What Killed the Giant Mammals?

As the huge glacial masses of 10,000 years ago melted, dozens of species of giant mammals crashed into extinction: was the culprit climate or human hunter?

Extinction events—large and small—punctuate the history of life, and thus produce a strikingly episodic pattern throughout the fossil record. The most recent event, which occurred at the end of the last glacial period about 10,000 years ago, was modest by comparison with most of its forerunners and unusual in that, according to some authorities, it disproportionately affected large terrestrial mammal species. The cause of this extinction episode is hotly debated.

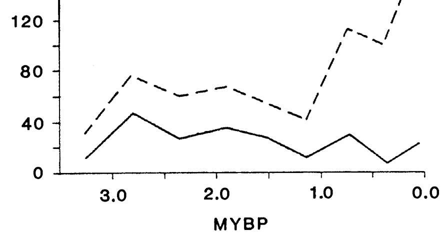
The coincidence of the extinction with the rapid termination of the most recent glaciation has inevitably encouraged the opinion that climatic and environmental changes delivered a fatal blow to many vertebrate species, at least in the terrestrial realm. Indeed, environmentally based explanations, which have encompassed perturbations in nutrient availability, reproductive physiology and overall biotic patterns, have assumed the dominant position in the debate.

A new development of the environmentalist view, which was presented by Russell Graham, of Illinois State Museum, Springfield, at a recent meeting at Northern Arizona University,* states that vegetational communities were not simply geographically displaced by the postglaciation climatic shift but were fragmented. Some of the species that were adapted to the ecological integrity of the community would, argues Graham, have been unable to cope with the disruption of their food resource and therefore became extinct.

The counterargument to the environmentalist view, which has been promulgated principally by Paul Martin of the University of Arizona, Tucson, is that the death blow suffered by many species was actually delivered by human hand. The late Pleistocene demise of some 55 species of large mammals in the Americas, which included the giant ground sloth, the mastodon, the mammoth, and the sabre tooth cat, was wrought by the advance of big game hunters—Clovis Man—through the continents, says Martin, who also spoke at Flagstaff.

With the two sides being presented it was obvious, both to protagonists and spectators, that neither set of arguments is without problems. For instance, if climate was the cause, why does one not see extinction events specifically marking the dozen or so glacial advances and retreats throughout the 2-million-year-long Pleistocene? And if the hunters' skill was so devastating on so many species, why did other equally vulnerable species, such as the bison, the musk ox, and the moose survive?

The late Pleistocene glacial retreat produced, of course, a global environmental readjustment: the cool but equable climes of the ice age gave way to the warmer but more seasonal climate of today. The contemporaneous extinction, however, was most marked in the Americas. Perhaps the poor Old World fossil record of the time obscures equally momentous events among the fauna there. Perhaps the qualitatively different ecological communities in different parts of the world responded differently to the post-Pleistocene climate. In any event, the debate over climate versus hunters also involved Australia, where humans arrived some 40,000 years ago, and Madagascar, which was first occupied at the beginning of this millennium.



Extinction and diversity among mammals

Solid lines shows extinction and dashed lines show standing diversity among large (more than 100 pounds) and small mammal species in the Americas.

The fossil record for Madagascar is exceedingly poor, but it is known that half a dozen species of giant lemur, bird, and hippopotamus disappeared about 1000 years ago, that is contemporaneously with human occupation. "I concede this extinction to Paul," says Graham. "Man clearly had considerable effect there." Martin is naturally happy with this concession, but notes that the island might present a useful test opportunity for the competing hypotheses. "As Madagascar was not peopled before 1000 years ago, an examination of the earlier fossil record should reveal whether the post-Pleistocene warm-up caused any extinctions there."

Australia is more complicated. Numerous archeological and paleontological sites confirm human immigration by about 40,000 years ago, but an ambiguous record leaves uncertain any associated or later large mammal extinctions. Graham notes some evidence that indicate disappearance of some giant mammalian species around 15,000 to 18,000 years ago, which coincides with a noticeable increase in aridity. There is, however, no convincing fossil evidence to support earlier or later extinctions.

Although there have been periodic extinctions throughout the Pleistocene in the Old World, there is nothing especially curious at the end of the epoch to match the pattern seen in the Americas. Humans evolved in Africa and spread to Eurasia at least a million years ago; their predatory effect, if any, might therefore be dissipated through the ages and be invisible in the record.

The focus of the debate, therefore, is on the Americas.

Fifty-seven species of large mammals became extinct at the late Pleistocene, compared with 54 in the previous 3 million years. The figures for small mammal species are 21 at the last Pleistocene and 200 earlier. Some critics of Martin's overkill hypothesis say that the disappearance of a large number of bird species at the same time as the mammal extinctions do not support a cause through human hunting. Martin contends that these bird species are mainly scavengers or commensals, which would likely be doomed to extinction by the

*Dynamics of Extinction, Northern Arizona University, Flagstaff, 10 to 12 August 1983.

disappearance of the large mammals.

Martin's case rests heavily on the date of human occupation of the Americas and the date of the last appearance of the extinct large mammals. No one doubts that the first Americans were on the continent by 12,000 years ago: there are many good archeological records of hunting people, characterized by a particular fluted point from this time onwards. There is contention, however, about occupation prior to 12,000 and up to 37,000, the earliest reasonably supported date for human presence.

Paleoanthropologists are divided over the probable date of entry into the Americas, but a head count would likely go against Martin. Furthermore, the rate of large mammal attrition by early hunters that is implied by the overkill hypothesis is considered by some to be unrealistic for any hunting population. Martin counters this by citing ethnological evidence that shows that in the face of superabundant game, the normal constraints on hunting are released. Clearly, this is an area of the hypothesis that is heavy with speculation, except to say that a prey-mortality rate little more than double the normal would plunge a species precipitously toward extinction.

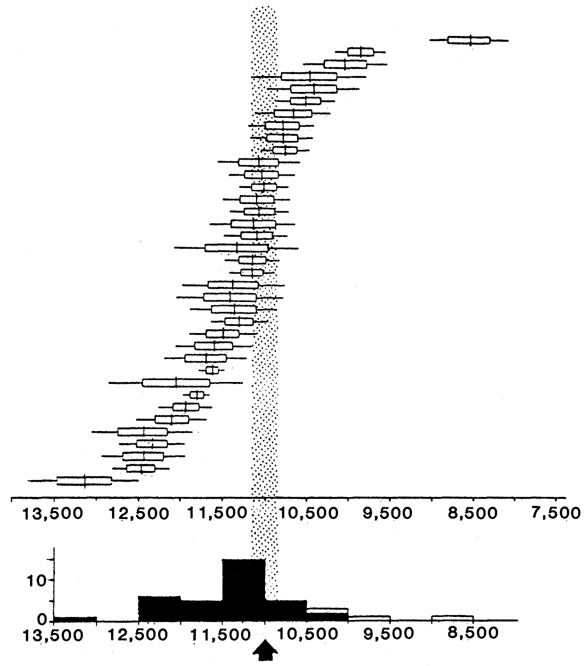
The dates for the last appearance of the extinct, giant herbivores and associated giant predators fall relatively cleanly at a little under 11,000 years. "The speed of the extinctions is fully consistent with the overkill hypothesis," says Martin, "whereas environmentally caused extinctions would be expected to be gradual." Graham demurs, and argues that rapid species loss is not inconsistent with his environmental model. And so the argument continues.

One aspect of dating the demise of the lost species could help settle a choice between these competing hypotheses: that is the geographical direction of the extinctions through time. The overkill model predicts that a wave of extinction would have passed from north to south through the continents, being complete in perhaps as little as a millennium. By contrast, an environmentally inflicted extinction would be more complicated but would proceed from south to north in North America, says Graham. The chances of being able to track extinction events over such a narrow time interval are, however, not great.

Graham's environmental model, which he developed with Ernest Lundelius of the University of Texas at Austin, is called coevolutionary disequilibrium. "Late Pleistocene communities are characterized by the coexistence of species that today are geographically and ecologically separated," says Graham. "This implies that communities did not migrate as intact or immutable units but instead individual species responded to environmental changes in accordance with their own tolerance limits." The result of these disruptions was that "significant adjustments in feeding strategies were required by many species."

Extinction profile

Forty-two radiocarbon dates on last appearing Shasta ground sloth dung from various sites in the U.S. southwest. The arrow and shaded panel indicate approximate time of activity of Clovis hunters in the region. Some of the earlier and later dates might not be valid, says Martin, which would make the extinction point sharp at close to 11,000 years.



The overall environmental switch between the glacial and postglacial times was a shrinking of forests and an expansion of grasslands. The switch, however, was not simple, otherwise extinction patterns would have reflected the change: more grassland species and less forest species. This did not happen, because, suggests Graham, plant species migrated idiosyncratically and animals dependent on the former communities as intact units had to search for new food supplies. This brought many of them into novel competition with each other, with the inevitable result that some were squeezed into extinction. Others, after losing their traditional food resource, might have consumed other plants that contain noxious chemical defenses and therefore "literally poisoned themselves into extinction."

This version of the environmental theme is very attractive, as the data on community fragmentation following climate change look persuasive. The hypothesis would also accommodate the survival of several large herbivores that surely would have been tempting targets for proficient hunters. (Martin says these survivors might have retreated to habitats that were free of hunters; in any case, their modern ranges are much reduced, as is their body size.) There are, however, problems, which Graham acknowledges.

The hypothesis rests on the assumption of tightly coevolved communities and intense competition between species once communities have fragmented, two concepts that are the subject of some debate among ecologists (see *Science*, 12 August, p. 636). "The scenario of tightly coevolved communities doesn't make any sense to me," says Daniel Simberloff, an ecologist at Florida State University. "Yes, we have emphasized competition heavily in our model," states Graham. "If competition turns out not to be an important factor in community organization, we are on thin ice."

A second possible weakness of this model, and all other environmental models, is the apparent lack of correlation between extinction events and the many glacial advances and retreats throughout the Pleistocene. Graham suggests that the rate of the late Pleistocene glacial melt was unusually rapid, thus offering a possible explanation for its novelty. Geochemical data indicate, however, that all Pleistocene glacial retreats were relatively rapid and that the final one was not especially unusual.

The debate, therefore, continues—a state of affairs that participants at the Flagstaff conference found quite understandable. Colleagues working with a superior fossil record and better time resolution cannot readily establish the cause of the late Pleistocene extinction only tens of thousands of years ago. What chance then is there of solving mysteries that are measured in tens of millions of years in the past (*Science*, 2 September, p. 935)?—**Roger Lewin**