Geography Compass (2012): 1–14, 10.1111/j.1749-8198.2012.00483.x

Mastodons and Mammoths in the Great Lakes Region, USA and Canada: New Insights into their Diets as they Neared Extinction

Catherine H. Yansa*, Kristin M. Adams
Michigan State University

Abstract

The conventional image of Ice Age environments of North America includes mammoths feeding on grasses in open tundra or steppe habitats and mastodons browsing on spruce branches in forests. However, re-examination of plant and animal fossil research in the Great Lakes region of the USA and adjacent Ontario, Canada provides new insights into the changing diets of mammoths and mastodons in this region, particularly as these animals neared extinction between 13,500 and 13,000 calendar years Before Present (cal yr BP). This paper reconstructs the following scenario at the end of the Ice Age. Woolly mammoths primarily inhabited tundra adjacent to the northward receding margin of the Laurentide ice sheet. Meanwhile, to the immediate south, Jefferson mammoths grazed on grasses, sedges and herbs around the edges of wetlands, while American mastodons consumed mainly the leaves and branches of spruce and other trees in first an anomalous spruce parkland/sedge wetland environment and later in spruce-dominated forest. However, mammoth and mastodon populations began to dwindle at a time when the succeeding vegetation became a closed forest with a lesser amount of spruce trees, grasses and sedges and a greater abundance of invading deciduous trees. The last mammoths and mastodons in the Great Lakes region bear signs of stress and competition for the same foods in dense coniferous-deciduous forest, which contributed to the extinction of these magnificent beasts by ∼13,000 cal yr BP. This extinction event highlights the fragility of mammal populations under stress; an important lesson given that numerous species today are similarly challenged by climate and landscape change.

Introduction

Mastodons (or mastodonts, *Mammut americanum*) and mammoths (*Mammuthus* species) are two of the ''charismatic megafauna'' of the Ice Age that have captured the public's imagination since their discovery as fossils in the late 18th century (Osborn 1936). The massive size of the skeletons and tusks of these extinct relatives of modern elephants (proboscideans) is part of the appeal of these animals to the public and scientists alike. Mammoths and mastodons disappeared before the end of the Pleistocene (Ice Age) along with several other ''megafauna'' weighing over 44 kg (Martin 1984; Grayson and Meltzer 2003). Given the dwindling numbers and even extinctions in many mammal populations today (e.g. Patterson 2010; Stone 2010; Drake and Griffen 2010), in response to climate change and other factors, there is much interest in understanding the environmental conditions that caused the demise of 35 genera of large mammals between 14,800 and 13,000 cal yr BP (calendar years Before Present) (e.g. Davies et al. 2009; Gill et al. 2009; Saunders et al. 2010; Faith 2011). The value of reconstructing past animal responses to changing climate is well articulated by Patterson (2010, p. 3019), who stated that we should ''use the 'lessons of the Pleistocene' to forecast the biotic effects of [future] climate change.''

Most research on Pleistocene megafauna, including that on mammoths and mastodons, has focused on identifying the cause(s) of their extinction. Various hypotheses have been proposed, and numerous debates have ensued over this controversial subject, which has become a ''hot topic'' in current scientific journals and popular media that may last into the foreseeable future. In brief, the following explanations have been evoked by some researchers and refuted by others: (i) the ''Pleistocene overkill hypothesis,'' where the newly arrived Paleoindians, the first humans to colonize the New World, were largely responsible for excessive hunting, and eventual extinction, of the megafauna in the Americas (e.g. Martin 1984; Fisher 1987; Surovell and Waguespack 2008). (ii) A killer pandemic disease (virus or bacterium) wiped out these Pleistocene megafauna (MacPhee and Marx 1997). (iii) An asteroid impact at 12,900 cal yr BP (calendar years Before Present) caused widespread fires that decimated much of the vegetation of North America, which ultimately caused the megafauna extinctions (Firestone et al. 2007). And, (iv) shifts in climate and vegetation at the end of the Pleistocene glaciation caused this major extinction event, either solo or in tandem with one or more of the above factors, such as human predation on megafauna (e.g. Guthrie 1984; Graham et al. 1996; Barnosky et al. 2004; Gill et al. 2009; Saunders et al. 2010).

In this paper we favor the last hypothesis, that of climate and attenuated ecological changes at the termination of the Pleistocene epoch, as it relates to our reconstruction of mastodon and mammoth habitats and diets in the Great Lakes region of the USA (Minnesota, Wisconsin, Illinois, Indiana, Michigan, and Ohio) and southern Ontario, Canada. Our goal is not to test the validity of this extinction hypothesis, per se. Instead, we (i) explain how three proboscidean species were able to coexist in this region during the terminal Pleistocene, and (ii) elucidate upon dietary shifts of these species as they neared extinction, in response to climate-driven habitat changes. Whereas other authors have focused on the extinction event or reconstructed paleoenvironments for specific mammoth and mastodon sites, this paper represents the first attempt to provide a synthesis of mastodon and mammoth habitats and diets for the Great Lakes region, with respect to these changing climate and vegetation regimes. But first, we describe what these mammals looked like, and explain how they came to live in the Great Lakes region during the Pleistocene.

Mastodon and Mammoth Origins, Morphology and Taxonomy

At first glance, mastodons and mammoths look alike, being elephant-like creatures, but upon closer examination there are several significant differences in the morphology of their teeth and skeletons (Figure 1). Of the two, mastodons have a more primitive body form, being an early offshoot of the ancestral proboscidean line (Haynes 1991). Specifically, mastodons have a robust pig-like body with all legs of the same length, and have flat skulls with tusks that exited the jaws horizontally (Skeels 1962; Holman 2001). Mastodon teeth are very distinctive, in that each tooth is comprised of two parallel rows of large knobs or cusps, a pattern called ''nipple tooth'' (Figure 1; Skeels 1962; Holman 2001). Given the arrangement of their jaws, mastodons chewed up and down, mashing their food, primarily leaves of shrubs and trees, between the knobs (Kurten and Anderson 1980; Holman 2001).

In contrast, mammoths (*Mammuthus* spp.) are more evolved, being closely related to living elephants, and as such they have longer front legs than back legs, creating a sloped

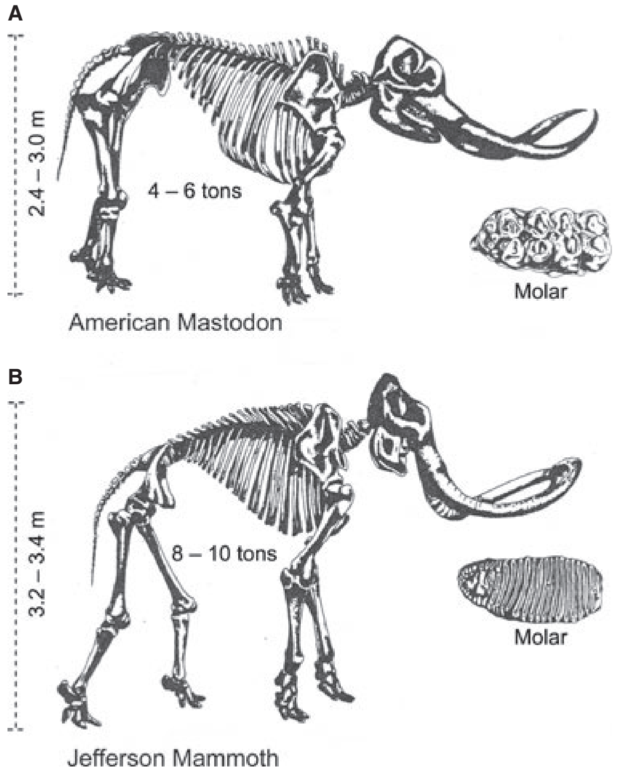


Fig. 1. Skeleton and molar of an American mastodon (A) compared to those of a Jefferson mammoth (B). The height and weight range of each species is shown. Figure is adapted from Holman (2001).

back with a hump behind the neck (Figure 1; Kurten and Anderson 1980). They also have domed skulls with tusks that exit the jaw downwards and then curl outwards (Skeels 1962; Haynes 1991). Mammoth teeth are very different than those of mastodons. Each mammoth tooth has a chewing surface composed of a series of parallel, transverse rows of thin enamel plates (Figure 1). Mammoths ground their food along the surface rows of these enamel plates, with the lower jaw moving backwards and forwards against the upper jaw (Holman 2001). Their teeth were designed to graze on primarily grasses and grass-like plants, such as sedges (e.g. Lister and Bahn 2007).

The ancestors of all proboscideans (mammoths and mastodons) in North America were originally derived from Eurasia and had crossed the Bering land bridge that once connected Siberia to Alaska (Kurten and Anderson 1980; Agenbroad 1984). Ancestral mastodons arrived in North America about 2 million years ago and developed into the American mastodon (*Mammut americanum*) (Kurten and Anderson 1980). By the late Pleistocene, mastodons (i.e., American mastodons) ranged from south of the glacier margins to Florida, and in smaller numbers inhabited presumably woody habitats in the Great Plains, western United States and Mexico (Kurten and Anderson 1980; McAndrews and Jackson 1988).

In contrast, there were two migration waves of mammoths across the Bering land bridge (Figure 2A). First, the steppe mammoth (probably *Mammuthus trogontherii*) arrived in North America at ~1.1 million yr BP (Lister and Bahn 2007). This species developed into the Columbian mammoth (*Mammuthus columbi*), which inhabited the western United

Fig. 2. (A) A generalized depiction of the two migrations of mammoth species from Siberia via Beringia; once in North American these species dispersed in more directions than indicated. (B) Site localities for American mastodon, Jefferson mammoth, woolly mammoth, mammoth (not identified to species) and proboscidean (not distinguished between mastodon or mammoth) in the Great Lakes region. Note the Mason-Quimby Line, which is the approximate northern limit of these taxa in this region: MN (Minnesota), WI (Wisconsin), IL (Illinois), IN (Indiana), OH (Ohio), MI (Michigan) and ON (Ontario). These data capture all fossil localities dated between 24,000 and 13,000 cal yr BP.

States south to Nicaragua, and hence never ventured into the Great Lakes region (Kurten and Anderson 1980; Lister and Bahn 2007). Later, a population of woolly mammoth (*Mammuthus primigenius*), which evolved from *Mammuthus trogontherii* in Siberia, arrived in Alaska at ~100,000 yr BP (Figure 2A), and from there spread to occupy land around the margins of the ice sheets to as far south as the mid-section of the United States (including the Great Lakes region) and the Atlantic coast (Figure 2B; Kurten and Anderson 1980; Agenbroad 1984).

A third type, called the Jefferson mammoth (*Mammuthus jeffersonii*), emerged in the Midwest USA during the Middle Pleistocene, although its identity has been a topic of debate among paleontologists. Some propose it to be a legitimate species (e.g. Madden 1981; Saunders et al. 2010), whereas others contend that the Jefferson mammoth was a Midwestern version (variant) of the Columbian mammoth (Kurten and Anderson 1980; Pasenko and Schubert 2004), or a hybrid of the Columbian and woolly mammoths (Fisher 2001, 2009). Regardless of the Jefferson mammoth's exact identity, we recognize that it was one of two types of mammoths that once inhabited the Great Lakes region and will now explore ideas of how they co-existed with each other and with mastodons (Figure 2B).

Data Sources

Mammoth and mastodon bones and teeth (including tusks, which are enlarged incisors) are more common within the Great Lakes region than in any other area of North America. In particular, they are most abundant within the area that was covered by the Laurentide ice sheet during the Late Wisconsin: all of Ontario, Canada, and in the United States, Michigan, most of Wisconsin and Minnesota, and the northern parts of Illinois, Indiana and Ohio (Holman 2001). This ice sheet reached this maximum limit between 24,000 and 18,000 cal yr BP (Figure 2B), and afterwards began to retreat by melting, to reach the northern limit of the Great Lakes region by 13,000 cal yr BP (Hupy and Yansa 2009). In the wake of the melting glacier, abundant glacial streams carried meltwater south and millions of ponds, lakes and lowlands were created (Hupy and Yansa 2009). Fragmentary proboscidean remains have sometimes been recovered from glacial till and glaciofluvial sand and gravel deposits, indicating ice and water transport of fossils from depositional sites, but the majority of finds, those from lake and pond sites, are intact (Holman 2001). Hundreds, if not thousands, of proboscideans (mammoths and mastodons) probably inadvertently fell into some of these ponds and lakes when walking over snow-covered thin ice (Holman 2001). The bones and teeth of many of these megafauna have been preserved in place, buried in clay-rich sediments below the water table (Holman 2001; Hupy and Yansa 2009).

South of the glacial limit there are fewer depositional sites with preserved fossils. Some caves, such as those in southern Indiana, contain mammoth and/or mastodon skeletons (Holman 2001). Most fossil remains in the ''unglaciated'' area, however, are fragmentary, in that they are recovered from glaciofluvial outwash (Holman 2001). Therefore, the dataset of megafauna and plants fossils are biased towards those records from within the formerly ''glaciated'' (northern) portion of the Great Lakes region (Figure 2B).

There are also several additional biases in the regional dataset. For example, recovered proboscidean materials come from accidental discoveries, such as by crews excavating and constructing roads and bridges, and farmers digging ponds and ditches. Only a few of these fossil sites have been properly excavated, studied and reported by scientists, and even a smaller number included analysis of the plant fossils from the sediments encasing the megafauna remains. So additional information about the vegetation at the times mammoths and mastodons were alive comes from temporal correlation to radiocarbon-dated pollen and macrofossils (cones, seed, leaves) records from nearby lake sites. However, not all mammal and plant fossil records are radiocarbon (^{14}C) dated. But for those that are, we calibrated the ^{14}C ages of fossils (bones, teeth and terrestrial plant fossils) using Calib 6.0 (http://calib.qub.ac.uk/calib/calib.html) and present the timing of events in ''cal yr BP.'' 3

For this paper we captured data from FAUNMAP, a web-based electronic database (http://www.neotomadb.org/), as well as gathered information from the ''gray literature,'' specifically newspapers, unpublished museum reports and state academic publications. Using these data, we explore ideas about how and why mammoths (Family Elephantidae) and mastodons (Family Mammutidae), while both being proboscideans (members of the Order Proboscidea), were able to occupy overlapping ranges in the Great Lakes region during a time of significant environmental changes. We also evaluate the hypothesis that after ~13,500 cal yr BP these species adapted their diets to new and less ideal habitats, which made them more vulnerable to extinction.

Mastodon and Mammoth Distribution and Relative Abundance in the Great Lakes Region

Figure 2B shows the site locations of American mastodon, Jefferson mammoth, woolly mammoth as well as unidentified mammoth and proboscidean (either mammoth or mastodon) sites in the Great Lakes region. This figure captures more site localities than available in FAUNMAP or in Holman (2001). The American mastodon data are accurate, but there are resolution problems with some of the mammoth data. Specifically, some mammoth remains were not identified to species, such as those in Ontario and, as mentioned above, not all paleontologists recognize the Jefferson mammoth (*Mammuthus jeffersonii*) as a viable species and identified it as such (Pasenko and Schubert 2004; Saunders et al. 2010). Nevertheless, a closer look at these data reveals several interesting patterns.

For starters, mastodons were 4:1 more abundant than mammoths in Michigan and Ohio, which Abraczinskas (1993) and Holman (2001) attributed to the greater abundance of trees and shrubs in these areas, compared to the western Great Lakes states. Most of these mammoths were probably Jefferson mammoths, including those unidentified in Ontario (Figure 2B). Conversely, mammoths (both species) were more common than mastodons westward, in Wisconsin and especially in Minnesota, because of the greater acreage of open habitats there (Figure 2B; Holman 2001).

Mastodons and woolly mammoths are documented to have occupied areas immediately south of the maximum limit of the Laurentide ice sheet, from ~24,000 to 18,000 cal yr BP (King 1973; Jackson et al. 2000; Saunders et al. 2010). These species migrated northwards with subsequent glacier retreat to occupy parts of northern Illinois, southern Wisconsin, Lower Michigan and southern Ontario until as late as 13,500 cal yr BP (woolly mammoths) and 13,000 cal yr BP (mastodons) (McAndrews and Jackson 1988; Holman 2001; Saunders et al. 2010). Fewer Jefferson mammoths have been recognized, for reasons discussed above, and hence dated, but those in Illinois, for example, range from 20,900 to 13,300 cal yr BP (Pasenko and Schubert 2004; Saunders et al. 2010).

The northern limit of mammoths and mastodons in the Great Lakes region (Figure 2B) has been referred to by Skeels (1962) and others as the ''Mason-Quimby Line;'' so named after the University of Michigan archaeologists, R.J. Mason and G.I. Quimby, who first mapped the northernmost occurrences of proboscidean remains and Paleoindian artifacts in the mid-section of Lower Michigan. This line was later extended roughly east-west into southern Ontario (McAndrews and Jackson 1988; Holman 2001), and in Figure 2B we took the liberty of continuing it farther, in a northwesterly direction across Wisconsin and Minnesota. The Mason-Quimby Line may reflect the timing of deglaciation, respective to the uncovering of land that allowed for plant and animal colonization (Holman 2001), prior to the megafauna extinction event.

Another interesting observation from Figure 2B is that mammoth and mastodon sites are most numerous in Michigan, compared to the other Great Lakes states and province (Ontario). Holman (2001) earlier noted this pattern and provided two explanations, the first being that numerous bogs, ponds and lakes in Michigan trapped some of these mega-herbivores. He further suggested that numerous salt seeps and shallow saline water were available in southern Lower Michigan, which periodically (annually?) attracted mammoths and mastodons from other areas of the Great Lakes region to replenish their salt supply. Holman's (2001) reasoning came from his readings of African elephant biology and behavior. Elephants must periodically intake salt to counteract the excessive potassium they ingest by consuming plants, and are reported to travel great distances to salt licks when they crave sodium (Haynes 1991). When waterholes dry up in Africa, elephants will use their tusks to dig up compacted salt-rich soil, which they then consume (Haynes 1991).

Available data suggest mammoths and mastodons similarly utilized salt deposits. For instance, Holman (2001) noted that many mammoth and mastodon sites cluster around known salt deposits in southern Lower Michigan. Furthermore, McAndrews (2003) analysis of dung associated with a mastodon skeleton indicates that mastodons regularly ate clay, rich in mineral salts, to detoxify the chemicals (terpenes) in the spruce needles and twigs they consumed.

Mastodon and Mammoth Habitats and Diets in the Great Lakes Region

For the most part, mastodons were browsers of shrub and tree leaves, including spruce twigs, needles and bark, whereas mammoths were grazers of grasses and grass-like plants. However, some dietary exceptions indicate that these two types of proboscideans were adaptable, to a point. After a thorough review we have detected patterns that allow us to pose tentative answers to several outstanding questions regarding mastodon and mammoth habitats and diets in the

GREAT LAKES REGION

How were the woolly and Jefferson mammoths able to co-inhabit the great lakes region? Both mammoth species apparently occupied a ''refugium,'' a vegetated area south of the Laurentide ice sheet, during the height of the last (Late Wisconsinan) glaciation, between 24,000 and 18,000 cal yr BP, as evidenced by a few skeletons of each species recovered from southern Illinois and other locales (e.g. King 1973; Saunders et al. 2010). Available pollen and plant macrofossil data reconstruct that these animals lived in a ''mosaic'' of various habitats, comprised of patches of tundra, open boreal woodlands, mixed coniferous-deciduous forest and pine woodlands (King 1973; Jackson et al. 2000; Webb et al. 2004). Compared to today, there was greater habitat diversity and a more open landscape with fewer trees in areas south of the glacier limit, which permitted a greater abundance of grasses and sedges (Webb et al. 2004), the favorite food of mammoths. But how the woolly and Jefferson mammoths were able to partition habitats is unknown. The climate was also unlike modern. Annual temperatures in this refugium were 5–10 °C less than modern during the height of the last glaciation, with greater cooling at any given time in areas closest to the Laurentide ice sheet (Jackson et al. 2000).

Available fossil data from within the formerly glaciated area, suggest that Arctic-adapted woolly mammoths, for the most part, tracked the northward shift of tundra, which hugged the retreating margin of the Laurentide ice sheet (Holman 2001; Agenbroad 2005; Saunders et al. 2010). For example, the Muirkirk woolly mammoth skeleton in southern Ontario is associated with tundra-boreal woodland plant fossils and dates to 14, 050 cal yr BP, shortly after deglaciation in the area (Harrington et al. 2011). We [5] assume that these animals consumed a diet similar to that of the woolly mammoths in northeastern Siberia during this time, the latter we know well from the intact stomach contents of numerous carcasses preserved in the Siberian permafrost (e.g. Lister and Bahn 2007). Studies of these frozen mammoths reveal that grasses and grass-like sedges comprised about 90% of their diet, supplemented by small amounts of the leaves and twigs of tundra shrubs (birch, alder, willow), and needles of a boreal tree (tamarack) (e.g. Lister and Bahn 2007). Similar Arctic tundra herb/shrub and boreal tree species existed in the Great Lakes region when woolly mammoths inhabited the region (Curry and Yansa 2004), and so we can suppose that woolly mammoths in North America ate a comparable diet. Tundra vegetation, perhaps occurring in patches, inhabited northeastern Illinois from 21,700 to 16,200 cal yr BP (Curry and Yansa 2004; Curry et al. 2010), eastern Wisconsin shortly after 14,500 cal yr BP (Maher et al. 1998; Yansa et al. 2009), and northern Lower Michigan at ~12,000 cal yr BP (Larson et al. 1994). The later dates towards the north result from the south-to-north recession of the Laurentide ice sheet margin.

While the woolly mammoths probably favored the tundra habitat closest to this ice sheet, the Jefferson mammoths seemingly preferred parklands with scattered trees located farther south (Oltz. and Kapp 1963; Pasenko and Schubert 2004; Saunders et al. 2010), thereby reducing competition for food between these two species. In post-glacial plant succession, the pioneering tundra vegetation was replaced by an anomalous spruce parkland/sedge wetland biome that extended from the eastern Dakotas to the Atlantic coast (Grimm and Jacobson. 2004; Webb et al. 2004; Yansa 2006; Hupy and Yansa 2009), and it was this habitat that the Jefferson mammoth apparently occupied until 14,100 to 13,300 cal yr BP (e.g. Pasenko and Schubert 2004; Joyce 2006; Yansa et al. 2009; Saunders et al. 2010). In this environment, uplands were covered by grasses, wormwood and other herbs and scattered trees, primarily of white spruce (*Picea glauca*) and black spruce (*Picea mariana*) with lesser amounts of balsam fir (*Abies balsamea*) and black ash (*Fraxinus nigra*), whereas lowlands were inhabited by shoreline herbs (e.g. *Ranunculus* sp.), sedges (*Carex* spp., *Cladium* spp.), and aquatic plants and some of the aforementioned trees (Hupy and Yansa 2009). Several of these species are shown in Figure 3, which is a photograph of fossils collected from a typical spruce parkland deposit. This vegetation was time-transgressive, following the distribution of tundra as it shifted northwards with the retreating Laurentide ice sheet (e.g. Yansa 2006). For example, this parkland/wetland existed from 19,000 to 14,100 cal yr BP in northern Illinois (Gonzales and Grimm 2009; Saunders et al. 2010), 15,500 to 14,100 cal yr BP in southern Wisconsin (Fredlund et al.

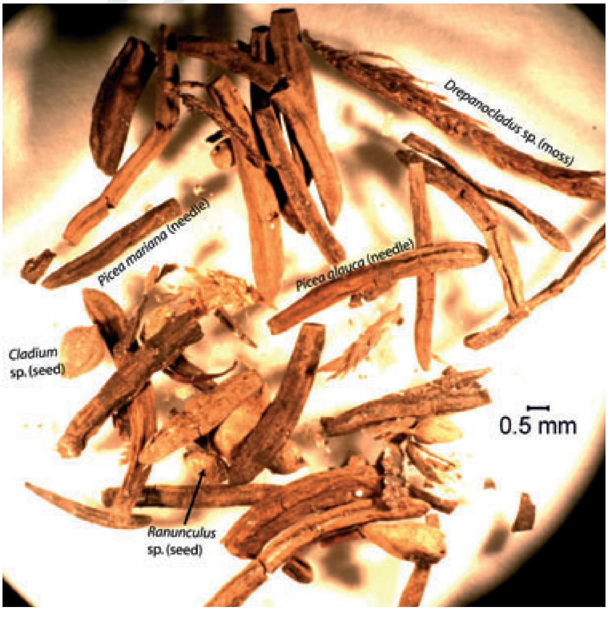


Fig. 3. Image of fossils representative of the spruce parkland vegetation – abundant needles of white spruce (*Picea glauca*) and black spruce (*P. mariana*) and some seeds of shoreline plants (e.g., *Cladium* sp. and *Ranunculus* sp.).

1996; Yansa et al. 2009), and 15,300 to 11,400 cal yr BP in southern Lower Michigan (Hupy and Yansa 2009).

We are the first to propose, here, that sedges and other herbaceous plants around the shorelines of numerous ponds, lakes and rivers in the spruce parkland biome were the primary food sources of the Jefferson mammoth in the Great Lakes region. And in doing so, the Jefferson mammoth probably came into more contact with the American mastodon than did the tundra-adapted woolly mammoth.

How did the mastodons and mammoths partition habitats in the great lakes region?

Mammoths, particularly the Jefferson mammoths, and American mastodons overlapped in range in the Great Lakes region (Figure 2B), which suggests that they partitioned plant foods by each consuming different plants within the same landscape. We propose that Jefferson mammoths consumed primarily herbaceous plants, probably those ringing ponds, lakes and streams, while mastodons browsed the leaves and stems of nearby trees and shrubs, as depicted in Figure 4. At times these two species co-occupied the same area, but at other times they may have favored different geographic locations according to their habitat preferences. Evidence for the latter assumption is based on fossil site locations in southern Ontario. McAndrews and Jackson (1988) reported that most (90%) of the mastodon sites are located in swampy lowlands and abandoned lake plains where black spruce and tamarack (*Larix*) were most abundant, whereas most of the mammoth (species undetermined) locales are situated on higher ground, primarily along the shorelines of lakes.

We have a better understanding of the American mastodon diet in the Great Lakes region because of a few studies of preserved dung and intestinal contents of this species (e.g. Dreimanis 1968; Kapp 1986; McAndrews and Jackson 1988; McAndrews 2003). From these sources we know that the conventional food stuff of mastodons was primarily spruce needles and twigs, although tamarack materials were sometimes eaten (e.g. Stoutamire and Benninghoff 1964; Dreimanis 1968; Shoshani et al. 1989; Holman 2001). Specifically, mastodons were most commonly associated with the spruce parkland described above (e.g. Dreimanis 1968; Jackson et al. 1986; Bearss and Kapp 1987; Shoshani et al. 1989), although they did inhabit the subsequent closed-forest vegetation (Whitehead et al. 1982; Graham et al. 1983). For example, while mastodons in southern Lower Michigan existed in an open spruce parkland at about 14,000 cal yr BP (e.g. Stoutamire and Benninghoff 1964; Holman 2001), those farther south, such as in northern Illinois, lived

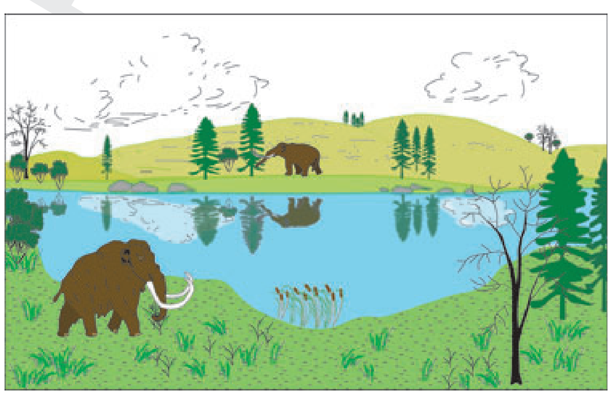


Fig. 4. A schematic of habitat partitioning during the spruce parkland-sedge parkland phase, with an American mastodon (background) browsing on spruce branches, while a Jefferson mammoth (foreground) is feeding on grasses and sedges.

in a closed, mixed coniferous-deciduous forest, the subsequent stage in postglacial plant succession (Gonzales and Grimm 2009; Saunders et al. 2010). Compared to before, this forest was comprised of lesser amounts of white and black spruce, the leaves of which mastodons likely consumed, and greater numbers of other trees (fir, hornbeam (*Ostrya*-type), oak (*Quercus*) and black ash), which were probably not eaten (Gonzales and Grimm 2009; Saunders et al. 2010). Curiously, there are a few reports of mastodons and mammoths consuming other plants (Graham et al. 1983; Lepper et al. 1991; Saunders et al. 2010), but these date to after 13,500 cal yr BP, and probably reflect a dietary widening under stress, as these mammals neared extinction.

A few researchers report dietary shifts for other herbivores at the end of the Pleistocene based on isotopic ratios obtained from teeth and bone, and microwear analysis of teeth. For example, Sánchez et al. (2004) attribute a narrowing of dietary choices in South American gomphotheres (a primitive relative of proboscideans) in the Late Pleistocene to be a major cause of their extinction. Rivals et al. (2007) infer bison adaptation to a change in forage type from the Pleistocene to Holocene, but in this case a species of bison survived in the U.S.A. Also, Koch et al.'s (1995) isotopic study of living and recently dead African elephants tracks their changes in diet from trees and shrubs to grasses in response to arboreal plant loss and range restrictions. These studies provide supporting evidence for our conceptual model regarding Great Lakes proboscideans.

Did mastodon and mammoth diets change as they neared extinction?

The youngest mastodons and mammoths in the Great Lakes region are those dating from 13,500 to 13,000 cal yr BP (Saunders et al. 2010). The teeth and skeletons of these last proboscideans show signs of stress, presumably from trying to adapt to closed-forest habitats, either that of an unusual black ash-spruce-fir forest or spruce-fir forest, in much of the region (Woodman and Branstrator 2008; Gonzales and Grimm 2009). In these forests there would have been lesser amounts of grass, sedge and other herbs favored by the mammoths, and diminished quantities of spruce for mastodons. The Bølling-Allerød warm episode (14,600 to 12,900 cal yr BP), as identified in the Greenland ice cores (Björck et al. 1998), favored the established of these forests, which differed significantly from the earlier tundra and open spruce parkland/wetland to which mammoths and mastodons were probably better adapted (Gonzales and Grimm 2009). A few relict pockets of tundra and spruce parkland persisted in southeastern Michigan and adjacent Ontario (Bearss and Kapp 1987; Kapp 1999), which may partly explain the abundance of proboscidean sites in these areas dating between 13,500 and 13,000 cal yr BP (Figure 2B).

Balsam fir and black ash in these forests of the southern Great Lakes region, during the Bølling-Allerød, indicate a very wet climate, but it may have been mainly in the form of heavy winter snowfall (Gonzales and Grimm 2009). We further reason that thick snow during winters made it difficult for mammoths and mastodons to uncover grasses and other plants to eat and traverse long distances. For comparison, African elephants eat 180 kg (400 lbs) of food per day and feed for about 20 hours a day (Lister and Bahn 2007), and if food stuffs for their relatives, the mastodons and mammoths, dwindled in quantity, these animals would have been undernourished. Fisher's (1987, 2009) analysis of tusks to determine growth rates of the youngest mastodons in Michigan reveal that these mammals shortened the number of years to sexual maturation, from 12 to 9 years, as they neared extinction. Earlier sexual maturity is a common response of animals to stress (Fisher 1987, 2009).

We propose that the last mammoths and mastodons shifted their diets as an adaptation to these deteriorating environmental conditions. Pollen and plant macrofossil analysis of the intestinal contents of a mastodon recovered from central Ohio reveal that this animal consumed primarily sedges, grasses, weeds and even mosses and aquatic plants along with some twigs of deciduous trees at 13,520 cal yr BP (Lepper et al. 1991). Given this information, we suggest that there was a decline in the abundance of spruce which forced this mastodon to consume herbaceous plants that brought it into direct competition with mammoths and other herbivores. Other competitors included the now extinct stag-moose (*Cervalces scotti*) and Harlan's (helmeted, woodland) muskox (*Bootherium bombifrons*), and several species that exist today, such as moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) (Shoshani et al. 1989; Holman 2001).

Surprisingly, the youngest mammoth so far reported for the Great Lakes region is a woolly mammoth (identity confirmed by an expert who recognizes both mammoth species) found on the grounds of Lincoln College, central Illinois, which dates to 13,500 cal yr BP (Saunders et al. 2010). Apparently, this mammoth, and presumably a few others, failed to track the northward shift of tundra vegetation, because pollen data indicate the Lincoln College woolly mammoth existed in a closed-canopy ash-spruce forest (Saunders et al. 2010). Extensive wear on its teeth suggest that this animal consumed leaves and other foods for which it was not adapted (Saunders et al. 2010). Moreover, the isotopic ($\delta^{13}C$) value from collagen of this woolly mammoth is nearly identical to the $\delta^{13}C$ values obtained for American mastodons of similar age from Illinois, which indicate that these last proboscideans shared a similar diet (Saunders et al. 2010). These data suggest that for the first time there was extensive niche overlap between mammoths and mastodons as they competed for the same foods, along with other herbivores, which made them highly vulnerable to regional extinction during a time of vegetation change. While other factors may have played a role in the extinction of mastodons and mammoths, such as human predation in some cases (e.g. Fisher 1987, 2009), without a doubt the changing climate and vegetation during the Bølling-Allerød was a significant contributor to the demise of these magnificent elephant-like creatures.

Summary and Final Remarks

At first glance, people have branded mammoths as grazers in open tundra or steppe and mastodons as browsers in parklands or forests, and consequently thought to have inhabited different habitats. Closer examination of the paleontological and paleobotanical data associated with two species of mammoth and one of mastodon in the Great Lakes region reveals a more complex situation, particularly as these megafauna neared extinction between 13,500 and 13,000 cal yr BP. This paper represents the first attempt to reconstruct mastodon and mammoth habitats and diets for this region of North America, a place where both types of proboscidean overlapped in range and their fossils have been commonly preserved along with plant remains in lowland settings.

During the height of the last glaciation (24,000 to 18,000 cal yr BP), mammoths and mastodons existed south of the maximum limit of the Laurentide ice sheet in a mosaic landscape with great habitat diversity. Upon melting of this ice sheet, woolly mammoths generally tracked the northward recession of the glacier, because they fed on the ice-front tundra plants. To the immediately south, Jefferson mammoths and American mastodons overlapped in range and probably partitioned habitats within the spruce parkland/sedge wetland biome. Specifically, the Jefferson mammoths may have favored sedges and herbs along the shores of wetlands, whereas the mastodons targeted the browse (leaves and twigs) of spruce trees and other plants within the parkland and later forested habitats. This dietary arrangement broke down as climate changed and impacted vegetation, as a result populations of these proboscideans dwindled. There is evidence for a woolly mammoth, and presumably a few others, competing with mastodons for the browse of deciduous trees and other plants in closed ash-spruce and spruce-fir forests in the southern portion of this region at 13,500 cal yr BP. Snowfall may have increased, making it more difficult for the proboscideans to obtain enough feed during winters. Mastodons, and presumably mammoths, matured at younger ages as they neared extinction, which is a typical mammalian response to environmental stress. But the changes in climate towards the end of the Bølling-Allerød warm episode, along with biome shifts and plant community reorganizations, and other factors were too much and both the mammoths and mastodons became extinct between 13,500 and 13,000 cal yr BP. This extinction event provides us an example as to the sensitivity of mammal populations to changing climates and habitats, a situation numerous species are experiencing now and into the near future.

Short Biographies

Catherine H. Yansa is an Associate Professor of Geography at Michigan State University. Her research and teaching focus on reconstructing past landscape changes since the last glaciation based on the analysis of fossil pollen and plant macrofossils (seeds, leaves and other remains) recovered from wetland sediments. Yansa studies tundra and spruce parkland/forest fossils at sites in the Midwest and Northern Plains of the United States and Canada. She also works with archaeologists and paleontologists in interpretation the paleovegetation associated with mammoths at several sites in Wisconsin and Michigan and plans to conduct similar environment reconstructions for other megafauna sites.

Kristin M. Adams is a M.S. student in the Department of Geography at Michigan State University, studying under Catherine Yansa. Her thesis research involves using GIS techniques to determine geographic ranges of mammoths and mastodons in the Great Lakes Region during the Late Pleistocene. Utilizing known proboscidean site localities associated, both directly and indirectly, with dates and documented pollen and plant macrofossil studies, Adams' research tests whether GIS and statistics can be utilized in determining mammoth and mastodon habitats and home ranges.

Note

* Correspondence address: Catherine H. Yansa, Department of Geography, Michigan State University, East Lansing, MI 48824, USA. E-mail: yansa@msu.edu.

References

Abraczinskas, L. M. (1993). Pleistocene proboscidean sites in Michigan: new records and an update on published sites. *Michigan Academician* 25, pp. 443–490.

Agenbroad, L. D. (1984). New World mammoth distribution. In: Martin, P. S. and Klein, R. G. (eds) *Quaternary extinctions: a prehistoric revolution*. Tucson: University of Arizona Press, pp. 90–108.

Agenbroad, L. D. (2005). North American proboscidean mammoths: the state of knowledge, 2003. *Quaternary International* 126, pp. 73–92.

Barnosky, A. D., et al. (2004). Assessing the causes of Late Pleistocene Extinctions on the continents. *Science* 306, pp. 70–75.

Bearss, R. E. and Kapp, R. O. (1987). Vegetation associated with the Heisler Mastodon site, Calhoun County, Michigan. *Michigan Academician* 19, pp. 133–140.

Björck, S., et al. (1998). An event stratigraphy for the last termination in the North Atlantic region based on the Greenland ice-core record: a proposal by the INTIMATE group. *Journal of Quaternary Science* 13, pp. 283–292.

Curry, B. B. and Yansa, C. H. (2004). Stagnation of the Harvard sublobe (Lake Michigan lobe) in northeastern Illinois, USA, from 24,000 to 17,600 BP and subsequent tundra-like ice-marginal paleoenvironments from 17,600 to 15,700 BP. *Géographie Physique et Quaternaire* 58, pp. 305–321.

Curry, B. B., et al. (2010). The DeKalb mounds of northeastern Illinois as archives of deglacial history and postglacial environments. *Quaternary Research* 74, pp. 82–90.

Davies, T. J., Purvis, A. and Gittleman, J. L. (2009). Quaternary climate change and the geographic ranges of mammals. *The American Naturalist* 174 (3), pp. 297–307.

Drake, J. M. and Griffen, B. D. (2010). Early warning signals of extinction in deteriorating environments. *Nature* 467, pp. 456–459.

Dreimanis, A. (1968). Extinction of mastodons in eastern North America: testing a new climatic-environmental hypothesis. *Ohio Journal of Science* 68, pp. 257–272.

Faith, J. T. (2011). Late Pleistocene climate change, nutrient cycling, and the megafaunal extinctions in North America. *Quaternary Science Reviews* 30, pp. 1675–1680.

Firestone, R. B., et al. (2007). Evidence for an extraterrestrial impact 12,900 years ago that contributed to the megafaunal extinctions and the Younger Dryas cooling. *Proceedings of the National Academy of Sciences* 104 (41), pp. 16016–16021.

Fisher, D. C. (1987). Mastodont procurement by Paleoindians of the Great Lakes Region: Hunting or scavenging? In: Nitecki, M. H. and Nitecki, D. V. (eds) *The evolution of human hunting*. New York: Plenum, pp. 309–421.

Fisher, D. C. (2001). Season of death, growth rates, and life history of North American mammoths. In: West, D. L. (ed.) *Mammoth site studies: proceedings of the first international conference on mammoth site studies*. Lawrence, Kansas: University of Kansas, Publications in Anthropology 22, pp. 121–135.

Fisher, D. C. (2009). Paleobiology and extinction of proboscideans in the Great Lakes region of North America. In: Haynes, G. (ed.) *American megafaunal extinctions at the end of the Pleistocene*. New York: Springer, pp. 55–75.

Fredlund, G. G., et al. (1996). Late Pleistocene vegetation of Hebior mammoth site, southeastern Wisconsin. *Current Research in the Pleistocene* 13, pp. 87–89.

Gill, J. L., et al. (2009). Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* 326 (5956), pp. 1100–1103.

Gonzales, L. M. and Grimm, E. C. (2009). Synchronization of late-glacial vegetation changes at Crystal Lake, Illinois, USA with the North Atlantic Event Stratigraphy. *Quaternary Research* 72, pp. 234–245.

Graham, R. W., Holman, J. A. and Parmalee, P. W. (1983). Taphonomy and paleoecology of the Christensen Bog Mastodon Bone Bed, Hancock County, Indiana. *Illinois State Museum, Report Investigations* 38, pp. 1–29.

Graham, R. W., et al. (1996). Spatial response of mammals to late Quaternary environmental fluctuations. *Science* 272 (5268), pp. 1601–1606.

Grayson, D. K. and Meltzer, D. J. (2003). A requiem for North American overkill. *Journal of Archaeological Science* 30, pp. 585–593.

Grimm, E. C. and Jacobson ., G. L. Jr. (2004). Late-Quaternary vegetation history of the eastern United States. In: Gillespie, A. R., Porter, S. C. and Atwater, B. F. (eds) *The Quaternary Period in the United States*. Amsterdam: Elsevier, pp. 381–402.

Guthrie, R. W. (1984). Mosaics, allochemics and nutrients: an ecological theory of late Pleistocene megafaunal extinctions. In: Martin, P. S. and Klein, R. G. (eds) *Quaternary extinctions: a prehistoric revolution*. Tucson: University of Arizona Press, pp. 259–298.

Harrington, C. R., Mol, D. and van der Plicht, J. (2011). The Muirkirk mammoth: a late Pleistocene woolly mammoth (*Mammuthus primigenius*) skeleton from southern Ontario, Canada. *Quaternary International* ??? pp. 1–8. in press. 6

Haynes, G. (1991). *Mammoths, mastodonts, and elephants*. Cambridge, UK: Cambridge University Press.

Holman, J. A. (2001). *In quest of great lakes ice age vertebrates*. East Lansing: Michigan State University Press.

Hupy, C.M. and Yansa, C.H. (2009). Chapter 7, The last 17,000 years of vegetation history [of Michigan]. In: Schaetzl, R.J., Darden, J.T. and Brandt, D. (eds) *Michigan geography and geology*. Boston: Pearson Custom Publishers, pp. 91–105.

Jackson, S. T., Whitehead, D. R. and Ellis, G. D. (1986) Late-glacial and early Holocene vegetational history at the Kolarik mastodon site, northwestern Indiana. *American Midland Naturalist* 111, pp. 361–373.

Jackson, S. T., et al. (2000). Vegetation and environment in eastern North America during the Last Glacial Maximum. *Quaternary Science Reviews* 19, pp. 489–508.

Joyce, D. J. (2006). Chronology and new research on the Schaefer mammoth (*Mammuthus primigenius*) site, Kenosha County, Wisconsin, USA. *Quaternary International* 142-143, pp. 44–57.

Kapp, R. O. (1986). Late-glacial pollen and macrofossils associated with the Rappuhn mastodont (Lapeer County, Michigan). *American Midland Naturalist* 116 (2), pp. 368–77.

Kapp, R. O. (1999). Michigan Late Pleistocene, Holocene and presettlement vegetation and climate. In: Halsey, J. R. and Stafford, M. D. (eds) *Retrieving Michigan's Buried Past: the archaeology of the Great Lakes State*. ???: Cranbrook Institute of Science, pp. 30–58. 7

King, J. E. (1973). Late Pleistocene palynology and biogeography of the western Missouri Ozarks. *Ecological Monographs* 43 (4), pp. 539–565.

Koch, P. L., et al. (1995). Isotopic tracking of change in diet and habitat use in African elephants. *Science* 267, pp. 1340–1343.

Kurten, B. and Anderson, E. (1980). *Pleistocene mammals of North America*. New York: Columbia University Press.

Larson, G. J., Lowell, T. V. and Ostrum, N. E. (1994). Evidence for the Two Creeks interstade in the Lake Huron basin. *Canadian Journal of Earth Sciences* 31, pp. 793–797.

Lepper, B. T., et al. (1991). Intestinal contents of a Late Pleistocene mastodont from midcontinental North America. *Quaternary Research* 36, pp. 120–125.

Lister, A. and Bahn, P. (2007). *Mammoths: giants of the ice age, revised edition*. Los Angeles: University of California Press.

MacPhee, R. D. E. and Marx, P. A. (1997). The 40,000-year plague: humans, hyperdisease and first-contact extinctions. In: Goodman, S. and Patterson, B. (eds.), *Natural change and human impact in Madagascar*. Washington, D.C.: Smithsonian Institution Press, pp. 169–217.

Madden, C. T. (1981). Origin(s) of mammoths from Northern Channel Islands, California. *Quaternary Research* 15 (1), pp. 101–104.

Maher, L. J. Jr, et al. (1998). Paleobiology of the sand beneath the Valders diamicton at Valders, Wisconsin. *Quaternary Research* 49, pp. 208–221.

Martin, P. S. (1984). Prehistoric overkill: the global model. In: Martin, P. S. and Klein, R. G. (eds) *Quaternary extinctions: a prehistoric revolution*. Tucson: University of Arizona Press, pp. 354–403.

McAndrews, J. H. (2003). Postglacial ecology of Hiscock site. In: Laub, R. S. (ed.) *The Hiscock site: late Pleistocene paleoecology and archaeology of Western New York State*. ???: Bulletin of the Buffalo Society of Natural Sciences 37, pp. 190–198. 8

McAndrews, J. H. and Jackson, L. J. (1988). Age and environment of Late Pleistocene mastodont and mammoth in southern Ontario. In: Laub, R. S., Miller, N. G. and Steadman, D. W. (eds) *Late Pleistocene and early Holocene paleoecology and archaeology of the eastern Great Lakes region*. ???: Bulletin of the Buffalo Society of Natural Sciences 33, pp. 161–172. 9

Oltz ., D. F. Jr and Kapp, R. O. (1963). Plant remains associated with mastodon and mammoth remains in central Michigan. *American Midland Naturalist* 70, pp. 339–346.

Osborn, H. F. (1936). *The Proboscidea: a monograph of the discovery, evolution, migration and extinction of the mastodonts and elephants of the world, Volume 1: Mœritherioidea, Deinotherioidea, Mastodontoidea*. New York: American Museum of Natural History Press.

Pasenko, M. R. and Schubert, B. W. (2004). *Mammuthus jeffersonii* (Proboscidea, Mammalia) from Northern Illinois. *Paleobios* 24 (3), pp. 19–24.

Patterson, B. D. (2010). Climate change and faunal dynamics in the uttermost part of the earth. *Molecular Ecology* 19, pp. 3019–3021.

Rivals, F., Solounias, N. and Mihlbachler, M. C. (2007). Evidence for geographic variation in the diets of late Pleistocene and early Holocene *Bison* in North America, and differences from the diets of recent *Bison*. *Quaternary Research* 68, pp. 338–346.

Sánchez, B., Prado, J. L. and Alberdi, M. T. (2004). Feeding ecology, dispersal, and extinction of South American Pleistocene gomphotheres (Gomphotheriidae, Proboscidea). *Paleobiology* 30, pp. 146–161.

Saunders, J. J., et al. (2010). Paradigms and proboscideans in the southern Great Lakes region, USA. *Quaternary International* 217, pp. 175–187.

Shoshani, J., et al. (1989). The Shelton Mastodon Site: multidisciplinary study of a late Pleistocene (Twocreekan) locality in southeastern Michigan. *University of Michigan Museum of Paleontology, Contribution to Paleontology* 27, pp. 393–436.

Skeels, M. A. 1962. Mastodons and mammoths of Michigan. *Papers of the Michigan Academy of Science, Arts, and Letters* 47, pp. 101–133.

Stone, R. (2010). Home, home outside the range? *Science* 329, pp. 1592–1594.

Stoutamire, W. P. and Benninghoff, W. S. (1964). Biotic assemblage associated with a mastodon skull from Oakland County, Michigan. *Papers of the Michigan Academy of Science, Arts, and Letters* 49, pp. 47–60.

Surovell, T. A. and Waguespack, N. M. (2008). How many elephant kills are 14? Clovis mammoth and mastodon kills in context. *Quaternary International* 191, pp. 82–97.

Webb, T., Shuman, B. and Williams, J. W. (2004). Climatically forced vegetation dynamics in eastern North America during the Late Quaternary Period. In: Gillespie, A. R., Porter, S. C. and Atwater, B. F. (eds) *The Quaternary Period in the United States*. Amsterdam: Elsevier, pp. 459–478.

Whitehead, D. R., Jackson, S. T., Sheehan, M. C. and Leyden, B. W. (1982). Late-glacial vegetation associated with caribou and mastodon in central Indiana. *Quaternary Research* 17, pp. 241–257.

Woodman, N. and Branstrator, J. W. (2008). The Overmyer Mastodon (*Mammut americanum*) from Fulton County, Indiana. *American Midland Naturalist* 159 (1), pp. 125–146.

Yansa, C. H. (2006). The timing and nature of Late Quaternary vegetation changes in the northern Great Plains, USA and Canada: a re-assessment of the spruce phase. *Quaternary Science Reviews* 25, pp. 263–281.

Yansa, C. H., Joyce, D. J. and Overstreet, D. F. (2009). *Paleoindian-mammoth interactions and Late Pleistocene environments in southeastern Wisconsin*. Annual Meeting of the Geological Society of America, *Abstract with Programs*, 37, p. 115.

Author Query Form

Journal: GEC3

Article: 483

Dear Author,
During the copy-editing of your paper, the following queries arose. Please respond to these by marking up your proofs with the necessary changes/additions. Please write your answers on the query sheet if there is insufficient space on the page proofs. Please write clearly and follow the conventions shown on the attached corrections sheet. If returning the proof by fax do not write too close to the paper's edge. Please remember that illegible mark-ups may delay publication.

Many thanks for your assistance.

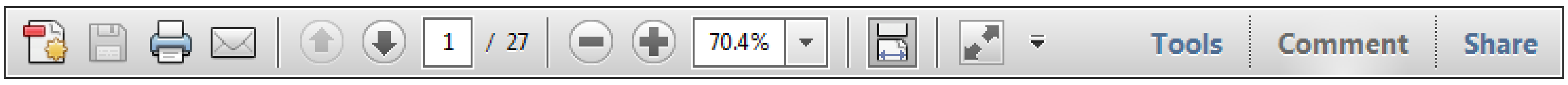
Query reference	Query	Remarks
Q1	**AUTHOR: A running head short title was not supplied; please check if this one is suitable and, if not, please supply a short title of up to 40 characters that can be used instead.**	
Q2	**AUTHOR: Please check affiliation.**	
Q3	**AUTHOR: Please check this website address and confirm that it is correct. (Please note that it is the responsibility of the author(s) to ensure that all URLs given in this article are correct and useable.)**	
Q4	**AUTHOR: Abraczinkas (1993) has been changed to Abraczinskas (1993) so that this citation matches the Reference List. Please confirm that this is correct.**	
Q5	**AUTHOR: Harington et al. 2011 has been changed to Harrington et al. 2011 so that this citation matches the Reference List. Please confirm that this is correct.**	
Q6	**AUTHOR: Please provide the volume number for reference Harrington et al. (2011).**	

Q7	**AUTHOR: Please provide the city location of publisher for reference Kapp (1999).**	
Q8	**AUTHOR: Please provide the city location of publisher for reference McAndrews (2003).**	
Q9	**AUTHOR: Please provide the city location of publisher for reference McAndrews and Jackson (1988).**	

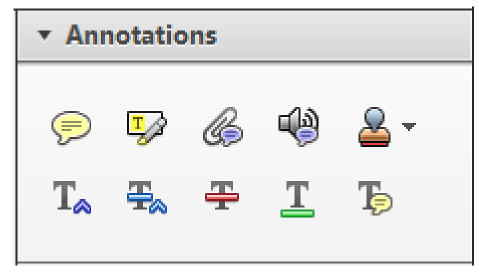
USING e-ANNOTATION TOOLS FOR ELECTRONIC PROOF CORRECTION

Required software to e-Annotate PDFs: Adobe Acrobat Professional or Adobe Reader (version 8.0 or above). (Note that this document uses screenshots from Adobe Reader X)
The latest version of Acrobat Reader can be downloaded for free at: http://get.adobe.com/reader/

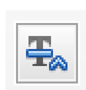
Once you have Acrobat Reader open on your computer, click on the Comment tab at the right of the toolbar:



This will open up a panel down the right side of the document. The majority of tools you will use for annotating your proof will be in the Annotations section, pictured opposite. We've picked out some of these tools below:



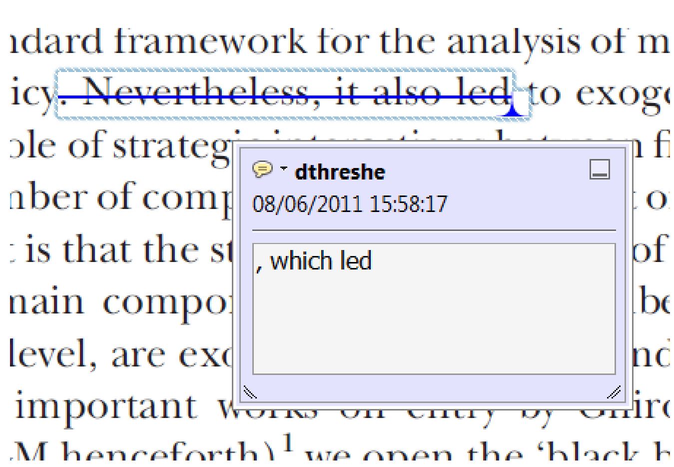
1. Replace (Ins) Tool – for replacing text.



Strikes a line through text and opens up a text box where replacement text can be entered.

How to use it

- Highlight a word or sentence.
- Click on the Replace (Ins) icon in the Annotations section.
- Type the replacement text into the blue box that appears.

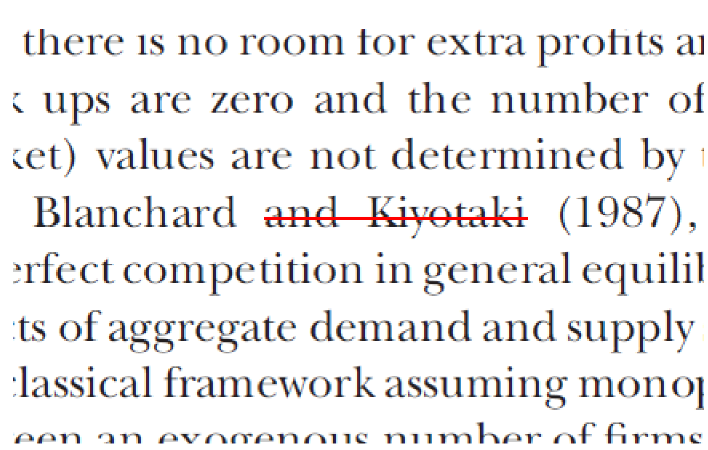


2. Strikethrough (Del) Tool – for deleting text.

Strikes a red line through text that is to be deleted.

How to use it

- Highlight a word or sentence.
- Click on the Strikethrough (Del) icon in the Annotations section.

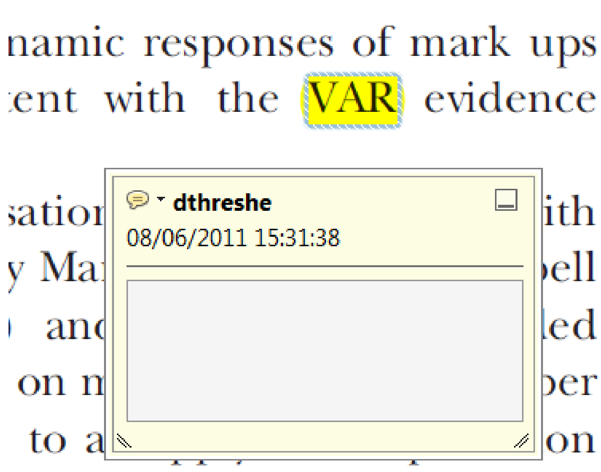


3. Add note to text Tool – for highlighting a section to be changed to bold or italic.

Highlights text in yellow and opens up a text box where comments can be entered.

How to use it

- Highlight the relevant section of text.
- Click on the Add note to text icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.

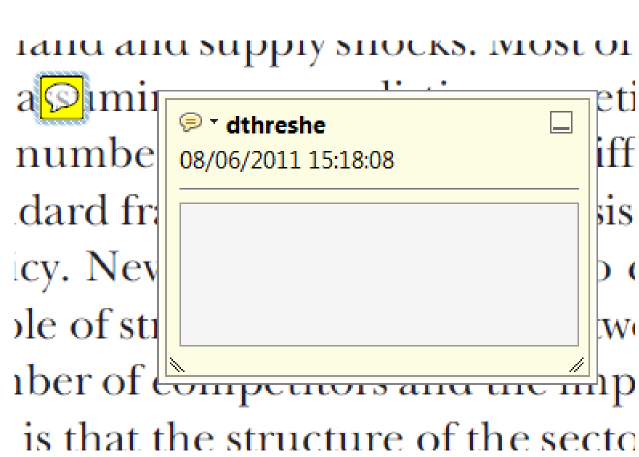


4. Add sticky note Tool – for making notes at specific points in the text.

Marks a point in the proof where a comment needs to be highlighted.

How to use it

- Click on the Add sticky note icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the yellow box that appears.



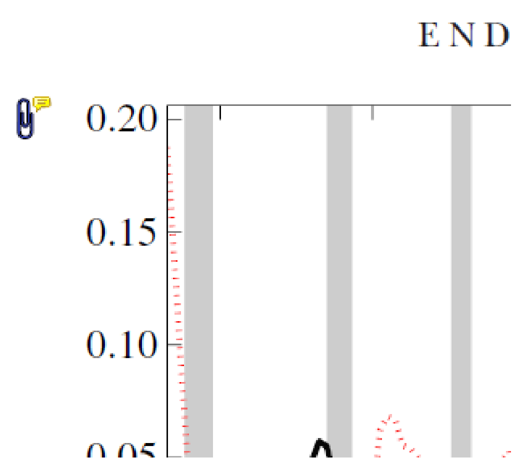
USING e-ANNOTATION TOOLS FOR ELECTRONIC PROOF CORRECTION

5. Attach File Tool – for inserting large amounts of text or replacement figures.

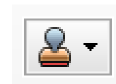
Inserts an icon linking to the attached file in the appropriate pace in the text.

How to use it

- Click on the Attach File icon in the Annotations section.
- Click on the proof to where you'd like the attached file to be linked.
- Select the file to be attached from your computer or network.
- Select the colour and type of icon that will appear in the proof. Click OK.



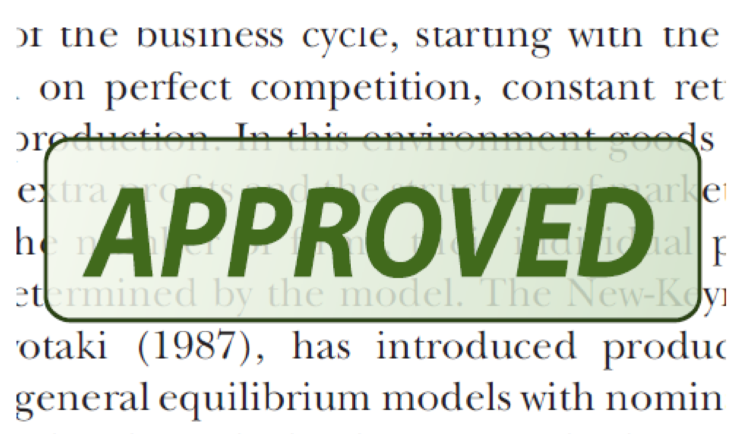
6. Add stamp Tool – for approving a proof if no corrections are required.

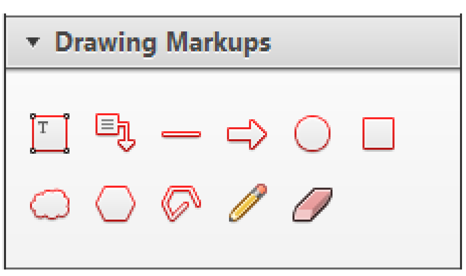


Inserts a selected stamp onto an appropriate place in the proof.

How to use it

- Click on the Add stamp icon in the Annotations section.
- Select the stamp you want to use. (The Approved stamp is usually available directly in the menu that appears).
- Click on the proof where you'd like the stamp to appear. (Where a proof is to be approved as it is, this would normally be on the first page).



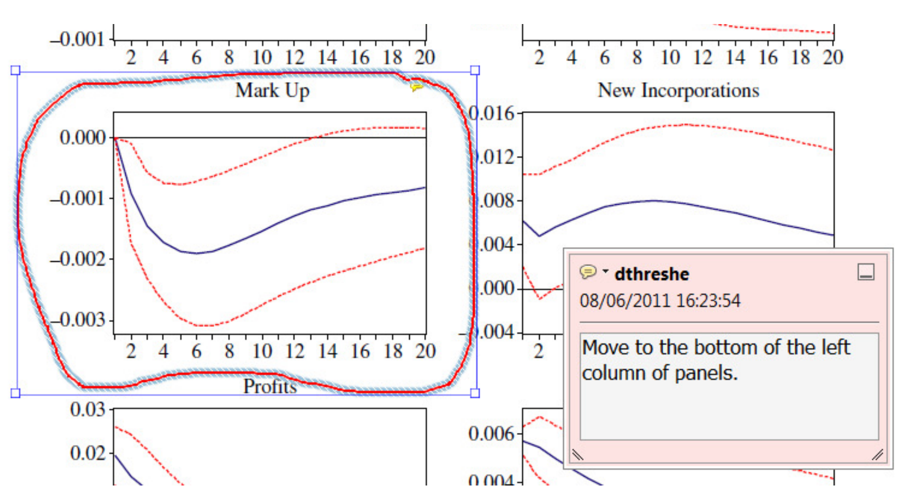


7. Drawing Markups Tools – for drawing shapes, lines and freeform annotations on proofs and commenting on these marks.

Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks..

How to use it

- Click on one of the shapes in the Drawing Markups section.
- Click on the proof at the relevant point and draw the selected shape with the cursor.
- To add a comment to the drawn shape, move the cursor over the shape until an arrowhead appears.
- Double click on the shape and type any text in the red box that appears.



For further information on how to annotate proofs, click on the Help menu to reveal a list of further options: