in the Khazar levels of the Volga valley, where they comprise 2–8 percent of all the bones found on sandbars (Vereshchagin 1959). Dwarf forms of large-antlered deer are known from southern Italy and from Mediterranean islands (Bonfiglio 1978).

The giant deer ranged throughout Europe, to Scandinavia and the Timanskij Ridge on the north, to North Africa, the Caucasus, Kazakhstan, and southern Siberia, as far north as Tyumen, and Transbaikal (Kyakhta). Giant deer remains are abundant in Mousterian sites on the Russian Plain: at Starye Duruitory (Moldavia) they represent 2 percent of all bones from economically important species (David 1980), and at Korman IV (Ukraine) they make up 2.2 percent (Tatarinov 1977). In the northern Caucasus they make up 1.3 percent at Il'skaya (Vereshchagin 1959) and 12.0 percent at Barakaevskaya (Baryshnikov 1979). Giant deer remains are very numerous in the Crimea: at Shajtan-Koba they represent 39.4 percent (Gromov 1948). In the Transcaucasus they are rare—only 0.07 percent in Akhshtyr Cave (Vereshchagin 1959).

The antlers of the male giant deer, reaching 3.7 m across, indicate that the species inhabited open landscapes—glades where these alternated with copses on river floodplains. This conclusion is confirmed by comparison with the moose, a forest animal. In the giant deer, the orbits were larger, the teeth more hypsodont, and the lower jaw more massive.

In the late Valdaj (Würm) the range of the giant deer shrank dramatically (fig. 22.6). It disappeared in Siberia, Kazakhstan, and the Caucasus. The latest finds in Siberia date from the beginning of the Upper Paleolithic (Verkholenskaya gora; Ermolova 1978). On the Russian Plain they are rare. Thus, in the Upper Paleolithic levels of Korman IV on the Dnestr, giant deer bones comprise only 0.1 percent of the remains of economically important species (Tatarinov 1977), and at Kostenki VIII on the Don only 0.2 percent (Vereshchagin and Kuz'mina 1977). It was more abundant in the Crimea—up to 7.8 percent of bones from herbivorous mammals (Bibikova and Belan 1979).

In western Europe giant deer bones are rare in sites dating from the Aurignacian and Magdalenian. In France it disappeared in the Allerød (Bouchud 1965), while in the northern part of West Germany it was still present in the Preboreal (Guenther 1960). It is possible that the giant deer survived into the Christian era in Ireland (Mitchell and Parkes 1949) and was destroyed by medieval Anglo-Saxons.*

In eastern Europe the species probably became extinct at the end of the Pleistocene, since it has not been recorded from any Mesolithic or Neolithic site (Paaver 1965, Vereshchagin 1979). Suggestions that some giant deer bones from the Ukraine (Tarasovka in Dneprepetrovsk oblast'; Pidoplichko 1951a) and Siberia (Kamyshlov; Cherskij 1891) date from the Holocene require confirmation.

It is not clear why this species became extinct. The most commonly cited reasons are the colossal energy demands of male antlers, low fertility, the need for relatively warm conditions, the shrinkage of mesophytic meadows during the Würm (Valdaj), and prehistoric hunting.

The Primitive Bison *Bison priscus* Bojanus, 1827

The bison probably originated in southern Asia, since the oldest known representative (subgenus *Eobison*) has been found in Pliocene deposits in India (the Siwaliks) and China. In the USSR remains of the small *B. (Eobison) tamanensis* N. Ver. occur in Upper Pliocene/Lower Pleistocene beds on the shore of the Sea of Azov in the Taman faunal complex.

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*Most authors place extinction of *Megaloceros* in Ireland at the Allerød. Mitchell and Parkes (1949) are very guarded about two poorly documented claims of Holocene survival.—Eds.

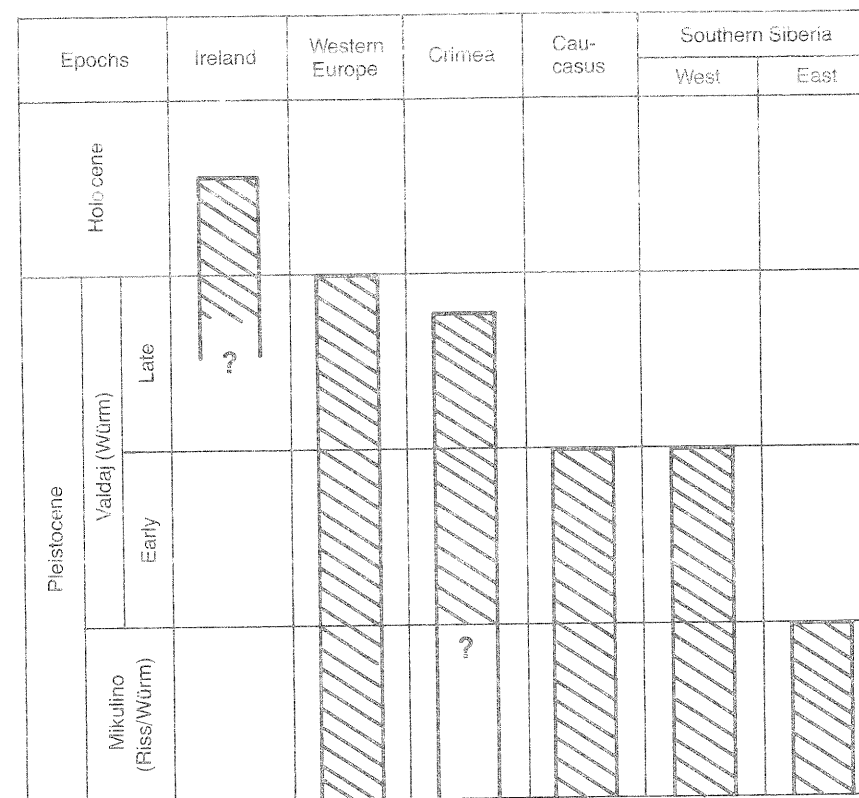| Epochs		Ireland	Western Europe	Crimea	Caucasus	Southern Siberia	
						West	East
Pleistocene	Holocene						
	Valdaj (Würm) Late	?					
	Valdaj (Würm) Early						
	Mikulino (Riss/Würm)			?			

Figure 22.6. Time of extinction of the giant deer.

Early Pleistocene deposits in Europe and northern Asia have provided remains of the larger *B. voigtstedtensis* Fischer (Germany, England) and *B. schoetensacki* Freud. *B. schoetensacki*, considered a forest species by Flerov (1979), ranged as far east as the Vilyuj River in Yakutia. By this time, bison had already reached America.

Bison probably divided into steppe and forest types in the early Pleistocene (Hilzheimer 1918, Flerov 1979). Short-horned forest forms rarely occur in Upper Quaternary deposits. A forest fauna from the Kudaro sites in the Caucasus contains fragmentary bison bones from the Acheulean to the Holocene (Vereshchagin and Baryshnikov 1980).

Considerably more may be said about the evolution of the steppe *Bison priscus*. It is represented by the huge *B. p. gigas* Flerov in the Middle Pleistocene Khazar fauna of the Povolzh'e and Kazakhstan. The hornspan of this subspecies reached 2 m. *B. p. crassicornis* Rich. was the contemporaneous subspecies in Siberia and Alaska. The great breadth and volume of its nasal cavity indicate that it was adapted to the cold climate of the northern forest-steppe (Flerov 1979).

B. p. mediator Hilzh. occupied the extensive Upper Pleistocene periglacial steppes of Europe and western Siberia, while *B. p. occidentalis* Lucas inhabited the tundra-steppe of eastern Siberia, Alaska, and Canada. It was the antecedent steppe forms that made it possible for these bison to penetrate arctic latitudes so extensively—reaching the Gydansk and Tajmyr peninsulas and the Bering Land Bridge. This is confirmed by paleogeographical data and by a comparison of the ecology of the bison with the ecology and distribution of the aurochs, a more mesophylic bovine.

Until the historic period in the Holarctic there existed four geographically isolated forms of bison, distinguished from one another by ecology and morphology. These were the forest bison, *Bison bonasus* L., an inhabitant of the forests of Europe and the Caucasus; a diminished *B. priscus* subsp., which survived in parts of the south Russian Plain (Don basin) until the fifth to the tenth centuries A.D. (Vereshchagin 1971) and in the steppic valley of the Angara and Cisbaikal until the sixth to the seventh centuries (Ermolova 1978); the forest bison, *B. priscus athabascae* Rhoads, which inhabited the woodland and the light-needle coniferous taiga of northeastern Siberia and the taiga of Canada and which survives today only in Canada; and the bison of the North American prairies, *B. bison* L., which flourished until the arrival of Europeans.

As a whole the evolution of forest and steppe adaptations in bison during the Quaternary was a complex process. Fluctuations in bison ranges and populations as a result of natural and anthropogenic factors were equally complex. It is known that bison do not tolerate a prolonged snow cover of more than 40 cm, which limits the restocking of reserves and parks in the USSR. Observations on a thousand head of hybrid bison that have lived in the Caucasus Nature Reserve for the past sixty to seventy years show that bison adaptation to forest and steppe conditions is not absolute. The hybrid individuals have acclimated well to the forest conditions of the western Caucasus. In summer they ascend to the mountain meadows of the alpine zone, but they do not enter the foothill steppe.

The huge range of prehistoric bison in the Eurasian Pleistocene suggests clearly that a natural catastrophe caused their decline in the Holocene. In the northern parts of the bison range the catastrophe was probably increasing warmth and precipitation, a thawing out of the Pleistocene tundra-steppe, and an increase in the depth of the snow cover. The bison populations that survived in the forests and steppes of Europe and the Caucasus and in the steppes of Siberia were almost wiped out by man at the beginning of the twentieth century. Geptner et al. (1961) and Kirikov (1959) review this destruction in detail.

The Musk Ox *Ovibos moschatus* Zimmerman, 1780

The musk ox, which flourished in large numbers in the Pleistocene, is especially interesting in the context of the extinctions problem, since it has survived to the present in parts of the Arctic. As a consequence, we have an actualistic basis for reconstructing its ecology.

The musk ox probably made its first appearance in northeast Siberia. This area has provided a series of ancestral forms belonging to the genus *Praeovibos* (Sher 1971), previously described from European early Pleistocene deposits (Frankenhausen). The oldest known fossils of modern *Ovibos* come from the Mindel gravel of Süssenborn in Germany (Soergel 1942). Pleistocene Eurasiatic musk oxen differ from modern American ones in several cranial features, leading some zoologists to place them in a distinct species, *O. pallantis* H. Smith, 1827 (Ryziewicz 1955). This position is debatable, however. During the Pleistocene, musk ox metapodials changed their proportions: they became shorter and more massive (Kahlke 1963), approaching metapodials of modern musk oxen in massiveness.

During the Middle and Upper Pleistocene the musk ox ranged through most of Europe and northern Asia. In western Europe it spread south to the Dordogne (Les Eyzies) in France, to southeastern Hungary, and to Dobruja in Rumania. In the coldest periods it apparently even reached Spain (Abreda; Estevez 1979). Its southernmost limit on the Russian Plain was at the latitude of Kiev and Volgograd. In Siberia its southern limit was further north, for musk ox bones are known from Paleolithic sites in Cisbaikal (Ermolova 1978). Its northern boundary passed onto the Tajmyr Peninsula and onto the continental shelf of the Arctic basin, where it occurred on the New Siberian Islands.

Modern musk oxen live in herds averaging from twenty to thirty individuals, of which two or three are adult bulls. In summer the males leave the herds. In European Upper Pleistocene sites males outnumber females seven to one. This fact led Soergel (1942) to suggest that carnivores and prehistoric hunters preyed selectively on solitary bulls that had been driven from herds during sexual conflicts.

It is now known that the musk ox does not tolerate a dense snow cover deeper than 30 cm and that it is unable to undertake long migrations. On the other hand, it tolerates temperatures of minus 50 degrees C and harsh winds on Canadian islands and the northeast coast of Greenland. In addition, it can survive on the sparse grass and shrub vegetation of the stony tundra.

Unsuccessful attempts were made in the 1970s to introduce Canadian and Alaskan musk oxen to the southern slopes of the Byrranga Mountains on the Tajmyr Peninsula and to Wrangel Island. This experiment showed that musk oxen could not inhabit large portions of the modern Eurasian arctic tundra.

Beginning in the late Valdaj (Würm III) the range of the musk ox probably retreated progressively northward. A small population survived longest on the Tajmyr Peninsula. Very late radiocarbon dates have been obtained on musk ox skulls and horn sheaths found on the surface in northern Tajmyr: 3800±200 and 2900±95 yr B.P. (Vereshchagin 1971b). In Europe the latest known occurrences are in late glacial deposits in Scandinavia, as exemplified by a skull from Estersund, Sweden, with an age of about 9000 yr B.P. (Borgen 1979).

The principal factor limiting musk ox distribution in the modern Siberian tundra is the dense snow cover, which prevents feeding. Dense snow cover probably accounts for the extinction of musk ox throughout Eurasia in the postglacial. Human activity is responsible for the sharp reduction in musk ox range in North America in recent centuries.

In summary, we can say first that not all the extinct Pleistocene species disappeared at the same time. Some of them apparently retreated into appropriate refugia. Second, the paleontological data provide no basis for the idea that any of the extinct species disappeared as a result of morphological defects.

Local Causes of Extinction and Local Range Displacements in the Pleistocene and Holocene

Modern partial extinctions show clearly how environmental factors affect mammal existence and distribution. Range fluctuations in mesophilic and relatively xerophilic species provide excellent examples.

In the western Ciscaucasus the Caucasian mole (*Talpa caucasica* Satun.) lives in river valleys and on the plain adjacent to the Caucasus foothills. In periodic drought years it becomes extinct over large areas. Extinction is caused by a dramatic reduction in soil invertebrates and probably also by microclimatic deterioration in the burrows—a sharp rise in temperature and a decrease in moisture. The species can disappear completely from sections of the plain when agricultural exploitation and the removal of riverine forests increase aridity and promote the expansion of steppe.

When large expanses of floodplain became more arid in the postglacial epoch, the moles became restricted to relatively moist relict areas surrounded by steppe and even semidesert biotopes. The Karayarsk Oak Forest in the Kura Valley east of Tbilisi is a remarkable example of a mole refugium (Vereshchagin 1959). Relict areas of mole occupation also occur on the Stavropol' Highland, surrounded by dry steppes, and in the alpine meadows of the Armenian Plateau.

The social vole, *Microtus socialis* Pall., a relatively xerophilic species, presents a similar example of range pulsation. This species flourishes in the eastern Transcaucasus (Azerbajdzhan) in semidesert and steppe with 350–800 mm of precipitation per year. A series of dry winters causes the vole to become extinct over large areas. At the same time, its range retreats progressively into the foothills of the Caucasus east of Baku 100–120 km in the course of one or two seasons.

Such local extinction, brought about by seasonal climatic events, can continue over long periods. Complicated by other, nonclimatic factors, it can lead to total extinction. The gradual disappearance of a group of steppe rodents and small carnivores in the Caspian Sea region over the past few centuries is probably another example of such climatically induced local extinctions.

Formozov (1938) described the extinction of the steppe pika (*Ochotona pusilla* Pall.), the yellow lemming (*Eolagurus luteus* Eversm.), the great gerbil (*Rhombomys opimus* Licht.), the northern mole vole (*Ellobius talpinus* Pall.), and the giant mole rat (*Spalax giganteus* Nehr.) in the steppes and semideserts on the northern margin of the Caspian Sea in the middle of the nineteenth and beginning of the twentieth centuries. In the middle of the present century new data appeared on the disappearance of the corsac fox (*Vulpes corsac* L.) and steppe polecat (*Putorius eversmanni* Lesson.) in the Volga-Don steppes and in the steppes north of the Caucasus (Vereshchagin 1959). In this instance, it is possible that a decisive factor was the use of poisons and gasses to destroy small ground squirrels that the carnivores ate. Also perhaps important was the intense exploitation of the carnivores for their skins.

The saiga antelope (*Saiga tatarica* L.) presents another obvious example of fluctuation in range size. This species is adapted to a sharply continental climate and to steppe and semidesert landscapes. It feeds on grasses and wormwood and depends on hard ground for rapid flight. Its heartland is the region of steppe plateaus of central Asia, where its relative, the chiru (*Pantholops hodgsoni* Abel), also occurs. During the Upper Pleistocene the saiga ranged from England on the west to Alaska on the east and from the New Siberian Islands on the north to the central Asiatic deserts on the south. It is possible, however, that a separate species (*Saiga borealis* Tscherskyi) inhabited the arctic steppes of Siberia.

In the historic period the saiga's range has shrunk progressively eastward. In the Middle Ages large numbers of saiga lived in the steppes of the Dnestr and Dnepr basins, and they probably also occurred in Hungary west of the Carpathians. By the 1920s no more than a few hundred animals survived in the Kalmyk steppes (on the Don/Volga interfluve), in the Karakumy adjacent to the Urals, and in the western part of the Bet-Pak-Dala. As a result of this decline in saiga numbers, the subcutaneous botfly, *Pallasiomyia antilopum*, disappeared. It is found today only in an isolated population of Mongolian saiga (Grunin 1957).

In Siberia the major factor in saiga extinction was the disappearance of Pleistocene tundra-steppe and the spread of taiga. On the Russian Plain and in Kazakhstan the extinction of saiga in the nineteenth and early twentieth centuries was directly linked to persecution by nomadic herdsmen and farmers, especially near water sources. The rapid growth in saiga numbers and the restoration of its range in the succeeding thirty to forty years reflect depopulation of the steppe and semidesert and state efforts at conservation—a full ban on hunting. In Kazakhstan today the total saiga population varies around 1.8 to 2 million head, thanks to regulated exploitation and to the shooting of wolves from airplanes.

Overall, the impression we gained is that the steppe group of central Asiatic species, including carnivores (corsac fox and steppe polecat), rodents (yellow lemming and steppe marmot), lagomorphs (steppe pika), and ungulates (kulan, tarpan, and saiga), retreated progressively eastward beginning at the end of the Pleistocene. They disappeared in western Europe very early on and in recent centuries they have also disappeared from eastern Europe. Today they are largely restricted to their central Asiatic homeland—the steppes of Kazakhstan and Mongolia. Their retreat appears to have retraced the route of their Pleistocene expansion.

In Europe and Asia there are numerous well-known examples of mesophilic rodent species that retreated into mountains from plains that became arid and steppic in the postglacial period. In Adam Cave in the semidesert of Dobruja on the right bank of the Danube, Romanian paleontologists have found remains of the snow vole (*Chionomys nivalis* Martins), which lives today in the southern Carpathians. In the Ciscaucasus the closely related Gudarsk vole (*Chionomys gud* Satun.), which presently lives in the high Caucasus, once lived at Pyatigor'e on Mt. Razvalka only 500 to 600 m above sea level in an area of permafrost in teshenite detritus.

The chromosomal species of common vole (*Microtus arvalis* Pall. and *M. subarvalis* Meyer, Orlov et Skholl) are broadly distributed in the mesophilic floodplains of the Russian Plain and in the high Caucasus, but on the southern limit of their range they have a patchy distribution in alpine meadows. The patchy distribution probably came about when populations living in degraded lowlands and intermontane valleys became extinct in the postglacial.

In general, there was considerable mobility in the ranges of mesophilic and xerophilic small mammals during the Pleistocene and Holocene. The discovery of the Binagadinsk Middle Pleistocene fauna in tars of the Aspheron Peninsula in the eastern Transcaucasus shows this mobility clearly.

During the Holocene (?), the corsac fox and the saiga retreated from the Transcaucasus into the Ciscaucasus, while the alpine mole vole and the porcupine retreated from the Transcaucasus onto the Iranian Plateau. Displacements in the ranges of other local species were less remarkable. Thus the boundary of the common vole's range moved 120 to 130 km to the northwest, while that of the golden hamster (*Mesocricetus raddei* Nehr.), which still survives in Dagestan, moved 200 to 250 km.

Other factors led to great variation in the range of the river beaver (*Castor fiber* L.). In the northeastern USSR there are places where the former presence of beavers is obvious from fossil ponds and fossil gnaw marks on branches and tree trunks. On the Enisej, Aldan, and Penzhina rivers, these places are many thousands of kilometers from relict beaver colonies found, for example, in the Tuva Autonomous Region and in the eastern foothills of the Urals along the Konda and Sos'va rivers (Grave 1931, Skalon 1951).

Historically in Siberia beavers were rare in the permafrost zone, because permafrost inhibits the construction of stable burrows in river banks and causes beaver ponds and lairs to freeze over. Beavers probably penetrated far to the north in Siberia during a period when permafrost disappeared. Thus, in our opinion, the relict beaver colonies that survive in the Irtysh Basin and in other parts of Siberia formed in the postglacial epoch no earlier than 8,000 to 9,000 years ago. Their "aboriginality" is therefore relative. Greater "aboriginality," dating from the Mio-Pliocene, may be ascribed to those beaver colonies which occurred in western Asia and Kazakhstan, and which still occur on the Bulugan River.

Until the twentieth century, beaver colonies survived only under the protection of monasteries in European Russia, and elsewhere under the protection of native shamans, that is, also on religious grounds. In the 1950s and 1960s a major state effort to promote the restocking of beavers in the European USSR and in southern Siberia were totally successful and showed clearly that human overexploitation constituted the principal reason for the historic disappearance of beavers from huge areas of eastern Europe, the Caucasus, western and central Asia, and Siberia. In the southern regions of the country beavers were also adversely affected by stockbreeders' destruction of the riverine, gallery forests that provided fodder for these remarkable rodents.

Climate and Landscape Changes on the Boundary Between the Pleistocene and Holocene as Causes of the Extinction of the Mammoth Group

As indicated earlier, in the eighteenth, nineteenth, and early twentieth centuries most European scholars believed that the mammoth fauna existed in Siberia under conditions that were much warmer and very different from modern ones. The zoologist Brandt (1865:3) was correct when he wrote that the scanty vegetation of the modern tundras would not sustain gigantic mammoths, rhinoceroses, and bison. He believed that a warmer climate promoted more luxuriant vegetation in the past.

Opinions changed in the first half of the twentieth century. It was supposed that temperatures approximated modern ones. The ornithologist Tugarinov (1928, 1934) believed that the tundra was "not the same as now" when the cave lion and saiga lived there. He postulated that it was "an open landscape with a remarkably xerothermic climate, rather cold, with little winter precipitation" (1928:669). In his opinion, an increase in moisture, a subsequent dry period, and a renewed increase in moisture caused horses, camels, and saigas to retreat from tongues of steppe in eastern Siberia into the region of unbroken steppes and deserts (1934:63–64). Mammoth, rhinoceros, bison, and cave bear did not become extinct as a result of a sharp climatic change or one "in the direction of deterioration." "They were living in marginal conditions to begin with, and a relatively small environmental change was enough to precipitate a crisis."

The excellent ornithologist and paleozoologist Serebrovskij (1935) apparently saw approximately the same landscape zones in the Würm (Valdaj, Wisconsin) as exist in northern Eurasia now; however, he also recognized the existence of a great European ice sheet.

The paleontologist Pidoplichko (1951a, 1969) consistently asserted that mammoths could live in the Ukraine today. He emphasized the lack of sharp climatic and landscape differences between the Pleistocene and the present and discounted such differences as a factor in Pleistocene extinctions. The glaciologist Dajson (1966:138) stated that, from the perspective of mammoth habitation, Pleistocene and modern environments were very similar.

Vague facts and speculative considerations led to such categorical conclusions, since detailed paleoclimatic investigations had not taken place. Different facts were discovered by numerous native paleogeographers, frozen-ground specialists, and geomorphologists working in the arctic and subarctic zones and in the region where permafrost developed during the Pleistocene.

Velichko (1973, 1982) and Tomirdiaro (1977, 1980) obtained very firm information on natural processes during the Pleistocene. From geomorphic observations on the Russian Plain and in northeast Siberia, and from paleogeographic comparisons, both investigators reconstructed the mammoth's environment during the period of peak cold in the Würm (Valdaj). Climate was sharply continental, leading to the development of permafrost up to 1.5 km below the surface and to the formation of subterranean ice vein-walls up to 40 m deep, pressing up columns of earth. Permafrost extended as far south as 46–48 degrees N in Europe. Low winter temperatures were characteristic: around minus 30 degrees C at the latitude of southern England, White Russia, and the Central Russian Highland, judging from paleobotanical data (Velichko 1982). Summer temperatures were not depressed as much. In the periglacial zone, precipitation was no more than 250 to 300 mm per annum.

In Europe the zonal mixed and broadleaf forests were replaced by periglacial vegetation which occupied a wide belt between the Scandinavian ice sheet on the north and the Alpine glacier on the south (Grichuk 1982). Periglacial steppes covered the south Russian Plain and the central Danube lowlands.

Winters with little snowfall and the development of a luxuriant grass cover on hard, dry ground with abundant summer insolation allowed horses, bison, and saiga to

Figure 22.7. Counting bones at the Berelekh mammoth "cemetery" (Yakutia). (Photo by A. V. Lozhkina 1970)

occupy huge expanses of northern Eurasia. The boundary between the Pleistocene and Holocene was characterized by sharp, short climatic oscillations: the Bølling interstadial (12,400–12,000 yr B.P.), the Middle Dryas stadial (12,000–11,800 yr B.P.), and the Allerød interstadial (11,800–11,000 yr B.P.), the Upper Dryas stadial (11,000–10,300 yr B.P.), and so forth, which affected the Pleistocene species decisively. It was precisely in this time range that the massive extinction of the mammoths and their "fellow travelers" occurred in the arctic zone. Testimony to this extinction are the hundreds of thousands of bones from disarticulated skeletons and the occasional frozen carcasses buried in Sartan deposits (late Wisconsin) in northern Yakutia and on the Tajmyr Peninsula (fig. 22.7). Judging from modern examples of mass death among wild and domestic ungulates in the Kazakhstan steppes (Sludskij 1963), the best explanation for such death at the end of the Pleistocene is the frequent occurrence of snowstorms (blizzards) in winter and the transformation of the nutritious Pleistocene tundra-steppe into a boggy, lake-dotted tundra. In subarctic latitudes at this time, taiga and mixed forests advanced rapidly onto open expanses, and a forest fauna developed.

From the paleozoologist's point of view, the most convincing proof that the landscape changed radically on the boundary between the Pleistocene and Holocene is the change from a steppe, mammoth fauna into a forest fauna on the Russian Plain, in the northern Urals (Kuz'mina 1971), in Siberia, and even in the Far East.

Animal Extinction Under Human Influence

Man's ability to destroy economically significant species, especially "harmful" ones, is widely appreciated in our technological age. It has found clear expression in numerous nature-preservation laws, legislative measures, books, pamphlets, and instruction on exploitation and destruction, and we need present no proof. However, the situation was different in the Paleolithic, when there were few people and when technology and economy were at a low level.

The primitive people of the Lower and Upper Paleolithic left abundant evidence of their exploitation of mammals, birds, and fish in western and eastern Europe, the Caucasus, central Asia, Siberia, and the Far East. This evidence comprises hundreds of thousands of artificially broken bones in open-air and cave sites dating from the Paleolithic, Mesolithic, and Neolithic. The mammals taken by primitive hunters included essentially all the large species that were available: carnivores, large rodents, lagomorphs, perissodactyls, artiodactyls, proboscideans, and occasionally even primates. Soergel (1922) and Lindner (1937) have reviewed the hunting methods used in the European Paleolithic and Neolithic. Further reviews may be found in the archaeological and ethnographic literature.

Gromov (1948) was the first to summarize the species composition of Paleolithic faunas in the Soviet Union. Special reviews relevant to ancient hunting are presented by Semenov (1968) and Vereshchagin (1971b). These publications show that on the Russian Plain and in the Caucasus, central Asia, Siberia, and the Far East, man obtained and butchered for food and technical purposes one species of monkey, twenty-eight carnivores, two proboscideans, five lagomorphs, five rodents, four perissodactyls, twenty-three artiodactyls—a total of sixty-seven to seventy species of terrestrial mammals.

Regional differences, linked to zoogeography and terrain, are very obvious. For example, the greatest variety of carnivores and ungulates was obtained on the Russian Plain and in the Caucasus, and the smallest in central Asia. These data are expanding and becoming more precise. One basic pattern is the use of local, immediately available, abundant resources. Taphonomic factors complicate attempts to evaluate objectively the significance of different mammal species in ancient human diets. The bones of large animals—mammoths and ungulates—are better and more readily preserved and thus appear more important than the bones of small and medium-size carnivores and rodents. We have no convincing data on how much meat ancient people ate. Different estimates vary widely. Ethnographic observations indicate that some modern natives of Siberia—Nentsy, Dolganes, Yukagirs, Yakuts, Evenki, and Evenni—can eat 2 to 5 kg or more of reindeer meat in twenty-four hours.

Mowat (1963) published a daily norm of 2 kg of caribou (reindeer) meat for Canadian Eskimos. Soviet investigators accept clearly lower norms for Upper Paleolithic people in eastern Europe: Bibikov (1966), 600 g in twenty-four hours, and Pidoplichko (1969), 800 to 1,000 g. These norms apparently differed sharply between summer and winter. In summer, people ate a great deal of vegetal food: roots of cattails and reeds, parts of umbelliferous plants, fruits and berries, nuts, edible herbage, and even tree bark—for example, willow bast. Pidoplichko (1969:153) thought that vegetal products, fish, and meat of small mammals and birds comprised one third of the entire diet in summer and fall. Over the entire year, he believed, vegetal foods and the meat of small mammals constituted one fourth of the diet, and mammoth meat three fourths. Data from the Kostenki (Don) sites suggest that in the majority of cases Paleolithic people got more meat from horses and hares than from mammoths (Vereshchagin and Kuz'mina 1977).

Given the severe climate of northern Eurasia in the Paleolithic epoch and the brief growing season, Vereshchagin (1971b) assumed that the average person consumed 2 kg of meat in twenty-four hours. At this level of consumption, an Upper Paleolithic population of 15,000 people (a conservative estimate) on the southern half of the Russian Plain would need up to 10,500 tons of meat per year—up to 60,000 horses (100 kg of meat after butchering) and up to 10,000 bison (300 kg of meat after butchering). Considering the difficulty of hunting large mammals with primitive weapons, the prehistoric hunters would have had to work hard all year. Nonetheless, these numbers suggest that Paleolithic people applied considerable pressure to the mammal populations of the plains. However, there is also reason to suspect that the ancient inhabitants of northern Europe often scavenged the bodies of mammoths and other animals that had drowned or frozen. We know this, for example, from the 1980 excavation of bajdzherakhs on the

Figure 22.8. A skull of one of the last mammoths of Berelekh. The tusks were removed by Stone Age hunters. (Photo by N. K. Vereshchagin, 1970)

Berelekh River in northern Yakutia, where there is a huge "mammoth cemetery," formed approximately 13,000 years ago (fig 22.8). (*Bajdzherakh* is a Yakut word for a column and mound of ground pushed out by veins of ground ice during polygonal cracking of the earth.)

Like the recent aborigines of Africa, the prehistoric hunters of northern Eurasia probably also used game killed by carnivores (cave lions and wolves). Such double pressure—from carnivores and settled human tribes—could have been fatal to Upper Pleistocene populations of mammoths and ungulates.

Irregular hunting success and the migratory habits of the mammoths and ungulates must have led Paleolithic people to develop methods for storing meat. They probably dried and cured it in the sun and wind, froze it in winter, and buried it in the permafrost in summer.

In the post-Paleolithic epoch the growth of stockherding and agriculture increased the pressure on exploitable animals, thanks to advances in the technology for capturing wild animals and to domestication of the dog and horse.

The use of the dog and the horse permitted improved methods for reconnoitering and catching large and small game. Numerous petroglyphs observed and described by ethnographers over a huge area, from Scandinavia to Kamtchatka and from the Mediterranean littoral to the Pacific Ocean, tell us about the animal species that were acquired and also about the invention and perfection of bows, harpoons, and boar spears in the Neolithic and the Bronze Age (Kuhn 1956, Savvateev 1970), Vereshchagin and Burchak-Abramovich 1948, Marikovskij 1953, Okladnikov 1959, Dikov 1971, Formozov 1969, Devlet 1980, and others).

Numerous bones of large wild animals (bear, boar, and moose) have been found in Neolithic pile-dwellings on the eastern Baltic littoral. Marine animals (dolphins and pinnipeds) played an important role in the economy of the shoreline settlements (Paaver 1965; Vereshchagin and Rusakov 1979). Neolithic and Bronze Age sites on the shores of the Far Eastern oceans present a similar picture.

Undoubtedly the Neolithic tribes of eastern Europe and Siberia obtained the last, sporadic mammoths, musk oxen, spiral-horned antelopes, Transbaikal buffalo, and Baikal yaks. On the steppes of eastern Europe and southern Siberia the Sarmatian and Scythian tribes were still able to exploit almost untouched herds of tarpan, kulan, saiga, aurochs, and bison.

Medieval manuscripts tell us about the grand battues the Mongol and Tatar cavalry of the Bronze Age conducted against steppe ungulates (bison, red deer, and saiga) (Rashid-Ad-Din 1946, Kirikov 1959). The existence of such hunts is confirmed by the numerous bones found in the eighth- to thirteenth-century Khazar town and fortress of Sarkel on the Don (Vereshchagin 1971a) and by the superb studies of Tsalkin (1962), Bibikova (1953) and Timchenko (1972) on bones excavated from several town sites on the Russian Plain in the middle of the present century. Even with the wide variety of available data it is difficult to evaluate the significance of hunting as a factor in the destruction of several mammalian species. Over the centuries there was a general tendency for the percentage of wild animals present to decline, while the percentage of domestic ones increased. Among the thousands of bones in the collections from medieval sites near the Dnepr River (Ukraine), bones of wild animals (boar, kulan, roe deer, red deer, moose, saiga, bison, and aurochs) comprise from 0.4 to 10.6 percent; on a minimum individual basis they comprise from 5.0 to 29 percent (Timchenko 1972).

The cases of the aurochs and the large cats illustrate what can happen to large mammals as a result of intense hunting, the cutting down of forests, and the plowing of virgin lands. The oldest fossil remains of the aurochs (*Bos primigenius* Bojanus, 1827) come from Lower Quaternary deposits in Europe, western Asia, and the Caucasus. Even then it was a very large animal. The Pleistocene range of the aurochs was extensive but considerably smaller than that of the bison. Besides Europe, remains of aurochs are known from western Asia, the Transcaucasus and Ciscaucasus, central Asia, and southern Siberia as far as Cisbaikal. During the Middle and Upper Pleistocene the aurochs became rather large, but toward the end of the Pleistocene and in the Holocene it split into large and small forms. Both forms of the aurochs were domesticated in the Neolithic.

Ecologically, the aurochs was more mesophilic and warmth-loving than the steppe bison. It inhabited the valleys and floodplains of rivers, especially during droughts or desiccation of interfluves. It penetrated high into mountain ranges. In the medieval forests of Lithuania and Poland, aurochs kept to dense mixed forests, even moist and boggy ones, feeding in part on sprigs and shoots (Geptner et al. 1961).

In the Ukraine, aurochs bones occur in Neolithic, Eneolithic, and Bronze Age sites as late as the tenth or eleventh centuries (Bibikova 1953). In the Caucasus there are Mesolithic and Neolithic depictions of aurochs on rocks. In western and central Asia, the species survived until the Bronze Age in riverine thickets and reed beds along the Euphrates, Amu-Darya, and Syr-Darya. The aurochs disappeared in western and central Europe in the fifteenth century, following the removal of forests. It survived only under feudal protection in some forests of modern Poland and White Russia.

Bones of Pleistocene tigers (*Panthera tigris* L.) have been found in India, China, and the southern part of the Soviet Far East. At the beginning of the twentieth century in the USSR the tiger occurred in Transbaikal, along the courses of central Asiatic rivers, in the Far East, and the Amur Valley. Occasional individuals were encountered in the southern part of western Siberia and Yakutia (Geptner and Sludskij 1972). In the northern Caucasus the tiger apparently disappeared in the twelfth century. By the 1920s persecution and agricultural development in the Transcaucasus led to a situation in which only occasional tigers came in from Iran. In central Asia tigers survived until the 1950s, when they disappeared completely as a result of direct persecution and the destruction of wild boar. The tiger population steadily declined in the Far East, where as of the early 1980s there were only 180 to 200 individuals enjoying state protection (Zhivotchenko 1981).

Figure 22.9. Skulls of the last Caucasian bison of northern Osetia, killed in the eighteenth and early nineteenth centuries. The Sacred Cave of Digorized. (Photo by N. K. Vereshchagin, 1947)

In the Middle Ages the range of the cheetah (*Acinonyx jubatus* Schreb.) included the plains of the eastern Transcaucasus, where it may have persisted until the eighteenth century (Vereshchagin 1959). In the present century in the USSR, cheetah occurred only in the desert regions of Turkmenia and Uzbekistan. Cheetah became rare as a result of direct persecution and of reduction in the numbers of goitered gazelle. As of 1982, there were probably no cheetah left.

To these examples we can add the well-known extermination of Steller's sea cow (*Hydrodamalis gigas* Zimm.) on the shores of the Commander Islands in 1768; the disappearance of the tarpan (*Equus ferus gmelini* Anton.) and the kulan (*E. hemionus* Pall.) in the mid-nineteenth century on the steppes of the south Russian Plain; and the destruction in the 1920s of the last Caucasian bison (*Bison bonasus caucasicus* Satun.) (fig. 22.9), as well as other data that provide a picture of faunal impoverishment.

The rapid disappearance of wild animals on the planet—of precious genetic resources—has forced biologists to seek ever more decisive measures to conserve them, including the publication of national and global "Red Books" and the development of conservation laws.

When we compare the rate of extinction today with the rate in the Paleolithic, Neolithic, and early metal periods, we are struck by how much it has increased in the age of technology. Besides direct and indirect human destruction of both valuable and harmful mammals, we are now increasingly aware of the strong influence of carnivores and epizootic diseases, and also of various kinds of stressful situations that disrupt population structure. Human exploitation may also disrupt population structure, thereby placing an intolerable burden on exploited animal populations. Hunting practices often inhibit the growth of a wild ungulate or carnivore population by disrupting its structure. Human concentration on large animals and the selection of males for trophies hinders normal reproduction, leading to population exhaustion. Carnivores, epizootic diseases, food shortages, and other factors can have a similar destructive effect on populations.

Conclusion

Analysis of the geography and ecology of extinct and declining Quaternary mammals in the USSR shows clearly that four groups or factors led to the destruction of the mammoth fauna and to the disappearance of a series of other species:

1. Changes in environment, including seasonal and secular climatic oscillations, involving changes in landscapes and biotopes. Here we include tectonic uplift and fluctuation in the level of the world ocean, which not only altered atmospheric circulation, but also weakened natural selection pressures in circumstances of insular and peninsular isolation.

2. The loss by species of resistance and of the ability to adapt quickly to new abiotic and biotic environmental conditions. Here we are talking about ecogenetic and phylogenetic defects, including the concept of excessive specialization and the nonadaptive character of evolution.

3. The disruption of population structure as a result of external factors such as more progressive competitors, carnivores, parasites, epizootic diseases, and stressful situations.

4. The direct destructive influence of people and the indirect action of their economic activity on exploited and unexploited animal species.

Once we postulate these groups of factors, the next step is to evaluate the relative weight of each in time and space, that is, in different stages and geographic zones.

The examples we have presented of extremely rapid decline in some nonexploited mammal species during the Quaternary and at present in northern Eurasia point to the supreme importance of external, abiotic environmental factors in their extinction. The nearly total extinction of large species of the mammoth fauna in the tundra and taiga zones and their partial survival in the forest steppe and steppe confirms the decisive effects of climatic and landscape changes for the life and death of this species group.

The best proof of what has been said is the ubiquitous transformation of the Upper Pleistocene "steppe" fauna into a forest and taiga fauna over huge areas in upper and middle latitudes in Eurasia. In this case, the primitive species were not crowded out by more progressive ones, nor were their population structures disrupted, nor were they destroyed by human activity. Environmental change was so radical and dramatic that morphological evolution simply did not have time to catch up.

The destructive activity of people is often thought to have been decisive in the extinction of Quaternary giants (mammoth, rhinoceros, cave bear, and others). However, while human influence on animal populations steadily increased in prehistory, it became definitive only in the last few millenia and centuries. In addition, the role of man has not been the same in all geographic zones. It has been greatest in the ancient heartlands of civilization in the Mediterranean Basin, western and central Asia, and China, and least in the polar desert.

The remaining causes of extinction have apparently been secondary, merely promoting further reduction in ranges and numbers of species after they had suffered from climatic and landscape changes or from human pressures.

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Mammoths in China

LIU TUNG-SHENG AND LI XING-GUO

MAMMOTH FOSSIL LOCALITIES ARE WIDESPREAD in China (fig. 23.1), from Raohe (#33) along the Wusuli River in the east to Tongwei (#146) of Gansgu Province in the west, and from Huma of Da Xingan Mountains (#79) in the north to Lushun (#141) in the south. Fossil localities are especially numerous in the Songliao Plain of northeast China (fig. 23.1). Mammoth is a representative of the *Mammuthus-Coelodonta* (woolly rhinoceros) fauna of the late Pleistocene in northeast China (Pei 1957).

The southern boundary of the distribution of the woolly mammoth (*Mammuthus primigenius*) in the northern hemisphere, Europe, and North America is roughly 40°N latitude (Zhou 1978). The distribution of the mammoth in China is approximately the same, occasionally reaching 35°N latitude.

Mammuthus and Its Distributional Characteristics in China

Mammoth were recorded 2,100 years ago in *The Book of Magic*. They were described in the Emperor Kangxi's *Inquiry on the Physical Law in Leisure*, written by Aixinjueluo Xuanhua of Qing dynasty (1654–1722 A.D.):

> The northern plain near the sea in Russia is the coldest place. There is a kind of beast, which like a mouse, is big as an elephant, crawls in tunnels, and dies as it meets the sun or the moon light. Its teeth are like an elephant's, white, soft and smooth with no crackles. The native people often find it near the river bank. Its bones are used for making bowls, dishes, combs, and double-edged fine-tooth combs. Its meat is chilly and cold in character. Taking it as food, uneasiness and fever can be ridded off and its Russian name is Momentuowa (Chen Zhen 1958).

Thus, as early as 300 years ago, there were narratives on mammoths in China telling of their bones being used for utensils and their meat for food.

According to the study by Zhou Ming-zhen et al. (1974), "The genus *Mammuthus* in China includes *Mammuthus* (*Parelephas*) *trogontherii* Pohlig, *Mammuthus* (*Parelephas*) *sungari* Chow et Chang, *Mammuthus primigenius* Blumenbach, and one subspecies, *Mammuthus primigenius liupanshanensis* Chow et Chang." From the structure and pattern of the molars it is evident that these species are in a continuous transitional series.