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GENERAL BIOLOGY

Glaciation as a Factor of Geographic Variation in the Long-Tailed Marmot (Bioacoustical Analysis)

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Among mammals the ranges of which are affected by mountain glaciation, the long-tailed marmot (*Marmota caudata* Geoffr.) is of particular interest. The pattern of species distribution suggests that the range is intimately associated with the history of glaciation in the highlands of Asia. This species inhabits the Western and Central Tien Shan, the Pamirs, Alai, Kashgaria, Hindu Kush, and Karakoram [1], where it occurs at elevations of up to 5000 m above sea level [2–4].

As glaciation is a potent ecological factor, the population structure of species inevitably bears evidence of glaciation history; the latter is reflected in the patterns of species ranges and geographic variation of animals. Thus, using the geographic variation of marmot vocalization as an example, populations from the Eastern Pamirs were shown to differ substantially from those inhabiting the Trans-Alai Range, Alai Valley, Alai Range, and the Talas Tau [5, 6]. The most probable explanation for this follows from glaciological data, as the Eastern Pamirs were isolated by the glacier for a long time. The data obtained during the last 20 years not only confirm that the geographic variation of the long-tailed marmot is associated with the processes of glaciation in the Pamirs, but also reveal new features of the population structure of this species, correlated with the glaciation in the highlands of Asia (see below).

In this paper, as in previous studies [5, 6], variation in long-tailed marmots is characterized through the variation of an alarm call, a sound signal which animals use to warn neighbors of approaching enemies. This signal is a series of short sounds rapidly following one another and complicated by a deep amplitude modulation. The alarm call as a test character has a number of methodological advantages, as it allows mass examination of animals in the field without killing them; in addition, tape-recorded signals can be input directly into a computer.

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Sound responses of 193 marmots were tape-recorded under field conditions at 16 geographic points in the Northern Tien Shan, Gissar–Darvaz Mountains, Alai, Eastern Pamirs, and in the northeastern part of the Karakoram. Some neighboring populations were combined into groups for convenience of data processing (Fig. 1). We used standard methods of data analysis.

The entire diversity of alarm calls can be divided into two main structural types (Fig. 2): (1) the sound duration increases from the second to subsequent sounds of a series and (2) the sound duration decreases from the beginning to the end of the series. Thus, this characteristic divides the populations into northern and southern groups. The durations of the third and subsequent sounds of alarm calls in these two large population groups differ significantly ($p = 0.95$, Fig. 3). The Bartang, Murghab, and Oxus rivers form the boundary between the groups (see Fig. 1).

In marmots inhabiting the region of the Pshartskii Pass and the upper reaches of the Muzkol and Koikubel' rivers (Fig. 1, populations *6* and *7*), changes in the duration of sounds within a series correspond to the northern type; however, the duration proper is intermediate between those in the main two types, being closer to the northern group (Fig. 4).

A stepwise pattern (see Fig. 3) of geographic variation in the long-tailed marmot allows us to propose that the initially continuous range of this species was divided into parts for some time. As a result, populations that probably deserve the subspecies rank were formed. One subspecies inhabits the Tien Shan, Gissar–Darvaz, and Alai; the second occurs in the Eastern Pamirs and Karakoram. The boundary between these presumed subspecies extends along the Bartang, Murghab, and Oxus rivers. We refrain from using the subspecies names proposed in the literature [1], as the variation and distribution of long-tailed marmot subspecies are extremely poorly understood. The northern and southern population groups come into occasional contact with one another. These contacts are more frequent and regular in the southeastern part of the Pamirs. This follows from the intermediate pattern of alarm call in the populations inhabiting the area between the Muzkol Mountains and Lake Karakul.

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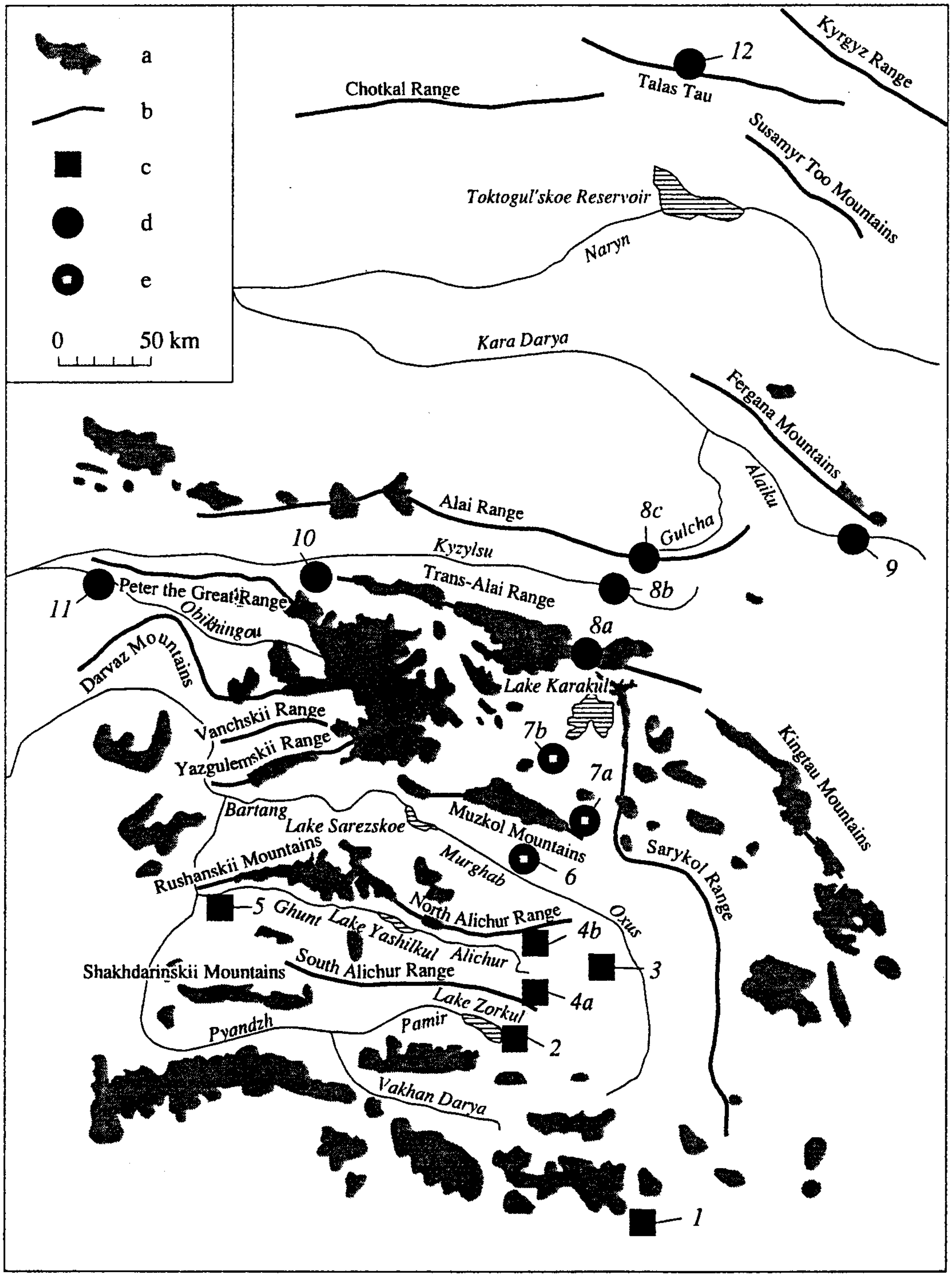

Fig. 1. Sampling sites (local populations of long-tailed marmots): (a) glaciers, (b) mountain Ranges, (c) southern group of local populations, (d) northern group of local populations, and (e) group of local populations with a signal pattern intermediate between the latter two groups (these populations presumably inhabit the zone of secondary intergradation of the subspecies); (*1–12*) populations.

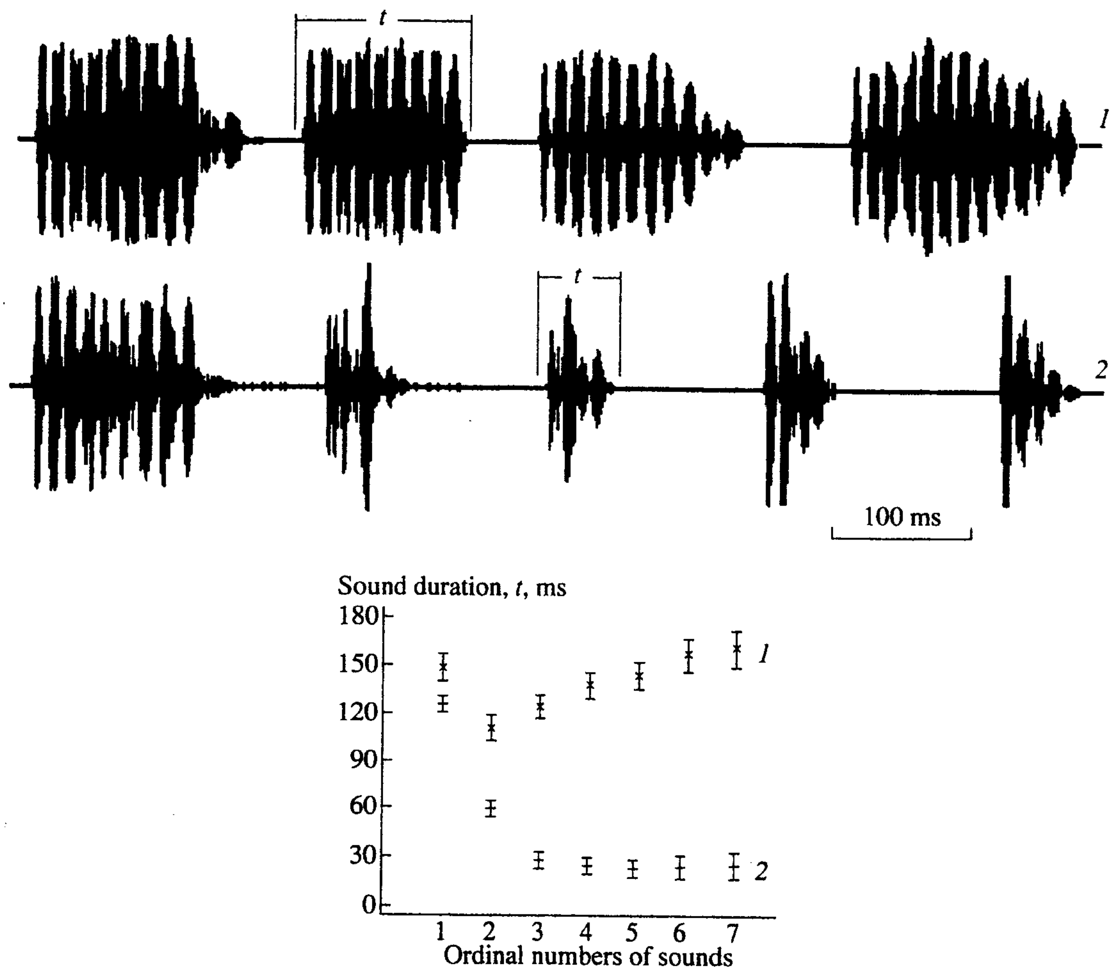

Fig. 2. Examples of the main types of alarm calls in long-tailed marmots: (a) oscillograms of the first sounds of a series and (b) the mean durations ($p = 0.95$) of the first seven sounds of a series; (t) duration of an individual sound of a series (pauses between sounds are reduced by half to save space); (*1*) local population *10* (see Fig. 1), western spurs of the Trans-Alai Range, and (2) local populations *4a* and *4b* (see Fig. 1), northern spurs of the South Alichur Range and southern spurs of the North Alichur Range.

The most probable barrier separating the northern and southern refugia for a long time could be a continuous glacier covering the Pamir Upland in the Late Pleistocene [7, 8]. As the glacial cover regressed, the upland was occupied by marmots from the north and south.

Currently, the contacts between presumed subspecies are weak not only because of the intraglacial position of the Eastern Pamirs [9–12], but also due to some factors accompanying glaciation. This is primarily the *nonsoil structures* [13] and the region of unstable snow cover forming a narrow zone along the Sarykol Range [12]. The nonsoil structures, including the glacial cover, enlarge the area unsuitable for marmots, and unstable snow cover weakly protects animal burrows from freezing during winter hibernation [14].

A comparison between the patterns of marmot occurrence [4] and the distribution of glaciation and accompanying factors shows that the northern and southern population groups are connected only by a narrow zone along the Oxus River. Occasional contact between the population groups occurs through this zone. This is confirmed by certain details of geographic variation in the alarm calls; thus, in 2 out of 13 marmots from population *3* (Kok-Dzhar Stow), the call is of the northern type.

On the assumption that glaciation had a determining effect on the geographic variation of the long-tailed marmot, we propose the following scheme for the historical development of the species range: (1) the Late Pleistocene glaciation was preceded by the expansion of the range; (2) in the Late Pleistocene, the range was disjoined, as the Pamir Upland was covered by glaciers, forming an insurmountable obstacle for marmots; (3) in the Holocene, secondary intergradation restored contact between the northern and southern population groups (subspecies); and (4) marmots inhabiting the

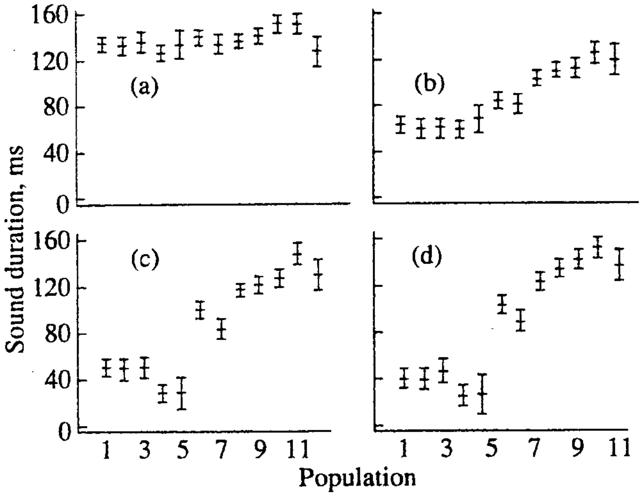

Fig. 3. Mean durations of the first four sounds of alarm calls in long-tailed marmots from different populations (Fig. 1), (a–d) ordinal numbers of sounds.

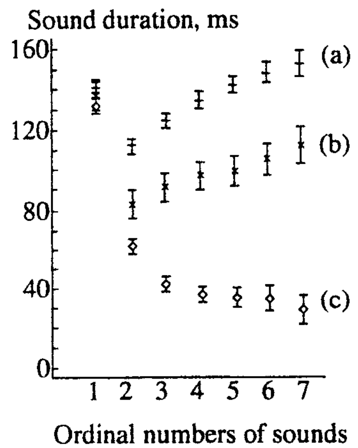

Fig. 4. Mean durations of the first seven sounds of alarm calls in long-tailed marmots from the following population groups: (a) northern population group (Fig. 1, populations *8–12*); (b) group of populations with intermediate characteristics of the signal (Fig. 1, populations *6* and *7*) (these populations presumably inhabit the zone of secondary intergradation); (c) southern population group (Fig. 1, populations *1–5*).

Eastern Pamirs retain a long-term partial isolation, as the upland is still an intraglacial region.

This scheme is not at variance with either early [9] or late [7] models of glaciation development in the Pamirs. Each model probably reflects different stages of Pamir glaciation from the Late Pleistocene to the present.

The upper boundary of marmot distribution [2] correlates with the lower boundary of the glaciers ($r = 0.85$; $p < 0.001$); $H_{max} = 1717\text{ m} + 0.61h_{min}$, where H_{max} is the upper boundary (m) of marmot occurrence and h_{min} is the lower boundary (m) of the glaciers [after 15]. In the Gissar–Darvaz Mountains, long-tailed marmots occur 200–300 m above the lower boundary of the glaciers, whereas in the Eastern Pamirs, they are recorded below this boundary. This is probably attributable to the differences in the glaciation patterns and to the relatively high location of glaciers in the Eastern Pamirs, where many slopes of the valleys are covered with broad slope glaciers [11, 12].

We believe that this study opens up fresh opportunities for glaciology, as it shows that geographic variation of alarm calls in long-tailed marmots can be used as an additional method for studying the glaciation history of the highlands of Asia.

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