ISSN 0012-4966, Doklady Biological Sciences, 2008, Vol. 422, pp. 324–327. © Pleiades Publishing, Ltd., 2008.
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GENERAL BIOLOGY

Increased Frequency of the Acoustic Signal Aberrations in the Peripheral Populations of the Steppe Marmot

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Presented by the Academician D.S. Pavlov January 21, 2008

Received February 14, 2008

DOI: 10.1134/S001249660805013X

Analysis of the frequency spectrum of the alarm call from the steppe marmot (*Marmota bobak* Müller, 1776) demonstrated aberrations in all populations throughout the major part of the species area. In the peripheral part, deviations from the normal type were much more frequent than in the center of the area. In biological literature, aberration means a noticeable deviation from the wild phenotype of the species. In population phenetics, aberrations are usually assumed to result from mutations, though this has been confirmed directly only in a few natural populations.

In this study, magnetic recordings of the vocal response of the steppe marmot to the presence of a human in the colony were collected under field conditions. By means of an acoustic signal, marmots alert their neighbors to the potential or real danger, including arrival of humans [1].

The signal was analyzed using the SpectraLab v.4.32.11 for Windows software. In total, the spectrograms obtained from 640 individuals from eight local populations were studied (table). The working names of the populations, their locations (the administrative region and district), and the year of collection are shown below.

(1) Kharkov: Velikoburlukskii raion, Kharkov oblast, Ukraine, 1994, 1997, 1998, 2007. (2) Lugansk: Melovskii raion, Lugansk oblast, Ukraine, 1969, 1987, 1988. (3) Ul'yanovsk: Novospasskii and Sengileevscii raions, Ul'yanovsk oblast, Russia, 1991. (4) Grachevka: Grachevskii raion, Orenburg oblast, Russia, 1997. (5) Kuvandyk: Kuvandykskii raion, Orenburg oblast, Russia, 1997. (6) Svetlyi: Svetlinskii raion, Orenburg oblast, Russia, 1997. (7) Astana: Shortandinskii raion, Akmolinsk oblast, Kazakhstan, 1981. (8) Karaganda: Karkaralinskii raion,. Karaganda oblast, Kazachstan, 1979.

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The local populations Kharkov, Lugansk, and Svetlyi are chronopopulations; i.e., the material was collected in the same place but at different times (table). Two marmot colonies (Nesterivka and Kopanki) were included into the local population Kharkov (table).

The number of observations (n) and the frequency of aberrations (p, %) of the steppe marmot acoustic signal in local populations and in chronopopulations

Populations	n	p
1. Kharkov*:	286	47***
(a) Nestrerivka, August 2–6, 1994**	36	61
(b) Nestrerivka, August 15–24, 1994	43	58
(c) Nestrerivka, 1997	46	61
(d) Nestrerivka, 1998	49	31
(e) Nestrerivka, 2007	51	41
(f) Kopanki, 1997	29	38
(g) Kopanki, 1998	21	29
(h) Kopanki, 2007	11	64
2. Lugansk:	145	37***
(a) Lugansk, 1969**	44	39
(b) Lugansk, 1987	34	47
(c) Lugansk, 1988	67	31
3. Ul'yanovsk	27	19
4. Grachevka	67	16
5. Kuvandyk	35	9
6. Svetlyi:	41	10***
(a) Svetlyi, 1968**	7	14
(b) Svetlyi, 1997	34	9
7. Astana	19	37
8. Karaganda	20	35

* 1–8, Local populations.
** (a–h), Chronopopulations.
*** The weighted average percentage of the aberration frequency in local populations relative to the aberration frequency in chronopopulations.

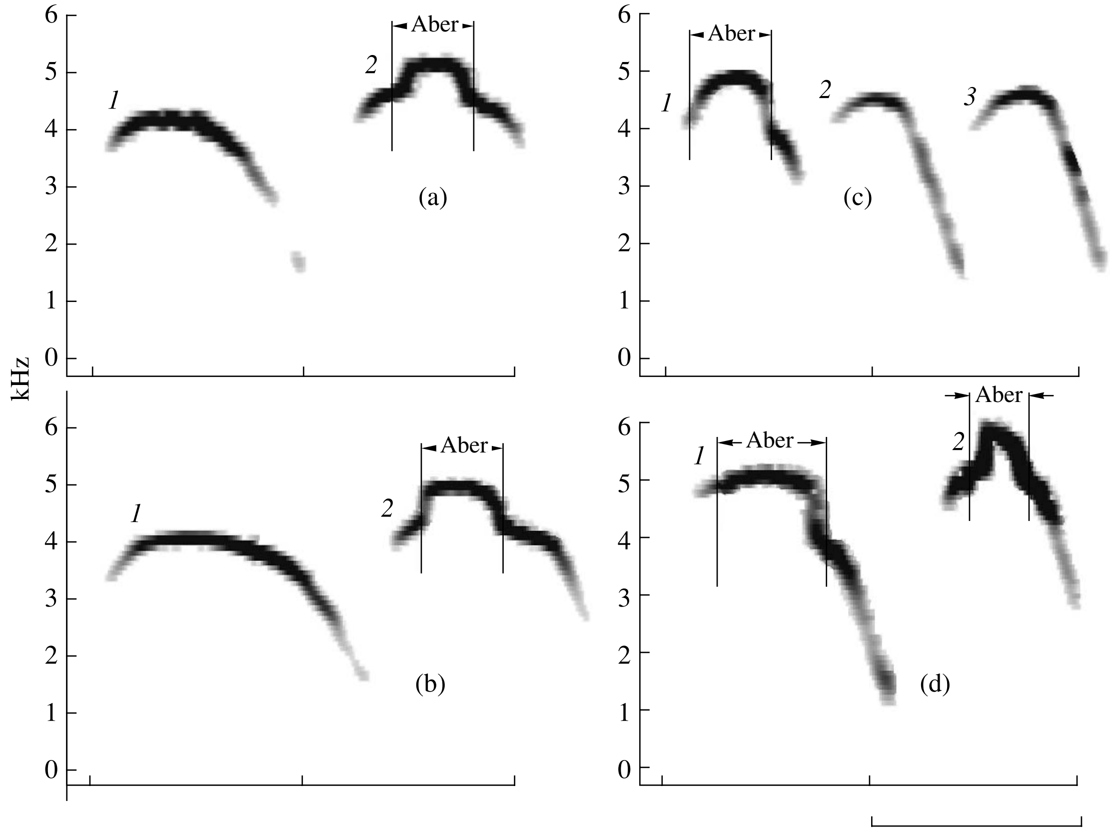

Fig. 1. Spectrograms of the major high-frequency component of the alarm call of the steppe marmot. (a, b) Sibs, local populations (a) Kharkov and (b) Lugansk: *1*, normal signal; *2*, aberrant signal. (c) Local population Karaganda: *1*, female, an aberrant signal; *2* and *3*, offspring, a normal signal. (d) Local population Karaganda: *1*, female, an aberrant signal; *2*, offspring, an aberrant signal. Aber, the region of signal aberration.

These colonies were close to each other (about 13 km apart), but in recent years, anthropogenic obstacles (arable lands, settlements, and roads) separated them. We combined these colonies into the same local population Kharkov for the sake of simplicity; however, it is reasonable to regard then as independent local populations in the future.

In some cases, we recorded signals from undoubtedly related individuals. These were either sibs or a mother and its offspring.

Using a GPS satellite navigator, we determined the spatial coordinates of marmot burrows with normal and aberrant signals.

The steppe marmot signal is normally a sequence of solitary sounds; each including both low- and high-frequency components separated with a pause of several tens of milliseconds [1]. The high-frequency component is represented by a harmonic spectrum. Asymmetric frequency modulation is characteristic of this component (Fig. 1): an increase in the frequency spans a smaller portion of the spectrum than frequency attenuation. Together with some other traits, this one distinguishes the steppe marmot signal from that of related marmot species from the bobak group [2].

An aberration was found in the high-frequency component. The frequency modulation of this component is normally smooth. The frequency increases and decreases gradually. Because of this, the high-frequency component looks like a parabolic curve, which is typical of rodent warning signals [1]. The frequency modulation in the aberrant signal is different: the frequency grows and decreases rapidly (Fig. 1). We were the first to discover this phenomenon.

Signal variations were the following:

(1) Different variants of the presence/absence of aberrant signals were found in groups of close relatives. Some sibs could utter a normal signal, whereas others, an aberrant signal (Figs. 1a, 1b). The progeny of a female uttering an aberrant signal could produce both normal (Fig. 1c) and aberrant signals (Fig. 1d). The material collected was insufficient to determine whether the offspring of a female uttering a normal signal could produce an aberrant signal;

(2) In chronopopulations, the frequency of aberrations could range noticeably; nevertheless, the corresponding local populations differed clearly. For example, in chronopopulations of the local population

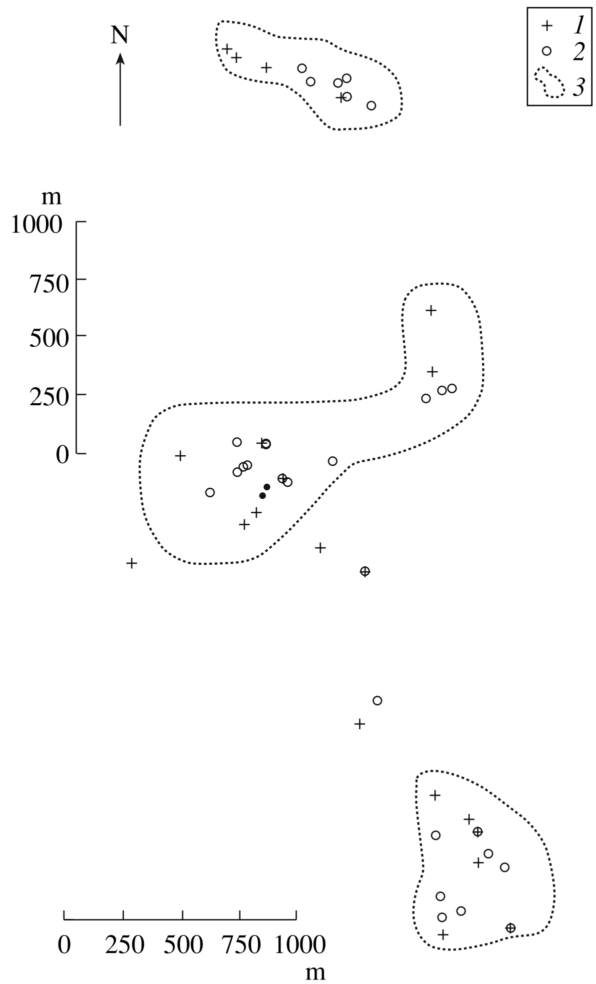

Fig. 2. Spatial distribution of the burrows populated by marmots uttering (*1*) aberrant and (*2*) normal signals (chronopopulation Nesterovka, 2007); (*3*) boundaries of relatively isolated parts of the colony.

Kharkov, the frequency of aberrations was relatively high in all years of the study. Conversely, in the local population Svetlyi, the frequency of aberrations remained low for as long as 30 years (table).

No chronoclines were found for this trait. Probably, longer observations are required to detect them. However, in the chronopopulations separated by a short time interval (two weeks), no noticeable distinctions in the frequency of aberrations were found. This phenomenon was observed in the colony Nesterivka in 1994, where two chronopopulations were determined: Nesterivka, August 2–6, 1994 (the frequency of aberrations was 61%) and Nesterivka, August 15–24, 1994 (the frequency of aberrations was 58%). The material from each chronopopulation was collected by different collectors. Similar frequencies of the aberrant signals produced by two chronopopulations separated by the short time interval indirectly confirm that the demographic and genetic structures of the given population remained unchanged during a short time interval;

(3) Animals uttering the aberrant signal were grouped, though these groups were indistinct (Fig. 2). Probably, marmots with aberrant signals were not found to form distinct aggregations because close relatives producing normal and aberrant signals could occupy the same burrows (Fig. 1).

(4) The frequency of aberrations is significantly higher in the peripheral populations of the steppe marmot (Fig. 3), which confirms previous data obtained on the morphological material of different animal groups [3]. The current area inhabited by the given marmot species is a long but narrow region stretched from Kharkov oblast (Ukraine) in the west to Pavlodar oblast (Kazakhstan) in the east [4]. The local populations Kharkov, Lugansk, Astana, and Karaganda inhabit the most peripheral regions of the species area. An increased frequency of aberrant signals is characteristic of these populations. This "peripheral" effect has been enhanced by a prolonged isolation of these four populations, especially the Kharkov population, from the major part of the species area. In the west, anthropogenic factors (human settlements, large arable lands, and roads) were the main factors responsible for the isolation. In the east, the Turgaiskaya Valley exerts an additional isolating effect. At present, this valley is more an ecological than a geographical obstacle [5]: its bottom, which was previously the bottom of a flow-through lake with a slow current, several hundred kilometers in length [6], is now formed by sodic and saline soils, where marmots cannot live.

Variations of the acoustic signal, like those in morphological traits, confirm the widely accepted notion that deviations from the normal phenotype occur mostly in the peripheral rather than in the central part of a species area. The genetic mechanisms of this phenomenon are related to the fact that the gene flow responsible for metapopulation integrity is interrupted in isolated populations that are not necessarily formally peripheral [3].

Of interest is a wide occurrence of the acoustic signal aberrations. It was characteristic of all local populations studied, though at different frequencies; it is as usual in nature as, e.g., the melanistic coat color of some mammalian species. The communicative processes based on acoustic warning seem to be independent of the aberrations. Anyway, aberrations fail to distort the key parameters of the normal signal; the range of frequencies, duration, and asymmetry characteristic of the high-frequency component of the normal signal are retained in the aberrant one.

Like that of other species of the ground Marmotinae, the acoustic warning signal of the steppe marmot is a suitable model for studying the natural population phenetics, including processes induced by interruption of the gene flow. This is of special interest because fragmentation of the natural habitats has been a common

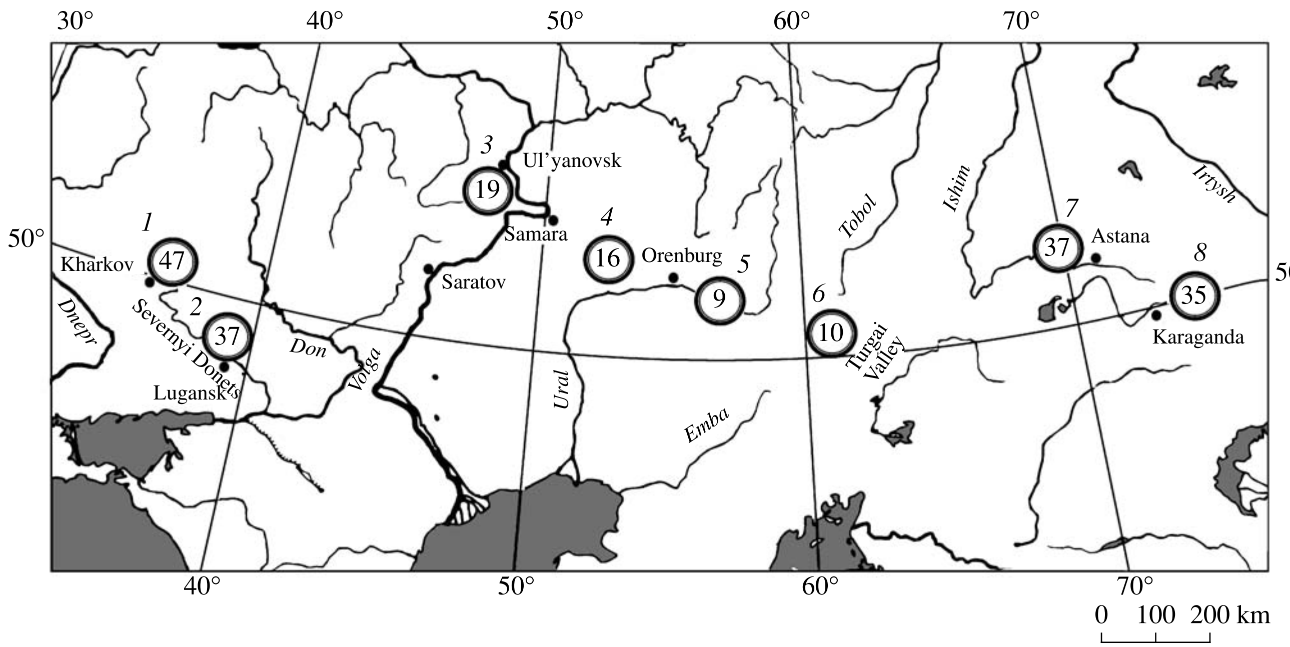

Fig. 3. Distribution of aberrant acoustic signals in a natural habitat of the steppe marmot. (*1–8*) Local populations. Figures in circles indicate the percentage of acoustic signal aberrations in local populations.

phenomenon during the past decades. Mayr [3] rightly noted that the effect of peripheral populations is characteristic of any local population isolated from the genetically integrated metapopulation, and not only at the periphery of the species areas.

ACKNOWLEDGMENTS

I am grateful to N.L. Nesterova, E.E. Roshchina, V.I. Rudi, M.V. Rutovskaya, O.V. Soroka, and N.A. Formozov for the help in collecting the field material; to V.I. Ronkin and G.A. Savchenko for organizing the field studies in Ukraine; to N.S. Vinogradov, I.M. Gribov, and An.A. Nikol'skii for the technical support in the field studies; and to O.A. Ermakov and A.S. Rubtsov for the help in manuscript preparation.

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