

The impact of large terrestrial carnivores on Pleistocene ecosystems

Blaire Van Valkenburgh^{a,1}, Matthew W. Hayward^{b,c,d}, William J. Ripple^e, Carlo Meloro^f, and V. Louise Roth^g

^aDepartment of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095; ^bCollege of Natural Sciences, Bangor University, Bangor, Gwynedd LL57 2UW, United Kingdom; ^cCentre for African Conservation Ecology, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa; ^dCentre for Wildlife Management, University of Pretoria, Pretoria, South Africa; ^eTrophic Cascades Program, Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331; ^fResearch Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool L3 3AF, United Kingdom; and ^gDepartment of Biology, Duke University, Durham, NC 27708-0338

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Large mammalian terrestrial herbivores, such as elephants, have dramatic effects on the ecosystems they inhabit and at high population densities their environmental impacts can be devastating. Pleistocene terrestrial ecosystems included a much greater diversity of megaherbivores (e.g., mammoths, mastodons, giant ground sloths) and thus a greater potential for widespread habitat degradation if population sizes were not limited. Nevertheless, based on modern observations, it is generally believed that populations of megaherbivores (>800 kg) are largely immune to the effects of predation and this perception has been extended into the Pleistocene. However, as shown here, the species richness of big carnivores 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 in 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 subadult 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.

predator | megafauna | hypercarnivore | Carnivora | megaherbivore

Large mammalian terrestrial herbivores have dramatic effects on the ecosystems they inhabit and at their highest population densities the environmental impact of the largest modern herbivores, such as elephants, can be devastating (1, 2). At the end of the Pleistocene, loss of large mammalian herbivores has been implicated in major shifts in vegetation structure and ecosystem processes, including transitions between biomes, such as from grass-dominated steppe biomes to moss-dominated tundra (3, 4). What prevented widespread habitat destruction during the Pleistocene, when ecosystems sustained multiple species of megaherbivores (>800 kg), including mammoths, mastodons, and giant ground sloths?

Although the role of predators in structuring terrestrial ecosystems is widely acknowledged (5, 6), it is also widely assumed that the large body size of megaherbivores renders their populations exempt from “top-down” limitation by predators both now and in the past (7–10). However, the impact of large terrestrial predators on Pleistocene ecosystems may be difficult to appreciate, because these carnivores interacted within much more species-rich guilds than exist today. In addition, these Pleistocene guilds included extinct species (such as sabertooth cats and very large hyenas) for which we have no close living

analogs, making their prey preferences a matter of inference, rather than observation.

In this article, we estimate the predatory impact of large (>21 kg, ref. 11) 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 the relationships between masses of extant predators and prey 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. On the basis of these data we suggest that Pleistocene carnivores had the capacity to, and likely did, limit megaherbivore population sizes through predation on juvenile and subadult individuals.

Guilds of Large Carnivores Then and Now

The importance of carnivores in shaping Pleistocene terrestrial ecosystems is readily underestimated because carnivore species diversity and body size are much reduced in modern communities. Using several localities with well-preserved fossils representing both the early (1–1.5 million years B.P.) and late (<500,000 y B.P.) Pleistocene of the Old and the New World, we compared the diversity in species size and richness among fossil and contemporary carnivore guilds (Fig. 1 and *SI Appendix, Table S1*). In general, Pleistocene guilds tended to have more

Significance

At very high densities, populations of the largest herbivores, such as elephants, have devastating effects on the environment. What prevented widespread habitat destruction in the Pleistocene, when the ecosystem sustained many species of huge herbivores? We use data on predator–prey body mass relationships to predict the prey size ranges of large extinct mammalian carnivores, which were more diverse and much larger than living species. We then compare these prey size ranges with estimates of young mammoth sizes and show that juvenile mammoths and mastodons were within predicted prey size ranges of many of the Pleistocene carnivores. From this and other fossil evidence we argue that, by limiting population sizes of megaherbivores, large carnivores had a major impact on Pleistocene ecosystems.

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¹To whom correspondence should be addressed. Email: bvanval@ucla.edu.

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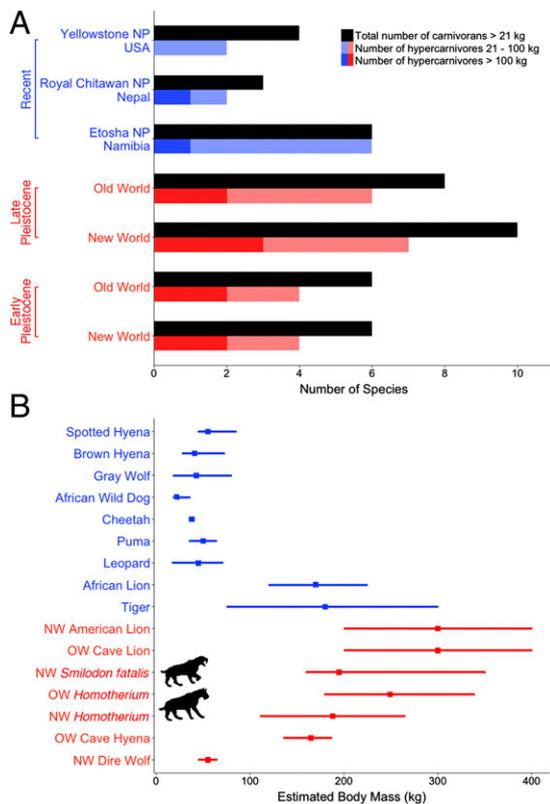


Fig. 1. (A) Predator guild composition for four Pleistocene (red) and three extant (blue) communities. Indicated for each guild are the total number of species of carnivorans (hypercarnivores and omnivores, e.g., ursids) with masses >21 kg (black), the subset of these that are hypercarnivores (two-toned bar), and the subset of these that are hypercarnivores with masses >100 kg (dark blue or red). (B) Estimated body masses (mean and range) of extant (blue) and extinct (red) hypercarnivores. Silhouettes are provided only for the sabertooth cats because they lack modern analogs. For details on the localities and species compositions, as well as body mass estimations, see *SI Appendix, SI Materials and Methods, section 1*.

species with masses greater than 21 kg, and these species tended to be larger than equivalent extant species (Fig. 1). Averaging across the species found within single communities, the mean size of large hypercarnivores (species whose diets consist of >80% meat) in the extant guilds ranges from 53 to 63 kg, whereas it spanned 96–135 kg in the fossil guilds. Although guilds in the most diverse modern African communities are similar to those in the late Pleistocene 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, who feed on marine resources), there are only two hypercarnivores that exceed 100 kg in mass, the aforementioned lion and the tiger (*Panthera tigris*), and these are not found in sympatry. In the late Pleistocene, there were four to five more large hypercarnivores and it was typical to find two to three in sympatry (Fig. 1). For example, there were massive sabertooth felids (*Smilodon* sp. and *Homotherium* sp.) in addition to much larger relatives of the extant lion (*Panthera leo spelaea* and *Panthera atrox*) in both the Old and the 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 possessed a suite of adaptations that enhanced their ability

to kill large prey, including enlarged knife-like upper canines, a long, thick neck, and robust, heavily muscled forelimbs (12). Notably, nearly all Pleistocene predator guilds found 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? Among most extant communities, large predator species richness is more closely linked to prey richness than either primary productivity or climate and this relationship is more pronounced within sets of similar sized predators and prey (13). To further examine this relationship, we surveyed 181 present day mammalian faunas (*SI Appendix, SI Materials and Methods, section 2, and Table S6*) that include at least one species each of large hypercarnivore and megaherbivore (species >800 kg), and we found that, 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 9 (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 association between hypercarnivore diversity and megaherbivore diversity suggests that the presence of huge herbivores promotes, or at least permits, coexistence among big predators. The correlation could arise from a variety of causes. Given the size of their carcasses, megaherbivores could be a significant food resource for scavenging and hunting predators (14). Megaherbivores themselves may 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 toward grassland, thus improving the habitat for cursorial hunters such as African wild dogs and spotted hyenas (9, 15). A dynamic cycle could arise where vegetation patterns shift with the relative dominance of megaherbivores or large predators. However, it is unclear to what extent such habitat modification would occur if the large carnivores exerted strong top-down pressure on the megaherbivores.

In contrast to the present, all four of the Pleistocene fossil communities we examined (*SI Appendix, Table S1*) had two to six megaherbivores and four to seven large hypercarnivores, two to three of which exceeded 100 kg in mass. In the Old World, the megaherbivores usually included mammoth (*Mammuthus* sp.), rhinoceros (*Stephanorhinus* sp. or *Coelodonta* sp.), and a giant bovid (*Praeovibos* sp., *Bison* sp., *Symbos* sp., or *Bos* p.) (16, 17). In North America, the species richness of megaherbivores was even greater, in part due to the immigration of giant ground sloths from South America at least 2.5 million years ago (18). At the late Pleistocene site of Rancho La Brea, California, there were six megaherbivores: two proboscideans (*Mammuthus columbi* and *Mammot americanum*), giant camel (*Camelops hesternus*), extinct bison (*Bison antiquus*), and two ground sloths (*Megalonyx jeffersoni* and *Paramylodon harlani*) (19). Not surprisingly, this site also exhibits the greatest richness of hypercarnivores >21 kg ($n = 7$) across all our fossil guilds.

Prey body size tends to increase with predator size (10, 20). Given the greater prevalence of very large (>100 kg) hypercarnivores in association with multiple megaherbivores in Pleistocene communities, it seems likely that predation pressure on megaherbivores was greater in the past than in modern mammalian communities. However, this idea is not so easily accepted, given the observation that even the largest of living carnivores, tigers and lions, rarely tackle adult elephants, hippos, or rhinos. But what about juveniles?

Predation on Extant Megaherbivores

Modern day megaherbivores may appear largely immune to the effects of predation because their bodies are massive and maternal protection of juveniles is strong (9, 10). Juvenile elephants do not stray far from their mother's side until they are about 5–7 years of age (*SI Appendix, SI Materials and Methods, section 6*). Nevertheless, our 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 (*SI Appendix, Table S2*). For example, 74 elephants were killed by lions over a 4-y period in Chobe National Park, Botswana, with nearly two-thirds of the kills on juveniles and subadults 9 y old or younger (21). Elsewhere in Africa, 44 kills of elephants by lions were observed in Zimbabwe over a 6-y span, with juveniles less than 8 years of age being targeted (22), and smaller numbers of kills have been documented in both the Central African Republic (23) and Kenya (24). 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 (25). Young rhinoceros are also not immune to predation by lions as evidenced by three kills of subadults that were made over 3 mo in Etosha National Park, Namibia (26). Goddard (27) estimated that 16% of black rhinos younger than 2 y 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 (28). Thus, it is clear that lions, and to a lesser extent, spotted hyenas, are fully capable of killing juvenile and subadult megaherbivores that can weigh as much as 1,500 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 accordingly, 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 others on the ground worked to sever the relatively thin flexor muscles of the hindlimb, resulting in rapid immobilization (29). Of 18 such attempts on elephants, 4 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 3 years in Botswana was also large, consisting of 18 individuals (21). These numbers suggest 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 pride size due to human persecution and reductions in prey numbers (29, 30). With the advent of large-scale human hunting, larger prides would have provided more conspicuous targets. The decline in lion numbers in Africa over the past 100 y is well known; whereas there were perhaps 500,000 lions on the continent in 1950, there are now fewer than 30,000 (31). Whether or how closely pride size should follow population size is unclear, but in Etosha National Park, a reduction in the mean number of adults per pride from 10 to 6 accompanied a 33% population decline over 12 y (30). Our review of African fauna historical records in the period 1835–1950 suggests that modern perceptions of typical lion pride size may reflect only what has been observed over the past 60 y (*SI Appendix, Table S3*). A published survey of pride size across 27 African reserves between 1997 and 2007 found a mean of 9 (± 4) adults (32), but older records include multiple reports of prides of 35–40 individuals, and in some instances such sightings were not unusual. For example, Sikes (ref. 33, p. 253) commented on predator group sizes in the period between 1901 and 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, as the historical record suggests, African lion prides were significantly larger in the past, 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 the behavior of extant predators suggests that conditions in the Pleistocene 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 woodlands, where lions, spotted hyenas, African wild dogs, and to a lesser extent cheetahs (*Acinonyx jubatus*) all hunt in groups. Beyond 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). Moreover, in aggressive interactions over carcasses between lions and hyenas, or wild dogs and hyenas, group size is an important determinant of who wins (34, 35).

Given the multiple anthropogenic forces that currently limit large carnivore abundance, such as habitat loss, competition for prey, and direct persecution, it seems likely that predator densities and group sizes could have been much greater in the Pleistocene than in even the recent past (5). If so, attempts at kleptoparasitism were probably a common occurrence, and this behavior also would favor large group sizes (36, 37). Larger groups in turn would favor more complete consumption of carcasses, including bones. Among modern carnivores, more bone is eaten when prey are more difficult to acquire, and this activity increases both the number of teeth broken in life and rates of tooth wear (38). Elevated tooth fracture frequencies observed among multiple species of Pleistocene carnivores suggest ecosystems in which the densities of predators relative to prey were high, and thus competition for carcasses was intense, leading to more frequent intra- and interspecific confrontations over kills (39). In large New World predators of the Pleistocene, for example, rates of tooth fracture are as much as three to five times that of their modern counterparts (38). Very high rates of tooth fracture are also present in Pleistocene gray wolves from Great Britain dated between 50 and 85 thousand years ago (40) and late Pleistocene cave lions and cave hyenas from Zoolithen Cave, Germany (our data, *SI Appendix, Table S4*).

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 (*SI Appendix, SI Materials and Methods, section 3*). These data are used here 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 the equations are extrapolated to predict the prey sizes of extinct species (Fig. 2 and *SI Appendix, Table S5* and Fig. S1). Based on their morphology and their extant relatives, several of the large Pleistocene hypercarnivores, such as the dire wolf (*Canis dirus*), gray wolf (*Canis lupus*), and cave hyena (*C. c. spelaea*) were probably social because all are large, cursorial predators that are unable to grapple with their prey, and instead must subdue prey with their jaws alone. When it is difficult for a solitary individual to kill prey much larger than itself, hunting in groups is favored. Felids are not so constrained by their anatomy and 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 each of these (12, 41) but

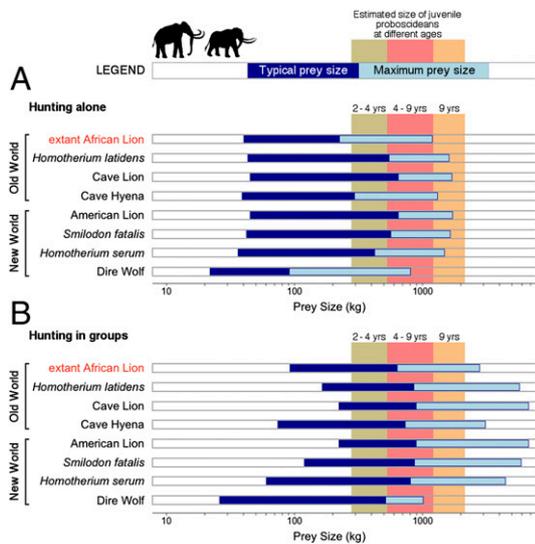


Fig. 2. Predicted typical (dark blue) and maximum (light blue) prey size ranges (horizontal bars) for the extant African lion (*Panthera leo*) and large extinct Pleistocene predators superimposed on the estimated sizes of juvenile proboscideans (mammoth and mastodons) at different ages (vertical stripes). 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 Appendix, SI Materials and Methods, sections 3 and 6*.

some workers have disagreed (42). Because it is difficult to be confident of the social behavior of extinct species, we estimated prey sizes for all species as both solitary and group hunters. These prey sizes are compared with our estimates of body sizes of proboscideans (the largest of the megaherbivores) in the most vulnerable age classes (*SI Appendix, SI Materials and Methods, section 6*).

With the exception of the dire wolf, estimated typical prey size ranges of the Pleistocene species exceed that of extant African lions (Fig. 2). Whereas we infer that the typical range of prey for a solitary African lion would not include 2- to 4-y-old mammoths, we predict that all four of the Pleistocene felids could have included them as typical prey, even without considering the special weaponry of the sabertooths. Our predictions of the maximum prey sizes for the fossil cats also exceed that shown for the extant lion, with each species, we infer, being capable of killing 9-y-old subadult 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. In groups, the extinct cats are estimated to have been able to kill adults with masses between 5,700 kg (*Homotherium* spp.) and 6,700 kg (*P. atrox* and *P. l. spelaea*), thus encompassing the size of female adult and male young adult proboscideans (Fig. 2 and *SI Appendix, 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 appear to have been outside the typical prey size range of Pleistocene hypercarnivores, but would have been accessible to most species hunting in groups. This situation suggests that, if predators did limit their populations, it would have been mainly through predation on younger individuals. In Africa today, predation on elephants by nonhuman predators is observed, but not top-down regulation, in large part because maternal defense of juveniles appears to greatly inhibit successful attacks by modern predators that hunt in groups that are comparatively small (see above).

The fossil record provides some limited data indicating that Pleistocene carnivores did in fact consume 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 (*SI Appendix, SI Materials and Methods, section 7*). In addition to the stable isotope data, there is evidence of a preference for megaherbivores from several fossilized den sites of both cave hyenas (43, 44) and the sabertooth cat, *Homotherium serum* (45). 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 (44, 45).

Could Pleistocene Carnivores Limit Megaherbivore Populations?

Others before us have viewed the large hypercarnivores of the Pleistocene as capable of killing megaherbivores (e.g., refs. 29, 46), but few have addressed the issue of whether this capability resulted in limiting megaherbivore populations (39). However, when the issue has been explicitly addressed, the prevailing opinion seems to be similar to that of Owen-Smith (9) who wrote, “prior to human arrival, populations of mammoths, mastodon, and ground sloth would have existed at saturation levels where further increase was prevented by food limitation,” or Sinclair et al. (10), who said, “A threshold occurs at prey body sizes of 150 kg, above which ungulate species have few natural predators and exhibit food limitation,”—statements based on observations of living systems. The conclusion that megaherbivores were immune to the effects of predation seems improbable given the greater size of the Pleistocene hypercarnivores. As we describe below, selective predation on juveniles would have intensified the effects of these carnivores on prey populations, given that species with the low reproductive rates typical of megaherbivores are susceptible to population reduction under conditions of relatively low predation pressure (47). 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-sized 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 (17). Clearly, this change in preference is a consequence both of their body sizes and of the much greater challenge of killing adults.

In the extreme, it is possible for relatively low rates of selective predation on juveniles to lead to extinction (47). As shown in an analysis of extinction patterns among nine groups of mammals (185 species) that lost three or more species at or near the end of the Pleistocene (47), 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. Some species of extinct megafauna, such as mammoths, mastodons, and ground sloths were not included in that analysis, but it is almost certain that all these species had very low reproductive rates. Using the PanTHERIA database for extant mammals (esapubs.org/archive/ecol/e090/184/metadata.htm), we find that 22 of the 29 ungulate species with masses greater than 200 kg have interbirth intervals that exceed 1 y, and of these, 9 of the 12 species with masses greater than 600 kg have interbirth intervals that exceed 2 y (*SI Appendix, Fig. S4*). Indeed, for woolly mammoths, weaning age has been estimated from stable isotope analysis and tooth wear to have been at least 1.5 y and in one case more than 5 y (*SI Appendix, SI Materials and Methods, section 6*), and patterns of tusk growth in female mastodons point to typical calving intervals of 3–4 y (e.g., ref. 48). Although there are small mammals with relatively slow reproductive rates, such as echidnas, there are no very large mammals with relatively high reproductive rates (47);

thus it is safe to assume that extinct megaherbivores had interbirth intervals that exceeded 1 y, and could have been 4 y or more, as is typical of African elephants (*SI Appendix, SI Materials and Methods, section 6* for more details). Given such low fecundity, the number of deaths due to predation and other causes, such as episodic droughts or wild fires, would not have had to be high to keep mortality rates above recruitment rates and thereby limit population growth.

Providing further confirmation, a recent study used a discrete, stochastic model (49) analogous to a life-table analysis to examine the long-term impact of age-specific mortality on African elephant population growth (50). Drawing values of life-history parameters from multiple studies of wild elephant populations, the authors estimated the age-specific mortality needed to achieve 0% population growth for simulations spanning hundreds of years. Model projections showed that annual mortality of just 17% of juveniles aged 0–9 y would be enough to halt population growth; by comparison, the death annually of 10.5% of all adults, aged 10–60, would be needed to yield the same effect (50). We find no data on percentages of juvenile elephants taken by extant lions in Africa, but in other large mammal predator–prey systems, annual percentages of juveniles killed easily exceed 17%. For example, in Wood Buffalo National Park, Canada, gray wolves regularly prey on bison, a species at the upper limit of their capabilities, and are documented to kill more than a third of all juveniles each year (51). Similarly, bears in Yellowstone National Park remove 40% of the elk calves annually (52). Like their modern counterparts, Pleistocene carnivores probably preyed preferentially on juvenile rather than adult megaherbivores, all of which fell within their predicted range of typical prey size.

Theoretical evidence has supported the idea that populations of medium to large sized herbivores were limited by large Pleistocene hypercarnivores (53), but it has been less clear whether the theory applies to megaherbivores. Based on studies of modern African elephants, it is not clear that they can effectively self-regulate and maintain their own numbers at levels that allow for a sustainable existence of a healthy population. Gough and Kerley (54), for example found no evidence for density-dependent regulation in a South African elephant population 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 before the expansion of modern and especially industrialized humans any appropriate habitats would have been fully occupied by elephants, thus limiting their ability to expand their foraging range. Africa was reportedly home to five species of elephants during the Pleistocene, with two or more inhabiting some regions (55). 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.

We suggest that large hypercarnivores must have limited at least the proboscideans, especially given the impressive impact these species have on vegetation structure and quality. Of course, predation would not have been the sole factor; periodic droughts can produce substantial mortality in modern elephant and rhinoceros populations, especially among juveniles and subadults (56). It is noteworthy that Pleistocene large mammal community composition is remarkably stable at a continental scale over at least the last 1 million years in both the Old and the New Worlds, despite glacial–interglacial fluctuations in climate (57–59). 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. Environmental reconstructions of late Pleistocene interglacial environments in the United Kingdom, for example, reveal an abundant, diverse large herbivore guild associated with a mosaic of vegetation structures that promoted biodiversity (60). In extant large mammal communities that lack big apex predators, large herbivores often experience rapid population expansions. For example, in Eurasia and North America, cervid densities were on average nearly six times greater in areas without wolves compared with areas with wolves (61). These impressive herbivore irruptions can have very negative impacts on vegetation and ecosystem services and can produce declines in floral and faunal biodiversity if they are persistent or occur repeatedly (62, 63). If megaherbivores had not been predator limited, the Pleistocene might be expected to have experienced a long-term 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, associated with the presence of humans (64), and potentially linked to the effects of human hunting/scavenging in addition to ongoing predation by large carnivores (39). The negative impact of human hunting on megaherbivore numbers could have been especially large if the prey species were already under pressure due to top-down forcing by large carnivores (39) and episodic environmental stressors, such as severe drought and wild fires.

Implications for the Future

Why should we 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 before 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. Secondly, studies of the Pleistocene reveal that the planet was capable of sustaining many more species-rich communities that included a greater proportion of megafauna than are found today (65). 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 before 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 processes that favored biodiversity by creating increased scavenging opportunities, refuges from herbivory for plants, and enhanced environmental heterogeneity and stability (5, 6, 66, 67). The late Pleistocene extinction of the largest of the 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 deeper timescales are an important piece of the puzzle.

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