The Impact of Large Terrestrial Carnivores on Pleistocene Ecosystems

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Submitted to Proceedings of the National Academy of Sciences of the United States of America

The impact of large mammalian carnivores on terrestrial ecosystems has almost certainly been underestimated, in large part because their numbers have been suppressed for at least the last two hundred years. Based on modern observations, it is generally believed that large carnivores are not capable of limiting populations of megaherbivores (>800 kg), such as elephants, and this perception has been extended into the Pleistocene, a time when many more huge herbivores, such as mammoths, mastodons, and giant ground sloths, roamed the landscape. However, as shown here, the species richness of big carnivores also was greater in the Pleistocene and many of them were significantly larger than their modern counterparts. Fossil evidence suggests that interspecific competition among carnivores was relatively intense, and reveals that some individuals specialized on consuming megaherbivores. To estimate the potential impact of Pleistocene large carnivores, we use both historic and modern data on predator-prey body mass relationships to predict size ranges of their typical and maximum prey when hunting as individuals and in groups. These prey size ranges are then compared with estimates of juvenile and sub-adult proboscidean body sizes derived from extant elephant growth data. Young proboscideans at their most vulnerable age fall within the predicted prey size ranges of many of the Pleistocene carnivores. Predation on juveniles can have a greater impact on megaherbivores because of their long interbirth intervals, and consequently, we argue that Pleistocene carnivores had the capacity to, and likely did, limit megaherbivore population sizes.

Pleistocene | megafauna | hypercarnivore | Carnivora | megaherbivore

The role of large predators in shaping and maintaining Pleistocene ecosystems has historically been greatly underestimated, largely because across much of the planet and over the last ∼200 years, humans have kept large extant predators at relatively low densities and potentially below levels where they clearly make a difference in ecosystem functioning. In addition, because the Pleistocene is characterized by a high diversity of megaherbivores (>800 kg), and because extant species in this size range, such as elephants, are known to reduce the densities and distributions of more abundant, medium-sized herbivores (1), it has been assumed that Pleistocene terrestrial communities were much more influenced by the megaherbivores than by the large carnivores. However, if the Pleistocene carnivores were capable of regulating the megaherbivore populations, then they would be classified as key elements of a top-down forced ecosystem. Pleistocene carnivores are not usually considered to have been regular hunters of megaherbivores based on observations that the largest of the living predators (lion, tiger) do not often kill extant megaherbivores, probably because of the latter's large size and well-developed maternal protection behaviors (1, 2). However, the role of terrestrial Pleistocene predators in their ecosystems is difficult to discern because they interacted within much more species-rich guilds than exist today, and these guilds included extinct species for which we have no analogs, such as sabertooth cats and very large hyenas, making it difficult to predict prey preferences.

In this article, we estimate the predatory impact of large (> 21 kg, ref. 3) Pleistocene carnivores using a variety of data from the fossil record, including species richness within guilds, population density inferences based on tooth wear, and dietary inferences based on stable isotope ratios as well as carnivore-produced bone accumulations. In addition we use both historical and recent data on extant predator-prey relationships to estimate the prey size preferences of prehistoric carnivores and compare these to the estimated sizes of their potential prey, specifically, juvenile and young adult mammoths and mastodons. Taken together, these data suggest that Pleistocene carnivores had the capacity to, and likely did, regulate megaherbivore population sizes through predation on juvenile and sub-adult individuals.

Guilds of Large Carnivores Then and Now

Using several well preserved fossil localities that represent both the early (1-1.5 million years bp) and late (<500,000 years bp) Pleistocene of the Old and New World, we compared the diversity in species size and richness among fossil and carnivore guilds (Fig. 1, Table S1). In general, relative to three representative guilds of extant carnivores, Pleistocene guilds tended to have more species of carnivores with masses greater than 21 kg, and these species tended to be larger in mass (Fig. 1). The mean size of large hypercarnivores (species whose diets consist of >

Significance

T The role of large carnivorous mammals in curbing the populations of the largest herbivores (>800 kg), such as elephants is thought to be minimal, both in modern and Pleistocene times. However, Pleistocene carnivores were more diverse and much larger than living species. To explore their ecological roles, we use data on predator-prey body mass relationships to predict the prey size ranges of these extinct carnivores. These prey size ranges are then compared with estimates of young mammoth size, and it is apparent that juvenile mammoths and mastodons were within the predicted prey size ranges of many of the Pleistocene carnivores. Based on this and other fossil evidence, we argue that Pleistocene carnivores were able to limit megaherbivore population sizes.

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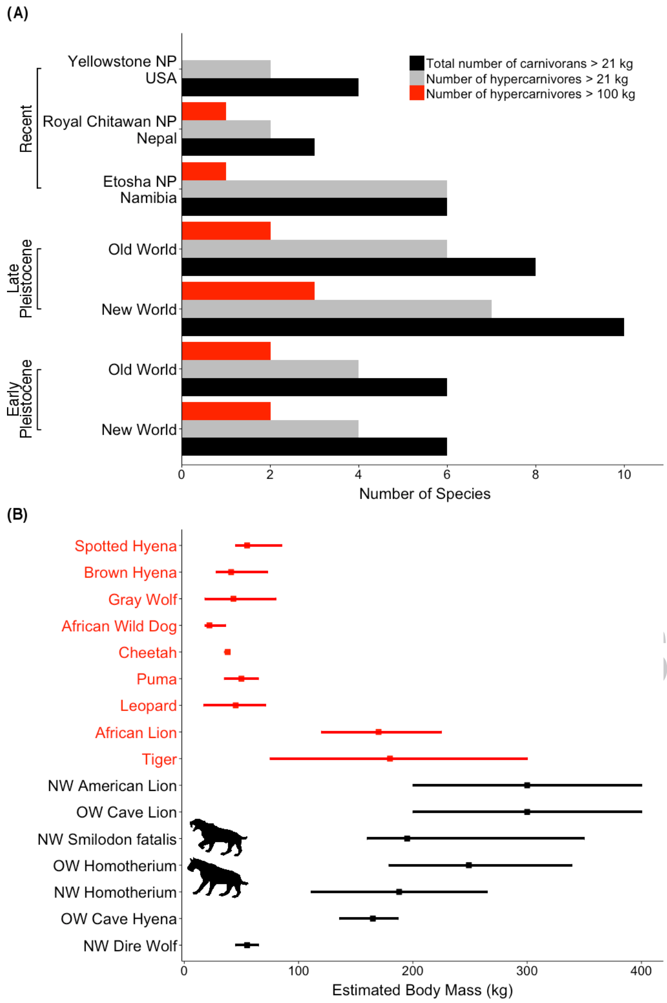

Fig. 1. (A) Predator guild composition for four Pleistocene and three extant communities. Indicated for each guild are the total number of species of carnivorans (hypercarnivores and omnivores, e.g. ursids) with masses >21kg (black), the subset of these that are hypercarnivores (gray), and the subset of these that are hypercarnivores with masses >100 kg (red) (B) Estimated body masses (mean and range) of extant (red) and extinct (black) hypercarnivores. Sabertooth cats are indicated by silhouettes. For details on the localities and species compositions, as well as body mass estimations, see *SI Materials and Methods.*

80% meat) in the extant guilds ranges from 53-63 kg, whereas it spanned 96-135 kg in the fossil guilds. Although the most diverse modern African communities are comparable to the late Pleistocene guilds in containing five to six large hypercarnivores, they include only one hypercarnivore that exceeds 100 kg, the lion (*Panthera leo*). At present (and excluding polar bears whose diet derives from marine ecosystems), there are only two hypercarnivores that exceed 100 kg in mass, the aforementioned lion and the tiger (*P. tigris*), and these are not found in sympatry. In the late Pleistocene, there were four to five more and it was typical to find two to three in sympatry (Fig. 1). For example, there were massive sabertooth felids (*Smilodon* sp., *Homotherium* sp.) in addition to much larger relatives of the extant lion (*Panthera leo spelaea, P. atrox*) in both the Old and New World, as well as huge spotted hyenas (*Crocuta crocuta spelaea*) in the Old World and a relatively carnivorous, enormous bear (*Arctodus simus*) in the New World. These Pleistocene giants were at least a third to more than twice the mass of their extant relatives (Fig. 1). Moreover, as noted above, some of these species were sabertooth cats, an ecomorph without a close modern analog. These imposing felids were characterized by a suite of adaptations that enhanced their ability to kill relatively large prey, including enlarged knife-like upper canines, a long neck, and robust, heavily muscled forelimbs (4, 5). Notably, nearly all Pleistocene predator guilds outside of Australia included at least one and often two species of large sabertooth cat.

What could have supported such a high diversity of coexisting, large predators? Sandom et al. (6) showed that at a global scale, large predator species richness was more closely linked to prey richness than either primary productivity or climate. This relationship was more pronounced within sets of similar sized predators and prey than across their entire sample. Our survey of 181 present day mammalian faunas (see *SI Materials and Methods)* that include at least one species each of large hypercarnivore and megaherbivore (species > 800 kg), suggests a positive association between hypercarnivore and megaherbivore diversity. As the number of megaherbivore species increases, so does the likelihood of finding three or more coexisting hypercarnivores. For example, of the 28 faunas that include one megaherbivore, only nine (32%) include three or more large hypercarnivores. By contrast, this percentage climbs to 52 % (11/21) when two megaherbivores are present, and further still to 91% (31/34) when three or more megaherbivores are present. The maximum richness of six coexisting large hypercarnivores is found only in communities with three or more megaherbivores. This positive correlation between hypercarnivore diversity and megaherbivore diversity suggests that the presence of huge herbivores promotes, or at least permits, coexistence among big predators. This could be due to a variety of causes. Given the size of their carcasses, it is possible that megaherbivores are a significant food resource for scavenging and hunting predators, especially over longer timescales (7). However, it is also possible that the megaherbivores themselves could modify the environment in ways that increase hunting success by creating more edge habitats that favor ambush predators, such as lions, or by shifting woodland and forest towards grassland, thus improving the habitat for cursorial hunters, such as African wild dogs and spotted hyenas (1,8).

All four of the Pleistocene fossil communities we included in our analysis have two to six megaherbivores and four to seven large hypercarnivores, two to three of which exceed 100 kg in mass. In the Old World, the megaherbivores usually include mammoth (*Mammuthus* sp.), rhinoceros (*Stephanorhinus* sp. or *Coelodonta* sp.), and a giant bovid (*Praeovibos* sp., *Bison* sp., *Symbos* sp., or *Bos* p.) (9,10). In the New World, the species richness of megaherbivores was even greater, in part due to the addition of giant ground sloths that emigrated from South into North America at least 2.5 million years ago (11). At the late Pleistocene site of Rancho La Brea, California, there were six megaherbivores: two proboscideans (*Mammuthus columbi, Mammut americanum*), giant camel (*Camelops hesternus*), extinct bison (*B. antiquus*), and two ground sloths (*Megalonyx jeffersoni, Paramylodon harlani*) (12). Not surprisingly, this site also exhibits the greatest richness of hypercarnivores >21 kg (n=7) across all our fossil guilds.

Given the greater prevalence of very large (>100 kg) hypercarnivores in association with multiple megaherbivores in Pleistocene communities, and the observation that prey size tends to increase with predator size (2, 13), it seems likely that predation pressure on megaherbivores was greater in the past than in the present mammalian communities. This scenario makes sense especially in light of evidence that supports selective predation by large extant hypercarnivores upon more vulnerable age classes of megaherbivores.

Predation on Extant Megaherbivores

It is often stated that modern day megaherbivores are largely immune to the effects of predation due to their massive bodies and their tendency to exhibit strong maternal protection of juve-

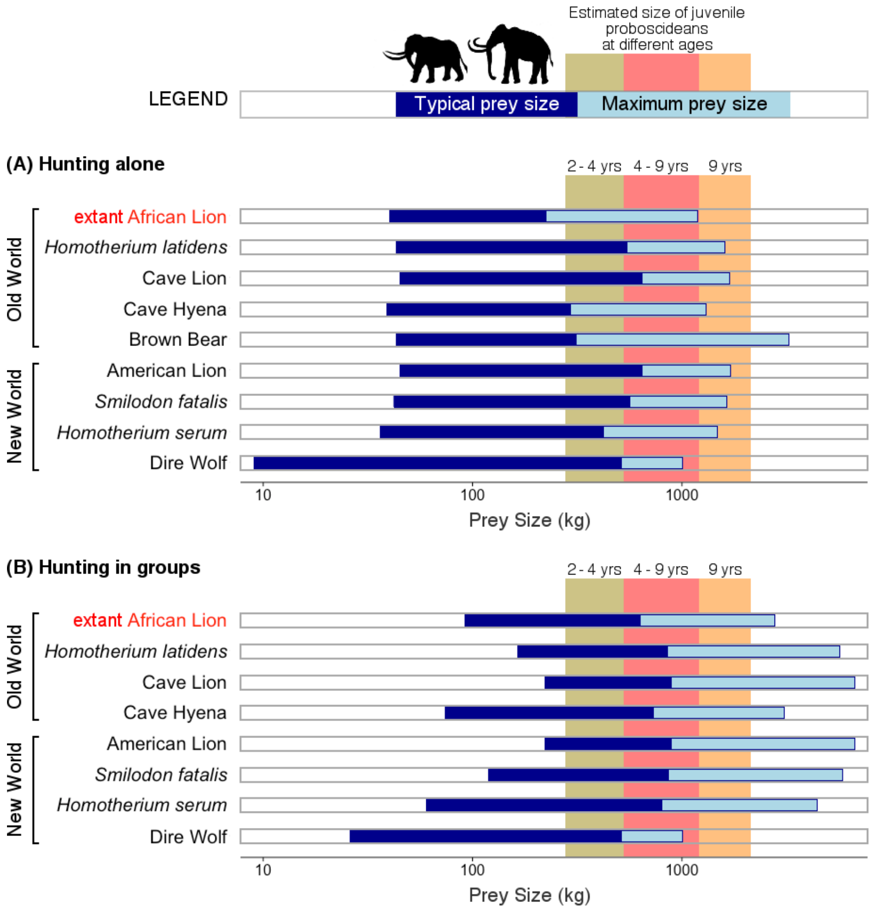

Fig. 2. Predicted typical (dark blue) and maximum (light blue) prey size ranges (horizontal bars) for the extant African lion (*Panthera leo*) and large extinct Pleistocene predators superimposed on the estimated sizes of juvenile proboscideans (mammoths and mastodons) at different ages (vertical stripes). Prey size ranges are estimated both for (A) solitary hunting, and (B) group hunting. Size estimates for mammoths are based on data from living elephants. Prey size ranges for the predators were based on known relationships between prey size and predator body mass for extant large carnivores. For details, see *SI Materials and Methods*.

niles (1, 2). Modern juvenile elephants do not stray far from their mother's side until they are about 5-7 years of age (*SI Materials and Methods*). Nevertheless, a review of the literature reveals that young African elephants are taken regularly, especially at the end of the dry season when they may be more susceptible (Table S2). For example, Joubert (14) observed 74 elephants killed by lions over a three-year period in Chobe National Park, Botswana, with two-thirds of the kills on juveniles and subadullts between 4 and 15 years old. Elsewhere in Africa, 44 kills of elephants by lions were observed in Zimbabwe over a six-year span, with juveniles less than eight years of age being targeted (15), and smaller numbers of kills have been documented in both the Central African Republic (16) and Kenya (17). In one study, elephant made up 20-23% of the total biomass consumed by lions annually, and exceeded the biomass contributions made by all other prey except buffalo (18). Young rhinoceros are also not immune to predation by lions as evidenced by three kills of subadults that were made over three months in Etosha National Park, Namibia (19). Goddard (20) estimated that 16% of black rhinos younger than two years old were killed by lions and spotted hyenas in East Tsavo Park, Kenya. Spotted hyenas were also observed to kill five young elephants in Hwange National Park, Zimbabwe in a single year (21). Thus it is clear that lions and to a lesser extent, spotted hyenas, are fully capable of killing juvenile and subadult megaherbivores that probably weigh as much as 1500 kg.

Most often, the killing of megaherbivores is accomplished by a group of individuals working together. Hunting in groups facilitates the killing of large prey and in accord with this, the success rate for lions taking elephants appears to be enhanced by large pride size. In Botswana, lions were observed to regularly use a strategy in which one to two lions leapt onto and bit the back of the victim while two to four others on the ground worked to sever the relatively thin flexor muscles of the hindlimb, resulting in rapid immobilization (22). Of 18 such attempts on elephants, four were successful, all of which involved more than 27 of the 30 lions in the pride. Similarly, the pride that took more than 70 elephants in three years in Botswana was also large, consisting of 18 individuals (14). This suggests that large prides are predisposed to attack large megaherbivores. If so, predation on elephants by lions may be less frequent now than in the past because of declines in lion pride size due to human persecution and reductions in prey populations (22, 23). Larger pride sizes may have been selected against with the advent of large scale human hunting, as they could have been a more conspicuous target. It is well known that the number of lions in Africa has declined over the past 100 years; whereas there were perhaps 500,000 lions on the continent in 1950, there are now less than 30,000 (24). It is not clear whether or how closely pride size should follow population size, but in Etosha National Park, a 33% population decline over 12 years was accompanied by a reduction in the mean number of adults per pride from ten to six (23).

A review of African fauna historical records in the period 1835-1950 suggests that our perceptions of typical lion pride size may be constrained by what has been observed over the past sixty years (Table S3). A survey of pride size across 27 African reserves between 1997 and 2007 found a mean of nine (+/- four) adults (25), but older records include multiple reports of prides of 35-40 individuals, and in some instances such sightings were not unusual (ref. 26:253). For example, Sikes (26) commented on predator group sizes in the period between 1901-1931, writing “In the days when such well-known personalities as Lord Delamere habitually encountered prides of up to 36 lions on their ranches in Kenya, when hunters all too frequently stumbled on prides of between 17 and 40 on a kill or when the lone horseman found himself surrounded by packs of between 25 and 40 Cape hunting dogs, these animals were sufficiently numerous to keep elephant calf mortality at a high level." If African lion prides were significantly larger in the past as the historical record suggests, then predation on elephants may have been a more regular occurrence than is observed today.

Pleistocene Predator Group Size and Population Density

Typical group sizes for Pleistocene predators are difficult, if not impossible, to determine, but there are reasons to believe that selection would have favored sociality and the existence of large prides, clans, and packs. The greatest diversity of social predator species today is found in African savannah-woodland environments where lions, spotted hyenas, African wild dogs, and to a lesser extent cheetahs (*Acinonyx jubatus*) all hunt in groups. In addition to expanding the size of prey that they can kill, working in groups allows all but the cheetah to better defend their kills against carcass theft (kleptoparasitism). In aggressive interactions over carcasses between lions and hyenas, or wild dogs and hyenas, group size is an important determinant of who wins (27, 28). The frequency of kleptoparasitism increases with the density of predators (29), and thus higher predator densities, such as those found in Africa, favor the evolution of sociality among large hypercarnivores. Moreover, in relatively open environments such as savannah-woodland with vultures circling overhead in search of carrion, the ability to detect kills made by others is probably enhanced (30), increasing the frequency of aggressive encounters over kills.

It seems likely that predator densities and group sizes could have been much greater than at present, given the multiple anthropogenic forces that currently tend to limit large carnivore abundance such as habitat loss, competition for prey, and direct persecution (31). If predator densities were higher in the Pleistocene than at present, then it is likely that attempts at kleptoparasitism were a common occurrence, and this in turn would favor large group sizes (32). Moreover indirect evidence from rates of tooth wear and fracture in Pleistocene carnivores suggests elevated levels of competition for food (ibid, Van Valkenburgh and Ripple 2010), a situation likely defined by high predator densities, where larger group sizes would be advantageous, both for defense of a kill and because prey could be more efficiently utilized (Vucetich et al. 2004). High rates of tooth wear and fractures are widespread among fossils of large Pleistocene carnivores. For example, large New World predators of the Pleistocene exhibit rates of tooth fracture that are as much as three to five times that of their modern counterparts (33). Very high rates of tooth fracture are also present in Pleistocene gray wolves from Great Britain dated between 50 to 85 thousand years ago (34) and late Pleistocene cave lions and cave hyenas from Zoolithen Cave, Germany (Table S4). Data from modern carnivores indicate that both the number of teeth broken in life and rates of tooth wear are greater when more bone is eaten, a behavior that increases when prey are more difficult to acquire (33, 35). The elevated tooth fracture frequencies observed among multiple species of Pleistocene carnivores suggest an ecosystem in which the relative density of predators to prey was high, and thus competition for carcasses was intense, leading to more frequent intra- and interspecific confrontations over kills. This in turn would favor larger group sizes as well as more complete consumption of carcasses, including bones.

Estimating Pleistocene Predator-Prey Preferences

The prey preferences of extant large carnivores have recently been reviewed in a series of papers by Hayward and colleagues (see *SI Materials and Methods*). These data were used to construct regression equations of accessible (typical) and largest prey body mass against predator body mass for extant species hunting alone or in groups, and these were extrapolated to predict the prey sizes of extinct species (Fig. 2, Table S5, Fig. S1). Several of the large Pleistocene hypercarnivores were likely to have been social, based on their morphology and their extant relatives, such as the dire wolf (*Canis dirus*), gray wolf (*C. lupus*), and cave hyena (*C.c. spelaea*). All of these species are large cursorial predators that are unable to grapple with their prey and instead must subdue prey with their jaws alone. Consequently, it is very difficult for a solitary individual cursor to kill prey much larger than itself, so hunting in groups is favored. Felids are not so constrained by their anatomy, and therefore single individuals can kill relatively large prey. Nevertheless, hunting in groups does extend the size range of prey that can be killed and may increase hunting success on very large prey (see below), so it is possible that some or all of the large Pleistocene felids (*Homotherium, Smilodon, P. atrox, P. leo spelaea*) were social at times. Arguments have been made in favor of sociality in all three (5, 36) but others have disagreed (37). Because it is difficult to be confident of the social behavior of extinct species, we estimated prey sizes for all species as both solitary individuals and groups.

With the exception of the dire wolf, the estimated typical prey size ranges of the Pleistocene species exceed that of the African lion (Fig. 2). Whereas the typical range of prey for a solitary African lion would not include 2-4 year old mammoths, all four of the Pleistocene felids are predicted to have included them as typical prey, and this is without any consideration of the special weaponry of the sabertooths. The maximum prey sizes for the fossil cats also exceed that shown for the extant lion, with each being capable of killing nine-year old sub-adult proboscideans. Hunting in groups increases the upper range of available prey sizes, and the difference between the extant lion and Pleistocene species is most apparent in terms of the predicted maximum size of prey. The extinct cats are estimated to have been able to kill adults with masses between 5700 kg (*Homotherium* spp.) and 6700 kg (*P.atrox, P.l. spelaea*), thus encompassing the size of female adult and young male adult proboscideans (Fig. 2. Fig. S2). These data suggest that juvenile proboscideans, rhinos, and ground sloths would all have been well within the realm of possibility for many of these extinct hypercarnivores. Adult megaherbivores do appear to have been outside the typical prey size range of Pleistocene hypercarnivores, even with group hunting, suggesting that the predators would have limited their populations through predation on younger individuals. In Africa today, top-down regulation of elephants by non-human predators has not been observed, in large part because maternal defense of juveniles appears to greatly inhibit successful attacks by predators hunting in the relatively small group sizes we currently observe (see above).

The fossil record also provides some limited data indicating that Pleistocene carnivores consumed megaherbivores. Studies of carbon and nitrogen stable isotope ratios in a number of large species suggest that most individuals were generalists that consumed a mix of large ungulates but some individuals of gray wolves and cave hyenas specialized on mammoth (see *SI Materials and Methods*). In addition to the stable isotope data, there is evidence of a preference for megaherbivores from several fossilized den sites of both cave hyenas (38, 39) and the sabertooth cat, *Homotherium serum* (40). These den sites include numerous tooth-marked bones of juvenile woolly mammoth and rhinoceros, in the case of the cave hyenas, and juvenile Columbian mammoth, in the case of the sabertooth cat. The predominance of juvenile prey suggests that most or all of these individuals were killed rather than scavenged (39).

Could Pleistocene Carnivores Limit Megaherbivore Populations?

Others before us have viewed the large hypercarnivores of the Pleistocene as effective predators of megaherbivores (e.g. refs. 22, 41), but few have addressed the issue of whether this resulted in limiting megaherbivore populations, though Ripple and Van Valkenburgh (35) synthesized multiple lines of evidence suggesting that the megafauna of the North American Pleistocene were primarily predator-limited and at low densities. The prevailing opinion seems to be similar to that of Owen-Smith (1) who wrote, "prior to human arrival, populations of mammoths, mastodont, and ground sloth would have existed at saturation levels where further increase was prevented by food limitation." This does not state directly that predators were irrelevant to reducing the numbers of megaherbivores, but it is strongly implied, and is based on observations of living systems. The conclusion that megaherbivores were at saturation levels seems improbable given the greater physical capacities of the Pleistocene hypercarnivores, as well as evidence that species with the low reproductive rates typical of megaherbivores, are susceptible to population reduction under conditions of relatively low predation pressure (42).

The greater vulnerability of species with low reproductive rates to extinction is apparent from a 2002 (ref. 42) analysis of extinction patterns among nine groups of mammals (1200+ species) that lost three or more species at or near the end of the Pleistocene. Species with reproductive rates of less than one offspring per female per year were much more likely to have gone extinct than those with faster reproductive rates. This analysis did not include some species of extinct megafauna, such as mammoths, mastodonts, and ground sloths, but it is almost certain that all these species had very low reproductive rates. According to the PanTHERIA database for extant mammals (http://esapubs.org/archive/ecol/e090/184/ metadata.htm), 22 of the 29 ungulate species with masses greater than 200 kg have interbirth intervals that exceed one year, and of these, nine of the 12 species with masses greater than 600 kg have interbirth intervals that exceed two years (Figure S4). Indeed, estimates of weaning age from stable isotope analysis and tooth wear in wooly mammoths point to weaning ages of at least 1.5 and in one case more than five years (see *SI Materials and Methods*), and Fisher (*e.g.,* ref. 43) presented evidence from cyclic patterns of annual growth increments in tusks of female mastodons that calving intervals were typically three to four years Although there are small mammals with relatively slow reproductive rates, such as echidnas, there are no very large mammals with relatively high reproductive rates (42), thus it is safe to assume that the extinct megaherbivores had interbirth intervals that exceeded one year, and could have been four years or more, as is typical of African elephants (see *SI Materials and Methods* for more details). Given such low fecundity, predation pressure would not have to be high in order to keep mortality rates above recruitment rates, thereby limiting population growth.

It is likely that Pleistocene carnivores preferentially preyed on juvenile rather than adult megaherbivores. Among extant large predators, the proportion of prey that are juveniles increases with prey size; living spotted hyenas tend to take juveniles of smaller and medium size ungulates in proportion to their abundance, but shift to taking mostly or all juveniles of very large prey such as giraffes, black rhinos, and elephants (10). Clearly, this is a consequence of the much greater challenge of killing adults. Predation on juveniles can have a significant impact on ungulate population growth. For example, more than 50% of the annual mortality of moose (*Alces alces*) can be ascribed to brown bear (*Ursus arctos*) predation on calves in some reserves (44). Similarly, brown bears in Yellowstone National Park, kill more than 1000 elk calves (*Cervus elephus*) every spring, a number that exceeds the combined total number of elk calves killed annually by wolves, coyotes, and cougars (45).

Although theoretical evidence supports the idea that populations of medium to large sized herbivore were limited by large Pleistocene hypercarnivores (46, 47), it is less clear whether this applies to megaherbivores. We suggest that large hypercarnivores must have limited at least the proboscideans, given the impressive impact these species have on vegetation structure and quality. Based on studies of modern African elephants, it is not clear that they can effectively self-regulate and maintain their numbers at levels that allow for a sustainable existence of a healthy population. Gough and Kerley (48) found no evidence for density dependent regulation in a South African elephant population that they studied between 1976-1979 and 1996-2006. Birth rates and overall population growth rate did not slow as elephant density rose despite serious declines in plant biomass and biodiversity. Of course, it might be argued that human activities have limited elephants to reserves that are too small, and in the past, they would have moved from areas of low forage quality to areas of better quality as needed. However, it seems likely that elephant densities would have been much greater prior to the expansion of modern and especially industrialized humans, and consequently any appropriate habitats would have been fully occupied by elephants, thus limiting their ability to expand their foraging range. Remarkably, Africa was home to four species of elephants over much of the Pleistocene, with three of them coexisting in some regions (49) It is hard to imagine how they partitioned their shared resources, but it certainly suggests a crowded system, in which top-down forcing was probably essential to ensure long term stability.

Notably, Pleistocene large mammal community composition is remarkably stable at a continental scale over at least the last one million years in both the Old and the New Worlds, despite glacial-interglacial fluctuations in climate (50-52). The apparently long term and persistent stability suggests the existence of rich and complex communities that included multiple species at different trophic levels playing similar roles (redundancies), thus enhancing their resilience in the face of environmental perturbations. Extant large mammal communities that lack large apex predators are often characterized by rapid population expansions among the large herbivores. For example, in Eurasia and North America, cervid densities were on average nearly six times greater in areas without wolves compared to areas with wolves (53). These impressive herbivore irruptions can have very negative impacts on vegetation and ecosystem services, and can result in declines in floral and faunal biodiversity if they occur repeatedly (44, 54). If megaherbivores had not been predator-limited, the Pleistocene might be expected to have been characterized by a longterm decline in ecosystem stability but there is no evidence of such a gradual decline. Instead, megafaunal extinctions are concentrated close to the Pleistocene-Holocene transition and associated with the presence of humans (55).

Implications for the Future

It is fair to ask why we should care about the role of extinct predators in their ecosystems. What bearing does it have on current struggles to preserve biodiversity? One answer is that many of the species we are most concerned about preserving evolved during or prior to the Pleistocene, and thus did so under very different conditions from the present. As a result, aspects of their behavior and morphology may be better explained as a response to ancient rather than current selection pressures. Second is that studies of the Pleistocene reveal that the planet was capable of sustaining much more species–rich communities that included a greater proportion of megafauna than are found today (56). It appears that the complexity of these communities and their trophic depth, especially the presence of large apex predators, contributed to their stability, and the same would apply to the many, more ancient communities that included megaherbivores prior to the Pleistocene. Recreating these communities is not possible, but their record of success compels us to maintain the diversity we have and rebuild it where feasible (e.g. rewilding). Then as now, it is likely that large predators influenced their communities via trophic cascades that favored biodiversity, including increased scavenging opportunities, the creation of refuges from herbivory for plants, and consequent enhanced environmental heterogeneity and stability (31, 57-59). The late Pleistocene extinction of the largest of these hypercarnivores almost certainly resulted from the disappearance of their preferred prey, including large equids, bovids, and we argue, young megaherbivores. It is probably not a coincidence that spotted hyenas and lions have persisted in Africa alongside megaherbivores, while disappearing from more northern latitudes. With a growing awareness of the prevalence of top-down forcing, we are just beginning to understand the ecological and evolutionary linkages among these large mammals, and studies of their interactions on evolutionary timescales are an important piece of the puzzle.

ACKNOWLEDGEMENTS We are grateful to the organizers of the 2013 conference on Megafauna and Ecosystem Function for inviting us to contribute to this issue. We also thank C Badgley, J Damuth, and the members of BVV's lab for comments on various drafts, and M. Balisi for help with illustrations. We acknowledge the support of National Science Foundation EAR 1237928 to BVV. .

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