# Pleistocene Niches for Alien Animals

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Massive extinction of animals at the end of the Pleistocene was the subject of a symposium held at the VIIth Congress of the International Association for Quaternary Research (INQUA) in Boulder, Colorado, in 1965. The meaning of Pleistocene extinction in understanding prehistory, paleoclimatology, and future resource planning has yet to be fully appreciated. The search for a cause (whether man or climate, or both), which occasioned some sharply conflicting interpretations at the Boulder symposium (Martin and Wright, 1967), need not be resolved before we may examine yet another provocative issue: What is to be done in those parts of the world where Pleistocene extinction decimated the native fauna and where man's primary Neolithic domesticates—cattle, sheep, and goats—seem to be inferior replacements?

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Outstanding features of Pleistocene extinction include the following: (1) It eliminated mainly large terrestrial mammals, with smaller terrestrial vertebrates affected only on certain oceanic islands. (2) The large herbivores (proboscidians, ungulates, perissodactyls), plus their associated carnivores, commensals, scavengers, and parasites, were not replaced by the evolution of new species (for which there was far too little time). There was no replacement by extensive immigration from other regions. Megafaunal extinction left empty niches. (3) Massive extinction took place with variable intensity, apparently striking first in Africa and Southeast Asia roughly 50,000 years ago, later reaching the Americas, and finally within the last 1000 years sweeping over the larger oceanic islands such as New Zealand and Madagascar (Fig. 1). (4) The phenomenon did not leave its mark on either the marine or the terrestrial plant fossil record of the Pleistocene.

Based on the sizable biomass of elephants, bovids, and zebra in protected parts of Africa (Table 1), plus the great number of mammoth, mastodon, bison, and horse teeth found in the fossil deposits of North America, it seems fair to assume that before their extinction the natural Pleistocene vertebrate fauna on this and other continents was also abundant. Mammoth were not rare, to be seen once in the lifetime of a Paleolithic hunter, as has been suggested by some. The Pleistocene game-carrying capacity of western North America must have equaled, and very likely exceeded, the 40 million units of livestock which it now supports (Stoddart and Smith, 1950).

With Pleistocene extinction, one may envision a reduction in pruned limbs, browse lines, and in the thorn frequency on branches of woody legumes, all features of African big-game country at present. Under recommended stocking capacity of the better grassland in Ari-

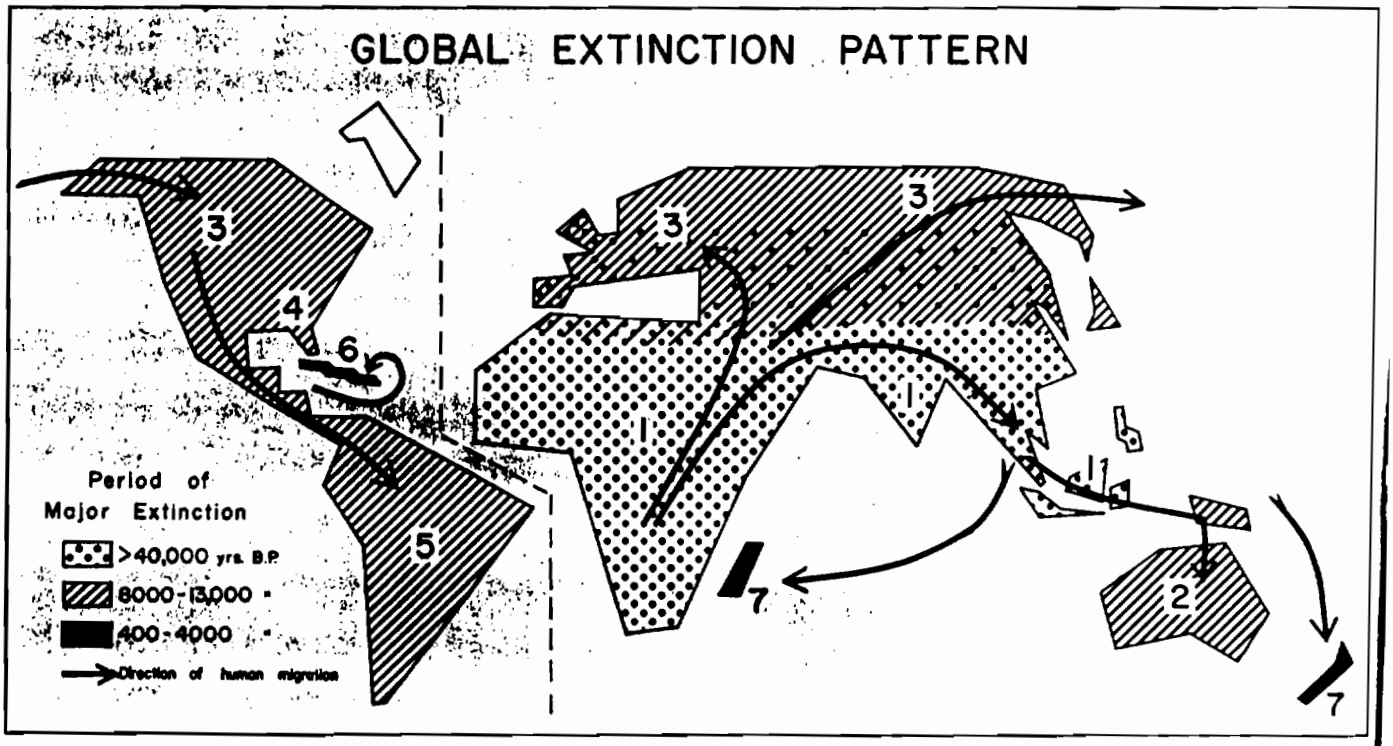


**Fig. 1. Late Pleistocene extinction and the path of human migration.**

TABLE 1. Megafauna biomass

| Locality | Area | kg/sq km | Animal units/ sq mi | Source |
|---|---|---|---|---|
| 1. Wyoming Bison Range | 75 sq km | 3,400 | 20 | Bourliere, 1963 |
| 2. Cochise Co., Arizona cattle on grassland | 1.7 million acres | 3,000 | 18 | Darrow, 1944 |
| 3. Cochise Co., Arizona cattle on mesquite, creosote bush | 1.6 million acres | 1,200 | 7 | Darrow, 1944 |
| 4. Lake Manyara, Tanzania elephant-buffalo | 30 sq mi | 20,800 | 125 | Watson & Turner, 1965 |
| 5. Luangwa Valley, Zambia elephant-buffalo-hippo | ? | 15,800 | 95 | D. R. Patton (pers. comm.) |
| 6. Albert Natl. Park, Congo elephant-buffalo-hippo | ? | 7,200 & 19,500 | 43 & 117 | Bourliere, 1963 |
| 7. Ngorongoro Crater, Tanzania zebra-wildebeest | 120 sq mi | 5,800 | 35 | Lamprey, 1964 |
| 8. Serengeti Plains, Tanzania zebra-wildebeest | 6,500 sq mi | 4,865 | 29 | Stewart & Talbot |
| 9. Tarangire Game Reserve, Tanzania | 1,583 sq km | >12,000 | >72 | Lamprey, 1964 |
| 10. Athi-Kapiti, Kenya (game only) | 2,090 sq km | 1,033 | 62 | Stewart & Zaphiro, 1963 |
| 11. Ghana (Tano Nimri) | 250 sq km | 5 | 0.030 | Bourliere, 1963 |
| 12. Tchad | 1,200 sq km | 80 | 0.500 | Bourliere, 1963 |

Key references:

*East African Wildlife Journal* for Lamprey, Watson & Turner.
*Mammalia*, 27(4): 483-496, 1963, for Stewart & Zaphiro.
*African Ecology & Human Evolution*, 1963, Aldine, Chicago, for Bourliere.

zona, cattle consume roughly 50% of the annual grass production (S. Clark Martin, pers. comm.). After extinction, much more plant productivity went by default directly to decomposers. Whether there was an increase in grassland at the expense of woody plants is less certain and would have depended upon the effectiveness of browsers as deterrents to the growth of shrubs and low trees competing with the grasses. More important to grass-bush dynamics of the time would have been a sharp increase in fire frequency that presumably accompanied the spread of the early hunters of the late glacial.

The fossil record is not too helpful on this point. Worse, the scattered evidence provided by pollen and macrofossil records in western North America has yet to establish just where high plains and desert grassland (tall- and short-grass prairie) actually was during the full and late glacial. Pollen diagrams suggest no true grassland in the northern Great Plains, the Texas Panhandle, eastern Arizona, or New Mexico until 12,000 years ago (Martin and Mehringer, 1965). Until this matter is settled, there seems little hope of resolving through the pollen record the more subtle question of how the grassland might have responded to the extinction of the grazers.

If one is concerned with the effect of exotic, large herbivores on native American ecosystems, it seems worth examining the fossil record of a time when natural immigration was underway. In the Rancholabrean, 12 Eurasian genera of large mammals entered North America over the Bering bridge (see Table 2, from Repenning, 1967; Hibbard et al., 1965). Evidently, most arrived well within the last 100,000 years. One might have expected them to compete with and replace certain of the native species. Yet very little megafaunal loss *caused by replacement* by Rancholabrean invaders has been claimed. Hibbard et al. (1965) cite the grizzly bear group of *Ursus* as replacing the short-faced bears, *Arctodus*. Alleged replacement of *Capromeryx* by the pronghorn *Antilocapra* was not the result of immigration. Other cases cited by Hibbard et al. (1965) are of invasions

preceding the Rancholabrean.

When it finally came, massive extinction struck many of the Eurasian newcomers such as *Symbos* and *Cervalces* (Table 2), as well as Pliocene relicts such as the peccaries and mastodonts. The case might seem to strengthen Guilday's (1967) hypothesis of competitive constriction as the cause of extinction on the continents. In a deteriorating environment, the large numbers of large herbivores made excessive demands on the ecosystem and finally exterminated themselves in what might be considered, a la Deevey (1960), pathological togetherness.

But most of the mammals which invaded North America from Eurasia in the last 2 million years (Table 2) did not penetrate the New World tropics where a wave of late Pleistocene megafaunal extinction also occurred. Nor is it possible to recognize any other deterioration of the North American environment, apart from the fact of extinction itself. If the only late Pleistocene fossils known were plants, their pollen, and small vertebrates, I doubt that anyone would have guessed at a major crisis in the life of the large mammals.

One serious objection to the introduction of African or Asian exotics has been the belief that the New World fauna of 1492 A.D. was in a "natural" state, a balance allegedly struck after millions of years of evolutionary adjustment among plants and animals throughout the late Cenozoic. Unaware of the fossil record, conservationists have inferred that new exotics would necessarily crowd native species out of their niches, vulgarize the habitat, and perhaps flood the countryside with an animal as destructive to native vegetation as the rabbit in Australia and the red deer in New Zealand (e.g., Laycock, 1966). But even in strictly genealogical terms, it is clear that certain supposedly "alien" mammals have a valid prior claim to the continent. At higher taxonomic levels, some of the "natives" are considerably less American than certain "foreigners."

Among the Asian invaders of the last 100,000 years was the mountain sheep or bighorn, genus *Ovis*, one of the prized native game mammals of the West. The current competitors of *Ovis* include some 500 to 15,000 feral burros (McKnight, 1958), progeny of animals that escaped from mining camps in the last century. Burros (*Equus hemionius*) occupy Death Valley and desert areas along the Colorado River. They have become more numerous than mountain sheep in parts of

TABLE 2. North American Pleistocene megafauna

| Order | Irvingtonian + Blancan extinction | Rancholabrean extinction (last 15,000 yr) | Living |
|---|---|---|---|
| Edentata | *Glyptotherium*<br>*Glyptodon* | *Megalonyx*<br>*Nothrotherium*<br>*Paramylodon*<br>*Eremotherium*<br>*Boreostracon*<br>*Brachyostracon*<br>*Chlamytherium* | |
| Carnivora | *Borophagus*<br>*Ischyrosmilus*<br>*Chasmaporthetes* | *Arctodus*<br>*Smilodon* (I)<br>*Dinobastis* (I)<br>*Tremarctos* * | *Euarctos*<br>*Ursus*<br>*Felis*<br>*Panthera*<br>*Canis* |
| Proboscidea | *Rhyncotherium*<br>*Stegomastodon* | *Mammut*<br>*Cuvieronius*<br>*Mammuthus* (I) | |
| Artiodactyla | *Pliauchenia*<br>*Titanotylopus*<br>*Hayoceros*<br>*Platycerabos* | *Platygonus*<br>*Mylohyus*<br>*Camelops*<br>*Tanupdama*<br>*Sangamona* (R)<br>*Cervalces* (R)<br>*Capromeryx*<br>*Stockoceros*<br>*Tetrameryx*<br>*Bootherium* (R)<br>*Symbos* (R)<br>*Euceratherium* (I)<br>*Preptoceras*<br>*Saiga* * (R)<br>*Bos* * (R) | *Cervus*<br>*Odocoileus*<br>*Oreamnos* (R)<br>*Ovibos* (R)<br>*Ovis* (R)<br>*Rangifer* (R)<br>*Antilocapra*<br>*Bison* (R)<br>*Alces* (R) |
| Perissodactyla | *Nannippus*<br>*Plesippus* | *Equus* * (I)<br>*Tapirus** | |
| Rodentia | | *Castoroides*<br>*Neochoerus*<br>*Hydrochoerus* * | |
| Reptilia (Testudinata) | | *Geochelone* * | |
| Total | 13 | 35 | 14 |

*Living species surviving south of the United States or in Eurasia.
R = Rancholabrean age immigrant from Eurasia.
I = Irvingtonian age immigrant from Eurasia.

the Southwest where the sheep are not flourishing. In the struggle for pasture and water, alien burros have played the villain in the opinion of some scientists (i.e., Buechner, 1960). Even those who do not find that burros are serious competitors regard mountain sheep as enjoying priority in their claim to the range (Welles and Welles, 1961). However, *Ovis* was one of the last of the Eurasian immigrants to arrive in America. It penetrated a continent already richly stocked with many species of native horses of all sizes, some as small as burros. *Ovis* managed to compete with native camels, ground sloths, mammoths, extinct bison, deer, and pronghorn, and to survive the predation of extinct jaguar, saber-toothed cats, dire wolves, and mountain lions. Finally, it survived the late Pleistocene extinction of the megafauna, the crisis that doomed the native horses. Having moved in millions of years after the evolution and radiation of the Equidae, it is not clear, to me at least, why the mountain sheep must be regarded as more "native" than the feral burros. Lacking trophy horns, the burros may be inferior game for the hunter, but at least they represent a lineage that, like the American Indian, occupied this part of the world long before the Pilgrim Fathers.

Again, in the perspective of the fossil record, one finds that Asian camels represent a family with a far longer history in America than the "native" American bison. Bison or buffalo began to roam their western home only in the middle of the Pleistocene, many millions of years after the American origin and radiation of camels. The Old World genus *Camelus* is morphologically close to the extinct *Camelops* of the New World (Webb, 1965). When introduced into the West 120 years ago by the U.S. Army, the former proved partial to mesquite, cactus, greasewood, and creosote bush (See Beal in Lesley, 1929).

In brief, the record of the last 2 million years reveals a number of invasions by alien large mammals entering over the Bering bridge, invaders which apparently caused little or no direct upset among pre-existing native mammals. Around 11,000 years ago, coincident with the arrival of big-game hunters, massive extinction was underway. The survivors—deer, antelope, wapiti, musk oxen, caribou, moose, pronghorn, mountain goats, mountain sheep, and bison—represent only 30% of the big-game fauna present earlier (Table 2). Despite the addition of domestic cattle, sheep, and goats, there is reason to suspect that numerous "empty niches" or "job opportunities" persist on the American range.

In the case of the brush country, the mesquite-dominated ranges of the Southwest and Mexico, ranchers obviously inherited the wrong species to fill local niches (Fig. 2). History and tradition demand the raising of *Bos*, a grass-preferring, water-dependent herbivore, in a land with little of either. Despite 60 years of range research that led to such sophisticated management techniques as careful pasture rotation, water development, chemical spray for "bush control," and the virtual elimination of screw worm and other diseases, the southwestern cattle industry is not a money-making proposition. The owner-operator of a sizable Arizona ranch (450 head of livestock) may expect an annual return to capital and

**Fig. 2. Browsing cow in Short Tree Forest near Alamos, Sonora, Dec. 1968. Vegetation is luxuriant; cattle carrying capacity is low.**

income of $9,000-$15,000, about 2.0-2.4% of the value of the fixed investment (Martin, 1968). Smaller outfits operate at a loss.

The only innovative approach to the problem not being attempted in federal and state agricultural experiment station programs is the search for some superior bovid, or combination of large herbivores, that might be better adapted to arid and subtropical ranges than *Bos*. The problem is not just a question of low total forage production. There are sizable stands of natural vegetation that cattle will not eat.

Foremost is the creosote bush (*Larrea tridentata*), called *La Governadora* in Chihuahua the Governor's Wife—"because she dominates." In one part of Cochise County, Arizona, desert shrub communities produced approximately 1400 kg/ha, the caloric equivalent of 6100 Mcal/ha/yr (Chew and Chew, 1965). Some 900 kg/yr were in the form of inedible (to cattle, not camels) creosote bush. Desert shrub communities dominated by creosote bush will support two to six head per square mile (Darrow, 1944). Five times as many cattle are supported on adjacent grassland under the same or slightly greater precipitation, yet Chew and Chew's data suggest that primary production (plant dry matter per year) is greater in a creosote bush community than in an adjacent grassland.

The repellent properties in the creosote bush and many other desert plants are the natural oils which occur in concentrations of up to 5% (McCaughey and Buehrer, 1961). The essential oils contained in sage brush (*Artemisia*) retard cellulose digestion by microorganisms in the rumen of mule deer and cattle (Nagy et al., 1964). The woody plants of the arid Southwest that do not contain repellent oils in their foliage are typically armed with thorns or else are deciduous. The thorny species increase in frequency toward the tropics. Apparently one adaptation is used largely to the exclusion of the other. There are very few species of desert shrubs, such as *Artemisia spinescens* and *Franseria bryanti*, that are both thorny and aromatic.

Range experts have long recognized that the oily, resinous, poisonous, harsh-leaved or thorn-protected shrubs are poor forage for domestic livestock (Thornber, 1910; Dayton, 1931). The expansion of mesquite, cactus, creosote bush, and other shrubs over arid grassland of the Southwest has been documented repeatedly (Buffington and Herbel, 1965; Hastings and Turner, 1965). What has not commonly been recognized is that the character of the vegetation was molded in the Pleistocene; few authors speculate about the foraging habits of Pleistocene mammoths, camels, ground sloths, and horses.

Any serious effort at introducing a new species should be attempted, if at all, only with the greatest care and only with recognition of the formidable problems in management and marketing that might remain even if large herbivores ecologically more efficient than *Bos* were found. However, the experiment has historical precedent.

There were a number of natural invasions of North America by alien animals over the past 2 million years. Eleven thousand years ago there was a major biotic catastrophe, an upset perhaps entirely caused by prehistoric man. One million square miles of arid and tropical vegetation on either side of the United States-Mexico International Boundary, land once occupied by ground sloths, mammoths, bison, native camels, and horses, have proved to be poor country for domestic cattle. Ten to 20 million new animal units (one animal unit equals 1000 lb., or the equivalent of a cow and a calf) consuming forage largely untouched by cattle is a rough, but perhaps not unreasonable, estimate of the outcome of a successful program of alien animal introduction. No stronger case need be made for primary productivity studies of the sort envisioned by the International Biological Program. Meanwhile, to tolerate further decimation of local populations of African and Asian wild ungulates—the gene bank for any future domestication experiments—is unthinkable, both for the conservationist and for the range industry of the future.

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