PALEOECOLOGY OF BERINGIA

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MAMMALS OF THE MAMMOTH STEPPE AS PALEOENVIRONMENTAL INDICATORS

R. Dale Guthrie

The most puzzling feature of the mammoth steppe is its great diversity of large mammals. The reasons for their diversity, their dietary specializations and their gigantism are examined here, in conjunction with other information, as clues to an investigation of the general paleoenvironment.

The mammalian evidence suggests a specific vegetational mosaic with certain seasonal characteristics. Mammalian growth patterns indicate a long growing season, requiring diets high in available energy and nutrients. These features would require a seasonally rich Pleistocene vegetation in comparatively fertile soil that utilizes antiherbivory defenses quite different from those used by the dominant plant forms now present in the North.

The annual seasonal cycle reconstructed here is characterized by cold, but perhaps variable, winters with very little snowfall. Most of the annual moisture would have fallen during spring and little to none during summer. Summer soils generally were warm, dry, and had a deep thaw. This intraannual variability in the growth season produced hydric, mesic, and xeric plants within the same local communities. Windy conditions were most common.

A new model is presented to explain the high species diversity of Pleistocene mammals, their large social organs and gigantism, as well as the converse: Holocene dwarfing, shrinking social organs, range contractions and extinction with the demise of the mammoth steppe.

Key words: mammoth steppe; mammals, Holocene dwarfing of; Pleistocene

INTRODUCTION

Our Pleistocene heritage is rooted in a large mammal fauna which, for the most part, no longer exists. Nowhere is this more true than in Europe, northern Asia and Beringia. Within this broad zone lived an array of creatures more bizarre than the imagination could invent—giant woolly forms with grotesque antlers, horns or tusks, long manes, humps, and trailing tresses.

If we had found only caribou, sheep, elk and musk-oxen bones in the cutbanks on the Yukon and the Kolyma, this symposium about the Arctic Pleistocene environment would probably not have taken place. It is the mysterious fauna on the cave walls, the frozen carcasses of strange species no longer living and their scattered bones in human middens which excite our imagination and wonder. When learning of this exotic mixture of hyenas, mammoths, sabertooth cats, camels, horses, rhinos, asses, deer with gigantic antlers, lions, ferrets, saiga and other Pleistocene species, one cannot help wondering about the world in which

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they lived. This great diversity of species, so different from that encountered today, raises the most obvious question: is it not likely that the rest of the environment was also different?

Given the immense size of the area involved there was a surprising continuity of large mammal species. Most of the species portrayed on the cave walls of southern France are also present as fossils in the muck deposits of Alaska and northeastern Canada. This continuity suggests a multicontinental mural composed of locally unique elements, each contributing to the character of the large mosaic (Fig. 1). An equally widespread distributional pattern seems to occur among the small mammals, birds, invertebrates and plants, but their fossil record is not as sharply resolved as is that of the large mammals.

As I see it, our present status in depicting this mosaic of related habitats depends heavily on the large mammals. Thus, in many past papers and discussions I have referred to these communities collectively as the *mammoth steppe*. The woolly mammoth seems to be a ubiquitous marker, both chronologically and spatially. Because of the steppic nature of the vegetation, this term seems to better capture the entirety than arctic steppe, tundra-steppe, steppe-tundra, loess-steppe, cold steppe and others that are more descriptively limited.

In this paper I use the fossil mammals as a focus to study not only how these species lived but also their environment in general. Historically, it was large mammal remains that first suggested the clearest outlines of the mammoth steppe. I

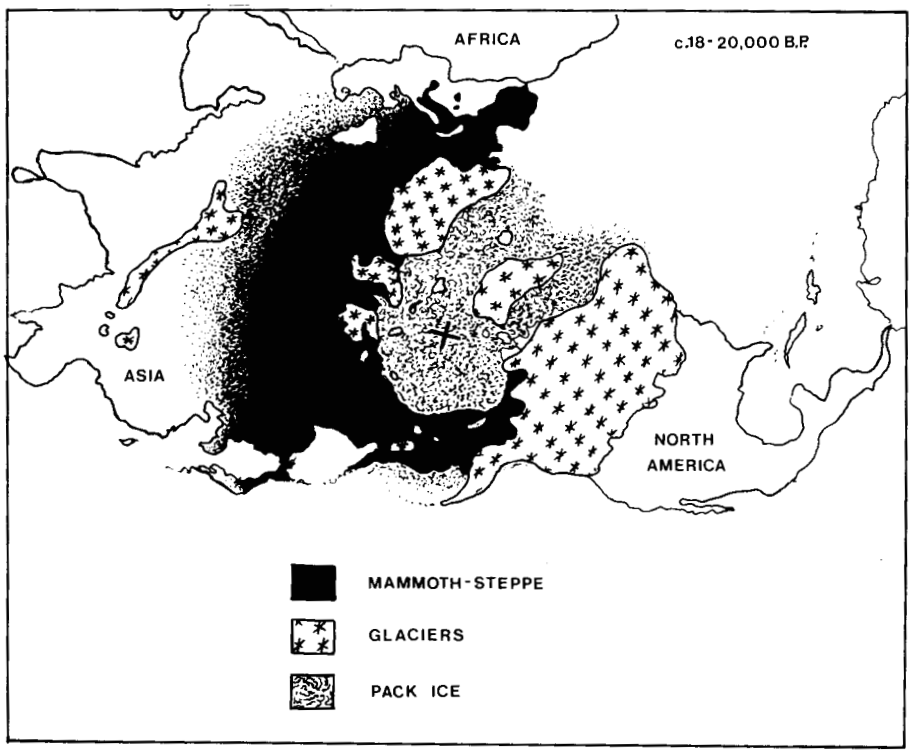

Figure 1. The mammoth steppe seems to have existed throughout the major part of the Pleistocene. Although there were spatial and temporal facies of diversity throughout this vast area, there was an identifiable integrity of xeric graminoid-forb dominance combined with a dominance of large grazing mammals, the 'mammoth fauna,' dominated by *Mammuthus, Bison,* and *Equus.* During the relatively short interglacials and interstadials, the mammoth steppe was disrupted by the northward invasion of more southern plant species and by the expansion of what had previously been minor community elements; both of these tended to be more mesic forms with better developed large mammal anti-herbivory defense systems

think the vegetation pattern of Europe and northern Asia is still misunderstood by many palynologists as a sort of low-latitude version of tundra or polar desert. In Alaska and northwestern Canada palynological interpretations of polar deserts (Cwynar and Ritchie, 1980; Colinvaux, 1980) are also at great divergence with the herbivore evidence for grasslands. The fauna, both taxonomically and in community composition, was quite different in the north during the Pleistocene—there was no homologous, nor even analogous, counterpart to extant zoogeographic biomes, provinces or life zones. This concept seems to be particularly heretical to many paleobotanists who are reluctant to abandon the "geoflora" concept and rather prefer to think in terms of cliseral shifts of biotic provinces altitudinally and geographically through time. However, there is accumulating evidence (mainly from macrofossils) that, like the fauna, plants during the Pleistocene occurred in distributions and associations that would be unthinkable today.

It is peculiar that the paleoclimatic indicators developed in more southern latitudes have not worked very well in the north. Northern herbaceous pollen lacks the arboreal diversity of southern woodlands, and graminoids are not distinctive at lower taxonomic levels (Johnson and Packer, 1967; Young, 1976). And because many northern plants reproduce vegetatively or are insect pollinated, the amount of pollen entering the fossil record may be an insensitive guide to diversity and biomass. Plant macrofossils and phytoliths, though common in some northern areas, have not been well exploited by paleoecologists. Because of their migratory abilities and tolerances of wide climatic regimes, large mammals are not necessarily the optimum paleoecological medium. In this case, however, it is the large mammals which create the puzzle, and as I shall argue, they are the best place to begin a search for the solution.

Our increasing understanding of the ecology of living large mammals can contribute much to our understanding of paleoenvironments. Using insights gained from extant mammal communities, I wish to present several new theories pertaining to the megafauna of the mammoth steppe and its environment. I will concentrate on a time during the last glacial maximum, around 17,000 BP, and then generalize this for earlier times, recognizing that our search at this point is for broad brush images.

We have thus far surmised several basic things about the "mammoth fauna." Foremost is that they were predominantly steppe-adapted species (e.g., Kowalski, 1967; Guthrie, 1968a). The pollen evidence also indicates predominantly non-arboreal plants (e.g., Colinvaux, 1967a).

There are several key pieces missing to the puzzle. One is why so much *species diversity* in large mammals? Only in central Africa do we find this megafaunal complexity today. How could such diversity have existed in the face of stringent interspecific competition? Did they adapt to different aspects of the topography or vegetation and, if so, how? A second piece is the question of *abundance*. Was this diverse fauna thinly spread or distributed at high densities? Proposals range from a rich, abundant fauna to a depauperate polar desert (see Ritchie and Cwynar, this volume). Most of the large mammals were well-dressed giants. So, our third missing piece to the puzzle is what central environmental feature could have been responsible for this *gigantism*? Many of the species would have been giants in any era, immense creatures, much larger than their modern counterparts. Fourthly, why where they *ornamented* with the physiologically costly social paraphernalia of shaggy ruffs, heavy horns, long tusks, or enormous antlers. These are traits wildlife managers recognize as indicators of high-quality habitat (e.g., Geist, 1971). How could this austere Arctic landscape, bounded by glaciers and frozen seas, be considered high quality?

Did these species have special adaptations which allowed them to tap diffuse northern nutrients; were the nutrients somehow greater in quantity than now, or was there possibly a greater turnover rate—a higher primary producivity? Were the soils more fertile? Did the vegetation use different antiherbivory defenses? Given a more herbaceous vegetation, are we dealing with a redistribution of extant northern species or intrusions of other species, and in what kind of communities? What kind of situation could maintain this herbaceous steppe—fire? Some type of climatic change? Was it windier, wetter, colder, dustier, cloudier—more arid? Was it continental—with the same seasonality of today?

In the fairly short interval of less than a millenium or two the megafauna changed dramatically (Guthrie, 1968a). There is evidence that the landscape, the vegetation, the climate, and the people

also changed (Guthrie, in press). How all of this took place, and why, are also parts of the puzzle.

The answers to these questions must fit. They must intermesh with the other pieces of our puzzle. In fact, I often feel much like a jig-saw puzzler holding several pieces in my palm, sensing that they are keys to the fragmentary pattern, yet not quite knowing where each goes. Then once in a while, one fits and an entire segment jumps into focus, giving meaning to other segments.

MEGAFAUNAL ADAPTATIONS

Although mammals may not be good "indicators" of precise environmental situations, they are affected by their surroundings. Not only can certain mammals do better than others in a given environment, each situation results in subtle evolutionary changes in their morphology—a sort of "fine-tuning" to a specific habitat, which can be very informative to a mammalian paleoecologist. Mammals are also informative about some aspects of seasonality. In this section I will review some of the major environmental implications derived from my studies of the mammoth fauna, some of which are published (Guthrie, e.g., 1966, 1968a, 1976, 1978), others as yet unpublished.

1) One of the more informative features is body size. There is a general tendency for northern species to be larger than their southern counterparts—this was particularly true during the Pleistocene. Because size is such a major adaptive theme, I discuss it in a separate section.

2) The faunal evidence strongly suggests a dominance of herbaceous vegetation. Though its character is still debatable, most of the evidence points toward a xeric steppe. The type of herbivore present indicates a major bent toward dependence on grass and grass-like plants. In a competitive situation, the living counterparts of those herbivorous species that dominated the mammoth steppe are grazers. Also mature grasses and grass-like plants have abrasive phytoliths (which cause rapid tooth wear), as their major herbivore defenses. Woolly mammoths, northern equids, and bison all show indications in their dental anatomy of quite complex antiwear defenses, indicating a diet of grass (stomachs of frozen mammoths have yielded high percentages and a diversity of grass fossils—Tikhomirov, 1958; Ukraintseva, 1979).

3) The hooves of the Pleistocene Beringian fauna (horses, hemionids, saiga, bison, etc.) are not broadly splayed like those of caribou, moose, and musk oxen of today which use increased hoof surface to negotiate the swampy muskegs, tussocky terrain, and sphagnum meadows of the Arctic and Subarctic. The small hooves of Pleistocene species indicate a firm ground surface. As the mammoth fauna is ubiquitous in its distribution throughout the northern landscape, one can surmise that this firm substratum was a dominant feature.

4) Several of the ungulates in the mammoth fauna are intolerant of deep snow. Bannikov (1963) contends that saiga cannot tolerate snow depths greater than 20 cm. Horses and hemionids also find it difficult to get adequate food by digging through deep snow.[1] Thus I have concluded that winter precipitation through the mammoth steppe was probably quite light, and that the little snow that did fall was redistributed into drifts.

5) The singing vole (*Microtis miurus*) and pika (*Ochotona collaris*), instead of hibernating, cache summer hay and use it as supplemental food during winter. They now most commonly winter under snow drifts in windy alpine areas. However, from fossil evidence we know that they did live on rolling hills and in lowlands during the Pleistocene. From this one can conclude that the Far North was a windswept area with intermittent snow banks, rather than the powder-snow-covered taiga and hard-crust-covered tundra that characterize the Arctic today.

6) At any one time there was considerable megafaunal diversity in comparison to living Holarctic communities. We know that the present vegetation in the North could not support so diverse a grazing community. It is quite possible, then, that several important climatic-environmental aspects were different from those of today.

7) Extant mammals (e.g., Dall sheep, *Ovis dalli*, singing voles, *Microtus miurus*), now confined to disjunct alpine habitats, were then more widespread and present at lower altitudes. This suggests that alpine habitats retain remnant characteristics of the mammoth steppe (Guthrie, 1968a).

8) Much of the mammoth fauna that did not

[1] I once raised miniature asses (the same size as Pleistocene hemionids) in Fairbanks, Alaska, and they had considerable difficulty with the snow.

become extinct is now limited to more southern latitudes (e.g., hyena, lion, saiga, equids, bison, badger and ferret), which indicates that the ecological barriers of the present northern distributional limits were absent or located much further north than they are today.

9) At the beginning of the postglacial period the long-standing equid, proboscidian, and bovid dominance of the mammoth steppe was replaced by that of cervids. Cervids as a group are more mesic-adapted species, usually avoiding mature grasses in their diet and preferring leaves of dicotyledons, twig tips, and lichens. This shift is undoubtably indicative of a corresponding change in the vegetation patterns.

10) The survivorship curves of the large mammals are instructive about winter severity (Guthrie, unpublished). The curves are of the usual semi-rectangular form (type 1), with the most mortality occurring very early or late in life. This indicates that, once mature, animals were well adapted to winter conditions, but that conditions were sufficiently severe to keep juvenile mortality high.

There are additional phenomena on which I have not yet published. One involves the much wider distribution of Arctic ground squirrels (*Spermophilus parryi* and *S. undulatus*). Their fossils occur in areas where they do not live today. Ground squirrels prefer open country and require energy-rich seeds to cache for spring sustenance because they must emerge from hibernation while the ground is still snow covered in order to breed and bear their young at the time new plant growth emerges. They also require protein-rich forbs in order to rear their young to maturity before winter. Prime habitat seems usually to involve well-drained sites composed of irregular surfaces and cut banks. These provide the favored early succession plants and easier excavating.

Bear teeth may also furnish new insights into the ecology of the mammoth steppe. Grizzly bears (*Ursus arctos*) often graze in spring and midsummer (Herero, 1978), when grasses are abundant. Bears which fill their protein requirements by excavating for ground squirrels must wait until later in the season, when the annual frost has receded to the lower reaches of the burrow systems (Carl, 1971). Pleistocene bear (both *Arctodus* and *Ursus*) teeth from Alaska, Asia, and Europe show much wear from grass consumption and none of the dental caries characteristic of extant bears, which get most of their late summer carbohydrates from berry sugars.

The above mammalian features, taken as a whole, suggest a diverse fauna in an open landscape, firm in substratum, dominated by a complex assortment of herbs with many grass-like plants, and a windy winter. With these pieces of the puzzle in hand I shall now turn to the phenomenon and question of faunal diversity.

MEGAFAUNAL DIVERSITY

How was the diverse mammal community on the mammoth steppe adapted to a sympatric life? The heart of the issue is the way in which the secondary producers (herbivores) partition their use of the primary producers (plants). There are several ways for herbivores to avoid direct competition. Let us take a look at these and see which might be relevant to the mammoth steppe:

(1) *Specialization for plant form or species.* Herbivore species living together may have entirely different diets. This is the case with the browsing black rhino (*Diceros bicornis*) and the grazing white rhino (*D. simus*).

(2) *Specialization for plant parts.* Different herbivores may specialize by consuming different portions of the same plant. Bell (1970) showed that zebra in East Africa select for mature grass stems, wildebeest for sheathes and leaves.

(3) *Specialization for different growth stages of plant succession.* The grazing of plants by one species may make the same plants more palatable to another. McNaughton (1976) has shown that the rich grass regrowth occurring in the wake of a wildebeest migration is the cause of the ensuing gazelle migration.

(4) *Separation by habitat.* Different herbivores may overlap in distribution and diet but normally remain separated by habitat (Fig. 2). This is the case with mountain goat (*Oreamnos*) and sheep (*Ovis*) in North America (Geist, 1971). It seems also to be the case with reindeer (*Rangifer*) and musk oxen (*Ovibos*) (Bos, 1967), although with musk oxen there are also major season dietary differences involved. Some species may appear to be quite competitive but occur at different altitudes or in different types of terrain. The various

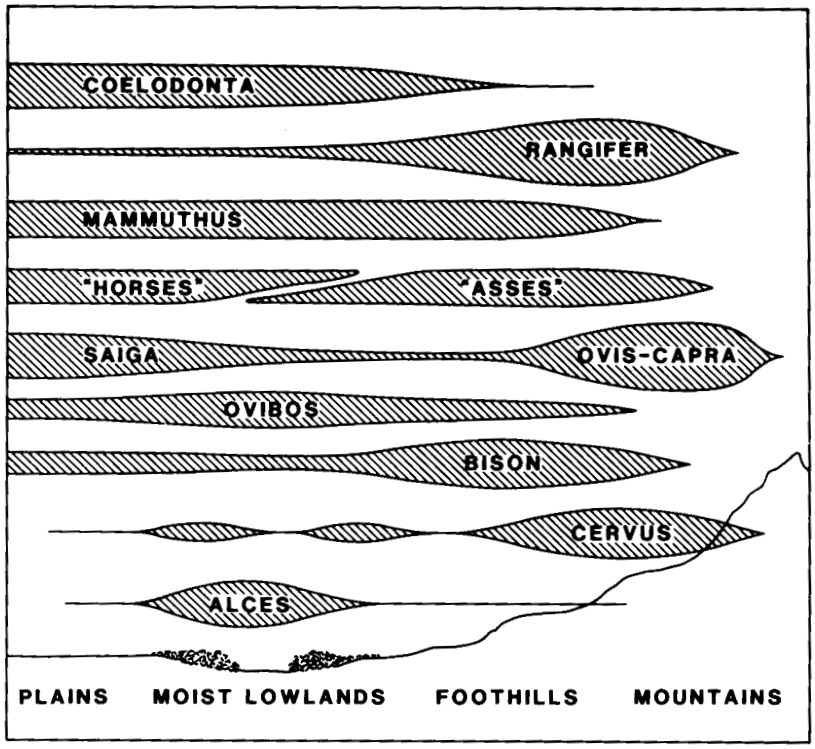

Figure 2. Mammalian herbivores are frequently separated by habitat preferences. We can assume that the same was true of the mammoth steppe and can reconstruct the rough outlines of large mammal habitat specializations by using distribution patterns of the modern analogs

Caprini of central Asia represent this kind of separation (Schaller, 1977).

It is a biological axiom that if phylogenetically (or ecologically) related species occurring together do not partition the available resources to avoid direct competition (as outlined above), one of the species is competitively eliminated. Schaller (1977) has proposed that the northern Caprini—goats, musk oxen, sheep, etc. are adapted to living in altitudinally partitioned areas, within which each species is a very adaptable feeder, occupying a wide dietary niche. Some component of the diversity of mammoth fauna seems to be explicable through spatial separation. The percentage of bison in Alaskan fossil localities increases with altitude (the same can be said for sheep), but the relative proportions of horses and mammoths decline (Guthrie, 1968a). Harington (personal communication) has observed that the frequency of horses among the equids is much greater in the lowlands (Old Crow Flats) and the percentage of asses (hemionids) higher in the hills (Dawson, Yukon Territory). Saiga (*Saiga tatarica*) seem to have a diet very similar to that of Dall sheep (*Ovis dalli*), but are specialized lowland runners, while sheep depend on steep upland escape terrain. Wapiti (*Cervus*) prefer high alpine meadows for spring and summer range (Murie, 1944), but normally graze below preferred sheep range.

There are other subtle spatial separations among living moose (*Alces*), wapiti (*Cervus*), musk oxen (*Ovibos*), caribou (*Rangifer*), and sheep (*Ovis*), where their ranges overlap. The same was probably true during the Pleistocene, and for many of the extant species as well—particularly in regard to seasonal use.

Nevertheless, topographic or altitudinal separations seem inadequate to explain all of the megafaunal diversity on the mammoth steppe. First of all, many, if not most, Pleistocene archaeological

and paleontological localities on the mammoth steppe have a diverse fauna no matter what their location in terrain or altitude. Secondly, large mammal communities of analagous complexity which exist today seem to rely more on other methods of partitioning resources (McNaughton, 1976).

Unfortunately there are few living analogs to the ungulate diversity of the mammoth steppe. East Africa stands alone as a community of roughly comparable ungulate complexity. Several authors have emphasized various ecological gradients of specialization in East Africa. Estes (1974) contends that the central theme of the ecological spectrum is sociality, which increases from the solitary woodland browsers (duiker or *Cephalophus*) to the open plains grazers (wildebeest or *Connochaetes*). He relates this shift to increasing grass in the diet, the increase in body size, development of social organs, polygamy, decreased territoriality, and changes in body shape. Jarman (1974) and Bell (1970) came to similar conclusions but emphasized *feeding styles*. Geist in a series of papers (e.g., 1971, 1974, 1977) has discussed this same spectrum but has chosen to emphasize a different series of features, particularly the degree of community *successional maturity* and the stage of colonization—a rendition of the *r* and *K* evolutionary strategies. Leuthold (1977) has amalgamated the Jarman-Estes approaches and Janis (1976) has expanded the Jarman-Bell emphasis on diet to include proboscidians and equids in a general review of the various advantages and disadvantages of rumen-cecal digesters.

To summarize their conclusions about the East African ungulates, there is considerable specialization among the grazers in the community for plants of different protein/fiber content as well as for different plant forms. The smaller the animal the higher the metabolic rate and thus the higher the protein and soluble carbohydrate requirements. The larger the animal the more fiber it can tolerate. Perissodactyls and proboscidians can process food faster (gut transit time) than ruminants of comparable size and can thus exist on a lower-quality/higher-fiber diet. The gradient of increasing fiber tolerance is thus: small ruminants, large ruminants, equids, and proboscidians. All these grazers may live sympatrically where there is an adequate diversity along this protein/fiber spectrum. In addition, there are ungulate specializations in plant species of form which are somewhat independent of this protein/fiber spectrum (for example the browser-gazer spread).

With this brief review in mind, we can now examine a few of the ungulates from the mammoth-steppe fauna. I should strongly emphasize that because of the abundance of new plant growth, there was probably little competition during spring. This is analogous to the rainy season in Africa (Bell, 1970) when the dietary specializations of the extant plains grazers also break down. Thus, we are looking for resource partitioning during the rest of the year. Utilizing the biology of the living counterparts, we can very briefly look at the ecological niches of the principal ungulates in the mammoth fauna:

Woolly mammoth. This species would probably have avoided competition with ruminants by eating a broad spectrum of herbaceous vegetation, principally coarse grass with supplements (Olivier, this volume). The extremely high-crowned, complex molars indicate a high percentage of mature coarse-stemmed grasses in the diet. The limiting parameter is sheer volume. Studies on African elephants have shown that they eat virtually around the clock and have a short gut-transit-time of around 12 hours (Laws, et al., 1975). Because sufficient volume is a potential problem the most common element in the mammoth's diet, aside from the early young spring growth, was probably the lower quality tall and mid-height bunch-grasses. Ceylonese elephants today are mainly grazers (Kurt, 1974); grass clumps are ripped from the soil—the roots shaken free of dirt and eaten whole. Mammoths, with their "fingered" trunks, would have been well suited to grazing. They were probably more migratory than living elephants are, but may have had traditional ranges on a large scale. Bulls were solitary or lived in small bands, and the females in reproductive-class herds (unlike the matriarchies of the African elephant, *Loxodonta,* and like the more closely related Asiatic elephant, *Elephus*) (Sykes, 1971). Mammoths had no obvious means of penetrating winter snow (the striations on tusks do not indicate wear from snow shoveling) for the quantity of necessary food and so probably used windblown winter ranges.

Horses and hemionids. (There may be several species, but their systematics are not yet clear.) In a complex grazing community equids specialize on grass stems of medium- to low-protein content,

usually in the mid-level height range. Remember that we are not talking now about spring plant growth. The living related hemionids are found on the high arid plateaus of central Asia. Horses and those species with more ass-like adaptations may have been spatially separated throughout the mammoth steppe, but their habitats may have been interspersed in many areas as both species did occur in the same localities and, in one case, are pictured in the same frieze (Sanctuary Cave). Horses are normally found in large mare herds with a single stallion, while hemionids generally have sexes separate except during the breeding season (Ewer, 1968). Both groups crater through snow for winter food, but are then in a negative energetic balance, so cannot tolerate deep snow for lengthy periods. Thus, they also would seek out snow-free areas swept clean by winter winds. Living Asian hemionids have small, cupped hooves for irregular hard-substrate terrain (as did those on the mammoth steppe) and cannot exist on soft ground or deep snows. The late Pleistocene Beringian equids were petite and short legged—with not much over 60 cm clearance between brisket and ground. They were probably seasonally migratory, but had large traditional ranges.

Steppe Bison. In comparison to other ruminants, bison can tolerate considerable fiber in the diet (Peden, et al., 1977), but unlike horses, bison cannot live on the low-protein high-fiber stems alone; they require a high fraction of grass sheaths and leaves. In addition, they seem unable to exist on the taller grasses, which also have a lower-protein higher-fiber content than short grasses (see Guthrie, 1978, for a review). In a diverse community bison seem to be short-grass specialists using, in addition, tall and mid-level grass new growth, or regrowth after grazing by other ungulates. Thus, bison could benefit from prior moderate grazing by horses which would have removed stems and increased the relative leaf fraction by stimulating vegetative proliferation. In contrast to horses or proboscidians, bison are fairly well adapted to snow: they sweep the snow aside with their nose and cheek, then eat in a repeated cycle. However, snow does reduce range access, so they also could be expected to have concentrated in snow-free areas during the Pleistocene. The manner in which bison use the landscape would have meant a migratory habit, but they also could have had traditional ranges with only a loosely predictable migratory route. Judging from their large horns, bison males were separated from the females throughout all seasons except the rut; they probably grazed alone, or in small herds (Guthrie, 1978).

Sheep were more widespread than at present, and occurred at lower altitudes. They consume a wide range of plants (Hoefs, 1974), but prefer new growth of high-quality forage when it is available. They are lip-feeders and can feed selectively on low-growing herbs in small tidbits—taking regularly up to 14,000 bites a day (Hoefs, 1974). They cannot feed through deep snow, and in winter are confined to the windblown high-mountain ridges. Sheep are social, but herd size varies with season. They have great fidelity to home range.

Moose or Eurasian elk are high-brush animals feeding predominantly on deciduous leaves and pond weeds in summer and twig tips of willow in winter. Because deciduous trees are most common in the North in well-watered, disturbed sites, moose are usually found along streams or in the early fire-succession communities of the boreal forest. Moose are well adapted to deep snow. Their winter food, twig tips, is above the snow, and their long legs allow them to travel in snows of considerable depth. They are one of the least social of the ungulates thus far discussed, and least traditional in their home range use.

Musk oxen, in contrast to moose, can probably be best thought of as mesic hydric low-brush feeders. Low deciduous shrubs and sedges form the bulk of their winter diet. They seem to be animals of the open country. The females are quite social. They are nonterritorial but tend to stay in large areas of familiarity (Jingfors, 1980). They seem to be well adapted to the extreme windy cold weather of the tundra and the shrubby northern steppe.

Caribou or reindeer are well adapted to cratering for lichens through soft snow. Their summer diet is diverse. In winter, they are among the more social of cervids. They are not territorial, but migrate seasonally within familiar home ranges, the size of which—a few to hundreds of square kilometers—depends mainly on the size of the herd.

Wapiti or red deer or American elk are extremely adaptable. More than any other cervid they have moved toward an open-country grazer pattern. As a consequence, their teeth are complex and moderately high-crowned. They prefer grass, when it is available, to other plants (Murie, 1944).

Wapiti are not territorial and highly social, but they often undertake extensive seasonal migrations on familiar ranges. They are tolerant of moderate snow depths, shifting to twig browsing in stress conditions of deep snow cover. (Murie gives a figure of 75 cm as the depth to which they can crater for grasses.) They do not compete seriously with moose for winter range. (See Boyce and Hayden-Wing, 1979, for a review.)

Saiga is a selective herbivore, requiring mainly high-quality forage. It inhabits hard flat lands because it can run fast, and for long distances, but it cannot jump well nor is it a nimble negotiator of rough terrain (Sher, 1967). Saiga are quite social and extremely migratory when faced with inclement weather or seasonal range changes, although they generally occur in the same large areas year after year (Bannikov, 1963). Saiga are markedly tolerant of halophytes and could have done well in the sandy-arid late Pleistocene conditions in Beringia (Bannikov, 1963).

Several things emerge in this quick review. Most of the ungulates of the mammoth steppe were open-plains forms and quite social, all were migratory to a great degree, yet complementary in their dietary preferences. This dietary diversity is especially revealing, for combined with the fact that there must have been a diversity of herbaceous plant forms on the mammoth steppe spanning the spectrum from the small, high-quality forbs and leafy grasses required to support sheep and saiga, to the short grasses for bison and the taller medium-short grasses for bison and the taller medium-quality grasses for horses, and finally the large-stem, low-quality grasses apparently required by mammoths. These plant communities were spread across a diverse topography, allowing some local spatial separation of ungulates, and causing further diversity among the grazers. In addition, there were a few riparian tall willows for moose, although *Alces* was uncommon on the mammoth steppe (Vereshchagin, 1967; Guthrie, 1968a). There must have been some upland short-shrub growth in order to support musk oxen, and possibly, some lichen habitat for caribou (although there is evidence that cryptogams were rare). Each of these ungulates had specialized anatomical means of exploiting its food resources (Fig. 3).

The mammoth steppe had a high diversity of microtine rodents. Grant and Birney (1979) show that the percentage of microtine biomass and diversity is highest in grasslands with high vegetation cover (tall and mid-level grasses) and least in bunchgrass and shortgrass habitats.

All of this information can be taken to suggest that the mammoth steppe was not characterized by homogeneous communities but a diverse, rather fine- to medium-grained vegetational mosaic. This diverse herbaceous vegetation base required by the megafauna of the mammoth steppe will be examined in the following section.

PLAIDS VS. STRIPES: OR VEGETATIONAL DIVERSITY

At this point I should note that the greater diversity of large mammals during the Pleistocene, in comparison to extant faunas, is not unique to the mammoth steppe. Virtually all large mammal faunas throughout the Holarctic had a more diverse assemblage during the Pleistocene than they do today. Moreover, this principle holds true for small mammals as well (e.g., Guilday, et al., 1977; Graham and Semken, 1976). In fact, it is also true of plant communities (e.g., Leopold, 1967). In trying to solve the puzzle of high megafaunal diversity on the mammoth steppe we are dealing with a global phenomenon and solutions to our specific concerns may have a more general application.

In the preceding section I concluded that the striking diversity of the ungulate community on the mammoth steppe was primarily the result of a more fine-grained, "mosaic" distribution of flora communities than exists today. Again, this seems to have been a worldwide phenomenon. The markedly regional biome zonation we take for granted seems to have been a Holocene derivation. The integrity of most extant biomes quickly disintegrates as one looks backward into the Pleistocene (Guthrie, in press).

The upshot of this lack of biome integrity among local primary producers is, of course, a greater potential local species diversity among secondary producers when compared to modern communities. For example, caribou (*Rangifer*) and musk oxen (*Ovibos, Symbos*) moved far southward and mixed with tapirs (*Tapirus*) and peccaries (*Platygonus*) (Guilday, et al., 1975) and wild cattle (*Bos*) (Kurtén, 1968). Thus, the greater species diversity during the Pleistocene at any one locality comprised not just a greater number of species

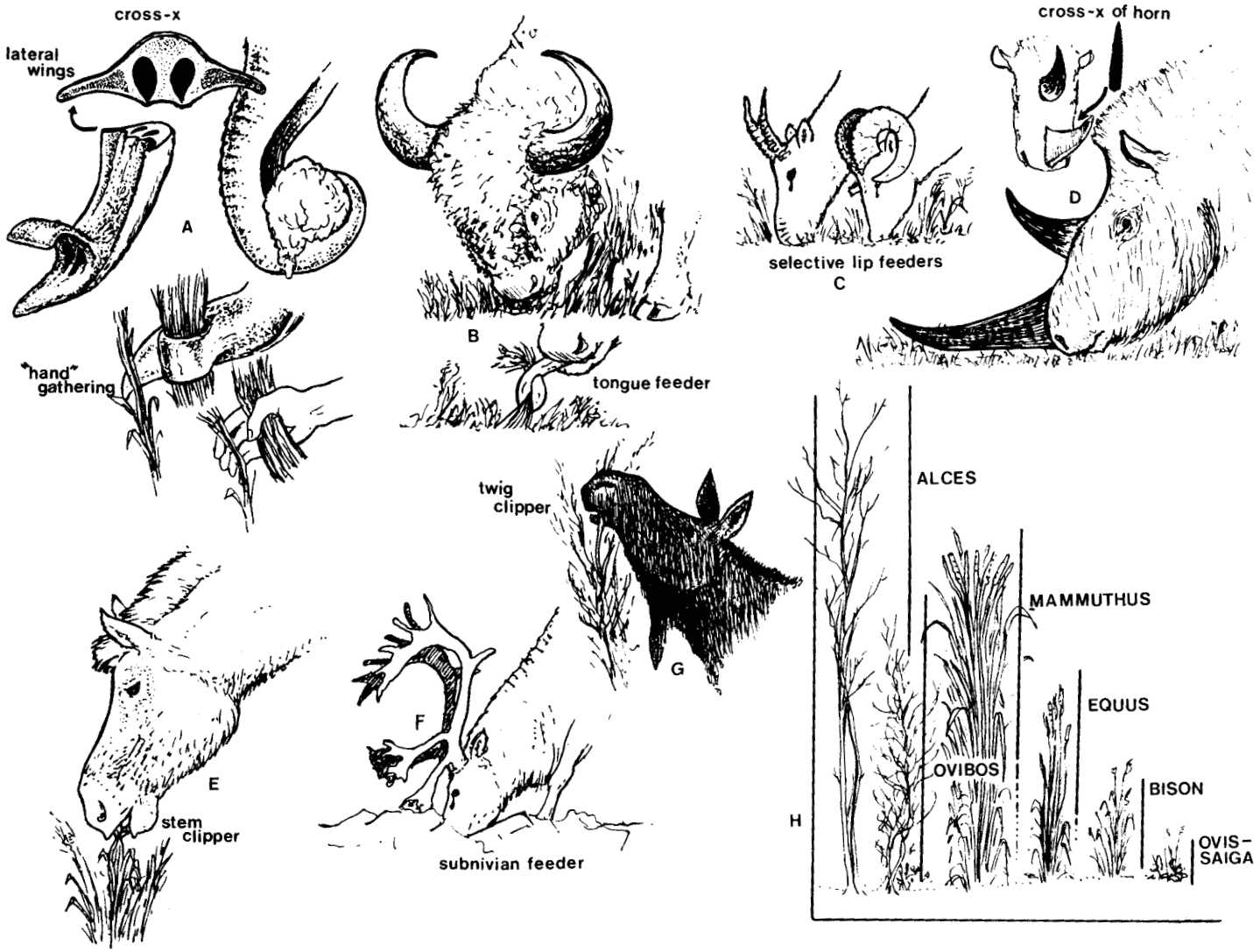

Figure 3. Large mammal species of herbivores are normally separated by the resources they use, at least during part of the year. This illustration shows some of these resources and anatomical specializations for their use by northern large herbivores. Most of the dietary specializations illustrated are for winter, the season when most resource separations occur

when the extinct ones are summed with extant ones, but it also was a distributional phenomenon resulting from the mixing of the extant biotic provinces. I suspect, then, that the solution to the causes of the greater biome blending during the Pleistocene will account for much of the greater species diversity and maybe most of it. So what were the causes?

Most animal physiologists would argue that neither temperature nor moisture deficit directly limits large mammal distributions. It is more a question of how the vegetation patterns affect interspecific competition. This then leads us back to ask why Pleistocene plant species may have been distributed in more diverse communities, in a more fine-grain mosaic, and how this would have affected competition among large mammals.

The reasons behind plant diversity are hotly contested, but there is a rough consensus that diversity increases with (1) increasing substratum fertility, (2) increased temperature equability (reduced seasonality), (3) diverse moisture conditions during different portions of the growth season, (4) a long stable evolutionary history, and (5) increased substratum and topographic diversity. These relations are not necessarily linear and their rank of importance may be contextual. The first three of these are particularly important in relation to the mammoth steppe.

(1) *Nutrient availability and recycling.* The soil mantle throughout most of the mammoth steppe consisted of loess (see Tomirdiaro, this volume). Its minerals and nutrients were thinly spread across the landscape by runoff water and wind. Unlike modern acidic boreal soils, mammoth steppe soils were probably alkaline and thus more conducive to herbaceous growth and nutrient release; newly formed loess soils were also comparatively rich in available potassium, phosphate, and calcium, which facilitated rapid nitrification. The pH in the Pleistocene loess averages around 8.2. By way of comparison, blueberry, *Vaccinium uliginosum,* so common throughout the North today, grows optimally at pH's of about 4.5. But more important than soil pH are soil temperature and plant growth strategies which determine nutrient turnover time (discussed later in this section). Increased nutrient availability would have decreased cryptogams and increased graminoids (McKendrick, 1980).

(2) *Length of growing season.* Equability, a concept used by several people (e.g., Axelrod, 1967), is central in importance, but needs some modification and elaboration for the North. I think that the most important component is *length of growth season,* i.e., number of days a plant can grow. Though many southern plant species would be killed by northern winter temperatures, the major *climatic* limitation for their growth and for that of most species is the abbreviated growing season on cool soils at high latitudes. The *biotic* component is even more important than climatic factors in creating the present zonation of plants and animals. Many southern forms are kept from moving northward by competition from species more precisely adapted to northern environments. A longer growing season on warm summer soils, especially one with changing moisture conditions, decreases competition because it allows for more sympatric sequential adaptations to growing, flowering, seeding, etc. A short growing season on cold summer soils thus intensifies competition by selecting for the taxa most precisely adapted to local conditions. I propose that the marked biome zonation during the Holocene was produced by shorter, and less diverse growing seasons throughout the Holarctic. Conversely, a longer growing season, on a fertile substratum, in the Pleistocene would have allowed forms with widely different adaptive strategies to reside together, thus decreasing zonation and fostering diversity.

Most of the Pleistocene physical evidence for the climate of the mammoth steppe relates to mean annual temperatures and tells us little about the growth season. It is the fossil biota which are most informative about seasonality. It appears that mean annual temperatures may be a nearly worthless ecological measurement; it is temperature patterns within the year, particularly spring to fall that are most revealing. There is evidence from the growth patterns of mammoth steppe ungulates that the growth season was longer than it is today. I will return later to the concept of the length of growth season during the Pleistocene because it is of critical importance in developing several other concepts.

(3) *Marked wet and dry conditions during different portions of the growth season.* As mentioned previously, the telling factor is not mean annual precipitation, but how and when precipitation

occurs throughout the year. Today, winter snowmelt quickly runs off of steep loess-covered terrain and remains in marshy flatland swamps all summer because of the poor drainage of the permanently frozen ground and the lack of summer aridity.

Though precipitation is very low in the North today it occurs in scattered rains throughout the growing season, generally peaking late in the summer. Thus it comes in the wrong form and at the wrong time to create and optimally maintain a productive steppe habitat with a solid substratum. For more herbaceous communities moisture limits quality and permits productivity to vary by several orders of magnitude during dry and wet growing seasons. There are several new lines of evidence which suggest a marked wet, and then dry, moisture regime throughout the North during the Pleistocene growing season. That late- and perhaps mid-summers were characterized by clear skies and arid conditions can be inferred from the presence, at least as far north as Fairbanks, Alaska, of numerous elements of the shortgrass plains fauna and flora (Guthrie, 1978, and in press): e.g., badgers (*Taxidea*), ferrets (*Mustela),* and gramma grass (*Bouteloua*). There is yet other evidence of heavy, warm spring rains manifest in the prominent silt erosional features throughout much of the mammoth steppe. Also, the high quality of individual ungulates during the Pleistocene would require significant spring moisture to maximize spring growth of herbaceous vegetation (Bunnell, 1978).

The nagging puzzle of large-mammal biomass invariably emerges from any discussion of the high diversity on the mammoth steppe. We may never know whether the actual primary productivity was quite different from now, but we can suppose that ungulate productivity was greater. A change in quality, not necessarily quantity, of the primary production must be the key. An herbaceous community has a much higher productivity than a woodland having the same biomass (in woodland, nutrients and energy are tied up in the form of wood). There is thus a higher turnover rate among herb biomass. Very few mammoth-steppe ungulates were adapted to eating plant parts from trees for their growth resources; rather, most are adapted to eating herbs or leaves of shrubs. The much greater sympatric ungulate diversity, combined with the more palatable and productive herbage, argues for a higher ungulate biomass on the mammoth steppe than is found today in the same areas. Generally, ungulate numbers are limited by winter range. The virtual lack of snow cover would have greatly increased the potential carrying capacity of the mammoth steppe.

I wish to propose that these changes we see at the end of the Pleistocene were a cycle or syndrome of events triggered by a seasonal change of moisture in the northern Holarctic which affected soil temperatures, floristic and vegetational composition, antiherbivory compounds, available nutrients in the substrate, litter decomposition, soil insulation, primary productivity, and finally, the kind, quality, and numbers of large herbivores.

Increasing snow cover and late summer moisture favored more mesic plants, which would tend to generate an insulative cover on the soil surface. Frozen winter soils insulated by this cover during the summer would show declines in summer temperatures and soil fertility, thus favoring nutrient-stress-tolerant plant species (Chapin, 1980). Among woody plant species so favored would be evergreens which produce much more toxic allelochemic antiherbivory defenses (Grime, 1979; Mattson, 1980). Among the deciduous species there are large quantities of tannins and resins. Ericaceous plants produce both digestibility-reducing and toxic antiherbivory compounds (Jung, et al, 1979). Because such toxic species are not eaten intensively the litter accumulates on the soil surface where decomposers are equally affected by its toxicity (Chapin, 1980). Summer moisture also favors the growth of cushion plants, which are at the same time shunned by large mammalian herbivores and are effective soil insulators.

The dominant northern graminoids today are also intolerant of grazing, but their antiherbivory defenses seem to involve a nutrient-deficiency strategy. They actively exclude sodium and calcium, which results in phenomenally low levels of these nutrients in their leaves (Chapin, et al., 1980). Also, Jung et al. (1979) found a wide distribution of various alkaloids among extant tundra grasses. Unbrowsed, and generally unburned because of the damp substrate, these graminoids, cushion plants, and evergreens accumulate as leaf litter, which creates more soil insulation. This further contributes to the cycle of colder soil temperatures and more nutrient-stress-tolerant plants. The accumulated litter and invasion by bryophytes clog drainage, magnifying the effect of the moisture, and further perpetuating the cycle.

Plants that are tolerant of nutrient-impoverished soils probably are not carbon limited and thus have extra resources to produce digestibility reducing compounds, particularly toxic resins (Mattson, 1980; Bryant and Kuropat, 1980). Another adaptation of these plant species to nutrient stress is slow leaf turnover time (evergreenness) and great root longevity (Chapin, 1980). However, the photosynthetic rate declines with leaf age, and nutrient absorption declines with root age, both of which greatly reduce productivity by slowing nutrient turnover rates. The slow vegetative turnover in the living plants due to their growth strategies and toxicity makes plant matter unavailable to herbivores and decomposers. The resultant considerable standing and litter biomass, and the decreased nutrient turnover in the soil due to coolness, must have created reduced primary productivity from the levels that existed during most of the Pleistocene. Even more critical to the large herbivores than the simple reduction in primary productivity was the increasing toxicity of the antiherbivory allelochemics and the decreasing nutrient quality. Thus for the Holocene large herbivore community the quantity of available utilizable resources must have declined several-fold from that of the late Pleistocene.

In contrast, plants adapted to more fertile soils, both the ruderals and those with more conservative strategies (Grime, 1979), capitalize on the spring flush of soil nutrients with a burst of growth and are generally not as well defended with toxic allelochemic compounds (Janzen, 1975). The large herbivores of the mammoth steppe were well adapted to these plants (Guthrie, in press).

In drier environments, like that of the northern Holarctic during the Pleistocene, grasses undergo considerable evapotranspiration, which moves both sodium and calcium into the grass leaves (Chapin, et al., 1980). Likewise, with warmer summer soil temperatures, deeper roots, and more rapid absorption rates, nutrients would have been more available. This would have shifted plant selection floristically and in vegetation patterns away from the more nutrient-stress-tolerant forms and toward a community that was more nutritious and more digestible (less defended with toxic allelochemics) for large herbivores. Such habitat would have been much more productive for the large mammals of the mammoth steppe.

As opposed to the view that glacial climate and soils are too hostile or rigorous for today's vegetation,[2] it is more likely that other stresses not now characteristic of the North were involved. That is to say the stresses to which the present vegetational dominants of the North are adapted were not intensified, but rather were actually less extreme in the glacial climates. It was not nutrient deficiency (the main limiting factor at present) but other stresses—most likely moisture stress—which made the mammoth steppe too rigorous for boreal forest and tussock muskegs. Most likely moisture stress was the limiting factor. On more fertile soils in climates with drier summers, other plants that are adapted to rapid uptake of soil nutrient pulses (Chapin, et al., 1980) outcompete the boreal nutrient-stress-tolerant species. Some of the same

[2]The "polar desert" interpretation of the glacial vegetation in Beringia by Ritchie and Cwynar (see this volume) is based on two main points: a lower than present total pollen influx during the Pleistocene and, secondly, no major influx differences of grass and wormwood, *Artemisia*, between Pleistocene and Holocene sediments. But what does this mean in terms of Pleistocene plant biomass or productivity? The plant biomass throughout most of the tundra and taiga today is relatively high—in fact, the vegetation is so thick as to be virtually impenetrable, making cross-country summer travel very difficult. In contrast, the productivity is quite low (see Brown, et al., 1980, for a discussion).

This plant biomass is so high principally because it consists largely of nutrient-stress-tolerant forms, which are mostly unusable by herbivores. Given the same biomass, but in utilizable plant forms, the environment would be an immensely rich rangeland.

This would hold true if northern vegetation during the Pleistocene had even 10% of its present above-ground biomass, in a more utilizable form to herbivores, and with increased productivity and greater winter access. These productive grazophilic communities would have produced much less pollen than is produced today in the tundra and taiga.

Grazing itself would also tend to reduce pollen production on the mammoth steppe. Most herbs respond to heavy grazing with vegetative growth and cease or limit flowering. For example, McNaughton (1979) found that ungulate grazing virtually prevented flowering in the Serengeti. If ungulates grazed one half of the mammoth steppe plants sometime during the growing season (theoretically removing a relatively small biomass—say in the range of 5-20%) the pollen production would have been considerably reduced. Pollen production, without a knowledge of the other forces at work, does not seem to be a good indicator of either plant biomass or productivity.

forces which now prevent spruce (*Picea*) in North America and larch (*Larix*) in the Old World from extending their ranges southward probably acted during most of the Pleistocene to prevent them from extending their ranges northward. These are the forces which determine their northern perimeter today.

In conclusion, the seasonally diverse growing season, the longer growing season than today, and the relatively fertile soils resulted in a complex vegetational mosaic of seasonally rich vegetation which was required to maintain the diversity of mammalian species and their inordinately high quality.

SUPERLATIVES ON THE MAMMOTH STEPPE

When one compares the Pleistocene large-mammal faunas to those of today there are several striking differences, foremost among them body size. Megafaunal gigantism was pronounced in almost all species, excepting some of the very late Pleistocene equids, mammoths and rhinos, which were smaller than their more southern contemporaries and closest modern analogs. I suspect that this was due to the generally more conservative growth strategies of equids, rhinocerids, and proboscidians. They can exist on low-quality forage (in sufficient volume), but grow slowly. The manner in which Pleistocene habitat was partitioned allowed species to coexist as long as some were able to use the less nutritous end of the vegetation spectrum during the summer. A second characteristic of the Pleistocene megafauna was the extreme development of social organs—extravagant horns, antlers, tusks, and tresses. Associated with these traits was a tendency for most forms to possess a large shoulder hump. I contend that these differences are central to an explanation of the character of the mammoth steppe and that a close examination of them can reveal much about their environmental features.

Wildlife managers have long recognized that "high quality" populations (large bodied, fast growing, with large trophy antlers and horns) are found where competition is light and food is both high in quality and abundant during the growth season (Geist, 1974). I have proposed elsewhere (Guthrie, 1976, and in press) that the seasonal distribution of competition and food quality and abundance is of major evolutionary importance.

It must first be understood that seasonality has both liabilities and assets. In the Far North, seasonality sets a narrow time limit on growth. Much of the year northern ungulates are in a state of obligate growth dormancy, because nutrients are insufficient not only for growth, but for maintenance as well. Northern ungulates gradually decline in weight and body condition during the winter. They lose the ability to grow during the winter even when they are artificially provided an abundant and nutritious diet (Wood, et al., 1962).

Yet, with the onset of spring and the subsequent explosion of new plant growth, northern ungulates have adapted by evolving an extremely rapid growth rate. In fact, so have some northern rodents. Not only is the arctic ground squirrel (*Spermophilus undulatus* and *S. parryii*) the giant of the genus, it has also, by far, the most rapid growth rate (Levenson, 1979). Klein (1970) has reviewed the advantages of northern ranges in detail. To summarize, he found that many northern plants have a greater quantity of nutrients per unit weight due to adaptations for rapid growth during the shorter season. Also, the absence of darkness results in less plant catabolic activity. Low sun angle and topographic relief result in a considerable variation in the chronology of new growth, allowing a long phenological sequence of high-quality forage for a mobile grazer—unlike in more southern latitudes, where new growth is more synchronized.

Additionally, Geist (1977) observes that the canalization of parturition (and hence rutting time) means that males have a long period to forage undisturbed by agonistic rutting behavior. Concentration of growth is heightened by the fact that ungulates feed less actively in hot sunny weather than on cool days (Leuthold, 1977; Fox, 1978). It should be remembered that most ungulates of the mammoth steppe had heavy pelts which probably were not shed until well into summer, after high-protein green growth was available to repay winter debts in order to afford moulting and new pelt growth. Females normally moult even later, due to the greater nutrient expense of nurturing young in spring and early summer.

Many ungulates decrease food consumption nocturnally (except on moonlit nights); however,

in the Arctic during most of the growth season there is no real darkness, allowing a longer daily activity period. Proboscidians (Laws, et al., 1975) and equids (personal observation) feed around the clock when food is limiting, and ruminants have to take time out to ruminate, which often means that they too benefit from nocturnal feeding to refill the rapidly emptying rumen in spring (Leuthold, 1977). The mammoth-steppe ranges thus seem to have been able to provide high quality forage. The matter in question is the abundance and duration of the quality peak.

The diversity of ungulates living sympatrically tells us that Pleistocene vegetation was not as sparse as the Middle Eastern arid lands, High Arctic barrens, or simple high-alpine systems of today. The concurrence of a diverse, sympatric ungulate community and high ungulate quality argues for heterogenous and adequate rangeland that includes medium or tall herbaceous growth forms. We can conclude from their large body size that, for a wide array of ungulate species, neither range quality nor abundance was growth-limiting during the peak of plant-growth season.

I propose that the critical variable was the duration of the peak in range quality. As I mentioned earlier, northern ungulates have a limited time in which to grow—they may not (and cannot) do so outside the short growing season, but within the growing season there are physical limits on the rate of growth. The physical aspects of consumption, rumen turnover, assimilation, and transit time create inherent limitations on maximum potential growth rate. Thus, an extremely high-quality diet when limited to a very brief season is unable to produce large-bodied animals. The dynamics of natural selection preclude ungulate growth programs that try to reach maximum genetic potential with insufficient resources. However, a long season of growth on quality resources without high interspecific competition would select for large-bodied individuals with elaborate social organs.

There are several lines of evidence which point to increased length of growth season, particularly an earlier spring. Pleistocene mountain sheep were larger than those living today (Harris and Mundel, 1974). When raised in captivity, mountain sheep are larger bodied and larger horned than in the wild. This larger size is *not* due to increased growth rate nor is it due to growth being extended over more years. Rather, the larger body and horn size in captive animals results from growth beginning earlier in spring and lasting later in fall due to supplemental feeding. These captive sheep almost equal their Pleistocene counterparts in body and horn size (Guthrie, unpublished). In captivity Dall sheep (*Ovis dalli*) begin growing horns in late January, but in the wild, horn growth does not commence until late April (Bunnell, 1978).

What could have produced an onset of spring plant growth much earlier than its present scheduling? I suspect that a partial cause was the lack of uniform snow cover. There is presently abundant solar energy during the long spring days, but most of this is reflected by the snow. The onset of spring green-up currently varies more than a month, depending on snow cover. If, during the late Pleistocene, spring began with bare ground and mild air temperatures, there would have been enough sunshine to accelerate the onset of the season. New growth would have been particularly encouraged by early spring rains on a dehydrated landscape. Spring soils would not have been insulated with litter as they are today. More digestible forage (less toxic antiherbivory defenses) would have resulted in more intense winter grazing. Drier autumns may have produced more grass fires—an important consequence of which would have been a rapid warming of soils in the spring.

Adequate spring precipitation also seems to be a necessary element in the model. Bunnell (1978) was able to show a positive correlation between early spring precipitation and horn size in Dall sheep. My work with the captive Dall sheep has shown that most horn growth occurs before the end of June, when protein is highest in plants. Resources during the rest of summer, when plant minerals and fiber increase, are devoted to more somatic growth and fat deposits.

New spring plant growth on a snow-bare landscape would have been profuse and widespread. As mentioned above, spring plant growth is exceptional in quality (high in protein, phosphorus, potassium, etc., and low in fiber, phytoliths and antiherbivory compounds). This abundant new growth is eaten by all ungulates and even some carnivores (grazing grizzlies) without much interspecific competition or compartmentalization. The same was probably true on the mammoth steppe. In East Africa, Bell (1970) found that after the rains a number of ungulate species could be found eating similar short new growth on the high grazing

catena. The frozen stomach contents of mammoths that died in spring bear this out. They reveal a diverse, relatively unselective dietary assortment of herbaceous spring growth (Tikhomirov, 1958). As these early spring plants began to mature and became shorter in supply, and as the later-blooming plants began to emerge, ungulate partitioning would have begun.

Although spring was likely of extreme importance in lengthening the growth season, a prolonged autumn may also have been involved. The decreased snow cover and accessible frost-hardy northern herbs could have provided growth nutrients well into early winter. Today many herbs are still green and growing (particularly those once grazed and on fertile soil) when they are first covered by snow in early October (personal observation).

During the end of the last glacial interval these conditions which promoted the biological superlatives on the mammoth steppe began to decline rapidly.

SOME RUMINATIONS ON CLIMATE

Scanning the various existing habitats in the Arctic and Subarctic, one sees a wide variety of seasonal patterns in temperature, moisture, wind, and weather. It is surprising that so few of these modern habitats are even approximate analogs to the mammoth steppe. One is thus reluctant to reject the conclusion that seasonal patterns in the Pleistocene must have been quite different, not just subtly different, to produce a change of so great a magnitude over such a large area.

In this section I shall briefly review the environmental implications of the large-mammal fossils and then speculate on the mammoth-steppe climate and its causes. The vertebrate faunal implications are:

(1) *A preponderance of herbaceous plants consisting for the most part of grass and grass-like species* is indicated by the grazing fauna (as well as by all the palynological evidence).

(2) *A long growing season of abundant high quality forage* is indicated by the well-developed social organs and gigantism of the large mammals.

(3) *A fine- to medium-grained mosaic of herbaceous plants* is indicated by the megafaunal diversity. Involved are plants which are tolerant of aridity as well as those adapted to more mesic conditions.

(4) *A light winter-snow cover* is indicated by the presence of some large mammals which are intolerant of deep snow.

(5) *Winds in both winter and summer* are indicated by the snowdrift adaptations of the small mammals occurring in combination with the large mammals which do poorly in snow, and by the relict aeolian features of the landscape.

(6) *Medium- to low-quality winter range and cold winters* are indicated by the ubiquity of cryogenic geologic features and by the deep annulae in the dental cementum of members of the mammoth fauna. Winter range was poor compared to that further south, however. Compared to that of the North today, Pleistocene rangeland was relatively good. Today it is virtually nonexistent for grazers.

(7) There was very little litter on the soil surface and *relatively high soil fertility,* in contrast to the modern syndrome of cold summer soil and nutrient-stress-tolerant plants.

(8) *Early spring snow melt,* critical in producing large body and horn size, are an expected result of the light snow cover (items 2 and 4) as are *postponed autumns.*

(9) The *firm, dry substratum* indicated by the small hooves of many of the ungulates means less insulative vegetation cover, which would promote *relatively deeper summer thaw.*

(10) A long summer, beginning with *spring rains* (very unlike the rain patterns which are usual in the North today), shifting to *clear skies with wind in late summer,* is indicated, resulting in *moderately warm and arid conditions long into autumn* (which would then be accompanied by very disparate day-night temperature cycles).

Assuming that this reasoning is sound, what could have produced this kind of climate? Undoubtedly, major cyclonic patterns were different than those of today.

It was probably windy throughout the year. Winter wind has several major environmental implications: (1) foremost, it would have made available to ungulates large areas of winter range. (2) Also, it would have speeded the first green growth of the spring by exposing the ground surface, thus eliminating the lag between first snow-

melt and soil exposure, and exposing land to winter deflation with dust accumulation on the existing snow mantle, thus speeding melting. (3) Direct wind disturbance of the vegetation and soil, and its secondary effects on snow redistribution (in combination with varying macro- and micro-topographic relief), would have further promoted vegetational diversity on a more fine-grained scale than exists today. Not only would there have been varying stages of succession present at all times and continued wind "tilling" of nutrients, but the microhabitats would have provided a greater potential range to accommodate varying plant adaptations and hence greater species diversity in a complex fine- to medium-grained mosaic. (4) The present severely cold temperatures in the North are normally the result of temperature inversions which would have been occasionally upset by winter winds, thus producing slightly warmer weather at lower altitudes. (5) Wind would have tumbled ice crystals and abraded woody plants. There are many alpine areas where shrubs can escape winter mortality from wind scouring by growing only in snow-drifted swales. New growth is pruned annually by windblown ice crystals at the snow surface. (6) Summer wind would also have heightened aridity.

Like wind, some degree of aridity is a relative certainty for the ecological requirements of the fossil mammals and plants (Guthrie, unpublished). All aspects of the evidence suggest that snowfall was light and what little occurred was greatly redistributed by wind, as in mountain-sheep ranges today. Low winter moisture also suggests clear winter skies. Because of the well-developed cryogenic features one can safely say there had to be rather severe cold episodes (even without the insulation blanket of snow), though these could have been interspersed with relatively warm episodes.

The amount of summer precipitation is quite another question. Presently, northern habitats have a wet substratum—the result of snowmelt water and decreased percolation (due to the high frost table) and not simply high precipitation. We assume that the Pleistocene summer frost table was probably lower because plant cover and litter were less insulative. Precipitation may not have been less than the 15–30 cm presently experienced in northern continental interiors, but it seems to have been more concentrated in the spring. The precipitation curve must have shifted from the autumn peak of today to a spring peak—which would select against woody plants (S. A. Bowling, personal communication).

The seasonal moisture diversity throughout the growing season on the mammoth steppe makes such dichotomies as "continental" and "oceanic" almost inapplicable. Those who argue simply for increased continentality miss the fact that it is difficult to get greater continentality than, in say, central Yakutia today. The weather which would best produce the mammoth steppe would be characterized by little snow, spring rains, and semi-drought conditions for the remainder of the summer. Aridity during the summer and autumn would have inhibited the high frost table that now generates the muskeg bogs and, instead, would have created a firm substratum and encouraged grasses and grass-like plants. Spring rains would have provided adequate moisture for optimum plant development (as well as allowing for medium or tall herbaceous growth habits). This model would allow a more northern distribution of the specialized xeric grasses (*Bouteloua*[3], etc.) from the arid temperature grasslands. Yet the spring rains would allow the coexistence of more mesic grass-like plants which are around today, e.g., *Carex, Hierochloë, Poa, Festuca, Calamagrostis, Arctagrostis,* and *Dupontia.*

At least two interrelated features of grasslands seem to combine to produce the characteristic plains life-history strategy of ungulates. One is the comparative synchrony of plant growth in any one spot, and the other is seasonal disparity (De Vos, 1969). The former makes territorial defense unwarranted, as neither food volume nor quality are concentrated for any length of time. The resulting

[3] In an unfinished study of fossil ground squirrels (*Spermophilus parryii*) conducted in Alaska, I have had nest materials identified at the Composition Analysis Laboratory, Colorado State University. Among the grass genera identified was *Bouteloua*, one of the dominants of the short grass plains. These finds from Wisconsin-age sediments are several thousand miles north of the present range of *Bouteloua*. This has important implications for northern paleoecologists because *Bouteloua* is a C_4 grass species. There are no native C_4 plants living in the Arctic today. C_4 herbs are adapted to summers having a long, warm, sunny, and arid segment in which water is quite limited. These C_4 herbs photosynthesize on a four-carbon molecule and open stomata at night, when the air moisture is highest.

animal mobility and the diffuseness of the forage reduces competition and gives rise to herding (for more opportunities to spot predators and better potential for group defense). The seasonal disparity characteristic of grasslands increases polygamy and promiscuity and reduces competition during the growth season, causing a selection for larger body size and more elaborate social organs. The dependence on a rapid canter, to efficiently cover long distances, results in a high shoulder hump (Guthrie, 1978). Combined with the phenomena of heavy antlers, tusks, and horns, shoulder humps become particularly exaggerated. This line of discussion demands a section in itself—but, basically, the direction of my argument is that the *mammoth-steppe ungulates exhibit these steppe adaptations more than any other faunas now living in open country.* This in turn suggests that the environmental factors, which contributed to the "grassland character" (e.g., Geist, 1974; Estes, 1974; Jarman, 1974; Bell, 1970) were also present to a greater extent on the mammoth steppe than in other areas at other times.

THE DEMISE OF THE MAMMOTH STEPPE

Some time around 14,000-10,000 BP—the exact chronology and sequence is still not totally clear—major changes occurred throughout the mammoth steppe. Large numbers of megafaunal species became extinct. Others greatly retracted their distributional ranges in a variety of directions, some to the south (e.g., *Saiga*) and some to the far north (e.g., *Ovibos*). Most species that remained in the Arctic and Subarctic experienced what has become known as "Holocene dwarfing"; they became smaller and their horns and antlers were greatly reduced in size and complexity. In the North there was a general increase in evergreen woody plant species to create the boreal coniferous forest and its various deciduous successional elements. Herbaceous communities remained dominant only in mountainous areas and lowland muskeg and even there, nutrient-stress-tolerant evergreens predominated.

I would like to outline and then discuss a series of propositions to form a general theory that accounts for the demise of the mammoth steppe:

1) The change was climatically induced.

2) It involved a change in the seasonal distribution of moisture particularly, but also of wind and temperature, and not necessarily great changes in their annual means.

3) The result was increased vegetation zonation and an increased abundance of plant species having strong ungulate antiherbivory defenses.

4) Concurrently, the wet swampy ground and deep winter snows made the remaining herbage inaccessible to all but the snow and muskeg specialists.

5) As a consequence, there was a radical decrease in food for ungulates—and increased competition for those that remained.

6) The ungulates most precisely adapted to the emerging vegetation zones and Holocene habitats outcompeted ungulate species with broader adaptations as well as those species closely adapted to the declining plant communities.

7) All potential ungulate niches in the area once occupied by the mammoth steppe are now filled to carrying capacity, except for a few special situations where reduced access to colonization or unstable environments of a long-term scale have limited colonization.

Evidence from a number of sources shows that a major climatic change took place during the recession of the Wisconsin-Sartan ice (Leopold, 1967). From what we can reconstruct, there was a less seasonal glacial environment in mid-continent North America and North Africa (Axelrod, 1967). I have proposed in earlier sections that something similar seems to be true of the mammoth steppe. Summers were long, having a wet season and a dry season, fostering a diverse, herbaceous landscape that contained only few woody plants. Plants, invertebrates and mammals were present that now are limited to more southern areas; these intermingled with more northern forms to produce heterogeneously complex floral and faunal communities. The greater nutrient-availability of the basic warm-summer soils resulted in high-quality herbs to which the grazing ungulates were adapted.

With the increased moisture of the Holocene—featuring wetter summers and more winter snows—cushion and evergreen woody plants were favored. Cool soils limited nutrient availability, which favored plants that produced more antiherbivory chemicals. For example, there are few mammals which can tolerate a diet high in alder (*Alnus*), dwarf birch (*Betula*), mature larch (*Larix*) or

spruce (*Picea*) needles, (porcupines, *Erethizon*, climb above the defenses concentrated on the lower portion of spruce trees and eat the upper bark).

The shorter growing season and increased competition among woody plants has resulted in the present degree of vegetational zonation which existing herbivores exploit thoroughly. If musk oxen (*Ovibos*), which have been reduced in historical times by hunting, were to be restocked in their original habitats, tundra vegetation would be used by the mammals to its current winter potential, because winter range is the critical bottleneck for survival. Moose (*Alces*) and hares (*Lepus*) now exploit to its maximum the deciduous successional growth available to mammalian herbivores in the northern boreal forests. Additionally, the alpine areas are occupied in some form of vertical stratification by the Caprini. There are some local exceptions but, in general, the pattern holds. If other ungulates were introduced on a wide scale they would be outcompeted by the existing fauna.

Caribou (*Rangifer*) is the snow craterer without parallel. It can smell lichen and other plants through deep snow, and quickly paw down to them with its broad rounded hooves. A wide syndrome of adaptations including locomotor modes, respiratory structures, and high growth rate during a short season, etc., make caribou a tundra and mixed woodland-muskeg specialist without peer.

The same is true for moose (*Alces*) in the boreal forests where deep snows preclude ungulate subnivian feeding. Moose are especially adapted to walking in the deep snow and to browsing on the deciduous twigs above the snow. They also are especially adapted to the wet muskegs and summer ponds.

Musk oxen (*Ovibos*) are likewise well adapted to their windswept tundra ranges where low-growing woody plants and forbs are found. The same is true for sheep and goats on the highest alpine slopes. From everything we can gather about the extinct species, it is unlikely that they could outcompete extant species where the latter are confined to their zone of specialty. Thus when one removes these present habitats for which living ungulates are well adapted, there is virtually nothing left for any other ungulate species. There are no empty widespread ungulate habitats in the Far North today which could conceivably be filled by either living or extinct species.

The combination of short growing season, wet substratum, deep snows, and reduced distribution and complexity of nutritious herbaceous plants drove the distributional limits of many ungulates (e.g., *Cervus, Equus, Bison,* and *Saiga*) southward during the Holocene. The shorter Holocene growing season has also reduced the body size of almost all species. Horn and antler size have also diminished. The surfeit of nutrients ceased to be available, placing at a selective disadvantage those genomes which provided for the elaborate excrescences of social stature (Geist, 1974). Rather, because of limited growth resources, the more conservative strategies of survival and maintenance were followed and horns and antlers were reduced in size.

This climatic shift in seasonal patterns also greatly affected the distribution of other elements of the mammalian fauna. (1) The collared lemming (*Dicrostonyx*) and Arctic fox (*Alopex*) are now confined to the High Arctic. (2) Where the arctic ground squirrel (*Spermophilus*) abounded, now tree squirrels (*Sciurus, Tamiasciurus, Glaçomys*) live. (3) Very large badgers (*Taxidae*) and ferrets (*Mustella*) which lived in central Alaska and the Yukon Territory (Anderson, 1973) are now found thousands of kilometers to the south.

The extinctions of long-standing members of the mammoth steppe such as mammoth (*Mammuthus primigenius*) and woolly rhino (*Coelodonta antiquitatis*) indicate that climatic shifts in the Holocene were of a unique character. This was corroborated by the evolutionary dwarfing during latest Pleistocene time of the northern steppe bison (*Bison priscus*), red deer (*Cervus elaphus*), some sheep (*Ovis dalli*), and other species, including carnivores (Kurtén, 1968). Similarly, Leopold (1967) proposes unique climatic conditions for the more southern latitudes during the early Holocene.

MODERN ANALOGS

Could such a widespread biome have so recently existed and not left a sizable remnant? The answer seems to be yes. There are two major herbaceous biomes existing today: the alpine, or high-latitude tundra, maintained ultimately by summer coolness, and the temperate grasslands. Neither seem to approximate the mammoth steppe.

The grassland biomes today are at mid-latitudes and are maintained by a combination of wind and aridity through several controversial proximate forces (fire, root competition for moisture, etc.). They are extremely continental in climate (De Vos, 1969), which produces a number of features very similar to those of the mammoth steppe (e.g., grazing faunas) and a number of other features quite dissimilar (e.g., highly zoned vegetation, and an absence of the cryophilic elements). Lowland arctic tundra is even less similar to the mammoth steppe, as the melted winter snows remain puddled on the frozen ground through most of the summer, creating an almost impenetrable muskeg or bog.

High alpine tundra has some similarities to the mammoth steppe. The topographic heterogeneity creates a patchwork of herbaceous vegetation and, because of the slope, it is well drained with sharp nutrient pulses. Winter winds drift the snow, creating exposed rangeland interspersed with subnivian habitats. It is probably not coincidence that a large segment of the survivors of the mammoth steppe now reside in alpine areas.

But alpine habitat is of limited value in our search for analogs. The relief and limited extent make this habitat unsuitable for animals such as saiga or mammoth. The short alpine summer creates the prostrate growth habits characteristic of alpine tundra. More importantly, the season is too short for production of the ungulate giants which marked the mammoth steppe.

The high plateaus of central Asia, sometimes called the "alpine steppe" (Schweinfurth, 1957) come close to what the mammoth steppe must have been like, particularly parts of the Tibetan Plateau and areas to the north. Though the vegetation and large mammals are altitudinally zoned (Schaller, 1977), they are fairly diverse. The large yak (*Bos grunniens*) survives in this area as do the wild hemionids (*Equus hemionus*). Historically, saiga (*Saiga tatarica*) occurred in the northern portion of the plateau and there are still small populations in Mongolia, just southeast of Lake Baikal. In the recent past, wild horses (*Equus przewalski*) were common throughout this area, as were bactrian camels (*Camelus bactrianus*). Both species may still exist in remnant populations. Additionally, several species of sheep (*Ovis*), antelope (*Procapra, Panthalops*), and goat (*Capra*) are found there. Because of its altitude, alpine-steppe summers are windy and relatively dry, cool, and often cloudy, and due to the latitude, moderately long. Winters are windy, with little snowfall. Most of the woody plants are willows or aspen, but the vegetation is mainly herbaceous.

Though somewhat analogous to the mammoth steppe, this area certainly is not a homologous relict. The central Asian plateaus seem to have had a relatively stable late Quaternary history without the dramatic ecological change that occurred in the North. They can best be thought of as a late Pleistocene relict pattern which existed to the south of the mammoth steppe in central Asia during the last glaciation (Schaller, 1977).

Throughout the North there are a number of small, well-drained grasslands (Guthrie, 1968a; Young, 1976) in special edaphic conditions such as steep bank, southern exposures, and major mountain-pass outwash deltas, but these are probably not microcosms of the general mammoth-steppe conditions, although they may support some of the same flora and fauna. The mammoth steppe may be gone forever.