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The Dynamics of Bioresources and Activity of the Paleolithic Man, Using the Example of Northwestern Altai Mountains

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Abstract—Long-term studies of living and fossil mammals of the Altai Mountains (= Gornyi Altai) revealed the pattern of the dynamics of small mammal communities in this region in the second half of the Pleistocene, in the Holocene, and the present time. The fossil fauna of the Anui River valley differs significantly from the modern one. The Pleistocene fauna of Paleolithic sites reflects a considerably more diverse biotopic situation and high landscape diversity compared with the present time. This diversity depended on a stronger role in the communities of steppe and highland elements. The influence of Paleolithic man on Late Pleistocene populations of ungulates and large predators is detected.

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Key words: Bioresources, mammals, Paleolithic Man, Late Pleistocene, Holocene, Recent, Altai Mountains.

INTRODUCTION

Today, faced with increasing economic activity and technological impact on natural resources, it is very important to get an insight into the trends of natural environmental transformations and human influences on it, in order to estimate possible consequences of such an influence. One of the sources of this information is the study of mammals in archaeological sequences, widely applied in both paleontology and archeology. As early as the 1930s Pidoplichko (1929, 1934, 1936a, 1936b, 1938) published a series of works devoted to small mammals from Paleolithic sites of the Dnieper River area. Later studies of Paleolithic sites were usually accompanied by investigations of the mammal fauna, including small mammals (Gromov, 1953, 1957, 1961; Aleksandrova and Tseitlin, 1965; Sukachev et al., 1966; Gromov and Fokanov, 1980; Agadjanian, 1982). Similar studies were conducted in Poland, Hungary, the Czech Republic, Germany, and France (Jánossy, 1963, 1964, 1970, 1976; Fejfar, 1971; Heller, 1971; Tobien, 1971; Chaline, 1972; Storch, 1973; Koenigswald, 1974; Kowalski and Nadachowski, 1982; Rzebik-Kowalska, 1982; Sych, 1982; Kowalski, 1990).

MATERIAL

The area studied is located in the western part of the Altai Mountains, in the middle and upper reaches of the Anui River. It is an eroded–denuded upland, ranging from 500 to 2300 m above sea level. Altitudinal zonation of vegetation and small mammals is marked in this area. The mountain slopes are mainly covered with taiga forests. River valleys mostly contain meadow–steppe associations. Communities of the nival type occur at elevations above 1800 m.

The composition and structure of modern vegetation, mollusks, and small mammals have been studied for more than ten years. Standard census trapping methods are used for mammalian studies. Mammals were collected from Paleolithic sites of the closed (Denisova cave) and open types (Ust'-Karakol, Anui-3, and others). The entire volume of excavated ground was hand sorted, then subjected to water maceration and screen-washed on sieves of 1 mm cell size. A total of more than 57 thousand bones were determined.

The data on the fossil material have been partly published (Ivleva, 1990; Ovodov and Ivleva, 1990; Germonpré, 1993; Derevyanko and Molodin, 1994; Vasil'ev and Grebnev, 1994; Agadjanian, 1998; Derevyanko et al., 1998; Shun'kov and Agadjanian, 2000; Agadjanian and Shun'kov, 2001). However, these works are far from covering all the results obtained. The present paper is aimed at filling this gap.

RESULTS

Modern Mammal Fauna of the Anui Basin

At present, the drainage basin of the Anui River is well developed by man. Only sites of bald mountains composed of granites are not affected by economic activity. However, due to the specific economic features of the human population of the Altai Mountains, the use of natural resources does not lead to a significant disturbance of local ecosystems. This leads to the ecological balance of humans and nature and preserves many natural systems in almost virgin condition.

The bottoms of valleys and all terrace levels are used for agricultural crops. The only large mammals are livestock, mainly dairy cattle *Bos*. The herbage–covered slopes of mountains are used for pasture and, in parts, as hayfields. The majority of large mammals here are sheep *Ovis ammon*, horses *Equus caballus,* and beef cattle *Bos*. The moderate load on these sites preserves pastures, and their vegetation remains close to natural meadows. Apparently, the general appearance of the modern biota of open slopes is close to that of the Early Holocene one when large mammals were mostly represented by the primeval bison *Bison priscus*, the wild horse *Equus caballus*, and the small caprines *Ovis* and *Capra*.

This territory has a particular taiga animal assemblage. As throughout northwestern Altai, deer-farming of Siberian red deer (maral) for antlers is an important branch of agriculture. Hundreds of square kilometers of taiga-covered slope have been withdrawn from economical land use and are managed as maral farms. These are protected areas, comparable in conservation conditions to the state nature reserves. These lands are formally included in the economic circulation, but, in fact, their vegetation and animal population correspond to natural assemblages of the taiga zone of the Altai Mountains. As in the whole Upper Pleistocene and Holocene, the prevailing species is the maral *Cervus elaphus maral.* At present, it is the largest and most numerous herbivore in the Altai taiga from the valley of the Charysh River in the west to the valley of the Abakan River in the east. The second, no less characteristic large mammal is the roe *Capreolus pygargus.* According to our observations, this species populates the slopes covered by larch–birch forests near Denisova cave and along the Shinok River valley and similar biotopes at Kaminnaya cave and in larch forests along the Tyumechin valley. It is a characteristic element of the taiga zone of the Altai Mountains. The third herbivore is the musk deer *Moschus moschiferus.* It occurs at rocky outcrops, rocks, and stone shelters. Traces and droppings of musk deer are found at the top of the Karakol Mountain above Denisova cave, in the area of Kaminnaya cave and in other places of the Anui basin. The only wild caprine in the modern fauna of the area is the Siberian goat *Capra sibirica.* The habitats of this species include rocky outcrops, open steppified slopes, and mountain ridges.

The wolf *Canis lupus* is a common large predator. The bear *Ursus arctos*, a typical representative of the taiga fauna of the Altai Mountains, is rather rare. Traces and droppings of bear were found in at the top of Karakol Mountain and along the Shinok valley. The woodlands are ubiquitously inhabited by the badger *Meles meles* (L.). Its paths and burrows are encountered near both Denisova and Kaminnaya caves. The badger is a frequent prey of local hunters. The sable *Martes zibellina* (L.) and marten *Martes martes* (L.) are the commonest smaller mustelines. The floodplains and screes are populated by the ermine *Mustela erminea* L. and the weasel *Mustela nivalis* L. The steppified sites of terraces with colonies of ground squirrels are populated by the Siberian polecat *Mustela (Putorius) eversmanni* Lesson. The Siberian weasel *Mustela (Kolonocus) sibiricus* Pallas is common, we caught one in a zokor borrow.

The study of the modern fauna shows the pattern of altitudinal zonation and the structure of the small mammal community in the Anui drainage basin, and their connection with certain types of vegetation. In the area of study, these are floodplain–meadow, meadow–steppe, larch–birch, birch–pine, cedar pine, subalpine moss–shrub, mountain–steppe petrophilous, and nival sedge–grass associations. The spatial distribution of the listed types of vegetation is connected to the absolute elevation, position on the relief, slope aspect, soil cover, and other factors. Each of the listed floral associations hosts the following types of small mammal associations: (1) the root vole and ruddy vole association in the floodplain–meadow biotopes; (2) the field mouse and common vole association in the meadow–steppe biotopes; (3) the field vole and ruddy vole association in the larch–birch forests; (4) the wood mouse and ruddy vole association in the birch–pine forests; (5) the ruddy vole association in the cedar pine forests; (6) the narrow-skulled vole and ruddy vole association in the moss–shrub subalpine biotopes; (7) the flat-skulled rock vole in the petrophyte mountain–steppe biotopes; and (8) the narrow-skulled vole association in the sedge–grass associations of highlands. Each of these associations is distinct in the composition and ratio of small mammal species.

To summarize, the Anui valley is predominantly populated by small mammals of the taiga association. In the vicinity of Denisova cave, this fauna dominates in both the area occupied and number of species. Meadow communities play an inferior role. Steppe associations are currently absent in this area. However, individual steppe species sporadically occur in communities of meadow landscapes and agricultural ecosystems.

For a better understanding of taphonomic processes under modern conditions of the northwestern Altai Mountains near Denisova cave, a ten-year-long study of regurgitated pellets of modern birds of prey, droppings of predatory mammals, and modern deposits of numerous niches, grottoes, and fissures was conducted. The comparison of the results obtained with the data on trapping censuses shows discrepancies added on the way from ecosystem to thanatocenosis.

The analysis of 140 kite pellets has shown that the association is dominated by remains of the common vole *Microtus arvalis* (Pallas) (35.5%). The proportions of other species are much lower. The ground squirrel *Spermophilus undulatus* (Pallas) and the mole *Asioscalops altaica* (Nikolsky) compose about 4% each. Shrews, mostly *Sorex araneus* L., make 7%. The share of the ruddy vole *Clethrionomys* is only 3.5% of the total rests. The zokor *Myospalax myospalax* (Laxmann) amounts to about 5% of remains. Mice and the Baraba

Table 1. Absolute dating of Pleistocene deposits of Denisova cave (Derevyanko et al., 1998)

	TL dates	^{14}C dates
Bed 11		>37335 (SO RAN-2504)
Bed 14	69 ± 17 ka (RTL-611)	
Bed 21	155 ± 31 ka (RTL-546)	
Bed 22.1	171 ± 43 ka (RTL-737), 182 ± 45 ka (RTL-738), 223 ± 55 ka (RTL-739), 224 ± 45 ka (RTL-547)	
Bed 22.2	282 ± 56 ka (RTL-548)	

(or Dahurian) hamster *Cricetulus barabensis* (Pallas) do not exceed 0.7% each. The pellets contained remains of the Norway rat *Rattus norvegicus* (Berkenhout) (2.1%), the water vole *Arvicola terrestris* (L.) (0.7%), and the common hamster *Cricetus cricetus* (L.) (0.7%). These three species add to the list of the modern fauna of the Anui Valley established by trapping. The Norway rat is connected with human buildings. The water vole, judging from its feeding stations, extensively inhabits the floodplain of the Anui and Karakol rivers. However, its numbers are low everywhere, which is also supported by the pellet material. The common hamster, as in other areas of Altai, is very likely confined to cultivated fields.

Two main conclusions are obvious on the basis of the data presented. First, the water vole, common hamster, and Norway rat should be added to the list of the modern fauna of the Anui valley. The quantitative ratios of small mammal species derived from pellets of predators do not directly reflect proportions in the wild (Gromov, 1957b; Kowalski, 1990). Birds of prey have a hunting selectivity and prefer forms of open biotopes. Species that inhabit meadows, forest margins, and glades are over represented in their pellets. The species living under the forest canopy and in shrub thickets are under represented in comparison with their actual proportions in nature.

Pleistocene Mammal Fauna of the Anui Basin Based on the Material of Paleolithic Sites

Paleolithic Site Denisova Cave

Denisova cave is located in the Soloneshskii District of the Altai Region, Russia, 1.8 km below the mouth of the Karakol River on the right bank of the Anui River valley. The cave's entrance is 28 m above the shore line of the Anui River. The cave is a karst cavity in Silurian limestone. The central hall is about 10 m high from the surface of the Holocene deposits. The depth of the bedrock floor in the central part is about 6 m. The Holocene deposits vary slightly in thickness along the strike, being on average 1.5 m thick. The Pleistocene deposits are about 4.5 m thick.

Table 1 shows the radiocarbon (^{14}C) and termoluminiscence (TL) dates of the Pleistocene part of the Denisova cave section.

Figure 1 shows the proportions of animal taxa identified in the material collected in 1995 in squares E-5 (subsquares a, b, c, d), E-6, E-7, E-8 (subsquares b and d), and E-9 (subsquares b and d) of the central hall (sector 4) of Denisova cave. The total list of taxa determined in the Pleistocene sequence of excavated squares of Denisova cave includes 50 taxa. Forty-three of them are small mammals. Quantitative analysis of horizontal and vertical distribution of bone remains and frequency of different taxa in the material collected in 1995 suggests a number of conclusions.

Notwithstanding the general uniformity of small mammal communities, the extensive material enables a recognition of a certain pattern of changes in the ratios of particular taxa.

Bats, Chiroptera, are the only component of the taphocenosis that demonstrates dramatic changes in abundance. In Bed 22, their relative quantity changes from 14.5% at level 3 to 63.8% at level 13. In Bed 21, the proportion of bats declines to 9.9%. Further up the section, it varies within the range of 3–6.6% till Bed 17; in the upper part of the section, they compose less than 3%. These data confirm the earlier noted trend, making it more reliable.

The greatest number of determinable specimens and the highest diversity of bats is in Bed 22. At the boundary of beds 22 and 21, both the absolute number and species diversity of Chiroptera sharply decrease. The upper member of the Pleistocene sequence (beds 13 to 9) is also poor in fossil Chiroptera. In general, the composition of the fossil bat fauna is close to the modern one. The majority of recognized species presently inhabit the forest zone of temperate latitudes. Only the lesser mouse-eared bat *Myotis* aff. *blythi*, a common element of the taphocenoses of Denisova cave, occupies both humid and arid landscapes from the Mediterranean to southern Kazakhstan (*Mammals*… 1999). It is remarkable that this species is found in the upper part of the Pleistocene sequence of Denisova cave.

The lower part of the Pleistocene sequence of Denisova cave, level 13 of Bed 22.3, is marked by relatively high numbers of red-backed voles (5.6%), zokor (14.5%), and flat-headed voles (15%). At level 12 of Bed 22.3, these species are nearly half as numerous. The same tendency is observed in the material collected in 1994. At level 10 of Bed 22.2, *Clethrionomys* and *Alticola* increase in number to 10 and 9.4%, respectively, while the proportion of *Stenocranius* decreases to 3.1%. This bed is characterized by an increase in the number of shrews and the Baraba hamster. Levels 9–2 of beds 22.2 and 22.1 show stable proportions of small mammal taxa. Red-backed voles, flat-headed voles (*Alticola*), and *Stenocranius gregalis* compose about 5–6,

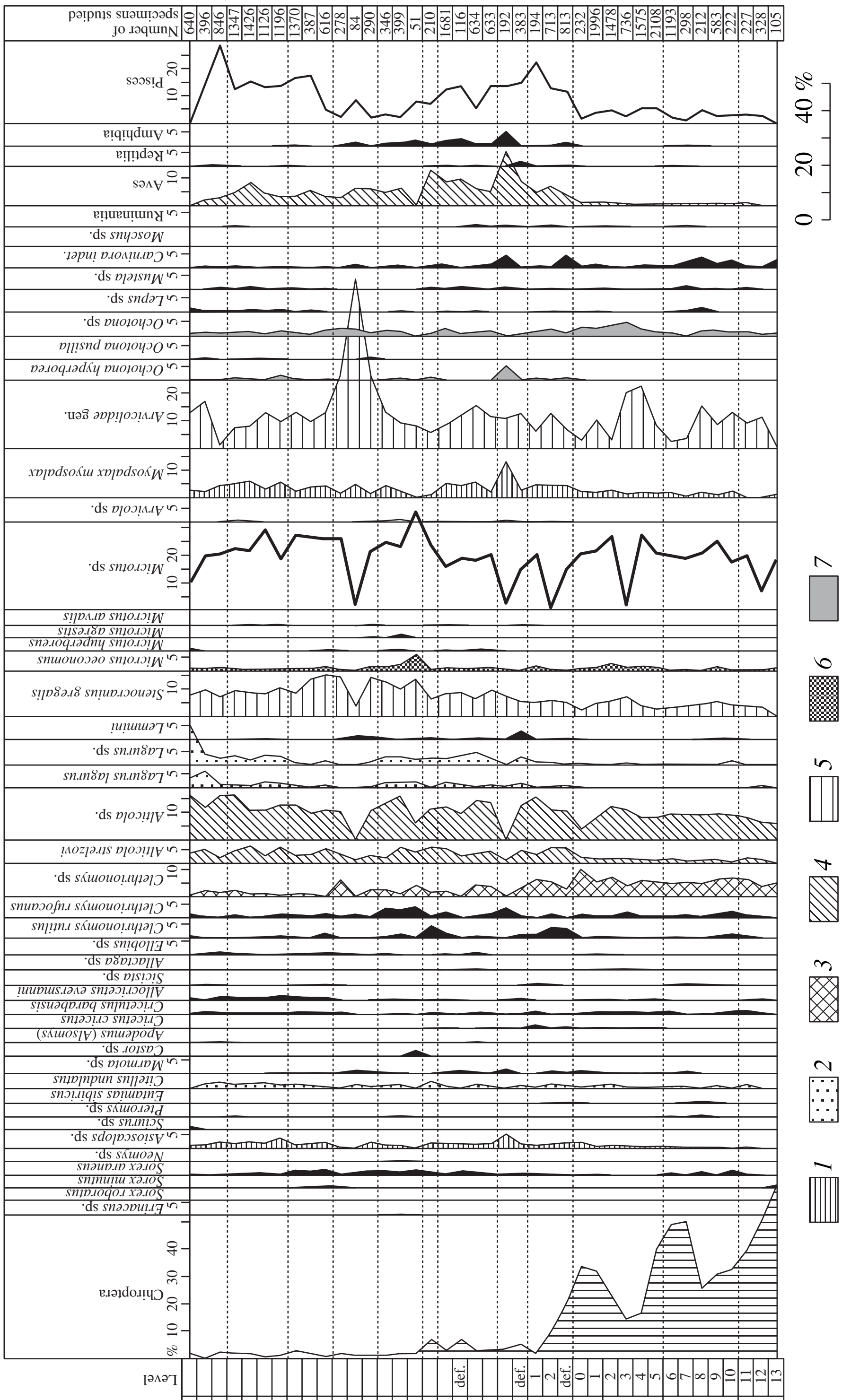

Fig. 1. General composition of small vertebrates in Pleistocene deposits of the central hall (sector 4) of Denisova cave, collected in 1995: (*1*) subterranean animals, (*2*) steppe species, (*3*) mammals of forest biotopes, (*4*) nival species, (*5*) species of highland meadows; (*6*) mammals of riparian biotopes, and (*7*) petrophilous species.

8–10, and 3–5%, respectively. Hamsters and shrews are common in these beds. The proportion of zokor varies from 0.6 to 1.8%. Pikas are relatively common. Birds, on the contrary, are very rare. Moles are rare (0.3–0.6%). The material collected in 1994 shows a similar picture. The exception is bats, with a local peak at levels 7 and 6 of Bed 22.2.

From level 1 of Bed 22.1, voles decrease in number, while zokors increase to 1.8%. The numbers of hamsters slightly increase.

Level 0 of Bed 22.1 shows the highest proportion of *Clethrionomys* (11% of specimens) and a certain increase in the proportion of moles. At the same time, it shows a decrease in the proportion of *Alticola* to 3.8%, very low number of *Lagurus,* and a decrease in the proportion of *Stenocranius gregalis.*

In general, it is possible to assume that beds 22.3–22.1 were formed under warm and moderately humid conditions. Forest associations were dominant in the Anui valley. The final accumulation stage of Bed 22 coincided with the greatest area of forested sites. The material collected in 1994 confirms this conclusion.

From the top of Bed 22.1, the number of bats sharply decreases, while red-backed voles decrease in number from Bed 21.2. The proportion of *Alticola*, after a minimum in Bed 20, on the contrary, grows to 17.7%, and the proportion of *Stenocranius gregalis* increases to 19.3% in Bed 19.3. *Lagurus* begins to play a notable role. The proportion of zokor slightly increases.

In the composition of the taphocenosis, Bed 20 is sharply dissimilar to the other beds. It lacks ground squirrels, shows a reduced proportion of red-backed voles, and *Alticola* and *Lagurus* almost disappear, although the proportion of *Stenocranius gregalis* is retained at the level of 7.2%. At the same time, Bed 20 is characterized by the highest proportion of mole (5.2%) and zokor (13.0%). It is this bed that shows the highest abundance of birds (19.7%). Apparently, Bed 20 was formed under special climatic and biotopic conditions. This period witnessed a simultaneous reduction of forested areas and mountain–steppe petrophilous associations, while meadow–steppe associations and larch–birch forests reached the maximum development. This was the time of meadow and forest herbage with minimum participation of gramineous plants. The climate was characterized by warm winters and wet summers.

Upward in the section, the basic small mammal groups restored their initial proportions and remained relatively stable to the boundary of beds 17 and 14. Thus, the proportion of *Clethrionomys* changed within the range of 5–7%; *Alticola*, 12–20%; and *Lagurus*, from 3.5–4.8%. Bed 14.3 is an exception with reference to the proportion of *Alticola*, which decreases to 9.8%. At the same time, red-backed voles and *Stenocranius gregalis* retained average values of 7.8% and 3.9%. The root vole (*Microtus oeconomus*) shows its maximum proportion (5.9%). On the contrary, moles, zokors, ground squirrels, and pikas completely disappear. This is probably connected to a swamping over of the territory, although this condition is difficult to imagine in the mountainous relief. An alternative explanation may be a considerable winter freezing of the ground during the formation of Bed 14.3. Unfortunately, these changes are not documented in the material collected in 1994 and need further verification.

In the deposits of Bed 13.4 and, especially, Bed 13.2, a sharp decrease in the proportions of *Clethrionomys* and *Alticola* is observed, the proportion of *Stenocranius gregalis* is reduced to 3.6%, while *Asioscalops, Lagurus lagurus*, and *Microtus oeconomus* disappear. *Lemmus* appears at the same time. It occurs in beds 14.1, 13.4, and 13.2. Marmots and ground squirrels are also present in these beds. The formation of these deposits probably took place during the epoch of dominant mountain–steppe petrophilous and nival grass–sedge associations in conditions of a relatively cold and dry climate. In the material collected in 1994, this phase is less pronounced.

Bed 13.1 records a restoration of favorable biotopic conditions. Red-backed voles reach 6.5%; *Alticola*, 13.3%; and the narrow-skulled vole, 14.4%. The marmot disappears, the proportion of ground squirrels decreases, whereas the mole, mole-vole, and root vole appear. However, this environmental stabilization was a short-term event.

From Bed 12.3 to the top of Pleistocene deposits, i.e., Bed 9.1, the proportion of *Clethrionomys* decreases to 1–2%, while *Alticola*, on the contrary, composes 12–17%. The proportion of *Stenocranius gregalis* decreases slightly, but remains not less than 8%. The relative quantity of *Lagurus* sharply increases and reaches 17.9% in Bed 9.1. The long-tailed ground squirrel and Eversmann's hamster become constant components of the assemblage. The proportions of shrews, root voles, and birds are, on the contrary, reduced. Beds 12.1, 11.4, 11.3, 11.2, and 11.1 constantly contain remains of lemmings.

These results allow several conclusions on the dynamics of ecosystems in the Anui valley in the Pleistocene.

(1) The species composition of small vertebrates only changes slightly from bed to bed, i.e., it shows low variation over time.

(2) Bats are the only vertebrate group that show a drastic change in abundance at the boundary between beds 22 and 21.

(3) In general, the fossil fauna of Denisova cave differs markedly from the modern fauna. This is particularly conspicuous when paleontological materials are compared with the modern fauna of the Anui basin. The Pleistocene fauna of Denisova cave suggests considerably more diverse biotope conditions and a high diversity of landscapes in comparison with the present situ-

ation. This diversity was caused by the important role of steppe and highland elements in communities.

Approximately the same changes in the taphocenosis are observed in the material collected in 1994, i.e., the material from other sites of the cave. This corroborates that, in the time of accumulation of beds 12–9, the forested areas decreased, while the area of open biotopes, primarily all mountain–steppe petrophilous associations, increased. It is worth noting that, from Bed 9.3 to Bed 9.1, this tendency was especially well expressed.

Fauna from Holocene Deposits of Denisova Cave

Small mammals from Holocene deposits of Denisova cave were investigated based on the material from the southeastern gallery (sector 5, squares A 2-6, B 2-6, C 2-6, D 2-6). Altogether 3823 bone fragments were used for determinations. The material contains 36 taxa, including birds, reptiles, fishes, and 33 mammal taxa. Fish bones and scales compose a significant proportion of specimens from the middle and upper beds. The most abundant material and, therefore, the most reliable information is obtained from beds 2 and 3. Beds 0, 1, and 8 are quite rich in bone remains. The data on Beds 5 and 6 are the least reliable.

Most of the bone remains belong to fish and small mammals, and in one case, to birds. The antiphase abundance pattern of birds and fish is remarkable. The highest abundance of birds is recorded in beds 0, 4, and 7, while fish prevail in beds 1, 2.1, 3, and 5; they are most abundant in bed 3, with 88.5% of the total number of specimens. In the lower beds, fish are rare or absent.

The bed-by-bed analysis of mammal species composition shows the similarity of the Holocene fauna of the Anui basin to both Pleistocene and modern faunas of small mammals. It is less diverse than any of the two associations; this is probably accounted for by an insufficient amount of material collected. The main characteristic feature of the fauna studied is the presence of Pleistocene species of *Lagurus* and *Ellobius*, which are absent from the modern biota of the Altai Mountains. The increasing number of *Microtus agrestis* is very indicative during the Holocene. It shows that ecosystem changes in the Altai Mountains do not accurately fit into rigid framework of stratigraphic units. These changes have proceeded gradually and continue into the present time. The data provided by E.M. Malaeva on the dynamics of vegetation and a study of the Holocene avifauna (Martynovich, 1998) corroborate this conclusion.

The quantitative ratios of different ecological groups of small mammals in the Holocene deposits look differently compared with those in the Pleistocene. The contrast between faunas from the Holocene and Upper Pleistocene of Denisova cave (Beds 11–9, sectors 4) is particularly sharp. This is evidence of a certain specificity of Holocene ecosystems. In addition, it may point to a sedimentation break at the boundary of Late Pleistocene Bed 9 and Holocene Bed 8.

A distinctive feature of Holocene communities is a higher proportion of forest animals, such as *Clethrionomys*, and lower proportions of nival and steppe species (*Stenocranius, Alticola*, and *Lagurus*). The upper part of the section shows an increased proportion of meadow and riparian taxa; the only record of chipmunk also comes from this level. All the above suggest gradual reduction of steppe landscapes and expansion of meadows and forests. This biocenotic rearrangement was probably caused by climatic changes towards a higher humidity and higher average annual temperatures than at the end of the Pleistocene. It is remarkable that, in the ecological pattern of the fauna, the upper part of the Holocene sequence is most similar to Bed 22 of the Pleistocene deposits of Denisova cave.

Environmental Changes in the Basin of the Upper Reaches of the Anui River, Inferred from the Small Mammal Record from Pleistocene Deposits of Denisova Cave

The distribution of vertebrate bone remains over the sedimentary sequence of Denisova cave allows the reconstruction of environmental changes in the vicinity of the cave during the accumulation of the Pleistocene beds. Comparison of the modern fauna of the Anui canyon, its slopes, and adjacent sites of the valley with the fossil fauna (taphocenosis) from the Pleistocene beds of Denisova cave shows their significant differences. Thus, the modern fauna of the Anui basin lacks characteristic elements of steppe communities, such as marmot, Eversmann's hamster, mole-vole (*Ellobius*), lemming, and *Lagurus lagurus.* All these taxa occur here as fossils. As for the species present in both modern and fossil communities, they substantially differ in abundance. As was shown above, the modern fauna of the Anui basin is dominated by voles of the genus *Clethrionomys*, characteristic indicators of taiga conditions. The Pleistocene fauna of the cave is dominated by the voles *Stenocranius gregalis* and *Alticola strelzovi*, which inhabit dry steppes and tundras, or highland steppes. In the modern fauna, Asian wood mice of the genus *Apodemus* (*A. uralensis* and *A. peninsulae*), representatives of the southern taiga subzone, play an important role. These species are extremely rare in the Pleistocene beds of the cave. In the modern fauna, the second most important group after red-backed voles is common voles (*Microtus*), specialized vegetarians living in herbage meadows. In the fossil fauna of Denisova cave, they compose not more than 5%. The pika *Ochotona* is currently not numerous and has a patchy distribution in the area studied, but it is relatively common in the fossil record.

This indicates changes in the composition of the small mammal fauna at the Pleistocene–Holocene boundary. They were expressed in a reduction of nival and steppe elements of the biota and increase in the proportion of taiga species due to reorganization of ecosystems in the Anui valley and, probably, throughout the Altai Mountains at the Late Pleistocene to Holocene transition.

However, the turnover of ecosystems should not be overestimated. Both the fossil record and extant fauna constantly include regional endemic species, such as the Altai mole *Asioscalops altaica* and the zokor *Myospalax myospalax.* Several characteristic East Siberian species occur in both the modern biota and the fossil record: long-tailed ground squirrel, chipmunk, Siberian ruddy vole, flat-headed vole, Dahurian hamster, and other forms. This suggests that changes in the ecological composition of communities proceeded against a background of a generally stable zoogeographic situation. The community of the area studied mainly originated from the Altai Mountains and adjacent territories.

The assumed role of nival and steppe communities in the Pleistocene of Denisova cave is probably slightly exaggerated, contrary to a certain underestimation of taiga communities due to the above noted taphonomic reasons of selective concentration of small mammals of open biotopes in pellets of birds of prey. Taking this into account, it is possible to reconstruct the habitats of small mammals in the Anui valley for both the entire Pleistocene and its particular phases. Nival (*Alticola*) and steppe (*Spermophilus, Stenocranius*, and *Lagurus*) taxa dominate along the studied sequence pointing to a more important role of communities of open landscapes than at present. The area of scree slopes occupied by mountain–steppe petrophyte associations was much larger. High terraces, gentle slopes, and near-top plateaus were occupied by light steppe vegetation rather than by high meadow herbage with dense turf, as today. The presence of marmots in the taphocenosis, though probably underestimated, confirms this. According to our observations, in modern conditions marmots avoid steppe sites with densely vegetated soil. Even within their individual ranges, marmots prefer to use their own previously trampled paths. For an ungainly animal, it is the only way of quick escape in case of a danger. An indicator of dry steppes and semideserts is the mole-vole *Ellobius*, which sporadically occurs in the Pleistocene beds of Denisova cave. Today, its nearest populations occur in steppe Altai. The continuous presence of the Altai pika indicates extensive scree areas.

However, the domination of steppe and nival communities was not constant and complete. All Pleistocene beds of the section contain remains of the Siberian ruddy vole *Clethrionomys rutilus.* This is evidence of a stable existence of forest vegetation in the site investigated in the Anui valley. The presence of chipmunk and, especially, red squirrel and flying squirrel, typical arboreal species, fully confirms this conclusion. The sites of larch–birch and birch–pine and possibly Siberian cedar-pine forests, similar to modern forests, existed throughout the Late Pleistocene.

The root vole, a species characteristic of floodplain biotopes, is present in almost all beds of the sequence. This is evidence of continuous existence of grass and sedge associations probably connected with the floodplains of the Anui River and its tributaries. This implies only slight variations of Anui's hydrological mode within the time span studied. This stability is supported by the constantly low proportion of the water vole *Arvicola* in the deposits of the cave.

Another important environmental indicators are mole and zokor. Finds of these large burrowing animals in almost all beds of the Pleistocene deposits of Denisova cave point to a rather warm climate in the Anui basin during the Pleistocene and indicate a lack of deep freezing of ground in this period.

Judging from the increase in abundance and diversity of steppe forms upward in the section, it is possible to assume a gradual expansion in the Anui valley of open biotopes, scree slopes, and lighted vegetation of dry steppes. This tendency reaches its maximum in beds 9.2 and 9.1. The incomplete appearance of the diagram in Fig. 1 suggests that deposits of the maximum steppe phase are not preserved in Denisova cave for some reason. This is corroborated by the material from Kaminnaya cave reported by T.A. Dupal and A.A. Pozdnyakov (Derevyanko et al., 1998). According to these data, the proportion of *Lagurus* in the Upper Pleistocene deposits of Kaminnaya cave (which is situated 20 km apart from Denisova cave) is up to 26.7% of the total number of specimens. In the deposits of Denisova cave, the share of *Lagurus* steadily increases upward the sequence, but does not reach 12%. The presence of a sedimentation break is confirmed by the character of the transition between the Pleistocene and Holocene deposits. Material from the entrance area of Denisova cave (sector 3) also validates this assumption. The proportions of *Lagurus* in beds 6.2 and 6.1 of the entrance area are 23% and 15%.

Fauna of the Paleolithic Site Ust'-Karakol

The multilayer Paleolithic site Ust'-Karakol is situated on the left bank of the Anui River at its confluence with Karakol River. The total number of determined specimens is 1908. They are unevenly distributed over the beds. The highest number comes from Bed 17 (299 specimens), the least fossiliferous (3 specimens) is bed 1. The taphocenosis of the Paleolithic site Ust'-Karakol differs essentially from cave Paleolithic sites in the Anui basin. All faunal material comes from the natural sequence of soils, loesses, floodplain and alluvial deposits. All bones of small mammals come from primary burial. A larger part of the material belongs to species that lived directly in this part of the valley. Thus, oryctocenosis, taphocenosis, tanatocenosis, and ancient biocenosis nearly coincide. The oryctocenosis of a particular bed is nearly identical to the composition of the past biocenosis from the time when these deposits were accumulated. However, this has its negative sides. The mate-

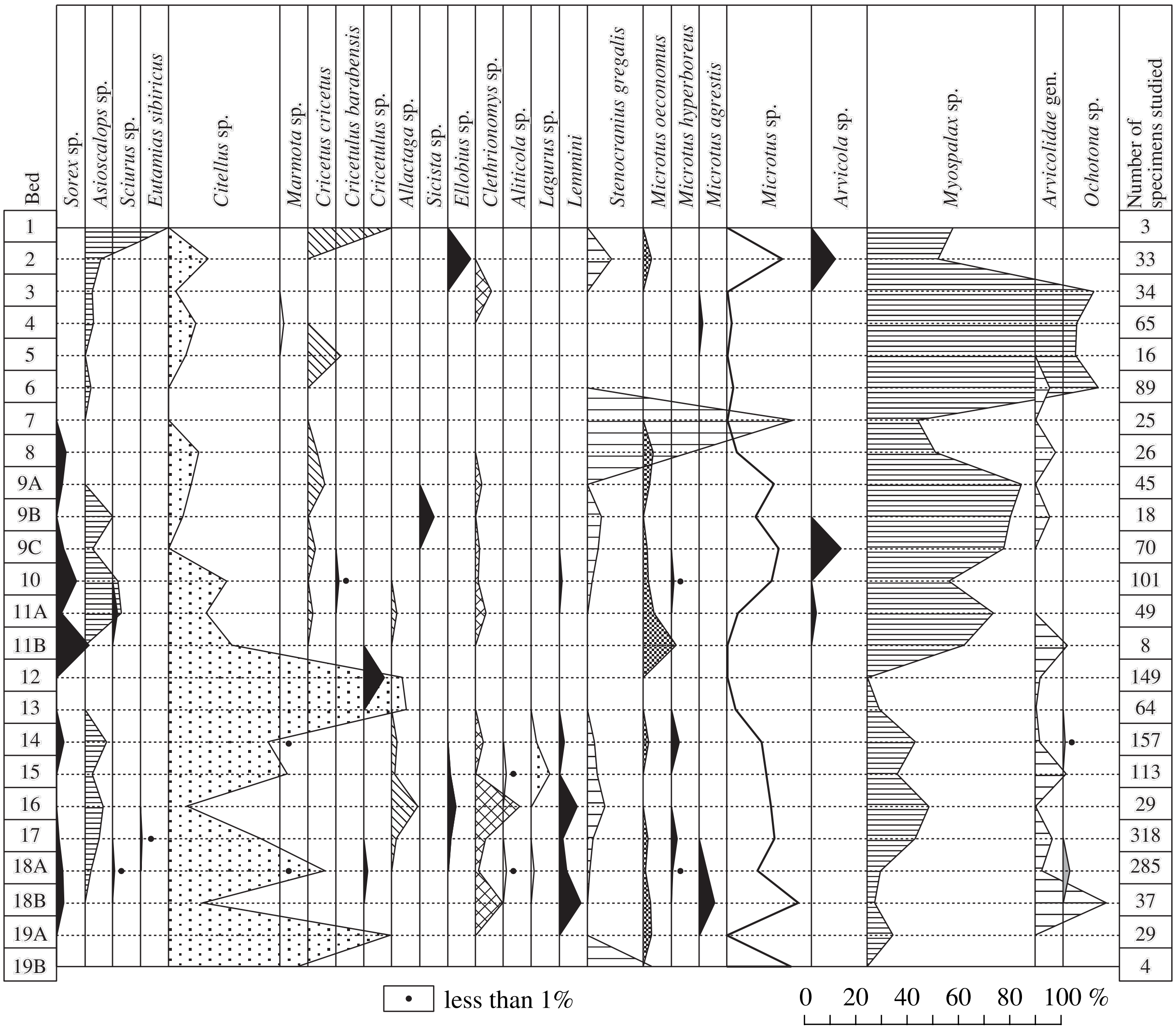

Fig. 2. General composition of small mammals from Pleistocene and Holocene deposits of the Paleolithic Ust'-Karakol site.

rial in the tanatocenosis of Ust'-Karakol was not concentrated and includes species from the immediate surrounding locations. Thus, it reflects a very local situation and the results could not be applied to the whole of the Anui basin. On the other hand, quantitative ratios of various species in oryctocenoses of each bed reflect their actual proportions in the ancient biocenosis of this area. This gives a special significance to the material of the open site Ust'-Karakol.

Figure 2 shows that ground squirrels and zokor were the major components of the small mammals community in the Anui valley during the accumulation of the sequence of the Paleolithic site Ust'-Karakol. The group of codominants includes shrews, mole, red-backed vole, narrow-skulled vole, and, partly, common hamster and root voles. The group of species with fewer numbers includes jerboa, mole-vole, *Lagurus*, lemmings of the tribe Lemmini, the gray voles *Microtus hyperboreus* and *M. agrestis*, the water vole *Arvicola*, and pika. The group of very rare species includes red squirrel, chipmunk, marmot, Baraba hamster, birch mouse, the Asian highland vole *Alticola*, amphibians, and reptiles. In all the features listed, the fossil fauna of Ust'-Karakol is essentially different from the taphocenosis of Denisova cave. In contrast to Denisova cave, the fauna completely lacks bats and fish, it has very rare *Alticola* and very few hamsters. This reflects local biotopic conditions.

The available material allows tracing the general pattern of the change in faunal composition in spite of some minor fluctuations. In general, from Bed 19B to beds 11B and 11A, the assemblage was dominated by ground squirrels, while from Bed 11B, by zokor. Forest species, such as the red squirrel, chipmunk, red-backed voles mostly occur in the lower part of the section in beds 18A–11A. Most records of Lemmini also come from this interval (beds 18B–14). In the taphocenosis of the upper part of the section, starting from Bed 11A, an important role is played by the common hamster and narrow-skulled vole with the total domination of zokor. Thus, essential changes of paleogeographic conditions at the boundary of beds 11B/11 are assumable.

The initial stage of the formation of the Ust'-Karakol section (beds 19B–19A) was probably connected with the domination in the Anui valley of steppe and meadow associations. A subsequent sharp reduction of steppe components and significant expansion of wooded biotopes was accompanied by the occurrence of moss bogs and (or) elements of fir-aspen taiga. This phase is reflected in beds 18B–18A. Bed 18E has a transitional appearance. The overlying Bed 18 reflects the second stage of steppification of the area, reduction of forests, moss, and meadow biotopes. This is a nonrandom paleogeographic parameter because of the significant material characterizing this bed.

The time of the formation of beds 17–14 had the highest biotopic diversity. On the one hand, the appearance of semidesert elements, with the maximum in Bed 16, is recorded. On the other hand, beds 17–16 show the highest proportion of forest species, which indicate an expansion of forest communities. Additionally, Bed 16 also shows the second peak of lemmings, reflecting an increase in moss associations and, probably, mire formation in the area. The numerical ratios of small mammal species have a natural appearance (Fig. 2). They show that the period of biotopic diversity of Bed 16 was followed by a gradual reduction of forest and bog associations and the onset of steppification.

Beds 13 and 12 correspond to the maximal steppe phase in the Anui valley, to a sharp reduction of meadow associations, disappearance of mole and shrews in the Ust'-Karakol site. The significant amount of studied material stresses the reliability of these conclusions. A new climatic improvement with an increase in humidity occurred during the accumulation of beds 11B and 11A. This was reflected in a substantial increase in areas of meadow and forest communities. However, in contrast to the previous periods, the lowered relief sites were occupied by sedge bogs rather than moss associations. Beds 11 and 10 indicate a new deterioration of the environment, though less intensive than in the previous phase. The reduction of forested areas was accompanied by an increase in the area of meadow and, to a lesser extent, steppe biotopes.

During the formation of beds 9B and 9C, the role of meadow communities increased even more, while steppe biotopes were reduced. This was a time of widespread dense grass vegetation on the valley slopes and sedge associations in the floodplain of the Anui River. Beds 9A, 9, and 8 accumulated in conditions of a certain increase in climatic aridity and expansion of both steppe and forest vegetation. This probably occurred on the background of increased summer temperatures.

Bed 7 corresponds to an environment with prevailing grassy vegetation, which, however, was not accompanied by the formation of a dense grass sod cover. This was possibly a time of marked climate cooling. This cold phase was followed by a significant warming reflected in beds 6, 5, 4, and 3. This was a period of maximal expansion of meadow associations occupied by herbage with dense grass sod cover. The role of steppe associations slightly increased. At the end of the phase (Bed 3), forested areas expanded.

During the accumulation of Bed 2, the area of meadow herbage reduced again and steppe areas on the slopes increased, although sedge associations expand onto the floodplain. Bed 1 reflects an improvement of climatic conditions and expansion of meadow herbage. However, these results are questionable due to the limited material from Bed 1.

Dynamics of Bioresources and Activity of the Paleolithic Man

The analysis of data on various Paleolithic sites in the Anui River basin shows that environmental and climatic changes in the Pleistocene were directional. The Late Pleistocene is characterized by a general decrease in the heat supply and an increase in the continentality of the climate. The general direction of the process was complicated by periodic fluctuations caused by alternation of relatively dry and more humid climatic phases.

During the Late Pleistocene, vertical zonation was more complex than in the present day. The mosaic structure of communities existed during the entire Middle and Late Pleistocene. It was determined by climatic features, slope aspect, orientation of mountains ridges and river valleys.

The autochthonous coniferous forests with a significant proportion of broad-leaved forms undoubtedly represented the core of biocenotic communities of the northwestern Altai Mountains. Steppe and semidesert species came from the south, from Kazakhstan and Mongolia, through a system of leveled intermontane depressions, for example, of the Chuya and Kansk steppes. Elements of tundra and boreal communities penetrated from the north, from the Ob River Plateau, and in part could spread from the bald mountain zone, which could be their refugium in interglacial epochs. Even little changes in average annual temperature and humidity resulted in increasing expansion of one or several zonal types of ecosystems, creating an overall unique mosaic of landscape conditions.

In general, the Sayan-Altai Mountains represented a refuge territory, which maintained rather stable and multicomponent ecosystems, which influenced the history of the formation and development of the Paleolithic people.

Against a background of gradual transformations of the environment inferred from the material of Paleolithic sites of the Anui valley, the sharp and significant drop in the number of bats at the transition from bed 22 to bed 19 and higher beds of Denisova cave is very surprising. This phenomenon is not accidental because it is well expressed in different squares of the excavation. The thickness of bed 22 is equal to that of the whole above-lying sequence of Pleistocene deposits. It essentially differs from it in lithology, structure, texture, and color. Even taken alone, this points to a change in sedimentation mode between beds 21 and 19. This transition also shows a reduction in the abundance of small forest mammals and an increase in the proportion of steppe species. The composition of large mammals experienced drastic changes. The brown bear prevails among carnivores in Bed 22, whereas remains of the cave hyena dominate in the upper part of Pleistocene deposits. The proportion of bear specimens in Bed 22 is 12.7% (179 specimens), and in beds 21–9 their abundance does not exceed 5.17% (73 specimens), i.e., they become less than half as frequent. Remains of hyena demonstrate the reverse distribution. In Bed 22, they are represented by 1.06% (15 specimens), while in Beds 21–9 their share totals 8.07% (114 specimens), i.e., their proportion is almost eight times greater.

In the upper part of Pleistocene deposits, the proportion of ungulate bones increases. Simultaneously, the amount of artifacts and tools grows drastically above Bed 22 (Derevyanko et al., 1998).

Judging from the small mammal fauna from the Pleistocene deposits of Denisova cave, the environment changed towards the expansions of open biotopes and a slight decline of forest vegetation during the accumulation of beds 21 and 20. This inevitably resulted in increased areas and biomass of grass communities. The increase in the area and productivity of pastures led to an increase in population numbers and species diversity of ungulates, which, in turn, determined the growth of the population density of Paleolithic people. As a consequence, humans visited the cave more frequently, which is reflected in the increased amounts of artifacts in cave sediments. Abundant charcoal and fire-spots in beds 21–9 indicate that the presence of humans became long-term and was accompanied by setting of fires. All these factors disturbed and negatively influenced bats and other inhabitants of the cave. This was the main reason for the sharp reduction of the bat colony.

The increased area of grasslands and density of ungulates resulted in the increase in the population of hyenas, as shown by the osteological material of Denisova cave. The quantitative ratio of bears and hyenas is also indicative. Bones of young animals prevail among bear remains in Bed 22. This suggests that bears used the cave in winter as hibernation shelter and birthplace of cubs. It is quite clear that the cave could not function simultaneously as a bear's lair and a human dwelling. This suggests infrequent visits of humans to the cave during the accumulation of Bed 22, which is supported by the small amount of artifacts found. After the change of environmental conditions, an increase in the areas of meadow and steppe biotopes, growth in numbers of ungulates, hyenas, and humans, the bear was forced out of the cave. The facts listed above confirm this conclusion.

It is more difficult to explain how humans and hyenas could share the cave in the periods of their activity. It is known that hyenas need a protected shelter for giving birth to cubs only in spring and early summer. On the contrary, humans probably used the cave as a shelter primarily in fall and winter periods. Cave walls, especially combined with the use of fire, gave protection from the cold. It is the fire use that would have had an unfavorable effect on the bat colony which inhabited the cave at previous stages of its history. However, the life in cave also had its limitations for humans. Denisova cave is located in a narrow part of the Anui canyon, which restricts a wide outlook on the area and prevents hunting of moving herds of ungulates. Therefore, at the beginning of a warm season, humans most likely moved to open-air sites, such as Ust'-Karakol, which provide an excellent view on the Anui and Karakol valleys and adjacent mountain slopes. This gave a visual control of an extensive space and, therefore, enabled a fast response by hunters to approaching ungulate herds. There were probably other reasons why humans seasonally abandoned the cave. For example, during the long winter season, sleeping skins and the people themselves could have been increasingly infected with ectoparasites. In addition, during the spring and summer period, the air temperature inside the cave is much lower than outside. Measurements carried out in July to August of 2002 showed that, in the galleries of the cave, the day temperature keeps within the interval of 8–9°C, and in the range of 12–14°C in the central hall. On the same days, the daily fluctuations of the air temperature in the Anui valley ranged from 14 to 23°C, the day temperature was at the of level 20–23°C, sometimes reaching 31°C. Therefore, additional efforts are required to keep the cave warm in summer. It is also noteworthy that most of the dry brushwood in the cave's vicinity was consumed during the fall–winter period. In this situation, the move of its inhabitants to open air summer sites became almost inevitable. Thus, humans and hyenas could use the cave in different seasons of the year.

The data on bones of large mammals of Denisova cave reveals another regularity. As indicated by archeological materials, the presence of humans in the cave during the accumulation of Bed 22 was minimal, as well as their influence on the formation of the taphocenosis of this bed. During this interval, bones of ungulates were brought into the cave only by carnivores. The quantitative ratio of bones of predators and ungulates in Bed 22 is 4.73 : 1, which corresponds to their natural ratio in taphocenoses formed without human influence. This ratio of predator to victim bones would have been retained during all the time of the formation of the cave's taphocenoses in the absence of humans. However, the actual data indicate a steady increase through the time in relative (and absolute) numbers of bones of herbivores

The proportions reported allow the share of bones brought by predators and by humans to be calculated

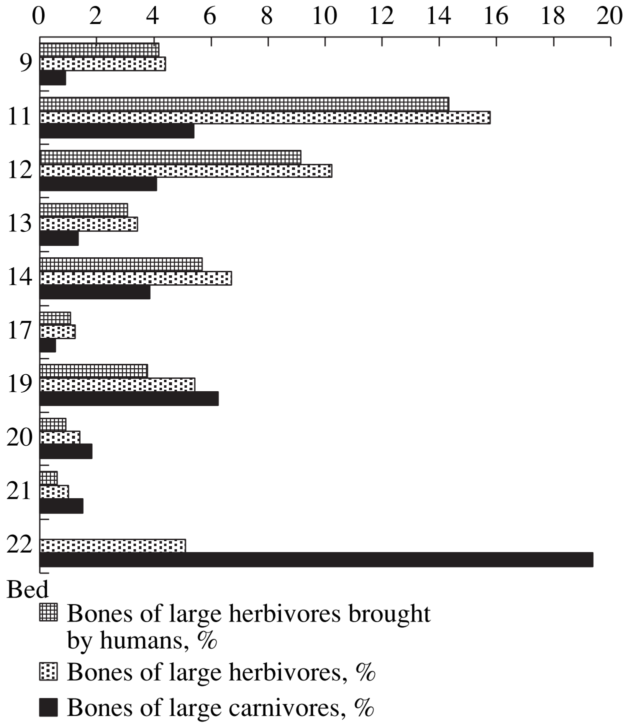

Fig. 3. Proportions of large herbivore bones brought to Denisova cave by large carnivores and humans.

for every bed of Denisova cave. The results obtained are shown in Fig. 3.

Figure 3 clearly shows a sharp increase during the Late Pleistocene in the amount of bones of herbivores brought by humans. This, in turn, reflects the increased human pressure on the populations of ungulates and the environment in general.

The data presented reveal the existence of intricate links between natural conditions of the Late Pleistocene, the composition of animal communities, the condition of populations and the economy of prehistoric people. It is assumed that these links were not only unidirectional but had a feedback. The activity of Paleolithic people exerted a considerable influence on natural resources of the Anui valley.

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