LATE PLEISTOCENE MAMMALIAN
EXTINCTIONS IN NORTH AMERICA:
EXTENT, THEORIZED CAUSES, AND IMPLICATIONS

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INTRODUCTION

Two of the greatest theories in the history of science—James Hutton and Charles Lyell's geological principle of uniformitarianism, and Charles Darwin and Alfred Wallace's biological theory of evolution—changed man's perception of himself, his past, and the natural history of the Earth and its biota. Uniformitarianism states that the present is the key to the past; that is, by observing present processes at work we can better understand past geological events as seen in rock strata. Classical evolutionary theory describes how changes in species come about through the orderly, relatively slow process of natural selection. Both theories in their original form tended to disregard the dramatic effects of rapid or catastrophic changes of the environment on the geological and biological history of the Earth. Modern expressions of these theories have modified the original concepts to account for the apparently rapid changes that took place at various times in the past, as revealed by the fossil and stratigraphic records. Geologists contend that the rates of the chemical and physical processes may have varied widely, but past geological events can still be explained by uniformitarian principles. Biologists hypothesize that relatively rapid (compared to pure natural selection) evolutionary change may occur due to isolating mechanisms, particularly geographical (allopatric speciation).
However, episodes of mass extinctions have not been satisfactorily explained by conventional evolutionary theory. George Cuvier, a pre-Darwinian naturalist, contended that animals became extinct only through natural catastrophe, rather than through an inability to adapt. In the view of the catastrophists, worldwide natural disaster would be followed by another act of creation. With the acceptance of Darwinian theory in the late 19th century, there was a turning away from any catastrophic explanation of past events. However, advancements in the techniques of dating geological and biological material in recent years have shown that there were periods of dramatic changes in the Earth and its biota. The temporal juxtaposition of the geological and biological events suggests some correlation between the two. Recent examples of interactions between geological and biological events show that significant events in one can have an effect on the other. For example, the volcanic eruption of Tamboro, in the East Indies, in April of 1815 is believed to have caused the disastrously cold year of 1816. On the other side of the coin, man's activities since the Industrial Revolution, such as the burning of fossil fuels, extensive mining, and hydrological modifications (e.g., damming rivers) have had a significant impact on geological conditions. There has always been a close interaction between the living and non-living components of Earth. Thus, a mass extinction may be explained as an inability of large numbers of
organisms to adapt to extensive environmental changes.

One familiar example of mass extinction occurred at the end of the Cretaceous, about 65 million years ago. Becoming extinct at this Mesozoic-Cenozoic boundary were: five prominent orders of reptiles, including the highly successful forms commonly termed dinosaurs; several planktonic forms, such as the chalk-forming coccoliths and types of foraminifera; many land plants; and the formerly abundant ammonites. A variety of theories have been proposed to explain this apparently synchronous devastation of prominent land and marine forms. Comparisons of the planktonic forms that survived the end-Cretaceous with modern forms as well as the changes in land plant forms, suggests that there was a drastic drop in world temperature. This would have placed severe stress on the prominent forms of the time, which had evolved and thrived in the warm Mesozoic. The cause of the hypothesized climatic cooling has been speculated as: 1) a change in the energy output of the sun; 2) volcanic episodes brought about by plate tectonic moving; 3) a change in the Earth's magnetic field, allowing in a greater amount of cosmic radiation, which affected weather patterns as well as mutation rates; and 4) the explosion of a close supernova, which would have contributed high radiation levels as well as climatic deterioration.

Due to the difficulty of uncovering and interpreting events that took place about 65 million years ago, we may
never know the cause or causes of this mass extinction. To fairly represent the literature, it should be pointed out that some investigators do not believe this mass extinction was synchronous, and thus indicative of cataclysmic causes. For example, Camp (1952) points out that the ichthyosaurs had dropped out well before most of the other Cretaceous extinctions occurred, and that the mosasaurs continued to thrive after the plesiosaurs had disappeared. Similarly, Colbert (1961) shows that a large part of the Cretaceous dinosaur fauna actually had disappeared before deposition of the Lance Formation several million years prior to the end of the Cretaceous, yet the carcharodontosaurus persisted well into the Eocene. Still, relative to their span of existence, the disappearance of the dinosaurs was a mass extinction, although the role of catastrophic events is in dispute.

Another mass extinction, although not as spectacular, occurred relatively recently—only about 11,000 years ago. Rather than being an all-encompassing disaster of many life forms, it was primarily restricted to large mammals. Also, the end of the Pleistocene had interacting factors not present in any previous time period: 1) severe climatic and vegetational changes associated with a receding ice sheet, and 2) the emergence of men as a significant ecological force. Due to its proximity to the present, there is more evidence available to interpret than for previous mass extinctions. Thus, research into its causes may prove
to be fruitful in shedding light on the phenomenon of mass extinction. This may have an impact on our interpretations of the fossil record as well as general evolutionary theory. Also, by studying the causes of the disappearance of the Pleistocene megafauna in many parts of the world, perhaps we can prevent the extinction of the essentially Pleistocene megafauna still existing in the African savannah. The major emphasis of this paper will be on the events in North America at the close of the Pleistocene, from about 10,000 to 15,000 years ago. Episodes of Pleistocene mammalian extinctions in other times and places will be referred to for comparison purposes.

EXTINCT NORTH AMERICAN PLEISTOCENE MAMMALS

Before considering the theories proposed to explain the extinctions, let's survey the mammals involved. Strictly speaking, we are dealing with Rancholabrean mammals at the end of the Wisconsin glaciation (Fig. 1). Table I lists the extinct mammals we will be treating in some detail. Included in this list are: 24 genera in which there are no surviving members, and 7 genera (starred) in which there were extinctions but have surviving representatives of the genus somewhere in the world today. The numbers of species involved cannot be accurately stated due to intraspecific variation and the difficulty in interpreting species level morphological differences from most fossilized bone fragments.
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Fig. 1 (After Wright and Frey, 1965)
Table I  Extinct Pleistocene mammals of continental North America  
(After Martin, 1967)
The known fossil history of each genus in North America is denoted by a horizontal line. Also, current information concerning direct association of the bones with human artifacts, as well as dating of the bones by the $^{14}$C method or stratigraphic location is provided.

**Edentates**

The first group of mammals considered are the edentates (Fig. 2). Included in this order are: *Nothrotherium*, the Shasta ground sloth; *Megalonyx*, Jefferson's ground sloth; *Eremontherium*, the giant browsing ground sloth; *Paramyloodon*, common ground sloth; *Pamatherium*, giant armadillo; and *Boreosracon*, a glyptodon. Generally, they are herbivorous or insectivorous forms that evolved in South America and moved into North America sometime after the linking of the two continents by the Panamanian isthmus during the Pliocene. For the most part they ranged in the southern areas of North America, with the exception of *Megalonyx*, whose remains have been found as far north as Alaska. There are no clear associations of any of these extinct edentates with early man, as will be discussed later.

**Rodents**

The next group to be discussed is the rodents. There was a great deal of range displacement in rodents due to
Fig. 2 (Martin and Guilday, 1967)
the advancing and retreating ice sheets during the Pleistocene. However, other than normal phyletic replacement, the only extinctions in North America experienced by this largest group of mammals at the end of the Pleistocene were the two largest forms: *Castoroides*, the giant beaver, and *Neochoerus*, a capybara (Fig. 3). *Castoroides* has been found throughout northern North America and *Neochoerus* is a South American form that ranged into Florida. As with the edentates, these extinct rodents have not been found to be in direct association with early man.

**Carnivores**

The extinct carnivores are represented by: *Arctodus*, the giant short-faced bear (Fig. 3); *Tremarctos floridanus*, a large spectacled bear; *Canis dirus*, the dire wolf; *Smilodon*, the saber-tooth cat (Fig. 3); *Dinobastis*, a specialized saber-tooth cat; and *Panthera atrox*, a giant jaguar. There are still living representatives of the genera *Tremarctos*, *Canis*, and *Panthera*. All the carnivores were wide-ranging and fierce predators. *Smilodon* was not fleet-footed for a felid, so it probably preyed on ground sloths and young proboscideans, while *Dinobastis* apparently had a specialized diet of young proboscideans. *Panthera atrox* was probably the most formidable predator of them all, ranging from Alaska to Mexico. There are questionable associations of *Canis dirus* and *Dinobastis* with early man.
Fig. 3 (Martin and Guilday, 1967)
Proboscideans

Much of the original interest in late Pleistocene extinctions was due to the discoveries of extinct proboscideans in the temperate and arctic regions of the world. There are only two living species, both tropical, of this ancient and formerly successful order of mammals. The extinct North American genera are: *Mammut*, the mastodon, and *Mammuthus*, the mammoth (Fig. 4). From dentition and pollen it is generally agreed that mammoths were primarily grazers and mastodons were browsers. Both of these proboscideans were abundant members of the late Wisconsin fauna, and both disappeared fairly rapidly. Consideration of the plight of the proboscideans will form a significant portion of the discussion on the causes of the extinctions.

Perissodactyls

The perissodactyls, whose diversity was already greatly diminished by Pleistocene times, experienced complete extinction in North America. Several species of horse (*Equus*) and tapir (*Tapirus*, Fig. 3) once flourished in North America, but disappeared in early Holocene time and, of course, have living representatives. European colonization resulted in the reintroduction of horses and burros into southwestern North America, although the ecological adaptations of the present feral equids are not necessarily the same as the
Fig. 4 (Martin and Guilday, 1967)
ones that became extinct. As with the proboscideans, the perissodactyls show some clear associations with early man.

Artiodactyls

The last major group of mammals we are concerned with are the artiodactyls. These are a diverse group of herbivores who, although they suffered much generic extinction, still comprise most of the mammalian megafauna. Included in this group are: the tayassuids Platygonyus (flat-headed peccary) and Mylohyus (long-nosed peccary), Fig. 5; the camelids Camelops (camel) and Tanupolama (llama-like camel), Fig. 4; the cervids Cervalces (moose) Fig. 5 and Sangamona (caribou-like deer); the antilocaprids Capromeryx (dwarf pronghorn) and Tetrameryx (four-horned pronghorn, represented by Stockoceros, a similar earlier form, Fig. 5); and the bovids Bootherium (southern woodland musk-ox), Symbos (northern woodland musk-ox), Euceratherium (shrub oxen, represented by Preptoceras, which may be merely the female of Euceratherium), Oreamnos harringtoni (mountain goat), Bison anticuus, and Bison occidentalis (Fig. 6). Generally, the tayassuids and cervids have not been found associated with early man artifacts, whereas the camelids, antilocaprids, and bovids have to a variable degree.
Fig. 5 (Martin and Guilday, 1967)
Fig. 6
(Martin and Guilday, 1967)
A variety of theories have been proposed to explain the disappearance of these mammals from North America. Before discussing the specific theories relating to the events in North America at the end of the Pleistocene, a discussion of some general concepts of extinction is in order. Generally speaking, there are three types of extinction inferred from the fossil record (Simpson, 1967, p. 198): 1) A group of organisms simply changes to such a degree that the ancestral form is no longer present. This is not true extinction, since the group lives on in a different form. 2) When two groups interact for the same resources (niche), and one of them becomes extinct. The interaction is sometimes called competitive exclusion and the observed result is ecologic replacement, as opposed to the phyletic replacement described in #1. This type of extinction would probably be caused by an immigration or a time of moderate ecological stress. 3) Disappearance of a group of organisms without any recognizable replacement. This last type would appear to suggest severe ecological stress and, therefore, a situation beyond the capabilities of many species to adapt (mass extinction). It is also the most disturbing type of extinction to biologists, who have generally not recognized the importance of dramatic environmental events on the course of evolution.
Differential Extinction

Related to the second, and perhaps the third type of extinction (depending on the degree of ecological stress), is the theory of differential extinction. It states that in any deteriorating ecosystem large herbivores are more drastically affected than are small herbivores by virtue of their greater demands upon the system for space, food, and cover. This produces a situation of differential extinction, whereby the megafaunal forms are drastically reduced or totally eliminated (again, depending on the degree of ecological stress), while the small forms are virtually unaffected. This is a natural consequence of interspecific ecological competition, operative throughout the history of terrestrial vertebrate evolution. How this theory explains the course of events in North America and elsewhere at the end of the Pleistocene was detailed by Guilday (1967), and will be dealt with later on in this paper.

Racial Senility

Another explanation sometimes given for extinction is that of "racial senility;" that is, just as individuals grow old and die, so do races of organisms. It is true that just as death is a fact of life, extinction is a fact of evolution. Most biologists accept the estimate that the number of living species is less than 1% of those that have
ever existed. However, this does not imply that there is a programmed longevity to a given group of organisms and that a type of "genetic senility" sets in that results in extinction. In fact, there are many organisms that have remained virtually unchanged for millions of years. Also, although extremes in size or external features such as horns are sometimes seen in groups just prior to their extinction, this does not necessarily imply either a "racial old age" or maladaptive genetic activity. First of all, structural peculiarities denote high specificity of adaptation, and it is this new specialization that limits flexible adaptation in the face of unfavorable changing environmental conditions. A second plausible explanation for "bizarre" forms prior to extinction is that of inbreeding and the lack of elimination of inadaptive mutations in a population that is already doomed to extinction (Simpson, 1967, p. 203). Therefore, it may be that impending extinction produces the peculiarities that have been associated with "racial old age," rather than the other way around. Thus, the true cause of extinction is an inability of a group of organisms to adapt to a change in its environment, which could include competitors, natural conditions, or both. Specializations, which are quite adaptive at the time they are developed, may result in an inability to adapt to new conditions, resulting in the extinction of the group. It is a general observation that existing organisms that have not changed perceptibly for a long time are well adapted to a specific ecological niche and exist in a stable environmental situation.
Population Dynamics and Extinction

Due to the variation present within every population of a species (differences in age, sex, and genetic endowment of individuals) and the often subtle morphological differences between species (and sometimes genera), the paleontologist describes an extinction on the species or even genus level only. However, evolution (and thus extinction) operate at the level of the population. It is when all the populations of a species become extinct that a true, observable extinction has taken place. Therefore, a discussion of the factors affecting the stability of a population may be relevant to problems of extinction.

The constancy of a population is related to its ability to withstand environmental change. Large organisms have small surface/volume ratios and their internal environments are more independent of the external environment than are the internal environments of small organisms. The accumulation of biomass and reduction of the turnover rate of individuals in populations also increases buffering against environmental variation. Immature stages of the life cycle are generally more vulnerable to environmental change than are adults because they are smaller, less experienced, and have more poorly developed mature functions. Populations with high proportions of immature individuals tend to be less stable than populations that consist predominately of mature individuals (Ricklefs, 1973, p. 764).
Another important component of stability is the response time of the population to fluctuations in the environment. Small organisms usually reproduce more rapidly than large organisms. Therefore, populations of small organisms can respond to environmental change rapidly and adjust their population levels to the conditions prevalent at a particular time. Furthermore, small organisms have more avenues of response to environmental change open to them. Developmental and evolutionary responses are practical ways of coping with short-term environmental change only for small organisms with short lifespans. Size and biomass/productivity ratios have two opposing influences on stability (Ricklefs, 1973, p. 764). Populations of large organisms fluctuate relatively little, but they respond slowly to change; the opposite is true of populations of small organisms. As one can see, this is the theoretical basis of the differential extinction model.

Obviously, the size of a population will determine the likelihood of its extinction. But what determines the absolute size of populations? Changes in the productivity of populations, effected by the relative success of their adaptations compared to the adaptations of their predators, parasites, competitors, and prey, directly determine the size of the population and its degree of specialization. Also, the diversity of predators which a population must avoid, and the diversity of prey that the population exploits, influences the productivity of the population, and thus its size (Ricklefs, 1973, p. 765). Diversity and complexity
of organization are thought to be greatest in tropical environments, suggesting that tropical populations may actually be inherently less stable than temperate and arctic populations. The apparent stability of tropical populations may be due only to the constancy of the tropical environment. The inherent instability of tropical populations is an important consideration in the effort to preserve the "remnant-Pleistocene" fauna of equatorial Africa.

Equilibrium Hypothesis

Related to extinction theory is the population ecology model known as the equilibrium hypothesis. MacArthur and Wilson (1963 and 1967) developed this model to explain the diversity of life in a given area. For example, the number of non-migrating bird species inhabiting an island is the product of an equilibrium between the intrinsic rate of extinction of indigenous species and the random rate of immigration of exotic species. The faunas of distant islands support fewer species, not because they have had insufficient time to be colonized, but because the rates of immigration are low relative to the rates of extinction.

Although the equilibrium hypothesis was formulated in the context of insular zoogeography, there is no reason why it should not extend to continents as well. However, certain structural differences between insular and continental faunas affect the way in which the equilibrium operates. One of the
The most important differences is that on continents new taxa may appear autochthonously, not merely by immigration. Thus, the term rate of origination, encompassing immigration and autochthonous development, is more appropriate for continental faunas. In a broad sense, the extinction curve represents the hostility of the environment to the fauna. In most insular situations, particularly in the tropics, area is the principal limiting factor. Nevertheless, other factors such as carrying capacity, habitat diversity, and climatic stability are also important. In a continental situation in the temperate zone, one or more of these other factors may become the critical one. The relationship between this model and the late Pleistocene megafaunal extinctions has been worked out by Webb (1969), and will be considered later in the paper with specific theories.

THEORIES ON SIZE AND STRUCTURE PHENOMENA

Much of the discussion concerning extinct Pleistocene mammals deals with their large body size and external structures. Four theories relating to size and structure phenomena are discussed below.

Cope's Rule

Cope's rule is a generalization that most animal groups have evolved toward larger body size. The usual explanation
given is that large size imparts a survival advantage, and thus an evolving population will tend toward larger individuals. This explanation for Cope's rule has been challenged and modified recently by Stanley (1973). He believes that Cope's rule is more fruitfully viewed as describing evolution from small size rather than toward large size. Whether body size will increase or decrease in a given population depends on whether mean body size is larger or smaller than the optimum for the population. It is the tendency of groups to arise at small body size relative to their optima that produces the widely observed pattern of net size increase. Size increase is not inherently favored in speciation, but prevails during diversification because origin of a higher taxon at small body size concentrates many early species in the small size range (Stanley, 1973).

Bergmann's Rule

Another generalization related to body size is Bergmann's rule, which states that races from cooler climates in species of warm-blooded vertebrates tend to be larger than races of the same species living in warmer climates. It is important to note that the validity of this ecological rule is restricted to intraspecific variation (Mayr, 1970, p. 193). A more northerly species is by no means always larger than its nearest more southerly relative, since separate species have different means of adaptation available to them than have
open populations within species. The usual physiological explanation of Bergmann's rule is based on the fact that the volume of the body increases as the cube and the surface area as the square of a linear dimension. The larger a body, the relatively smaller is its surface area. In a cool climate there should be a selective advantage in the relative reduction of surface area resulting from increased size, since the metabolic rate is more nearly proportional to body surface than to body weight. In hot climates the advantage should be on small body size and relatively large surface area. It should be pointed out that the validity of the empirical findings supporting the generalization is independent of the physiological interpretation given to explain the observed regularities. An alternative explanation of Bergmann's rule, as it relates to ungulate evolution in the Pleistocene, is found in the dispersal theory. This theory also relates to the concept of allometry, and so discussion of it will be delayed until after the presentation of allometric principles.

Allometry

Allometry involves the recognition that different parts of the body grow at different rates. These rates change during the course of the individual's development, and may vary with the season of the year and the sex of the individual. Thus, a small increase in body size (overall growth
rate) can result in a great increase of some body part (e.g., horns). This concept removes the necessity for postulating large numbers of more or less independent mutations, each affecting some particular structure of the body and each acted on by natural selection (Moooy, 1970, p.457).

The allometric-type principle of comparing measurements of body size and external structure was used by Gould (1974) in explaining the immense antlers of the extinct Pleistocene Eurasian cervid Megaloceros giganteus, the famed "Irish Elk." Megaloceros had been considered a classic example of maladaptive evolution; that is, their extreme development of large antlers was the direct cause of their extinction. After taking a variety of measurements, Gould concluded that Megaloceros had about the predicted antler size for its body size. Actually, moose (Alces) have smaller antlers than expected by this relationship in cervids. Antlers are weapons for combat against predators or conspecific rivals. However, a more important function may be as "visual dominance-rank symbols" and attraction of females. The immense antlers of Megaloceros were selectively advantageous and at a predictably appropriate size. There must be a strong selection against large antlers for a large cervid not to possess them. The opposing selective force operating in the moose may be its forested environment and the difficulties large antlers would pose. The reforestation following deglaciation may have caused the extinction of Megaloceros, which was specialized to an open forest-steppe habitat.
Dispersal Theory

The recognition of the importance of "social organs" such as antlers in the evolution of ungulates brings us to the dispersal theory (also termed glaciation theory) as expounded by Geist (1971). There were several general observations that led Geist to formulate this theory. A study of Ovis (mountain sheep) revealed an association between evolutionary advancement and geographic distribution. Two ways in which this association may be seen are: 1) A species evolves and the individuals enlarge during dispersal across a continent. Reproductive and/or geographic isolation brings about clinal variation. 2) Evolutionarily advanced forms (extinct or living) tend to be found close to centers of continental glaciations, while closely related but primitive ones tend to be found in the tropics or subtropics.

The next general observation was that, in ungulates, the decision whether to call a species primitive or advanced is usually based on structures that have social significance, rather than habitat adaptations. These include horn-like organs, skin glands, hair color and patterns, and rump patches. Other characters, such as teeth and skull proportions, have both social and habitat adaptations. Canines and incisors are frequently sexually dimorphic and the skull may be contoured for intraspecific collisions in sexual combat (rutting). Another general observation leading to the theory was that intraspecific combat is more characteristic
of northerly ungulates, whereas territoriality (which reduces combat) is widespread in tropical (e.g., African) ungulates. Finally, a type of parallel evolution during the Pleistocene is seen among various ungulate and subungulate forms, suggesting an overall mechanism in operation.

The dispersal theory fuses concepts from animal behavior, nutrition and growth physiology, population dynamics, and zoogeography. The theory states that when ungulates disperse into new habitats that follow retreating glaciers, they form pioneering populations which find a superabundance of excellent forage. These excellent food sources cause high birth rates, high birth weights, high milk production, rapid growth of young, early sexual maturation, large body size of adults close to the genetic maximum, rigorous social interactions (frequent and intense combat), and short life expectancy. The aggressive interactions increase the reproductive fitness of males with a large body, improved weapons, defenses, and combat techniques. The selection for large body and horn size results in a selection for physiological mechanisms that maintain the animal in a physiologically "juvenile" state (neotony), permitting longer and more intense body growth. Once the habitat is saturated this selection ceases, resulting in smaller, long-lived, and slow-growing individuals. There are two conditions in cold regions that permit the growth of large horn-like structures: 1) seasonal superabundance of forage, and 2) sharp seasonal differences in climate that restrict breeding activity to a short span.
of the year. Thus, males may be idle during the growing season and divert their energies into horn growth. Also, a large fat deposit may be accumulated for use in the rutting season, so that breeding time is well spent (instead of feeding). The last contention of the theory is that the further the species disperse and the longer the time of dispersal, the greater is the difference between individuals of the parent population and the pioneer population; that is, geographic isolation from dispersal results in clinal variation.

There are many predictions and implications of the dispersal theory. For one thing, the individuals from populations within regions previously glaciated should be larger in body and the size of horn-like organs, and more specialized in intraspecific combat than individuals of the same species from glacial refugia. There should be a close correlation between dispersal and changes in "social structures." The further that members of a family live from areas affected by glaciations, the closer they will resemble pre-Pleistocene relatives. The paleontological record should show that individuals of an invading species will be largest in the early populations and decline in size in succeeding populations. Also, a primitive race living in a glacial refugium may give rise to similar advanced forms with every glacial retreat. Rapid evolutionary change is thus linked to colonization, with a long period of evolutionary quiescence thereafter. This apparently challenges the concept of continuous,
progressive evolution. Rapid evolutionary change may occur without ecological differentiation, since the animals invade vacant habitat to which they are already adapted. Generally, the periglacial zones are characterized by rapid evolutionary changes, while the tropics are characterized by evolutionary stagnation. Yet, generalizing this theory can explain evolutionary change in the tropics. An ecological specialization is followed by dispersal, colonization, and this in turn by a specialization in combat and display adaptations.

Although this theory was formulated largely through investigations of living species (Ovis), it has a great deal of relevance to the stated problem of this paper; that is, the late Pleistocene extinctions in North America. The dispersal theory appears to more satisfactorily account for the size and external structures of the Pleistocene mammals (particularly ungulates) in the temperate zones than Cope's rule, Bergmann's rule, or allometry. It closely relates the glacial events of the Pleistocene with the faunal changes observed in the paleontological record. Perhaps most important of all, it explains the higher fitness of invading glacial forms, and thus may explain the so-called "immigration extinctions" caused by Palearctic forms invading North America.

The concepts of this important, unifying theory have been presented in their entirety primarily for reference purposes. We will have occasion to refer to it in the discussion of the specific mechanisms of extinction in North America, with a detailed account concerning the various Bison species.
SPECIFIC THEORIES

The specific theories that have been proposed to explain the extinctions in North America will now be presented. Basically, the theories fall into three categories: direct implication of Early Man, indirect affects of Early Man, and various ecological-climatological explanations of the extinctions.

Overkill Hypothesis

One theory that has attracted a great deal of attention in recent years, but not a great deal of support, is the theory of Paleo-Indian overkill. Its main proponent and defender is Paul S. Martin, of the University of Arizona. Martin (1967) contends that there is a global extinction pattern in the late Pleistocene that correlates strongly with prehistoric man's spread and his development as a big-game hunter (Fig. 7). For events in the Americas, Martin (1973) asserts that there is no convincing evidence of man in the New World prior to the end of the Wisconsin glaciation. At about 13,000 years ago, deglaciation had proceeded to the point that a corridor on the eastern foothills of the Canadian Rockies had opened up, once again establishing a migratory route from Alaska to the conterminous United States. There is sufficient evidence to show the complete coalescence of the Cordilleran ice sheet of the Northwest with the
FIG. 7. The global pattern of late-Pleistocene extinction in sequence: 1, Africa and southern Eurasia; 2, New Guinea and Australia; 3, Northern Eurasia and northern North America; 4, southeastern United States; 5, South America; 6, West Indies; 7, Madagascar and New Zealand. In each case, the major wave of late-Pleistocene extinction does not occur until prehistoric hunters arrive. (Martin, 1967)

Laurentide ice sheet of the Northeast and Middle West from 20,000 to 13,000 B.P. (before present). Martin hypothesizes the entrance of early man (Paleo-Indians) into the continental United States as a skilled hunter of the first magnitude, complete with a tool kit of fine projectile points and miscellaneous implements for processing a kill (Martin, 1973). Finding a new land teeming with game with no fear of man, the Paleo-Indians experienced a population explosion, as they spread rapidly southward along a widening front (Mosimann and Martin, 1975, Fig. 8). Their impact on the game, primarily
Fig. 8. Overkill scenario for North America. (Nosimann and Martin, 1975)

large herbivores, was to reduce the populations below the minimal level necessary to sustain the species. Presumably, carnivores became extinct as their prey was eliminated by man. This wave of slaughter spread southward to the tip of South America in a matter of only about 1,000 years. The requirements of this theory are: no evidence of man in the New World (except Alaska) older than 12,000 B.P.; evidence of an advanced hunting culture in Alaska prior to the opening
of the Canadian corridor; no significant extinctions of mega fauna prior to 13,000 B.P.; the latest dates for extinct forms must proceed from North to South America; large accumulations of bones of extinct animals (kill sites) should be found with convincing associations with human artifacts; no preference for any particular game species should be seen, since we are dealing with the synchronous extinctions of many forms; evidence of large populations of skilled hunters dispersed across North America should be found; and, the effects of climatic and vegetational changes on the now extinct species must be proven to be minimal.

Before presenting a critique of this theory, a discussion of its strengths is in order. The strongest evidence for this theory is coincidental in nature. Not only in the Americas, but also in Eurasia, Africa, Australia, Madagascar, and New Zealand extinctions in the local fauna apparently coincided with the first arrival of modern man (Homo sapiens sapiens), a skilled hunter surpassing the abilities of any prior predator. We will take a closer look at the evidence supporting man’s role in these regions after completing the summary of the strengths of the overkill hypothesis. It is also contended that climatic and vegetational changes were typical throughout the Pleistocene, and large-scale extinctions did not result from past ice ages. The only truly unique feature of the terminal Wisconsin glaciation was the appearance of man. Also, it is pointed out that severe ecological stress results in phyletic replacement, and not the complete abandonment of niches, as was seen at the end of the Pleistocene. The
circumstantial evidence appears to point to man. Also, Martin contends that critical analysis of alleged early man artifacts in the Americas prior to 12,000 B.P. will prove them to be erroneous. Further, he contends that there is no clear-cut case of loss of any Rancholabrean mammals prior to 12,000 years ago and no extinct genera have been found in cultural deposits of the last 10,000 years. There is evidence for a widespread hunting culture, termed Clovis or Llano, in association with some extinct genera, particularly mammoth (Table I).

There are many serious problems with the overkill hypothesis. The late and explosive entrance of man into North America has not been supported by archeological finds. There is adequate evidence of man in the Americas prior to the end of the Wisconsin (MacNeish, 1976). According to MacNeish, man entered the New World not as a skilled hunter, but rather as a primitive, generalized hunter-gatherer. He places the first crossing of migrating bands across the Bering Strait at 70,000 ± 30,000 years ago and subsequent southward movement at a very slow rate. Early man sites and dates in the New World are shown in Table II and Fig. 9. MacNeish divides Paleo-Indian prehistory into four general stages of development based on tool assemblages (Fig. 10). The fourth stage corresponds to the skilled Clovis mammoth hunters in Martin's model. Besides the old sites found, mostly in Texas, Mexico, and Peru, there is every reason to believe that man entered the New World prior to 12,000 B.P. when one examines
Siberian and Alaskan archeological evidence as well as the history of the Bering land bridge (Hopkins, 1967). The Bering land bridge has provided the migration route of faunal exchange between Eurasia and the New World several times in the past. Due to the binding up of a great deal of water in a continental ice sheet during an ice age, sea level is greatly

(MacNeish, 1976)
Figure 9. The map shows the location of major sites where remains of early man have been found in the Western Hemisphere. The "stage," or characteristic technology complex, of each site is indicated by the circular symbols. Site numbers are keyed to Table 1, opposite, which summarizes tool complexes, site names, dates, and sources.

(MacNeish, 1976)
Stage IV: Begins ca. 13,000 B.P. in North America and ca. 11,000 B.P. in southern South America, ending ca. 9,000 B.P.
21. Western Inmexicam point—Lind Coulee, Washington
22. Lerna point—Tehuacan, Mexico
23. Hardaway point—North Carolina
24. Plainview point—Texas
25. Folsom point—Lind Coulee, Colorado
26. Clovis point—New Mexico
27. Felt’s Cave flint point—Patagonia, Chile
28. Lauercocha point—Peru
29. Broad-stem point—Tequendama, Colombia

Stage III: Begins ca. 20,000 B.P. in northern North America and ca. 15,000 B.P. in southern South America
12. Lerna point—Yuma, Mexico
13. Serrated leaf point—El Jobo, Venezuela
14. Retouched prismatic blade—Wilson Butte Cave, Idaho
15. Pointed side-blade—El Jobo, Venezuela
17. Burin—El Jobo, Venezuela
18. Bone needle—Flint Creek, Yukon, Canada
19. Bone pin—Flint Creek, Yukon, Canada
20. Bone awl—Flint Creek, Yukon, Canada

Stage II: Begins ca. 40,000 B.P. in northern North America and ca. 18,000 B.P. in southern South America
6. Flute projectile point or knife—Vallequillo, Mexico
7. Bone projectile point—Ayacucho, Peru
8. Pebble chopper—Ayacucho, Peru
9. Plane-convex denticulated scraper—Ayacucho, Peru
10. Burin—Ayacucho, Peru
11. Rib bone刷新—Ayacucho, Peru

Stage I: Begins 70,000 ± 30,000 B.P. in northern North America and ca. 20,000 B.P. in southern South America
1. Pointed flake—Pacifica, Peru
2. Side chopper—Pacifica, Peru
3. Pebble chopper—Lewisville, Texas
4. Retouched flake—Lewisville, Texas
5. Volcanic obsidian projectile point—Pacifica, Peru

Fig. 10 (MacNeish, 1976)
lowered. The depths between the tips of northeastern Siberia and western Alaska are shallow enough that a broad land bridge has probably existed for every Pleistocene ice age and was inundated during each interglacial (as it is today). One must keep in mind, though, that entrance into the rest of North America was not possible during the existence of the continental ice barrier (20,000-13,000 B.P.). On the basis of a great amount of geological data, the sequence of events towards the end of the Wisconsin is believed to be:
1) The land bridge was exposed for several thousand years up to 35,000 B.P.;
2) A glacial regression interrupted the land bridge until about 26,000 B.P.;
3) Glacial readvance exposed the land bridge until about 15,000 B.P.;
4) The terminal stages of the Wisconsin were marked by several major oscillations of sea level, which periodically severed and connected the land bridge;
5) The land bridge has been severed since 10,000 B.P.;
6) During times of severance man could cross on winter pack ice or in simple boats during summers;
7) The main obstacle to North American entrance was the continental ice barrier, which has been estimated at 1,300 meters thick at its southern border;
8) Sea level and glacial dynamics are such that the land bridge would be open before continental ice coalescence and would be closed before corridor reestablishment;
9) Correlations of land bridge and corridor existence place the possible entrances of men into the New World at prior to 35,000 B.P., between 20,000 and 26,000 B.P., and between 10,000 and 13,000 B.P. Entrance prior to 35,000 B.P.
is considered unlikely on anthropological grounds, since the transition from the Neanderthal (Homo sapiens neanderthalensis) to the fully modern stage is believed to have occurred somewhere between 35,000 and 45,000 years ago, and the absence of any trace of Neanderthal-like remains in the New World suggests that the first migration probably occurred after this date (Wendorf, 1966).

Thus, there was ample opportunity for modern man to enter North America between 20,000 and 26,000 years ago. Ancient campsites in Siberia and Alaska are still inconclusively dated, but it would have been strange indeed if man the hunter did not follow the vast numbers of herds of herbivores, which have been dated in this time range, across the Bering land bridge and along the corridor of the Canadian Rockies (Sher, 1974). Furthermore, there is no evidence of a late Wisconsin pre-Clovis culture in Siberia and Alaska. The archeological evidence points to indigenous development of the Clovis industry (Müller-Beck, 1967 and Bryan, 1969).

Now let's take a look at the evidence concerning overkill in other regions of the world. In the Palearctic (northern Eurasia) at the end of the Pleistocene only five genera (each with only one species) became extinct (Reed, 1970). These were: Mammuthus primigenius (woolly mammoth), Coelodonta antiquitatis (woolly rhinoceros), Megaloceros giganteus, Ovibos moschatus (musk ox), and Homoioioceros antiquus (a buffalo related to the Cape Buffalo). This relatively minor episode of extinction occurred in a region
where man as a skilled hunter had existed for many thousands of years. Neanderthal and Neanderthal-like remains have been found in Europe, the Middle East, and Africa from 125,000 to 35,000 years ago. Artifacts and other cultural remains of European Neanderthals indicate that they hunted large mammals along the borders of the ice fields and glaciers. However, reindeer, red deer, aurochs, and wild horse—all which were extensively hunted—were able to survive while the more formidable mammals became extinct (Kowalski, 1967). The possible cause of this apparent contradiction will be discussed with the indirect effects of hunting man on animal populations. The most frequently cited explanation for the Eurasian extinctions is the effect of the habitat changes, due to climatic change, from cold-steppe throughout Eurasia to steppe-forest in northern Eurasia and full forestation in southern Eurasia (Reed, 1970; Kowalski, 1967; Axelrod, 1967).

The example of Africa can neither support nor refute the overkill hypothesis. Most of the African fossil material is beyond the limits of radiocarbon dating (>40,000 years ago). Stratigraphic associations have not been conclusively worked out for Africa (Cooke, 1972). Many fossil species of mammals have been found in Africa. However, as we have shown, this is to be expected during the normal course of evolution, particularly in an ancient tropical continent such as Africa. Much of man's evolution is believed to have taken place in Africa. Yet, the fact remains that Africa has the most varied and abundant megafauna in the world.
Man has not been able to make a significant impact on this fauna until very recent times.

Australia presents some special problems. No one can seem to agree on the approximate date of man's entry. Although Gill (1963) concludes that aboriginal entry began at least 20,000 years ago, this evidence has been questioned by several workers. More convincing dates on prehistoric man date from 11,600-16,000 B.P. (Martin, 1967). Ethnologists have not been able to determine the exact affinities between the Australian Aborigines and other races of man. This inability to trace Australoid ancestry, along with the doubtfully dated fragments, makes it difficult to even approximate the original entry date of man in Australia. The Pleistocene marsupial fauna of Australia was spectacular, both in its diversity and in that it included giant terminal forms of the now extinct Diprotodontidae, Thylacoleoninae, and Sthenurinae (Keast, 1972). Large body size also characterized some Pleistocene species in various contemporary groups, such as echidnas, wombats, macropodid kangaroos, and "Tasmanian devils." One of the striking features of the late Pleistocene to Holocene transition in Australia is the curtailment in the ranges of many of the dominant faunal elements. For example, the koala (Phascolarctos), today confined to the eastern forests, is known as a fossil in southwestern Australia and Lake Menindee, now a desert area. Also, fossils of the arboreal ringtail possum, Pseudochierus, have been found at the eastern limits of the southwestern woodland
belt, proving the former existence of scrub or forest there. Both Keast (1972) and Tedford (1967) feel that only dramatic climatic shifts can explain such striking distributional changes. Thus, the possible effects of early man on Australian Pleistocene extinctions are too uncertain to support Martin's overkill hypothesis. The only places in the world where man can directly be implicated in a mass extinction are Madagascar and New Zealand, both involving insular situations in very recent times. Madagascar is almost 250 miles from the African continent and is separated from it by an old and deep channel. The ancient character of the fauna, its largely African affinities and the high degree of endemism, suggest very early colonization by a few ancestral types (Bigalke, 1972). The first arrival of man on Madagascar is believed to have been as recently as 900 A.D. Since that time there has been a severe ecologic disturbance to the island in the form of reduced forests, accelerated erosion, and extinction of faunal elements (Battistini and Verin, 1967). These extinctions included seven genera of lemurs, the pigmy hippopotamus, two species of giant tortoise, and two genera of struthious birds. Signs of human destruction of these animals as well as nearby weapons and tools can argue convincingly for the hand of man in these extinctions (Walker, 1967). Some indirect effects of man, such as habitat destruction, may also have contributed significantly to the demise of these animals. There is no evidence of recent climatic or natural habitat changes in Madagascar. The
inherent instability of tropical insular populations probably accounts for the rapid demise of these animals once man arrived on the island.

New Zealand is a slightly different situation. There were no native terrestrial mammals here, but 27 species of extinct moas have been discovered in astonishing numbers in postglacial deposits. Twenty-two of the extinct moa species have been found in association with human artifacts (Martin, 1967). The exact arrival time of man in New Zealand is unknown, but it is believed to be as late as 800 A.D. Despite piedmont glaciation and widespread periglacial phenomena on South Island and despite volcanism with the extensive blanketing of North Island by nutrient-poor pumice and ash, no species of these giant flightless birds are definitely known to have disappeared before man's arrival (Martin, 1967). These large, flightless, and probably relatively unintelligent members of an ancient order of birds, were probably easy prey for the moa hunters. The insular situation of New Zealand also made it impossible for the moas to escape from the ceaseless predatory pressure of man.

Thus, only in recent times and only in insular situations has man been convincingly implicated in a faunal extinction. In a temperate continental situation, such as North America, prehistoric man just would not have been capable of rendering massive populations of large terrestrial mammals extinct on the basis of overkill alone. Also, it is a general biological principle that a predator almost never, if ever, reduces a
prey population to the point of extinction (Ricklefs, 1973, p. 531). As the number of prey individuals are reduced, hunting success is greatly lowered, until the prey population is able to reestablish itself. In the meantime, the predator must be able to switch prey species or suffer a drastic reduction in its own numbers. It is extremely unlikely that any predator, even as skilled as human hunters were, could successfully reduce a prey population below its minimum level for sustenance unless the population was already doomed to extinction due to severe ecological stress. The numbers of human hunters required to have an impact on faunal extinction is also beyond what has been observed in hunting cultures. A computer simulation model of overkill (Mosimann and Martin, 1975) contains some serious false assumptions which render it invalid. One of the assumptions is that a hunter-gatherer society is capable of a sustained growth rate. In fact, anthropological studies of modern hunting societies such as the Eskimos and the African Bushmen show that their populations are relatively constant over a long period of time and are controlled by the abundance of game, which fluctuates. The only time a sustained growth rate is accomplished is when man begins planting crops, which did not occur in the New World until much later (Freedman and Berelson, 1974). Extinctions and range shrinkages for mammals since the Agricultural Revolution initiated civilization have been due to destruction of habitat for farming and herding and wanton killing for sport (Reed, 1970).
Another reason to discount the overkill theory in North America is the fact that only two animals were hunted extensively—mammoth and bison. From 34 archaeological sites, camel and horse were found at 3 sites only, pronghorn at two, tapir, peccary, musk ox, caribou, cervid and bear at one each (Butzer, 1971, p. 509). Also, 160 specimens of mastodon have been found in Michigan alone, and not a single specimen there, or any other part of the eastern United States, has been found in clear association with human artifacts or with evidence of human alteration. Total faunal counts at Paleo-Indian sites are small. The earliest evidence of mass slaughter comes from Plano sites dated at 9,000 B.P. (after the major wave of extinctions) and these were exclusively bison (Butzer, 1971, p. 509). Also, Martin's assertion about no survival of extinct forms later than 10,000 B.P. has been shown to not apply to horses and camels, which survived in New Mexico until at least 7,800-8,000 years ago (Schultz, 1968). Lundelius (1957) reported that a fauna consisting of proboscideans, sloths, glyptodonts, saber-tooth cats, Bison antiquus, Bison occidentalis, Camelops, Tanupolama, horses and peccaries persisted in central Texas until approximately 8,000 years ago. Certainly, there is no evidence to support a blitzkreig of human hunters through North America. As has been noted, few extinct animals have been found in direct association with human artifacts or have signs of human disturbance (Table I). Of those that do show the direct effect of men,
only a very small percentage of the fossils found have shown this association.

Finally, the overkill hypothesis denies the uniqueness and severity of the late Wisconsin's climatic and vegetational changes. A sizeable portion of this paper will be devoted to explaining the climatic and vegetational changes of the late Pleistocene and the hypothesized effects on the now extinct mammalian genera.

Indirect Effects of Man

But before we leave the subject of man, let's explore the possibility of man influencing megafaunal extinction indirectly, rather than directly. This concept was elucidated by Krantz (1970), who described three possible indirect means: 1) competition between man and carnivores for a particular food supply, 2) man's hunting practices causing one herbivore to exterminate other herbivores, and 3) agricultural practices altering ecological relationships. This last method describes mechanisms of modern agricultural man's impact on mammals, and since we are dealing with extinctions that occurred before agricultural practices in the New World, we need not concern ourselves with this point. The first two means though, have relevance to our discussion.

The first method refers to the extinctions of the large carnivores. Man need not kill a single animal to eliminate the species—he needs merely to deprive them of their normal
food supply by getting it first. This would be especially effective at times of seasonal crisis, such as northern winters, when food resources are reduced to a minimum and competition is most intense. It is not the entire prey population we are concerned with here, but rather the most vulnerable members (young, lame, ill, and aged) who would be the food resource for both man and the large carnivores. Thus, we would expect that carnivore extinction would precede the herbivore extinction when man was competing, and this is in fact seen. Without man's intervention, carnivore extinction would follow herbivore extinction. Evidence for this effect is clearly seen in North America in the last records of extinct species (Table III; carnivores are starred).

The second indirect method is in direct opposition to the overkill hypothesis. It contends that heavy hunting by early man preserved at least one type while unhunted species became extinct. Apparently, while man preyed heavily on the bison it increased in numbers and range. Archeological and paleontological evidence seems to support these conclusions. Recall the analogous situation that occurred in Eurasia, where the most easily hunted species survived and the most difficult to hunt became extinct. Demonstration of the mechanism of this phenomenon involves principally a comparison of human predation practices with those of other carnivores. Large carnivores prey mainly on young herbivores in the warmer half of the year, and the old, diseased, and injured ones in the colder months. The resulting survivorship curve of a popula-
Table III. Stages of late Pleistocene and early Holocene extinctions in North America (from Butzer, 1971)

Last dated record prior to 12,000 B.P.

- *Bison latifrons* (32,000 B.P.)
- *Bison alleni* (31,000 B.P.)
- *Boreostracon* (23,000 B.P.)
- *Papoatherium* (16,000 B.P.)
- *Dinobastis* (Friesenhahn Cave)
- *Felis bituminosa*
- *Felis dasgatti*
- *Smilodon*
- *Canis furlongi*
- *Canis milleri*
- *Ursus optimus*

La Brea Tar Pits, 13,890 B.P. ?)*

Last record contemporary with Llano (ca. 11,600-10,900 B.P.)

- *Panthera atrox*
- *Arctodus*
- *Mammutbus exilis, M. imperator*
- *Equus hemionus*
- *Sangamon*
- *Bison priscus crassicornis*
- *Rangifer fricki*
- *Bootherium, Symboe*
- *Capromeryx, Stockoceros, Tetrameryx*
- *Eucatherium, Preptoceras*

Last record contemporary with Folsom (ca. 10,800-10,300 B.P.)

*Paramylodon* (?)

Last record contemporary with Plano (ca. 10,300-7900 B.P.)

- *Canis dirus, Aeonocyon*
- *Mammutbus columbi, M. primigenius*
- *Tapirus*
- *Equus*
- *Mylohyus, Platysonus*
- *Camelops*
- *Tanucolama*
- *Bison bison antiquus*
- *Oreamnos harringtoni*
- *Ovibos*
- *Castoroides*
- *Dasycus bellus*
- *Megalonyx, Nothrotherium*

Last record after 7900 B.P.

* Mammut americanus (?)*
* Bison occidentalis (7350 B.P.)*
tion of large herbivores under natural predation is seen in figure 11a. However, data on human game kills tend to indicate a more nearly equal take at all ages of the prey species, due to the development of projectile weapons capable of killing adult animals as easily as the more vulnerable prey individuals (Hester, 1967). The survivorship curve under human predation is depicted in figure 11b. Superposition of the two survivorship curves is in figure 11c. Most conspicuous is the difference in numbers of surviving young adults, which constitute the major breeding stock. Thus, when hunting man replaces natural predators a population increase is likely to occur. This prey species will then exert considerable population pressure against any competing species in the area with similar ecological requirements. Conditions under which these first two methods may not occur are: 1) The predator which man competes with has another major food supply during seasons of stress, and 2) Other competing carnivores are taking significant numbers of the young of the prey species.

This model explains the success of the bison and the demise of its competitors—horses, camels, pronghorn, and cattle. But what about the mammoth? Indications are that it was hunted by the early Clovis culture. Perhaps its disappearance is due to changed preference by hunters for bison. Success of the bison would have doomed the mammoth, also a grazer of open plains. Perhaps the late onset of reproductive maturity in elephants would result in decline of the population under any sizeable predation pressure.
Fig. 11a Typical survivorship curve of large herbivore under natural predation.

Fig. 11b Typical survivorship curve of large herbivore under human predation.

Fig. 11c Superimposed survivorship curves showing differences between natural and human predation. (Krantz, 1970)
Lastly, there is the possibility that the vegetational changes at the end of the Pleistocene had a more significant impact on the mammoth than on other herbivores.

Krantz (1970) points out that these indirect influences of man cannot entirely explain the megafaunal extinctions of the late Pleistocene. He concedes that the combination of an unusually abrupt end to the last glaciation with the subsequent altithermal warming may have been unique in the Pleistocene, and its effect on the extinctions cannot be ignored. With this in mind, let's explore the merits of the theory of climatic and vegetational change being the prime cause of the megafaunal extinctions.

Climatic-Vegetational Theory

The central dogma of this theory is that the late Pleistocene was characterized by rapid and extreme fluctuations of climatic conditions, compared to earlier times. These climatic changes may have affected the large mammals directly (severe drought, cold arctic air masses, severe winter storms, floods) or indirectly through vegetational change. Changes in vegetational patterns would have weakened the specialized herbivores to the point where they were more susceptible to disease, parasites, extremes in the weather, or predators, including early men. With the decline of the large herbivore populations, the carnivores that depended on them were doomed to extinction.
In the first place, how do we determine that a climatic change has taken place in the past? Basically, there are six indicators: 1) surface-ocean temperature, as recorded in deep-sea sediments; 2) the volume of glacial ice, as recorded by fluctuations in sea level; 3) the extent of major ice sheets, as recorded by glacial deposits and dated materials; 4) the aridity of desert areas, as recorded by the size of closed-basin lakes; 5) plant-growth environment, as recorded by the type of pollen grains in Pleistocene sediments; and 6) changes in the fossil distribution of animals whose ecological requirements are well known. The first four may be characterized as geophysical in nature, and due to their complexities we will only summarize the pertinent information gained from them rather than going into detail about the methods. The last two are biological in nature, and have a more direct bearing on the theory at hand.

As for the first indicator, Broecker and his associates (Broecker et al., 1960) concluded from changes in the coiling direction of Foraminifera and sedimentation rates in carbon-dated deep-ocean cores that there was an abrupt change in ocean-water temperatures, and therefore climate, approximately 11,000 years ago. This presumably correlates with the warm and dry post-glacial conditions which affected the vegetational patterns in North America, as we shall see later.

Fluctuations in sea level have correlated well with glacial advances and retreats (Fig. 12). For sea levels to fluctuate significantly, major climatic changes have to occur.
Fig. 12 Fluctuations in Sea Level

(After Creager and McManus, 1967)

Fig. 13 Fluctuations in lake level of two Great Basin lakes (Bonneville, Utah and Lahontan, Nevada)

(After Broecker, 1965)
Late Wisconsin deglaciation, as well as readvancements, must have been in response to major changes in temperature and precipitation. In general, we can say that the late Pleistocene has been characterized by a trend to warm and dry conditions, with several fluctuations. On a yearly basis, it is contended by several paleo meterologists that the seasonal fluctuations we experience today in temperate regions (extremely cold winters and hot summers) are a recent weather phenomenon and were not typical of the pre-Wisconsin Pleistocene (Taylor, 1965). Perhaps the lack of adaptability to seasonal extremes explains some of the extinctions.

Major ice sheet movement has been determined by radiocarbon ages on wood from glacial tills (marking the position of an advancing ice front), from the beaches of proglacial lakes and from basal bog deposits. These dates correlate well with sea level fluctuation (Fig. 12). The sequence of late Wisconsin glacial events in North America is considered to be: 1) the ice achieved its maximum extent about 18,000-20,000 years ago; 2) the ice sheet retreated until about 15,000 years ago, and then had a short readvancement (Port Huron); 3) ice sheet retreat resumed up until about 12,000 years ago (Two Creek); 4) a short-lived readvance (Valder's) took place at about 11,800 years ago; 5) except for some minor oscillations, the glacial retreat was completed and modern sea level restored by 4,000 years ago.

Variations in the size of lakes confined to closed basins are undoubtedly related to climatic change. High stands
broadly correlate with cold and wet periods and low with
warm and dry (Fig. 13). Clearly, the geophysical evidence
supports the contention that major fluctuations in climate
have characterized the late Pleistocene and early Holocene.

It is not only major fluctuations over a number of years
that have an impact on plant and animal distributions. The
seasonal variations in temperature are also important. This
climatic variable has been termed equability, and its relevance
to the Pleistocene mammalian extinctions has been detailed
by Axelrod (1967). A region that has high equability, such
as a tropical rain forest, has very little variation in its
temperature on a yearly basis. High equability is strongly
correlated with adequate levels of precipitation and humidity.
Areas of high equability support mixtures of plants and
animals that otherwise are widely separated geographically,
and, generally, a high level of overall biomass. A region
that has low equability, such as a temperate plains, has
a large average annual range of temperature. When low
equability is coupled with low levels of precipitation and
humidity, overall biomass and species diversity are much
lower. The role of equability in mammalian history is sug-
gested by the conditions under which the richest ungulate
fauna has survived. The African fauna south of the Sahara
has the aspect of the Quaternary fauna of middle North America.
Its area of optimum development includes the largest region
of high equability close to the equator. It is a climate
characterized by a lack of extremes which enables a rich
ungulate fauna to extend into temperate areas well outside the margin of tropical climate. Thus, tropical biota in temperate regions of high equability are very sensitive to a small change in temperature; that is, they are close to their limits of tolerance. Thus, an occurrence such as tapir and mammoth at Rancho La Brea, or porcupine and capybara at Seminole, Florida, is not paleoclimatically unexpected. The Tertiary was generally characterized by global high equability due to lower continents, lower mountain systems, and marine embayments of moderate extent. Regional polar, tundra, steppe, and desert climates were not yet in existence. The Pleistocene and Holocene have been characterized by episodes of severely decreased equability, particularly in temperate regions (Axelrod, 1967).

What about the biological evidence for climatic change? Deevey (1965) stated that vegetation is often a surer guide to the climate of a region, or to the microclimate of a locality, than any physical measurement yet devised. Vegetational change, and thus climatic change, is inferred from analysis of fossil pollen spectra from lakes and bogs. Different plants vary in their production and dissemination of pollen, so minor fluctuations in the pollen percentages of species found in the spectrum may have no ecological significance. However, dramatic shifts in pollen percentages or the timing of the first or last appearance of a species in the pollen profile may have considerable ecological significance. These lake or bog sediment cores can also be
dated by radiocarbon method to correlate the vegetational changes with absolute chronology, although carbonate contamination from limestone and mixing of lake sediments by bottom organisms may affect the accuracy of the results (Ogden, 1967). With these limitations in mind, what is the pollen evidence for late Pleistocene climatic change? From lakes and bogs in the Great Lakes region comes evidence of climatic change at about 10,000-11,000 years ago (Ogden, 1967). What is seen is a transition from spruce pollen to either pine or deciduous species in an apparently short period of time across a wide area of eastern North America. Ogden concludes that the distance covered is too great, and the time available too short for mild climatic changes to account for the replacement of spruce with other species. Only a widespread, rapid, and dramatic change in temperature and/or precipitation could account for the vegetational change observed in the pollen spectra. A full sequence of the late Pleistocene vegetational changes in North America and their impact on the various faunal elements will be detailed later.

A final indicator of climatic change is an observed change in the fossil distribution of an animal whose ecological requirements and tolerances are well known due to contemporary research. The most frequent terrestrial faunal indicators of environmental change are non-marine mollusks, insects, and small mammals. The duration of the Pleistocene is short in comparison to the evolutionary rate of mollusks. Thus, a change in the molluskan community species composition reflects
a change in habitat brought on by climatic shift. The appearance of a certain land snail only in the Wisconsin has suggested uniquely extreme glacial conditions. Also, a decrease in diversity is seen in the late Pleistocene-early Holocene molluscan fauna, reinforcing the contention that aridity and strong seasonal contrast are a late Wisconsin development, not only in the Great Plains but also in the Southwest (Taylor, 1965).

The use of insect remains, usually beetles, grasshoppers, or chironomid larvae, to infer climatic change is relatively recent. Insect remains are abundant in Quaternary deposits, the number of extinct forms is extremely small, and the response of insects to changes in climate is extremely rapid. A study of present and past grassland insects by Ross (1971) has shown that the prairie biome in North America during the glacial optimum of the Wisconsin was very small, but expanded greatly and quickly in post-Wisconsin time. Paleoentomology may make significant contributions to knowledge of climatic and vegetational changes in future research.

Small mammals, also due to their rapid response to ecological change and their lack of recent extinctions, have been used to show climatic changes. Comparison of late Wisconsin ranges of several extant species with their current ranges shows some remarkable northward shifts after deglaciation (Hibbard, et al., 1965). This readjustment has not been gradual up to the present time, but rather was occurring rapidly and was essentially completed during the most intense
period of megafaunal extinction (Slaughter, 1967).

Now that it has been established through a variety of sources that—1) the Wisconsin glaciation was unique in its intensity, 2) rapid climatic fluctuations marked the end of the Wisconsin, and 3) post-glacial conditions were marked by warm and dry conditions, as well as seasonal extremes—a climatic-vegetational theory of megafaunal extinction can be properly developed.

The maximal extent of the Wisconsin glaciation and isochrones of its deglaciation are shown in Fig. 14. This establishes the minimal dates for vegetational, and thus faunal, invasions of formerly glaciated areas. The vegetational pattern of eastern and central United States at the late-Wisconsin glacial maximum is believed to be as shown in Fig. 15. The current vegetational pattern is shown in Fig. 16. Conspicuous differences exist between the vegetational patterns of the present and during the glacial maximum. The periglacial environment of tundra and park tundra has been displaced northward at least 1,920 km (1200 miles). This was accomplished rather quickly (Fig. 14) and was essentially completed by 8,000 years ago. The boreal coniferous forest, an approximately 200 mile wide strip of predominately spruce south of the periglacial environment, has seen a displacement of at least 960 km (600 miles) and a great expansion in its width up to the present. Recall from the pollen spectra, that this change was extremely rapid in eastern North America, and was more rapid than
what would be expected in a gradual invasion of a deglaciated area with mild climatic changes pushing the species northward. Spruce forests were maintained in isolated lowlands while the deciduous forest spread rapidly around them, forming a wide belt of deciduous forest between spruce enclaves and the new spruce forest in Canada (Dreimanis, 1968). Other startling differences in the vegetational patterns are the former small prairie and large forested areas of the Great Plains and the present expanded prairie and reduced open woodlands of the Great Plains. The last major observation is the expanded desert shrub and grasses in the Great Basin, Southwest, and portions of the Great Plains where there formerly existed savannah—forest.

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**Figure 14** Speculative model of deglaciation by the Laurentide Ice Sheet from ~18,000 BP to disappearance of the ice sheet. Isochrons are based on C¹⁴ dates as well as end moraines and other field data. Short arrows indicate significant readvance. (Prest, chap XII in Douglas, ed., 1970.) For more detail see Canada Geol. Survey Map 1237A, 1969. (Flint, 1971)
Fig. 15 Probable distribution of principal biomes in North America during glacial optimum of the Wisconsinan. Stippled area is the prairie biome.

(Ross, 1970)
<table>
<thead>
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<th>Explanation</th>
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<tr>
<td>Tundra and park tundra</td>
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<tr>
<td>Boreal coniferous forest</td>
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<tr>
<td>Boreal coniferous forest (montane)</td>
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<tr>
<td>Hemlock-northern hardwood forest</td>
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<tr>
<td>Temperate mixed forest</td>
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<tr>
<td>Temperate mixed forest (montane)</td>
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<tr>
<td>Prairie, steppe, and savanna</td>
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<td>Dry steppe</td>
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<td>Desert shrubs and grasses</td>
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<tr>
<td>Subtropical scrub</td>
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<td>Tropical woodland</td>
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Figure 1b. Natural vegetation zones in North America today, much generalized. (Compiled from various sources by R. F. Flint and prepared by L. A. Sirkin.) (Flint, 1971)
Now that the climatic and vegetational changes of the late Pleistocene in North America have been presented, it is appropriate to discuss the differential extinction model. These environmental changes resulted in different ecological stresses, depending primarily on the size of the mammal. Differential extinction is schematically represented in Fig. 17. This explains why the large herbivores, primarily ungulates, showed a drastic reduction in their diversity, while the small herbivores, primarily rodents, survived with their diversity unaffected. It is an interesting observation that the only rodents in North America to become extinct at this time were the very large North American capybara and the giant beaver. The Pleistocene survival of the African megafauna is schematically diagrammed in Fig. 13. The large mammals of the Sahara survived by migrating into the southern and eastern savannas of Africa. The small mammals were able to survive much better in the Sahara than the large mammals, although many migrated to the savannas also. Evidently, the North American large mammals were unable to migrate to a region of high equability and precipitation due to the expanding Mexican desert cutting off the passage to Central and South America.

A different perspective on this whole problem is Webb's (1969) viewpoint of the equilibrium hypothesis and Pleistocene extinctions. Webb contends that the abruptness of the late Pleistocene extinctions, as opposed to earlier extinction episodes, is due only to the refined state of knowledge
Fig. 17. Differential extinction model. (Guilcay, 1967)

concerning the late Pleistocene, as opposed to earlier times. This is reminiscent of the rationale used to allay the fears of Americans in the late 1960's to a rising crime rate. It's not that there is more crime, we were told, it's just that modern police techniques have resulted in more crime being reported. This analogy aside, let's examine what else Webb contended. He feels that much insight can be gained by examining the mammalian extinction phenomena of the last 12 million years. Thus, the late Pleistocene extinctions
may be only a small "pulse" in an otherwise smooth extinction curve over millions of years. The originations (including immigration and internal development) and extinctions of late Cenozoic land mammals in North America are shown in Table IV. The "total firsts/lasts" category refers to the total number of genera of that particular type of mammal that made their first appearance or last appearance during that time period.
General observations on this data are: 1) Other ages, particularly the Hemphillian, which is pre-Pleistocene, have seen large numbers of mammalian extinctions. 2) There is a general trend in the decline of large herbivores and the expansion of small rodent and rodent-like forms ("glires"). None of this is really very startling, since we have already recognized the routine occurrence of extinction during the course of evolution, and differential extinction predicts and explains the differences between large mammal and small mammal extinctions. The fact still remains that the late Pleistocene extinctions in North America were indeed abrupt, relative to geologic history. This widespread and dramatic phenomenon can not be regarded lightly by incorporating it into an overall scheme. So many variables are different for each age, even within the same region, that attempts to generalize are only exercises in statistical manipulation.
Now that the major contentions of the environmental theories have been discussed, let’s systematically consider how well they explain the disappearance of the various megafaunal elements in North America. The ground sloths are specialized herbivores. Any change in the vegetation would have had dire consequences to these formerly South American species. The broadly expanding Mexican desert would have prevented them from returning to their native South America. Their numbers probably dwindled in the face of this vegetational change brought on by the warm and dry post-glacial environment. At least one sloth, *Megalonyx*, tried to follow the vegetation northward, but most likely perished as a result of the seasonal extremes in the post-glacial temperate regions. As for the other edentates, *Pampatherium*, the giant armadillo, apparently could not adjust to the new environment, whereas another armadillo, *Dasyx novemcinctus*, phylogenetically replaced a larger form, *D. bellus*, and has enjoyed a successful range expansion in recent times (Slaughter, 1967). The glyptodon *Boreostracon* was a tropical form, which apparently could not adapt to the late-glacial conditions in North America. As was pointed out before, there are no direct associations of these edentates and early man. The climatic and vegetational changes associated with the transition from Wisconsin glacial to recent times satisfactorily explains the disappearance of these edentates.

*Castoroides*, the giant beaver, evidently preferred lakes and ponds bordered by swamps in the northeast and similar
environments as well as large streams farther west. Their dentition suggests that they were not as efficient in gnawing down trees, and thus building dams, as present day Castor. The reduction and disappearance of their water environments during the post-glacial warming undoubtedly contributed to their demise (Stirton, 1965). Also, Stirton determined from skull casts that the brain of Castoroides was considerably more primitive than that of modern Castor. Thus, the disappearance of Castoroides may also be explained as a case of being outcompeted by a more intelligent, better dam-building, and generally more adaptive beaver, Castor. The disappearance of Neochorerus, an extinct capybara, may be explained as another example of a South American tropical form that could not adjust to post-glacial conditions, particularly low equability. These semi-aquatic animals probably suffered as their habitats dried up, and could not successfully migrate back to Central and South America through Mexico.

The demise of the carnivores—the bears, saber-tooth cats, dire wolves, and jaguars—can be explained as a result of the decline in their food source, the large herbivores. Perhaps competition from early human hunters also contributed to their extinction. The surviving bears in North America mostly consume small game and vegetation. The mountain lion, which had an extensive range until European colonization, apparently was successful due to its chief food source, Odocoileus, expanding its range greatly in post-glacial time after the disappearance of so many of the herbivores. The fate of the saber-tooth cats was probably determined by the
decline of the ground sloths and proboscideans. The disappearances of Canis dirus and Panthera atrox may have been as a result of competition and replacement by timber wolves and mountain lions, or competitive pressure by early man.

The extinctions of the proboscideans, which has intrigued paleontologists and the general public for years, can be satisfactorily explained by this model. Recall that through dentition and pollen studies it is generally agreed that Mammut, the mastodon, was a browser in open spruce woodlands or spruce forests. It has also been pointed out that in eastern North America post-glacial drying resulted in the rapid movement of spruce northward and replacement by deciduous species in the south, except in swampy lowlands. Dreimanis (1968) has hypothesized that the mastodons became trapped in ever-drying up spruce swamp enclaves while a wide-belt of deciduous woodlands prevented them from reaching the new spruce forests just south of the receding ice. The palynological evidence supports such a scenario in the east, as well as the numerous mastodon finds with no evidence of man's influence. The possibility that many of them died in swamps and bogs by becoming stuck is supported by several finds. Skeels (1962) described the sequence of events as: 1) glacial retreat was marked by the formation of depressions, which were filled with melting glacial ice; 2) as these depressions or kettle holes filled with sand, silt, and clay, they began to support a growth of aquatic and semiaquatic vegetation; 3) heavy animals, such as proboscideans, venturing out on "quaking"
portions commonly broke through, became mired, and died. Due to the quick preservation by this process, most of the good mammoth and mastodon sites are from present or former bogs. In Alaska and Siberia, thousands of mammoths have been found in frozen mud (Farrand, 1961), which may explain the disappearance of the arctic species of mammoth. The disappearance of mammoths in the United States, though, is somewhat problematical. By their dentition, mammoths are believed to have been grazers. There are two lines of paleontological evidence that mammoths were under a severe ecological stress prior to their extinction: 1) A progressive diminution of size of many mammalian species, including mammoth and bison, is evident throughout the later Pleistocene, (Reed et al., 1965; Flerow, 1967; Edward, 1967), which may be interpreted as a population response to deteriorating resources or increased competition (Butzer, 1971, p. 505), and 2) During the late Pleistocene mammoth teeth developed thinner plates, and the enamel also was thinner and more crenulated. This trend continued up to the time of their extinction, about 12,000 years ago (C.B. Schultz and L.D. Martin, 1970). Mammoth extinction can thus be seen as a combination of factors: 1) rapid change in the vegetational pattern of the region in which they inhabited; 2) competition from an expanding bison population; 3) death in migration to new areas by becoming stuck in bogs, mud, or ice; 4) non-adaptive dental evolution; 5) hunting by early men; and 6) inability to adjust mating habits, gestation, and parental
care to the presence of man. This last possible cause points out the vulnerability of elephants in their reproductive behavior and physiology. Sexual maturity is attained late (16 years old), gestation is long (2 years), reproductive potential is low (1 calf born per litter, 1 litter every 3 years), and they generally are easily disturbed by man or carnivores. This information on elephants is valid for mammoths, since many studies show the close morphological similarity between mammoths and present day elephants, and some authorities even consider them to be of the same genus.

The extinctions of the North American perissodactyly can also be explained as the result of climatic and/or vegetational factors. Horses disappeared from North America not long after: 1) warm and dry post-glacial conditions expanded the desert and dry prairie areas, and 2) the bison expanded its range. The combination of having to adjust to a new food source and competition from an invader with similar ecological requirements may have weakened the horses to the point that they were more susceptible to disease, weather extremes, and predators, including early man. The tapirs, which only inhabit humid areas today, may have been doomed in North America as a result of the warm and dry post-glacial conditions, seasonal extremes, as well as vegetational changes.

The artiodactyly, being a diverse group, probably have a variety of causes associated with their extinctions. *Platygonus*, the flat-headed peccary, is believed to have
been primarily a prairie-plains form, in contrast to *Mylohyus*, the long-nosed peccary, which was primarily a woodland browser and omnivore. *Platygonus* may have been another form that was successfully outcompeted by the bison for grazing areas. *Mylohyus* may have become extinct as a result of not successfully migrating to northern woodlands. Both species, evolved from South American tayassuids, may have been unable to successfully adapt to the extreme seasonal changes in temperate North America since the late Pleistocene. Man may have had a secondary role in the disappearance of these peccaries, although there are no definite associations.

The extinct camelids, *Camelops* and *Tanupolama*, are not as satisfactorily explained by the ecological model as others. The transition to drier conditions should not have adversely affected them. Most of their range (Great Basin and Southwest) was not extensively invaded by bison. Seasonal extremes may have had an impact on them. However, charred and broken bones of them have been found in caves occupied by Paleo-Indians. Perhaps this is one group that early man may have played a significant role in exterminating.

On the other hand, the extinct cervids, *Cervulces* (moose) and *Sangamone* (large deer) show absolutely no associations with early man in North America. In the case of *Cervulces*, it may have been outcompeted by the modern moose *Alces*, a recent immigrant from Eurasia. It is a basic biological principle that when two species with identical ecological niches are present in the same region one will eventually
outcompete the other. As predicted by the dispersal theory, the recent Eurasian immigrants have been shown to be more adaptive than the American endemics by their intercontinental dispersals. The proportion of Palearctic emigrants to the New World, relative to Nearctic emigrants to the Old World is about 3:1 in the Blancan, 5:1 in the Irvingtonian, and 23:0 in the Rancholabrean (Repenning, 1967). As for Sangamon, so little is known about it that no definite statements can be made about the probable cause of its disappearance. Perhaps it never really has a firm foothold in the New World and was outcompeted by other large deer such as Rangifer (caribou) and Cervus canadensis (elk).

The antilocaprids, Capromeryx and Tetrameryx, probably disappeared as a result of phyletic replacement by Antilocapra (modern pronghorn). Perhaps vegetational changes resulted in competition among these similar forms, with the swift and adaptable Antilocapra winning out. There is some evidence that Paleo-Indians took some pronghorns, but it is doubtful that this played even a minor role in the disappearance of Capromeryx and Tetrameryx.

The bovids provide some special problems. Bootherium, an extinct woodland musk-ox, ranged from Alaska to the east coast of North America and south to Texas. Spruce and pine pollen have been found in the endocranial matrix of a specimen from Saltville, Virginia, suggesting a boreal woodland habitat (W. Beninghoff, unpublished, in Martin and Guilday, 1967, p. 57). If Bootherium favored boreal coniferous forest, then
its demise may be seen as an inability to relocate successfully in the post-glacial Canadian spruce forest. Another possible cause of its demise was the lack of suitable forage in northern areas due to the formation of Sphagnum associations (muskegs) in the Canadian boreal forest as compared to the spruce forests in the United States in glacial time (Flerow, 1967). Perhaps the same reasons can be applied to Symbos, another boreal woodland musk-ox, and apparently a late migrant from Eurasia. The type of forage available in the New World's spruce forests did not suffice to maintain the population. It is unlikely that severe winter conditions could have killed these bulky, hairy animals directly, but perhaps heavy snows could have covered their main sources of forage and resulted in severe winter starvation and susceptibility to timber wolves. Bones of these woodland musk-ox have never been found in association with early man. Euceratherium (Preptoceras is female?), the shrub oxen, were larger than mountain sheep and probably occupied lower slopes of hilly country. Being a part of the Irvingtonian fauna, they were in North America long before the late Wisconsin and have been found from coast to coast. Their disappearance may have been as a result of vegetational changes eliminating their favorite forage, or unsuccessful competition with a late Wisconsin immigrant from Eurasia, such as Ovis (mountain sheep) or Bison. There are a few remains of Euceratherium (and Preptoceras) associated with early man sites, but they are not abundant enough to support the contention that man seriously affected the fate
of the shrub oxen through overkill. As for *Oreamnos harringtoni*, an extinct mountain goat, competition by its close relative and ecological equivalent *Oreamnos americanus* appears to account for its disappearance. Again, this competition may have been triggered by the ecological stress of changing climate and vegetation. The extinct species of bison, *B. antiquus* and *B. occidentalis*, have a great deal of uncertainty and debate surrounding them. The evolution of the various bison forms has two general theories (Fig. 19): 1) *Bison priscus*, the cold-steppe bison of Europe depicted in cave man drawings, is considered the prototype, from which the wisent of Europe, *B. bonaesus*, the wood bison of Canada, Alaska, and Siberia, *B. priscus athabascae*, and the extinct giant-horned *B. latifrons* were derived. Through isolation in its southern range, *B. latifrons* developed into *B. allenii*, which gave rise to *B. bison antiquus*. *B. bison antiquus* developed into the modern plains bison, *B. bison bison*, perhaps through an intermediate stage, *B. bison occidentalis* (Flerow, 1967). 2) *Bison bonaesus*, the wisent, was the generalized form from which two lines developed. One line led to *Bison priscus*, the cold-steppe bison, which gave rise to *B. latifrons* and then *B. antiquus*. The other line had as its intermediate *B. occidentalis*, which gave rise to *B. athabascae*, the wood bison of Canada, and *Bison bison*, the modern plains bison (Geist, 1971). If one accepts the first theory, then there really were no bison extinctions in North America after all, just evolu-
Fig. 19  Two theories of bison evolution.
tionary development to the modern form. The second theory depicts *B. antiquus* as the end of an extinct line of bison and the modern plains bison, *B. bison*, and the Canadian wood bison, *B. athabascae*, to be evolved forms from *Bison occidentalis*. Geist supports his theory with comparisons of facial hair, horns, relative body proportions, and tail length for *Bison priscus*, *B. bonasus*, and *B. bison* (Fig. 20). As you may recall, the dispersal theory states that for a variety of
physiological and behavioral reasons, improved combat techniques are selected for in pioneering populations after a glacial retreat. These combat modifications manifest themselves in bison in larger horns, exaggerated front quarters, and a more distinctly patterned hair coat. Thus, *B. criscus* could have evolved as the pioneering population of a generalized form, *B. bonesus*. After a habitat becomes saturated, the features become less extreme. Linking *B. latifrons* and *B. antiquus* to the short facial hair group is the relatively small protrusion of their orbitals (Guthrie, 1966), compared to the present *B. bison*. The evolutionary sequence of the first theory does not take into account the unlikelihood of reverse morphological trends in the evolution of the bison, so let's assume that indeed *B. antiquus* represented a true North American late Pleistocene extinction. This extinction can best be explained as successful competition from an invading ecological equivalent, *B. occidentalis*, which then evolved into *B. bison*. Although many bones of *B. antiquus* have been found in association with Paleo-Indian sites, the principle of inevitable competition and elimination of one form between two ecologically equivalent forms better explains the disappearance of *B. antiquus*. This is more logical than trying to explain how a small population of paleolithic hunters selectively exterminated a herd of probably millions, but managed to preserve a smaller form in huge numbers.
The major theories of the causes of the extinctions have been presented. Other minor theories have been suggested, but they are mostly speculative and have very little evidence to support them. It has been shown that no one theory satisfactorily explains all the extinctions, since we are dealing with many types of animals, with different ecological requirements and tolerances, in different biomes of North America.

The late Pleistocene was characterized by both severe environmental changes as well as the emergence of man as a significant ecological force. The author contends that, at least in North America, man did not play a decisive direct role in mammalian extinctions. His presence may have been a contributing factor in various indirect ways, though. The climatic and vegetational changes of the late Pleistocene and early Holocene would have had a more far-reaching effect on the herbivores, either directly through individual inability to adapt to new conditions or more indirectly through enhanced competition among ecological equivalents.

IMPLICATIONS AND CONCLUSION

Before concluding, it may be of value to reflect on the implications of the Pleistocene extinctions. Four points to ponder are: 1) What was the effect on mammalian evolution? 2) What was the effect on human cultural evolution? 2) What
factors will be important in the preservation of the African megafauna? 4) Could the events of the late Pleistocene happen again, and if so, what would be the effects on the world's biota, including man?

The effects on mammalian evolution are readily apparent when one compares the megafauna of the past with that of the present. The ungulates and subungulates experienced a drastic reduction in their diversity, while the carnivores were reduced some or favored forms that were smaller or more omnivorous. The rodents, for the most part adaptable small forms, were relatively unaffected by the course of events, except for strengthening their position as the most successful group of mammals in terms of numbers of species, numbers of individuals, and variety of niches inhabited.

The effects on human history may be more important than most people realize. It was probably due to the disappearance of his favorite game that caused man to put down his spear and pick up a plow. The transition from man the hunter-gatherer to man the planter-herder was probably the single most significant event in the history of man. The first civilizations, made possible by agriculture and animal husbandry, arose after the worldwide late Pleistocene extinctions. Larger populations could now be maintained, and now it was possible to develop more fully man's capacities in art, music, philosophy, and science. Without this impetus for man to organize his food sources, man might still be in the stone age. There is no reason to believe we today are inherently more intelligent
or more refined than Paleolithic man. There are some philosophers who feel that these are really the Dark Ages of man, where individuality has perhaps forever become subordinated to the common good by making one's own small contribution to the workings of society. Paleolithic man may have led a more complete existence as a human being than anyone in modern society can strive to attain. Also, genetically, man as a species is probably declining since selective factors are no longer operating to insure that only the most adaptable are reproducing. Many of us could probably not survive under the rigors of Paleolithic life.

How can we apply the knowledge gained from studying the late Pleistocene extinctions to the preservation of the rich megafauna of Africa? First of all, we must be aware of the inherent instability of tropical populations. A severe enough ecological stress may result in rapid eradication of many forms. It is obvious that the stable climate of high equability has been primarily responsible for the richness and the persistence of the sub-Saharan fauna. If an unforeseen climatic cooling affects the African savannas, then man will probably be powerless to change the fate of the animals. However, this being an unlikely event for equatorial Africa, other factors are more relevant. An equally serious ecological stress would be habitat destruction by man. Every effort must be made to preserve the wilderness areas of Africa. This may soon become extremely unlikely, with the enormous population pressures now being exerted by uncontrolled birth rates and medical
advances lowering death rates in Africa. Also, with the critical population levels being higher than most people realize, killing for sport and commercial selling must cease. All things considered, the outlook is not good for the continued natural existence of the African megafauna. Zoos would most likely be their final holding ground before ultimate extinction.

Could the environmental events of the late Pleistocene happen again? Many geologists believe that the entire Holocene is merely another interglacial of the Pleistocene Ice Ages. A glacial period even more intense than the Wisconsin may be in store for man in the not too distant future. The global forces involved are probably beyond the control of even the technological man of the centuries to come. Cities in the northern areas would be reduced to rubble under the weight and movement of ice thousands of feet thick. Of course, this will not happen suddenly, but some major adjustments in where and how people live could come at some time in the future. Another glacial and post-glacial could result in the extinctions of many forms familiar to us today. Thus, by studying the causes of the late Pleistocene extinctions, man may gain a new perspective on the history of the world's animals, his own history, and the possible course of events in the future.
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