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ECO-GENETICALLY FACTORS DETERMINING THE STRUCTURE AND FUNCTION OF THE SOUND SIGNAL OF EURASIAN MARMOTS

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Marmots are a life form (or ecotype), characterized by diurnal activity, high population density and dwelling in open landscapes. The key behavioral component of this life form is the timely warning of neighbors about the danger by means of a sound signal. Among ecological determined factors, I distinguish selection for the specialization of vocal activity of marmots, selection for optimization of the rhythmic structure of signal and selection for increasing the noise immunity of the transmitted message. Among the genetically determined factors, I distinguish the process of speciation, geographical variability, and gene drift in small isolated populations and variability in joint settlements of different species of marmots. The role of the landscape is so great that it even affects the rhythmical structure of the alarm call. The rhythmical structure of the signal is controlled by a vertical dismemberment of the relief of the terrain populated by marmots. The alarm call is designed not only for the animals outside of the burrow but also for those in the burrow. Similar to tubes, burrows have radial resonance. Judging from their diameter marmot burrows suppress the frequencies higher than 1 kHz but amplifies the lower frequencies. In order to increase noise immunity in the burrows the marmot alarm call has the low frequency component and an amplitude modulation. All the marmot species are characterized by species-specificity of structure of the alarm call. The genetically-determined species specificity of the signal structure encodes the population genotype. As a result; different species encode the same function using different symbols.

By this report, I sum up the long-term field studies of the vocal activity of Eurasian marmots, associated with an acoustic warning of danger.

All species of plants and animals are affected by two main factors – ecologically determined and genetically determined. Among ecological determined factors, determining the structure and function of the sound signal of Eurasian marmots, I distinguish selection for the specialization of vocal activity of marmots, selection for optimization of the rhythmic structure of signal and selection for increasing the noise immunity of the transmitted message. Among the genetically determined factors, I distinguish the process of speciation, geographical variability, and gene drift in small isolated populations and variability in joint settlements of different species of marmots. The above factors confirm that the alarm call performs two basic functions: facilitates the implementation of the ecological niche of species and the realization of the gene pool of populations (Nikol'skii, 2016).

Among the ecological factors responsible for the alarm call key factor is selection for specialization of vocal activity. Marmots are a life form (or ecotype), characterized by diurnal activity, high population density and dwelling in open landscapes. Open landscapes make it possible to see danger at a great distance and warn neighbors of it. The key behavioral component of this life form is the timely warning of neighbors about the danger by means of a sound signal.

The role of the landscape is so great that it even affects the structure of the signal. The rhythmical structure of the alarm call is controlled by a vertical dismemberment of the relief of the terrain populated by marmots. The greater the dismemberment of the relief the shorter the period of sound sequence producing the call. On the plain these are normally series of slow sound sequences. In the mountains these are series of rapid sequences.

Regressive analysis (Fig. 1) has supported a strong relationship between the relief of the terrain populated by marmots and the period of sound sequence.

$$t=(1.88731–0.00172041\text{x}h)^2;\ R^2=89.8\%,\ p<0.001.$$

Where t is the period of sound sequence, h is the vertical dismemberment of the relief.

Assumed to be an independent variable is the vertical dismemberment of the relief - the distance from the nearest mountain top to the bottom of the valley. The relationship revealed is supported both on the intra- and inter-specific level (Никольский, 1984, Nikol'skii. 2002, Nikol'skii. 1994).

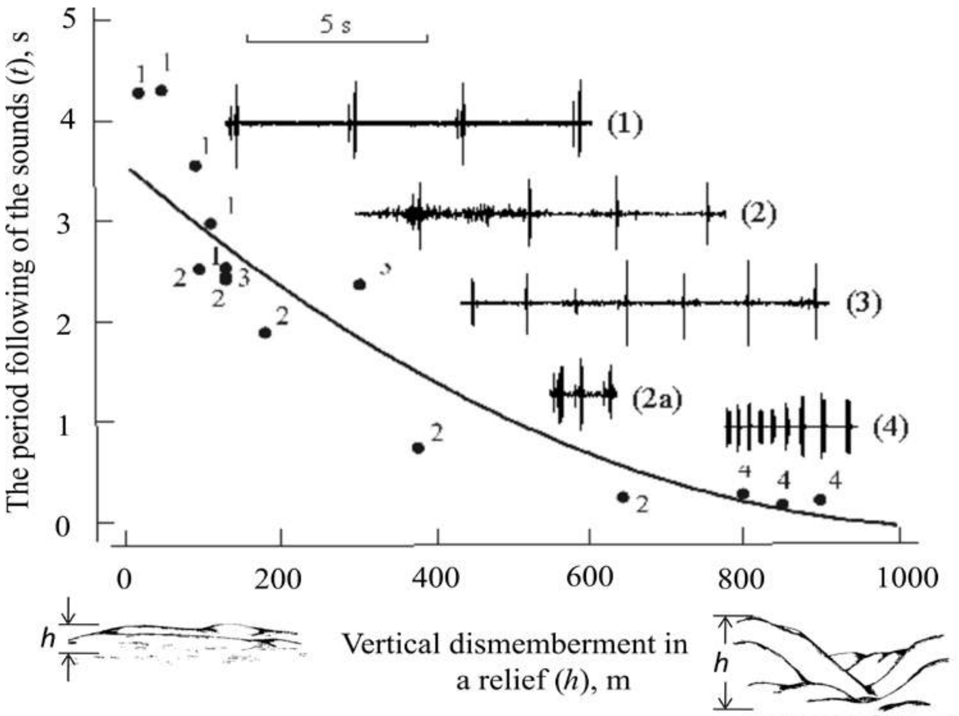


Fig. 1. *The relationship between extent of a vertical dismemberment (h) in a relief and the period following of the sounds (t). Species of marmot: 1 – M. bobak, 2 – M. baibacina, 3 – M. sibirica, 4 – M. caudata. Fragments of the signal of the listed species in one time scale – (1), (2, 2a), (3), (4).*

I believe that the selection mechanism is a high probability of marmots facing danger at an unexpectedly short distance. This is promoted by the down cuttings to the main slope, divided by ridges (Fig. 2).

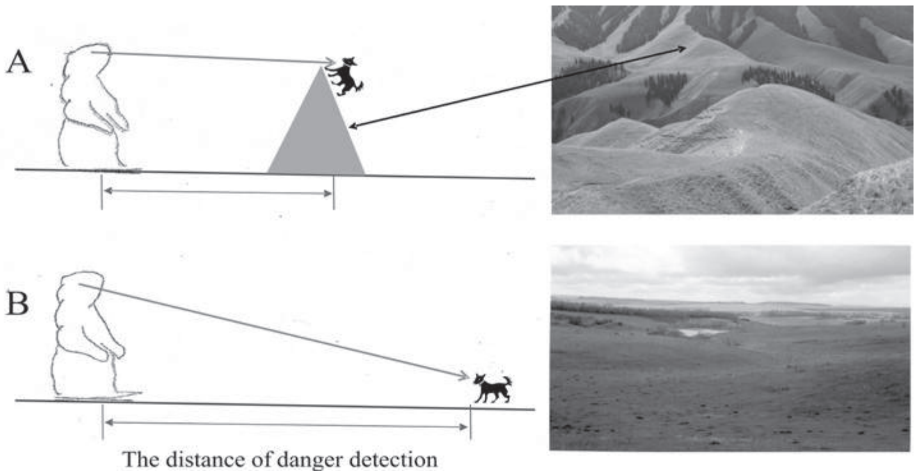


***Fig. 2.** Influence of relief on the perception of danger by marmots. A – Mountainous relief. B – Flat relief.*

We do not know what factors are selected at the nervous system level.

There are grounds to believe that selection fixes different levels of reactivity in marmots. The levels of reactivity can be estimated by the gradients of situational changes in the rhythmical structure of the signal, as shown in Figure 3. The Situation "A" of moderate danger is associated with a low level of reactivity. The Situation "B" implies an increased danger level and is associated with a high level of reactivity. An increase in the level of reactivity is accompanied by a reduction in the periods of following the sounds in the signal. In extreme cases, the signal turns into a series of rapidly following sounds, which is typical for all species of marmots (Fig. 3). In the mountains the probability of increased danger (Situation "B") is higher than in a plain area. As a result, selection extracts a high reactivity of the animals and respective rhythmic structure of the signal from the gradient of situational changes.

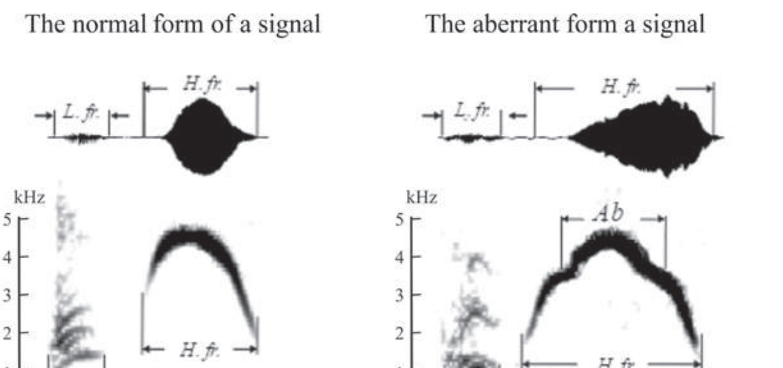


***Fig. 3.** Situational changes in the signal. A - The rhythmic structure of the signal corresponding to situation "A". B - The same is situation "B".*

A special case is the variability of the rhythmic structure of the signal of the Marmota sibirica. In the signal of one individual, there may be single sounds, doubles and a series of three sounds, as shown on the Figure 4. In my opinion, the signal of the Mongolian marmot is an intermediate (or transitional) form of the rhythmic structure of the alarm call. Further research may be useful for understanding the evolutionary mechanisms of signal structure formation.

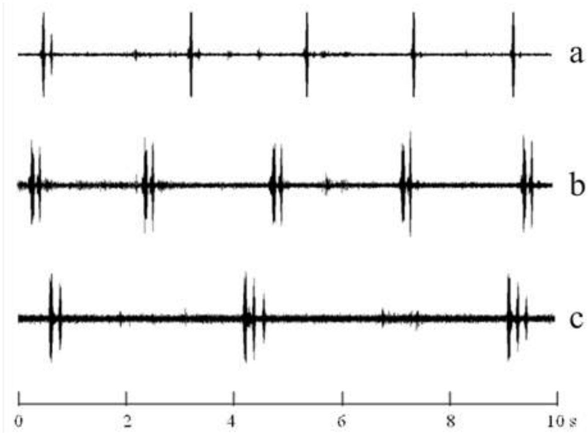


Fig. 4. *The diversity of the rhythmic structure of the signal of Marmota. sibirica. The signal forms: a – Single sounds predominate, there are double; b – Absolutely dominate the dual sounds; c – Doubled sounds predominate, there are a series of three sounds.*

The structure of any signal is to have some properties ensuring noise immunity of the messages transmitted .The alarm call is designed not only for the animals outside of the burrow but also for those in the burrow. Similar to tubes, burrows have radial resonance. Judging from their diameter marmot burrows suppress the frequencies higher than 1 kHz but amplifies the lower frequencies (Nikol'skii, Vinogradov, 2000).

In order to increase noise immunity in the burrows the marmot alarm call has two sources of lower frequency – the low frequency component and an amplitude modulation (Nikol'skii et al., 2015). The main energy of the low-frequency component is concentrated in the range lower than 500 Hz. The frequency of modulating oscillation ranges from several dozens to hundreds of Hz.

On an example of the Marmota bobak (Figure, 5). The Figure 5 demonstrates the function of the low-frequency component as a source of low frequency augmenting the noise immunity of the call in the burrows. We see that dominant on the surface is the high frequency component, whereas in the burrow, the low-frequency component predominates.

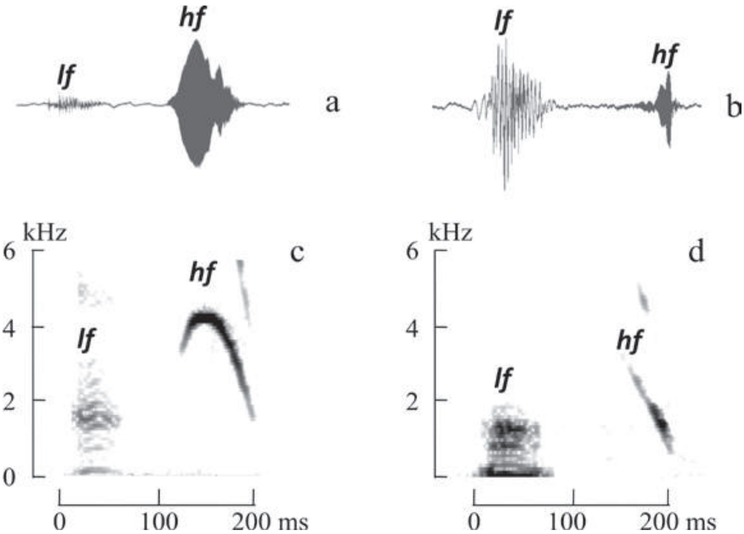


Fig. 5. *Low-frequency component as a source of low frequency. M. bobak. The signal on the surface of burrow: a – oscillation, c – sonogram. The signal into burrow: b – oscillation, d – sonogram. lf – low-frequency component; hf – high-frequency component.*

On an example of the call of the Marmota caudate the Figure 6 shows the functions of the amplitude modulations as a source of low frequency increasing the noise immunity of the call in case of its distribution in the burrows. The source of low frequency is a slow modulating oscillation. One can see that in the burrow the rapid carrier frequency is suppressed but the slow frequency of the amplitude modulation is dominant.

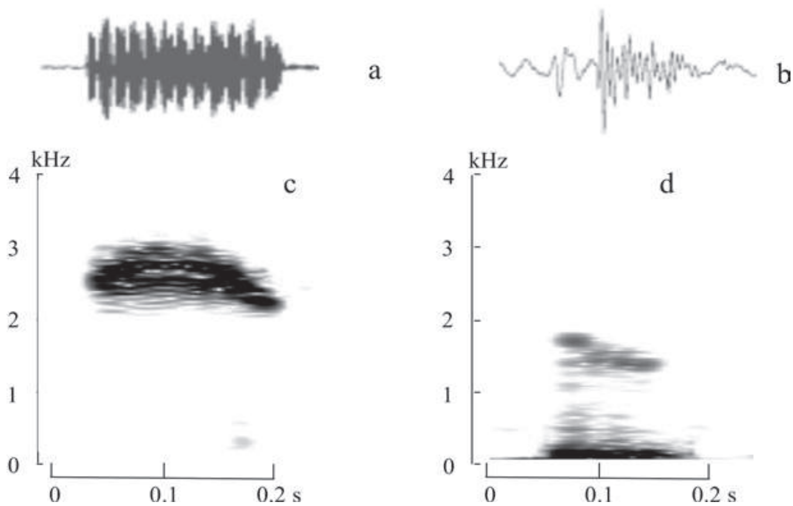


Fig. 6. *Amplitude modulation as a source of low frequency. M. caudate. The signal on the surface of burrow: a – oscillation, c – sonogram. The signal into burrow: b – oscillation, d – sonogram.*

In some species as, for instance, the Marmota baibacina and the Marmota sibirica the call may contain both sources of low frequency – the high frequency component and amplitude modulation (Nikol'skii, 2014).

The signal structure is highly-sensitive to genetically-determined variability. We have found 4 forms of genetically-determined structure variability of the signal, reflecting species-specificity, geographic variability and aberrations in small-number populations and also variability in joint inter-species settlements.

All the marmot species are characterized by species-specificity of the alarm call (Nikol'skii, 2014).

The genetically-determined species specificity of the signal structure encodes the population genotype and the ecologically-determined function (danger warning). As a result; different species encode the same function using different symbols (Figure 7).

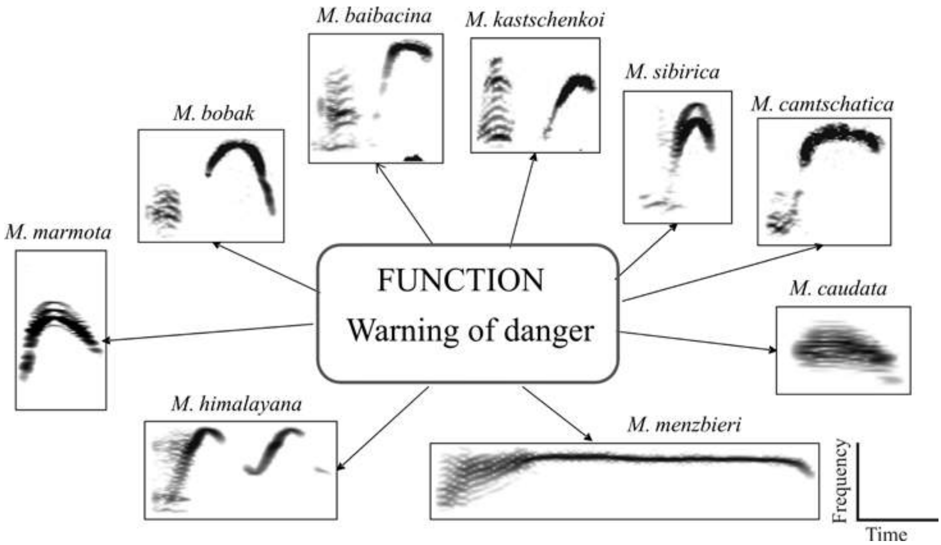


Fig. 7. *The same ecologically determined function of the alarm call is encoded by different genetically determined symbols.*

This phenomenon of parallelism of function and divergence of the structure of sound signals is widespread in many groups of animals, but has not been practically studied. These indicate to two relatively independent directions of evolution: ecological expediency and genetic uniqueness.

Naturally, in the course of geographical (allopathic) species formation was preceded by geographic variability of the populations divided by eco-geographical barriers.

A characteristic example is the geographic variability of the signal of the Marmota caudata in the Central Pamir, where the southern and the northern population groups (Fig. 8), which are attributed the subspecies status were for a long time isolated by a thickness of the glacier (Nikol'skii et al., 1999). The boundary passes along the deep valleys of modern rivers Bartang, Murgab and Aksu (Fig. 9).

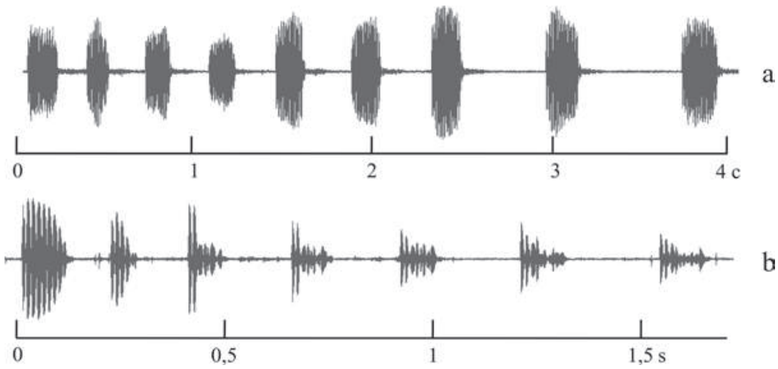


Fig. 8. *Geographic variability of the signal. M. caudate. a – the north form of signal; b – the southern form of signal .*

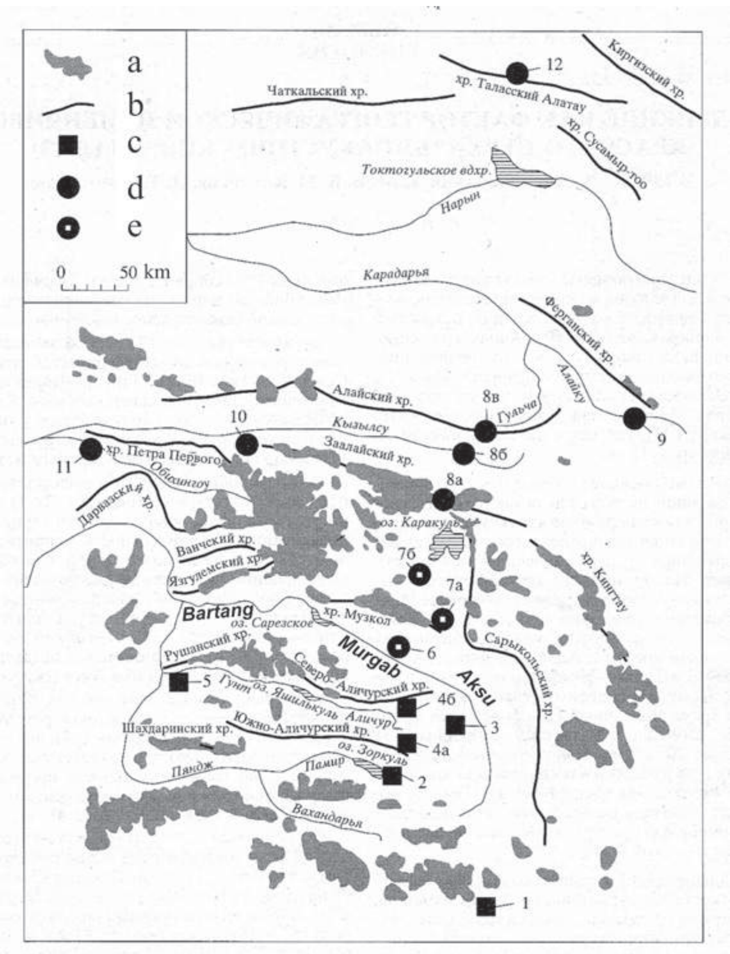


Fig. 9. *Local populations of M. caudate. 1 – 12 – local populations. a – glaciers; b – ridges; c – southern group of local populations; d – northern group of local populations; e – group of populations with intermediate signal signs.*

Another example of genetically-determined variability of the signal is the high probability of the aberrations that occur in small isolated populations, which is in keeping with the theory of gene drift.

A very high frequency of signal aberrations was revealed in the most distant population of the Marmota bobak in Ukraine (Nikol'skii, 2008a, b). This small population is isolated in main portion of the species distribution range along hundreds of miles (Fig. 10).

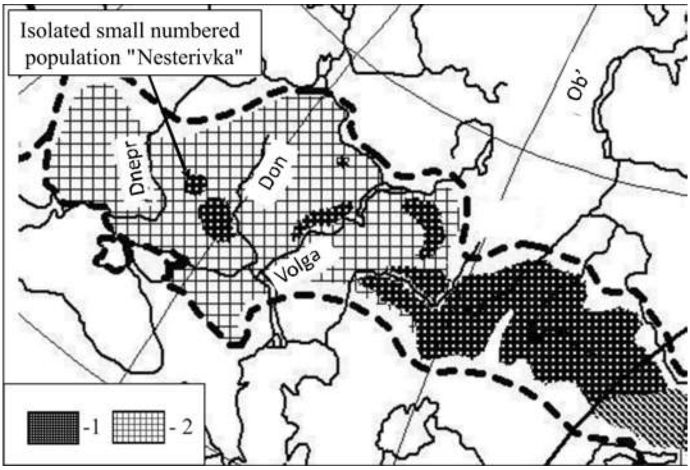


Fig. 10. *The modern (1) and restored (2) area of M. bobak.*

An aberration is a distorted characteristic of frequency modulation as shown in the Figure 10. This is the most common aberration that is found not only in the Steppe marmot but also in the Marmota baibacina and Marmota sibirica.

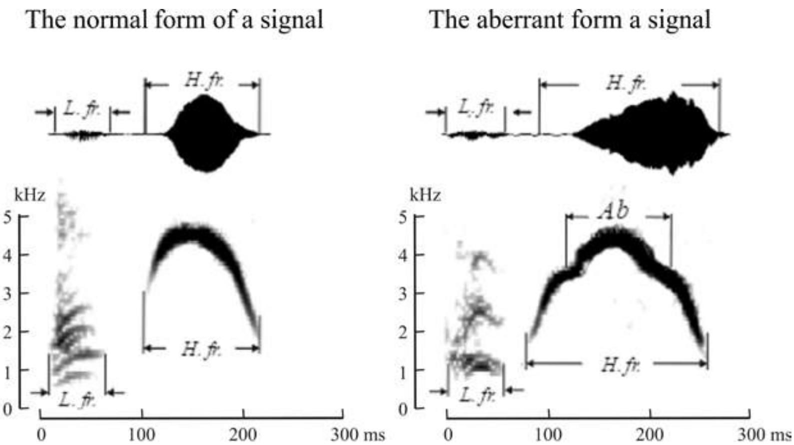


Fig. 11. *Aberration of a frequency modulation of the signal of M. bobak. L. fr. – Low-frequency component; H. Fr – High-frequency component; Ab – aberration.*

The Steppe marmot has a rare aberration of "amplitude modulation". There are only 3 instances per over 400 observations. The aberrant alarm call of the Steppe marmot is little different from the normal call of the Mongolian marmot. For it, the amplitude modulation is common. The distance between the species is several thousand kilometers.

The Fig. 12 shows that the probability of the signal aberration in the Steppe marmot increases from the center of the species range to its periphery, where fragmentation is particularly great.

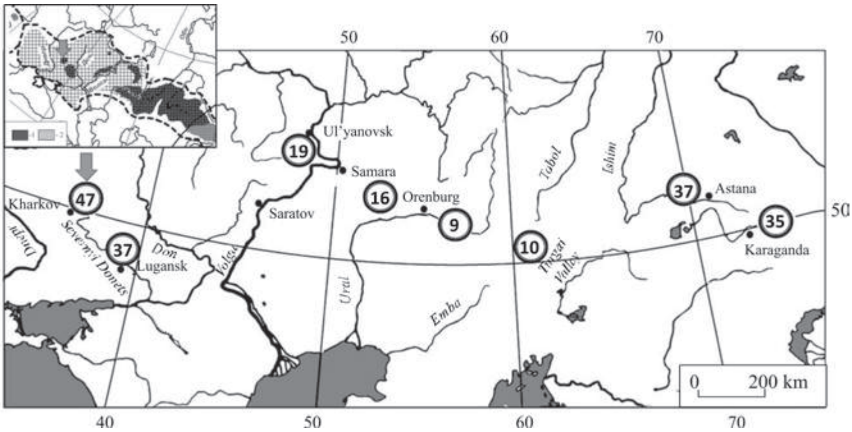


Fig. 12. *Probability (percents, in circles) of aberrations in populations of M. bobak.*

The fourth genetic factors are the variability of the signal in the zone of secondary contacts. In joint interspecies settlements variability is such that there are grounds to infer hybridization between the species.

In particular, in the joint settlements of Marmota baibacina and Marmota bobak in Central Kazakhstan we revealed a great diversity of signal forms – from species-specific to intermediate forms (Никольский и др., 1983). In intermediate forms the relationship between the ascending and descending branches of frequency modulation shows a great diversity. As demonstrated in the Figures 13, they are normally equal.

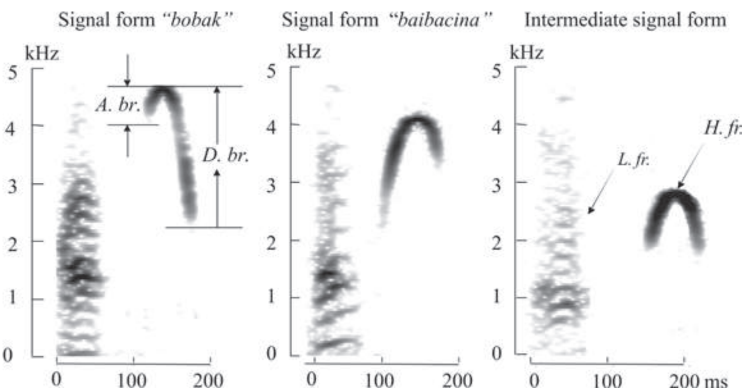


Fig. 13. *The signal of Marmota. bobak and Marmota. baibacina from the contact zone in the Central Kazakhstan. The ascending branch (A. br.) and descending branch (D. br.) of the frequency modulation characteristic. L. fr. – low-frequency component; H. fr – high-frequency component.*

With increasing distance from the boundary of the contact between the species the probability of species-specific forms of the signal increases (Fig. 14).

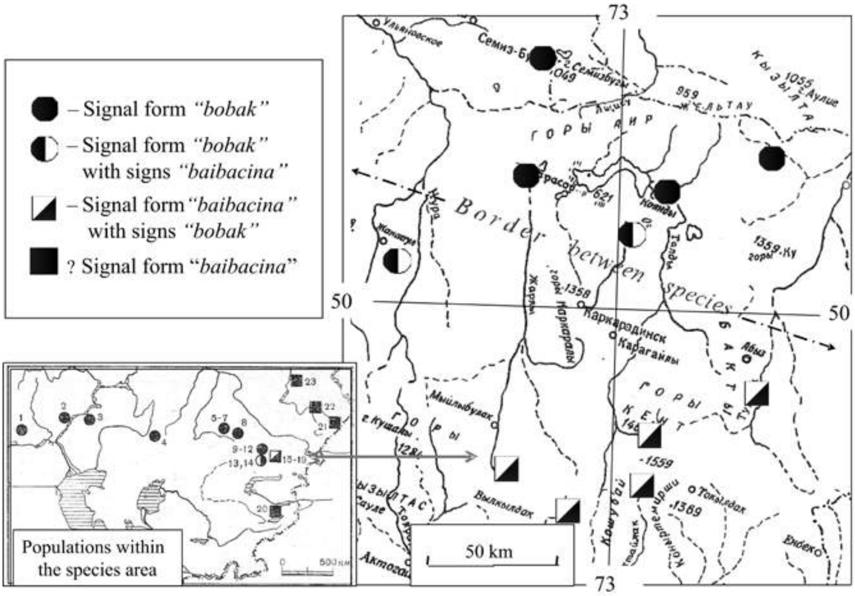
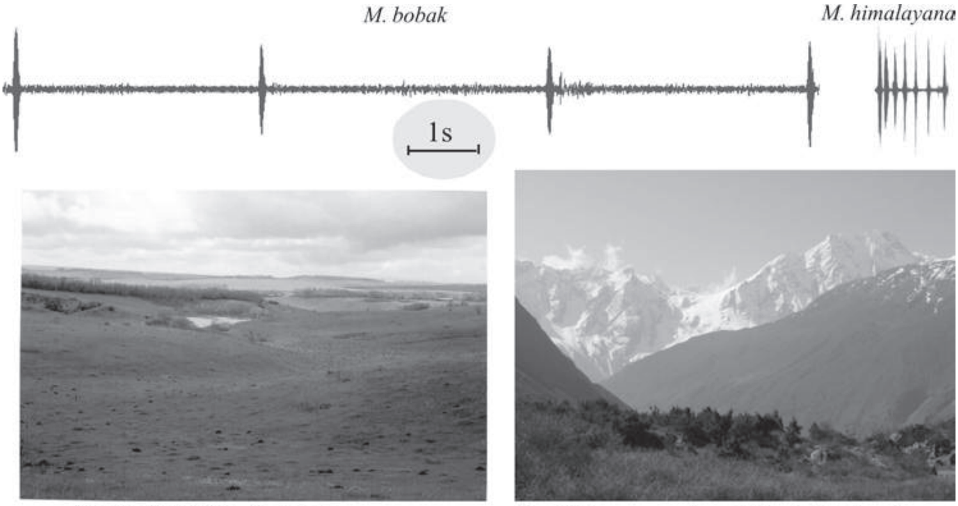


Fig. 14. *Populations in the contact zone of Marmota. bobak and Marmota. Baibacina.*

The results obtained confirm the existence of two relatively independent processes: 1) the influence of ecologically determined factors on the vocal activity of marmots and the structure of the sound signal associated with increasing the noise immunity of the transmitted message; 2) the influence of genetically determined factors on the structure of the signal. These two processes are relatively independent, and their most significant result is: 1) inter specific parallelisms of the signal function and 2) inter- and intr a specific divergence of the signal structure. The relative independence of the two directions of evolution confirms that the signal performs two basic functions – the realization of the species of ecological niches and the realization of the population's genotype.

The above suggests the most unexpected and intriguing conclusion is the effect of the relief of the terrain populated by marmots on the rhythmic organization of the signal. The greater the dismemberment of the relief, the shorter the periods of sound sequence. The extreme forms differ by an order of magnitude as demonstrated by the Figure 15. The main intrigue lies in the fact that so far we can only state a strong effect of selection on the signal structure. But we do not know that is the object of selection at the nervous system level. True enough, selection does not affect the signal directly but rather its source – the nervous system of marmots.



Plains of Ukraine. *M. bobak* The highest mountains of Nepal. *M. hymalayana*

Fig. 15. *The extreme forms of the dismemberment of the relief and their respective the extreme forms of the rhythmic organization of the signal.*

REFERENCE

1. *Nikol'skii A.A.* The basic functions of sound signals in mammals // Вестник Российского университета дружбы народов. Серия: Экология и безопасность жизнедеятельности. 2016. № 3. С. 7-15.
2. Nikol'skii A.A. Topographic relief as a factor in the geographical variation of the rhythmical structure of alarm calls of the steppe marmot *(Marmota bobak)*. // Holarctic Marmots as a Factor of Biodiversity (K.B. Armitage & V.Yu. Rumiantsev Eds.) - Proceedings of the 3d International Conference on Marmots, Cheboksary, Russia, 25 - 30 August 1997. - Moscow: ABF P.H., 2002. P. 299 - 307.
3. Nikol'skii A.A. Geographical variability of the alarm call rhythmical structure in *Marmota baibacina*. / Actual problems of marmots investigation. (Collection of Scientific Articles). // Theriology Society (Russian Academy of Sciences), Marmots Investigation Committee. - Moscow, ABF Publishing House, 1994. P. 111 - 126.
4. Nikol'skii A.A., Vinogradov N.S. Burrows of Mammals as Acoustic Devices: A Study of the Bobac Burrow as an Example // *Doklady Biological Sciences, 2000, Vol. 374, pp. 509–513.*
5. *Nikol'skii A.A., Wang Chi, Vanisova E.A., and Lisitsyna T.Yu.* Amplitude Modulation as a Source of Low Frequency Facilitating the Propagation of Marmot (Mammalia, Rodentia) Vocal Signals in Burrows // Doklady Biological Sciences, 2015, Vol. 463, pp. 193–199.
6. *Никольский А.А.* Видовая специфика и географическая изменчивость звукового сигнала сурков (*Marmota*, Sciuridae, Rodentia) Евразии // Зоологический журнал, 2014, том 93, № 8, с. 1026–1043.

7. Nikol'skii A.A., Academician Kotlyakov V.M., Blumschtein D.T. Glaciation as a Factor of Geographic Variation in the Long-Tailed Marmot (Bioacoustical Analysis) // Doklady Biological Sciences. Vol. 368, 1999, pp. 509 - 513.

8. Nikol'skii A.A. Increased frequency of the acoustical signal aberration in the peripheral populations of the Steppe marmot // Doklady Biological Sciences, 2008a, Vol. 422, No 2, pp. 279–282.

9. Nikol'skii A.A. Aberration of the alarm call of the steppe marmot, *Marmota bobak* (Rodentia, Sciuridae) // Biology Bulletin, 2008b, Vol. 55, No 6, Pp. 718-729.

10. Никольский А.А., Янина И.Ю., Рутовская М.В., Формозов Н.А. Изменчивость звукового сигнала степного и серого сурков в зоне вторичного контакта. Зоол.ж.,Т.62, вып.8, с.1258 - 1266. 1983.