

ЭКОЛОГИЯ

THE BASIC FUNCTIONS OF SOUND SIGNALS IN MAMMALS

A.A. Nikol'skii

Peoples' Friendship University of Russia
Podolskoye shosse, 8/5, Moscow, Russia, 113093

All the diversity of sound signals by mammals is subordinated two basic functions: function implementation of the populations of genotype and function realization of the ecological niche of species populations. The basic functions have resulted from some relatively independent trends in the evolution of sound signals as those developing the genetically determined structure and the ecologically determined functions. A relative independence of the above trends in the sound signal evolution supports variation.

Key words: behavioral ecology, biocommunication, bioacoustics, geographical variation, species specificity, mammals

Intra-specific communication processes are most important mechanism of ecosystem organization. Acoustic communication has a special status in intra-species communication. In fact, owing to acoustical oscillations acoustic signals have a number of advantages as compared to the signals of other sensory modalities, both in terms of encoding information and with respect to interference immunity of the transmitted message. Sound signals are common in all mammalian orders and the diversity of sound signals appears to be limitless.

Biocommunication, including acoustic communication, is a form of adaptive behavior. Similar to morph physiological adaptations, communicative behavior promotes implementation by the species of their respective ecological niches that they use efficiently. The concept of the “implementation of the ecological niche” is not new. It is directly associated with the concept of the “implemented niche” as part of the area successfully mastered by the population [14]. Hence, my purpose is not to introduce a new concept but rather demonstrate that acoustic communication is a part of the process of implementation of the ecological niche by the population.

The process of communication involves the exchange of information between the genotype carriers, and the acoustical communication, similar to any other type of communication, creates a behaviorally determined gene flow to implement the population gene pool in the species ecological niche. The latter is essential, indicating a relationship between the species ecology and the population-genetic processes.

Thus, the present communication advances a hypothesis whereby the entire diversity of mammalian sound signals has two basic functions as follows: — 1) the function of

implementation of the genotype by the populations and 2) the function of implementation of the species ecological niche by the population. The basic functions result from some relatively independent trends of the evolution of sound signals as the formation of 1) a genetically determined structure and 2) ecologically determined function. **The function** of sound signals in the present context implies the effect of the sounds produced by the animals on the motor and vocal activity of the recipients and on their hormonal and physiological condition. **The basic functions** are regarded here as one of the trends in the adaptive strategy of the evolutionary process.

The relative independence of the two above trends of the evolution of sound signals is confirmed by the evident variation phenomena. The variation of signal structure is controlled by the population genetic processes. This is testified by the existent forms of variation: intra- and inter-specific divergence [6], an increase in aberration frequency in peripheral relatively small-numbered populations [9], variation in the secondary contact zones [2, b, 12], with typical hybridization characters. Characteristically, all the above variability forms are only typical of the signal structure, whereas *the signal function remains unchanged*.

The signal function is controlled by selection, which is supported by intra-specific parallelisms of similar life forms, i.e., partial overlapping of ecological niches (ecological parallelisms) are accompanied by parallelisms in vocal activity of mammals, a presence of identical sound signals in the repertory of different species is accompanied by parallelisms in mammalian vocal activity and a presence of functionally identical signals in the acoustical repertory of different species. For instance, an alarm call is typical of numerous rodent and lagomorphs species — those dwelling in open space and characterized by a high population density [6]. It is exactly in such ecological conditions that the alarm call is efficient and feasible. Another example of parallelisms in systematically distant groups is provided by the attracting calls of domestic sheep (*Ovis aries*) and northern fur seals (*Callorhinus ursinus*) whereby the sound communication between mothers and their young is effected [11]. Both have to communicate in numerous and dense herds under conditions of intensive masking noise created by concurrently calling co specific.

Strictly speaking both the ecologically determined function and the signal structure are genetically determined as selection necessarily involves some genetic processes. In its turn, a genetically determined structure of the signals is ecologically determined to the extent by which ecological factors affect the gene flow to create or destroy inter-population barriers. To emphasize the effect of ecological factors on the population “gene content” N.P. Dubinin and D.D. Romashov proposed the term “ecogenotypes” [1. P. 89].

The examples below demonstrate that the variation of a genetically determined structure does not affect the ecologically determined function of sound signals. Even in case of a wide geographical variation of inter-species divergence of the signal function remains unchanged. It is the absence of the relationship between the structure and function that suggests a relative independence of the two trends in evolution resulting in the formation of the basic acoustic signals of mammals.

The present study is mainly based on the unique collection of the sound signals of mammals acquired over 50 years of field studies in the expanse of the former Soviet Union and some findings of my colleagues. The technique of recording and analysis of data under discussion were presented earlier [6].

The geographic variation of the sound signal structure supports the well-known fact of the effect of the eco-geographical barriers that isolate populations on the intra-specific divergence. Fig. 1 shows some examples of the geographical variation of the spectral structure of the bellow of the red deer (*Cervus elaphus*), the songs of the northern pika (*Ochotona hyperborea*) and the rhythmic structure of the alarm call of the long-tailed marmot (*Marmota caudata*).

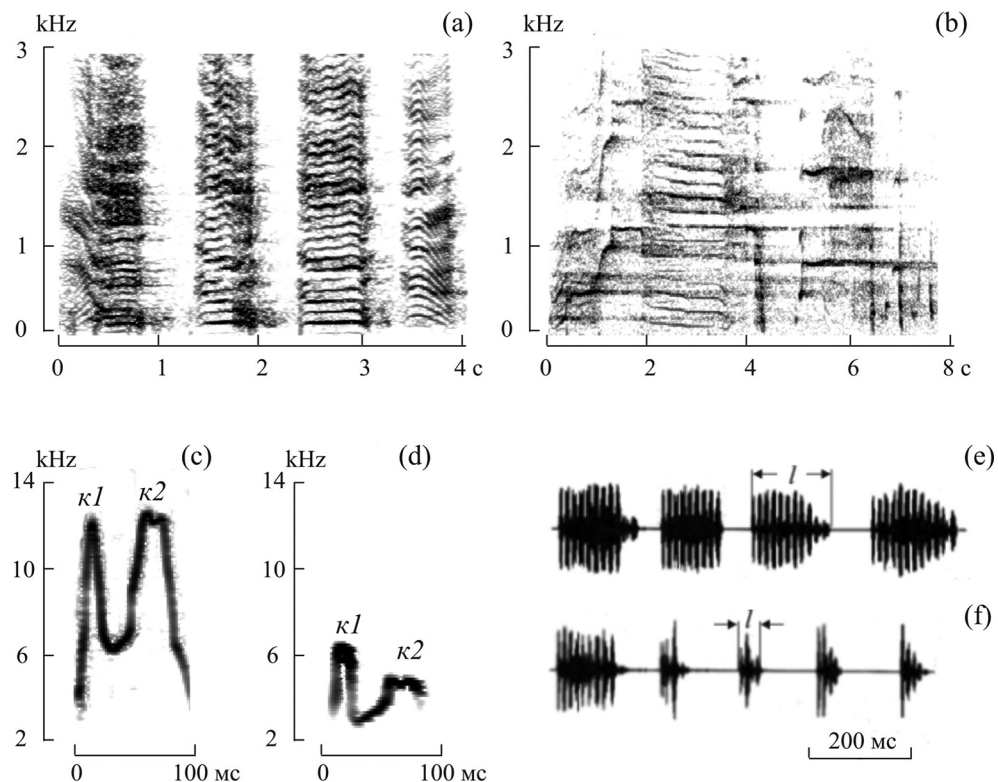


Fig. 1. Geographical variation of the sound signals of mammals:

a — spectrogram of the bellow of the Carpathian deer (*C. e. montanus*); *b* — the bellow of the Altai red deer (*C. e. sibiricus*); *c* — the spectrogram of the song of the northern pika (*O. hyperborea*), recorded in the mountains of the South Siberia; *d* — the spectrogram of the northern pika song in Chukotka; *e* — the oscillogram of an alarm call of the long-tailed marmot (*M. caudata*) from the northern group of the populaions in Pamir; *f* — the oscillogram of the alarm call of the long-tailed marmot from the southern group of populations. $\kappa 1$, $\kappa 2$ — species-specific components of the call of song of the northern pika; *l* — the duration of the sounds in the long-tailed marmot signal

On the whole vast area of species habitat from Scotland to the Far East deer form about 20 subspecies [4], united into two supra-species complexes — the western elaphoid group of subspecies and the eastern maraloid group. A steep variation gradient of not only morphological characters but also of the signal structure passes between the subspecies group along the south of the Russian Plain. In the Pleistocene that frontier repeatedly created an unsurpassable barrier separating the supra-species complexes of deer [6].

The northern pika, which populates a considerable portion of Eastern Siberia, forms a large number of isolated populations not only on the periphery but also in the depth of the species range, which is reflected in the geographical variation of sound signals [3, 5].

Fig. 1 shows the spectrograms of the northern pika call recorded in the mountains of Southern Siberia (Fig. 1c) and in Chukotka (Fig. 1d). Against the background of a wide geographical variation, there are two spectral components ($\kappa 1$, $\kappa 2$ — Fig. 1c), that are sustainably repeated from population to population throughout the entire range of the northern pika to confirm the species specificity of the signal [5].

A clearly steep gradient of geographical variation is that of the alarm call of the long-tailed marmot (Fig. 1e, f). The boundary between the population groups passes in Pamir in the intra-glacial area, which in the upper Pleistocene divided the species range into population groups north and south of the Murgab River [10]. In the southern population group, from the beginning of the signal series towards its end, the duration of the sounds (l , Fig. 1e, f) rapidly decreases.

The *inter-species divergence* of the signal structure produces a result similar to that of geographical variation, i.e., marking of the genotype. Examples of interspecies divergence (species specificity) of mammalian sound signals are presented in Fig. 2. In particular, species specificity of ground squirrel alarm calls (Fig. 2a) and pikas (Fig. 2b) and species specificity of the pika song (Fig. 2c) were demonstrated.

The genetically determined variation of the sound signal structure is also confirmed on the periphery of the area of distribution, where the isolation of small-numbered population is accompanied by a relatively high probability of *aberrations* [9], which agrees with the concept of genetic automated processes [1], or according to a different terminology — gene drift [18].

Fig. 3 shows examples of aberrations of the alarm call in the steppe marmot. Some aberrations occur regularly (Fig. 3b), whereas others are very rare (Fig. 3d) — one instance per hundred of observations.

Some particular form of genetically determined variation is the variation in the *secondary contact zones*, where as a result of hybridization the structure of sound signals acquired diversified forms in joint colonies (Fig. 3d) [2, 6, 12].

All the above examples indicate that as a result of population-genetic variation, the structures of sound signals some acoustic genotype markers, i.e., phonotypes, are formed. The phonotypes restrict communication by the population gene pool. In the space of the ecological niche they maintain the genetic integration of the signal producers whose function is in conformity with the ecological niche of the population concerned.

However, the signal structure can be not only be determined genetically (as shown above) but also ecologically in case the structural elements affect the jamming resistance of the transmitted messages facilitating the transmission of information in the environmental where the signal is distributed (for example, [13]).

In fact, Fig. 4 shows the main structural components of the low and high-frequency (Fig. 4, lf , hf), alarm calls in the Altai marmot and the steppe marmot. The high-frequency component is genetically determined. The species are absolutely different in relation to the phases of frequency modulation of the high-frequency component (Fig. 4, hf) [6]. By contrast, the low-frequency signal component (Fig. 4, lf) is determined ecologically. The low-frequency component is characterized by wide parallelism. It is present in the signal of the majority of the Eurasian marmot species [6]. Being a source of low frequency that signal promotes distribution of the signal in the burrows [13], where high frequencies weaken whereas the low frequencies are strengthened, which is shown in Fig. 4 (d, h).

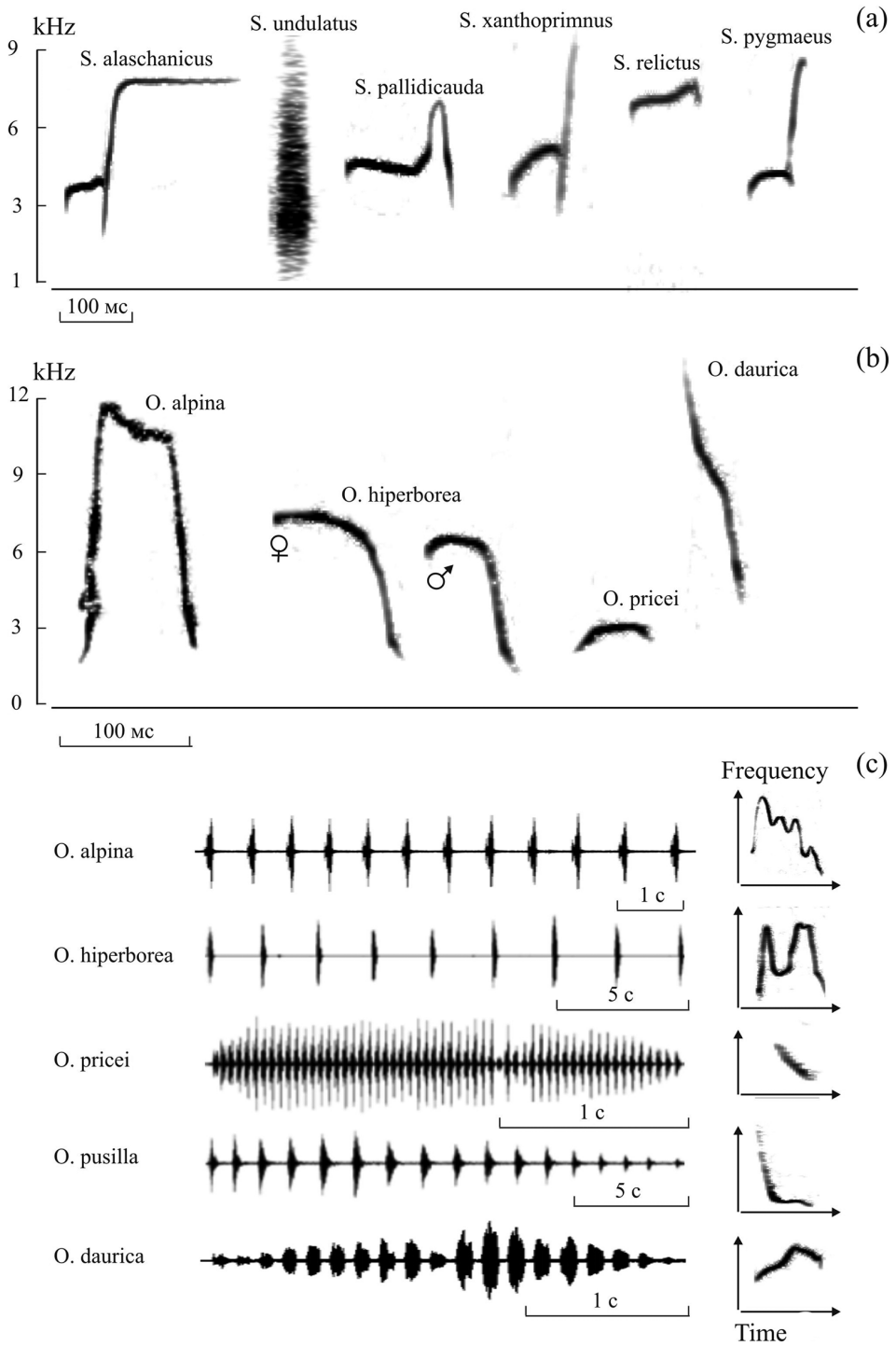


Fig. 2. Species specificity of the mammalian sound signals:
 a — spectrograms of ground squirrel alarm call (*Spermophilus*) (a) and the pika alarm call (*Ochotona*) (b); c — oscillograms (on the left) and spectrograms (on the right) of the pika song.
 (For convenience, the scale of the spectrograms has been changed)

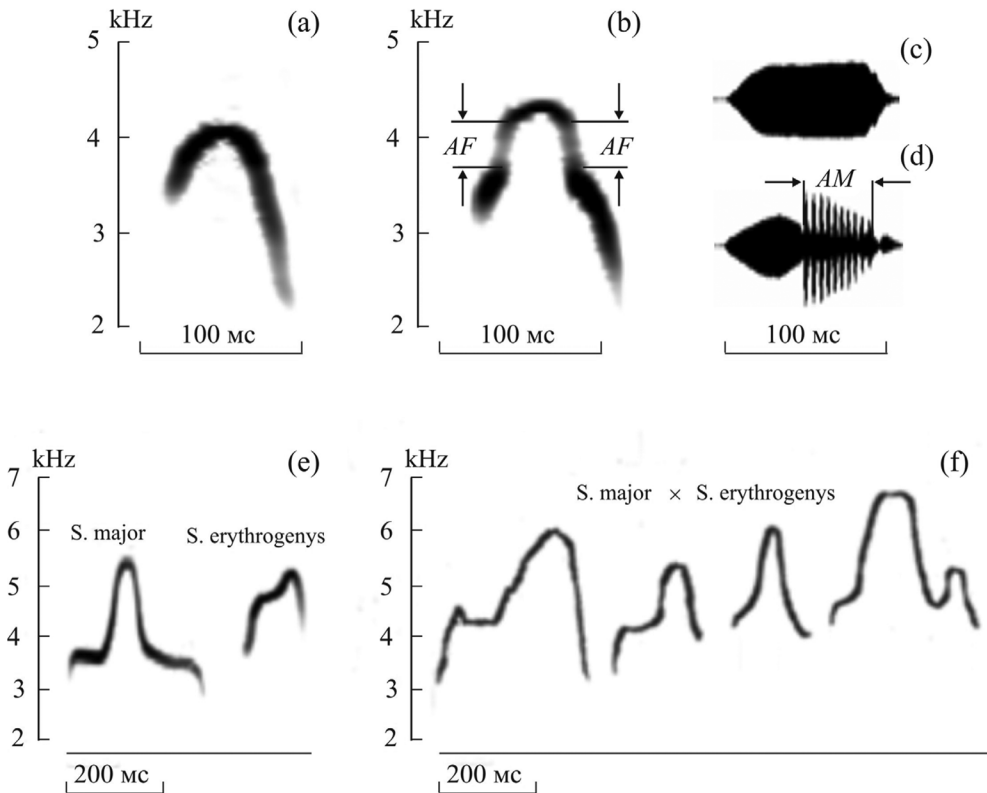


Fig. 3. Aberrations of the alarm call of the steppe marmot and variation of the alarm call in the zone of the secondary contact of russet ground squirrel (*S. major*) and the red-cheeked ground squirrel (*S. erythrogegens*):
a — species-specific frequency modulation in the steppe marmot (*M. bobak*) alarm call;
b — an aberrant frequency modulation in the steppe marmot alarm call; *c* — species-specific amplitude-temporal characteristic of the steppe marmot alarm call; *d* — aberrant amplitude-temporal characteristics of the steppe marmot alarm call; *e* — spectrograms of the alarm call of the ground squirrel parental species; *f* — spectrograms of the alarm call of the ground squirrels in the contact zone;
AF — aberrant phase of frequency modulation; *AM* — amplitude-modulated fragment of the steppe marmot call, which is the most rare aberration

The structure of advertisement calls of domestic sheep and northern fur seals discussed above is also ecologically determined: the amplitude modulation of the signal and its long duration increase the jamming resistance of the transmitted message under conditions of intensive masking noise.

An increase in the jamming resistance of the transmitted messages is a relatively independent trend in the evolution of the structure of the transmitted signals. A prerequisite condition, irrespective of the acoustic properties of the environment, i.e., a communication channel of information transmission, the signal parameters are to reflect the properties of the recipient hearing as for instance, absolute and differentiated frequency thresholds.

The main conclusion from analysis of the variation of mammalian sound signals is that the signal structure is distinguished by augmented sensitivity to the gene flow and relatively independent of the function. Importantly, the variation of the signal genetically determined structure is not associated with the vocal apparatus periphery (the larynx, etc.), but rather with changes in respective parts of the brain respective for vocal activity.

This is supported by the variable characteristics of the frequency modulation of the signals in various species and subspecies of mammals (Figs. 1c, d; 2a, b; 3e; 4e, g; [2, 3, 5, 6, and 12]). (I do not consider here some particular cases of the effect of the periphery on the signal structure, e.g., in the case of the saiga — “an antelope calling through the nose” [17]).

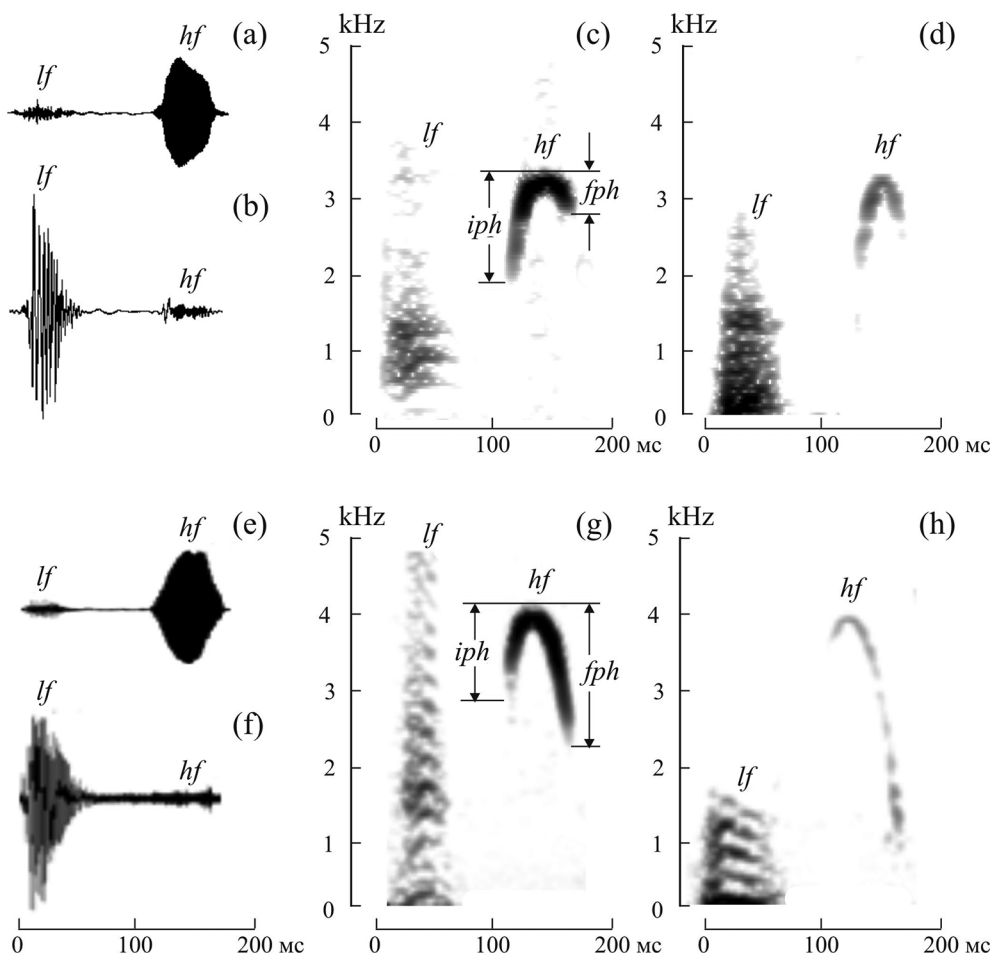


Fig. 4. The divergence and parallelism of the alarm call in the Altai marmot and the steppe marmot. The Altai marmot:

a — amplitude-temporal characteristics of the signal beyond the burrow; *b* — amplitude-temporal characteristics of the signal in the burrow; *c* — spectrogram of the signal beyond the burrow; *d* — spectrogram of the signal in the burrow. The steppe marmot: *e* — amplitude-temporal characteristics of the signal beyond the burrow; *f* — amplitude-temporal characteristics in the burrow; *g* — spectrogram of the signal beyond the burrow; *h* — spectrogram of the signal in the burrow. *lf* — low-, *hf* — high-frequency component; *iph* — initial; *fph* — final phase of the frequency modulation

Incidentally, it is noteworthy that the cultural traditions in acoustic communication (as capacity for vocal learning), including vocal communication, are aimed against the dependence against the genetically-determined structure of sound signals to expand the capacities of inter-population communication.

When performing the basic functions any signal includes two contexts — genetic and situational. The former context includes information about some individual genotypic characters of the signal carriers. The latter provides information of the signal motivation and the motivation factors as physiological and hormonal condition of the communication and the status of communication partners, the external triggers of vocal activity, etc.

The population genetic variation processes of the sound signals are generally understood. In principle, they do not differ from the regularities of the morphological characters and are accountable by genetic-automatic processes of alternation of the panmixia periods and isolation periods, brilliantly described by N.P. Dubinin and D.D. Romashov [1]. Less understood is the effect of selection on the formation an ecologically determined function. For instance, it is not clear why the repertoire of some pika species have a song whereas it is absent from the repertoire of others although there may be no notable ecological differences between the species concerned. Actually, we do not know all the numerous factors concerning the multidimensional space of the species ecological niche.

The variation regularities forming the basic functions of the sound signals are universal. They are common not only among mammals but also in other groups of both vertebrates and invertebrates [7, 8, 15, 16], and, presumably, applicable to the signals of other sensory modalities but not only to sound signals.

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БАЗОВЫЕ ФУНКЦИИ ЗВУКОВЫХ СИГНАЛОВ МЛЕКОПИТАЮЩИХ

А.А. Никольский

Российский университет дружбы народов
Подольское шоссе, 8/5, Москва, Россия, 113093

Все разнообразие звуковых сигналов млекопитающих подчинено двум базовым функциям — функции реализации популяциями генотипа и функции реализации популяциями экологической ниши видов. Базовые функции являются результатом относительно независимых направлений эволюции звуковых сигналов, таких как формирование генетически детерминированной структуры и экологически детерминированной функции. Относительную независимость двух направлений эволюции звуковых сигналов подтверждает изменчивость.

Ключевые слова: поведенческая экология, биокоммуникации, биоакустика, географическая изменчивость, видовая специфика, млекопитающие