megafauna. Were the extinctions sudden or gradual? Did other landmasses experience similar waves of extinction, and if so, were they synchronous across regions? Did small animals and plants become extinct at the same time? Were the Pleistocene extinctions caused by climatic and geological changes, or did intense hunting by humans result in the extirpation of these large beasts? These are questions that must be answered if we are to understand faunal change and biogeography in the Pleistocene.

The Overkill Hypothesis

The prehistoric, or Pleistocene, **overkill hypothesis** states that humans were responsible for the mass extirpation of large herbivorous mammals (over 50 kg), and the carnivores and scavengers dependent upon them, after the Wisconsin glaciers had retreated. This is an old hypothesis, but is also one that has been most clearly presented as a straightforward explanation with potentially

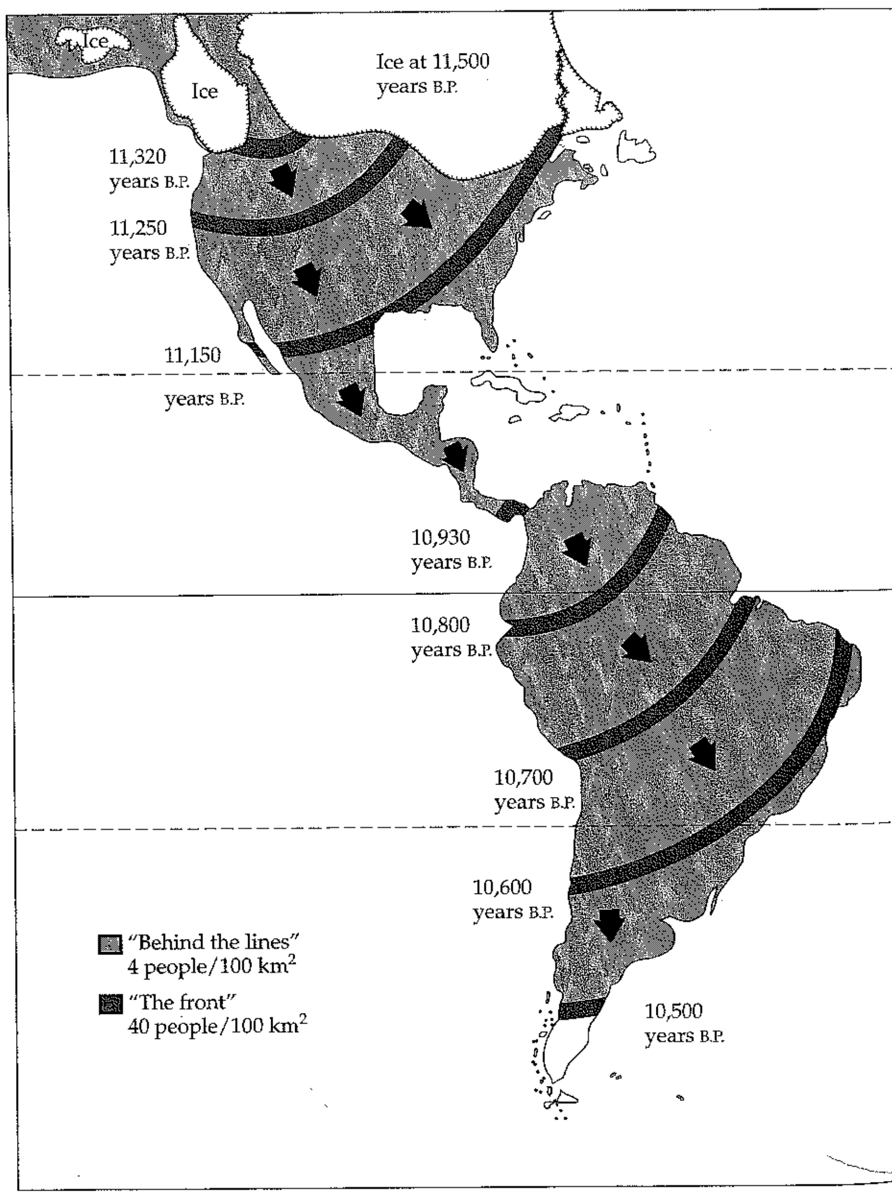


Figure 7.30 The temporal sequence of advancing populations of human big-game hunters correlates well with the progressive extinction of large Pleistocene mammal species. According to the Pleistocene overkill hypothesis, sophisticated hunters crossed Beringia and expanded southward, maintaining a relatively dense population by subsisting on large mammals. Human populations may have colonized the America's well ahead of these dates, but their population densities, technology, and ability to cause significant ecological disturbance were very limited in comparison to the more sophisticated hunting societies that followed. (After Martin 1973.)

falsifiable assumptions and predictions (Martin 1967, 1973, 1995). Let us consider this hypothesis in detail for comparison with alternative explanations.

The overkill model suggests that a population of aggressive and skillful human hunters entered North America during the late Wisconsin by crossing Beringia from Asia. Once these hunters colonized America, they spread southward and eastward through North America and into South America, killing large animals as they went (Figure 7.30). The native American animals lacked adequate defensive behaviors to outwit or elude their new predators. The abundant food supplies obtained from their hunts permitted human populations to remain high and in constant need of new and massive food sources. Behind this trail of carnage, there were no more waves of mammalian immigrants from Asia to replace those species that became extinct. Most of the large mammals that survived were those that had spread to the New World from the Old World since the evolution of Pleistocene humans, so they were presumably already adapted to human hunters.

The evidence supporting this scenario is of several types. First, fossil evidence shows that prehistoric humans and large mammals coexisted in the Americas and that the people hunted the extinct herbivores. Arrow points in carcasses and remains of massive animal kills are clearly demonstrated. Second, late Wisconsin extinctions in North America were nonrandom in that many more large and very large mammals than smaller ones became extinct during the period from 12,000 to 10,000 years B.P. (Figure 7.31). Third, as noted above, immigrants from Beringia and Eurasia, including caribou, moose, deer, and Dall's and bighorn sheep, fared much better than native species (Figure 7.32; Kurtén and Anderson 1980). Fourth, extinctions of large mammals appear to have begun in the north and proceeded rapidly and systematically southward (compare to Figure 7.30). Finally, when the dates of the last known occurrences of species are compared with a computer simulation of southward human migration (assuming high human population densities), the two appear to coincide rather closely (Mosiman and Martin 1975).

The Pleistocene overkill model could be tested and possibly falsified by showing that many different types of animals and plants became extinct at the same time, that extinctions were under way before humans arrived, that aggressive human hunters coexisted with large mammals for long periods, that human populations were never at high densities, or that comparable extinctions on other continents did not correspond with an invasion by ecologically significant human societies.

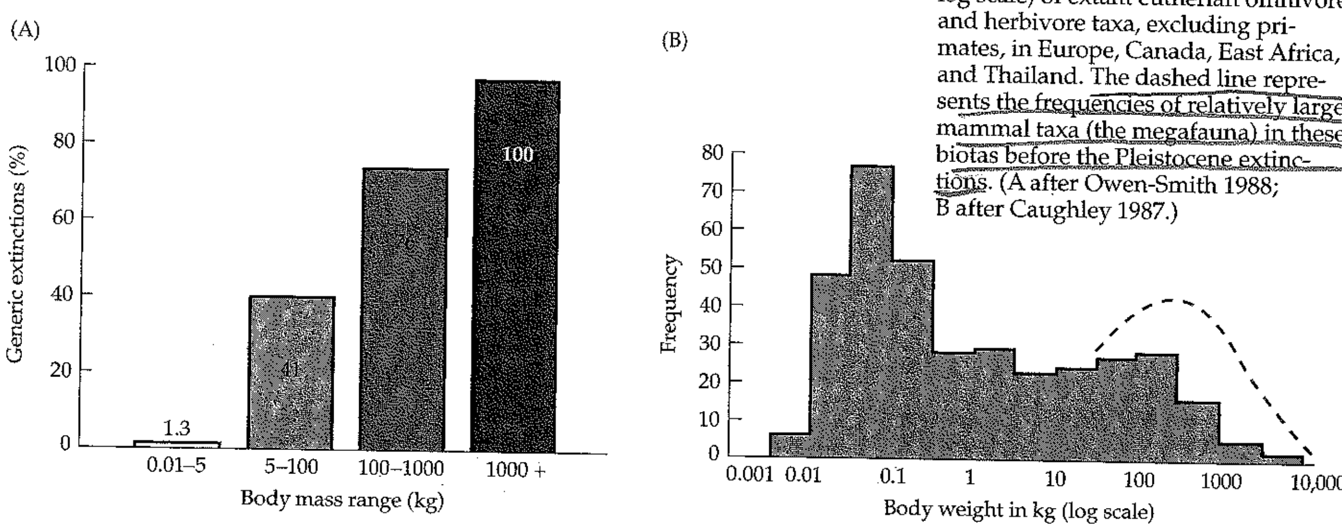


Figure 7.31 Pleistocene extinctions of mammals tended to be highly nonrandom, disproportionately affecting relatively large taxa. (A) Extinction rates among mammalian herbivore genera of different body sizes in North America, South America, Europe, and Australia during the late Pleistocene. (B) Distribution of body weights (on a log scale) of extant eutherian omnivore and herbivore taxa, excluding primates, in Europe, Canada, East Africa, and Thailand. The dashed line represents the frequencies of relatively large mammal taxa (the megafauna) in these biotas before the Pleistocene extinctions. (A after Owen-Smith 1988; B after Caughley 1987.)

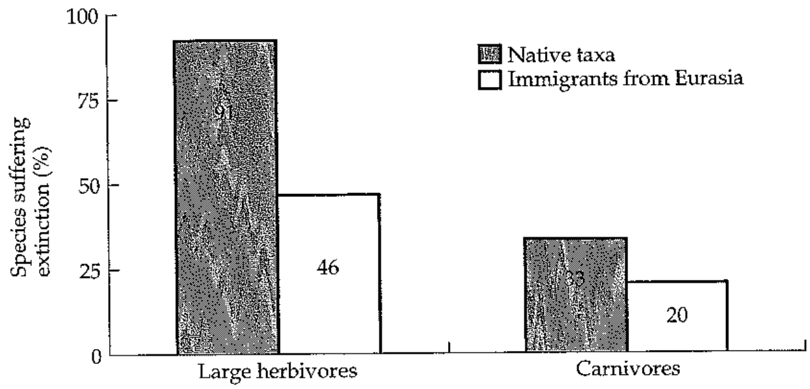


Figure 7.32 Extinction rates among native and immigrant large herbivores and carnivores in North America during the late Wisconsin. (After Kurtén and Anderson 1980.)

Alternative Explanations for Pleistocene Extinctions

As with any controversial theory in biogeography, there are several alternative explanations to account for Pleistocene extinctions of mammals. The overkill hypothesis, if correct, paints a rather brutal and disparaging picture of the early human pioneers in North America. Some authors feel that these colonists have been given a "bum rap"—they may have been instrumental in reducing prey population sizes, but extinctions were already occuring in response to climatic shifts at the end of the Ice Age. They point to other groups of organisms, such as raptors and large scavenging birds, that experienced high rates of extinction at the same time as large herbivores (Grayson 1977). However, as we noted earlier, such extinctions are entirely consistent with the overkill hypothesis, which predicts a loss not just of the megafauna, but of dependent predators and scavengers as well (see Owen-Smith 1988).

Raptors + Scavengers also went extinct (but argue either way)

One observation that has always been puzzling is that the North American fauna did not disappear until after the Wisconsin glaciers retreated. Hence the late Pleistocene extinctions cannot be related directly to glaciation, cold climate, or any other catastrophic geological event, such as flooding. Nevertheless, many researchers contend that climatic changes were the direct cause of the extinctions, either through increased aridity (Guilday 1967) or by decreased equability (Slaughter 1967; Axelrod 1967).

Extinctions After Wisconsin Glacier retreat ∴ not climate?

An excellent discussion of Pleistocene extinctions by Kurtén and Anderson (1980) explains why paleontologists generally prefer a climatic explanation. Pleistocene extinctions of mammals were not restricted to the period of 12,000 to 10,000 years B.P., but were part of a fairly continuous series of episodes during the latest Cenozoic (Table 7.3). The Pliocene Blancan extinction (mainly

Extinctions not restricted to time of human habitation.

Table 7.3
Extinction of North American mammals during the last 4 million years

Animal size	Blancan (3.5–1.8)	Irvingtonian (1.8–0.7)	Rancholabrean (0.7–0.01)	Extinction total	Surviving species	Percent extinct
Small (1–907 g)	97	55	29	181	166	52%
Medium (908 g–181 kg)	31	25	33	89	50	64%
Large (182–1730 kg)	5	12	35	52	16	76%
Very large (> 1730 kg)	1	2	5	9	1	90%

Source: After Kurtén and Anderson (1980).

Note: Duration of periods is in million years B.P.

between 3.3 and 2.4 million years B.P.) resulted in the disappearance from North America of at least 125 mammalian species, of which three-fourths were animals smaller than 1 kg in body mass. During that time, aridity increased, grasslands replaced forests, and many forest dwellers and browsers died out. Following that depletion of the fauna, surviving grazers and rodents underwent evolutionary radiation, and small carnivores also increased in abundance and diversity. In the Irvingtonian extinction of the Pleistocene (1.8 to 0.7 million years B.P.) only 89 taxa disappeared, 80% of which were small or medium-sized (< 180 kg). Extinction rates during the Pleistocene were fairly low and constant until the late Wisconsin, when many small, medium, and large animals disappeared. However, as stated earlier, a highly disproportionate number of large mammals became extinct in the late Wisconsin as compared with other episodes (see Figure 7.31A).

The cause of the late Pleistocene extinctions remains one of the most important and intriguing mysteries of our field. In a wonderful essay on the nature and causes of historic extinctions, Jared Diamond (1984) called on one of the world's greatest detective minds to help solve the mystery: Sir Arthur Conan Doyle—alias Sherlock Holmes. In "Silver Blaze," Holmes called attention to "the curious incident of the dog in the night-time." When the dim-witted Inspector Gregory observed that "the dog did nothing in the night-time," Holmes remarked that "that was the curious incident"—it indicated that the stables pet was familiar with the "intruder." The decisive clues to the causes of Pleistocene extinctions also may be the "dogs that did nothing in the night-time," namely, the species and biotas that survived while others became extinct.

Champions of the overkill hypothesis call our attention to four such "curious incidents." First, they ask, why did the North American megafauna diversify when climatic conditions seemed least favorable during the Wisconsin, only to suffer so many extinctions when climates warmed and environmental conditions became more favorable? Second, why did the megafaunal extinctions not occur during an earlier glaciation? Third, why were most groups of small animals spared from mass extinctions while their larger counterparts were devastated? Finally, why didn't the megafaunal species of Africa suffer extinctions comparable to those among biotas on other large continents (Figure 7.33)?

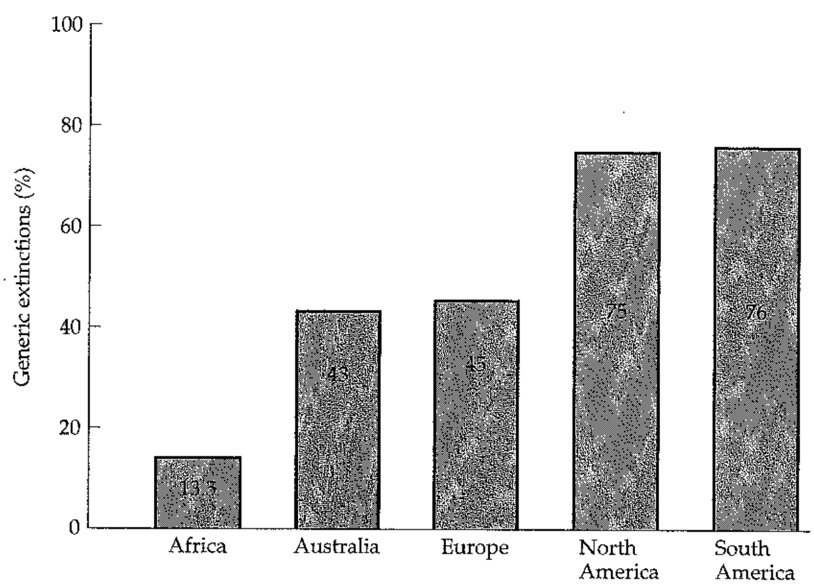


Figure 7.33 Extinction rates among mammalian herbivore genera with medium to large body sizes (> 5 kg) on different continents during the late Pleistocene. (After Owen-Smith 1988.)

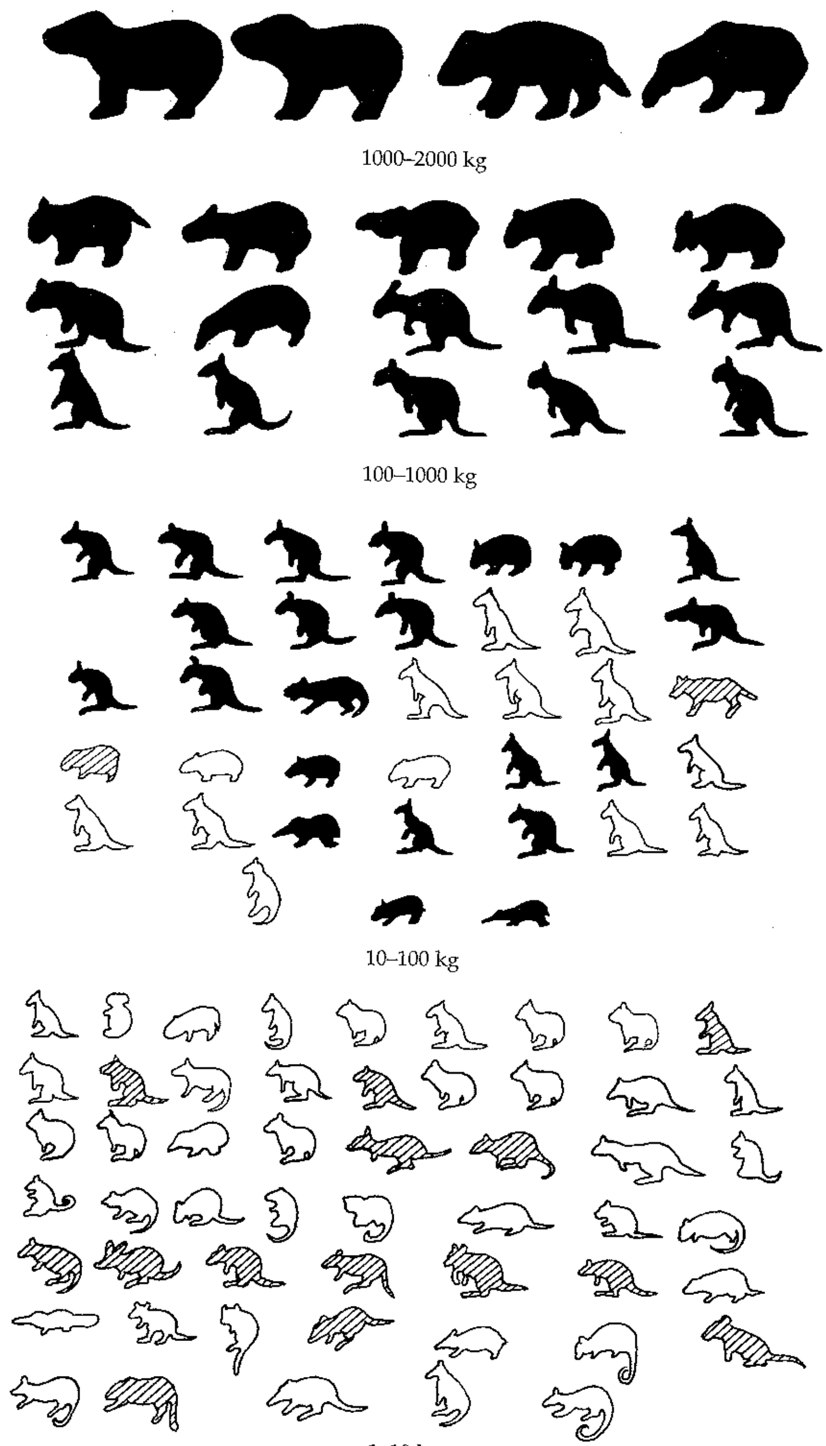
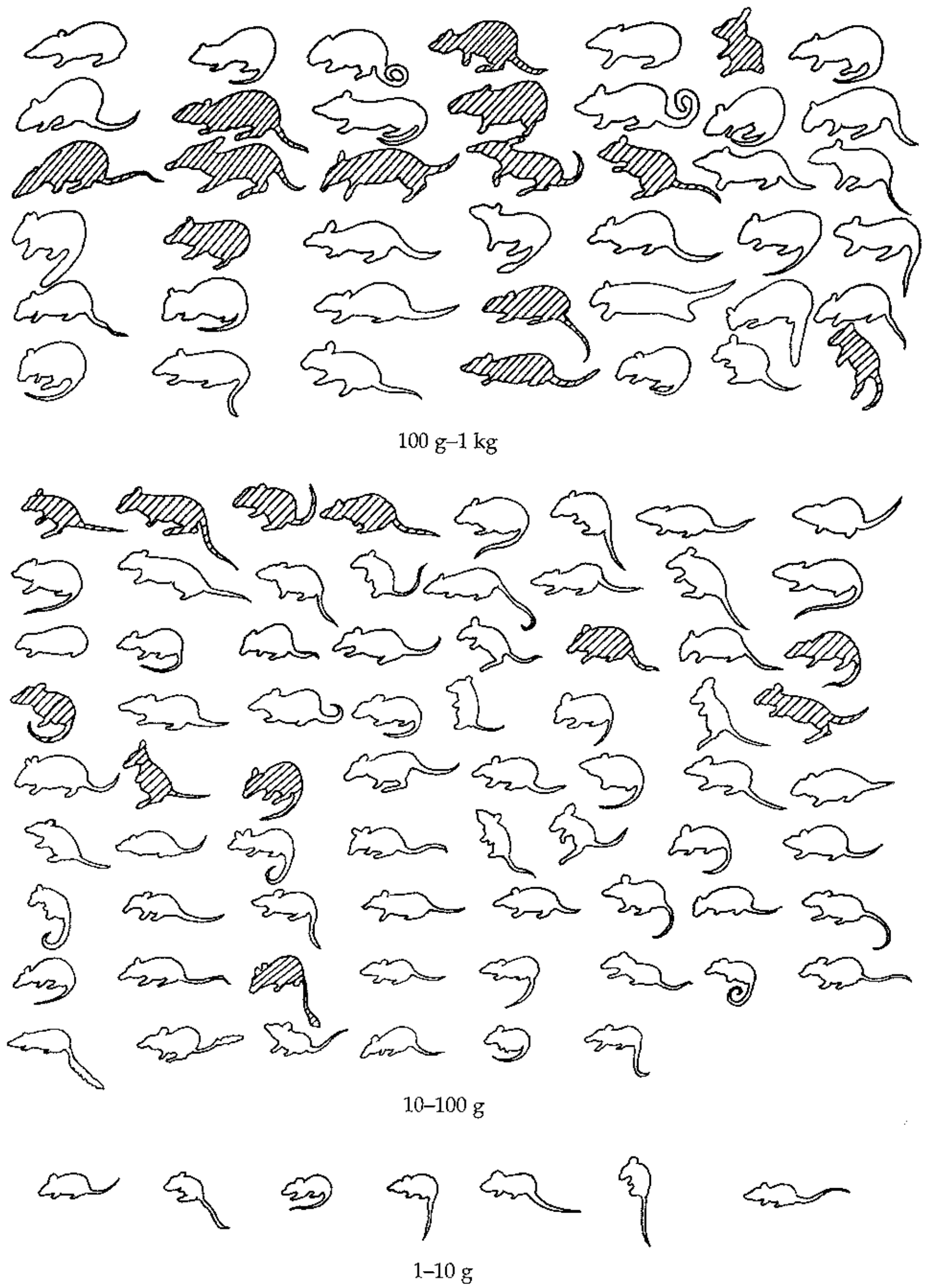


Figure 7.34 Selective extinctions of large, megafuanal mammals in Australia during the Pleistocene and Holocene. Shown are outline drawings of species known to occur in these regions when they were colonized by aboriginal humans. Species suffering extinction during the Pleistocene and early Holocene are shown in black, while those that became extinct or endangered following European colonization are shaded (open outlines indicate extant, nonendangered species). (Information courtesy of T. F. Flannery, art based on original drawings by Tish Ennis, Australian Museum, Sydney.)

No big extinction in Africa because animals coevolved with humans.

Some have argued that familiarity is the key to the last question: *Homo sapiens* has had such a long history in Africa that, at least until modern times, native African societies have had little impact on the megafauna that coevolved with them. Proponents of the overkill hypothesis note that Africa may be the exception that proves the rule. In fact, the megafauna of most landmasses suffered mass extinctions during the Pleistocene, but they were far from synchronous. A mass extinction of the Australian megafauna for exam-



ple, occurred roughly 35,000 years B.P. (Figure 7.34), while mass extinctions on Madagascar and the Galápagos Islands have occurred within the last 1000 years (Figure 7.35). These chronologies are difficult to explain according to the climate-based hypothesis, since climatic reversals were synchronous across the globe. On the other hand, the timing of these waves of megafaunal extinction is coincident with invasions by aggressive hunting societies, increased human population levels, extensive use of fire, and other activities that significantly modified native ecosystems.

Despite these arguments, champions of the climate-based hypothesis continue to take issue with the overkill hypothesis. Webb and Barnosky (1989), for example, recognized six major episodes of Neogene extinctions of North American mammals, each thought to be coincident with rapid climatic changes. But

Rapid Climate Change may be cause

Afroeurasia: No major episodes of extinction during past 100,000 years, although some losses occurred.

Meganesia: Humans arrive 40,000–60,000 years B.P.; major extinction episode follows, but extends to circa 15,000 years B.P. (or later?).

Americas: Ecologically significant human populations arrive 12,500 years B.P.; major extinction episode terminates circa 10,500 years B.P., few extinctions thereafter.

Mediterranea: Humans arrive 10,000 years B.P.; major extinction episode follows and terminates circa 4,000 years B.P., few extinctions thereafter.

Antillea: Humans arrive 7000 years B.P.; major episode of extinction follows, but extends to circa A.D. 1600 (or later?).

Madagascar: Humans arrive 2000 years B.P.; major episode of extinction follows and terminates circa A.D. 1500, few extinctions thereafter.
Mascarenes (Ms): Humans arrive A.D. 1600; major episode of extinction follows and terminates circa A.D. 1900.
New Zealand: Humans arrive 800–1000 years B.P.; major episode of extinction follows and terminates circa A.D. 1500.

Commander Islands (C): Humans arrive A.D. 1741; Steller's sea cow extinct by A.D. 1768.
Wrangel Island (W): Humans arrive ?; mammoths survive to 4000 years B.P.
Galápagos Islands (G): Humans arrive A.D. 1535; modern-era extinctions only.

Figure 7.35 The geography and chronology of Pleistocene extinctions may be correlated with major episodes of human colonization. Extinction episodes during the Pleistocene were relatively minor in regions with a long history of human occupation, but severe and coincident with colonization by ecologically significant human cultures elsewhere (see also Chapter 18). (After MacPhee and Marx 1997; based on drawings by Clare Flemming.)

why, then, ask the advocates of the overkill hypothesis, were these extinctions not synchronous across the continents, and why were they not recorded for all of the ten or so major climatic reversals of the Pleistocene?

But if rapid climate Δ, why not same everywhere?

As we can see, this debate is far from over, and it is likely that the pendulum of consensus will swing many times between champions of the competing theories. In fact, it is likely that the true causes of the Pleistocene extinctions involve a multitude of factors, including anthropogenic as well as climate-driven changes in native ecosystems, physiological effects of altered climates, and biotic exchanges and resultant changes in interspecific interactions, including the appearance of new predators, competitors, diseases, and parasites (see MacPhee and Marx 1997; Flannery 1994). In other words, many combinations of ecological or evolutionary factors (anthropogenic and otherwise) might have contributed to the waves of Pleistocene extinctions, and hunting by early human colonists may merely have delivered the final and fatal blow to some species. Unfortunately, this explanation is difficult to evaluate, even if it is correct.

Regardless of its cause or causes, the elimination of the majority of large mammals and birds has been one of the most important events in the relatively recent history of terrestrial biotas. Not only did these animals themselves experience reductions in their populations and geographic ranges ending in their extinction, but their disappearances may also have had important effects on other species. The herbivores that did survive were faced with fewer potential competitors, and the surviving carnivores had to make do with fewer prey. Parasites, scavengers, and mutualists of the extinct species either switched to new associates or became extinct themselves (see Owen-Smith 1988). For example, Steadman and Martin record high extinction rates among carrion-feeding birds at the end of the Pleistocene, including eagles, vultures, teratorns, and condors. Finally, it is known from fossil feces (**coprolites**) that the extinct large herbivores consumed large quantities of certain extant plant species. To what extent has release from such herbivory contributed to the shifts in plant species ranges and the changes in the distribution of vegetation types that are known to have occurred within the last 20,000 years? It is perhaps as important to investigate these questions as it is to solve the riddle of the extinctions of the Pleistocene megafauna. To paraphrase G. G. Simpson, our ability to understand and effectively curtail the ongoing wave of extinctions may well depend on our ability to learn the lessons of these prehistoric extinctions (see Chapters 17 and 18).

extant = existing.

elephant, sloth, camel, tiger, lion, horse, mastodon.

Today: both factors 1) climate Δ 2) Human etc.

Anti-overkill Hypoth.

- many small species went extinct too.
- possible disease?
- drought: large animals most vulnerable
- plants of herbivores still present today, but plants more tolerant to drought.
- climate Δ not same everywhere, but N. Am. Hardest?
- Eagles extinct too...
- space Aliens

Box 7.1
Biogeographic responses to climatic cycles of the Pleistocene

1. The gradual period of cooling during the mid-Cenozoic was followed by repeated and dramatic climatic reversals during the Pleistocene.
2. Communities and coevolved assemblages of plants and animals that may have persisted for tens of millions of years during the equable Mesozoic were disrupted, with many species responding independently of one another based on their particular physiological tolerances, life history strategies, and dispersal abilities.
3. Many species were able to track the geographic shifts of their prime climates and habitats, but they typically lagged behind, often by centuries, sometimes by millennia.
4. Vegetation zones tended to shift toward the equator (or lower elevations) during glacial periods and toward the poles (or higher elevations) during interglacials, but the shifts were complicated and strongly influenced by geographic features (e.g., mountains, ocean basins, prevailing winds, and proximity to the ice sheet).
5. In general, open-canopied biomes (tundra, savannas, grasslands, and prairies) expanded during glacial maxima at the expenses of closed biomes (i.e., forests). These trends were reversed during periods of global warming, but again, the rates of shifts varied substantially among biomes, as did the particular species composition of each biome and community.
6. Despite substantial variation among regions, glacial climates tended to be dry as well as cool. On the other hand, glacial warming resulted in flooding of coastlines, submergence of landbridges, introgression of marine waters onto land, and formation of extensive shallow seas and great, post-glacial lakes and rivers.
7. On land, climatic zones changed dramatically, not only in location and areal coverage, but also in their characteristic nature (i.e., combinations of temperature, seasonality, precipitation patterns, and soil conditions). As a result, the Pleistocene events created novel environments, fostering development of novel communities, while other communities disappeared.
8. Although there was much variation within taxonomic groups, plants tended to shift more slowly than animals. The geographic dynamics of species during the Pleistocene created many isolated populations, in some cases promoting evolutionary divergence and diversification of certain biotas.
9. Many plants and animals that were unable to track their shifting environments were able to remain in situ by adapting to the altered conditions.
10. The remaining species, unable to shift or adapt, went extinct. During the initial cycles of climatic reversals, extinctions were much more common among plants than animals. This may have been a consequence of the comparatively limited ability of plants to disperse and the decoupling of associations among plants and between plants and animals that served as pollinators, parasites, and herbivores.
11. In contrast, until the most recent glacial cycles, animal extinctions were relatively few, and many groups, especially the large herbivores and carnivores, underwent major radiations.
12. The tables were turned, however, during the more recent glacial cycles, which witnessed waves of extinctions of many animals, especially larger ones, while comparatively few plants suffered extinctions. It appears that the initial climatic reversals may have "weeded out" most of the intolerant plants, leaving behind those more capable of dispersing with, or adapting to, climatic reversals.
13. During the most recent glacial cycle, large mammals may have become too specialized on the now waning glacial habitats (especially steppes and savannas). Alternatively, these "megafaunal" extinctions may have resulted from biotic exchanges associated with glacial events, which, again, decoupled coadapted groups of species or introduced novel competitors and predators, including *Homo sapiens* (see Chapters 17 and 18).

dinal shifts in isotherms and biogeographic patterns have tended to be substantial in the mid-latitudes (35° to 55°), but relatively minor at lower latitudes (Figure 7.12).

Shifts in climatic zones and biomes, however, are complicated by currents and topographic features, including mountain ranges, large rivers, and other bodies of water. In Europe, the southward shift of some biomes during the most recent glacial maximum was blocked by the Alps, Pyrenees, and Mediterranean Sea (Figure 7.13). In contrast, the north-south-running rivers and mountain ranges of North America facilitated extensions of high-latitude biomes deep into subtemperate and subtropical latitudes. During the Wisconsin maximum (about 18,000 years B.P.), boreal forests and tundra penetrated deep into the interior of the continent along the Mississippi River valley and