

The role of traditional nomadic pastoralism in the spatial and genetic subdivision of the distribution of populations of small mammals in mountain areas and their sanitary and epidemiological significance (on the example of Tuva)

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Abstract. The data on the genetic and spatial subdivision of populations of synanthropic species of small mammals, their dependence on the intensity with the territories of distant-pasture cattle tending are presented, and some patterns of indicators of ectoparasite infestation of their communities are revealed. The factor determining the genetic and spatial differentiation of populations of small mammals can be attributed to the relationship of small mammals with ungulates that has long historical roots (Neogene, Anthropogen). At present, these relations have been preserved with domestic ungulates, which, along with physical and geographical ones, determine the genetic and biotopic differentiation of populations of small mammals. The assumption is made about the deep historical roots of the establishment of such relationships by pasture ungulate animals from the neogene and pleistocene.

1 Introduction

The purpose of our work is to analyze the mechanisms of achieving ecological specialization that accompanies adaptation to transformed ecosystems, to establish the mechanisms of formation of spatial and genetic subdivision of populations and the epizootological role of synanthropic species of small mammals in the conditions of traditional distant-pasture cattle tending. Many species of small mammals of such families as Insectivora, Chiroptera, Lagomorpha, the family Ochotonidae, Rodentia and Chiroptera are associated with the territories of intensive development of distant-pasture cattle tending. All studied species are intermediate carriers and / or carriers of pathogens of acute infectious diseases [1, 2, 3].

The territory of modern Tuva is characterized by a complex geological history. Paleontological material from the Neogene localities of Tuva "Holu" and "Taralyk-Cher" [4, 5], from the Pleistocene — "Ak-Tal" and "Mogen-Buren" [6], testifies to the rich fauna of pasture ungulates and small mammals of the region. By the beginning of the anthropogenic period (~ 2 million years ago), the unified steppe and forest spaces in the region were torn apart. The Tuvan steppes were separated from the Khakass steppes, but they represented a single whole with the Mongolian steppes, which have survived to the present day. The latest orogenic stage of the relief development was caused by block uplifts. The Sayans finally took shape and the was formed Western Tannu-Ola Mountains ridge [7]; as a result of weak upward movements, a number of intra-mountain

depressions were formed in the Tuva basin: the Khemchik, Ulug-Khem and Kyzyl depressions, bounded by low-mountain ridges – Adar-Tosh and Bert-Dag, which, along with mountain-valley glaciations, contributed to the formation of a watershed between the Siberian and Mongolian flow directions. As a result of the activity of tectonic processes in combination with glacial and volcanic, the main hydro - and morphostructures of the region were formed, which divided the main areas of small mammals into several groups of populations isolated by physical and geographical barriers. The habitats of many steppe species of small mammals (jerboa, hamsters) in Tuva have significantly decreased, they are torn into separate foci and their mutual spatial isolation has become close to absolute.

The spatial organization of settlements of steppe species, which, in combination with biotopic confinement, causes the effect of isolation pressure by distance on the differentiation process is almost the same as due to a complete violation of panmixia with complete isolation of local populations. Moreover, the isolation of local settlements can also be ensured outside of biogeographic or ecological barriers, due to limited dispersion or, for example, epizootics in buffer zones [8].

The data on the distribution of settlements from different localities located on different sides of the main regional physical and geographical barriers, both hydrological and orographic, were obtained: delimiting the biomes of the Central Asian deserts from the Siberian taiga zone (Fig. 1).

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Fig. 1. Points of research ● Tuva basin (Khemchik depression – the valley of the Shemi River); ● Tuva basin (Ulug-Khem depression – Khayyrakan); ● Tuva basin (Khemchik and Ulug-Khem depressions-hr. Adar-Tosh ● Tuva basin between (Khemchik depression-lime sands); ● Ubsu-Nur basin (valleys of the Tes-Khem, Khol-Oozhu and Kholu rivers); ● Ubsu-Nur basin (Irbitey pass); ● Tuva and Ubsu-Nur basins (southern environs of the city of Kyzyl-hr. Tannu-Ola - southern foothills of Tannu-Ola); ● the Mongun-Taiga mountain range

The observed high rates of intrapopulation genetic and morphological variability in populations of synanthropic small mammal species with the biotopic subdivision of transformed ecosystems (seasonal pastures, outbuildings in camps, such as goats, etc.).

2 Material and research methods

The work was carried out from 2012 to 2021 in order to test the hypothesis about the role of spatial heterogeneity of the landscape, physical barriers, as well as demographic processes in the formation and dynamics of the genetic and spatial structure of populations of synanthropic / semi-synanthropic species of small mammals in Tuva, determining the epizootic situation.

Trapping and route studies of the distribution of local populations of small mammals in the mountainous and lowland regions of Tuva (total length – 2.3 thousand km) were carried out. The capture of the animals was carried out with Hero crushers and hunting grooves. A total of 1035 trap-days were worked out, 757 samples were obtained for molecular genetic analysis and morphometric and parasitological studies.

A systematic list of species, the order of their location, their Russian and Latin names according to the systematic and geographical reference book "Mammals of Russia" [9].

The characteristics of the relative abundance of species are given by categories with the following designations in Table 1: d-numerous (dominance index ≥ 10); c-common - ≤ 10 ; r-rare - ≤ 3 ; s-single - ≤ 1 ; n-the species is not marked.

To analyze the influence of physical and biotopic barriers on the genetic structure of spatially subdivided populations of ground squirrels, the primer SB10, IGS 9, CAG, IGS-bm, CK, ST7, STR 3 was used for microsatellite analysis with a wide allelic spectrum (25 variants), necessary for population analysis [10, 13], and the mtDNA locus was used as a marker of phylogenetic lines: the complete cyt b gene (1140 bp) 11, 12, 13, 14, 15].

In parallel, the collection of material was carried out to determine and study the fauna of ectoparasites. A total of 262 individuals of various species of small mammals from 8 different model sites were examined during the studies (see Figure 1). Fixation and treatment of

ectoparasites were carried out by generally accepted methods [6]. The following information is provided about the parasites found by us: the total number of parasites collected, the occurrence index (IV – the percentage of animals on which ectoparasites were found) and the abundance index (IO – the average number of ectoparasites per animal in the study sample).

3 Features of the genetic structure of populations of synanthropic species of small mammals

The analysis of microsatellites showed the existence of genetic differentiation both between the two complexes of populations of the Yenisei basin and the terminal lakes of Mongolia, and between the populations within each of the complexes. The genetic diversity within both population complexes is quite high with an equally low and significantly different degree of heterozygosity, especially in the populations of the Mongolian lake basin, which may be due to the discrete distribution of individual settlements in combination with inbred crosses within them [10]. The Altai lineage represents western populations and is significantly more diverse than all the others. It is well genetically separated from the other clades ($dp = 0.039 - 0.071$) and unites two branches: the Altai lineage proper and the branch on its right bank geographically remote from it and isolated by the Yenisei in the central group of populations (Tuva) [13].

The number of unique haplotypes for the samples of the haplotypes of *Cricetulus barabensis tuvinicus* (the Mongun-Taiga mountain range, the Tuva and Ubsu-Nur basins), no repeating haplotypes were found. They are all unique. A total of 495 samples from the Central Asian area were used. Of these, 189 unique haplotypes were recorded in 496 sequences. The observed number of nucleotide substitutions was 251, including 212 transitions and 39 transversions. The total number of non-synonymous changes according to the DnaSP estimate was 20 [3, 4, 5]. High individual diversity in the *cytb* gene was also noted for *Cricetulus longicaudatus* (4 samples from different populations), 8 haplotypes from 11 samples of *Alexandromys oeconomus* were unique [5].

According to the work Kovalskaya et al. [15], it seems plausible that *S. subtilis* s.l. from Tuva represents a rare case of extremely rapid speciation via fixation of aberrant karyotypes. The gene flow between the incipient species is blocked not through gene divergence but rather due to meiotic incompatibility. Similar cases of genetically close but chromosomally divergent species are known in other groups of mammals [11; 12].

4 Spatial structure of populations of synanthropic species of small mammals in Tuva

The analysis of the spatial distribution and the number of small mammals of Tuva showed that many population parameters are directly correlated with the intensity of development in the territory of driving-nomadic cattle breeding (see Fig. 1).

Model area 1 (Fig. 1). The valley of the Shemi River (absolute heights-871-878 m above sea level) with erosive and erosive-accumulative relief. There are a complex of terraces of different levels with sandy, loamy-sandy material, occupied by grass-grass steppes, in places with willows, poplars and shrub communities (*Caragana*) on alluvial chestnut and light chestnut steppe soils in the valley.

Model area 2 (Fig. 1) is represented by the Khayyrakan limestone rock massif at absolute altitudes of 585-903 m with calciferous flora. In low-mountain and medium-mountain erosion-denudation complexly divided relief, on the plains of intermountain basins, in denudation-accumulative, accumulative forms of relief, represented by elevated, inclined, hilly, small-mound ridges and ridges, sometimes strongly dissected, with calcifilic flora, and in the northern part of the mountain range dry fine-grain grass steppes on chestnut and chestnut saline soils.

Model area 3 (Fig. 1). It is represented by the meridially oriented Adar-Tosh ridge, which separates the intermountain super-depressions (Ulug-Khem and Khemchik) with elevated, inclined, flat relief forms, in places with fine-grained, fractional, fan-shaped forms, in real steppes in places with shrubs, on chestnut soils. The research sites are confined to the valleys of the Kara-Dyt, Kara-Sug rivers and their tributaries. The relief is low- and medium-mountain denudation-erosive, denudation steep-, medium- and weakly dissected with a low-power gravelly-loamy soil cover, sometimes rocky.

Model area 4 (Fig. 1) The Khemchik basin is represented by the western slopes of the spurs of the Adar-Tosh ridge with accumulative-aeolian relief forms (bumpy-ridge aeolian) with psammophytic and halophytic variants of desolate steppes with turf-grass and shrub vegetation on light chestnut sandy loam and sandy soils. It is composed of ridge, bumpy, sand dunes.

Model area 5 (Fig. 1). The Ubsunur basin. The southern foothills and the leveled plain of hr. Tannu-Ola and the valleys of the rivers Tes-Hem, Holu, Khol-Oozhu and their tributaries. The territory belongs to the medium- and high-mountain denudation-erosion relief with steeply sloping, deeply divided, sometimes peneplenized hilly-remnant-uvallist forms. Low-power sandy loam and sandy-gravelly soils dominate. There are rocky outcrops and stony-talus deposits on pastures, parking lots and near settlements in some places.

Table 1. Relative abundance of small mammals in pastures and natural areas

Animal species	1		2		3		4		5		6		7		8	
	T	N	T	N	T	N	T	N	T	N	T	N	T	N	T	N
<i>Talpa altaica</i>	s	r	n	n	n	n	n	n	n	r	n	s	n	s	n	r
<i>Sorex minutus</i>	n	s	n	r	n	s	n	n	n	s	n	s	n	r	n	r
<i>Sorex caecutiens</i>	n	c	n	c	n	r	n	n	n	c	n	r	n	c	n	c
<i>Sorex araneus</i>	n	r	n	r	n	c	n	n	n	r	n	r	n	c	n	r
<i>Sorex tundrensis</i>	n	r	n	r	n	n	n	n	n	r	n	c	n	c	n	c
<i>Meomys fodiens</i>	n	r	n	r	n	r	n	n	n	r	n	r	n	r	n	r
<i>Vespertilio murinus</i>	n	n	s	r	s	s	s	s	r	s	n	n	r	s	r	s
<i>Eptesicus niessoni</i>	c	r	c	r	r	s	c	s	c	s	r	n	s	r	c	r
<i>Eptesicus gobiensis</i>	n	n	n	n	n	n	n	n	c	r	r	r	n	n	r	s
<i>Myotis davidii</i>	c	r	c	r	r	s	r	s	c	r	r	r	c	r	r	s
<i>Peccotus ognevi</i>	c	r	r	r	c	r	r	s	s	r	r	n	c	c	c	s
<i>Ochotona dauurica</i>	c	r	c	c	n	n	c	r	d	c	d	c	d	n	d	r
<i>Ochotona alpina</i>	n	n	n	n	n	n	n	n	n	n	r	r	s	r	c	c
<i>Ochotona hiperborea</i>	n	n	n	n	n	n	n	n	n	n	s	r	s	s	s	r
<i>Ochotona (pallasi) pricei</i>	n	n	n	n	n	n	n	n	s	r	d	c	n	n	c	r
<i>Urocitellus undulatus</i>	d	c	d	n	d	r	s	n	c	r	c	r	c	r	c	r
<i>Meriones meridianus</i>	d	c	d	r	c	n	c	r	n	n	c	r	d	r	c	n
<i>Meriones unguiculatus</i>	n	n	n	n	n	n	n	n	d	r	n	n	d	r	c	n
<i>Cricetulus barabensis</i>	d	r	c	r	c	r	c	s	c	s	c	r	d	c	c	r
<i>Cricetulus longicaudatus</i>	n	n	s	n	r	n	c	s	n	n	c	s	c	n	n	n
<i>Cricetulus curtatus</i>	n	n	n	n	n	n	n	n	r	c	r	r	s	s	r	r
<i>Phodopus campdelli</i>	n	n	n	n	n	n	n	n	s	r	r	r	r	r	r	r
<i>Lasiopodomys gregalis</i>	c	n	c	n	c	r	n	n	c	r	d	c	d	r	c	r
<i>Alticola strelzowi</i>	c	n	c	r	n	n	n	n	c	s	d	c	c	r	d	c
<i>Alticola tuvinicus</i>	n	n	r	n	n	r	n	n	n	r	n	n	n	n	n	n
<i>Ellobius talpinus</i>	n	n	n	n	n	n	n	n	d	n	d	r	d	n	c	n

Note: The designations of the study points as in Figure 1; T-transformed territories – seasonal pastures, shepherd camps and the vicinity of settlements; N — natural territories corresponding to zonal analogues.

Model area 6 (Fig. 1). In physical and geographical terms, the Mongun-Taiga massif is located at the junction of latitudinal zones of steppes and semi-deserts and longitude-climatic sectors with continental and sharply continental climates, which creates a mosaic variety of landscapes against the background of a significant height difference in a highly dissected high-altitude relief and on multi-level alignment surfaces. There are no vegetation belts in the Mongun-Taiga massif and the structure of the vegetation cover is represented by a different mosaic of cryoxerophilic, cryohydrophilic, mesophilic and floodplain floral complexes. In the northern part of the massif, rare larch forests and tundra associations are confined, and in the southern part, arid steppe communities predominate. Cryopetrophytic floral complexes rise to a height of 3400 m, tundra communities are confined to altitudes of 2200-3000 m, alpine meadows (2400-3000 m) are fragmentally distributed on brown soils mainly confined to the heated slopes of the southern exposure, various steppes are distributed from the foothills to a height of 2800 m.

Model area 7 (Fig. 1). The system of the Tannu-Ola ridges. To the south of the Eastern and Western Sayan ranges lies the mountain arc of the Western and Eastern Tannu-Ola, adjacent to the Sangilensky Highlands, and the system of the Academician Obruchev ridge. The Tuva Basin is located between the ridges at different hypsometric levels, and part of the Ubsu-Nur basin, which belongs to the drainless and most arid region of Inner Asia, enters Tuva to the south of the ridges. The model section begins from the south-eastern outskirts of the city of Kyzyl through (Tuva basin), the Mezhegeysky wetland complex with abs. with a height of 667 m above sea level, along the northern forest macroscline and through the high-mountain lake. Kara-Khol on the ridge (height 2298 m) and the southern macrosclines of the East Tannu-Ola ridge to the floodplain of the Tes-Khem River (Ubsu-Nur basin 1026 m).

Model area 8 (Fig. 1). The Ubsu-Nur basin. It is represented by a profile from the pass (height above the sea level of 1988 m) along the Irbitey River valley to the south (height of 1353 m). The vegetation is represented by forest tundra with cedar with an undergrowth of dwarf birch, which abruptly passes to the south down the profile into a gravelly-stony shrub steppe, which is winter pastures.

5 Epizootological characteristics of populations of synanthropic species of small mammals

The relations between epizootic systems formed on the burrows of colonial mammalian species and humans are unpredictable, dramatic and multifaceted. Since 2012, cardinal changes have been registered in the Tuva plague center, as an unusually high epizootic activity with a predominance of epizootics of various types [17, 18, 19].

The plague microbe began to be detected in a wide altitude range from the desolate steppes (1500 m above sea level) to the upper borders of the subalpine (2550 m above sea level). A more frequent involvement of secondary, accidental carriers and carriers in the epizootic process was established (9.3% for the entire previous period and 12.1% in 2012-2017; 39.1% in recent years). The duration of the epizootic process has become much more extended in recent years – infected animals are now registered from April to September, 81.5% of crops were isolated in July – the first half of August. The total area of the hearth has almost doubled in recent years and by 2017 reached 10826.2 km².

In faunistic terms, the territory of the Republic of Tuva has been studied extremely unevenly. The most complete collections were carried out in Southern and, especially, South-Western Tuva, which is associated with long-term studies of the Tuva natural plague center and the adjacent territory. During the reconnaissance research works carried out by the staff of the Tuva State University in Tuva, some materials on the fauna of ectoparasites of synanthropic species of small mammals were collected, which served as the basis for this report [20].

The main carriers of the plague microbe are the long-tailed ground squirrel (*Urocitellus undulatus*), Mongolian and midday gerbils (*Meriones unguiculatus*, *M. meridianus*). To a lesser extent, mammals of other species are involved in epizootics caused by this variant of the pathogen: the Daurian pipit (*Ochotona dauurica*), the Barabinsky hamster (*Cricetulus barabensis*), the long-tailed hamster (*C. longicaudatus*), mountain voles (*Alticola strelzowii*, *A. tuvinicus*), narrow-crusted vole (*Lasiopodomys gregalis*) and the housekeeper vole (*Alexandromys oeconomicus*), common blindfold (*Ellobius talpinus*). The research involved 8 localities of the populations of the above-mentioned species (see Figure 1). A detailed study of these issues is necessary due to the fact that the data available in the literature do not allow us to unambiguously interpret the role of secondary carriers in the course of the epizootic process in the focus.

757 individuals of various species of small mammals were studied, of which 57.8% were infected with various types of ectoparasites — ticks, lice and fleas. The maximum indices of the occurrence and abundance of ectoparasites are observed in the ground squirrel, two species of gerbils and the Barabinsky hamster. Parasitization of 26 forms was revealed. The predominant and common for the studied species are *Haemogamasus ambulans*, *Hirstionyssus isabellinus*, *Laelaps clethrionomydis*, *Laelaps hiliaris*, *Hyperlaelaps arvalis* and *Ceratophyllus tesquorum*, regardless of the point of study.

In general, a number of patterns can be traced in the distribution of ectoparasites associated with small mammals in the studied territories: 1) in the general ectoparasitocenosis, IV and IO are maximal in pastures, shepherd sites and near settlements where livestock are traditionally kept, minimal in non-transformed territories;

in ectoparasitocenoses of small mammals, the species composition has practically not changed for individual localities; 2) the change in the species composition of ectoparasites due to the inclusion or "loss" of individual species is accompanied by a redistribution of the abundance of background species and a corresponding restructuring of the structure of dominance in communities; 3) in ectoparasites adapted to parasitism on a limited range of hosts, the spectrum of the main hosts and the structure of parasite-host relations changes from high points to lowlands; 4) the most common set of ectoparasite species is noted on animals in anthropogenically transformed territories.

6 Conclusion

The modern orographic scheme, the hydrographic network of the territory is a factor determining the spatial and genetic subdivision of populations of small mammals. On the one hand, along with physical and geographical groups of factors, pasture conditions with ancient roots of their structural and functional organization are a factor of biotopic differentiation of various natural and climatic zones (vertical and horizontal zonality), and on the other hand, the formation of identical pasture biotopes is the dominance of soils of light mechanical composition, the spread of xerophytic vegetation, the introduction of steppe species of small mammals, changes in soil chemistry due to an increase in the balance of some macronutrients – nitrogen, phosphorus, calcium and some trace elements, the formation of specific pasture vegetation, etc., which serve as ecological "bridges" for the penetration of synanthropic species. Together with them, migration and interspecific exchange of ectoparasitocenoses are carried out, which ensures high transmissivity and stability of the Tuvan focus of epizootics.

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