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Late Pleistocene Mammalian Extinctions in North America: Taxonomy, Chronology, and Explanations

Donald K. Grayson[1,2]

Toward the end of the Pleistocene, North America lost some 35 genera of mammals. It has long been assumed that all or virtually all of the extinctions occurred between 12,000 and 10,000 years ago, but detailed analyses of the radiocarbon chronology provide little support for this assumption, which seems to have been widely accepted because of the kinds of explanations felt most likely to account for the extinctions in the first place. Approaches that attribute the losses to human predation depend almost entirely on the assumed synchroneity between the extinctions and the onset of large mammal hunting by North American peoples. The fact that only two of the extinct genera have been found in a convincing kill context presents an overwhelming problem for this approach. Climatic models, on the other hand, are becoming increasingly precise and account for a wide variety of apparently synchronous biogeographic events. While a role for human activities in the extinction of some taxa is fully possible, there can be little doubt that the underlying cause of the extinctions lies in massive climatic change.

KEY WORDS: extinctions; North American prehistory; Pleistocene; vertebrate paleontology.

INTRODUCTION

Toward the end of the Pleistocene, some 35 genera of mammals became extinct in North America (northern Mexico, the United States, and Canada),

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[1] Department of Anthropology and Quaternary Research Center, University of Washington, Seattle, Washington 98195.

[2] To whom correspondence should be addressed at Department of Anthropology, University of Washington, Seattle, Washington 98195.

either in the sense that they ceased to exist anywhere on earth (29 genera) or in the sense that they ceased to exist here, while living on elsewhere (6 genera). The cause or causes of these extinctions have been controversial for well over a century (Grayson, 1984c), but debate became particularly heated in 1967 with the publication of a powerful argument by Paul S. Martin that attributed the losses to human predation. Since that time, the literature on North American Pleistocene extinctions has become voluminous, yet there exists no single source that presents a synthesis of the mammals involved, of our understanding of the chronology of extinction, and of the nature and status of current explanations of the extinctions. This paper is offered to fill that gap. Avian extinctions also occurred; these are not treated here (see Grayson, 1977; Steadman and Martin, 1984).

THE EXTINCT LATE PLEISTOCENE MAMMALS OF NORTH AMERICA

The extinct late Pleistocene mammals of North America belong to 35 genera, distributed across 21 families and seven orders (Table I). Although a diverse lot, most were either herbivores or carnivores possibly dependent on them, and many were large. To increase the utility of my synopsis, I have included a number of mammals that entered the extinctions debate between the 1960s and the 1980s but that no longer play a role, either because they survived the Pleistocene or because of changed assessments of their chronologic or taxonomic status; these do not appear in Table I. Throughout, I focus on species of mammals belonging to genera that became extinct, although I also discuss some well-defined extinct species that belong to genera that still occur in North America.

I follow Richmond and Fullerton (1986) in placing the boundary between the middle and the late Pleistocene at the end of the Illinoian (penultimate) glaciation in North America. As such, the late Pleistocene includes the Sangamon (last) interglaciation and the Wisconsin (last) glaciation (ca. 132,000–10,000 years B.P.). Although the chronology of North American Pleistocene mammal extinction is, as I discuss, poorly known (and not all of the distributional records mentioned below are necessarily late Pleistocene), all of the taxa listed in Table I appear to have survived well into Wisconsin glacial times.

Chiroptera (Bats)

The extinct vampire bat *Desmodus stocki* was first reported in 1958 from San Josecito Cave, Nuevo Leon, northeastern Mexico; North American records are now also known from California, the Southwest, and Florida (Jones, 1958;

Table I. Extinct Late Pleistocene North American Mammalian Genera

Order	Family	Genus	Common name
Xenarthra	Dasypodidae	*Pampatherium*	Southern pampathere
		Holmesina	Northern pampathere
	Glyptodontidae	*Glyptotherium*	Simpson's glyptodont
	Megalonychidae	*Megalonyx*	Jefferson's ground sloth
	Megatheriidae	*Eremotherium*	Rusconi's ground sloth
		Nothrotheriops	Shasta ground sloth
	Mylodontidae	*Glossotherium*	Harlan's ground sloth
Carnivora	Mustelidae	*Brachyprotoma*	Short-faced skunk
	Canidae	*Cuon*[a]	Dhole
	Ursidae	*Tremarctos*[a]	Florida cave bear
		Arctodus	Giant short-faced bear
	Felidae	*Smilodon*	Sabertooth
		Homotherium	Scimitar cat
		Miracinonyx	American cheetah
Rodentia	Castoridae	*Castoroides*	Giant beaver
	Hydrochoeridae	*Hydrochoerus*[a]	Holmes's capybara
		Neochoerus	Pinckney's capybara
Lagomorpha	Leporidae	*Aztlanolagus*	Aztlan rabbit
Perissodactyla	Equidae	*Equus*[a]	Horses
	Tapiridae	*Tapirus*[a]	Tapirs
Artiodactyla	Tayassuidae	*Mylohyus*	Long-nosed peccary
		Platygonus	Flat-headed peccary
	Camelidae	*Camelops*	Yesterday's camel
		Hemiauchenia	Large-headed llama
		Palaeolama	Stout-legged llama
	Cervidae	*Navahoceros*	Mountain deer
		Cervalces	Elk-moose
	Antilocapridae	*Capromeryx*	Diminutive pronghorn
		Tetrameryx	Shuler's pronghorn
		Stockoceros	Pronghorns
	Bovidae	*Saiga*[a]	Saiga
		Euceratherium	Shrub ox
		Bootherium	Harlan's musk ox
Proboscidea	Mammutidae	*Mammut*	American mastodon
	Elephantidae	*Mammuthus*	Mammoths

[a] Genus survives outside of North America.

Gut, 1959; Ray *et al.*, 1988). Including this bat on the list of North American late Pleistocene extinctions is marginal on two scores: *Desmodus* is today found well into northern Mexico, and records for *D. stocki* from San Miguel Island, California, appear no older than middle Holocene. However, a large vampire from New Trout Cave, West Virginia, may represent a second extinct species, *Desmodus draculae*, and is late Pleistocene (>29,400 years B.P.) in age (Ray *et al.*, 1988).

Xenarthra (Sloths, Vermilinguas, and Armadillos)

Seven genera of now-extinct xenarthrans, ranging from giant armadillos to enormous ground sloths, marked the North American late Pleistocene mammalian fauna, especially across the southern United States. The southern pampathere *Pampatherium* has been securely reported only from a single site in Texas, but the northern pampathere *Holmesina septentrionalis* ranged from Florida to Texas and Mexico and as far north as Kansas. Like extant armadillos, pampatheres were covered with a flexible armor of bony scutes, but *H. septentrionalis* was some 2 m long and 1 m high (James, 1957; Kurtén and Anderson, 1980; Edmund, 1985a, b).

The North American glyptodont *Glyptotherium floridanus* is known primarily from near-coastal localities in Texas, Florida, and South Carolina and south into Mexico. Enclosed in a turtle-like carapace with armored tail and skull, this remarkable animal had massive limbs and a pelvic girdle that was fused to its carapace and weighed about a ton. Some 3 m long and 1.5 m tall, these cumbersome beasts appear to have lived along lakes, streams, and marshes and may have been semiaquatic (Gillette and Ray, 1981).

Missing from extinction tallies that focus only on losses at the generic level is the beautiful armadillo, *Dasypus bellus*. Known from a wide variety of sites ranging from eastern New Mexico to Iowa and Florida, this animal was extremely similar to its modern counterpart, the nine-banded armadillo *Dasypus novemcinctus*, but was two to three times larger (Simpson, 1929; Slaughter, 1961; Klippel and Parmalee, 1984).

Modern sloths are arboreal; widely distributed in the forests of Central and South America, fat ones may weigh 10 kg. During the late Pleistocene, four genera of ground-dwelling sloths occupied various parts of North America, the smallest of which (*Megalonyx jeffersonii*) was the size of a black bear (*Ursus americanus*) and is known from Florida to Alaska. The largest of the North American ground sloths, *Eremotherium rusconii*, was roughly the size, but not the shape, of a mammoth and is known only from the southeast and Texas. *Glossotherium harlani*, characterized in part by the presence of pebble-like bones ("dermal ossicles") embedded in its skin, was larger than *Megalonyx* and is the most abundant ground sloth in the asphalt deposits of Rancho la Brea. The best known of the extinct North American sloths, however, is the Shasta ground sloth, *Nothrotheriops shastense*, known from northern Mexico, the western United States, and Alberta. A number of dry caves in the American southwest contain the well-preserved dung of this bear-sized sloth. Analyses of that dung have shown that the Shasta ground sloth ate plants still common in the area, suggesting to some that the diet may live on without the animal, though others disagree [(Stock, 1925, 1956; Martin, 1975; Hansen, 1978; Kurtén and Anderson, 1980; Engelmann, 1985; Webb, 1985; Naples, 1987, 1989); for the argument that the plants live on but the diet does not, see Guthrie (1984b)].

Carnivora (Carnivores)

The short-faced skunk *Brachyprotoma obtusata* is known from a series of sites in the eastern United States. A second species, *B. brevimala*, has been defined on the basis of material from western Utah, and the genus has also been reported from the Yukon. *Brachyprotoma* seems to have occupied boreal habitats and to have been more carnivorous than any living skunk (Heaton, 1985). A second mustelid, the noble marten, *Martes nobilis*, was once thought to have become extinct at the end of the Pleistocene, but a series of records now suggests that it survived well into the Holocene (Anderson, 1970; Kurtén and Anderson, 1980; Grayson, 1984d, 1987c; Mead and Mead, 1989b). The genus *Martes* is represented in North America by martens (*M. americana*) and fishers (*M. pennanti*).

The dhole, *Cuon alpinus*, is currently found through much of Asia. Weighing about 15 kg, this canid is highly carnivorous and appears to subsist primarily on large mammals (Cohen, 1978; Nowak and Paradiso, 1983). In North America, it is known from late Pleistocene contexts at San Josecito Cave, northern Mexico, and from Alaska and the Yukon (Harington, 1970; Kurtén and Anderson, 1980). One presumes that it also occurred in intervening areas, but there are no records to show it. On the other hand, the massive dire wolf (*Canis dirus*) appears to have been heavily dependent on scavenging and was widespread in North America south of glacial ice (Nowak, 1979; Van Valkenburg and Ruff, 1987).

The North American spectacled bear, *Tremarctos floridanus*, seems to have been almost entirely vegetarian. Most abundant in the southeastern United States during the late Pleistocene, records are also available from as far west as New Mexico and south into northern Mexico. Today, the less powerfully built and smaller spectacled bear *T. ornatus* occupies the mountainous areas of northwestern South America. The giant short-faced bear, *Arctodus simus*, in contrast, is known from northern Mexico, much of the contiguous United States, Saskatchewan, the Yukon, and Alaska. Long-limbed and huge, some 30% larger than the North American grizzly bear (*Ursus arctos*), the short-faced bear was at one time thought to have been the most powerful predator on the late Pleistocene North American landscape, perhaps feeding on such animals as ground sloths, horses, and bison. However, recent analyses of relatively complete *Arctodus* skeletal material from eastern Nevada suggest instead that the large size of this bear is to be accounted for by the fact that it was largely omnivorous or herbivorous (Kurtén, 1966, 1967; Kurtén and Anderson, 1980; Nowak and Paradiso, 1983; Emslie and Czaplewski, 1985).

Known from Alberta in the northwest to Florida in the southeast, the lion-sized sabertooth cat *Smilodon fatalis* possessed upper canines that were laterally compressed and serrated on anterior and posterior edges, forming efficient cutting tools some 15 cm long. Detailed studies of the morphology of *Smilodon* canines and molars strongly suggest that little contact was made between those teeth and the bones of *Smilodon* prey. This, in turn, suggests that a good deal of meat was left on the carcasses of sabertooth victims, providing opportunities for such scavengers as dire wolves. Indeed, sabertooth feeding behavior may account for the great similarity in the distribution of *S. fatalis* (Kurtén and Anderson, 1980, Fig. 11.17) and *C. dirus* (Nowak, 1979, Fig. 54) south of glacial ice in North America and for the fact that sites that contain the remains of sabertooth cats frequently contain the remains of dire wolves as well. For instance, of the sample of 16 sites listed by Lundelius *et al.* (1983) as having provided the remains of *S. fatalis*, 15 also provided the remains of *C. dirus* (Merriam and Stock, 1932; Webb, 1974c; Gonyea, 1976; Emerson and Radinsky, 1980; Marcus and Berger, 1984; Akersten, 1985; Van Valkenburgh and Ruff, 1987; Van Valkenburgh *et al.*, 1990b; Berta, 1985 argues that *S. fatalis* is conspecific with the South American *S. populator*; if so, *S. populator* becomes the proper name for the North American form).

The more gracile scimitar cat *Homotherium serum* is not nearly as well known but appears to have been widely distributed, with fossils known from as far north as Alaska and the Yukon and from as far south as Texas. While this cat had smaller canines than *S. fatalis*, they were also serrated fore and aft and laterally compressed; the association of *H. serum* with a large number of juvenile mammoths at Friesenhahn Cave, Texas, suggests that young elephants may have formed a significant part of the scimitar cat's diet (Meade, 1961; Churcher, 1966; Waldrop, 1974; Kurtén and Anderson, 1980).

The late Pleistocene American cheetah *Miracinonyx trumani* is known from Nevada, Wyoming, and Colorado. This New World cheetah differs from its Old World counterpart, *Acinonyx jubatus*, in many ways, including larger size and the possession of fully retractile claws, more powerful forelimbs, and greater limb mobility. Indeed, many of the similarities between the New World and the Old World forms are now suspected to reflect convergent evolution rather than common ancestry. Although it has been suggested that cheetahs may have originated in the New World, the evidence is equivocal (Adams, 1979; Emslie, 1986; Van Valkenburgh *et al.*, 1990b).

Lions (*Panthera leo*) were widespread in North America during the late Pleistocene, found from California to Florida and from Alaska into Mexico and beyond. Populations south of glacial ice, assigned to the subspecies *P. l. atrox*, were somewhat larger than their modern African counterparts; those from eastern Beringia are somewhat smaller than *P. l. atrox* and are quite similar to the cave lion (*P. l. spelaea*) of Pleistocene Europe. The fact that these animals have never been found in the forested east suggests that they were similar to modern lions in their preference for open habitat (Merriam and Stock, 1932; Simpson, 1941; Harington, 1969; Harington and Clulow, 1973; Kurtén, 1985).

The genus *Panthera* lives on in the southern United States and northern Mexico in the form of the jaguar [*P. onca*; see Hall, (1981); taxonomy follows Honacki *et al.* (1982)].

Rodentia (Rodents)

Only three genera of rodents were lost from North America toward the end of the Pleistocene, but those three were impressive. The giant beaver *Castoroides ohioensis* ranged from New York to Florida in the east to Alaska in the northwest but appears to have been most common south of the Great Lakes. Probably weighing some 100 kg (roughly the size of a black bear), giant beavers frequented marshes, lakes, and ponds. Although their incisors were about 20 cm long and 2.5 cm wide, the tips of these teeth were rounded and this, as well as other aspects of their morphology, documents that giant beavers were not dam builders (Simpson, 1930b; R. A. Martin, 1969; Saunders, 1977; Parmalee and Bogan, 1976; Kurtén and Anderson, 1980).

The two remaining genera of rodents that were lost to North America were capybaras. Today, the single species of capybara (*Hydrochoerus hydrochoerus*) provides the world with its largest living rodent, adults weighing some 55 kg and reaching a length of well over 1 m. Found from Panama to Uruguay, capybaras inhabit dense vegetation near water and use their excellent swimming abilities to escape danger (Nowak and Paradiso, 1983). Similar habits seem to have characterized both North American capybaras. *Hydrochoerus holmesi*, known only from Florida, was somewhat larger than its modern congeneric counterpart, but *Neochoerus pinckneyi*, known from South Carolina and Florida, was half again larger (Hay, 1926; Simpson, 1930a, b; R. A. Martin, 1974; Kurtén and Anderson, 1980).

Lagomorpha (Pikas, Rabbits, and Hares)

Aztlanolagus agilis is a diminutive rabbit known from the Chihuahuan Desert of New Mexico, Texas, and northern Mexico. Analyses of its limb bones suggest that it was hare-like in its specialized adaptations for running, while the few radiocarbon dates available suggest that it did not survive the Wisconsin glacial maximum, some 20,000 years ago (Russell and Harris, 1986).

Perissodactyla (Odd-Toed Ungulates)

Horses (*Equus* sp.) evolved in the New World and crossed into Asia via the Bering Land Bridge. They became extinct in the New World at the end of the Pleistocene, only to be reintroduced by Europeans during early historic times (Crosby, 1986). Approximately 10 species of late Pleistocene North American horses are currently recognized, but many of the named species may have little biological meaning (Dalquest, 1978; Kurtén and Anderson, 1980). The only other perissodactyl known from the late Pleistocene of North America is the tapir, of which two species are currently recognized: *Tapirus veroensis*, comparable in size to the living *T. terrestris* of South America, and the larger *T. haysii*. Between the two, late Pleistocene tapirs are known from California on the west to Pennsylvania and Florida on the east; many other species of Pleistocene tapirs have been named, the validity of which remains to be determined (Ray and Sanders, 1984; see also Jefferson, 1989).

Artiodactyla (Even-Toed Ungulates)

Thirteen genera of five families of artiodactyls were among North America's late Pleistocene losses, ranging from peccaries to musk oxen.

Today, the collared peccary, *Tayassu tajacu*, ranges north into the southwestern United States and Texas, but it appears to be a recent arrival, and peccaries were far more widespread during the late Pleistocene. The long-nosed peccary *Mylohyus nasutus*—characterized in part by its long and slender snout—is known from a wide variety of sites in the eastern half of North America, east of about 100° longitude. Apparently occupying woodland environments, *M. nasutus* may have been the rough ecological equivalent of the more massive European wild boar *Sus scrofa*. *Platygonus compressus*, the flat-headed peccary, was even more widely distributed, known from coast to coast and from the edge of glacial ice in the north into Mexico on the south. Both the morphology of *P. compressus* and its faunal and floral associates show that this animal occupied open environments and, in this way, differed from *M. nasutus*. It also differed from *M. nasutus* in social life: while the long-nosed peccary appears to have been solitary, discoveries of tightly associated multiple skeletons (''fossil herds'') of *P. compressus* show that this animal was gregarious (Gidley, 1921; Lundelius, 1960; Semken and Griggs, 1965; Guilday *et al.*, 1969; Ray *et al.*, 1970; Finch *et al.*, 1972). Remarkably, a peccary closely related to *Platygonus*, the chacoan peccary *Catagonus wagneri*, was discovered alive and well in the Paraguayan Chaco during the 1970s. Prior to its discovery on the hoof, the chacoan peccary had been known only from subfossil material (Wetzel *et al.*, 1975; Wetzel, 1977; Mayer and Wetzel, 1986).

Like horses, camels are New World natives, evolving here and subsequently entering the Old World via a land bridge in the far northwest. Unlike horses, however, some camelids—and, in particular, llamas (*Lama* and *Vicugna*)—survived in the New World. During the late Pleistocene, North America supported one genus of llama-like camel and two of llamas. The camel *Camelops hesternus* was then widespread in western North America; in life, it would have looked much like a large version of a dromedary (*Camelus drome-*

darius), although its legs were longer, its head narrower and longer, and its single hump placed somewhat further forward. The large-headed llama *Hemiauchenia macrocephala* was widespread in the more southerly United States, known from southern California to Florida. Long-limbed with high-crowned cheek teeth, *H. macrocephala*, a relatively fast animal with a diet oriented toward grasses, appears to have been adapted to open terrain. *Palaeolama mirifica*, on the other hand, was of stockier build with lower-crowned cheek teeth and appears to have been adapted to more rugged terrain and to a more mixed diet. Known primarily from near-coastal settings in Florida, Texas, and California, a nearly complete skeleton was recently discovered in southern Missouri (Webb, 1965, 1974b; R. W. Graham, personal communication, 1990).

The mountain deer, *Navahoceros fricki*, was a stout-legged cervid intermediate in size between mule deer (*Odocoileus hemionus*) and wapiti or "elk" (*Cervus elaphus*). Closely related to the caribou (*Rangifer tarandus*), this was an alpine deer; all records are from localities in or near the Rocky Mountains and from the mountains of northern Mexico (Kurtén, 1975; Kurtén and Anderson, 1980; Webb, 1990). Remains of the elk-moose *Cervalces scotti*, on the other hand, come primarily from the central and eastern United States and Canada north of 36°N latitude and from the Yukon Territory and Alaska. The size of a moose (*Alces alces*), but with complexly palmate antlers and relatively long limbs, *C. scotti* is very similar to the extinct Old World *C. latifrons*, and it is possible that the elk-moose from far northwestern North America intergraded with their Eurasiatic counterparts (Churcher and Pinsof, 1987).

Two additional genera of cervids are at times seen in lists of North American late Pleistocene extinctions. In 1928, Simpson reported a single specimen of *Blastocerus*, the genus of extant South American marsh deer, from late Pleistocene (Sangamonian?) deposits in Sabertooth Cave, Florida, but no further records have been forthcoming. Simpson himself noted the similarity between this single specimen and the extant North American *Odocoileus*, and in a later review placed Pleistocene *Blastocerus* in South America only, suggesting that he had little faith in the identification (Simpson, 1928, 1945; Webb and Wilkins, 1984). There are fewer problems with the aptly named fugitive deer *Sangamona fugitiva*. This animal, Churcher (1984, p. 330) has convincingly argued, "is a construct of diverse and disparate skeletal elements" that originally came from either *Odocoileus* or *Cervus elaphus*.

Today, there is but a single surviving species of Antilocapridae, the pronghorn, *Antilocapra americana*, of western North America. This speedy animal has two laterally compressed horn cores, each covered by a sheath with a small anterior prong. All three genera of extinct late Pleistocene North American antilocaprids had four-pronged horn cores, two anterior and two posterior. The smallest of the three, *Capromeryx minor*, was only some 0.5 m tall at the shoulder, with long and slender limb bones. Known from California to Texas, this tiny pronghorn appears to have been adapted to open country. *Tetrameryx shuleri* was nearly the size of the modern pronghorn, had posterior horn cores more than twice the size of the anterior ones, and is apparently known only from Texas, although *Tetrameryx* sp. has been reported from a very late Pleistocene context in southern Nevada. The third late Pleistocene genus, *Stockoceros*, has two described species, *S. conklingi* and *S. onusrosagris*, but these may refer to the same animal. *Stockoceros* had anterior and posterior horn cores that were roughly equal in size; this animal was shorter than, but about the same length as, the modern pronghorn, although the two described species of *Stockoceros* differ in size. Known from Texas, Arizona, New Mexico, and northern Mexico, the relatively short lower limbs of *Stockoceros* suggest that it was not as speedy as the extant pronghorn (Lull, 1921; Colbert and Chaffee, 1939; Skinner, 1942; Furlong, 1943, 1946; Kurtén and Anderson, 1980; Lundelius *et al.*, 1983; Czaplewski *et al.*, 1989).

Of the three genera of bovids that became extinct in North America toward the end of the Pleistocene, the saiga *Saiga tatarica* now thrives on the arid steppes of the Soviet Union. During the late Pleistocene, its range extended into Alaska and the Northwest Territories (Frick, 1937; Harington, 1971, 1981; Heptner *et al.*, 1988). The shrub ox *Euceratherium collinum* has been reported from late Pleistocene deposits from California to Iowa and from as far south as central Mexico. Apparently related to musk oxen, *E. collinum* is characterized by horns that arise from the posterior edge of the frontal bones and sweep up and back, and then out and forward, curling up near their tips. The morphology of their cervical vertebrae suggests that, like modern mountain sheep (*Ovis canadensis*), these animals were head-butters; they also appear to have been grazers that occupied hilly, but not mountainous, terrain (Sinclair and Furlong, 1904; Furlong, 1905; Stock and Furlong, 1927; Stovall, 1937; Hibbard, 1955). Harlan's musk ox *Bootherium bombifroms* is known from nearly all of unglaciated North America, with the exception of the far southeast and southwest. Able to cope with warmer climates than the extant musk ox *Ovibos moschatus*, *B. bombifroms* seems to have occupied fairly open terrain. *B. bombifroms* was longer-limbed and stood taller than the extant musk ox but was significantly shorter from head to tail (Semken *et al.*, 1964; Harington, 1968, 1975; McDonald, 1984a; McDonald and Ray, 1989).

Two bovids were removed from the extinctions list during the late 1980s. The extinct yak *Bos bunnelli*, reported by Frick (1937) from Alaska and the Yukon, was based on modern cattle bones that had become mixed with the remains of Pleistocene mammals (Frick, 1937; Guthrie, 1990a, b). McDonald and Ray (1989) have demonstrated that the extinct musk oxen *Symbos* and *Bootherium* were males and females of the same species.

While the genus *Oreamnos*, in the form of the mountain goat *O. americanus*, is doing well in northwestern North America, Harrington's mountain goat *Oreamnos harringtoni* failed to survive the late Pleistocene. Known from a variety of sites in the Great Basin and Colorado Plateau of the arid American west, all of which are well south of the distribution of its modern relative, Harrington's mountain goat occupied environments ranging from open juniper (*Juniperus* spp.) woodlands to subalpine coniferous forests. Compared to *O. americanus*, *O. harringtoni* was as much as 30% smaller but possessed more robust, albeit shorter, mandibles and metapodials; preserved hairs of this animal are pure white, strongly suggesting that it was similar in pelage to *O. americanus* (J. I. Mead, 1983; Mead *et al.*, 1986a, b, 1987).

Finally, while the genus *Bison* was thriving in North America at the time of European occupation, the species involved—*B. bison*—differed from that, or those, present here during the latest Wisconsin. The classification of the latest Pleistocene bison of North America has long been a contentious matter. In eastern Beringia, those bison are often assigned to the same species as the late Pleistocene European steppe bison, *B. priscus*, or to a descendant species, *B. occidentalis*. South of glacial ice, the latest Pleistocene North American bison are usually assigned to *Bison antiquus*. In both areas, bison decrease in size toward or at the end of the Pleistocene and into the Holocene, ultimately resulting in the bison encountered by Europeans when they first arrived. While the late Pleistocene bison are thus technically "extinct," this was phyletic replacement, not true extinction: their descendants live on. Indeed, the similarities between latest Pleistocene and modern bison are so great that some authors, with good justification, assign them to the same species (*B. bison*) as the modern forms and treat them as differing only at the subspecific level (Wilson, 1974; McDonald, 1981; Guthrie, 1990a).

Proboscidea (Mastodons, Gomphotheres, and Elephants)

The American mastodon *Mammut americanum* was widespread in unglaciated North America, from coast to coast and from Alaska to Mexico, but appears to have been most abundant in the woodlands and forests of the east. Mastodons had upper tusks that projected horizontally from their skulls, then curved gently outward and, finally, inward. Their distinctive cheek teeth had large cusps arranged in pairs to form ridges that ran at right angles to the main axis of the tooth. Mastodons were browsers, apparently thriving in open spruce woodlands. They were also massive, stockier in build than both modern elephants and extinct North American mammoths. They were, however, shorter than mammoths, standing from 2.7 to 3.0 m at the shoulder. The fact that mastodon remains are frequently found as single individuals suggests that these were fairly solitary animals (Skeels, 1962; Kurtén and Anderson, 1980; Miller, 1987; Haynes, 1989; Shoshani, 1990).

The gomphothere *Cuvieronius* frequently occurs on lists of North American late Pleistocene extinctions (e.g., P. S. Martin, 1984) but was primarily South American in distribution at this time. Although a single record (Crystal River, Florida) has suggested that this large browser occurred in southern North America during the latest Pleistocene, this occurrence probably predates the last interglaciation. The youngest North American records for *Cuvieronius* appear to be at least Sangamonian in age (Lundelius, 1972; Lundelius *et al.*, 1983; Webb, 1974a; S. D. Webb, personal communication, 1990).

Closely related to living elephants, late Pleistocene North American mammoths possessed flat, high-crowned cheek teeth, each composed of a series of enamel-bordered plates running at right angles to the main axis of the tooth, forming an efficient shearing device. Unlike mastodon tusks, mammoth tusks point downward as they leave the skull, then curve down, out, and back in. Mammoths were primarily grazers; their remains, known from throughout unglaciated North America, are most abundant in environments that were open grasslands. Of the two species of late Pleistocene North American mammoths, the woolly mammoth *Mammuthus primigenius* was northern in distribution and is well known not only from bones and teeth, but also from frozen carcasses found in Alaska and Siberia. The Columbian mammoth *Mammuthus columbi* (also called Jefferson's mammoth, *M. jeffersonii*) has been found from the far north into Mexico and reached a shoulder height of some 3.5 m, comparable to the height of an African elephant (*Loxodonta africana*). In addition to differing in morphology and diet, mastodons and mammoths also seem to have differed in social behavior. Since the remains of mammoth are frequently discovered in groups of multiple animals, it seems likely that, in contrast with mastodons, mammoth were gregarious (Skeels, 1962; Maglio, 1973; Kurtén and Anderson, 1980; Agenbroad, 1984; Haynes, 1989; Agenbroad and Mead, 1989).

THE CHRONOLOGY OF EXTINCTION

Prior to the advent of radiocarbon dating, the precise timing of the North American extinctions was not at all clear. Romer (1933), for instance, suggested that they had begun no more than 20,000 years ago and had continued to within at least the past few thousand years. Greater precision was hardly possible in the absence of a valid means of extracting absolute dates.

Radiocarbon dating seemed to provide that means, and some of the earliest published radiocarbon dates were for extinct mammals. By 1958, sufficient dates were available that Paul Martin (1958) was able to provide a radiocarbon-based chronology of Pleistocene extinctions. The 35 dates available to him strongly suggested that while different taxa became extinct at different times in different places, the extinctions as a whole were largely Holocene in age, the final losses perhaps occurring as late as 2000 years ago.

Two years later, Hester (1960) reanalyzed the extinction chronology, relying primarily on 86 dates. Rejecting all dates whose validity had been questioned, Hester (1960) concluded that the extinction of most herd animals, including mammoth, horse, and camel, had occurred at about 8000 years ago and that most extinctions were under way by at least this time. As had Martin (1958), Hester concluded that different taxa may have become extinct at different times at different places.

The conclusion that the extinctions were largely a Holocene event and may have occurred in piecemeal fashion remained intact through the middle 1960s (e.g., P. S. Martin, 1963). In 1967, however, Martin returned to the ever-growing list of relevant radiocarbon dates. Arraying the dates available for each taxon against time, he showed that those dates reached well into the Holocene (see Fig. 1). He also observed that if such animals as mammoth, horse, and camel had survived beyond 10,000 years ago, "their remains are unaccountably absent" from Holocene-aged archaeological sites (P. S. Martin, 1967b, p. 89). Accordingly, he truncated the chronology at the Pleistocene/Holocene boundary and concluded that the main wave of extinctions had occurred around 11,000 years ago.

In arguing that the extinctions had occurred between 12,000 and 10,000 years ago, Martin made two critical assumptions. First, he assumed that since no Holocene site had ever provided the remains of any of the extinct mammals in a secure context, they must have been extinct by 10,000 years ago. That

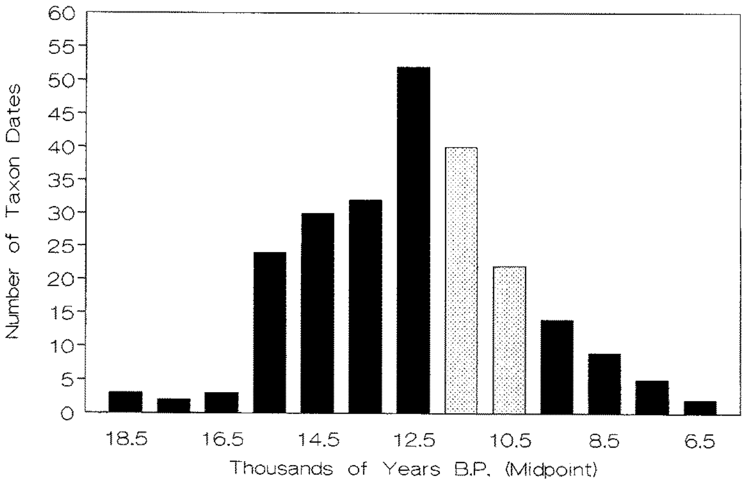

Fig. 1. The distribution of dated taxonomic occurrences ("taxon dates") used by Martin (1967b) to construct an extinctions chronology; dates falling between 12,000 and 10,000 years ago are stippled.

assumption was reasonable at the time and appears compelling today, given the vastly larger sample of excavated Holocene sites.

Since Martin believed that what had caused the extinction of some of the animals had caused the extinction of all of them, he also assumed that the extinctions were synchronous. Since he had dates falling between 12,000 and 10,000 years ago for 13 of the 34 genera on his extinctions list, he concluded that all of the extinctions had occurred in this interval.

If this second assumption is wrong, the effects are fairly profound, requiring that we attribute to the extinction "event" certain properties, notably speed and breadth (some 35 genera lost within 2,000 years), that it may or may not have possessed. Once that is done, explanations of the extinctions must be structured to account for those assumed parameters.

Martin's 1967 paper is the most influential analysis of the North American extinctions ever written and fundamentally altered the way in which people thought about those extinctions. Martin's arguments regarding the chronology of the extinctions may have fit his own ideas concerning the causes of those extinctions (see Pleistocene Overkill below), but the dates he provided also aligned the extinctions with increasingly secure evidence for major climatic change at this time (e.g., Adam, 1967; Davis, 1967; Ogden, 1967). As a result, his chronology fit almost everyone else's ideas on those causes as well. *That is, Martin's position concerning the timing of the extinctions seems to have been widely accepted not so much because of the strength of the radiocarbon chronology that was then available, but because of the kinds of explanations felt most likely to account for those extinctions.* It is thus no surprise that most scientists quickly abandoned the notion that the extinctions may have been spread over thousands of years. In its place, they adopted the position that all or virtually all of the losses had occurred between 12,000 and 10,000 years ago.

Unfortunately, analyses of the radiocarbon dates now available for these animals do not provide much support for this belief.

It is a truism of radiocarbon dating that not all dates are created equal, and both Hester (1960) and Martin (1967b) tried to ferret out the good dates from the bad. Since Martin published his analysis, a tremendous amount has been learned about the extraction of radiocarbon dates that accurately reflect the time of death of an organism. As a result, better dates can be produced, and the potential validity of dates produced in the past can be better evaluated.

Meltzer and Mead (1985) compiled a sample of 363 radiocarbon dates for extinct North American Pleistocene mammals, drawn from 163 North American sites. Although this list is not exhaustive (for instance, it does not include Alaska and Arctic Canada), it is the most extensive compilation of such dates ever published. Meltzer and Mead (1985) also devised a radiocarbon date rating system to allow the separation of good dates from the bad. This system takes into account both the material dated and the strength of association between that material and the target taxon (Table II). Assuming, as Martin (1967b) did, that Holocene dates for extinct Pleistocene mammals are likely to be invalid given the lack of remains of these mammals in Holocene archaeological sites, it can be shown that dates as high as rank 7 in their system are likely to be invalid (Meltzer and Mead, 1985; Grayson, 1989). As a result, any attempt to build an acceptable radiocarbon chronology for the extinctions must focus on dates of ranks 8 and 9. These I call simply "good dates."

At the time of the Meltzer and Mead (1985) compilation, only nine genera had good dates, and only seven had good dates falling between 12,000 and 10,000 years ago (Grayson, 1989; see also Grayson, 1987a). Since the publication of their list, many new radiocarbon dates for the extinct mammals have become available, but only one additional taxon, *Palaeolama*, has both received a good date (rank 9) and been placed in the final 2000 years of the Pleistocene (R. W. Graham, personal communication, 1990).

Of the eight genera that can be shown to have survived to the end of the Pleistocene, six had received the dates that place them there by 1969 (Grayson, 1989). During the last 20 years, a time of intense investigation of the latest Pleistocene paleontology and archaeology of North America, only two additional genera have been placed on the list of extinctions that occurred during this narrow time interval (Table III).

Table II. Meltzer and Mead (1985) Radiocarbon Date Rating System (Ranks Are Derived by Tallying Separate Scores for Material Dated and Strength of Association)

	Score
1. Material dated	
A. Derived from extinct taxon	
Body perishables (dung, keratin, etc.)	6
Primary humates or amino acids	5
Collagen	4
Apatite	3
Whole bone	1
B. Derived from other material	
Charcoal (elemental carbon)	6
Wood (logs, twigs, leaves)	5
Peat	3
Organic mud (includes gytjja)	3
Soil	3
Shell (freshwater/terrestrial)	2
Terrestrial carbonate (marl/tufa)	1
2. Strength of association	
Strong	3
Medium or unknown	2
Weak	1

Table III. Youngest Good Date for Extinct Late Pleistocene North American Genera (After Grayson, 1989) (Abbreviations of Taxon Names Are Used in Fig. 2)

Genus	Youngest good date	Site	Year received
Pampatherium	None		
Holmesina	None		
Glyptotherium (Gly)	None		
Megalonyx (Meg)	12,190 ± 215		
Eremotherium	None		
Nothrotheriops (Not)	10,035 ± 250	Aden Crater	1969
Glossotherium	20,450 ± 460		
Brachyprotoma	None		
Cuon	None		
Tremarctos	None		
Arctodus	None		
Smilodon	11,130 ± 275	Rancho La Brea	1984
Homotherium	None		
Miracinonyx	None		
Castoroides (Cas)	None		
Hydrochoerus	None		
Neochoerus	None		
Aztlanolagus	None		
Equus (Equ)	10,370 ± 350	Lehner Ranch	1958
Tapirus (Tap)	10,900 ± 450	Lehner Ranch	1958
Mylohyus (Myl)	None		
Platygonus (Pla)	None		
Camelops (Cam)	10,900 ± 450	Lehner Ranch	1958
Hemiauchenia (Hem)	None		
Palaeolama	10,890 ± 130	Woody Long	1990
Navahoceros	None		
Cervalces	None		
Capromeryx	None		
Tetrameryx (Tet)	None		
Stockoceros	None		
Saiga	None		
Euceratherium	None		
Bootherium	None		
Mammut (Mas)	10,395 ± 110	Rodney	1960
Mammuthus (Mam)	10,550 ± 350	Santa Rosa	1957

Most of the dates available to Martin in 1967 were for taxa that can now be shown to have survived to between 12,000 and 10,000 years ago. Of the 62 dated taxonomic occurrences used or referred to by Martin (1967b) and that fell into this interval, 47 (76%) were for *Equus*, *Mammuthus*, *Camelops*, *Mammut*, *Tapirus*, and *Nothrotheriops*. The other 15 dated occurrences were spread across the remaining seven genera; none of those dates are now regarded as acceptable (Fig. 2). It may well be that the genera that survived beyond 12,000 years ago have misled us into thinking that all of the extinct genera survived this late.

This is not to say that the period of time focusing on 11,000 years ago is

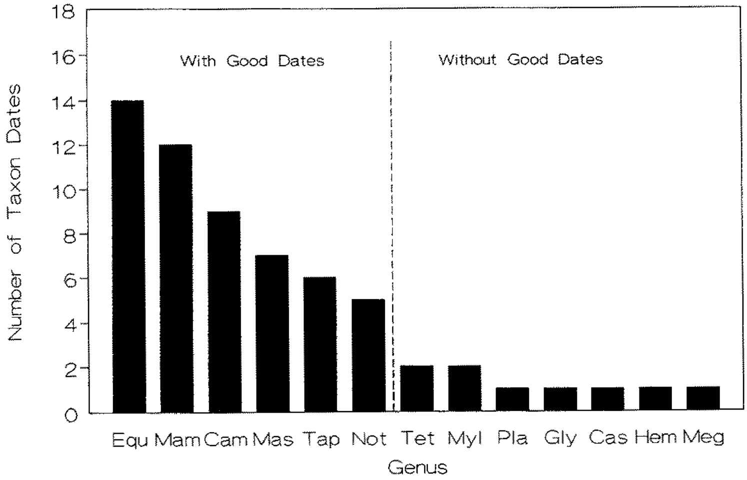

Fig. 2. The distribution of dated taxonomic occurrences ("taxon dates") falling between 12,000 and 10,000 years ago and used by Martin (1967b) to construct an extinctions chronology. Taxa falling to the left of the dashed vertical line currently have good dates placing them in this interval; those to the right of this line do not. See Table III for abbreviations of taxon names.

not critical to our understanding of the extinctions. It clearly is: elegant work has documented the extinction of *Mammuthus*, *Nothrotheriops*, and *Oreamnos harringtoni* at almost precisely this time in the Southwest (Long and Martin, 1974; Mead *et al.*, 1986b, 1987; P. S. Martin, 1987; Agenbroad and Mead, 1989). Nonetheless, it is also true that of the 35 or so genera of mammals that became extinct toward the end of the Pleistocene, only 8 can be convincingly shown to have survived beyond 12,000 years ago. As the years go by, it seems to be getting harder, not easier, to extend this list. As a whole, these facts provide little convincing support for the argument that all of the extinctions occurred during the last 2000 years of the Pleistocene. Although it is fully reasonable to expect that coming years will see additions to this list (*Megalonyx*, for instance, is not too far off now), it is equally reasonable to suspect that many of the extinct genera were gone well before 12,000 years ago. If we are to understand what caused the extinctions, building a solid extinctions chronology must become a top research priority.

PROPOSED EXPLANATIONS

Until the middle 1960s, most explanations of Pleistocene extinctions were broadly multivariate, calling on some combination of human activities and climatic change to account for the losses. Martin (1967b) argued in detail that human predation had caused the extinctions. In so arguing, he presented the first precise explanation of those extinctions, and did so in a form that appeared readily testable. Martin's account was so powerfully framed that henceforth, most scientists were to argue either for or against a critical human role: that either climate or people, but not both, had been the cause (Grayson, 1984b). It is only recently that multivariate explanations have begun to regain their popularity, but most explanations remain decidedly univariate in scope. Here, I review Martin's hypothesis and then turn to the climatic accounts that seem to offer the greatest explanatory potential.

Pleistocene Overkill

The notion that human activities may have played a role in causing the extinction of late Pleistocene mammals in both Europe and the Americas is an old one (Grayson, 1980, 1984c), but the most forceful elaboration of that argument has been provided by Martin.

Martin first addressed the North American extinctions in 1958, when the radiocarbon chronology suggested that many of the losses had occurred during the Holocene, and archaeological work suggested a human presence south of glacial ice prior to 20,000 years ago (P. S. Martin, 1958). Martin observed that most of the mammals that became extinct were large, that no ecological replacements for them seem to exist, and that the available chronology showed no correlation between the extinctions and major climatic change. He concluded that human predation must have been to blame: that, as he suggested a few years later, "large mammals disappeared not because they lost their food supply, but because they became one" (1963, p. 70).

Martin began developing this position in great detail in 1967. At this time, the earliest unequivocal archaeological sites in North America, Clovis sites, appeared to date to between 12,000 and 11,000 years ago (Haynes, 1967). Martin (1967b) argued at length that the similarity between the extinctions chronology he constructed and the emerging dates for Clovis was not likely to be coincidental. Of course, insofar as the extinctions chronology was built in part by assuming that all taxa had been driven to extinction by the same cause, the correlation was not coincidental. However, even without this assumption, the 13 taxa that could then be placed between 12,000 and 10,000 years ago would have provided sufficient ammunition for the argument he now developed.

In addition to being impressed by the magnitude and apparent speed of the extinctions, Martin (1967b) was struck by the fact that most of the animals that became extinct were large mammalian herbivores or were carnivores, scavengers, and commensals that may have been ecologically dependent on those herbivores. He was also struck by the fact that, unlike earlier episodes of extinction during the Cenozoic, there had been no comparable losses of small mammals, amphibians, reptiles, mollusks, or pelagic invertebrates. To him, it seemed that these were taxonomically unbalanced extinctions that could not be explained by known aspects of late Pleistocene climatic change. Only human predation, Martin (1967b) felt, could account for all this.

During the following years, Martin made his arguments increasingly precise. Clovis hunters, he argued, had moved south through an ice-free corridor east of the Canadian Rockies, emerging south of glacial ice at about 11,500 years ago. Here they found themselves in a vast expanse of territory that lacked people but that contained a vast supply of what were, from the point of view of the new arrivals, large game mammals. Because these mammals had never before encountered human predators, they lacked the defensive behaviors possessed by their Old World counterparts. Clovis hunters, however, were exceedingly well adapted for big game hunting [''expert at tracking, killing, butchering, and preserving meat from large mammals . . . it appears that they ate little else'' (Mosimann and Martin, 1975, p. 303)]. Taking rapid advantage of this massive, naive, and accessible food supply, they multiplied quickly and spread southward explosively. Behind themselves, they left a trail of extinct populations, and, ultimately, extinct genera (P. S. Martin, 1967b, 1973, 1990b; Mosimann and Martin, 1975).

The general notion that human predation was the ultimate cause of the extinctions is usually termed ''Pleistocene overkill'' (P. S. Martin, 1967a). The argument that the extinctions resulted from the rapid expansion across the landscape of a group of finely tuned hunters is generally termed ''blitzkrieg'' (P. S. Martin, 1973; Mosimann and Martin, 1975). The blitzkrieg argument has been applied not only to North America, but also to South America, Australia, and oceanic islands (P. S. Martin, 1984, 1990a).

During the 1980s, paleontological and archaeological work established beyond a doubt that people played a major role in the extinction of a broad variety of birds, and perhaps other organisms, on oceanic islands during the Holocene (e.g., Olson and James, 1982, 1984; Steadman, 1989; Steadman *et al.*, 1991). This information is important not only for understanding past extinctions, but also for managing modern populations of birds and other animals on these islands. There is, however, little reason to think that the same processes that caused the extinction of birds on the restricted geographic settings presented by islands must also have caused the extinction of mammals on a continental scale. This is especially true since most of the island losses are likely due to habitat disruption associated with human occupation. Even though some scientists whose work has focused on the avifaunas of modern oceanic islands disagree (e.g., Diamond, 1982, 1989a, b), little support for continental overkill is to be found in the faunal record of those islands.

Indeed, support for a human role in causing North American Pleistocene extinctions continues to come primarily from the temporal correlation between the appearance of fluted points and the disappearance of at least eight genera of mammals. Most scientists who reject overkill are impressed by the fact that there are so few associations between artifacts and the extinct mammals in convincing kill contexts.

While many taxa have been claimed to have been found in such a context, the number of genera for which such an argument can be convincingly made has actually declined over the years, in concert with the development of our taphonomic skills. For instance, a number of claims have been made for *Camelops* in kill association, but detailed review of such sites shows none to be convincing (Haynes and Stanford, 1984; Frison and Todd, 1986; Haynes, 1988). The apparently burned *Tapirus* mandible from the Lehner site, southwestern Arizona, appeared to suggest a tapir kill here (Haury *et al.*, 1959), but recent examination of that specimen suggests that the discoloration is a manganese oxide stain (C. V. Haynes, personal communication, 1990). The superb taphonomic work conducted by Johnson on faunal material from Clovis-aged feature FA2-1 at Lubbock Lake, northwestern Texas (Johnson, 1987, 1990; see also Holliday and Johnson, 1990), may establish human modification of the bones of *Artodus simus* and, perhaps, *Equus* sp. [discussed by Johnson (1987) but not by Johnson (1990)]. This feature, however, is not a kill site (nor is it claimed to be such) and has had a complex postdepositional history (Kreutzer, 1988): whether or not extinct Pleistocene mammals were, in fact, killed nearby and processed here remains a matter for debate. As it stands now, only two extinct genera can be convincingly shown to have been hunted—mammoth (e.g., Haury, 1953) and mastodon (e.g., Graham *et al.*, 1981; Graham and Kay, 1988).

What appear to have been some of the most abundant mammals on the North American late Wisconsin landscape have never been found in a kill asso-

Table IV. Percentage of Sites in the Lundelius *et al.* (1983) Sample of Wisconsin-Aged Paleontological Sites Containing a Given Extinct Genus: Ten Most Common Genera (Genera for Which Kill Sites Are Known Are in Boldface)

Genus	Percentage of sites containing genus
Equus	44.9
Mammuthus	23.6
Camelops	21.9
Mammut	19.1
Tapirus	16.3
Platygonus	15.2
Hemiauchenia	12.9
Megalonyx	11.8
Mylohyus	11.8
Glossotherium	11.2

ciation. Table IV presents the proportion of sites in which the 10 most common extinct genera are found in a sample of 178 North American late Pleistocene paleontological sites compiled by Lundelius *et al.* (1983). *Equus* is the most common of all late Pleistocene genera in this compilation, appearing in 44.9% of the sites. *Camelops* is the third most common genus, occurring in 21.9% of the sites. Neither horse nor camel has ever been found in convincing kill association. [A previous version of this argument, presented by Grayson (1984a) and Meltzer (1986), was based on earlier interpretations of the meaning of associations between extinct taxa and artifacts and is now outdated.]

Responding to those who felt the lack of kill sites to be a critical issue, Martin has argued that the extinctions took place so quickly that the chances for preservation of the results were slim. The wonder, he has argued, is not that there are so few kill sites, but that there are any at all (e.g., P. S. Martin, 1973, 1984; Mosimann and Martin, 1975). There are several problems with this position, one of which is that Martin has taken the abundance of moa kill sites in New Zealand as prime evidence for the extinctions of these birds by human predation (P. S. Martin, 1967b), creating a situation in which either many kill sites or none at all count as evidence for overkill. He has also noted that ''the first centuries following historic contact of native Americans and Europeans offer an analogue'' (P. S. Martin, 1984, p. 370) to the speed with which overkill occurred. However, archaeological sites from that period of time are abundant and have provided a prime source of information on the disastrous effects of contact on Native Americans (e.g., Ramenofsky, 1987).

Even if one accepts Martin's argument concerning the lack of kill sites, that argument predicts that kill sites for all taxa will be scarce; it does not predict that kill sites for one taxon will be scarcer than for another. Yet the archaeological record clearly shows that differential scarcity characterizes Paleoindian sites. Mammoth kills are relatively abundant, mastodon kills are rare but known, but horse and camel kills do not exist, even though the paleontological record shows that horses and camels were abundant on the landscape. Such differential associations are not predicted by overkill and imply that insofar as Paleoindians hunted large mammals—and the degree to which they did so is also in contention (e.g., Grayson, 1988; Meltzer, 1988; Dillehay, 1989)—they primarily took proboscideans.

The application of overkill to the North American setting thus continues to depend primarily on the correlation of the extinction of some of the mammals with the appearance of fluted points. The lack of kill sites for all but two of the taxa involved is a serious problem for the overkill position. It is also problematic (1) that Martin's argument appears to require that fluted point users were obligate large-mammal hunters, a view that does not accord well with our admittedly poor understanding of the adaptations of those people, and (2) that so few of the taxa involved can be shown to have survived until fluted point times. Given that this is the case, perhaps a more convincing explanation is to be found in climatic change.

Climatic Change

While scientists who argue for overkill as the prime cause of the extinctions tend to focus strongly on the genus as the analytic unit, those who emphasize climatic change as the prime cause often couch their arguments in terms of the species of mammals involved. The reasons are fairly simple. In the overkill perspective, the most important attributes of the animals that became extinct are their size (they were big) and their diet (they were herbivorous or were carnivores, scavengers, or commensals ecologically dependent on the herbivores). Big herbivores were driven to extinction by human predation; ecologically dependent forms were driven to extinction by the loss of the herbivores. In the climatic perspective, however, it is the interface between changing climates and the adaptations of the mammals that became extinct that counts, and those adaptations are generally to be understood at the species level. In addition, the climatic approach, unlike overkill, lays heavy emphasis on the fate of small mammals at the time the extinctions were occurring. Since small mammal genera were not lost, species-level analyses are called for here as well.

It is well established that at the time the extinctions were occurring, small mammals were undergoing tremendous changes in their ranges. For instance, the yellow-cheeked vole *Microtus xanthognathus* is now found in Alaska and the northern Yukon; toward the end of the Pleistocene, this vole was living in Tennessee (Guilday *et al.*, 1978). The collared lemming *Dicrostonyx torquatus* now lives no farther south than far northern Manitoba; toward the end of the Pleistocene, it occurred in Iowa, Nebraska, and southern Wyoming (Foley, 1984; Semken and Falk, 1987; Walker, 1987; Mead and Mead, 1989b). Many similar instances of substantial range changes among small mammals at about the time of the extinctions exist—for the heather vole *Phenacomys intermedius*, the northern bog lemming *Synaptomys borealis*, the yellow-bellied marmot *Marmota flaviventris*, and many other species (Lundelius *et al.*, 1983; Graham, 1985a, b; Harris, 1985).

It is a fact of life history that during significant episodes of extinction, larger species of vertebrates are more prone to extinction than are smaller ones (A. D. Barnosky, 1989). There are many reasons that this is so, but one is that larger vertebrates have greater food and space requirements than smaller ones: the bigger the vertebrate, the fewer there are of them in a given area. The inverse relationship between body size and population size plays a powerful role in increasing the risk of extinction faced by larger animals. In addition, larger vertebrates tend to have slower rates of reproduction than smaller ones, countering the fact that they also tend to be longer-lived. Indeed, analyses of modern populations have shown that except at extremely small population sizes (where the greater longevity associated with larger body size looms large), the risk of extinction is greater for larger-bodied birds than for smaller ones even when population size is taken into account. These facts make larger vertebrates far more vulnerable to extinction in the face of environmental change [(Pimm *et al.*, 1988; Brown and Maurer, 1989); for arguments within the context of North American Pleistocene extinctions, see Guilday, (1967, 1984), Grayson (1987b), and A. D. Barnosky (1989)].

Faunal change at the end of the Pleistocene in North America appears to have formed a continuum, with many larger mammals becoming extinct and many smaller ones undergoing range changes. Focusing only on extinction forces us to isolate the large-mammal end of this continuum for analysis, since the extinctions were clustered at this end. Even if overkill can account for the extinction of the large mammals, it cannot account for temporally correlated range changes among the small ones. Climatic explanations can account for the entire continuum, and this is one of the facts that gives them such potential power (Grayson, 1987b). Whether that potential has been realized, however, is a very different matter.

When the yellow-cheeked vole was living in what is now Tennessee, the small mammals that occupy this area today were not forced far to the south. Many late Pleistocene faunas contain mammals that are now arctic or boreal in distribution, living alongside mammals that now occupy temperate North America. At Baker Bluff Cave, northeastern Tennessee, for instance, the same depositional unit that provided *M. xanthognathus* also provided the remains of the eastern woodrat *Neotoma floridana*, an animal that is still found here. Throughout much of unglaciated North America, the same pattern has emerged: taxa that are today northern in distribution apparently living alongside (i.e., sympatric with) southern taxa. Because the combinations of taxa that these faunas contain no longer exist, the faunas themselves have been termed ''disharmonious'' (Graham and Lundelius, 1984; Semken, 1984; Lundelius, 1989), but the label ''intermingled'' (Graham, 1985b) is far preferable, since it does not imply, in contrast, that Holocene faunas are somehow ''harmonious'' or that late Pleistocene sympatries were odd.

While it is possible that some of the stratigraphic cooccurrences of northern and southern taxa in Late Pleistocene paleontological sites reflect stratigraphic mixture or extremely slow sedimentation rates (Semken, 1984), it is extremely unlikely that all do. Not only have such cooccurrences been replicated in many sites, but Semken and Stafford (1990) have recently shown that the members of one such pair—the eastern woodrat *Neotoma floridana* and the red-backed vole *Clethrionomys gapperi* from Peccary Cave, northeastern Arkansas (Semken, 1984)—have virtually identical radiocarbon ages (16,830 B.P. ± 210 years and

16,660 B.P. ± 165 years, respectively). While the eastern woodrat still exists in the area surrounding Peccary Cave, the red-backed vole is found no closer than 830 km to the north.

Paleontologists have long argued that these intermingled faunas most likely reflect late Pleistocene climates that were more equable than those of the Holocene: that while the late Pleistocene saw colder average annual temperatures, seasonal swings in those temperatures were less severe than they are now. According to this argument, lower average summer temperatures during the late Pleistocene allowed a number of northern taxa, such as the yellow-cheeked vole, to live much further south than they do today. Marginally higher average winter temperatures allowed a few southern taxa to expand northward. This cold equable climate resulted in faunas that contained taxa that, by today's standards, are ecologically incompatible (e.g., Hibbard, 1960, 1970; Taylor, 1965; Axelrod, 1967; Slaughter, 1967; Graham, 1976, 1990; Graham and Mead, 1987; Graham and Semken, 1976; Harris, 1976; Guilday *et al.*, 1978).

Given that the extinction of late Pleistocene mammals appears to have occurred at the same time as the intermingled faunas were being broken apart, many feel that the two processes are integrally related. This argument has been developed in most detail by Graham and Lundelius (e.g., Graham and Lundelius, 1984; Graham, 1985a, b, 1986, 1990; Graham and Mead, 1987; Lundelius, 1988, 1989). They argue that the demise of the intermingled faunas is a direct reflection of the loss of climatic equability, and in particular to an increase in summer temperatures, that occurred at the end of the Pleistocene, perhaps due in part to the fact that the glacial ice mass that covered much of Canada prevented the southerly movement of Arctic air masses (Ruddiman and Wright, 1987; see also Webb and Barnosky, 1989; Van Devender, 1990). As climate changed from the cold equable condition that characterized the late Pleistocene to the warm continental condition that has marked the Holocene, the diversity of plant communities decreased. This decrease, Graham and Lundelius suggest, created habitats that, by their structural simplicity, could not support a diverse mammalian fauna. In this view, the reorganization of vegetational communities caused increased competition among herbivores and decreased the availability of the plant foods to which these animals were adapted. This severe ecological disruption caused tremendous range changes for many smaller mammals and extinction for many larger ones [see Lundelius (1983) for an application of this argument to Australia, where late Pleistocene extinctions were also severe].

The equability model developed by Graham and Lundelius is meant to apply to all North American extinctions, but it is hard to see how it might apply to Pacific coastal settings, from California to Washington. In at least the northern parts of this region, equability appears to have increased at the close of the Pleistocene (C. W. Barnosky, 1985; Barnosky *et al.*, 1987). This, of course, is the reverse of what the model requires, yet mammoth, mastodon, ground sloth, camel, and other components of the late Pleistocene fauna became extinct here as well. The equability model appears to apply best to central and perhaps eastern North America, although evidence for decreased equability is also mounting in the Southwest (Van Devender, 1990; but see Spaulding, 1990).

Guthrie (1982, 1984a, b, 1990a, b) also looks to the changing nature of the seasons in his explanation of the extinctions, but he argues that the critical shift was in the length of the growing season, coupled with the demise of arid grasslands. Although Guthrie's argument is meant to apply to all North American (and Eurasian) extinctions, it was developed on the basis of data from unglaciated Alaska and adjacent Canada and would apply best to that region.

Guthrie believes that a huge area stretching from Europe to Alaska and northwestern Canada was covered by a spatially complex arid grassland, which he terms the ''Mammoth Steppe'' [for a history of similar concepts, see Hibbert (1982); for a very similar argument, see Harington (1981)]. Guthrie observes that the ruminants that survived the Pleistocene in far northern North America underwent substantial decreases in body size; these animals include bison, musk ox, mountain sheep, moose, and caribou. The large size of these mammals during the late Pleistocene leads him to infer that growing seasons during this period were longer, and he argues that these longer growing seasons were separated by short, severe winters. The longer growing seasons provided greater amounts of nutrients for larger mammals, while heavy winter mortality reduced competition for those nutrients. Guthrie also argues that by providing a longer period of time during which nutrients could be gathered, the lengthened growing season allowed a more diverse set of mammals to coexist. In his view, the diversity of these faunas was further enhanced by the spatially complex vegetational mosaic that characterized eastern Beringia at this time: by their very complexity, eastern Beringian habitats were able to support more complex mammalian faunas.

In Guthrie's account, then, the remarkable late Wisconsin mammalian fauna of the far north was supported by long growing seasons and a spatially complex arid grassland. As the Pleistocene came to an end, so did these critical attributes of the northern environment. Growing seasons were dramatically shortened and homogeneous plant communities replaced the more heterogenous mosaics of the late Wisconsin. These shifts caused tremendous changes in the distribution of some mammals, caused the dwarfing of mammals that were able to survive the transition in place, and caused the extinction of such mammals as camel, mammoth, and horse.

Guthrie's intriguing arguments are not well received by paleobotanists working in eastern Beringia. The relatively small number of lacustrine pollen sequences available from lakes in the far north suggests that the vegetation of this area *was* a complex mosaic of plant associations. However, they also suggest that higher elevations, and far eastern Beringia, were covered by unproductive tundra, while lower elevations supported more productive tundra vegetation (Ritchie and Cwynar, 1982; Ritchie, 1984; Ager and Brubaker, 1985; Anderson, 1985, 1988; Colinvaux, 1986; Barnosky *et al.*, 1987). These reconstructions do not coincide well with Guthrie's Mammoth Steppe.

The nature of the vegetation of full glacial eastern Beringia would be clarified if more information were available on the density of large grazing mammals that occupied this area during that time. Guthrie, observing the hundreds of thousands of late Pleistocene mammalian fossils that have been collected from this region, believes that large mammal densities were high. However, most of those fossils have been collected as lag deposits from placer mining in the Alaskan interior. In this process, jets of water are used to remove thick deposits of reworked loess in order to expose underlying gold-bearing gravels [Westgate *et al.*, (1990) discuss the chronology of this fossiliferous loess, the base of which is late Pliocene in age]. As a result, there is no way of knowing whether the immense number of fossils reflects high mammal densities during glacial times, as Guthrie assumes, or the concentrating effects of placer mining. What would solve the issue is the calculation of an ''animal influx rate'' comparable to the pollen influx rate of palynologists, but this we do not have.

Without such information, the pollen data provide the only secure access to the nature of full glacial vegetation in eastern Beringia, and they indicate a complex mosaic of different kinds of tundra. Significantly, pollen data also suggest that this mosaic came to an end with the development of birch shrub tundra between 14,000 and 12,500 years ago, coinciding well with the onset of the extinctions, which appear to have occurred earlier in the far north than south of glacial ice.

There is less debate over changing seasonal swings in temperature from full- to post-glacial times in the far north. Simulation models of the climate at 18,000 years ago for this region suggest that winter temperatures were no cooler than those at present, and may have been warmer, while summers appear to have been substantially cooler. At 12,000 years ago, summer temperatures were near their modern levels, while winter temperatures had decreased significantly from their earlier values. These interpretations do not conflict with Guthrie's model. In his account, increased winds, not decreased temperatures, produce severe winters; increased length of the growing season, not increased temperatures, led to larger ruminants and to more diverse mammalian faunas. The simulated climate is also in accord with reconstructed vegetation, with the tundras and ''steppe-tundras'' of 18,000 years ago having given way to birch shrub tundra by 12,000 years ago (Kutzbach, 1987; Barnosky *et al.*, 1987; Anderson, 1988). As in the midcontinent and eastern North America, seasonal temperature differences appear to have increased as the Pleistocene ended.

Thus, in many areas both south and north of the ice sheet, there is substantial evidence for both changing seasonal temperature regimes and vegetational simplification as the Pleistocene came to an end, changes that were contemporaneous with the extinctions. Although the Graham, Lundelius, and Guthrie explanations differ in many ways, they all attribute the extinctions to this massive and documented loss of habitat.

It is important to recognize that one of the most frequent criticisms leveled at climatic arguments now seems to have little power. Those who object to climate-based explanations routinely point to earlier glacial terminations in North America. They note, with good reason, that while those terminations seem as substantial as the Pleistocene/Holocene transition, they were not associated with equally dramatic extinction events (e.g., Spaulding, 1983; P. S. Martin, 1984, 1990b). Those arguments, however, are routinely based on oxygen-isotope ratios from deep sea cores (e.g., Ruddiman and McIntyre, 1982). These ratios provide unparalleled insight into changing continental ice volumes on a global scale and into changing ocean temperatures during the Pleistocene (Williams *et al.*, 1988). However, they do not monitor the same variables as are now being implicated in climatic models of late Pleistocene extinctions: vegetational complexity, seasonal temperature regimes, and length of growing season. Thus, criticisms based on sea-core data do not address climatic explanations as they are currently constituted. Unfortunately, we simply do not have empirical access to the state of these critical variables at the time of earlier glacial terminations.

Regardless of the nature of these previous terminations, however, climatic models are not fully convincing for North America as a whole. Insofar as Guthrie's account is dependent on the existence of a Mammoth Steppe in eastern Beringia, it receives little support from palynology. However, even if the mammals were there at low densities, the environments in which they lived supported them, and those environments were changing as the extinctions were occurring. The arguments developed by Graham and Lundelius appear to fail for at least the Pacific Coast, although in the northwestern United States, vegetational simplification seems to have occurred at around the time of the extinctions (Barnosky *et al.*, 1987). Debates over the causes of the extinctions are now likely to focus on areas for which massive habitat loss at the time of extinctions has yet to be convincingly documented: coastal California, for instance, and, to a lesser extent, the Southwest.

CONCLUSIONS

Many other attempts to explain Pleistocene extinctions have been offered. Most form subsets of the arguments developed by Graham and Lundelius (e.g., Slaughter, 1967; Kiltie, 1984) or by Martin (e.g., McDonald, 1984b). Owen-Smith (1987, 1989), for instance, has argued that such huge herbivores as mammoth and ground sloths maintained habitat diversity by their physical impact on the environment. When human predation caused the demise of these keystone ''megaherbivores,'' habitat simplification ensued. This simplification then caused the extinction of other, smaller, mammals, by making them more vulnerable to climatic change or to human predation or both. This ecologically sophisticated argument appears to fail on two grounds. First, with the exception of mammoth, and perhaps mastodon, there is little evidence to support a human role in the extinction of the ''megaherbivores.'' Second, the keystone hypothesis requires that the megaherbivores became extinct first, a requirement for which there is little empirical support. Insofar as Owen-Smith's arguments stress complex mutual relationships between mammals and their environments, however, they do open avenues that should be explored in the future.

A Final Note on Causation

In the 25-year interval between 1965 and 1990, tremendous progress was made in our understanding of late Pleistocene extinctions. Some of this progress was due to the normal accumulation of facts that occurs in active disciplines—more sites excavated, more pollen counted, more bones identified. Some was due to technological innovation and, in particular, to the advent of methods that allow the extraction of valid radiocarbon dates from bone (e.g., Stafford, 1990; Nelson, 1991). Much, however, was due to Paul Martin and to the powerful ways in which he structured his arguments implicating human predation as the cause of the extinctions. All of the climatic arguments, and much of what we have learned about the chronology of the extinctions, have developed in response to the strong position he has taken regarding overkill. His hypotheses have done what good hypotheses are supposed to do: lead to the search for information that would support or falsify them.

The results of that search strongly suggest that overkill could not have been the force that Martin has claimed. The differential appearance of kill sites (only proboscideans, and within the proboscideans, almost only mammoth) and the strong hints that many of the taxa involved may have been on their way to extinction, if not already gone, by 12,000 years ago imply a far lesser human role in the extinctions than the overkill model allows. The climatic models account not only for the extinctions, but also for the histories of smaller mammals during the late Pleistocene. With greater explanatory power, most scientists studying the extinctions issue accept climatic, not overkill, accounts, while recognizing that far more precision is needed in these accounts.

This does not mean that people played no role in causing the extinctions. A multivariate explanation may yet provide the best account of the extinctions. But no matter what the human role might have been, overkill was not the prime cause of the extinctions. That cause rather clearly lies in the massive climatic change that marks the end of the Pleistocene in North America.

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REFERENCES

Ackersten, W. A. (1985). Canine function in *Smilodon* (Mammalia; Felidae; Machairodontinae). *Natural History Museum of Los Angeles County Contributions in Science* **356:** 1–22.

Adam, D. P. (1967). Late-Pleistocene and recent palynology in the Central Sierra Nevada, California. In Cushing, E. J., and Wright, H. E., Jr. (eds.), *Quaternary Paleoecology*, Yale University Press, New Haven, Conn., pp. 275–301.

Adams, D. B. (1979). The cheetah: Native American. *Science* **205:** 1155–1158.

Agenbroad, L. D. (1984). New World mammoth distribution. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, University of Arizona Press, Tucson, pp. 90–108.

Agenbroad, L. D., and Mead, J. I. (1989). Quaternary geochronology and distribution of *Mammuthus* on the Colorado Plateau. *Geology* **17:** 861–864.

Ager, T. A., and Brubaker, L. (1985). Quaternary palynology and vegetational history of Alaska. In Bryant, V. M., Jr., and Holloway, R. G. (eds.), *Pollen Records of Late-Quaternary North American Sediments*, American Association of Stratigraphic Palynologists, Dallas, pp. 353–384.

Anderson, E. (1970). Quaternary Evolution of the Genus *Martes* (Carnivora, Mustelidae). *Acta Zoologica Fennica* **130**.

Anderson, P. M. (1985). Late Quaternary vegetational change in the Kotzebue Sound area, northwestern Alaska. *Quaternary Research* **24:** 307–321.

Anderson, P. M. (1988). Late Quaternary pollen records from the Kobuk and Noatak River drainages, northwestern Alaska. *Quaternary Research* **29:** 263–276.

Axelrod, D. I. (1967). Quaternary extinctions of large mammals. *University of California Publications in Geological Sciences* **74:** 1–42.

Barnosky, A. D. (1989). The Late Pleistocene event as a paradigm for widespread mammal extinction. In Donovan, S. K. (ed.), *Mass Extinctions: Processes and Evidence*, Belhaven Press, London, pp. 235–253.

Barnosky, C. W. (1985). Late Quaternary vegetation in the southwestern Columbia Basin, Washington. *Quaternary Research* **23:** 109–122.

Barnosky, C. W., Anderson, P. M., and Bartlein, P. J. (1987). The northwestern U.S. during deglaciation: Vegetational history and paleoclimatic interpretations. In Ruddiman, W. F., and Wright, H. E., Jr. (eds.), *North America and Adjacent Oceans During the Last Glaciation*, The Geology of North America, Vol. K-3, Geological Society of America, Boulder, Colo., pp. 289–321.

Berta, A. (1985). The status of *Smilodon* in North and South America. *Natural History Museum of Los Angeles County Contributions in Science* **370:** 1–15.

Brown, J. H., and Maurer, B. A. (1989). Macroecology: The division of food and space among species on continents. *Science* **243:** 1145–1150.

Churcher, C. S. (1966). The affinities of *Dinobastis serus* Cope 1893. *Quaternaria* **8:** 263–275.

Churcher, C. S. (1984). *Sangamona*: The furtive deer. In Genoways, H. H., and Dawson, M. R.

(eds.), Contributions in Quaternary vertebrate paleontology: A volume in memorial to John E. Guilday. *Carnegie Museum of Natural History Special Publication* **8:** 233–240.

Churcher, C. S., and Pinsof, J. D. (1987). Variation in the antlers of North American *Cervalces* (Mammalia; Cervidae): Review of new and previously recorded specimens. *Journal of Vertebrate Paleontology* **7:** 373–397.

Cohen, J. A. (1978). *Cuon alpinus. Mammalian Species* **100:** 1–3.

Colbert, E. H., and Chaffee, R. G. (1939). A study of *Tetrameryx* and associated fossils from Papago Spring Cave, Sonoita, Arizona. *American Museum Novitates* **1034.**

Colinvaux, P. A. (1986). Plain thinking on Bering Land Bridge vegetation and mammoth populations. *Quarterly Review of Archaeology* **7:** 8–9.

Crosby, A. W. (1986). *Ecological Imperialism*, Cambridge University Press, Cambridge.

Czaplewski, N. J., Mead, J. I., Ku, T.-L., and Agenbroad, L. D. (1989). Radiometric age assignment for Papago Springs Cave deposits, southeastern Arizona. *Southwestern Naturalist* **34:** 278–281.

Dalquest, W. W. (1978). Phylogeny of American horses of Blancan and Pleistocene age. *Annales Zoologica Fennici* **15:** 191–199.

Davis, M. B. (1967). Late-Glacial climate in the northern United States: A comparison of New England and the Great Lakes region. In Cushing, E. J., and Wright, H. E., Jr. (eds.), *Quaternary Paleoecology*, Yale University Press, New Haven, Conn., pp. 11–43.

Diamond, J. M. (1982). Man the exterminator. *Nature* **298:** 787–789.

Diamond, J. M. (1989a). Quaternary megafaunal extinctions: Variations on a theme by Paganini. *Journal of Archaeological Science* **126:** 167–175.

Diamond, J. M. (1989b). The present, past and future of human-caused extinctions. *Royal Society of London Philosophical Transactions B***325:** 469–477.

Dillehay, T. D. (1989). *Monte Verde: A Late Pleistocene Settlement in Chile. Vol. 1. Palaeoenvironment and Site Context*, Smithsonian Institution Press, Washington, D.C.

Edmund, G. (1985a). The armor of fossil giant armadillos (Pampatheriidae, Xenarthra, Mammalia). *Texas Memorial Museum Pearce-Sellard Series* **40.**

Edmund, G. (1985b). The fossil giant armadillos of North America (Pampatheriinae, Xenarthra = Edentata). In Montgomery, G. G. (ed.), *The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas*, Smithsonian Institution, Washington, D.C., pp. 83–94.

Emerson, S. B., and Radinsky, L. (1980). Functional analysis of sabertooth cranial morphology. *Paleobiology* **6:** 295–312.

Emslie, S. D. (1986). Late Pleistocene vertebrates from Gunnison County, Colorado. *Journal of Paleontology* **60:** 170–176.

Emslie, S. D., and Czaplewski, N. J. (1985). A new record of giant short-faced bear, *Arctodus simus*, from western North America with a re-evaluation of its paleobiology. *Natural History Museum of Los Angeles County Contributions in Science* **371:** 1–12.

Engelmann, G. F. (1985). The phylogeny of the Xenarthra. In Montgomery, G. G. (ed.), *The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas*, Smithsonian Institution, Washington, D.C., pp. 51–64.

Finch, W. I., Whitmore, F. C., Jr., and Sims, J. D. (1972). Stratigraphy, morphology, and paleoecology of a fossil peccary herd from western Kentucky. *U.S. Geological Survey Professional Paper* 790.

Foley, R. L. (1984). Late Pleistocene (Woodfordian) vertebrates from the driftless area of southwestern Wisconsin: The Moscow Fissure local fauna. *Illinois State Museum Reports of Investigations* **39.**

Frick, C. (1937). Horned ruminants of North America. *Bulletin of the American Museum of Natural History* **69.**

Frison, G. C., and Todd, L. C. (1986). *The Colby Mammoth Site*, University of New Mexico Press, Albuquerque.

Furlong, E. L. (1905). *Preptoceras*, a new ungulate from the Samwel Cave, California. *University of California, Department of Geology Bulletin* **4:** 163–169.

Furlong, E. L. (1943). The Pleistocene antelope, *Stockoceros conklingi*, from San Josecito Cave, Mexico. *Carnegie Institute of Washington Publication* **551:** 1–8.

Furlong, E. L. (1946). Generic identification of the Pleistocene antelope from Rancho La Brea. *Carnegie Institute of Washington Publication* **551:** 135–140.

Gidley, J. W. (1921). Pleistocene peccaries from the Cumberland Cave deposit. *Proceedings of the United States National Museum* **57:** 651–678.

Gillette, D. D., and Ray, C. E. (1981). Glyptodonts of North America. *Smithsonian Contributions to Paleobiology* **40.**

Gonyea, W. J. (1976). Behavioral implications of saber-toothed felid morphology. *Paleobiology* **2:** 332–343.

Graham, R. W. (1976). Late Wisconsin mammalian faunas and environmental gradients of the eastern United States. *Paleobiology* **2:** 343–350.

Graham, R. W. (1985a). Diversity and community structure of the Late Pleistocene mammal fauna of North America. *Acta Zoologica Fennica* **170:** 181–192.

Graham, R. W. (1985b). Response of mammalian communities to environmental changes during the Late Quaternary. In Diamond, J., and Case, T. J. (eds.), *Community Ecology*, Harper and Row, New York, pp. 300–313.

Graham, R. W. (1986). Plant-animal interactions and Pleistocene extinctions. In Elliot, D. K. (ed.), *Dynamics of Extinctions*, Wiley, Chicago, pp. 131–154.

Graham, R. W. (1990). Evolution of new ecosystems at the end of the Pleistocene. In Agenbroad, L. D., Mead, J. I., and Nelson, L. W. (eds.), Megafauna and Man. *Mammoth Site of Hot Springs Scientific Papers* **1:** 54–60.

Graham, R. W., and Kay, M. (1988). Taphonomic comparisons of cultural and noncultural faunal deposits at the Kimmswick and Barnhart sites, Jefferson County, Missouri. In Laub, R. S., Miller, N. G., and Steadman, D. W. (eds.), Late Pleistocene and Early Holocene Paleoecology and Archeology of the Eastern Great Lakes Region. *Bulletin of the Buffalo Society of Natural Sciences* **33:** 227–240.

Graham, R. W., and Lundelius, E. L., Jr. (1984). Coevolutionary disequilibrium and Pleistocene extinctions. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, University of Arizona Press, Tucson, pp. 223–249.

Graham, R. W., and Mead, J. I. (1976). Environmental fluctuations and evolution of mammalian faunas during the last deglaciation. In Ruddiman, W. F., and Wright, H. E., Jr. (eds.), *North America and Adjacent Oceans During the Last Glaciation*, The Geology of North America, Vol. K-3, Geological Society of America, Boulder, Colo., pp. 371–402.

Graham, R. W., and Semken, H. A. (1976). Paleoecological significance of the short-tailed shrew (*Blarina*), with a systematic discussion of *Blarina ozarkensis*. *Journal of Mammalogy* **57:** 433–449.

Graham, R. W., Haynes, C. V., Johnson, D. L., and Kay, M. (1981). Kimmswick: A Clovis-mastodon association in eastern Missouri. *Science* **213:** 1115–1117.

Grayson, D. K. (1977). Pleistocene avifaunas and the overkill hypothesis. *Science* **195:** 691–693.

Grayson, D. K. (1980). Vicissitudes and overkill: The development of explanations of Pleistocene extinctions. *Advances in Archaeological Method and Theory* **3:** 357–403.

Grayson, D. K. (1984a). Archaeological associations with extinct Pleistocene mammals in North America. *Journal of Archaeological Science* **11:** 213–221.

Grayson, D. K. (1984b). Explaining Pleistocene extinctions: Thoughts on the structure of a debate. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, University of Arizona Press, Tucson, pp. 807–823.

Grayson, D. K. (1984c). Nineteenth-century explanations of Pleistocene extinctions: A review and analysis. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, University of Arizona Press, Tucson, pp. 5–39.

Grayson, D. K. (1984d). The time of extinction and nature of adaptation of the noble marten, *Martes nobilis*. In Genoways, H. H., and Dawson, M. R. (eds.), Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday. *Carnegie Museum of Natural History Special Publication* **8:** 233–240.

Grayson, D. K. (1987a). An analysis of the chronology of Late Pleistocene mammalian extinctions in North America. *Quaternary Research* **28:** 281–289.

Grayson, D. K. (1987b). Death by natural causes. *Natural History* **5**(87): 8–13.

Grayson, D. K. (1987c). The biogeographic history of small mammals in the Great Basin: Observations on the last 20,000 years. *Journal of Mammalogy* **68:** 359–375.

Grayson, D. K. (1988). Americans before Columbus: Perspectives on the archaeology of the first Americans. In Carlisle, R. C. (ed.), Americans Before Columbus: Ice-Age Origins. *Ethnology Monographs* **12:** 107–123.

Grayson, D. K. (1989). The chronology of North American Late Pleistocene extinctions. *Journal of Archaeological Science* **16:** 153–165.

Guilday, J. E. (1967). Differential extinction during Late-Pleistocene and recent times. In Martin, P. S., and Wright, H. E., Jr. (eds.), *Pleistocene Extinctions: The Search for a Cause*, Yale University Press, New Haven, Conn., pp. 121–140.

Guilday, J. E. (1984). Pleistocene extinction and environmental change. In Martin, P. S., and Klein, R. G. (eds.) *Quaternary Extinctions: A Prehistoric Revolution*, University of Arizona Press, Tucson, pp. 250–258.

Guilday, J. E., Hamilton, H. W., and McCrady, A. D. (1969). The Welsh Cave peccaries (*Platygonus*) and associated fauna, Kentucky Pleistocene. *Annals of the Carnegie Museum* **43:** 249–320.

Guilday, J. E., Anderson, H. W., Anderson, E., and Parmalee, P. W. (1978). The Baker Bluff Cave deposit, Tennessee, and the Late Pleistocene faunal gradient. *Bulletin of the Carnegie Museum of Natural History* **11**.

Gut, H. J. (1959). A Pleistocene vampire bat from Florida. *Journal of Mammalogy* **40:** 534–538.

Guthrie, R. D. (1982). Mammals of the mammoth steppe as a paleoenvironmental indicator. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *The Paleoecology of Beringia*, Academic Press, New York, pp. 307–326.

Guthrie, R. D. (1984a). Alaskan megabucks, megabulls, and megarams: The issue of Pleistocene gigantism. In Genoways, H. H., and Dawson, M. R. (eds.), Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday. *Carnegie Museum of Natural History Special Publication* **8:** 482–510.

Guthrie, R. D. (1984b). Mosaics, allelochemics, and nutrients: An ecological theory of Late Pleistocene megafaunal extinctions. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, University of Arizona Press, Tucson, pp. 259–298.

Guthrie, R. D. (1990a). *Frozen Fauna of the Mammoth Steppe*, University of Chicago Press, Chicago.

Guthrie, R. D. (1990b). Late Pleistocene faunal revolution: A new perspective on the extinction debate. In Agenbroad, L. D., Mead, J. I., and Nelson, L. W. (eds.), Megafauna and Man: Discovery of America's Heartland. *The Mammoth Site of Hot Springs Scientific Papers* **1:** 42–53.

Hall, E. R. (1981). *The Mammals of North America, Vol. 2*, Wiley, New York.

Hansen, R. M. (1978). Shasta ground sloth food habits, Rampart Cave, Arizona. *Paleobiology* **4:** 302–219.

Harington, C. R. (1968). A Pleistocene muskox (*Symbos*) from Dease Lake, British Columbia. *Canadian Journal of Earth Sciences* **5:** 1161–1165.

Harington, C. R. (1969). Pleistocene remains of the lion-like cat (*Panthera atrox*) from the Yukon Territory and Northern Alaska. *Canadian Journal of Earth Sciences* **6:** 1277–1288.

Harington, C. R. (1970). Ice Age mammal research in the Yukon Territory and Alaska. In Smith, R. A., and Smith, J. W. (eds.), *Early Man and Environments in Northwest North America*, Student's Press, Calgary, pp. 35–51.

Harington, C. R. (1971). Ice Age mammals in Canada. *Arctic Circular* **22:** 66–89.

Harington, C. R. (1975). Pleistocene muskoxen (*Symbos*) from Alberta and British Columbia. *Canadian Journal of Earth Sciences* **12:** 903–919.

Harington, C. R. (1981). Pleistocene saiga antelopes in North America and their paleoenvironmental implications. In Mahaney, W. C. (ed.), *Quaternary Paleoclimate*, Geo Abstracts, Norwich, England, pp. 193–225.

Harington, C. R., and Clulow, F. V. (1973). Pleistocene mammals from Gold Run Creek, Yukon Territory. *Canadian Journal of Earth Sciences* **10:** 697–759.

Harris, A. H. (1976). Wisconsin age environments in the northern Chihuahuan Desert: Evidence from the higher vertebrates. In Wauer, R. H., and Riskind, D. H. (eds.), *Transactions: Sym-*

posium on the Biological Resources of the Chihuahuan Desert, National Park Service, Washington, D.C., pp. 23–51.

Harris, A. H. (1985). *Late Pleistocene Vertebrate Paleoecology of the West*, University of Texas Press, Austin.

Haury, E. W. (1953). Artifacts with mammoth remains, Naco, Arizona. 1. Discovery of the Naco mammoth and associated projectile points. *American Antiquity* **19:** 1–14.

Haury, E. W., Sayles, E. B., and Wasley, W. H. (1959). The Lehner mammoth site, southeastern Arizona. *American Antiquity* **25:** 2–30.

Hay, O. P. (1926). A collection of Pleistocene vertebrates from southwestern Florida. *Proceedings of the United States National Museum* **68**(24).

Haynes, C. V., Jr. (1967). Carbon-14 dates and early man in the New World. In Martin, P. S., and Wright, H. E., Jr. (eds.), *Pleistocene Extinctions: The Search for a Cause*, Yale University Press, New Haven, Conn., pp. 267–286.

Haynes, G. (1988). Spiral fractures, cutmarks, and other myths about early bone assemblages. In Willig, J. A., Aikens, C. M., and Fagan, J. L. (eds.), Early Human Occupation in Far Western North America: The Clovis-Archaic Interface. *Nevada State Museum Anthropological Papers* **21:** 1435–149.

Haynes, G. (1989). Mammoth and mastodon socioecology. *Current Research in the Pleistocene* **6:** 67–68.

Haynes, G., and Stanford, D. (1984). On the possible utilization of *Camelops* in North America. *Quaternary Research* **22:** 216–230.

Heaton, T. H. (1985). Quaternary paleontology and paleoecology of Crystal Ball Cave, Millard County, Utah: With emphasis on mammals and description of a new species of fossil skunk. *Great Basin Naturalist* **45:** 337–390.

Heptner, V. G., Nasimovich, A. A., and Bannikov, A. G. (1988). In Hoffmann, R. S. (ed.), *Mammals of the Soviet Union, Vol. 1. Artiodactyla and Perissodactyla*, Smithsonian Institution Libraries and the National Science Foundation, Washington, D.C.

Hester, J. J. (1960). Late Pleistocene extinction and radiocarbon dating. *American Antiquity* **26:** 58–77.

Hibbard, C. W. (1955). Pleistocene vertebrates from the Upper Becerra (Becerra Superior) formation, Valley of the Tequixquiac, Mexico, with notes on other Pleistocene forms. *University of Michigan Museum of Paleontology Contributions* **12**(5): 47–96.

Hibbard, C. W. (1960). An interpretation of Pliocene and Pleistocene climates in North America. *Annual Report of the Michigan Academy of Science, Arts and Letters* **62:** 5–30.

Hibbard, C. W. (1970). Pleistocene mammalian local faunas from the Great Plains and Central Lowland provinces of the United States. In Dort, W., Jr., and Jones, J. K., Jr. (eds.), Pleistocene and Recent Environments of the Central Great Plains. *Department of Geology, University of Kansas, Special Publication* **3:** 385–493.

Hibbert, D. (1982). History of the steppe-tundra concept. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *The Paleoecology of Beringia*, Academic Press, New York, pp. 153–156.

Holliday, V. T., and Johnson, E. (1990). The Lubbock Lake landmark. In Holliday, V. T., and Johnson, E. (eds.), Fifty Years of Discovery: The Lubbock Lake Landmark. *Lubbock Lake Landmark Quaternary Research Center Series* **2:** 19–54.

Honacki, J. H., Kinman, K. E., and Koeppl, J. W. (1982). *Mammal Species of the World: A Taxonomic and Geographic Reference*, Allen Press and The Association of Systematics Collections, Lawrence, Kans.

James, G. T. (1957). An edentate from the Pleistocene of Texas. *Journal of Paleontology* **31:** 796–808.

Jefferson, G. T. (1989). Late Cenozoic tapirs (Mammalia: Perissodactyla) of western North America. *Natural History Museum of Los Angeles County Contributions in Science* **406:** 1–22.

Johnson, E. (ed.). (1987). *Lubbock Lake: Late Quaternary Studies on the Southern High Plains*, Texas A&M University Press, Lubbock.

Johnson, E. (1990). Human modified bones from southern Plains Sites. In Bonnichsen, R., and Sorg, M. H. (eds.), *Bone Modification*, Center for the Study of the First Americans, University of Maine, Orono, pp. 431–471.

Jones, J. K., Jr. (1958). Pleistocene bats from San Josecito Cave, Nuevo Léon, México. *University of Kansas Publications, Museum of Natural History* **9**(14): 389–396.

Kiltie, R. A. (1984). Seasonality, gestation time, and large mammal extinctions. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, University of Arizona Press, Tucson, pp. 299–314.

Klippel, W. E., and Parmalee, P. W. (1984). Armadillos in North American Late Pleistocene contexts. In Genoways, H. H., and Dawson, M. R. (eds.), Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday. *Carnegie Museum of Natural History Special Publication* **8:** 149–160.

Kreutzer, L. A. (1988). Megafaunal butchering at Lubbock Lake, Texas: A taphonomic reanalysis. *Quaternary Research* **30:** 221–231.

Kurtén, B. (1966). Pleistocene bears of North America. 1. Genus *Tremarctos*, spectacled bears. *Acta Zoologica Fennica* **115.**

Kurtén, B. (1967). Pleistocene bears of North America. 2. Genus *Arctodus*, short-faced bears. *Acta Zoologica Fennica* **117.**

Kurtén, B. (1975). A new Pleistocene genus of American mountain deer. *Journal of Mammalogy* **56:** 507–508.

Kurtén, B. (1985). The Pleistocene lion of Beringia. *Annales Zoologici Fennici* **22:** 117–121.

Kurtén, B., and Anderson, E. (1980). *Pleistocene Mammals of North America*, Columbia University Press, New York.

Kutzbach, J. E. (1987). Model simulations of the climatic patterns during the deglaciation of North America. In Ruddiman, W. F., and Wright, H. E., Jr. (eds.), *North America and Adjacent Oceans During the Last Glaciation*, The Geology of North America, Vol. K-3, Geological Society of America, Boulder, Colo., pp. 425–446.

Long, A., and Martin, P. S. (1974). Death of American ground sloths. *Science* **186:** 638–640.

Lull, R. S. (1921). Fauna of the Dallas sand pits. *American Journal of Science* **202:** 159–176.

Lundelius, E. L., Jr. (1960). *Mylohyus nasutus*, long-nosed peccary of the Texas Pleistocene. *Texas Memorial Museum Bulletin* **1.**

Lundelius, E. L., Jr. (1983). Climatic implications of Late Pleistocene and Holocene faunal associations in Australia. *Alcheringa* **7:** 125–149.

Lundelius, E. L., Jr. (1988). What happened to the mammoth? The climatic model. In Carlisle, R. C. (ed.), Americans Before Columbus: Ice-Age Origins. *Ethnology Monographs* **12:** 75–82.

Lundelius, E. L., Jr. (1989). The implications of disharmonious assemblages for Pleistocene extinctions. *Journal of Archaeological Science* **16:** 407–417.

Lundelius, E. L., Jr., Graham, R. W., Anderson, E. Guilday, J., Holman, J. A., Steadman, D. W., and Webb, S. D. (1983). Terrestrial vertebrate faunas. In Porter, S. C. (ed.), *Late Quaternary Environments of the United States, Vol. 1. The Late Pleistocene*, University of Minnesota Press, Minneapolis, pp. 311–353.

Maglio, V. J. (1973). Origin and evolution of the Elephantidae. *Transactions of the American Philosophical Society* **63**(3):.

Marcus, L. F., and Berger, R. (1984). The significance of radiocarbon dates for Rancho La Brea. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, University of Arizona Press, Tucson, pp. 159–183.

Martin, P. S. (1958). Pleistocene ecology and biogeography of North America. In Hubbs, C. L. (ed.), Zoogeography. *American Association for the Advancement of Science Publication* **51:** 375–420.

Martin, P. S. (1963). *The Last 10,000 Years*, University of Arizona Press, Tucson.

Martin, P. S. (1967a). Pleistocene overkill. *Natural History* **76:** 32–38.

Martin, P. S. (1967b). Prehistoric overkill. In Martin, P. S., and Wright, H. E., Jr. (eds.), *Pleistocene Extinctions: The Search for a Cause*, Yale University Press, New Haven, Conn., pp. 75–120.

Martin, P. S. (1973). The discovery of America. *Science* **179:** 969–974.

Martin, P. S. (1984). Prehistoric overkill: The global model. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, University of Arizona Press, Tucson, pp. 354–403.

Martin, P. S. (1987). Late Quaternary extinctions: The promise of TAMS 14C dating. *Nuclear Instruments and Methods in Physics Research* **B29:** 179–186.

Martin, P. S. (1990a). 40,000 years on the Planet of Doom. *Palaeogeography, Palaeoclimatoloy, Palaeoecology* **82:** 187–201.

Martin, P. S. (1990b). Who or what destroyed our mammoths? In Agenbroad, L. D., Mead, J. I., and Nelson, L. W. (eds.), Megafauna and Man. *Mammoth Site of Hot Springs Scientific Papers* **1:** 109–117.

Martin, R. A. (1969). Taxonomy of the giant Pleistocene beaver *Castoroides* from Florida. *Journal of Paleontology* **43:** 1033–1041.

Martin, R. A. (1974). Fossil mammals from the Coleman IIA Fauna, Sumter County. In Webb, S. D. (ed.), *Pleistocene Mammals of Florida*, University of Florida Press, Gainesville, pp. 35–99.

Mayer, J. J., and Wetzel, R. M. (1986). *Catagonus wagneri. Mammalian Species* **259:** 1–5.

McDonald, J. N. (1981). *North American Bison: Their Classification and Evolution*. University of California, Berkeley.

McDonald, J. N. (1984a). An extinct muskox mummy from near Fairbanks, Alaska: A progress report. In Klein, D. R., White, R. W., and Keller, S. (eds.), Proceedings of the First International Muskox Conference. *University of Alaska Biological Papers Special Report* **4:** 148–152.

McDonald, J. N. (1984b). The reordered North American selection regime and Late Quaternary megafaunal extinctions. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, University of Arizona Press, Tucson, pp. 404–439.

McDonald, J. N., and Ray, C. E. (1989). The autochthonous North American musk oxen *Bootherium*, *Symbos*, and *Gidleya* (Mammalia: Artiodactyla: Bovidae). *Smithsonian Contributions to Paleobiology* **66.**

Mead, E. M., and Mead, J. I. (1989a). Quaternary zoogeography of the Nearctic *Dicrostonyx* lemmings. *Boreas* **18:** 323–332.

Mead, E. M., and Mead, J. I. (1989b). Snake Creek Burial Cave and a review of the Quaternary mustelids of the Great Basin. *Great Basin Naturalist* **49:** 143–154.

Mead, J. I. (1983). *Harrington's Extinct Mountain Goat* (Oreamnos harringtoni) *and Its Environment in the Grand Canyon, Arizona*, Ph.D. dissertation, University of Arizona, Tucson.

Mead, J. I., O'Rourke, M. K., and Foppe, T. M. (1986a). Dung and diet of the extinct Harrington's mountain goat (*Oreamnos harringtoni*). *Journal of Mammalogy* **67:** 284–293.

Mead, J. I., Martin, P. S., Euler, R. C., Long, A., Jull, A. J. T., Toolin, L. J., Donahue, D. J., and Linick, T. W. (1986b). Extinction of Harrington's mountain goat. *Proceedings of the National Academy of Science* **83:** 836–839.

Mead, J. I., Agenbroad, L. D., Phillips, A. M., III, and Middleton, L. T. (1987). Extinct mountain goat (*Oreamnos harringtoni*) in southeastern Utah. *Quaternary Research* **27:** 323–331.

Meade, G. E. (1961). The saber-toothed cat, *Dinobastis serus. Texas Memorial Museum Bulletin* **2**(2): 23–60.

Meltzer, D. J. (1986). Pleistocene overkill and the associational critique. *Journal of Archaeological Science* **13:** 51–60.

Meltzer, D. J. (1988). Late Pleistocene human adaptations in eastern North America. *Journal of World Prehistory* **2:** 1–52.

Meltzer, D. J., and Mead, J. I. (1985). Dating Late Pleistocene extinctions: Theoretical issues, analytical bias, and substantive results. In Mead, J. I., and Meltzer, D. J. (eds.), *Environments and Extinctions: Man in Late Glacial North America*, Center for the Study of Early Man, Orono, pp. 145–173.

Merriam, J. C., and Stock, C. (1932). The Felidae of Rancho La Brea. *Carnegie Institute of Washington Publication* **422.**

Miller, W. (1987). *Mammut americanum*, Utah's first record for the American mastodon. *Journal of Paleontology* **61:** 168–183.

Mosimann, J. E., and Martin, P. S. (1975). Simulating overkill by Paleoindians. *American Scientist* **63:** 304–313.

Naples, V. L. (1987). Reconstruction of cranial morphology and analysis of function in the Pleistocene ground sloth *Nothrotheriops shastense* (Mammalia, Megatheriidae). *Natural History Museum of Los Angeles County Contributions in Science* **389:** 1–21.

Naples, V. L. (1989). The feeding mechanism in the Pleistocene ground sloth, *Glossotherium*. *Natural History Museum of Los Angeles County Contributions in Science* **415:** 1–23.

Nelson, D. E. (1991). A new method for carbon isotope analysis of protein. *Science* **251:** 552–554.

Nowak, R. M. (1979). North American Quaternary *Canis*. *University of Kansas Museum of Natural History Monograph* **6.**

Nowak, R. M., and Paradiso, J. L. (1983). *Walker's Mammals of the World*, 4th ed., Johns Hopkins University Press, Baltimore.

Ogden, J. G., III (1967). Radiocarbon determinations of sedimentation rates from hard- and soft-water lakes in northeastern North America. In Cushing, E. J., and Wright, H. E., Jr. (eds.), *Quaternary Paleoecology*, Yale University Press, New Haven, Conn., pp. 175–183.

Olson, S. L., and James, H. F. (1982). Fossil birds from the Hawaiian Islands: Evidence for wholesale extinction by man before Western contact. *Science* **217:** 633–635.

Olson, S. L., and James, H. F. (1984). The role of Polynesians in the extinction of the avifauna of the Hawaiian Islands. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, University of Arizona Press, Tucson, pp. 768–780.

Owen-Smith, N. (1987). Pleistocene extinctions: The pivotal role of megaherbivores. *Paleobiology* **13:** 351–362.

Owen-Smith, N. (1989). Megafaunal extinctions: The conservation message from 11,000 years B.P. *Conservation Biology* **3:** 405–412.

Parmalee, P. W., and Bogan, A. E. (1976). First records of the giant beaver (*Castoroides ohioensis*) from eastern Tennessee. *Journal of the Tennessee Academy of Science* **51**(3): 87–88.

Pimm, S. L., Jones, H. L., and Diamond, J. (1988). On the risk of extinction. *American Naturalist* **132:** 757–785.

Ramenofsky, A. F. (1987). *Vectors of Death*, University of New Mexico Press, Albuquerque.

Ray, C. E., and Sanders, A. E. (1984). Pleistocene tapirs in the eastern United States. In Genoways, H. H., and Dawson, M. R. (eds.), Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday. *Carnegie Museum of Natural History Special Publication* **8:** 283–315.

Ray, C. E., Denny, C. S., and Rubin, M. (1970). A peccary, *Platygonus compressus* Le Conte, from drift of Wisconsin Age in northern Pennsylvania. *American Journal of Science* **268:** 78–94.

Ray, C. E., Linares, O. J., and Morgan, G. S. (1988). Paleontology. In Greenhall, A. M., and Schmidt, U. (eds.), *Natural History of Vampire Bats*, CRC Press, Boca Raton, Fla., pp. 19–30.

Richmond, G. M., and Fullerton, D. S. (1986). Introduction to Quaternary glaciations in the United States of America. *Quaternary Science Reviews* **5:** 3–11.

Ritchie, J. C. (1984). *Past and Present Vegetation of the Far Northwest of Canada*, University of Toronto Press, Toronto.

Ritchie, J. C., and Cwynar, L. C. (1982). The Late Quaternary vegetation of the North Yukon. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *The Paleoecology of Beringia*, Academic Press, New York, pp. 113–126.

Romer, S. (1933). Pleistocene vertebrates and their bearing on the problem of human antiquity in North America. In Jenness, D. (ed.), *The American Aborigines: Their Origin and Antiquity*, University of Toronto Press, Toronto, pp. 47–84.

Ruddiman, W. F., and McIntyre, A. (1982). Severity and speed of Northern Hemisphere glaciation pulses: The limiting case? *Bulletin of the Geological Society of America* **93:** 1273–1279.

Ruddiman, W. F., and Wright, H. E., Jr. (1987). Introduction. In Ruddiman, W. F., and Wright, H. E., Jr. (eds.), *North America and Adjacent Oceans During the Last Glaciation*, The Geology of North America, Vol. K-3, Geological Society of America, Boulder, Colo., pp. 1–12.

Russell, B. D., and Harris, A. H. (1986). A new leporine (Lagomorpha: Leporidae) from Wisconsinan deposits of the Chihuhuan Desert. *Journal of Mammalogy* **67:** 632–639.

Saunders, J. J. (1977). Late Pleistocene vertebrates of the Western Ozark Highland, Missouri. *Illinois State Museum Reports of Investigations* **33.**

Semken, H. A., Jr. (1984). Paleoecology of a Late Wisconsinan/Holocene micromammal sequence in Peccary Cave, northwestern Arkansas. In Genoways, H. H., and Dawson, M. R. (eds.), Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday. *Carnegie Museum of Natural History Special Publication* **8:** 405–431.

Semken, H. A., Jr., and Falk, C. R. (1987). Late Pleistocene/Holocene mammalian faunas and environmental changes on the northern plains of the United States. In Graham, R. W., Semken, H. A., Jr., and Graham, M. A. (eds.), Late Quaternary Mammalian Biogeography and Environments of the Great Plains and Prairies. *Illinois State Museum Scientific Papers* **22:** 176–313.

Semken, H. A., Jr., and Griggs, C. D. (1965). The long-nosed peccary, *Mylohyus nasutus*, from McPherson County, Kansas. *Papers of the Michigan Academy of Science, Arts, and Letters* **50:** 267–274.

Semken, H. A., Miller, B. B., and Stevens, J. B. (1964). Late Wisconsin woodland musk oxen in association with pollen and invertebrates from Michigan. *Journal of Paleontology* **38:** 823–835.

Shoshani, J. (1990). Distribution of *Mammut americanum* in the New World. *Current Research in the Pleistocene* **7:** 124–127.

Simpson, G. G. (1928). Pleistocene mammals from a cave in Citrus County, Florida. *American Museum Novitates* **328**.

Simpson, G. G. (1929). Pleistocene mammalian fauna of the Seminole Field, Pinellas County, Florida. *Bulletin of the American Museum of Natural History* **56:** 561–599.

Simpson, G. G. (1930a). Additions to the Pleistocene of Florida. *American Museum Novitates* **406**.

Simpson, G. G. (1930b). Rodent giants. *Natural History* **30:** 305–313.

Simpson, G. G. (1941). Large Pleistocene felines of North America. *American Museum Novitates* **1136**.

Simpson, G. G. (1945). The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* **85**.

Sinclair, W. J., and Furlong, E. L. (1904). *Euceratherium*, a new ungulate from the Quaternary caves of California. *University of California Publications, Department of Geology* **3**(20): 411–418.

Skeels, M. A. (1962). The mastodons and mammoths of Michigan. *Papers of the Michigan Academy of Science, Arts, and Letters* **47:** 101–134.

Skinner, M. F. (1942). The fauna of Papago Springs Cave, Arizona, and a study of *Stockoceros*. *Bulletin of the American Museum of Natural History* **80**(6): 143–220.

Slaughter, B. H. (1961). The significance of *Dasypus bellus* (Simpson) in Pleistocene local faunas. *Texas Journal of Science* **13:** 311–315.

Slaughter, B. H. (1967). Animal ranges as a clue to Late-Pleistocene extinctions. In Martin, P. S., and Wright, H. E., Jr. (eds.), *Pleistocene Extinctions: The Search for a Cause*, Yale University Press, New Haven, Conn., pp. 155–167.

Spaulding, W. G. (1983). The overkill hypothesis as a plausible explanation for the extinctions of Late Wisconsin megafauna. *Quaternary Research* **20:** 110–112.

Spaulding, W. G. (1990). Vegetational and climatic development of the Mojave Desert: The last glacial maximum to the present. In Betancourt, J. L., Van Devender, T. R., and Martin, P. S. (eds.), *Pack Rat Middens: The Last 40,000 Years of Biotic Change*, University of Arizona Press, Tucson, pp. 166–199.

Stafford, T. W., Jr. (1990). Late Pleistocene megafauna extinctions and the Clovis Culture: Absolute ages based on accelerator 14C dating of skeletal remains. In Agenbroad, L. D., Mead, J. I., and Nelson, L. W. (eds.), Megafauna and man: Discovery of America's heartland. *The Mammoth Site of Hot Springs Scientific Papers* **1:** 118–122.

Stafford, T. W., and Semken, H. A., Jr. (1990). Accelerator ^{14}C dating of two micromammal species representative of the late Pleistocene disharmonious fauna from Peccary Cave, Newton County, Arkansas. *Current Research in the Pleistocene* **7:** 129–132.

Steadman, D. W. (1989). Extinction of birds in eastern Polynesia: A review of the records, and comparisons with other Pacific island groups. *Journal of Archaeological Science* **16:** 177–205.

Steadman, D. W., and Martin, P. S. (1984). Extinction of birds in the Late Pleistocene of North America. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, University of Arizona Press, Tucson, pp. 466–477.

Steadman, D. W., Stafford, T. W., Jr., Donahue, D. J., and Jull, A. J. T. (1991). Chronology of Holocene vertebrate extinctions in the Galápagos Islands. *Quaternary Research* (in press).

Stock, C. (1925). Cenozoic Gravigrade Edentates of Western North America. *Carnegie Institute of Washington Publication* **331**.

Stock, C. (1956). Rancho La Brea: A record of Pleistocene life in California. *Los Angeles County Museum of Natural History Science Series 20, Paleontology* **11**.

Stock, C., and Furlong, E. L. (1927). Skull and skeletal remains of a ruminant of the *Preptoceras-Euceratherium* group from the McKittrick Pleistocene, California. *University of California Publications, Department of Geological Science* **16**(10): 406–434.

Stovall, J. W. (1937). *Euceratherium bizzelli*, a new ungulate from Oklahoma. *Journal of Paleontology* **11:** 450–455.

Taylor, D. W. (1965). The study of Pleistocene nonmarine mollusks in North America. In Wright, H. E., Jr., and Frey, D. G. (eds.), *The Quaternary of the United States*, Princeton University Press, Princeton, N.J., pp. 597–611.

Van Devender, T. R. (1990). Late Quaternary vegetation and climate of the Sonoran Desert, United States and Mexico. In Betancourt, J. L., Van Devender, T. R., and Martin, P. S. (eds.), *Pack Rat Middens: The Last 40,000 Years of Biotic Change*, University of Arizona Press, Tucson, pp. 134–165.

Van Valkenburgh, B., and Ruff, C. B. (1987). Canine tooth strength and killing behavior in large carnivores. *Journal of Zoology* **212:** 379–397.

Van Valkenburgh, B., Grady, F., and Kurtén, B. (1990a). The Plio-Pleistocene cheetah-like cat *Miracinonyx inexpectatus* of North America. *Journal of Vertebrate Paleontology* **10:** 434–454.

Van Valkenburgh, B., Teaford, M. F., and Walker, A. (1990b). Molar microwear and diet in large carnivores: Inferences concerning diet in the sabretooth cat, *Smilodon fatalis*. *Journal of Zoology* **222:** 319–340.

Waldrop, J. S. (1974). The scimitarcat, *Homotherium serum*, from the Florida Late Pleistocene. In Webb, S. D. (ed.), *Pleistocene Mammals of Florida*, University of Florida Press, Gainesville, pp. 154–157.

Walker, D. N. (1987). Late Pleistocene/Holocene environmental changes in Wyoming: The mammalian record. In Graham, R. W., Semken, H. A., Jr., and Graham, M. A. (eds.), Late Quaternary Mammalian Biogeography and Environments of the Great Plains and Prairies. *Illinois State Museum Scientific Papers* **22:** 334–393.

Webb, S. D. (1965). The Osteology of *Camelops*. *Los Angeles County Museum Science Bulletin* **1**.

Webb, S. D. (1974a). Chronology of Florida Pleistocene mammals. In Webb, S. D. (ed.), *Pleistocene Mammals of Florida*, University of Florida Press, Gainesville, pp. 5–31.

Webb, S. D. (1974b). Pleistocene llamas of Florida, with a brief review of the Lamini. In Webb, S. D. (ed.), *Pleistocene Mammals of Florida*, University of Florida Press, Gainesville, pp. 170–213.

Webb, S. D. (1974c). The status of *Smilodon* in the Florida Pleistocene. In Webb, S. D. (ed.), *Pleistocene Mammals of Florida*, University of Florida Press, Gainesville, pp. 149–153.

Webb, S. D. (1985). The interrelationships of tree sloths and Xenarthra. In Montgomery, G. G. (ed.), *The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas*, Smithsonian Institution, Washington, D.C., pp. 105–112.

Webb, S. D. (1990). On the relationship of *Navahoceros* to other New World Cervidae. *Journal of Vertebrate Paleontology* (*Suppl.*) **10**(3): 48A.

Webb, S. D., and Barnosky, A. D. (1989). Faunal dynamics of Pleistocene mammals. *Annual Review of Earth and Planetary Sciences* **17:** 413–438.

Webb, S. D., and Wilkins, K. T. (1984). Historical biogeography of Florida Pleistocene mammals. In Genoways, H. H., and Dawson, M. R. (eds.), Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday. *Carnegie Museum of Natural History Special Publication* **8:** 233–240.

Westgate, J. A., Stemper, B. A., and Péwé, T. L. (1990). A 3 M.Y. record of Pliocene-Pleistocene loess in interior Alaska. *Geology* **18:** 858–861.

Wetzel, R. M. (1977). The Chacoan peccary *Catagonus wagneri* (Rusconi). *Carnegie Museum of Natural History Bulletin* **3**.

Wetzel, R. M., Dubos, R. E., Martin, R. L., and Myers, P. (1975). *Catagonus*, an "extinct" peccary, alive in Paraguay. *Science* **189:** 379–381.

Williams, D. F., Thunell, R. C., Tappa, E., Rio, D., and Raffi, I. (1988). Chronology of the Pleistocene oxygen isotope record: 0–1.88 m.y. B.P. *Palaeogeography, Palaeoclimatology, Palaeoecology* **64:** 221–240.

Wilson, M. (1974). The Casper local fauna and its fossil bison. In Frison, G. (ed.), *The Casper Site: A Hell Gap Bison Kill on the High Plains*, Academic Press, New York, pp. 125–171.