Habitat fragmentation and the extinction of mammoths (*Mammuthus primigenius*, Proboscidea, Mammalia): arguments for a causal relationship

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**Abstract**

The extinction of mammoths and other members of the *Mammuthus-Coelodonta* Faunal Complex is here attributed to the effects of natural habitat fragmentation occurring as the result of the climatic changes of the Late Pleistocene. This habitat fragmentation led to isolated populations of megafauna, which populations eventually underwent phenomena of insular evolution. This explains the presence of diminutive or supposed “dwarf” mammoths and other mammal species on several localities in Eurasia and N. America. Human predation then contributed to the demise of vulnerable isolate populations living in the refugial habitat fragments. This hypothesis combines the influence of both climate changes and human hunters.

**Key words**: extinction, habitat fragmentation, climate change, overkill hypothesis, Pleistocene, Holocene

**Introduction**

The extinction of mammoths is one of the most intriguing problems that has arisen from our study of the past. The reason for the Late Pleistocene/Holocene extinction of mammalian megafauna such as *Mammuthus primigenius*, *Mammut americanum*, *Coelodonta antiquitatis*, *Equus* spp. (in America only), *Bison priscus*, *Ovibos moschatus* (in Eurasia only), *Megaloceros giganteus*, and the like, is subject of quite some debate. The extinction – even though not 65 million years ago like that of the dinosaurs, but ‘only’ 10,000 to 5,000 years ago – poses a problem. There was no cataclysmic meteorite impact around the Pleistocene-Holocene transition, and nothing alike the Deccan Trap volcanism either. There was a rapid climatic change though, and there were human hunters. Hence, the two major reasons for mammoth extinction advocated are climate-driven habitat changes (Webb 1984) and human overkill (Martin 1984, Alroy 1999), in addition to other arguments such as hyperdisease (MacPhee & Marx 1997). It now seems that the scientific discussion on the subject is paralyzed by prejudiced opinions that hamper the free development of thought. It may even seem that the science of mammoth extinction is the only science that has made no appreciable progress in some 150 years. Donald Grayson wrote in 1984: “We still debate the differential merits of overkill and climatic change much as those merits were debated during the 1860s and 1870s” (Grayson 1984: 807). The situation has not appreciably changed since Grayson wrote this statement, as scientists still discuss “the questions associated with the extinction of megafauna in general: environmental stress against human presence” (Gonzalez et al. 2001). Thus, we are now again twenty years further in time and the arguments are same. ‘Climatists’ and ‘overkill proponents’ try to outcompete each other, either by trying to falsify the arguments of the other (implicitly providing support for the own view by default, e.g., Webb 1984: 192) or by finding arguments for the own view (and thereby implicitly falsifying the other view). If these two strategies seem to fail, a third strategy can be proposed that circumvents both other views, of which strategy the hyperdisease theory is an example.

Yet both opinions (‘climate’ and ‘overkill’) have certain merits. And if, after nearly a century and a half of discussion, the two competing points of view both have their merits, it may seem that in fact both are true, or, they should be united into a model that includes the positive aspects of both. It is true that, in the geological history, most extinctions or faunal revolutions took place at moments that climatic or environmental changes occurred: examples such as the K/T boundary, the mid-Vallesian crisis, or the Messinian salinity crisis are just some of a large number. On the other hand, it is also true that many Late
Pleistocene and Holocene extinctions took place shortly after the arrival of *Homo sapiens*: whether the Australian extinctions around 40,000 years BP, or the North American ones around 12,000–9,000 years BP, or the disappearance of the dodo in the 17th century and the passenger pigeon in the late 19th, man seems to be involved.

Here, the extinction of (mammalian) megafauna is attributed to habitat fragmentation, a phenomenon that is a normal attribute of natural systems but that has aggrava
ted its influence since humans manipulate the natural environment. Natural habitat fragmentation is a climate driven process causing populations to retreat into smaller areas (refugia), and to eventually become prone to island phenomena including inbreeding, genetic drift, morphological change and increased vulnerability to extinction.

**Patchiness of the fossil landscape**

The reasoning of this paper focuses around the patchiness of the Late Pleistocene and Holocene landscape, which patchiness increased in time as far as the mammalian megafauna is concerned. Increasing patchiness translates into habitat fragmentation, this in its turn implies splitting up of populations into subpopulations or metapopulations. If the connectivity between the fragments becomes too low (i.e. when the connecting environmental ‘matrix’ becomes too inhospitable for migration) this may lead to the possibility of island evolutionary phenomena.

Zazula et al. (2003) described patchiness in the landscape of Beringia. On the basis of studies of plant macrofossils they concluded that local ecological mosaics existed, and their results indicated that there were “marked ecological differences between the central and easternmost regions of Beringia during the late Pleistocene”. Markova et al. (2001) described a similar situation for the Russian Plain during the Valdai Briansk interstadial (the Valdai corresponds to the American Wisconsinan and the European Weichselian; the Briansk interstadial is equivalent to the Denekamp interstadial in W. European terms, i.e. the interstadial just before the Last Glacial Maximum [LGM]). Here, five major biomes are distinguished, some of which are more favourable to mammoths than others due to a higher production of vegetal biomass. Some biomes occurred with mosaics of forest islands; especially the periglacial forest-tundra steppe is described by Markova et al. (2001) as “a mosaic of plant communities, including Betula-Pinus and Picea forested ‘islands’, meadow and halophytes steppes, and tundra vegetation patches”. Simakova (2001) comes to similar results for the Russian Plain for both the Briansk interstadial and the LGM, mapping forest vegetation refugia and concluding the existence of a wide distribution of different types of forest-steppe and tundra-steppe landscapes. These descriptions illustrate the patchiness or mosaicity as a constant but varying attribute of the Late Pleistocene landscape, whether before, during, or after the LGM.

Such mosaicity is the result of complicated interactions between flora, fauna and the climate. Due to climatic changes, biotopes such as forests or grass communities can expand or contract, producing habitat islands during the process. Mosaicity and the formation of habitat islands exert constraints on the co-evolutionary relationship between herbivores and the vegetation (e.g., Graham & Lundelius 1984). When mosaicity leads to formation of habitat islands, and when the connectivity between the fragments becomes too low, these habitat islands will be subject to phenomena of island biogeography such as described and modelled by MacArthur & Wilson (1967). The evolutionary model of island biogeography predicts different rates of settlement or extinction of the (mammalian) inhabitants that live in the expanding or shrinking habitat islands.

Populations living in the habitat islands (provided that they are sufficiently isolate) will be subject to island evolution sensu Son
daar (1977), including a higher vulnerability to extinction by either natural or human-induced causes.

**Refugia, indication of habitat fragmentation**

When taxa originally live in a large area, and subsequently become restricted to smaller contracted and isolated habitat patches, we can speak of habitat refugia. Refugia are a well-known indicator of large-scale habitat fragmentation. Modern examples of this are the present European range of the once ubiquitous brown bear *Ursus arctos*, as a result of human-induced habitat fragmentation (Mitchell-Jones et al. 1999). There are small islands of bear habitat in Spain, France, Italy and the Balkans. This pattern is largely the result of human influence: habitat destruction and hunting the bears to oblivion. The same fragmented distribution is seen in the Alpine grouse *Lagopus mutus*, a bird living in Scotland, Scandinavia, the Alps and the Pyrenees (Peterson et al. 1965). Like the bear, its range is split into fragments. Yet this is NOT due to human intervention but to climatic change, forcing the bird to retreat to cold regions in either high altitude or high latitude. It is obvious that many such examples can be found, not only among vertebrates but also in invertebrates and plants. Habitat fragmentation is a natural phenomenon, although nowadays it is strongly aggravat ed by man who disturbs the environment. Another well-known example of natural habitat fragmentation is found in the Amazonian rainforest, which contracted into small forest islands during glacial maxima and expanded during minima (Haffer 1969, Müller 1974, Terborgh 1992). These forest islands acted as refugia for the inhabiting species.

Climate driven changes in the vegetation are generally slow processes, and it can be expected that they occur over larger areas – if not continents – contemporaneously. Gilbert & Martin (1984) described such phenomenon for North America, where vegetational changes (e.g., replacement of the Pleistocene boreal woodland by a mixed forest)
at the end of the Pleistocene seem to have occurred roughly contemporaneously throughout the continent. Yet, on a more regional scale these changes took several millennia to be accomplished, with modern vegetational aspects appearing by 12,000 years BP, and remnants of Pleistocene vegetation lingering on until 9,000 years BP (Gilbert & Martin 1984). This can only have occurred with habitat fragmentation as a temporary result, and such fragments of Pleistocene vegetation will have acted as refugia for Pleistocene (mega)fauna.

Thus, in the case of Late Pleistocene megafauna, evidence of fossil refugia as an indication of habitat fragmentation can be seen in the existence of locally restricted areas where mammoth steppe taxa could survive. Tikhonov & Vartanyan (2001), in their short abstract for the 2001 Rome meeting, wrote “at the end of the Pleistocene the range of woolly mammoth in Eurasia became dissected into isolated populations. (...) On Wrangel Island and the Taimyr peninsula, they crossed the boundary into the Holocene, surviving into the Holocene global warming”. In a more elaborate study, Stuard et al. (2002) showed that mammoth survived in the Russian Plain in a refugium at Cherepovets until ca. 9,800 BP and on the Taimyr peninsula until roughly the same date. Another such indication is presented by Boeskorov (2003) for several species in NE Siberia. Not only did mammoth survive on Wrangel Island until about 3,700 years BP, Boeskorov also found evidence for refugia of horse until 3,000–2,000 years BP in the lower reaches of the Enisey river, the Novosibirskie Islands and the E. Siberian coast; of muskoxen on the Taimyr Peninsula and in the Lena river delta until 3,000 years BP; and of bison in E. Siberia in the Holocene (unspecified).

In North America, mastodonts (Mammut americanum) probably disappeared in a causal connection to habitat fragmentation. Mastodonts were linked to a coniferous forest habitat with spruce and pine and were unable to live outside this biome. King & Saunders (1984) studied the decline of the coniferous forest biome and its replacement by deciduous forest in relation to the population structure of the mastodont. As the coniferous habitat collapsed after the LGM (Wisconsinan glacial), these authors state (for the locality of Boney Spring, W. Missouri): “As the coniferous habitat was collapsing, it appears (...) that mastodonts were undergoing self-regulation, evidenced by low recruitment and high modal age class analogous to the African evidence (Laws & Parker 1968), during a time of environmental stress. (...) This self-regulation was in vain, and mastodonts became locally extinct”. King & Saunders (1984) inferred “that a mastodont-coniferous vegetation linkage was vital for the maintenance of healthy (...) mastodont populations during the late Wisconsinan. When pine collapsed into island-like distributions, this linkage was effectively broken and mastodonts, retreating into these islands, would be expected to decline rapidly as a consequence of natural self-regulation. When these islands disappeared, the mastodonts vanished (...)”.

It is tempting to draw a parallel between the mastodont and the coniferous forest biome on the one hand, and mammoths and the mammoth steppe ecosystem on the other. One then envisages mammoths surviving for some time in mammoth steppe habitat islands, until these islands disappeared and mammoths became extinct. The question that then arises is how to prove the existence of such habitat islands, either directly (e.g., the mentioned paper of Boeskorov 2003) or through inference.

Dwarfism, a parallel with island mammals

Sondaar (1977) was one of the first to describe the effect of island evolution on larger mammals. Many taxa of larger mammals, having had the opportunity to go through a phase of endemic evolution due to isolation on an oceanic island, underwent (sometimes considerable) size reduction: dwarfism. Examples are dwarf hippos on Cyprus and Crete (Mediterranean), dwarf stegodonts on Sulawesi, Flores and Java (SE Asia), dwarf mammoths on Santa Rosa Island (California) and dwarf elephants on Sicily, Malta, and Tilos (Mediterranean). Dwarfism of larger mammals, along with other phenomena such as gigantism (among small mammals and tortoises) or flightlessness (among insects and birds), counts as a typical trait indicating endemic or island evolution, taking place on oceanic islands. One of the major reasons for these traits is supposed to have been the absence of mammalian predators Sondaar (1977). It is thus no surprise that the discovery of small mammoths on Wrangel Island dated ca. 4,000 years BP was interpreted as indicating oceanic island evolution (Vartanyan et al. 1993; see also Lister & Bahn 1994). It is, however, a classic example of circular reasoning: because oceanic island proboscideans developed into dwarf forms as a rule (e.g., Santa Rosa, Sicily, Malta, Crete), this dwarf form was hence considered an (oceanic) island proboscidean and published as such.

It is important to delimitate the meaning of dwarfism to island situations: not all small specimens (i.e. the smaller end of any bell-curve distribution, or small continental populations due to – for example – Bergmann’s Rule, are necessarily dwarfs. I propose to restrict the meaning of ‘dwarfism’ to island forms.

Small mammoths conforming the diagnosis of the Wrangel ‘dwarf mammoth’ Mammutthus primigenius vrangeliensis Garutt, Averianov & Vartanyan, 1993 are known from several other regions. Small mammoths from the North Sea (Mol et al. 1999) are dated as > 30,000 years BP (Essen 2003), those from Taimyr ca. 10,000 years BP (we have a Taimyr ‘dwarf’ jaw dated 9,920 +/− 60 years BP [Laboratory # GrA–17350/DM5, delta13C: -22.80 %o]; Reumer et al. 2002). The phenomenon of diminutives is also known from Mexico (Joaquin Arroyo-Cabrales, pers. comm. 2004) and further examples (e.g., a population of mammoth from Kirby, England showing...
diminutive sizes) are to be found in Essen (2003) who briefly discusses the matter. Even if the Wrangel population were indeed oceanic island dwarfs paralleling the Santa Rosa dwarf mammoths (which we consider rather improbable as Wrangel is only an oceanic island during the summer; Reumer et al. 2002), it is a taxonomical oddity to see morphologically identical dwarfs in England, in the North Sea (aged > 30,000 y) and in the Taimyr region (aged 10,000 y) well before the taxon itself emerged on Wrangel by ca. 8,000 years BP.

So, the question arises what really happened here. The climatic warming after the LGM caused a generally northward shift of the various vegetation belts, including the mammoth steppe ecosystem. However, due to the geography of the Eurasian terrain, this was not a smooth process, like the rolling up of a projector screen after the slide-show. Mountain ranges, surfaces of sea water or estuaries, or glaciers, could have caused the split-up of the mammoth steppe into several habitat fragments. Northward directed slopes could retain a tundra-like vegetation while southward directed slopes developed forest or steppe. The present North Sea region, the Taimyr peninsula, and the Wrangel Island region could have constituted habitat islands. It is in these three regions that small mammoths were found. Are these supposed dwarfs a taxon (which should then be named Mammutthus primigenius vrangeliensis) or a development (for which a taxonomic epitheton is not applicable)? Are they real dwarfs or just the smaller end of a bell-curve? And if it is a development that occurred in several places, what is/are its common cause(s)? Part of the size difference could be explained by sexual dimorphism, females being smaller than males. But it is equally plausible that the size reduction is (at least partly) the result of an isolated fragmented population suffering from ecological stresses such as food shortage, followed by selective processes (including inbreeding and genetic drift) leading to diminutives. The development then paralleled oceanic island evolution, but took place in a habitat island on the continent.

Schmidt & Jensen (2003) demonstrated that mammals that become isolated in habitat fragments respond by showing the same phenomena as mammals on oceanic islands do: small mammals become larger, while large mammals become smaller. They attribute this to an island effect. Size reduction or dwarfing of larger mammals is a response to adverse situations in the environment. It is explained by putting a premium on becoming sexually mature at a younger age. When animals are able to reproduce at a younger age, they have a relative advantage compared to animals that wait a longer period before starting to reproduce, as they require less nutrition during the lifetime of their generation (an adaptation to a low carrying capacity). Schilthuizen (2001) reported this for eucalyptus skunks in Australia that became smaller when living outside the advantageous rainforest environment.

Reports on Late Pleistocene megafauna becoming smaller are not restricted to the Eurasian mammoths. Guthrie (2003) reported size decline in Alaskan Pleistocene caballoid horses, and noted: “The significance of this size decline among Alaskan horses just before their regional extinction is that environmental pressures provoking smaller body size may well have been the same ones that ultimately resulted in their extinction.” This is explained by changes in the vegetation from a cold and arid version of the mammoth steppe towards a more mesic (warmer yet less arid) vegetation. King & Saunders (1984) reported dwarfing in their studied mastodont populations: “during the terminal late-glacial period, some evidence shows that mastodonts again decreased in size, perhaps reflecting incipient dwarfing in response to insular distributions”.

Guthrie (1984) reported on body size reduction in Bison, Cervus, Rangifer, Ovibos and Alces, and Guthrie (2003) observed the same in Equus before extinction. Marshall (1984: 796) noted that many taxa in North America underwent some degree of dwarfing: Alces, Ovis, Ovibos, Rangifer, Bison, Felis, Hydrochoerus, Panthera, Tapirus, and Ursus. Apparently, there is a general trend to be observed. This would plead in favour of (at least some) role for another cause here. Size decrease could also be a response to changes in overall temperature: i.e., Bergmann’s rule. A nice example of this was published by Kurten (1973) for American puma (Felis concolor), animals being smallest near the equator, and becoming larger towards both the North and the South. Size increase is explained as an adaptation to relatively cooler climates, as the surface/volume ratio becomes smaller with increasing body size, thus keeping body heat inside. If this trend be spread out over time, animals could tend to become smaller when temperature increases, and larger when temperature drops. This would imply that the Late Pleistocene/Holocene warming episode could result in animals becoming smaller.

It is a challenge to unravel both influences: size reduction through Bergmann’s Rule (sensu Kurten 1973) spread out over time, versus size reduction (dwarfism) as a result of island evolution in habitat fragments (sensu Schmidt & Jensen 2003). A third factor to be considered in some published cases is sexual dimorphism, females being smaller than males (Mor et al. 1999). As the Late Pleistocene trend towards smaller body size is seen in so many species (mammoth, bison, horse, mastodont, …) it seems unlikely that sexual dimorphism is involved. Pro-bosceids and bovids are known to respond to insular conditions by dwarfing; this is not known from perissodactyls, but these mammals normally do not reach oceanic islands (Sondaar 1977).

Overhunting

The Latest Pleistocene was a period in which modern humans (Homo sapiens) entered Eurasia and the Americas
and dramatically increased in number. This is explained by the release from the regulation of their number by predatory larger mammals (PUTSIKOV 1997). The escape from this regulatory mechanism, result of advancing defense technology, development of language, and possibly other such factors, led to considerably higher numbers of humans in comparison to earlier phases in the Quaternary. This is an important difference (and arguably the major difference between the post-Pleistocene warming and earlier ones), leading to the possibility of overhunting.

Overhunting of Late Pleistocene – Holocene megafauna in their habitat islands shows parallels with the effects of overhunting on islands (the most noted example of which is the effect of 17th century seafarers on the dodo). ROBINSON et al. (2003) noted the resemblance between population collapse, followed by extinction as a result of human action, on Madagascar (a large oceanic island) and in Late Pleistocene megafauna in the Hudson Valley area (New York State, US). They interpreted the observed sequence of events "with the hypothesis that humans precipitated these extinctions by setting in motion a process of ecosystem failure driven by the synergistic interactions of overhunting and landscape transformation", but failed to include the possibility that the observed transformation of the landscape can also be climate-driven next to being the result of diminishing grazing pressure. Overhunting may well have killed the last remaining populations in an already drastically changed ecosystem.

Such has been documented for Eurasian bison (Bison bonasus). VERESHCHAGIN & BARYSHNIKOV (1984) noted that the bison populations that survived in the forests and steppes of Europe and the Caucasus and in the steppes of Siberia were almost wiped out by man at the beginning of the twentieth century. They barely escaped extinction; bison survives to the present day in a forest refugium in E. Poland (Białowieża Forest), and only strict conservation measures kept the species from becoming extinct (MICHTELL-JONES et al. 1999).

In a fossil context, it has been documented that, in N. America, Clovis culture people opportunistically targeted megamammals in habitat refugia around the time of the Pleistocene – Holocene transition in N. America, ca. 11,500 years BP (KING & SAUNDERS 1984, HAYNES 2001). Proboscideans (or other large mammals) in habitat refugia may provide human foragers with scavengable carcasses, as stated by HAYNES (2001), the more so when environmental pressure such as water or food shortage leads to die-offs. Also KVASOV (cited in PUTSIKOV 1997) noted that small residual populations of mammoths and other megafauna, hidden in refugia from the effect of the Late Pleistocene warming, were overhunted by man. Eventually, if there would not have been man, mammoths and woolly rhinos could have "sat out" the Holocene warm period up to the present day in their refuge areas, just as they apparently did during earlier warmings (such as during the Eemian interglacial or the mentioned Bransk/Denkamp interstidial).

A synthesis

The demise of North American mastodonts that were restricted to their coniferous forest biome islands can be explained by a cascading suite of causes:

- climatic changes after the Last Glacial Maximum;
- changes in the vegetation regime i.e. breaking up of the coniferous forest area into small habitat fragments ('coniferous islands' sensu KING & SAUNDERS 1984);
- splitting up of the mastodont population into a metapopulation with separate subpopulations in various coniferous islands;
- overaiging of the population, leading to environmental stress such as food shortage;
- reduced population viability due to loss of genetic variation and to inbreeding depression;
- size reduction of the mastodonts starting in the late glacial;
- hunting (and/or scavenging after stress-induced die-offs) of the animals by Clovis people starting some 10,000 years ago;
- overhunting and collapse of the mastodont (sub)populations;
- increase of plants that were so far restricted by grazing or browsing leading again to habitat alteration; and finally
- extinction of the mastodonts.

Note that climatic factors, habitat alteration and human overhunting all played a role in this scenario.

The extinction, at the end of the Late Pleistocene and the early phases of the Holocene, of a large number of large mammal species is similarly explained as being connected to environmental changes, of which habitat fragmentation formed a crucial factor. Rapid climatic changes led to the splitting up of previously existing biomes into shrinking habitat islands that proved too small to sustain mammal populations for a longer period of time. The mammoth steppe (home of the woolly mammoth), the American coniferous forests (home of the mastodont), and other biomes reduced to habitat fragments. Populations living in these fragments developed adaptations to the environmental stresses encountered (such as food shortage) by selectively evolving into dwarf forms. This process, driven by inbreeding and genetic drift, parallels island evolution on oceanic islands. At the same time, the remaining populations became vulnerable to both evolutionary chance (cf. the island biogeographical model of MACARTHUR & WILSON 1967) and to overhunting by humans. The Latest Pleistocene saw the release of human populations from numbers regulation by larger carnivores due to advancing defence technologies, thereby causing a plummeting number of people able to hunt.

So, in a scenario that mirrors the above-mentioned scheme that led to the extinction of the American mastodont, I propose the following scenario that led to the extinction
of the mammoth and most of the Mammuthus-Coelodonta Faunal Complex (MCFC) sensu Kahlke (1999):

Step 1. Climatic change after the LGM caused a splitting up of the mammoth steppe into fragments, first large fragments and subsequently smaller fragments. This is a natural form of what is presently known as habitat fragmentation.

Step 2. Populations of MCFC species were driven into a metapopulation structure, with subpopulations in each habitat fragment.

Step 3. When the fragments became smaller and situated at greater distances, with decreasing connectivity due to inhospitality of the interspersed habitat matrix, the fragments became true habitat islands and the subpopulations became isolated populations.

Step 4. The populations started to evolve island phenomena as a result of environmental stress, inbreeding, and genetic bottleneck effects. In the case of mammoths, this led to smaller (diminutive) individuals such as *Mammuthus primigenius* *vrangeliensis* or such as the Holocene small mammoths from the Taimyr peninsula (Wrangel Island and Taimyr being such habitat islands). Other examples are known from Mexico and England (the Kirby population).

Step 5. Island populations, due to their low genetic plasticity, are extremely vulnerable to influences from outside, such as the introduction of predators, competitors, parasites, or disease. We may call this the ‘dodo effect’.

Step 6. One extremely dangerous predator is man. So when Clovis culture people started to hunt the mastodont in its remaining conifer forest fragments, they caused the extinction of the mastodont. When Eurasian hunters started to hunt mammoths for their meat, skin and bones, they did the same. They killed the mammoth that lived in its habitat island in exactly the same way as men killed the dodo in the seventeenth century.

Discussion

The splitting up of the mammoth steppe of Eurasia into terrestrial habitat islands is a hypothesis that could explain the many dwarf mammals occurring at the end of the Quaternary, such as the supposed dwarf mammoths of Wrangel Island. These dwarfs, described by Vartanyian et al. (1993) and Garutt et al. (1993), were long considered a separate subspecies occurring on Wrangel Island as a discrete taxon, but are here considered not a taxon, but a phenomenon that results of habitat fragmentation. Late Pleistocene dwarfs, or diminutive mammoths are they are more aptly called (e.g., Essen 2003), are found in several localities of Late Pleistocene, but not necessarily latest Pleistocene/Holocene, age. As the taxon *vrangel-

iensis* (which is a morphotaxon in the paleontological taxonomical sense) is therefore polyphyletic, I consider it a nomen nudum. The phenomenon of diminutive mammoths parallels the dwarfing of oceanic island populations (Mediterranean, Californian Channel Islands, SE Asia) as a result of ecological stress and facilitated by genetic bottleneck effects in small subpopulations.

The fragmentation of the mammoth steppe was illustrated by Listler & Bahn (1994: 121) in three small maps showing the advancement of forests over Eurasia, replacing the mammoth steppe biome. Ward (1997) also indicated the influence of habitat fragmentation on the fate of the mammoth. He wrote: “The largest single habitat of the mammoths (…) was split into many isolated pieces when the last glacial interval came to an end. The various populations of mammoths were split into many tiny populations” (Ward 1997: 178), and: “With the end of the Ice age, the ancient elephants lived in an increasingly fragmented habitat, just as today’s elephants do. Within these islands of favorable habitat, the declining elephant populations are especially vulnerable to human predation, even if that predation seems to occur at a very low rate” (Ward 1997: 213). Listler & Bahn (1994) and Ward (1997) are thus the first to have observed a relation between habitat fragmentation and the extinction of the mammoth, but both these revelations were published in books for the general public and not in the mainstream scientific journals; they apparently escaped notice of the scientific community.

This model also explains the vulnerability to human overhunting of the last megamammals in their respective habitat islands; this parallels the vulnerability of oceanic island populations. Island populations are more vulnerable than (larger) continental populations: 71.7 % of all mammals extinct since AD 1500 lived on islands (MacPhee & Flemming 1999), and at least part of the remaining 26.1 % of continental losses may involve species that lived in fragmented habitats. The ultimate collapse of the populations, leading to their eventual extinction, is due to continuously shrinking habitat, environmental stress, inbreeding, genetic drift, and overhunting. In some cases even a disease (caused by a parasite or a contagious viral or bacterial infection sensu the overkill model of MacPhee & Marx 1997) may have been the culprit. The mammoth being a keystone species, its demise could in turn have led to a cascading extinction wave: removal of the proboscideans from an ecosystem (the keystone removal concept cf. Putshkov 1997) leads to habitat alteration and to subsequent extinctions, from other herbivores up to the top-predatory sabretooth cats (*Homotherium, Smilodon*).

This model combines a) the influence of climatic change that led to the formation of habitat islands with b) the influence of man who finished off the island-like and vulnerable populations living in the shrinking habitat fragments, and c) also explains the island-like evolutionary phenomena such as the supposed dwarf mammoths.
from Taimyr and Wrangel Island. But maybe the best aspect is that it also seems that during 150 years of scientific discussion everybody was somehow right, and nobody was entirely wrong. It may thereby put an end to the fruitless and never-ending dispute between so-called climatists and overkill proponents.

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