

Linking Top-down Forces to the Pleistocene Megafaunal Extinctions

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Humans, in conjunction with natural top-down processes and through a sequence of cascading trophic interactions, may have contributed to the Pleistocene megafaunal extinctions. The arrival of the first humans, as hunters and scavengers, through top-down forcing, could have triggered a population collapse of large herbivores and their predators. We present evidence that the large mammalian herbivores of the North American Pleistocene were primarily predator limited and at low densities, and therefore highly susceptible to extinction when humans were added to the predator guild. Our empirical evidence comes from data on carnivore dental attrition, proboscidean age structure, life history, tusk growth rates, and stable isotopes from the fossil record. We suggest a research agenda for further testing of this hypothesis that will provide a more detailed comprehension of late Pleistocene megafaunal ecology, and thereby allow us to better understand and manage remaining megafauna.

Keywords: Pleistocene, megafauna, extinctions, large carnivores, humans

Two-thirds of North America's large mammal genera became extinct during the late Pleistocene. The cause for this massive extinction has been debated for decades, with most authors favoring either aboriginal overkill or climate change as the primary driver (Grayson and Meltzer 2003, Barnosky et al. 2004, Burney and Flannery 2005, Haynes 2009). The aboriginal overkill hypothesis posits that extinctions occurred as a result of the human hunting of large herbivores, whereas the climate hypothesis suggests that extinctions are attributable to a climatically controlled food or resource limitation on large herbivores. Arguments for humans as the primary cause of the extinctions have gained great momentum from recent research on archaeology, paleontology, chronology, paleoclimatology, and simulations, but much uncertainty persists as to the actual causal mechanisms (Barnosky et al. 2004, Koch and Barnosky 2006). Therefore, we agree with Burney and Flannery (2005) that it is more interesting to investigate what the role of humans might have been rather than debate the merits of overkill versus climate hypotheses. Here, we present a hypothesis of how humans, in conjunction with natural top-down processes, and through a sequence of cascading trophic interactions, could have contributed to the extinctions. Critics of the aboriginal overkill hypothesis emphasize that there are few

sites that show evidence of human association with extinct megafauna (Grayson and Meltzer 2003, but see Surovell and Waguespack 2008). Notably, the hypothesis proposed here is not dependent on a minimum number of known kill sites, and a relatively low number of these sites would be expected under our scenario. In addition, although this hypothesis points to human hunting as the main trigger, it does not preclude climate change or other environmental factors (anthropogenic or naturally caused) as contributing and interacting causes.

The idea that Pleistocene hunters had help from predators in causing the extinctions was first put forth by Janzen (1983) in a little-known, two-page paper, and has largely been ignored over the last 25 years, with a few significant

exceptions in recent years (especially further developments in Kay 2002; also see Fiedel and Haynes 2004, as well as Koch and Barnosky 2006). Here, we further develop Janzen's idea, but propose the opposite emphasis: that the predators, operating within a cascading top-down process, had help from the humans in causing the extinctions. The predators, which were much more abundant than the humans, most likely killed the vast majority of the megafauna (Kay 2002). In developing this hypothesis, we draw on theories of trophic cascades, predator-prey dynamics, and optimal foraging. We provide evidence from studies of the North American late

We live in a zoologically impoverished world, from which all the hugest and fiercest, and strangest forms have recently disappeared.

—Alfred Russell Wallace, 1876

Pleistocene that examined the foraging patterns and other characteristics of extinct and extant mammals, using data from carnivore dental attrition, proboscidean tusk growth rates, and stable isotopes to reveal possible environmental stresses as well as competition or flexibility in megafaunal diets. We also investigate predator-prey associations, megafaunal track sizes, and prey abundance from the fossil, historical, and modern records. Although our focus for this article is on the North American extinction event, the results should be applicable to late Quaternary extinctions elsewhere. We recognize that although the data presented here support the top-down hypothesis, uncertainty remains; therefore, we suggest a research agenda for the future and hope our article stimulates further investigations.

The top-down hypothesis

The top-down hypothesis is based on the premise that the arrival of the first humans as hunters and scavengers in the New World at the end of the Pleistocene triggered a sequential collapse of large herbivores and their predators. We argue that humans were able to do this because they entered a system in which many large herbivores were already predator limited (Geist 1998, Kay 1998). In a predator-limited system, herbivore populations are held at low densities, well below carrying capacity, and the ratio of predators to prey is relatively high (Gasaway et al. 1992, Messier 1994, Peterson et al. 2003). Humans most likely opportunistically included meat in their diets by scavenging predator kills and hunting to the point that they competed with large carnivores (Janzen 1983, Kay 2002, Fiedel and Haynes 2004, Koch and Barnosky 2006). Furthermore, both humans and many of the large carnivore species were capable of prey switching, forcing both humans and predators to intensify pressure on alternative prey. Notably, whereas previous additions of new carnivores to North America, such as lions (*Panthera leo atrox*) and gray wolves (*Canis lupus*), did not result in many or any extinctions, humans would have played a different and distinct role within the large-predator guild. Unlike other mammalian carnivore systems, in which interspecific competition is known to affect species densities (Van Valkenburgh 2001, Donadio and Buskirk 2006), humans were omnivorous and probably less subject to intraguild predation, allowing their numbers to increase independently of large-carnivore densities and diversity. Moreover, relative to other large predators such as dire wolves (*Canis dirus*) and sabertooth cats (*Homotherium serum*, *Smilodon fatalis*), humans most likely had a reduced risk of predation because of several advantages, such as living in groups, fire, weapons, dogs, and language. Another possible advantage is that North American carnivores were unlikely to recognize humans as prey at the time people arrived on the continent in the late Pleistocene because most animals had evolved without humans (Hart and Sussman 2005). Even those predator species that emigrated from the Old World, such as the gray wolf and lion, did so earlier, and had not encountered humans for at least 100,000 years (Kurten and Anderson 1980, Barnett

et al. 2009). In essence, humans joined a highly competitive predator guild but were able to do so without paying the usual costs of competition and intraguild predation.

The top-down forcing hypothesis relies on humans favoring large prey (ungulates, proboscideans, etc.) that were also preferred by large carnivores, such as dire wolves and sabertooth cats. When humans began taking a small proportion of these highly ranked prey, carnivores were forced to switch to lower-ranked prey (Kay 2002). While subsisting on alternative prey, carnivores (and humans) would then provide intense predation pressure on remaining highly ranked prey, driving them to extinction. This extinction process has been modeled in a modern wolf-moose (*Alces alces*)–sheep (*Ovis canadensis*) system in Alaska. In this system, the introduction of relatively limited human hunting on predator-limited moose triggers a drastic decline in moose, cascading to a steep decline in sheep due to intensified predation and prey switching to sheep by wolves, and finally resulting in a precipitous decline of wolves, moose, and sheep (Walters et al. 1981).

Current ecological literature contains compelling empirical support for the limiting effect of large carnivores on their prey. Numerous studies have found that predation by large mammalian carnivores, especially by sympatric wolves and bears (*Ursus arctos*, *Ursus americanus*), limits the densities of large mammalian herbivores in the Northern Hemisphere (Gasaway et al. 1992, Messier 1994, Crête 1999, Flueck 2000, Peterson et al. 2003), thus demonstrating widespread and strong top-down forcing by large carnivores on large herbivores. When predators are removed, herbivore populations irrupt and these dense herbivore populations most likely become limited by resources or human hunting (Beschta and Ripple 2009). An exception to the above pattern is that some migrating ungulates are not limited by predation and can cycle over a wide range of abundance. Migration creates an advantage for prey species because it significantly reduces predation, as most predators are confined to a specific area for at least part of the year, usually when denning or caring for dependent offspring (Fryxell et al. 1988). Evidence exists that Pleistocene megafauna, such as equids and mastodons (*Mammuthus americanum*), may have undertaken migrations of at least 120 to 300 kilometers, whereas mammoths (*Mammuthus* spp.) appear to have ranged more locally (Hoppe et al. 1999, Hoppe and Koch 2007). Nevertheless, all three of these species became extinct, suggesting migratory habits (or the lack thereof) did not guarantee survival.

For predators to drive prey to extinction, three criteria must be met: (1) prey population recruitment must be less than losses, (2) this imbalance must be maintained even when prey become scarce, and (3) predator-free refugia must be absent (Owen-Smith 1999). We hypothesize that a prey-recruitment imbalance may have been maintained late in the North American Pleistocene through prey switching by both omnivorous human hunters and opportunistic large carnivores, many of which were generalist predators, and that these carnivores were especially important in

eliminating prey in much of the hunter-free refugia. Unlike blitzkrieg hypotheses (rapid overkill), the top-down forcing hypothesis is not weakened by the possible presence of people south of the ice in North America as far back as 15,000 years ago (Goebel et al. 2008). The unraveling of the megafaunal ecosystem may have taken a few thousand years (Gill et al. 2009), but we would not be surprised if the final extinction event were associated with the widespread but late appearance of Clovis culture.

To support the hypothesis that human hunting tipped the balance against the Pleistocene megafauna, we provide evidence that (a) herbivore populations, including mammoth and mastodon, were predator rather than food limited; (b) large carnivores competed intensely for food, suggesting high predator-to-prey ratios; and (c) humans and large carnivores prey switched.

Predator-limited herbivores

The late Pleistocene of North America was characterized by a much higher diversity of large carnivores and large herbivores than occurs today. For example, only one-fifth of the 51 herbivore (ungulates, sloths, proboscideans) species survived to the present, and only 8 of 21 carnivore species survived. In both groups, large species with low reproductive rates suffered to a greater degree (McDonald 1984, Johnson 2002, Lyons et al. 2004). Among the herbivores, mammoths, mastodons, ground sloths (three genera), camels (three genera), horses (*Equus* spp.), and one or more species of bison (*Bison* spp.) were lost, and among the carnivores, American lions, dire wolves, short-faced bears (*Arctodus simus*), and two forms of sabertooth cat (*Homotherium*, *Smilodon*) are among the missing. We believe these predators held prey populations in check, such that the prey were not food limited and existed at densities far below the carrying capacity. Here we present fossil evidence for predator-limited prey from data on extinct proboscidean growth rates and patterns of carnivore dental attrition.

Fisher (2001) tested for food-limited megafauna by examining annual growth increments (rings) on fossil mammoth (*Mammuthus* spp.) tusks. Thick growth rings are indicative of abundant forage; narrow rings reflect food stress. His data include tusk thickness growth rates at nine sites for males and seven additional sites for females across North America, with dates ranging from 42.0 thousand to approximately 10.8 thousand years before present (YBP). (All dates are uncalibrated radiocarbon years.) Results show high

mammoth tusk growth rates in North America from 11.3 thousand to 10.8 thousand YBP (figure 1). Interestingly, this suggests that food availability was increasing in the latest Pleistocene near the time of mammoths' extinction, and this evidence does not support climate-induced habitat declines as a cause of their demise (Fisher 2001). This finding is consistent, however, with increased predation pressure just before mammoth extinction.

Fisher (2009) has also shown that the age of sexual maturity in proboscideans can be read from tusk growth patterns. For males, a sharp decline in growth rate is apparently due to eviction from the family unit, whereas in females, a decline in tusk growth rate marks the age of first conception. Fisher (2001, 2009) pointed out that in modern African elephants (*Loxodonta africana*), conditions of plentiful food favor earlier maturation, whereas the opposite is expected under conditions of limited food. In an analysis of seven male and three female mastodons dated from about 12.0 thousand to 9.6 thousand YBP, he recovered a pattern suggestive of decreasing age of maturation with time (figure 2). As with the tusk growth data, this is not what would be expected if environmental conditions were declining before mastodon extinction, but is consistent with increased predation pressure.

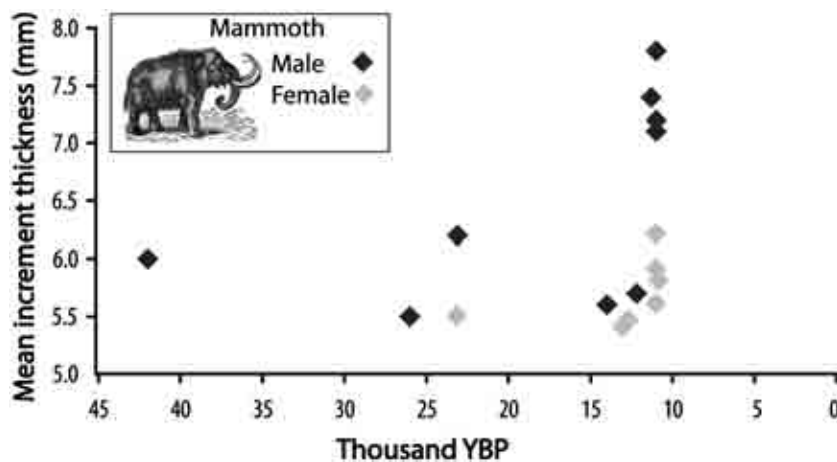


Figure 1. Mammoth tusk thickness growth rates (in millimeters) from 15 different sites across North America with dates ranging from 42 thousand to approximately 10.8 thousand years before present (YBP). Sites from oldest to youngest for males include Field Museum, Arkansas; Hot Springs, South Dakota; Poyser, Indiana; Jensen, Nebraska; Moon, Pennsylvania; Union Pacific, Wyoming; Hughes, Michigan; Mott Community College, Montana; and Randolph, New York. For females, locations include Field Museum, Arkansas; Lamb Springs, Colorado; Maine State Museum, Maine; Hunter Ranch, Wyoming; Colby, Wyoming; Chittenango, New York; and Dent, Colorado. Each point on the graph represents the mean increment thickness for one mammoth except for the point at 26 thousand YBP for the males, which represents the average increment thickness for eight mammoths at the Hot Springs site. The number of annual increments analyzed per specimen ranged from 1 to 12, $\bar{x} = 2.7$. These data do not point to environmentally induced habitat declines as the cause of extinction, but are consistent with increased predation pressure just before extinction (adapted from Fisher 2001).

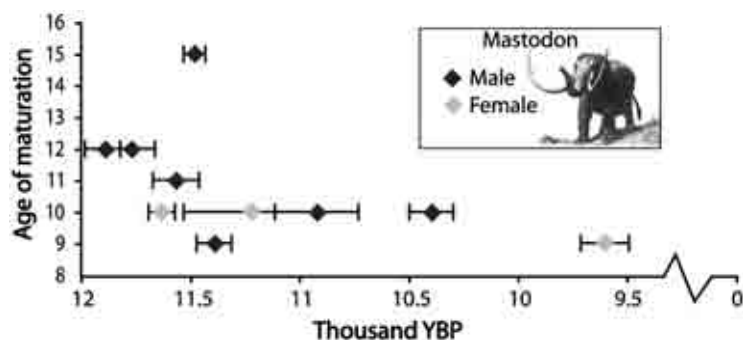


Figure 2. Radiocarbon age estimates (x-axis) and estimated age of maturation of mastodons of the Great Lakes region (y-axis). Maturation ages were inferred from annual increment measurements in tusks. Horizontal bars represent uncertainties of the dates for the specimens. The trend toward a younger age of maturation is not expected if environmental conditions were declining, but is consistent with increased predation pressure near the extinction event (adapted from Fisher 2009). YBP, years before present.

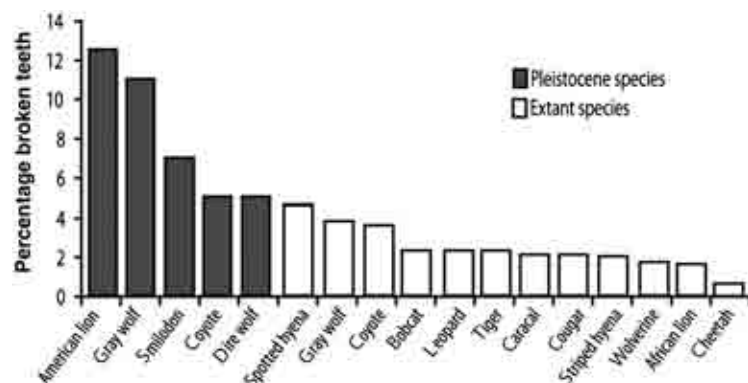


Figure 3. Comparison of mean tooth fracture rates (percentage broken teeth) between Pleistocene and modern carnivores greater than or equal to 10 kilograms in body mass. Five species of Pleistocene carnivores included American lion, gray wolf, sabertooth cat (*Smilodon fatalis*), coyote (*Canis latrans*), and dire wolf. Twelve extant species include spotted hyena (*Crocota crocuta*), gray wolf, coyote, bobcat (*Lynx rufus*), leopard (*Panthera pardus*), tiger (*Panthera tigris*), caracal (*Caracal caracal*), cougar (*Puma concolor*), striped hyena (*Hyaena hyaena*), wolverine (*Gulo gulo*), African lion, and cheetah (*Acinonyx jubatus*). The high tooth fracture rates during the Pleistocene may represent a time of strong top-down forcing and a predator-limited system (adapted from Van Valkenburgh 2009).

An alternative view would be that proboscideans were food limited before humans arrived, so that with greater predation (by people) and a reduction in proboscidean population density, food availability increased. In this scenario, prey populations would have been only transiently predation limited as they declined to extinction. A direct impact of hunting by people could explain this without invoking interactions in the predator community. However, we find it likely that the large predators of the Pleistocene were capable of exerting significant predation pressure on the proboscideans (see below), and thus

it is reasonable to assume some interaction because both people and predators were killing megafaunal prey at that time.

We recognize that others have argued on the basis of declines in body mass before extinction that some herbivores were food limited in the latest Pleistocene. They include mastodons (King and Saunders 1984), Alaskan horses (Guthrie 2003), and Irish elk (*Megaloceros giganteus*; Barnosky 1986). As noted by Koch and Barnosky (2006), changes in body size are difficult to interpret given that they can result from changes in climate, nutrition, predation intensity or selectivity, as well as anthropogenic effects or other variations with little or no consequence to extinction. For example, body size decreased in many taxa that did not go extinct during earlier climate warming periods of the Pleistocene (Kurten 1968). Clearly, to understand such size changes we need better indicators of herbivore nutritional status, such as variation in dental incremental growth lines that are applicable to the ungulate fossil record.

Teeth are also key to understanding late Pleistocene predator ecology: In this case, it is rates of dental wear and fracture rather than growth rings. Large carnivores tend to exhibit heavier tooth wear and greater numbers of broken teeth when they consume carcasses more completely, actively feeding on bones (Van Valkenburgh and Hertel 1993, Van Valkenburgh 2009). These carnivores will ingest more of a carcass when food is limited and intraguild competition is elevated. For example, Van Valkenburgh (2009) found significantly lower tooth fracture frequencies for wolves in elk (*Cervus elaphus*)-rich Yellowstone National Park (1.6%) than in other areas of North America (4.8%). Elk, the primary prey of Yellowstone's wolves, existed at some of the highest densities in North America and were near a food-limited population density at the time the wolves were sampled (NRC 2002). The Yellowstone results suggest that the frequency of tooth fractures in Pleistocene predators could be a good indicator of whether prey populations were food limited or predator limited. Low fracture rates indicate plentiful, food-limited prey, whereas high fracture rates suggest lower-density prey that are probably predator limited.

Samples of late Pleistocene gray wolves spanning from more than 45 thousand to 11 thousand YBP display consistently heavy tooth wear, with dental fracture rates (11%) that exceed anything observed in a modern sample of more than 275 gray wolves (Van Valkenburgh 2009). Similarly, Pleistocene dire wolves, sabertooth cats (*Smilodon* and *Homotherium*), American lions, and coyotes (*Canis latrans*), spanning 30 thousand to 11 thousand YBP, exhibit tooth fracture rates that are up to six times higher than those observed in living carnivores (figure 3; Van Valkenburgh 2009). These high fracture rates are observed

across a range of localities (Alaska, California, Mexico, Peru) and do not appear to follow any temporal trends, such as increasing in the latest Pleistocene (Leonard et al. 2007, Binder and Van Valkenburgh 2010). Moreover, as implied by comparisons of dental wear and canine tooth growth rates in the dire wolves and sabertooth cats of Rancho La Brea, the high tooth fracture rates are probably not a result of Pleistocene individuals living longer on average than their extant counterparts, and thus having a higher probability of having fractured a tooth (Van Valkenburgh and Hertel 1993, Binder et al. 2002, Binder and Van Valkenburgh 2010). Although it was not possible to assess ontogenetic ages for all the sampled Pleistocene carnivores, it seems unlikely that late Pleistocene carnivores would have lived longer on average than extant carnivores of similar size. Large carnivores often kill one another in acts of predation or, more typically, in intra- or interspecific battles over territory or carcasses (Van Valkenburgh 2001, Donadio and Buskirk 2006). Given that anthropogenic influences probably limit the present-day abundance of large predators to levels well below those reached in the late Pleistocene, encounters among and within species must have been more frequent and dangerous in the past, making it difficult for species to survive to old age. Thus, a better explanation for the elevated dental wear and fracture rates observed among large Pleistocene carnivores is that the late Pleistocene was a period of strong top-down forcing, in that these species fully utilized carcasses and competed intensely for food. This is further evidence of a predator-limited system or a low ratio of prey relative to carnivore densities.

The life history traits found by both Van Valkenburgh (2009) and Fisher (1996) are consistent with the hypothesis that the large herbivores (e.g., mammoths, mastodons, ground sloths, camels, horses, and others) of the late Pleistocene were under intense predation pressure and were predator, not food, limited. Any vegetation changes during this time most likely had less of an effect on these megafauna populations than did predation. Interestingly, Gill and colleagues (2009), in analyzing dung fungus spore counts, contended that their data rule out hypotheses that the megafaunal decline was driven by climate-forced changes in vegetation. Furthermore, McDonald (1984), Martinez-Meyer and colleagues (2004), and Agenbroad (2005) argued that vegetation changes in the late Pleistocene caused megafaunal habitat to improve rather than decline. These results strongly suggest that the extinction of megafauna was not driven primarily by environmental changes such as climate, vegetation, fire, or habitat deterioration; however, they do not rule out environmental factors having played a secondary role.

A final argument against the idea that large herbivores of the late Pleistocene were food limited comes from paleontological analyses of diet

that provide evidence for high levels of flexibility. For example, Rivals and colleagues (2007) demonstrated that the dental microwear of Pleistocene bison (*Bison* spp.) is more consistent with mixed feeding than pure grazing, suggesting that bison readily altered their diets according to food availability. Similarly, stable isotope analyses of Pleistocene large herbivores (mammoth, horse, bison, camel) document shifts from eating predominantly C3 browse species to C4 grasses and sedges over time and across space (figure 4; Feranec 2003, 2004). These data cast doubt on the idea that changes in vegetation abundance or distribution could have been fatal at the time the extinctions occurred. However, stable isotope data provide information only on diet composition or flexibility, and are not direct evidence of the degree of predation pressure.

Large carnivores of the Pleistocene preyed on proboscideans, the largest of the herbivores (figure 5). Because proboscideans produce offspring at a very low rate, any consistent predation pressure may have limited their populations. For example, mammoth weaning could have been a lengthy process, thus slowing the reproductive rate such that predation at any level may have had serious effects (Rountrey et al. 2007). Using a model, Brook and Johnson (2006) demonstrated that remarkably low levels of juvenile exploitation could have driven Pleistocene megafauna in Australia to extinction as a result of their “slow” life histories. Similarly, Carbyn and colleagues (1993) found that gray wolves in Wood Buffalo National Park, Canada, were able to drive a modern bison population to low levels by preying primarily on bison calves. Carbyn and colleagues (1993) also described how bison could die from blood poisoning as a result of simple puncture wounds infected by bacteria on wolves’ teeth.

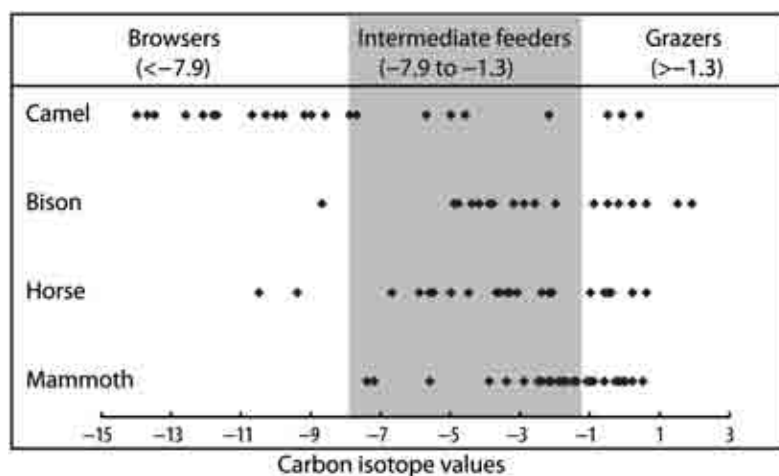


Figure 4. Stable carbon isotope values of camel, bison, horse, and mammoth during the Rancholabrean period in Florida. The plotted values show the flexibility in herbivore diets along a gradient from a browsing C3 diet to a grazing C4 diet. These data indicate high flexibility in megafaunal diets, shown by a mixture of both browsing and grazing for these taxa, making it unlikely that a lack of food or changes in forest cover (browse) due to a changing climate caused megafaunal extinctions (adapted from Feranec 2004).

The cranial morphology of sabertooth felids suggests a specialization for very large prey such as proboscideans (Marean 1989) and the fossil record reveals frequent associations of sabertooth cats with proboscideans (Rawn-Schatzinger 1992). For example, scimitar-toothed saber cats (*Homotherium serum*) specialized on a diet of mammoth on the late Pleistocene Mammoth Steppe in eastern Beringia (Matheus et al. 2003). At Friesenhahn Cave in Texas, the scimitar cat has been intimately associated with proboscideans, mainly mammoths, up to approximately two years of age (Rawn-Schatzinger 1992, Marean and Ehrhardt 1995). Juvenile mammoths apparently were a preferred prey of scimitar cats, suggesting the possibility that mammoths may have lacked the protective social structure currently found with elephants (Marean and Ehrhardt 1995, but see Joubert 2006 below). Alternatively, scimitar cats may have ambushed juvenile mammoths, inflicted serious wounds, and then retreated to safety and waited to eat until the young mammoth died and the remaining herd left the scene.

Modern elephant species have social behaviors that help guard juveniles against predation, but contrary to conventional wisdom, recent research shows that lions can be highly

successful. Loveridge and colleagues (2006) reported that elephant calves comprised nearly a quarter of all lion kills they recorded during a six-year period in Zimbabwe. The calves became more vulnerable during periods of low rainfall, when elephants had to travel large distances between limited water sources, and calves sometimes became separated or lost. In addition, play among modern juvenile elephants is common, and “whenever the group of [adult] females is feeding in a relatively stationary position, older infants frequently stray from them and indulge in fairly extensive play behavior” (McKay 1973, p. 69). In Botswana, Joubert (2006) observed 74 elephants killed by lions during a four-year period, with two-thirds of the kills in the elephant age range of between 4 and 15 years (figure 6). The predation success rate was 88% on elephants aged 4 to 9 years, and 50% on those aged 9 to 15 years. The elephants killed were typically on the periphery of the herd, with nearly half of them killed more than 50 meters from the herd (Joubert 2006). If similar situations existed with mammoths and mastodons, predators may have had regular opportunities to prey on these taxa.

Finally, McNeil and colleagues (2005) used preserved footprint size in 51 mammoth tracks and trackways in

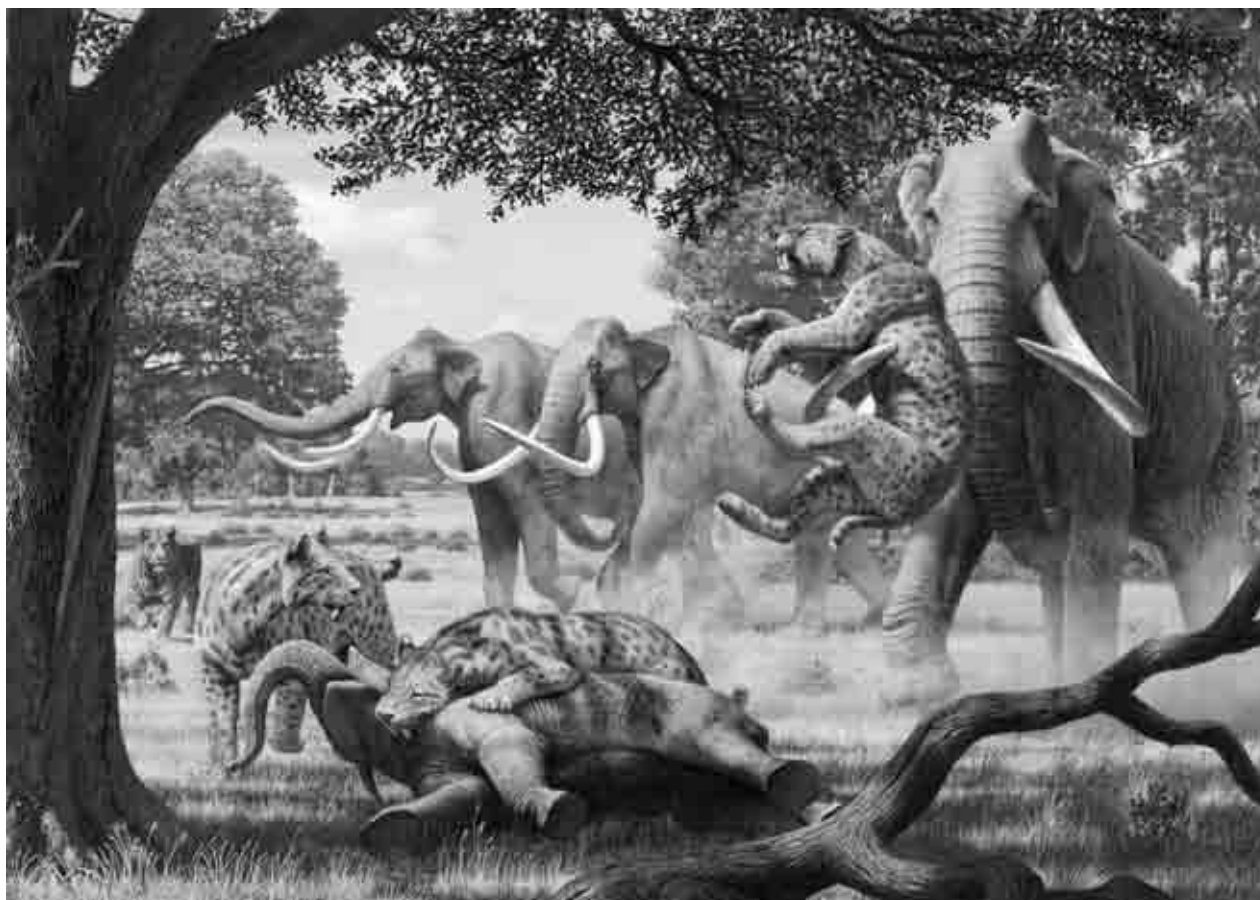


Figure 5. In the late Pleistocene (Rancholabrean) of western North America, a small group of sabertooth cats (*Smilodon fatalis*) attack a young mammoth (*Mammuthus columbii*), risking retaliation from the adult members of the herd, seen in the background. Such scenes exemplify the interrelations between large mammalian herbivores and predators during the Pleistocene. Artwork: Mauricio Anton.

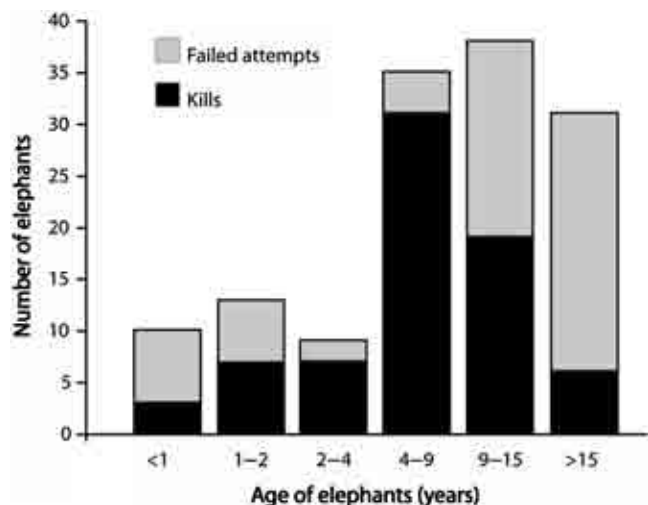


Figure 6. Successful kills (black bars) of elephants by lions versus failed attempts (gray bars) in Botswana during a four-year period as documented by Joubert (2006). He observed a total of 74 elephant kills by lions with highly successful kill rates on elephants less than 15 years old.

southwestern Canada, dated from between 11.3 thousand and 11.0 thousand YBP to determine population age distribution. Compared with extant African elephant trackways, the mammoth population had fewer juveniles than would be expected for a stable population. These results on mammoth age distribution are consistent with our hypothesis of heavy predation on juvenile mammoths just before species extinction and coincident in time with Fisher's data set (figure 1; 7 of 15 sites at 11.3 thousand to 11.0 thousand YBP) that shows mammoths possibly under greater predation stress. Alternatively, the lack of juvenile mammoths could reflect nutritional or other limitations that affected offspring viability and heightened their vulnerability to predation. Given the small sample size and the uncertainty in how many track-making events are represented in the data set, it is difficult to draw strong conclusions.

The top-down forcing hypothesis presented in this article is plausible even if the proboscideans, because of their large size, were not completely predator limited before the arrival of humans to North America. In this scenario, humans would have competed with predators by (a) killing proboscideans, (b) usurping and scavenging proboscidean carcasses, thereby forcing predators to (c) intensify predation pressure on remaining proboscideans, as well as (d) causing both predators and humans to switch to smaller prey, resulting in sequential collapses and extinctions of the megafauna.

Prey switching by humans and carnivores

As noted by others, the ability of both predators and humans to change to alternative food sources may be key to the Pleistocene megafaunal extinctions. Because of their ability to switch foods, both the carnivore and human predators of megafauna could persist, and in the case of the omnivorous

humans, continue to thrive on alternative, plentiful foods (fish, plants)—despite reductions in the numbers of their preferred prey. Consequently, predation pressure by humans on the large herbivores would have continued to increase, even as they became difficult to find. In addition, we think that humans most likely had a further survival advantage over the carnivores in that they were less vulnerable to the intraguild predation and kleptoparasitism that characterize large terrestrial mammal carnivore guilds (Donadio and Buskirk 2006).

Humans are well-documented optimal foragers, and in general, large prey (ungulates) are highly ranked because of the greater return for a given foraging effort. A survey of the association between mammal body size and the current threat of human hunting showed that large-bodied mammals are hunted significantly more than small-bodied species (Lyons et al. 2004). Studies of Amazonian Indians (Alvard 1993) and Holocene Native American populations in California (Broughton 2002, Grayson 2001) show a clear preference for large prey that is not mitigated by declines in their abundance. After studying California archaeological sites spanning the last 3.5 thousand years, Grayson (2001) reported a change in relative abundance of large mammals consistent with optimal foraging theory: The human hunters switched from large mammal prey (highly ranked prey) to small mammal prey (lower-ranked prey) over this time period (figure 7). Grayson (2001) stated that there were no changes in climate that correlate with the nearly unilinear decline in the abundance of large mammals. Looking further back in time, Stiner and colleagues (1999) described a shift from slow-moving, easily caught prey (e.g., tortoises) to more agile, difficult-to-catch prey (e.g., birds) in Mediterranean Pleistocene archaeological sites, presumably as a result of declines in the availability of preferred prey.

More recent examples of optimal foraging and prey switching include data from the Lewis and Clark expedition. As they traversed the North American continent in

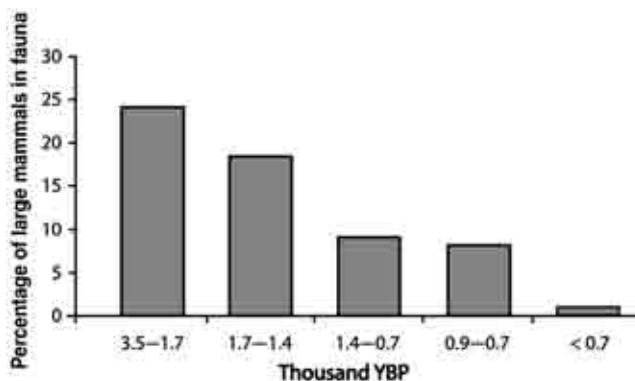


Figure 7. The relative abundance of artiodactyls found at an archaeological site in the White Mountains of southeastern California. A relatively high percentage of large mammals (artiodactyls) was found early in the sequence, with declining representation over time, possibly due to prey switching (adapted from Grayson 2001). YBP, years before present.

the very early 1800s, they found aboriginals subsisting on lowly ranked small game, fish, and plants because of an apparent scarcity of large mammals near their occupations. Conversely, highly ranked large mammals were found to be abundant in prey refugia within buffer zones between the warring tribes (Martin and Szuter 1999, Laliberte and Ripple 2003). Similarly, Kay (1998) documented very low numbers of large game in more than 400 pre-Columbian archaeological sites in North America, and argued convincingly that this reflects low densities of large mammals (as a result of overhunting) during these times. Instead of elk and moose, early Native Americans thrived on nonungulate foods, but as optimal foragers they undoubtedly killed large prey when they had the opportunity.

Large carnivores also prey switch regularly in response to changes in prey availability. In general, large carnivores tend not to specialize on single herbivore species; instead, they take a broad range of prey, allowing them to sustain themselves through varying conditions (Sinclair et al. 2003, Owen-Smith and Mills 2008a). For example, an examination of 70 years of data on lion prey preference in South Africa revealed that lions shifted their focus from more- to less-common species in response to changing prey abundance or increases in prey vulnerability as a result of drought (Owen-Smith and Mills 2008b). Importantly, the prey-switching behavior of lions resulted in marked declines in some uncommon prey species.

Isotopic studies of Pleistocene carnivore diets confirm that carnivores were flexible in prey choice. Fox-Dobbs and colleagues (2008) found that during the late Pleistocene in Alaska, carnivore diets included all measured large herbivore species. In eastern Beringia, Matheus and colleagues (2003) found that among extinct carnivores, lions (*P. l. atrox*) were bison specialists, scimitar cats were mammoth specialists, short-faced bears were generalist scavengers, gray wolves and wolverines (*Gulo gulo*) had diverse prey bases, and brown bears were omnivorous. Using a robust data set, Coltrain and colleagues (2004) found that the diets of Pleistocene Rancho La Brea lions, sabertooth cats (*S. fatalis*), and dire wolves were similarly broad and included horse, camel (*Camelops hesternus*), bison, ground sloth (*Paramylodon harlani*), and mastodon. This type of dietary breadth can make prey switching and herbivore declines possible under certain conditions, as in the African example discussed above.

A modern example of potential prey switching in a carnivore resulting in a cascade of prey declines comes from the oceans, with striking, unexpected consequences arising from humans overhunting marine megafauna. Springer and colleagues (2003) hypothesized that as the great whales declined from human hunting in the last century, predatory killer whales (*Orcinus orca*) were forced to turn to smaller prey, causing a collapse of several smaller prey populations (sea lions [*Eumetopias jubatus*], seals, and sea otters [*Enhydra lutris*]). The collapse of sea otter populations likely caused a trophic cascade, with sea urchins overgrazing kelp forest ecosystems. The social system of transient orcas is

optimized for foraging on very large prey. The typical predation pattern involves silent hunting, followed by intense vocalizations that may attract other transient killer whales that assist in the attack and the kill (Pitman et al. 2001). This strategy rewards reciprocity at minimal cost, since killing a single great whale provides a copious feast.

A final caveat

The impetus for this article was in large part the growing realization of the importance of top-down forcing in modern terrestrial and marine ecosystems (Beschta and Ripple 2009, Terborgh and Estes 2010), combined with the appearance of new fossil data on Pleistocene mammal dental wear and growth. We recognize that modern, terrestrial, large-mammal ecosystems are not close analogs of those in the late Pleistocene. Almost all our examples of predator-limited prey are from western and northern North America, where the diversity of large carnivores and herbivores is greatly diminished relative to the past. Perhaps our best data on the impact of adding a top carnivore to a community are from Yellowstone National Park, where gray wolves were reintroduced after a 70-year hiatus. There, the impacts on prey (elk) and consequently the vegetation and associated fauna are clear and pervasive (Ripple and Beschta 2007), leading us to ponder the impact of the first arrival of humans to North America. However, the relative clarity of the trophic cascade in Yellowstone might be partly a result of the relatively small number of species compared with the Pleistocene. How would a system with significantly more large predators behave? Would negative interactions among predators act to limit their abundance below a level at which they limited their prey? Could periodic disease prevent predators from reaching carrying capacity? To answer these questions, we need more long-term data from undisturbed predator-rich ecosystems such as occur in parts of Africa, as well as theoretical studies on complex multipredator systems. Available data do seem to suggest that (a) intact predators prevent irruptions of nonmigrating herbivore prey, and (b) competition for food is a key determinant of predator coexistence. Consequently, the addition of a new, probably dominant species, such as humans, is likely to have precipitated significant changes in predator-prey dynamics.

Research agenda for testing the top-down forcing hypothesis

To further test the top-down forcing hypothesis, a more detailed picture of late Pleistocene megafaunal ecology is required. We need additional data on the health of large herbivore and carnivore populations, as well as time-transgressive studies of their life-history parameters, such as age of maturation and reproductive cycling. Clearly, these data are difficult to extract from the fossil record, but, as shown above, it is remarkable how much can be learned from studies of dental growth and wear. Below, we propose several lines of research that could help paint a more complete picture of the late Pleistocene. We suggest:

- Additional documentation in modern ecosystems of the association between dental wear and fracture patterns of large carnivores and the relative numbers of their prey. Low densities of prey relative to predators should be associated with high dental fracture frequencies and heavy wear. If they are not, then carnivore dental attrition may not be a good indicator of prey density.
- Documentation of dental attrition patterns in Pleistocene large carnivores outside of North America. The permafrost deposits of Eurasia are especially likely to produce sufficient numbers of individuals for this kind of analysis. If predator-limited populations of herbivores were a global phenomenon in the late Pleistocene, then relatively high dental fracture rates among the large carnivores should be prevalent, regardless of geographical location. In addition, it would be useful to explore temporal trends in Pleistocene carnivore tooth fracture frequencies alongside similar indicators of health for their prey (see below).
- Additional data on tusk growth rates to look for signs of food limitation in Pleistocene proboscideans, as well as more data on season of death, age of maturation, and reproductive cycles.
- Development of a methodology for assessing levels of environmental stress in fossil ungulates, such as bison, horses, and camels. For example, studies of incremental growth lines in teeth have been used to infer life history events and growth rates in a variety of extant mammal species, but have yet to be applied to many extinct species other than proboscideans (Smith and Tafforeau 2008).
- More analysis of the spatial and temporal distributions of both the large carnivores and large herbivores during the late Pleistocene. Additional precise radiocarbon dating is needed to better define the extinction window.
- Additional analysis of megafaunal diets in both predators and prey, using stable isotope analyses, especially as they approached extinction, to assess possible environmental impacts.
- Additional studies, both theoretical and empirical, on the effects of large predators on ecosystems in diverse communities with multiple carnivores.
- Development of new numerical modeling techniques to analyze food webs as complex systems to understand the ecology of extinctions and ecosystem reorganization.

Conclusions

Trophic cascades science suggests that predators typically limit the number of herbivores and prevent overuse and suppression of plant communities. Evidence for top-down forcing and trophic cascades in terrestrial and aquatic ecosystems has been mounting in recent years, with a growing number of scientists suggesting that top-down forces contribute strongly to regulating and sustaining the diversity of life on our planet. Did similar top-down forces govern Pleistocene ecosystems and contribute to the mass extinctions of megafauna in North America after the arrival of humans? We propose that multiple lines of evidence suggest this was the case. A key point relates to the prey-switching abilities of both the predators and humans and that the human

population was able to continue growing, applying more predation and scavenging pressure, even as the megafaunal prey declined, because humans were subsidized by smaller game and plant food sources.

We urge paleontologists, conservation biologists, ecologists, and physical scientists to work together to develop a deeper comprehension of how nature was structured during the Pleistocene. This knowledge is crucial when we consider questions about sustaining or restoring ecological and evolutionary processes in both terrestrial and aquatic ecosystems. In the terrestrial realm, it is important that we have a better understanding of how Pleistocene ecosystems were structured as we proceed in maintaining and restoring today's ecosystems. In the aquatic realm, Earth's oceans are the last frontier for megafaunal species declines and extinctions. If the top-down forcing idea advocated by Springer and colleagues (2003) is true, then the current tragic cascade of species declines due to human harvesting of marine megafauna may be a repetition of the cascade that occurred with the onset of human harvesting of terrestrial megafauna more than 10,000 years ago. This is a sobering thought, but it is not too late to alter our course this time around in the interest of sustaining Earth's ecosystems.

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