Ann. Zool. Fennici 28:253–259
Helsinki 19 February 1992

ISSN 0003-455X

The ecological structure of the "Mammoth Fauna" in Eurasia

N. K. Vereshchagin & G. F. Baryshnikov

Vereschagin, N. K. & Baryshnikov, G. F., Zoological Institute of the USSR Academy of Sciences, University Embankment 1, 199034 St. Petersburg, USSR

Received March 1990, accepted 1 May 1990

The so-called "Mammoth fauna" lived during the Late Pleistocene in northern Eurasia and in Alaska. About 30 indicator species inhabited a single hyperzone of "tundra-steppe" that existed where today there is recent steppe, taiga, and tundra. The ecological structure of the mammoth fauna was similar to that of recent communities of animals in African savannas. These ecological parallels of taxa inhabiting very different climatic zones may be analogized as a pyramid, one lateral half of which consists of beasts of the tundra-steppe, and the other half beasts of the savanna. The levels of the pyramid indicate biomass and feeding ecology. The lowest level of the pyramid is made up of grazers: Eurasian horses and kulan on the Pleistocene side, corresponding to zebra and African donkey on the Recent side; along with saiga and zeren, which correspond to African gazelles; bison, yak, and muskox, corresponding to African buffalo and eland. The next level consists of mixed feeders, consumers of grass, leaves, and woody sprouts, and includes Mammoth on the Pleistocene side, corresponding to African elephant; woolly rhinoceros, corresponding to white rhinoceros; roe deer and elk, corresponding to gerenuk and kudu. The third level contains carnivores: wolf and dhole on the Pleistocene side, corresponding to hunting dog and cheetah; and cave lion, corresponding to African lion. In the fourth level are scavengers: cave hyaena, polar fox and glutton, corresponding to spotted hyaena and jackal. Reindeer, lemming, and polar bear survived the disappearing Pleistocene tundra–steppe, and had no analogues in Africa.

1. The Pleistocene tundra-steppe

A cold-tolerant mammalian fauna developed during the Late Pleistocene in the Beringian part of the Arctic, where the most ancient remnants of lemmings, reindeers and musk-oxen are known (Sher 1971, 1976). During the Pleistocene this fauna was spread by several waves of expansion or "migration" throughout northern Eurasia. The complex of cold-resistent species attained its highest development in the Late Pleistocene, and is known as the "mammoth fauna" which existed during the Würm (Valdai) Glaciation in northern Eurasia and Alaska, in its southern extent found

as far west as the Pyrenees, as far south as the Caucasus and Tibet, and as far east as Korea. Particularly highly evolved in response to cold conditions was a group of large herbivores, rodents, and predators consisting of species typical of recent zonal landscapes: i.e., in the tundra, musk-ox, reindeer, lemmings, *Microtus*, and arctic fox; in the steppe, horses, primitive bison, saiga, Irish elk, wolf, and marmot; in the deciduous and coniferous forests (taiga), maral, moose, Siberian roe, cave bear, and glutton; in the mountains and semideserts, onager and yak. Coexistence of "tropical" mammalian families, such as elephants (mammoth), rhinoceros (woolly rhinoceros), hyaena (cave hyaena), and giant cats (cave lion), appear somewhat paradoxical.

The ecological type of this mammoth fauna, its tropical relations and the morphological adaptations known from frozen carcasses of mammoths, rhinoceroses, horses, and bisons in Siberia show that this faunal group existed in a sharply continental dry climate having cold winters and short, hot summers on hard frozen grounds in open steppe, meadow-steppe, and tundra-steppe landscapes. Some idea of such landscapes can be drawn from relict parts of the Yakut steppes possessing gophers, marmots, and steppe species of annual groundcover plants.

The vast territory inhabited by the mammoth fauna and especially by its "indicator group" (mammoth, horse, bison, lion, etc.), allows us to conclude that recent landscape zones of steppes, forest-steppe, taiga, and tundra did not exist separately in the last glacial interval, but instead were altered to a single hyperzone of frozen tundra-steppe (Velichko 1968, 1973; Tomirdiaro 1972). Some tracts of leaf-bearing and coniferous forests were found along river valleys or in canyon-bottoms in low mountain ranges.

2. Specific adaptations

One can find indications of the high number of herbivorous and predatory animals in this hyperzone in the abundance of fossil remains in the region of recent permafrost (Vereshchagin 1979). Such an abundance and diversity of large animals, particularly hoofed animals in the mammoth fauna, could exist only at the high biological productivity of Pleistocene tundra-steppes, resulting from the presence of diverse ecological niches (biotypes), which considerably exceed recent subarctic and arctic niches.

Species composition and morphophysiological adaptations of animals of the mammoth fauna confirm conclusions of paleogeographers and geologists about the ecological conditions of the Pleistocene tundra-steppe. The thick-fur-covered exterior of mammoths, woolly rhinoceros, horses, and primitive bisons are known from well preserved carcases, and confirm that these animals were resistant to extreme cold. The same can be inferred from the small size of the ears of the mammoths (i.e., 6–7 times smaller than of the Asian elephant, and 10–12 times smaller than of the African elephants.

A study of the stomach contents of frozen mammoths, rhinoceroses, and horses has shown that the basic food of these species were cereal grains (grasses) and sedge. Pleistocene alpine hares fed on grass that was heavily covered with mineral particles, inferred from the greater hypsodontism of teeth as compared to teeth of recent hares. This perhaps reflects dusty conditions, such as loess-carrying winds during the time. The presence of saiga antelope with their narrow feet providing small support area suggests that the tundra-steppe landscapes in summer and winter were solid and hard surfaces.

3. The ecosystem

Attempts to reconstruct the climate, landscapes, and comparative productivity of this hypothetical tundra-steppe have been undertaken by several scientists, such as paleogeographers, paleobiologists, and geologists (e.g. Hopkins 1976, Tomirdiaro 1972, Guthrie 1982, Vereshchagin 1974; see also Hopkins et al. 1982). Following from these publications, our earlier suggestions (Vereshchagin 1979) about the dry and cold climate, hard ground, thin snow cover, high insolation throughout the year, and lowered water tables in the Pleistocene tundra-steppe, were confirmed. However, details about the weather conditions, productivity of the primary and secondary biomass in figures, preservation of organic remains, and the possibility for hoofed ani-

mals to gain access to grass cover in winter still remain unknown and call for further study.

One ecological approach to the problems of reconstructing the landscape, climate and structure of the northern Eurasian mammal fauna in the Würm (Valdai) interval is a search for recent ecological analogues. The ecological structure of the mammoth fauna of Eurasia and Alaska is in many ways similar to the structure of the mammal fauna of the equatorial African savanna.

An alternation of humid and dry periods, responsible for seasonal cycles in the life of most mammals, is typical of the African savannas with their cover of tall grasses, baobabs, *Acacia* groves, and gallery forests along river valleys. During the unfavourable dry season some species do not stay in their wet season ranges or do not feed (and therefore do not deplete their food supply), and instead hibernate in shelters (for example, some rodents), while others migrate long distances in search of water and palatable food. Still others (elephants, ungulates, predators) concentrate in small areas at water bodies (Brown 1970).

In the Pleistocene tundra—steppes of Eurasia the seasonal rhythm of life was determined by two different periods of the year — cold and warm. In winter, Pleistocene marmots and gophers hibernated, as can be concluded from the frozen corpses of these Pleistocene animals that perished in the not-yet-thawed nest chambers (covered by landslips). Lemmings lived below the snow cover.

A shallow snow cover allowed mammoths, bisons, saigas, and reindeer to reach dry grass for feeding, as well as Iceland moss, and to migrate relatively long distances in search of convenient areas, whereas rhinoceroces, muskoxen and yaks led a more settled life, feeding in the same places preferred in the warm season. When water bodies were frozen many animals were satisfied with snow as a water source. Mammoths may have scraped the ice from precipices or broke it away from ground clefts, using their tusks. In summer, thawing and draining of the soil allowed the growth of abundant herbage. It is likely that the following groups of animals grazed along watersheds, and especially within river valleys: herds of mammoths (including hundreds of individuals), herds of horses, bison, deer (including thousands of individuals), packs of wolves, lions and hyenas.

4. Tundra-steppe and African savanna

The dramatic difference in life conditions and seasonal cycles of mammals living in the Eurasian tundra-steppe, and those living in African savanna, nevertheless also gives clues to the similarity of the ecological structures and faunas of these two communities.

The ecological parallelisms and exterior similarities among species of the above biomes can be represented as a "biotic pyramid", one half of which includes inhabitants of the extinct tundra-steppe, and the other half inhabitants of the African savanna (Fig. 1). Here are the most representative examples of ecological analogues: on the first level (i.e., consumers of herbs, forbs, and grass): Eurasian horses (*Equus latipes* V. Grom., *E. lenensis* Russ.) and onager (*E. hemionus* Pall.) on the extinct side, and African wild ass (*E. africanus* Fitz.) and zebras (*E. qreyvi* Oust., *E. burchelli* Gray) on the African savanna side; saiga (*Saiga tatarica* L.) and zeren (*Procapra gutturosa* Pall.), matched against African gazelles (*Gazella granti* Brooke, *G. thomsoni* Günth.); kiakhta antelope *Spirocerus kiakhtensis* M. Pavl.) and transbaikalian bubalis (*Parabubalis capricornis* V. Grom), matched against African gnu (*Connochaetes taurinus* Burch.), hartebeest (*Alcelaphus buselaphus* Pall.), and topi (*Damaliscus korrigum* Ogilby); primitive bison (*Bison priscus* Boj.), aurochs (*Bos primigenius* Boj.), Baikal Yak (*Bos baikalensis* N. Ver.), and muskox (*Ovibos moschatus* Zimm.), matched against African buffalo (*Syncerus caffer* Sparrm.) and eland (*Taurotragus oryx* Pall.); pika (*Ochotona pusilla* Pall., *O. alpina* Pall.) matched against dassi (*Procavia capensis* Pall., *Heterohyrax brucei* Gray). In Africa there are evidently no species directly analogous to three other taxa of tundra–steppe herbivores, namely reindeer (*Rangifer tarandus* L.) and two kinds of lemming (*Dicrostonyx*, *Lemmus*).

Under normal conditions the abundant species of recent savanna ungulates do not directly compete for food because the different taxa consume forage (especially grass) at different stages of its growth (Bell 1971, Hoffman & Stewart 1972, Grunow 1980). The first to eat tall, coarse grasses are zebra and buffalo, followed by gnu, hartebeeste, and gazelles. Topi mainly feed on the dry

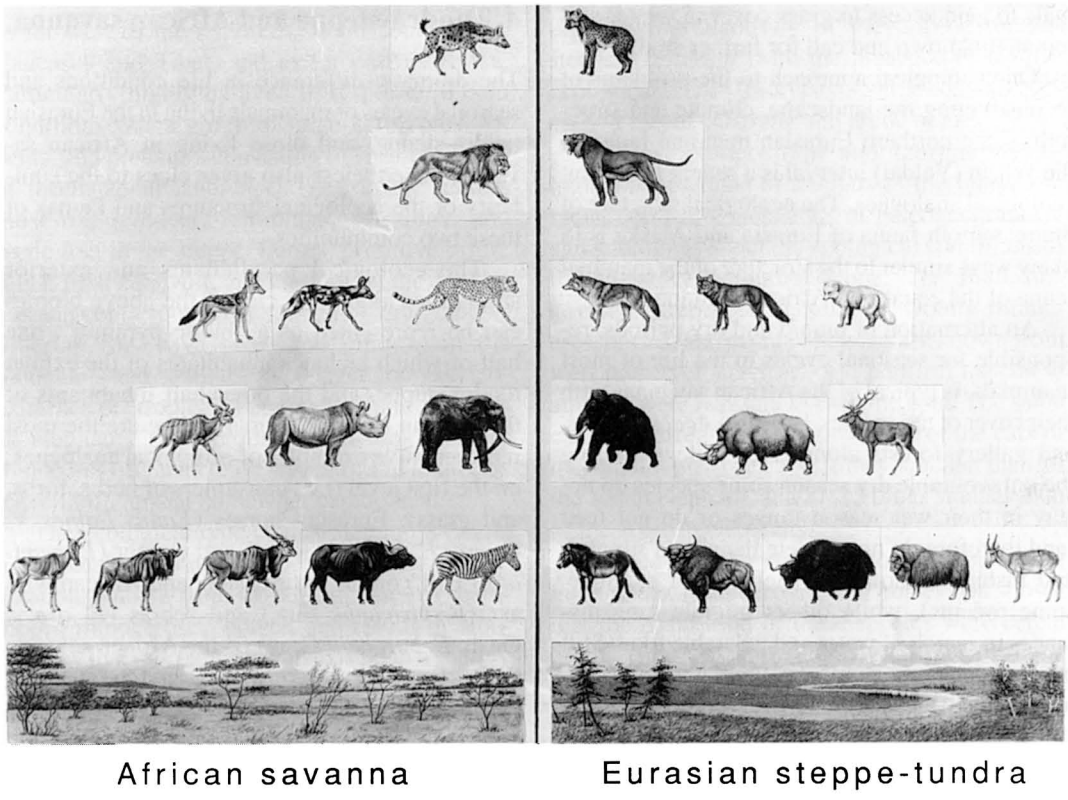

Fig. 1. Schematic comparison of the faunas of the African savanna and the Pleistocene steppe-tundra.

stems of old grass. A similar situation probably existed in the tundra-steppe, where ungulate feeding behaviour changed significantly in different seasons. In summer, horses, bisons, musk-oxen, and saigas consumed herbs (mainly cereals and Chenopodiaceae), twigs of shrubs, berries, mushrooms, and mosses. In winter they fed on dry grass obtained under the snow, while reindeers fed on lichens.

The second level of the comparative pyramid are the animals consuming herbs, leaves of shrubs, twigs and bark: namely mammoth (*Mammuthus primigenius* Blum.), matched against African elephant (*Loxodonta africana* Blum.); woolly rhinoceros (*Coelodonta antiquitatis* Blum.) matched against white rhinoceros (*Ceratotherium simum* Burch.); Siberian roe (*Capreolus pygargus* Pall.), maral (*Cervus elaphus* L.) and moose (*Alces alces* L.) matched against gerenuk (*Litocranius walleri* Brooke) and kudu (*Tragelaphus strepsiceros* Pall., *T. imberbis* Blyth).

It would be particularly interesting to compare the mammoth with the African elephant, i.e., the biggest animals of the studied communities. Tusks of male mammoths were up to 3.5 m long, with possible weights of up to 100–110 kg each, greatly surpassing female tusk-sizes, as in *Loxodonta*. Elephants of the African savanna live mainly in small groups of 10–20 individuals each, consisting of adult females, young, and juveniles (Glover 1963; Laws 1970). In the arid season of the year, during migrations they temporarily group into large herds containing 700–1000 individuals (Nasimovich 1975). Adult males usually keep away from the herd. The study of bones of the Berelyokh population of mammoths from Yakutia has shown that herds of this species also consisted of females, young, and juveniles (Vereshchagin 1977; Baryshnikov et al. 1977).

Very few bones of old males were found there. Possibly adult males of mammoths lived separately like those of African elephants.

African elephants move on long seasonal migrations in search of water and food. Their trampling creates nearly permanent paths in the shrubs and grass. They need water virtually every day, and in the dry season dig out with the feet (not using their tusks) pit wells in sandy river beds. Adult elephants consume up to 100 kg of grass, sprouts, and shrub leaves per day. They break off branches and destroy and fell trees, such as baobabs, or peel the bark using the tusks.

There are only indirect data on possible migrations of mammoths. However, to judge by analogy with African elephants, mammoths probably also migrated long distances along river valleys. Such herd migrations under conditions of recent tundra would have led to the creation of boggy ditches filled with water (the remains of mammoth paths) as the frozen groundwater in them melted. In summertime these animals probably fed on herbs, woody twigs and alders; in wintertime they grazed around river thickets. The wearing down of mammoth tusk tips perhaps resulted from mammoths scraping the bark of trees such as willow, *Chozenia*, poplar, spruce, and larch. From the bark they extracted essential nutrients such as calcium, needed tor the formation of the huge skeleton and tusks.

It is also interesting to compare the woolly rhinoceros to the African white rhinoceros. Both taxa are rather similar in body proportions. Grass sprouts, *Eriophorum*, and sedges were extracted from the large intestine of the Pleistocene rhinoceros from Churapcha and Central Yakutia (Vereshchagin & Baryshnikov 1982). The structure of the skull and the upper lip also confirm that this species was a grazer (Garutt et al. 1970). African white rhinoceroses of the savanna also feed on grass. They are nonmigratory, live in small groups including up to 20 individuals, consisting of females, young, and subadult animals. In case of danger they assume the same defense position as do arctic muskoxen or bison: the animals arrange themselves in a tight circle, with heads facing outward, thus sheltering their vulnerable young.

The cave bear (*Ursus spelaeus* Rosenm. & Hein.) and brown bear (*U. arctos* L.) constitute a transitional "link" between the herbivorous and the predatory taxa; they partly existed in intrazonal biotopes.

The third level of the pyramid includes consumers of ungulates and rodents, active predators of the first order: steppe polecat (*Mustela eversmanni* Less.) and ermine (*M. erminea* L.), matched against African zorilla (*Ictonyx striatus* Perry) and ichneumon (*Herpestes ichneumon* L.); arctic fox (*Alopex lagopus* L.) and wolverine (*Gulo gulo* L.) matched against jackals (*Canis mesomelas* Schreb, *C. adustus* Sundev.) and African civet (*Viverra civetta* Schreb.); wolf (*Canis lupus* L.) and dhole (*Cuon alpinus* Pall.) matched against African hunting dog (*Lycaon pictus* Temm.) and cheetah (*Acinonyx jubatus* Schreb.). Typical of the large canids (wolf, wild dog, and dhole) is the formation of complex social groups that hunt in organized packs, particularly efficient under conditions of open landscapes.

The differences among the trophic characters, activity patterns, and social structures of different African predators reduce interspecific competition (Rautenback & Nel 1978), probably typical also of Pleistocene tundra–steppe forms.

Almost all surviving species of the mammoth fauna's predators at present live in the high latitudes of the Holarctic. Only the area of the wild dog (dhole) in Eurasia has been reduced to south and east.

The fourth level of the pyramid contains predators of the second order: cave lion (*Panthera spelaea* Goldf.) matched against African lion (*P. leo* L.). Taxonomically these species are very close. Recent lions feed on large and small ungulates, rodents, reptiles, insects, and also carrion. They live in prides including 2-3 adult lions and up to 20 cubs. The animals either consume prey immediately, or keep guard over it in turn, while others in the pride move temporarily to water. Otherwise the prey would be quickly captured by hyenas, jackals, or griffon-vultures. The presence of hyenas, wolverines, wolves, and polar foxes in the mammoth fauna probably indicates that cave lions lived in temporary, cooperating groups.

The fifth and final level of the biotic pyramid contains consumers of carrion: cave hyena (*Crocuta spelaea* Goldf.) matched against spotted hyena (*C. crocuta* Erxl.) and striped hyena (*Hyaena hyaena* L.). African species of hyenas

also obtain live prey, but in many areas mainly feed on carrion such as dead elephants, buffalo, antelopes, and remnants of lion kills. The presence of cave hyena in the mammoth fauna confirm, the former abundance of the ungulates in tundra-steppes of Eurasia; otherwise this scavenger would probably not have been able to exist there.

5. Conclusion

Based on our recent knowledge of the fauna of north Eurasia in the Late Pleistocene, we draw the following conclusions:

1. The "mammoth fauna" in north Eurasia during the Late Pleistocene (Würm, Valdai) was a group of herbivorous and predatory animals, including up to 30 indicator species, living in the cold and dry climate of the extensive zone of tundra—steppe that existed in the place of recent steppe, taiga, and tundra.

2. The ecological structure of this fauna resembled that of the present savanna group of animals in Equatorial Africa.

3. The ecological parallels of the extinct steppe-tundra community and the recent savanna community can be presented as a pyramid, one half of which are animals of the Eurasian tundra-steppe, and the other half savanna animals.

4. The traits of similarity between the tundra-steppe and savanna ecosystems are striking, but do not form a perfect analogy. The differences are expressed primarily in the relatively impoverished systematic composition and simplified trophic relations of the mammoth fauna, namely the absence of several mammalian life forms, such as frugivores (primates and large insectivores (pangolins, antbear).

5. It is important to note that the species that survived the disappearance of the Pleistocene tundra-steppe landscape and became widely spread in the recent arctic have no direct analogues in Africa; these animals are reindeer, lemmings, and polar bear.

6. Ecological parallels in the structure of the mammal faunas of the Eurasian tundra-steppe and African savanna are due to the similar requirements of species to landscape conditions. Such parallels exist in the peculiar faunistic variants known in other parts of the world; for example, marsupials in Australia have adapted in ways very similar to placental animals on other continents; Tertiary marsupials and primitive ungulates in South America developed similar to advanced ungulates in the Northern continents. In the case of the mammoth steppe fauna, there is an interesting paradoxical "inversion": the structure of a boreal mammal fauna parallels the structure of a tropical fauna, in spite of diametrically opposite physiological adaptations of species to the temperature factor in the local environment.

7. The above ecological and morphological parallels may prove useful for archaeologists and ethnographers searching for analogies to help in reconstructing the primitive hunting practices of prehistoric people in Africa and north Eurasia.

Acknowledgements. The editors thank Dr. Gary Haynes (University of Nevada, Reno) for editing the manuscript.

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