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ZOOLOGY

Aberrations of the Alarm Call of the Steppe Marmot, *Marmota bobak* (Rodentia, Sciuridae)

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Abstract—Aberrations, or deviations from the normal type of alarm call, have been studied in the steppe marmot. One regular and several rare aberrations have been identified. The regular aberration manifests itself in all six populations studied, from the Kharkov Region in the west to the eastern border of the Orenburg Region in the east, with its frequency in the populations varying in different years from 10 to 66%. Rare aberrations occur sporadically and not in all populations.

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INTRODUCTION

The term "aberration" in the biological literature refers to a sharp, distinct deviation from the wild phenotype in a certain species. In studies on population phenetics, aberrations are usually attributed to mutations, although direct evidence for this in natural populations in absent, with very rare exceptions (Dubinin et al., 1937).

As shown previously (Nikol'skii, 2007), aberrations manifest themselves in the alarm call of the steppe marmot (*Marmota bobak* Müller, 1776). In this preliminary study, I suggested that aberrations as a variation phenomenon are characteristic of acoustic responses, a major means of communicative behavior in all orders of mammals.

The alarm call of marmots is a convenient model for studying the communicative behavior. Firstly, it is species-specific, as has been repeatedly confirmed in studies on this call among marmots of the world fauna (Nikol'skii, 1976; Blumstein, 2003); secondly, it can be effectively analyzed with the aid of recent computer programs; and, finally, modern equipment allows large scale collection of the material in the field and its long-term storage for further analysis.

MATERIALS AND METHODS

Tape recordings of vocal responses of the steppe marmot to the presence of a human within its field of view were made in the field using tape recorders and microphones operating within a frequency range of 60 to 12 000–16 000 Hz (Nikol'skii, 1984). They were digitized, recorded on a compact disc, and analyzed using a computer with the program SpectraLab v. 4.32.11 for Windows.

The analysis was performed with oscillograms and spectrograms (sonograms) of the alarm calls of 475 individuals from six steppe marmot populations, from the Kharkov Region in the west to the eastern border of the Orenburg Region in the east. In the norm, the alarm call of this species is a sequence comprising an uncertain number of single sounds. The spectral–temporal structure of this signal was analyzed by oscillograms and spectrograms of no less than five (in most cases, 10–20) sounds from the sequence emitted by each individual. The number of sounds considered in each particular case depended on the quality of recording, the number of sounds in the sequence, and their variation.

Frequency–time diagnosis of aberrations was based on four characteristics of the signal:

(1) An amplitude–time characteristic (oscillogram) with a low temporal resolution allows estimation of the rhythmic structure of the signal and the sequence of its constituent sounds.

(2) An amplitude–time characteristic (oscillogram) with a higher temporal resolution makes it possible to estimate the general pattern of changes in the amplitude of the signal with time and, in a first approximation, to reveal its regular amplitude modulation (if any).

(3) A spectrogram (sonogram) makes it possible to reveal deviations in the pattern of frequency modulation and the presence (absence) of additional frequencies not characteristic of the normal signal.

(4) An oscillogram with a high temporal resolution allows deviations from the norm in the fine structure of oscillations to be revealed.

Parameters of the SpectraLab program common to all cases of sound spectrum analysis were as follows: a Hamming smoothing window, a 75% overlap on the frequency axis, and 512 or 1024 rapid Fourier transform points.

General characteristics of the material are shown in the table. The term "population" refers to the groups of

General characteristics of the material and frequencies of regular signal aberration in different marmot populations

Population	Sampling site	Sampling period	Number of animals	Aberration frequency, %
Kharkov 94	Kharkov Region, Velikoburlukskii district	August 1994	41	59
Kharkov 97	»	July 1997	100	66
Kharkov 98	»	July 1998	70	30
Lugansk 69	Lugansk Region, Melovskii district	June 1969	27	19
Lugansk 87	»	August 1987	19	21
Lugansk 88	»	May 1988	55	16
Ulyanovsk	Ulyanovsk Region, Novospasskii and Sengilevskii districts	July 1991	27	19
Grachevka	Orenburg Region, Grachevskii district	June 1997	67	16
Kuvandyk	Orenburg Region, Kuvandykskii district	June 1997	35	9
Svetlyi	Orenburg Region, Svetlinskii district	June 1997	34	10

individuals inhabiting certain sampling sites. The names of populations living in the same sites but sampled in different years have corresponding numerical indices. N.L. Nesterova, A.A. Nikol'skii, E.E. Roshchina, V.N. Rudi, O.V. Soroka, and M.V. Sukhanova participated in collecting the field material in different years.

RESULTS

The alarm call of the steppe marmot was described in detail previously (Nikol'skii, 1974, 1976; Nikol'skii et al., 1983). Basic characteristics of the normal signal are shown in Fig. 1. The signal is a sequence of single sounds monotonically emitted at intervals of several seconds (Figs. 1a). Each sound has a low-frequency component that is followed by a high-frequency component after a pause of several tens of milliseconds (Figs. 1a–1c). In the former, energy is concentrated in a higher frequency range than in the latter (Fig. 1c). The entire high-frequency component is usually filled with quasi-harmonic oscillation (Fig. 1d–1f) (it cannot be harmonic in a strict physical sense, since the basic vibration frequency of vocal cords is subject to random fluctuations; Fant, 1964). Correspondingly, the signal spectrum (Fig. 1c) has the main (dominant) frequencyF_0, which carries the maximum amount of energy, and several harmonics (the first harmonic F_1 is shown in this figure). Higher-order harmonics rapidly fade and can rarely be detected in spectrograms. The frequency modulation pattern of the high-frequency component is asymmetric, with the increase in frequency taking less time than its fading.

Several aberrant forms of the steppe marmot alarm call were detected. One of them, which occurred with a high probability in all populations studied, was named regular aberration. All other aberrations were combined in the group of rare aberrations, as they occurred sporadically and not in all populations.

The regular aberration (Fig. 2) differed from the normal signal in the frequency modulation pattern of the high-frequency component. Its frequency first increases slowly and then abruptly, reaching a fairly long plateau (Fig. 2b, A_{br}); this is followed by an abrupt frequency drop and gradual signal fading. Asymmetry characteristic of the normal signal is also observed in the regular aberration; thus, the signal retains the main diagnostic parameter differing the steppe marmot from other marmots of the bobak group (Nikol'skii et al., 1983).

As in the normal signal, the whole high-frequency component of the aberrant signal is filled with harmonic oscillations (Figs. 2c, 2d), and its spectrum (Fig. 2b) has the main (dominant) frequency F_0, which carries the maximum amount of energy, and several harmonics (the first harmonic F_1 is shown in Fig. 1b).

As noted above, the regular aberration was recorded in every population studied (Fig. 3). However, its frequency proved to vary between populations, reaching a peak in the Velikoburlukskii district of Kharkov Region and decreasing to a minimum in Kuvandykskii and Svetlinskii districts of Orenburg Region. Moreover, its frequency in the same populations (e.g., in the Kharkov population) could also change more than twofold in different years.

There is evidence that deviations from the norm are better manifested when the animals enhance the power of the emitted signal. When the signal is several minutes long and the animal gets tired (the call begins to sound much softer and is no more accompanied by active movements),

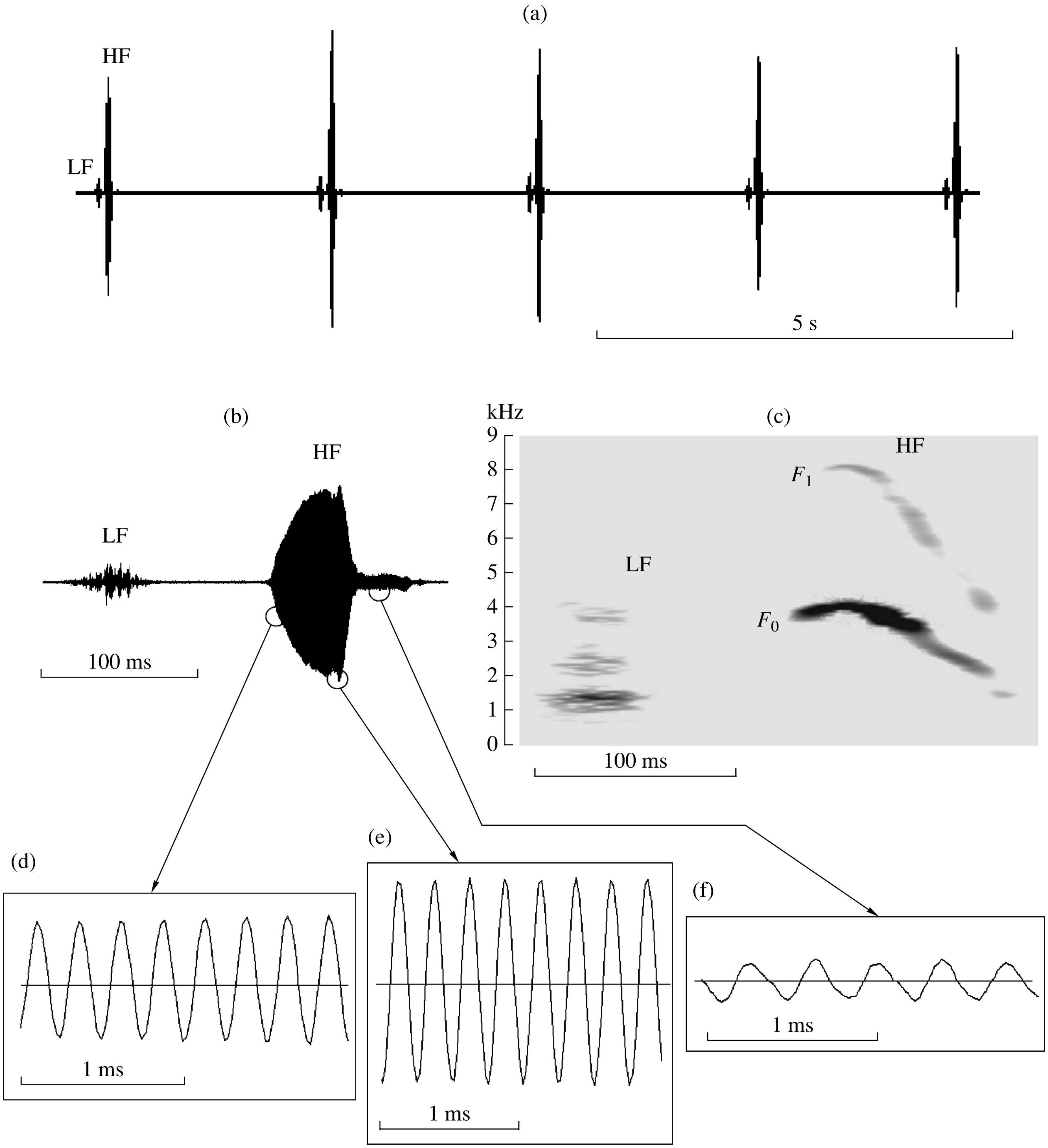

Fig. 1. Normal signal: (a) rhythmic structure (a sequence of five sounds), (b) an oscillogram of one sound, (c) a sonogram of the same sound, and (d–f) oscillograms of fragments of the high-frequency component; (LF) the low-frequency component, (HF) the high-frequency component, (F_0) the main frequency, and (F_1) the first harmonic. Here and in Figs. 2 and 4–9, arrows indicate oscillograms corresponding to the encircled fragments of the high-frequency component.

the spectral structure of the high-frequency component approaches the norm (Fig. 3g, *1–3*). The same tendency is observed in the vocalization of marmots hiding in burrows upon detecting a source of danger (e.g., a human occurring at a short distance or making abrupt movements). Such an animal emits a rapid sequence of cries, with the first cry always being the loudest. In the case of aberrant signals, deviations from the norm are distinct only in this first cry, whereas the following low-intensity sounds in the sequence are usually almost normal.

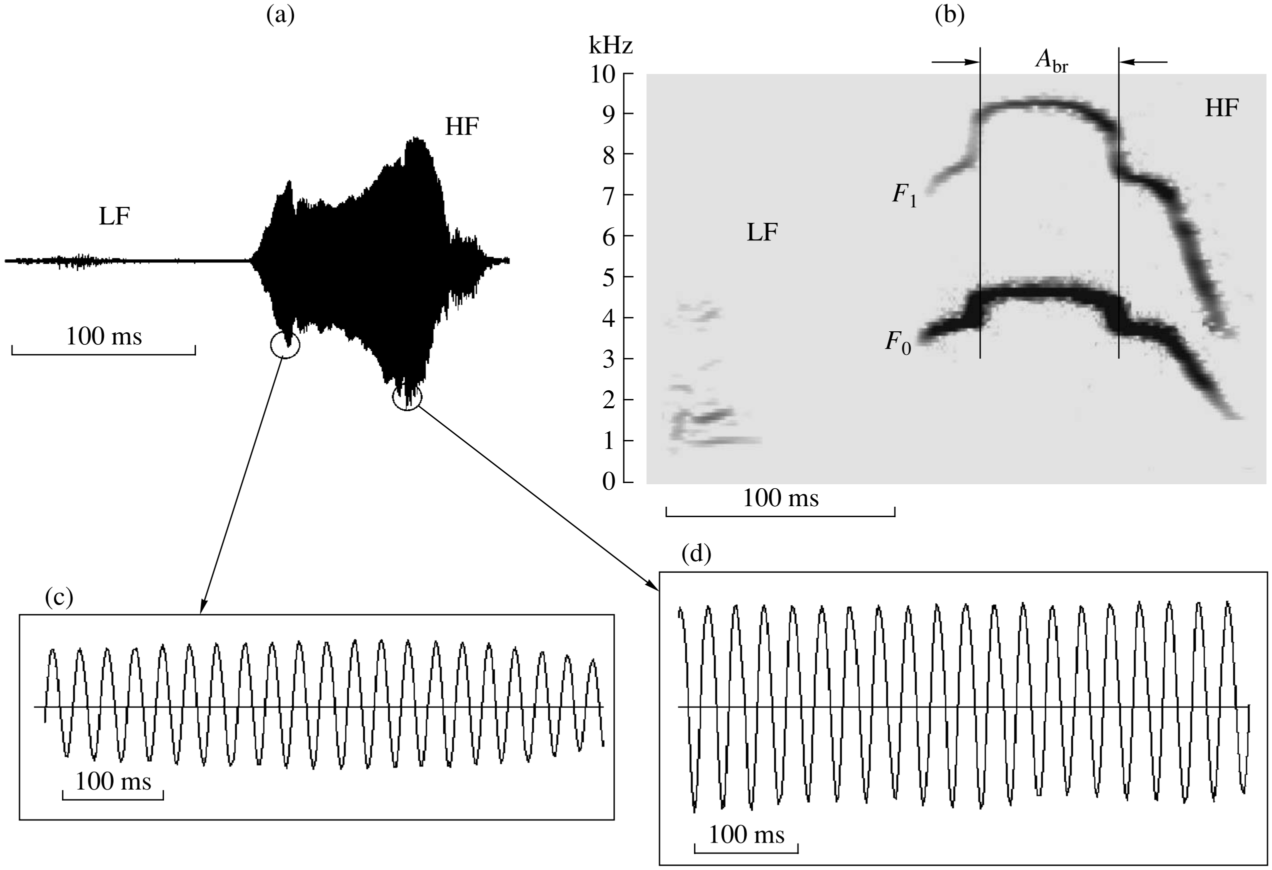

Fig. 2. Regular signal aberration: (a) an oscillogram of one sound, (b) a sonogram of the same sound, and (c, d) oscillograms of fragments of the high-frequency component; A_{br} is the aberrant region of signal frequency modulation pattern.

Rare aberrations can be divided into three subgroups: (1) aberrations in the spectral structure of the high-frequency component, (2) the absence of the pause between high- and low-frequency components, and (3) aberrations in the rhythmic structure of the signal.

Rare aberrations in the spectral structure of the high-frequency component (Figs. 4–7), unlike the regular aberration, are characterized by periodic amplitude modulation. On the whole, four rare aberrations of this type (less than 1% of the total samples (475)) were recorded in three populations: Kharkov (Kharkov 94 and Kharkov 98), Lugansk 69, and Kuvandyk.

The aberration recorded in the Kuvandyk population has the simplest pattern (Fig. 4). The second part of the signal (Fig. 4a) shows profound amplitude modulation, with the period of modulating oscillation being markedly longer than the period of oscillations in the filling frequency of the signal (Figs. 4c, 4d). As expected (Sergienko, 2006; Nikol'skii, 2007), this results in generation of lateral frequencies, in addition to the main frequency and its harmonics (Fig. 4b).

The pattern of aberration recorded in the Kharkov 98 population is similar (Fig. 5). The only difference is that amplitude modulation is observed almost throughout the high-frequency component (Figs. 5a, 5b) and the modulating oscillation frequency is higher (the modulation period is shorter; Fig. 5d) than in the Kuvandyk population. As a result, the lateral frequencies are distributed more loosely (Fig. 5b).

Aberrations in populations Kharkov 94 and Lugansk 69 (Figs. 6, 7) have more complex patterns of oscillations than in the above two cases. The oscillation process can be described in detail only after its physicomathematical diagnosis, which is beyond the scope of this study. Here, both aberrations are described briefly, taking into account published examples of oscillation processes (Sergienko, 2006).

In the aberrant signal recorded in the Kharkov 94 population (Fig. 6), the quasi-harmonic oscillation at the beginning of the high-frequency signal component (Figs. 6a, 6c) passes into the oscillation that probably is a sum of several oscillations with different frequencies (Figs. 6a, 6d). In addition to the main frequency F_0 and its harmonics F_1–F_3 (Fig. 6b), the signal spectrum contains a number of other components.

The aberrant signal recorded in the Lugansk 69 population is characterized by a complex oscillation throughout the high-frequency component (Fig. 7a), which is probably the sum of two oscillations and a

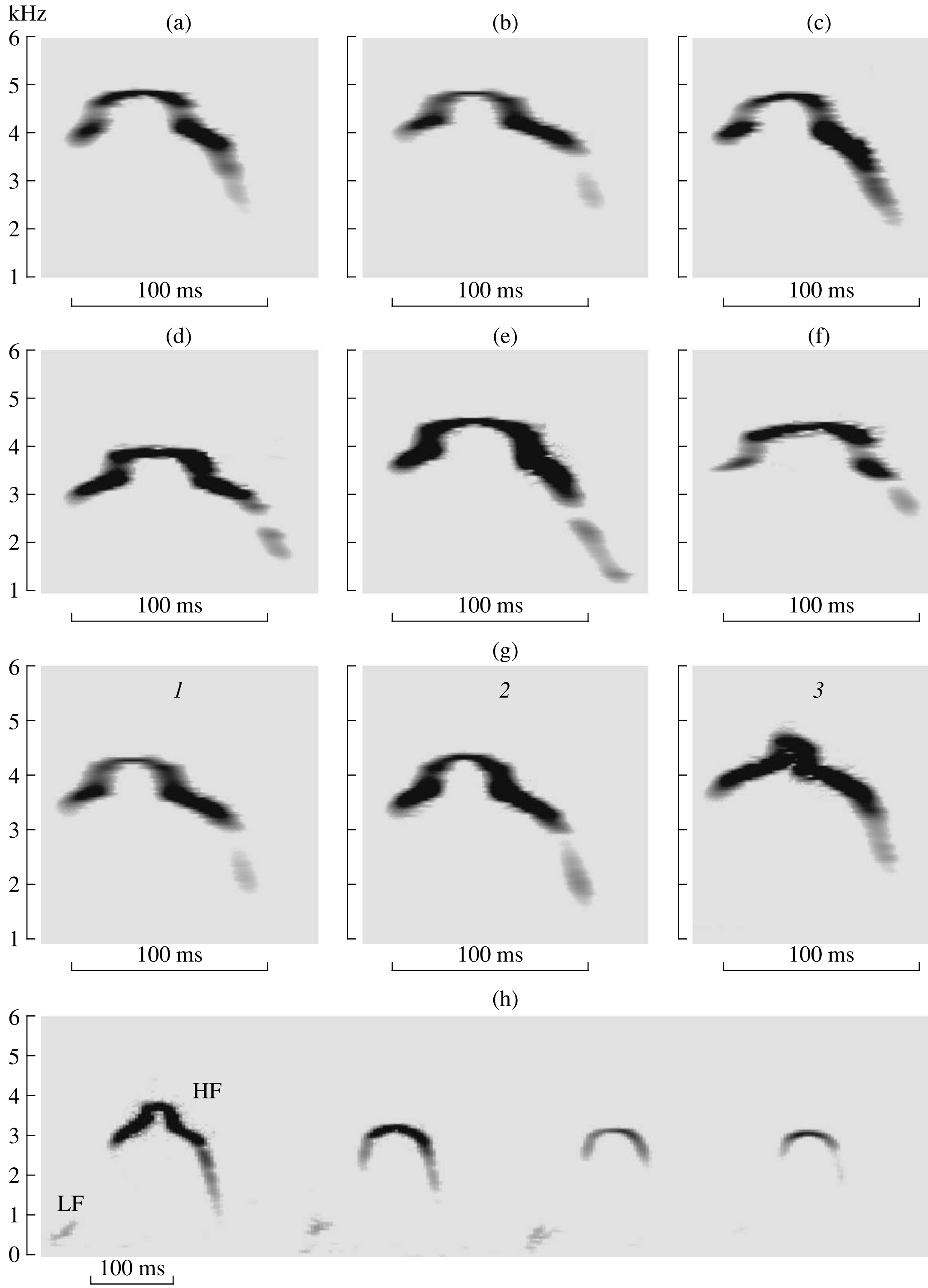

Fig. 3. Sonograms of regular signal aberration in populations (a) Kharkov 97; (b) Lugansk 69; (c) Ulyanovsk; (d) Grachevka; (e) Kuvandyk; (f) Svetlyi; (g) Lugansk 87, individual sounds from (*1*) the beginning, (*2*) the middle, and (*3*) the end of sequence; and (h) Kharkov 97, a rapid sequence of sounds emitted by the marmot hiding in the burrow.

constant component (Figs. 7c, 7d). In addition to the main frequency F_0 and its harmonics F_1 (Figs. 7b), the signal has a few more spectral components. In both these cases, there are reasons to consider summation of two oscillations, which are probably generated by the vocal cords vibrating independently of each other.

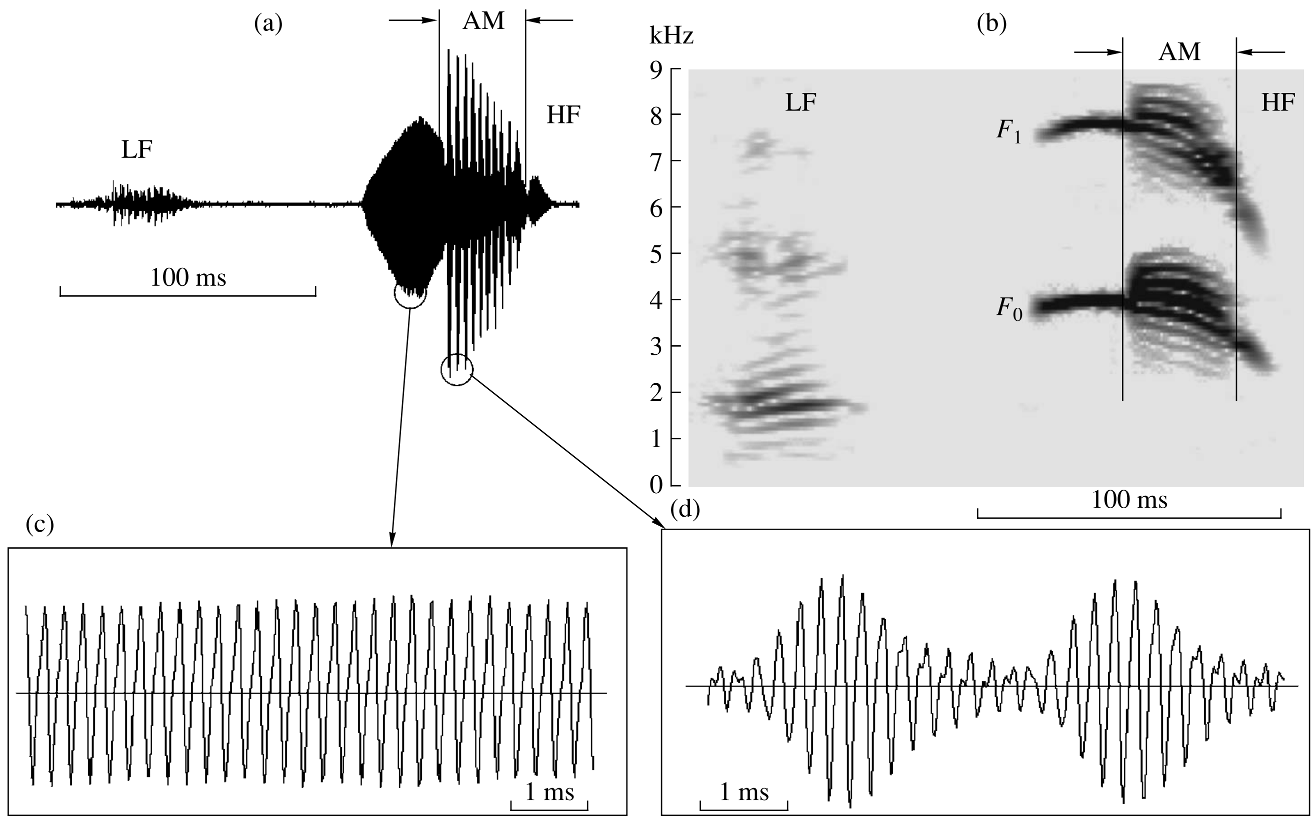

Fig. 4. A rare aberration of the signal spectral structure in the Kuvandyk population: (a) an oscillogram of one sound, (b) a sonogram of the same sound, (c, d) oscillograms of fragments of the high-frequency component; (AM) an amplitude-modulated fragment of the high-frequency component (here and in Fig. 5).

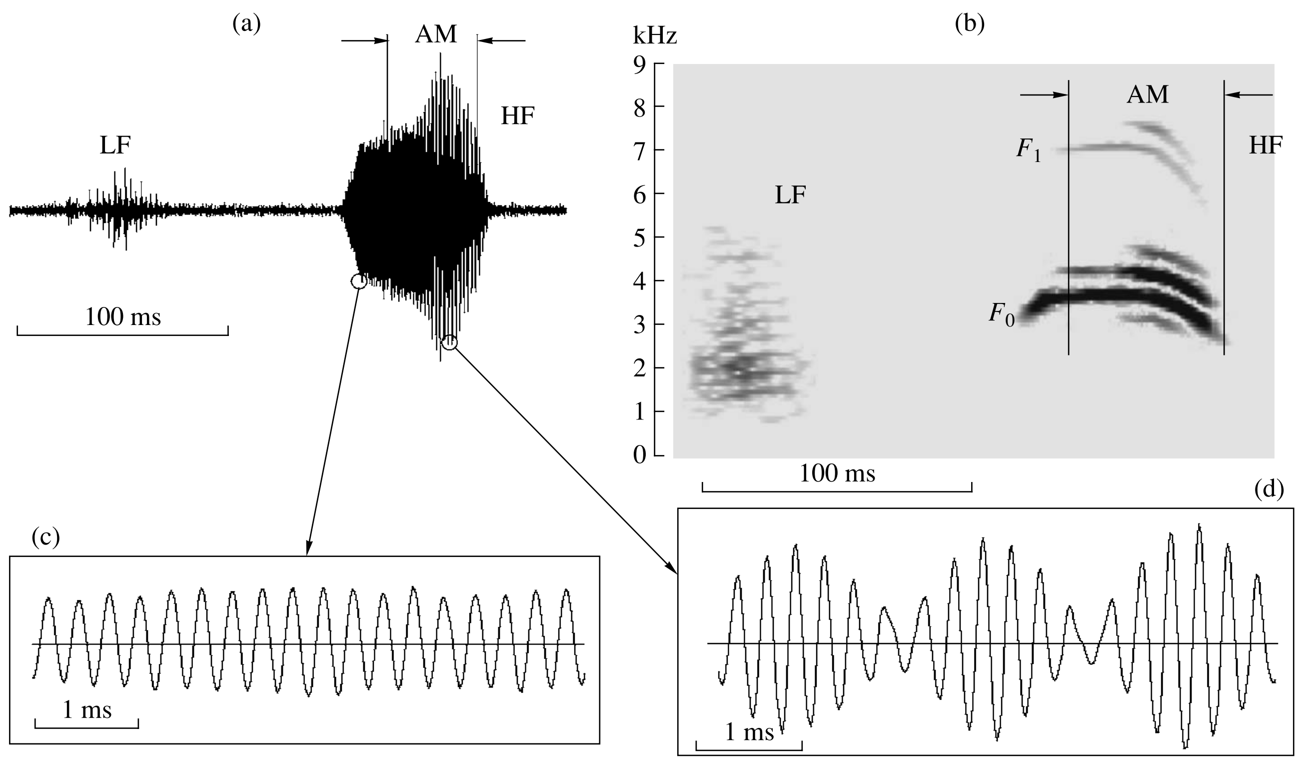

Fig. 5. A rare aberration of the signal spectral structure in the Kharkov 98 population: (a) an oscillogram of one sound, (b) a sonogram of the same sound, (c, d) oscillograms of fragments of the high-frequency component.

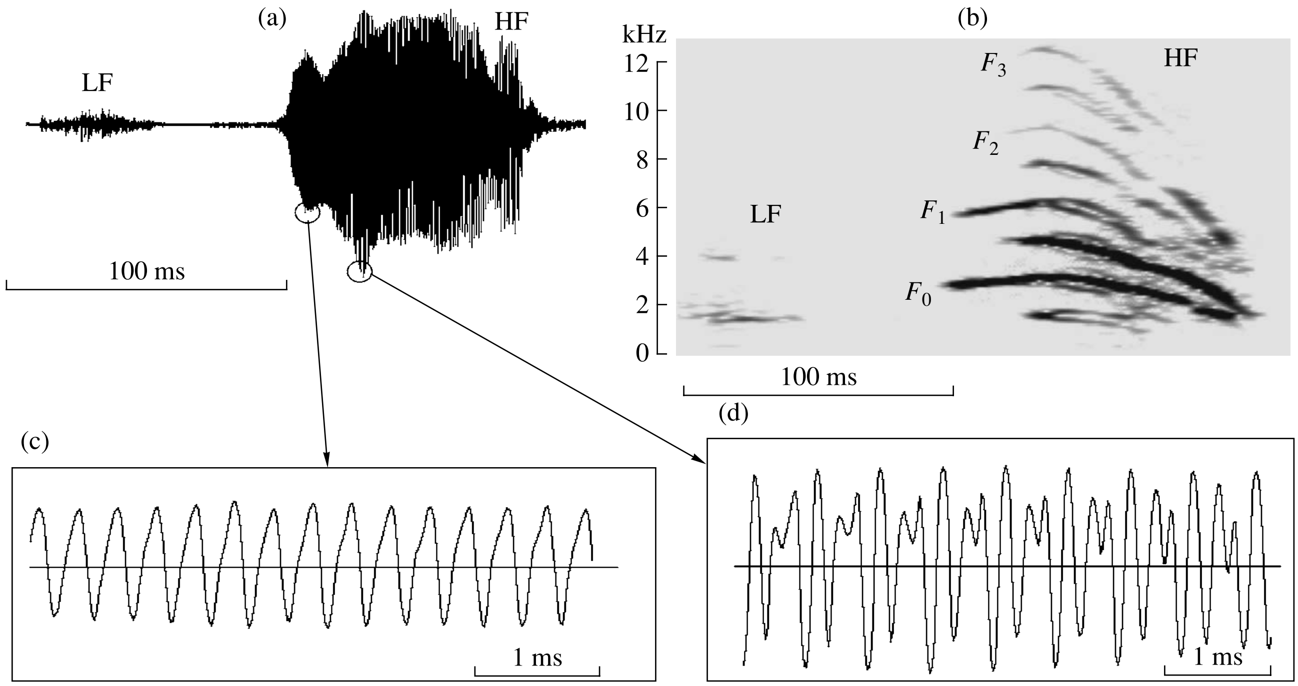

Fig. 6. A rare aberration of the signal spectral structure in the Kharkov 94 population: (a) an oscillogram of one sound, (b) a sonogram of the same sound, (c, d) oscillograms of fragments of the high-frequency component; (F_2, F_3) the second and third harmonics.

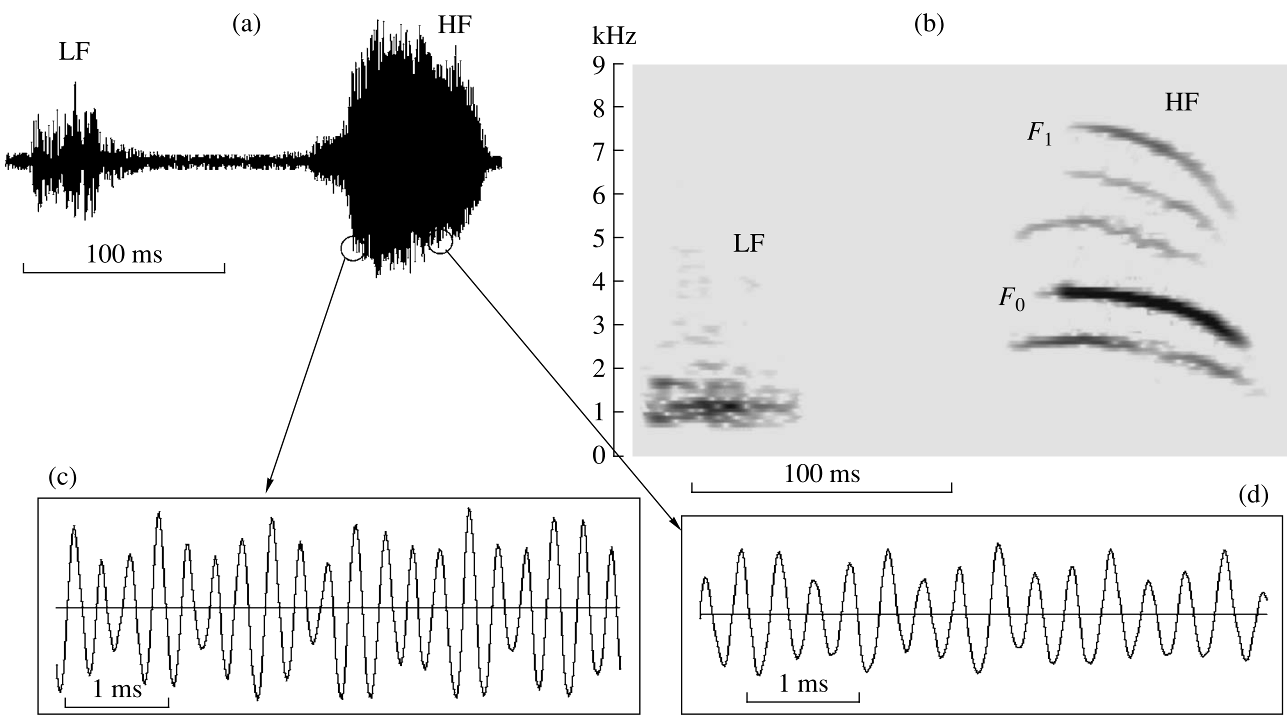

Fig. 7. A rare aberration of the signal spectral structure in the Lugansk 69 population: (a) an oscillogram of one sound, (b) a sonogram of the same sound, (c, d) oscillograms of fragments of the high-frequency component.

The absence of the pause between low- and high-frequency signal components was recorded in the Kharkov 94 population (Fig. 8). The sound filling the pause has a low amplitude and is barely detectable on the oscillogram (Fig. 8a), but the fragment connecting the two components at the main frequency level F_0 is distinct on the sonogram (Fig. 8b). In addition, this aberration is similar to the regular aberration (see Fig. 2) in the absence of any amplitude modulation of the high-frequency component.

Aberrations in the rhythmic structure of the signal were detected in two forms: (1) a short series of rapidly following sounds (Fig. 9a) and (2) a sequence of paired sounds, with the first and second sounds of each pair being separated by a short pause (Fig. 9b). The first was recorded in only one animal from the Kharkov 97 population; the second, in eight animals (23%) from the Kuvandyk population.

DISCUSSION

Aberrations of the steppe marmot alarm call are nothing else than deviations from the norm in control over the vocal apparatus. They are unlikely to result from any abnormal morphological changes, e.g., in the trachea or larynx. The rhythmic structure of this signal (Fig. 9) is initially independent of the vocal apparatus morphology. The regular aberration varies in degree so that the signal may be almost normal (Fig. 3g), and rare aberrations deviate from the norm only in a certain part of the high-frequency component, rather than in this component as a whole (Figs. 4–6). If aberrations were due to some changes in the vocal apparatus, their manifestation in the course of vocalization would apparently be more consistent. Although such a situation cannot be excluded, the results of this study indicate that signal aberrations are apparently a direct result of deviations at the highest level of sound generation control. The corresponding structures include the gray matter near the Sylvian aqueduct and some other brain regions (Vartanyan and Shmigidina, 1990).

In principle, acoustic signal aberrations as a variation phenomenon do not differ from aberrations of morphological characters described previously (Kirikov, 1934; Romashov and Il'ina, 1943; Southern, 1951; Obukhova, 2007): (1) aberrations occur in many characters; (2) their frequency depends on a character, with some aberrations being extremely rare, whereas others occurring in all populations with a high probability (as is the case with the regular aberration of the alarm call); (3) the spatial distribution of aberrations usually has no distinct pattern, but a tendency toward clinal variation is observed in some cases; (4) some populations are especially susceptible to aberrations; and (5) the frequency of some aberrations in the same population may change severalfold in different years.

As noted above, aberrations in the steppe marmot alarm call concern its frequency modulation (Fig. 2), spectral structure (Figs. 4–7), the pause between low- and high-frequency components (Fig. 8), and rhythmic structure (Fig. 9).

The regular aberration (Fig. 2) occurs in all populations studied, with its frequency reaching 66% (table). Other (rare) aberrations occur sporadically and not in all populations.

Some populations within the steppe marmot range are characterized by accumulation of aberrations. This is especially true of the Kharkov population inhabiting the Velikoburlukskii district of Kharkov Region, in which almost all aberrant forms of the signal have been recorded and the frequency of the regular aberration is higher than in all other populations. This fact may be explained by long-term isolation of the Kharkov population from the main part of the species range, which is accounted for mainly by anthropogenic factors (Tokarsky, 2003).

No distinct clinal variation in signal aberrations has been revealed; there is only a tendency toward a decrease in the regular aberration frequency in the west–east direction.

The regular aberration obviously deviates from the normal signal but retains its basic characteristics such as asymmetry in the frequency modulation of the high-frequency component and a relatively long pause between the low- and high-frequency components. Such a mutation can be classified as neutral, which is indirectly confirmed by the results of field experiments on playing tape-recorded signals to steppe marmots of the Lugansk population. Their responses to conspecific calls proved to differ only slightly and nonsignificantly from those to heterospecific calls of the Altai marmot *M. baibacina* (Nikol'skii and Nesterova, 1988). Interspecific differences in the signals concern parameters of frequency modulation and the length of the pause between low- and high-frequency components (Nikol'skii, 1976).

A probable interpretation to the high frequency of aberrations in the rhythmic structure of the signal in the Kuvandyk population (23%) is different. Unlike most steppe marmot populations living in the plains, this population inhabits the Guberlinskie Mountains (the Southern Urals), the region with a moderately dissected topography. The results of previous studies (Nikol'skii, 1974), including those on the Kuvandyk population (Nikol'skii, 2002), show that dissected topography is a factor affecting the rhythmic structure of the signal: the higher the degree of dissection, the more rapid the sequence of sounds in the alarm calls of all marmot species (Nikol'skii, 1984). In mountain species, the signal consists of short series of rapidly following sounds or a sequence of paired sounds, as shown in Fig. 9. The Kuvandyk population lives in the low mountains, which is not characteristic of the steppe marmot, and this aberration of the signal rhythm in it is apparently maintained by selection. Conversely, the Kharkov population lives in the plain landscape typical of the species,

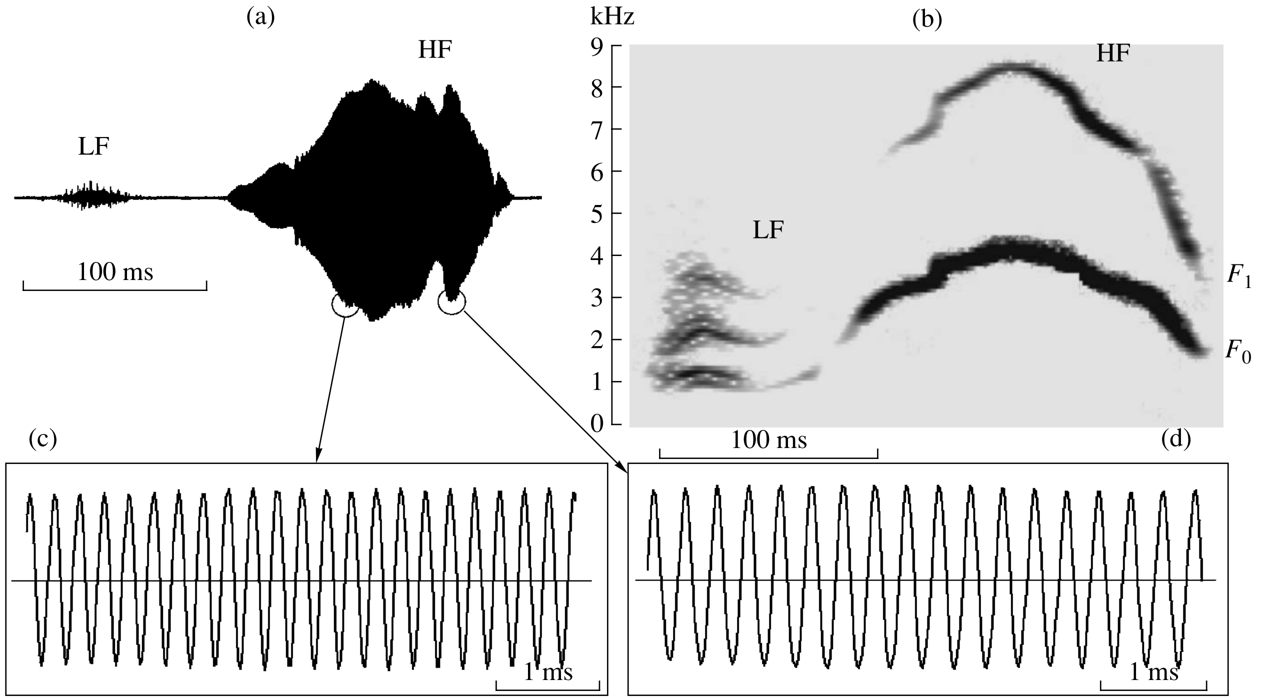

Fig. 8. A rare aberration of the pause between the low- and high-frequency signal components in the Kharkov 94 population: (a) an oscillogram of one sound, (b) a sonogram of the same sound, (c, d) oscillograms of fragments of the high-frequency component.

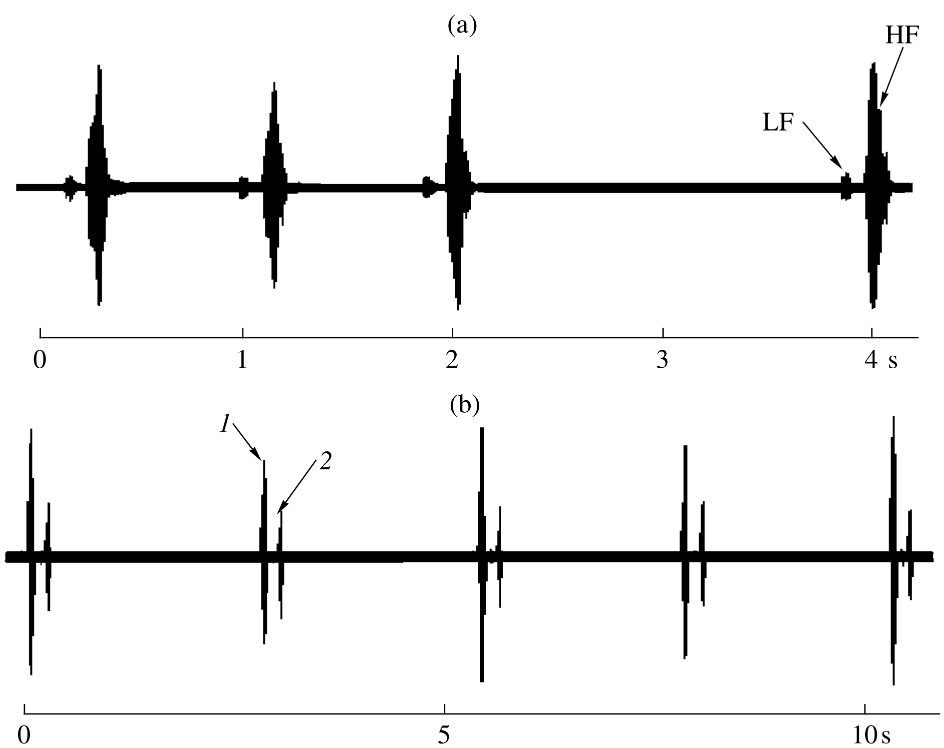

Fig. 9. Aberrations of rhythmic signal structure: (a) short series of rapidly emitted sounds, population Kharkov 98; (b) a sequence of paired sounds, population Kuvandyk (*1* and *2* are the first and second sounds of a pair).

and the low frequency of aberrant rhythmic structure of the signal is evidence for its elimination by selection. The total sample from this population (including Kharkov 94, 97, and 98) consisted of 211 individuals, and such an aberration was detected in only one case (0.47%). A major factor of selection is that marmots are highly responsive to the rhythmic structure of the signal: as shown in field experiments, the rhythm of the signal, compared to its spectral characteristics, has a significantly stronger effect on motor responses of marmots (Nikol'skii and Nesterova, 1989, 1990).

A noteworthy fact revealed in this study is an abrupt decrease in the frequency of regular aberration in the Kharkov population: from 66% in 1997 to 30% in 1998 (table); i.e., its frequency decreased by more than half, while no apparent events were detected in the population in those years. Rapid changes in aberration frequencies are known for morphological characters of some invertebrate and vertebrate species (Dubinin et al., 1937; Southern, 1951).

Signal aberrations result in interspecific parallelisms. The signal regarded as aberrant in the steppe marmot may be normal in other marmots of the bobak group, the Mongolian (*M. sibirica*) and Altai marmots (Nikol'skii, 1974, 1976). The spectrum of the steppe marmot signal resulting from rare aberrations of the high-frequency components (Figs. 4–7) has signs characteristic of the Mongolian marmot signal. The aberration of the pause between low- and high-frequency components (Fig. 8) results in the form of the signal that is typical of the Altai marmot. Aberrant forms of the rhythmic structure of the steppe marmot signal (Fig. 9) resemble the normal signals of the Altai marmot (series) and the Mongolian marmot (the sequence of paired sounds).

There results provide additional evidence for the phenomenon of homologous variation, which, according to the law of homologous series in hereditary variation (Vavilov, 1967), limits the diversity of characters (Dubinin et al., 1937; Rautian and Rautian, 1985).

Considering that all aberrations (except for those in the signal rhythmic structure) apparently result from neutral mutations, it may well be that aberrant forms of the signal accumulate in some populations under conditions of long-term isolation. The probability of such events increases under anthropogenic impact, which is known to result in fragmentation of plant and animal species ranges and, consequently, in increasing isolation of disjoined populations. Since acoustic signaling is involved in this process as well as is communicative behavior as a whole, the accumulated aberrations may be an additional factor of behavioral isolation in cases of secondary contacts between the animals.

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