Finding meaning in mammoth age profiles

Gary Haynes

University of Nevada, Reno, USA

ARTICLE INFO

ABSTRACT

This paper summarizes standard methods for estimating ontogenetic ages of individual proboscideans and alternative approaches to presenting the data. Age (a.k.a. mortality) profiling of multiple-mammoth assemblages can provide information about possible causes of death, population health, and other ecologically significant topics, even when the assemblages have been time-averaged. However, caution must be exercised in how the age profiles are calculated and interpreted, to avoid potential misdirection or error.

© 2016 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

Larry Agenbroad devoted much of his career to interpreting the spectacular mammoth accumulation at the Mammoth Site of Hot Springs, South Dakota, and found unique meaning in the site's mammoth age profile (also called a mortality profile; Van Valen, 1964; Voorhies, 1969; Klein, 1982). In this paper I briefly review methods often used in determining ontogenetic ages of proboscideans, and discuss how various age-profiling methods may lead to different interpretations of multiple-mammoth assemblages. The goal of this paper is to raise several issues for analysts to be aware of when examining multiple-mammoth assemblages.

Several multiple-mammoth sites in North America are the remains of human-made kills or scavenged carcasses which date to 13.5 to 12.2 ka (thousand years before 1950 CE) (Haynes and Hutson, 2014). A number of other multiple-mammoth sites are noncultural, such as Hot Springs, and occur over a wide chronological span. Widga et al. (2015) found that "single-[proboscidean] localities are by far the most common," compared to multi-animal and multi-taxic sites in the American midcontinent, a pattern that seems to be true for the rest of the continent. Single-mammoth sites probably have been found for centuries by non-scientists who left no reliable documentation, but multi-animal localities often attract more attention. Table 1 lists some multi-animal sites. Not on the list are several of the more spatially expansive collecting localities such as Old Crow (Yukon), with minimum number of individuals (MNI) of mammoths >5, and Big Bone Lick (Kentucky), with estimated MNI of mastodons in the dozens.

The starting point in age-profiling death assemblages is to determine the frequencies of animals at different life-stages. This is done by plotting MNI in progressively older age groups. The graphic display of data is most often a bar graph or histogram, where the height of the bars indicates number or percentage of individuals in designated age intervals. Each interval represents a fixed portion of lifespan, such as youth, prime adulthood, and old adulthood, but age groups need not explicitly represent ontogenetic age in years. However, in the case of proboscideans, ages in real years are usually assigned to individuals and to the age-groups.

2. How are ontogenetic ages of mammoths determined?

Several methods can be applied to assign ontogenetic ages in multiple-mammoth death assemblages to allow interpretations of the age distribution (e.g., Saunders, 1977a, 1980; Agenbroad, 1994). The methods include counting rhythmic growth increments in hard tissue, assessing the extent of skeletal maturation, and analysis of tooth progression and wear.

2.1. Counting growth increments in hard tissue

One age-determination method requires laboratory preparation of hard tissue specimens. Several studies have shown that proboscidean dentin grows in hierarchical microscopic increments, with first-order light and dark couplets representing seasonal contrasts thought to record one year, and second-order increments that represent multiples of seven days (Fisher, 1987, 1996; Koch, 1989). Rountrey et al. (2012) counted what were interpreted as third-order or daily growth increments in a thin section of the unworn first tooth of a newborn Siberian woolly mammoth

Table 1
Some multiple-mammoth sites in North America. The reference cited for each one provides background summary; other publications with more detail are also available in most cases.

Site and reference	Mammoth MNI	Range or midpoint of ^{14}C date(s) or estimated age (yrs)	Sedimentary/depositional setting
Blackwater Draw, New Mexico (Hester, 1972)	8+	11,630 − 11,040	lake
Colby, Wyoming (Frison and Todd, 1986)	7	11,200	small stream
DeLong, Nevada (Livingston, 1991)	3+	16,000−10,000	stream/lake
Dent, Colorado (Brunswig, 2007)	14	11,200; 10,980 − 10,670	streamside/ford?
Hajny, Oklahoma (Wyckoff et al., 1992)	2	34,000−21,500 (also 165,000−140,000 U/Th dates)	floodplain spring
Hot Springs, South Dakota (Agenbroad and Mead, 1994)	60+	26,000	sinkhole pond
Koehn-Schneider, Kansas (Johnson et al., 1990)	2	11,050 (bone/ivory); 11,170 (overlying sediment)	slow stream
Lamb Spring, Colorado (Rancier et al., 1982)	30+	13,000−11,000	spring pond/stream
Lange-Ferguson, South Dakota (Hannus, 1990)	2	11,140	pond/marsh
Lehner, Arizona (Saunders, 1977a)	13	11,470 − 10,620	streamside/pond
Leikum, Arizona (Saunders, 1980)	2	12,000−10,000	stream
Lubbock Lake, Texas (Johnson, 1987)	3	11,100	point bar in stream
Miami, Texas (Holliday et al., 1994)	5	12,000−10,000	pond in loess
Murray Springs, Arizona (Haynes and Huckell, 2007)	4	11,190 − 10,710	streamside/pond
Rancho La Brea, California (Harris and Jefferson, 1985)	5+	20,000−10,000	slow stream/ephemeral ponds
Saskatoon, Saskatchewan (Pohorecky and Wilson, 1968)	2	35,000+	meltwater stream
Selby and Dutton, Colorado (Stanford, 1979)	2+	16,000−12,000	pond/loess
Tocuila, Mexico (Morett Alatorre and Arroyo Cabrales, 2001)	5+	11,188	atop volcanic ash, in mudflow
Tolo Lake, Idaho (Miller et al., 1996)	10+	[4300 and 5100, both rejected]	lakeside
Waco, Texas (Bongino, 2007)	24	73 − ~50,000	stream

(*M. primigenius*), producing a tally of the few days this animal lived after it was born.

Proboscidean teeth erupt, wear down, and are serially replaced from behind. Each quadrant of the mouth will have six teeth in a lifetime, although supernumerary teeth are also possible (e.g., Burns et al., 2003) but infrequent. The method of counting dentin increments for age determination of animals older than newborns is currently impractical because the precise ages are not known when dentin in each tooth begins to develop in different proboscidean taxa, and the ontogenetic ages when each tooth appears and erupts are at best only estimates. For the counting of increments in tooth dentin to be more widely applicable to all teeth that erupt in life following the first one, the ages when each tooth begins to grow must first be known, requiring further research, as Metcalfe et al. (2010) noted in their study of woolly mammoth growth.

Proboscidean tusks, a specialized type of incisor tooth, can also provide records of the full ontogenetic ages. Their record is visible in section as nested dentin structures laid down in rhythmic layers daily, weekly, and annually over life (Fisher, 2001). The oldest dentin is present at the tip of the ever-growing tusk, and the most recent is at the base, where outward growth occurs. But because the tusks are used frequently to aid in feeding, to move objects, to interact aggressively with conspecifics, and in other actions, the tips continually wear or are serially broken, and over time may not record all years lived.

2.2. Assessing extent of skeletal maturation

Another possible reflection of ages is the extent of epiphyseal fusion on skeletal elements. Epiphyses fuse to diaphyses at patterned rates in maturing mammals. The timing of epiphyseal fusion on certain skeletal elements in *Loxodonta* and *Mammuthus* has been studied to a limited extent (Haynes G., 1991:341−353; Lister, 1994, 1999). Lister (1999) found that the sequence of epiphyseal fusion is similar in *Loxodonta*, *Elephas*, and *Mammuthus*.

Although variability is expected, the application of this age-determination method can place proboscideans into narrowed age categories (which have been defined by tooth wear and progression; see Section 2.3 below), if enough bones are available and

can be reliably associated with specific individuals. This method is not applied as often as analysis of dentitions, because postcranial skeletal elements may not preserve as well as teeth, or may be scattered, commingled, and fragmented by natural or human-induced processes. Another complicating factor is that epiphyses in males and females fuse at different ages. Therefore, an individual's sex must be known before assigning probable ontogenetic age ranges based on degree of skeletal maturation. Sexual dimorphism is pronounced in mammoths and elephants (Haynes G., 1991; Averianov 1996; Lister, 1996), and most elements in mature males differ in size and often shape from those of same-age females. After about 10 years old, some skeletal elements in males may be significantly larger than those of females of the same ages, but they will have more unfused epiphyses than in the same-age females.

Fig. 1 shows estimated ages of fusion scheduling in female (on the left) and male (on the right) *Loxodonta*. The data on Fig. 1 came from a sample of 63 individual African elephants whose ages were determined by matching tooth wear and progression to Laws (1966) age groups I—XXX, during field studies in Zimbabwe (Haynes G., 1991). The Laws age groups with added "a" or "b" indicate slight differences in tooth-wear/progression that fit within the group designation. Also displayed are the numbered tooth or teeth in wear at specific ages and the likely ontogenetic ages in years, which are based on age assignments in Laws (1966) and recent revisions by Lee et al. (2012) and Stansfield (2015). Further research is needed to support the proposed correlations of *Loxodonta* data on this Figure, and their applicability to *Mammuthus*. Lister (e.g., 1994) estimated fusion ages for *M. primigenius* and found similar timing for epiphyseal fusion in a sample of *M. columbi* (North American Columbian mammoth). Both mammoth species showed comparability with *Loxodonta africana* in their fusion scheduling, although with some differences.

2.3. Analysis of progression and wear of mandibular teeth

This method requires careful observation of age-related changes in mammoth mandibular dentition, and most often uses as guidelines the results of studies of free-roaming and captive African elephants (*Loxodonta africana*) (Laws, 1966; Sikes, 1966, 1968) and