	3	3	4	
Loc. 64	57A	3	244	Bovidae	1	MT, PX – MSH	0	3	4	
Loc. 64	57A	3	71	Bovidae	1/2	MT, PX – MSH	2	3	4	
Loc. 64	57A	3	20	Bovidae	2	MT, PX – MSH	3	4	4	
Loc. 64	57A	3	315	Bovidae	1	RAD, PX – MSH	0	3	4	
Loc. 64	57A	3	434	Bovidae	3B	RAD, MSH – DS	4	3	0	
Loc. 64	57A	3	31	*Lepus*	1	FEM, PX – MSH	0	3	4	
Loc. 64	57A	3	336	Primate	2	HUM, MSH – DS	4	3	0	
Long K	51	3	16	Mammal	2/3	LB, MSH	4	3	4	
Long K	51	3	19	Vertebrate	indet	NID				1
Long K	51	3	18	Equidae	4	LB, MSH	4	3	4	
Long K	51	3	15	Mammal	2/3	LB, MSH	4	3	4	
Long K	51	3	17	Mammal	2/3	LB, MSH	4	3	4	
Long K	51	3	22	Mammal	2/3	LB, MSH	4	3	4	
Long K	51	3	26	Mammal	1	LB, MSH	4	3	4	
Long K	51	6	53	Bovidae	2	HUM, DS	4	4	3	

MNK	19	1Z	1	Mammal	3	LB, EPI				3
MNK	101	3	8	Mammal	3	LB, MSH	4	3	4	
MNK	101	4	11	Mammal	2B/3A	LB, MSH	4	3	4	
THC	56	7	6	Mammal	1/2	HUM, MSH	4	3	4	
THC	56	7	7	Mammal	1/2	LB, MSH	4	3	4	
THC	56	7	8	Mammal	2/3	LB, MSH	4	3	4	
THC	56	7	10	Mammal	2/3	LB, MSH	4	3	4	
THC	56	7	11	Mammal	2/3	LB, MSH	4	3	4	
THC	56	7	12	Mammal	2/3	LB, MSH	4	3	4	
THC	56	7	13	Mammal	1/2	LB, MSH	4	3	4	
THC	56	7	14	Mammal	1/2	LB, MSH	4	3	4	
THC	56	7	15	Mammal	1/2	ILB or LLB, MSH	4	3	4	
THC	56	7	16	Mammal	3	ILB or LLB, MSH	4	3	4	
THC	78	4	2	Mammal	2/3	LB, MSH	4	3	4	
THC	79	4	2	Mammal	3/4	LB, MSH	4	3	4	
THC	80	1	1	Mammal	2/3	LB, MSH	4	3	4	
THC	80	5	2	Mammal	1/2	LB, MSH	4	3	4	
THC	80	5	3	Mammal	2/3	LB, MSH	4	3	4	
THC	80	5	4	Mammal	2/3	LB, MSH	4	3	4	
THC	80	5	5	Mammal	2/3	LB, MSH	4	3	4	
THC	80	5	6	Mammal	2/3	LB, MSH	4	3	4	
THC	80	5	7	Mammal	2/3	LB, MSH	4	3	4	
THC	85b	2	5	Mammal	indet	LB, EPI – SH	4	3	4	
TK-Loc 20	41	1	12	Vertebrate	2/3	LB, MSH	4	3	4	
TK-Loc 20	41	1	3	Vertebrate	2/3	LB, MSH	4	3	4	
TK-Loc 20	41	1	14	Vertebrate	2/3	LB, MSH	4	3	4	
TK-Loc 20	41	4	47	Vertebrate	2/3	LB, MSH	4	3	4	
VEK	21	1	301	Bovidae	2B/3A	MP, DSH – DS	4	4	3	
VEK	21	1	264	Equidae	3/4	FEM, MSH	4	3	4	
VEK	21	1	271	Mammal	2/3	LB, MSH	4	3	4	
VEK	21	1	17	Mammal	3	LB, MSH	4	3	4	
VEK	21	1	15	Mammal	3	LB, MSH	4	3	4	
VEK	21	1	85	Mammal	1/2	LB, MSH	4	3	4	
VEK	21	1	11	Mammal	1/2	LB, MSH	4	3	4	
VEK	21	1	113	Mammal	3/4	ILB or LLB, MSH	4	3	4	
VEK	21	1	84	Mammal	1/2	THO, R				3
VEK	21	2	200	Bovidae	2B/3A	MC, PX – DSH	0	0	4	
VEK	21	2	291	Bovidae	3B/4	MP, DS	4	4	3	
VEK	21	2	297	Bovidae	1	MT, PX – MSH	0	3	4	

VEK	21	2	284	Bovidae	1	MT, PX – MSH	4	3	4	
VEK	21	2	298	Bovidae	1	MT, PX – MSH	4	3	4	
VEK	21	2	299	Mammal	2/3	LB, MSH	4	3	4	

Table 7.3. Specimens from the Olduvai sub-sample with carnivore tooth marks. Length and width of tooth marks are measured to the nearest hundredth of a centimeter. See Table 7.2 caption for more details.

Locale	Trench	Level	Specimen #	Tooth Mark Type	Skeletal Element	Location of Tooth Mark	Length	Width	Length	Width	Length	Width	Length	Width
DK	75	8	18	score	LB	MSH	1.55	0.09						
DK	75	9	22	score	LB	MSH	2.52	0.38						
HWKE	104.5	4	784B	scores	FEM, PX	PSH	3.38	0.18	9.79	0.51				
HWKE	104.5	4	784A	pits	FEM, DS	ANT	1.04	1.31	1.31	1.77	1.07	1.31	4.81	1.78
HWKE	104.5	4	696	pit	FEM	MSH, POST/LAT	4.65	4.18						
HWKE	104.5	4	698	score	MAND	HRAM, MED	2.04	0.18						
HWKE	104.5	4	653	score	MC	MSH	2.60	0.02						
HWKE	104.5	4	821	scores	THO	V	2.86	0.02	3.71	0.76				
HWKE	104.5	4	700	scores	RAD	PSH + MSH	3.28	0.48	8.23	0.41				
HWKE	104.6	2	5	score	CER	V, INF	4.58	0.09						
JK-WK	98	5	31	score	LB	MSH	2.14	0.17						
JK-WK	98	5	20	scores	LB	NEF	2.80	0.12						
Loc. 64	57	3	236	scores	HUM	DSH	3.32	0.50						
Loc. 64	57	3	802	pit	HUM	MSH, DSH	2.28	1.06						
Loc. 64	57	3	802	score	HUM	MSH, DSH	3.35	0.87						
Loc. 64	57	3	665	pits	RAD	PX, MSH	2.87	1.94	6.25	5.96				
Loc. 64	57	3	661	puncture	ULN	PX	9.07	9.03						
Loc. 64	57	3	780	score	RAD	MSH	5.34	1.79						
Loc. 64	57A	3	319	scores	RAD	MSH	5.54	0.45						
Long K	51	3	16	score	LB	MSH	6.31	0.41						
Long K	51	3	19	score	NID	n/a	1.52	0.10						

Different methods were used to investigate the three research questions introduced above.

1. Did the intensity of carnivore activity change through time during lowermost Bed II?

To address this question, two different scales of analyses were conducted using the same data set. To look at change through time, a comparison of the "pre-incision" and "post-incision" sub-assemblages was done. The specimens falling into each sub-assemblage ("pre", N = 154, and "post", N = 487,) can be found in Table 7.1, in the last column. Specimens whose Pre/Post designation is "Mixed" or "n/a" were not included. The three types of data used for analysis are 1) proportion of specimens with carnivore gross bone damage, and 2) long bone epiphysis to shaft ratio of size 1-4 mammals.

2. Does the activity of different carnivore taxa or ecotypes vary in different geographic locales? If so, is this variability predicted by the hypothesized vegetation of the locales?

To address these questions, I mainly used different data than above. The subset of carnivore damaged and tooth-marked specimens (Tables 7.2 and 7.3) was analyzed for carnivore gross bone damage (on a prey size-specific basis, following Chapter 3) and tooth mark location and dimensions (following Chapter 4). This time, I calculated epiphysis to shaft ratios for size 1-2 and 3-4 prey separately. The former is more indicative of lion or leopard modification, and the latter is indicative of spotted hyaena modification. Geographic localities from three fault compartments were used, as follows: FLK/VEK – HWKE – HWKEE-KK; TK-Loc 20 – MCK – Long K; and JK-WK – DK – THC.

3. Can carnivore-specific gross bone damage and tooth marking be used to identify consumption of individual prey animals in the landscape assemblage?

The data collected to answer this question were similar to #2, but the methodologies used during data collection and analysis were slightly different. During data collection, all of the bones from each trench and level were examined together to determine if any prey carcass units (one or more bones from a single prey individual) could be identified. Carcass units were identified based on snug fit of joint articulations and morphometric compatibility of non-articulating bones. The prey carcass unit or individual, rather than the bone specimen, is the unit of analysis. This methodology was only used on the following locale samples: HWKE Trench 104.5 Level 4; and Trench 104.6 Level 2 from lowermost Bed II, and Loc. 64 Trench 57 Level 3 from middle-upper Bed I. I chose these samples because they have some of the highest NISPs of any locales in my Olduvai sample. Time constraints limited the Loc. 64 sample to long bones only.

Results

1. Does the intensity of carnivore activity vary through time during lowermost Bed II?

The frequency of carnivore damaged bone did not change between pre- and post-valley incision times: 16 to 17% of the bones had carnivore damage, including both tooth marking and gross bone damage (Table 7.4). This implies that carnivore activity did not vary through time during lowermost Bed II. However, the long bone epiphysis to shaft ratio decreased from .25 in the pre-valley incision sub-sample to .04 in the post-valley incision sub-sample, meaning that there were relatively fewer epiphyses in the latter. These proportions include specimens with recent breaks and poorly preserved surfaces.

Therefore, the actual proportion of carnivore damaged and tooth-marked bones is likely to be much higher if these specimens are excluded, as has been found by R. Blumenschine and J. Njau (unpublished data).

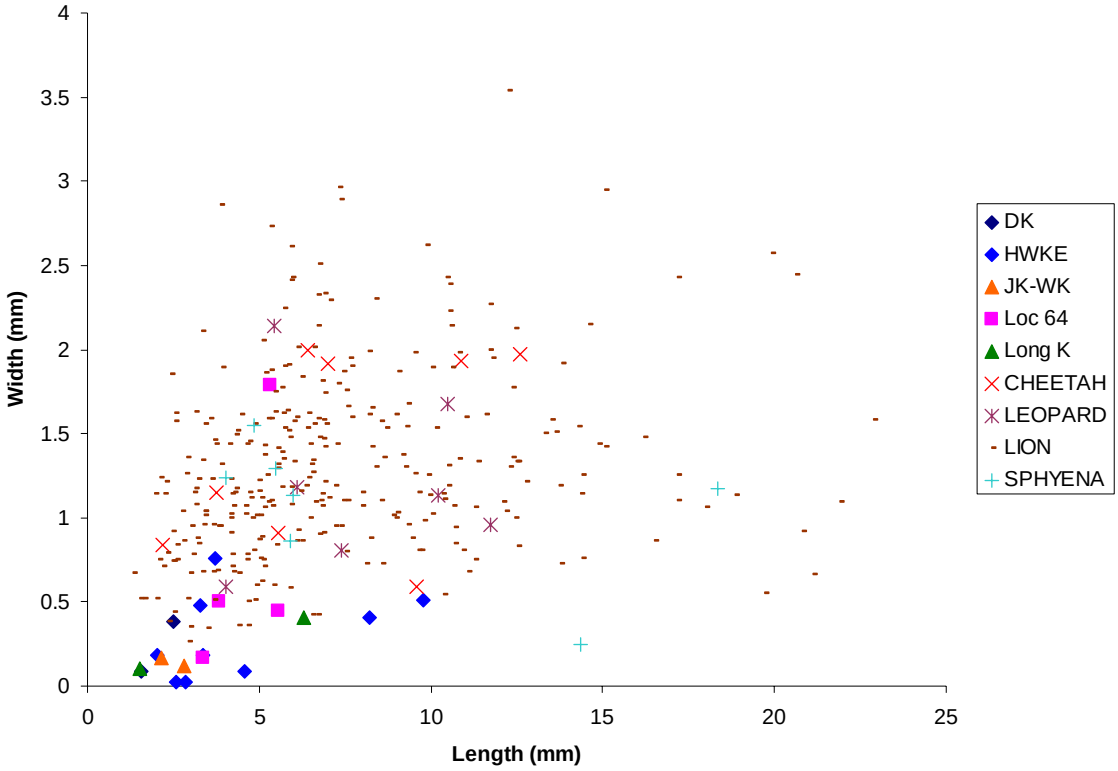
Table 7.4. Characteristics of carnivore damage on pre- and post-valley incision phase sub-samples of lowermost Bed II Olduvai fauna. Epiphysis to shaft ratio was calculated by dividing the number of epiphyses by the number of shafts.

	NISP	NISP with Carnivore Gross Bone Damage	% with Carnivore Gross Bone Damage	Number of Long Bone Epiphyses	Number of Long Bone Shafts	Epiphysis to Shaft Ratio
Pre-Valley Incision	487	25	16%	42	165	.25
Post-Valley Incision	154	84	17%	3	74	.04

2. Does carnivore activity vary in different geographic locales? If so, is the variation predicted by the hypothesized vegetation of the locales?

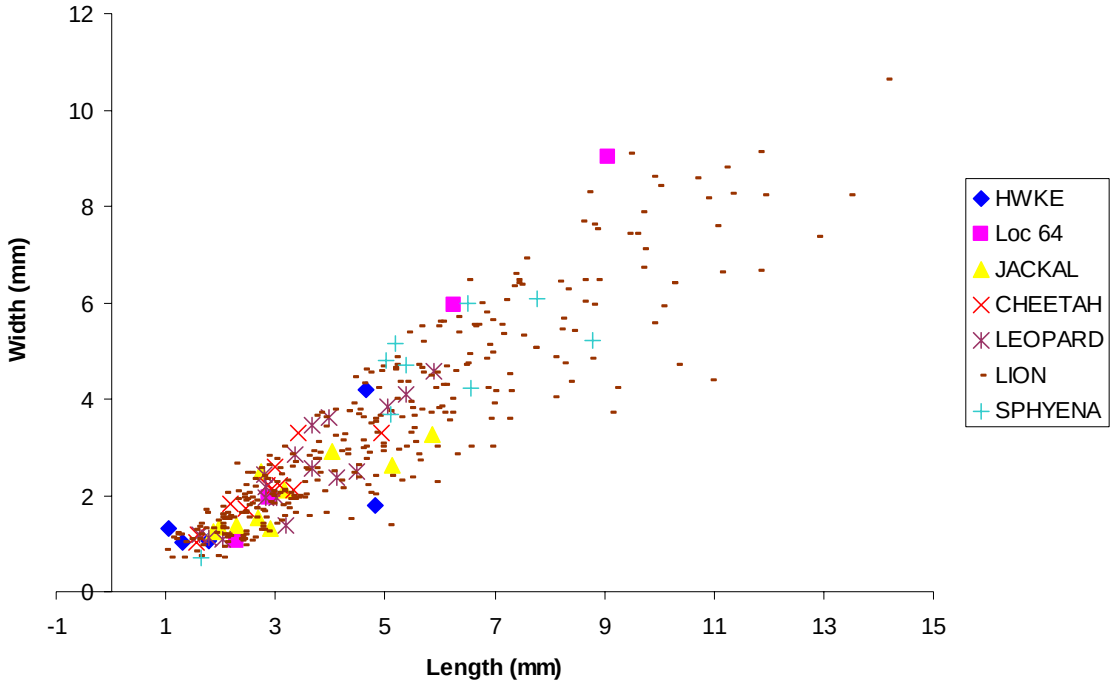
The number of tooth marks in this sub-sample of bones from Olduvai is small (N = 21, Table 7.3, Figures 7.4 and 7.5), and most tooth marks from this sample had measurements falling below the 95% confidence intervals of a single modern carnivore taxon that I measured. Possible carnivore taxa modifying bones at Olduvai during lowermost Bed II could only be identified from four tooth marks from HWKE. The length of one tooth score on a size 2 suid cervical vertebra from HWKE (4.58 mm) is within the low end of the 95% confidence interval range for spotted hyaenas (4.28 – 12.56 mm; Table 4.10), while the lengths of two others, one on a size 2 suid radius midshaft and one on a size 2/3 bovid femur proximal near-epiphysis, fell comfortably within this range (8.23 mm, 9.79 mm). However, these latter two scores are also within the 95% confidence interval of leopards and cheetahs, and the gross bone damage

Figure 7.4. Distribution of lengths and widths of tooth scores of modern carnivores, and tooth scores from the Olduvai sample. Measurements from both the modern and the Olduvai sample are of individual tooth marks.



patterns on the tooth-marked specimens do not preclude leopards from being the agents of bone modification. Therefore, a definitive identification of the carnivore that created these tooth marks is not possible. Nevertheless, the length (4.65 mm) and width (4.18 mm) of a tooth pit on a size 3 juvenile bovid femur midshaft from HWKE falls only within the 95% confidence interval of spotted hyaena, using both length (4.45 – 7.11 mm) and width (3.44 – 5.56 mm). Unfortunately, this sample does not help to identify which carnivores may have been modifying bones in any of the hanging walls or foot walls in the Olduvai sample. The tooth scores from Olduvai are short and narrow compared to my modern sample, which may be due to my choosing only the largest tooth scores on each modern bone to measure. Alternatively, the tooth scores at Olduvai could have been created by a carnivore for which I do not have a modern comparative sample.

Figure 7.5. Distribution of lengths and widths of tooth pits and punctures of modern carnivores, and tooth pits and punctures from the Olduvai sample. Measurements from both the modern and the Olduvai sample are of individual tooth marks.



The overall epiphysis to shaft ratio substantially decreases from FLK/VEK (.57) to HWKE (.20) to HWKEE-KK (.06), which what would be predicted by a decrease in spotted hyaenas (which destroy grease-rich epiphyses during consumption) over this gradient (Table 7.5). FLK/VEK is a hanging wall, which is predicted to have more wooded vegetation, supporting a lower spotted hyaena population than at HWKEE-KK, predicted to be more open and/or marshy with more spotted hyaenas. This relationship breaks down within prey size categories, due to small sample sizes. The epiphysis to shaft ratio at TK-Loc 20 (.10) is slightly lower than at Long K (.13), which follows the expected direction of change. Additionally, the proportion of bones with carnivore damage increased from 5% at TK-Loc 20 to 20% at Long K. The epiphysis to shaft ratio of size 1-2 long bones at Long K is the highest of any of the locales, at 1, but there are 10

Table 7.5. Characteristics of carnivore damage on foot and hanging wall sub-samples of three compartments of the lowermost Bed II Olduvai fauna. Subsamples are FLK+VEK – HWKE – HWKEE-KK, TK-Loc 20 – MCK – Long K, and JK-WK – DK – THC. Hanging walls are FLK/VEK and TK-Loc 20; HWKE and MCK are intermediate; and foot walls are MNK (just to the west of FLK/VEK), HWKEE, and Long K. The JK-WK, DK, THC compartment is slightly different, where the elevation likely increases slightly from former to latter. Possible carnivore ID from tooth mark refers to the species of carnivore which *may* have created a tooth mark or modified a bone in the assemblage from that locale, based on actualistic models outlined in this dissertation. Specimens originally classified as size 2/3 or 2B/3A are included in size 3-4 here. Specimens included in the overall epiphysis to shaft ratio calculation, but not in the calculations of epiphysis to shaft ratios of size 1-2 and 3-4 prey were of indeterminate size.

	NISP	Possible Carnivore ID from Tooth Mark	NISP with Carnivore Gross Bone Damage	% with Carnivore Gross Bone Damage	Number of Long Bone Epiphyses	Number of Long Bone Shafts	Epiphysis to Shaft Ratio	Number of Size 1-2 Long Bone Epiphyses	Number of Size 1-2 Long Bone Shafts	Size 1-2 Epiphysis to Shaft Ratio	Number of Size 3-4 Long Bone Epiphyses	Number of Size 3-4 Long Bone Shafts	Size 3-4 Epiphysis to Shaft Ratio
FLK+VEK	78	n/a	30	38%	12	21	0.57	1	11	0.09	0	18	0
HWKE	216	spotted hyaena or leopard	9	4%	17	84	0.20	2	15	0.13	0	2	0
HWKEE-KK	46	n/a	7	15%	1	16	0.06	1	11	0.09	0	3	0
TK-Loc 20	65	n/a	3	5%	2	21	0.10	0	3	0	1	16	0.6
MCK	5	n/a	0	0%	0	5	0	0	0	0	0	5	0
Long K	40	leopard	8	20%	2	16	0.13	2	2	1	0	10	0
JK-WK	140	n/a	12	9%	12	46	0.26	3	12	0.25	1	2	0.5
DK	33	n/a	19	58%	2	15	0.13	1	4	0.25	0	2	0
THC	27	n/a	20	74%	1	21	0.05	0	7	0	0	13	0
MNK	9	n/a	3	33%	0	7	0	0	4	0	0	3	0

size 3-4 long bone midshafts and no epiphyses; this also speaks to hyaenid activity. It seems that this compartment provisionally accords with the predicted differences in carnivore communities based on geographic locale vegetation reconstructions. However, these data include specimens with recent breaks, which may confound these calculations. The data from JK-WK, DK, and THC are more enigmatic. The proportion of carnivore damage on bones increases across the gradient from west to east (from 9% to 58% to 74%), but the epiphysis to shaft ratio decreases (from .26 to .13 to .05).

3. Can the consumption of individual prey animals in the landscape assemblage be identified from carnivore-specific gross bone damage and tooth marking?

Table 7.6 details butchery marks from the Olduvai sample, and Tables 7.7, 7.8, and 7.9 outline the results of the carcass unit-based analyses from HWKE (Trench 104.5 Level 4, and Trench 104.6 Level 2) and Loc. 64 (Trench 57 Level 4). Identification of the most likely consumer access scenario for each individual prey animal was based on presence and location of bone surface modifications (cut, percussion, and tooth marks); measurements of individual tooth marks; and prey size-based and skeletal elements combined with carnivore gross bone damage data (e.g., hyaenas are assumed to consume all or most of size 1 and 2 prey, and to destroy most limb epiphyses of size 3 prey). The individuals for which consumer access scenarios could be proposed will be discussed below. Tooth mark measurement data for modern carnivores are from Tables 4.10 and 4.15. This is a unique analytical method which has only been applied once before (R. Blumenschine, pers. comm.) to a sample of long bones from Trench 57. This analysis incorporates more detailed taxon-specific gross bone damage criteria, as well as tooth mark measurement data.

Table 7.6. Specimens with definite butchery marks from the Olduvai sub-sample. Skeletal element abbreviations are in Appendix 3.

							Butchery Mark		
Locale	Trench	Level	Specimen Number	Taxon	Size	Skeletal Element	Mark Type	Location	Description
HWKE	104.5	4	41	Mammal	indet	LB MSH	CM	MSH	single long slice mark, longitudinal
HWKE	104.5	4	792	Bovidae	2/3A	ULN	CM	PSH	3 short transverse cut marks, posterior, likely from disarticulation
HWKE	104.5	4	644	Mammal	2/3A	RIB SH	CM	SH	good patch of cut marks
HWKE	104.5	4	819	Ungulate	2/3A	LB EPI + NEF	CM	NEF	patch of several oblique cut marks
HWKE	104.5	4	700	Suid	3A	RAD PX – MSH	CM	MSH	cut mark with internal striae, anterior-lateral MSH
Loc. 64	57	3	802	Bovidae	3B	HUM, MSH	CM	MSH	single long curving cut mark, posterior
Loc. 64	57	3	662	Bovidae	3A	MCM, PX – MSH	CM	PX	patch of transverse cut marks at neck, anterior
Loc. 64	57	3	155	Bovidae	1/2	ULN, MSH – DS	PM	MSH	percussion pit and separate but nearby patch of striae on medial MSH
Loc. 64	57	3	566	Equidae	3B/4	FEM, MSH	CM	MSH	patch of cut marks, oblique
Loc. 64	57	3	822	Mammal	2	LB, MSH	CM	MSH	2 patches of cut marks, one emanating from edge of bone
Loc. 64	57	3	600	Mammal	1/2	RIB, SH	CM	SH	one good slice mark with multiple internal striae
Loc. 64	57	3	780	Ungulate	5	RAD, PSH – MSH	PM	PSH, MSH	battering with striae PSH POST-MED; striae POST- MSH at green broken edge
Loc. 64	65	3&4	247	Mammal	indet	NID	CM	n/a	patch of 3-4 slice marks, slightly worn
Loc. 64	65	3&4	582	Ungulate	3/4	ILB MSH	CM	MSH	long double striation
Loc. 64	57A	3	71	Bovidae	1/2	MT PX – MSH	PM	MSH	percussion striae medial SH, battering lateral SH
Loc. 64	57A	3	31	*Lepus*	1	FEM PX – MSH	CM	PSH	single short oblique cut mark, anterior

Table 7.7. Carcass parts from individual prey specimens from HWKE, Trench 104.5, Level 4 (lowermost Bed II), with possible consumer access scenarios based on carnivore and hominin bone modification. Specimen numbers are listed in parentheses after the skeletal element description. Most likely consumer access scenario listed is for entire individual, not for any single skeletal element. PX = proximal epiphysis; PNEF = proximal near epiphysis; MSH = midshaft; DNEF = distal near epiphysis; DS = distal

Prey Individual	Most Likely Consumer Access Scenario	Skeletal Element	Bone Modification
Size 1 bovid	Single or small group of lions, or leopard, bulk defleshing; possibly followed by hominin marrow extraction and/or skinning	Isolated palate (813B)	None
		Unfused thoracic vertebral body with no spine (821)	2 tooth scores on superior body
		Radius DNEF (781)	Green break
		First phalanx, complete (637)	Possible percussion pit with striae, anterior; 2 possible cut marks, anterior DS condyle
		Third phalanx, complete (624)	None
cf. *Theropithecus oswaldi*	Unknown	Palate fragment with right M^2 and M^3 (812)	None
		Palate fragment with right M^2 and M^3 (807)	None
Size 2/3A bovid, immature (cf. *Parmularius altidens)*	Single or a few lions, or leopard, bulk defleshing; followed by hominin disarticulation	Horizontal ramus of mandible with dM_1, M_1, M_2, M_3, horizontal ramus (708)	Patch of several light tooth marks (could be crocodile?); sedimentary abrasion
		Thoracic vertebra without spine (824)	None
		Left femur, complete (748A+B)	Tooth score, posterior neck of greater trochanter; tooth score, anterior, towards greater trochanter; several small tooth pits and marginal gnawing on anterior DS articulation
		Right ulna, PX to MSH (792)	3 short transverse cut marks, posterior, PX end; very weathered/exfoliated
		Left radius, complete (777)	Root etching; ambiguous marks inferior to number and on anterior MSH
		Scaphoid, complete (806)	None
		Lunate, complete (818)	None
		Left metatarsal, complete (653)	Possible cut or percussion mark, anterior DNEF; tooth score, MSH; possible tooth pit, anterior DNEF; ambiguous score-shaped mark at label
Size 2/3A bovid (cf. *Parmularius*	Spotted hyaena (though proximal radii suggest a	Right mandibular condyle (827c)	Sedimentary abrasion
		Right horizontal ramus of	Inferior portion chewed; 1 definite and 1 possible tooth score, lingual,

altidens)	felid species instead)	mandible with M_1, M_2, M_3 (698)	below first loph of M_3; sedimentary abrasion
		Right maxilla with P^4, M^1, M^2, M^3 (692)	None
		Left maxilla with M^1, M^2, M^3 (797)	None
		C-2 fragment (813A)	None
		Left radius, PX to PNEF (787)	None
		Right radius, PX to MSH (786)	None
		Scaphoid, complete (807)	None
Size 3 bovid, immature	Unknown	Left radius with unfused epiphysis to MSH (766)	None
		DS femur with unfused epiphysis to MSH (696)	Possible large tooth pit, anterior (original surface not present); probable cut mark or percussion striae on DS shaft, side
Size 3A suid	Lion (bulk?) defleshing followed by hominin (scrap?) defleshing and possible marrow extraction	Left ulna, PX to MSH (788)	PX end gnawed off with small possible tooth notches
		Left radius, PX to MSH (700)	Isolated tooth score on anterior-lateral PNEF; isolated tooth score anterior-medial MSH; cut mark with internal striae, anterior-lateral MSH; possible percussion pits with striae, anterior-lateral MSH
Size 3B bovid, immature	Unknown	C-2, ~complete (706)	Chemical pitting
		Cervical vertebra inferior body fragment (709)	None
		Cervical vertebra, ~complete (694)	None
		Thoracic vertebra spine, near base (808)	Very exfoliated
		Thoracic vertebra centrum inferior, unfused (814)	None
Size 5, probable giraffid	Spotted hyaena	Thoracic vertebra with 1/3 spine present and one rib articulated (691)	Tooth score and possible tooth pit on anterior centrum
		Scaphoid 2/3 complete (711)	Several possible tooth scores; one preparation mark

Table 7.8. Individual prey specimens from HWKE, Trench 104.6, Level 2 (lowermost Bed II), with possible consumer access scenarios based on carnivore and hominin bone modification. See Table 6.7 caption for more details.

Prey Individual	Most Likely Consumer Access Scenario	Skeletal Element	Bone Modification
Size 1 bovid (cf. *Antidorcas recki*)	Unknown	Ulna, posterior PNEF fragment (27)	None
Size 2 ungulate	Unknown	Humerus, anterior DNEF (56)	None
Size 2 suid	Cheetah, leopard or lion (one or small group) defleshing	Cervical vertebra centrum (5)	Several possible and one definite small tooth scores
Felid, leopard-sized	Unknown	Cervical vertebra (2B)	None
Size 3A bovid (cf. *Parmularius altidens*)	Unknown	Left scapula, ~2/3 complete (9)	Possible sedimentary abrasion
		Right femur, MSH to DS (8a+b)	Possible cut mark, DS, medial; green break at MSH
		Left femur, MSH to DS (1)	Sedimentary abrasion
		Metatarsal, posterior shaft fragment (79)	None
Size 3B bovid	Unknown	Left horizontal ramus of mandible with P_3, P_4, M_1, M_2, M_3 (4a+b)	Preparation mark
		Right metacarpal, PX to shaft (7a+b)	None
Size 3B/4 equid	Unknown	Second phalanx, complete (58)	Root etching

Table 7.9. Individual prey specimens from Loc. 64, Trench 57, Level 3 (middle-upper Bed I), with possible consumer access scenarios based on carnivore and hominin bone modification. See Table 6.7 caption for more details.

Prey Individual	Most Likely Consumer Access Scenario	Skeletal Element	Bone Modification
Lepus sp.	Hominin defleshing	Right femur, PX to MSH (31)	Single short cut mark, anterior PNEF
Size 1 bovid, immature	Cheetah, leopard or jackal defleshing	Metapodial MSH (316)	Small tooth marks on MSH, anterior
		Right humerus, MSH to DS (405)	None
Size 1 bovid, immature	Unknown	Right humerus, MSH to DS (670)	None
Size 1 bovid (cf. *Antidorcas recki*)	Lion defleshing	Left radius, PX to MSH (315)	None
		Right ulna, PX to MSH (661)	Olecranon process missing (chewed?); huge tooth puncture in lateral olecranon
		Left metatarsal, PX to MSH (244)	Probable small tooth scores on anterior PNEF
		Left femur, head (663)	None
		Left humerus, DS (828)	None
Size 1/2 bovid (cf. *Antidorcas recki*)	Hominin fracture	Left ulna, MSH to DS (155)	Percussion pit and separate patch of striae on medial MSH
		Right metatarsal, PX to MSH (71)	Percussion striae medial, battering lateral; green fracture
Size 2 bovid (Antilopini or *Aepyceros*)	Leopard defleshing	Right humerus, DNEF to DS (664)	None
		Left humerus, MSH to DS (236)	Green fracture; tooth mark on MSH
		Right metatarsal, PX to PNEF (20)	None
Size 2 primate (*Theropithecus*?)	Unknown	Right humerus, MSH to DS (336)	Possible tooth marks, DS anterior
		Left humerus, MSH to DNEF (336)	None
Size 2 suid	Unknown	Carpal, complete (333)	None
		Second phalanx, complete (158)	None
Size 2/3A bovid (cf. *Parmularius altidens*)	Unknown	Right humerus, DS (667)	None
		Right metacarpal, PX to PNEF (171)	None
		Metapodial, single condyle (269)	None
Size 3A bovid (cf. *Parmularius altidens*)	Spotted hyaena, small group eating left forelimb	Left radius, PX to MSH (665)	Tooth puncture, posterior-medial MSH; tooth pit, posterior-medial PX end; green fracture
		Left metacarpal, MSH to DS (162)	Green fracture
		Left metatarsal, MSH to DS (760)	None
Size 3A bovid (cf. *Parmularius altidens*)	Hominin disarticulation or defleshing, followed by crocodile consumption	Left ulna, PX to MSH (58)	Cut marks on medial MSH; crocodile tooth puncture, medial PX end; possible carnivore damage on olecranon process

Size 3A bovid (cf. *Parmularius altidens*)	Lion bulk defleshing, followed by hominin skinning or periosteum removal and possible marrow extraction	Left radius, PX to MSH (319)	Light tooth scores, posterior-lateral shaft; green fracture
		Left metatarsal, PX to MSH (662)	Cut marks, anterior-lateral PNEF; green fracture
		Left metacarpal, MSH to DS (763)	Possible tooth pits on condyles
Size 3A bovid (*T. imberbis* or *K. sigmoidalis*)	Unknown	Right humerus, MSH to DS (666)	Possible tooth marks
		Left humerus, MSH to DS (240)	None
Size 3B bovid (Reduncini or Tragelaphini)	Lion bulk defleshing, followed by hominin skinning or periosteum removal	Right ulna, PX to MSH (764+756)	Probable carnivore damage on olecranon process
		Left metatarsal, PX to MSH (160)	Indeterminate marks
		Left metacarpal, MSH to DS (no number)	Cut marks, anterior DNEF; green fracture
		Right humerus, posterior-lateral MSH to DS (802)	Tooth score, lateral MSH; tooth pit, lateral DNEF; cut mark, posterior DNEF; green fracture
		Left radius, MSH to DS (434)	Green fracture
		Left tibia, MSH to DS (158)	None
Size 3B/4 equid	Hominin defleshing?	Right radius, DNEF to DS (161)	None
		Right metacarpal, PX to MSH (889)	Green break
		Femur, MSH (566)	Possible cut mark
Size 5 ungulate (*Sivatherium?*)	Hominin fracture, followed by spotted hyaena	Right radius, PNEF to MSH (780)	Percussion battering with striae, posterior-medial PNEF; percussion striae, posterior MSH at green broken edge; tooth mark, PX end

Of the eight individual animals identified from HWKE Trench 104.5 (lowermost Bed II), five have gross bone damage which suggest a particular consumer or consumers (Table 6.7). Three of these may have been defleshed by felids, followed by hominin scrap defleshing, and possibly marrow extraction and skinning. One of these animals was a size 1 bovid, possibly defleshed by a leopard or lion(s), based on gross bone damage to and tooth scores on a thoracic vertebra. This apparent felid defleshing was possibly followed by hominin marrow extraction and/or skinning, based on possible percussion and cut marks on a first phalanx. An immature size 2/3 bovid (possibly *Parmularius altidens*) was possibly defleshed by one or a small group of lions, based on a complete femur with tooth marks on the proximal and distal ends and marginal gnawing damage on the distal end, a tooth score on the metatarsal, and several tooth scores (which could be crocodile) on the mandible. The four tooth scores on the femur and the tooth score on the metatarsal are all short, but within the range of lengths of tooth scores made by lions. This may have been followed by hominin disarticulation, based on cut marks on the proximal ulna. A large (size 3A) suid distal forelimb was possibly bulk defleshed by lions, based on damage to the proximal ulna and tooth marks on the proximal radius. The length of one of the tooth scores on the proximal radius, the only tooth mark that was measured, is just above the 95% confidence interval and well within the standard deviation of tooth score length of lions. Hominins may have then defleshed the radius; cut marks on the midshaft indicate some access to bulk flesh or flesh scraps, and possible percussion marks may indicate marrow extraction.

Two other individuals from HWKE Trench 104.5 may have been modified solely by hyaenids. A larger size 2/3 bovid (again, possibly *Parmularius altidens*) was possibly

eaten by a hyaenid, which fragmented the inferior mandibular horizontal ramus to consume the marrow within, though the survival of both proximal radii would be unusual for modern spotted hyaenid consumption, and the tooth score length is shorter than expected based on modern spotted hyaenids. A size 5 giraffid was likely modified by a hyaena, based on tooth marks on the thoracic vertebral centrum and damage to the neural spine.

Only one of the seven individuals identified from HWKE Trench 104.6 (lowermost Bed II) has bone modification suggesting feeding by a particular consumer (Table 6.8). A size 2 suid cervical vertebral centrum has a tooth score shorter than the 95% confidence interval for most of the carnivores except spotted hyaenas, but as it is from a smaller prey animal, it was likely modified by a felid (cheetah, leopard, or lion).

Sixteen individuals were identified from Loc. 64, Trench 57 (Bed I; Table 6.9). Most (11) of those have bone modification suggestive a particular consumer or consumers; hominins were involved with 6 (possibly 7). The smallest individual, a *Lepus* (hare), has a single cut mark on the near epiphysis of the femur, indicating hominin defleshing. Hominin fracture of a size 1/2 bovid (likely a larger *Antidorcas recki*) is indicated by percussion marks on both the ulna and metatarsal. Hominin disarticulation or defleshing of a size 3A bovid forelimb, indicated by cut marks on the medial ulna midshaft, may have been followed by crocodile consumption, as indicated by the tooth puncture on the medial proximal ulna. Tooth marks on a size 3A bovid (probably *Parmularius altidens*) radius shaft suggest bulk defleshing by lions; the length of the measured tooth score is slightly shorter than the 95% confidence interval for lion tooth score length, but well within one standard deviation. Cut marks on the metatarsal

proximal near-epiphysis indicate hominin skinning or periosteum removal, and the green fracture of the metatarsal and radius could be indicative of hominin bone breakage for marrow processing. The right forelimb of a larger, size 3B bovid, has evidence suggesting lion bulk defleshing in the form of probable carnivore damage on the ulna olecranon process, a tooth score on the humerus midshaft, and a tooth pit on the humerus distal near-epiphysis. Both tooth marks are small, but within the range of tooth scores inflicted by lions. This was likely followed by hominin skinning or periosteum removal on the left forelimb, indicated by cut marks on the distal metacarpal near-epiphysis; the green fracture of the humerus, radius and metacarpal could be indicative of hominin bone breakage of both forelimbs for marrow processing. Percussion striae and battering damage indicated that hominins broke open the radius of a size 5 ungulate (possibly a *Sivatherium*), and the tooth score at the proximal end of the near epiphysis could only have been caused by a large hyaenid during bone breakage. The length of the tooth score is within the 95% confidence interval for spotted hyaenas. Hominins may have defleshed an equid femur, which has a possible cut mark.

Four individuals from Loc. 64 were modified only by carnivores. An immature size 1 bovid has small tooth marks on a metapodial midshaft, probably caused by a cheetah, leopard or jackal. A lion may have defleshed a size 1 bovid (probably *Antidorcas*) right forelimb, based on a large tooth puncture on the lateral ulna olecranon. This tooth puncture is larger than those created by smaller carnivores, but hyaenas would have consumed the entire prey carcass. A tooth score on a size 2 bovid humerus midshaft is within the 95% confidence interval for leopard tooth score length. Hyaenid modification of a size 3A bovid (probably *Parmularius altidens*) forelimb is suggested by

a tooth pit on the proximal radius and a tooth puncture on the radius midshaft; the tooth puncture length and width fall within or just above the 95% confidence interval for spotted hyaenas. Green fracture on the radius and metacarpal were possibly caused by hyaenid bone breakage for marrow consumption.

Discussion and Conclusions

Carnivore bone damage patterns do not indicate substantial variation in the intensity of carnivore activity through time during lowermost Bed II at Olduvai Gorge. The proportion of bones with carnivore damage remained the same, but the epiphysis to shaft ratio decreased from .25 to .04. This could indicate higher impact on the landscape bone assemblage by bone-crunching hyaenids during this time. Alternatively, comparisons of these values to those from modern studies of spotted hyaena bone modification of both whole carcasses (carnivore only) and human butchered assemblages (simulated sites) may be informative. An epiphysis to shaft ratio of .25 is within the range of carnivore only assemblage epiphysis to shaft ratios, but these assemblages usually exhibit more tooth-marked long bone shafts (Blumenschine and Marean, 1993: Figure 16-5). An epiphysis to shaft ratio of .04 is within the range of that exhibited by (fat-rich) simulated sites, but the tooth mark long bone shafts is always higher. This suggests that fragmentation at these sites was inflicted by factors other than carnivores. The high proportion of specimens with a recent break (842/1518, 55%) supports this alternative interpretation.

The sample of tooth marks from lowermost Bed II is too small to discern potential differential feeding by carnivores in different geographic locales during this time, and to

determine if these differences are predicted by the hypothesized vegetation of the locales. Most of the measurements of the tooth marks from the Olduvai lowermost Bed II fossils are small, and fall below the 95% confidence intervals of the measurements of modern carnivore tooth marks (Figures 7.6, 7.7). While the actualistic model used here only includes modern carnivores, several fossil carnivore taxa were present at Olduvai during Beds I and II including flesh-specializing sabertoothed felids such as *Dinofelis* and *Megantereon* (Cushing, 2002), and these may have been the primary modifiers of these bones. Sabertoothed felids likely avoided bone during carcass processing (e.g. Marean, 1989; see Chapter 5), and may have left smaller tooth marks when they did have tooth to bone contact. Some of the small tooth marks at these sites, then, may have been inflicted by sabertoothed felids or smaller carnivores.

Using the carcass unit as the basis for analysis, a combination of carnivore and hominin inflicted gross bone damage patterns can imply a particular carcass consumption scenario for individual prey animals. During lowermost Bed II, at HWKE Trench 104.5, hominins scavenging flesh and/or marrow from felids is hypothesized for three prey animals: a size 1 bovid, an immature size 2/3A bovid, and size 3A suid. Here, hyaenas are likely consumers of a size 5 giraffid and possible consumers of a size 2/3A bovid. At HWKE Trench 104.6, the only discernable consumer is a possible small carnivore or a single lion which consumed a size 2 suid. During middle-upper Bed I, at Loc. 64, hominins removed flesh from a hare, broke open a size 1/2 bovid ulna and metatarsal, and disarticulated or defleshed a size 3A bovid forelimb (which then may have been eaten by crocodiles). They also left cut marks from skinning or periosteum removal on metapodials of two bovids (size 3A and 3B), which may have been defleshed by lions.

They extracted marrow from a size 5 ungulate radius, which was then likely modified by large hyaenids. Four other prey animals (an immature and an adult size 1 bovid, a size 2 bovid, and a size 3A bovid) were possibly eaten by small carnivores (cheetah, leopard or jackal), lions, leopards, and hyaenids, respectively.

The original carcass unit-based methodology used in the analysis conducted on the Beds I and II sample is still being developed. Applying a combination of modern carnivore taxon-specific gross bone damage and tooth mark measurement criteria to this fossil sample allow additional interpretations of carnivore presence not possible otherwise. However, there are methodological challenges inherent in this analysis. For instance, there are many equifinalities that currently remain in modern samples of carnivore-modified bones. Nevertheless, using this methodology increases the detail available for hypothesis-building aimed at identifying carnivores involved with fossil bone assemblages. Also, tooth marks created by fossil taxa are currently unidentifiable; but along with bone damage, their dimensions can be hypothesized. Future analyses using this methodology should incorporate hypotheses of extinct carnivore bone modification.

Chapter Eight
Conclusions

This dissertation reports the results of neotaphonomic research on bone modification by larger African carnivores. It contributes to the growing literature on taxon- and/or size-specific taphonomic traces, specifically gross bone damage and tooth mark patterns and tooth mark morphology (Miller, 1969; Brain, 1980, 1981; Haynes, 1980, 1981a, 1982, 1983; Richardson, 1980; Sobbe, 1990; Fiorillo, 1991; Andrews and Fernandez-Jalvo, 1997; d'Errico and Villa, 1997; Domínguez-Rodrigo, 1999; Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Pobiner and Blumenschine, 2003). It is the first study to outline a replicable methodology to systematically quantify gross bone damage by carnivores applicable to the fossil record. As well, it is the first study to strongly emphasize the utility and necessity of prey size-based analyses of carnivore bone modification.

This dissertation applies the above-mentioned neotaphonomic results to several Plio-Pleistocene archaeofaunas from Koobi Fora, Kenya and Olduvai Gorge, Tanzania. In doing so, it contributes to the "hunting and scavenging" debate (e.g. Binford, 1981; Brain, 1981; Bunn, 1981, 1982, 1983, 1986, 2001; Bunn and Kroll, 1986; Shipman, 1986; Blumenschine, 1987, 1995; Potts, 1988; Blumenschine and Cavallo, 1992; Bunn and Ezzo, 1993; Lupo 1994; Oliver 1994; Capaldo, 1997; Domínguez-Rodrigo 1997, 2002; Selvaggio, 1998; Domínguez-Rodrigo *et al.*, 2002), aiming to construct hypotheses regarding the timing of access of hominins and (specific) carnivores to larger mammal carcasses. These samples expand the currently small number of published Oldowan archaeofaunas with hominin and carnivore bone modification, increasing the known

variability of reconstructed interactions between hominins and carnivores during this time. Through these samples, I also attempt to broaden the current interpretation of Oldowan hominin dietary behavior, previously derived primarily from studies of FLK Zinjanthropus which is often implicitly used as the archetype of Oldowan hominin carnivory (cf. Plummer, 2004).

The main conclusions from each chapter (excluding Chapters 1 and 5) will be reiterated here. Additionally, I will present a synthetic hypothesis towards identification of a carnivore taxon or ecomorph based on gross bone damage levels, tooth mark patterning, and tooth mark morphology on prey of different sizes.

The Types and Scale of Scavenging Opportunities for Early Hominins

Documentation of the types and scale of potential hominin scavenging opportunities in different ecosystems was not a central focus of this dissertation, but was one result of data collection on fresh prey carcasses or carcass parts eaten by different free-ranging and captive carnivores. Different types of scavenging opportunities have been previously hypothesized, and scales of these opportunities have been partially documented via actualistic studies (Blumenschine, 1986a, 1986b, 1987; Turner, 1988, 1992; Cavallo and Blumenschine, 1989; Marean, 1989; Selvaggio, 1994, 1998; Marean and Ehrhardt, 1995; Tappen, 1995; Arribas and Palmqvist, 1999; Domínguez-Rodrigo, 1999, 2001).

At Sweetwaters, lion consumption of size 3/4 carcasses leaves at least marginal scavengeable resources (flesh scraps, with less than 10% of original muscle mass remaining) 95% of the time, and large muscle masses over 50% of the time. This is a

much higher amount of scavengeable resources in the form of meat from size 3 and 4 lions kills than previous studies (Blumenschine, 1986a; Dominguez-Rodrigo, 1999). This may be a result of sampling a different ecosystem with a lower level of interspecific competition from spotted hyaenas than those previously sampled (Serengeti, Maasai Mara, Tsavo).

When smaller carnivores (jackal, cheetah and leopard) had access to size 3/4 prey, which in my sample was always in a captive setting, the bones always remained with at least flesh scraps after consumption. In contrast, over 70% of the bones left from spotted hyaena consumption of size 3 and 4 prey were completely defleshed. These findings are similar to previous studies (e.g. Blumenschine, 1986a; Selvaggio, 1994) which document striking differences between the completeness of lion and hyaena consumption of size 3/4 prey.

Lions much more thoroughly defleshed carcasses of size 1/2 prey; only a single bone from a size 2 animal retained bulk flesh. About half of the sample of size 2 bones exhibited flesh scraps, and half were completely defleshed. The differential was even stronger in the size 1 sample, where nearly 80% of the bones were completely defleshed. This size-based difference in lion flesh consumption agrees with previous studies (e.g., Blumenschine, 1986a, Selvaggio, 1994). Spotted hyaenas consumed all flesh and virtually all bone from size 1 and 2 prey. Leopard flesh consumption from size 1 and 2 prey is generally similar to that of lions, but slightly less intense (cf. Blumenschine, 1986a; Cavallo and Blumenschine, 1989; Selvaggio, 1994).

There was little patterning in the flesh distribution both within and among different skeletal elements on carnivore-eaten carcasses. On limbs, epiphyses generally

remained with less flesh than did shafts, but not markedly so. This is likely due to the systematic presence of flesh on distal intermediate limbs (radio-ulna and tibia), which normally remained with flesh on the shafts and distal epiphyses. Intermediate limbs sometimes remained with relatively more scavengeable flesh (in terms of proportion of original flesh present) than upper limbs, but not consistently so. Carnivore number, age, habitat, and season of kill may all influence flesh availability, especially in lion kills, as found by Blumenschine (1986a).

Clearly, there is an important difference in scavenging opportunities from lion-eaten carcasses based on prey size. Regardless, calculating the amount of caloric resources available from any of these lion-modified carcasses reveals the significant amount of potential energy from even small amounts of scavengeable meat. This underscores my support of the hypothesis of scavenging as a profitable, though potentially dangerous, foraging strategy for early hominins (e.g., Blumenschine 1986a, Selvaggio 1994).

Additionally, it emphasizes the need to exercise caution in applying results from studies in modern ecosystems to prehistoric ecosystems with different ecological structures. Van Valkenburgh (1988) cautions that the modern Serengeti ecosystem, with high carnivore species richness and close species packing, is unusual. This unusual carnivore guild structure may result in lower passive scavenging opportunities in the Serengeti relative to other ecosystems, though a high prey biomass could offset this effect. Therefore, thought it is a more artificial and managed ecosystem, Sweetwaters may offer at least an alternative model for prehistoric carnivore guild structures. At Sweetwaters, which has high numbers of felids especially in relation to hyaena

populations, opportunities for passive scavenging include large amounts of flesh and marrow from lion kills, even in more open environments. If sabertoothed felids were solitary, and consumed less flesh per kill than modern felids, Sweetwaters may be a useful model for the overall scale of scavenging opportunities for early hominins in an ecosystem dominated by flesh-specialist felids. *Pachycrocuta* is absent from the Okote Member of Koobi Fora, as it is from Beds I and II at Olduvai; the only hyaenid present in these time horizons is *Crocuta ultra*, which likely did not have modern *Crocuta crocuta* prey carrying and bone consumption capabilities, or social structure with high intraspecific competition (Lewis and Werdelin, 2000).

Carnivore Gross Bone Damage and Destruction and Tooth Marking Patterns: Taxonomic Specificity

Gross Bone Damage and Destruction

This study documents and quantifies gross bone damage and destruction by larger African carnivores on different sized prey. Carnivore gross bone damage on forelimbs is usually greater than on hindlimbs, and damage generally decreases from upper to intermediate to distal limb elements. Lumping all limb elements, or even limb portions, may mask important patterning which allows the identification of the carnivore taxon responsible for the damage to an individual bone or a bone assemblage. Gross bone damage by different carnivores to similar sized prey can often be distinguished by the patterning of bone damage across specific skeletal elements and portions.

The predator taxon/prey size-specific bone modification patterns shown in Chapter 3, and documented previously (Pobiner and Blumenschine, 2002, 2003) attest to

the scaling relationship of gross bone damage levels with increasing prey size and predator specialization on within-bone nutrients. The characterization of this relationship allows zooarchaeologists of identify the last carnivore to modify particular bones or bone portions. For clear examples: leopard (and most probably cheetah)-like felids and jackal-like canids can be excluded as agents of fragmentation of limb shafts of size 1 and 2 carcasses, while lion-like felids can be excluded as agents of fragmentation of limb shafts of size 3 and 4 (cf. Pobiner and Blumenschine, 2003). Conversely, for size 3 and larger carcasses, hyaenids are the only carnivores capable of destroying long bone shafts, severely reducing and fragmenting the mandible, innominate and scapula.

This carnivore taxonomic or ecomorphic identification can be extended to an assemblage-level scale, permitting the identification of the carnivores with which hominins interacted over carcass resources, especially in conjunction with tooth mark analyses. Additionally, the scaling relationship means we can model potential bone modification capabilities of extinct carnivores if we know their body size and edible tissue specialization. The results in Chapter 3 demonstrate that at least for lions modifying zebra skeletal elements, this scaling relationship is conditioned at least in part by bone density.

If there is a predictive relationship between gross bone damage level and edible tissue remaining on particular bones or bone portions, it could be possible to construct hypotheses about the amount of edible tissue available from a fossil bone specimen based on the amount of carnivore damage that bone has sustained. This could then be extrapolated on a bone-by-bone basis to an archaeofaunal assemblage exhibiting carnivore and hominin damage, characterizing the amounts and types of edible resources

scavenging hominins could have encountered. Ultimately, relative amounts and types of edible tissues available to hominins from different archaeofaunal assemblages could be compared. In the future, I plan to collect systematic data on both edible tissue availability and gross bone damage level by bone portion, to test the hypothesis that there is a relationship between these two variables. Additionally, I hope to collect data on larger canid (i.e., African wild dog or wolf) gross bone damage and tooth marking comparable to those I have collected for other carnivores.

Tooth Mark Frequency and Distribution

The proportion of skeletal elements bearing tooth marks varies from 0-100% across different carnivore taxa/prey size samples from both naturalistic and captive settings. Compared with gross bone damage patterning, tooth mark frequency and location is generally less useful in differentiating between carnivore agents who may have modified bones of a particular sized prey. The main exception is lions modifying size 1 and 2 prey, which create significantly more tooth-marked specimens (58% across all skeletal elements) than other taxa (<26%). The propoprtion of tooth-marked specimens varies by prey size: the average proportion of tooth-marked specimesn for size 3&4 prey is 58% (range: 43-60%), and the average propoprtion of tooth-marked specimens for size 1&2 prey is 39% (range: 9-58%). Tooth marks are differentially distributed across prey skeletal elements, but not in any discernable pattern.

The relative proportion of tooth-marked limb specimens decreases distally down the limb, from upper to intermediate to lower limb bones. This holds true in this sample except for in spotted hyaenas, which have a low sample size of intermediate limb bones. This relationship is likely due to the distribution of meat and marrow on ungulate

carcasses (cf. Blumenschine, 1986a), which also decreases distally down the limb. There is no consistent difference between frequency of tooth-marked limb epiphyses and shafts in the sample as a whole. However, the carnivores capable of higher damage levels on a particular prey size (e.g. lions versus jackals on size 1 prey) tended to produce lower epiphyseal tooth mark frequencies on that prey size, probably because some of the previously tooth-marked epiphyses were destroyed during consumption.

Fragmentation (measured by NISP/MNE) does not have a strong relationship to the proportion of tooth-marked specimens across all skeletal elements. However, fragmentation of size 1 and 2 bones by lions and size 3 and 4 bones by spotted hyaenas creates a higher proportion of tooth marks on limb shaft versus limb epiphyses, presumably due to destruction/deletion of epiphyseal limb portions. Consequently, the relative proportion of limb shaft tooth marking can be related to carnivore *fragmentation*, but not overall carnivore *access or involvement*. Across all samples, the number of tooth-marked limb shafts is inversely related to the number of epiphyses/shafts. The relationship between the proportion of tooth-marked skeletal elements and intensity of carnivore involvement or competition varies depending on the capability of particular carnivore taxa to fragment and destroy bones of a particular prey size.

Tooth Mark Measurements

When the total sample is analyzed, the length and width of tooth pits and punctures are statistically distinguishable among carnivore taxa, *contra* Domínguez-Rodrigo and Piqueras (2003). However, all of the carnivore taxa in this study (except spotted hyaenas) can create small tooth pits and punctures (< 6mm in maximum length), but only the larger taxa (lion and spotted hyaena) can create large tooth pits and

punctures (> 6mm in maximum length). The statistical differences in the length and width of tooth pits and punctures created by different carnivore taxa are both being driven by tooth punctures; the length and width of tooth pits created by different carnivores are not statistically distinguishable. However, when comparing length and width measurements of tooth punctures only of similar sized carnivores, even tooth punctures are not identifiable to a specific carnivore taxon. Pairwise difference tests among tooth punctures created by smaller taxa (jackal and leopard) and larger taxa (lion and spotted hyaena) demonstrate that carnivore tooth punctures cannot be statistically distinguished among taxa of similar sizes. Therefore, it is the relative size of the carnivore rather than the taxon which is most conservatively distinguishable using measurements of a single tooth mark.

The ranges of the length and width of tooth scores overlap for all variables analyzed: carnivore taxa, prey size, skeletal group, and long bone portion. This agrees with results of a previous study where tooth pit size was more useful than tooth score size for distinguishing between carnivores (Domínguez-Rodrigo and Piqueras 2003). Tooth score length may distinguish between smaller and larger carnivores, as only lions and hyaenas created tooth scores longer than 13 millimeters in my sample, with most of the longer tooth scores having been created by lions. It is unclear if this difference is taxonomic, or the result of a much larger sample size of lion tooth scores compared with other carnivores.

Tooth score, pit and puncture size is inversely correlated to cortical bone thickness, where tooth marks are largest on epiphyses, smaller on near-epiphyses, and smallest on midshafts. Selvaggio and Wilder (2001) and Domínguez-Rodrigo and Piqueras (2003) also found larger tooth pit sizes on cancellous versus cortical bone, and

concluded that tooth pit size is at least partially conditioned by bone density. Because of this relationship, long bone specimens should be stratified by portion for analyses if trying to distinguish carnivore taxon, or even carnivore size, from tooth mark size.

Towards Identifying Carnivore Involvement with an Archaeofauna: Multiple Lines of Evidence

While measurements of individual tooth marks do not always statistically distinguish carnivores taxonomically, hominin interactions with specific carnivores over prey carcasses are still knowable to a certain degree. We can still test several hypotheses of hominins scavenging from different carnivores (lions versus leopards) using tooth mark measurement data, and combined with gross bone damage and destruction data, we can even recognize the involvement of different larger carnivores on an assemblage (lions versus hyaenas). Tables 4.26 and 4.27, which include data on gross bone damage level, tooth mark frequency, and tooth mark measurements on each skeletal element on a prey size-specific basis, can be used as the basis for constructing hypotheses regarding the involvement of specific carnivore taxon with a bone assemblage. These hypotheses can be depicted with a flow chart, shown in Figure 4.14. Prey taxa should first be stratified by size, and then each skeletal element and portion examined for gross bone damage patterns, tooth mark patterns, and tooth mark metrics. Then, particular patterning across an assemblage can be used to construct a hypothesis for the involvement of a particular carnivore or carnivores with the assemblage.

Hominin Carcass Foraging Strategies and Hominin-Carnivore Interactions at ~1.5 Ma at Koobi Fora, Kenya

Introduction and Setting

This section of the dissertation summarizes the zooarchaeology and taphonomy of three sites from Koobi Fora, Kenya: FwJj14A, FwJj14B, and GaJi14. The sites lie stratigraphically within the Okote Member of the Koobi Fora Formation. FwJj14A and FwJj14B lie just atop the Northern Ileret Tuff dated to ~1.52 Ma; GaJi14 is just below the Lower Koobi Fora Tuff Complex, dated to ~1.49 -1.62 Ma (Brown *et al.*, 2006).

The FwJj14A fauna accumulated in a small flood basin within a channel system, adjacent to a watercourse, subsequently infilled by fine-grained sediment (C. Lepre, pers. comm.). The fauna at FwJj14B accumulated on the margin of a broad and shallow stream. The lithology and facies associations at GaJi14 indicate lake shore environments with small, marginal channels and floodplains (R. Quinn, pers. comm.). GaJi14 is preserved within small, shallow tributaries of an ancient transgressing and regressing lake, the precursor of Lake Turkana, which is reconstructed at this time on the Koobi Fora Ridge (Feibel, 1988, 1997; Brown and Feibel, 1991; Feibel *et al.,* 1989).

The fauna from FwJj14A indicate a paleoenvironment with a significant shallow-water component, suggesting an oxbow lake or a delta component of a riverine environment. This was accompanied by swampy areas, possibly in valleys, and also possibly undergoing seasonal flooding events. The fauna from FwJj14B is similar to that at FwJj14A, with the addition of a more open, grassy component and a nearby gallery forest. The fauna from GaJi14 is similar to that at FwJj14A as well, with a more woody component to the vegetation, as well as drier, open grassy areas nearby.

These three sites are relatively unique in that they consist entirely of fauna, with several hundred specimens bearing hominin-induced modification from butchery, but no stone tools. The likelihood is that these three sites were each amenable to butchery activities by offering hominins particular resources, such as shade and water, but not stone raw material. A total of 5945 faunal specimens were analyzed from FwJj14A, FwJj14B, and GaJi14. Sedimentological and taphonomic analyses support an interpretation of low energy deposition followed by relatively rapid burial. Size 2 and especially 3 mammals dominate all of the assemblages, and bone surface preservation is generally very good.

Taphonomic Analyses and Site Formation Processes

A total of 147 of the 1653 mammal bones (9%) from FwJj14A have hominin bone surface modifications. From FwJj14B the number of hominin-modified bones is 74/1713 (5%), and from GaJi14, 92 of 1659 mammal bones (6%) are hominin-modified. Cut marks occur on a variety of skeletal elements and carcass sizes (1-6), with a predominance of cut marks on size 3 limb shaft fragments. Notable cut-marked specimens include hyoids of three size 3 bovids, a primate humerus, and a fish spine. Hyoid, especially cut-marked hyoids, are unusual in the fossil record, and cut marks on the primate and fish specimens expand the evidence for the diet of Plio-Pleistocene hominins. Application of an actualistic model which uses cut mark locational data as indicative of butchery activity (Nilssen, 2000) suggests that both flesh removal (filleting) and disarticulation occurred, as well as periosteum removal in preparation for hammerstone breakage. Hammerstone breakage is evident from percussion marks on 27 specimens from the three sites. At least 31 individual carcasses were butchered at the

three sites, including water-dependent taxa (hippos, fish), a monkey which presumably required tall trees (*Cercopithecus)*, water-dependent alcelaphines, and a grass-eating hippotragine. This indicates that hominins acquired meat from animals associated with a variety of habitats: water edge, riverine forest, and open, grassy areas.

The proportion of butchered bones in each size class category (size 1 and 2 - small, size 3 and 4 - medium, size 5 and 6 - large) is not statistically significant at any of the three sites. Actualistic and archaeological studies indicate that higher cut mark frequencies are expected on larger carcasses; in one actualistic study, bones from size 3 carcasses had over four times as many cutmarks on average than those from size 1 carcasses (Pobiner and Braun, 2005). The relatively equal proportions of cut marks on bones from different sized animals could indicate that hominins were butchering small and medium size mammals in different ways at these sites. The proportion of butchery marks across skeletal groups (axial, appendicular, and compact) is also statistically similar at all three sites. This finding could support a behavioral interpretation of hammerstone breakage followed by carnivore activity (cf. Capaldo, 1995), with an overabundance of cut marks on podials, possibly resulting from disarticulation.

Spearman's rank correlation coefficient indicates that there is no correlation between the proportion of size 3 and 4 skeletal elements bearuing cut marks and the order of carnivore consumption of these skeletal elements at any of the three sites. This indicates that hominins were not butchering different skeletal elements in the same order as carnivores consume those elements, assuming similar fragmentation rates during butchery and carnivore consumption, and assuming a strong linear relationship between frequency of butchery of an element and the frequency of cut-marked specimens of that

element in the assemblage. If these assumptions are upheld, hominin butchery strategies of size 3 and 4 mammals may have been based on variables other than relative proportion of meat and marrow extractable from particular skeletal elements.

The dominance of percussion marking on upper limbs at FwJj14A and FwJj14B, though the sample size is small, may indicate that hominins preferentially hammerstone-broke these bones. This supports a hypothesis of early access to these carcasses by hominins; presumably, if (bone-crunching) carnivores had first access to them, they would have consumed the meat and marrow from the higher-utility upper limbs before the lower-utility intermediate and lower limbs (e.g. Blumenschine, 1986a). At GaJi14B, though, the percussion-marked limbs are all intermediate and lower limbs. At this site, hominins were breaking open less attractive bones in terms of marrow yields (unless the bones were mainly from juveniles, which have a different inter-limb distribution of marrow than adults; Blumenschine and Madrigal, 1993).

There are only four tooth-marked specimens from these sites: three from FwJj14A, two of which also exhibit cut marks, and one from GaJi14, which also exhibits cut marks. On one of the tooth- and cut-marked specimens from FwJj14A, a sequence of hominin-carnivore can be discerned from the overlap of the marks, but there is no evidence for order of access on the other. The tooth marks on the specimen from GaJi14 are likely crocodile tooth marks. The tooth marks on the specimens from FwJj14A are all small (<4mm long), and neither the gross bone damage nor the tooth mark measurements are diagnosable to carnivore taxon.

The low frequency of carnivore tooth marks does not necessarily indicate a lack of carnivore activity at these three sites. However, it probably indicates that if carnivores

were consuming bones from these carcasses, they were not doing so on site. If carnivores were consuming limb epiphyses in the same place that hominins were butchering these carcasses, one would expect much higher frequencies of tooth-marked limbs, comparable to experimental models. Combined with the low proportion of epiphyses and near-epiphyses, the very low number of tooth-marked limbs can probably be explained by this scenario: hominin meat and marrow processing, which fragmented the limbs, occurred. Subsequently, carnivores deleted greasy epiphyses from the assemblage for consumption off site. This may also apply to axial and compact elements, the latter of which are underrepresented at the sites. However, this is hard to evaluate without knowing how the un-marked limb bones were broken. Alternatively, the virtual lack of complete limb epiphyses and relative relative paucity of epiphyseal fragments may have been caused by *in situ* density-mediated attrition.

Evaluation of the possibility of hominins butchering felid kills at these sites, based on cut mark frequencies in actualistic models (Domínguez-Rodrigo 2002, Domínguez-Rodrigo and Barba, 2006) is inconclusive. The taphonomic data relevant to answering this question are the tooth mark data, which do not support the scenario of hominins butchering felid kills based on available experimental models. If this was the case, again, we would expect higher frequencies of tooth-marked limb midshafts (Blumenschine, 1995). Therefore, the hominins at these sites likely acquired these carcasses via hunting, confrontational scavenging, or scavenging mass deaths of ungulates (cf. Capaldo and Peters, 1995). Experimental models of carcass procurement modes, based on cut and tooth marks frequencies, differentiating between hunting and high-yield scavenging (regardless of whether this scavenging involved early or late

access by hominins to carcasses) are currently lacking, rendering these hypotheses currently untestable.

3. Summary: Hominin Carcass Foraging Behavior

Hominins had early access to the majority or all of the carcasses they butchered at these sites, based on cut, percussion, and tooth mark frequencies and locations, though whether they had access to bulk or scrap flesh is unknown. They probably disarticulated some elements or groups of elements for transport (crania, vertebrae, possibly innominates from femora and scapulae from humeri, forelimbs, and hindlimbs), but whether this articulation was indeed in preparation for transport or was part of on-site butchery activities is uncertain. Hominins conducted various butchery activities at these sites, including defleshing of ribs, vertebrae, innominates, scapulae, and limbs. Tongue removal was also practiced. Percussion marks and scrape marks indicate marrow access to all classes of limbs (upper, intermediate, and lower), though scrape marks only occur on intermediate and lower limbs. Evidence of skinning on metapodials is also present.

After hominins had extracted the meat and marrow from the limbs, bone crunching carnivores (hyaenids) may have deleted the grease-rich limb epiphyses for consumption off site. This may indicate that even after hominins extracted the resources from these carcasses usable to them, their presence in the general vicinity of the site prevented hyaenids from processing the grease-rich epiphyses on site. Alternatively, hyaenid off site consumption may have occurred due to high intraspecific hyaenid feeding competition (as is modern *Crocuta crocuta*), though the instraspecific competition level within fossil *Crocuta* may have been lower (Lewis and Werdelin, 2000). Hyaenid deletion of limb epiphyseal portions may have also removed evidence for

disarticulation of limbs, in the form of cut marks, especially on upper limbs. The presence of cut marks on three out of four of the tooth-marked specimens from these sites indicates that carnivore activity was not completely independent of hominin carcass processing.

Implications: Variability in Hominin Carcass Foraging Behavior

The results of these analyses are important because they demonstrate the variability in hominin-carnivore interactions during Oldowan and Developed Oldowan times. As has been noted (Monahan, 1996, Domínguez-Rodrigo, 2002, Plummer, 2004), there has been a disproportionate focus for decades on the evidence from the large, well-preserved FLK *Zinjanthropus* assemblage (e.g. Bunn, 1986, 2001; Bunn and Kroll, 1986; Shipman, 1986; Potts, 1988; Lupo, 1994; Oliver, 1994; Blumenschine, 1995; Capaldo, 1997; Selvaggio 1998). The current accepted interpretation of hominin-carnivore interactions at FLK *Zinjanthropus* involves hominins scavenging at least partially defleshed carcasses from felids (Blumenschine, 1995 but see Dominguez-Rodrigo and Barba, 2006). Recently, other assemblages with traces of hominin and carnivore bone modifications during the Oldowan and Developed Oldowan/early Acheulean (2.5-1.5 Ma) are being analyzed or re-analyzed and published, yielding evidence for earlier access by hominins to larger mammal carcasses, followed by bone-crunching carnivores (Domínguez-Rodrigo, 2002: FxJj50; Domínguez-Rodrigo *et al.*, 2002: Peninj; Monahan, 1996: BK and MNK Main, Olduvai Gorge, Bed II) or independence of hominin and carnivore access (Egeland *et al.*, 2004: Swartkrans Member 3; Monahan, 1996: HWKE 1-2, Olduvai Gorge Bed II; Plummer, 2004: Kanjera South). FwJj14A, FwJj14B, and GaJi14 fall either within the former or latter category; it is likely that carnivores were

occasionally active at these sites, so it is more accurate to categorize them as sites with evidence for early hominin access followed by bone-crunching carnivores.

The results from this study add to the current known realized vertebrate dietary niche of Oldowan and Developed Oldowan hominins. A recent study (Blumenschine and Pobiner, 2006) inventoried the known prey taxa, identified to at least the tribe level, with butchery marks from Oldowan sites (<1.7 Ma). These are (in order of increasing body size): *Antidorcas recki,* size 2 Antilopini*, Kolpochoeres limnetes, Metridiochoerus andrewsi, Tragelaphus strepsiceros, Parmularius altidens, Kobus sigmoidalis, Connochaetes* cf. *gentryi, Hipparion* sp., *Syncerus* cf. *acoelotus, Oryx* sp., *Giraffa* sp., *Hippopotamus* cf. *gorgops,* and possibly *Elephas recki*. Additionally, cut marks on *Erinaceous broomi* during this time period have been observed (Fernandez-Jalvo *et al.* 1999). This analysis adds dietary information to the realized behavioral niche of Developed Oldowan hominins, which were likely members of the species *Homo erectus* or *ergaster*. Their diet included mammals ranging in size from 1 to 5 including bovids and suids, fish, an arboreal monkey (*Cercopithecus* sp.), size 3 Tragelaphini, size 3 Hippotragini, and hippopotamids. Hominin procurement of fish at Olduvai Gorge was suggested by Stewart (1994), but butchery marks on Plio-Pleistocene fish have not been reported until now.

How does hominin foraging behavior vary among penecontemporaneous sites during the early Developed Oldowan (from 1.6-1.3 Ma)? Is there a single dominant behavioral pattern during this time period, or is there variation among sites? A simple examination of archaeological sites from this time period, including assemblages with stone tools and/or butchered bones, reveals a lack of concordance between the presence

or number of stone tools and the presence or number of butchered animal bones (Table 8.1). This is also the case for earlier Oldowan sites (Table 8.2). This suggests that hominin stone tool manufacture and discard, as well as butchery activities, varies at different sites with local conditions which probably include (on a basic level):

1. availability of stone raw material (distance to, quality and quantity of each source)
2. availability of carcasses (encounter frequency, predation and competition risk associated with carcass utilization, amount of meat, marrow, and brain)
3. hominin biology and ecology (species, body size, group size, home range)
4. site-specific affordances and risks not considered above (shade, water, sleeping trees, other resources such as edible plants)

Archaeologists should not assume a single hominin carcass foraging pattern during the Oldowan and Developed Oldowan. Instead, it should be assumed, like other biological organisms, hominin foraging patterns changed within lineages or when variables in their environments changed. Understanding how butchery patterns at specific sites are related to other ecological variables can be an informative a goal of Oldowan and Developed Oldowan hominin foraging ecology studies (cf. Potts, 1994).

Table 8.1. Evidence of stone tools and butchery-marked bones at African early Developed Oldowan sites (dated to ~1.7 – 1.3 Ma). Sites which have no butchery-marked bones present can mean bones either have or have not been examined for butchery marks. Numbers of lithics and fauna include surface and *in situ* specimens. "Probable" or "possible" cut marks are not included in counts here. For butchery and carnivore tooth mark details, CM = cut marked, PM = percussion-marked, TM = tooth-marked. For industries, Old = Oldowan, D-Old = Developed Oldowan, D-OldA = Developed Oldowan A, D-OldB = Developed Oldowan B, Kar = Karari, ProtoAch = proto Acheulean, Indet = indeterminate, N/A = not applicable (no lithics). Butchery-marked bones are only detailed when present. Tooth marks are only noted for archaeofaunas with butchery-marked bones. Sites are arranged in decreasing order of number of lithics reported.

Site	Number of Lithics Reported	Industry	Fauna Present	Butchery Marks Present	Butchery and Carnivore Tooth Mark Details
MNK Chert Factory Site[1]	>30,000+	D-OldA	No*	No	
Gomboré I B, Melka-Kunturé[2]	8000†	Old	Yes	No	
Garba IV D, Melka-Kunturé[2]	8000†	Old	Yes	No	
BK[5]	7220	D-OldB	Yes	Yes	46 CM, 49 PM, 83 TM
TK Upper Occupation[3,4]	5319	D-OldB	Yes	No	
MNK Main[4]	5315	D-OldB	Yes	Yes	13 CM, 15 PM, 45 TM
FxJj20M, Koobi Fora[2]	4437	Karari[13]	Yes	Yes	1 CM
FxJj20AB, Koobi Fora[2]	3476	Karari[13]	Yes	No	
FxJj18IH, Koobi Fora[2]	3272	Karari	Yes	No	
HWK E 3, 4, 5[4]	3173	D-OldA	Yes	No	
TK Lower[4]	2174	D-OldB	Yes	No	
FxJj20E, Koobi Fora[5]	1819	Karari[13]	Yes	No	
FxJj18GL, Koobi Fora[5]	1645	Karari	No	No	
FxJj50, Koobi Fora[5,6]	1535	Old[14]	Yes	Yes	12 CM, 12 PM, 45 TM
TK Channel[4]	1436	D-OldB	Yes	No	
FC West, Occupation[4]	1435	D-OldB	Yes	No	
FxJj18NS, Koobi Fora[5]	1012	Karari	Yes	Yes	1 CM
FxJj16, Koobi Fora[5]	980	Karari[13]	Yes	No	
SHK Tuff[4]	953	D-OldB	Yes	No	
FxJj37, Koobi Fora[5]	946	ProtoAch[15]	Yes	No	
MNK Skull Site[4]	834	Old	Yes	No	
FC West, Tuff[4]	780	D-OldB	Yes	No	
TK Tuff[4]	733	D-OldB	Yes	No	
FxJj11, Koobi Fora[5]	661	Karari[13]	Yes	No	
HWKE 1-2, Olduvai Gorge[3,5]	651	Old /D-OldA[16]	Yes	Yes	5 CM, 3 PM, 127 TM
FxJj20S, Koobi Fora[5]	646	Karari[13]	Yes	No	
SHK Channel[4]	643	D-OldB	Yes	No	
TK Intermediate[4]	614	D-OldB	Yes	No	
Nyabusosi[7]	536	Old	No	No	
FwJj1, Koobi Fora[5]	432	Karari[17]	Yes	No	
Swartkrans Member 2[8]	403	D-Old	Yes	No	
ST Site Complex, Peninj[9]	354	D-Old	Yes	Yes	17 CM, 30 PM, 7 TM
FxJj17, Koobi Fora[5]	294	Karari[13]	Yes	No	
FLK N Sandy Conglomerate[4]	234	D-OldA	No	No	
FxJj18GU, Koobi Fora[5]	229	Karari	No*	No	
FxJj23, Koobi Fora[5]	205	Karari[18]	Yes	No	
SHK Annexe[4]	185	D-OldB	Yes	No	
FxJj38NW, Koobi Fora[5]	172	Old[19]	No*	No	
FC[4]	170	D-OldB	No	No	
FxJj33, Koobi Fora[5]	155	ProtoAch[20]	No	No	
Swartkrans Member 3[8,10]	72	D-Old	Yes	Yes	60 CM, 45 PM, 70 TM
FxJj64, Koobi Fora[5]	45	Karari	Yes	Yes	1 CM
FLK N Deinotherium, Olduvai Gorge[3]	23	Indet[21]	Yes	No	
FLK N Clay with Root Casts[4]	21	Indet[21]	Yes	No	
FC West[4]	17	D-OldB	Yes	No	
FxJj38E, Koobi Fora[5]	9	Indet	Yes	No	
FxJj38SE, Koobi Fora[5]	4	Indet	Yes	No	
GaJi0[11]	0	N/A	Yes	Yes	31 CM
FwJj0[11]	0	N/A	Yes	Yes	7 CM
GaJi5, Koobi Fora[5]	0	N/A	Yes	Yes	11 CM
FwJj14B[12]	0	N/A	Yes	Yes	70 CM, 8 PM
GaJi14[12]	0	N/A	Yes	Yes	90 CM, 5 PM, 1 TM
FwJj14A[12]	0	N/A	Yes	Yes	132 CM, 14 PM, 4 TM

+ Only 7,373 studied

*One or a few non-identifiable bone fragments, so a “practical absence” of fauna

†Total number of lithics for Gomboré IB and Garba IV D combined
[1]Stiles *et al.*, 1974
[2]Chavallion *et al.*, 1979
[3]Monahan, 1996
[4]Leakey, 1971
[5]Harris and Isaac, 1997
[6]Domínguez-Rodrigo, 2002
[7]Texier, 1995
[8]Brain *et al.*, 1988
[9]Domínguez-Rodrigo *et al.*, 2002
[10]Egeland *et al.*, 2004
[11]Bunn, 1994
[12]this study
[13]J. W. K. Harris, pers. comm.
[14]"The high proportion of choppers and modified battered cobbles makes the FxJj50 assemblage typologically more similar to the KBS Member assemblages that to the other Okote assemblages with which it is contemporary…" (Harris and Isaac, 1997:203)
[15]"… the flaked pieces include eight bifacially flaked items that are suggestive of Acheulean forms, although none of them is a classic Acheulean tool." (Harris and Isaac, 1997:182)
[16]Level 1 is Oldowan, Level 2 is Developed Oldowan A.
[17]"The assemblage consists of a failry generalized set of flakes and flake fragments that could perfectly well fit within the Karari Industry series. However, the characteristic Karari core/scrapes are not represented in the sample." (Harris and Isaac, 1997:119)
[18]"…it can be said that the flakes and the few flaked pieces, choppers, cores, etc., are all consistent with an attribution of this sample to the Karari Industry. However, the sample is too small and the items too nondescript for this attribution to be more than tentative." (Harris and Isaac, 1997:171)
[19]"…it resembles assemblages from sites in the KBS member at Koobi Fora and in Bed I at Olduvai Gorge." (Harris and Isaac, 1997:190)
[20]"Although there is an absence of classical bifacial forms, the varied evidence for the production of large flakes at FxJj 33 may imply that this artifact series is drawn from am early Acheulean stone-flaking system that was starting to be established in the basin." (Harris and Isaac, 1997:178)
[21]"The industry appears to represent a stage intermediate between the Oldowan of Bed I and the Developed Oldowan of Bed II." (Leakey, 1971: 87)

Table 8.2. Evidence of stone tools and butchery-marked bones at African Oldowan sites (~2.6 – 1.75 Ma). Assemblages from Koobi Fora described as belonging to the KBS industry are subsumed under Oldowan industry here. See Table 8.1 for more details.

Site	# Lithics	Fauna	BM	Butchery and Carnivore Tooth Mark Details
Kanjera South 1 (KJS-1)[1]	>4500	Yes	Yes	Present, but unspecified
Fejej[2]	2610	Yes	No	
Sterkfontein Oldowan Infill[3]	2797	Yes	Yes	1 CM, 122 TM
Lokalalei 2C[4]	2583	Yes	No	
FLK 22 (Zinj)[5,6]	2470	Yes	Yes	233 CM, 200 PM, 444 TM
EG 10 (Gona)[7]	2216	No	No	
Ain Hanech, Deposit B[8]	2097	No	No	
Omo 123, Upper[9,10]	1781	No	No	
Omo 123, Lower[10]	1314	No	No	
FLKN 1-2[11]	1205	Yes	No	
DK1,2,3[12]	1198	Yes	Yes	9 CM, 6 TM
DAN-2 (Gona)[13]	hundreds	Yes	Yes	5 CM
Senga 5A[14]	915	Yes	No	2 TM
Ain Hanech, Deposit A[8]	827	No	No	
EG 12 (Gona)[7]	754	No	No	
FxJj10[15]	689	Yes	No	
FtJi 1 (Omo)[16]	647	Yes	No	
El Kherba[8]	510	Yes	No	
Lokalalei 1[17,18]	466	Yes	No	6 TM
FtJi 2 (Omo)[9]	355	No	No	
Omo 84[9]	290	Yes	No	
OGS-7 (Gona)[19]	263	Yes	No	
Omo 57[9]	253	No	No	
FxJj1[15]	227	Yes	No	
Kanjera South 2 (KJS-2)[20]	223	Yes	No	
DAN-7 (Gona)[21]	190	No	No	
EG 13 (Gona)[13,21]	179	Yes	Yes	1 CM
FxJj3[15]	175	Yes	No	
FLKN 3[12]	171	Yes	No	
FLKN 5[12,]	151	Yes	Yes	3 CM
FLKN 6[12]	123	Yes	No	1 CM, 6 TM
DAN-1 (Gona)[21]	112	No	No	
FtJi 5 (Omo)[9]	101	No	No	
OGS-6a (Gona)[21]	100	No	No	
FLKN 4[11]	73	Yes	No	
DAN-2d (Gona)[21]	60	No	No	
FLKNN 3[11,12]	48	Yes	Yes	2 CM, 5 TM
WG 7 (Gona)[7]	43	No	No	
West Gona 1[23]	39	Yes	No	
AL-666[24]	34	Yes	No	
Ain Hanech, Deposit C[8]	31	Yes	No	
Kada Gona 2-3-4[23]	21	No	No	
FLKNN 1[11]	17	Yes	No	
Omo 71[10,25]	12	Yes	No	
FLK 13[11]	11	Yes	Yes	
FLK 15[11]	9	Yes	Yes	
FLK 10[11]	8	Yes	Yes	
FLK 17[11]	5	No	No	
Kromdraai B[26]	2	Yes	No	
FLKNN 4[11]	1	Yes	No	
OGS-6 (Gona)[13,19]	0	Yes	Yes	1 CM
WG 9 (Gona)[13]	0	Yes	Yes	2 CM
Bouri[27]	0	Yes	Yes	3 CM

[1]Plummer, 2004
[2]de Lumley *et al.*, 2004
[3]Pickering, 1999
[4]Roche *et al.*, 1999
[5]Blumenschine, 1995
[6]Oliver, 1994
[7]Semaw *et al.*, 1997
[8]Sahnouni and de Heinzelin, 1998
[9]Howell *et al.*, 1987
[10]Chavallion, 1976
[11]Leakey, 1971
[12]Potts, 1988
[13]Domínguez-Rodrigo *et al.*, 2005
[14]Harris *et al.*, 1987
[15]Isaac, 1997
[16]Merrick and Merrick, 1976
[17]Roche, 2000
[18]Kibunjia, 1996
[19]Semaw *et al.*, 2003
[20]Plummer *et al.*, 1999
[21]Stout *et al.*, 2005
[22]Fernandez-Jalvo *et al*, 1999
[23]Harris, 1983
[24]Kimbel *et al.*, 1996
[25]de la Torre, 2004
[26]Kuman *et al.*, 1997
[27]de Heinzelin *et al.*, 1999

Landscape-Scale Carnivore and Hominin Traces During Upper Bed I and Lowermost Bed II, Olduvai Gorge

Introduction, Sample, and Methods

This part of the dissertation focused on applying the taphonomic test criteria developed in Chapters 3 and 4 to a landscape-scale sample of 2196 specimens (1518 of these, the macromammal bones, were analyzed taphonomically) from excavations in Bed I (1.84-1.79 Ma, Blumenschine *et al*., 2003) and lowermost Bed II (1.75-1.70 Ma, Manega, 1993) by the Olduvai Landscape Paleoanthropology Research Project (OLAPP). Data collection on the fossil samples included standard zooarchaeological variables and bone surface modifications (Appendix 5), as well as data on carnivore gross bone damage patterns and measurements of carnivore tooth marks (following Chapters 3 and 4).

Carnivore Activity Through Time

The first analysis used only the sample from lowermost Bed II, and explored possible changes in the intensity of carnivore activity through time. The sample was divided into "pre-incision" and "post-incision" sub-samples, referring to the valley incision occurred during lowermost Bed II. Two of the three taphonomic variables did not measure any change through time in the intensity of carnivore activity (NISP bones with carnivore damage: 16% pre-incision, 17% post-incision). However, the epiphysis to shaft ratio decreased substantially, suggesting that the relative abundance of bone-crunching carnivores may have increased after valley incision.

Carnivore Activity Through Space

The second analysis was also conducted only on the sample from lowermost Bed II. The spatial analysis units were the geographic locales currently used by the Olduvai Landscape Paleoanthropology (OLAPP) project, which are defined by geographic proximity of trenches and take several variables, including lithology and faulting, into account. One of OLAPP's hypothesized reconstructions of the vegetation in each of these locales is sensitive to the synsedimentary faulting that compartmentalized the lowermost Bed II eastern basin. Based on these two types of vegetation regimes reconstructed for the upthrown foot walls (more wooded, with tree stands) and downthrown hanging walls (more open, marshy terrain), differential carnivore activity would be predicted: evidence of lions, leopards, possibly spotted hyaenas, and an absence of cheetah in the former; and evidence of cheetah and spotted hyaena, possibly with lions, but an absence of leopards in the latter. The activities of extinct carnivores found in Bed II at Olduvai (based on Cushing, 2002 and Lewis, pers. comm.) that might be expected to be focused in the more

wooded upthrown foot walls include the sabertoothed felid *Dinofelis*, while *Canis africanus* and *Crocuta ultra* may have focused their activities in the more open downthrown hanging walls. I attempted to identify particular modern carnivores using taxon-specific carnivore traces, including gross bone damage and tooth mark measurements, outlined in the first part of this dissertation (Chapters 3 and 4).

The tooth scores in this sample were narrow and short compared with my modern sample, rendering them less useful for identifying specific carnivore taxa present, though the length and width of one tooth pit from HWKE is within the 95% confidence interval for modern spotted hyaenas and outside that of other modern carnivores. Other measures of carnivore activity, including epiphysis to shaft ratio and proportion of bones with carnivore damage, seem to follow some of the expected patterns. Epiphysis to shaft ratios substantially decreased over the FLK/VEK – HWKE – HWKEE-KK gradient, which is expected if hyaena activity was greater in HWKEE-KK (a foot wall, with open, marshy terrain) than FLK/VEK (a hanging wall, with trees). The epiphysis to shaft ratio at TK-Loc 20 is slightly lower than at Long K, while the proportion of bones with carnivore damage increased from the former to the latter, also supporting predicted carnivore abundances from hypothesized vegetation regimes. The lack of any size 3-4 long bone from Long K also speaks to hyaenid activity there. The results from the JK-WK, DK, THC compartment are difficult to interpret, as the proportion of carnivore-damaged bones follows the expected trend, but the epiphysis to shaft ratio does not.

Carnivore and Hominin Consumption of Individual Prey Animals

I attempted to identify consumption of individual prey animals in the Bed I landscape assemblage from carnivore-specific gross bone damage and tooth marking. I

used the Bed I samples for this analysis they have the highest NISPs in my overall Olduvai sample. The purpose of this analysis was partially to test the utility of this novel methodology and analytical technique, which was successful. Seventeen individual prey carcasses or carcass parts, for which specific consumer(s) could be suggested (including a variety of carnivores and hominins), were identified. This validates the use of this analytical technique and helps to suggest possible carnivores that may have been active in these particular geographic locales within the same time frame as hominins were.

Future directions

This dissertation successfully built on previous studies of carnivore-specific gross bone damage patterns and tooth mark measurements, and focused on *quantifying* these taxon-specific traces for applicability to the fossil record. I would like to expand on these results by:

1. Specifically linking carnivore gross bone damage and destruction to flesh availability information. If zooarchaeologists were able to quantify, or even identify, carcass resources available based on gross bone damage data (e.g., a damage level 2 on a size 3 ungulate femur is correlated with flesh scrap availability), we could then hypothesize specific resources extracted by hominins from bones on which carnivores had already fed. This requires new samples to be collected, which I plan to do at Sweetwaters Game Reserve (now Ol Pejeta Conservancy).

2. Gathering data on my entire sample of carnivore tooth marks. It is unknown if, and how, choosing only the largest tooth score and pit on each bone may have skewed my results.
3. Augmenting my samples of carnivore-damaged bones from naturalistic settings. My sample sizes of bones damaged by cheetahs, leopards, and jackals are small, and I was unable to collect any samples of bones damaged by wild dogs. To this end, I plan to continue my work at Ol Pejeta Conservancy, as well as initiate projects in other modern study locales.
4. Determining if the butchery-marked bone at the Koobi Fora sites are discrete occurrences, or part of more extensive scatters of butchery events. Surface fauna has been collected in several 2 x 2m meter squares in the vicinity of FwJj14A and FwJj14B, and analysis of this material, and especially material from future excavation at and near these sites, could provide information relevant to answering this question. Analysis of the fauna from FwJj1 could also shed light on the potentially specialized nature of the archaeological occurrences from Koobi Fora at this time.

Measuring tooth marks on fossils from Olduvai underscores the limits of the direct applicability of modern carnivore bone modification studies. The carnivore paleoguild present at Early Pleistocene sites includes some modern carnivores, but also includes many extinct taxa, such as sabertoothed felids (*Homotherium, Megantereon,* and *Dinofelis*) and two hyaenids (*Pachycrocuta* and *Chasmaporthetes*) for which models of gross bone damage capabilities are underdeveloped. I would like to see these models improved, and I am especially interested in the use of modern cheetahs as models for the

gross bone damage capabilities of sabertoothed felids. Recognizing sabertoothed felid gross bone damage and tooth marking is of great importance for testing hypotheses of early hominin scavenging.

Results from the three sites at Koobi Fora suggest hominin access to meat and marrow from ungulate carcasses on a relatively large scale. The analysis of the Bed I and lowermost Bed II samples at Olduvai, however, indicates low levels of hominin activity. Is this discrepancy related to the ~300,000 year time difference, and likely species level difference in the hominins (*Homo habilis/rudolfensis* versus *Homo erectus/ergaster*), between the two faunal samples? Different environmental settings? Different ecological settings, with different risks and affordances, and different carnivore communities (cf. Blumenschine and Peters, 1998; Tables 8.3)? More recent analyses of some other Oldowan or early Acheulean sites have evidence for hominin and carnivore interaction where hominins are thought to have had access to meat and marrow, including FxJj50 (Koobi Fora), FLK *Zinj* (Olduvai Bed I), BK and MNK Main (Olduvai Bed II), and Peninj (Blumenschine, 1995; Monahan, 1996; Domínguez-Rodrigo, 2002; Domínguez-Rodrigo *et al.*, 2002). Tables 8.1 and 8.2 are the beginnings of an attempt to relate hominin carcass foraging behavior to other measurable lithic and paleoecological variables. It is only with a focus on more integrative approaches will paleoanthropologists be able to recognize changes in behavioral patterns across time and space and identify factors influencing the evolution and ecology of the genus *Homo*.

Table 8.3. Carnivore taxa found during the Okote Member of the Koobi Fora Formation and Beds I and II at Oldvuai Gorge. An "X" in a cell indicates that a particular taxon is present in that time-stratigraphic interval. Data are from Cushing, 2002; Werdelin and Lewis, 2005, and references therein; M. Lewis and L. Werdelin, pers. comm..

Carnivore Family	Carnivore Species	Okote Member, Koobi Fora	Bed I, Olduvai Gorge	Bed II, Olduvai Gorge
Viverridae	*Genetta genetta*	X		
	Pseudocivetta ingens		X	X
Mustelidae	*Mellivora* sp.	X		
	cf. *Torolutra*	X		
	Aonyx sp.		X	X
Herpestidae	*Herpestes* aff. *ichneumon*		X	
	Galerella primitivus		X	
	Galerella debilis		X	
	Ichneumia aff. *albicauda*		X	
	Mungos dietrichi		X	
	Mungos minutus		X	
	Atilax sp.			X
Canidae	*Canis* cf. *mesomelas*		X	
	Prototocyon recki		X	
	Canis africanus		X	X
Hyaenidae	*Crocuta ultra*	X	X	X
	Hyaena sp.	X[1]	X[2]	X[3]
Felidae	*Dinofelis piveteaui*	X		
	Dinofelis sp.		X	X
	Megantereon whitei	X	X[4]	
	Homotherium sp.	X		
	Panthera leo	X	X	X
	Panthera pardus		X	X
	Acinonyx sp.	X		X

Notes:

A. A small viverrid or herpestid from the Okote Member is not listed on this chart, as it has not been further identified.

B. *Panthera leo* in the Okote Member includes Panthera sp. (lion-sized) specimens (M. Lewis, pers. comm.)

C. The *Machairodus* sp. listed by Cushing (2002) in Bed II, Olduvai, is likely a misidentification; *Macharodus* is an Upper Miocene genus, and the youngest known occurrence of its successor, *Amphimachairodus*, is from Langebaanweg at 5.3-5.0 Ma (Werdelin and Sardella, 2006). It is possible that this specimen is actually *Homotherium*, since the *Machairodus africanus* described by Petter and Howell (1987) from Aïn Brimba is a skull of *Homotherium* (L. Werdelin, pers. comm.)

[1] Likely either *Hyaena hyaena* or *Hyaena makapani* (L. Werdelin, pers. comm.)

[2] *Hyaena hyaena* (M. Lewis, pers. comm.)

[3] Identified as *Hyaena brunnea* by Cushing (2002), but this is a difficult taxon to identify and the presence of it in Bed II, Olduvai is highly unlikely (L. Werdelin, pers. comm.)

[4] Both *Megantereon eurynodon*, a junior synonym of *M. whitei*, and *Megantereon* sp. were listed by Cushing (2002); these are subsumed under *M. whitei* here.

Appendix 1
Carcass Retrieval Site Data Sheet

Carcass ID # _____
GPS location _____
habitat _____
initial spotting by _____ date/time _____
my initial observation (date/time) _____ when picked up _____
people/time spent searching for bones _____
herbivores present _____

Prey

taxon _____ age _____ sex _____ size _____
number of patches bones are scattered in _____ max scatter dimension _____
bones present bulk flesh flesh scraps no flesh
_____
_____
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Predator(s)

identification by _____
taxon _____
number of predators, age(es)/sex(es) _____
other mammalian predators present/distance _____
vultures present/number _____

other comments/observations _____
_____
_____
_____
_____
_____
_____

The following is a more detailed account of the data collected on this data sheet:
GPS location was recorded using map datum WGS 84.
Habitat refers to major habitat classification as detailed previously, as well as microhabitat, such as in a patch of tall grass or near an Acacia tree on the plains. Initial spotting by, date/time: this is who originally found the carcass and when they first saw it. I recorded not only my initial observation, but any subsequent observations if they were made before I picked the carcass up.
Age recorded was relative age: fetal, juvenile, sub-adult, adult.
Size was following the classification of Bunn (1982), sizes 1-6.
Maximum scatter dimension was an estimate of how far the farthest patches were from each other, to the nearest meter.
I recorded each bone present as well as what portions were present if some portions had been destroyed. Under bones present, I also noted if the bones had skin and/or were articulated and noted articular units. Flesh (bulk, scraps, none) was recorded following descriptions in Dominguez-Rodrigo (1997).

Appendix 2
Sweetwaters Kill Data

ID#	East	North	habitat	initial spotting by
SWT001	273462	-359	grass clearing; scattered bushes & trees nearby	Willy - Rongai gate
SWT002	272389	1175	bushy terrain	BLP
SWT003	271751	6120	tall grass with scattered bushes near water edge (30m)	Felix Patton
SWT004	271575	6124	tall grass with scattered bushes near water edge (30m)	Felix Patton
SWT005	271830	6305	bushes near Ol Pejeta Dam	Alan Birkett's daughter
SWT006	269233	4998	open plains (Oryx Plains)	STC night drive
SWT007	269300	4986	open plains (just next to road through Grant's Plains)	STC night drive
SWT008	269300	4986	open plains (just next to road through Grant's Plains)	STC night drive
SWT009	273854	2962	open Acacia woodland	Sweetwaters Research Centre
SWT010			open plains (Serat Plain)	Dixon
SWT011	261817	9003	open Acacia woodland	Earthwatch
SWT012	267870	2529	riverine woodland (leopard bait tree)	BLP
SWT013	270284	6643	open plain	STC morning drive
SWT014	272830	7408	open Acacia/Euclea woodlands	Rhino Patrol
SWT015	270426	6089	open Acacia woodland	BLP/Dixon/KWS
SWT016	267255	976	open Acacia woodland	Dixon
SWT017	267255	976	open Acacia woodland	Dixon
SWT018			airstrip	BLP
SWT019			airstrip	BLP
SWT020			airstrip	BLP
SWT021	269376	2730	open plain with scattered bushes nearby	Dixon
SWT022	272839	1799	open grass (jackal den)	n/a
SWT023	274197	7120	open grassy area	askari
SWT024	270867	7463	grassy woodland	Whisky Patrol
SWT025	266795	1396	mixed Acacia/Euclea but mostly Acacia; pretty thick bush	Earthwatch
SWT026	266795	1396	mixed Acacia/Euclea but mostly Acacia; pretty thick bush	Earthwatch
SWT027	269753	4875	open plain	Earthwatch
SWT028	267856	2550	riverine woodland (leopard bait tree)	BLP

SWT029	269700	7200	open plain	Alan Birkett
SWT030	267856	2550	riverine woodland (leopard bait tree)	BLP
SWT031	267856	2550	riverine woodland (leopard bait tree)	BLP
SWT032	274019	4168	open plain near open woodland & Acacia Dam	patrols
SWT033	271602	5990	on edge of Ol Pejeta Dam	patrols
SWT034	271641-50	5118-5130	open plains	Felix Patton/Andrew
SWT035	266334	1326	airstrip	Dixon
SWT036	268776	4617	open plains edge	Dixon
SWT037	273654	103	bushy grassland	night game drive
SWT038	272476	802	grassy bushland	Dixon

ID#	spotting date/time	my initial spot	when picked up	# people/time collection
SWT001	13 Sept 02 0200	13 Sept 02 1210	13 Sept 02 1210	3/30 min
SWT002	14 Sept 02 0700	14 Sept 02 0700	not picked up	n/a
SWT003	17 Sept 02 1720	17 Sept 02 2000	18 Sept 02 0630	3/45 min
SWT004	17 Sept 02 1720	17 Sept 02 2000	18 Sept 02 0630	3/45 min
SWT005	19 Sept 02 1700	19 Sept 02 0940	not picked up	n/a
SWT006	21 Sept 02 2200	21 Sept 02 2218	22 Sept 02 0645	3/20 min
SWT007	26 Sept 02 2210	26 Sept 02 2245	27 Sept02 0620	2/30 min
SWT008	26 Sept 02 2210	26 Sept 02 2245	27 Sept02 0620	2/30 min
SWT009	27 Sept 02 1945	27 Sept 02 2030	28 Sept02 0630	3/20 min
SWT010	1 Oct 02 1000	n/a	1 Oct 02 1000 (Dixon)	n/a
SWT011	5 Oct 02 (AM)	5 Oct 02 afternoon	5 Oct 02 afternoon	3/15 min
SWT012	11 Oct 02 (PM)	11 Oct 02 evening	12 Oct 02 0600	1/10 min
SWT013	13 Oct 02 0700	13 Oct 02 0800	13 Oct 02 0815	2/15 min
SWT014	13 Oct 02 0800	13 Oct 02 0830	13 Oct 02 0830	2/30 min (mainly disarticulating, defleshing)
SWT015	2 Nov 02 1800	2 Nov 02 1800	3 Nov 02 0900	4/5 min (all articulated)
SWT016	6 Nov 02 0600	6 Nov 02 0820	6 Nov 02 0830	2/20 min
SWT017	6 Nov 02 0600	6 Nov 02 0820	6 Nov 02 0830	2/5 min (all articulated except patella)
SWT018	20 Nov 02 1530	20 Nov 02 1530	21 Nov 0830	1/15 min
SWT019	20 Nov 02 1530	20 Nov 02 1530	21 Nov 0845	1/15 min
SWT020	20 Nov 02 1530	20 Nov 02 1530	21 Nov 0900	1/15 min
SWT021	1 Dec 02 1430	2 Dec 02 1130	2 Dec 02 1130	5/10 min
SWT022	n/a	16 Dec 02 0905	16 Dec 02 0905	n/a (all articulated)
SWT023	17 Dec 02 0830	17 Dec 02 1500	17 Dec 02 1500	4/10 min
SWT024	25 Dec 02 1100	25 Dec 02 1215	25 Dec 02 1215	3/15 min
SWT025	22 Jan 03 (AM)	22 Jan 03 1300, 2100	could not relocate	n/a
SWT026	22 Jan 03 (AM)	22 Jan 03 1300, 2100	could not relocate	n/a
SWT027	22 Jan 03 0745	23 Jan 03 0900	23 Jan 03 0900	3/15 min

SWT028	n/a	30 Jan 03 1700	30 Jan 03 1700	1/n/a
SWT029	11 Feb 03 2030	n/a	not picked up	n/a
SWT030	n/a	18 Feb 03 1730	18 Feb 03 1730	n/a
SWT031	n/a	21 Feb 03 0830	21 Feb 03 1930	n/a
SWT032	25 Feb 02 (AM)	25 Feb 03 1600	not picked up	n/a
SWT033	13 March 03 0730	13 March 03 0900	14 March 03 1530	3/20 min
SWT034	19 March 03 2135	21 March 03 1630	21 March 03 1630	4/10 min
SWT035	21 March 03 1700	n/a	not picked up	n/a
SWT036	25 March 03 1545	25 March 03 1645	28 March 1545	2/ 5 min (rain)
SWT037	18 June 03 2130	19 June 03 2150	not picked up	n/a
SWT038	18 June 03 (AM)	20 June 03 1000	20 June 03 1000	4/15 min

ID#	prey taxon	prey age	prey sex	prey size	# bone patches	max scatter dimension
SWT001	Zebra	AD	unknown	3	2	2m
SWT002	Hare	unknown	unknown	1	2	10m
SWT003	Thomson's gazelle	JUV	M	1	2-3	30m
SWT004	Grant's gazelle	JUV	unknown	1-2	1-2	10m
SWT005	Warthog	AD	unknown	2	n/a	n/a
SWT006	Zebra	AD	F	3	2	1m (head from rest of carcass)
SWT007	Zebra	AD	F	3	7	20mX10m
SWT008	Zebra	FET	unknown	2	3	3mx3m
SWT009	Grant's	JUV	unknown	1	2	4mx2m
SWT010	Thomson's gazelle	AD	unknown	1	unknown	unknown
SWT011	Zebra	AD	unknown	3	2	2mx2m
SWT012	Domestic goat	JUV	unknown	1	n/a	n/a
SWT013	Warthog	AD	unknown	1-2	5	1mx2m
SWT014	Zebra	AD	F	3	1	0
SWT015	Zebra	AD	M	3	1	1m
SWT016	Zebra	FET	unknown	1	2	1mx1m
SWT017	Zebra	AD	F	3	2 (incl. patella)	5m
SWT018	Domestic cow	JUV	unknown	2	1	n/a
SWT019	Domestic sheep	AD	unknown	1	1	n/a
SWT020	Domestic cow	JUV	unknown	2	0	n/a
SWT021	Zebra	JUV	F	3	6	10mx3m
SWT022	Domestic sheep	AD	unknown	1	0	n/a
SWT023	Impala	unknown	unknown	2	multiple	3mx10m
SWT024	Zebra	AD	M	3	2 (+ ribs)	10mx3m
SWT025	Zebra	AD	F	3	n/a	n/a
SWT026	Zebra	FET	unknown	1	n/a	n/a
SWT027	Grant's gazelle	JUV	unknown	1	4	15mx5m
SWT028	Domestic cow	JUV	unknown	2	n/a	n/a

SWT029	Zebra	?AD	unknown	3?	n/a	n/a
SWT030	Domestic sheep	AD	unknown	1	n/a	n/a
SWT031	Domestic sheep	?JUV	unknown	1	n/a	n/a
SWT032	Zebra	AD	unknown	3	n/a	n/a
SWT033	Eland	AD	M	4	3	15m
SWT034	Zebra	JUV	M?	2	3 (main)	12m
SWT035	Thomson's gazelle	AD	unknown	1	n/a	n/a
SWT036	Zebra	AD	F	3	3	11m
SWT037	Hare	unknown	unknown	1	n/a	n/a
SWT038	Warthog	JUV	unknown	2	2+	1m

Note:
AD = adult
JUV = juvenile
FET = fetus

ID#	predator ID by	predator taxon	#/age/sex of predators
SWT001	Willy - Rongai gate	Lion	~7
SWT002	BLP	Lion	10 - 2ADF, 3JUVF, 5JUVM
SWT003	FP/BLP	Lion	8 - 1ADM, 2 JUVF, 5 JUVM
SWT004	FP/BLP	Lion	8 - 1ADM, 2 JUVF, 5 JUVM
SWT005	Alan Birkett's daughter	Lion	9 - same pride as @ SWT004
SWT006	BLP	Lion	8 - 1ADM, 2ADF, 2JUVM, 3JUVF
SWT007	STC/BLP	Lion	7 - 1ADM, 1ADF, 3JUVM, 1JUVF, 2CUB
SWT008	STC/BLP	Lion	7 - 1ADM, 1ADF, 3JUVM, 1JUVF, 2CUB
SWT009	SRC/BLP	Lion	5 - 2ADF, 3CUB
SWT010	no ID	unknown	unknown
SWT011	Elijah (guard) via footprints	Spotted hyaena	1?
SWT012	BLP	Leopard	1?
SWT013	STC/BLP	Lion	2 - 2JUVM
SWT014	Rhino Patrol	Lion	3
SWT015	BLP	Lion - Spotted Hyaena	3 - 3 ADF
SWT016	Dixon/rangers in nearby huts	Lion	>1 (seen walking away)
SWT017	Dixon/rangers in nearby huts	Lion	>1 (seen walking away)
SWT018	BLP	Spotted Hyaena	unknown
SWT019	BLP	Spotted Hyaena	unknown
SWT020	BLP	Spotted Hyaena	unknown
SWT021	Dixon	Lion	12
SWT022	BLP	Black-Backed Jackal	unknown
SWT023	askari @ junction 7	Lion	unknown
SWT024	Whisky Patrol (by footprints)	Lion	unknown
SWT025	Earthwatch/BLP	Lion	3 - 1ADF, 1JUVF, 1 JUVM
SWT026	Earthwatch/BLP	Lion	3 - 1ADF, 1JUVF, 1 JUVM
SWT027	Earthwatch	Lion	4
SWT028	BLP	Leopard	1?

SWT029	Alan Birkett	Lion	5 - 2ADF, 3JUVM
SWT030	BLP	Leopard	1?
SWT031	BLP	Leopard	1?
SWT032	BLP	Lion	5 - 2ADF, 3CUB
SWT033	BLP/patrol	Lion	10 - 1ADM, 2ADF, 6JUVM, 1CUB
SWT034	Felix Patton/Andrew	Lion	10 - Ol Pejeta Pride
SWT035	BLP	Spotted Hyaena	unknown
SWT036	Dixon/BLP	Lion - Spotted Hyaena	LI 4 - 2ADF, 1JUVF, 1 JUVM
SWT037	BLP	Lion	1 - 1ADF
SWT038	Dixon	Lion	1 or 2; 1 seen was ADF

Note:
ADF = adult female
ADM = adult male
JUVF = juvenile female
JUVM = juvenile male
CUB = cub

ID#	other mammalian predators	vultures present/#
SWT001	none	none (but seen in early morning)
SWT002	none	none
SWT003	none	none
SWT004	none	none
SWT005	none	none
SWT006	none	none
SWT007	none	none
SWT008	none	none
SWT009	none	none
SWT010	unknown	unknown
SWT011	none	none
SWT012	spotted hyaena @ 2115, 3m	none
SWT013	none	1 medium bird of prey (hawk?)
SWT014	none	none
SWT015	none	~30
SWT016	none	none
SWT017	none	none
SWT018	none	none
SWT019	none	none
SWT020	none	none
SWT021	none	none
SWT022	lions in bushes 100m away	none
SWT023	unknown	vultures & 1 marabou stork in morning
SWT024	none	none
SWT025	none	none
SWT026	none	none
SWT027	Black-backed jackal - pretty close	none
SWT028	none	none

SWT029	none	none
SWT030	none	none
SWT031	none	none
SWT032	2 BBJ, 3 SH	> 25
SWT033	none	2 marabou storks in dam; vulture evidence at collection
SWT034	none	none
SWT035	none	none
SWT036	none	35 vultures/6 marabou storks @ ~200m
SWT037	none	none
SWT038	none	none

ID#	comments
SWT001	
SWT002	lions settled down so I could not pick up remains, but from consumption observation I think there were none
SWT003	killed with SWT004 (at least found together); could not pick up night of 17 Sept b/c lions still in vicinity; red jelly marrow
SWT004	found with SWT003
SWT005	could not relocate to collect
SWT006	collared male
SWT007	kill was pregnant F - fetus is SWT008
SWT008	fetus of SWT007; only fragments, no flesh
SWT009	one ADF with collar; probably incomplete recovery b/c 1) tall grass 2) lions moved around and ate
SWT010	possibly cheetah kill; found and collected by Dixon
SWT011	found on ranch; probably a day old - dried skin, lots of maggots; picked up and put out for bait for more hyaena damage
SWT012	leopard bait; only remaining limb was one wired to tree, rest of carcass probably on the ground and carried off by hyaenas
SWT013	got good video of consumption
SWT014	entire skeleton articulated; lots of flesh remaining (unusual); had to disarticulate and deflesh (carefully) to transport
SWT015	at pick up no lions but vultures in trees; limbs disarticulated from girdles, attached by skin; stomach cavity w/o no guts
SWT016	fetus of SWT017; killed @ 2300, lions still there 0600
SWT017	left for bait for hyaenas
SWT018	left all but hindlimbs & lumbars for hyaena bait; only saw isolated palate & upper cranium on opposite site of airstrip
SWT019	left all but hindlimbs & lumbars for hyaena bait; only L SCAP recovered ~25m from original placement; did not pick up
SWT020	left all but hindlimbs & lumbars for bait for hyaenas; nothing recovered
SWT021	
SWT022	sheep left as bait at jackal den; some internal organs still present (not gut); also dead jackal cub ~20m away
SWT023	know it was an impala only b/c askari saw skin in morning
SWT024	left stomach
SWT025	pregnant F; on 1st look, neck, stomach, anus eaten; couldn't relocate to pick up, kill dragged a few hundred meters!
SWT026	fetus of SWT025
SWT027	
SWT028	not sure how long this bait was up; lost after boiling!

SWT029	GPS is estimate - was 10m L of Oryx Plain Rd; neither Dixon nor I could relocate to collect
SWT030	I was not present at collection but bones were given to me for boiling; lost after boiling!
SWT031	
SWT032	could not collect b/c nothing left!!; lion ADF with collar
SWT033	observed 3/13 9AM, 5:30PM, 10PM
SWT034	could not pick up 3/20 b/c car trouble
SWT035	could not relocate to collect, assume moved/consumed by spotted hyaena
SWT036	at 1st obs. vultures, lions there, dragged kill behind tree; rain so no pickup 3 days; at pick up signs of vultures, sp. hyaenas
SWT037	observed consumption for 15 min until complete; got out to check area; no bones left, only large intestines; with RJB
SWT038	probably killed evening of 18 June; guts w/ 2 rib frags 10m from main patch

Appendix 3
Skeletal Element, Portion, and Segment Abbreviations

Skeletal Element Abbreviation	Skeletal Element Name
TTH	Tooth
MAND	Mandible
MANT	Mandible with teeth
HMAND	Hemimandible
MAX	Maxilla
MAXT	Maxilla with teeth
CRAN	Cranium
HC	Horn core
HYO	Hyoid
AX	Axial
RIB	Rib
VRT	Vertebra
C-1	Atlas
C-2	Axis
CER	Cervical vertebra
THO	Thoracic vertebra
LUM	Lumbar vertebra
SACR	Sacrum
CAUD	Caudal vertebra
INN	Innominate
SCAP	Scapula
LB	Long bone
ULB	Upper long bone
HUM	Humerus
FEM	Femur
ILB	Intermediate long bone
PAT	Patella
RADU	Radio-ulna
RAD	Radius
ULN	Ulna
TIB	Tibia
FIB	Fibula
CARP	Carpal
TARS	Tarsal
CALC	Calcaneum
AST	Astragalus
NAVC	Navicular-cuboid
LLB	Lower long bone
MP	Metapodials
MC	Metacarpal
MCM	Main Metacarpal (MTIII, equids)
MT	Metatarsal
MTM	Main Metatarsal (MTIII, equids)
PHA	Phalanx
PHA1	1st phalanx
PHA2	2nd phalanx
PHA3	3rd phalanx
SES	Sesamoid
NID	Non-identifiable bone

Portion Abbreviations and Categories

Long Bone:
A = proximal
B = proximal near-epiphyseal
C = midshaft
D = distal near-epiphyseal
E = distal
Rib:
6 = head
7 = neck
8 = shaft
9 = distal end (all 9's have to have some 8)
Vertebra:
V = centrum
R = neural spine
T = transverse process
Z = zygopophysis
Scapula:
G = glenoid
Y = blade
Innominate:
L = ilium
S = ischium
P = pubis
U = acetabulum
Mandible:
M = vertical ramus
N = gonial angle
H = horizontal ramus

Segment Abbreviations

CO = complete
PX = proximal
PSH = proximal shaft
PNEF = proximal near-epiphysis
MSH = midshaft
DNEF = distal near-epiphysis
DSH = distal shaft
DS = distal
MED = medial
LAT = lateral
ANT = anterior
POST = posterior
SUP = superior
INF = inferior
(Note: segment can also be a more precise skeletal element identification not listed here, such as a specific carpal or tarsal bone)

Appendix 4
Tooth Mark Frequency and Distribution Data

These counts of tooth marks include those with ambiguous morphologies that could not be measured, as noted in the methods section of Chapter 4.

Nairobi Animal Orphanage

Sample	Consumer	Prey Size	Element	Portion	# Scores	# Pits	# Furr	# Punct
NAO5	cheetah	4	CER	ZYGOPO		5		
NAO5	cheetah	4	CER	ZYGOPO		5		
NAO5	cheetah	4	CER	ZYGOPO		2		
NAO34	cheetah	4	HUM	MSH	2			
NAO7	cheetah	4	HUM	PSH	5	5		
NAO20	cheetah	4	HUM	PSH, MSH, DSH	13			
NAO22	cheetah	4	HUM	PX				2
NAO9	cheetah	4	INN	ILL		3		
NAO7	cheetah	4	RADU	PX	5			
NAO20	cheetah	4	RADU	PX, PSH	8			
NAO20	cheetah	4	SCAP	BLADE	7			
NAO10	cheetah	4	SCAP	BLADE		30		
NAO10	cheetah	4	SCAP	BLADE		12		
NAO15	cheetah	4	SCAP	BLADE		2		
NAO33	jackal	4	LUM	PROC		1		
NAO14	jackal	4	THO	NSPINE		1		
NAO18	leopard	4	CER	ZYGOPO	1			
NAO18	leopard	4	CER	ZYGOPO	1			
NAO8	leopard	4	INN	ILL		1		
NAO30	leopard	4	INN	ILL	2			
NAO8	leopard	4	LUM	PROC		2		
NAO8	leopard	4	LUM	PROC		3		
NAO30	leopard	4	LUM	PROC	7	9		
NAO30	leopard	4	SACR	PART	5			
NAO18	leopard	4	THO	PROC	1			
NAO12	lion	4	CALC	TUBERCLE	4	5		
NAO13	lion	4	CALC	TUBERCLE	6			
NAO26	lion	4	CALC	TUBERCLE				1
NAO28	lion	4	CARP			3		
NAO17	lion	4	CER	BODY		1		
NAO17	lion	4	CER	BODY				
NAO4	lion	4	FEM	DSH	6			
NAO13	lion	4	FEM	DSH, DS	1			1
NAO32	lion	4	FEM	MSH, DSH, DS	4			2
NAO16	lion	4	FEM	PX, MSH, DSH, DS	10	4		1
NAO26	lion	4	FEM	MSH, DSH	11			
NAO28	lion	4	HUM	PSH	10	7		
NAO6	lion	4	INN	ILL	2			
NAO16	lion	4	INN	PUB				1
NAO23	lion	4	INN	ILL	11	2		
NAO26	lion	4	INN	ACE	4			

NAO17	lion	4	LUM	ZYGOPO				
NAO17	lion	4	LUM	BODY				
NAO4	lion	4	NID		3			
NAO4	lion	4	NID			2		
NAO4	lion	4	NID		4			
NAO28	lion	4	RADU	PX		2		
NAO17	lion	4	RIB	SH	1			
NAO17	lion	4	RIB	SH	5			
NAO17	lion	4	RIB	SH	2			
NAO17	lion	4	RIB	SH	2			
NAO17	lion	4	RIB	SH	1	2		
NAO17	lion	4	RIB	SH		2		
NAO17	lion	4	RIB	SH		1		
NAO17	lion	4	RIB	SH	9	5		
NAO17	lion	4	RIB	SH		6		
NAO17	lion	4	RIB	SH	1			1
NAO17	lion	4	RIB	SH	1			
NAO17	lion	4	RIB	SH	2			
NAO17	lion	4	RIB	SH	3			1
NAO6	lion	4	RIB	SH	1			
NAO6	lion	4	RIB	SH		1		
NAO11	lion	4	RIB	SH	4	1		
NAO12	lion	4	TIB	MSH	15			
NAO4	lion	4	TIB	MSH	4	6		
NAO4	lion	4	TIB	PSH, MSH	11			
NAO32	lion	4	TIB	PSH	11			
NAO19	lion	4	TIB	PSH	1			
NAO26	lion	4	TIB	PSH	1			
NAO17	lion	4	THO	ZYGOPO				3
NAO17	lion	4	THO	ZYGOPO, BODY		3		
NAO17	lion	4	THO	NSPINE	1	1		
NAO17	lion	4	THO	ZYGOPO				1
NAO17	lion	4	THO	BODY, ZYGOPO				5
NAO17	lion	4	THO	BODY, ZYGOPO				2
NAO17	lion	4	THO	BODY		3		1
NAO6	lion	4	THO	BODY, ZYGOPO				2
NAO6	lion	4	THO	NSPINE		1		
NAO11	lion	4	THO	ZYGOPO		1		
	TOTAL				**209**	**140**	**0**	**24**

Sweetwaters Game Reserve

Hyaena is always spotted hyaena. Furr = furrows, punct = punctures.

Sample	Consumer	Prey Size	Element	PORTION	# Scores	# Pits	# Furr	# Punct
SWT022	jackal	1	CAUD	BODY		5		
SWT022	jackal	1	FEM	PX				5
SWT022	jackal	1	FEM	DS				1
SWT022	jackal	1	INN	ISCH		1		
SWT022	jackal	1	INN	ISCH, ILL		1		2

SWT022	jackal	1	RIB	SH	3			
SWT022	jackal	1	RIB	SH				1
SWT022	jackal	1	RIB	SH		1		
SWT022	jackal	1	RIB	SH		1		
SWT022	jackal	1	RIB	SH		1		
SWT022	jackal	1	RIB	SH				1
SWT012	leopard	1	AST	INFERIOR				2
SWT012	leopard	1	CAUD	BODY, PROC				2
SWT031	leopard	1	FEM	PSH, MSH, DSH, DS	15	2		4
SWT012	leopard	1	FEM	DS				1
SWT012	leopard	1	LUM	BODY	1	2		1
SWT028	leopard	2	AST	INFERIOR				2
SWT028	leopard	2	CALC	POSTERIOR	1	8		2
SWT028	leopard	2	FEM	PX, DSH, DS	1		1	11
SWT028	leopard	2	TIB	PSH, DSH		1	3	
SWT003	lion	1	AST		6	3		
SWT009	lion	1	CALC	CO		4		2
SWT009	lion	1	CALC	CO		1		
SWT003	lion	1	CARP	1		1		
SWT009	lion	1	CRAN	MAX	1			
SWT003	lion	1	CRAN	FRONTAL	6			1
SWT003	lion	1	CRAN	FRONTAL	1			
SWT003	lion	1	CRAN		1			
SWT027	lion	1	FEM	MSH	5	1		
SWT009	lion	1	FEM	PSH, MSH	2	2		
SWT009	lion	1	FEM	MSH, DSH, DS	10	10		
SWT009	lion	1	FEM	PSH, MSH, DSH	16	9		
SWT003	lion	1	FEM	PSH, MSH, DSH				
SWT003	lion	1	FEM	DSH	12	5		
SWT016	lion	1	FEM	PSH				1
SWT016	lion	1	FEM	PSH, DSH				2
SWT027	lion	1	HMAND	HRAM	2			
SWT027	lion	1	HMAND	HRAM	2	6		
SWT009	lion	1	HMAND	HRAM	3	5		
SWT009	lion	1	HMAND	HRAM	16			
SWT003	lion	1	HMAND	HRAM	20	4		
SWT003	lion	1	HMAND	HRAM	4	3		
SWT009	lion	1	HUM	MSH	3			1
SWT009	lion	1	HUM	MSH, DSH, DS	11	13		
SWT003	lion	1	HUM	MSH, DSH, DS	30	11		
SWT003	lion	1	HUM	MSH, DSH, DS	37	9		
SWT009	lion	1	INN	ACE	20	8		4
SWT009	lion	1	INN	ACE	13	1		
SWT003	lion	1	INN	ILL, ACE, PUB	35	3		3
SWT027	lion	1	LB	MSH	1	2		
SWT027	lion	1	LB	MSH	3	4		
SWT027	lion	1	LB	MSH	2	2		
SWT003	lion	1	MCM	PSH, DSH, DS	48	9		
SWT003	lion	1	MCM	PSH, MSH, DSH, DS	54	38		
SWT009	lion	1	MTM	DSH	2	2		
SWT009	lion	1	MTM	PSH, MSH, DSH	6	3		

SWT003	lion	1	MTM	PX, PSH, DSH	29	27		
SWT027	lion	1	NID		2	4		
SWT027	lion	1	NID		2			
SWT027	lion	1	NID		1			
SWT009	lion	1	RAD	PX, PSH, MSH	5	15		
SWT003	lion	1	RAD	PSH, MSH	25	4		
SWT003	lion	1	RADU	PX, PSH, MSH, DSH	49	10		1
SWT003	lion	1	RADU	PX, PSH, MSH	40	8		
SWT016	lion	1	RIB	SH	2			
SWT016	lion	1	RIB	SH	1			
SWT016	lion	1	RIB	SH	2			
SWT016	lion	1	RIB	SH	4			
SWT016	lion	1	RIB	SH	3			
SWT016	lion	1	SACRUM					2
SWT003	lion	1	SCAP	GLENOID, NECK	19	2		3
SWT016	lion	1	SCAP	GLENOID		1		
SWT027	lion	1	TIB	PSH, MSH, DSH	3	7		
SWT027	lion	1	TIB	MSH		1		
SWT009	lion	1	TIB	PSH, MSH, DSH	1	10		
SWT009	lion	1	TIB	PSH	13	3		
SWT003	lion	1	TIB	MSH, DSH, DS	18	4		
SWT003	lion	1	TIB	PSH, MSH, DSH	35	4		
SWT003	lion	1	TIB	PSH	1	3		
SWT016	lion	1	TIB	DSH			1	3
SWT013	lion	2	AST	PART		1		
SWT004	lion	2	AST	CO	2			
SWT013	lion	2	C-1	BODY	1			
SWT013	lion	2	C-2	SPINE				1
SWT004	lion	2	CALC	CO	35	4		2
SWT004	lion	2	CARP	CO		1		
SWT034	lion	2	CRAN	PREMAX				1
SWT034	lion	2	CRAN	PALATE	5	1		
SWT034	lion	2	CRAN	SKULL	1	1		
SWT034	lion	2	CRAN	SKULL	2	4		
SWT004	lion	2	CRAN	MAX	4			
SWT034	lion	2	FEM	PSH, MSH, DSH	24	28		
SWT034	lion	2	FEM	PSH, MSH, DSH	10			4
SWT008	lion	2	FEM	DSH	4			
SWT008	lion	2	FEM	PSH	3	1		
SWT034	lion	2	HUM	PSH, DSH	5	3		
SWT034	lion	2	HUM	PSH, MSH	16	8		
SWT013	lion	2	HUM	PSH, MSH	10	2		
SWT008	lion	2	HUM	PX, PSH				2
SWT038	lion	2	HUM	PSH, DSH	2	3		
SWT013	lion	2	INN	ILL, ACE, PUB, ISCH	19			
SWT013	lion	2	INN	ISCH	2			
SWT008	lion	2	INN	ILL	1			
SWT008	lion	2	INN	ACE, ILL				6
SWT004	lion	2	INN	ILL, ACE	38	3		
SWT013	lion	2	LUM	ZYGOPO, PROC	5			
SWT013	lion	2	LUM	BODY	1			

SWT013	lion	2	LUM	BODY, ZYGOPO	2			
SWT013	lion	2	LUM	PROC	2			
SWT034	lion	2	MAND	VRAM, HRAM	3	2		1
SWT004	lion	2	MAND	HRAM	11	4		2
SWT004	lion	2	MAND	HRAM	18			1
SWT038	lion	2	MAND	HRAM, GONA	11	3		
SWT034	lion	2	MCM	PSH, DSH	10	21		
SWT034	lion	2	MCM	MSH, DSH	7	11		
SWT004	lion	2	MCM	PSH, MSH, DSH, DS	64	7		2
SWT034	lion	2	MTM	PSH, DSH	3	28		
SWT004	lion	2	MTM	PSH, DSH, DS	48	14		
SWT004	lion	2	MTM	PSH, MSH, DSH	40	5		
SWT008	lion	2	NID		15			
SWT008	lion	2	NID			1	2	
SWT008	lion	2	NID			3		2
SWT008	lion	2	NID			2		
SWT038	lion	2	NID		4			
SWT038	lion	2	NID		7	3		
SWT038	lion	2	NID		4	1		
SWT038	lion	2	NID		1	1		
SWT038	lion	2	NID			1		
SWT034	lion	2	RAD	PSH, MSH, DSH	12	3		4
SWT034	lion	2	RAD	PSH, MSH, DSH	4	12		
SWT038	lion	2	RAD	PSH, MSH	5			
SWT013	lion	2	RADU	PX, PSH	4	2		1
SWT013	lion	2	RIB	HEAD, SH	6			2
SWT013	lion	2	RIB	SH	27	1		2
SWT013	lion	2	RIB	HEAD, SH	17			
SWT013	lion	2	RIB	SH	5	6		
SWT013	lion	2	RIB	SH	1			
SWT013	lion	2	RIB	SH	13			
SWT013	lion	2	RIB	SH	4			
SWT013	lion	2	RIB	SH	3	1		
SWT013	lion	2	RIB	SH	5			
SWT013	lion	2	RIB	SH	2			
SWT013	lion	2	RIB	SH	8			
SWT013	lion	2	RIB	SH	2	3		1
SWT013	lion	2	RIB	SH	16	2		
SWT013	lion	2	RIB	SH	3			
SWT008	lion	2	RIB	SH	1			
SWT038	lion	2	RIB	SH	8	4		
SWT038	lion	2	RIB	SH	2			
SWT034	lion	2	SCAP	NECK, BLADE	28			1
SWT034	lion	2	SCAP	NECK, BLADE	15	18		1
SWT013	lion	2	SCAP	NECK, BLADE	12	2		
SWT008	lion	2	SCAP	BLADE	1			
SWT038	lion	2	SCAP	GLENOID, NECK, BLADE	2			1
SWT034	lion	2	TIB	PSH, MSH, DSH	16	6		
SWT034	lion	2	TIB	PSH, DSH	10	3		
SWT004	lion	2	TIB	PSH, MSH	7	6		
SWT038	lion	2	TIB	PSH, MSH, DSH				

SWT013	lion	2	THO	NSPINE	3			
SWT013	lion	2	THO	BODY, ZYGOPO, SPINE	11			
SWT013	lion	2	THO	NSPINE	2	1		2
SWT013	lion	2	THO	BODY				1
SWT013	lion	2	THO	NSPINE	6			
SWT013	lion	2	THO	ZYGOPO				
SWT038	lion	2	ULN	PX, PSH, MSH	9	2		
SWT013	lion	2	VRT	ZYGOPO	7			1
SWT013	lion	2	VRT	ZYGOPO	2			
SWT013	lion	2	VRT	ZYGOPO, PROC		3		
SWT021	lion	3	AST	CO		2		
SWT021	lion	3	AST	CO	2		1	
SWT006	lion	3	C-1	PROC	5	1		
SWT007	lion	3	C-1	PROC	7		1	1
SWT014	lion	3	C-1	PROC	2			
SWT021	lion	3	C-1	PROC	1			1
SWT007	lion	3	C-2	BODY, ZYGOPO	1	1		
SWT021	lion	3	C-2	BODY				2
SWT021	lion	3	CALC	CO	7	1		
SWT021	lion	3	CALC	CO	1			1
SWT006	lion	3	CRAN	OCCIPITAL				1
SWT021	lion	3	CRAN	FACE, OCCIPITAL		3		7
SWT024	lion	3	CRAN	FACE				2
SWT001	lion	3	CER	ZYGOPO				
SWT001	lion	3	CER	ZYGOPO	1			
SWT006	lion	3	CER	BODY, PROC	6			
SWT006	lion	3	CER	PROC	2			
SWT006	lion	3	CER	BODY, ZYGOPO, PROC	9			
SWT006	lion	3	CER	BODY, ZYGOPO, PROC	1	2		3
SWT006	lion	3	CER	ZYGOPO		1		
SWT007	lion	3	CER	BODY	1			1
SWT007	lion	3	CER	PROC				3
SWT007	lion	3	CER	PROC	5			1
SWT007	lion	3	CER	PROC				1
SWT007	lion	3	CER	BODY, PROC	2			3
SWT021	lion	3	CER	BODY, PROC	3	1		5
SWT021	lion	3	CER	BODY, ZYGOPO, PROC	5	1	1	5
SWT021	lion	3	CER	BODY, PROC		7	2	5
SWT021	lion	3	CER	PROC	2			
SWT021	lion	3	CER	PROC	2			1
SWT021	lion	3	CER	PROC	1			
SWT001	lion	3	FEM	PX, PSH, MSH, DS	14			3
SWT001	lion	3	FEM	PX, PSH, MSH, DSH, DS	19			
SWT006	lion	3	FEM	PX, MSH, DSH, DS	35			1
SWT006	lion	3	FEM	PX, PSH, MSH, DSH, DS	14		1	
SWT007	lion	3	FEM	PX, PSH, DSH, DS	26	2	4	
SWT007	lion	3	FEM	PX, PSH, MSH, DSH, DS	18	2	1	4
SWT014	lion	3	FEM	PX, PSH, MSH, DSH, DS	16		2	2
SWT014	lion	3	FEM	PX, PSH, MSH, DSH, DS	22			3
SWT021	lion	3	FEM	PSH, DSH	11	7		
SWT021	lion	3	FEM	PSH, MSH, DSH, DS	17	2	1	3

SWT024	lion	3	FEM	PX, DS	2	8	8	2
SWT024	lion	3	FEM	PX, PSH, MSH, DSH, DS	16	1	7	
SWT006	lion	3	HUM	PSH, DSH	6			
SWT006	lion	3	HUM	PX, PSH, MSH, DSH, DS	23	1		2
SWT007	lion	3	HUM	PX, PSH, MSH	3			2
SWT007	lion	3	HUM	PX, PSH, MSH, DS	19			1
SWT021	lion	3	HUM	PSH, DS	8		2	6
SWT024	lion	3	HUM	PX, PSH	11	5		
SWT024	lion	3	HUM	PX, PSH, MSH, DSH, DS	10		1	4
SWT001	lion	3	INN	ILL, ACE, PUB, ISCH	85			
SWT006	lion	3	INN	ILL, ACE, ISCH	14	2		
SWT006	lion	3	INN	ILL, ACE, ISCH	21	2		1
SWT007	lion	3	INN	ILL, ACE, PUB, ISCH	53			3
SWT014	lion	3	INN	ILL, ACE, PUB, ISCH	31			
SWT021	lion	3	INN	ILL, ACE, PUB, ISCH	12	2	4	
SWT024	lion	3	INN	ILL, PUB	5			2
SWT001	lion	3	LUM	BODY	5			
SWT001	lion	3	LUM	PROC	2			
SWT006	lion	3	LUM	PROC	1	1		
SWT006	lion	3	LUM	PROC	3	1		
SWT006	lion	3	LUM	PROC				4
SWT007	lion	3	LUM	PROC				2
SWT007	lion	3	LUM	BODY, PROC	5			
SWT007	lion	3	LUM	BODY	4			1
SWT007	lion	3	LUM	PROC		1		
SWT014	lion	3	LUM	PROC	1			
SWT014	lion	3	LUM	PROC	1			
SWT014	lion	3	LUM	BODY, PROC	7			5
SWT014	lion	3	LUM	PROC	6			1
SWT024	lion	3	LUM	ZYGOPO, PROC	1			1
SWT024	lion	3	LUM	BODY	1			
SWT024	lion	3	LUM	BODY, PROC	3			2
SWT024	lion	3	LUM	PROC				1
SWT024	lion	3	LUM	PROC				1
SWT007	lion	3	MAND	VRAM	5			
SWT021	lion	3	MAND	VRAM				3
SWT021	lion	3	MC	PSH	2			
SWT021	lion	3	MCM	PX, PSH, DSH, DS	4	20	1	1
SWT021	lion	3	MT	PSH				1
SWT024	lion	3	MT	CO	2			
SWT024	lion	3	MT	CO	3			
SWT021	lion	3	MTM	PX, DSH, DS	4	4		
SWT021	lion	3	MTM	PSH, MSH, DS	1	1		1
SWT024	lion	3	MTM	MSH	1			
SWT021	lion	3	PHA1	CO	5	8	4	
SWT021	lion	3	PHA1	CO	5	4	14	
SWT021	lion	3	PHA2	CO		1		
SWT006	lion	3	RADU	PX	13	1		
SWT006	lion	3	RADU	MSH	5			
SWT007	lion	3	RADU	PX, PSH, MSH, DSH	12	1		
SWT007	lion	3	RADU	PX, PSH, MSH	7	4		2

SWT021	lion	3	RADU	PX, DSH	5	2	2	2
SWT024	lion	3	RADU	PX, MSH	19			
SWT024	lion	3	RADU	PX, DSH	16			1
SWT001	lion	3	RIB	SH	1			
SWT001	lion	3	RIB	SH	12			
SWT001	lion	3	RIB	SH	11	2		
SWT001	lion	3	RIB	HEAD, SH	14	4		1
SWT001	lion	3	RIB	SH	17			
SWT001	lion	3	RIB	SH	3			
SWT001	lion	3	RIB	SH	9	1		
SWT001	lion	3	RIB	SH	2			
SWT001	lion	3	RIB	SH	4			
SWT001	lion	3	RIB	SH	12			
SWT001	lion	3	RIB	SH	16			
SWT001	lion	3	RIB	SH	2	4		
SWT001	lion	3	RIB	SH	1	1		
SWT001	lion	3	RIB	SH	2			
SWT001	lion	3	RIB	SH	7	1		
SWT001	lion	3	RIB	SH	22	2		
SWT001	lion	3	RIB	SH	9	1		
SWT001	lion	3	RIB	SH	2			
SWT001	lion	3	RIB	SH	2			
SWT001	lion	3	RIB	SH	1	2		
SWT001	lion	3	RIB	SH	7	1		
SWT001	lion	3	RIB	SH	5			
SWT001	lion	3	RIB	SH	7			
SWT001	lion	3	RIB	SH	6	4		
SWT001	lion	3	RIB	SH	24			
SWT001	lion	3	RIB	SH	4	1		
SWT001	lion	3	RIB	SH	10	1		
SWT001	lion	3	RIB	SH	2			
SWT001	lion	3	RIB	SH	5	2		
SWT001	lion	3	RIB	SH	15			
SWT001	lion	3	RIB	SH	2			
SWT001	lion	3	RIB	SH	7			
SWT001	lion	3	RIB	SH		2		
SWT001	lion	3	RIB	SH	6			
SWT001	lion	3	RIB	SH	34	3		
SWT001	lion	3	RIB	SH	14	2		
SWT006	lion	3	RIB	SH	2			
SWT006	lion	3	RIB	SH	4	1		
SWT006	lion	3	RIB	SH	1			
SWT006	lion	3	RIB	SH	2			
SWT006	lion	3	RIB	SH	5			
SWT006	lion	3	RIB	SH	4			
SWT006	lion	3	RIB	SH	21			
SWT006	lion	3	RIB	SH		2		
SWT006	lion	3	RIB	SH	16	1		
SWT006	lion	3	RIB	SH	4			
SWT006	lion	3	RIB	SH	3			
SWT006	lion	3	RIB	SH	9			

SWT006	lion	3	RIB	SH	14	4		
SWT006	lion	3	RIB	SH	18	2		
SWT006	lion	3	RIB	SH	2			
SWT006	lion	3	RIB	SH	10			
SWT006	lion	3	RIB	SH	8			
SWT006	lion	3	RIB	SH	14			
SWT006	lion	3	RIB	SH	10			
SWT006	lion	3	RIB	SH	3			
SWT006	lion	3	RIB	HEAD, SH	10	1		1
SWT006	lion	3	RIB	SH	18			
SWT006	lion	3	RIB	SH	1	2		
SWT006	lion	3	RIB	SH	2			
SWT006	lion	3	RIB	SH	7			
SWT006	lion	3	RIB	SH	10			
SWT006	lion	3	RIB	SH	2			
SWT006	lion	3	RIB	SH	5			
SWT007	lion	3	RIB	SH	1			1
SWT007	lion	3	RIB	SH	2			
SWT007	lion	3	RIB	SH	7	2		
SWT007	lion	3	RIB	SH	1			
SWT007	lion	3	RIB	SH	6			
SWT007	lion	3	RIB	SH	3			
SWT007	lion	3	RIB	SH	2			1
SWT007	lion	3	RIB	SH				1
SWT007	lion	3	RIB	SH	4	1		
SWT007	lion	3	RIB	SH	4	2		
SWT007	lion	3	RIB	SH	8			
SWT007	lion	3	RIB	SH	5			
SWT007	lion	3	RIB	HEAD, SH	13			2
SWT007	lion	3	RIB	SH	6	3		
SWT007	lion	3	RIB	SH	40			
SWT007	lion	3	RIB	HEAD, SH	8		1	1
SWT007	lion	3	RIB	SH	4	1		
SWT007	lion	3	RIB	SH	15	6		
SWT007	lion	3	RIB	SH	15			2
SWT007	lion	3	RIB	SH	9	7		
SWT007	lion	3	RIB	SH	27			
SWT007	lion	3	RIB	HEAD, SH	6	4		
SWT007	lion	3	RIB	SH	19			
SWT007	lion	3	RIB	SH	1			
SWT007	lion	3	RIB	SH	8			
SWT007	lion	3	RIB	HEAD, SH	17			
SWT007	lion	3	RIB	SH	10	1		
SWT007	lion	3	RIB	SH	1			1
SWT007	lion	3	RIB	SH	8			
SWT007	lion	3	RIB	SH	12			
SWT014	lion	3	RIB	SH	10			
SWT014	lion	3	RIB	SH		3		1
SWT014	lion	3	RIB	SH	3		1	1
SWT014	lion	3	RIB	SH	3			
SWT014	lion	3	RIB	SH	1			

SWT014	lion	3	RIB	SH	6			
SWT014	lion	3	RIB	SH	2			1
SWT014	lion	3	RIB	SH	2			
SWT014	lion	3	RIB	SH	4			
SWT014	lion	3	RIB	SH		2		1
SWT014	lion	3	RIB	SH	2			3
SWT014	lion	3	RIB	SH	2			
SWT014	lion	3	RIB	SH	9			
SWT014	lion	3	RIB	SH	1	1	1	
SWT014	lion	3	RIB	SH	6			
SWT014	lion	3	RIB	SH	3	1		
SWT014	lion	3	RIB	SH	5			
SWT014	lion	3	RIB	SH	3			
SWT014	lion	3	RIB	SH	2			
SWT014	lion	3	RIB	SH	1	4		
SWT014	lion	3	RIB	SH	17			
SWT014	lion	3	RIB	SH	5	1		
SWT014	lion	3	RIB	SH	7			
SWT014	lion	3	RIB	SH	2			
SWT014	lion	3	RIB	SH	2			
SWT021	lion	3	RIB	SH		1		1
SWT021	lion	3	RIB	SH	8			
SWT021	lion	3	RIB	SH	11			
SWT021	lion	3	RIB	SH	2			
SWT021	lion	3	RIB	SH	5		6	
SWT021	lion	3	RIB	SH	8			
SWT021	lion	3	RIB	SH	4			
SWT021	lion	3	RIB	SH	12			2
SWT021	lion	3	RIB	SH	1			3
SWT024	lion	3	RIB	SH	8			
SWT024	lion	3	RIB	SH	6			
SWT024	lion	3	RIB	SH	1			
SWT024	lion	3	RIB	SH	5	1	1	1
SWT024	lion	3	RIB	SH	11			
SWT024	lion	3	RIB	SH	11		1	
SWT024	lion	3	RIB	HEAD, SH	7	2		1
SWT024	lion	3	RIB	SH	10			
SWT024	lion	3	RIB	SH	18			1
SWT024	lion	3	RIB	SH	16	1		
SWT024	lion	3	RIB	HEAD, SH	4			3
SWT024	lion	3	RIB	SH	5			
SWT024	lion	3	RIB	SH	3			
SWT024	lion	3	RIB	SH	6		2	
SWT024	lion	3	RIB	SH	1	2		
SWT024	lion	3	RIB	SH	10			
SWT024	lion	3	RIB	SH	9			
SWT024	lion	3	RIB	SH	15			
SWT024	lion	3	RIB	SH	5			
SWT024	lion	3	RIB	SH		1		
SWT024	lion	3	RIB	SH	6			
SWT024	lion	3	RIB	SH	1	1		

SWT001	lion	3	SACR	DS	8	3		
SWT007	lion	3	SACR	~CO	5	3		
SWT014	lion	3	SACR	CO				2
SWT024	lion	3	SACR		3			1
SWT006	lion	3	SCAP	BLADE, NECK	7	4		2
SWT006	lion	3	SCAP	BLADE	5			
SWT007	lion	3	SCAP	BLADE	28	3		
SWT007	lion	3	SCAP	BLADE	7	1		
SWT014	lion	3	SCAP	BLADE	1			
SWT021	lion	3	SCAP	BLADE	12			1
SWT021	lion	3	SCAP	BLADE	10	10		5
SWT024	lion	3	SCAP	BLADE		3		
SWT024	lion	3	SCAP	BLADE	5			
SWT001	lion	3	TIB	PSH	8			
SWT006	lion	3	TIB	PSH	4			
SWT006	lion	3	TIB	PSH	6			
SWT007	lion	3	TIB	PSH, MSH	5			
SWT007	lion	3	TIB	PSH, MSH, DSH	4			
SWT021	lion	3	TIB	PSH	5			
SWT021	lion	3	TIB	PSH	8		1	
SWT024	lion	3	TIB	PX, PSH	1			1
SWT024	lion	3	TIB	PSH, MSH	12			
SWT001	lion	3	THO	BODY, NSPINE	29			1
SWT001	lion	3	THO	BODY, NSPINE	18		1	
SWT001	lion	3	THO	BODY, NSPINE	18			
SWT001	lion	3	THO	BODY	2			
SWT001	lion	3	THO	BODY	11			
SWT001	lion	3	THO	BODY	5			2
SWT001	lion	3	THO	BODY, NSPINE	9			
SWT001	lion	3	THO	BODY, NSPINE	15	3		2
SWT001	lion	3	THO	BODY, NSPINE	11	2		1
SWT001	lion	3	THO	BODY, NSPINE	7			
SWT001	lion	3	THO	BODY	1			
SWT001	lion	3	THO	NSPINE	1			
SWT001	lion	3	THO	NSPINE	5	2		
SWT001	lion	3	THO	NSPINE	5	3		
SWT001	lion	3	THO	NSPINE		1		
SWT001	lion	3	THO	NSPINE	1			
SWT006	lion	3	THO	ZYGOPO, NSPINE	1	1		
SWT006	lion	3	THO	NSPINE	4			
SWT006	lion	3	THO	NSPINE	6			
SWT006	lion	3	THO	NSPINE	4	1		
SWT006	lion	3	THO	BODY, NSPINE	4	1		1
SWT006	lion	3	THO	BODY, NSPINE		2		3
SWT006	lion	3	THO	BODY, NSPINE	2		1	3
SWT006	lion	3	THO	BODY, NSPINE	8	1		2
SWT006	lion	3	THO	BODY, NSPINE	1	1		2
SWT006	lion	3	THO	BODY, NSPINE	5	2		
SWT006	lion	3	THO	BODY, NSPINE	1		1	1
SWT006	lion	3	THO	BODY, NSPINE	2	2		4
SWT006	lion	3	THO	BODY, ZYGOPO	2	1		3

SWT006	lion	3	THO	BODY, NSPINE		1		3
SWT006	lion	3	THO	BODY, NSPINE	1		1	3
SWT006	lion	3	THO	BODY, NSPINE	7			
SWT006	lion	3	THO	BODY	3			
SWT006	lion	3	THO	BODY	5			
SWT007	lion	3	THO	NSPINE	2			
SWT007	lion	3	THO	NSPINE	1			
SWT007	lion	3	THO	NSPINE	3			
SWT007	lion	3	THO	BODY, NSPINE	4			4
SWT007	lion	3	THO	BODY, NSPINE	4			3
SWT007	lion	3	THO	BODY, ZYGOPO, NSPINE	16			5
SWT007	lion	3	THO	BODY, NSPINE	2			1
SWT007	lion	3	THO	BODY, NSPINE	2			2
SWT007	lion	3	THO	BODY				10
SWT007	lion	3	THO	BODY, ZYGOPO, NSPINE	2			10
SWT007	lion	3	THO	BODY, NSPINE	3			8
SWT007	lion	3	THO	BODY, NSPINE	1	2		2
SWT007	lion	3	THO	BODY, NSPINE	2	2		2
SWT007	lion	3	THO	BODY, NSPINE	2	3		3
SWT007	lion	3	THO	BODY, NSPINE	12		1	
SWT007	lion	3	THO	BODY, NSPINE	1	1		4
SWT007	lion	3	THO	BODY		1		1
SWT014	lion	3	THO	NSPINE	4			
SWT014	lion	3	THO	BODY			1	1
SWT014	lion	3	THO	BODY	7			
SWT014	lion	3	THO	BODY	5		2	
SWT014	lion	3	THO	BODY	7	1	1	
SWT014	lion	3	THO	BODY	3			
SWT021	lion	3	THO	BODY				4
SWT021	lion	3	THO	BODY				3
SWT024	lion	3	THO	BODY, ZYGOPO, NSPINE	4			3
SWT024	lion	3	THO	BODY, NSPINE	2			1
SWT024	lion	3	THO	BODY, ZYGOPO, NSPINE	6		3	4
SWT024	lion	3	THO	BODY, ZYGOPO, NSPINE	3		1	2
SWT033	lion	4	C-1	PROC	3	5		3
SWT033	lion	4	C-2	PROC	5			5
SWT033	lion	4	CER	BODY, PROC	10			
SWT033	lion	4	CER	BODY, PROC	2			3
SWT033	lion	4	CER	PROC	3	1	1	
SWT033	lion	4	CER	BODY, PROC	6			3
SWT033	lion	4	CER	BODY, PROC	3			
SWT033	lion	4	FEM	PX, PSH, DSH, DS	15		1	4
SWT033	lion	4	FEM	PX, DSH, DS	4		5	5
SWT033	lion	4	HMAND	VRAM	1			
SWT033	lion	4	INN	ILL, ACE, PUB, ISCH	10		1	5
SWT033	lion	4	INN	ILL, ACE, ISCH	11	3		1
SWT033	lion	4	LUM	BODY, PROC	4	1		
SWT033	lion	4	LUM	BODY, PROC	2			
SWT033	lion	4	LUM	PROC	2	1		
SWT033	lion	4	LUM	PROC	1			
SWT033	lion	4	LUM	PROC	9			

SWT033	lion	4	LUM	PROC	6			
SWT033	lion	4	MCM	PSH	3			
SWT033	lion	4	RADU	PX, PSH	1	1		
SWT033	lion	4	RIB	SH	1			
SWT033	lion	4	RIB	SH	1			
SWT033	lion	4	RIB	SH	6			
SWT033	lion	4	RIB	SH	1			1
SWT033	lion	4	RIB	SH	16			
SWT033	lion	4	RIB	SH	22			
SWT033	lion	4	RIB	SH	3			1
SWT033	lion	4	RIB	SH	1	1		
SWT033	lion	4	RIB	SH	4			
SWT033	lion	4	RIB	SH		1		2
SWT033	lion	4	RIB	SH	5	1		
SWT033	lion	4	RIB	SH	8			
SWT033	lion	4	RIB	SH	3			1
SWT033	lion	4	RIB	SH		1		
SWT033	lion	4	RIB	SH	1			
SWT033	lion	4	RIB	SH	1			
SWT033	lion	4	SACR		4			
SWT033	lion	4	SCAP	BLADE	11	3		2
SWT033	lion	4	SCAP	BLADE	9	3		1
SWT033	lion	4	TIB	PX	1		1	1
SWT033	lion	4	THO	NSPINE	2			
SWT033	lion	4	THO	ZYGOPO, NSPINE	2	1		
SWT033	lion	4	THO	NSPINE	1			
SWT033	lion	4	THO	NSPINE		1		
SWT033	lion	4	THO	BODY	4			
SWT017	lion-hyaena	3	C-1	PROC	1	1		
SWT015	lion-hyaena	3	CRAN					6
SWT015	lion-hyaena	3	CER	ZYGOPO, PROC	15			
SWT015	lion-hyaena	3	FEM	PX, MSH	11			1
SWT036	lion-hyaena	3	HUM	PX, MSH, DS	2		1	
SWT015	lion-hyaena	3	HUM	MSH, DSH	6	1		
SWT015	lion-hyaena	3	HUM	MSH	6			
SWT015	lion-hyaena	3	INN	ILL, PUB, ACE	9	3		3
SWT015	lion-hyaena	3	LUM	BODY	1			
SWT015	lion-hyaena	3	NID		4			
SWT015	lion-hyaena	3	RADU	MSH	4			
SWT015	lion-hyaena	3	RADU	MSH	3			
SWT036	lion-hyaena	3	RIB	SH	3			
SWT036	lion-hyaena	3	RIB	SH	6			
SWT036	lion-hyaena	3	RIB	SH	12			
SWT036	lion-hyaena	3	RIB	SH				2
SWT036	lion-hyaena	3	RIB	SH	4	1		
SWT036	lion-hyaena	3	RIB	HEAD				2
SWT036	lion-hyaena	3	RIB	SH	6			
SWT036	lion-hyaena	3	RIB	SH	1			
SWT036	lion-hyaena	3	RIB	SH	4	1		
SWT036	lion-hyaena	3	RIB	SH	8	1		
SWT036	lion-hyaena	3	RIB	SH	2			

SWT036	lion-hyaena	3	RIB	SH	26			
SWT036	lion-hyaena	3	RIB	SH	6			
SWT036	lion-hyaena	3	RIB	SH	1			
SWT036	lion-hyaena	3	RIB	SH	10			
SWT036	lion-hyaena	3	RIB	SH	2			
SWT036	lion-hyaena	3	RIB	SH	7	1		
SWT036	lion-hyaena	3	RIB	SH	6			
SWT036	lion-hyaena	3	RIB	SH	8	1		
SWT015	lion-hyaena	3	RIB	SH	13	2		1
SWT017	lion-hyaena	3	RIB	SH	9			
SWT017	lion-hyaena	3	RIB	SH	1	3		
SWT017	lion-hyaena	3	RIB	SH	1			
SWT017	lion-hyaena	3	RIB	SH		2		
SWT017	lion-hyaena	3	RIB	SH	7			
SWT017	lion-hyaena	3	RIB	SH	3			
SWT017	lion-hyaena	3	RIB	SH	11	1		
SWT017	lion-hyaena	3	RIB	SH	1			
SWT017	lion-hyaena	3	RIB	SH	2			1
SWT017	lion-hyaena	3	RIB	SH				1
SWT017	lion-hyaena	3	RIB	SH	12			
SWT017	lion-hyaena	3	RIB	SH	7			1
SWT017	lion-hyaena	3	RIB	SH	6			
SWT017	lion-hyaena	3	RIB	SH	1			
SWT017	lion-hyaena	3	RIB	SH	1			
SWT017	lion-hyaena	3	RIB	SH				2
SWT017	lion-hyaena	3	RIB	SH		1		
SWT017	lion-hyaena	3	RIB	SH	1	2		
SWT017	lion-hyaena	3	RIB	SH	1	1		
SWT017	lion-hyaena	3	RIB	SH	1			
SWT017	lion-hyaena	3	RIB	SH	2			
SWT017	lion-hyaena	3	RIB	SH	1			
SWT017	lion-hyaena	3	RIB	SH		1		
SWT017	lion-hyaena	3	RIB	SH	1			
SWT015	lion-hyaena	3	SACR		8			
SWT036	lion-hyaena	3	SCAP	BLADE	1			1
SWT015	lion-hyaena	3	SCAP	GLENOID, BLADE	7			1
SWT017	lion-hyaena	3	SCAP	GLENOID, BLADE	5			
SWT017	lion-hyaena	3	SCAP	BLADE	1			
SWT015	lion-hyaena	3	THO	NSPINE	7	2		
SWT017	lion-hyaena	3	THO	BODY, NSPINE	5			2
SWT017	lion-hyaena	3	THO	BODY	7			1
SWT011	hyaena	3	CER	PROC				3
SWT011	hyaena	3	CER	PROC				2
SWT011	hyaena	3	CER	PROC				1
SWT011	hyaena	3	FEM	PX, PSH, MSH	10		3	
SWT011	hyaena	3	FEM	PSH, DSH	8			
SWT011	hyaena	3	LUM	PROC				2
SWT011	hyaena	3	MAND	VRAM	5			
SWT011	hyaena	3	RIB	SH		2		
SWT011	hyaena	3	RIB	SH	8	2		
SWT011	hyaena	3	RIB	SH	1			1

SWT011	hyaena	3	RIB	SH	1			
SWT011	hyaena	3	RIB	SH	3			
SWT011	hyaena	3	RIB	SH	2			
SWT011	hyaena	3	RIB	SH	1	1		
SWT011	hyaena	3	RIB	SH	1	1		
SWT011	hyaena	3	RIB	SH	1			
SWT011	hyaena	3	RIB	SH	3	1		
SWT011	hyaena	3	RIB	SH	1			
SWT011	hyaena	3	RIB	SH	3			
SWT011	hyaena	3	SACR					1
SWT011	hyaena	3	THO	PROC				1
SWT011	hyaena	3	THO	BODY, ZYGOPO, PROC				3
SWT010	cheetah	1	SCAP	BLADE				1
SWT010	cheetah	1	SCAP	BLADE				1
SWT010	cheetah	1	CRAN	TEMPORAL, PARIETAL				3
SWT010	cheetah	1	INN	ILL				1
SWT010	cheetah	1	SACR			1		
SWT010	cheetah	1	FEM	DS		1		
SWT010	cheetah	1	C-1	PROC	3	1		
SWT010	cheetah	1	C-2	PROC	3	1		
SWT010	cheetah	1	CER	PROC	1	1		
	TOTAL				**4160**	**847**	**104**	**439**

Appendix 5
Zooarchaeological and Taphonomic Data Sheet

This appendix refers to all of the data collected on the Koobi Fora archaeofaunas. Each category of data collected was the heading of a column in an Excel spreadsheet.

CATALOGUE NUMBER
CATALOGUE NUMBER SUFFIX
NORTHING
EASTING
LEVEL
ORIENTATION
DIP
YEAR EXCAVATED
ORIGINAL ANALYST
ORIGINAL/CATALOGUE IDENTIFICATION
TAXON
SIZE (1-6, following Bunn 1982)
AGE (relative age: juvenile or adult)
SIDE
SKELETAL ELEMENT
BLUMENSCHINE'S PORTION

1	proximal
2	distal
3	near-epiphyseal
4	midshaft

FERRARO-POBINER'S PORTION

A	proximal
B	proximal near-epiphyseal
C	midshaft
D	distal near-epiphyseal
E	distal

SEGMENT
CIRCUMFERENCE (for long bones only)

1	1-25%
2	26-50%
3	51-75%
4	76-99%
5	100%

MAX LENGTH (in millimeters)
MAX WIDTH (in millimeters)
GREEN FRACTURE
RECENT FRACTURE
WEATHERING STAGE
SURFACE READABILITY (CORTICAL, FRACTURE, MEDULLARY)
proportion of bone surface 'readable' for modifications

1 0-25%
2 25-50%
3 50-75%
4 75-99%
5 100%

SURFACE CONDITION (CORTICAL, FRACTURE, MEDULLARY)

if surface is not 100% readable, reason(s) why

1 Weathered
2 Adhering matrix
3 Exfoliation
4 Chemical corrosion
5 Mechanical rounding (may include polish)
6 Not Applicable
7 Immature

MISCELLANEOUS MARKS

0 NO MISCELLANEOUS MARKS
1 indeterminate lineation - cut-mark-like
2 indeterminate lineation - tooth-mark-like
3 sedimentary abrasion
4 excavator/preparator mark
5 root etching
6 rodent gnawing
7 indeterminate marking
8 hammerstone pit- or striae-like mark

TOOTH MARK (on cortical surface)

N None
S Score
P Pit
B Both

TOOTH MARK LOCATION
TOOTH MARK COMMENTS
PERCUSSION MARK (on cortical surface)

N None
S Striae
P Pit
B Both

PERCUSSION MARK LOCATION
PERCUSSION MARK COMMENTS
CUT MARK (on cortical surface)

N None
S Slice
P Scrape
C Chop
M Multiple

CUT MARK LOCATION
CUT MARK COMMENTS

FRACTURE MARKS (TM, PM or CM on fracture surface)
MEDULLARY MARKS (TM, PM or CM on fracture surface)
TOOTH NOTCH (presence/absence)
TOOTH NOTCH LOCATION
TOOTH NOTCH ASSOCIATES

- N No Associated Mark
- S Associated Carnivore Score
- P Associated Carnivore Pit
- C Associated Carnivore Pit and Score
- A Associated Ambiguous Marks

TOOTH NOTCH COMMENTS
PERCUSSION NOTCH (presence/absence)
PERCUSSION NOTCH LOCATION
PERCUSSION NOTCH ASSOCIATES

- N No Associated Mark
- S Associated Hammerstone Striae
- P Associated Hammerstone Pit
- H Associated w/ Classic HSTN Impact Mark (both Pit and Striae)
- A Associated Ambiguous Mark

PERCUSSION NOTCH COMMENTS
BEHAVIORAL AGENT(S)

- C Carnivore
- H Hominid

ADDITIONAL COMMENTS

Appendix 6
Modified Bones from Koobi Fora Archaeofaunas (Key)

This key is for the headings of columns in Appendices 6a-6d.
Cat #: Catalogue number
Taxon: Taxonomic identification
Size: Size classes 1-6, following Bunn, 1982 and Brain, 1981
Age: Relative age (J = juvenile, AD = adult); blank cells indicate an assumed adult
Side: L, left; R, right
Skel Elem: Skeletal element, following Appendix 3
Portion: Portion of skeletal element, following Appendix 3
Segment: Segment of skeletal element or portion, following Appendix 3
Circ: Circumference, following Appendix 5
MaxL: Maximum length, in millimeters
MaxW: Maximum width, in millimeters
GF: Green fracture (Y = yes, N = no); for long bones only
RF: Recent fracture (Y = yes, N = no); recent fractures of >10% of the bone edge
WS: Weathering state: 1-6, after Behrensmeyer (1978)
CRead: Cortical surface readability, following Appendix 5
CCond: Cortical surface condition, following Appendix 5
MiscM: Miscellaneous bone surface marks, following Appendix 5
Context: Surface, *In Situ,* or Geo Trench
TM: Tooth mark type(s) (if present), following Appendix 5
TM Loc: Tooth mark location(s), following Appendix 5
TM Comments: Description and/or additional information about tooth mark(s)
PM: Percussion mark type(s) (if present), following Appendix 5
PM Loc: Percussion mark location(s), following Appendix 5
PM Comments: Description and/or additional information about percussion mark(s)
CM: Cut mark type(s) (if present), following Appendix 5
CM Loc: Cut mark location(s), following Appendix 5
CM Comments: Description and/or additional information about cut mark(s)
Agent(s): H = hominin, C = carnivore
Comments: Any additional information about recent breaks, refitting, gluing, curation, possible further identification, analytical methods, etc.

Appendix 6a
Modified Bones from FwJj14A

Cat #	Taxon	Size	Age	Side	Skel Elem	Portion	Segment	Circ	MaxL	MaxW	GF	RF	WS	CRead	CCond	MiscM	Context
2562j	Mammal				NID				9	3		y		4	2,4		*In Situ*
6006	Mammal				NID				10	6				5			Surface
1467a	Mammal				NID				10	9		y		4	4		Surface
601	Mammal				NID				11	5		y		4	4		Surface
1454b	Mammal				NID				11	6		y		5			Surface
1554b	Mammal	2/3A			LB	C		1	11	7		y		4	4		Surface
1225	Mammal				NID				12	8		y	0	5			Surface
656	Mammal				NID				13	4		y	0	5			Surface
349	Mammal				NID				13	6		y		2	3,4		Surface
6009	Mammal				NID				13	6				5		1,3	Surface
6161	Mammal				NID				13	7				4	4		Surface
1420d	Mammal				NID				14	6		y		4	4		Surface
1342a	Mammal				LB	C		1	14	7				4	4		Surface
6005	Mammal				NID				15	7		n		4	4		Surface
121	Mammal				NID				15	9		y		4	4		Surface
1477a	Mammal				NID				16	4		y		4	4		Surface
1067	Mammal	2/3A			LB	C		1	16	11	y		0	4	2,4		Surface
1417b	Mammal				NID				16	11		y	0	5			Surface
1224	Mammal				NID				16	12		n		4	4		Surface
1546b	Mammal	1/2			LB	C		1	16	13	y	n		4	4		Surface
615	Mammal				NID				16	13		y		4	4		Surface
6222	Mammal				NID				17	7		y		4	4		Surface
6115a	Fish				spine				17	8		y		4	2		Surface
6140	Mammal				NID				17	9		y		4	4		Surface
2028	Mammal	1/2			LB	C		1	17	9		y		4	4		*In Situ*
323	Mammal				NID				18	9		n		4	4		Surface
1213	Mammal				NID				18	9		y	0	5			Surface
1346a2	Mammal				NID				18	10		y		3	3		Surface
1367a	Mammal	3			LB			1	18	12	y	n		5			Surface
1512e	Mammal				NID				18	13		y		4	4		Surface
508	Mammal	2/3A			LB	C		1	19	7	y	y		4	3,4		Surface
6342d	Mammal				NID				19	7		y		4	4		Surface
1246a	Mammal				NID				19	12		y		4	4		Surface

Cat #	Taxon	Size	Age	Side	Skel Elem	Portion	Segment	Circ	MaxL	MaxW	GF	RF	WS	CRead	CCond	MiscM	Context
6099	Mammal				NID				19	20		n		4	4		Surface
1300	Mammal				NID				20	15				4	4		Surface
6004	Mammal	2/3A			LB	C		1	20	16	y	y	0	4	3	3	Surface
6098	Mammal	1/2			LB	C		1	21	6				4	4		Surface
1403a	Mammal				NID				21	12		y		4	4		Surface
1390	Mammal				NID				21	14		y		4	4		Surface
1275	Mammal	3			LB	C			21	16	y	y		4	4		Surface
652	Mammal				NID				22	9		y		4	4	2	Surface
1406d	Mammal				LW LB	C		1	22	11	y	y		4	4		Surface
6342b	Mammal				NID				22	11		y		4	2,4		Surface
216	Mammal	2/3A			LB	C		1	22	15	y	n	0	5			Surface
1051	Mammal	>=2			LB	C		1	22	19	y	y		5		2	Surface
1384b	Mammal				NID				23	9		y		4	4		Surface
610	Mammal	2/3A			LB	C		2	23	15	y	y		4	4	3	Surface
6059	Mammal				NID				23	19		y		4	4		Surface
321	Mammal	2/3			ULN	A	POST		25	11		y		4	4		Surface
348	Mammal				ULN	A			25	11		y		4	4		Surface
1013a-97	Mammal	3B/4			LB	C		1	25	17	y	y	0	5		3	Surface
1028	Mammal	2	J		VRT	V			25	21				4	4		Surface
6084	Mammal	2/3A			ULN	C			26	11	n	y		4	4		Surface
1384a	Mammal				NID				26	18		y		4	4		Surface
1266	Mammal				NID				27	16		y		4	4		Surface
1008-97	Mammal				NID				27	19		y		4	4		Surface
666	Mammal				NID				28	11		y		4	4	1	Surface
6132	Mammal	2/3A			LB	C		1	28	14	y	y		1	3	1	Surface
506	Mammal				NID				28	16		y		4	4		Surface
314	Mammal	3			LB	C		1	29	8				4	3		Surface
1369c	Mammal	3			LB	C		1	30	15	y	n		4	4		Surface
1006-97	Mammal	>=3			NID				30	16	n	n	1	4	4		Surface
1010-97	Mammal	>=2			NID				30	18	n	n	0	4	3		Surface
614	Mammal	2/3A			LB	C		1	31	8	y	y		5			Surface
1172	Mammal				NID				32	10		y		4	4		Surface
1289	Mammal				NID				32	11		y		4	2		Surface
6138	Mammal	3			LB	C		1	32	16	y	y		4	4		Surface
14	Mammal	2/3A			LB	C		1	32	16	y	y	0	2	3,4		Surface

Cat #	Taxon	Size	Age	Side	Skel Elem	Portion	Segment	Circ	MaxL	MaxW	GF	RF	WS	CRead	CCond	MiscM	Context
27	Mammal	2/3A			LB	C		1	32	16	y	y	0	2	3,4		Surface
6111	Mammal				NID				32	16		y		4	4		Surface
1088	Mammal				NID				32	22				4	4		Surface
2611a	Mammal	3			HUM	C		1	32	25	y	n		4	2,4		*In Situ*
6118	Mammal	2/3A			LB			1	33	14	n	y		4	4		Surface
1252	Mammal	3			LB	C		1	33	18	y	y	0	5			Surface
6324	Mammal	1/2			LB	C		1	34	9	y	n		4	4		Surface
1448a	Mammal	3B/4			LB	C		1	34	12	n	y		3	4		Surface
1208	Mammal	3			LB	C		1	34	16	n	y		4	4	1,3	Surface
6070	Mammal	2/3			RIB	8			34	17		n		4	4		Surface
1369d	Mammal				NID				34	21		y		4	4	3	Surface
665	Mammal	3B/4			LB	C		1	36	21	y	y		3	2,3	3	Surface
5007	Bovidae	3		R	MAND	N			36	29		y		4	2	1	*In Situ*
1101	Mammal	1		L	FEM	A-C		4	37	17	n	y		4	2	7	Surface
1015-97	Bovidae	3			MTP	C	POS	1	37	25	n	n	0	4	4		Surface
623	Mammal	2/3A			LB	C		2	38	14	n	y		4	4		Surface
2591a	Mammal				NID				38	16				4	4		*In Situ*
303	Mammal	3B/4			LB	C		1	39	18	y	n	0	4	4		Surface
304	Mammal	3B/4			LB	C		1	39	18	y	n	0	4	4		Surface
1320	Mammal				NID				39	28				4	4		Surface
1132	Mammal	2/3A			LB	C		1	41	14		y		3	3		Surface
1095	Mammal				NID				41	18		y		4	4		Surface
1007-97	Bovidae	2/3A		L	MTM	C,E		5	41	35	n	n	1	4	3		Surface
1202	Mammal	3			LB	C		2	42	18		y	1	4	4		Surface
6167	Mammal	3			LB	C		1	42	21	y	n		4	2,4		Surface
1019-97	Bovidae	3A		L	FEM	C-D	POS-MED	2	42	28	y	n	0	5			Surface
1238	Mammal	>=2			MAND	G			42	30		n		4	4		Surface
6010	Mammal	3			LB	C		1	43	17	y	n	0	4	3		Surface
154	Mammal	3B/4			RAD	C		2	43	20	y	y		4	4		Surface
173	Mammal	3B/4			RAD	C		2	43	20	y	y		4	4		Surface
6114	Mammal				NID				43	26	n	y	0	4	4		Surface
655	Mammal	3			LB	C		1	45	13	y	y	0	5			Surface
1107	Bovidae	3		L	TIB	C	POS-MED	1	45	16	y	n		4	4		Surface
107	Mammal	2/3A			LUM	T			45	16		y		4	3		Surface
140	Mammal	3			LUM	Z			45	25		n		3	2		Surface

Cat #	Taxon	Size	Age	Side	Skel Elem	Portion	Segment	Circ	MaxL	MaxW	GF	RF	WS	CRead	CCond	MiscM	Context
1205	Mammal	1/2			RIB	8			48	12		y		4	4		Surface
1020-97	Mammal	2/3A			RIB	8			48	13		y		4	4		Surface
1016-97	Bovidae	3			RAD	C		1	48	15	y	n	0	4	4		Surface
668	Mammal	2/3A			UP LB	C		2	48	21	y	n		5		3	Surface
1	Bovidae	3		R	PAT		CO		48	40			0	5			Surface
1203a	Bovidae	3			CRAN		OCCIPITAL		49	42		y	0	4	3		Surface
1240	Mammal	3			LB	C		1	50	14	n	y		4	4		Surface
409	Mammal	3			LB	C		1	50	19	n	y		2	4		Surface
412	Mammal	3			LB	C		1	50	19	n	y		2	4		Surface
1226	Mammal	3		L	INN	L			50	24		y		4	4		Surface
418	Mammal	3		L	HUM	C		2	51	19	y	y		4	4		Surface
6073	Bovidae	3		L	ULN	A	PX-POS	5	51	24	y	n		4	4		Surface
1014-97	Mammal	2		L	INN		ILL		51	25	n	n	1	5			Surface
6113	Mammal				NID				51	26		n		4	4		Surface
1056	Mammal	2/3A			FEM	C	POS-MED	2	52	23	y	y	0	5		1	Surface
1021-97	Mammal	3			LB UP	C		4	52	29	y	n	0	5			Surface
6063	Mammal	2/3A			RIB	8			53	17		y		4	4		Surface
1397a	Mammal	2/3A			FEM	C		2	53	23	y	y		4	4	3	Surface
431	Mammal	>=4			RIB	8			54	14		y		4	4		Surface
1022-97	Mammal	3			HUM	C	POS-LAT	2	54	25	y	n	0	4	3		Surface
1108	Bovidae	3A		R	TIB	C		2	56	22	y	n		4	3,4		Surface
1130	Bovidae	3		L	TIB	C	ANT-LAT	2	57	20		y		4	4		Surface
1131	Bovidae	3		L	TIB	C	ANT-LAT	2	57	20		y		4	4		Surface
1093	Suidae	3A		R	AST		CO		59	33				3	3,4		Surface
1003-97	Bovidae	3A	A	R	MCM	C,E		5	61	40	y	n	0	4	3		Surface
1141	Bovidae	3		L	TIB	C	POS	2	62	31	y	y		2	3,4		Surface
1206	Mammal	>=3			NID				66	27		n		4	4		Surface
1112	Bovidae	3A		L	MAND	H			68	27		y	0	4	3		Surface
1170	Mammal	3			LUM	N			68	36		y		4	4		Surface
1017-97	Bovidae	3A			ULN	C		4	69	14	n	y	1	4	3		Surface
12	Mammal	2/3			INN	U			69	30		y		4	4		Surface
1115	Mammal				NID				71	22		y		4	4		Surface
6346	Mammal	>=4			RIB	8			73	35		y		4	2,4		Surface
2560a	Mammal				LB	C		1	74	14	y	y		4	4,5		*In Situ*
102	Mammal	3		L	INN				74		n	y		5			Surface

Cat #	Taxon	Size	Age	Side	Skel Elem	Portion	Segment	Circ	MaxL	MaxW	GF	RF	WS	CRead	CCond	MiscM	Context
1210	Mammal	>=3B			RIB	8			83	35		y	0	4	4		Surface
1024-97	Bovidae	3		L	TIB	B-C	ANT-LAT	3	86	47	y	n	1	5			Surface
1122	Bovidae	3		L	TIB	C	POS-MED	2	90	23	y	y		4	3,4		Surface
1125	Bovidae	3		L	TIB	C	POS-MED	2	90	23	y	y		4	3,4		Surface
1221	Hippopotamidae	5			CER	VZ			95	90		y		4	4		Surface
2034a	Bovidae	3		L	TIB	C		2	96	19	y		1	4	2,3	7	*In Situ*
1002c-97	Mammal	3B/4			RAD	C		3	105	26	y	y		3	4		Surface
1111	Suidae	3A			CER		C-1		111	66		y		4	4		Surface
no #	Bovidae	3			CER		CO		112	73		n		4	2		Surface
148	Bovidae	3		L	RAD	C	LAT	3	117	24	y	n		4	4		Surface
1012-97	Hippopotamidae	5			CER	VZ			121	86		y		4	2,4		Surface
1201	Suidae	3		R	INN	LU			143	75		y		4	3,4		Surface
103	Hippopotamidae	5			HUM	C		2	155	54	y	n		4	2,4		Surface

Cat #	TM	TM Loc	TM Comments
2562j			
6006			
1467a			
601			
1454b	S		3 parallel scores, oblique to bone axes
1554b			
1225			
656			
349			
6009			
6161			
1420d			
1342a			
6005			
121			
1477a			
1067			
1417b			
1224			
1546b			
615			
6222			
6115a			
6140			
2028	S	4C	single score
323			
1213			
1346a2			
1367a			
1512e			
508			
6342d			
1246a			

Cat #	TM	TM Loc	TM Comments
6099			
1300			
6004			
6098			
1403a			
1390			
1275			
652			
1406d			
6342b			
216			
1051			
1384b			
610			
6059			
321			
348			
1013a-97			
1028			
6084			
1384a			
1266			
1008-97			
666			
6132			
506			
314			
1369c			
1006-97			
1010-97			
614			
1172			
1289			
6138			
14			

Cat #	TM	TM Loc	TM Comments
27			
6111			
1088			
2611a			
6118			
1252			
6324			
1448a	S	4C	3 wide scores near broken bone edge
1208	P	4C	single pit overlying CMs
6070			
1369d			
665			
5007			
1101			
1015-97			
623			
2591a			
303			
304			
1320			
1132			
1095			
1007-97			
1202			
6167			
1019-97			
1238			
6010			
154			
173			
6114			
655			
1107			
107			
140			

Cat #	TM	TM Loc	TM Comments
1205			
1020-97			
1016-97			
668			
1			
1203a			
1240			
409			
412			
1226			
418			
6073			
1014-97			
6113			
1056			
1021-97			
6063			
1397a			
431			
1022-97			
1108			
1130			
1131			
1093			
1003-97			
1141			
1206			
1112			
1170			
1017-97			
12			
1115			
6346			
2560a			
102			

Cat #	TM	TM Loc	TM Comments
1210			
1024-97	P	3B&C	5: one large, lat of tibial crest; one large, midway down near broken lat edge; three small on most dist-lat part
1122			
1125			
1221			
2034a			
1002c-97			
1111			
no #			
148			
1012-97			
1201			
103			

Cat #	PM	PM Loc	PM Comments
2562j			
6006			
1467a			
601			
1454b			
1554b	S	4C	very light striae emanating from one edge, concentrated in 2 patches
1225			
656			
349			
6009			
6161			
1420d			
1342a			
6005			
121			
1477a			
1067			
1417b			
1224			
1546b			
615			
6222			
6115a			
6140			
2028			
323			
1213	S		2 long striae emanating from broken fracture edge
1346a2			
1367a	S	3	2 partial sets of striae, emanating from same rounded edge
1512e			
508			
6342d			
1246a	S		patch of short striae emanating from cortical flake scar

Cat #	PM	PM Loc	PM Comments
6099			
1300			
6004			
6098			
1403a			
1390	S		thick patch of striae emanating from fracture edge
1275	S	4C	one long striae emanating from fracture surface
652			
1406d			
6342b			
216			
1051	S	4C	patch of short striae emanating from fracture edge
1384b	S		patch of short percussion striae near "A"
610			
6059			
321			
348			
1013a-97			
1028			
6084			
1384a			
1266			
1008-97			
666			
6132			
506			
314			
1369c			
1006-97			
1010-97			
614	S	4C	light patch of striae extending from mini-notch
1172			
1289			
6138			
14			

Cat #	PM	PM Loc	PM Comments
27			
6111			
1088	S		several patches of small striae emanating from one broken surface (left)
2611a	S	4C	several long striae emanating from cortical flake removal
6118			
1252	S	4C	2 striae emanating from fracture edge
6324			
1448a			
1208			
6070			
1369d			
665	S	4C	patch of striae emanating from fracture edge
5007			
1101			
1015-97			
623			
2591a			
303			
304			
1320			
1132			
1095			
1007-97			
1202			
6167			
1019-97			
1238			
6010			
154			
173			
6114			
655	S	4C	unusually long percussion striae patch emanating from fracture surface
1107	S	4C	on lateral side, near CMs
107			
140			

Cat #	PM	PM Loc	PM Comments
1205			
1020-97			
1016-97			
668	S	4C	patch of short, relatively deep striae near fracture edge
1			
1203a			
1240			
409	S	4C	patch of fairly long striae
412	S	4C	patch of fairly long striae (on 409)
1226			
418			
6073			
1014-97			
6113			
1056			
1021-97			
6063			
1397a	S	4C	a few patches of striae emanating from fracture edge near label
431			
1022-97			
1108			
1130			
1131			
1093			
1003-97			
1141			
1206			
1112			
1170			
1017-97			
12			
1115			
6346			
2560a			
102			

Cat #	PM	PM Loc	PM Comments
1210			
1024-97			
1122			
1125			
1221			
2034a			
1002c-97			
1111			
no #			
148			
1012-97			
1201			
103			

Cat #	CM	CM Loc	CM Comments
2562j	S		2 parallel CMs with 2 shorter CMs in same direction nearby
6006	S		4 CMs/CM patches, parallel, fairly deep, perpendicular to bone axis
1467a	S		2 CMs made of many linear marks each, obliquely oriented to each other
601	S		several patches of deep CMs oblique to bone axis
1454b			
1554b			
1225	S		patch of deep CMs extending from broken edge
656	S		6-7 distinct CMs or groups of CMs
349	S		two small, deep CMs near one edge
6009	S		3 light CMs on one side of bone
6161	S		2 wide CMs on one end of bone spanning from one broken edge to the other; 2 short, narrow CMs on other end
1420d	C		two deep marks
1342a	S	4C	several CMs/patches in tight group
6005	S		patch of light, medium length CMs, partially obscured by surface condition
121	S		patch of CMs, fairly short & deep
1477a	S		single, fairly deep CM
1067	S	4C	several deep CMs or patches of CMs, perpendicular to long bone axis
1417b	S		swipe/patch of CMs
1224	S		single long CM
1546b	S	4C	several patches of light, short CMs emanating from fracture edge
615	S		two CM patches, one heavier and shorter, one lighter and longer
6222	S		several CMs stretching across entire width of bone
6115a	S		a series of CMs cutting across bone ridges; perpendicular to bone axis
6140	S		2 deep CMs coming from bone edge
2028			
323	S		several patches of CMs going in two directions
1213			
1346a2	S		two long CMs emanating from area on surface where bone was removed
1367a			
1512e	S		several CMs/patches in linear group, oblique to bone axis
508	S	4C	several CMs parallel to long bone axis, on both sides of exfoliated patch
6342d	S		2 short CMs near one broken edge
1246a			

Cat #	CM	CM Loc	CM Comments
6099	S		3-4 light, longish CMs, parallel to each other
1300	S		several patches of deep, medium length CMs
6004	P	4C	very light scrape marks along one side of bone, partially covered by sedimentary abrasion
6098	S	4C	3-4 patches of long, fairly deep CMs/patches
1403a	S		several isolated CMs and patches, in a group, oblique to bone axis
1390	S		patch of CMs across modern break, going in several directions
1275			
652	S		single, long, medium depth CM, oblique, emanating from edge
1406d	P		two parallel scrape marks, pretty far apart, on bone edge, perpendicular to long bone axis
6342b	S		2 longish CMs with same origination going to broken edge
216	S	4C	6 patches of fairly deep, short CMs perpendicular to the long bone axis
1051			
1384b			
610	P	4C	several rather light, short marks perpendicular to long bone axis
6059	S		multiple CMs along one side of bone, most short & deep, some perpendicular to bone axis, some oblique
321	S	1A	several CMs along posterior margin
348	S	1A	several CMs along posterior margin
1013a-97	S	4C	several "V" CMs, long, medium depth
1028	S	V	long, deep CMs across specimen
6084	S	C	3 patches of very short CMs along posterior margin
1384a	S		three longish CMs on a less-than-ideal surface
1266	P		4 deep, parallel marks on point
1008-97	S		one fairly heavy & fairly long CM
666	S		2 deep CMs coming from same origin point ("V")
6132	S	4C	single longish CM on unexfoliated surface
506	SC		one patch & one single heavy CM, one chop mark; all at one (broken) end
314	S	4C	one patch of several CMs near one end, oblique to long bone axis; another group of much lighter CMs near other end
1369c	S	4C	2 parallel shallow, oblique, medium-length CMs emanating from one edge
1006-97	S		several patches of medium CMs, subparallel, linear group
1010-97	S		several CMs whose length are abbreviated by surface exfoliation; a few are light and look like P striae
614			
1172	S		6 CMs/CM groups, in 2 intersecting directions, both oblique to bone axis
1289	P		several short, medium depth, CMs perpendicular to bone axis
6138	S	4C	2 deep, short CMs (almost chop marks) coming from bone edge
14	S	4C	multiple series of short CMs perpendicular to long bone axis and across both bone frags

Cat #	CM	CM Loc	CM Comments
27	S	4C	multiple series of short CMs perpendicular to long bone axis and across both bone frags
6111	S		2 short, deep CMs on bone edge near "6"
1088			
2611a			
6118	S	3	two fairly deep parallel CMs emanating from bone edge
1252			
6324	P	4C	long series of very light scrape marks down one side of bone
1448a			
1208	S	4C	several long both light and heavy CMs
6070	S	8	>=7 patches or individual CMs along one side, coming off lower edge
1369d	S		two long deep parallel linear marks, apparently overlying sed abrasion?
665			
5007	S	1A	a few patches of short, light to deep CMs near modern break
1101	S	1C	two relatively deep, curvilinear marks, posterior
1015-97	SP	3C	4 or 5 distinct patches of very fine to medium CMs, each @ slightly different orientations; incl. scraping marks (down long. bone axis)
623	S	4C	several patches of deep, short CMs along 'leading edge'
2591a	S		several short-medium CM patches in a tight group, perpendicular to bone axis, along one edge
303	S	4C	a series of several individual or patches of CMs perpendicular to long bone axis
304	S	4C	a series of several individual or patches of CMs perpendicular to long bone axis
1320	S		single 'flying V' near one broken edge
1132	S	4C	about 4 individual or parallel paired long, medium depth CMs, oblique to long bone axis
1095	S		several long CMs, parallel, oblique to bone axis
1007-97	S	2E	2 heavy & one medium CMs, medial, on condyle
1202	S		several well-defined CMs or CM patches in a linear group, generally perpendicular to bone axis, at edge
6167	S	4C	several CMs in two distinct intersecting groups, one parallel to long bone axis and one slightly oblique
1019-97	S	3C	CMs in 2 groups, one heavy, one light
1238	S	H	3 long CMs all coming from similar origin point; partially obscured by poor surface
6010	S	4C	4 groups of short to longish CMs, in exfoliated area
154	S	4C	two fairly heavy marks emanating from broken edge (on 173)
173	S	4C	two fairly heavy marks emanating from broken edge
6114	S	4C	2 very long, medium depth, sets of double CMs
655			
1107	S	4C	on lateral side, coming off of posterior-lateral eminence
107	S	T	several patches of CMs emanating from (recent) broken edge
140	S	Z	patch of short, light CMs

Cat #	CM	CM Loc	CM Comments
1205	S	8	1 main patch of heavy CMs, perpendicular to bone axis; a few other, lighter patches, same orientation
1020-97	SP	8	several scrape marks and some lighter CMs
1016-97	P	4C	linear group of >=10 CMs
668			
1	S		single CM, lateral/superior
1203a	S		one longer CM and a patch of >=3 short CMs (on bone ridge), perpendicular to bone axis
1240	S	3C	several fairly deep CMs in linear group all along one side of bone, oblique to long bone axis
409			
412			
1226	S	L	several patches of faint CMs on medial side, below auricular
418	S	3C	single long deep CM extending from fracture edge, with shorter, lighter parallel CM
6073	S	A	patch of short CMs on posterior margin -> as actualistics
1014-97	SC		some heavy CMs interspersed with some light CMs (medial); a single heavy chop mark (posterior)
6113	S		2 deep CMs on bone edge, continuing into 2 lighter slice marks
1056	S	4C	one patch of good CMs, oblique
1021-97	S	C	patch of CMs, missed at first b/c specimen has slightly abraded surface
6063	S	8	3 patches of CMs along one side, all short
1397a			
431	SP	8	a single long CM, oblique and a patch of scrape marks along the bone edge
1022-97	S	3C	group of >=3 CMs near PL nutrient foramen; group of other possible fine CMs
1108	S	3C	patch of several CMs/CM patches (coming from same origin point but probably made by single motion), oblique to long bone axis
1130	S	3C	2 extended CM groups, on lateral side, one shorter & one longer (in length of individual CMs), both perpendicular to long bone axis
1131	S	3C	2 extended CM groups, on lateral side, one shorter & one longer (in length of individual CMs), both perpendicular to long bone axis
1093	S		patch of short, deep CMs on lateral eminence of tibial articulation
1003-97	P	2C	cut marks in two groups, one along PL, one along PM
1141	S	4C	single CM ending in 3 'tails', on grey (more readable) part of surface, below site name and to right of number
1206	S		several long, heavy CMs/CM patches, parallel to each other but oblique to bone axis
1112	S	H	2 deep CMs/CM patches at lateral inferior margin of horizontal ramus, posterior of mental foramen, next to fracture edge
1170	S	N	2 tightly packed groups of several CMs, one on either (lateral) side of neural spine base
1017-97	S	4C	on posterior shaft, as in actualistics
12	S	U	single heavy CM just below acetabulum
1115	S		one main CM, with part of another small linear mark, next to fracture edge
6346	S	8	2 long & deep CMs;2 patches of short, lighter CMs on same side but near bone edge
2560a	S	4C	>=6 CMs or CM patches along edge of bone; possibly scrape marks but surface slightly rolled, so not sure
102	S	L	an "extended linear group" of CMs (>=12) along inferior border of ILI from near ACE towards articulation with SAC

Cat #	CM	CM Loc	CM Comments
1210	S	8	4-5 short, deep CMs perpendicular to bone axis, on thicker edge; partially obscured by poor surface
1024-97	S	3B&C	several parallel light CM patches along lateral side
1122	S	4C	patch of 4 closely associated CMs, with another nearby (same cutting episode), emanating from the broken med margin, perp. to bone axis
1125	S	4C	CMs on 1122
1221	S	V	2 deep CMs on posterior centrum
2034a	S	4C	2 parallel CMs coming off of pointy fracture edge, oblique to long bone axis
1002c-97	P	4C	small patch of closely associated, short CMs located @ MSH, P, M
1111	S	VZ	single group of 4-6 very fine, short CMs just left (and outside of) left posterior zygopop.; two deeper CMs just outside of cranial articulation
no #	S	V	matching long slice marks on either size of the vert head
148	S	3C	series of short and fairly deep CMs, perpendicular, starting at NEF end and continuing to SH
1012-97	SC	V	3 groups of fine CMs, one pair chop marks on ant epi; >=7 groups of fine CMs at diff locations @ centrum, processes/zygopop. Junctions
1201	S	L	4 locs: 3-4 heavy @ lat sup ILI; several fine @ lat inf margin ILI; 6-8 heavy near ACE @ lat sup ILI base; 6-8 fine near ACE @ med inf ILI base
103	S	C	3 parallel patches of medium length and fairly deep CMs with several individual CMs in between; third patch lighter and with more CMs

Cat #	Agent(s)	Comments
2562j	H	level bag
6006	H	
1467a	H	
601	H	
1454b	C	
1554b	H	
1225	H	
656	H	
349	H	
6009	H	
6161	H	
1420d	H	
1342a	H	surface bag; embedded in CaC03
6005	H	
121	H	
1477a	H	
1067	H	
1417b	H	
1224	H	
1546b	H	
615	H	
6222	H	
6115a	H	
6140	H	
2028	C	
323	H	
1213	H	I think these are percussion striae and not CMs even though they are long b/c they are so shallow
1346a2	H	
1367a	H	
1512e	H	
508	H	
6342d	H	
1246a	H	also cortical flake scar

Cat #	Agent(s)	Comments
6099	H	
1300	H	
6004	H	
6098	H	
1403a	H	
1390	H	
1275	H	
652	H	
1406d	H	
6342b	H	
216	H	
1051	H	a piece of only cortical bone, I think; some odd TM-like marks nearby
1384b	H	
610	H	
6059	H	
321	H	refit & glued to #348; CMs in the 'typical' ulna spot
348	H	refit & glued to #321
1013a-97	H	
1028	H	unfused vert centrum epiphysis
6084	H	
1384a	H	
1266	H	
1008-97	H	
666	H	CM-like marks are longer and near CMs but surface is too poor to diagnose
6132	H	
506	H	
314	H	
1369c	H	
1006-97	H	
1010-97	H	
614	H	
1172	H	possibly LB
1289	H	
6138	H	
14	H	refits & glued to #27

Cat #	Agent(s)	Comments
27	H	refits & glued to #14
6111	H	
1088	H	
2611a	H	level bag
6118	H	
1252	H	
6324	H	
1448a	C	
1208	HC	SEQUENCE - hominid (CM) to carnivore
6070	H	
1369d	H	readable part is a 4, but 1/2 encased in CaC03 so readability could be coded 2
665	H	refits & glued to #667
5007	H	
1101	H	
1015-97	H	
623	H	
2591a	H	
303	H	refits & glued to #304
304	H	refits & glued to #303
1320	H	
1132	H	
1095	H	
1007-97	H	
1202	H	
6167	H	
1019-97	H	
1238	H	
6010	H	
154	H	refits & glued to #173; CMs are on 173
173	H	refits & glued to 154
6114	H	Paul says humerus; med completely cancellous
655	H	
1107	H	
107	H	
140	H	

Cat #	Agent(s)	Comments
1205	H	
1020-97	H	
1016-97	H	percussion flake scar on medullary surface
668	H	a few patches that could be PMs, including one on opposing edge, but only one definite
1	H	
1203a	H	related to removal of head?
1240	H	
409	H	Paul says femur frag; refit & glued to #412
412	H	Paul says femur frag; refit & glued to #409
1226	H	
418	H	
6073	H	
1014-97	H	segment of inferior horizontal ramus near AR
6113	H	
1056	H	1 patch of good CMs and 2 patches of CM-like marks, probably CMs but not definitive, all oblique
1021-97	H	slightly abraded/polished
6063	H	
1397a	H	
431	H	
1022-97	H	
1108	H	
1130	H	refits & glued to #1131
1131	H	refits & glued to #1130
1093	H	removing feet?
1003-97	H	
1141	H	
1206	H	
1112	H	portion includes mental foramen & partial mandibular symphysis
1170	H	portion is partial (dorsal) neural arch and base (+2/3) of neural spine
1017-97	H	?ULN SH; kind of sketchy
12	H	refits & glued to #19, #1482
1115	H	
6346	H	
2560a	H	
102	H	

Cat #	Agent(s)	Comments
1210	H	
1024-97	HC	can't tell sequence
1122	H	refits & glued to #1125
1125	H	refits & glued to #1122
1221	H	
2034a	H	
1002c-97	H	
1111	H	
no #	H	C-7
148	H	
1012-97	H	
1201	H	about the size of modern giant forest hog
103	H	

Appendix 6b
Modified Bones from FwJj14B

Cat #	Taxon	Size	Age	Side	Skel Elem	Portion	Segment	Circ	MaxL	MaxW	GF	RF	WS	CRead	CCond	MiscM	Context
6028c	Mammal				NID				9	9		y		4	4		Geo Trench
4048a	Mammal				NID				12	5		y		4	4		*In Situ*
5291	Mammal				NID				12	7		n		4	4		*In Situ*
5236	Mammal				NID				13	5		y		4	2		*In Situ*
5256	Mammal	2/3			LB	C		1	14	11		y		4	4		Surface
3040	Mammal				RIB				16	6		y		4	4		*In Situ*
3141	Mammal				NID				17	8		y		4	4		*In Situ*
6016	Mammal				NID				17	8		y		4	3,4		Surface
3031	Mammal	2			LB	C		1	18	12		y		4	4		*In Situ*
3124	Bovidae - Alcelaphini	3			HYO				19	7		y		5			*In Situ*
5261	Mammal	2/3			RIB	8			22	8		y		4	4		Surface
6015	Mammal				NID				22	10		y		3	4	7	Surface
5109	Mammal	3			LB	C		1	22	16	n	n		4	2,4		*In Situ*
5027	Mammal	3/4			LB			1	23	21	y	n		4	2,4		*In Situ*
3147a	Mammal	3			LB	C		1	24	22	y	y		5			*In Situ*
3038	Mammal	2/3A			LB	C		1	25	15	y	n		4	4		*In Situ*
4063a	Mammal				NID				26	9		y		4	4		*In Situ*
3165	Bovidae	2			MCM	C	ANT	1	26	11	y	n	0	5			*In Situ*
4053a	Mammal				RIB	8			27	8		y		4	2,4		*In Situ*
4115k	Mammal				NID				28	8		n		4	2,4		*In Situ*
3099	Mammal				NID				28	10				4	2,4		*In Situ*
4092c	Ungulata	2/3			THO	R			30	12		n		4	2,4		*In Situ*
3055	Suidae			L	CAR		MAGNUM		30	19		y		4	2,4		*In Situ*
6031	Mammal	2/3A			LB	C		1	31	14	y	y		4	4		*In Situ*
4066aj	Mammal				LB	C		1	33	7	y	y		4	4		*In Situ*
5234	Mammal	2/3			LB	C		1	34	14	y	y		4	4		*In Situ*
5070	Mammal	>=3			NID				34	17		n		4	4		*In Situ*
3075a	Mammal	3			UP LB	C		1	34	20	y	n	0	5			*In Situ*
6011	Mammal	2/3			NID				35	11		y		4	4		Surface
5119b	Mammal				RIB	8			36	10		n		4	2,4		*In Situ*
5043a	Mammal	1/2			LB	C		2	37	11		y		4	2,4		Surface
4007r	Mammal				NID				39	14		y		4	4		Surface

Cat #	Taxon	Size	Age	Side	Skel Elem	Portion	Segment	Circ	MaxL	MaxW	GF	RF	WS	CRead	CCond	MiscM	Context
3131	Mammal	3			LB	C		1	39	28	y	n		4	4		*In Situ*
4025e	Mammal	3			LB	C		1	40	10		y		4	3,4		Surface
6021	Bovidae	2		L	RAD	C	POST-MED	2	42	24	y	n		4	2,3,4		*In Situ*
5212	Mammal				NID				42	25		n		4	4		*In Situ*
6090a	Bovidae	3		R	RAD	A-C	LAT		42	27		n		4	2,4		*In Situ*
5230	Bovidae	2			ULN	C			44	12		y		4	2,4		*In Situ*
3097	Bovidae - Hippotragini	3			HYO				44	24		y		4	4		*In Situ*
3088	Mammal				RIB	8			46	9		y		4	2,4		*In Situ*
5222	Bovidae - Alcelaphini	3			HYO				46	14		y		4	2		*In Situ*
5016	Mammal	3			UP LB	C		1	46	22	y	n		4	2,4	8	*In Situ*
5146	Mammal	>=3			NID				47	23		y		4	2,4,5		*In Situ*
5220	Suidae			L	MCIII	A-C			47	30	y	y		4	2,4		*In Situ*
5128	Bovidae	3		R	RAD	A-C		5	47	47		y		4	2		*In Situ*
3120	Mammal	>=3			CRAN				50	47		n	0	3	2		*In Situ*
3159	Mammal	3		R	HUM	C		1	51	22	y	n		4	3,4		*In Situ*
3015	Mammal				NID				53	14		y		4	2,4		*In Situ*
5117	Bovidae	3A		L	ULN	C		5	53	17		n		4	2,4		*In Situ*
5119a	Mammal	>=3			RIB	8			53	17		n		4	2,4		*In Situ*
5060	Mammal	3			UP LB	C		2	53	24	y	n		4	2		*In Situ*
5130	Ungulata	3			THO	R			54	14		n		4	4		*In Situ*
3035	Bovidae	3			MCM	C		2	55	23	y	y	1	4	2,4		*In Situ*
3005	Bovidae	3A			INN		S		57	55		y	0	4	4		*In Situ*
5165	Mammal				NID				60	24		n		3	4		*In Situ*
5099	Bovidae	3A		R	HUM	C-D	POS-LAT	4	60	30	y	y		4	4	1,3,5,8	*In Situ*
5097	Bovidae	3A			MAND	H			61	23		y		4	4		*In Situ*
6057	Mammal	>=3			NID				64	25		y		4	2,4	1	*In Situ*
5214	Bovidae	2/3A		R	MAND	H	ANT		64	26		y		4	4		*In Situ*
3092	Mammal				NID				67	11		n		4	2,4		*In Situ*
4071a	Mammal	3			LW LB	C		1	67	23	y	n		4	2		*In Situ*
3090	Bovidae	3B/4		L	HUM	C	MED		67	33	y	n		4	4		*In Situ*
6037	Mammal	3		L	TIB	C	POST-LAT	2	67	33	y	y		4	4		*In Situ*
5067	Bovidae	2		R	ULN	A	PX		74	35		n		4	2		*In Situ*
3058	Bovidae	3			MTM	C	POS	1	85	16	y	n		4	2,4	7	*In Situ*
6040	Mammal	3		R	FEM	C	POST	2	86	27	y	y		4	2,4		*In Situ*
6038	Bovidae	2		R	FEM	C	POST-LAT	3	87	24	y	y		4	2		*In Situ*

Cat #	Taxon	Size	Age	Side	Skel Elem	Portion	Segment	Circ	MaxL	MaxW	GF	RF	WS	CRead	CCond	MiscM	Context
3085	Mammal	>=2			RIB	8			93	13		y		4	2,4		*In Situ*
3091a	Mammal	2/3A			RIB	6-8			93	20		y		4	4		*In Situ*
6063	Mammal	3			LB	C		2	98	28	y	y	0	4	2		*In Situ*
5113	Bovidae	3A			LW LB	C		1	104	22	y	y		4	2,4	2,8	*In Situ*
3096	Bovidae	3		R	TIB	C		3	105	24	y	y		4	4		*In Situ*
3132	Suidae			L	MTIV		CO		112	31				4	4		*In Situ*
5233	*Cercopithecus* sp.	1			HUM	C-D			120	18		y		3	2		*In Situ*

Cat #	PM	PM Loc	PM Comments
6028c	S		2 patches of striae, fairly deep, medium length
4048a			
5291			
5236			
5256			
3040			
3141			
6016			
3031			
3124			
5261			
6015	S		patch of light striae under "Fw"
5109	S	4C	2 patches of long striae
5027			
3147a			
3038			
4063a			
3165			
4053a			
4115k			
3099			
4092c			
3055			
6031			
4066aj			
5234			
5070			
3075a			
6011			
5119b			
5043a			
4007r			

Cat #	PM	PM Loc	PM Comments
3131			
4025e			
6021			
5212			
6090a			
5230			
3097			
3088			
5222			
5016			
5146			
5220			
5128			
3120			
3159	S	4C	long striae patch emanating from exfoliated area; pit with striae near spiral fracture edge
3015			
5117			
5119a			
5060			
5130			
3035	S	4C	patch of striae emanating from cortical flake removal
3005			
5165			
5099			
5097			
6057			
5214			
3092			
4071a	S	4C	very light patch of striae at area of spiral fracture (not quite notch), opposite number
3090			
6037			
5067			
3058			
6040	B	4C	hammerstone pit with two sets of long striae (1 associated) near less broken end
6038	S	4C	4 short striae patches on posterior surface opposite percussion fracture-y edge

Cat #	PM	PM Loc	PM Comments
3085	SP	8	percussion pit with long striae on larger bone
3091a			
6063			
5113			
3096	S	4C	one patch of striae situated on break edge
3132			
5233	S	4C	single striae emanating from (recent?) fracture near DS NEF

Cat #	CM	CM Loc	CM Comments
6028c			
4048a	S		covered with long, shallow CMs
5291	S		single long CM
5236	S		2 CMs in same area, oblique, coming off edge
5256	S	4C	5-6 CMs coming from one edge
3040	S		5-6 CMs, oblique, down one side of bone; long CM crossing these longitudinal to bone
3141	P		4 patches of light scrape marks
6016	S		3-4 short CMs, partially obscured by kind of crappy surface
3031	S	4C	patch of CMs near one edge, under 'Fw"
3124	S		numerous fairly deep CMs and one very deep CM in patches virtually covering one side
5261	S	8	several single & patch CMs, medium length & deep, perpendicular/oblique
6015			
5109			
5027	C	3	single chop mark
3147a	S	4C	a patch of relatively faint CMs near (recent) fracture edge, under "B"
3038	S	4C	several CM patches down one side, 2 CMs down other side, all fairly deep & short
4063a	P		single deep and associated light scrape marks
3165	S	4C	several CMs, light, long, perpendicular/oblique to long bone axis
4053a	P	8	deep scrape marks along one side
4115k	SP		single short CM and 2 series of light scrape marks
3099	S		2 longish, deep CMs coming from one broken edge
4092c	S	R	single slice mark on bone edge
3055	SC		several slice and 2 chop marks on most rugose part of largest fragment
6031	S	4C	single light CM
4066aj	S	4C	set of 2 definite CMs coming from edge underneath "Jj"; another set of possible CMs
5234	S	4C	2 long-ish CMs coming from modern break; slightly sketchy surface
5070	S		1 classic cm oblique left
3075a	S	4C	single, short, very light mark coming off of one of the cortical flake edges
6011	SP		one definite scrape mark, one definite CM, the rest sketchy
5119b	S	8	several CMs in patches near edge
5043a	P	4C	series of scrape marks, fairly deep
4007r	S		5 associated CMs, oblique, emanating from bone edge

Cat #	CM	CM Loc	CM Comments
3131	S	4C	patch of several deep CMs along one part of bone, oblique
4025e	S	4C	2 CMs emanating from small patch of exfoliation on one end of bone
6021	S	4C	a few fairly deep CMs along lateral side, oblique
5212	S		5-6 CMs in 2 groups, long
6090a	S	1C	patch of short CMs, perpendicular, down lateral margin of bone
5230	SP	4C	1 patch of longer CMs, oblique; a series of scrape marks, shorter; both posterior
3097	SC		2 patches of CMs on one end, 2 chop marks on another end
3088	P	8	2 scrape marks near one end; one deep, one more shallow
5222	S		single CM
5016	S	4C	several parallel deep, short CMs
5146	S		single long oblique CM
5220	S	1A	several perpendicular CMs, posterior, between PX art facet and MCII facet
5128	S	1A	CM on ant medial side just below articular surf
3120	S		a series of fairly deep, fairly short, CMs near one edge without adhering sed
3159			
3015	S		several CMs down both side margins of bone frag
5117	C	C	several chop marks along posterior ULN
5119a	S	8	2-3 CMs near edge
5060	S	4C	several patches of CMs coming from one broken side, in at least 2 oblique directions
5130	S	R	long CM patches nearly covering part of the bone
3035	SP		slice and scrape marks along edge where cortical flake was removed
3005	S	isch	2 CMs near left lower margin, one coming off of eminence
5165	S		patch of short CMs near one edge
5099	S	4C-D	1 deep CM from most PX; a few short, shallow CMs just inf; several long CMs, post-lat edge
5097	S	H	cluster of 6 transverse cm's on inferior margin; 2 oblique on lingual surf
6057	S		2-3 CMs, longish, perpendicular, sort of odd looking
5214	P	H	5 small scrape marks on inferior symphysis
3092	SP		cut and scrape marks along entire bone length, perpendicular
4071a			
3090	S	4C	several CMs on most posterior part of bone, oblique, not associated with muscle attachment
6037	S	3C	two short CMs, V-shape, oblique, on rugosity/muscle attachment on posterior-lateral margin
5067	P	1A	scrape marks along posterior side of PX ulna
3058	S	4C	2-3 patches of light CMs along margin of bone
6040	S	4C	1 CM 'set' continuing across two bone ridges, on more broken end, near nutrient foramen
6038			

Cat #	CM	CM Loc	CM Comments
3085	S	8	very light scrape marks down side of smaller bone, oblique
3091a	S	7	several CMs, fairly deep, on neck
6063	S	4C	3-4 CMs with a single origin, on 6063b, termination obscured by adhering matrix
5113	S	4C	short CMs on smaller glued piece
3096	S	4C	small, shallow to deep CM patches in 6+ different places, but none OK on muscle attachment
3132	S	4C	on posterior muscle attachment
5233	S	4C	several patches of perpendicular CMs on posterior surface closer to PX NEF

Cat #	Agent(s)	Comments
6028c	H	
4048a	H	
5291	H	
5236	H	goes with 5234?
5256	H	
3040	H	
3141	H	
6016	H	
3031	H	
3124	H	
5261	H	
6015	H	chemical pitting & some other unidentifiable marks
5109	H	
5027	H	
3147a	H	
3038	H	
4063a	H	
3165	H	
4053a	H	4 frags, assume refit, measured largest
4115k	H	
3099	H	
4092c	H	
3055	H	4 fragments total, assume refit
6031	H	
4066aj	H	
5234	H	
5070	H	
3075a	H	a few cortical flake removals
6011	H	
5119b	H	
5043a	H	11 frags, recent breaks, data from largest (2 glued)
4007r	H	2 frags, refit & glued

Cat #	Agent(s)	Comments
3131	H	
4025e	H	
6021	H	
5212	H	
6090a	H	
5230	H	
3097	H	
3088	H	
5222	H	modern breaks glued
5016	H	
5146	H	recent break, not glued
5220	H	slightly larger than giant forest hog--same morphology; with 17 associated frags
5128	H	
3120	H	
3159	H	
3015	H	7 pieces total, measured large one, assume related
5117	H	
5119a	H	
5060	H	
5130	H	
3035	H	
3005	H	
5165	H	surface pretty weird; a few small associated frags, assuming recent breaks
5099	H	
5097	H	
6057	H	& 12 more frags, assume refit
5214	H	larger than impala, smaller than waterbuck
3092	H	
4071a	H	
3090	H	
6037	H	
5067	H	entire proximal bit, in 3 pieces, coded largest
3058	H	
6040	H	
6038	H	

Cat #	Agent(s)	Comments
3085	H	in 2 refitting pieces (modern break)
3091a	H	in 2 pieces, refit (modern), glued
6063	H	nice percussion flake scar; ancient breaks (a-c) not reglued
5113	H	TM-like are three small pits on the smaller glued piece; a few pieces, modern breaks, glued
3096	H	
3132	H	
5233	H	

Appendix 6c
Modified Bones from GaJi14a

Cat #	Taxon	Size	Age	Side	Skel Elem	Portion	Segment	Circ	MaxL	MaxW	GF	RF	WS	CRead	CCond	MiscM	Context
108	Mammal	2			FIB		SH		10			y		3	2		*In Situ*
508e	Mammal				NID				13	8		n		4	3,4		*In Situ*
1209e	Mammal				NID				17	13		y		4	2,4		Surface
1214d	Mammal				NID				18	9		n		4	4		Surface
1067	Mammal	1			LB	C		2	20	8	n	y		4	4		Surface
1065	Mammal	2/3A			RIB	8			23	11		y		4	2		Surface
601	Mammal				NID				28	22		n		4	4	2	Surface
3	Bovidae	2		L	TIB	C	ANT-LAT	3	31	12	y	y		4	2,4		Surface
1035	Mammal	2/3A			RIB	8			31	14		y		4	4		Surface
1086f	Mammal				RIB	8			32	15		y		3	4		Surface
1025d	Bovidae	2			MAND	H			33	15		y		4	4		Surface
7	Hippopotamidae	3/4	J		PHA1		CO		37	25				3	2,4		Surface
1092	Mammal	2/3A			LB	C		1	38	18	n	y		4	4		Surface
1061	Mammal	3			TIB	C		1	38	29	y	n		4	2,4		Surface
307	Mammal	3/4			LB	C		1	39	24	y	y		4	2,3,4		Surface
1119	Bovidae	3		R	NAVCUB		CO		39	29				4	4		Surface
1093	Mammal				NID				40	23		n		4	3,4		Surface
568	Mammal				NID				42	22		y		4	4		Surface
1053b	Mammal	>=3			LB	C		1	43	15	y	n		4	3,4		Surface
1066	Mammal				NID				43	17		y		4	2,4		Surface
1051	Mammal	3			LB	C		1	44	18	y	y		4	4		Surface
1069	Mammal	3			LB	C		1	46	17	y	y		4	4	1,3	Surface
1058	Mammal	3			FEM	C		1	48	22	y	y		4	4		Surface
1075	Mammal	3			LB	C		1	48	26	n	y		4	3		Surface
605	Mammal	>=2			RIB	8			49	10		y		4	4		Surface
107	Mammal	2/3			RIB	8			49	24		y		4	2,4	2	*In Situ*
1032	Mammal	2/3A			LB	C		1	50	17	y	n		4	4		Surface
1071	Mammal	>=3B			THO	R			50	31		y		3	2,3,4		Surface
321	Mammal	2/3A			LW LB	C		2	51	14	n	y		4	2,4		Surface
101a	Ungulata	3/4		R	HUM	C-D	MED	2	52	41	y	n		4	2		*In Situ*
1062	Mammal	3/4			INN	L			52	50		y		4	2		Surface
218	Mammal	>=2			RIB	8			53	11		y		4	2		*In Situ*
1038	Mammal	3			RIB	8			53	16		y		4	4		Surface

Cat #	Taxon	Size	Age	Side	Skel Elem	Portion	Segment	Circ	MaxL	MaxW	GF	RF	WS	CRead	CCond	MiscM	Context
1036	Bovidae	4			MCM	C-E		5	54	48	n	y		4	2,4		Surface
1054	Mammal	3			UP LB	C		2	57	34	y	n		3	2,3		Surface
1059	Bovidae	3B			MCM	C		4	58	35	n	y		4	3,4		Surface
1044c	Mammal	>=4			LB			1	58	40	y	n		4	4		Surface
1041	Mammal	3			LB	C		1	60	22	y	n		4	4	2	Surface
1014	Mammal	3			LB	C		2	60	30	y	n		4	4		Surface
1018	Mammal	3			LB	C		1	61	28	y	n		4	3,4	3	Surface
1010	Mammal				RIB	8-9			63	19		y		4	3,4	3	Surface
510	Mammal	3/4			RIB	8			65	22		y		4	2,4		Surface
1055	Bovidae	3		L	HUM	C		2	67	29	y	y	0	5			Surface
4	Mammal	>=3			NID				67	45		n		3	2,4,5	1,3	Surface
1009	Mammal	3			UP LB	C		2	68	27	y	n		4	2		Surface
1028	Mammal	3			NID				69	17		y		4	4		Surface
1001	Mammal	3/4			LB	C		1	69	25	y			4	4		Surface
527	Mammal	3			LB				69	29	y	y		4	3,4		Surface
1031	Mammal	3			UP LB	C		2	70	29	y	n		3	2,3,4		Surface
1056	Mammal	>=4			SCAP	Y			71	48				4	4		Surface
1030	Bovidae	2		L	RAD	C	ANT-MED	1	72	18	n	y		4	4		Surface
1052	Bovidae	3		L	TIB	C	POS	1	73	30	y	n		4	2,4		Surface
1042	Mammal	3			FEM	C		1	74	18	y	y		4	4		Surface
1085b	Mammal	3			RIB	8			74	28		y		3	3,4		Surface
1080	Mammal	3/4			UP LB	C		2	74	32	y	y	1	4	4,5		Surface
203	Bovidae	2	J	R	INN	S			78	41		y		4	4		*In Situ*
1013	Mammal	3/4			RAD	C		2	79	23	y	y		4	4	1,8	Surface
1034	Bovidae	3		L	CALC				79	32		y		4	4		Surface
1040	Mammal	>=4			LB	C		1	79	42	y			4	4		Surface
109	Bovidae	3			MP	C		2	81	24	y	y		4	2		*In Situ*
1039	Mammal	>=4			LB	C		1	83	32	y			4	4		Surface
1019	Mammal	3/4			TIB	B	PX	2	83	39	y	n		4	4		Surface
1008	Ungulata	>=3		R	SCAP	GY			83	70		n		4	3,4		Surface
1017	Ungulata	3/4			THO	R			85	27		y		4	2,4		Surface
313	Ungulata	3/4			LW LB	C		1	86	26	y	y		4	2		Surface
1044a-b	Mammal	>=4		L	FEM			2	86	57	y	y		4	3,4		Surface
1007	Bovidae	3		R	MCM	C-E		5	89	42	n	y		4	4		Surface
1079	Bovidae	3		L	SCAP	Y			100	45		y		4	2		Surface

Cat #	Taxon	Size	Age	Side	Skel Elem	Portion	Segment	Circ	MaxL	MaxW	GF	RF	WS	CRead	CCond	MiscM	Context
1026a-b	Mammal	3B/4		R	SCAP	Y			103	37		y		4	2,4		Surface
1021	Mammal	3			RIB	8			104	17		y		4	4		Surface
543	Bovidae	4			MP	C		2	110	49	y	y		3	2,3	3	Surface
6	Bovidae	3		R	MTM	A,C	ANT-MED	3	112	34	y	n	0	4	2,4		Surface
1064	Bovidae	3A		L	ULN	1A	PX	5	112	55		y		4	2,4		Surface
1096	Bovidae	3		L	RAD	A-C	ANT-MED	3	113	40	n	y	2	3	2,3		Surface
1090	Mammal	5/6		L	INN	L			120	98		y		3	3		Surface
1089	Mammal	3			LB	C		1	148	23	n	y		3	3	1	Surface
1045	Mammal	>=4			RIB	8			163	35		y		4	2,4		Surface
1047c	Bovidae	3		L	MCM	A-C		5	180	41	n	y	2	3	2,3		Surface
1033	Mammal	3			RIB	8			243	22		y		4	2,4		Surface

Cat #	TM	TM Loc	TM Comments
108			
508e			
1209e			
1214d			
1067			
1065			
601			
3			
1035			
1086f			
1025d			
7			
1092			
1061			
307			
1119			
1093			
568			
1053b			
1066			
1051			
1069			
1058			
1075			
605			
107			
1032			
1071			
321			
101a			
1062			
218			
1038			

Cat #	TM	TM Loc	TM Comments
1036			
1054			
1059			
1044c			
1041			
1014			
1018			
1010			
510			
1055			
4			
1009			
1028			
1001			
527			
1031			
1056			
1030			
1052			
1042			
1085b			
1080			
203			
1013			
1034	P		several pits on both sides of calcaneum
1040			
109			
1039			
1019			
1008			
1017			
313			
1044a-b			
1007			
1079			

Cat #	TM	TM Loc	TM Comments
1026a-b			
1021			
543			
6			
1064			
1096			
1090			
1089			
1045			
1047c			
1033			

Cat #	PM	PM Loc	PM Comments
108			
508e			
1209e			
1214d	S		large patch of striae
1067			
1065			
601			
3			
1035			
1086f			
1025d			
7			
1092			
1061			
307			
1119			
1093			
568			
1053b			
1066			
1051			
1069	S	4C	long striae emanating from fracture edge
1058			
1075			
605			
107			
1032			
1071			
321	S	4C	long striae emanating from ancient break of smallest reglued specimen
101a			
1062			
218			
1038			

Cat #	PM	PM Loc	PM Comments
1036			
1054			
1059			
1044c	S	3	at least one, and maybe more, striae patches, near number
1041			
1014	S	4C	2 long striae emanating from fracture edge, ~'flying V', longitudinal
1018			
1010			
510			
1055			
4	S		2 patches of long striae, emanating from same place (corner) but going in 2 different directions
1009	S	4C	2 patches of striae, one with more robust marks, the other with very light marks, both not associated with fracture edge
1028			
1001	S	4C	several patches of light, fairly long striae emanating from ancient fracture edge, posterior
527	S		on both bones, patches of light, long striae
1031			
1056			
1030			
1052	S	4C	patch of short striae near chemical pitting
1042			
1085b			
1080			
203			
1013	S	4C	patch of striae emanating from (chemical?) pitting
1034			
1040			
109	B	4C	one pit w/ striae, several isolated striae patches coming from percussion fracture surface, not ass. w/ percussion notch
1039			
1019			
1008			
1017			
313			
1044a-b			
1007			
1079			

Cat #	PM	PM Loc	PM Comments
1026a-b			
1021			
543			
6			
1064			
1096			
1090			
1089	S	4C	3 light perc striae emanating from modern fracture/cortical flaking edge; one long, two short
1045			
1047c			
1033			

Cat #	CM	CM Loc	CM Comments
108	S		3 patches of deep, short, perpendicular CMs on edge; smaller patch of light, oblique CMs further down towards middle
508e	S		long scraping marks extending across bone surface
1209e	S		2 short CMs
1214d			
1067	S	4C	two long, thin oblique CMs coming from broken pointed edge
1065	S	8	patch of short, light CMs near broken end
601	S		
3	S	4C	several patches of light CMs
1035	C	8	3-4 chop marks, dorsal
1086f	P	8	series of 4-6 very light scrape marks down one side of bone
1025d	S	H	2 heavy, short CMs coming from ancient fracture
7	S		one larger and one smaller patch of CMs, perpendicular, on larger side, at PSH & MSH (if it was a LB)
1092	S	4C	several patches of light to heavy, long-ish CMs; all generally in the same direction
1061	P	4C	several scrape marks along one side of bone, at edge
307	S	4C	two light CMs near bone edge, partially exfoliated
1119	S		3 deep, medium length CMs, on bone spur, perpendicular to limb axis
1093	S		several patches of deep and long CMs, going in 2 directions and overlapping
568	C		single heavy chop mark near edge with associated smaller mark
1053b	S	4C	isolated long CM and patch of medium length CMs on edge, patch is near end and partly obscured by surface alteration
1066	S		several oblique CMs along one edge
1051	S	4C	4 patches of long CMs, 3 in one oblique direction and 1 (overlapping) in another
1069			
1058	S	4C	several patches of CMs at one end - on both edges and in middle of bone
1075	S	4C	several patches of medium length and depth cut marks
605	S	8	3 isolated chop marks, short, one really good
107	C	8	3-4 chop marks on one side of the bone
1032	S	4C	several long CMs in a patch emanating from fracture edge
1071	S	R	several long striae on both sides of neural spine
321			
101a	S	3C-D	several patches of classic CMs on medial side
1062	S	L	series of medium length, deep CMs on one margin; small patch of short CMs on other margin; single deep CM anterior
218	S	8	several CMs including a patch at rugosity (muscle attachment?)
1038	S	8	2 sets of CMs: one perpendicular, on more ventral edge, short; the other oblique, on side, more dorsal, long

Cat #	CM	CM Loc	CM Comments
1036	S	2E	2 short, deep CMs, perpendicular, on anterior surface of L condyle
1054	S	4C	isolated long CM and patch of short to medium length CMs, patch is near end
1059	S	3C	patch of short CMs, perpendicular, on lat/med border of a, partially obscured by surface alteration
1044c			
1041	S	4C	at least one good isolated CM
1014			
1018	S	4C	one pair of long, deep-ish CMs near end; the other, in middle of specimen, is equivocal as surface is altered
1010	S	8	extended group of dozens of short, classic CMs
510	S	8	2 CMs, associated, ventral side
1055	S	4C	1=series of oblique CM patches on edge; 2=long, lighter CMs near modern glued break; 3=weird curvy CM (larger piece)
4			
1009			
1028	S		patch of 4 short CMs in middle of bone
1001			
527			
1031	SC	4C	single heavy chop mark and several isolated CMs
1056	S	Y	several isolated wide, short CMs along scap margin
1030	S	4C	series of patches of short CMs along margin
1052	S	4C	isolated long CM
1042	S	4C	2 patches of 4 and one isolated CM, all oblique
1085b	P	8	a patch of scrape marks, would have been banner if bone surface was better
1080	S	4C	several patches of light CMs, oriented in different directions, mainly along ridge
203	S	S	deep CMs, bordering on chop marks, anterior - on area of maximum curve
1013	S	4C	two light, fairly long CMs, near number
1034	C		patch of chop marks on superior side of ankle bit
1040	S		several short CMs
109	SC	4C	single short chop mark near percussion damage; short CMs on other end, same side; single short CM in middle of bone
1039	S		several isolated or paired short CMs
1019	S	3B	2 patches of medium depth, short CMs, near NEF end
1008	S	Y	multiple short CMs, perpendicular to bone axis
1017	S	R	3 relatively heavy CMs in sub-parallel group, middle one 'flying V'
313	S	4C	single CM emanating from spiral fracture area
1044a-b	S	3	2 short, medium depth CMs near spiral fracture edge on b
1007	S	2E	short to medium deep CMs in 3 areas on medial side of medial condyle
1079	S	Y	a few CMs/patches on the 2 largest pieces and largest flat piece (3 total)

Cat #	CM	CM Loc	CM Comments
1026a-b	S	Y	light, medium-long CMs on dorsal side of scap blade at base of spinous process (on a)
1021	S	8	one main CM/patch on each side of shaft (dorsal and ventral), relatively heavy and isolated
543	S	4C	2 patches of short CMs, truncated by surface flaking
6	SP	4C	several short scrape marks on anterior-lateral margin; two patches of more classic CMs, anterior, coming off fracture edge
1064	S	1A	short, oblique CMs in the 'usual' ulna CM place - inferior part of posterior PX
1096	S	4C	2-3 long CMs on MSH edge, partially obscured by surface alteration
1090	S		several patches of light, short CMs concentrated in one area of bone
1089			
1045	S	8	3 patches of short CMs, dorsal side - one on end, two in middle, all oblique but in varying directions
1047c	S	1C	several patches or isolated short to medium CMs along medial side of shaft
1033	C	8	single heavy chop mark on rib edge

Cat #	Agent(s)	Comments
108	H	possibly suid, but can't get a definite ID
508e	H	level bag
1209e	H	
1214d	H	
1067	H	very thin bone - cortical only? bird?
1065	H	
601	H	could be non-mammal
3	H	
1035	H	
1086f	H	
1025d	H	
7	H	juvenile based on size and lack of PX fusion
1092	H	
1061	H	
307	H	
1119	H	
1093	H	
568	H	
1053b	H	
1066	H	
1051	H	
1069	H	
1058	H	
1075	H	
605	H	
107	H	
1032	H	
1071	H	
321	H	in 3 pieces, modern break, glued; MCM or RAD
101a	H	
1062	H	
218	H	
1038	H	

Cat #	Agent(s)	Comments
1036	H	in 2 pieces, not glued
1054	H	MSH ID made on shape b/c med bone obscured by matrix
1059	H	
1044c	H	not sure how a-b and c are related, cannot refit, treated as separate specimens
1041	H	with cancellous bone
1014	H	
1018	H	
1010	H	broken after analysis
510	H	
1055	H	
4	H	whole bone surface has 'beat up' appearance
1009	H	
1028	H	fairly rounded
1001	H	
527	H	recent break, assume refit, measured larger
1031	H	
1056	H	
1030	H	surface pretty crappy w/ chemical corrosion
1052	H	sort of a percussion notch, but truncated and obscured by adhering matrix
1042	H	
1085b	H	
1080	H	some CMs look like sed abrasion but some are good
203	H	
1013	H	
1034	HC	can't tell sequence - croc TM?
1040	H	really cool bone flake, from v large animal
109	H	percussion notch
1039	H	
1019	H	
1008	H	could be juvenile of large mammal (could be hippo ?)
1017	H	
313	H	
1044a-b	H	not sure how a-b and c are related, cannot refit, treated as separate specimens
1007	H	
1079	H	in 5 pieces, modern break, assume refit; measured largest

Cat #	Agent(s)	Comments
1026a-b	H	
1021	H	
543	H	possible that marks are P striae; with cancellous bone
6	H	
1064	H	
1096	H	
1090	H	really big animal, piece of flat bone
1089	H	
1045	H	
1047c	H	one piece not refit, assume associated
1033	HC	can't tell sequence; in several broken pieces, most glued, now in 2 pieces

Appendix 6d
Modified Bones from GaJi14B

Cat #	Taxon	Size	Age	Side	Skel Elem	Portion	Segment	Circ	MaxL	MaxW	GF	RF	WS	CRead	CCond	MiscM	Context
865d	Mammal				NID				10	8		y		4	2		*In Situ*
830c	Mammal				NID				15	11		y		4	2		*In Situ*
235	Bovidae	2/3A		R	TIB	B-C	POS	1	19	24	n	y	0	5			*In Situ*
924	Mammal				NID				20	19		n		4	3		*In Situ*
637	Fish				spine				22	8		y		4	4		Surface
892c	Mammal	1/2			LB	C		1	22	8		y		4	4		Surface
979	Mammal				NID				24	19		y		3	2,4		*In Situ*
987	Mammal	3			LB	C			25	12	n	y		4	2,4		*In Situ*
522	Mammal	2/3			LB	C		1	26	12	y	y		4	4		Surface
897j	Mammal	2/3			LB	C		1	30	14		n		4	2,4		*In Situ*
689	Fish				NID				33	9		y		4	2		Surface
712	Mammal	3			LB	C		1	33	25	n	n	1	4	1	1,5,7	*In Situ*
531	Mammal	>=2			RIB	8			35	16		y		4	4		Surface
784	Mammal	1/2		R	HUM	A	SUP	1	38	29	y	n	0	3	2		*In Situ*
549b	Mammal				NID				43	10		n		4	2,4		*In Situ*
604	Mammal				NID				52	16		y		4	4		Surface
101	Bovidae	3B/4		L	HUM	C-D	ANT-MED	1	52	41	n	n	0	5		1,3	*In Situ*
902	Bovidae	3A	AD		MP	C-E		3	56	30	n	y	0	4	2		*In Situ*
630	Mammal	2/3A			HUM	C		1	57	17	y	y		3	2,3		*In Situ*
931	Mammal	3/4			INN	L			65	49		y		4	2	4	*In Situ*
547	Mammal	3		L	FEM			2	79	28	y	y		3	3,4		Surface
724	Suidae	2		R	MAND				122	29		n	0	4	2	1,3	*In Situ*
213	Mammal	3/4			RIB	8			137	30		y		4	2,4		*In Situ*
703	Mammal			L	MAXT				n/a	n/a		y	0	4	2	1	*In Situ*

Cat #	PM	PM Loc	PM Comments
865d			
830c			
703			
924			
637			
892c			
979			
987	P	4C	pit underneath cut marks
522			
897j			
689			
712			
531			
784	S	1A	under number, near possible loadpoint
549b	S		set of striae emanating from bone edge
604			
101			
902			
630	S	4C	several sets of striae emanating from end of (smaller) bone, in several directions
931			
547			
724			
213			
703			

Cat #	CM	CM Loc	CM Comments
865d	S		4-5 CMs emanating from one side of bone
830c	S		short CMs, perpendicular to bone axis, all along one side of the bone
703	S	1B	two deep, short, parallel CMs, offset, just below where rugose bone starts
924	S		patch of short CMs emanating from broken edge
637	S		series of short CMs coming off of ridge
892c	S	4C	4 patches of CMs, 3 emanating from the bone side, one in the middle
979	S		patches of long-ish cut marks, all in same direction
987	S	4C	cut marks overlying percussion pit
522	S		one long & deep and a few accompanying lighter & shorter CMs, extending from bone edge
897j	S	4C	2 patches of light CMs near one end
689	C		single chop mark
712	S	4	two sets of very short medium depth CMs that probably would join together if bone surface was better
531	S	8	4 patches of a few short CMs (multiple marks made by one cutting motion), near edge opposite labeling
784			
549b			
604	P		2-3 patches of scrape marks
101	S	3C	a series of short, medium depth marks along medial side
902	S	2D	patch of short light CMs, posterior, above epiphysis
630			
931	S		patch of very short CMs just at curve
547	S	3	patch of 3 and single short CMs, on bone ridge (unexfoliated surface)
724	S		one deep and at least one shallow mark towards one end of the bone
213	S	8	patch of short CMs coming from bone edge
703	S		CMs near tubercle, in 4 parallel patches of very short marks

Cat #	Agent(s)	Comments
865d	H	
830c	H	
703	H	
924	H	
637	H	
892c	H	
979	H	
987	H	
522	H	
897j	H	
689	H	
712	H	
531	H	
784	H	part of head and greater tubercle
549b	H	
604	H	
101	H	
902	H	modern break @ SH transverse, fossil break longitudinal
630	H	modern break, not glued
931	H	neck of iliac blade; 3 other frags from modern break, analyzed biggest
547	H	
724	H	
213	H	refits with #214, recent break, not glued, measured together
703	H	in 11 bone fragments + tooth; largest 6 examined

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Academic and Related Positions

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2005: Adjunct Faculty, Rutgers University (Anthropology 326: Pleistocene Hominid Adaptations)
2002-2004: Field Director, Koobi Fora Paleoanthropology Field School, Kenya
2001: Instructor, Koobi Fora Paleoanthropology Field School, Kenya
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1997: Research Associate, Florisbad Quaternary Research Station, South Africa
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Publications

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