

西伯利亚南部旧石器时代晚期 哺乳动物群动态学

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摘要: 旧石器时代晚期至全新世发生了广泛而迅速的动物群更替,为研究动物群对快速环境变化的反应提供了有益的信息。自中新世以来中亚地区一直是欧亚大陆向更开阔和干旱环境转变的焦点。利用已发表的俄罗斯贝加尔湖和阿尔泰山区域旧石器时代晚期的文献资料,通过对大型食草动物白齿齿冠高度、食性和体型大小的分析,绘制了环境变化图。结果表明,在旧石器时代最晚期(晚冰期),平均齿冠高度、平均体型大小均有所减小,食物取向从食草向食树叶转变,这意味着气候变得温暖,降雨量增加,森林也有可能扩展。常见种(出现于超过25%的地点)更强烈地表现出这一趋势。齿冠高度随海拔高度而增大,提示降雨量减少。从齿冠高度得出的降雨量数值与根据其他指标所估算的数值之间的偏差可能随海拔高度而增大。影响西伯利亚南部猛犸象动物群消亡的主要变化可能开始于末次冰期冰盛期(LGM)之后。猛犸象和奇蹄动物出现频率的降低与大型哺乳动物的绝灭相一致,它们和偶蹄类的差异则反映了气候的变化。人类的过度开发可能给区域环境带来了更大的压力,使得哺乳动物的种群数量下降,导致它们更迅速地绝灭。

关键词: 贝加尔湖,阿尔泰山,旧石器时代晚期,食草动物,齿冠高度,出现频率,食性,体型大小,降雨量

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DYNAMICS OF THE MAMMALIAN FAUNA IN SOUTHERN SIBERIA DURING THE LATE PALAEOOLITHIC

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Abstract The extensive and rapid faunal alteration occurring at the late Pleistocene-Holocene is an informative period for studying faunal responses to rapid environmental change. Since the Miocene Central Asia has been the focal point of the transformation in Eurasia towards more open and dry environment. Here I use published literature data on the late Palaeolithic of Lake Baikal and Altai Mountains region in Russia to map environmental changes through molar crown height (hypsodonty), diet and body size in large herbivores. The results demonstrate a decrease in mean hypsodonty, mean body size, and the shift in dietary preferences from grazing towards browsing during the latest late Palaeolithic or Late Glacial (LG), which implies climatic warming, precipitation increase and, probably, spread of forests. Common species, present in ≥ 25 per cent of localities, produced these trends

more strongly and responded faster to changing environments. Hypsodonty increased with altitude, which suggests precipitation decrease. Deviation between precipitation values derived from hypsodonty and estimated from other paleoindicators might be increasing with altitude. The major change that influenced the demise of the mammoth fauna in southern Siberia was probably initiated after the Last Glaciation Maximum (LGM). Decrease in mammoth and perissodactyl commonness is consistent with large mammal extinctions and different from artiodactyls response to climatic change. Human overexploitation could regionally add more stress to the declining mammalian populations and lead quicker to their extinction.

Key words Baikal, Altai, late Palaeolithic, herbivore, hypsodonty, commonness, diet, body size, precipitation

1 Introduction

Dynamic environmental fluctuations of the last 25 000 years are an important time period to understand drastic faunal turnover between the last Glaciation of the Pleistocene-Weichselian and the interglacial period - Holocene. The rapid environmental changes that occurred during the Pleistocene (1.65 ~ 0.01 Ma) have been linked to extensive evolution in mammalian faunas across the world. All modern species in Europe and Northern Asia are Pleistocene in origin, and most show adaptations to the Pleistocene environments like permafrost, tundra or steppe-tundra (Lister, 2004). Fragmentation of dry and cold tundra-steppes was initiated at the end of the Weichselian Glaciation when increased temperature and humidity produced boggy tundra in the north (Sher et al., 2005) and forests, including taiga, in the south of the most part of Northern Eurasia (Blyakharchuk et al., 2004).

Central Asia was the focal point of an environmental change in Eurasia towards increasingly more open and dry environments beginning in the middle Miocene (Fortelius et al., 2003). The Holocene backward transition towards more closed and humid environment could have started in Europe since Western Europe was closer to the Atlantic and consequently experienced more climatic fluctuations than Siberia. The expansion of temperate broad-leaved forest in the mountains of Europe, e. g. Alps, at the beginning of the Holocene was matched only 2000 years later by the expansion of coniferous forest in southern Siberia (Blyakharchuk et al., 2004). However, the major change that influenced the mammoth fauna demise was probably initiated in Central Asia (Tormidiaro, 1977; Kvasov, 1977; Sher, 1997).

Mammal evolutionary responses to climatic change can be measured by proxies such as tooth height, body size, taxonomic change, species richness, abundance and commonness. If warming lasts over 100 years extinction of some species occurs, taxonomic composition of communities changes and reduction in species richness can follow (Barnosky et al., 2003).

The recent Russian literature offers an opportunity to evaluate faunal changes of large herbivores on a more restricted temporal and geographic scale – the latest Pleistocene of southern Siberia, in the region of Lake Baikal and Altai Mountains in Russia. This area is elevated 200 to 400 meters above the sea level and rises northward to a height over 3 000 meters (Karabanov et al., 1998). The modern climate of the Baikal Lake region resembles a maritime climate due to the moderating influence of the large body of water. Baikal Lake is the deepest and oldest lake in Eurasia, situated in the middle of the continent at 52° ~ 56°N latitude. In the past Lake Baikal was not covered by ice sheets nor was it desiccated, despite glaciers that developed in the adjacent Altai Mountains and the mountains north of the lake (Karabanov et al., 1998).

Fortelius et al. (1996, 2003) used hypsodonty, which is a measure of molar crown-height, of large herbivores to broadly map environmental changes across Eurasia through the Neogene. Hypsodonty has been correlated with the preferred diet of a species (Flerov, 1962; Janis and Fortelius, 1988), as well as the environmental conditions in which it lived. In fact, Damuth and Fortelius (2001) used hypsodonty values to calculate rainfall values. Previous studies have shown that common species (and common tooth crown types) drive the evolutionary increase in hypso-

donty (Jernvall and Fortelius, 2002, 2004). They further indicated the importance of common species, found in $\geq 25\%$ localities, in retrieving the general evolutionary trends and showing them stronger irrespective of the rare groups.

Here I demonstrate changes in species commonness, molar crown height, dietary preferences and body size during the latest Pleistocene. Specifically I examine locality coverage or species' commonness, similarity, mean hypsodonty (transferred into precipitation), mean diet and mean body size within the three stages of the Weichselian Glaciation or the late Palaeolithic.

2 Material

All data were obtained from Vasil'ev et al. (2002) and Vasil'ev (2003), who described radiocarbon-based chronology of the late Palaeolithic localities and their large mammal fauna in Siberia. From Vasil'ev's articles I have used 119 localities with two or more species. Of these, 46 localities are situated in Lake Baikal area ($50^{\circ}\sim 60^{\circ}\text{N}$; $103\sim 117^{\circ}\text{E}$) and 73 localities in the Altai Mountains region ($51^{\circ}\sim 60^{\circ}\text{N}$; $84\sim 100^{\circ}\text{E}$). The dates varied from about 34 000 to 10 500 y BP ^{14}C representing the early, middle and latest late Palaeolithic. On the basis of the fossil insect faunal zones in East Siberian Arctic (Sher et al., 2005) the localities dated 34 000 ~ 24 000 y BP, representing the early late Palaeolithic or late middle Weichselian (referred in text as late MW) were correlated to the late Oxygen Isotope Stage 3 (OIS3); 24 000 to 15 000 y BP, representing the middle late Palaeolithic, early late Weichselian or Last Glacial Maximum (referred as LGM) - to early OIS2; and 15 000 to 10 500 y BP representing the latest late Palaeolithic, latest late Weichselian or Late Glacial (referred as LG) - to the late OIS2. Calibrated radiocarbon years are denoted as cal. y BP.

Overall 38 species were analysed. The late MW contains 18 localities with 34 species, LGM - 26 localities with 25 species and LG - 75 localities with 29 species (Fig. 1).

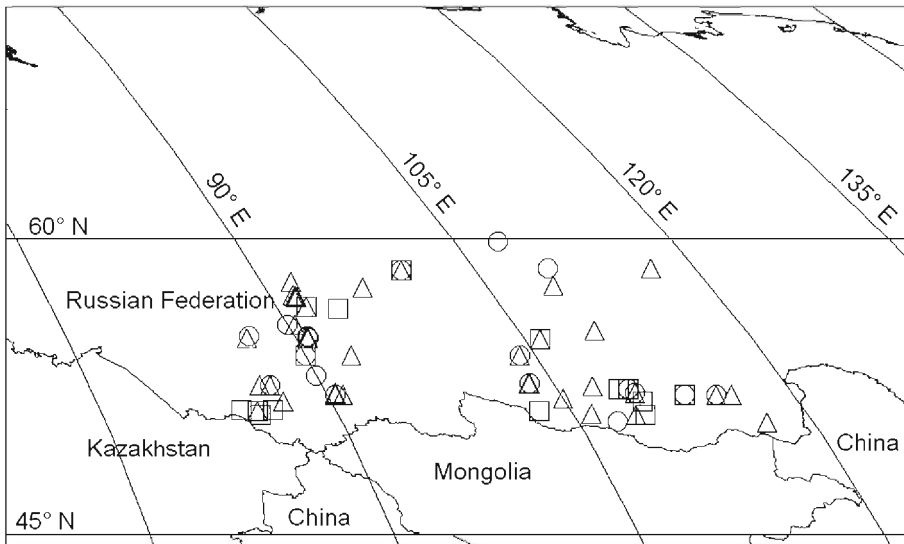


Fig. 1 The study area and localities

The squares represent the early late Palaeolithic or late MW (late OIS3), the circles - the middle late Palaeolithic or LGM (early OIS2), and the triangles - the latest late Palaeolithic or LG (late OIS2)

3 Methods

Molar crown height (hypsodonty), body size and diet for each species were obtained from Nowak (1991) and NOW database (M. Fortelius, personal communication, 2004). Analysis of variance (ANOVA) and post hoc analyses on differences among groups were conducted on all species and only common species. A species was considered common if it was present in 25 and more percent of localities. **Species commonness** was calculated for each time stage dividing the number of localities, where the species occurred by the number of all localities in that stage (Jernvall and Fortelius, 2004).

Hypsodonty class is usually attributed to each species according to the ratio of height to length or sometimes the ratio of the molar width to height (Janis and Fortelius, 1988). A tooth is hypsodont when its height to length or dorsal-ventral to anterior-posterior ratio is higher than 1.2, mesodont when the ratio is between 0.9 and 1.2, and brachydont when the ratio is below 0.9 (M. Fortelius, personal communication, 2004). I follow the classification of Fortelius et al. (2003): high-crowned or hypsodont and ever-growing or hypselodont - class 3, medium-crowned or mesodont - class 2, low-crowned or brachydont - class 1. Increased hypsodonty indicates an adaptation to higher rates of tooth wear experienced in open and dry habitats (Janis and Fortelius, 1988).

The mean hypsodonty value was translated into **precipitation** in mm per year. Mean hypsodonty (H) at a locality divided by the number of the large species is related to mean annual precipitation (P) by the formula $\log_{10}P = -1.27(\log_{10}H) + 1.36$ (Damuth and Fortelius, 2001). The absolute rainfall estimates are regarded as very approximate but the relative difference as significant and it is still possible to detect general trends in the rainfall change in an area (Fortelius, personal communication, 2005). Taphonomic factors can result in low rainfall estimates (Damuth and Fortelius, 2001; Fortelius, personal communication, 2005). Here I compare the LGM precipitation values derived from hypsodonty with precipitation values estimated from other paleoindicators.

Diet for each species was ordinated into the grazers as 1, mixed grazers-browsers as 2, browsers as 3. Instead of the actual body masses the body length was categorised into **body size** classes of 2 - the body length between 10 cm and 1 m; 3 - the length between 1 m and 2 m; 4 - 2 m and 5 m; and 5 - over 5 m.

Dice similarity index was applied to assess taxonomic differences among the Weichselian stages. The Dice index better explains cases where the number of occurrences is considerably less than 50 per cent, which is common in paleontological sparse data (Maples and Archer, 1988). $Dice = 2A / (2A + B + C)$, where A - number of species present in both adjacent intervals, B - species present only in one interval, C - present only in another. The Dice index value of 0.5 is interpreted as two faunas being rich but not similar, more than 0.5 as very similar and less than 0.5 as dissimilar (Maples and Archer, 1988).

4 Results

Mean hypsodonty is shown to decrease from 2.63 in the late MW to 2.38 in the LG (ANOVA $F_{2,578} = 5.99$, $p = 0.003$) (Fig. 2A). The LG is significantly different from the late MW (post hoc Tukey HSD, $p = 0.009$) and the LGM ($p = 0.032$). The same trend is seen in the common species, only their hypsodonty descent is stronger from 2.66 to 2.19 ($F_{2,395} = 13.95$, $p < 0.001$). The LG differs from the two previous stages (post hoc both $p < 0.001$). The rare species response is not statistically significant ($F_{2,145} = 1.92$, $p = 0.151$) (Fig. 2B).

Hypsodonty and derived rainfall values changed along a latitudinal gradient ($F_{2,4654} = 7.59$, $p = 0.001$, post hoc hypsodont from mesodont ($p = 0.009$), from brachydont ($p =$

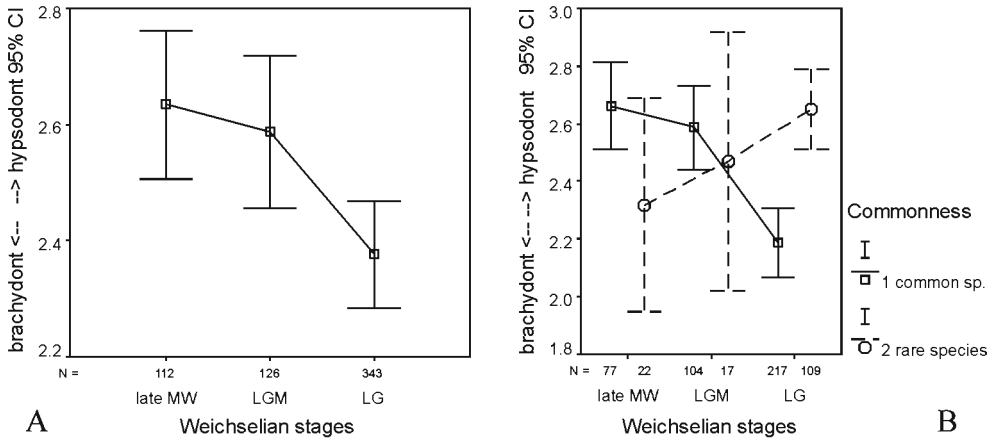


Fig. 2 Mean hypsodonty in all species (A) and in common vs. rare species (B)

Mean hypsodonty in all species declines between late middle Weichselian and Late Glacial; mean hypsodonty in common species shows a decreasing trend between late MW and LG, while in rare species an increasing trend

0.001)).

Hypsodont species were distributed further in the south, which is more elevated, as shown by a negative correlation between hypsodonty and latitude ($r_p = -0.131$, $p = 0.001$, $N = 657$).

In terms of **rainfall** the hypsodonty values indicate an increase from approximately 245 to 330 mm per year between the late MW and LG, producing a difference in about 100 mm. Hypsodonty value for the maximum Weichselian cooling (LGM) of the Altai-Baikal region is the same in all and in common species. Translated into precipitation it produces 256 mm/year, crudely between 200 ~ 300 mm per year. These values indicate rather dry climatic conditions close to desert or mountainous landscape. In common species a more dramatic rainfall increase is estimated, from 237 to 411 mm/year. The precipitation value of the LG matches the precipitation of the middle taiga forest or forest-steppe, and suggests that the common species responded faster to changing environments.

Dietary preferences shifted slightly from grazing to browsing into the Late Glacial (ANOVA $F_{2,552} = 7.69$, $p = 0.001$) (Fig. 3A). Significant differences in diets exist only between the LG and the two previous stages (post hoc tests Tukey HSD $p = 0.014$ between late MW and LG, $p = 0.002$ between the LGM and LG). This change is more pronounced in the common species ($F_{2,395} = 14.79$, $p < 0.001$, post hoc $p \leq 0.001$ both) (Difference between the common and rare $F_{2,520} = 12.91$, $p < 0.001$). The rare species show an opposite trend ($F_{2,125} = 3.66$, $p = 0.029$). Only the last stage is close to be significantly different from the LGM (post hoc $p = 0.065$) (Fig. 3B).

Mean body size does not change significantly in all species during the late Middle and Late Weichselian. Common and rare species have different trends (ANOVA $F_{2,650} = 12.33$, $p < 0.001$). The body size of the common species declines into the LG ($F_{2,432} = 6.19$, $p = 0.002$, post hoc Tukey HSD between the late MW and LGM ($p = 0.072$), the LGM and the latest period ($p = 0.003$)). An apparent rise into the LGM is not significant. The rare species body size increases into the LG ($F_{2,218} = 5.27$, $p = 0.006$). The LGM body size also differs only from the latest period (post hoc $p = 0.006$) (Fig. 4).

The **species composition** is very similar among the Weichselian stages, and similarity tends to increase into the latest stage despite that it is subject to substantial change due to small

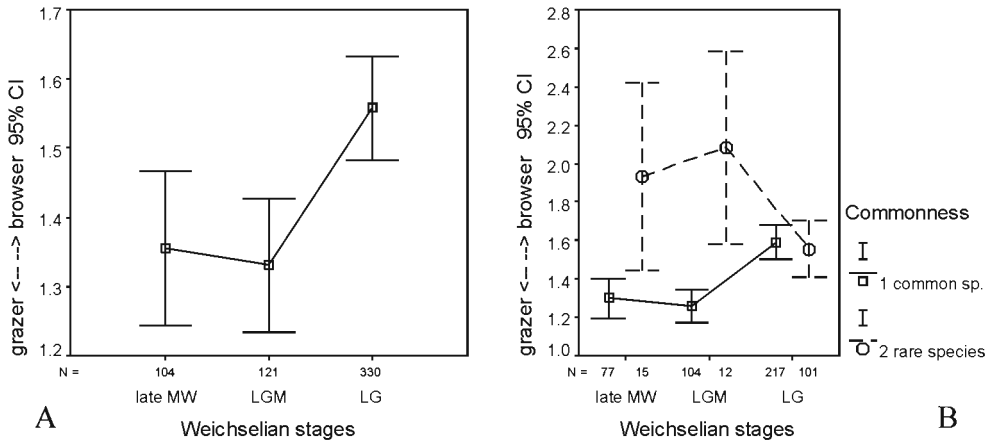


Fig. 3 Mean dietary preferences in all species (A) and in common vs. rare species (B)

Mean diet shifts towards browsing between late middle Weichselian and Late Glacial in all species and in the common species; difference between late middle Weichselian and LGM is not significant; in the rare species mean diet shifts towards grazing

numbers. The **Dice similarity** index is $D = 0.8$ between the late MW and LGM, and $D = 0.9$ between the LGM and LG. The latter two stages show similarity due to the absence of many rare species (frequency of one, small mustelids, felids). Carnivores added the most change. Without them the Dice index produces the same values. Similarity among the common species, which are mostly ungulates, decreases ($D = 0.8$ and 0.6) due to the drop of the mammoth *Mammuthus primigenius*, woolly rhinoceros *Coelodonta antiquitatis* and kulan *Equus hemionus*. Without the common carnivores – arctic fox *Alopex lagopus*, red fox *Vulpes vulpes* and wolf *Canis lupus* it is $D = 0.9$ and 0.7 , respectively.

Mean locality coverage and species commonness varies in time from the late MW to the LG. Only 5 ungulate species - the steppe bison *Bison priscus*, reindeer *Rangifer tarandus*, red deer *Cervus elaphus*, mouflon *Ovis ammon*, horse *Equus caballus* (*E. ferus*) are present in more than 25% of localities during all stages. The woolly rhinoceros, woolly mammoth and kulan are common during the first two stages (Fig. 5).

Although the proboscideans (the mammoth) and perissodactyls (the woolly rhinoceros and horses) are very common their commonness steadily declines from the late MW to LG. Concurrently, an overall declining trend is observed in other ungulates (the mouflon, red deer, Siberian ibex *Capra sibirica*) and carnivores (the brown bear *Ursus arctos* and red fox) in Altai and Baikal region. In addition, Baikal yak *Poephagus baikalensis*, Spiral horn antelope *Spirocerus hiakhtensis*, Mongolian gazelle *Gazella gutturosa*, giant deer *Megaloceros giganteus*, hyena

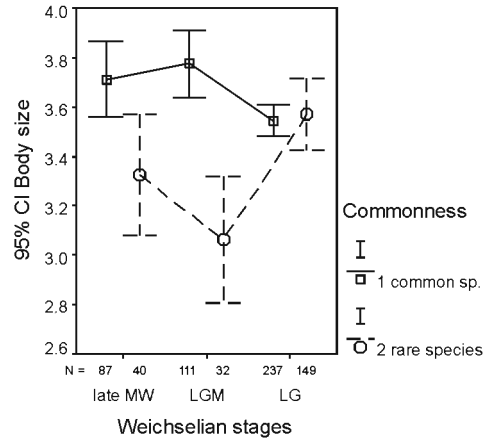


Fig. 4 Mean body size in common and rare species. Body size in common species shows an overall decreasing trend between late MW and LG, while rare species show an overall increasing trend with a drop during the LGM

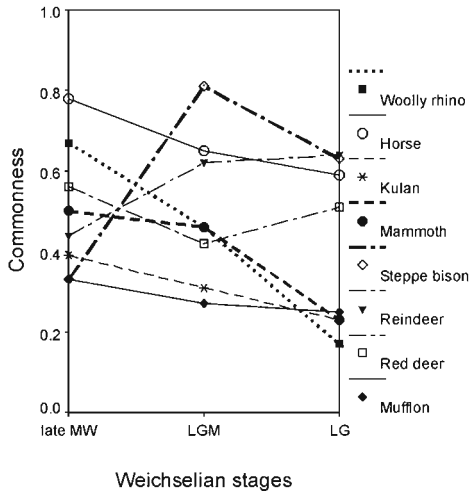


Fig. 5 Changes in mean locality coverage (species commonness) of the most common herbivore species in the late Palaeolithic localities

as the same species), moose *Alces alces*, saiga antelope *Saiga tatarica*, aurochs *Bos primigenius*, arctic fox and, probably, wolverine *Gulo gulo*. The wolverine is rather infrequent. On the contrary to many species experiencing a depression in commonness during the LGM the bison, reindeer, arctic fox and wolverine show increasing commonness. In the following stage the bison and arctic fox commonness falls but not below the late MW.

The musk ox *Ovibos moschatus* and cave bear *Ursus spelaeus* are probably not present in the late Palaeolithic localities of Altai and Baikal regions at all.

5 Discussion

5.1 Hypsodonty, diet and body size

Both a high hypsodonty index of the large mammal species and many grazing herbivores in southern Siberia throughout the late MW to LG indicate a rather dry environment with open habitat and a continental climate. The reason for this is the situation of the study localities in Altai and around Lake Baikal in a mountainous landscape with assorted steppe vegetation. Dry steppe patches still linger in the Altai Mountains and on gentle slopes and valley bottoms in the Transbaikalian area (Sher et al., 2005). During the Weichselian Glaciation southern Siberia was covered by montane subarctic desert along with periglacial steppes and refuge forests at lower than 1 000 m mountain area (Grichuk, 1984; Frenzel et al., 1992; Blyakharchuk et al., 2004). The mammals of the mountainous regions are often ecologically and morphologically adapted to severe climatic conditions like the tundra-steppe, e. g. Tibetan Plateau mountain desert (Baryshnikov and Markova, 1992). In Eastern Eurasia the species of the cold-adapted *Mammuthus-Coelodonta* complex are divided into two associations, a more cold-adapted arctic association in the north and a boreal association in the south, characterised by the musk ox absence (Baryshnikov and Markova, 1992). The mammals of the study area represent the boreal association on elevated drier landscapes.

During the late MW and LGM eco-morphological features of large mammals were similar to each other. This similarity is consistent with the recent data from the East Siberian Arctic,

Crocota crocota and cave lion *Panthera leo* also become less common although there are fewer occurrences. The giant deer is extremely rare.

Among carnivores only the wolf is common during nearly all stages. Its commonness decreases to 19% during the LGM. In contrast the arctic fox is common only during the LGM. The red fox, brown bear and hyena are rather common during the late MW.

The rareness during the LG can be explained by the presence of many sites with a small number of species, which produce low mean locality coverage ($r_p = -0.205$, $p = 0.025$). For example, the LG contains 14 localities with 2 species in comparison to 2 localities in the LGM and one in the late MW.

Quite the opposite increasing trends in commonness are seen in the bison, reindeer, roe deer (*Capreolus capreolus*, and *C. pygargus* listed in some localities but treated

where no major climatic or vegetation fluctuations occurred during the assumed Karginskij interstadial (OIS3) to actually signify its existence (Sher et al. , 2005). The whole middle Weichselian (OIS3) was highly continental, and the LGM was an impoverished cold variant of the late MW (Sher et al. , 2005). This faunal resemblance is also suggested in European Russia where the faunal composition was not much affected by the assumed Bryanskij interstadial, equivalent to the Karginskij in Siberia (Markova, 1984).

However, during the LG the large mammal data imply a considerable environmental change that started in southern Siberia. Decreasing hypsodony and the shift towards browsing, more obviously portrayed by the common species, suggest that environment was becoming more humid and, probably, forested after the LGM as a consequence of the LG warming. Former steppe landscapes in southern Siberia gradually transformed into closed forests at altitudes below 2 100 m and into high mountain tundra and shrub above 2 100 m most significantly between 11 500 ~ 9 500 cal y BP (Blyakharchuk et al. , 2004).

The decline in body size of the common mammals suggests a response to warming and a possibility of temporal application of Bergmann's rule, where mammals with a wide distribution should be smaller in warmer areas. Also Guthrie (2003) showed that Alaskan horses experienced body size decline prior to their extinction at the end of the last ice age. The Younger Dryas (YD) cooling is not apparent in the mammal response as the data in this case do not provide high temporal resolution. In Europe the warming that could have continued after the LGM was set back because the YD cooling event was more profound in Europe. In the gradually transforming southern Siberia the climate and mosaic vegetation were not affected much by the Younger Dryas cooling (Blyakharchuk et al. , 2004).

The Late Glacial replacement of rather dry and cold conditions that remained in southern Siberia during the middle and late Weichselian led to the demise of the *Mammuthus-Coelodonta* fauna. Precipitation increase was suggested as one of the main causes for this demise because large glacial species required low precipitation and low temperatures, and would not survive a thick winter snow cover or softening of substrata (Kvasov, 1977; Tormidiaro, 1977; Vereshchagin and Baryshnikov, 1985). The warming was also suitable for human populations and enabled their dispersal northward.

5.2 Precipitation values from hypsodony versus other paleoindicators

Hypsodony increased with altitude indicating that precipitation decreased. The rainfall values obtained from hypsodony indicate desert conditions in the European part of Russia while in southern Siberia (Transbaikal region) it indicates the middle taiga larch forests with steppes and mountain tundra (Savina and Khotinsky, 1984).

According to published maps (Velichko, 1984; Frenzel et al. , 1992) there was no deviation in mean rainfall values between the late MW and LGM in the study area. During the LGM the mean annual rainfall was 350 mm per year (Velichko, 1984). The rainfall values for the LGM obtained from hypsodony are different – 256 mm/year. However, absolute values are not critical but rather the hypsodony data predicts a general trend in southern Siberia. These variations in precipitation value predictions can mean that deviations are greater in the elevated areas. The LGM supposedly deviates in rainfall from contemporary time by -100 mm to -250 mm (Frenzel et al. , 1992). Present rainfall values vary for Lake Baikal region from 495 mm/year in the south to 258 mm/year in the north (<http://www.irkutsk.org/baikal/climat.htm>), and in Altai region from 460 mm/year to 271 mm/year, respectively (Blyakharchuk et al. , 2004). Therefore, the LGM rainfall value should vary for Baikal area from 395 ~ 245 mm/year in the south to 158 ~ 8 mm/year in the north, and for Altai from 360 ~ 210 mm/year in the south and 171 ~ 21 mm/year in the north. The precipitation values derived from hypsodony are comparable with the precipitation values derived from other paleoindicators although deviation between

them might be increasing with altitude. As such the rainfall estimations obtained from hypsodonty in the elevated landscape might be less humid than expected. However, this relationship is not straight forward and further research is needed to investigate it.

5.3 Commonness

Species commonness variation in the late Palaeolithic localities used here can reflect not only environmental trends but also species that were more utilised by humans. Human occupation of Central Asian mountains was continuous from the middle Pleistocene to the Holocene, and was shifted northwards during the LGM by an increased aridity in Central Asia (Madeyska, 1992).

The drop in commonness of many species during the LGM is consistent with the study in East Siberian Arctic by Sher et al. (2005). Sher et al. (2005) noticed that the populations' numbers were lowered and true steppe species were eliminated from the fossil record because the LGM conditions were less favourable for grazers, yet not intolerable. Sher et al. (2005) described the mammoth and bison decline in the East Siberian Arctic populations during the LGM as abrupt for the mammoth, while delayed for the bison. However, both species rose during the LG (Sher et al., 2005). In southern Siberian late Palaeolithic sites the mammoth demise into the LG was continuous and could be related both to deterioration of ecological conditions and human interactions. The species retreated northwards (Sher, 1997; Vasil'ev, 2003).

According to this study the only successful and more intensely hunted species during the coldest Weichselian period were the bison, reindeer, arctic fox and, possibly, wolverine. The bison and arctic fox were less common during the LG, correlating with an increased stress on their populations by humans. Furthermore, a deterioration of favourable conditions, to which both species were best adapted in southern Siberia, occurred during this period. This study depicts the steppe bison commonness already during its genetic decline started at 37 000 y BP ^{14}C (Shapiro et al., 2004) but still caught the variation in commonness, namely lower coverage at the late MW and higher at the LGM that could reflect past demographic signals. Some sufficient ecological stress that decreased the bison population (Shapiro et al., 2004) could be related to its increased occurrences in the archaeological sites. The combination of the hunted ungulates and carnivores during the late Palaeolithic varied in different parts of Siberia (Vasil'ev, 2003) but the extinct steppe bison was the major game animal throughout Siberia.

The commonness value for the wild horse and kulan, presented in this analysis, decreased throughout the late MW to LG, which is congruent with Sher et al. (2005), where they point out the fact that horses enigmatically did not rise during the LG. The saiga antelope numbers are small but still consistent with Sher's observation of a decline during the LGM and increase during the LG.

A difference in commonness patterns between the horse and the bison in the late Palaeolithic localities is intriguing and implies both differences in human preferences and in food consumption strategy, even though both are grazers and members of the mammoth glacial fauna. Artiodactyls are more efficient digesters and can live longer in areas with short food supply (McDonald, 1989). Extinct hind-gut fermenters like horses were more susceptible to nutritional stress in the Holocene biomes (mosaic nutrient model) because they needed a greater diversity of forage types than ruminants (Guthrie, 1984), the surviving herbivores of which (e. g., bison, deer) had very homogeneous diets (Barnosky et al., 2004).

Horses seem to have been less adapted to the fragmentation of tundra-steppe mosaic (Sher et al., 2005) than the bovids and cervids, numerous species of which survived despite the human impact. However, the large mammal species responded individualistically to the late Pleistocene environmental changes (Guthrie, 2003). Horses survived in north-eastern Asia (Vasil'ev, 2003), possibly owing to decreasing human procurement.

Overall, the large species that went extinct during the late Weichselian or early Holocene decreased in commonness during the LG, except for the aurochs that survived well into the later Holocene. These large extinct species were heavily relied on in human subsistence activities (Vasil'ev, 2003), and only the hunted deer, except the extinct giant deer, are still successive.

The causes of the Late Pleistocene extinctions have been hotly debated during the past years. In Northern America they are suggested to be a result of human overexploitation (Alroy, 2001; Barnosky et al., 2004), while in Northern Eurasia they are believed to be a result of rapid environmental changes towards more humid and forested (Tormidiaro, 1977; Kvasov, 1977; Vereshchagin and Baryshnikov, 1985; Sher, 1997). Under these circumstances the Northern Eurasia mammal populations were severely stressed and their decline was initiated prior to the presence of large populations of humans (Shapiro et al., 2004).

Thus, humans are not implicated directly although the earliest modern human occupation is recorded for southern Siberia at 43 ~ 39 000 y BP ^{14}C , prior to the bison genetic decline, and the human populations were increasing considerably to occupy all of northern Asia by 13 000 y BP ^{14}C (Vasil'ev et al., 2002). Human overexploitation could stress the declining mammalian populations in southern regions and accelerate their extinction. Perhaps, the difference in species commonness between archaeologically and paleontologically associated localities will shed a light on this paradigm.

6 Conclusions

The abundant large mammal fossil record from the late Palaeolithic localities in southern Siberia offers a means of seeing trends in the changing paleo-environment via eco-morphological changes, especially in common taxa. Decreasing hypsodonty and body size of common species and the shift in their diet from grazing towards browsing suggest that environment was becoming more humid and forested during the LG as a consequence of the warming.

Hypsodonty increased with altitude whereas precipitation decreased. The precipitation values derived from hypsodonty are comparable with the precipitation values derived from other paleoindicators, although the deviation between them might be increasing with altitude.

A considerable environmental change that influenced the demise of the cold-adapted *Mammoth-Coelodonta* fauna was initiated in southern Siberia after the LGM. Different trends in commonness between the mammoth and perissodactyl species, on one hand, which steadily declined from the late MW to the LG, and artiodactyls, on the other, can probably be associated with human exploitation as well as different response in digestive strategies and is consistent with their late Weichselian or Holocene extinction or survival. It is possible that regionally human overexploitation added to the stress of the declining mammalian populations even more to lead quicker to their disappearance from southern Siberia and to their extinction in Northern Eurasia, since human populations were rapidly expanding in area and numbers.

Although mammalian communities showed the general trends the response to environmental change was not necessarily the same in individual species. Further work on morphological and ecological characteristics within species will be valuable to demonstrate and understand the relationship between these features and changes in environment.

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