

Mammoth (*Mammuthus* spp.) and American mastodont (*Mammut americanum*) bonesites: what do the differences mean?

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Based on dental anatomy, bone geochemistry, pollen analyses, and paleoecological studies of fossil bonesites, it seems clear that mastodonts did segregate from mammoths in habitat choices and diets. But based on analogical studies of modern elephant (*Loxodonta africana*) biology, behavior, and bonesites, there is no strong reason to believe that mastodont social behavior differed from that of mammoths in significant ways. The distribution of modern elephant bonesites reflects both habitat features (such as the distribution of water and forage) as well as features of elephant behavior. Mastodont and mammoth bonesites also probably reflect the same kinds of features. Allowing for differences in habitats between the North American Pleistocene contexts and the recent African contexts, it is possible to use observations and principles derived from the modern elephant studies to reconstruct important characteristics of extinct mammoth and mastodont life. The death processes affecting mastodonts were not necessarily distinct from the processes affecting mammoths.

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INTRODUCTION

American 'elephants': their biological and archeological importance

Several different species of mammoth and mastodont lived in North America during the last part of the late Wisconsin glaciation. The taxon *Mammuthus* had arrived in North America around two million years ago, crossing the Bering land connection from Asia. No mammoths dispersed farther south than central America. The late Wisconsin mammoth taxa were *Mammuthus primigenius* in the northern part of the continent, and *M. imperator*, *M. columbi*, and *M. jeffersoni* to

the south. The earliest mastodonts may have been present in North America some time after 15 million years ago. Adaptive radiations and other migrations from Eurasia resulted in related taxa dispersed throughout North, Central, and South America by the late Pliocene (Simpson & de Paula Couto 1957). By the late Wisconsin, only one taxon of mastodont (*Mammut americanum*) was found north of Mexico, although earlier in the Pleistocene at least two mastodont-like gomphotheres (*Stegomastodon* and *Cuvieronius*) co-existed with *Mammut* in the southern part of the United States (Kurtén & Anderson 1980). The mammutids and mam-

moths are not especially closely related, with the common ancestor shared about 20 million years ago (Lowenstein & Shoshani 1996; Saunders 1996). Both lineages arose originally in Africa, and dispersed through the Old and New Worlds. Yet while only distant relatives, both creatures were elephant-like in many ways, and both *Mammuthus* and *Mammuthus* were present in the ranges first occupied by the earliest human colonizers of the Americas.

The contemporaneity of the extinct American proboscideans and human beings was strongly doubted until archeological discoveries of the 1920s, which demonstrated that people and Pleistocene fauna did indeed see each other face to face. The Dent mammoth, excavated in the early 1930s, was the first clear example of mammoth hunting or scavenging by late Pleistocene people, but it was the finds near Clovis, New Mexico, whose name eventually became connected with the human-mammoth associations. Over the past 65 years, several discoveries of stone tools and mammoth skeletons have been made, and a few of mastodont remains with possible artifacts in association. While other animal taxa are known from the late Pleistocene sites that contain undoubted artifacts, it is by far mammoth that appears to be the preferred prey. Scientific studies of the biology and behavior of mammoths and mastodonts are not especially abundant in the paleontological or archeological literature, but over the last century valuable work has been done in taxonomy (for example, Graham 1986; Maglio 1973; Osborn 1936; 1942; numerous papers in Shoshani & Tassy 1996), taphonomy (for example, Saunders 1977a; Saunders & Daeschler 1994), and other aspects of mastodont and mammoth life. However, a relatively full picture of the day to day life of these taxa is not yet available, especially as regards their social behavior and ecology. Some of the probable differences and similarities between mammutids and mammoths can be surmised, based on anatomy, distribution, dietary remains, pollen

associations, and so forth. In this paper we begin by examining fossil bone deposits that have yielded mastodont and mammoth remains, and we make behavioral, ecological, and biological comparisons between the taxa, based on the characteristics of the bone assemblages.

Sampling the Late Pleistocene population of *Mammuthus* and *Mammuthus* in North America

Hundreds of finds of proboscidean fossil are known from the Americas. To make the sampling manageable, we have drawn examples from an extensive literature search and also from compilations such as FAUNMAP. Thus, our sample is one of practicality and convenience. Its make-up depends on the availability of the literature and the willingness of scholars to report the finds, and especially on the skills of scholars in securing necessary funding or assistance for salvaging information from discoveries that for the most part were not well funded or expected. Perhaps a critically important factor in the widespread availability of information is any site's potential evidence about human activities in the past - in other words, those discoveries of mastodont or mammoth bones that plausibly may be interpreted as prehistoric kills or sites where human beings left evidence of their behavior have greater chances for their reports to be published even more widely and discussed. Hence, those sites that contain bone modifications interpreted as, for example, butcher marks - the proboscidean sites with both paleontological and archeological interest - tend to become much more visible in the literature than the sites described in purely paleontological terms.

There are 107 sites in our selected sample (see Appendix) with an estimated total of 377 animals in them. These numbers may be roughly 10% of the total numbers known in the scientific literature (see Agenbroad 1984, Shoshani 1990). The total number of mastodont sites in our sample is 54, containing 137 individuals, and the total of mammoth sites is

53, containing 240 individuals. Of the 107 sites, 73 contained only solitary individuals; 45 (62%) of these were mastodont and 28 (38%) were mammoth. Table 1 shows the proportions of these 73 sites for which the sex of the animal has been firmly determined or suggested. In both the mammoth and masto-

dont subsamples, there are few sites with large numbers of individuals. Table 2 shows the numbers of sites with different MNI measurements.

Of the total 107 sites, 44 contained broken or flaked, 'butcher-marked', or burned bones. This proportion may or may not be represen-

Table 1 Sites at which the sexes of animals have been identified.

SITE	TAXON	MNI	AGE/SEX	DATE estimate or midpoint
Alma, MI	mastodont	1	adult female	
Babine Lake, BC	mammoth	1	adult male(?)	34,000
Boaz, WI	mastodont	1	adult male	12,000-10,000
Burning Tree, MI	mastodont	1	adult male	11,660; 11,450 (gut contents?)
Cole, MI	mastodont	1	adult male(?)	
Cooperton, OK	mammoth	1	young adult male	20,400 - 17,575
Dansville, MI	mastodont	1	young adult female	
Denver, IN	mastodont	1	adult male	
Domebo, OK	mammoth	1	young adult female	11,490-10,810
Duewall-Newberry, TX	mammoth	1	young adult male	12,000-10,000
Elkhart, MI	mastodont	1	young adult male	
Escapule, AZ	mammoth	1	adult male	12,000-10,000
Farview, MI	mastodont	1	young adult male	
Grandville, MI	mastodont	1	adult male	
Hajny, OK	mammoth	2	adult males	34-21,500 (also 165-140,000)
Heisler, MI	mastodont	1	adolescent male	11,770
Hot Springs, SD	mammoth	50+	males, mixed ages	26,000
Huntington Canyon, UT	mammoth	1	adult male	11,500 - 9,500
Inglewood, MD	mammoth	1	adolescent male	20,070
Johnson, MI	mastodont	1	adult male	
Kuhl, MI	mastodont	1	middle-aged male	
Manis, WA	mastodont	2?	old adult male and subadult	12,000; 11,850
Murray Springs, AZ	mammoth	4	adult females(?)	11,190-10,710
New Hudson, MI	mastodont	1	female(?)	
Owosso, MI	mastodont	1	adult female	
Parker, MI	mastodont	1	adult male	
Pleasant Lake, MI	mastodont	1	middle-aged male	12,845; 10,395
Powers, MI	mastodont	1	adult female	
Quagaman, MI	mastodont	1	adult male	
Rawlins (U.P.), WY	mammoth	1	adult male	11,280
Russell Farm I, MI	mastodont	1	adult male	
Russell Farm II, MI	mastodont	1	female	
Sakstrup, MI	mastodont	1	middle-aged female	
Sheathelm, MI	mastodont	1	young adult female	
Shelton, MI	mastodont	1	adolescent female	
Taylor, MI	mastodont	1	male	
Valley of Mexico, Mex	mammoth	2	adult male (?)	16,000; 11,003; 9,670
Van Sickle, MI	mastodont	1	adult male	
Warren (NY)	mastodont	1	adult male	
Wattles, MI	mastodont	1	young male	

Table 2. Number of sites with different MNI measurements (N=32). (nota bene, this is a sampling and not necessarily a truly representative one from all sites known in the New World)

MNI range	No. Of <i>Mammuthus</i> Sites	No. Of <i>Mammut</i> Sites
1	28	45
2 - 5	14	3
6 - 10	6	2
over 10	5	3

tative of the much greater number of proboscidean fossil sites ever discovered and reported in North America. Over the last two decades such marks on bone surfaces have been interpreted more often as traces of human actions, and as a result many sites containing incised and fragmented elements create sensations whenever reported, especially those sites that date to unexpectedly early time periods or those sites that otherwise lack clear evidence for human activity, such as flaked stone tools. The existence of these sites in our sample reflects their high profile in the literature, although we do not know if this high proportion is fairly representative. A sustained search for details about the thousands of fossil mastodont and mammoth finds may discover how often green-bone breaks and sharply incised 'cutmarks' or other marks occurred on the discoveries that were made in the days before attention was drawn to the potential meaning of such modifications. Of the sites in the sample that have bone modifications, at least 30 (68%) are late glacial in age (younger than 13,000 radiocarbon years old). Table 3 shows the sites containing modified bones. Dates were either estimates based on chronostratigraphic data, or were determined radiometrically (or in one case by the use of luminescence dating). Individual females (either adult or subadult) are relatively rare in sites of both taxa, but in the mastodont sample females are apparently less rare: there are half as many occurrences of individual female mastodonts as there are of individual males. However, we note that relatively few finds of the hundreds of mastodonts and mammoths were analyzed for sex and life-age information, except by certain

researchers (for example, see Fisher 1984, 1987, 1996; Lister & Agenbroad 1994). There are no clear and direct correlations of chronostratigraphic or chronometric dates with animal life-ages or sex. Mixed groups or solitary individuals of either sex have been found that date to several different time intervals. Once again we must point out that our sample may not be a representative one, and that such correlations indeed may become apparent as a result of a much more conscientious and thorough analysis of the thousands of finds recorded over the last two centuries. The subsample of finds with ages and sexes identified is disappointingly small. Many finds may never be amenable to analysis of age and sex, simply because the discoveries were too fragmentary or incomplete. Of the finds where sex has been assigned to individual animals, further analysis may be prudent. The large-sized individuals of *M. columbi*, *M. imperator*, or *M. primigenius* often have been identified as males, without reference to support provided by a cross-check of epiphyseal fusion and tooth progression, which are known to vary by sex, or an examination of incremental growth tissue in the tusks.

EVIDENCE ABOUT ECOLOGY, DIET, BEHAVIOR

The evidence for dietary and habitat segregation

There is ample evidence from North American fossil proboscidean finds that *Mammut* and *Mammuthus* segregated in terms of habitat and diet. Dreimanis (1967) found that Ontario mastodonts seemed to have preferred spruce forests or woodlands, especially those with poor drainage. These same habitats yield a much poorer record of mammoths. In Shoshani's (1990) 'census' of *Mammut* finds reported from all of North America, the distribution of the total number of 1,473 individuals clearly shows most sites to be in the eastern United States, with noticeable clustering in the Great Lakes region and Florida. While mammoths also were found in

Table 3 Sites in the sample that contained modified bones interpreted as artifactual

SITE	TAXON	EVIDENCE
Boaz, WV	mammoth	Broken bones
Burning Tree, MI	mastodont	Butcher marks; Cached bones?
Case High School, WI	mammoth	Butcher marks;
Cooperton, OK	mammoth	Broken bones, transported boulders
Crappie Hole, NE	mammoth	Broken bones
Deerfield, WI	mastodont	Butcher marks
Dent, CO	mammoth	Clovis points; butcher marks; season-of-death
Duewall-Newberry, TX	mammoth	Flaked bones
Fenske, WI	mammoth	Butcher marks
Grundel, MO	mastodont	Broken bones
Haley, IN	mammoth	Broken bones
Hebior, WI	mammoth	Lithics; Butcher marks
Heisler, MI	mastodont	Butcher marks; Season-of-death
Hot Springs, SD	mammoth	Flaked bones
Huntington Canyon, UT	mammoth	Lithics? Cutmarks(?)
Inglewood, MD	mammoth	Broken bones
Ivory Pond, MS	mastodont	Cutmarks; toothmarks
Koehn-Schneider, KS	mammoth	Butcher marks; Bone distribution
La Sena, NE	mammoth	Flaked bones
Lake Mills, WI	mammoth	Butcher marks
Lamb Spring, CO	mammoth	Flaked bones
Lange-Ferguson, SD	mammoth	Flaked bones
Lindsay, MT	mammoth	Cutmarks; Transported rocks; Stacking
Lubbock Lake, TX	mammoth	Butcher marks
Marion County, OH	mammoth	Broken bones
Miami, MO	mastodont	Piled ribs; Boiled bone scraps? Cut tusks?
Miami, TX	mammoth	Fluted points and lithics; cutmarks?
Monte Verde, Chile	mastodont	Flaked bones; bone tools; burned bones
Moon, PA	mammoth	Netstones; Butcher marks; Bone distrib.
Mud Lake, WI	mammoth	Butcher marks
Oak Creek, NE	mammoth	Broken bones
Oakes, WI	mammoth	Butcher marks
Old Crow, Yukon	mammoth	Flaked bones
Owl Cave, ID	mammoth	Flaked bones
Petronila Creek, TX	mammoth	Cutmarks; Flaked mammoth teeth
Pleasant Lake, MI	mastodont	Butcher marks; cut & burned bones; bone tools
Rappuhn, MI	mastodont	Pole platform? Burnt and cut bones
Saltville, VA	mastodont	Flaked bones; Transported rocks; lithics
Saskatoon, Sask.	mammoth	Broken bones; cut marks; lithics
Schaeffer, WI	mammoth	Lithics; butcher marks; piled bones
Selby and Dutton, CO	mammoth	Flaked bones; 7 tiny lithic flakes
Sloth Hole, FL	mastodont	Ivory "foreshaft;" cut/chopped bone
Stolle, NM	mammoth	Broken bones
Tocuila, Mex	mammoth	Flaked bones

these same subregions, the evidence about the mastodonts shows that the genus *Mammut* without doubt 'preferred' the east-ern USA, where wooded habitats were more extensive and thicker than in other parts of the continent. Saunders (1996) described the distribution of *Mammut* as effectively continent-wide, but unmistakably the most dense in the Great Lakes area of the eastern USA. The implication is that specific kinds of wooded habitats made up the mastodont's preferred range. Johnson & Kost (1988) reported that most mastodonts found in Kansas were from the eastern half of the state, where woods were denser. McAndrews & Jackson (1988) described far more mastodont finds than mammoths in southern Ontario, a mostly wooded part of the province. The evidence is very strong that mastodonts predominated in woodlands and forests; mammoths, on the other hand, probably survived well in some wooded habitats but seem to have preferred the more open grassland or steppe-like regions of North America. Judging from tooth morphology (specifically the enamel configurations) *Mammut* was well adapted to browsing diets, and *Mammuthus* was efficiently adapted to a grazing diet. Fisher (1996), based on studies of isotopic bone chemistry, concluded that *Mammut* had a mixed browsing and grazing diet, but with at least seasonally apparent preferences for browse. Agenbroad (1984) and associates (Agenbroad & Mead 1987; Agenbroad *et al.* 1984; Mead *et al.* 1986) analyzed *Mammuthus* habitats and the evidence about diets, and determined that grasses were the preferred food of mammoths, although browsing also was done. These and other studies (for example, Drumm 1963; King & Saunders 1984; Koch 1991) show that *Mammut* and *Mammuthus* were segregated in terms of preferred habitats and diets, although overlapping ranges were probable in certain regions and at certain times during the late Pleistocene.

The evidence about social differences and similarities

Other characteristics of the two proboscidean taxa may have been distinct, as well. Many finds of *Mammut* and *Mammuthus* have been made of single individuals whose bones were discovered in waterlain sediments. It would be useful to determine whether there are relatively more finds of single *Mammut* skeletons than of *Mammuthus*. It also would be useful to determine if the age profiles are different between 'typical' mass sites of mastodont and mammoth. The depositional environments do not appear to be greatly different in mammoth and mastodont sites. If some differences do exist in the proportions of single animals found dead for each genus, compared to the total population of dead animals, what reasons could be found to explain them? Are there ecological and behavioral distinctions between *Mammut* and *Mammuthus* that would have led to different proportions of ages and sexes in mass sites, or different kinds of sites where the deaths occurred? We attempt to provide answers to these questions in the rest of this paper.

WHAT ARE THE BEHAVIORAL AND ECOLOGICAL DIFFERENCES BETWEEN MASTODONTS AND MAMMOTHS?

Bone input and deposition in general

Some general predictions about rates and density of bone input can be made, based on actualistic models and observations of both high-input and low-density field situations (see Haynes 1991). These models are derived from studies of natural river courses, seepage springs and ephemeral water sources, and rockshelters in south-central Africa. Along rivers, input of bones from natural deaths may be steady, unspectacular, incremental, continuously variable, and somewhat scattered through space, occurring in different densities in riverine woods, on streambanks, atop channel bars, within channels, or on floodplains. Occasionally the input is punctu-

ated by a mass death event, or by floods scouring surficial bones or depositing transported bones. At points where deposition occurs (such as seepage springs, pans, ponds, and caves or rockshelters), input also may be steady and incremental, but with episodic punctuation when deposition changes. For example, within rockshelters, single-grain wall breakdown may change to slab and roof-fall input, increasing the burial potential of surficial bones. Or bone input rates may change, as when mass death events occur where previously only rare individual deaths took place, or denning-site bone input is replaced by predation-event input. We see no compelling reasons to expect depositional input processes to have been significantly different during the late Pleistocene. The important generalization to note is that incremental, low-density bone input may be ‘punctuated’ by short-term or extended, higher-density input, especially around water sources. Another point that should be made here is that not all elephants die at water sources, but bone input rates are greatest at water sources, contributing to a higher density of bones in sediments and also to a higher probability that bones will be preserved through burial.

Minimum numbers of individuals (MNI)

They died in heaps and were buried in heaps.

Daniel Defoe

(describing plague victims in 17th Century England)

The variable MNI figures of the multi-animal assemblages do not correlate clearly with chronometric age, although the very largest assemblages (referring to MNI) are pre-late Glacial. However, in terms of numbers of such sites, the late Glacial examples predominate. Of the 16 sites with MNI greater than 5, 11 (69%) are late Glacial in age. Mammoth sites containing more than one animal are more numerous than mastodont sites in the sample, which includes the best known sites in the Americas. Especially numerous are mammoth small-group sites (n=14), each

containing from two to five individuals. The mammoth subsample contains almost twice the number of mastodont ‘crowd’ sites (sites with MNI above 5) (mammoth n = 11; mastodont n = 5). A possible pattern that may need explaining is the larger number of mammoth sites with high MNI. If this sort of apparent disproportion is not merely a sampling error, and far more mammoth sites actually do have a higher MNI, the pattern may reflect either a behavioral or biological difference between the genera, or, alternatively, may result from other factors such as habitat differences, taphonomy, or simply biased reporting. Certain researchers (such as, for example, Fisher 1996) conscientiously publish the results of rigorous studies of individual finds in specific geographic regions of the USA, such as the Great Lakes, where mastodonts are much more numerous than mammoths, therefore increasing the total of well-published mastodont sites whose MNI equals 1. Although single-mammoth sites have been published widely in paleontological journals or local periodicals, their visibility in the literature may be relatively low by comparison with the well-studied single-mastodont sites. Nonetheless, it may be a true pattern of the mastodont fossil record that individuals died alone more often than in groups. Also it may be a pattern that mammoths died more often in relatively larger numbers at specific sites than mastodonts did. As a possible explanation, we suggest that the distribution of water sources in prehistory had a measurable effect on the numbers of proboscidean skeletons found together, and the high proportion of single-mastodont sites may be (at least partly) a reflection of the greater abundance of water that existed in mastodont ranges. More will be said about this suggestion in the section that deals with bonesite settings (see below).

Age (or mortality) profiles

Until about 30 years ago, mortality profiles were rare to nonexistent in the literature about fossil proboscidean sites, mainly due to

the fact that no really useful method of determining the life-age of mammoths or mastodonts was available until Laws (1966) published a graphical and descriptive study of molariform tooth progression and wear in African elephants. C.V. Haynes (1966) and J. Saunders (1977b, 1980, 1992) saw the advantages of applying the Laws age-determination criteria to mastodonts and mammoths in North America, and other researchers followed suit (Graham 1986; G. Haynes 1985) as they realized how valuable this sort of analysis can be. Unfortunately, many discoveries of mammoths and mastodonts were made before the ageing criteria were known, and experienced workers have never properly aged thousands of individual proboscideans. On the other hand, quite a few well-documented finds have been studied over the last decades, and there is a growing body of information about the ages of mammoths and mastodonts that died in the late Wisconsin glacial interval.

The sample used in this paper includes all the larger assemblages of proboscidean bones, and a large number of smaller ones. The African elephant mortality profiles described in G. Haynes (1991) seem adequate to characterize the fossil multi-animal assemblages. The four types of death profile described are Type A, a stair-step shaped profile in which progressively decreasing proportions of successively older age categories are present; Type B, a U-shaped profile containing a noticeably large proportion of very young animals, but very few prime-age and middle-aged adults, and a relatively large proportion of old adults; Type C, in which few very young and old individuals are found, but relatively many prime-aged individuals; and Type D, which includes any shape other than these three (Fig. 1).

Type A profiles are seen in some noncultural assemblages such as Waco and Boney Springs. This type is the expected outcome of nonselective mortality in stable populations. Type B profiles are seen in larger assemblages such as Lehner and Dent, which are

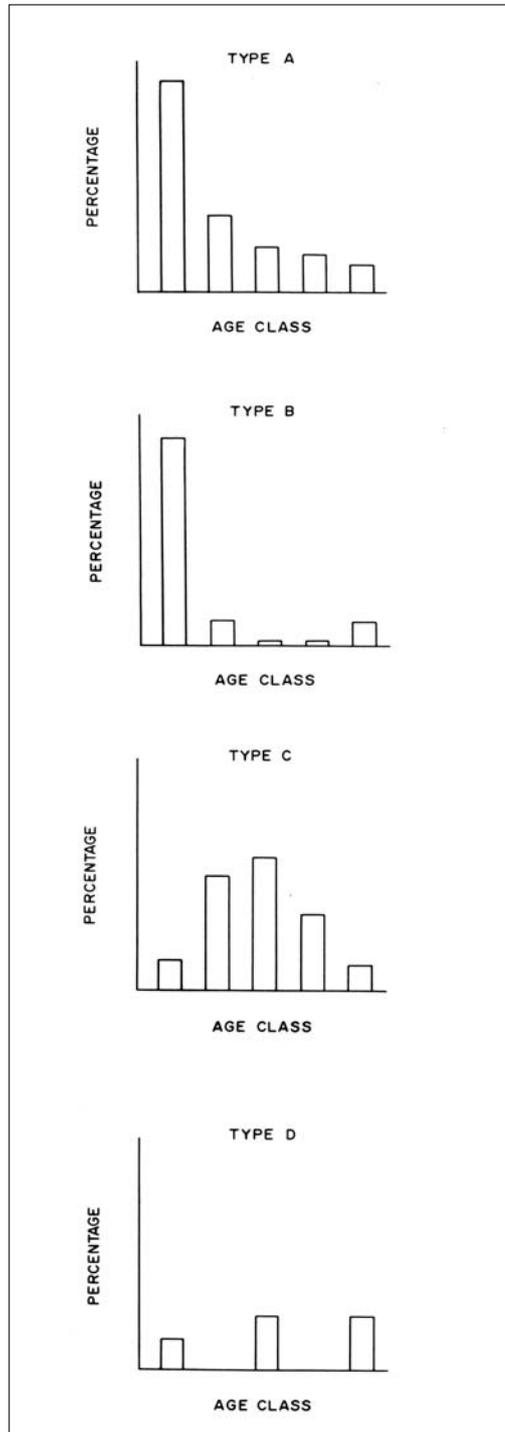


Figure 1 Shapes of patterned mortality (age) profiles seen in recent elephant-bone assemblages and fossil mammoth and mastodont assemblages.

Clovis cultural associations. This type of profile is the predicted outcome of selective mortality events. Type C profiles are not common, but an example can be seen in the Mammoth Site of Hot Springs. It is possible that this type is the result of a different kind of selective mortality, such as that affecting only one sex in populations.

Bone assemblage characteristics

I: cultural associations

It was once thought that Pleistocene foragers in North America hunted or scavenged mammoths, at least to some extent, but much more rarely - if ever - hunted mastodonts. No unambiguous associations of mastodont bones and cultural remains were known. However, over the past 10 years a number of mastodont sites have been announced as showing such associations. For example, at Kimmswick, Missouri, excavations revealed the presence of fluted projectile points bedded with *Mammuth* bones (Graham *et al.* 1981). In Michigan, D. Fisher (for example, 1984, 1987, 1996) published a series of papers describing mastodont bones that bear 'butcher marks', although stone tools that made at least some of the marks were themselves not found at the sites. Laub and colleagues (for example, Laub & Haynes 1998; Laub 1990, 1995) described fluted points, possible bone and stone tools, and modified mastodont bones from the Hiscock site in New York state. These discoveries may indicate that fluted-point-makers chose to hunt or scavenge mastodonts much more frequently than previously thought, perhaps even as frequently in the eastern woodlands as mammoths were hunted or scavenged in western plains and steppes.

However, the evidence in favor of mastodont-hunting and butchering is not always clear and undoubted. For example, bone scratches and incisions that are called 'butchery marking' often are proposed as proof that mastodont sites contain evidence of human behavior. The butcher marks may be scrapes and incisions on articular surfaces,

or on bone shafts. These sorts of marks must be very carefully evaluated. The bones from many fossil sites were preserved in excellent condition in waterlogged or anaerobic sediments, which means that postdepositional modifications to bone surfaces would not be always distinct from predepositional modifications. We suggest that in many cases the bone marking may have occurred while bones were still buried. The 20,000 year old Inglewood mammoth site in Maryland (G. Haynes 1991:199, 235, 236f) yielded bones with green-bone fractures and flaked cortical surfaces, the result of heavy equipment distorting the bones while they were still embedded within a clay that had preserved them very well for 20 millennia. The heavy equipment not only caused the fragmentation to happen underground, but also created gouges and incisions in bone surfaces, probably as bones grated against other bones, or clasts in the sediments (sand-sized particles, mollusc shells, bone fragments, etc.) were forced against the bone surfaces. The incised surfaces were stained an identical color to the unmodified surfaces, thus making the recency of the scratching impossible to discern.

Marks on well-preserved fossil mastodont and mammoth bones - marks interpreted as wedging or butchering traces - in fact may have been made after the skeletons were defleshed, and it is quite possible that they were made on the bones sometime immediately prior to the discovery of sites or the bones' recovery. The main implication of this empirical observation is that some mastodont sites (and some mammoth sites, too) do not contain evidence about human hunting or scavenging behavior. It follows that the number of mammoth sites showing unambiguous association with humans - stone projectile points and tools bedded within bonebeds - is still much larger than the number of mastodont sites. Therefore, one obvious difference between the two proboscidean taxa, based on the firmest evidence at hand, is that mammoths were much preferred for hunting or scavenging.

Bone assemblage characteristics 2: element proportions

Many bonesite discoveries were not excavated carefully, due to time and funding restraints. The very well studied and excavated multi-animal examples - such as Boney Springs and Colby - show variability in element representation (which is a statistic determined by comparing each skeletal element's occurrence against a predicted number based on the site's greatest MNI). Some sites may have suffered bone subtraction by weathering, erosion, scavenging, or other processes; some sites may be very completely preserved. But the similarities between some sites such as Boney Springs and the well-known actualistic sites of modern African elephants (described in Conybeare & Haynes 1984; G. Haynes 1988, 1991) perhaps indicate that the fossil and the modern sites may share taphonomic pathways. In other words, the subtractive processes of carnivore scavenging, bone weathering, etc., are similar, and the bone susceptibility and resistance to decay are also similar. Sites from which the element representation numbers are different may have undergone unusual subtractive processes, such as human selectivity in removing or destroying elements, or erosional events not repeated at other sites.

At this time, until detailed and comparable studies are carried out, it can be proposed only that different fossil sites may have different taphonomic histories, just as modern elephant bonesites may, and that these fossil-site histories are similar to those of the modern sites.

Bonesite settings

*Say, you are in the country; in some high land of lakes.
Take almost any path you please, and ten to one it carries
you down in a dale, and leaves you there by a pool...*

Herman Melville (1948 [orig. 1851]: 2),

Moby Dick, or The Whale

The greater number of fossil proboscidean sites in North America is located in former

watercourses or waterholes. Likewise, the overwhelming majority of modern large-mammal bonesites are also located in settings where there is or has been water. However, we repeat that not all elephants die at or in water sources, and elephant carcasses or skeletons may be found in upland areas. In this section of the paper we draw upon data and generalizations derived from a comparative examination of the fossil proboscidean site settings and the settings of recent large mammal deaths studied in our own actualistic research. The actualistic work behind the propositions in this paper was carried out (by GH) over the last 30 years in North America, Australia, and Africa. The fieldwork in North America and Australia involved studies of horses, camels, bison, moose, deer, and numerous other wild-roaming mammals in roadless or protected parks, game reserves, or national forests and public lands. In Africa the fieldwork has involved two decades of examinations of many different settings where elephant bones were found, all of them located in strictly protected national parks or game reserves, where all human activity is closely monitored and the animals live and die completely in the wild. The settings ranged from large 'water hole locales' (containing several ponds or seepage springs in extensive spatial areas up to 3 km² in size), to long-term but spatially limited single water sources such as basin depressions that ranged in size up to one hectare, to seasonal or ephemeral ponds or pools ranging up to 10 m² in size, formed temporarily in streamways.

We do not discuss the upland skeletal sites we have examined away from water sources, but we do intend in the future to publish descriptions and generalizations about them. A number of the large water hole locales have been described before (G. Haynes 1985, 1987, 1988, 1991, 1995), as have some smaller water source areas. The attention of archeologists directed at these papers has been focused on the larger bone accumulations in elephant die-off sites, where dozens of elephants died and left behind many hun-

dreds of bones. Unfortunately, the smaller sites - where bones of single elephants were found - were not as widely described, and it has been mistakenly assumed that bone-modifying processes and events in single-animal sites (either fossil or modern) must be very different from the bone-modifying events in larger accumulations. Hall (1997), for example, quoted one archeologist as stating that the sites he analyzed (yielding mammoth bones with green-bone breaks and flakes removed from some specimens) are different from the sites examined in Africa (G. Haynes 1991), because the African sites contained bones of "many animals scattered near African watering holes where elephants and other animals congregate, whereas each of [the mammoth sites in question] consists of a single large male mammoth." In other words, the premise is that the African studies are hardly relevant, in this way of looking at the literature, because certain characteristics of the modern sites do not closely enough match the fossil sites' characteristics.

What needs to be emphasized here is that all elephant bonesites studied in Africa, numbering in the dozens, whether they contained one animal's skeleton or hundreds of animals', and regardless of whether they were located at water sources or in upland settings, showed the same ranges of bone modifications. When we make this statement we are not saying that every site showed the same modifications. We are saying that the same range of modifications can appear in any kind of site, large or small, mass or serial, transported or *in situ*, as long as the same natural agents are able to be present at any site.

Mastodont finds are noted from prehistoric water sources such as glacial lakes, kettle-hole ponds, stream ways, salt licks, and so forth. Mammoth finds are noted just as often from water sources, too. Clearly, these are the sorts of sedimentary situations that allow bones to be preserved. But the existence of proboscidean bones in association with water is not exclusively the result of taphonomic biasing; it must be just as clearly a reflection

of the tendency of proboscideans to keep close to water, and to die at water sources as often as not, to judge from observations of the living elephants. There does not seem to be a clear behavioral or ecological difference between the associations of mammoth bones with ancient water loci and the association of mastodont bones with water.

Within the general category of water-association, we see several possible patterns of variability. These patterns are in numbers of animals that may have died at the same time (the range is many, a few, or one individual); extent of bone scattering and modifications possibly due to trampling and other non-cultural processes (the range is very scattered, a mixing of scattered skeletons and tightly clustered skeletons, or very tightly clustered skeletons only); ages of dead animals represented at the sites; and so on. It should be understood that variability is expected in bonesites. Patterning across the variables is well documented, but the fact remains that variability is also observable in the modern elephant-bone sites. In the sections of this paper to follow, we discuss some of the variability that perhaps has been underemphasized in the African studies, and propose some 'meaning' that can be assigned to different types of variability.

REFERENTIAL MODELS: ELEPHANT SITE VARIABILITY, AND THE MEANINGS TO BE FOUND

Die-off age profile variability

In the African elephant localities with larger and permanent water sources, differences in the patterns of mortality profiles resulting from starvation and drought have been well documented. When a serious drought (characterized by at least 20% reduced rainfall) follows good years, there is generally a high proportion of very young animals and older females in death assemblages. Under conditions of chronic or frequently recurring droughts (for example, reduced rainfall lasting 1-3 years and occurring about every 4-8

years), there are proportionately more young adults, and a reduced input of immature animals dying in and around water sources; and under conditions of sustained drought (rainfall reduced at least 10% below the long-term average, occurring in as many years as average rainfall amounts occur), the main skeletal input at water sources consists of adults, especially the so-called prime age individuals. These animals are generally the last to die during serious environmental stress.

The density of water source distribution is extremely important in explaining mortality profiles. Where the water sources are close together and relatively abundant, only single individuals are expected to be found dead at each source. Where the sources are scattered and rare, several deaths are possible at each one if the water was not rapidly used up or evaporated. At smaller water sources, or seasonally dry ones that are not widely separated, single animals may be found dead. Only individuals die at the smaller sources, rather than masses or groups of elephants, before the water is fully exhausted. Variability in age and sex at different water sources is common.

Feeding habits

During changing environmental conditions, elephants change their feeding behavior. Their preferred or optimized diets consist of forage obtained during nomadic grazing with the addition regularly of seasonal browsing; however, under stress conditions such as during drought intervals interrupting normal rainfall years, diets may be heavier in browse, and feeding movements are extremely nomadic when compared to the normal pattern. Elephants in droughts endure more frequent and longer periods of fasting while they move longer distances more often, seeking water. The greatest degree of changed habits is seen following chronic droughts, when elephants noticeably reduce their range movements, as they attempt to stick closely to known permanent or semi-permanent water sources rather than to food patches. Elephants

will often re-sample the nearby food patches, sometimes exhausting all the available forage, but do not habitually attempt to make long-distance treks when drought conditions are well established.

Site variability 1: who dies? how many die?

At slightly scattered but relatively abundant water sources (those located within a day's travel apart), normally the deaths recorded at each water source are adults who died alone; the bones from each death are generally scattered in and around the water sources. When serious drought follows after good rainfall years, the larger or more reliable water sources contain many skeletons (Fig. 2), mostly from young animals. The skeletons are mainly scattered and incomplete, although a few may be relatively more complete. This is a result of lighter scavenging by carnivores that find the carcasses to be so abundant. The skeletons of some old adults may be distributed amongst the younger animals', and their bones are also mostly scattered, although the occasional complete skeletons may be found, too (Fig. 3). Under conditions of chronic drought, water sources see bursts of skeletal input, coming from individuals that range in age from half-grown to adults. The skeletons may occur in tight clusters; the bones will show mixed stages of weathering.

Site variability 2: taphonomic trajectory of bones

During 'normal years' when rainfall is within 10% of long-term average, and water sources are not unusually distributed in elephant ranges, small proportions of many differently weathered partial skeletons of adults may characterize bone deposits at water sources. However, other possibilities have been observed, such as water sources that contain a few skeletal elements from several individuals, or water sources that contain only one or a few complete skeleton(s). When droughts are repeated or chronic, small parts of many skeletons of adults and subadults may be



Figure 2 Bones from numerous individual elephants that died during a two-year drought in northwestern Zimbabwe, scattered around a perennial water source called Nehimba. [Photo: G. Haynes]



Figure 3 A nearly complete carcass of a mature female elephant lying next to the bone scatter from another mature female that died the previous year. The view is of a perennial water source called Shabi Shabi, in Hwange National Park, Zimbabwe. [Photo: G. Haynes]

found in the longest-lasting water sources, as well as nearly complete skeletons of adults and subadults.

Site variability 3: bone breakage, pseudo-artifactual modifications

In water sources that last beyond a single season, normal years (or decades, or centuries) see an input of well preserved bone specimens, plus a proportion of broken and rounded specimens. If water sources are single season or ephemeral, fewer bones will be present, and bones from different years may be differentially preserved. When drought is chronic or repeated, trample-broken and sharply incised (trample-marked) elements will be intermixed with well preserved examples.

INTERPRETING MAMMOTH AND MASTODONT BEHAVIORAL AND ECOLOGICAL DIFFERENCES, BASED ON BONESITES

We believe that the social groupings of both *Mammuthus* and *Mammut* were similar. The basic social group was probably mother and young, and individual mothers preferred to associate with other adult females and young in bonded groupings called mixed herds. Sexually mature males did not stay in mixed herds, but instead lived on their own or in fluid-membership male bond groupings. Sexually active females and males sought each other out for mating, but there was probably no seasonal synchrony of mating activity. The mixed herds and the males in groups or alone were generally segregated throughout the year.

Both taxa would have been water-dependent, although at certain times of the year the available forage would have provided abundant moisture content along with nutrition, allowing longer intervals of time between trips to water. Seasonal feeding preferences and habits would have changed to optimize diets, as is seen with modern Asian and African elephants. During the seasons when moisture was least available in forage and in

water sources, members of each taxon would have centered their nomadic feeding movements around water sources. These seasons would have been the times of the year when proboscideans were most vulnerable to human hunting, because feeding and socializing movements were much limited, precise tracking of targeted individuals could be easily done by foraging humans, and the animals themselves would have been continually losing condition and vigor.

We recognize that some differences between mammoth and mastodont sites may be explained by behavioral or ecological distinctions between *Mammuthus* and *Mammut*, but we think the greater explanatory power for the differences of interest to paleoecologists and archeologists is in habitat and environment. The behavioral responses of mammoths and mastodonts to habitat characteristics and climatic change were probably identical, and when bonesites do differ between the genera, the differences may be due more often to water distribution than to taxon-specific behavioral distinctions.

The proportion of single-mastodont bonesites may seem to be large, when compared to mammoths (see Table 2), and this difference has led to speculation that mastodonts were perhaps solitary animals, or lived in smaller groups than mammoths or the recent elephants. We suggest that the single-mastodont sites may be accounted for by the distribution of water sources in the ranges preferred by *Mammut*. Both mammoths and mastodonts were water-dependent, but paleoenvironmental studies show that the genera did not uniformly inhabit ranges with identical water source distributions. In mastodont ranges, water sources may have been closer together and perhaps less often strictly ephemeral or seasonal than in mammoth ranges, since in general the precipitation totals would have been greater during the year than in mammoth ranges. One predicted result of the denser water distribution (including point sources and ribbon, linear, or streamway sources) is that in mastodont ranges - in general and more

often than not - one should find bones of single individuals. The deaths may have resulted either from normal mortality over the range, or from serious and sustained drought. Mammoths, on the other hand, including any of the several species within the genus *Mammuthus*, preferably inhabited grasslands, open woodlands, and steppes, which are habitats that probably would not have had the same relatively dense distribution of water sources throughout many geographic regions. Their water-related skeletal sites should frequently contain several individuals.

Another possible difference in bonesites is the scarcity of fluted-point associations with mastodonts, when compared to mammoths. Some researchers believe that a relatively large number of mastodont sites do contain evidence of butchering by humans, although stone tools may be lacking in the assemblages. These sites are dated to a time interval consistent with the fluted-point cultures in the United States. One possible explanation for the difference in fluted-point associations between *Mammot* and *Mammuthus* may have to do with the distance between water sources in woodland *versus* grassland or wooded steppe, and with the nomadic movements of mastodonts in their more closed and better-watered habitats versus the movements of mammoths in their drier and more open habitats. If fluted-point-makers were targeting proboscideans to hunt in the late Glacial interval, the relatively greater distances separating mammoth water sources from feeding patches probably led to widely scattered mammoth killsites in large ranges, although multiple-kill locales should be clustered at the largest and longest-lasting water sources. In mastodont ranges, the kills could be more closely spaced and selective, since mastodont populations may have been spread more evenly or distributed more accessibly throughout the woodland habitats.

To conclude, we re-state our propositions: (1) Mammoth and mastodont bonesites do differ in some features; (2) The differences are most apparent in proportions of sites con-

taining single individuals, and proportions of sites showing unambiguous cultural affiliation. Mastodonts appear to have died alone more frequently than did mammoths. Mammoths appear to have been hunted or scavenged by prehistoric people more often than were mastodonts in North America; (3) The possible differences in the proportions of mammoth and mastodont MNI may be due to differences in the Pleistocene distribution of water (in streams, as point sources such as springs, or in ephemeral ponded sites).

We have not discussed in depth any of the possible differences in mammoth and mastodont social behavior or ecology that could explain the taxon-specific proportions of MNI. Instead we have offered what we consider to be a plausible but still hypothetical reason behind some bonesite differences. The main implication of what we have said here is that social differences were not necessarily great between mammoths and mastodonts.

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APPENDIX

All sites selected in the sample.

SITE	TAXON	MNI	AGE/SEX	PLACE OF DEATH	DATE estimate or midpoint	EVIDENCE
Alma, MI	mastodont	1	adult female			
Angus, NE	mammoth	1	adult male(?)	stream	12,000-10,000?	Fluted point? (maybe not contemp.)
Babine Lake, BC	mammoth	1	adult male(?)	pond	34,000	
Barnhart, MO	mastodont	17	mixed	streamside/slackwater	12,000-10,000	
Big Bone Lick, KY	mastodont	10+	mixed	salt springs/pond	10,600	
Blackwater Draw, NW	mammoth	8+	adults	lake	11,630 - 11,040	Fluted points and lithics
Boaz, WI	mastodont	1	adult male	bog/marsh	12,000-10,000	Fluted point?
Boaz, WV	mammoth	1			13,510	Broken bones
Boney Spring, MO	mastodont	31	mixed	springfed pond	16,540-13,550	
Burning Tree, MI	mastodont	1	adult male	small lake	11,660; 11,450 (gut contents?)	Butcher marks; Cached bones?
Case High School, WI	mammoth	1		bog/marsh?	13,000-10,000	Butcher marks;
Coats-Hines, TN	mastodont	1		small stream		
Colby, WY	mammoth	8	mixed (incl. fetal)	small stream	11,200	Fluted points and lithics
Cole, MI	mastodont	1	adult male(?)			
Cooperton, OK	mammoth	1	young adult male	stream/pond	20,400 - 17,575	Broken bones; transported boulders
Crappie Hole, NE	mammoth	1+		stream/lake?		Broken bones
Dansville, MI	mastodont	1	young adult female	marsh		wooden spear
Deerfield, WI	mastodont	3			11,140 - 9,065	Butcher marks
DeLong, NV	mammoth	3+		stream/lake	16,000-10,000	Fluted, stemmed, square-based points
Dent, CO	mammoth	14	mixed	streamside/ford?	11,200; 10,980-10,670	Clovis points; butcher marks; season-of-death
Denver, IN	mastodont	1	adult male	bog		
Domebo, OK	mammoth	1	young adult female	slackwater stream/pond?	11,490-10,810	Fluted points and lithics
Dry Gulch, NM	mammoth	1		springfed pond		Transported boulders
Duewail-Newberry, TX	mammoth	1	young adult male	streamside	12,000-10,000	Flaked bones
Elkhart, MI	mastodont	1	young adult male			
Escapule, AZ	mammoth	1	adult male	small stream	12,000-10,000	Fluted points and lithics
Farview, MI	mastodont	1	young adult male	bog/marsh?		Butcher marks
Fenske, WI	mammoth	1			13,470	
Grandville, MI	mastodont	1	adult male	loess	25,100 (large sigma errors)	Broken bones
Grundel, MO	mastodont	1		floodplain spring	34-21,500 (also 165-140,000)	
Hajny, OK	mammoth	2	adult males		13,850	Broken bones
Haley, IN	mammoth	1		kettle-hole lake	13,695 - 12,685	Transported boulders
Hallsville, OH	mastodont	1				
Hazen, AR	mammoth	1		pond	12,480; 12,250	Lithics; Butcher marks
Hebior, WI	mammoth	1	adolescent male	pond	11,770	Butcher marks; Season-of-death
Heisler, MI	mastodont	1	adolescent male	pond	11,770	lithics; bead; 4% of bones are tools?
Hiscock, NY	mastodont	9+	mixed	springfed lake	10,945 - 9,150	Flaked bones
Hot Springs, SD	mammoth	50+	males, mixed ages	sinkhole pond	26,000	
Huntington Canyon, UT	mammoth	1	adult male		11,500 - 9,500	Lithics? Cutmarks(?)
Ingleswood, MD	mammoth	1	adolescent male	stream/marsh	20,070	Broken bones
Ivory Pond, MS	mastodont	1		bog	11,440 - 11,630	Cutmarks; toothmarks

APPENDIX (continued)

Johnson, MI	mastodont	1	adult male	point bar in stream	12,000-10,000	Fluted points and lithics
Kimmswick, MO	mastodont	8+	mixed	spring/pond/stream	11,050; 11,170 (overlying sediment)	Butcher marks; Bone distribution
Koehn-Schneider, KS	mammoth	2	middle-aged male	slow stream		
Kuhl, MI	mastodont	1		pond margin		
La Sena, NE	mammoth	1		loess?	18,000	Flaked bones
Lake Mills, WI	mammoth	1		bog/marsh	9,065	Butcher marks
Lake Willard, OH	mastodont	1			9,250	
Lamb Spring, CO	mammoth	30+	mixed	spring pond/stream	13,000-11,000	Flaked bones
Lange-Ferguson, SD	mammoth	2	adult and subadult	pond/marsh	11,140	Flaked bones
Lavis/Simpson, FL	mastodont	1		sinkhole in river channel		
Lehner, AZ	mammoth	13	mixed	streamside/pond	11,470-10,620	Fluted points and lithics
Leikum, AZ	mammoth	2		stream	12,000-10,000	Fluted points assoc. with 1
Lindsay, MT	mammoth	1		loess	11,925; 10,980; 10,700; 9,490	Cutmarks; Transported rocks; Stacking
Lubbock Lake, TX	mammoth	3	adult and 2 subadults	point bar in stream	11,100	Butcher marks
Manis, WA	mastodont	2?	old adult male and subadult	stream/pond	12,000; 11,850	Bone point (?) embedded in rib
Marion County, OH	mammoth	1	young adult	lake	10,340	Broken bones
McLean, TX	mammoth	1				Fluted point?
Miami, MO	mastodont	1		loess	35,900; 35,773 ; 41,700 (TL)	Piled ribs; Boiled bone scraps? Cut tueks?
Miami, TX	mammoth	5	mixed	pond in loess	12,000-10,000	Fluted points and lithics; cutmarks?
Milwaukee, WI	mastodont	1		bog		hair
Monte Verde, Chile	mastodont	7	mixed	streamside	12,500	Flaked bones; bone tools; burned bones
Moon, PA	mammoth	1		springfed kettle-hole lake	12,210	Neistones; Butcher marks; Bone distrib.
Mud Lake, WI	mammoth	1		bog/marsh?	13,440	Butcher marks
Murray Springs, AZ	mammoth	4	adult females(?)	streamside/pond	11,190-10,710	Fluted points and lithics
Naco, AZ	mammoth	1	adult		12,000-10,000	Fluted points and lithics
New Hudson, MI	mastodont	1	female(?)	point bar in stream		
Oak Creek, NE	mammoth	1				Broken bones
Oakes, WI	mammoth	1		bog/marsh	13,000-10,000	Butcher marks
Old Crow, Yukon	mammoth	5+	mixed	lake/stream	290,000-13,000	Flaked bones
Orleton Farms, OH	mastodont	1	adult	bog/marsh?		
Owl Cave, ID	mammoth	1+		cave	12,800-10,920	Flaked bones
Owosso, MI	mastodont	1	adult female			
Parker, MI	mastodont	1	adult male			
Petronia Creek, TX	mammoth	1+		sandbar beside slow stream	18,180 (bone); 16,880 (overlying clay)	Cutmarks; Flaked mammoth teeth
Pleasant Lake, MI	mastodont	1	middle-aged male	bog/lake	12,845; 10,395	Butcher marks; cut & burned bones; bone tools
Powers, MI	mastodont	1	adult female			
Quagaman, MI	mastodont	1	adult male			
Rancho La Brea, CA	mammoth	5+	mixed	slow stream/ephemeral ponds	20-10,000	Pole platform? Burnt and cut bones
Rappuhn, MI	mastodont	1		bog/pond	9,250	
Rawlins (U.P.), WY	mammoth	1	adult male		11,280	Lithics
Russell Farm I, MI	mastodont	1	adult male			
Russell Farm II, MI	mastodont	1	female			
Sakstrup, MI	mastodont	1	middle-aged female			

