Reconstructions of Woolly Mammoth life history

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SUMMARY: How can we know about the life history of an extinct species, such as woolly mammoths? The Pleistocene fossil record can add considerableinformation and inference to help us reconstruct mammoth life history. So also can data from analogies with modern elephants combined with patterns seen among extant northern large-mammals. I focus here on three main categories of very non-elephant like adaptations in the areas of reproductive specialization, the dietary resources available from the unique steppic vegetation in the Pleistocene far north, and life exposed on the cold-arid open steppe. The repercussions of these three to woolly mammoth life history not only form an interesting contrast to the rest of the proboscidians, they make an interesting story of Pleistocene specializations.

1. Introduction

The ecology of an extinct species, like woolly mammoths (*Mammuthus primigenius*), is not easy to reassemble. Fortunately, several ways of approaching this are available. There is a wealth of research on general adaptive patterns in northern ungulates which can help us in this matter, especially when we combine that with details of the frozen mammoth carcasses from the far north. I will focus on three interrelated ecological aspects of woolly mammoths which provide the most contrast with more tropical elephants: (2) the likelihood of adaptive canalization of parturition (and hence conception) into a closely delimited time of the year, (3) adaptations to a dramatically different dietary resource, the low-growth steppic vegetation, (4) and several unusual adaptations to the very open and exposed environment found on steppes. I review but a few of the repercussions within these three categories.

2. Reproductive Adaptations on the Mammoth Steppe

In the far north there is a strikingly predictable contrast to the harshness of winter and the lush greenery of summer. This disparity selects for female ungulates which are more genetically predisposed to ovulating during optimum times of this annual cycle in order to maximize benefits of seasonal timing of that birth. Spring green-up with plants of highest nutrient quality is rather abrupt (at present late May to early June in the north). This nutrient spike (Guthrie 1984) forms a narrow window, a young born too early risks late winter storms, and yet, being born too late loses precious days of the optimum growing season.

There are many evolutionary repercussions of these dynamics which undoubtedly figured into woolly mammoth life history:

• Judging from most ungulate species in the far north, the timing of that birth season would have been targeted on the period of green-up. Pleistocene solar angles, which determine green-up, would likely have been little different than today, but there may have been less cloud cover and less snow cover (Guthrie 2001) which may have pushed the green-up to slightly earlier. As with other northern ungulates a short “canalized” birth season would have been maintained among mammoths by opposing forces of stabilizing selection.

• Assuming a rough 22 month gestation time, as in most living proboscidians, that would have dictated a rut time of sometime near late

July to early August-well past the northern summer's nutrient-caloric peak. Thus, bulls and cows (especially those without calves) would have had time to recover from winter debilitation. This late summer rut would have allowed both sexes to lay down significant fat reserves. For gravid females these future reserves would have been critical because they had to nurse young during the following winter (unlike any other northern ungulate today). Elephants nurse young for 3-5 years (Spinage 1994), and woolly mammoths may have been even more conservative in weaning due to difficulty in finding volumes of easily digestible winter forage. Fat would have been critical for these mothers of nursing young. For males, fat would have been important addition to body mass which increased force and leverage in upcoming rut battles (again, this is the way many northern ungulate males use fat today). Dominant males of several species forgo eating during this sharply defined rut peak and enter winter with reduced body fat.

• Since the mammoth cows coming into estrus would have all done so at almost the same time, there is no selective value for staggered musth year-around as in bull elephants. Rather among mammoths it would have been focused in a two-week, or so, period (the build-up of pre-rut activity may have added another week or two). Sometime in the last half of July, mammoth bulls and cows must have coalesced into mating herds in which all bulls ultimately compete directly for access to each cow as she came in to heat. As with all northern ungulates today, rut would have consisted of a wild melee of courtship, copulation, and aggression. Constraining rut in time and space results in more overtly violent confrontations, favoring dominant bulls and selecting for aggressive qualities and exaggerated weaponry. We can, in fact, see this effect among mammoth fossils-for proboscidians, mammoths have enormously exaggerated tusks in comparison to their body size.

• The special tusk size and shape of mammoths apparently relates to different fighting postures of mammoths in comparison to other proboscidians-again, driven by steppic adaptations of more frequent and violent fights resulting from canalized rut timing. Because of the mammoth's more vertical head (another steppic grazing adaptation), fights took place frontal-to-frontal, very unlike the way elephants fight. Mammoth tusks are curved, each in an opposing gaining-helix toward one another, such that they arc around, and point inward left-and-right, toward the opponent, while two bulls are engaged in a head-to-head position. From this position a strong bull can twist his head and dig the tusk tip into the opponent's vulnerable shoulder or thoracic region. Once engaged in this manner it is very difficult for the weaker one to safely uncouple and retreat, so this kind of fighting would likely be expected either between two playfully sparring adolescents or between two very serious and more equally matched prime-aged opponents. Yet, the situation where no bull would have experienced musth throughout the 11 month remainder of the year, likely firmed the bachelor bands into more permanent groups. This is an important item in reconstructing male social behavior. But there is an important point to be noted, as discussed under the next bullet.

• Trying to decipher tusk use in musth battles of mammoth bulls from the fossil record can easily lead to a mistake for several interrelated reasons: without significant predators mammoths continued to live into post-reproductive years and their tusks continue to grow, the long tusks ultimately spiral beyond a configuration useable as a dangerous weapon. So in old age, the arcing tusk-tips of an old bull approach one another and occasionally even cross. However, this dysfunctional configuration would have presented few difficulties as older animals would be reproductively senile. Musth weakens dramatically among older aged elephants and they are unable to stage a threatening combat with younger prime-aged competitors.

Yet, tusks from older mammoth bulls tend to be over-represented in our fossil sample, because of the taphonomic nature of the record (really a skewed graveyard assemblage where few prime aged bulls died) leading us to the mistaken presumption that long-tusked bulls were the functional norm. It is an interesting evolutionary case of a character using a growth pattern that results in an effective design, but once past an optimal time window this configuration inherently loses its utility. There are some similar examples of this phenomenon among living large mammals-like the horns on some individual African buffalo that ultimately hook back on themselves.

3. Adaptations to an Unusual Dietary Resource

Woolly mammoth adaptations revolved around life on a more open cold steppe of low sward graminoids, unlike that experienced by most other proboscidians. There were several evolutionary repercussions that accompanied this dietary specialization:

• The traditional proboscidian diet is large quantities of easily available, but low quality, vegetation, taken from a very eclectic seasonal variety of species. Woolly mammoths, too, utilized a diverse diet; however, they seem to have focused primarily on thin tufts of sparsely dispersed graminoids, those were the most common plant species (Goetcheus and Birks 2001). These would have had lower biomass per bite but higher quality of nutrient content and caloric digestibility than what is eaten by elephants. Because of the small bite size, mammoths likely spent a large part of the day grazing. Also, the low plant biomass meant that woolly mammoths could quickly exhaust local ranges, particularly in winter, and thus had to be more mobile, on a seasonal scale of large migrations or a semi-nomadic life.

• Both the canalization of rut and the cold and windy winter climates seem to have selected for individual mammoths which acquired large fat reserves. Northern male ungulates today characteristically add 20% of body fat beyond lean winter values. How much fat did mammoth lay down? It is not easy to tell. There are few if any frozen mummies available from the season of peak obesity, just prior to rut (taphonomic circumstances make quality preservation of such a large animal at this warm time of year rare), but frozen mummies, preserved from other seasons, show at least significant fat reserves.

• Bone construction, especially cortex thickness is evolutionarily matched to the intensity of bone loading experienced by the animal. Bone loading of course pertains to the animal's activity, but especially to its body weight, which is to say, its weight at the heaviest time of the year. Of course with seasonal fat, mammoths body weight was probably considerably higher than an elephant of the same stature. This seasonally heavy body may be one of the forces involved in producing the significantly higher bone density of mammoths when compared to elephants (Haynes 1991).

4. The Ecology of Life in the Open

Mammoth life in the vast expanses of treeless steppes was a rather novel niche for proboscidians. To prosper on the steppes probably required many evolutionary changes, including those involving social structure, mobility, dispersal rates, vagility, communication, traditional ties to landscape, and much else:

• Elephant communication in woodlands or savannas occurs mainly within long-distance infrasonic sound ranges. Elephant's large ears not only help in cooling and in visual communication, they may also help in the reception of these long distance sounds. But among woolly mammoth living in the open vistas of the Mammoth Steppe, one could argue that vision is more critical than hearing in spotting and identifying other mammoths. The selective pressures for a protruding "cup" of an external ear would be much weaker among animals in this kind of habitat. Rather, the pressures to conserve heat loss apparently favored small-sized external ear structure of mammoths, quite unlike that of any other living elephants.

• It is possible that various elements of this niche (high mobility, type of food, and climate) on the Mammoth Steppe may have selected for a more conservative life history than among proboscidians in tropical-temperate regions. For example, that the timing of life-junctures we see among today's elephants could have been slowed down among mammoths: lengthening time young males spent in the female herd, and age of female sexual maturity. There are hints of this in the reconstructed survivorship curves using molars from fossil Alaskan mammoths. Those curves show that mortality accelerates rapidly around 20 years of age, which may help us identify the social transitions into adulthood and the higher risks which accompany these life changes.

5. References

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