

# 4. Paleobiology and Extinction of Proboscideans in the Great Lakes Region of North America

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**Keywords** Mastodon • mammoth • tusk growth • season of death • life history

## Introduction

I would like to address the topic of this chapter in calm reflection on a mature body of data, representing a balanced sampling of the empirical record and unhurried evaluation of its possible interpretations. I would also like to be 5 – no, 10 – years further along in the very labor-intensive process of compiling that empirical record! For now, however, I will have to settle for a status report on a series of ongoing investigations designed to assess the nature of late Pleistocene proboscidean occurrences and evaluate aspects of proboscidean paleobiology that have the potential to yield insights concerning the ecological stresses encountered by these animals during the centuries and millennia leading up to the time of their ultimate extinction.

This book focuses on the broad problem of late Pleistocene losses of megafaunal taxa across the Americas, which is itself a geographically, taxonomically, and temporally restricted subset of the larger problem of worldwide losses of megafaunal diversity. In contrast, my title carves out an even smaller region (and set of taxa) as the domain for my analysis. Work in progress actually involves proboscideans from more diverse regions of the Americas and from Siberia as well, and it has involved a variety of aspects of proboscidean paleobiology, but only for the Great Lakes region of North America are there enough data in hand at this time to warrant a summary of trends that offer evidence of the cause of extinction.

The strategy on which this work is based is to investigate the behavior, physiology, and life history of proboscidean victims of the late Pleistocene extinction. My emphasis on victims is in part because generations of scholars working before me have already shed much light on factors that might have been responsible for this extinction – essentially, the “cause” end of the chains of cause-and-effect relationships that brought about the extinction. We of course know the ultimate “effect” end of the chains, the extinction itself, but what remains to be identified and evaluated are intermediate effects that might constitute evidence that one or another causal factor was at work. The advantage of seeking these intermediate effects within the biology of victim species is that only an effect documented there, ideally as a change in “state” that is temporally associated with, and plausibly premonitory to, the extinction event, can be said to have really “completed” one of the hypothesized chains of cause-and-effect relations. Changes wrought in victim species, beyond serving as evidence for identifying causes, also demonstrate, as nothing else can, that the identified cause had an *impact* on the victim (Fisher, 1996a, 2001a).

Since we have no direct, observational access to most of the behavior and physiology that we think is important for understanding late Pleistocene events, we would have little chance of following the strategy described above were it not for the remarkable records of growth and life history that are encoded in the tusks of mastodons and mammoths (most observations presented here involve *Mammot americanum*, but some deal with *Mammuthus primigenius*, *M. columbi*, and specimens referred to as *M. jeffersonii*, which I have suggested may represent hybrids between *M. primigenius* and *M. columbi* (Fisher, 2001a; Hoyle et al., 2004). Other victims of the late Pleistocene extinction offer dental records that might prove tractable in certain respects, but no other animal offers a structure quite like a tusk, capable of recording virtually the entire life.

Tusks are enlarged incisors that grow continuously, without remodeling. In tusks of older individuals, especially males,

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G. Haynes (ed.), *American Megafaunal Extinctions at the End of the Pleistocene*, 55–75.

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the earliest part of the record may be missing due to tip fracture or abrasion, but typically the middle and late portions of life are preserved in their entirety. Periodically formed laminae within tusk dentin provide internal temporal control, and changes in dentin composition provide clues to aspects of life history and environment. In some cases, parts of this record may help to constrain causes of death, but an even more general outcome is that the record clarifies circumstances under which animals *lived*. After all, most of the tusk is a record – many years long – of life and growth; only the last layers pertain to the time of death.

## Morphologic and Taphonomic Contexts for Tusk Studies

Tusk analyses that are most informative about environment and life history involve fine structural and compositional details that could be documented and interpreted on an essentially microscopic scale, without explicit reference to the larger geometry of the tusk, let alone the rest of the animal or its conditions of preservation. However, a tusk always has some larger-scale morphological configuration, and it is often found associated with additional parts of the animal, within a particular depositional setting and taphonomic context. Each of these successively larger contextual scales comes with its own potential for recording information that can be relevant for interpreting even the finest details of tusk structure and composition.

## Sexual Dimorphism of Tusks

Previous workers have remarked on the pronounced dimorphism of proboscidean tusks, in which tusks of adult males are typically longer and much larger in diameter, while those of females are shorter and more slender (Osborn, 1936; Vereschagin and Tikhonov, 1999; Fig. 4.1A). Still, distinguishing sex from tusk size and shape is not trivial when a sample includes tusks of younger individuals. In particular, tusks of a young, incompletely grown male can be difficult to distinguish from tusks of adult females. However, Elder (1970) recognized that male African elephants of intermediate and larger size have pulp cavities that are longer, extending distally past the alveolar margin, while females have shorter pulp cavities that end proximal to the alveolar margin. This same difference has been observed in both mastodons and mammoths (Sher and Fisher, 1995; Smith and Fisher, 2007; Fisher, 2008, and unpublished data, 2001, on *M. primigenius*), although pulp cavities for both sexes get shorter in the oldest individuals, as tusk diameters also begin to decrease. More informative than single extremal measures such as tusk length, maximum diameter, or pulp depth, are series of measurements (e.g., diameter or girth) made at a sequence of positions relative to the tusk tip (Fig. 4.1B). These comprise a “profile” or a time series (uncalibrated to time-in-life, if the independent variable is *distance* from the tusk tip) for the measurement in question. Profiles of tusk girth vs. length for nine males and eight females in Fig. 4.1B trace out largely non-overlapping trajectories. Only one young male (the Heisler mastodon; all specimens referred to here are listed in Table 4.1) occupies the

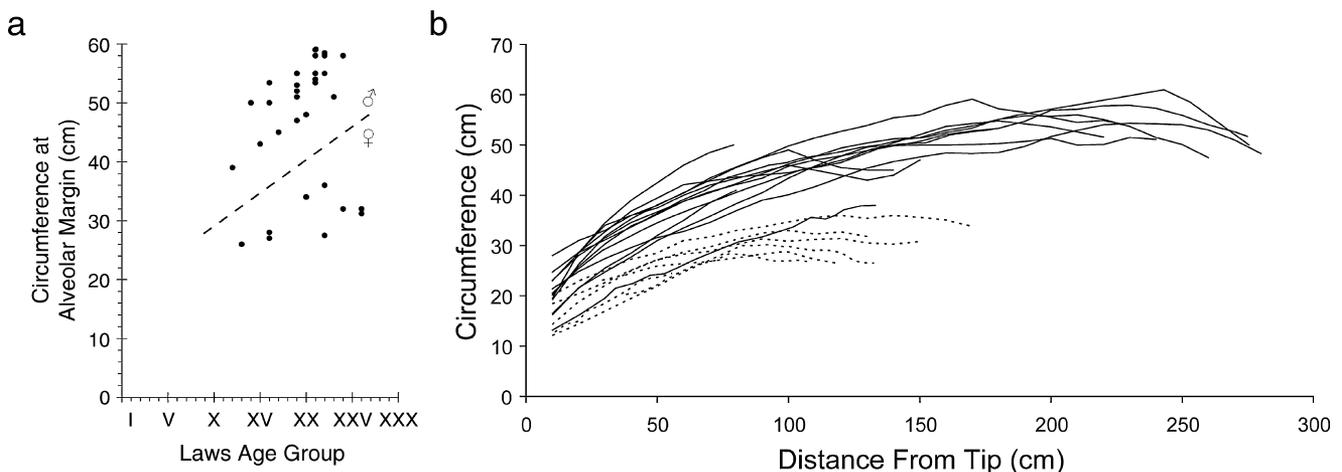


FIGURE 4.1. Sexual dimorphism in tusks of *Mammut americanum* (after Fisher 2008). a. Graph of tusk circumference (averaged when both tusks are present) near the alveolar margin vs. Laws' Age Group, based on cheek tooth dentition, for all specimens listed in Table 4.1 (Krugler has no associated molars, but is given an approximate Laws' age group, based on epiphysis fusion; Fisher, 2008). Tusk circumference increases with age for both male and female mastodons, but males of a given age, or stage of molar development, show greater tusk girth than do same-stage females. Dashed line (placed by eye) follows separation between putative male and female morphs. b. Tusk girth profiles measured relative to distance from the tusk tip. Solid lines, inferred males (Hyde Park, Buesching, Burning Tree, Cohoes, Farview, Grandville, Heisler, Parker, Pleasant Lake); dashed lines, inferred females (Alma, Laur, Miller, North Java, Owosso, Powers, Sheathelm, Shelton).

TABLE 4.1. American mastodon specimens referred to in this work. Institutional abbreviations: AC, Alma College, Alma, MI; CIS, Cranbrook Institute of Science, Bloomfield Hills, MI; INSM, Indiana State Museum, Indianapolis, IN; KPMNH, Kanagawa Prefectural Museum of Natural History, Yokohama, Japan; MSU, Michigan State University, East Lansing, MI; NYSM, New York State Museum, Albany, NY; PMGR, Public Museum of Grand Rapids, Grand Rapids, MI; PRI, Palaeontological Research Institution, Ithaca, NY; RMSC, Rochester Museum & Science Center, Rochester, NY; UM, University of Michigan, Ann Arbor, MI. Sex (M, F) inferred from data presented in Fisher (2008). LAG, Laws' (1966) Age Groups (assignments in brackets based on estimated number of years in tusk, rather than cheek teeth); TG, tusk girth (cm) near alveolar margin (values in brackets estimated from partial tusks or alveoli).

Specimen name	Specimen number	Sex	Material available	State	LAG	TG
Hyde Park	PRI	M	Partial skeleton	NY	XXII	55.0
Cohoes	NYSM V101	M	Partial skeleton	NY	XX	48.0
East Bloomfield	RMSC	M	Partial skeleton	NY	XXII	58.1
Farview	RMSC	M	Partial skeleton	NY	XXI	53.4
Bloomfield Hills	UM 11308	M	Partial skeleton	MI	XVI	50.0
Pleasant Lake	UM 57705	M	Partial skeleton	MI	XXI	58.0
Brennan	UM10627	M	Partial skeleton	MI	XVI	53.4
Darling	UM 22273	M	Cranium	MI	XXI	59.0
Kuhl	UM 59936	M	Partial skeleton	MI	XXIV	58.0
Johnson	UM 57648	M	Partial skeleton	MI	XXII	58.5
Smith-Running	UM 10934	M	Partial skeleton	MI	XV	43.0
Parker	AC	M	Partial skeleton	MI	XXI	54.0
St. Johns	UM 12306	M	Palate	MI	XXI	55.0
McAlpin	UM 11731	M	Partial skeleton	MI	XIX	55.0
Quagaman	UM 24240	M	Cranium	MI	XIX	52.0
Heisler	UM 61888	M	Partial skeleton	MI	XII	39.0
Russell Farm I	UM 37811	M	Partial skeleton	MI	XVII	45.0
Krugler	UM 16303	M	Tusk, misc.	MI	[XXII]	[58]
Grandville	PMGR	M	Partial skeleton	MI	XXIII	51.0
Striker	UM 3489	M	Cranium	MI	XIX	47.0
Winnamag	UM 11230	M	Partial skeleton	OH	XIX	[51]
Burning Tree	KPMNH	M	Partial skeleton	OH	XIX	53.0
Buesching	INSM 71.3.261	M	Partial skeleton	IN	XXI	55.0
Elkhart	UM 34302	M	Cranium	IN	XIV	50.0
North Java	PRI	F	Tusk	NY	[XXVI]	31.2
Shelton	CIS	F	Partial skeleton	MI	XIII	26.0
Sakstrup	UM 54910	F	Cranium, misc.	MI	XXIV	32.0
Sheathelm	MSUVP 1355	F	Cranium, tusk, mand.	MI	XVI	28.0
Owosso	UM 23498	F	Partial skeleton	MI	XXII	36.0
Alma	AC	F	Tusk	MI	[XXII]	30.2
Eldridge	UM 58075	F	Partial skeleton	MI	XX	34.0
Laur	UM 16190	F	Tusk	MI	[XXII]	27.5
Powers	UM 13971	F	Partial skeleton	MI	XXVI	32.0
Miller	UM 16191	F	Tusk, molars	IN	XVI	27.0

portion of the morphospace in which females fall. It falls below the plots for most male tusks because it has not experienced appreciable tip breakage (making it longer, relative to its girth), but it matches males, and is distinguished from females, by its rapid rate of increase of girth with length.

### Skeletal Evidence of Sexual Dimorphism and History of Injuries

As informative as tusks can be, we would be remiss to ignore the larger anatomical system of which they are but one element. Part of the value of associated skeletal material, when it is avail-

able, is its ability to refute or confirm tusk-based determinations of sex. In all extant proboscideans and in woolly mammoths where preserved genitalia permit unambiguous sex determination, adult males are significantly larger than adult females (Vereshchagin and Tikhonov, 1986; Haynes, 1991). Body size dimorphism is also conspicuous in mastodons (Fisher, 2008) and Columbian mammoths (Lister and Agenbroad, 1994). Using bone size for sex determination requires some comparative framework, but this can be provided by comparing bone size among individuals and by referencing bone size to stages of epiphysis fusion on the same or other bones (Roth, 1984; Haynes, 1991) or to stage of molar eruption and wear.

The clearest and most easily understood example of sexual dimorphism in bone shape involves the innominates, or pelvis. As shown by Deraniyagala (1955), Haynes (1990), and Lister (1996; Coope and Lister, 1987; Lister and Agenbroad, 1994), females have a broad (and high) pelvic aperture relative to the width of the shaft of the ilium (a useful measure of size and robustness, even when there is peripheral damage to other parts of the innominate), giving them a large birth canal relative to their body size. In addition, recent work on mastodon pelvises (Fisher, 2008) has shown that there is striking dimorphism in the ischia, replicating a pattern seen in other mammals as well (Warwick and Williams, 1973). In posterior aspect, looking along the axis of the birth canal, the ischial tuberosities of females form a broad, U-shaped trough (with outwardly directed limbs, forming an angle  $\geq 90^\circ$ ), while in males, they form an acutely angled V-shape. In addition, the ventral extremity of the ischia of the male pelvis protrudes anteriorly as a prominent buttress for the closely adherent corpora cavernosa (Fisher, 2008).

Skeletal material also offers the prospect of gaining information on events during the life of an animal, via evidence of injury or pathology, and on postmortem events, including bone modification by human or nonhuman agents. Although analyses of this sort represent a distinct line of investigation from tusk studies, there is rich potential for complementary perspectives. Notable cases of injury in mastodons include only two females (Powers [Garland and Cogswell, 1985] and Eldridge [Kapp et al., 1990]) but are much more common among males. Another categorization relevant to injuries is between those that had healed (without returning to a normal configuration) prior to death and those that did not heal. Cases in the former group reflect to some extent conditions of life, but those in the latter group may be associated with the cause of death. On the other hand, they may be difficult to distinguish from postmortem bone modification caused by any of a number of agents. Further descriptions of cases of injury are given below, where they can be presented in conjunction with details of taphonomic context.

Recovery and documentation of skeletal material took on new urgency following the sale of the Burning Tree mastodon, an important specimen on which a great deal of work had already been done (Lepper et al., 1991; Fisher et al., 1994). This specimen was purchased by the Kanagawa Prefectural Museum of Natural History in Yokohama, Japan, and although the work interrupted by this sale could be resumed, the logistics are now far more complex. In retrospect, the sale of this specimen both resulted from, and contributed to, the growing commercialization of fossils. In the short run, it led to overestimation of the commercial value of mastodon material, and this misreading of the market complicated negotiations over the disposition of subsequently excavated specimens almost as much as if the market had in fact been more vigorous. One of the important specimens lost to commercial interests in the wake of Burning Tree was the Manitou Beach mastodon, discussed below. The combination of excavators trying to reach firm agreements with landowners before investing a

great deal in sites and landowners looking for opportunities for commercial gain has made for challenging times. With the loss of some opportunities to document sites thoroughly, it has become even more important to do so whenever the chance arises. This has led to redoubled efforts to encourage placement of specimens into the public trust and to document osteological material as thoroughly as possible. Products of these efforts now nearing completion include complete photographic series (six standard anatomical views of each bone) and complete sets of research-quality molds and casts of two relatively complete, adult males, the Buesching and Hyde Park mastodons. In addition, the Buesching mastodon and parts of several others have been digitized to produce 3D models that are being prepared for use in comparative and biomechanical studies and development of mapping protocols for documenting newly excavated sites (e.g., Fisher, 2005, 2008).

### Taphonomic Patterns and Their Association with Sex, Age, and Season of Death

Two decades have passed now since taphonomic patterns of Great Lakes region mastodon sites were systematically reviewed (Fisher, 1987). Some aspects of the pattern of occurrences remain stable, but, not unexpectedly, new sites have brought some new perspectives.

#### *Two Site Types Recognized in Fisher (1987)*

In Fisher (1987) one series of sites was distinguished as showing patterns of bone modification suggestive of carcass processing (butchery) by humans. Mastodons recovered at these sites were predominately males, with a younger age distribution than was observed in a complementary group of specimens interpreted as not showing evidence of human association, and they all turned out to have died in autumn or earliest winter (based on analysis of their last-formed dentin). All of these specimens came from wetland depositional settings, with bones occurring in marl or peat, and were interpreted as meat-caches consisting of minimally butchered carcass parts submerged in shallow ponds or along lake margins to promote preservation and extended access to the meat (Fisher, 1995). Some of these caches had apparently been abandoned without utilization, while others probably were utilized, in some cases after retrieval through a hole in ice (evidence for this includes burned wood, thought to represent a fire built on the frozen surface of the pond, associated with the bones in utilized caches, but not with unutilized caches at the Heisler site [Fisher, 1987]; other sites preserve cobble- to boulder-sized rocks that may represent a strategy [Fisher, 1995] for “passive-solar-ice-entry” ... let them melt their own way through as far as they will go and then punch through the remainder). These sites included some for which contextual data were available and others, excavated by previous University of Michigan staff, for which minimal contextual data had been recorded. However, all were united by occurrence of shared patterns of bone modification.

The complementary series of sites interpreted as not butchered included relatively few for which detailed contextual data were available. One of these few was the Johnson mastodon, a relatively complete skeleton of an old male preserved in a quasi-articulated condition within a small-scale fluvial setting, with the most conspicuous disarticulation being downstream displacement of small foot bones (Fisher, 1984a). Most of the other specimens in this group were categorized with Johnson because of the absence of bone modification like that observed on the specimens interpreted as butchered, though in some cases patterns of presence and absence of bones different from those seen in the butchered cases also played a role. These not-butchered cases showed an “even” sex ratio, an older age distribution than in the other group, and season of death ranging from the end of winter to late spring, with one midsummer death. Given the disparate sex, age, and season of death traits shown by these two groups, I proposed an argument framed in Bayesian terms that the butchered animals were most likely procured via hunting.

I had intended to document each of these assemblages in greater detail in the following years, but a steady stream of new sites was reported and took precedence until they could be secured and accessioned. These efforts, coupled with increased emphasis on tusk analysis and initiation of the digitizing project that would make site descriptions more effective, delayed completion of assemblage and site reports, though the first of many of these is now complete (Fisher, 2008). With this steady growth in the number of sites, my initial two-fold classification has become increasingly inadequate, while not completely breaking down.

#### *New Sites and New Observations Complicate the Picture*

One of the first sites that showed differences from the patterns reported in Fisher (1987) was the Eldridge mastodon, described briefly by Kapp et al. (1990). This was an adult female with evidence of butchery, but she turned out to be a spring death. Unfortunately, she had lost one tusk in life, and the other was not recovered at the site (season of death was determined from a molar), so a full life history was not available (though much might be learned from further analysis of cheek teeth). She also showed a complex array of healed injuries on her facial region, including several large perforations of parts of the skull that would normally be solidly ossified. We were unable to determine what caused her facial injuries or whether the loss of the tusk during life was related, but both of these events probably predated death by more than a year. Since most other spring deaths had shown no evidence of butchery, it seemed most parsimonious to interpret Eldridge as a natural death, of unknown cause, and therefore to consider the butchery as representing an instance of human scavenging of a natural death.

Another female previously interpreted as not butchered (Fisher, 1987) is the Owosso mastodon. This interpretation was

based on examining the full skeletal mount displayed in the University of Michigan Exhibit Museum. Although it was clear that a few parts of the skeleton had been restored, the apparent absence of butchery damage on exposed areas provided no basis for interpreting the specimen as associated with humans. However, when a skeletal cast of the adult male Buesching mastodon was recently mounted alongside the adult female Owosso mastodon, the latter had to be partly dismantled to reconfigure its permanent base to match the style of mobile base used for Buesching. In cleaning and remounting Owosso foot bones, it became clear that they showed types of damage previously observed only on butchered specimens. We know that the Owosso skeleton occurred in peat, in a lacustrine setting, but the skeleton was excavated by the neighbor of the landowner (leading to a dispute over ownership), and no data are available now on the spatial structure of the site.

Two of the sites interpreted as not butchered in Fisher (1987), Sheathelm and Quagaman, were unusual in preserving only heads, and each was encountered in nearly pristine condition (though Sheathelm was damaged by the landowner’s efforts to extract it). These were interpreted as non-butchered because the hypothesis of “no human association” was treated as a null hypothesis, and at the time, there were no grounds for rejecting it, even though I had no good explanation for why a mastodon head might occur in isolation. Both were recovered from sediments suggestive of shallow ponds, as were the sites interpreted as meat caches, but this was not considered sufficient reason to suggest human association. However, my perspective on these sites changed with recovery of the St. Johns mastodon, an adult male represented only by a palate (with upper cheek tooth dentition) and basicranium (Fisher, n.d.). This too was from a lacustrine setting (marl) comparable to those of meat caches, but the season of death was spring, as had been observed for Sheathelm and Quagaman, and different from all prior meat caches (except Eldridge). Though severely broken, the specimen was essentially unweathered. We expected to find other bone fragments nearby, representative of other parts of the highly pneumatized skull typical of proboscideans, but a major recovery effort supported by the Michigan Department of Transportation produced nothing. A “fresh”-looking skull remnant was even more difficult to account for out in a shallow lake than had been the heads of Sheathelm or Quagaman, the intact condition of which might permit them to be interpreted as having floated out into deeper water from a carcass on the pond margin that ultimately failed to be preserved.

Heightening the sense that a new pattern was emerging, UM collections contained two additional specimens that were almost indistinguishable from St. Johns (UM 3488 and UM 3489) and more that probably were similar at the time of discovery (e.g., UM 11308), but had been restored with plaster, making them difficult to compare. These were also spring deaths. I subsequently proposed (Fisher, n.d.) that “heads-alone” represent a distinct type of occurrence.

Although I cannot rule out the possibility that these animals were hunted, I regard them, conservatively, as natural deaths scavenged by humans, where the main tissues that warranted caching were those associated with the head, especially the brain and extensive nasal mucosa lining the *dipl e* of the greatly expanded system of cranial sinuses. In any death due to non-human causes, humans might be lucky enough to be first on the scene and scavenge an entire carcass, as in the case of Eldridge, but often other scavengers might be expected to find the carcass first, such that when humans arrived, many of the most accessible parts might already have been eaten. However, even in such cases, important fat reserves inaccessible to most other scavengers remain in the brain and nasal mucosa, and the nutritional importance of lipids for humans subsisting on high-protein diets (Speth and Spielman, 1983) may have made these tissues attractive. More to the point, spring deaths might often have involved fat-depleted animals in which much of the meat was lean enough to impose a calorie deficit on humans eating it, but this would not apply to brain tissue, which retains its lipid content even in starving animals (Speth and Spielman, 1983). Heads cached, but never retrieved, might account for pristine skulls such as those of Sheathelm and Quagaman. In contrast, specimens consisting of a palate+basicranium would be ones that were cached subaqueously, retrieved in winter (when the need for lipids was greatest) through a hole in the iced-over surface of the pond, “harvested” by breaking away upper portions of the skull, where the brain and *dipl e* are located, and then abandoned on the ice surface after the lipid-rich tissues attached to the broken fragments had been gathered and returned to a camp where they could be rendered. After limited exposure on the surface of the frozen pond, the palate+basicranium would have melted through the ice and been preserved on the pond bottom (if breakup of the skull did not occur on the ice, it is hard to explain how this dense part of the skull got out into a central area of a pond, since without *dipl e*, it could not have floated). An Inuit practice of storing heads of game underwater and returning to harvest the brain and nasal mucosa (Taylor, 1969) was part of the ethnographic support for the hypothesis of subaqueous meat-caching in the first place (Fisher, 1995), and deer heads that I stored in ponds and bogs at the E.S. George Reserve (prior to legs of lamb and a draft horse) retained brain tissue over summer and through the next winter. This hypothesized behavior has another parallel in the winter “head-collecting” documented for Neanderthals by Stiner (1991).

Another type of site for which we now have additional examples is the multiple death site, where more than one individual is preserved. Russell Farm I and II were discussed in Fisher (1987), and at least one additional mastodon was discovered at the Johnson site. There is no reason to assume that all individuals preserved at a site represent the same taphonomic history, but in any given case, there may be evidence supporting such a conclusion. The Bothwell site, excavated by R. Richards (Indiana State Museum) in northern Indiana

and under collaborative study with K. Smith (UM), yielded 13 tusks and additional cranial and postcranial remains, all apparently representing adult females (Smith and Fisher, 2007). We know nothing yet about site formation processes in this case, but determining season of death for all individuals will provide a good starting point.

Another interesting multiple death site is Manitou Beach (UM 18288 and 18289), where an adult female mastodon and a young calf were found. The calf was represented by only a left malar (= jugal) and several ribs, but from their size, age at death was estimated as 1–2 years. Measurements of annual increment lengths on a tusk of the adult female at the site, interpreted as in Fisher (1996a) to present a record of calving intervals, suggested that she had given birth to a calf about 1.5 years prior to death. The adult female was originally donated to the University of Michigan, but just as detailed analysis was about to begin (and after a great deal of fieldwork and lab work cleaning and stabilizing the specimen), the landowner demanded its return and sold it to a private collector (though several small samples were at least left to document the find in part). Through a complicated arrangement involving neighbors of the landowner who had assisted with much of the fieldwork (H. and D. Hoppe), the remains of the calf were acquired and (except for one rib) donated to the University of Michigan. Analysis of these specimens has been deferred in the hope that access to the remains of the adult might again be arranged, but a provisional interpretation of this site is that it represents a mother and her own calf, probably autumn deaths, and probably hunted and cached for later use.

#### *An Important Cause of Natural Death for Adult Males*

Another new development has been recognition of what may have been an extremely important cause of natural death for (mainly) adult males – death as a victim of musth battle. “Musth” refers to the hormonally mediated season of fasting, heightened aggression, and nearly exclusive focus on mating that is well known in extant Asian and African elephants (Poole and Moss, 1981). Musth has been recognized as an important cause of death in adult male elephants (Buss, 1990), but from a behavioral and life history point of view, this is only part of its significance. The frequency and duration of musth is related to dominance rank of a male, with larger and/or more highly ranked males remaining in musth longer (up to three months) and coming into musth at the optimum time of year (given the 22-month gestation period of extant elephants and the optimum season for calf birth). Less dominant males are inhibited from coming into musth in “prime-time,” showing shorter musth intervals, timed either earlier or later in the year (Poole, 1987). Independent of size, non-musth males typically give way to musth males, and females in estrous typically consent to mate with a musth male in preference to any non-musth male. Musth behavior and the physiological ability to enter and maintain a musth

episode are thus prime determinants of reproductive success. Musth battles in elephants may be brief and are generally non-lethal when disparity in size and power is clear, but cases in which two well matched musth males come into contact can lead to serious injury or death (Buss, 1990).

The first mastodon musth victim identified was the Cohoes mastodon, but its fate might not have been recognized had I not decided to test an earlier tusk-based season-of-death determination by repeating the analysis for one of the molars (lower left quadrant). To my surprise, the molar yielded a season of death about one month later! Both showed a spring death, but the tusk had stopped forming dentin before the molar. This refocused attention on a small puncture in the bone of the lateral aspect of the left temporal fossa, near the growing end of the tusk that yielded the earlier time of death. The fragments of bone surrounding this puncture were still attached along their margins and had all been rotated toward the skull interior, forming a round hole (Fig. 4.2A). I now interpret this hole as a bone puncture formed by the tip of an opponent's tusk, after plunging through much of the masticatory musculature on this side of the head. This would have caused a great deal of blood loss, and perhaps an infection that "killed" the tusk physiologically, soon after the injury was sustained. The animal itself, however, did not die immediately, but slowly starved. Its injury precluded mastication on the left side of its mouth, and ironically, the right side of its dentition had already been incapacitated by a developmental anomaly that I trace to an earlier injury that was probably incurred in an adolescent precursor to a full-fledged musth battle (Fisher and Fox, 2007b). Unable to eat, the Cohoes mastodon may have nursed a fever until he finally succumbed, about a month after his injury. Coincidentally,

there was also evidence of butchery and meat-caching, implying that his carcass was scavenged by humans who must then have perceived some residual value in it. With additional analyses of state of health at death, we might make sense of some of the contrasting fates of different carcasses (i.e., whether they are scavenged or not), but it seems most conservative for now to attribute such outcomes (without claiming independent evidence at this time) to variability in timing of access to the carcass and in the condition of remaining tissue when a carcass was encountered by humans.

Unfortunately, circumstances of access to the Cohoes mastodon (assisting with its remounting in the New York State Museum) did not allow for detailed study of all postcrania. However, two other parallel cases were recognized in quick succession – the Buesching and Hyde Park mastodons – and the first trait linking them all, beyond the fact that they were all adult males that died in spring, was the occurrence of remarkably similar, unhealed puncture wounds in the same anatomical position as the puncture on Cohoes. Both Buesching and Hyde Park show evidence of old, healed injuries like those sustained by extant elephants in musth battles (ribs broken by impact of the ventrolateral surface of a tusk, proximal caudal vertebrae broken and/or dislocated, probably by a tusk blow to the rump, as an unsuccessful competitor beat a hasty retreat, and zygapophysial remodeling following transient dislocation of thoracic vertebrae by ramming a tusk into a victim's flank). In addition, Hyde Park (which has been studied in greatest detail) shows evidence of fresh tusk blows to the lateral flank and associated vertebral dislocation and an injury from a tusk tip driven between two thoracic vertebrae from a dorsolateral direction, an indication that the Hyde Park mastodon was already recumbent when it sustained this injury (Fisher, 2008).

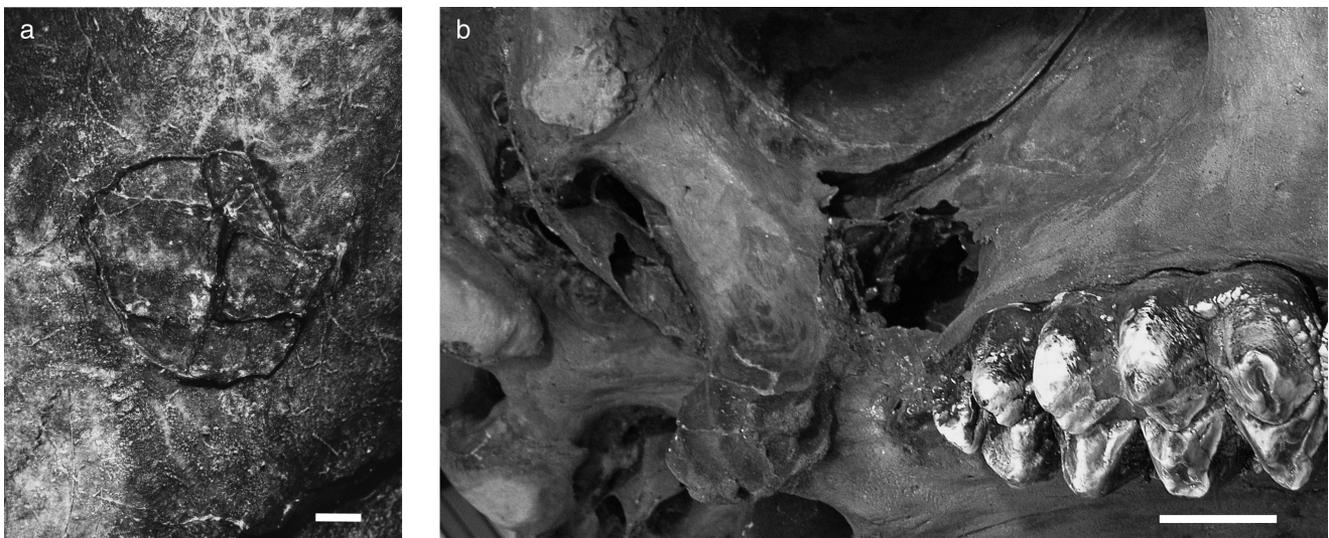


FIGURE 4.2. Bone punctures in the alisphenoid region (inner wall of temporal fossa) on adult male victims of musth battles. a. Cohoes mastodon, left temporal fossa; circular puncture restored by rotating fragments back into plane of bone surface (all remained partly attached); scale = 1 cm. b. Buesching mastodon, right temporal fossa; circular puncture left as found (for orientation, tooth is the right  $M^3$ , foramen magnum is dark opening at left of image, and the puncture is just below the alisphenoid canal; scale = 5 cm.

I interpret repeated occurrences of wounds implying tusk penetration of masticatory musculature and puncture of the lateral aspect of the skull bordering the temporal fossa as a result of a stereotyped mode of fighting in which opponents engaged each others' tusks, twisting their necks and driving forward to try to catch the other off balance. The key "move" would have come when one of the adversaries sensed even a momentary advantage of orientation or balance, dropped his head and tusks suddenly, and then vigorously thrust them upward and toward his opponent, on whichever side seemed vulnerable for a strike. The upward and inwardly turned tusk tip in the opportune position would then have caught the opponent in the cheek, or even entered his mouth, tearing through the masseteric and pterygoideus musculature, driving upward and toward the midline, and penetrating the alisphenoid bone, which formed the bony wall of the temporal fossa. This damage was usually unilateral, perhaps because the recipient of such a blow either withdrew from battle immediately or was sufficiently incapacitated by the blow that no comparable opportunity would likely be presented again. However, Quagaman, though identical in all other respects (except that as an isolated head, it lacked associated postcrania), shows identical damage bilaterally. This damage was observed during review of specimens prior to Fisher (1987), but it did not fit patterns of bone modification associated with butchery, and without the parallel examples of Cohoes, Buesching, and Hyde Park, it was assigned to an uninterpreted residue of perior or postmortem damage that did not (fortunately) compromise interpreting Quagaman as a natural death.

The skull damage described above does not replicate the style of damage seen on extant elephant victims of musth battles, but this may be a consequence of different tusk geometry in these taxa. Wounds inflicted by elephant tusks are described as perforations of the temporal margins of the skull (or of other parts of the body) that suggest thrusting of their much straighter tusks in a direct "jab" at the opponent's head or body (Buss, 1990). The "upper cut" style of motion implied by mastodon tusk wounds is functionally similar in that the tusk is moved along a trajectory parallel to its tip axis, but kinematically distinct, in association with the greater tusk curvature of mastodons. In addition, the alveolar surface of the dorsolateral portion of adult male mastodon premaxillary bones shows a localized specialization implying hypertrophy of the periodontal ligament precisely in the area needed to serve as a shock-absorber for the stresses of impact of an upthrust tusk tip (Fisher, 2008). Finally, as discussed below, use of the tusk in this way leaves a signature style of damage in dentin and cementum along the outer curve of the tusk (described below) such that individual bouts of fighting are visible in the record of tusk growth.

The only case in which I now feel reservations about a specimen interpreted in Fisher (1987) as probably hunted is the Heisler mastodon. This specimen has a small perforation of the alisphenoid region on the right side of the skull, which could be a tusk wound. As with Quagaman, this was noted before, but these two cases alone were not enough for me to

recognize the pattern. If Heisler was killed in a musth battle, two points are unusual. First, his autumn death would be the only exception to the otherwise exclusive association between musth battles and spring. Second, as a young male only about 16 years old at death, Heisler seems too young to have yet experienced onset of typical musth. This did not occur in Hyde Park until an age of about 23 and is commonly delayed in extant elephants until even later (Poole and Moss, 1981). One interpretation of these two anomalies is that as a young male in musth for one of his first times, Heisler may have been inhibited from going into musth in spring, when older, larger males were in musth, and may instead have delayed his novice musth episode until autumn. Even so, it is not clear that musth in this young a male is plausible, unless the local population was characterized by notably few adult males (Slotow et al., 2000). A second possibility is that perhaps this was not really a full-blown musth episode at all, but an example of the kind of fighting in young males that occurs throughout adolescence and that, bout by bout, prepares them for the onset of typical musth. The alisphenoid perforation on Heisler does suggest a very sharp tusk tip, like that of Heisler's own tusks, so perhaps he was just an unlucky pre-musth teen. This may be resolved by closer analysis of Heisler's tusk record, but this work is not yet complete. However Heisler died, the site still presents a compelling case of butchery and meat-caching.

Since it is now clear that some adult male mastodons met extremely violent ends in musth battles, and since some musth victims have been interpreted as scavenged and butchered (e.g., Cohoes, Buesching), it is worth asking whether some of the bone modification interpreted as due to butchery could be reinterpreted as damage sustained in musth battles. This might be difficult to assess without comparative observations from a musth victim that was not butchered, but this is exactly what we encountered in the Hyde Park mastodon (Fisher, 2008). Despite the damage evident on his skeleton, none of it resembles the types of damage interpreted as indicative of butchery (Fisher, 1984a, b, 2008; Fisher et al., 1994). This makes him, like Johnson, an important reference for documenting the contrasting patterns of "butchered" and "non-butchered" carcasses. We also still have cases such as Pleasant Lake and Burning Tree that appear to have been butchered but show no evidence of perimortem musth battle.

A final note on musth battles is that they constitute the first positive indication of a cause of death (normally applicable only to adult males) unrelated to human activity. In principle, studies of dentin increments and isotope profiles might allow recognition of death due to drought and/or nutritional stress (recorded as thin increments and elevated oxygen and/or nitrogen isotope values; Heaton et al., 1986; Hobson et al., 1993; Koch, 1998; Fisher and Fox, 2003), but we have not yet studied cases that appear to fit such patterns. Rather, as explained in Fisher (1987), most deaths now attributed to "natural" causes are identified as such because we have made the conservative choice to treat natural death as a null hypothesis that has to be rejected before an interpretation of hunting can be put forward.

I would not want to defend this as necessarily the best choice in all cases; for example, Fisher and Fox (2003) note as “suspicious” that three, or possibly four, of four females analyzed at the Hiscock site show no evidence of nutritional stress or severe seasonality, but all died between winter and early summer, each apparently with a yearling calf. As new evidence emerges, we may well want to revisit default “natural death” interpretations, but in the context of a debate where skeptics regard hunting as an extraordinary claim requiring extraordinary evidence, I am willing to maintain a conservative stance.

#### *Additional Findings at New Sites*

The presence and certain aspects of the behavior of mastodons are documented by footprints as well as bones. At the Brennan site, while excavating remains of a butchered, cached mastodon, footprints were discovered that record passage of a solitary adult male and, sometime after, a group that appears to have been composed of two females and at least one calf (Fisher, 1994). We followed the trackway of the male for about 60 m, paralleling a lake margin at about 1 m paleodepth and exposed a profusion of additional mastodon footprints just at and beyond the lake margin. Subsequently, with more of an idea of what to look for, abundant mastodon footprints were exposed just shoreward of the pond margin at the Heisler site. These footprints, in conjunction with the finely laminated character of the peaty marl of the bone horizon within the pond sediments, suggest that mastodon behavior was characterized by an appropriate avoidance of the soft, yielding substrates encountered within the pond itself.

The typical circumstances that bring new sites to our attention (receipt of a call from a landowner who has discovered large bones) represent a strong bias favoring animals as large as mastodons, and against specimens in a body size range that would permit them to be interpreted by landowners as simply domestic livestock buried by some prior property owner. Nevertheless, once working at a site, we sometimes find remains of taxa other than proboscideans. Perhaps the most notable case was recovery of limited remains of two *Cervalces scotti* at the Brennan mastodon site. One of these was represented by a partial cranium, with antlers broken off, that could plausibly be a cached Scott’s moose head retrieved for recovery of its brain. Likewise, at the Dempsey site, in what may be a Holocene assemblage, white-tailed deer (*Odocoileus virginiana*) crania with antlers girdled by stone tools, before being snapped off at the base, were recovered from lacustrine marl. Muskox crania in our collection also show damage that could reflect subaqueous caching and subsequent recovery for harvesting of brain and nasal mucosa.

## Discussion of Morphologic and Taphonomic Context of Tusk Studies

The sites reviewed by Fisher (1987) still warrant more detailed analysis, but only one site interpreted then as reflecting hunting is now viewed conservatively as a result of scavenging

(Heisler). Slightly more change in interpretation has affected sites thought to show no evidence of human association, with one (Owosso) now interpreted as a scavenged natural death and two others (Sheathelm and Quagaman) now interpreted as cached heads scavenged from natural deaths. Even with these changes, sites without human association comprise a set with a more even distribution of sexes and an older age distribution. With respect to season of death, specimens that show evidence of human association are still mostly autumn deaths, a season not represented at all among specimens without human association. This means they cannot all be readily interpreted as scavenged natural deaths. Instead of suggesting that all human-associated carcasses were probably hunted, I would now treat them as including both cases of hunting and cases of scavenging, but the inclusion of scavenging is mostly in the direction of considering scavenging for specimens that were formerly not recognized as involving humans at all.

The picture of human subsistence adaptation that emerges from these patterns is consistent with a generalist, opportunistic strategy in which megafauna are hunted or scavenged as circumstances allow, and in which proboscideans, predominantly mastodons in the Great Lakes region, represent a source of protein, fat, and possibly other materials that is at least seasonally important. The occurrence of these remains in the context of resource stores suggests some risk-reduction strategy, implying that humans in the Great Lakes region during the latest Pleistocene may have had to deal with some uncertainty in access to food, especially to lipid-rich dietary components. This would have been a human-scale problem, affecting human nutrition, and it would be a mistake to generalize this without further evidence to other contemporary mammals, especially proboscideans. The nature of proboscidean response to environmental conditions will be best determined from records of proboscidean growth and life history in tusks.

## Elements of Tusk Structure and Their Interpretation

Tusk and cheek tooth structure in mastodons and mammoths has been reviewed previously (e.g., Fisher, 1987, 1988, 1996a, 2001a; Fisher and Fox, 2003), but each of these treatments introduced elements that significantly change our understanding, and the pace of new observations is such that I doubt the last of these revisions is behind us. Because enamel is present on tusks only near their tips and is removed from cheek teeth by occlusal attrition, it does not tend to provide a long and continuous record for either. Cementum on tusks is subject to information loss due to abrasion following eruption and is generally not thick enough in any one area, especially on cheek teeth, to provide adequate temporal resolution. Tusk cementum does figure in studies of adult male mastodons, but except for this, I focus here on dentin. To keep the scope of this discussion manageable, even some unique aspects of

proboscidean dentin (such as the “Schreger” pattern; Espinosa and Mann, 1993; Trapani and Fisher, 2003) must give way to an exclusive focus on the patterns of layering that record the appositional history of this tissue.

### Proboscidean Dentin: Themes and Variations

The most basic aspect of proboscidean dentin structure is the existence of a hierarchical organization of laminar features, such that laminae at coarser scales are composed (typically) of a relatively fixed number of laminae at the next finer spatial scale. In tusk dentin there appear to be at least three orders of laminar features, and cheek teeth show two clearly (and probably three, but we do not usually use magnifications high enough to resolve the finest; Fisher, 1987, 1988, 1996a). The largest-scale layering in dentin is the repetition of so-called “first-order features” reflecting an annual periodicity, the cycle of seasons. This is expressed in variation in dentin color, density, the spacing of the next-finer laminar elements, and often the topography of the dentin-cementum junction. The next finer scale of lamination is the repetition of “second-order” features, reflecting a different period in different contexts, as discussed below. Second-order features are bounded, in general, by more strongly marked versions of the same type of structural discontinuities that demarcate the next-finer, or third-order, laminae. Third-order laminae are couplets of more and less dense dentin, where the less dense layers are essentially zones of vacuities, left in intertubular dentin as the mineralizing front passes a given locus of apposition. Third-order laminae appear to recur with daily periodicity and may be some reflection of circadian physiological rhythms.

First- and third-order features thus have at least plausible physiological causes, but second-order features are more variable and less well understood. Their apparent period in mastodon tusks is one fortnight, or two weeks, repeating about 26 times per first-order unit. However, in mastodon molars, I have observed about 13 second-order features per first-order feature, suggesting a period close to a lunar month. Both of these periods are different in mammoths, where second-order features in tusks recur at about one-week intervals, with about 52 per first-order unit, in mammoths living at temperate latitudes (Fisher et al., 2003). Mammoth molars, in contrast, show second-order features with a two-week period (Fisher and Fox, 2007a). Thus, each taxon shows a different period (related by a factor of 2) in tusks and molars, and controlling for the type of tooth, there is another factor-of-2 difference between mastodons and mammoths. At this point, insufficient work has been done on cheek teeth to say much about variability, but enough tusks have been analyzed to show that there can be variation within and between individuals. Some of this is attributable to the uncertainty in where exactly to say a given first-order feature begins. Seasonal changes are, after all, gradual on some scale; spring, for example, can come early or late in any given year. However, cases where one mastodon, for example, shows 25 second-order increments per first-order increment

for several years running (Fisher et al., 2008) imply real variation from the more common value of 26.

It is worth pausing here to note that the periodicities in mammoth tusk dentin are almost identical to those of human tooth enamel and dentin (Dean and Scandrett, 1996) and that other mammals show comparable hierarchical patterns (Klevezal, 1996). What I refer to as second-order features figure in literature on primate dental anatomy as “long-period striations,” while third-order features are “short-period striations.” Without dwelling on terminology, reference to “orders” implicitly addresses the hierarchical character of the system, acknowledges existence of annual as well as shorter-term features, and promotes the concept that relative position within the hierarchy may be more relevant for some problems than the actual duration of a period.

The interpretation of these patterns of tusk lamination is more complex than can be treated fully here. However, an overview of my working hypothesis is that second-order laminae are a reflection of a “beat-frequency” (see also Newman and Poole, 1974) driven by interaction of circadian rhythms and some other rhythm, possibly a spatiotemporal rhythm of dentin mineralization that is endogenous to the tusk itself (and likewise, but with different parameters, to cheek teeth). This physical model allows me to calculate the frequency and period of this hypothesized rhythm, even though its actual identity remains unresolved. As long as circadian rhythms are entrained to environmental light-dark cues, cycling with a 24-h period, as will always obtain at temperate (or equatorial) latitudes, the beat-frequency retains its period of about 7 days. However, for animals living north of the Arctic Circle, a portion of the year (winter and summer) lacks 24-h light-dark cues, and under those conditions, the circadian rhythm shifts to its endogenous “free-running” frequency, for which the period is generally longer (or shorter) than 24 h. This induces a change in the pattern of lamination for mammoths living above the Arctic Circle (Fisher, 2001b, 2007), but since these populations are not the subject of this chapter, I defer additional discussion of this phenomenon. In any case, the relevance of this model for mastodons and mammoths of the Great Lakes region (not to mention other instances of hierarchical dentin lamination) is that it provides insight into the cause of second-order lamination and supports treating second-order laminae as periodic features that can be used to extract data on short-term variation in rates of dentin apposition.

### *Isotope Evidence of Annual Nature of First-Order Features*

Analyses of light stable isotope compositions of mineralized tissues of organisms have recently become a major source of new perspectives on paleobiology and paleoenvironments. The isotope systems we have used for working on North American mastodons and mammoths are carbon and oxygen from structural carbonate of hydroxyapatite, phosphate oxygen from hydroxyapatite, and carbon and nitrogen from collagen.

The systematics of these isotopes have been reviewed on many occasions (e.g., Koch et al., 1994; Koch, 1998; Cerling and Harris, 1999; Kohn, 1996; Fisher and Fox, 2003). Factors that contribute to variation in isotope composition are broadly understood, and many aspects of such variation are highly predictable. However, the nature of isotope records, depending as they do on the actual fluxes of isotopes in and out of the body and all the environmental, physiological, and behavioral factors that control these, is highly contingent. This is the basis for the strength of isotope records as proxies for real variation in causal factors, but it is also a source of potential problems because, especially in the case of a large, mobile animal such as a proboscidean, we are monitoring a system in which relevant factors do not always maintain constant relations to one another.

For example, the most fundamental aspect of dentin lamination that has been addressed using isotope composition is the annual nature of first-order features. These highly regular, but not invariant, largest-scale features of dentin lamination could in principle have been under some hypothetical system of spatial or structural control, producing layers of roughly constant thickness but with no consistent temporal dimension. However, this interpretation has been effectively ruled out by finding patterns of variation in isotope composition matching those expected for seasonal variation on an annual cycle in nearly constant association with particular parts of the structural cycle. This was first established using oxygen from structural carbonate in hydroxyapatite, in the first study of intra-annual isotopic variation in dental remains (Koch et al. 1989), but it has been replicated many times over using all the isotope systems noted above (e.g., Fisher and Fox, 2003, 2007a; Fisher, 2001a; Hoyle et al., 2004). The fact that the expected patterns are not observed in every case is explained by variations in behavior and context. For instance, under temperate-latitude conditions, patterns of seasonal variation in meteoric water composition (Gat, 1980; Rozanski et al., 1993) and the calculated lag (reservoir effect) due to gradual shift in body water composition relative to inputs from drinking water and food water (Koch, 1989) lead us to expect the lowest oxygen isotope values ( $\delta^{18}\text{O}$ ) near the winter-spring boundary and the highest values in late summer or early autumn (Stuart-Williams and Schwarcz, 1997). This is seen often enough that we are confident that first-order features really are annual; yet the expected pattern of variation is based on the assumption that drinking water and food water are dominated by meteoric sources that display the usual seasonal pattern of compositional change. In work on four Hiscock mastodon females, from western New York, Fisher and Fox (2003) found a limited annual range of variation in oxygen isotope ratios ( $< 3\text{‰}$  in most tusk-years), no consistent pattern of intra-annual variation either within or between individuals, and little correspondence to the typical pattern of variation in meteoric water composition. Given the highly regular patterns of oxygen isotope variation observed for other sites, failure to observe the same patterns here cannot

be treated as refuting the annual nature of first-order features. Based on where the Hiscock mastodons died, they probably lived near glacial meltwater sources that were relatively stable isotopically and different in composition from meteoric waters. The most plausible interpretation of these animals' oxygen isotope profiles may therefore be that they reflect largely stochastic, individual histories of switching between water sources. If so, their profiles carry little information on local seasonality though they may still, to some degree, "reflect behavior."

The contingent nature of compositional profiles also means that the observed pattern of variation depends on the pattern of environmental change in the locale inhabited by the animal under study. Temperate-latitude settings in North America may show a simple, sinusoidal pattern of change in oxygen isotope values, one cycle per year, as seen today in meteoric water values in the same regions, but at lower or higher latitudes qualitatively different patterns may emerge. In a Florida mastodon, for example, there were two cycles of variation in oxygen values per first-order feature, interpreted as reflecting a more "tropical" pattern of two wet and two dry seasons per year (Fisher and Fox, 2006). On the other hand, woolly mammoths in Chukotka (northeastern Siberia) show an annual cycle that appears to depend entirely on seasonal shifts in the vapor source and rain-out history of air masses (Fox et al., 2007).

In many studies of intra-tooth variation in isotope composition, samples provide a time series of compositional data only in the sense that measured values are ordered in time; the amount of time represented by the whole series may be estimated if a large enough fraction of an annual cycle is recorded, but there is typically little independent control on the amount of time represented in each sample. In contrast, sampling proboscidean dentin, where first-order features are often marked by color banding or repeating patterns of accentuation or spacing of second-order features, provides an opportunity for greater precision in relating samples to time in the life of the animal. This also lets us express compositional time series in either the spatial domain (as in distance from the pulp surface at the time of death) or the temporal domain (as in weeks or fortnights since the last winter-spring boundary). Thus far, this temporal resolution has served mainly to control the sampling process itself and insure that we achieve comprehensive but minimally overlapping recovery of dentin from consecutive intervals of time, but we could in principle evaluate rates of change in composition as well as the general pattern of change.

Just as the pattern of oxygen isotope variation over the course of a year depends on the local hydrologic cycle (and an animal's behavioral interaction with it), the pattern of variation of other isotope systems is a function of behavioral and physiological interactions with locally available plants and environmental conditions. One interesting example of this may become an increasingly important pattern in studies of temperate-and high-latitude ecosystems. We are used to consulting oxygen isotope profiles to monitor seasonal

changes in environment, seeing only moderate changes seasonally in carbonate carbon profiles and interpreting them as indicative of subtle changes in diet (switching between  $C_3$  and  $C_4$  plants) or habitat use (habitats that are more or less arid, or closed-canopy; e.g., Koch, 1998). However, in the northern portions of temperate-latitude ranges,  $C_4$  plants become rare or drop out of floras completely (Teeri and Stowe, 1976). Although this might be expected to subdue seasonal patterns in carbon isotope profiles, profiles of carbonate carbon isotope composition recovered from the North American Great Lakes region and from Siberia often show a strong seasonal signal (Fisher and Fox, 2003; Gohman et al., submitted). Especially in Siberia,  $C_4$  photosynthesis would have been functionally absent, and there would have been no closed-canopy habitats in which more  $^{12}C$ -enriched isotope values would have been generated.

What we suspect is going on here is a seasonal cycle between fat utilization and fat formation, usually expressed most clearly in carbonate carbon, which reflects the carbon isotope composition of bulk diet (Ambrose and Norr, 1993). Because lipids tend to be depleted in  $^{13}C$  (DeNiro and Epstein, 1981), when late winter caloric deficits are balanced by metabolizing stored fat reserves, the body's carbon reservoir (and thus the carbonate carbon in newly mineralized dentin) is shifted toward lighter values (Polischuck et al., 2001). The opposing phase of this cycle, showing heavier values in late summer and fall, could reflect in part simply the opposite effect; that is, as caloric intake exceeds immediate needs, and excess energy is stored as fat, preferentially sequestering  $^{12}C$  in adipose tissue, the body's carbon reservoir is shifted toward heavier (more  $^{13}C$ -enriched) values. However, other carbon fluxes are important as well (P. Koch, 2007 personal communication), so additional investigation of this cycle is needed. In some cases, these patterns in carbonate carbon isotope composition may provide a clearer seasonal signal than corresponding patterns in oxygen isotope composition, especially where oxygen is influenced by vapor source and rainout history more than local temperature of condensation.

### *Age Determination*

A prerequisite for quantitative studies of life history is a means of determining individual age, ideally at critical points during life as well as at the end of life. Counting first-order features in tusk dentin satisfies much of this requirement, providing a minimum constraint on age at any given point in the development of the recovered part of a tusk. However, it leaves unaccounted for the number of years missing from the tusk tip due to breakage and abrasion, and these "missing years" may comprise a larger portion of life the longer an individual lives. In certain cases, useful information may be gained by correlating between teeth of the same individual, but by the time a tusk tip is broken, the cheek tooth that was forming during the corresponding part of life may have been worn down and lost long before.

The most effective response to this problem is to develop a composite reference frame (i.e., based on multiple individuals) for interpreting age relative to temporal reference features involving tusk composition and/or geometry. Rountrey et al. (2007a) have shown that compositional time series through the tusks of juvenile mammoths can track seasonal changes in the relative importance of milk and plant components of the diet and the longer-term trends associated with weaning. We expect the timing of weaning to be environmentally dependent itself, but it should be less variable than the number of years missing from a tusk tip. We are now documenting weaning in a number of calves that have lost little or no material from their tusk tips, and in some cases, we observe a record of birth itself via recognition of a neonatal line (Rountrey et al., 2007b, submitted). There may also be other transitions in juvenile tusk development, such as shifts in the composition of milk, that can be used to define reference features within tusks.

Tusk geometry is also important for building this composite reference frame. In both mastodons and mammoths (and in extant elephants; Elder, 1970), tusks develop as conical structures with proximally increasing circumference (except for parts of the tusk formed late in adult life) at the dentin-cementum boundary and externally, on the outside of the cementum. Distal-to-proximal gradients of increasing dentin radius (distance from the axis to the dentin-cementum boundary at a given radial position and distance from the tip) appear to be less variable among individuals of the same sex than between individuals of different sexes, possibly even starting with the earliest stages of tusk formation. In addition, the thickness and length of first-order dentin increments display sexual dimorphism during later tusk growth (Fisher, 2008; Fisher et al., 2008), and possibly in early years. Differential provisioning of male and female calves by mothers (Lee and Moss, 1985) may provide the nutrient influx critical for supporting higher tusk growth rates in males. Additional aspects of geometry include the transverse cross section of increments, which changes from elliptical to a more nearly circular configuration along both distal to proximal and axial to external gradients.

Although breakage and abrasion remove material from the tip and dynamically reconfigure it to yield a secondarily acute appearance, loss of material can always be recognized and to some degree estimated. In the first place, material loss is almost always asymmetrical, such that the structural axis of dentin increments is displaced from the morphologic tip of the tusk. This asymmetrical loss can usually also be seen by following the outcrop of the dentin-cementum boundary, which is typically displaced farther proximally on the outside (ventral) curve of the tusk (Fisher, 2008). Wherever cementum has been lost from the tusk surface, it is likely that some dentin has been removed too, but as long as even traces of cementum are left, the dentin radius at that position cannot yet have been altered. Measurements of unaltered dentin radii

can then be used to correlate between tusks with different degrees of tip loss.

### *Male Life History*

The most striking feature of male life histories, viewed from the perspective of records of tusk growth, is eviction of males from their matriarchal family units upon sexual maturation. Observations of extant elephant males undergoing this transition show that this is a time of increased stress and risk of mortality (Moss, 1988). This is partly because recently evicted males waste much time and energy “appealing” the sentence pronounced against them by the matriarch, and partly because they simply have not yet acquired the knowledge of local resources from which they benefited while in the company of their matriarch. Even records of tusk growth rate compiled at an annual scale show a pronounced drop in year length (i.e., first-order increment length measured along the dentin-cementum junction) that has been interpreted as indicative of eviction, and records of second-order increment thicknesses (Fisher, 1996a, 2008, and unpublished work on an African elephant tusk) show an abrupt, mid-year drop in tusk growth rate that is sustained, with only gradually moderating effects, for a period of 2–3 years. Annual records of tusk growth rate based on year thickness show a similar drop, though usually not as pronounced, as first-order increment thickness is inherently less variable over the whole ontogeny than first-order increment length (Fisher, 2001a). For the Hyde Park mastodon, examination of both types of annual increment profile has been augmented by pair-wise comparison of each of the 32 complete years in the tusk. Year 12 in the tusk, interpreted as year 15 in life, is the year that matches criteria for eviction on annual increment profiles, and it also stands out as the most distinctive year in the tusk from the perspective of Kolmogorov-Smirnov tests of both the temporally ordered sequence of second-order increment thicknesses and the temporally unordered distribution of second-order increment thicknesses (Fisher, 2008). We have not yet had a chance to “ground-truth” these interpretations by analyzing tusks from male elephants with known life histories, but the appearance of this depression in tusk growth is so consistent in character in all male proboscidean tusks we have examined that no other interpretation seems plausible. On any given tusk, we see no more than one depression in tusk growth rate matching the pattern interpreted as eviction, and it always occurs between the ages of 9 and 20 years, the same range attributed to eviction in extant elephants (Sikes, 1971).

Attainment of physiological sexual maturity in male elephants is the first but not the only threshold leading to full reproductive function. At a more advanced age, often in the later 20s or even 30s, comes the onset of musth, beginning with short, irregular periods of fasting and aggressive behavior lasting days or weeks, and later developing into longer and more regular episodes. In mature males, musth may recur annually as long as physical condition is sufficient to sustain

the fasting and high levels of aggressive interaction associated with the state (Poole, 1987). In less mature males, even the presence of more mature males within the population tends to inhibit musth or displace its timing to less opportune parts of the year. Comparisons between local populations where older bulls are and are not present have made it clear that the timing of musth is not programmed into individual development but is rather a reversible, inducible response to social interaction (Slotow et al., 2000).

For *Mammuthus columbi*, the most dramatic evidence of musth is presented by the Crawford mammoths (University of Nebraska State Museum 2448 and 2449), a pair of mature males that died with their tusks interlocked; in the end, both were victims of a musth battle from which neither could retreat. Recent studies (Fisher, Rountrey, and Voorhies, unpublished) of dentin increments and carbon and oxygen isotope compositions of hydroxyapatite carbonate show that both died in mid- to late-spring, roughly 22 months from what would have been an optimum early spring calving season. This same season of death and, implicitly, musth was observed for the Brooks mammoths (University of Nebraska State Museum 1384, 1952, 1953, 1954), an assemblage of four tusks that shows every indication of being analogous to the Crawford mammoths, but without such spectacular preservation of the rest of the skeletons (Fisher, 2004b). Musth at this time of year is also indicated by intervals of slow tusk growth (thin second-order increments) induced by the musth fast in years prior to the time of death, recorded in the tusks of all of these individuals.

*Mammuth americanum* offers no pairs of gladiators like the Crawford mammoths, but we do have inferred solitary victims of musth battles such as the Cohoes, Hyde Park, and Buesching mastodons. Again, death and musth were in the mid- to late-spring, implying a roughly 22-month gestation period if the calving season was in early spring, as seems optimal. As with mammoths, we also have indications of earlier musth episodes in the form of intervals of reduced rate of dentin apposition, presumably induced by the musth-fast. In addition, the Hyde Park mastodon shows a recently recognized type of tusk record that is in its own way almost more dramatic than pairs of victims. As argued at length elsewhere (Fisher, 2008), forceful upthrusting of its tusks during musth battles displaced its tusks within their alveoli to the extent that the proximal, growing margin was fractured along an arcuate tract on the ventral aspect (outer curve) of the tusk. After each such battle, tusk growth resumed, but odontoblasts and cementoblasts along the damaged locus produced anomalous dentin and cementum for many years after, leaving a visible record (externally and in thin section) of each significant battle in the life of this individual. The first recorded battle was at an age of 23, and more or less severe battles recurred in every subsequent year, always in mid- to late spring, until the death of this animal in a musth battle at an estimated age of 36. The combination of healed injuries and fresh injuries attributable to the final battle make it clear that such battles were brutal even when not lethal, taking a mounting toll on

the physical condition of the animal. Nonetheless, annual increments of dentin thickness (rate of apposition) maintain roughly constant values through most of life, and there is no long-term diminution in the length or severity of musth episodes, suggesting that this was simply the lifestyle to which mastodons were adapted, and which they successfully maintained within late Pleistocene environments. Patterns of tusk growth throughout life suggest that the seasonal cycle was quite variable from year to year, but in general, neither winter cold nor summer drought were harsh enough to impact tusk growth adversely. Clearly this work needs to be replicated on other individuals, but it promises to bring the lives and fates of individual mastodons into spectacular focus.

Beyond descriptive detail concerning the lives of individuals, comparative treatment of comparable records of maturation and musth battles may provide demographic evidence that is ordinarily extremely difficult to extract from the fossil record. Other mastodon males have not yet been studied in as great detail as Hyde Park, but specimens such as the Buesching and Pleasant Lake mastodons appear to have been involved in fewer severe musth battles. Those that are recorded show the same seasonal timing, but they do not occur in every year of these animals' adult lives. I suspect this means that the populations in which they lived were characterized by lower densities of adult males, leading to encounters that were less regular, though no less severe when they did occur. This suggests a social context in which young males would be expected to mature at younger ages. As noted below, eviction does seem to have occurred earlier for Pleasant Lake than for Hyde Park, but more work is needed to make this determination for Buesching.

Concerning the possibility of human-induced mortality (i.e., hunting), the evidence is still indirect. Roughly half of the mastodons recovered in the Great Lakes Region are young adult males that died in autumn (Fisher, 1987). If there was ever any suspicion that these were musth deaths, the emerging record of mid- to late spring musth argues against such an interpretation. The sole exception to this pattern, as noted above, is the Heisler mastodon, who, if he was even in musth at all at the time of his death, was probably a case of early onset of musth, at a completely inopportune time of year. Most other males dying at this time of year are not nearly this young and show no evidence of having died in musth battles.

### *Female Life History*

Tentative interpretations of tusk records of female mastodon life histories were proposed in Fisher (1996a) and discussed further in Fisher (2001a). Although all details require further evaluation, a recent comprehensive analysis of a tusk of the North Java mastodon (Fisher et al. 2008) corroborates earlier suggestions and provides much additional data, including comparisons and contrasts with male life history. There is some age uncertainty due to fracture of the tusk tip, but our best estimate of age for the North

Java mastodon suggests first conception at 9–10 years and a lifetime total of 6–7 calves, most at 3–4-year intervals (based on cycles of variation in annual increments of tusk length and dentin thickness), prior to death at an age of about 40. To carry the analysis beyond simple profiles of variation in annual increment dimensions, pair-wise comparisons between each year in the tusk (evaluated, as for Hyde Park, by Kolmogorov-Smirnov tests of both the temporally ordered sequence of second-order increment thicknesses and the temporally unordered distribution of second-order increment thicknesses) showed a pattern of similarities and differences between years that was dramatically different from the pattern seen in an adult male (Hyde Park; Fisher, 2008) and reflective of the inferred calving cycles. Results of these comparisons make it clear that there are objective differences in the growth histories of these tusks. North Java's tusk growth record is compatible with conception in mid- to late spring (equivalent to the timing of musth in males) and calving in early spring, roughly 22 months later. The pattern of seasonal variation in tusk growth rate, compared year-to-year, suggests that conditions for growth were highly variable but generally good. Slow-growth intervals in winter were not protracted and in most cases not extreme (Fisher et al., 2008). The emphasis of new studies of female life histories, beyond simply replicating prior analyses on additional individuals, is to identify additional structural and compositional factors in tusk growth that might provide independent evaluation of the calving cycles inferred from tracing changes in tusk growth rate (Fisher and Fox, 2003).

One pattern noted in Fisher and Fox (2003) and Fisher et al. (2008) is that female mortality does not seem to be associated with the time – either the season or the particular year – of calving, but rather with the time of mating. This needs to be addressed with larger samples, but it raises the question of what factors are responsible for most deaths of females. Neither tusk growth rates nor nitrogen isotope values of dentin collagen (evaluated for four females from the Hiscock site; Fisher and Fox, 2003) give any hint (e.g., elevated  $\delta^{15}\text{N}$  values; Hobson et al., 1993) that nutritional stress is involved.

Whether or to what extent there was human hunting of adult female mastodons and/or mastodon calves is not yet clear. The Manitou Beach mastodons are suggestive, but we have not even completed a formal season-of-death analysis on this material. Likewise, the Hiscock mastodon females analyzed by Fisher and Fox (2003) were difficult to explain as natural deaths, though terminal growth histories extracted from isolated tusks do not provide much to go on.

The possibility of a completely different source of mortality was proposed by Fisher et al. (2008) based on injuries on the Powers and Eldridge mastodons that are similar to injuries caused in tusk battles. Although this is “all wrong” in terms of normal proboscidean behavior (i.e., musth males might fight with each other, but ordinarily not with the females

with whom they should be mating), it is reminiscent of the misdirected aggression of young male elephants showing premature onset of musth in populations where poaching has removed most or all of the older bulls (Slotow et al., 2000). This mechanism does not address the issue of how the density of older bulls was reduced, but it does represent one possible behavioral pathology that could emerge in populations that display, for whatever reason, this type of demographic structure.

At present, much less has been done on life histories of North American mammoth females, but some information on tusk growth rates was presented in Fisher (2001a), and oxygen isotope time series for the last year or more of dentin formation in three of the Dent mammoths (Fisher and Fox, 2007a) suggest that this site (with at least 15 mammoths, all either young or adult females; Brunswig, 2007) preserves remains of individuals that died on at least three (and very likely more) occasions. Ironically, although this may strike some readers as less dramatic than Saunders' (1980) "herd confrontation hypothesis", in which hunters are envisioned as killing an entire matriarchal family unit on one occasion, the seasonal selectivity and site fidelity that our analysis revealed (also compatible with results of Hoppe, 2004) seem to us to strengthen the inference of human agency in site formation. Finally, the autumn season of death of one of the Colby mammoths (an adult female; Fisher, 2001a) is compatible with Frison and Todd's (1986) analysis of that site and with other evidence that autumn deaths may reflect hunting.

## Life History Changes as Tests of Hypothesized Causes of Extinction

Changes in life history traits are not necessarily useful for resolving every question regarding mechanism of extinction. For example, it is not clear that any prediction can be made about how life history should respond to "hyperdisease" (MacPhee and Marx, 1997) or to an extraterrestrial impact (Firestone et al., 2007). This is not to say that there would *be* no life history response to such events, but rather that the details of any response would depend on too many local factors and environmental contingencies to predict an overall response. In contrast, climate change as a mechanism of extinction, whether affecting animal populations directly or through mediation of a vegetational response, works by depressing organisms' capacity for growth and reproduction. If it was the principle driver of extinction, we should see evidence of reduced growth rates and retarded reproductive schedules. Whether or not this is a general prediction, it seems quite secure for a large-bodied herbivore with long gestation time, single births, and a social organization involving dominance hierarchies based largely on body size (Fisher, 1996a, 2001a, 2004a). Lower growth rates are essentially a direct response to environmental degradation, and delays in reproductive

schedules tend to mitigate the effects of resource limitations. The fundamental trade-offs between growth and reproduction (e.g., Clutton-Brock et al., 1982) are probably especially strong for proboscideans, where females incur the substantial energetic cost of producing, carrying, and provisioning large-bodied young, and males endure the rigors of the musth fast, not to mention the risks of encounters with dominant adversaries among older males. Enduring lower growth rates without a delay in reproductive schedules implies reproduction at smaller body size. This is bad enough for females, as it would tend to lead to reduced calf size, reduced survivorship (perhaps for both mother and calf), and reduced status for both mother and calf (to the extent that this is related to body size). However, it is even worse for males, for whom body size is a strong predictor of reproductive success (Hollister-Smith et al., 2007). In the absence of significantly elevated risk of adult mortality, delay of reproductive schedules is thus usually the best strategy. Proboscideans must have operated under this regime throughout much of their evolutionary history, and they have evolved behavioral and physiological traits that serve to regulate their life history response to environmental stress on ecological time scales. It is thus no surprise that under conditions of resource limitation, extant elephants show delayed maturation and prolonged calving intervals (Douglas-Hamilton, 1973; Laws et al., 1975).

In cases of moderate resource limitation, moderate delay of reproductive schedules might allow maturation at nearly the ancestral body size, but this is not to say that any amount of environmental stress can be accommodated in this way. If only because lifespan itself is finite, a proboscidean living under conditions of chronic resource limitation must eventually commit to reproduction, even if at a less than optimal body size. If further delay of reproductive schedules is not likely to lead to realized gains in fitness, then the "time-value" of earlier reproduction will begin to dominate the calculus of tradeoffs that control life histories (Clutton-Brock et al., 1982). This is the type of scenario generally called upon to explain the phenomenon of island dwarfing that has occurred so many times within proboscidean history, though to be sure, the developmental mechanisms behind this phenomenon have not yet been documented to the degree that would be possible with tusk-based studies of life history. Similarly, King and Saunders (1984) have appealed to resource limitation within the continental setting to explain reduction in mastodon body size during the late Pleistocene. Although this is certainly plausible, without actual data on ages and reproductive schedules, we cannot distinguish this cause of body size reduction (essentially a nutritionally induced neoteny, or retardation of growth and maturation) from an alternative scenario according to which smaller body size is viewed as a consequence of accelerated reproductive schedules (essentially progenesis). To understand why this might occur, we have but to consider hunting.

Hunting tends to reduce population densities and relax constraints on growth and reproduction imposed by resource

limitations. Females that are in adequate condition to go into estrous do so, and those that lose a calf for any reason typically cycle again with little delay. Losses from any portion of the spectrum of age classes remove potential competitors for reproductive opportunities and diminish any expected benefits of delaying reproduction until greater size can be attained. Under this regime, when survival to successful reproduction is itself less certain, the “time-value” of early reproduction (like compound interest) assumes greater importance than any “strategic” delay of reproductive effort. This effect may be especially strong for males, who are normally capable of reproduction long before the social hierarchy affords them significant opportunities. When that social hierarchy is “thinned out” by elevated mortality rates, onset of musth and reproductive function may be accelerated (Slotow et al., 2000). A relevant example of this phenomenon, though not involving elephants, was documented by Carrick and Ingham (1962) in southern elephant seals. On South Georgia Island, where hunting had been allowed for years, females matured about a year earlier, and males 2–3 years earlier, than on Macquarie Island, where no hunting had been allowed. Again, because these responses are mediated by behavioral and physiological mechanisms, they maintain a dynamic equilibrium with the social and environmental circumstances encountered by individual organisms.

It would be unreasonable not to consider what might happen under the combined assault of environmental deterioration and hunting pressure, but because these ecological forces have such diametrically opposed effects, a situation in which they were precisely matched would be expected to yield little change in life histories. In a less precisely balanced scenario, the stronger force would likely prevail, and we would see evidence of its action in the direction of change of life history traits. Before we get caught up, however, in worrying about still more complex scenarios (e.g., temporally varying combinations of opposing forces), we should remember that our role as empiricists is not so much to predict what would happen under any and all circumstances, but rather to document the patterns that history actually presents for our evaluation and correctly assess their differential likelihood under (and thus their differential support for) competing causal hypotheses.

As a proxy for somatic growth rates, two different measures of tusk growth rate (rate of dentin apposition, measured by thickness of increments, and rate of tusk extension, measured by length of annual increments) were considered in Fisher (2001a). Annual length increments may be easier to observe (as periradicular features near the growing end of the tusk, especially under conditions of high seasonality), but studies of their pattern of variation throughout the lifespan (e.g., Fisher, 2008; Fisher et al., 2008) make it clear that there is a strong ontogenetic component in both sexes and pronounced sex differences, making appropriately controlled comparisons critical. In contrast, thicknesses of annual dentin increments are more nearly constant throughout the adult portions of tusks (though they still differ between males

and females) and can be compared more easily. Both sets of tusk growth rates reported by Fisher (2001a), for North American mammoths showed higher values toward the end of the Pleistocene than for times earlier in the Pleistocene. I do not yet have this much time depth for mastodons, but their tusk growth rates are on par with those of late Pleistocene mammoths.

As noted above, calving intervals are tentatively recognized based on relatively regular cycles of variation in tusk growth rate in adult female mastodons. These patterns differ from what is seen in immature females and males of any age (Fisher, 1996a). Annual increments within such time series have been corroborated by oxygen and carbon isotope profiles (Fisher and Fox, 2005), and the pattern taken as characteristic of adult females has been documented at high temporal resolution and with interannual statistical comparisons (Fisher et al., 2008). We still need more individuals to be analyzed in these ways, and we especially need to trace structural and/or compositional traits that provide independent indications of calving cycles. Despite these reservations, all indications in hand now point toward late Pleistocene calving cycles in mastodons as lasting an average of 3–4 years, equivalent to those of African elephants under the most benign environmental conditions (Douglas-Hamilton, 1973; Laws et al., 1975).

Age of maturation is the life history trait for which some of the best data exist currently. For males, this is the time of eviction of adolescent males from the matriarchal family unit, and for females, it is the time of first conception. Males in particular are not fully mature until later, on or after the onset of musth, but eviction shows up clearly in the tusk record as a year of sharply reduced tusk growth rate, and it is at least one important point of reference. Some of the first data on age of maturation in mastodons were presented in Fisher (1996a), and a graph like Fig. 4.3, showing age of maturation vs. radiocarbon years before present, has been shown publicly on multiple occasions since then, starting with Fisher (1996b). In each case, these data have been described as preliminary: not yet based on sufficiently detailed tusk analyses, not yet fully accounting for loss of years from the tusk tips, and some requiring additional radiocarbon dating. Improving on these deficiencies is a priority, but unfortunately, it has at times had to be deferred to address newly discovered specimens and ephemeral opportunities for progress on other critical issues. For these reasons, the data themselves remained unpublished for over a decade, until my colleague Michael Foote convinced me they were useful enough as an example of the kind of argument being envisioned that they should be reported (Foote and Miller, 2007). Having now given permission for the graph to be published, I feel obliged to present the data on which it is based, and this is done in Table 4.2. In the intervening years, new data have been obtained, some of which are actually more highly resolved (Fisher, 2008; Fisher et al., 2008), and at the risk of mixing generations of results of differing inherent quality, these are added (where radiocarbon dates are available). All the caveats listed above still apply, and I would certainly entertain the

FIGURE 4.3. Graph showing age of maturation, inferred from annual increment measurements in tusk, relative to radiocarbon age estimates; data provided in Table 4.2. Males are shown as open circles, females as solid circles, labels as the initials of the site name, and reported uncertainties on age estimates as solid bars.

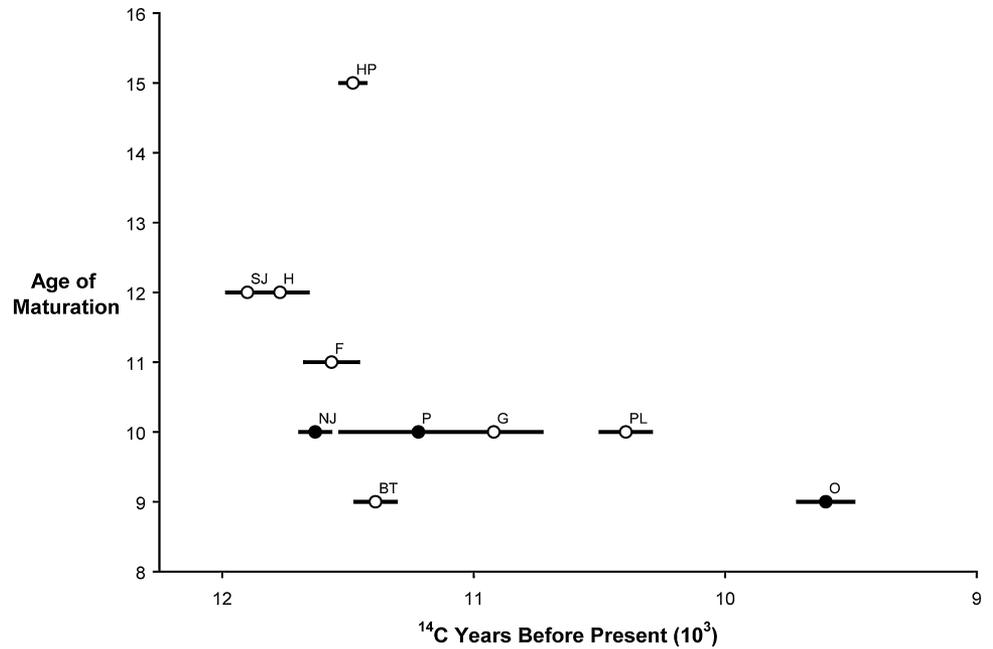


TABLE 4.2. Radiocarbon age estimates and ages of maturation for Great Lakes Region mastodons; sex of each individual is listed in Table 4.1.

Specimen name	Radiocarbon age estimate	Laboratory number	Age of maturation
St. Johns	11,900 ± 80	Beta 78626	12
Heisler	11,770 ± 110	AA 6979, NSRL 282	12
North Java	11,630 ± 60	Beta 176928	10
Farview	11,565 ± 105	AA 7397, X 359	11
Hyde Park	11,480 ± 50	Beta 141061	15
Burning Tree	11,390 ± 80	AA 6980, NSRL 283	9
Powers	11,220 ± 310	Beta 9482	10
Grandville	10,920 ± 190	Beta 15265	10
Pleasant Lake	10,395 ± 100	Beta 1388	10
Owosso	9600 ± 110	Beta 74159	9

possibility that something on the order of two years should be added to many of these ages to account for time missing from the tip. However, I think it unlikely that as many as 5 or 7 years should be added, and that is what would be required to make these data match the ages of maturation of elephants under conditions of environmental stress. Moreover, even this would leave unexplained the pronounced decline in age of maturation toward the end of the Pleistocene. I keep an open mind, but I see strong indications that age of maturation for Great Lakes Region mastodons declined as they neared extinction.

## Discussion: Extinction Scenarios

This chapter is not intended as a general discussion of the merits, relative or absolute, of all scenarios under consideration for explaining late Pleistocene megafaunal extinctions. Other

recent discussions address a wider range of factors than I can treat here (e.g., Alroy, 2001; Haynes, 2002; Barnosky et al., 2004; Martin, 2005). I have attempted to show, however, that if we focus on resolving the relative merits of climate change and human hunting as potential causes of extinction, life history data derived from tusk analyses of Great Lakes Region mastodons run counter to expectations based on climate change models, but follow closely the patterns expected for hunting. Interestingly, the duration of human-proboscidean interaction implied by Fig. 4.3 is much longer than suggested for Martin's (1967) "Blitzkrieg" style of overkill and suggests rather a more protracted attrition of proboscidean populations. Much of the hunting appears to have focused on adult males (Fisher, 1987), but agents of mortality for females are not well resolved.

Each determination in Table 4.2 and Fig. 4.3 deserves its own discussion, but this would take us into more detail than is possible here. One maturation age that stands out from the rest is the 15-year age for Hyde Park. Although this is higher than other maturation ages, this is also the animal that shows annual musth battles in his tusk record, implying a dense local population of adult male adversaries. Delayed maturation (though this is still not "late" by African elephant standards) is the expected response in this social setting. No other male in this data set shows a comparable frequency of musth battles, which could mean that other males are derived from populations that had already experienced some reduction in the density of adult males.

Likewise, one date that stands out is the figure of 9,600 rybp for the Owosso mastodon. This is the individual interpreted in Fisher (1996b) as having lost a large number of calves prior to weaning. At the time, this seemed suggestive of human predation, and subsequent discovery of what could

be a mother-calf pair at the Manitou Beach site enhances this impression, without of course yet providing firm evidence. This date for Owosso is later than is generally accepted for mastodons in North America (the youngest currently accepted date being 10,395 rybp for the Pleasant Lake mastodon; Fisher, 1984a; Meltzer and Mead, 1983) and it needs to be replicated, but it raises the possibility of a late phase of human-mastodon interaction in which hunting of females and calves became more common. As if this were not enough, the possibility (discussed above) that misdirected aggression of novice males in premature musth was responsible for some deaths of adult females adds an even darker note to the last days of mastodons in North America.

Data on mammoth life histories in North America are not yet plentiful enough to resolve a pattern as clear as that for mastodons, but they are compatible with the same broad trends. We simply need more analyses of more tusks with a wider sampling of regions and time intervals. Parallel studies are underway on life histories of Siberian woolly mammoths (*Mammuthus primigenius*), which offer the promise of large numbers of exquisitely well preserved specimens of male and female adults (e.g., Fisher et al., 2007; Gohman et al., 2007) and juveniles of both sexes (e.g., Rountrey et al., 2007a, b). Whether woolly mammoths show life history changes like those of North American mammoths and mastodons is much too soon to tell, but we are eagerly at work deciphering their tusk records.

*Acknowledgments.* I am grateful to Gary Haynes for inviting this contribution and to Paul Koch and an anonymous reviewer for comments that greatly improved its clarity. Scott Beld has provided able assistance during much of the work reported here; Paul Koch and David Fox remain valued colleagues in multiple ongoing projects; and Adam Rountrey and Kathlyn Smith have already taken on significant roles in moving this work forward. We have also benefited from many undergraduate assistants and volunteers in fieldwork and laboratory phases of documenting mastodon skeletons. Finally, Larry Agenbroad, Warren Allmon, Bruce Bourque, Robert Brunswig, George Frison, Elizabeth Garland, Alan Holman, Gary Hoyle, Ronald Kapp, Jude Kirkpatrick, Richard Laub, Bradley Lepper, George McIntosh, Norton Miller, Ron Richards, Jeffery Saunders, Ed Smith, Dennis Stanford, and Mike Voorhies have provided access to many important specimens and participated in rewarding collaborations on North American material.

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