

QUATERNARY EXTINCTIONS OF
LARGE MAMMALS

BY
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UNIVERSITY OF CALIFORNIA PRESS
BERKELEY AND LOS ANGELES
1967

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN GEOLOGICAL SCIENCES
ADVISORY EDITORS: D. I. AXELROD, G. H. CURTIS, A. E. J. ENGEL, C. H. HIGGINS, R. M. KLEINPELL,
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Volume 74

Approved for publication June 7, 1967
Issued December 27, 1967
Price, \$1.50

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY AND LOS ANGELES
CALIFORNIA

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CAMBRIDGE UNIVERSITY PRESS
LONDON, ENGLAND

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ABSTRACT

Tertiary climates of high equability enabled "tropical" and "temperate" biota to intermingle throughout temperate latitudes. As the climatic trend toward lowered temperature progressed, the mammal fauna adapted to it.

The fauna was subjected to at least four major periods of colder Quaternary climate. Widespread extinction, chiefly of "tropical" mammals,¹ occurred because of the high mortality of calves born in the colder half of the year, and because both young and old perished during colder winters. Episodes of dry climate characterized parts of all interglacial ages, but they evidently were not sufficiently severe to cause major extinctions. After the last glacial, however, severe drought and cold evidently played important complementary roles in extinction of large mammals.

Different degrees of extinction in distant regions (central North America vs. Central Europe) and in nearby areas (Argentine pampas vs. adjacent forest-border fauna; central Europe vs. Mediterranean Basin) appear to reflect areal differences in equability, with the highest extinction occurring in areas of lowest equability.

The rich African ungulate fauna escaped periods of major Quaternary extinction because its equatorial position was well removed from the theater of change, and its richest phase inhabited a plateau typified by pronounced equability throughout the period.

Unlike their large contemporaries, small mammals do not show major episodes of extinction. They escaped times of lowered equability—and extinction—by retreating into protected habitats (burrows, caves, dens, nests), and by their habits or patterns of activity (spring mating, short gestation period, polyestry, food gathering).

INTRODUCTION

AMPLE EVIDENCE supports the fact, well known to Darwin (1845, p. 173) and Lyell (1837, vol. 2, p. 295), that widespread extinction of large mammals followed the last glacial age. At that time North America lost numerous genera which now exist only in the Old World (horse, saiga) or in South America (llama, tapir, capybara), or are extinct (dire wolf, mammoth, ground sloth, sabertooth). Comparable changes occurred in southern Europe, where there are records of present-day European mammals associated with those now confined to Africa (rhinoceros, hippopotamus, elephant), as well as genera now extinct. Similar faunal change is recorded in South America, Australia, and eastern Asia (for general lit. see Flint, 1957; Zeuner, 1959; Charlesworth, 1957). In the United States, radiocarbon and archaeological dates imply that the major episode of extinction commenced with the culmination of the last glacial age and was largely completed during Altithermal

¹The term "tropical" is used here more in a popular than in a strictly scientific sense (i.e., climate with the mean temperature of the coldest month above 64.4°F). Informal usage has seemed desirable because many of the larger animals under consideration—tapir, capybara, hippopotamus, rhinoceros, peccary—are popularly equated by vertebrate paleontologists and mammalogists with "tropical" climates, when in fact they lived in areas far outside that climatic zone, and some of them still do if temperatures are not too severe. This phenomenon reflects the climatic property of equability, or thermal moderation, and is discussed in detail below.

It is also recalled that many large mammals wander widely, whereas plants are more sharply confined in a climatic sense. Owing to the complications of defining climatic properties for biota in general, it has seemed best to use "tropical" in the sense of mild climates that may support denizens of tropical as well as extratropical (mild temperate to warm temperate) climates which are characterized by the absence of extreme temperatures, and especially low ones.

time, approximately 8,000 years ago (Hester, 1960). Relict populations lingered on into historic time, their duration evidently being a function both of local climate and of man's activities.

Table 1 lists the important large mammals that disappeared from North America after the last glacial age (Hibbard, *et al.*, 1965). They represent a loss of fully 30 percent of the large browsers and grazers that were present during early post-

TABLE 1
LARGE MAMMALS THAT BECAME EXTINCT IN POSTGLACIAL TIME, OR DISAPPEARED THEN FROM NORTH AMERICA AND SURVIVE ELSEWHERE

EXTINCT GENERA			
Genus	Common name	Genus	Common name
<i>Mammut</i>	Mastodon	<i>Tetrameryx</i>	Pronghorn
<i>Cuvieronius</i>	Mastodon	<i>Arctodus</i>	Short-faced bear
<i>Mammuthus</i>	Mammoth	<i>Chlamytherium</i>	Giant armadillo
<i>Paramylodon</i>	Ground sloth	<i>Dinobastis</i>	Sabertooth
<i>Megalonyx</i>	Ground sloth	<i>Smilodon</i>	Sabertooth
<i>Nothrotherium</i>	Ground sloth	<i>Euceratherium</i>	Shrub ox
<i>Ereotherium</i>	Ground sloth	<i>Preptoceros</i>	Shrub ox
<i>Tanupolama</i>	Llama	<i>Bootherium</i>	Bovid
<i>Mylohyus</i>	Woodland peccary	<i>Cervalces</i>	Moose
<i>Platygonus</i>	Peccary	<i>Brachyostracon</i>	Glyptodon
<i>Camelops</i>	Camel	<i>Boreostracon</i>	Glyptodon
<i>Capromeryx</i>	Pronghorn	<i>Nechoerus</i>	Capybara

GENERA NOW EXOTIC TO NORTH AMERICA

Genus	Common name	Present habitat	Genus	Common name	Present habitat
<i>Equus</i>	Horse	Asia	<i>Saiga</i>	Antelope	Asia
<i>Hydrochoerus</i>	Capybara	South America	<i>Bos</i>	Yak	Asia
<i>Tremarctos</i>	Speckled bear	South America	<i>Symbos</i>	Woodland musk ox	Asia

Source: Hibbard *et al.*, 1965.

glacial time. In attempting to explain this extinction we must remember that similar episodes preceded it. As now known, the fossil record indicates that about 18 percent of the genera of large mammals recorded from North America did not survive the late Pliocene; approximately 23 percent made their last appearance in late Blancan time (early Kansan); 18 percent, in Rancho La Brea time; and 30 percent in postglacial time (Hibbard, *et al.*, 1965, table 2). In central Europe (Thenius, 1962), 50 percent of the large mammal genera did not survive the first glacial (Gunz); 25 percent of the genera of Mindel to Riss time did not persist beyond the Riss (fig. 1); of the thirty-two genera recorded from the Würm only three (9 percent) are extinct; and of the sixteen genera and species of the post-glacial period, all are living except one species. Furthermore, in North America and Europe the small-mammal faunas show no significant change at the time of large-mammal extinctions.

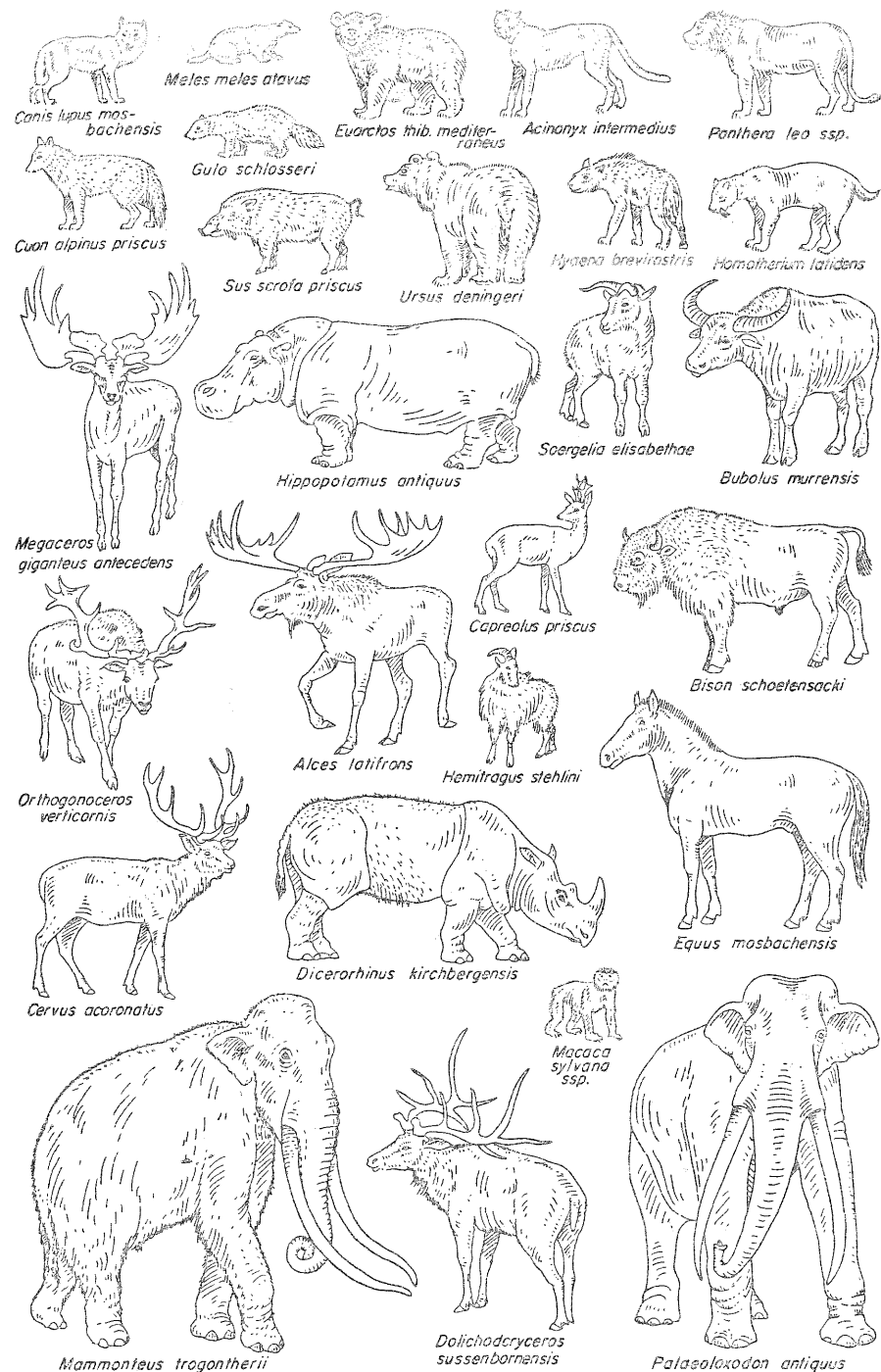


Fig. 1. Important large mammals of the middle Pleistocene (Mindel to Riss) of middle Europe. All species drawn to same scale. Of the twenty-seven species, seven belong to extinct genera (*Palaeoloxodon*, *Mammonteus*, *Orthogonoceros*, *Dolichodoryceros*, *Megaceros*, *Soergelia*, and *Homotherium*). Seven are Recent species which differ subspecifically from living forms, and the remaining thirteen represent extinct species. (From Thenius, 1962, with permission.)

The cause, or causes, of the postglacial and earlier extinctions are not known. The consensus usually reduces the explanation to the interaction of all factors (climate, predation, competition, pandemics, man, evolutionary lag) that may limit populations.² A multiple-factor hypothesis, however, can scarcely account for the differential loss of large animals, for the brief period during which postglacial extinctions occurred, or for the survival of a large ungulate fauna in Africa (Martin, 1958). Furthermore, it does not explain the recurrent, selective nature of extinction with respect to large grazing mammals during the Quaternary, as well as important regional (as between North America and Europe) and local (as between central and southern Europe, or between the forest-savanna and the pampas-steppe in southern Argentina) differences. Martin (1958) rejected climatic change as a factor, and emphasized the coincidence of extinction with the arrival of man in North America during early postglacial time. In a later study, Martin and Mehringer (1965) conclude that man probably was responsible for this "age of overkill." Martin (1966) also suggests that early man may account for a major episode of mid-Pleistocene extinction in central Africa. As Leakey (1966) notes, however, there is no clear evidence today to demonstrate that there was such an episode, or that man was responsible for it. Furthermore, man cannot be the sole agent because there were important large-mammal extinctions in North America and central Europe long before man arrived there.

Since there were various times and degrees of extinction of large mammals during the Quaternary, presumably a highly selective factor was at work during these episodes which was common to many regions. The record shows that this factor was more important in some areas than in others, and that it operated with varying degrees of effectiveness in the same area at different times during the Quaternary. The contention (Martin, 1958; Martin and Mehringer, 1965) that climatic change cannot account for this record is belied by many data. Changing climate appears to explain most of the puzzling features of the postglacial event, as well as extinctions earlier in the Quaternary.

A KEY TO THE CAUSE?

Quaternary and earlier faunas lived in environments that were suited to large animals whose closest descendants are basically "tropical" in their requirements, yet in these same environments lived mammals that are now adapted to cool or cold temperate climates. For example, the Rancho La Brea fauna (Stock, 1963) contains peccary, ground sloth, and tapir, together with bison and mammoth. The Seminole fauna of Florida (Cooke, 1945) has tapir, capybara, and ground sloth in addition to porcupine and mammoth. Although such faunal mixtures have been considered unique, and without paleoclimatic significance (Martin, 1958, p. 396), they typify *all* Pleistocene faunas at middle latitudes, as well as those of the later and middle Tertiary. This was apparent to A. R. Wallace (1876, vol. 1, p. 113), who emphasized that the Pliocene and younger deposits of Europe show that

... the presence of numerous large carnivora and ungulates (now almost wholly tropical) in the post-Pliocene period, was due to no exceptional or temporary cause, but was the result of a

² The general problem is discussed by many authors. References to the older literature are in Colbert (1938), Gill (1955), Osborn (1906), and Simpson (1931). Current discussions are listed under "Extinction" in Camp *et al.* (1940-1964).

natural succession from similar races which had inhabited the same countries for long preceding ages. . . . Various forms of monkeys, hyaenas, lions, horses, hipparions, tapirs, rhinoceroses, hippopotami, elephants, mastodons, deer, and antelopes, together with almost all the forms now living, produced a rich and varied fauna as we now see only in the open country of tropical Africa. . . . We must look upon them, therefore, as true indigenes of the country, and their comparatively recent extinction or banishment as a remarkable phenomenon for which there must have been some adequate cause. What this cause was we can only conjecture.

The association in these faunas of mammals that are now found in climatically different areas, or have their nearest descendants there, is paralleled by the composition of the earlier Pleistocene floras and also by those of Pliocene and earlier times (e.g., see Depape, 1928; Chaney, *et al.*, 1944). For instance, the early Pleistocene Soboba flora of southern California (Axelrod, 1966) represents vegetation like that at the lower margin of yellow pine forest in southern California, yet the flora contains *Magnolia grandiflora*, now found near the coast in the Gulf and South Atlantic states. The nearby, slightly younger Bautista fauna includes tapir and ground sloth, as well as antelope, deer, and horse (Frick, 1921). In central California, the late Pliocene Sonoma flora shows that avocado (*Persea*) was an associate of coast redwood forest (Axelrod, 1944). The nearby, contemporaneous Tehama formation yields a palm (U.C. Mus. Pal.) and a vertebrate fauna composed of tortoise, ground sloth, camel, horse, and mastodon (Russell and VanderHoof, 1931; VanderHoof, 1933). Such relations are not unique to California; they occur also in Europe, Japan, and elsewhere, as noted below. The data suggest that a change in the factor that explains the association of animals and plants of tropical and temperate requirements in Quaternary and Tertiary communities may be responsible for the widespread selective extinctions during the Quaternary.

EQUABILITY AND BIOTIC COMPOSITION

Darwin pointed out that equability (or "temperateness"; see Bailey, 1960, 1964) accounts for the present-day association of plants and animals that otherwise represent widely disparate ecologies. In his journal, dated June 9, 1834, we read (Darwin, 1845, pp. 243-244):

Inhospitable as this climate [of Tierra del Fuego] appears to our feelings, evergreen trees flourish luxuriantly under it. Hummingbirds may be seen sucking the flowers, and parrots feeding on the seeds of Winter's Bark, in Lat. 55°S. . . . The native forests [near Lat. 45°S] almost rival in luxuriance those of the glowing innertropical regions. Stately trees of many kinds . . . loaded by parasitical monocotyledonous plants; large and elegant ferns are numerous, and arborescent grasses . . . flourish. . . . An equable climate, evidently due to the large area of sea as compared with land, seems to extend over the greater part of the southern hemisphere; and as a consequence, the vegetation partakes a semi-tropical character.

The belief that Pleistocene glaciers may have existed at sea level in middle latitudes under climate of high equability also finds support in Darwin's observations (1845, p. 247):

In Europe, the most southern glacier which comes down to sea level is met with . . . on the coast of Norway, in Lat. 67°. Now this is more than 20° of Lat., or 1230 miles, nearer the pole than the Laguna de San Rafael. The position of the glaciers . . . [in southern Chile] may be put even in a more striking point of view, for they descend to the sea coast within 7½° of latitude, or 450 miles, of a harbor where three species of *Oliva*, a *Voluta*, and a *Terebra* are the commonest shells, within less than 9° from where palms grow, within 4½° of a region where jaguar and

puma range over the plains, less than $2\frac{1}{2}^{\circ}$ from arborescent grasses, and (looking westward in the same hemisphere) less than 2° from orchidaceous parasites, and within a single degree of tree-ferns!³

Two decades later, J. D. Hooker (1854, vol. 1, p. 158) made similar observations on his Himalayan travels:

... certain tropical genera are more abundant in the temperate zone of the Sikkim mountains and ascend much higher there than in the western Himalaya: of this fact I have already cited conspicuous examples in the [figs], palms, plantains, and tree ferns. This ascent and prevalence of tropical species is due to the humidity and equability of the climate in this temperate zone, and is, perhaps, the direct consequence of these conditions. An application of the same laws accounts for the extension of similar features far beyond the tropical limit in the Southern Ocean, ... where, various natural orders, which do not cross the 30th and 40th parallels of N. latitude, are extended to the 55th of S. latitude.

Equability is not only operating today; it is a significant and overlooked factor that controlled the composition of all past faunas and floras (Axelrod, 1964, p. 54). Implicit in the observations of Darwin and Hooker is the notion that equability relates to temperature. Since equability varies in degree, and applies to warm tropical as well as to cold temperate regions, it is one of two aspects of temperature which affect life. These have been clarified significantly by Bailey (1960, 1964), who distinguishes between effective temperature and equability (his "temperateness"). Effective temperature (*ET*) is a measure of the warmth of climate (e.g., tropical, warm temperate, tundra, polar), and is determined from the mean temperatures of the warmest month and the coldest month. The warmth of several selected stations is indicated in figure 2, with Abercorn, Rhodesia, and Cloncurry, Australia, close to the edge of tropical climate (*ET* 64.4°F), and Ushuaia, Tierra del Fuego, and Nome, Alaska, at the margin of polar climate (*ET* 50.0°F). By contrast, equability (*M*) expresses the departure from a constant temperature of 57.2°F , which is midway between *ET* 64.4°F and *ET* 50.0°F and has an ideal rating of *M* 100. If mean temperature is higher or lower than 57.2°F , or if the annual range of temperature increases, then equability is less than *M* 100. The contrast in the equability of the stations in figure 2 (read from arcs) at the edge of polar climate (Ushuaia, *M* 57; Nome, *M* 31) and at the edge of tropical climate (Abercorn, *M* 62; Cloncurry, *M* 42) accounts for the spacing of the stations along lines (radii) of effective temperature on the nomogram. The *ET* and *M* of the areas referred to by Darwin (Isla Guafu, Ushuaia) and Hooker (Darjeeling, Chumbi) are plotted in figure 2. From the relations incorporated in the statistician's normal frequency distribution, as applied to monthly and annual means of temperature by a method provided by Bailey (1967), Ushuaia would be expected to have no more than 2 percent of the hours of the year with temperatures below 32°F , and thus has a climate of higher equability (*M* 57, read from arcs) than Nome (*M* 31), where the mean temperature of the coldest month is 3°F ; the nearest parrots and tree ferns to Nome are in Mexico and Japan.

It is only areas of high equability which support mixtures of plants and animals that otherwise are widely separated geographically. This relation may be further

³ It is now known that on the west coast of South Island, New Zealand, palms are within 1 degree of glaciers, and tree ferns are within 3-4 miles of them.

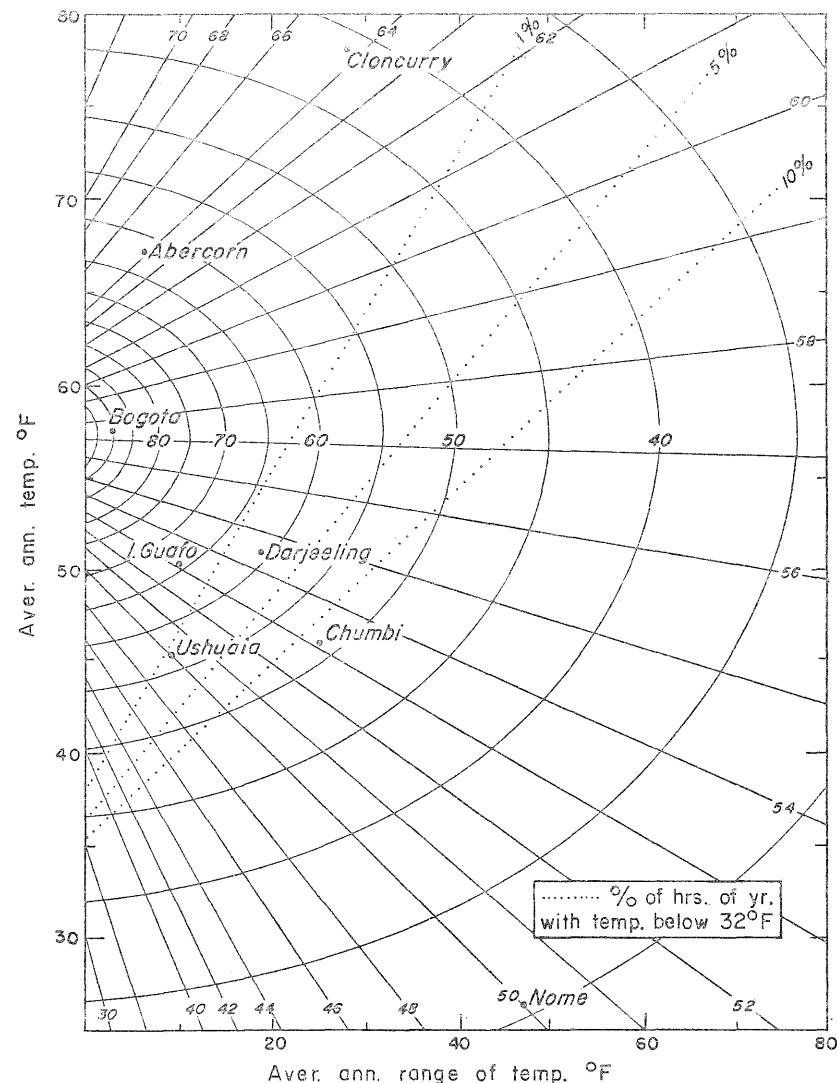


Fig. 2. Effective temperature (*ET*, radii) and equability (*M*, arcs) at several stations, including those referred to by Darwin and Hooker. Ushuaia and Nome are at edge of polar climate (*ET* 50°F); Abercorn and Cloncurry, at margin of tropical climate (*ET* 64.4°F). Note pronounced equability at Bogota (*M* 90+).

clarified by noting an additional example of biotic composition in an area of high equability. The cloud forest of Mexico is distinguished by a mixture of tropical trees mingled with those of temperate climates. In southern Tamaulipas and Puebla (Hernandez *et al.*, 1951; Miranda and Sharp, 1950) common temperate Appalachian species of *Rhus*, *Liquidambar*, *Rhamnus*, *Parthenocissus*, *Carpinus*, *Ostrya*, *Nyssa*, *Hammamelis*, and *Cercis* mingle with tropical species of *Turpinia*, *Phoebe*, *Bocconia*, *Beilschmedia*, *Magnolia*, *Trichilia*, *Eugenia*, *Cyathea*, *Chamaecodora*, *Meliosma*, *Piper*, and *Xylosma*. All are festooned with tropical mosses, and heavily

covered with large orchids and bromeliads. An analysis (Martin, 1955; Martin and Harrell, 1957; Leopold, 1959) of the vertical distribution of birds, reptiles, amphibians, and mammals in the region shows that the cloud forest zone is a meeting area for species from higher (cooler) and lower (hotter) altitudes, where they are found in oak-pine forest and tropical deciduous forest, respectively. Typical tropical mammals include spider monkey, anteater, peccary, coati, ocelot, and jaguar. Precipitation is high, drought largely absent, and evaporation low owing to clouds and high humidity. Meteorological records for the forest at Huauchinango show that the mean temperatures of the warmest (66.7°F) and coldest (52.1°F) months yield an effective temperature of only 58.4°F . But the mean annual range of temperature is 14.6°F , giving an equability rating of M 69. By contrast, Greenville, eastern North Carolina, also has an ET 58.4°F , and the area supports the deciduous hardwoods that occur at Huauchinango, as well as many others. Tropical evergreens, however, are reduced to three rare species (oak, magnolia, and avocado); tropical mosses, large orchids, bromeliads, and lianas are absent, and so are tropical mammals. Equability is much lower (M 52), with 4 percent or more of the hours of the year subject to freezing⁴ as compared with its essential absence in cloud forest. Figure 3 illustrates temperature conditions in these areas of similar warmth (ET , radian 58.4°F) but different equability (M , arcs).

Under conditions of high equability, temperatures are neither so high as to discourage temperate forms, nor so low as to prevent the success of tropical ones. High equability enables species to be associated which otherwise would be confined to widely separate ecosystems. High equability accounts for the mixtures of tropical and temperate plants and animals in the cloud forest of Mexico, and also in the rich, mixed deciduous hardwood forest in the uplands of western Hupeh-Szechuan, which has preserved much of the aspect of the Miocene forests from the middle latitudes of Holarctica (see Wang, 1961; Chaney, 1940; Chaney and Hu, 1940; Chu and Cooper, 1950). In this region, which is rarely subject to freezing, the forest has numerous evergreens, lianas, and epiphytes, and it also shelters tropical mammals, notably monkey, panda, and tiger. Thus, it is high equability—the absence of extremes of heat or cold—which enables parrots to live at Punta Arenas and on Kerguelan Island, sphenodon to persist in New Zealand, palms to live in a climate that is as “cold” as Boston’s, and figs to survive near 9,500 feet in the eastern Himalayas, within a stone’s throw of subalpine conifer forest. High equability not only seems to account for the mixture of tropical and temperate plants and animals in the Tertiary, as well as in earlier times, but it also appears to explain the occurrence of tapir and mammoth at Rancho La Brea, of capybara and porcupine at Seminole, Florida, and of rhinoceros and hippopotamus with mastodon in France and Spain during postglacial time.

The role of high equability in mammalian history is suggested by the conditions under which the richest ungulate fauna has survived. The African fauna south of the Sahara has the aspect of the Quaternary fauna of middle North America.

⁴ Estimates from the normal frequency distribution underestimate the frequency of subfreezing temperatures in middle latitudes if the site is subjected to cold waves. Observations from other North Carolina lowland stations (Raleigh, Winston-Salem) indicate a frequency of subfreezing temperatures as high as 5 percent.

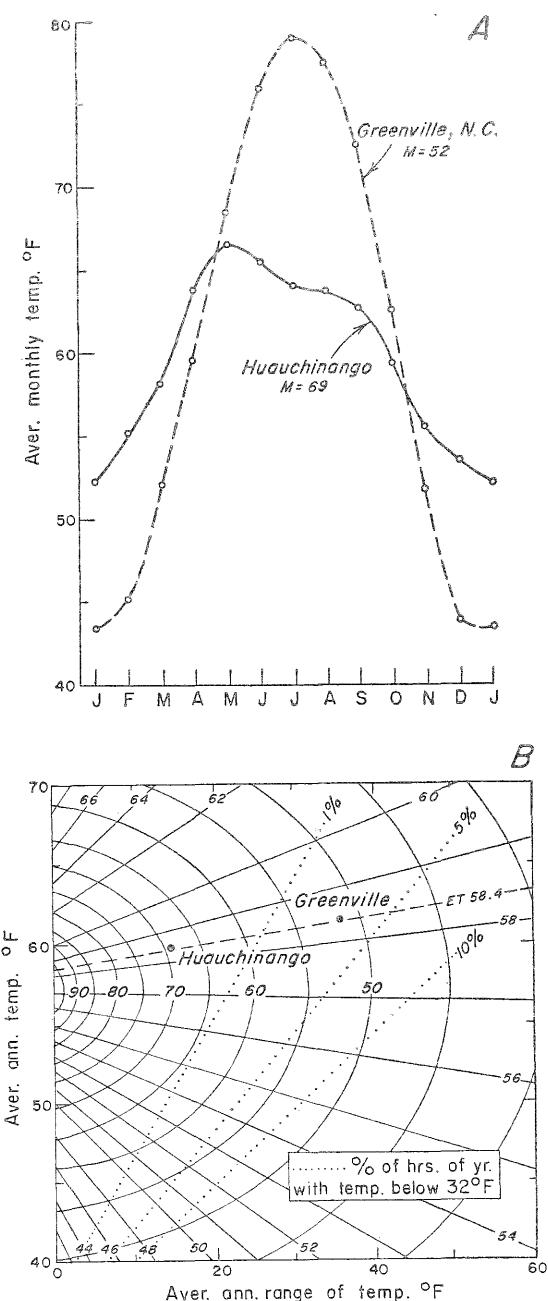


Fig. 3. *A* depicts mean monthly temperatures at Greenville, North Carolina, and at Huauchinango, Mexico, and shows the greater equability of latter area. *B* plots the equability (M , arcs) of the stations on the radian ET 58.4°F , the effective temperature at each locality.

Its area of optimum development includes the largest region of high equability close to the equator (Bailey, 1964, fig. 2). Conditions at a number of meteorological stations where the fauna occurs today, or at the time of white man's entry into the region, are shown in figure 4.⁵ The fauna ranges from deep tropical into subtropical regions, and finds optimum development on the open savannas. Note that the stations (fig. 4) that are warmer than ET $64.4^{\circ}F$ (radii) have, for the most

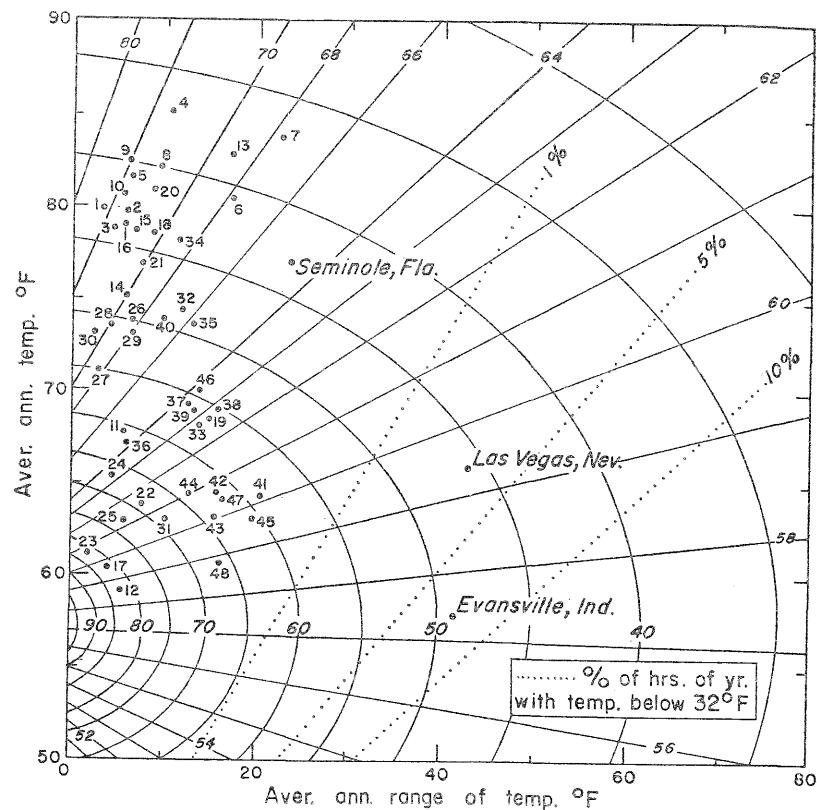


Fig. 4. Effective temperature (ET , radii) and equability (M , arcs) at stations in Africa south of the Sahara where there is a rich ungulate fauna today, or where it was present at the time of white man's entry into the region. (For stations, see n. 5.) Note that stations with lower warmth (ET , radii) have higher equability (M , arcs). For comparison, three stations in the United States where tapir, ground sloth, and other large tropical mammals occurred in postglacial time are shown. Note that these stations have warmth similar to that in Africa, but equability (M) is much lower, $<M$ 50.

⁵ The following stations are represented in figure 4. The Sudan west of Lake Chad: 1—Free-town, 2—Accra, 3—Calabar, 4—Ouagadougou, 5—Lokoja, 6—Kano, 7—Zinder. The Sudan east of Lake Chad: 8—Malakal, 9—Juba, 10—Wau. Ethiopia (Abyssinia): 11—Harar, 12—Addis Ababa. French Equatorial Africa: 13—Fort-Lamy, 14—Yaunde, 15—Duala, 16—Libreville. Belgian Congo: 17—Tshibinda, 18—Léopoldville, 19—Elisabethville. East Africa (Kenya, Tanganyika, Uganda): 20—Mombasa, 21—Voi, 22—Kabete, 23—Nanyuki, 24—Nakuru, 25—Eldoret, 26—Kisumu, 27—Entebbe, 28—Masindi, 29—Tabora, 30—Musoma, 31—Mbeya. Angola: 32—Luanda, 33—Mossamedes. Portuguese East Africa: 34—Mossuril, 35—Malema. Northern Rhodesia—Nyasaland: 36—Abercorn, 37—Kasama, 38—Broken Hill, 39—Zomba, 40—Fort Johnston. Southern Rhodesia: 41—Bulawayo, 42—Salisbury. Cape Province—Natal: 43—Cape-town, 44—Port Elizabeth, 45—Worcester, 46—Durban, 47—Pietermaritzburg, 48—Mbabane.

part, an equability index lower than M 50 (read arcs); those with high ET and relatively high M are in upland areas. All stations with ET below $64.4^{\circ}F$ have high equability (M 55+), and those with the lowest ET (58–61) have the highest M , mostly above M 60. Furthermore, these stations are well removed from freezing (diagonal, dotted lines), even though they are in temperate climates (ET 58–61 compares with the Middle Atlantic states).

It is a climate characterized by a lack of extremes which enables the rich ungulate fauna to extend today into temperate areas well outside the margin of tropical climate (ET $64.4^{\circ}F$). In areas of pronounced equability ($>M$ 60), a small change in mean annual temperature leads to a considerable shift in ET (see fig. 4). Thus, tropical biota in temperate regions of high equability are very sensitive to a small change in temperature: they are close to their limits of tolerance but are "protected" because there is sufficient warmth, or better, an absence of relative cold. For comparison with central Africa, present conditions near fossil localities in the United States where ground sloth, capybara, or tapir have been recorded in postglacial time are shown in figure 4. These areas have warmth (ET , radii) similar to that of stations in Africa, but equability (M , arcs) is considerably lower. The data support the inference that a climate of high equability is the critical factor that enabled tropical and temperate mammals (and plants) to mingle in Quaternary and earlier faunas, and that this factor is operating today. We conclude that an occurrence such as tapir and mammoth at Rancho La Brea, or porcupine and capybara at Seminole, Florida, is not paleoclimatically unique (Martin, 1958, p. 396), but is expectable if equability is high—as it was.

HIGH EQUABILITY DURING TERTIARY TIME

During most of the Tertiary, generally lower continents, lower mountain systems, and marine embayments of moderate extent all contributed to a better distribution of warmth across the surface of the earth, and hence to climatic moderation. *Regional* polar, tundra, steppe, and desert climates were not yet in existence.⁶ Under conditions of greatly reduced climatic contrasts with latitude, equability was much higher over broad regions than it is today, thus enabling tropical and temperate plants and animals to penetrate far into higher middle latitudes. Although the occurrence of early Tertiary tropical with temperate plants in Alaska and other areas above lat. 45° recurrently give rise to the notion that they lived under subtropical climate (e.g., Wolfe, 1966, pp. B4–B5), it was the condition of high equability that accounts for these mixtures (see Axelrod, 1964, pp. 54–59). As noted above, the modern forest at Huauchinango has a dominantly tropical aspect, yet deciduous hardwoods live with it in a region of mild temperate climate (ET 58) and pronounced equability (M 69).

As the trend to cooling progressed during the Tertiary, climatic contrasts increased only gradually. Tropical and temperate plants and mammals were associated well into the Miocene at middle latitudes. These mixtures persisted into the Pliocene, though the numbers of tropical plants were reduced owing to cooling

⁶ Dorf (1960) apparently is alone in the belief that the Arctic Basin and border areas supported *regional lowland* tundra and cold temperate climates during the early Tertiary, and tundra climate in the middle and late Tertiary. Fossil evidence supporting this idea has not been presented. The available record implies that climates were not so cold, and were highly equable.

climate. The later Pliocene floras still contain a few relicts of older, more equable climates, and were accompanied by mammalian faunas that regularly represent mixtures of tropical and temperate taxa. High equability during the middle and later Tertiary is clearly implied by faunal similarity over a wide range of latitude. For example, a Hemingfordian (middle Miocene) fauna from the Cucuracha formation, Canal Zone, compares closely in composition with faunas of similar age in the northern Great Plains and Montana (Whitmore and Stewart, 1965). In addition, the Tapasuna fauna of Honduras (Olson and McGrew, 1941) is similar in composition to the Gulf Coast and southern Great Plains faunas of the same age. Although there were some latitudinally limited taxa in the middle and late Tertiary faunas of North America, they do not obscure the striking faunal similarity that existed then over a much wider band of latitude than it does today. It is apparent that the conditions of the Tertiary—which set the framework for the changes of the Quaternary—were conducive to high equability over much wider regions than they cover today. Extreme summer temperatures were not so high, and extreme winter temperatures were not so low; as seasonal contrasts were not so sharp, equability was higher. With the coming of the first glacial stage, the situation was rapidly altered because equability was reduced. Equability was progressively lowered during the successive stages of the Quaternary, and it is this relation that appears to account for the several episodes of mammalian extinction.

DECREASED EQUABILITY DURING QUATERNARY TIME

In considering the problem of extinction, Martin (1958), Martin, Sabels, and Shutler (1961), and Martin and Mehringer (1965) rejected climatic change as a factor bearing on extinction. Their evidence seems to rest primarily on an interpretation of the ecologic and climatic conditions under which the ground sloth (*Nothrotherium*) lived in southern Nevada and adjacent Arizona after the last glacial. They note that at Gypsum Cave east of Las Vegas, Nevada, and at Rampart and Mauv caves, in the lower Grand Canyon east of Lake Mead, Arizona, the ground sloth was feeding on shrubs that are dominant in the Mohave and adjacent desert region today. Hence they assert that climate was much like that at present. Actually, there is ample evidence to show that regional conditions were not like those of today. Some of this evidence, as well as evidence for climatic change in other areas, must now be reviewed because it provides a basis for evaluating the cause, the different times, and the different degrees of extinction which occurred in different areas during the Quaternary.

1. The Gypsum Cave deposit (alt. 1,500 ft) comes from a low desert basin where a *Larrea-Franseria* community now dominates. Plants identified in the sloth dung (Laudermilk and Munz, 1934) indicate that when the fauna lived there the vegetation included agave, Joshua tree, and juniper. They now live in the adjacent region, but 3,000 feet higher in altitude, which implies a moister climate and also one of greater equability (see below). The dung from the surface of the cave gives radiocarbon dates ranging from 8,500 to 11,700 years (in Wells and Berger, 1967). The sloth dung from Rampart and Mauv caves (Laudermilk and Munz, 1933) contains plants similar to those near the caves today, such as creosote bush (*Larrea*), saltbush (*Atriplex*), cacti (*Opuntia*), nolina (*Nolina*), and Mojave yucca

(*Yucca*). The dung on the floor of the cave, from which the plants were identified, is dated at $9,900 \pm 400$ years (Olson and Broecker, 1961), and it also yields pollen of plants like those in the vicinity of the cave today (Martin, Sabels, and Shutler, 1961). Pollen analysis of a sample from a depth of 18 inches (radiocarbon age: $12,000 \pm 400$ years), however, reveals significant amounts of pinyon pine, juniper, and *Artemisia* pollen (*ibid.*), indicating a downward displacement of woodland vegetation fully 3,000 feet during this period, and in earlier times as well. The evidence implies cooler and moister conditions only 2,000 years earlier than suggested by the flora from the dung on the floor of the cave. It is apparent that in this local area, desert conditions developed slightly earlier than to the northwest and west, where at the same time juniper woodland was widespread in the region.

The regional occurrence of juniper woodland is demonstrated by megafossil remains preserved in ancient wood rat middens at approximately twenty localities in the Mohave and adjacent desert area (Wells and Jorgensen, 1964; Wells and Berger, 1967). As recently as 10,000 to 12,000 years ago, in the Frenchman Flat area north of Las Vegas, juniper woodland descended to an altitude of about 3,300 feet, or fully 1,800 feet below its present lower limit. Desert and semidesert shrubs existed with the woodland over much of the area, as they do today. Joshua trees, agave, and juniper descended to 1,500 feet in the Gypsum Cave area, and to the same level in the Muddy Mountains 25 miles northeast (Wells and Berger, 1967). As noted above, 50 miles southeast only desert shrubs are recorded in the sloth dung on the floor of Rampart and Mauv caves in the lower Grand Canyon. To judge from the widespread occurrence of juniper woodland in the nearby region, as shown by the wood rat middens, the absence of juniper woodland in the lower Grand Canyon cave deposits clearly was only a local feature. It may have resulted from the position of the sites in the deep canyon where precipitation may have been slightly lower than in the nearby area. This is implied by the presence of juniper and pinyon pine in the cave at a depth of 18 inches and dated only 2,000 years earlier, and by the distribution of juniper in wood rat middens at about the same altitude in the area to the north. It seems probable that the ground sloths were attracted to the cave region because of water, not food, for they obviously were browsing on plants that range into desert areas today.

That regional climate was not desert, as it is today, is apparent from the occurrence in southeastern Mohave Desert (Lucerne Valley area) of wood rat middens that also record the downward displacement of the pinyon-juniper zone (Wells and Berger, 1967). This is paralleled by the occurrence of pinyon pine and juniper at an altitude of 1,500 feet in the arid Turtle Mountains of the southwestern Mohave region, a range where these trees do not live today. Although the deposit is slightly older ($13,900 \pm 200$ years), it is symptomatic of the rapid climatic shift that was taking place in the region. At a minimum, evidence from the wood rat middens demands continuity for many now disjunct stands of conifer woodland over the region. They probably extended along the higher divides connecting most of the ranges (Wells and Berger, 1967), reaching down close to the edge of the lower flats as recently as 10,000 years ago. This supposition is consistent with the pollen samples from Tule Springs, now situated in a desert basin just north of Las Vegas, which indicate that the higher-elevation Mohave Desert or Great Basin

desert vegetation occupied the valley flats about 8,000 years ago (Mehringer 1965, p. 183). This implies a minimum climatic shift comparable to a change in altitude of 1,500 to 2,000 feet.

Present temperature conditions at the fossil localities in southern Nevada may be judged from meteorological data for Las Vegas, Indian Springs, Boulder City, and Overton (fig. 5), all situated near localities that yield pollen records or the

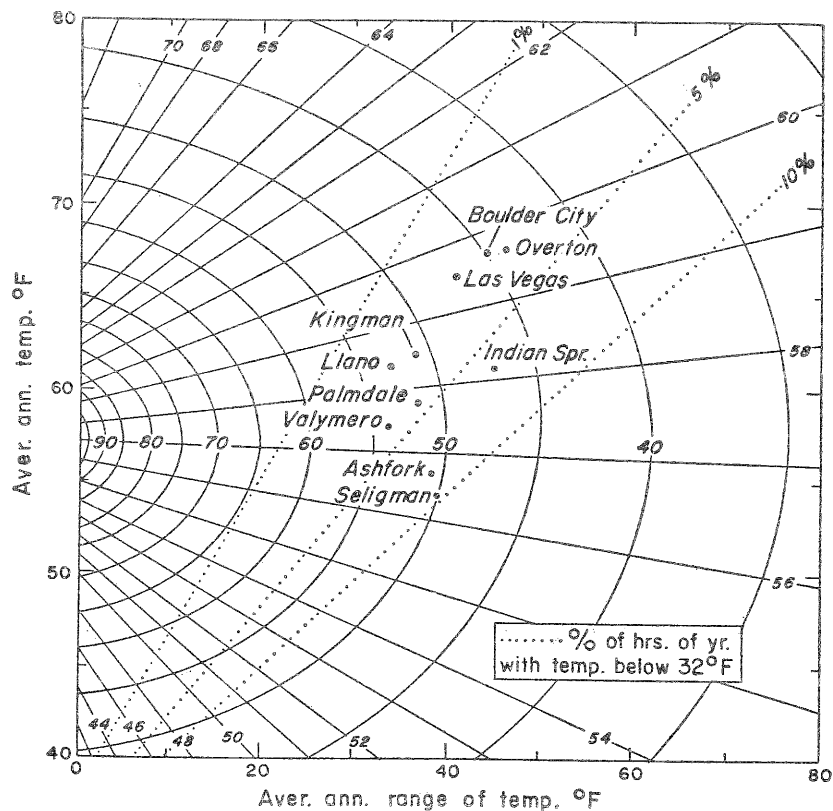


Fig. 5. Comparison of conditions in low desert (Las Vegas, Indian Springs) with those inferred for late Pleistocene floras in the same region which resemble the juniper zone above the desert today (Valymero, Ashfork, Seligman). Note higher equability (read from arcs) at latter three stations.

remains of juniper woodland in wood rat middens. All of them are about 10,000 years old, and occur in areas that receive 3.4 inches (Indian Springs) to 5.4 inches (Boulder City) of precipitation. For comparison, figure 5 shows temperature conditions at localities that are in the lower juniper zone (Ashfork, Ariz.; Valymero, Calif.), at the lowest margin of that zone (Llano and Palmdale, Calif.) at the upper edge of desert, or in the grassland (Seligman and Kingman, Ariz.) at the upper edge of desert. Average annual rainfall in all these areas ranges from 11 (Valymero) to 13 (Ashfork) inches in the lower juniper zone, to 9.5 inches (Palmdale, Llano) at its lower margin where it merges into the upper Mohave Desert, to about 10 inches (Seligman, Kingman) in the grassland at the upper margin of

desert in western Arizona. Present conditions at these localities approximate those of 10,000 years ago in the lower parts of the Mohave region when ground sloth lived in southern Nevada and adjacent Arizona, and when juniper woodland was widespread over the lowland of the region. Manifestly, a climate of higher equability (M 51-54 vs. M 47-48) and heavier rainfall (10 vs. 5 inches) typified the lowlands then as compared with today. Equability was higher than suggested by the meteorological data (fig. 5) because the present regional desert climate was not yet in existence, and lakes were present over the interior lowlands. These features would decrease the annual range of temperature, and thus increase equability which may have been near M 55-56 as compared with M 47-48 in the low desert today.

2. A significant change in equability is suggested by the record at Rancho La Brea, where plants of widely different environments occur in the tar pits. One ecologic assemblage includes Monterey pine (*Pinus radiata*) and bishop pine (*P. muricata*), implying pronounced equability (M 70) like that now along the outer coast from San Simeon to Monterey (fig. 6). The other, dominated by juniper, indicates conditions like those in interior southern California near San Bernardino where juniper and walnut now occur (Axelrod, 1966). Desert-border lizards (Brattstrom, 1953) and a desert shrew (Compton, 1937) from the tar pits presumably were contemporaneous with juniper because they live together today. The climatic contrasts between the former (representing the last glacial-pluvial) and the latter (probably representing postglacial, Altithermal time)⁷ are indicated in figure 6. Present conditions at Rancho La Brea are represented by the average temperatures for Culver City and Los Angeles, situated 7 miles east and 4 miles southwest of the tar pits, respectively. That equability was sharply reduced during the Altithermal (= Xerothermic period) is also evident from discontinuous distributions of desert and desert-border plants in southern California today. They occur in relict sites in the coastal strip, surrounded by more mesic, cooler types of vegetation which spread with climatic moderation after the Altithermal (Axelrod, 1966, p. 45).

3. The Pleistocene plant record in California, in Japan, in western Europe-Russia, and in the Mediterranean area indicates that earlier glacial and interglacial climates had higher equability than those of Wisconsin-Würm and later times. For instance, the early Pleistocene Coso pollen record from Owens Valley area east of the Sierra Nevada represents a rich, yellow pine forest like that now on the windward side of the range (Axelrod and Ting, 1960, 1961). Species of desert and desert-border requirements are not recorded, yet they occurred in the area during

⁷ The exact age of the juniper community has not been established. It may represent a dry interglacial of the Wisconsin. Even so, floristic evidence (Axelrod, 1966, pp. 45-54) supports the nature of the change suggested here.

The Monterey pine cone and cypress cone are from pits 67 and 16, respectively, both of which yield numerous extinct mammals (Marcus, 1969) and birds (Howard, 1962). The depth at which the pine cone was recovered is not known, however, and as the cypress cone was picked up on a dump its stratigraphic position also is uncertain. The age of the cone of *Pinus attenuata* (= *tuberculata*) from pit 9 at a depth of 12.5 feet is not known, though the cone from a depth of 17 feet is older than 40,000 years because wood at a depth of 16 feet is of that age (Berger and Libby, 1966, p. 492).

It is to be regretted that the precise age of the ecologically significant plants at Rancho La Brea cannot be determined. They are represented only by the type specimens, and thus cannot be used for dating.

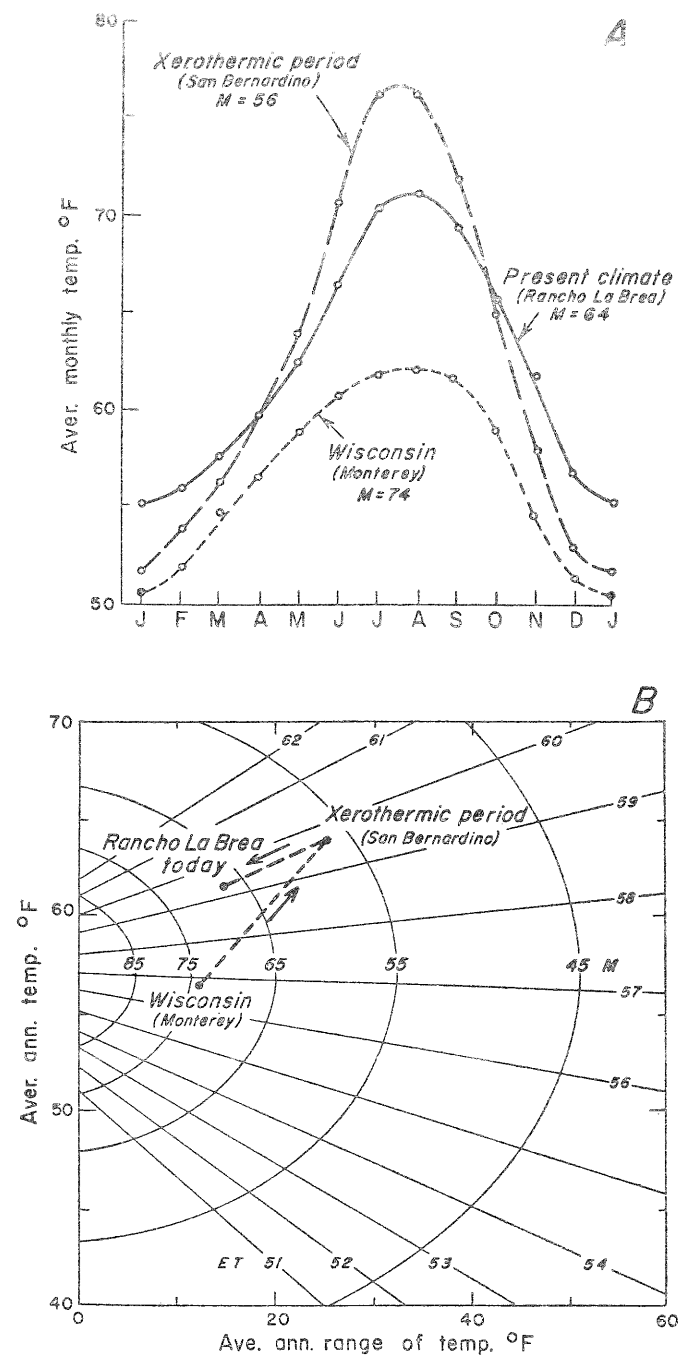


Fig. 6. Changing equability at Rancho La Brea during late Pleistocene and post-Pleistocene time. A. Curves show march of mean monthly temperature as inferred from modern stations with vegetation like that at Rancho La Brea which represents the late Wisconsin and Xerothermic period. Equability ratings (M) are also shown. B. Nomogram showing changing effective temperature (ET , radii) and equability (M , arcs) for the same stations, with the arrows indicating general direction of climatic change during time.

late Pleistocene when lowland vegetation was like that now found in juniper country on mountain slopes bordering the desert today (Roosma, 1958).

In central Japan (Uegahara, near Osaka) climate was sufficiently mild during an early interglacial (post-*Larix* bed) to support numerous trees that are now found to the south, either in Kyushu or in central China (Miki *et al.*, 1957).

Quaternary floras suggest that climates of higher equability characterized the region from the Russian Plain to the Netherlands early in the epoch, and that extremes of temperature increased only gradually, reaching a maximum during the last glacial (see Butzer, 1964; Duigan, 1963; Godwin, 1956; Reid, 1920; Szafer, 1946; Zagwijn, 1957). Rich, broad-leaved forests with conifers which characterized the early interglacials were replaced by progressively more impoverished forests—forests lacking species that now survive only in eastern Asia, eastern North America, or in the Colchic region. Critical evidence is provided by the rather complete sequence in the Netherlands (van der Vlerk and Florschuz, 1953; Florschuz and Van Someren, 1950) where a gradual diminution of exotics (*Liquidambar*, *Taxodium*, *Pseudolarix*, *Parrotia*, *Zelkova*, *Magnolia*) is recorded. The late Pliocene Reuver flora has 79 percent of species that are now extinct in the Netherlands, the Tiglian has 41 percent, the Holstein 17 percent, the Eem 9 percent; a similar sequence is recorded on the Russian Plain (Grichuk, 1960). The change implies gradually increasing extremes of temperature—decreasing equability—during the Pleistocene. Evidence for mild climate not only includes the persistence of species of these alliances in western Europe into mid-Pleistocene (Mindel-Riss), but the occurrence of present-day Mediterranean species (e.g., *Rhododendron ponticum*) in central Europe in the last (Eem; Riss-Würm) interglacial (Walter, 1954). Furthermore, species now found only in western and southern Europe (e.g., *Ilex aquifolium*, *Fagus sylvatica*, *Carpinus betulus*) ranged into eastern Europe and Russia during the later (Eem, Holstein) interglacials (Walter, 1954), implying not only a warmer climate, but one of greater equability. The composition of the middle European mammalian faunas (see Thenius, 1962) also suggests climates of high equability early in the Quaternary, and the gradual appearance of more severe, less equable conditions later in the period.

The early Pleistocene (Villafranchian = Günz) flora from Lac Ichkeul near Bizerte and the mid-Pleistocene (Riss) Maison-Carrée flora near Algiers contain species (e.g., *Laurus canariensis*) that now live only in the Canary Islands, where equability is high, as well as members of the widely distributed Mediterranean oak zone and a few Oriental relicts (Arambourg *et al.*, 1953; see Butzer, 1964). *Laurus canariensis* persisted in coastal Libya (near Derna) into the late Pleistocene, in an area now subdesert (McBurney and Hey, 1955). Faunal evidence in the Mediterranean Basin reinforces the plant record, for large mammals, now found only on the savannas south of the Sahara, inhabited the Mediterranean Basin and ranged southward into the region now desert (see Zeuner, 1959; Charlesworth, 1957; Monod, 1963; Butzer, 1964).

4. The rich African ungulate fauna was eliminated from the Saharan-Libyan desert region by increasing aridity and decreasing equability after the last glacial. This is shown by records, in the area now desert, of upper Paleolithic and Neolithic fossils and petroglyphs that represent elephant, rhinoceros, buffalo, crocodile, hip-

popotamus, and giraffe (Monod, 1963). Figures 7 and 8, redrawn from Mauny (1957), show the early postglacial occurrences of elephant and giraffe as compared with their present areas; Mauny presents similar maps for camel and rhinoceros. They indicate that under the moister conditions of late Pleistocene to early post-glacial times the region had sufficient forage for big game. That there was ample

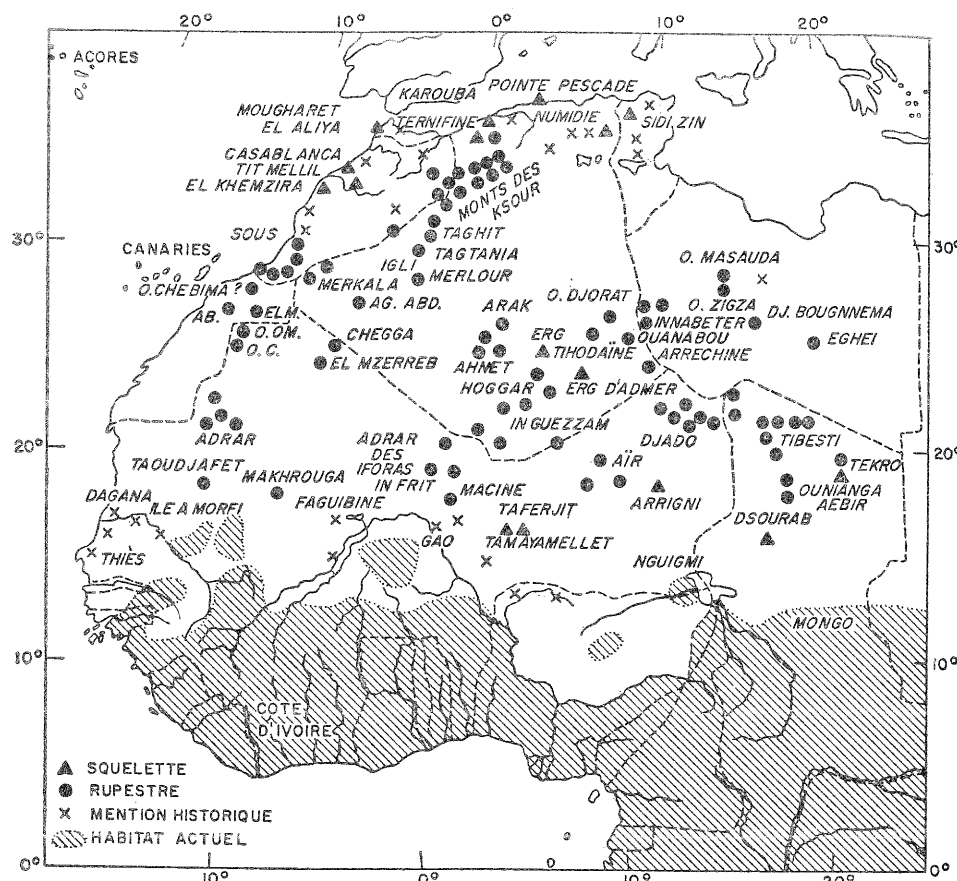


Fig. 7. Distribution of elephant in Saharan region during postglacial time as judged from fossil evidence, rock paintings, and historical records (from Mauny, 1957).

water in the area at these times is implied also by the presence of relict colonies of freshwater fish and crocodiles of Congo affinity at water holes in the mid-Saharan (Hoggar, Tibesti massifs) region (McBurney, 1960, pp. 70, 76). Furthermore, baboon and red monkey have relict colonies in the Air and Tibesti massifs, well isolated from their occurrences to the south of the Sahara (Monod, 1963, fig. 6). In addition, some of the fossil finds in the desert, including hippopotamus, buffalo, elephant, crocodile, and giraffe, are dated archaeologically as only 4,000 years old (*ibid.*, p. 183).

Paleobotanical evidence (in Monod, 1963; Alimen, 1965; Butzer, 1964) indicates that during the last glacial and in postglacial time the central Saharan region

locally supported Mediterranean vegetation of subhumid type, including forest (Atlas cedar, Aleppo pine, juniper) and woodland (oak, linden, pistachio, maple, alder) at levels where minimum precipitation was near 20 inches. These communities occurred chiefly on the higher plateaus and massifs of the region, including much of the Hoggar-Tibesti ridge. They evidently occupied the uplands of this

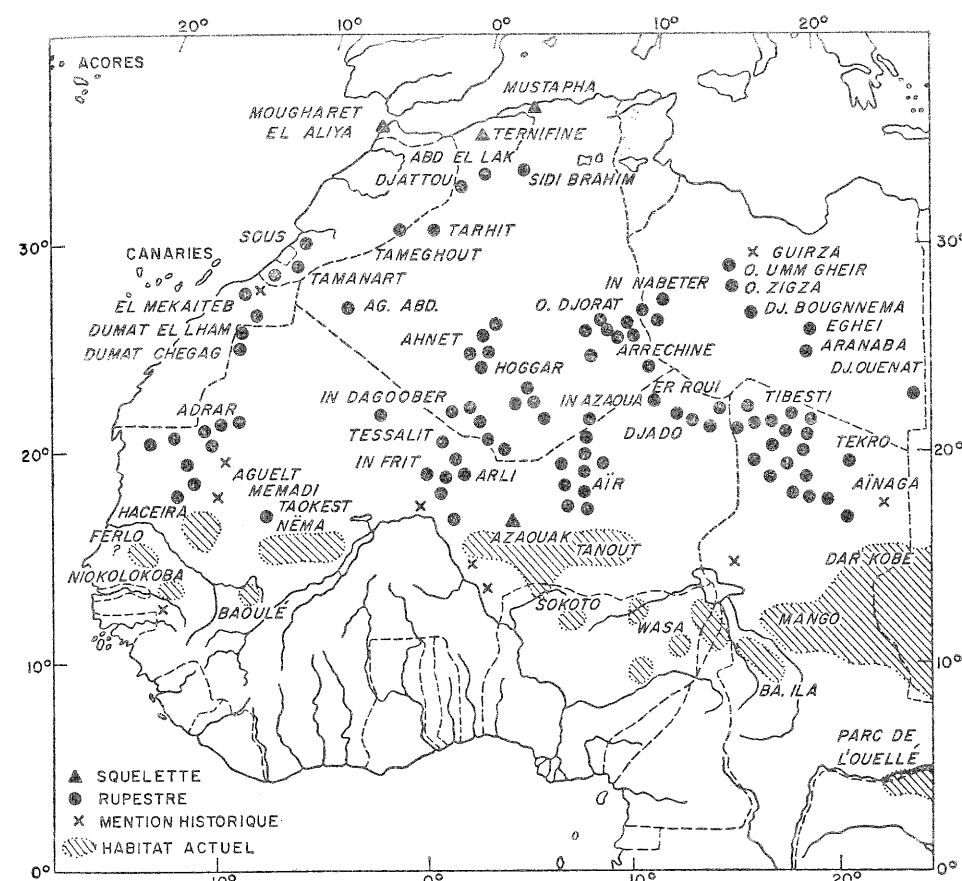


Fig. 8. Distribution of giraffe in the Saharan region during postglacial time as judged from fossil evidence, rock paintings, and historical records (from Mauny, 1957).

area during the earlier Pleistocene, to judge from the record at the Atakora Mountains, where elements of Irano-Caucasian, Mediterranean, and Saharo-Sudanese forest and woodland are recorded from sedimentary rocks at an altitude near 6,000 feet (van Campo *et al.*, 1964). During the last glacial, over most of the Saharan region there probably were scattered areas of tall-grass savanna (15 inches annual precipitation) interrupted in drier, lower areas by patches of short-grass savanna (10 inches annual precipitation), with subdesert scrub confined to locally more arid sites. These estimates represent minimal requirements for the large-mammal fossil fauna (giraffe, elephant, rhinoceros) which needs adequate forage, and for large animals that demand water (crocodilians, hippopotamus). Slightly drier

conditions were present during the Saharan subpluvial (ca. 5000–2350 B.C.), as described by Butzer (1964, pp. 449–453). The record implies that the Saharan region was subject to a rapidly spreading, successively drier, progressively less equable climate which confined surviving remnants of the late Pleistocene-Recent

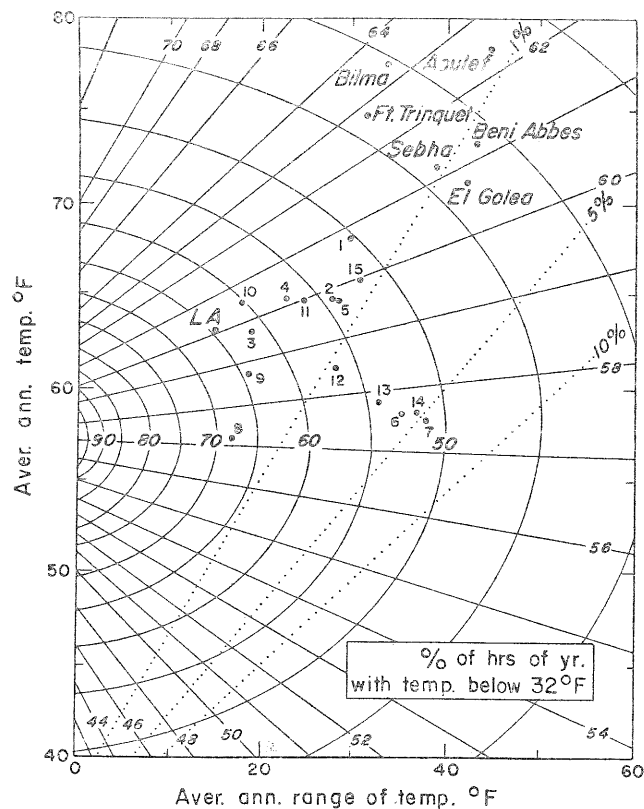


Fig. 9. Effective temperature (ET , radii) and equability (M , arcs) at stations in western Mediterranean region today (text gives stations). Large mammals (rhinoceros, giraffe, elephant) now found south of the Sahara lived in the western Mediterranean region into Neolithic time, and relicts of that fauna (monkey, lion, cattle) still persist in this highly temperate region. For comparison, present conditions are shown for several Saharan stations where a rich ungulate fauna existed into Neolithic time, a fauna that lived under conditions more nearly like those now in the western Mediterranean region, to judge from associated floras.

Mediterranean flora and large-mammal fauna to the higher, moister, more equable parts of the Hoggar-Tibesti ridge, and also to the northwest—to the moister west Mediterranean area of higher equability.

Relicts of the fauna in the Morocco-Algeria-Tunisia region occur with the same vegetation zones they occupied during early postglacial time. Monkey (*Macaca*), lion (*Panthera*), warthog (*Phacochoerus*), and native cattle (*Bos*) now occur there, and elephant, giraffe, and hippopotamus lived there into Neolithic (Cooke,

1963) and historic times (Mauny, 1957). Thus, tropical animals inhabited areas of high equability well outside the tropics, as indicated by the stations in figure 9 (1—Marrakesh, 2—Fez, 3—Casablanca, 4—Algiers, 5—Tunis, 6—Sétif, 7—Géryville). The postglacial record in Spain and Portugal also includes remains of large mammals that are now found south of the Sahara (see Charlesworth, 1957; Butzer, 1964). The region has a climate (fig. 9, stations 8—Corunna, 9—Lisbon, 10—Gibraltar, 11—Cartagena, 12—Barcelona, 13—Saragossa, 14—Madrid, 15—Seville) slightly cooler than that of Algeria-Morocco, but it also has high equability. Climate of the western Mediterranean Basin is similar to southern California, where the Rancho La Brea fauna (Los Angeles = LA in fig. 9) has many ecologic counterparts that occur in the fossil faunas of the western Mediterranean Basin. Figure 9 also shows present conditions at several stations (named) in the Saharan region. The fossil biota recovered from the area imply an equability somewhat less than that now in the Atlas region (fig. 9, stations 1–7), but considerably higher than that of the present regional desert which was not yet in existence.

5. Important climatic and faunal changes have occurred in north central China (northernmost Honan) during historic time. The archaeological site at Anyang yields fossil mammals (de Chardin and Young, 1936; Young and Liu, 1949) many of whose bones are engraved with oracle inscriptions which represent the Yin period, Shan Dynasty, dated between 3,350 and 3,000 years ago (Chang, 1963; Ting, 1966). The fossils reveal an intermingling of northern mammals (bear, sheep) with those of southerly affinity or distribution today (tiger, bamboo rat, tapir, horse, ox, water deer, two extinct deer, extinct sheep, cattle, elephant, monkey). Crocodile and tortoise also give a southern aspect to the fauna. Today elephant does not range north of southernmost China; water deer (*Hydropotes*) is on the southeast China coast; wild ox is of a type now in Indonesia; the tapir is in the deep tropics; the extinct species of deer represent genera now in Indochina; the bear is also extinct, and similar to one in the Pleistocene deposits at Choukoutien. Some of the other mammals of southern affinity also occur at Choukoutien, notably tapir, tiger, bamboo rat, and water deer, which shows that they were indigenous to the region. The inscriptions on the fossil bones refer to many of the mammals, and they also show that bamboo was common, yet neither the bamboo nor the bamboo rat ranges north of the Yangtze River today, which is situated 500 miles south. The bones also have inscriptions that represent common hardwoods (apricot, elm, oak, chestnut, mulberry) now in the region, but none refer to the conifers (pine, spruce, fir, juniper) which are frequent in the foothills there today, and clearly require a colder climate than that of the Yin period. The minimum climatic contrasts are suggested by Ichang, Hankow, and Engshih in the central Yangtze drainage as compared with Kaifeng situated 90 miles south of Anyang, and a little lower in altitude in the valley of the Hwang Ho. It is apparent (fig. 10) that at Kaifeng (and Anyang) the mean temperature of the coldest month is below 32°F, whereas at Ichang, Hankow, and Engshih less than 5 percent of the hours are subject to freezing. Ichang, Hankow, and Engshih have a warmer (ET 58°F) climate of higher equability and, at a minimum, suggest the conditions 500 miles north during the Yin period.

6. The composition of the fossil floras and faunas suggests that although

equability decreased gradually during the Quaternary, times of high alternated with episodes of lowered equability. On the Great Plains, the successive climates inferred for the sequence of Pleistocene mammalian faunas (Hibbard, 1960; Hibbard *et al.*, 1965) and freshwater molluscan faunas (Taylor, 1965) indicate that mesothermal subhumid climates typified the interglacials, whereas microthermal

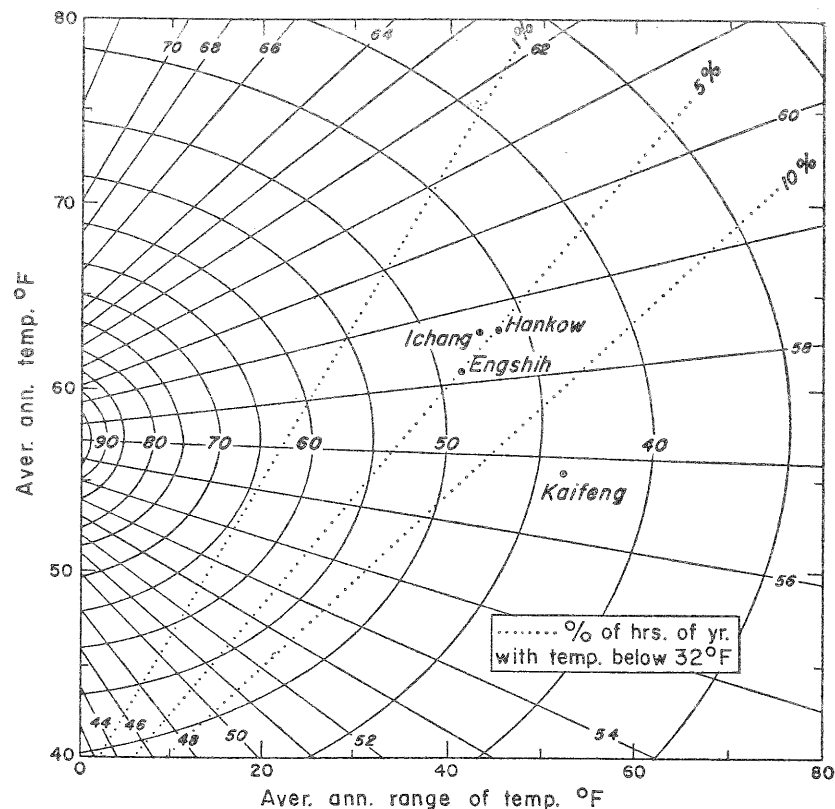


Fig. 10. Climatic differences between Kaifeng (near Anyang, China) and Yangtze River area (Hankow, Ichang, Engshih). Large animals now in latter area, and also well to south, lived 500 miles north at Anyang during Yin period, Shan Dynasty (3,350–3,000 years ago).

subhumid climates are inferred for the glacials. Climates of medium equability comparable to those of the present day (M 45–50) can be inferred only for the latest part of the sequence. All pre-Wisconsin mammalian faunas of interglacial ages indicate more moderate winters than at present. Probably none of the faunas, either mammalian or molluscan, could have survived the present hot, dry summers and cold winters: they required milder climates, climates of less extremes, and hence of greater equability. Taylor (1965) notes that land snails like those now at high altitudes in the Rocky Mountains appeared on the Great Plains only during the Wisconsin. Like the rodents and other mammals, they indicate cooler summers and a lower annual range of temperature than at any previous time in the Pleistocene. Thus the pronounced seasonal contrasts that are a Wisconsin and

post-Wisconsin phenomenon throughout the High Plains, and the Southwest in general (Malde, 1964), were not paralleled earlier in the Pleistocene, a time when equability was higher.

The faunas imply that interglacial climates were sufficiently mild so that the Arctic Ocean probably was not frozen during the earlier interglacials (Hibbard and Taylor, 1960; Taylor, 1965). This is consistent with the temperature indications of molluscan faunas and fossil plants recovered from sedimentary rocks representing the Beringian transgression in northwest Alaska, and from correlative rocks of the Konyatkhun suite, Chukotski Peninsula, Siberia (Hopkins *et al.*, 1965). Although rocks of the Beringian transgression have been considered late Pliocene (*ibid.*), their radiometric age (2.2 million years) indicates that they are Pleistocene, and transitional Aftonian-Kansan.⁸ The floras represent conifer and conifer-hardwood forests like those now on Hokkaido and in southern British Columbia, whereas the fossil sites are at lat. 64°–65°N in tundra, close to the region of continuous permafrost. Deposits of the Beringian transgression were followed by Iron Creek glaciation (Kansan), and succeeded by Anvilan deposits which indicate much warmer seas than at present near Nome, as does a small pollen flora which represents spruce-fir forest (in *ibid.*). Mild climate in the Arctic Basin during an early interglacial is also indicated by a pollen flora from Banks Island, lat. 73°N (Terasmae, 1956). It represents a conifer hardwood forest similar to those now in the upper Great Lakes area or on Hokkaido, yet the site is 200 miles north of the tree line today.

These records support the suggestion that during the early glacial ages the Arctic Ocean may not have been permanently frozen. With an open polar sea in winter (or most of the year), much more water vapor would be supplied to the air because it would have been fairly cold and therefore dry. When the air left the ocean it would be thoroughly charged with water vapor which would greatly increase the greenhouse effect, and substantially delay cooling of the atmosphere over landmasses around the polar basin. Although the land was still the source of the coldest air, the humid air would not have allowed so complete a radiational cooling. With a stronger greenhouse effect and a more favorable topography, climates associated with the earlier glaciations were characterized by considerably higher equability than during Wisconsin time. The open Arctic Ocean also supplied much of the snowfall that caused the widest extent of continental glaciation. Thus, although the earlier glacial epochs produced the largest ice sheets, they were associated with climates of higher equability than those of the later Quaternary. The conditions of higher equability which evidently characterized the northern hemisphere during the early Quaternary find a modern parallel in the present occurrence of glaciers near sea level in southern Chile and on South Island, New Zealand, where they are in proximity to tropical biota, as recorded by Darwin (see p. 5, above).

As the Pleistocene progressed, major cordilleras were lifted to greater heights, continents were elevated, and continuously frozen polar seas appeared during

⁸ The potassium-argon date of 2.2 million years reported by Hopkins *et al.* (1965) is of Pleistocene age because the Coso fauna of California, dated at 2.3 million years (Evernden *et al.*, 1964), is a correlative of the early Pleistocene faunas on the Great Plains, which are Aftonian to transitional Kansan (in Hibbard *et al.*, 1965).

middle (?) and later glacial ages. Air masses now brought colder and drier climates to central latitudes, with sharper seasonal contrasts and lowered equability. Such a climatic trend is implicit in the Great Plains faunal sequence, and also in the relatively complete floral and faunal sequences recorded in the Netherlands, European Russia, and the Mediterranean Basin. Periods of lowered equability during the glacial ages thus appear to account for most of the episodes of Quaternary mammalian extinction.

ROLE OF EQUABILITY IN EXTINCTION

The richest part of the surviving African ungulate fauna has persisted on the central plateau, a region of high equability (fig. 4). Of the large mammals on the African savannas only a few (e.g., hippopotamus, elephant, giraffe) seem to calve at nearly any time of the year, and they have a relatively constant food supply except towards the margins of their range. For the rest, including buffalo, chimpanzee, baboon, rhinoceros (black and white), wildebeest (black and brown), sable and roan antelope, ghemsbok (oribi), impala, puku, reedbuck, bushbuck, bushpig, honey badger, Thomson's gazelle, Grant's gazelle, gerenuk, lesser and greater kudu, eland, hartebeest, tsessebe, topi, nyala, zebra, ostrich, cob, leopard, and lion, the dry season of the savannas imposes a seasonality on calving (A. S. Boughey, written comm., 1966). As distance from the central equatorial savanna region increases, the calving season becomes more marked owing to the longer period of drought and also to decreased warmth. Although the young are very vulnerable for some days following birth, only rarely in areas of high equability and sufficient moisture would climatic stress result in mass mortality from critically high or low temperatures, or from severe drought. This relation appears to explain the persistence on the African plateau of a rich ungulate fauna that basically has remained unchanged since the Pliocene. The African savannas are deep within the tropical zone, and well removed from extremes of temperature or severe drought. Furthermore, the fauna on the central plateau (3,000–6,000 ft) inhabits an area that has high to pronounced equability today (fig. 4), and no doubt throughout the Quaternary and earlier. Thus, as compared with the United States, Australia, China, and southern South America, there was relatively little extinction of the African ungulate fauna after the last glacial, and probably earlier to judge from the available record:⁹ it was largely removed from the theater of climatic change which, fundamentally, was decreased equability.

Recall now that equability during Pliocene and earlier times was high, enabling tropical animals to have a wide distribution, ranging well into temperate latitudes. Under conditions of high equability and heavier rainfall over the savanna and steppe regions, most large mammals, which presumably bred only once a year, probably were somewhat seasonal in their mating habits, much as they are today on the African savannas and elsewhere (Asdell, 1964). Seasonality in mating is

⁹ Martin (1966) reports that a major period of extinction coincides with Achulean culture in central Africa. Leakey (1966) disagrees, however, and points out that there is good faunal and geological evidence for its more remote age. Leakey also notes that it was chiefly the larger mammals—the giant forms—which died out at that time. He also emphasizes that “the animals that needed the greatest number of calories suffered most, while their contemporaries survived into the upper Pleistocene.” Furthermore, he emphasizes that the period of change was a time of desiccation (end of Bed IV time) and a time of lowered equability (see discussion below).

also implied by studies of large samples of middle and late Tertiary fossil ungulates from single fossil sites (Kurten, 1953). Clearly, if equability decreased rapidly, as it did at the close of the Pliocene and also during the succeeding glacial ages, then high loss of young of large mammals might reasonably be expected throughout extratropical regions. According to these precepts, at times typified by cycles of rapidly increased cold to which biota were not adapted there should have been widespread extinction in areas previously typified by higher equability, and there was. As noted earlier, in North America 18 percent of the late Pliocene large-mammal fauna did not survive the first glacial, 23 percent of the large-mammal fauna became extinct at the close of the second glacial, and so on (see Introduction). In order to show that there probably is a direct relation between varying degrees of equability in different regions and the degree of extinction of large mammals in those areas, it is necessary to recall the effects that severe weather may have on biota.

LARGE MAMMALS

Effect of cold.—Increased cold is precisely the condition that sets a limit to the northern and southern distribution of biota today. An occasional freeze kills trees at the northern margin of the cloud forest in Mexico (Hernandez *et al.*, 1951, p. 463), controls the northern limit of redwood in California–southwestern Oregon (MacGinitie, 1933), and is the critical factor determining the northern distribution of subtropical plants in the Sonoran desert (Turnage and Hineckley, 1938). At the eastern margin of that region, about 200 miles south of the Lehner, Arizona, site where mastodon and tapir lived 10,000–12,000 years ago, ocelot, peccary, coati, and other tropical mammals occur today (Leopold, 1959). They inhabit short-tree forest and the adjacent oak zone, and occur in an area where cycads are common, with trunks 5–6 feet in height and up to 10 inches in diameter (John Rees, written comm., 1967). These tropical mammals do not survive conditions only 200 miles north probably because equability is lower there; presumably, cold waves periodically kill much of the tropical biota that may become established temporarily in the region.

Blizzards on the Great Plains and in the Great Basin may bring snow so deep that cattle starve on the range, and temperatures sufficiently low that they freeze. In 1965 the loss of antelope young during spring kidding season on Hart Mountain Antelope Refuge, southeastern Oregon, was approximately 70 percent during the thirty-six hour period of cold rain in early May (D. Weide, oral comm., 1967). The winter season of 1904–05 on St. Lawrence Island, Bering Sea, was unusually stormy, with high winds and low temperatures. That spring about 10 percent of the mature deer and 55 percent of the reindeer fawns died from cold. “When born, the fawns were licked dry, after which they lay down, only to be quickly covered by the drifting snow and deserted by the mother who moved off with the herd in the face of the gale” (Jackson, 1905). Blanford (1954) reports that in June, 1947, a blizzard caused 80 percent loss of the reindeer calf crop in the Canadian Arctic. Repeated freezing and thawing, and freezing rain, may form a snow crust so hard that caribou, deer, and reindeer can not paw through it to reach food, and thus starve (Scheffer, 1951; Rood, 1942).

We can now appreciate the effect that the rapid appearance of the cold waves that accompanied the first major glacial, and the later ones, would have had. Recall that there was a widespread, highly diversified, large-mammal fauna, composed of a mixture of taxa adapted to both tropical and temperate conditions (fig. 1). They were living in a world typified by much larger areas of high to pronounced equability than exist today. With the first wave of severe cold, or of temperatures appreciably lower than those previously present in their areas, widespread extinctions can reasonably be inferred, especially for the tropical mammals. Many adults would freeze because of lower temperatures, accentuated by wind and evaporation at times of storm. In snow-covered areas some large mammals would be unable to reach forage under the snow and ice crust, and either starve or freeze to death. For those that had survived the new winter conditions, and had mated in the preceding late summer or fall, spring and early summer could be a time of mass mortality. The calves would be vulnerable to snows and cold lasting well into late spring and early summer (see Appendix). This "out of step" mating (Slaughter, 1965) results from mating habits not adapted to producing young at a time appropriate for survival.

The fossil record shows that the degree of extinction was not equal in different regions at the same times during the Quaternary. This inequality may be explained by the selective role of equability with respect to local conditions. For instance, the late Pliocene faunas of central Europe (Thenius, 1962) and the central United States (Hibbard *et al.*, 1965) were about equally rich in large mammals. The first major glacial resulted in fully 50 percent extinction in Europe as compared with about 30 percent in the United States. The European fauna was largely trapped behind the Alpine barrier and could not escape the cold (lower equability) from the nearby ice sheets, whereas the American fauna could shift southward to areas of higher equability and hence would sustain fewer losses.

Regional differences in equability also seem to explain the different aspects of the faunas north and south of the Alps. During the last glacial age the fauna north of the Alps had a more "modern" aspect than the fauna to the south (see Thenius, 1962). In the north only three of some thirty-two genera are extinct, but in the Mediterranean area there were a larger number that are now exotic or extinct, including hippopotamus, giraffe, elephant, buffalo, and others that are now found only south of the Sahara. Colder climate in the north—a climate of lower equability—also accounts for the more modern aspect of the Würm fauna in that area: the "relicts" were eliminated there at an earlier date. It is apparent that the Alpine belt sheltered the Mediterranean Basin from cold air masses to the north, much as it shelters the area of southern Europe today, which has a climate of higher equability and supported relicts of the African fauna into historic time.

The effects of colder weather may be damped by local ecologic conditions. For instance, it has been found that removal of forest cover results in higher mortality in big game at times of severe cold than in areas where the cover has not been removed (J. Ashley, written comm., 1966). On this basis, it seems reasonable to suppose that during Quaternary time forest and forest-border mammals might find shelter in the forest, as compared with those adapted to the adjacent open plains. This possibility may explain the differential extinction shown by the

Pampean fauna of Argentina-Patagonia (Simpson, 1940; Martin, 1958). Ground sloths, glyptodonts and other edentates, camels, horses, and native ungulates such as maraheeniids, toxodonts, mesotheres, and hegetotheres, disappeared from the plains. There was some extinction of forest mammals, but survival there was much higher than on the plains. Tapirs, capybaras, peccaries, large edentates, monkeys, and deer of forest and forest-border habitats provide a marked contrast to the presence of only two large herbivores (pampas deer, llama) on the pampas and in Patagonia. This differential survival is probably owing to the greater equability in the shelter of the forest, where large mammals would be protected from occasional spells of severe weather in this region of high equability. Such a relation finds analogy in the southern Appalachians where a rich bryophyte and fern flora, composed of many species with disjunct distributions in subtropical Mexico, live in deep, mist-shrouded canyons under dense forest (Billings and Anderson, 1966; Farrar, 1967). They do not occur on the bordering slopes (analogous to the plains) where there are wider ranges of temperature (lower equability) and more drought, or else are very rare there. Comparable relations are seen in the scattered pockets of cloud forest in Mexico, and the discontinuous patches of evergreen subtropical forest on the central east coast of Australia which occupies deep, sheltered valleys; both inhabit areas of higher equability than the surrounding forests. It is apparent that while southern Argentina has relatively high equability (see Bailey, 1964, fig. 2), somewhat more severe cold on the plains than in the shelter of the forest may account for the higher degree of extinction of large mammals in the former area during postglacial time.

Effect of drought.—The hotter, drier, more intemperate climate of the Alti-thermal (= Xerothermic) period brought drought, heat, and stress. Similar episodes occurred earlier in the Quaternary though they evidently were not so severe as the postglacial trend toward aridity. Such a trend has a bearing on the problem of extinction because the amount of precipitation determines the density of plants and forage production on which herbivores depend; the numbers of large animals reflect primarily the mean annual precipitation through its influence on vegetation. For example (Teer *et al.*, 1965), as annual precipitation decreases from about 32 inches at the east margin of the Edwards Plateau, Texas, to less than 12 inches at its west edge 400 miles distant, population densities of deer also decrease—from about ten to fifteen per 100 acres in the east to less than two per 100 acres in the west. Field estimates show extremely high mortality during years of drought and food shortage, and much lower mortality after the drought (fig. 11). In 1954–1956, when precipitation was less than half the average and the range was in poor condition, losses amounted to as much as 52 percent of the herd, with starvation the primary cause. In periods of more extreme drought, the percentage of loss of young would no doubt rise.

According to Martin (1966), drought (and increased heat) would not be a critical factor in survival because large animals may migrate to suitable areas, as in the 800-mile annual migration of wildebeest from the desertic Serengeti Plains to the humid shores of Lake Victoria. Talbot and Talbot (1963), however, show that as wildebeest leave for preferred water and food areas as the plains dry, movement follows an irregular, not a steady, migration route. The migration is

dispersed over a wide region determined primarily by availability of grass at the right stage of growth, and by surface water. The distribution and the amount of rainfall affect herd size: typically the rainfall-grass complex encourages concentrations of wildebeest at the end of the wet period and to a lesser extent at the start, with a wider dispersion during the middle of the period. Wildebeest born near the start of the dry season obviously have less chance of survival than those born in the middle of the wet period, for food may disappear as well as water.

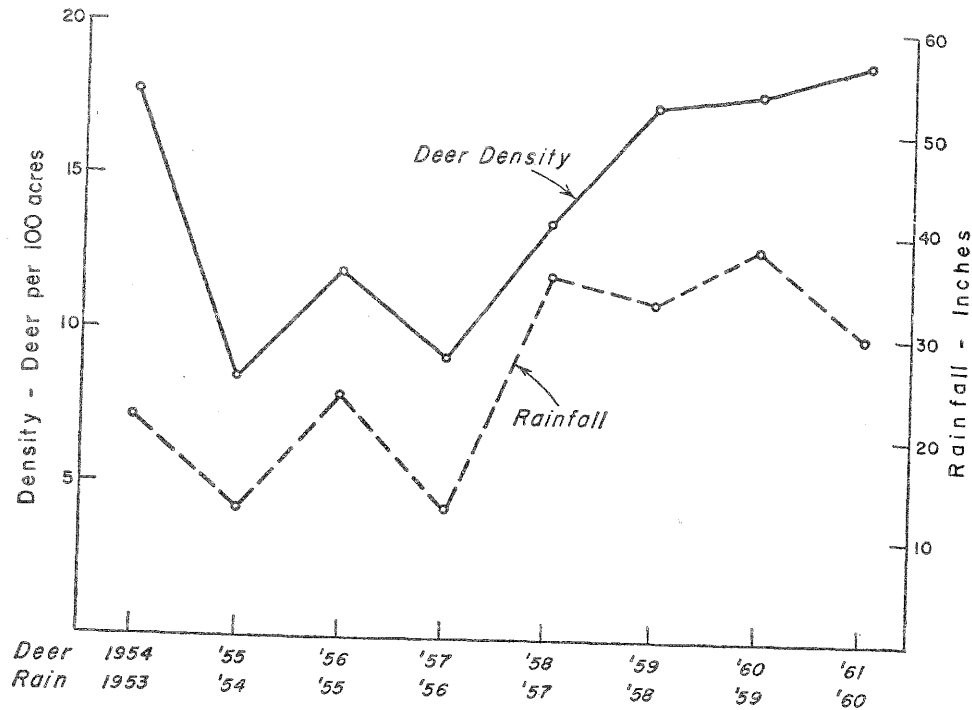


Fig. 11. The relationship of population levels of deer in the Llano Basin to annual precipitation of the preceding year (from Teer *et al.*, 1965).

Seasons with relatively poor and irregularly distributed rain produce much higher postnatal mortality. The forage-water relation is crucial not only to wildebeest, but to all the other grazers on the plains because they have highly specific food requirements. The different species, often seen feeding side by side, are eating different kinds of grasses, or different growth stages of the same grass (Talbot and Talbot, 1963). The complementary, nonduplicating diets of plains wildlife explain why so many species coexist in high numbers without overgrazing any one component of the grassland. If rains are delayed, or do not continue, then forage and water are in short supply for many different grazers, and drinking holes (often puddles) dry up. Under conditions of severe, long-continued drought—as during the Altithermal—adults may have been able to migrate to other water holes, but the young of many alliances probably would perish, either from lack of water, from excessive heat, or from starvation due to shortage of forage.

It seems clear that as the postglacial trend to aridity commenced, the shrinking back of the more humid climates toward the inner tropical zone was not even. It occurred irregularly and at uneven rates, more like the evaporation of a thin sheet of water. The geographic pattern of a shrinking area would produce progressively more disjunct islands of habitable ground which may be thought of as areas of positive relief (water, more food, above level of frost) separated by uninhabitable areas of negative relief (less or little water, less or no food, frost). The migratory ability of animals probably did them little good if they reached the geographic limits of their refuge, because they would be wandering aimlessly. In other words, Nature probably divided and conquered. This pattern appears to have been true of the Saharan region, where relicts on the plateaus and massifs

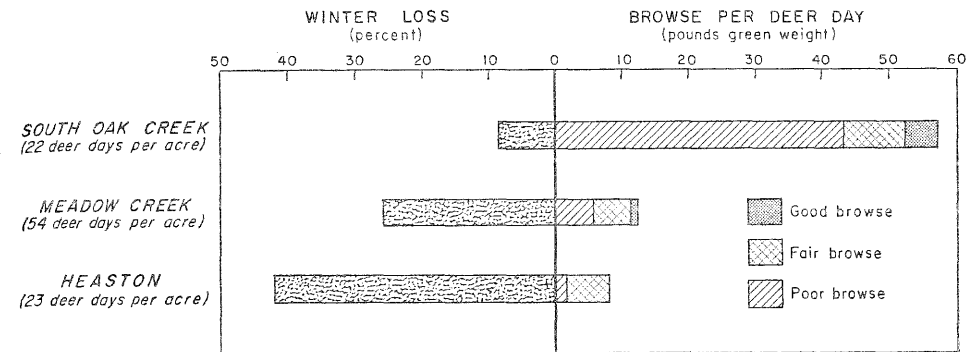


Fig. 12. Winter deer losses are inversely related to the amount of available browse (from Robinette *et al.*, 1952).

(positive relief) still survive, and where evidence suggests a wider distribution for forest and woodland in a steppe region well into postglacial time (Monod, 1963; Cooke, 1963; Butzer, 1964, pp. 449-453).

In middle North America, drought was a highly important factor controlling the distribution of all large mammals of plains and forest-border habitats. Relict areas within the present desert probably supported isolated, relict large-mammal populations, like the islands of forest, pinyon-juniper, and grassland which occur in the higher eastern Mojave and southern Great Basin region today. In a region changing from savanna to open steppe as aridity increased, the effects on large grazing and browsing mammals seem obvious. Since large animals need more area to maintain population size, they would disappear sooner than the smaller ones, chiefly by starvation due to overcrowding and overgrazing.

During an episode of increasing drought, as in postglacial time, the degree of loss of large browsers and grazers would depend on forage supply. The argument is supported by deer mortality and range condition studies made in Utah after the winter of 1948-49 (Robinette, *et al.*, 1952), the severest on record according to the United States Weather Bureau. Studies of three deer ranges showed that winter deer loss varied inversely with forage supply. Herd losses of 9, 26, and 42 percent were determined for the three areas which, forage inventories showed, had had respectively 57, 13, and 9 pounds of green forage at the start of winter for each deer day of use (fig. 12). As winter commenced much of the forage was made un-

available, with resulting serious food shortages on two overbrowzed ranges. The loss on ranges depleted by drought or overgrazing in severe winters may exceed by several times the mortality incurred during a moderate winter.

Recurrent spells of severe drought during a trend toward increased aridity may deplete the range of forage and browse, and man's activities may make the depletion worse. The goats and sheep used by early herdsmen were no doubt important contributory factors in depleting natural rangelands in the Old World, and hence in the extinction of marginal populations of large grazing and browsing mammals. The effects would have been especially important during late postglacial time. This inference may be drawn from the records of deer die-offs on the Edwards Plateau, western Texas (Taylor and Hahn, 1947). During the drought in July and August, 1942, the deer die-off on overgrazed land amounted to about 50 percent, and became more severe in the fall when, it is estimated, overpopulation reduced the herds by 65 to 70 percent. During the fall of 1954, after a spell of cold weather, another big die-off occurred. The fawns were the first to die, followed by the yearlings, the does, and finally the bucks. Mortality increased when large numbers of goats were added to the pasture for kidding. Apparently the deer did not move out, but held to their normal range. As pasture became depleted many deer died because of food shortage. With narrowing areas of favorable environment during a trend to aridity, the overcrowding of natural range would lead to starvation and extinction of large mammals.

Evidence suggests that the chief role played by aridity in extinction was a complementary one: together with cold, aridity helped to exterminate faunal components during postglacial time. Although dry climates were present earlier, deserts of regional extent probably were not. Recall now the trend to postglacial aridity, the resultant shrinking of grazing areas which would localize populations, the overcrowding of range owing to confinement of large browsers, decreased precipitation, and hence a further shortage of forage. Superimpose on this situation a period of severe winters such as occur sporadically even today (see Appendix), and were more frequent in the past—then it should not be surprising to find that many larger mammals disappeared. Most adults probably fell to the absence of food owing to drought and overgrazing, to its unavailability (under snow), or to low temperatures. The young also were reduced by cold snaps and blizzards in late spring and early summer because they were born "too early" in a region where climate formerly had higher equability.

SMALL MAMMALS

The preceding analysis provides a clue to the survival of small mammals. In North America, all the sixty-four nonvolant genera recorded as fossils which ranged up to the last glacial survived to the present day except for giant beaver (*Castoroides*). These small mammals include various species of the following genera (from Hibbard *et al.*, 1965):

<i>Sorex</i>	long-tailed shrew	<i>Sciurus</i>	tree squirrel
<i>Bassariscus</i>	ringtail cat	<i>Citellus</i>	ground squirrel
<i>Peromyscus</i>	white-footed mouse	<i>Vulpes</i>	fox
<i>Scapanus</i>	western mole	<i>Martes</i>	marten, fisher

<i>Perognathus</i>	pocket mouse	<i>Neofiber</i>	water rat
<i>Oryzomys</i>	grasshopper mouse	<i>Erethizon</i>	porcupine
<i>Ochotona</i>	pika	<i>Sylvilagus</i>	cottontail rabbit
<i>Baiomys</i>	pygmy mouse	<i>Lepus</i>	hare
<i>Blarina</i>	Short-tailed shrew	<i>Neotoma</i>	wood rat
<i>Cryptotis</i>	least shrew	<i>Procyon</i>	raccoon
<i>Notiosorex</i>	desert shrew	<i>Spilogale</i>	spotted skunk
<i>Urocyon</i>	gray fox	<i>Lutra</i>	otter
<i>Mustela</i>	weasel, mink	<i>Geomys</i>	eastern pocket gopher
<i>Lynx</i>	lynx	<i>Scalopus</i>	eastern mole
<i>Taxida</i>	badger	<i>Parascalopus</i>	hairy-tailed mole
<i>Marmota</i>	woodchuck, marmot	<i>Mephitis</i>	striped skunk
<i>Castor</i>	beaver	<i>Tamias</i>	eastern chipmunk
<i>Thomomys</i>	western pocket gopher	<i>Tamiasciurus</i>	red squirrel
<i>Sigmodon</i>	cotton rat	<i>Clethrionomys</i>	redback vole
<i>Reithrodontomys</i>	harvest mouse	<i>Dasybus</i>	armadillo
<i>Zapus</i>	jumping mouse	<i>Didelphis</i>	opossum
<i>Synaptomys</i>	bog lemming	<i>Conepatus</i>	hog-nosed skunk
<i>Cynomys</i>	prairie dog	<i>Gluacomys</i>	flying squirrel
<i>Microsorex</i>	shrew	<i>Orozomys</i>	rice rat
<i>Gulo</i>	wolverine	<i>Condylura</i>	starnose mole
<i>Dipodomys</i>	kangaroo rat	<i>Aplodontia</i>	sewellel
<i>Ondatra</i>	muskrat	<i>Eutamias</i>	western chipmunk
<i>Phenacomys</i>	phenacomys	<i>Cratogeomys</i>	Mexican pocket gopher
<i>Microtus</i>	vole	<i>Liomys</i>	Mexican pocket mouse
<i>Pedomys</i>	prairie vole	<i>Dicrostonyx</i>	collared lemming
<i>Pitymys</i>	pine vole	<i>Napaeozapus</i>	woodland jumping mouse

These small mammals apparently survived the period of crisis which affected their larger contemporaries because of behavioral and ecologic factors (see Bartholomew, 1958). They have two means of escaping spells of severe weather: (1) they either burrow into the ground, live in caves and dens or holes in trees, or build nests or houses; (2) they have short gestation periods, they mate in early or late spring so that climate and food will be favorable for the young, and under very favorable conditions they may breed several times (polyestry). Thus their mating habits as well as the habitats they occupy enable them to survive late (May, June, July) severe cold waves. Furthermore, the foraging, food-storage habits of many of them make it possible to survive times of severe drought. Hence, it has been by their behavioral (daily and seasonal) and ecologic (habitat) relations, rather than by a physiologic tolerance of great extremes, that they have been able to escape episodes of severe heat or cold or drought, and have survived times of decreased equability.

SUMMARY

Since Darwin's day various explanations have been offered to account for the postglacial extinction of numerous large mammals, chiefly grazers, browsers, and their dependent carnivores and scavengers. This event was not unique, for there were other major episodes of faunal turnover during the Quaternary. The same factor probably accounts for all these recurrent times of extinction.

Wallace pointed out that the postglacial faunas are similar in composition to those of Pleistocene and earlier times: they are composed of mixtures of large

mammals that are basically either tropical or temperate in their climatic requirements. A similar relation is also displayed by Quaternary and older floras.

Today, such climatically discordant taxa are regularly associated only in regions of high equability. Evidence is adduced to support the thesis that equability was much higher throughout Quaternary and earlier times than it is today. Periods of decreased equability which accompanied the glacial climates may therefore have been the selective agent that led to extinction of large mammals, and also to important changes in floral composition.

Modern studies of mass mortality of big game suggest that in areas where snow and freezing occur in late spring and even in early summer, the young, conceived in late summer to autumn, are born too early and thus die of cold. Also, in severe winters deep snow seals off food supply and adults and young both die, either from starvation or cold. These relations appear to explain most of the episodes of Quaternary extinction.

With a trend to aridity, areas of favorable food would be reduced in size, resulting in overpopulation and hence overgrazing on the range. Shortage of grass and reduced browse, owing to insufficient moisture and to overgrazing, would lead to mass starvation. Coupled with cold winters, severe losses could be expected. These factors appear to explain much postglacial extinction, at a time when drought was more extreme than earlier, and when equability was considerably lower.

The African fauna persisted in scarcely modified form on the savannas because it was largely removed from major climatic change owing to its equatorial position, and because the plateau has had high equability throughout the Quaternary. In other regions, differences in degrees of extinction seem to reflect local differences in equability. The occurrence of more numerous exotic and extinct genera in the late Quaternary fauna of the Mediterranean Basin as compared with central Europe probably was due to the protection afforded the former area by the Alps, giving it a climate of higher equability. The loss of 50 percent of large mammals in central Europe as compared with 30 percent in North America during the first glacial probably owes to the trapping of the former fauna behind the Alpine barrier, whereas the latter could migrate south. Greater extinction of the late Quaternary fauna on the Argentine-Patagonian pampas and steppe, as compared with that in the adjacent forest and forest-border environment, is probably owing to the higher equability in the shelter of the forest.

The small-mammal fauna survived without displaying important episodes of extinction, chiefly because of the habitats they occupy and the seasonal and daily habits they follow. They live in protected areas (dens, caves, burrows, nests), commonly store food, and mate in spring so that the young start life during a season of nonstress.

Man's activities, resulting in overgrazing and overpopulation of natural range by goats, sheep, and cattle during the past several millennia, appear to account for the extinction of local, relict populations of large mammals and for the disruption of range of others.

ACKNOWLEDGMENTS

Thanks are extended to several people who have helped in certain aspects of this study. Professor A. S. Boughey made available information concerning the fauna of Africa south of the Sahara, drawn from his many years of field experience there. Professor Marshal White, Ronald Skoog, and James F. Ashley provided references to mass mortality in big-game herds. Professor H. P. Bailey has made several helpful comments concerning the factor of equability, and has given permission to reproduce the nomogram he constructed.

The manuscript was read by the following, all of whom have provided constructive comments: Harry P. Bailey, George A. Bartholomew, Ted Downs, Clarence Hall, N. Gary Lane, Jere Lipps, Richard Tedford, and James Valentine.

The idea presented here emerged as an outgrowth of paleoclimatic problems raised by my studies of Tertiary floras in Nevada, a research project generously supported by National Science Foundation grants (GB 2625, GB 4926).

APPENDIX

A well-documented instance of the duration and effect of cold weather lasting through much of the year has been presented by the National Geographic Society (*News Bulletin* no. 12,311—PS, dated May 10, 1966). It was published in the *New York Times* and is reproduced here with the kind permission of the National Geographic Society.

Publication of the article was prompted by the abnormally cold spring of 1966. In this connection, it is recalled that in the winter of 1966-67 both Chicago and New York were immobilized by snowstorms; temperatures dropped as low as the sixties in Saigon; snow blanketed areas from Monterrey and Saltillo south to Mexico City; and in the Midwest warnings of invading air masses sufficiently cold to endanger cattle were issued into May.

SUMMER SKIPPED NEW ENGLAND IN 1816's FAMOUS COLD YEAR

Summer never came at all in the dismal year of "eighteen-hundred-and-froze-to-death."

The chilly spring of 1966 was nothing compared to that of 1816. The weather 150 years ago turned New England into a frigid disaster area, the National Geographic Society says.

Heavy frosts were recorded every month, a blizzard struck in June, ice storms coated trees in July, birds froze, hundreds of cattle and sheep died, crops failed, farmers perished in snowdrifts.

Scholars variously blamed a volcanic eruption and sunspots for the cold, bleakly speculating what would happen if "the sun should become tired of illuminating this gloomy planet."

January in June

Curiously, the cold year started with an unseasonably warm January, according to the *Old Farmer's Almanac*. Three days in May also were abnormally warm. In Salem, Massachusetts, the temperature rose to 101 degrees on May 23.

In June, things changed drastically. Salem's temperature dropped from 92° to 42° overnight. It snowed in many parts of the state. On June 7 a foot of snow blanketed Williamstown.

During the next few days, there were severe frosts every night as far south as Virginia. Snow fell all across New England, in New York, and Ohio.

On June 15, the Danville (Vermont) *North Star* reported that "on the night of the 6th water froze an inch thick, and on the night of the 7th and morning of the 8th a kind of sleet or exceedingly cold snow fell, attended by high wind, and measured in places where it drifted 18 to 20 inches in depth. . . . The shoots of leaves of forest trees which were just putting forth, and corn and garden vegetables that were out of the ground were mostly killed."

A Vermont farmer ventured out in the midst of the storm to tend his sheep. As he went out the door, he said jokingly to his wife, "If I am not back in an hour, call the neighbors and start them after me. June is a bad month to get buried in the snow." Three days later searchers found his frozen body.

Orioles in Kitchen

So many birds were frozen that relatively few were seen in New England the next few years. One farmer regularly brought orioles into his kitchen to warm them up.

In many parts of New England, the vital corn crop failed. Those who managed to raise some food helped their neighbors. The inscription on a gravestone in Ashland, New Hampshire, reads: "Son of a Revolutionary Soldier, a pioneer of this town. Cold Season of 1816 raised 40 bushels of wheat on this land which kept his family and neighbours from starvation."

The sun that chill year of 1816 rose every morning red and rayless, as in a cloud of smoke. Scientists thought the sun may have been obscured by a globe-girdling cloud of volcanic dust thrown up by the tremendous eruption of Tamboro, in the East Indies, in April of the year before.

Dudley Leavitt, a 19th-century astronomer and almanac maker, attributed the weather to a large number of sunspots. Present-day meteorologists speculate that a combination of volcanic dust and sunspots may indeed have caused "eighteen-hundred-and-froze-to-death."

(Sources for release on "COLD YEAR" of 1816: *Why the Weather?* by Brooks; *Our American Weather* by Kimble; *The Connecticut*, Hard; *The Merrimack*, Holden; *Old Farmer's Almanac*, 1966.)

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UNIVERSITY OF CALIFORNIA PUBLICATIONS IN
GEOLOGICAL SCIENCES

Volume 75

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY AND LOS ANGELES
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