PNAS COMMENTARY

Wandering mastodons reveal the complexity of Ice Age extinctions

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The extinction of more than 100 genera of giant terrestrial vertebrates in the Quaternary Ice Ages left an indelible imprint on the biodiversity of our planet. These so-called megafauna included a diverse variety of turtles, lizards, snakes, crocodiles, birds, and mammals (1). Although the exact drivers of the losses are unclear, the dominant extinction hypotheses are centered around the impacts of climate change or humans (2). In recent years, there has been a sideways shift in the field of Quaternary biodiversity studies toward metanalytical approaches (3). Vast datasets are routinely compiled from the literature about the extinct giants, mostly centered around geological ages of fossils. If statistical analyses of those datasets indicate that the losses occurred during extreme climate change events or at times of human incursions into new regions, extinction hypotheses are tested and drivers inferred by examining those temporal relationships (4).

Although proponents of "big data" modeling approaches claim to be able to provide substantive insights into patterns and processes of extinction, studies are sometimes limited in scope and utility because they rarely integrate crucial paleobiological and paleoecological information of the extinct species (3). In many cases, megafauna are reduced to little more than names and numbers (in this case, dates) in databases; subtle but critical nuances of life histories are overlooked, basically homogenizing megafaunal biology and ecology. It therefore becomes difficult, if not impossible, to determine if the modeled patterns of extinction in any way truly reflect nature. In PNAS, Miller et al.'s (5) new investigation of the life history of the American mastodon (*Mammut americanum*; Fig. 1) reminds us that the vanished giants of the Quaternary were real animals, ecologically complex, and had life histories that cannot be captured by ones and zeroes in massive databases.

Mastodons are members of the Proboscidea, a diverse order of afrotherian mammals including modern elephants as well as numerous extinct families. The order emerged around 60 Ma in Africa, with subsequent radiations taking place in the latest Oligocene and early Miocene (*ca*. 25 to 20 Ma) (6). The earliest fossil record of the American mastodon dates to around the middle Pliocene (*ca*. 3.5 Ma), having arisen from an ancestor that had earlier crossed the Beringian Isthmus from Eurasia. They dispersed widely through North America and were among the largest megaherbivores on the continent until their extinction in the late Quaternary. Despite having fossils relatively widespread and abundantly represented in collections, little is known about their life history (7).

Miller et al. (5) have made great strides to redress this situation by using a combination of microscopy and geochemical data to reconstruct the paleobiology and paleoecology of the so-called Buesching mastodon from Indiana. The individual is an impressively preserved, nearly complete skeleton of a male that died around 13 ka. They sectioned part of the well-preserved tusk with an aim to understand its growth history, examining sequential layers of dentine from the tip to the cavity. The dentine layers form in a similar fashion to growth rings in a tree, being laid down progressively as the individual matures. The varying thicknesses of the layers can be used to determine responses to both maturation and seasonal changes. Like in modern elephants, mastodon tusks grew continuously through the life of the animal, from the time of eruption to the time of death. By counting the repeating couplets of dentine banding along the tusk, Miller et al. (5) were able to determine that the individual was around 34 y old at the time of its death.

The dentine couplets also provide evidence that the individual separated from the matriarchal herd at around 12 y of age. For the last 8 y of its life, it routinely engaged in combats with other males during musth as it fought to compete for mates. Indeed, it is likely that intrasex fighting led to its death, as suggested by a 5-cm-diameter tusk-shaped puncture wound in its skull.

Miller et al. (5) used a variety of geochemical tools to reconstruct the life history of the Buesching mastodon, including both stable and strontium isotopes focused on the tusk. As per the proverbial saying that "you are what you eat," the chemical signature of food and water intake becomes fixed into mineral tissues as an organism grows. Teeth (including tusks) are unlike bone in that they are not remodeled throughout life. Thus, the chemical signature of diet becomes fixed into the various layers of a tooth as an individual ages. Oxygen isotope data along the tusk (in this case showing water uptake), in conjunction with that of dentine formation, demonstrates that the mastodon mating season occurred during spring to early summer; this was also the time of the Buesching individual's death.

Geochemically speaking, it is also true that "you are where you ate." Strontium signatures from local bedrock become fixed into plants and subsequently the growing tissues of herbivores upon consumption of vegetative matter (8). By examining strontium variations in local geology and comparing that to the signatures preserved in the tusk, Miller et al. (5) were able to infer landscape use and

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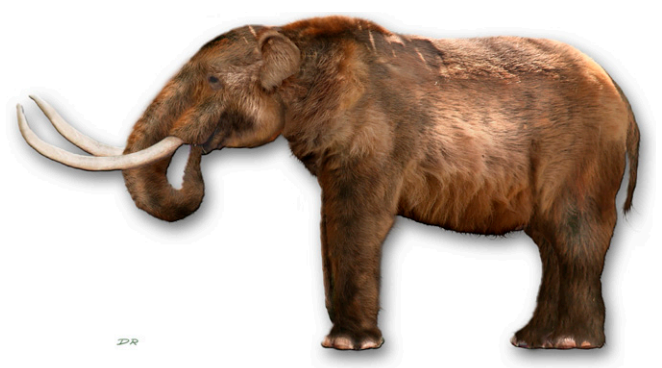

Fig. 1. Reconstruction of the American mastodon (*M. americanum*), an extinct megaherbivore of North America. As a distant relative of modern elephants, the American mastodon stood up to 2.8 m in height at the shoulder and weighed more than 5,000 kg. Image credit: Wikimedia Commons/Dan Reed, licensed under CC BY-SA 3.0.

the core range of the Buesching mastodon. The individual likely called central Indiana home, but as it matured it undertook seasonally patterned migration. The extent of its travels increased through its adulthood, with several northward excursions in the warmer months, traveling several hundreds of kilometers. This migration broadly corresponds with the mating season, suggesting that the Buesching mastodon periodically engaged in reproduction with individuals from a population outside of its natal herd. Strontium data demonstrate that it was somewhat of a wandering vagabond at the time of its death, spending only little time in the area where its fossilized skeleton was eventually discovered.

Miller et al. (5) note that the Buesching mastodon's inferred behavior is similar to that observed in extant elephants. The lineages that eventually led to mastodons (Mummutidae) and elephants (Elephantidae) diverged more than 24 Ma (9), with possible homology in life history due to shared ancestry (5). Interestingly, though, emerging evidence suggests that seasonal migration in Quaternary megafauna may be more widespread than previously thought, and not necessarily tied to phylogeny. For instance, employing a geochemical approach similar to that of Miller et al. (5), an independent study suggested that seasonal migration was also a phenomenon exhibited by the giant wombat-like marsupial Diprotodon (*Diprotodon optatum*) of late Quaternary Australia (10). The lineages that led to marsupials and placentals diverged in the Jurassic (>160 Ma), with the common ancestor being small-bodied, arboreal, and with shrew-like behavior (11). It is possible that the evolution of migration in megaherbivores of the Quaternary may be better explained as behaviorally adaptive responses to enhanced seasonality, especially in resource-limited environments.

Modern megaherbivores are commonly regarded as "ecosystem engineers" considering the dramatic role that they can have in shaping habitats. Given that species such as the American mastodon and other Quaternary North American proboscideans such as the woolly mammoth (*Mammathus primigenius*) were seasonal migrants (5, 12), it is likely they could cause significant and widespread impacts on habitats as they traveled great distances throughout the years. It remains uncertain how the relaxation of herbivory following extinction may have affected remnant ecosystems though, if at all. Emerging evidence from Beringia (centered around Alaska), however, suggests that the processes that drove the extinctions may have been temporally progressive, "bottom-up," and climate-induced, whereby habitat changes preceded the loss of migratory megafaunal herbivores (13, 14). The American mastodon became extirpated from the region around 75 ka following a climate-driven shift in habitat from boreal forest to steppe vegetation (13); the extirpation of the woolly mammoth took place around 14 ka when the steppe reverted back to more woody vegetation (14) but without replacement by mastodons. Although the removal of seasonal migratory species may have had little impact on remnant ecosystems, it is possible that the return to climatic conditions similar to that preextinction may have led to new ecosystem configurations without analog to anything earlier in the Quaternary.

Miller et al. (5) have demonstrated the elegance of applying cutting-edge, integrated methodologies to reveal paleobiological information of species known only from fossils. The sort of data that can be generated using their approach is unparalleled and cannot be gleaned solely from traditional paleontological techniques. It may also be true that it is the kind of information that cannot easily be fed into the "big data" approaches that presently seem to dominate the field of Quaternary extinction studies. This is not to say that metanalytical approaches are not without their value for revealing fundamental insights about Earth's fossil record (15, 16). However, where used incautiously by overlooking crucial aspects of paleobiology and paleoecology of individual species through time and space, they run the risk of complicating scientific discourse with more noise than actual insight (17).

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