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INTRODUCTION

The excavations at Natural Trap Cave have stimulated our interest in the changes that took place some 12,000 to 8,000 years ago that mark the end of the Pleistocene. Of these changes, the extinction that occurred at the end of the Pleistocene in North and South America is near enough in time, and the animals involved are well enough known, to stimulate interest in the causal mechanism. With the possible exception of the extinction of dinosaurs at the end of the Cretaceous, none other has been the subject of more varied and extensive speculation. One of the most attractive hypotheses is the suggestion that the early peoples of North America were in some way responsible for the demise of many of their mammalian contemporaries. Samuel Aughey (1874) was one of the earliest proponents of this idea, suggesting that the Indians may have been responsible for the extermination of the mammoths in North America. Other workers have supported the same general causal mechanism, but P. S. Martin has presented during the last decade the most comprehensive and convincing arguments for this model of extinction which has won popular acceptance as the "Overkill Hypothesis." While many people accept the overkill hypothesis as the only reasonable explanation for the extinction at the end of the Pleistocene in the western hemisphere, the idea has not received general acclaim among vertebrate paleontologists, many of whom favor models featuring environmental change (Guilday, 1968; Lundelius, 1968; Slaughter, 1968, 1975; Schultz and Hillerud, 1976). The various environmental models are united by a common thread of climatic change. Acceptance of either the overkill model or a climatic model determines the types of research possible or worthwhile and the extent to which the end Pleistocene extinction can be used as a model for understanding older but similar extinctions.

The overkill model is based on certain assumptions. Its reasonability as an explanatory model depends upon the validity of these assumptions, and its testability is, in a large sense, based on tests of the assumptions themselves. Fundamentally the overkill model states that humans entering the New World from Asia as predators found prey not co-adapted to their predation. These new predators were thus able to expand their populations very rapidly while at the same time over-exploiting the native mammals. Assumptions which would support this model include: (1) man's appearance in the New World did not antedate the extinction by very much or predator and prey would have become co-adapted; (2) populations of humans were adequate to account for the extinction; (3) the extinction was very rapid; (4) the extinction proceeded from north to south; (5) the extinction was restricted to species hunted by humans and any predators dependent on these as prey species; (6) the extinction was unique in earth history as human colonization of North America was a unique event; (7) the extinct animals were not replaced by ecological equivalents; and (8) climatic change at the end of the Pleistocene was not unique.

MAN'S APPEARANCE IN THE NEW WORLD

P. S. Martin (1973) argues that the correspondence between the advent of man in the New World and the beginning of the extinction is good. However, in supporting this argument he rejects all dates for paleo-Indians in North America much older than 12,000 B.P. (Mosimann and Martin, 1975). The validity of doing so has recently been questioned by MacNeish (1976) who points out that there are over fifty radiocarbon dates on paleo-Indian sites in the New World dated earlier than 12,000 B.P. and some of these dates are in excess of 35,000 years B.P. Rouse (1976) also accepts dates in excess of 12,000 B.P. and suggests that the peopling of the Western Hemisphere must have taken place before 14,000 B.P. He concludes (Rouse, 1976:610) that "the rapid spread of the Clovis complex and the accompanying extinction of many

big-game species can no longer be ascribed to a sudden perfection of big-game hunting, as Martin (1973) and Mosimann and Martin (1975) have assumed."

Perhaps the greatest danger in the analysis of radiocarbon dates thought to date the apperance of man in the New World is the tendency to reject dates that do not fit a given model of human immigration, although they otherwise appear as reliable as dates which are accepted. If such a procedure is practiced one might still argue that no dates reliably reject the model, but one could scarcely claim that the remaining dates *support* it.

HUMAN POPULATION SIZE

Little real evidence is available for estimating the size of the human population prior to the extinction. The assumption that human predators were numerous enough to account for the extinction would seem to require abundant paleo-Indian sites and many associations of man with extinct fauna. This prediction has not been fulfilled. Most of the Pleistocene megafauna has never been found in association with human artifacts, and estimates of the Pleistocene human population in North America (MacNeish, 1976) would seem inadequate to account for megafaunal extinction. Mosimann and Martin (1975) deal with this problem by postulating a high rate of population growth coupled with the organization of the paleo-Indians into a densely populated front that moved south from Alaska and northern Canada. This front is postulated to have been so structured as to prevent the re-establishment of populations of large mammals behind it and is assumed to have taken only about 1,000 years to move from Edmonton, Alberta to Patagonia. The rapidity of the front's movement would account for the lack of association of extinct animals with human artifacts as only a very narrow band of sediments in any one area could record its passing (one could extrapolate that only about twenty years would be required for the front to pass through Nebraska). MacNeish (1976) regards as unlikely both the high speed of migration through varied ecological zones and P. S. Martin's estimates of population growth. We concur with MacNeish and also regard the organization of a hunting population into a coordinated front that would prevent large mammals from establishing populations behind it as equally unlikely. As far as we can determine, the existence of a front, the speed of its movement and its impenetrability to large mammals are not testable with present data and such assumptions are not strong enough to stand without evidence other than computer simulations.

SPEED OF THE EXTINCTION

No one really quarrels with the speed of the extinction (probably less than 3,000 years) nor with its scope (around 50 percent of the genera of large mammals). Martin (1973)

terminates the entire extinction at about 11,000 B.P. and rejects a large set of radiocarbon dates associated with extinct animals that are younger. While some of these dates may be inaccurate, many workers (Slaughter, 1968; Hester, 1968; Lundelius, 1968) accept dates as late as 8,000 B.P. for some of the Pleistocene megafauna. Alford (1974) points out that 50 percent of the dated mastodon sites are younger than the 11,000 years B.P. that Mosimann and Martin (1975) set as the latest "undeniable survival" of extinct animals other than bison.

DIRECTION OF MOVEMENT OF THE EXTINCTION

If we accept the existence of a front as suggested by Mosimann and Martin (1975), we would expect the latest dates for extinct mammals to occur in southern North America and South America. However, Alford (1974) has shown that the dates associated with remains of American mastodons are older in the south and younger in the north, the exact opposite of what the overkill model predicts.

TYPES OF ANIMALS INVOLVED

It is often stated that extinction swept through the large mammals at the end of the Pleistocene but had little or no effect on the small mammals (Martin, 1973). In reference to complete extinction of a species this is generally true, but this is an unnecessarily stringent view of the process of extinction. The lower the taxonomic rank, the more common extinctions tend to be. For instance, extinction of demes due to local environmental change is probably not uncommon today, and extinction of subspecies is certainly more common than the extinction of species. In other words, extinction is qualified both by the taxonomic level we utilize and by the geographic area we examine. The process of extinction proceeds through local populations in restricted areas, and species extinction occurs when the last of these local populations disappears. We see many examples of local extinction at the end of the Pleistocene. For instance, the northern subspecies of the jaguar, *Panthera onca augusta,* became extinct, while the southern subspecies survived.

At the family level, camels became extinct in North America but not in South America; at the generic level, bison became extinct in Siberia and Alaska but not in the remainder of North America and Europe; at the species level, musk oxen became extinct in Eurasia but not in North America. Exactly the same thing may be observed with the small mammals. *Dicrostonyx torquatus* and *Microtus xanthognathus* among other forms became extinct south of Canada, and the modern populations are probably derived from Alaska. Bog lemmings disappeared completely from Texas and Florida. Extinction of this sort occurred in small mammals at various geographic

levels simultaneously with the extinction of the megafauna, although no one has suggested any cause other than vegetational change due to climatic change. It would be strange indeed if environmental changes in local areas were able to exterminate these small animals with high reproductive rates and an ability to maintain populations in small refugia, while not severely affecting the populations of large mammals in the same area.

The selectiveness shown in the extinct species of large mammals is also hard to understand. For instance, why were tapirs and llamas such easy and preferred prey in North America but permitted to survive in South America? Or why did moose and bison survive and in fact prosper at the same time that every last one of the camels, horses, and stag-moose (Cervalces) were sought out and destroyed?

THE UNIQUENESS OF THE EXTINCTION

The strength of the overkill hypothesis is largely a function of how unique we think the extinction was. If such a rapid and widespread extinction cannot be duplicated elsewhere then we must seek a unique explanation, and the coming of skilled hunters to North America would be a likely possibility. If, on the other hand, the extinction is one of a group of extinctions, then a more general model is to be preferred.

How similar are the changes in faunal composition that took place in the Western Hemisphere to those that occurred elsewhere? We can get some estimation by looking at extinction (both local and general) in Europe. Of about 82 species of carnivores, proboscidians, perrisodactyls, and artiodactyls known from the Late Pleistocene of North America, some 48 percent became extinct. According to Kurten (1968) there are 56 species belonging to these orders in the Late Pleistocene of Europe and 36 percent became extinct. Most of these forms had surviving populations elsewhere, but *Mammuthus primigenius* (woolly mammoth), *Coelodonta antiquitatis* (woolly rhinoceros), *Megaloceros giganteus* (giant elk), *Ursus spelaeus* (cave bear) disappeared completely around 10,000 B.P. (Reed, 1970). Is it coincidence that the latest dates for mammoths are around 10,000 B.P. in North America and around 9,000 B.P. in Eurasia (Vereshchagin, 1968)? The most striking difference between the European and North American extinction is, in fact, not the somewhat greater diversity of species that became extinct in North America, but that the distributions of so many European animals included areas outside of Europe where populations survived. It has been generally accepted that the changes of ranges of mammals in Europe due to local extinction were caused by vegetational changes (Kowalski, 1968).

Perhaps of greater significance is the fact that extinctions of the same magnitude as occurred in the Pleistocene

are not unique but have occurred in North America a number of times during the Tertiary (Martin and Neuner, unpublished). Because of their greater age, it is not possible to date these earlier extinctions as accurately as has been done for the Pleistocene, yet they too appear to have occurred over relatively short periods. The most recent Tertiary extinction similar to the extinction at the end Pleistocene took place at the end of the Ogallala Pliocene. Some 78 genera of carnivora, proboscidea, artiodactyla, and perrisodactyla are known from faunas of this age (Kimballian and Hemphillian in part). The latest Ogallala rocks containing these typical fossils appear to date something less than 7 m.y. (Boellstorff, 1976). About 70 percent of these genera became extinct prior to the appearance of oldest Blancan faunas, some of which may date as early as 6.2-4.4 m.y. (Smith, 1975).

While the resolution of the interval involved is not comparable to the duration of 3,000 years or less indicated by the dating of the Pleistocene extinction, it is still short in terms of both geologic time and the kinds of absolute dating used.

By comparison, about 64 genera in these four orders are known from the Wisconsinan (if the subgenera of *Equus* are given generic rank), and of these 59 percent became extinct. Even taking into account possible errors in recognition of either extinctions or taxa, it is hard to see how the terminal Pleistocene extinction can have been any more severe than that at the end of the Ogallala. The relative contribution of these orders to the extinction was similar in both cases, and of the adaptive types that became extinct (Fig. 1), analogous animals (camels, horses, proboscidea, and saber-toothed cats) were included in both cases.

ECOLOGICAL

Martin (1970) has argued that the depauperate nature of the present North American large mammal fauna supports the overkill hypothesis. However, this is only true if the alternative cause of extinction is competition with invading forms. A climatic model results in a depauperate fauna just as does the overkill model, and the time since the extinction has been too short for the immigration or evolution of replacements in either case. Lack of replacement is not unusual for Tertiary extinctions. In North America at the end of the Ogallala three genera of rhinoceroses became extinct without ecological replacement, and cats became extinct at the end of the Arikarrean without replacement in the following Hemingfordian.

UNIQUENESS OF PRESENT CLIMATE

It has been argued that the climate that exists at the present is that of a typical interglacial (Mossiman and Martin, 1975). However, little evidence has been presented to support this contention (Slaughter, 1975). There is evidence to support
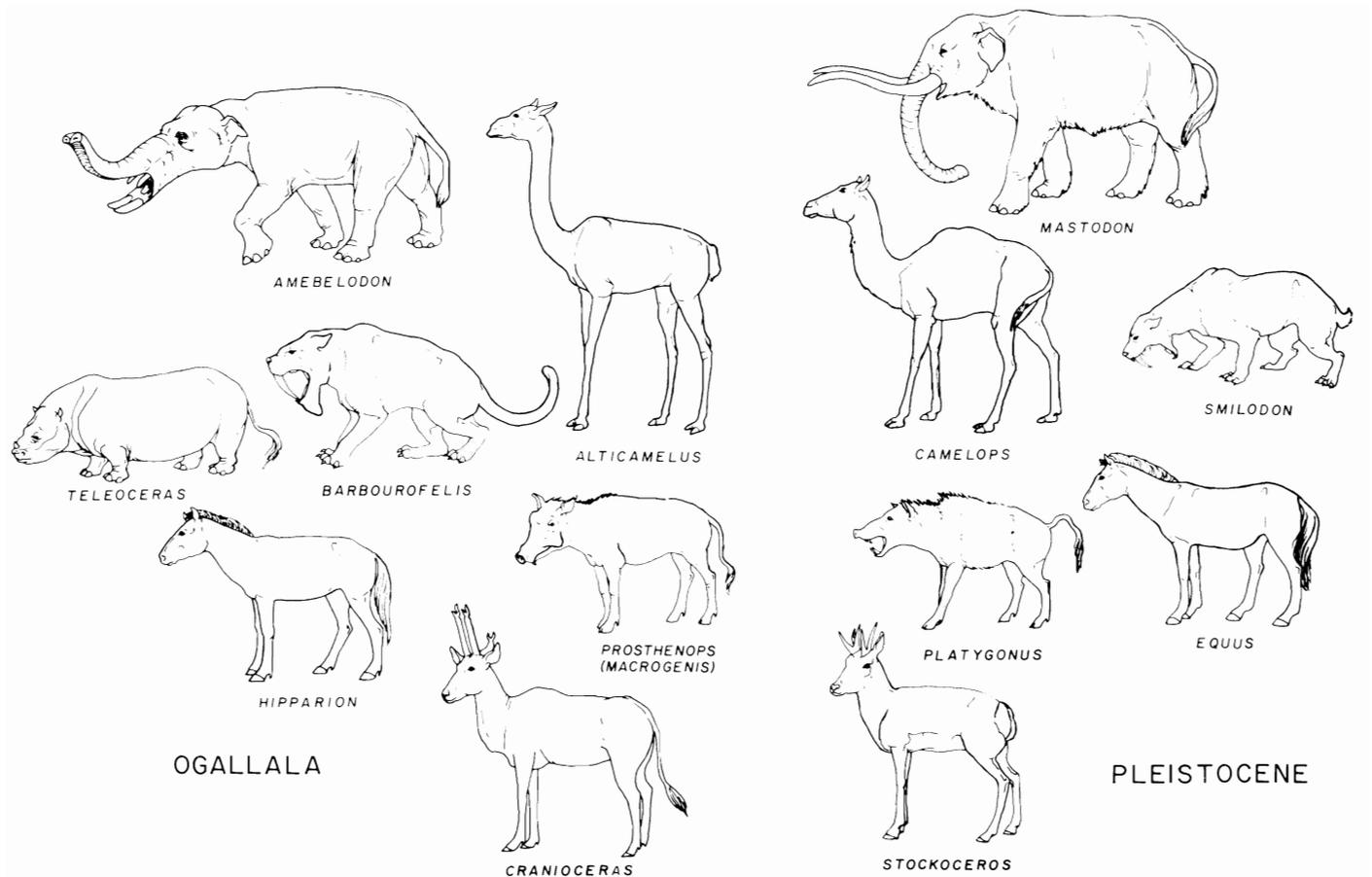
Figure 1. Representative animals which became extinct at the end of the Ogallala and at the end of the Pleistocene in North America.

the idea that the climate became more seasonal throughout the Pleistocene finally culminating in the severe biotic turnover at its end. This interpretation is supported by the slow general loss of diversity in molluscan faunas from the Illinoian on the Central Great Plains with a final depauperization of the fauna sometime after 10,500 years B.P. (Miller, 1975), the notable increase in eolian sediments which may indicate increasing aridity during the Pleistocene (Schultz, et al., 1972), and the absence of any sizable Pleistocene small mammal fauna where there are no extant forms beyond their present ranges (Slaughter, 1975). In fact, the difference between interglacial and glacial climates may be generally overrated. Few faunas have been confidently assigned to interglacial periods and even those generally resemble glacial faunas except for the addition of a few southern taxa, a condition that also characterized glacial faunas in the Wisconsinan. There is also no substantive evidence that extensive treeless prairies or deserts existed at any time in the North American Pleistocene. In other words, the amount of ice fluctuated as did the boundaries of the biomes, but there is no convincing evidence for any other episode that even approaches the biotic reorganization taking place from 11,000 to 8,000 years ago.

EVALUATION OF THE OVERKILL MODEL

We have shown that extinction similar in both number and kind occurred elsewhere in the world at the end of the Pleistocene as well as in the Western Hemisphere. We have also demonstrated the existence of similar extinctions in the Tertiary of North America when man could not have been a factor. The existence of environmental causes adequate to cause similar extinctions suggests that we should accept the overkill model only if there is strong supporting evidence. Much of Mosimann and Martin's (1975) paper is an explanation of why we should not expect to find such compelling evidence and why Mosimann and Martin (1975) state, "In our model, overkill is almost invisible."

EXTINCTION THROUGH CLIMATIC CHANGE

Both the Ogallala Pliocene and the Late Pleistocene contained a much wider diversity of large mammals than does the present North American fauna. The depauperate nature of the modern large mammal fauna is well illustrated by the many

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close relatives of modern genera which have become extinct since the Late Pleistocene. For instance, during the Late Pleistocene there were six genera of antilocaprids: *Antilocapra, Hexameryx, Tetrameryx, Capromeryx, Hayoceros,* and *Stockoceros;* four genera of musk oxen: *Ovibos, Symbos, Preptoceros,* and *Bootherium;* and six species of large cats: *Puma concolor, Panthera onca, P. atrox, "Felis" trumani, Dinobastis serus,* and *Smilodon californicus.* Of these only *Antilocapra* is more numerous and has a wider range than it once had. *Puma concolor* is still abundant and ranges throughout most of North and South America. The range of *Panthera onca* was much reduced by the disappearance of the large North American subspecies *P. onca augusta,* and *Ovibos* became extinct in Eurasia and restricted in North America to the Arctic tundra.

Almost one-half of North America was covered by continental ice, so about twice the diversity of large mammals lived in about one-half the area occupied by large mammals today. Coupled with this is the fact that a higher percentage of the plant biomass was tied up in conifers and thus unavailable to most of the large ungulates.

Coexistence of so many related taxa in the Late Pleistocene suggests a close partitioning of the environment. We might expect that the "niche breadth" occupied by these animals was somewhat smaller than the average for the modern North American fauna. This interpretation is partially supported by the close correlation between their ranges and the vegetational types. Some Pleistocene floral assemblages also differed from those of the present and sometimes contained combinations of taxa which presently do not occur together over any extensive area. According to Maxwell and Davis (1972), "The full-glacial forest communities of eastern North America were different from modern boreal forest, especially the boreal forest of eastern Canada, where fir is relatively abundant and jack pine is rare. Before these recent data came to light, biogeographers visualized a southward displacement of existing vegetation formations (Martin, 1958; Dillon, 1956). But this simple scheme is insufficient to explain the full glacial distribution of forest trees. Full-glacial communities were different both in species composition and species abundance from any modern vegetation. This difference has a further implication: the modern Canadian boreal forest is a new formation a recent development." Hare (1976) states that "scattered boreal elements are often identified from fossil assemblages in the deciduous forest zone, implying that it differed significantly from the modern forest." The areas presently occupied by deserts and grasslands were occupied by open woodlands dominated by montane conifers (Wells, 1966; Wells and Berger, 1967; Van Devender, 1977), and associations of taxa in those areas which do not occur together today have been reported (Van Devender and Mead, 1976; Van Devender, 1976). Apparently much of unglaciated Alaska also differed, most of it being covered with Steppe-Tundra, a type of boreal grassland that does not presently occur in

North America (Guthrie, 1968).

Recently we (Martin, Neuner and Wells, unpublished) have mapped the distributions of four faunal complexes in the North American Late Pleistocene (Fig. 2). In the west we have the *Camelops-Navahoceros* Faunal Provience based on the distribution of *Camelops, Capromerx, Navahoceros, Nothrotheriops, Arctodus simus* and *Panthera atrox.* In the southeast there is the *Chlamytherium*-glyptodont Faunal Province based on Chamytherium, glyptodonts, capybaras and the spectacled bear, *Tremarctos.* In the northeast occurred the *Symbos-Cervalces* Faunal Province with *Castoroides ohioensis, Cervacles, Symbos* and *Sangamona.* In the periglacial tundra is the *Ovibos* Faunal Province based on the distribution of *Ovibos, Dicrostonyx* and *Rangifer.*

These distributions of fossil mammals closely corresponded to the Pleistocene floral distributions mapped by Wells (unpublished) (Fig. 2). *Ovibos,* the modern tundra musk ox, was confined to the periglacial tundra, while its relative, *Symbos,* occurred in the conifer-hardwood forest and another relative, *Euceratherium,* occurred mostly in the western montane conifer woodlands. *Panthera atrox* was also found in these pine-park lands, while the jaguar, *Panthera onca,* was generally limited to the southern part of deciduous forest. Because the extinct animals are restricted to these particular environments, it seems reasonable to assume that these are the habitats to which they were adapted.

The combination of these factors suggests that the recent biomass of large mammals in North America just prior to European settlement might have equaled or exceeded the Pleistocene large mammal biomass at any one time and that most Pleistocene taxa were present in relatively small populations. Clearly this inerpretation—smaller populations with more restricted ranges—facilitates any model of extinction.

Intuitively we would expect widely distributed and abundant organisms to have a better chance of escaping extinction than those which are rare and of limited distribution. This was not the case at the end of the Pleistocene, or, for that matter, with the extinction at the end of the Ogallala Pliocene. The most widely distributed and abundant large mammals of the Pleistocene in North America became extinct. The survivors of the Pleistocene extinction are often rare as fossils.

For example, the North American Pleistocene lacks records of the javelina, *Tayassu,* while *Platygonus* and *Mylohyus,* extinct peccaries, are both numerous and widely distributed. *Capromeryx* is relatively common and has been found in some twelve widely scattered localities, while *Antilocapra* is known from only a few localities prior to 10,000 years B.P. Short-horned bison are extremely rare prior to 12,000 years B.P., and the moose, *Alces,* is virtually unknown in the Pleistocene record of North America. On the other
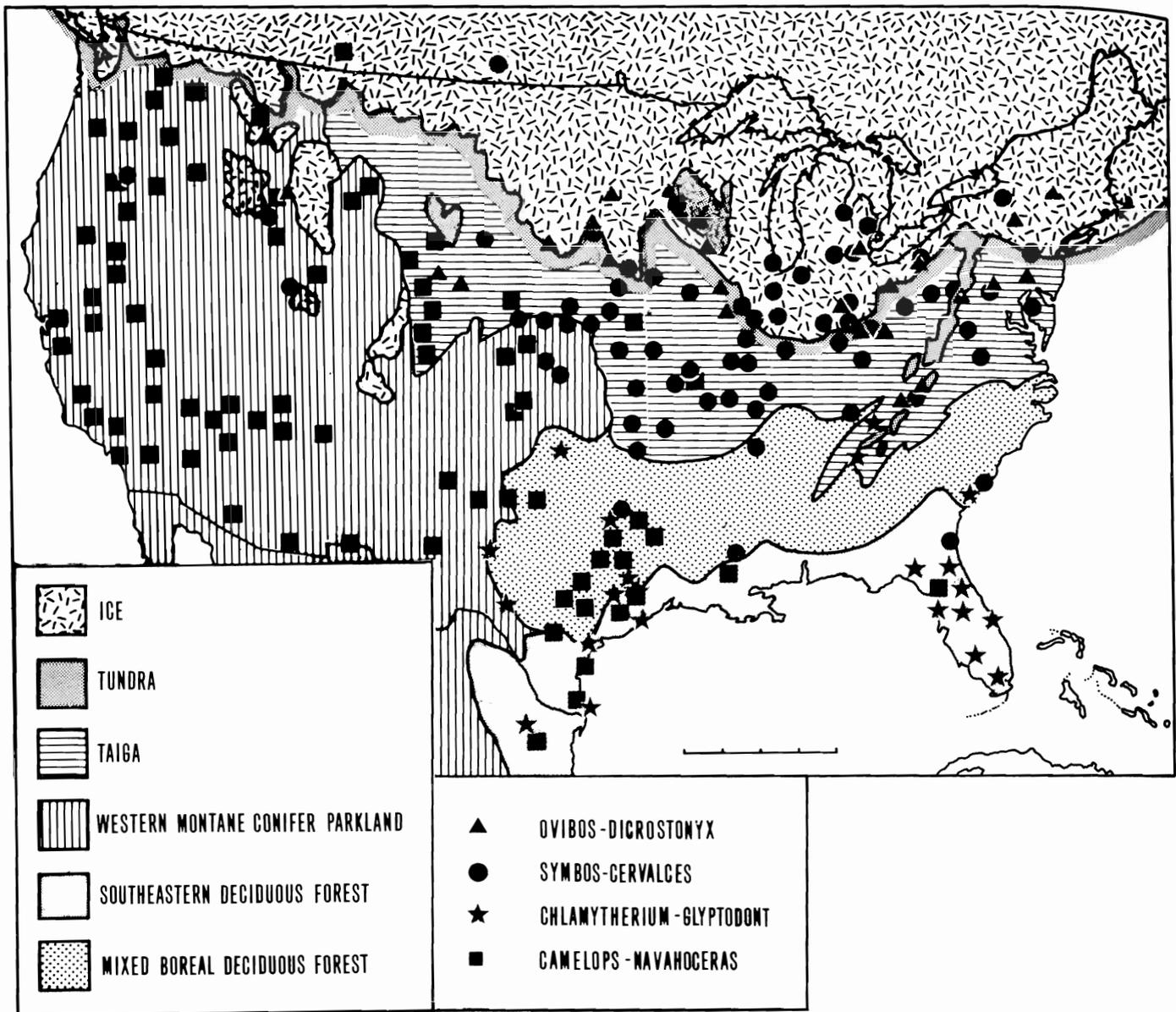
Figure 2. Distributional map of the full-glacial Wisconsinan flora (modified from Wells, unpublished) and Wisconsinan faunal complexes.

hand, extinct forms such as horses, camels, and proboscideans are all common and widespread during the Late Pleistocene.

We thus assume that the animals that became extinct occupied the most dominant and widespread habitats while the survivors often occupied habitats that were rare and restricted in distribution. An interesting aspect of this is that many of the large mammal survivors occupied essentially the same range in the Pleistocene as they occupy today suggesting that their particular niches remained after the niche of other animals were destroyed. On the other hand, their rarity in the more widely distributed biotas indicates that

these Pleistocene communities were less suited for them. The great heterogeneity of Pleistocene communities is expressed not only by the diversity of extinct mammals, but also in combinations of animals that cannot be found living together today. Some of these forms are presently allopatric by hundreds of miles. Examples of these combinations can be found in Pleistocene mollusks (Taylor, 1965), amphibians and reptiles (Holman, 1976), and mammals (Graham and Semken, 1976; Semken, 1974; Guilday, 1971; and Dalquest, 1965). Their Pleistocene sympatry has been interpreted as indicating a less seasonal climate with relatively milder winters, cooler summers, and more rainfall than at present. The ranges of

organisms are often limited by seasonal extremes rather than the yearly averages of rainfall, temperatures, etc. Reduction of these seasonal extremes permits the ranges of more organisms to overlap creating a more heterogeneous community structure which may support a greater taxonomic diversity. While cold temperature extremes may have been severe near the continental ice as evidenced by frozen ground structures (Wayne, 1967) and tundra animals (Fig. 2), there is no evidence that the tundra extended very far south of the ice margin (Wayne, 1967). In fact, Pleistocene distributions of animals regarded as having southernly distributions (tapirs, jaguars, giant armadillo, cotton rats, and rice rats) ranged at least as far north in the Pleistocene as they do today. This is emphasized by the discovery of the tropical-subtropical tortoise, *Geochelone*, in Texas and Oklahoma in deposits of glacial age (Slaughter, 1966; 1975). These areas presently experience seasons that are too cold for such tortoises. Van Devender (1976) reported a similar northern extension of the range of *Gopherus* in New Mexico during glacial times. On the other hand, animals having northerly distributions *(Synaptomys, Clethrionomys, and Sorex cinereus)* had the southern boundaries of their ranges in such areas as Georgia, Florida, and Texas where they overlapped the ranges of animals with southern distributions. In fact we can generally recognize three components to any Pleistocene fauna at the time of the megafaunal extinctions: (1) animals that became extinct throughout North America, (2) animals that became extinct locally but colonized deglaciated areas to the north, and (3) animals that make up the modern fauna of the area today. There is little evidence to support the expansion of warm-climate adapted animals farther north at the close of the Pleistocene. The northern surviving animals already occupied northern ranges, and their southern populations became extinct. An excellent example of this is the yellow-checked vole, *Microtus xanthognathus*, which had a large Pleistocene range south of the ice (Guilday, 1971), but whose living survivors in Alaska and Canada must be derived from an Alaskan population, while the entire southern population became extinct.

We may then characterize the change that took place at the end of the Pleistocene as being the loss of boreal and montane components in the south, along with the development of newly deglaciated areas which were invaded by the northern component of the fauna.

Proximate "causes" of extinction that are embraced by a climatic model have been suggested for various species. Dreimanis (1968), for instance, proposed that the extinction of the American mastodon was due to the disappearance of their spruce woodland and forest habitat with increasing dryness of the climate 10,000 to 11,000 years ago. He suggested that mastodons did not migrate from relict spruce stands in the Great Lakes region to more northerly spruce forests because these areas were "probably separated by a rapidly expanding belt of pine and hardwood forests over the better-drained morainic, kame, and dunes areas." Alford

(1974) points out that mastodons became extinct in a generally west to east and south to north pattern that is consistent with Dreimanis's (1968) proposal. It should be noted, however, that mastodons were probably already extinct before continental ice had melted off the area presently occupied by spruce forest.

Other "causes" have been generalized to explain most or all of the post-Pleistocene extinction rather than that of a single species. These "causes" too are embraced by a climatic model. Slaughter (1975) hypothesized that "out-of-step" mating might have been a prime cause of past extinctions. He argued that large mammals with long gestation periods synchronize the birth of young with the abundance of food available to the species in the spring. A slight change in the length of the winter season for just a few years would seriously reduce the survival chances of the newborn, and if this climatic change lasted long enough, the species could become extinct, even though the adult population was not adversely affected. In more southerly regions, a few degrees lowering of winter temperatures could destroy populations not adapted to such extremes. Similarly, raising summer temperatures could reduce fertility or increase mortality in species which were not adapted to higher temperatures.

Wilson (1973) proposed yet another climatic cause for the terminal Pleistocene extinction. He pointed out that C_4 plants (those which use a four carbon atom product as the start of the photosynthetic pathway) are a less valuable food source than C_3 plants (which use a three carbon atom product). The end of the Pleistocene brought a warmer, dryer summer climate to North America and an increase in the number of C_4 plants which are more efficient in hot, dry areas than are C_3 plants. Mulkern, et al. (1962) and Barnes (1955) demonstrated that an exclusive diet of C_4 plants caused starvation in organisms (grasshoppers) that had co-evolved with C_3 plants, while Tauber, et al. (1945) demonstrated that lower reproductive rates also resulted from feeding on C_4 plants. Wilson suggested that changes in the extremes of winter and summer temperatures, with longer, colder winters reducing winter food supplies and hotter, dryer summers reducing the quality of summer forage through the expansion in C_4 plants, led to the post-Pleistocene extinction. Drought is a related cause often invoked for the terminal Pleistocene extinction, most recently promoted by Schultz and Hillerud (1976).

It is the argument presented in part by Axelrod (1967) that we find most compatible with our data as a general explanation of the nature of the climatic change reflected by vegetational change. He showed that decreased seasonality would result in a more complex biota. These biotas formed communities which do not exist today although the species of plants that composed them do. In place of the deciduous woodlands and taiga, there was a hardwood forest; in place of extensive prairies, pine-parklands; and instead of tundra, a

steppe-tundra. An examination of the pollen and wood-rat records of glacial times shows that there were no extensive grasslands and that the tundra was restricted to a narrow band at the ice margin. Conifers were distributed throughout North America with spruce often present; in most cases there was probably not a closed forest, but instead open woodlands which would provide for a greater variety of habitats.

We now conclude that the world-wide climate during the Pleistocene was different than it is is today and that the plant communities were also significantly different in North America. The distribution of extinct mammals was very closely correlated with these plant communities. According to Hare (1976), "It seems likely that a nonglacial mode of climate was established quite rapidly about 11,000 B.P., and that since that time the circulation of the Northern Hemisphere has had a basically modern look." At this time the plant communities in North America change precipitously and begin to take on a modern aspect. In fact, the vegetational change was much faster than the retreat of the continental ice, thus trapping many boreal forms in the south of it. The collapse of the southern boreal flora may have been so rapid that its remnants were restricted to high altitude refugia if any existed at all. This was also the case with the western montane conifer parklands. Mountains might serve as refugia for forms that would otherwise become extinct in the area, as the last remnants of the Pleistocene southern conifer forests would occur on their slopes. Such areas might be adequate refugia for small animals, but would be too small for the large mammals. However, we would expect that the latest survivals of many forms to be in montane sites and that "primitive" species in species complexes would tend to be montane forms. In the southeast the most notable change except for the loss of some boreal forms was the loss of the truly tropical portion of the fauna including *Geochelone*, capybaras, tapirs, jaguars and giant armadillos. It is hard to conclude anything other than a loss of "tropicalness" in this area with the close of the Pleistocene.

The climatic model is in fact a unifying principle for many diverse causes of extinction. A change of climate on a continental or world-wide scale will affect almost all aspects of the environment, favoring some elements and removing others. One of the difficulties with extinction models has been the search for a single cause when, in fact, there were many causes. The decline in diversity of the habitat may have been an underlying cause, but on a species-by-species basis the "cause" may have been loss of a seasonal source of food, change in the time favorable for having offspring, loss of suitable prey, or loss of cover or of suitable nesting sites. While a species-by-species examination of these causes might be of some interest, the results are apt to be ambiguous. The critical point is that animals are so closely attuned to their habitat that whatever the proximate causes of individual extinctions, massive climatic and vegetational change of the sort that occurred between 12,000 and 10,000 B.P. would almost

certainly result in commensurate extinction of the most sensitive portion of the biota (the large mammals). However, we would not expect such an extinction to be all-inclusive as some habitats are favored by climatic change and we would expect their occupants to become more numerous and widely distributed as the other habitats decline. We can see this in the huge numbers of bison occurring both in and out of kill sites from 11,000 B.P. to the near-present; whereas, before this time they were much rarer than horses. In terms of the overkill model this expansion of bison seems difficult to explain. Why did the relatively large population of Indians proposed by its proponents not exterminate the bison or at least severely decrease its numbers (the exact opposite of what the fossil record shows) after the extinctions of the other large mammals left it almost their only prey?

SUMMARY

All of the assumptions upon which the "overkill hypothesis" is based are strongly contested or refuted. In its place we substitute a general model of rapid climatic change which may be applied to extinction elsewhere in the world and at other times. This model incorporates many of the existing hypotheses for proximate causes of extinction.

P. S. Martin has stressed the coincidence of the Pleistocene extinction with the expansion of man in the New World. There is an equal and perhaps more important coincidence with climatic change at this time. The Pleistocene shows a trend toward increasing seasonality which appears to culminate between 10,000 and 8,000 years B.P. This same period included the final extinction of most Pleistocene large mammals.

We believe that the low seasonality of Pleistocene environments permitted the establishment of very complex communities that lack modern analogues. These communities were composed in part of animals and plants extant today but presently allopatric and by animals which are now extinct. The modern highly seasonal environment is thought by us to be unique for the Pleistocene and its establishment along with the modern pattern of floral distributions is the underlying cause of the end-Pleistocene extinction. This mechanism would be world-wide in scope and applicable to Tertiary extinctions.

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