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NUMBER 2

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BREATHING LIFE INTO FOSSILS:

Taphonomic Studies in Honor of C.K. (Bob) Brain

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Front cover, clockwise from top left.

Top left:
Artist's reconstruction of the depositional context of Swartkrans Cave, South Africa, with a leopard consuming a hominid carcass in a tree outside the cave: bones would subsequently wash into the cave and be incorporated in the breccia deposits. © 1985 Jay H. Matternes.

Top right: The Swartkrans cave deposits in South Africa, where excavations have yielded many hominids and other animal fossils. ©1985 David L. Brill.

Bottom right: Reconstruction of a hominid being carried by a leopard. © 1985 Jay H. Matternes.

Bottom left: Photograph of a leopard mandible and the skull cap of a hominid from Swartkrans, with the leopard's canines juxtaposed with puncture marks likely produced by a leopard carrying its hominid prey. © 1985 David L. Brill.

Center: Photo of Bob Brain holding a cast of a spotted hyena skull signed by all of the taphonomy conference participants. © 2004 Kathy Schick, Stone Age Institute.

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CHAPTER 3

THE DESTRUCTION OF SKELETAL ELEMENTS BY CARNIVORES: THE GROWTH OF A GENERAL MODEL FOR SKELETAL ELEMENT DESTRUCTION AND SURVIVAL IN ZOOARCHAEOLOGICAL ASSEMBLAGES

NAOMI CLEGHORN AND CURTIS W. MAREAN

ABSTRACT

In the 1960s, Brain published on a series of taphonomic studies in which he observed the destruction of goat bones by pastoralists and domestic dogs. Those studies were notable and novel for a variety of reasons: 1) the attempt to control for complex parameters through the use of what we now recognize as experimental and naturalistic actualism, 2) documentation of the destructive impact on skeletal element abundance by secondary carnivore consumers, and 3) the attempt to understand the mechanical aspects of this process, and thus establish the foundation for justifiable uniformitarianism. This work set the stage for a proliferation of research, and today the differential destruction of bone by secondary carnivore consumers is considered a significant, perhaps the most important, determinant of zooarchaeological patterning. This process selectively removes less dense portions of bones (the articular ends, in the case of long bones), and therefore demands a methodological shift away from the easily identified articular fragments to the more challenging shaft portions. Carnivore ravaging also destroys greasy and less dense elements such as axial bones disproportionately, resulting in different survival potentials between elements. This paper reviews the long accrual of knowledge initiated by Brain, evaluates what is known and unknown, re-examines the relationship between mechanical properties (density) and skeletal element survival, develops a general model of archaeological bone survival, and concludes with a methodological roadmap for zooarchaeology's future studies of skeletal element abundance.

INTRODUCTION

It is now widely recognized that taphonomic analysis founded on actualistic research is fundamental to all zooarchaelogical interpretation. Two books published in 1981—Brain's *The Hunters or the Hunted* and Binford's *Bones: Ancient Men and Modern Myths*—set off a flurry of research leading to the widespread acceptance of taphonomy in zooarchaeology. Despite the equally revolutionary nature of both books, Binford's was easily the more controversial of the two. Writing in a pointed, sometimes bombastic style, Binford sought to educate the archaeological community as to how proper research should be done. He was harshly critical in his treatment of some established ideas about early hominid behavior and evolution, as well as the people who put them forth. Although *Bones* presented very little new data, it overflowed with analyses of research originally presented elsewhere by Binford (1978) and others. Chapter two of *Bones* remains one of the clearest articulations of the essential nature of taphonomy and actualistic studies (along with Gifford-Gonzalez, 1991). Binford could have been pointing to Brain's work as an example.

By contrast, Brain (1981) writes in a subdued, balanced, and understated manner, giving careful thought to caveats and competing hypotheses (as in the "leopard hypothesis" of chapter 14). Brain's book is also more empirical. It is full of direct observations and data, many of these packed into an appendix that has been mined and re-used by a multitude of researchers. Although lacking explicit discussions of epistemology and never taking on the tone of a lecture, the text is replete with lessons by example. The message and significance of the book is subtle but transformational once realized. It is a lesson plan for studying the past grounded in more than 14 years of research. The book was an epiphany for many young taphonomists starting out in the early 1980s, and a model of research for many participating in this symposium.

Together, Brain and Binford provided the following guidelines for actualistic research:

1. Make the uniformitarian assumption that physical and biological systems operated in the past as they do today.
2. Ground inferences about the past in an understanding of processes operating in the present.
3. Justify the relevance of these modern processes to the past, insuring that cause and effect are well understood and would likely apply to the past.
4. Isolate all the processes that can produce the physical traces and patterns that comprise archaeological evidence.
5. Study these processes in the modern world to develop criteria for their recognition in an archaeological context. This is what Binford meant by the search for "signature patterns."
6. Insure that there is little or no doubt about the link between the agent and the resulting traces.

Gifford-Gonzalez (1991) provided a much-needed re-statement and terminological clarification of these principles along with a research protocol for actualistic studies seeking to develop the uniformitarian assumptions referred to above. In the Gifford-Gonzalez system, a *trace* is a visible attribute displayed by a bone that has undergone a taphonomic process. The *causal agency* is the immediate physical cause producing a trace, such as a tooth skidding across a bone. The *effector* is the item or material that effects the modification of a bone, such as the tooth. The *actor* is the source of the force or energy that creates the trace, such as a hyena biting on to a bone. This analytical construct provides a protocol for evaluating the strength of bridging arguments linking actor to trace (cause to effect), and thus a procedure to evaluate the robustness of uniformitarian propositions.

Over the 20 plus years since Brain (1981) and Binford (1981) laid the foundations, the taphonomic approach has been embraced by many zooarchaeologists, ignored by others, and argued against by still others. In 1995, Marean noted that the field had largely split into two camps: one practicing "actualistic taphonomy," and the other relying on "comparative taphonomy." The former examines processes in the modern world to make inferences about these in the past, while the latter makes these inferences by comparing patterns from the past.

Actualistic taphonomy covers a spectrum of methodology ranging from naturalistic to experimental, in which the analyst observes the relationship between the trace, causal agent, effector, and actor. In a fully naturalistic context, the analyst only observes and records without intentionally manipulating the parameters of the process. In experimental studies, the analyst actively controls the parameters of the observed process to better understand the relations linking the actor to the trace. There are also intermediate approaches in which the analyst controls some parameters, but only observes the actors. Ideally, there is a dynamic relationship between naturalistic and experimental studies, as there is between analogous fields of endeavor such as field and laboratory primatology. Naturalistic studies often set the research agenda while experimental studies refine one's knowledge of the bridging arguments.

Proponents of comparative taphonomy cite two main arguments in its favor. The first is that the range of modern processes is insufficient for understanding the past because there were conditions in the past that do not exist today. For example, since sabertooth cats are now extinct, we cannot observe their bone chewing behavior, and we must therefore rely on studies of fossil bone assemblages where we are reasonably confident that sabertooths were the agent of accumulation and destruction. The second argument for comparative taphonomy is that there are geological processes acting on the fossil record that are impossible to model on anything less than geologic time scales. These can only be understood by trying to control for their effects through the comparison of fossil assemblages. Perhaps the strongest advocates and applicants of the comparative approach are Klein (Klein et al., 1999) and Stiner (1994, 2002).

While it is certainly true that adaptively unique taxa were present in the past, and that geologic processes operate at time scales that cannot be directly replicated, neither proposition provides compelling support for the comparative method, nor overturns the primacy of the actualistic method. Interpretations based on comparative taphonomy fail Gifford-Gonzalez's (1991) litmus test for method: there is no direct control over the links between trace, causal agent, effector, and actor. Thus, the results are bridging arguments reliant on circumstantial evidence. Comparative studies can only produce unverified models that, if left unverified, have a good probability of producing a Type II error—that is, the erroneous acceptance of the hypothesis that similar ancient patterns are indicative of similar processes. What then is the proper role of comparative studies in taphonomy? These studies form a fertile source of hypotheses that can guide research design and testing using actualistic methods; first in a naturalistic context, then further refined by experimental studies. The result is a robust bridging argument that can then be effectively applied to the interpretation of traces and their patterns in the fossil record.

Modern approaches to skeletal element analysis (SEA) developed out of this heuristic process and have been strongly influenced by actualistic studies. As early as the 1950's, White (1954, 1955) recognized that element profiles, although a potentially rich source of information on human behavior, were skewed by taphonomic processes related to both marrow processing and carnivore ravaging. Brain (1967, 1969) brought this idea into the realm of actualistic research in his now classic studies with goat remains at Hottentot camps. It has since become apparent that many factors affect the SEA, including prey/carcass availability, transport decisions, butchery destruction, carnivore ravaging, sedimentary processes, and excavation/curation procedures. It is no wonder that the interpretation of SEA remains contentious (Stiner, 2002; Pickering et al., 2003).

In this paper, we review and analyze the history of research examining the impact of carnivore destruction on the SEA. In particular, we will do the following: 1) review the evidence for the impact of carnivore ravaging on bone, 2) focus on data from actualistic research, 3) re-examine the idea that bone density is the primary mediator of SEA, 4) develop a general model for bone survival and destruction, and 5) suggest a course for future research.

CAUSE AND EFFECT: THE ROLE OF CARNIVORES IN THE SEA

Discarded food remains have been magnets attracting carnivores to hominin locales (i.e., FLK *Zinj*) for at least 1.7 million years. Despite the debate over the interpretation of the Plio-Pleistocene faunal assemblages, all would agree that there is excellent evidence that at least some carcass remains discarded by hominins were ravaged by carnivores. Actualistic studies demonstrate that defleshed carcasses discarded in natural habitats are rapidly discovered and ravaged by carnivores (Blumenschine, 1988; Capaldo, 1995). By the Late Pleistocene, sites in Eurasia and Africa document intense carnivore ravaging of hominin-discarded carcass parts (Marean and Kim, 1998; Marean et al., 2000). It is likely that this attraction to human refuse eventually put canids on the path to domestication. Once canids were domesticated around 12,000 BP, the discarded carcass parts became one of their primary sources of nutrition, and carnivore ravaging probably became even more regular and intense. Despite clear evidence for carnivore damage to faunal assemblages, the extent to which ravaging could affect element representation was not always appreciated.

Brain (1967, 1969) was one of the first to recognize and study this process, and he did so with the goal of explaining a pattern of element representation observed by Dart (1957) at Makapansgat. In his 1967 paper, Brain addressed two patterns identified by Dart. The first was the abundance of cranial fragments in the Makapansgat assemblage. Dart had argued that the abundance of heads resulted from intentional collection habits of the early hominins, resulting from their desire to have mandibles as saws. The second pattern was the differential survival of the ends of limb bones—particularly the great distinction between proximal and distal humeri. Dart (1957) also noted that lower limb bones (specifically metapodials) occurred in much larger numbers than expected.

Skeletal patterns such as this typically result in negative curvilinear correlations between element representation and food utility (the so-called "reverse utility curves", Marean and Frey, 1997). This head-and-foot, head-dominated, and reverse utility pattern is the most widespread skeletal element distribution in zooarchaeology. Although it occurs in paleontological, Paleolithic, and complex society sites, it is still commonly attributed to selective transport (by humans) when found in archaeological contexts. For example, head-dominated Middle Paleolithic assemblages in Italy are interpreted as an indication that Neanderthals were scavenging the heads of carcasses and bringing them back to caves (Stiner, 1991). The one thing these assemblages share is a collection or quantification procedure that excludes isolated shaft fragments from analysis (Marean and Kim, 1998; Bartram and Marean, 1999), a practice shown to result in this typical element distribution (Marean and Frey, 1997; Marean, 1998). Although these methodological issues were raised much later, Brain's (1969) work showed beyond a doubt that post-depositional process could significantly alter the distribution of skeletal elements.

Brain (1969:13) presciently noted "The reconstruction of events from the remote past is always an indirect process" and "In such circumstances it is enormously helpful when contemporary situations can be found in which comparable events are taking place." The contemporary situation to which he referred was the butchery and discard of goat bones by Khoi-khoi pastoralists (Kuiseb River, Namibia), and the subsequent carnivore (canid) ravaging. Brain collected the discarded bones from meals for which he had reliable estimates of the original number of carcasses entering the taphonomic system. He also procured an entire goat and observed its butchery and consumption, isolating the carcass from dogs so he could see the difference in destruction. The study illustrates the dual use of the naturalistic and experimental models. The canid ravaging of the discarded goat bones produced an assemblage that mimicked many of the patterns present in the Makapansgat assemblage, and Brain (1969:22) concluded, "The bones preserved would have been those best able to survive the destructive treatment to which they had been subjected." Thus, the resulting skeletal element pattern required no special appeal to hominin behavior.

In 1969, Brain expanded his 1967 study in two exciting ways. First, he calculated a percent survival of skeletal elements. In the case of limb bones, Brain (1969: 19, table III) calculated survival for both proximal and distal portions. Calculating a percent survival was reasonable because Brain could legitimately assume that the entire goat carcass entered the deposit, and he could estimate the original minimum number of carcasses. Second, he estimated the resistance of skeletal elements to destruction by calculating a specific gravity per element portion, which is a gross estimate of density as a proxy for resistance to destruction. He concluded (1969:20): "survival is not haphazard, but is determined by inherent qualities of the parts." Here, as early as the 1960s, we see a search for cause and effect between skeletal element survival and a contemporary process. That work set in motion two parallel research trajectories that often intersected: the study of carnivore ravaging's impact on the skeletal element profile, and the attempt to estimate bone's structural properties as a tool for understanding bone survival. We now turn to a critical review of both.

Carnivore impact on skeletal element survival

Skeletal element survival can be studied in at least two dimensions: intra-bone survival (variation in the survival of different element portions) and inter-bone survival (variation in the survival of different elements). The two are intimately related. The relationship between intra-bone survival and the element portions coded for analysis will affect the analytical results of inter-bone survival. In other words, if limb bone ends and shafts survive at different rates, then inter-bone survival will appear distinct depending on whether one codes ends, shafts, or both. Table 1 provides a summary of the published record on carnivore destruction of bone in which data are relevant to either intra- or inter-bone survival.

Actualistic studies of how carnivores destroy bone range from experimental to naturalistic approaches. In Table 1 we have made a distinction between procedure ("type of study") and context in indicating whether or not a study is experimental or naturalistic. The study type is experimental if the analyst presented the carcass or carcass parts for study, and naturalistic if the analyst simply observed behavior that was occurring naturally. The context of a study was also classified as experimental if it took place in some type of controlled environment, such as an enclosure or zoo, and naturalistic if out in an area where wildlife occur free-ranging (preserve, park, or ranch).

Studies of carnivore impact on skeletal element survival have focused on patterning at dens, kill sites, and the scavenged remains from human butchery. These contexts can be anticipated to have widely varying results. In the first two situations, carnivores encounter a carcass (through either hunting or scavenging), conduct at least some on-site consumption, and then may elect to transport a small selection of carcass parts back to a den. Importantly, the den researcher only sees the outcome of this process, and cannot determine the original number of carcasses or elements. In the last context, carnivores encounter skeletal elements or carcasses that humans may have modified in any of the following ways: selective transport, defleshing, demarrowing, cooking, and then discard. The differences in the initial carcass conditions affect carnivore behavior and will likely have a major impact on what elements survive (Blumenschine and Marean, 1993; Lupo, 1995). However, all the processes of the latter two contexts can be observed, and in some cases controlled, by the researcher. Our review will segregate the literature based on this distinction between den recovery and behavioral observation.

Bone collection at carnivore dens

Many of the first carnivore taphonomy studies were based on den research (see Table 1, "Context" column), and most of these focused on the frequency of taxa and skeletal elements. Den studies are distinct from other actualistic research in that they do not allow direct observation of the process of destruction. Many of these studies were done, we believe, with the hope that there would emerge a carnivore specific skeletal element pattern that could then be used to identify carnivore accumulations (Brain, 1981). Stiner has argued that it is unlikely that skeletal element abundance can be used to diagnose agents of collection, but that this instead "reflects the predominant foraging strategy employed" (i.e. scavenging or hunting; Stiner, 1991: 169).

However, the data from these studies are of limited use for pattern identification for several reasons. First, in most (but not all) of the studies the thoroughness of the collection method is unclear. Was there an excavation below the sediment surface, were the sediments sieved, and was everything picked up? Two studies employed archaeological recovery methods (Kerbis-Peterhans and Horwitz, 1992; Lam, 1992). This is particularly significant given the fact that hyenas fragment bones, often consuming articular ends and other greasy parts, and thus produce shaft fragments. Small shaft fragments quickly penetrate the sediment surface (Gifford-Gonzalez et al., 1985), protecting them from surface collection. Unexcavated assemblages would likely be biased toward larger fragments that, for one reason or another, have survived ravaging.

Second, the methods used in many of the den studies to quantify skeletal element abundance are unclear, and almost certainly do not meet the standards set today in zooarchaeology. This is further complicated by the fact that some of the analysts are not zooarchaeologists (i.e. Bearder, 1977 and Skinner et al., 1980) and thus would not be expected to have robust methods for estimating skeletal element abundance from highly fragmented specimens, while others (e.g., Bunn, 1983) are zooarchaeologists and would likely have better developed zooarchaeological methods.

Third, the data are reported in ways that vary both in the measure being reported and the grouping of skeletal elements and portions. For example, Henschel et al. (1979) provide a table listing bone abundance, but it is unclear if this is the number of individual specimens (NISPs) or minimum number of elements (MNEs). Some bones are listed twice (e.g., "Tibia, complete" and "Tibia, distal") and are not collated into a final measure of abundance. Lam (1992) provides data consistent with modern usage, including NISPs and MNEs on all bones and individual portions. Data of these two types are not comparable.

Despite these problems, some valuable information has emerged from these studies. One of the initial questions asked of den assemblages was simple: do hy-

Table 1. Summary of actualistic studies documenting or discussing carnivore destruction of bone

Source	**Type of study**	**Context**	**Consumer taxon/taxa**	**Original condition of elements when encountered by carnivore**	**Type of Intra-Element Presentation**	**Intra-Element Data NISP or MNE/ MNI**	**Shaft Portions or Fragments Included in Quant Analysis**	**Type of Inter-Element Presentation**	**Inter-Element Survival Control**	**Inter-Element Data NISP, MNE, MNI, or MAU**	**Consumed taxon/taxa**	**Locality**
Brain (1967, 1969)	Natur.	Natur. (village refuse)	Human, domestic dog	complete carcass	quantitative	NISP and MNI	In NISP analysis only	quantitative	yes	NISP and MNI	Size class 1 – 2 bovids	Namibia
Brain (1970)	Exper.	Exper. (feeding in enclosure)	Cheetah	complete carcass	narrative description	nr	nr	brief comments	yes	nr	Baboon	Namibia
Sutcliffe (1970)	Natur.	Natur. (dens)	Spotted hyena	unknown	narrative description	nr	nr	none	nr	nr	Size class 1 – 3 mammals	Kenya
Lyon (1970)	Natur.	Natur. (house refuse)	Human, domestic dog	unknown	narrative description	nr	nr	none	nr	nr	Size class 1 – 2 mammals	Peru
Binford & Bertram (1977)	Natur.	Natur. (camp refuse)	Domestic dog	Cooked, uncooked, defleshed	quantitative	MNI	**no**	quantitative	yes	MNI	Size class 1-3 caribou and sheep	USA
Mills & Mills (1977)	Natur.	Natur. (dens)	Spotted hyena	unknown	narrative description	nr	nr	none	nr	nr	Size class 1-4	South Africa
Bearder (1977)	Natur.	Natur. (dens)	Spotted hyena	unknown	narrative description	nr	nr	quantitative	**no**	NISP	Size class 1-4	South Africa
Henschel et al. (1979)	Natur.	Natur. (dens)	Spotted hyena	unknown	narrative description	nr	nr	none	nr	nr	Size class 1 – 3 animals	Namibia
Richardson (1980)	Natur. and Exper.	Natur. (ranches and wildlife reserves)	Feral dog, jackal, spotted hyena, brown hyena, lion	complete carcass	quantitative	MNI	no	quantitative	yes	MNI	Size class 1 – 5 bovids	South Africa, Zimbabwe
Haynes (1980, 1981, 1983a, b)	Natur.	Natur. (wilderness areas)	Wolf, bear	various (complete carcass and unknown)	narrative description	nr	nr	none	nr	nr	Size class 1-4	North America

“Natur.” = Naturalistic, “Exper.” = Experimental, nr = not relevant, NISP = number individual specimens, MNI = minimum number individuals.

Table 1. Summary of actualistic studies documenting or discussing carnivore destruction of bone (continued)

Source	Type of study	Context	Consumer taxon/taxa	Original condition of elements when encountered by carnivore	Type of Intra-Element Presentation	Intra-Element Data NISP or MNE/MNI	Shaft Portions or Fragments Included in Quant Analysis	Type of Inter-Element Presentation	Inter-Element Survival Control	Inter-Element Data NISP, MNE, MNI, or MAU	Consumed taxon/taxa	Locality
Haynes (1980, 1981, 1983a, b)	Exper.	Exper. (zoos)	Wolf, bear, large cats, hyenas	defleshed tibia and femora	narrative description	nr	nr	none	nr	nr	Size class 4 (*Bos taurus*)	North America
Skinner et al. (1980)	Natur.	Natur. (dens) and Exper.	Striped hyena	unknown for den, complete carcass for feedings	quantitative	NISP	yes	quantitative	no for den, yes for feedings	NISP	Size class 1-4	Israel
Binford (1981)	Natur.	Natur. (den and kill sites)	Wolf	unknown for den, complete carcass for kills	quantitative	MNI	no	quantitative	no for den, yes for kill sites	MNI	Size class 3 (*Rangifer tarandus*)	Alaska
Hill (1981, 1984), Potts (1988)	Natur.	Natur. (dens)	Spotted hyena	unknown	narrative description	nr	unclear	quantitative	no	MNE	Size class 1-4 mammals	Kenya
Bunn (1983)	Natur.	Natur. (dens)	Spotted hyena	unknown	narrative description	nr	yes	quantitative	no	unclear	Size class 1-4 mammals	Kenya
Stallibrass (1984)	Exper.	Natur. (farm)	Foxes	complete carcass	quantitative	MNI	no	quantitative	yes	MNI	Size class 1-2 sheep	England
Payne & Munson (1985)	Exper.	Exper. (enclosure)	Domestic dog	Cooked, uncooked, defleshed	none	nr	no	quantitative	yes, but not precise	MNE	Size class 2 bovids, small mammals	USA
Snyder (Snyder, 1988; Klippel et al., 1987)	Exper.	Exper. (enclosure)	Gray wolf	complete carcass	quantitative	MNI	no	quantitative	MNI	MNI	Size class 2 cervids	USA

"Natur." = Naturalistic, "Exper." = Experimental, nr = not relevant, NISP = number individual specimens, MNI = minimum number individuals.

Table 1. Summary of actualistic studies documenting or discussing carnivore destruction of bone (continued)

Source	Type of study	Context	Consumer taxon/taxa	Original condition of elements when encountered by carnivore	Type of Intra-Element Presentation	Intra-Element Data NISP or MNE/ MNI	Shaft Portions or Fragments Included in Quant Analysis	Type of Inter-Element Presentation	Inter-Element Survival Control	Inter-Element Data NISP, MNE, MNI, or MAU	Consumed taxon/taxa	Locality
Binford et al. (1988)	Exper.	Natur. (wildlife reserve)	Spotted hyena	defleshed limb bones	narrative description	nr	nr	none	nr	nr	Size class 4 bovids	South Africa
Blumenschine (1988)	Exper.	Natur. (wildlife reserve)	Spotted hyena, lion	defleshed limb bones	quantitative	NISP	yes	none	nr	NISP	Size class 1 – 3 bovids	Tanzania
Horwitz (Horwitz & Smith, 1988)	Natur.	Natur. (den)	Striped hyena	unknown	narrative description	nr	nr	narrative description	nr	nr	human	Israel
Marean (Marean & Spencer, 1991)	Exper.	Exper. (enclosure)	Spotted hyena	defleshed limb bones	quantitative	MNE	yes	quantitative	MNE	yes	Size class 1-2 sheep	USA
Kerbis-Peterhans and Horwitz (1992), Horwitz (1998)	Natur.	Natur. (den)	Striped hyena	unknown	narrative description	nr	no	quantitative	no	MNI	various mammals and reptiles	Israel
Lam (1992)	Natur.	Natur. (den)	Spotted hyena	unknown	quantitative	NISP/ MNE	yes	quantitative	no	NISP/ MNE	Size class 1–2 bovids	Kenya
Bartram (1993; Bartram & Marean, 1999)	Natur.	Natur. (abandoned human sites)	Human, Brown hyena, jackal,	unknown	quantitative	NISP/ MNE	yes	quantitative	no	NISP/ MNE	Size class 1–5 mammals	Botswana
Bunn (1993)	Natur.	Natur. (abandoned human sites)	Human, spotted hyena, jackal,	unknown	none	nr	yes	quantitative	no	MAU	Size class 1–4 bovids	Tanzania

"Natur." = Naturalistic, "Exper." = Experimental, nr = not relevant, NISP = number individual specimens, MNI = minimum number individuals.

Table 1. Summary of actualistic studies documenting or discussing carnivore destruction of bone (continued)

Source	Type of study	Context	Consumer taxon/taxa	Original condition of elements when encountered by carnivore	Type of Intra-Element Presentation	Intra-Element Data NISP or MNE/ MNI	Shaft Portions or Fragments Included in Quant Analysis	Type of Inter-Element Presentation	Inter-Element Survival Control	Inter-Element Data NISP, MNE, MNI, or MAU	Consumed taxon/taxa	Locality
Hudson (1993)	Natur.	Natur. (occupied campsites)	Human, domestic dog	defleshed and some hammer-stone broken	quantitative	MNE	yes	quantitative	yes	MNE	Size class 1–2 mammals	Central African Republic
Selvaggio (1994, 1998)	Natur.	Natur. (wilderness areas)	Large felids, spotted hyena, jackal, human	complete carcass	none	nr	nr	quantitative	yes	NISP	Size class 1 and larger	Tanzania
Lupo (1995)	Natur.	Natur. (abandoned human sites)	Human, unknown East African carnivores	unknown	quantitative	NISP, some MNE	yes	quantitative	some	NISP, some MNE	Size class 2-3 bovids, Size class 3 Equid	Tanzania
Capaldo (1995)	Exper.	Natur. (simulated abandoned human sites)	Unknown East African carnivores	defleshed bones	quantitative	NISP	yes	quantitative	yes	NISP	Size class 1 – 3 bovids	Tanzania
Domínguez-Rodrigo (Domínguez-Rodrigo, 1997; Pickering et al., 2003)	Exper.	Natur. (simulated abandoned human sites)	Unknown East African carnivores	defleshed bones	quantitative	NISP	yes	none	nr	nr	Size class 3 bovids	Kenya
Pickering (Pickering et al., 2003)	Exper.	Exper. (enclosure)	Spotted hyena, leopard	complete carcass	quantitative	MNE	yes	none	nr	nr	Size Class 2 primates	South Africa

"Natur." = Naturalistic, "Exper." = Experimental, nr = not relevant, NISP = number individual specimens, MNI = minimum number individuals.

enas accumulate bones at dens? Dart (1956) argued no, but these studies overwhelmingly provide an answer in the affirmative, and thus accumulation by carnivores in caves and rock shelters is a potentially serious problem for zooarchaeologists. The more complicated question addresses the issue of patterning in skeletal element representation and whether this can be used to diagnose an accumulator or identify a particular type of predatory niche.

Stiner (1991) argues that there is a pattern in the collections. Her analysis draws on a selected series of carnivore dens, including several unpublished dens from data provided by Gary Haynes and Lewis Binford. She indexes skeletal element completeness and finds that striped and brown hyenas (obligate scavengers) tend to have horn- or head- dominated assemblages, wolves tend to have assemblages dominated by the more meaty parts of the skeleton, and spotted hyenas vary between the two extremes.

The complicating factor here of course is that skeletal element abundance at dens minimally reflects both transport behavior and bone consumption capabilities. Hyenas are far more capable bone consumers than wolves (Ewer, 1973), and it is likely that their assemblages will display more attrition of the trabecular portions of postcranial elements than those of wolves. The result would be a greater relative representation of head, horn, and limb bone cortical fragments at hyena accumulations. This means that any (particularly hyena) study that fails to include shaft fragments in the analysis (most of these studies do not include shafts) will inevitably underestimate the number of limb bones present. This is clearly displayed in Lam's (1992) data (not included in Stiner's 1994 survey), which shows a strong representation of limb bones and a low frequency of horn and head parts. Another problem with comparing these carnivores is that cervids (the main prey of the wolves) only have antlers for part of the year (and these are in a soft state for some of that time). By contrast, bovids (the main prey of the hyenas) have horns (which survive well) all year round (Brain, 1967, 1969). Thus, it is inevitable that hyena assemblages will have more horns than wolf assemblages will have antlers without any appeal to differences in the carcass portions transported.

Several of these studies have noted that carnivores, in the process of accessing within-bone nutrients, chew away and consume the softer, greasy, cancellous portions of bones, and leave behind the harder cortical bone fragments. Sutcliffe (1970) studied several hyena dens in East Africa, leading him to develop a list of four types of hyena damage to bones. "Type 1" damage is typified by a regular pattern of relative bone destruction—robust bone portions survive, while cancellous portions are commonly destroyed. Sutcliffe goes on to note that when hyenas feed on human remains, the ends of limb bones are destroyed, but the shafts survive. Most of the den reports make similar observations on various prey taxa (Henschel et al., 1979; Lam, 1992; Kerbis-Peterhans and Horwitz, 1992).

Juvenile hyenas break bones far less effectively than do adults, and their gnawing creates multiple striations perpendicular to the long axis of the bone (Sutcliffe's "Type 2" damage), sometimes even wearing a hole. Various authors have noted that den assemblages typically have reasonable frequencies of "bone cylinders"—limb bone shafts that retain the complete circumference (Potts, 1988). However, they are rare to absent in assemblages where adult hyenas have been presented with complete long bones. One of us (CWM) has observed that juvenile hyenas, through this regular bone gnawing, produce cylinders because they cannot reduce the more resistant shafts. Thus, gnawed bone cylinders implicate juveniles when hyenas are the agent, and perhaps smaller adult carnivores of taxa less capable of crushing bone.

One pattern that has arisen from the den studies, but has been widely ignored in zooarchaeological literature, is the presence of regurgitations and their potential as an indicator of the persistence of hyena activity in caves and rockshelters. Bearder (1977) notes that spotted hyenas regurgitate in and around their dens on a regular basis (see also Brain, 1981). Although we lack precise data on transit times, we noted that regurgitations among the captive hyenas at Berkeley occurred at least several hours after consumption. Hyena den assemblages should therefore display fairly high frequencies of regurgitated bone. Along with tooth mark frequencies, this is likely to provide a useful measure of the contribution of hyenas to fossil bone assemblages.

In summary, we have gained a modest amount of knowledge from the currently published studies of den assemblages but these have had a limited impact on our interpretation of the SEA. Their importance in identifying a skeletal profile unique to dens could be revitalized by renewed research using strictly controlled collection and analysis procedures. However, unless done in very controlled situations, these will always lack the critical link between observer and initial conditions.

Bone ravaging at kills and areas of human discard

Studies examining how carnivores ravage bones discarded by humans have been done in at least three contexts: 1) studies of people living in traditional economic pursuits (ethnoarchaeology), 2) studies of carnivore kills, and 3) simulations of human butchery and discard. The first two contexts have necessarily less control over the process, but they at least have a more naturalistic context. We have lumped carnivore kill studies together with hominid-first research for two reasons. First, the process of observation can be done completely—that is, all skeletal inputs to the system can be known. Second, these studies are done in order to identify basic parameters of carnivore destruction and to put hominid-first destruction into perspective.

Ethnoarchaeological contexts have included both residential and butchery sites of hunter-gatherers or pastoralists. Some researchers observed behavior at occupied sites, making it easier to estimate the original number of elements entering the system (Brain, 1967, 1969; Hudson, 1993). However, when studying sites abandoned for varying lengths of time, researchers (e.g. Bartram, 1993) sometimes had little knowledge of the original number of carcasses.

Experimental studies provide a direct measure of the impact of carnivore feeding and ravaging through direct observation (securing the link between trace and actor), controlled input of skeletal elements, and thorough collection of bone fragment output. With such control over the parameters of the experiment, one can confidently estimate a percentage survival (Brain, 1967) or percentage change (Marean and Spencer, 1991). Without these statistics, the cause and effect relationship between carnivores and element representation is obscured by other factors that could affect representation (such as variation in human transport decisions) and thus diminishes the predictive power of the model. We have indicated in Table 1 whether this control applies in each study in the column titled "Inter-Element Survival Control."

Several studies maintained control over input parameters (in both naturalistic and experimental contexts) by providing carnivores with complete fleshed carcasses, observing the process of destruction, and then collecting the remains. More recent studies (such as those of Capaldo, Selvaggio, Domínguez-Rodrigo, and Marean) have focused on gaining even greater control through the use of a "simulated site" approach as first illustrated by Binford et al. (1988) and Blumenschine (1988). These studies typically model several scenarios of carcass part access by hominins and carnivores, preparing carcass parts accordingly. For example, the hominid-first (a.k.a. "hominid to carnivore") scenario involves defleshing bones, processing them for marrow, and then allowing carnivores to ravage them. These have since been permutated into a variety of sequences (e.g. carnivore only, carnivore to hominid, carnivore to hominid to carnivore, etc.).

Brain (1967, 1969) conducted one of the earliest studies of sequential carcass access, and documented both intra-bone and inter-bone survival. He found that human food preparation, followed by dog ravaging of the discarded bones, typically resulted in the elimination of limb bone epiphyses (except for those epiphyses with greater "specific gravity" and earlier fusion). His inter-bone analysis showed that the mandible survived the best (nearly 100% survival), while vertebrae, pelves, scapulae, ribs, small compact bones, and phalanges survived at rates less than 30%. Without a percentage survival based on shafts, limb bone portions other than the distal humerus survived poorly.

Brain (1970) also fed baboons and size 1 and 2 bovids to cheetahs, a felid with a rather flesh-specialized dentition (Ewer, 1973; see Brain, 1981: 9 for size class definitions). He found that cheetahs minimally damaged the bones of even small bovids such as springbok, but did far more damage to the skeletons of similarly sized baboons. The cheetahs consumed the entire baboon vertebral column, hands, and feet, and did significant damage to the ends of the limb bones. Brain (1970) argued that baboon skeletons were less dense than those of bovids, even those of the same body size, and thus were more susceptible to carnivore destruction. There are no quantitative data on survival presented in the study.

Lyon (1970: 214) studied the Wachipaeri of eastern Peru and observed the ravaging of size class 1 and 2 mammal bones that were discarded after human processing. These studies were done in the context of village sites with domestic dogs. Lyon notes "dogs generally chewed off all the articulations and occasionally completely consumed the long bones." The dogs totally consumed all the bones of small animals including fish, birds, and small mammals, but only damaged most of the bones of the larger mammals. There are no quantitative data presented in the study.

Binford and Bertram (1977) provided data and analyses of Nunamiut and dog destruction of caribou bones, and Navaho and dog destruction of sheep bones. Importantly, in one Nunamiut study the authors had nearly perfect control over the percentage survival (Binford and Bertram, 1977: 81, table 3.2, last column) and in two Navaho studies they had good, though not perfect, control. They did not present any data on shaft portions, but did document differential inter-bone survival that they argued was due to differences in density. Axial parts such as vertebrae, ribs, and pelves did not survive well, nor did small compact bones and phalanges.

Binford (1981) also reports on the inter-bone survival from 24 individual caribou killed by wolves. As in the Nunamiut study (Binford and Bertram, 1977), inter-bone survival does not appear to be density dependent, and axial elements have high rates of survival. Binford (1981) also provides useful information on the relative representation of intra-long bone survival, although not for individual elements. These data show that shaft splinters are nearly eight times more numerous than articular ends. Of course, this does not tell us that MNE would have been higher if calculated on shafts, but it suggests this possibility. Bone cylinders are also reported, but it is unclear whether they might have been included in the calculation of MNI per long bone end. Binford (1981: 210-217) compares the wolf kill data with a couple of dens and another suspected kill site, but he expresses some doubts about the agents of accumulation in these latter contexts.

Between 1977 and 1981, Haynes (1980, 1981, 1982, 1983a, 1983b) observed carcass destruction in natural contexts and bone destruction in zoo feeding experiments. In the former, he observed the effects of wolf (*Canis lupus*) and bear (*Ursus sp.*) ravaging of primarily large and medium ungulates (e.g., *Bison bison, Odocoileus virginianus, Alces alces*). These carcasses were examined seasonally for progressive change. Fieldwork was complemented by experimental research in which tibia and femora of *Bos taurus* were fed to several carnivores (bear, wolf, large cats, and hyenas). Haynes (1980, 1982, 1983a, 1983b) published detailed narrative descriptions of the resulting damage (including fracture type, surface marks, and general extent of destruction). In addition to the morphological distinctions between damage caused by different carnivores, Haynes noted that the hyenas were generally much more destructive than the wolves, and both generally did more damage to bone than the other carnivores surveyed. Even so, Haynes (1982) documented at least one instance in which wolves reduced a white-tailed deer carcass to a handful of isolated limb shaft fragments—very similar in appearance to the remains from Marean's (Marean and Spencer, 1991) hyena feeding experiments.

Richardson's (1980) study of the damage inflicted by various carnivores on 89 bovid, equid, and giraffe carcasses (size classes 1–5) shows differential destruction of limb bone ends relative to shafts across all body sizes. Richardson had control over the number of carcasses set out, and therefore provided a true percentage for inter-element survival. He found remarkable similarity in bone survival when comparing carnivore ravagers, but hyenas inflicted far more damage than other taxa. The idea that hyenas can have such a significant impact on large mammal skeletons has recently come under attack by Klein et al. (1999), who argue that hyenas are unable to chew the ends off size 4 and 5 mammals. As evidence, they provide a drawing of a hyena skull at maximum gape attacking the proximal tibia of *Pelorovis* just as a human would eat a hot dog. Both Richardson (1980: 113, figure 3b) and Brain (1981: 71, figure 63) illustrate giraffe proximal humeri that were completely removed by hyena chewing. Blumenschine (1988) and Capaldo (1995) both report destruction of size 4 and 5 limb bone ends in their hyena observations. One of us (CWM) has fed whole size 4 bones to hyenas, and found that hyenas have a standard approach to reducing large mammal bones. Rather than attacking the bone like a hot dog, hyenas grip protuberances in their teeth and exert leverage with their powerful neck muscles. They snap off chunks (some of which are swallowed) and thus produce craggy areas that can be gripped and attacked again, eventually opening the medullary cavity. These multiple actualistic observations, including Richardson's (1980), clearly falsify the Klein et al. (1999) hypothesis that hyenas are unable to destroy bones that exceed their maximum gape.

Stallibrass (1984) observed the impact of scavenging foxes and birds on 18 complete sheep carcasses with no human processing, and reported percentage element survival. She found significant variation in survival between elements as well as density related differences in intra-bone survival (in tibia and humerus). Small elements such as phalanges and compact bones survived poorly, and ribs and vertebrae survived the worst. Overall, limb bones with very dense epiphyses survived best. She does not provide survival data on limb bone shafts.

Payne and Munson (1985) fed the bones of squirrels, rabbits, and goats to a dog. They found that teeth survive well, as do early-fusing long bone ends. Survival is moderate for foot bones and low for late-fusing long bone ends, scapulae, pelves, and phalanges. They had good control over the original number of bones fed to the dog and were able to calculate percentage survival, but their data do not include shaft fragments, and some of the survival estimates are given as ranges.

Snyder (Klippel et al., 1987; Snyder, 1988) observed the feeding behavior of gray wolves on fleshed white-tailed deer carcasses. She found that limb bone end survival ranged from 87.5% (distal humerus) to 0% (distal radius and distal metacarpal). Axial remains such as vertebrae, pelves, and ribs survived very poorly, as did smaller bones like phalanges and carpals. Snyder had excellent control of percentage survival, but did not report the survival of limb bone shafts.

Binford and colleagues (1988) simulated hominid bone discard followed by hyena ravaging in a park in South Africa in which size 4 bovid bones (African buffalo) were defleshed and broken open with hammerstones. The researchers observed, "the bone elements remaining in their original positions were either long-bone splinters or impact chips, and none of them had been gnawed by hyenas" (Binford et al., 1988: 125). The focus was on limb bones and there are no data presented on inter-bone survival.

Blumenschine conducted similar, but more extensive, studies in northern Tanzania using size 1–3 mammals and presents NISP data on limb bone portion survival (including mid-shaft survival; Blumenschine, 1988: 488, table 2). He concludes:

> "The most conspicuous effect [of scavenger disturbance] is the virtually complete deletion or on-site destruction of hammerstone-produced epiphyseal fragments, a pattern that mirrors carnivore consumption of whole bone…At the same time, midshaft fragments produced by hammerstone breakage seem to be largely if not totally ignored by scavengers and to bear features distinctive of hammerstone breakage only" (Blumenschine, 1988: 495-496).

Marean and Spencer (1991) reported on the destruction of defleshed sheep limb bones, offered to hyenas as either unbroken bones or hammerstone broken fragments. They documented survival across five portions of each limb bone. They had excellent control of both the number of bones presented and of recovery, and their results showed significant destruction of end portions and rather complete survival of shafts. A subsequent paper (Marean et al., 1992) examined inter-bone survival and provided data on both the sequence of skeletal element choice by the hyenas and on ultimate levels of destruction. Axial bones tended to be chosen first and ravaged more intensely. The combined results of both papers indicate that only the middle shaft portions of long bones regularly withstand hyena attack.

Bunn (1993) described carnivore ravaging at Hadza base camps, noting that long bone ends were preferentially removed, but that this bias was less pronounced when sites were occupied for prolonged periods. He noted similar destruction of ends at San sites in the Kalahari. He did not include quantitative data on intra-element survival at the Hadza camps, but he did publish some graphs showing relative element representation. No information was given indicating the original number of skeletal elements that entered the system.

Hudson (1993) detailed the destruction of size 1 and 2 mammal skeletal elements by domestic dogs in Aka pygmy camps. Her observations with regard to the impact of dog ravaging are clear and "can be used to suggest a baseline of expected survival frequencies on an ordinal scale: the preferential survival of heads, the loss of the articular ends of limb bones, and of carpals, tarsals, phalanges, and the under representation of vertebrae and ribs" (Hudson, 1993: 320). Hudson also presents excellent control data on percentage of inter-element survival. The results of the study are somewhat limited, however, in that excavation occurred after Aka camps were abandoned and the assemblage included multiple taxa. In fragmented assemblages, taxonomic variability will naturally result in a higher proportion of unidentifiable bone specimens. Indeed, Hudson (1993: 305) reported a 48% loss of the original minimum number of individuals (MNI).

Bartram (1993; Bartram and Marean, 1999) conducted research among Kua San hunter-gatherers of Botswana, in which he regularly monitored the bone refuse from their kills of sizes 1 to 5 mammals. His (1993) data, presented in detail in a series of appendices and summarized in a clear discussion, show that carnivores at Kua camps regularly deleted the ends of limb bones while leaving shafts undisturbed. Furthermore, Bartram's results show that the deletion of ends over shafts is elevated in size 3 and 4 versus size 1 and 2 mammals. Bartram (1993) did not have control over the number of skeletal elements that entered the system, so percentage survival data are not available, but his published quantification, including NISP and MNE on all long bone portions is unmatched in completeness.

Selvaggio (1994, 1998) observed various carnivores consuming prey taxa in naturalistic contexts in Tanzania. For 19 of the 32 carcasses studied, she was able to document the process beginning with the hunt. She then collected long bones from the carcasses and marrow-processed all but 35 of these, simulating a "carnivore to hominid" assemblage. Carnivores were allowed to continue ravaging nineteen carcasses from this sample, creating a "carnivore to hominid to carnivore" assemblage. Although her published research focused on the resulting bone surface modification, she provided some information on bone portion (epiphysis, near-epiphysis, and shaft) representation after marrow processing. For all long bones combined, there was little epiphyseal destruction within her carnivore to hominid sample. However, an additional period of ravaging dramatically reduced epiphyseal survival (from 42% to 11%) while increasing midshaft representation (46% to 74%; Selvaggio, 1998: 196, table 4). Because she did not segregate her data by element, it is not possible to determine whether density influenced the initial survival of bone ends. The fact that bones were collected shortly following the initial episode of carnivore consumption may have also affected bone survival data. It is possible that there is more intra-bone survival information within her original data.

Capaldo (1995) simulated hominid discard assemblages ravaged by carnivores in semi-naturalistic contexts in northern Tanzania. He had excellent control over the number of bones that entered the system. To date Capaldo has reported the survival potential of skeletal elements and portions in NISP, but not in MNE, limiting the value of the results. These data together with data collected in a similar study by Domínguez-Rodrigo (Pickering et al., 2003) document severe preferential destruction of limb bone ends of size 1–3 bovids. Pickering (Ibid.) reports the same pattern for a study of carnivore ravaged baboon limb bones.

Summary of skeletal element survival

There are several clear patterns documented in the literature reviewed above, and we will review these both qualitatively and quantitatively. First, carnivores have a dramatic impact on intra-bone survival. The literature shows time and again that carnivores selectively destroy limb bone ends in preference to limb shafts. Pickering et al. (2003) provide a quantitative analysis of these data showing that, when presented by portion, limb shafts nearly always provide higher MNE estimates than ends. The critical implication of this pattern is that long bone counts that include isolated shaft portions are more accurate than counts based only on long bone ends. There is less discussion in these studies, and certainly no quantitative description, of intra-bone survival among other bones, such as axial elements. The literature agrees that when axial elements survive at all, their protuberances are most likely to be destroyed. It might be useful in future studies to examine this pattern in more detail.

Carnivores also have a dramatic impact on inter-bone survival. The question "how do different skeletal elements survive carnivore destruction?" is best answered by examining the rate of survival, not the skeletal element pattern (i.e. head and foot) that results from the process. The latter may be partly an outcome of selective transport and not only a measure of destruction. We must therefore first identify those studies in which we can directly measure rate of survival—that is, those studies with accurate quantification of element input and output.

Because the quantification of long bone shafts is so essential to accurate reporting of percentage survival (as discussed above), we have divided the analyses into those studies where shaft portions of limb bones were included, and those where they were not. For the majority of the studies surveyed here, data from limb shafts were

Table 2. Percentage survival of skeletal elements in studies that ***did not*** *report long bone shaft survival*

	A.		B.		C.		D.		E.		F.		G.	All Studies		
	MNI	**% Survival**	**MNI**	**% Survival**	**MNI**	**% Survival**	**MNI**	**% Survival**	**MNE**	**% Survival**	**MNE**	**% Survival**	**% Survival MNE**	**Mean % Survival**	**Min % Survival**	**Max % Survival**
Skull	11.0	47.8	16.5	76.7	11.0	61.1	ni	ni	ni	ni	1	25.0	ni	52.7	25.0	76.7
Mandible	18.5	80.4	21.5	100.0	14.0	77.8	ni	ni	117	91.4	8	100.0	47.0	82.8	47.0	100.0
Atlas	12.0	52.2	4.0	18.6	5.0	27.8	3.0	75.0	12	18.8	2	50.0	33.0	39.3	18.6	75.0
Axis	17.0	73.9	4.0	18.6	5.0	27.8	2.0	50.0	14	21.9	1	25.0	28.0	35.0	18.6	73.9
Cervical	12.8	55.7	3.7	17.2	8.3	46.1	3.0	37.5	12	3.8	3	15.0	40.0	30.8	3.8	55.7
Thoracic	12.2	52.8	3.2	14.9	3.0	16.7	3.2	35.0	21	2.5	2	3.8	23.0	21.2	2.5	52.8
Lumbar	15.6	67.8	4.5	20.9	5.6	31.1	6.7	47.8	31	8.1	7	29.2	30.0	33.6	8.1	67.8
Sacral	ni	ni	ni	ni	ni	ni	ni	ni	1	1.6	ni	ni	28.0	14.8	1.6	28.0
Caudal	ni	ni	ni	ni	ni	ni	ni	ni	0	0.0	ni	ni	ni	0.0	0.0	0.0
Pelvis	23.0	100.0	9.5	44.2	13.0	72.2	9.0	81.8	34	26.6	7	87.5	60.0	67.5	26.6	100.0
Rib	10.8	47.0	1.9	8.8	2.4	13.3	2.6	22.7	170	10.2	1	1.0	18.0	17.3	1.0	47.0
Scapula	12.0	52.2	6.0	27.9	14.5	80.6	2.5	50.0	35	27.4	4	50.0	47.0	47.9	27.4	80.6
Humerus Prx.	2.5	10.9	1.5	7.0	2.5	13.9	ni	ni	0	0.0	2	25.0	19.0	12.6	0.0	25.0
Humerus Dis.	9.5	41.3	7.0	32.6	18.0	100.0	ni	ni	82	64.0	7	87.5	58.0	63.9	32.6	100.0
Rad.-Ulna Prx.	8.0	34.8	7.5	34.9	12.5	69.4	ni	ni	65	50.8	6	75.0	71.0	56.0	34.8	75.0
Rad.-Ulna Dis.	4.5	19.6	2.5	11.6	10.0	55.6	ni	ni	22	17.2	0	0.0	67.0	28.5	0.0	67.0
Carpals	3.5	15.2	2.7	12.6	1.8	10.0	ni	ni	ni	ni	2	4.2	ni	10.5	4.2	15.2
Metacarpal Prx.	5.5	23.9	2.5	11.6	5.0	27.8	0.5	100.0	32	25.0	6	75.0	35.0	42.6	11.6	100.0
Metacarpal Dis.	5.5	23.9	2.5	11.6	3.5	19.4	0.0	0.0	23	18.0	0	0.0	33.0	15.1	0.0	33.0
Femur Prx.	7.0	30.4	1.5	7.0	7.0	38.9	1.0	50.0	18	14.1	2	25.0	36.0	28.8	7.0	50.0
Femur Dis.	3.5	15.2	2.5	11.6	3.5	19.4	0.5	25.0	9	7.0	3	37.5	31.0	21.0	7.0	37.5
Tibia Prx.	5.0	21.7	4.5	20.9	8.0	44.4	1.0	40.0	13	10.1	1	12.5	58.0	29.7	10.1	58.0
Tibia Dis.	11.0	47.8	7.5	34.9	13.0	72.2	1.5	60.0	72	56.3	4	50.0	80.0	57.3	34.9	80.0
Tarsals	5.0	21.7	3.6	16.7	4.0	22.2	0.5	25.0	ni	ni	18	45.0	ni	26.1	16.7	45.0
Astragalus	5.5	23.9	3.0	14.0	5.0	27.8	1.0	50.0	16	12.5	5	62.5	19.0	29.9	12.5	62.5
Calcaneum	5.5	23.9	2.5	11.6	5.0	27.8	0.5	25.0	14	10.9	4	50.0	7.0	22.3	7.0	50.0
Metatarsal Prx.	8.5	37.0	4.0	18.6	4.5	25.0	1.0	40.0	39	30.4	7	87.5	36.0	39.2	18.6	87.5
Metatarsal Dis.	4.5	19.6	2.5	11.6	5.5	30.6	0.5	25.0	20	15.6	1	12.5	33.0	21.1	11.6	33.0
Phalanx 1	2.6	11.4	0.9	4.0	0.9	4.8	0.4	18.5	ni	ni	1	3.1	ni	8.4	3.1	18.5
Phalanx 2	1.9	8.1	0.6	2.9	0.6	3.4	0.3	12.5	ni	ni	0	0.0	ni	5.4	0.0	12.5
Phalanx 3	1.5	6.5	0.4	1.7	0.4	2.1	0.1	6.0	ni	ni	0	0.0	ni	3.3	0.0	6.5
Phalanges	2.6	11.4	0.9	4.0	0.9	4.8	0.4	18.5	21	2.7	1	0.0	9.0	7.2	0.0	18.5

Raw values such as surviving MNIs or MNEs are listed if provided in the original study. ni = element not included in study. A. Binford (1981: 211-213, Table 5.01, total wolf kills). B. Binford and Bertram (1977: 101, Table 3.5, winter sheep). C. Binford and Bertram (1977: 101, Table 3.5, summer sheep). D. Binford and Bertram (1977: 81, Table 3.2, record B). E. Brain (1967: 109, Table 3). F. Klippel et al. (1987: 158, Table 1). G. Stallibrass (1984: Figure 1, data extracted by digitizing bar graph).

not included (Table 2). Quantifying only cancellous bone portions may provide a good measure of the impact of carnivores on those portions, but not on skeletal element abundance as a whole.

Since carnivores are the secondary or only agents of destruction in all of these studies, we hypothesized that skeletal elements would show similar levels of destruction across the different studies. To test this, we ran a correlation analysis on each pair of samples. We first standardized each pair of samples to the range of elements present. For instance, if one study provided percentage survival for the caudal vertebrae and the other did not, this element was removed from the analysis and the ranking procedure that followed. The remaining elements were then ranked in abundance, and a bootstrap correlation and probability statistic were generated from 1000 permutations of the datasets. The null hypothesis in this case was that the paired samples were not correlated. Table 3 shows that 19 out of 21 pairs of samples are strongly correlated ($p < .05$), and one of the remaining pair are nearly correlated at this level. We therefore reject the null and conclude that these five studies show us that carnivore destruction of human discarded bone results in very similar inter-element levels of destruction when shafts are not included in analysis.

Given this concordance, we calculated a mean percentage survival for each skeletal element in order to show a general pattern (Table 2, last column; Figure 1). Head elements survive best (particularly the mandible), while scapulae and pelves survive reasonably well. The limb bone ends show wide variation (both between elements and between studies). Distal humeri, proximal radius-ulnae, distal tibiae, and proximal metapodials survive well, while all other limb bone ends have mean survival rates below 30%. Vertebral portions, ribs, carpals, tarsals, and phalanges survive quite poorly (all means below 31%). Among these non-shaft portions, there is generally a close relationship between the average rate of survival and the range of variation in survival. That is, those element portions that survived well on average vary more in survival between studies. The fact that an element portion survives well in this grouping is therefore not an indication of consistent high survival.

We conducted the same analysis on those few studies that include shaft portions in their calculations (see Table 4 for the raw data). These were the small and medium duiker samples from Hudson's (1993) Aka study, and Marean's Berkeley hyena colony study (Marean and Spencer, 1991; Marean et al., 1992). The Berkeley hyena MNE's have been recalculated using an updated zooarchaeological coding system, and the numbers differ slightly from those in Marean et al. 1992. The correlation between Hudson's duikers was very low, as was the correlation between Marean's data (either whole bone or hammerstone broken) and the medium duikers (Table 5). However, Marean's data were highly correlated with the small duiker sample. The medium duikers appear to have undergone some taphonomic process different from either Marean's sheep or other duikers in the same study. Although we do not have the contextual data that could clarify this issue, we believe we can show a mechanistic difference when we examine the relationship of these elements to density. We will return to the problem below.

In Figure 2, we compare percentage survival in Hudson's small duiker sample to that of Marean's sheep. In Marean's study, negative values indicate elements not included in the research (no upper limbs were used), while zero values represent elements that were initially present but completely destroyed. Overall, survival is lower in Hudson's study, due in part to some loss during bone recovery (as discussed above). However, the pattern of destruction is quite similar in the two studies, despite differences in carnivores, prey, and fragment collection. Vertebrae survive poorly relative to other post-

*Table 3. Paired rank correlations of skeletal element survival in studies **without** long bone shaft data*

Study and carnivore taxon	A. Wolf	B. Domestic dog	C. Domestic dog	D. Domestic dog	E. Domestic dog	F. Wolf
B. Domestic dog	0.737 (.001)					
C. Domestic dog	0.632 (.001)	0.819 (.001)				
D. Domestic dog	0.618 (.002)	0.714 (.001)	0.783 (.001)			
E. Domestic dog	0.408 (.033)	0.694 (.001)	0.672 (.002)	0.620 (.003)		
F. Wolf	0.498 (.008)	0.659 (.001)	0.633 (.001)	0.795 (.001)	0.681 (.001)	
G. Fox	*0.246 (.138)*	0.673 (.001)	0.794 (.001)	0.496 (.010)	0.675 (.001)	*0.330 (.057)*

Correlation coefficient and p value (in parentheses) are given for paired samples. Insignificant results are indicated in italics. A. Binford (1981: 211-213, Table 5.01, total wolf kills). B. Binford and Bertram (1977: 101, Table 3.5, winter sample). C. Binford and Bertram (1977: 101, Table 3.5, summer sample). D. Binford and Bertram (1977: 81, Table 3.2, record B). E. Brain (1967: 109, Table 3). F. Klippel et al. (1987: 158, Table 1). G. Stallibrass (1984: Figure 1).

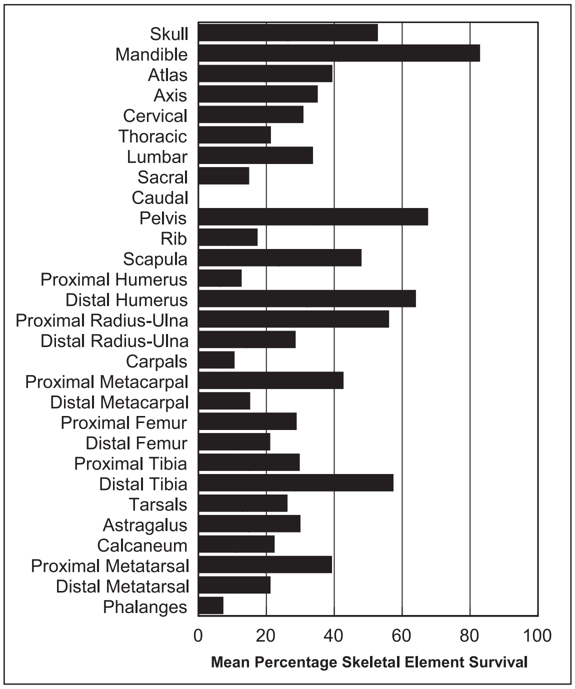

*Figure 1. Mean percentage skeletal element survival from studies that **did not** report long bone shaft survival (see Table 2).*

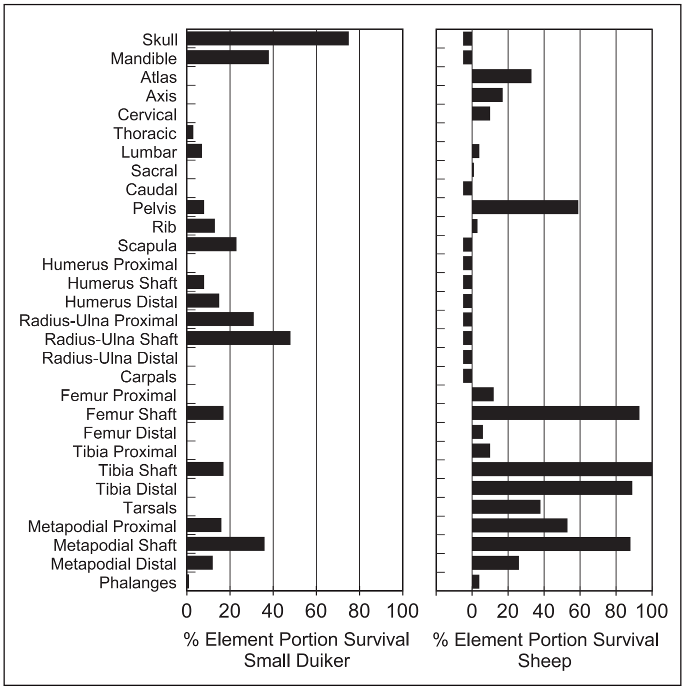

Figure 2. Percentage element survival from two studies that report long bone shaft survival. Small duiker sample is from Hudson (1993: 316, Table 17.4). Sheep sample is from Marean's hyena feeding experiment (described in Marean and Spencer, 1991). Negative values indicate elements not included in the study. Zero values indicate elements were originally present but completely destroyed.

cranial elements, and limb shafts generally survive well and give the highest MNE per element (with the exception of small duiker humeri). We now turn to the question of why carnivore ravaging has such an unequal effect on different skeletal portions, and thus wreaks havoc with the skeletal element analysis.

BONE DENSITY AS A MEDIATOR OF SKELETAL ELEMENT SURVIVAL

Structural properties have long been recognized as important to bone survival (White, 1953, 1954; Brain, 1969; Binford and Bertram, 1977; Lyman, 1984). The two most important of these properties are bone mineral density and within-bone nutrient distribution—two intimately linked factors. The latter can be determined by observing the distribution of trabecular (grease-bearing) bone, a task that can be accomplished using either comparative or archaeological assemblages. The techniques for estimating bone mineral density are far more complicated, but a consensus is emerging (Lam et al., 2003).

Brain (1967, 1969) made some of the earliest attempts to accurately estimate the structural properties of bone and compare it to skeletal element survival. He used the low-tech, but remarkably effective technique of water displacement to determine "specific gravity" (g/cm^3) in goat bones. Lyman (1984), however, pointed out that this technique tended to measure bulk density rather than true density because it inadequately accounted for pore space, particularly within trabecular bone. Recognizing the importance of developing a reliable, widely reproducible method for measuring density, Lyman (1984) turned to photon densitometry. This technique measures the attenuation of a photon beam as it passes through an object. The greater the mineral content of the object, the greater the attenuation of the beam, resulting in a true measure of bone mineralization. Numerous researchers (Kreutzer, 1992; Stahl, 1999; Pickering and Carlson, 2002) saw the practicality of this approach and began producing density value measurements for various species. However, in order to derive density from the mineralization value, it is necessary to know the area of bone over which the beam has passed—that is, the cross-sectional area. Researchers have measured this cross-sectional area in different ways with varying degrees of accuracy, a fact that has created methodological incompatibilities among studies (Lam et al., 2003).

The problem of inaccurate shape estimation introduces considerable error when calculating the density of long bone shafts, fragments of which are common in the archaeological record. Unlike the trabecular portions of skeletal elements, medullary shafts have a dense area of bone around a large empty canal. If cross-sectional area of the bone is calculated based on the external dimensions of the shaft, the mineral content of the cortex is effectively smeared out over the empty medullary cavity. This

Table 4. Percentage survival of skeletal elements in studies that reported long bone shaft survival

	Hudson's (1993) dog ravaging study		**Marean's hyena feeding experiments***		**All Studies**
	Medium duiker % survival	**Small duiker % survival**	**Original MNE**	**% Survival Sheep**	**Mean % Survival**
Skull	67	75	ni	ni	71
Mandible	50	38	ni	ni	44
Atlas	50	0	6	33	28
Axis	50	0	6	17	22
Cervical	40	0	30	10	17
Thoracic	21	3	18	0	8
Lumbar	15	7	56	4	9
Sacral	33	0	140	1	11
Caudal	0	0	ni	ni	0
Pelvis	40	8	49	59	36
Rib	74	13	36	3	30
Scapula	50	23	ni	ni	37
Humerus Proximal	0	0	ni	ni	0
Humerus Shaft	67	8	ni	ni	38
Humerus Distal	47	15	ni	ni	31
Radius-Ulna Proximal	33	31	ni	ni	32
Radius-Ulna Shaft	17	48	ni	ni	33
Radius-Ulna Distal	0	0	ni	ni	0
Carpals	0	0	ni	ni	0
Femur Proximal	0	0	50	12	4
Femur Shaft	0	17	50	93	37
Femur Distal	0	0	50	6	2
Tibia Proximal	0	0	50	10	4
Tibia Shaft	40	17	50	101	53
Tibia Distal	0	0	50	89	30
Tarsals	3	0	150	38	14
Astragalus	ni	ni	50	36	36
Calcaneum	ni	ni	50	28	28
Metapodial Proximal	18	16	50	53	29
Metapodial Shaft	27	36	50	88	50
Metapodial Distal	0	12	50	26	13
Phalanges	6	1	100	4	4

*Hudson (1993: 316, Table 17.4). *Marean's hyena data (combined hammerstone broken and whole bone feeding experiments) recalculated from original hyena data (experiment details given in Marean and Spencer, 1991). ni = element not included in study.*

Table 5. Paired rank correlations of skeletal element survival in studies **with** long bone shaft data (insignificant results indicated with italics)

Study, carnivore, and carcass type	A. Domestic dog consuming medium duiker	B. Domestic dog consuming small duiker	C. Spotted hyena consuming sheep (broken bone)*
B. Domestic dog consuming small duiker	*.341 (.063)*		
C. Spotted hyena consuming sheep (broken bone)*	*-.170 (.703)*	.500 (.039)	
D. Spotted hyena consuming sheep (whole bone)*	*.182 (.324)*	.758 (.009)	.968 (.001)

A. Hudson (1993: 316, Table 17.4, medium duiker). B. Hudson (1993: 316, Table 17.4, small duiker). C. Marean's hyena study (hammerstone broken feeding experiments)*. D. Marean's hyena study (whole bone feeding experiments)*. *Recalculated from original hyena data (experiment details given in Marean and Spencer, 1991).

calculation significantly underestimates the true density of the shaft. Lam et al. (1998,1999, 2003) proposed computed tomography as an alternative method that would return simultaneous accurate estimates of cross-sectional areas and mineral density. These researchers point out that photon densitometry can provide accurate values for long bone shafts if used in conjunction with a technique that accurately estimates shape (i.e. radiograph or water displacement), but that these have not been widely employed.

Early studies of the effect of density on the SEA

Although earlier researchers had guessed that bone mineral density probably had an effect on representation, Brain was one of the first to discuss (1967) and show (1969) an actual correlation between these values. Lyman (1984, 1985) and Grayson (1989) recognized the serious implications this would have for faunal analysis. They pointed out that density partially correlated with the bone utility indices, making it difficult to determine whether *in situ* destruction or selective transport were responsible for shaping the final element profile. Both researchers thought that the reverse utility curves found at numerous sites were possibly the result of differential preservation rather than human selectivity. Lyman (1991, 1993, 1994) tested this idea by performing correlation tests between his photon densitometry data and element representation in 143 published archaeological assemblages. Of these, 53% had a positive, significant correlation between density and representation. Furthermore, 71% of the sites (n=38) that had a reverse-utility curve also had a correlation with density (Lyman, 1994: 264). Thus, Lyman showed that density-mediated destruction was widespread in the archaeological record, and would severely limit the application of utility indices. If representation was unrelated to density in any given assemblage, Grayson (1989) had suggested the analyst might avoid the difficulty of disentangling selective transport from *in situ* attrition. Unfortunately, Lyman's study showed that this might obtain in less than half of the record. Marean and Frey (1997) showed that the reverse utility curve in the long bone set collapses when shafts are included, and thus argued that non-cortical bone portions drive much of the patterning in the relation between survivorship and density.

Earlier studies of the relationship between density and element representation (Lyman, 1991, 1993, 1994) were based on photon densitometry data without shape correction (Lam et al., 1998). As discussed above, these values significantly underestimate the density of long bone shafts. In addition, the assemblages used in Lyman's literature survey provided minimum number of elements (MNEs) based on long bone end counts, and did not include shaft portions (Lyman, 1993: 326). At that time, few researchers were publishing derived estimates (such as the MNE) for shaft portions of long bones. Actualistic studies in the 1980s (Blumenschine, 1986, 1988) and early 1990s (Marean and Spencer, 1991, Marean et al., 1992) demonstrated that carnivore ravaging (a significant agent of density-mediated destruction) preferentially deletes long bone ends. As a result, MNEs calculated solely on the basis of ends are almost certain to severely underestimate long bone representation. Pickering et al. (2003) demonstrated this bias in both archaeological and ethnographic sites. Thus, Lyman's (1993) study used data that underestimated both long bone representation and the density of long bone shaft portions. It now seems prudent to revisit the relationship between density and skeletal element survival for the following reasons. We now have more accurate density values. We now have several archaeological studies for which shaft portions are included in limb bone MNE estimates (thus, we have more accurate estimates on those skeletal elements). Finally, we now have some data on skeletal element survival (with shaft portions) following carnivore destruction (see above).

A new analysis of the relationship between density and skeletal element survival

Based on a survey of actualistic data, we have thus far established that carnivores systematically damage skeletal elements in a way that is consistent across predator and carcass type—that is, trabecular portions are variably affected by the intensity of ravaging, while certain non-trabecular portions are more consistently preserved. We will now re-test the hypothesis that density moderates this pattern of destruction. If supported, the result would present an equifinality problem for skeletal element analyses. That is, in assemblages impacted by carnivores, the archaeologist would not be able to simply differentiate an element pattern shaped by hominid transport decisions from one shaped by carnivore ravaging.

Density and carnivore ravaging

Our first question here is straightforward, and follows Brain's original (1967, 1969) search for the cause of differential skeletal element survival: is carnivore destruction of skeletal elements mediated by density? In order to develop a reliable model for interpretation, we again turn to the actualistic research to secure the link between agent and taphonomic pattern. Using the datasets listed in Table 2, we test the hypothesis that there is a significant (p ≤ .05) positive correlation between density and percentage survival. Because these studies quantify long bone portions on the basis of ends, we are strictly testing the effect of density on cancellous bone portions. The advantage of this is that we can make inferences about the role density has played in earlier zooarchaeological reports that lack shafts in the analysis.

Because the studies listed in Table 2 used bovids or cervids as prey carcasses, we compare representation to Lam et al.'s (1999) density values for wildebeest (*Connochaetes taurinus*) and reindeer (*Rangifer tarandus*), but not for *Equus*. We are primarily interested here in inter-bone survival, so we use only one density value (the highest) per element. This also precludes any bias that might have resulted from the variability in the number of scan sites and landmarks per element.

Table 6. Correlation between percentage element survival and bone mineral density (BMD) (insignificant results indicated with italics)

6.1. Studies *without* long bone shaft data	**R**	**p**
A. Wolf consuming caribou	0.313	*0.064*
B. Dog consuming sheep	0.384	0.024
C. Dog consuming sheep	0.408	0.012
D. Dog consuming reindeer	*0.270*	*0.101*
E. Dog consuming goat	0.578	0.006
F. Wolf consuming whitetail deer	0.363	0.026
G. Fox consuming sheep	*0.186*	*0.189*
H. Spotted hyena consuming size 3 bovid	0.346	0.045

A. Binford (1981: 211-213, Table 5.01, total wolf kills). B. Binford and Bertram (1977: 101, Table 3.5, winter sample). C. Binford and Bertram (1977: 101, Table 3.5, summer sample). D. Binford and Bertram (1977: 81, Table 3.2, record B). E. Brain (1967: 109, Table 3). F. Klippel et al. (1987: 158, Table 1). G. Stallibrass (1984: Figure 1). H. Richardson (1980: 116-117, Figures 8 and 10, spotted hyena data). Rank order from Richardson's study is extrapolated from published bar graphs (no quantitative data provided). Bone mineral density values per element from Lam et al. (1999: Table 1, wildebeest column).

	Wildebeest BMD		**Reindeer BMD**	
6.2. Studies *with* long bone shaft data	**R**	**p**	**R**	**p**
A. Dog consuming medium duiker	*0.314*	*0.080*	*0.254*	*0.116*
B. Dog consuming small duiker	0.790	0.001	0.806	0.001
C. Spotted hyena consuming sheep (broken bone)*	0.712	0.009	0.816	0.002
D. Spotted hyena consuming sheep (whole bone)*	0.674	0.001	0.680	0.003

A. Hudson (1993: 316, Table 17.4, medium duiker) . B. Hudson (1993: 316, Table 17.4, small duiker). C. Marean's hyena study (hammerstone broken feeding experiments). D. Marean's hyena study (whole bone feeding experiments)*. *Recalculated from original hyena data (experiment details given in Marean and Spencer, 1991). Bone mineral density values per element from Lam et al. (1999: Table 1).*

Table 6.1 shows the results: the null hypothesis can be rejected in 5 of the 8 samples, and in the 3 that do not meet the .05 limit, the probability of attaining that correlation through a random process is less than 20%. These results support our hypothesis that carnivore destruction, whenever it occurs, has a significant density-dependent effect on representation.

Ideally, we should be able to test whether the hypothesis holds for the overall skeletal element profile—not just the cancellous portions. Unfortunately, there are only two published actualistic datasets that incorporate shafts into the quantification of percentage survival: Hudson's (1993) Aka research and Marean's hyena colony study (Table 4). In Hudson's (1993) data, density and percentage survival correlate insignificantly among medium duikers, but are very highly correlated among small duikers (Table 6.2). Marean's data (Table 6.2) show a significant correlation between density and survival, comparable to that seen in Hudson's small duikers. As discussed above, element representation correlates well between Marean's study and the small duikers, while the medium duikers appear to be taphonomically distinct. These combined results strongly suggest that the medium duiker component was subjected to relatively less ravaging than the other two datasets.

The critical difference between these actualistic studies (Tables 2 and 4) and archaeological assemblages is, of course, time. A host of taphonomic processes contributes to the formation of an archaeofaunal assemblage (including variable transport, and biogenic and geologic destruction), and actualistic models are not meant to replicate the full range of possible events. Instead, the purpose of these experiments is to develop reliable inferences about parts of the system. The above results demonstrate that carnivores can significantly and systematically modify skeletal element representation even when they are not the primary agents of accumulation. As noted above, this creates a problem of equifinality for the archaeologist.

High and low survival elements

Our review of the record shows that carnivores, when presented with either fleshed or defleshed skeletal remains, will consume and fragment some skeletal portions in preference to others. Our understanding of this process, combined with our understanding of bone density, led us to propose a general model of skeletal element survival in archaeological sites (Marean and Cleghorn, 2003). To explain that model, we will distinguish between nutritive and non-nutritive processes of bone destruction (Blumenschine, 1986, 1988; Capaldo, 1997).

Nutritive processes of destruction are those resulting from attempts to extract nutrition, particularly from bone portions where nutrients and bone are not easily separated. Nutrients include marrow within the cortical portions of long bones and mandibles, grease stored in cancellous bone, and brain matter. Importantly, marrow is separable from cortical bone before consumption, and carnivores typically crack, spit out, ignore, or avoid the surrounding cortical bone portions (Bunn and Kroll, 1986; Blumenschine, 1988; Binford et al., 1988; Marean and Spencer, 1991; Blumenschine and Marean, 1993). Bone grease is not mechanically separable from cancellous bone by non-human animals. As our review above documents, carnivores adapt to this problem by chewing and swallowing the cancellous portions and allowing the digestive tract to render out the grease. To survive these nutritive processes of destruction and thus be countable by the zooarchaeologist, a bone must have a substantial portion of thick cortical bone free of cancellous bone (Figure 3). Any bone portion with associated cancellous bone is more likely to be destroyed or deleted by carnivores scavenging from human meals, and our review above documents that this process is geographically and environmentally widespread. It is now safe to say that nutritive attrition can be considered a law of site formation process that must guide all zooarchaeological analyses where carnivore involvement has been verified.

Non-nutritive bone destruction includes those processes that are not the result of animals attempting to derive nutrients. These include trampling, sediment compaction, chemical leaching, burning, and any other chemical or mechanical process that destroys bone. It is widely believed that these processes are density mediat-

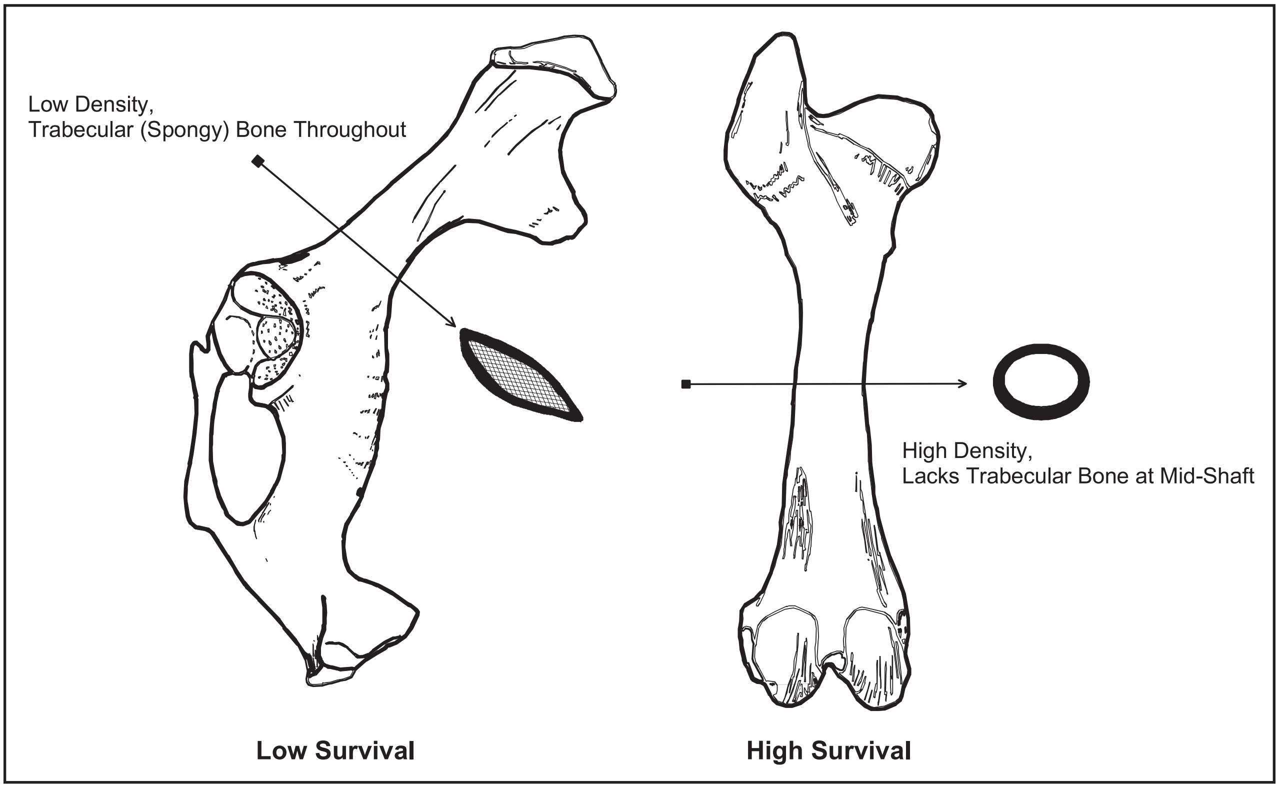

Figure 3. Trabecular content distinction between high and low survival elements. Although the innominate may sometimes survive well (as noted in the text), this survival is highly variable (as seen in Table 2 and Figure 2).

ed, meaning that the potential for non-nutritive destruction correlates inversely with bone mineral density (Lyman, 1984, 1985; Grayson, 1989; Lyman, 1992). There is still little experimental research documenting this relationship. If true, however, then there are two important propositions that arise. First, skeletal elements that lack at least some reasonably dense portion will have a lower frequency of survival (in an identifiable state). Bone density studies have shown that the densest parts of bovid and cervid skeletons are the thick cortical portions of long bones, the petrosal, and the teeth (Lyman, 1984; Kreutzer, 1992; Lam et al., 1998). Second, the only skeletal elements that will record relative abundances that reflect their original discard abundance are those that have similar high-density cortical portions free of cancellous bone.

We believe these nutritive and non-nutritive processes of bone destruction divide the skeleton into ***high survival*** and ***low survival*** elements. High survival elements are those that accurately represent their frequency (relative to each other) as it was before carnivore ravaging and other density-mediated destruction. These bones may be consistently useful when investigating hominid behavior through skeletal element analysis. The following three criteria distinguish the high survival set:

1. Each skeletal element has a substantial portion of thick cortical bone, lacking cancellous bone (Figure 3).
2. The density throughout the cortical portion is high and relatively homogeneous among the elements chosen for analysis.
3. The cortical portion is identifiable to skeletal element, and zooarchaeologists can identify and quantify it accurately.

High survival elements include all of the limb bones (excluding the carpals and the phalanges of size 1 and 2 animals), mandibles (which have dense cortical bone and an open medullary cavity similar to long bones), and crania (due to the presence of teeth and the petrosal).

By contrast, the relative representation of low survival elements will reflect their ability to survive the variety of processes that affect the assemblage after transport and discard. These bones include all vertebrae, ribs, pelves, scapulae (which have thick cortical bone but may be difficult to identify and quantify when fragmented), tarsals, carpals, and the phalanges of size 1 and 2 animals since these tend to be swallowed by carnivores (Marean, 1991; see our discussion above and Figure 1). These elements may be useful for evaluating the level of destruction to which the assemblage has been subjected, but their variation may also be the result of differential transport in an archaeological assemblage. The difficulty in distinguishing between the effects of transport and *in situ* destruction make these elements unreliable indicators of either taphonomy or behavior.

It is important to emphasize that the high and low survival elements are not distinguished based on an arbitrary bisection of the density scale. In fact, the primary evidence suggesting the presence of only two real survival sets comes from the data on nutrient-based destruction by carnivores, as discussed above. However, when comparing the density values of the two sets using Lam et al.'s (1999) shape-corrected data, two important differences emerge. First, the highest value per element is generally greater in the high survival set. The exception is the ulna. In bovids and cervids, however, the ulna has a quantifiable landmark (the mid-shaft radius articulation) that often fuses with the cortical portion of the radius and is then preserved along with the radius shaft. The second and more important difference is that there is much less variation in bone mineral density within the high survival set when compared to either the low survival set (Table 8) or to the full spectrum of bone density.

We can now examine the usefulness of the high-low survival dichotomy by testing the following three hypotheses:

Table 7. Results of correlations between percent survival and bone mineral density (BMD) by high and low survival sets (insignificant results indicated with italics)

Hudson's (1993) dog ravaging study	**Wildebeest BMD**		**Reindeer BMD**	
	R	**p**	**R**	**p**
medium duiker				
High Survival	*0.120*	*0.380*	*0.140*	*0.340*
Low Survival	*0.330*	*0.100*	*0.190*	*0.240*
small duiker				
High Survival	*0.078*	*0.428*	*-0.109*	*0.589*
Low Survival	*0.393*	*0.076*	0.492	0.048

Bone mineral density values per element from Lam et al. (1999: Table 1).

Table 8. Summary statistics for bone mineral density values

	High Survival			**Low Survival**		
	Mean	**sd**	**CV**	**CV**	**sd**	**Mean**
Zebra	1.05	0.15	14%	32%	0.20	0.64
Wildebeest	1.11	0.11	10%	30%	0.21	0.70
Reindeer	1.10	0.12	11%	27%	0.18	0.68

Highest bone mineral density values per element from Lam et al. (1999: Table 1). sd = standard deviation, CV = coefficient of variation.

Table 9. Archaeofaunal assemblages used in the evaluation of the high and low element survival sets

Site	**Taxa**	**Site Type**	**Location**	**Zooarchaeologist**
Ain Dara	Size 1 & 2 (mostly Sheep & Goat)	Iron Age Tell	Syria	C. Frey
Ain Dara	Bovid/Cervid Size 3 & 4	Iron Age Tell	Syria	C. Frey
Mezmaiskaya, MP levels	Size 2 (mostly Sheep & Goat)	Mousterian Cave	Caucasus Mtns., Russia	N. Cleghorn
Mezmaiskaya, MP levels	Bovid/Cervid Size 3 & 4	Mousterian Cave	Caucasus Mtns., Russia	N. Cleghorn
Die Kelders I	Bovid Size 2	MSA Cave	South Africa	C. Marean & Students
Die Kelders I	Bovid Size 3 & 4	MSA Cave	South Africa	C. Marean & Students
Kunji	Size 1 & 2 (mostly Sheep & Goat)	Mousterian Cave	Zagros Mtns, Iran	C. Marean & Students
Kobeh	Size 1 & 2 (mostly Sheep & Goat)	Mousterian Cave	Zagros Mtns, Iran	C. Marean & Students
Porc Epic	Bovid Size 2	MSA Cave	Ethiopia	Z. Assefa
Agate Basin, Folsom Comp.	Bison	Open-air Kill	Plains, USA	M. Hill
Agate Basin, Folsom Comp.	Pronghorn	Open-air Kill	Plains, USA	M. Hill
Agate Basin, Hell Gap Comp.	Bison	Open-air Kill	Plains, USA	M. Hill
Agate Basin, Agate Basin Comp.	Bison	Open-air Kill	Plains, USA	M. Hill
Clary Ranch	Bison	Open-air Kill	Plains, USA	M. Hill

MP = Middle Paleolithic, MSA = Middle Stone Age

H1 there is a significant ($p \leq .05$) positive correlation between density and representation in the low survival set.

H2 this correlation, while not significant, is greater in the low than in the high survival set.

H3 there is a significant positive correlation between density and representation among the high survival set.

Of these hypotheses, H1 and H2 are mutually exclusive but H3 may co-occur with H1. A high correlation in both high and low survival sets indicates a degree of density-mediated attrition high enough to differentiate even elements that have relatively similar density values. In this case, we can still examine the relative correlations between high and low survival sets.

Ideally, we would like to first test these hypotheses using a large sample of actualistic data. Unfortunately, only two published studies, Marean and Spencer (1991) and Hudson (1993) so far meet the standards of MNE quantification required (i.e., they include long bone shafts). Marean's hyena research is precluded from this analysis by the limited range of carcass elements studied. We compared percentage survival of small and medium duikers (Hudson, 1993) to both wildebeest and reindeer density values (Lam et al., 1999) using a rank correlation test as described above.

The results (Table 7) were not significant. Within the medium duiker set, the correlation is slightly higher within the low survival set, a result supporting our secondary hypothesis (H2). The small duiker results are mixed. This test of this particular dataset suffers from the possible disadvantage of comparing percentage survival with the density values of much larger taxa. Our analysis of the limited actualistic data is therefore inconclusive. A re-analysis of the original collections of Binford and Bertram (1977), Binford (1978), Brain (1969), Stallibrass (1984), and Snyder (Klippel et al., 1987; Snyder, 1988), including a recalculation of percentage survival with limb bone shafts, could usefully expand this investigation.

Table 10. Correlations between element representation and bone mineral density (BMD)

10.1 Correlations using minimum number of element (MNE) representation

	Highest BMD				Representative BMD			
	High Survival		Low Survival		High Survival		Low Survival	
Archaeofaunal Assemblage	**R**	**p**	**R**	**p**	**R**	**p**	**R**	**p**
Ain Dara size 1 & 2	-0.145	0.659	0.647	0.005	0.000	0.499	0.663	0.009
Ain Dara size 3 & 4	0.033	0.479	0.631	0.009	0.620	0.058	0.803	0.006
Kobeh size 1 & 2	0.018	0.474	0.625	0.004	0.656	0.047	0.529	0.027
Kunji size 1 & 2	0.018	0.470	0.538	0.022	-0.171	0.685	0.243	0.184
Mezmaiskaya MP size 2	-0.127	0.620	0.526	0.021	-0.356	0.752	0.366	0.142
Mezmaiskaya MP size 3 & 4	0.052	0.439	0.500	0.034	-0.342	0.794	0.358	0.091
Porc Epic size 2	-0.018	0.503	0.499	0.020	-0.151	0.649	0.499	0.020
Agate Basin bison	0.431	0.119	0.575	0.017	-0.131	0.573	0.410	0.069
Clary Ranch bison	-0.519	0.905	0.501	0.030	-0.305	0.706	0.345	0.112
Hell Gap bison	-0.430	0.845	0.362	0.101	0.368	0.202	0.427	0.082
Agate Basin, Folsom component bison	-0.142	0.614	0.379	0.103	-0.084	0.586	-0.062	0.572
Agate Basin, Folsom component pronghorn	0.050	0.041	0.464	0.047	0.384	0.181	0.290	0.186
Die Kelders I size 2	0.824	0.012	0.316	0.109	0.678	0.035	-0.102	0.649
Die Kelders I size 3 & 4	0.013	0.501	0.286	0.140	0.021	0.461	0.177	0.278

Bone mineral density values are from wildebeest (Lam et al., 1999, Table 1).

10.2 Correlations using minimum animal unit (MAU) representation

	Highest BMD				Representative BMD			
	High Survival		Low Survival		High Survival		Low Survival	
Archaeofaunal Assemblage	**R**	**p**	**R**	**p**	**R**	**p**	**R**	**p**
Ain Dara size 1 & 2	-0.178	0.667	0.770	0.001	-0.071	0.552	0.631	0.018
Ain Dara size 3 & 4	0.033	0.479	0.636	0.012	0.620	0.058	0.512	0.073
Kobeh size 1 & 2	0.018	0.474	0.847	0.001	0.656	0.047	0.742	0.003
Kunji size 1 & 2	-0.021	0.522	0.545	0.019	-0.239	0.750	0.418	0.065
Mezmaiskaya MP size 2	-0.127	0.620	0.510	0.032	-0.356	0.752	0.175	0.312
Mezmaiskaya MP size 3 & 4	-0.053	0.571	0.431	0.049	-0.379	0.794	0.386	0.109
Porc Epic size 2	-0.018	0.503	0.423	0.056	-0.151	0.649	0.423	0.056
Agate Basin bison	0.431	0.119	0.504	0.038	-0.131	0.573	0.713	0.003
Clary Ranch bison	-0.519	0.905	0.394	0.073	-0.305	0.706	0.255	0.183
Hell Gap bison	-0.430	0.845	0.415	0.074	0.368	0.202	0.597	0.022
Agate Basin, Folsom component bison	0.050	0.419	0.285	0.147	-0.084	0.586	0.231	0.263
Agate Basin, Folsom component pronghorn	0.606	0.041	0.015	0.476	0.384	0.181	0.112	0.378
Die Kelders I size 2	0.824	0.012	0.372	0.098	0.678	0.035	0.306	0.145
Die Kelders I size 3 & 4	0.036	0.452	0.444	0.052	-0.013	0.529	0.384	0.107

Bone mineral density values are from wildebeest (Lam et al., 1999, Table 1).

Table 11. Summary of hypothesis support among archaeofaunal components

	Highest Density				**Representative Density**			
	Wildebeest BMD		**Reindeer BMD**		**Wildebeest BMD**		**Reindeer BMD**	
Archaeofaunal Assemblage	**MNE**	**MAU**	**MNE**	**MAU**	**MNE**	**MAU**	**MNE**	**MAU**
Ain Dara size 1 & 2	H1	H1	H1	H1	H1	H1	H1	H2
Ain Dara size 3 & 4	H1	H1	H1	H1	H1	-	(H1)/H3	H3
Kobeh size 1 & 2	H1	H1	H1	H1	H1/H3	H1/H3	H3	H1/H3
Kunji size 1 & 2	H1	H1	H1	H1	H2	H2	H2	H1
Mezmaiskaya MP size 2	H1	H1	H1	H1	H2	H2	-	-
Mezmaiskaya MP size 3 & 4	H1	H1	H1	H1	H2	H2	H2	H1
Porc Epic size 2	H1	H2	H1	H2	H1	H2	H1	H2
Agate Basin bison	H1	H1	H2	H2	H2	H1	H2	H2
Clary Ranch bison	H1	H2	H2	H2	H2	H2	H2	H2
Hell Gap bison	H2	H2	H2	H2	H2	H1	H2	H2
Agate Basin, Folsom component bison	H2	H2	-	-	-	H2	-	H2
Agate Basin, Folsom component pronghorn	(H1)/H3	H3	H3	H3	-	-	-	-
Die Kelders I size 2	H3	H3	H3	H3	H3	H3	H3	H3
Die Kelders I size 3 & 4	H2	H2	H2	H1	H2	H2	H2	H1

H1: there is a significant ($p \leq .05$) positive correlation between density and representation in the low survival set. H2: this correlation, while not significant, is greater in the low than in the high survival set. H3: there is a significant positive correlation between density and representation among the high survival set. Parentheses indicate the relationship is weaker in the low survival set than in the high survival set.

Table 12. Percentage support for each hypothesis and the high-low survival model

	Highest BMD				**Representative BMD**			
	Wildebeest		**Reindeer**		**Wildebeest**		**Reindeer**	
	MNE	**MAU**	**MNE**	**MAU**	**MNE**	**MAU**	**MNE**	**MAU**
H1	64%	50%	50%	43%	29%	29%	14%	29%
H2	21%	36%	29%	29%	50%	50%	43%	43%
H3	14%	14%	14%	14%	14%	14%	21%	21%

Combined positive (H1 and H2) versus negative (H3) support for the high-low survival model:

	Highest BMD				**Representative BMD**			
	Wildebeest		**Reindeer**		**Wildebeest**		**Reindeer**	
	MNE	**MAU**	**MNE**	**MAU**	**MNE**	**MAU**	**MNE**	**MAU**
H1 and H2	86%	86%	79%	71%	79%	79%	57%	71%
H3	14%	14%	14%	14 %	14%	14%	21%	21%

H1: there is a significant ($p \leq .05$) positive correlation between density and representation in the low survival set. H2: this correlation, while not significant, is greater in the low than in the high survival set. H3: there is a significant positive correlation between density and representation among the high survival set.

Density and the final shape of the skeletal element profile

We can test the power of the high and low survival model within the archaeological record. This may be an appropriate test, since archaeological assemblages have typically undergone both nutritive and post-nutritive processes of destruction. However, this is admittedly a comparative taphonomy approach, resorted to because of the scarcity of appropriate actualistic datasets. We therefore view our results as a guide for future research, and note that the consistency and strength of these results make our conclusions even more compelling.

Table 9 lists the 14 archaeological samples used to test the relationship between density and the final representation of skeletal elements. These samples fulfill two necessary criteria: 1) the analysts present MNE estimates on both shaft and end portions for the limb bones, and 2) we are certain that the procedure used to estimate MNEs provides an adequate estimate for both the shaft and end portions. Our analysis of these assemblages tested whether human, carnivore, and other depositional and post-depositional processes acting on an unknown number of skeletal elements could produce the hypothetical patterns (H1, H2, and H3) as described above. To insure that quantification and data formats minimally affected our test, we tested correlations using several different parameters. For representation, we used both the minimum number of elements (MNE) and the minimum animal units (MAU). Focusing our analyses on the combined bovid/cervid portion of the test assemblages (segregating size 1 and 2 from size 3 and 4 animals), we again used Lam et al's (1999: table 1) wildebeest and reindeer bone mineral density (BMD) values. We used "BMD_2" values (as defined in Lam et al., 1999) whenever given, as these have the most accurate area calculation for portions with a medullary cavity. Finally, we ran our correlation tests using two different selection criteria for density. In the first (*highest BMD*), we paired the highest representation of a bone with the highest density value for that element. In this case, we considered that the highest density on a bone represented that element's best chance at entering the archaeological record. In the second comparison (*representative BMD*), we examined each element to find the portion that gave the highest representation, and then compared this to the specific density value from that scan site. Because we were primarily interested in inter-bone survival, we used only one density value per element. This also precluded any bias that might have resulted from variability in the number of scan sites and landmarks per element. Table 10 lists the results of rank correlation tests, and Table 11 provides a summary of hypothesis support.

Table 13. Hypothesis support and assemblage size

Archaeofaunal Assemblage	**H1**	**H2**	**H3**	**Maximum MAU**
Porc Epic size 2	√	√		59.4
Kobeh size 1 & 2	√	√	√	57.0
Kunji size 1 & 2	√	√		45.5
Agate Basin bison	√	√		39.0
Ain Dara, size 1 & 2	√	√		31.5
Mezmaiskaya MP size 2	√	√		25.6
Clary Ranch bison	√	√		20.0
Die Kelders I size 3 & 4	√	√		13.5
Mezmaiskaya MP size 3 & 4	√	√		13.5
Hell Gap bison	√	√		11.0
Agate Basin, Folsom comp. bison		√		7.0
Ain Dara size 3 & 4	√	√	√	7.0
Die Kelders I size 2			√	5.0
Agate Basin, Folsom comp. pronghorn			√	3.0

H1: there is a significant ($p \le .05$) positive correlation between density and representation in the low survival set. H2: this correlation, while not significant, is greater in the low than in the high survival set. H3: there is a significant positive correlation between density and representation among the high survival set.

Eleven out of the 14 archaeological components we examined supported our primary hypothesis (H1) in at least one (but usually more) of the correlation tests (Figures 4 and 5). Among these assemblages, almost all the tests that did not support H1 supported H2. An additional assemblage (Agate Basin, Main Folsom Component, pronghorn) supported H1 only in a test where H3 was also supported. Another assemblage (Agate Basin, Main Folsom Component, bison) provided some support for only H2. Finally, Die Kelders Cave I (body size 2) did not support either of our main hypotheses, but in fact supported only H3. These last three assemblages, however, appear to be the exceptions to a pattern of significant support for our main hypothesis within the archaeological datasets (Table 11). In seven tests, we found both H1 and H3 to be true. In five of those, the correlation was still much stronger in the low survival set. In the other two, it was not, and we did not count these as supportive.

Table 12 compiles the percentages of support for each hypothesis. This gives us a way to grossly assess the various types of comparisons we made, and show the overall strength of our results when approached with different datasets. Our main hypothesis, H1, was best supported in tests where we compared representation to the maximum density of a given element. Using the best represented density lessened the significance, but did not alter the main trend. Element representation in the low

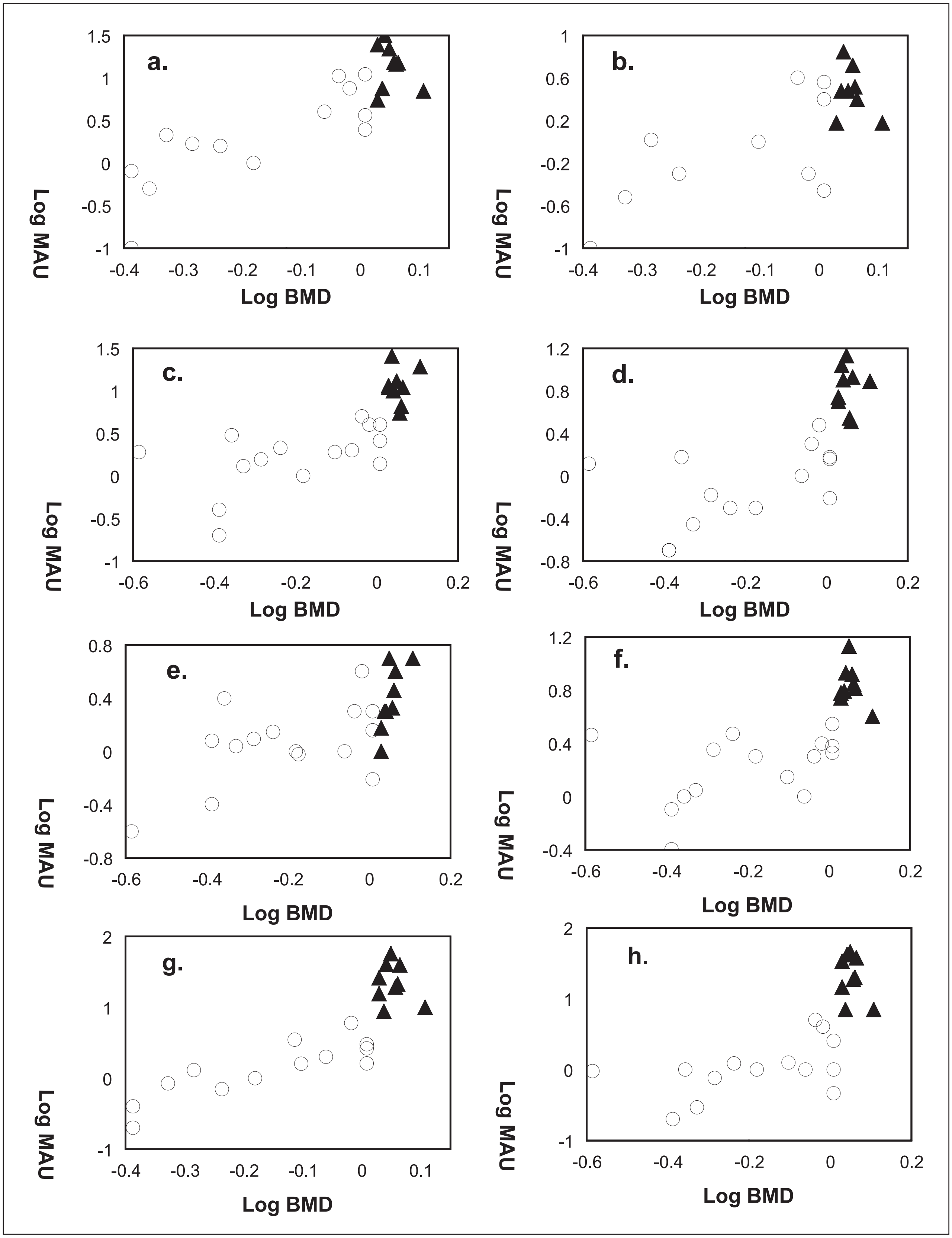

Figure 4. The relationship between bone mineral density (BMD) and minimum animal unit (MAU) within the archaeological components discussed in the text. High survival elements are shown with triangles (▲), low survival elements are shown with open circles (○). BMD values are from Lam and colleagues (1999, Table 1, wildebeest column). a) Ain Dara, Size Class 1-2. b) Ain Dara, Size Class 3-4. c) Mezmaiskaya, Size Class 2. d) Mezmaiskaya, Size Class 3-4. e) Die Kelders I, Size Class 1-2. f) Die Kelders I, Size Class 3-4. g) Kobeh, Size Class 1-2. h) Kunji, Size Class 1-2.

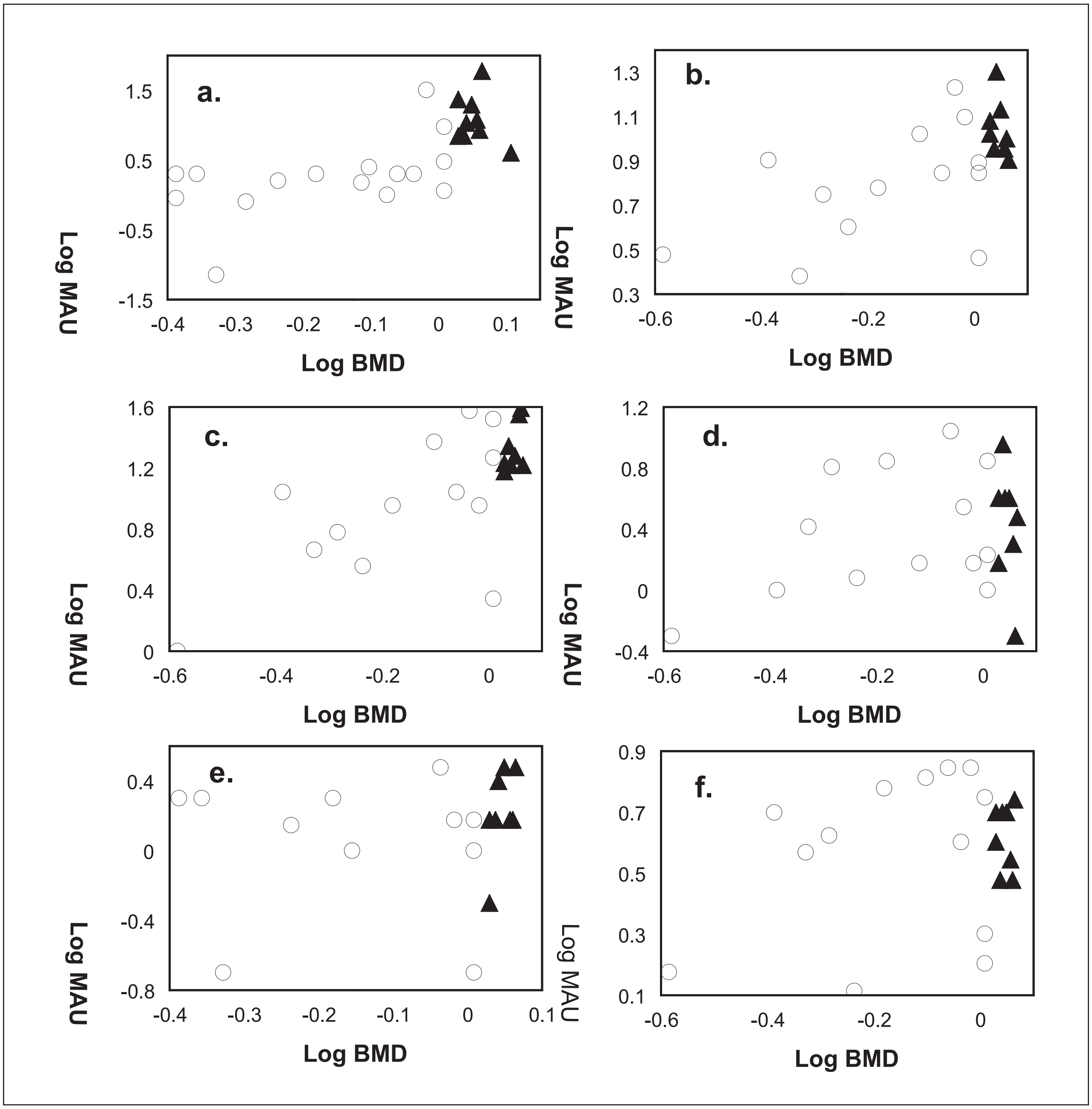

Figure 5. The relationship between bone mineral density (BMD) and minimum animal unit (MAU) within the archaeological components discussed in the text. High survival elements are shown with triangles (▲), low survival elements shown with open circles (○). BMD values are from Lam et al. (1999, Table 1, wildebeest column). a) Porc Epic, size 2 (from Assefa 2003). b) Clary Ranch, Size Class 4. c) Agate Basin, Size Class 4. d) Hell Gap, Size Class 4. e) Agate Basin, Main Folsom Component, Size Class 4 (bison). f) Agate Basin, Main Folsom Component, (pronghorn). MAU data for graphs b through f from Hill (2001).

survival set was still positively correlated with density to a much greater extent than in the high survival set.

The choice between the two ways of comparing density (highest per bone or best represented) did not have much of an effect on the rate of our third hypothesis. This is not surprising, since the highest MNE often coincided with the densest scan site per element.

Finally, we return to the question of why our model fits some sites but not others. In Table 13, we show the assemblages sorted by size (maximum MAU) and with the hypotheses they support. Once the assemblages get above a certain size (in this case an MAU of 11), both of our main hypotheses are supported in all assemblages. Lack of support for our model is concentrated in the smaller samples, and could therefore represent a simple sampling error.

Discussion and Conclusions

About 40 years ago Brain initiated a field of research into actualistic taphonomy and stimulated two parallel research trajectories that regularly intersected: 1) studies of the impact of multiple carnivore agents on skeletal element survival, and 2) studies of bone density with the goal of understanding the mechanical causes for differential bone survival. In reviewing several of these studies of carnivore ravaging, we found investigations set in the following contexts: naturally occurring dens, kill sites with complete prey carcasses, and areas of human refuse involving various states of butchery (from whole defleshed to hammerstone-broken bone). These studies vary widely in usefulness, as can be expected of research in its formative stage. Our review highlights some areas where taphonomists need to revisit old issues.

We have learned some valuable things from studies of dens, but the research return has been rather modest due to highly variable, and sometimes inadequate, methods of assemblage collection and description. The existence of species-specific skeletal element patterns in dens, whether resulting from transport or destruction, is still unresolved. We need new studies with comprehensive fragment collection (i.e., excavation), capturing even very small fragments. We also need studies that apply zooarchaeological standards to quantification methods in order to estimate skeletal element abundance using all bone portions. However, unless the agents of collection are monitored, the researcher will never fully understand the system parameters. For this reason, we remain skeptical that den studies can be used to usefully interpret skeletal element profiles in archaeological contexts.

The results from observations of carcass destruction have been more rewarding. Our review of the literature, of both qualitative observations and quantitative presentations, shows that there is a regular intra- and inter-element pattern of carnivore destruction of skeletal elements. Carnivores of all types preferentially destroy the cancellous portions of bones, though the extent of destruction varies as a function of several factors (e.g., carnivore's bone-crushing abilities, hunger, carnivore group size). Even small domestic dogs follow this generalization. This means that portions of hard cortical bone will survive better when lacking any attached cancellous bone. The implication is that zooarchaeological methods must be able to accurately estimate skeletal element abundance from both types of bone portions. Cortical portions will provide the most accurate estimates of skeletal element abundance as it was before carnivore ravaging, while the relative representation of cortical to non-cortical portions may provide a measure of the intensity of carnivore destruction. It would be useful in future studies to document this pattern in more detail.

These findings have implications for relative skeletal element survival. Our analysis of the percentage survival data from the studies lacking shaft portion estimates closely resembled the pattern Brain (1967) originally described. Head parts, metapodials, and distal humeri survive best. Pelves, scapulae, and the denser long bone ends survive moderately well. Ribs and vertebrae rarely survive. Small bones like phalanges, carpals, and tarsals survive poorly. The survival rate of this sample correlates tightly with density, though it is likely that variation in survival not explained by density is a function of the size and greasiness of bones and bone portions, and the agent of destruction.

When isolated shaft fragments are included in estimates of abundance, long bones and other elements with dense, cortical portions lacking trabeculae generally increase in relative abundance (a function of resistance to carnivore attack and a low nutrient value). This results in a more accurate estimate of element survival. It would therefore be extremely useful to re-study the samples in Table 2 and include shafts in the analyses.

We conducted an updated analysis of the relationship between bone density and skeletal element survival in archaeological faunal assemblages. This was done to overcome two deficiencies in prior analyses (the lack of limb bone shaft portions in quantification and the use of bone density estimates that were not shape-corrected) and to test the explanatory power of our high and low survival set model. We found that the standard analytical practice of setting up regression or rank correlation tests between density and skeletal element abundance using the entire skeleton masks the divergent patterning in these two sets of elements. Within the archaeological assemblages, we found that element representation in the low survival set is largely dictated by the density gradient. This is not the case in the high survival set. Thus, the destruction of cancellous portions of the skeleton is highly variable and subject to a variety of factors related to the identity and condition of the ravaging carnivore. By contrast, high survival portions tend to survive well regardless of these factors.

We conclude that a skeletal element analysis of archaeofaunal assemblages including the low survival set will not generally aid our interpretation of human behavior. Further, the low and high survival sets cannot be compared in order to characterize transport or butchery decisions. The good news is that the high survival set may yet provide answers to some questions of human behavior, with some important caveats. We reiterate that if MNEs are calculated based only on long bone ends or if density values are not shape-corrected, then real distinctions between the high and low survival sets will be lost.

Our conclusions regarding the high and low survival dichotomy, however, derive largely from a comparative taphonomic analysis. As we have noted above, this approach is best used as a means to develop hypotheses to be further tested by actualistic research. Although the published data re-confirm the general relationship between carnivore ravaging and element attrition, a significant expansion of actualistic research is needed to appreciate the subtler (and perhaps more constructive) patterns within this relationship.

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