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The hibernation temperature niche of the steppe marmot *Marmota bobak* Müller 1776

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Before hibernation, steppe marmots (*Marmota bobak* Müller 1776) close their burrows to prevent convection transfer of heat to the inside of the burrow. As a result, the temperature inside the burrow differs only slightly from that of the surrounding soil. Using data on soil temperature, I described the temperature regime of steppe marmot burrows (depth from 140 to 450 cm) during hibernation (from August to April), within the species and subspecies ranges. Taking into account the total soil depth of the hibernation chamber and the dates for the beginning and end of hibernation, the steppe marmot enters hibernation at a temperature of 8-16 °C, and ends hibernation at a temperature of 2-4 °C. The hibernation temperature regime differs significantly between the subspecies. *M. b. bobak* winters at a temperature of 3-4 °C higher than *M. b. schaganensis*. In the range of *M. b. schaganensis* marmots start hibernation 1 to 2 months earlier than in the range of *M. b. bobak*. The cause of subspecies differences in dates of onset of hibernation appear to lie in the zonal properties of seasonal changes in air temperature. In the course of hibernation, the soil temperature declines gradually at a rate approaching 1 °C per month.

KEY WORDS: steppe marmot, *Marmota bobak*, hibernation, burrows temperature.

INTRODUCTION

The steppe marmot *Marmota bobak* Müller 1776 hibernates 7 to 8 months per year. In contrast to the period of above-ground activity, marmots during hibernation are limited in the use of *behavioral* mechanisms for thermoregulation. Thus, a major requirement to survive long hibernation periods for marmots is a reduction of daily and seasonal temperature fluctuations. In marmots, this is accomplished by a unique behavioral adaptation: before hibernation they seal the burrow with a compact multi-meter plug. The plug virtually excludes heat exchange between the internal burrow environment and the external environment. After sealing, the burrow temperature is dependent on the temperature of the surrounding soil. Thus, marmot burrows are similar in thermal properties to the burrows of other subterranean mammals, such as, mole rats (*Spalax*) (Nikol'skii 2007).

The present-day range of the steppe marmot covers a vast area from west to east, along a narrow strip near the 52nd latitude. In most of the range, steppe marmots are not found above 300 m elevation.

The species *Marmota bobak* comprises two well-defined subspecies: the European steppe marmot, *M. b. bobak*, and the Kazakhstan steppe marmot, *M. b. schaganensis* (Gromov et al. 1965). The boundary between them passes through the Obshchy Syrt Upland (Sludskii et al. 1969). *M. b. bobak* lives under fairly even and moist climate conditions. The range of *M. b. schaganensis* is characterized by a drier climate with higher temperature amplitude during the year. There is reason to believe that these climate differences should influence the temperature regime of steppe marmot hibernation. As it will be shown below, comparative analysis has demonstrated that the hibernation temperature niche of the European subspecies significantly differs from that of the Kazakhstan subspecies. I define "temperature niche", as the entire diversity of temperature conditions of marmots, taking into account the depth of the burrows, season of the year and the geographical situation of local populations.

Previous studies established that steppe marmots begin hibernation between August and October (Sludskii et al. 1969, Shubin et al. 1978, Tokarskii 1997). Within this period, *M. b. schaganensis* starts hibernation 1 to 2 months earlier than *M. b. bobak*. The period for the end of hibernation is relatively short. Within their entire range, marmots appear above ground during March and April (Sludskii et al. 1969, Shubin et al. 1978, Tokarskii 1997)

My objective is to describe the temperature regime of steppe marmot hibernation to include:

1. The temperature of the soil within the species and subspecies ranges.
2. The temperature of the soil at the depth of the hibernation chamber.
3. Seasonal changes in the soil temperature over the period of hibernation.

METHODS

I used soil temperature data from the "Handbook on the Climate of the Soviet Union" (Spravochnik 1965a, 1965b, 1965c, 1965d, 1966, 1967). The *Handbook* provides tables of soil temperature at a depth from 20 to 320 cm, at intervals of 20, 40, 60, 80, 120, 160, 240, and 320 cm.

According to published data, the hibernaculum of steppe marmots is situated at a depth from 140 to 450 cm (Shubin et al. 1978, Tokarskii 1997). Hence, I assume 160 cm as the minimum depth of the soil surrounding the chamber and used that depth

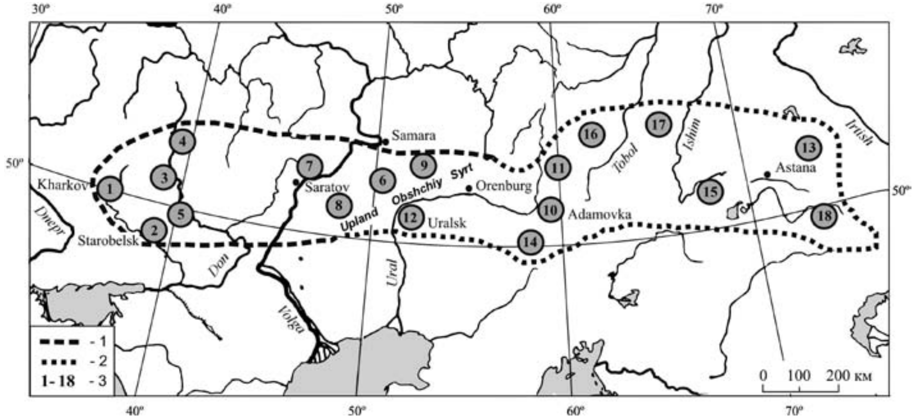

Fig. 1. — Distribution of the steppe marmot, *Marmota bobak*: 1, the boundary of the range of the European steppe marmot, *M. b. bobak*; 2, the boundary of the range of the Kazakhstan steppe marmot, *M. b. schaganensis*; 3, weather stations covering virtually the entire range of the steppe marmot were selected from the "Handbook on the Climate of the Soviet Union". The numbers show the location of the stations.

interval from the *Handbook* to determine soil temperature. To determine the temperature at the maximum depth of 450 cm, an interpolation was used. Temperature interpolation was made for each station and for each month separately, totally 162 equations (18 stations × 9 months).The interpolation used the linear equation $T(h) = a + b_1 h$, where $T(h)$ is the soil temperature in °C, h is the soil depth in m (thus 450 cm = 4.5 m), a is an intercept and b is a slope. Values are calculated separately for each station and corresponding month.

This equation is based on the observation that beginning from some depth the soil temperature is not affected by seasonal changes in ambient air temperature fluctuations. This depth is known as the "neutral layer". As a result, the temperature at a depth of 450 cm can be interpolated in the following interval: the soil temperature at a depth of 320 (stated in the *Handbook*) — neutral layer temperature. Information about temperature and depth of the neutral layer is published in the "Hydrogeothermal Atlas of the USSR" (HIDROGEOTERMICHESKI 1983). Within the range of the steppe marmot, the depth of the upper boundary of the neutral layer fluctuates between 15 to 25 m and its temperature ranges from 5 to 10 °C. In order to determine the depth and temperature of the neutral layer for each weather station, station location were projected onto the map of the "Hydrogeothermal Atlas of the USSR" (HIDROGEOTERMICHESKI 1983). For this study 18 meteorological station sites were selected (9 for each subspecies). The sites represent almost all of the steppe marmot's range (Fig. 1).

RESULTS AND DISCUSSION

Using the 18 meteorological stations, I compared the seasonal changes in soil temperatures at depths of 160 cm and 450 cm from August to April. Soil temperatures within the geographical range of the European subspecies were significantly ($P \leq 0.05$) higher than those of the Kazakhstan subspecies

(Fig. 2). At both soil depths, the seasonal changes in soil temperature are described by a third degree equation: $T_h\ (t) = a + b_1 t + b_2 t^2 + b_3 t^3$, where T_h = mean monthly air temperature °C at the soil depth of (h) 160 cm or 450 cm; t = the time (month) of observations.

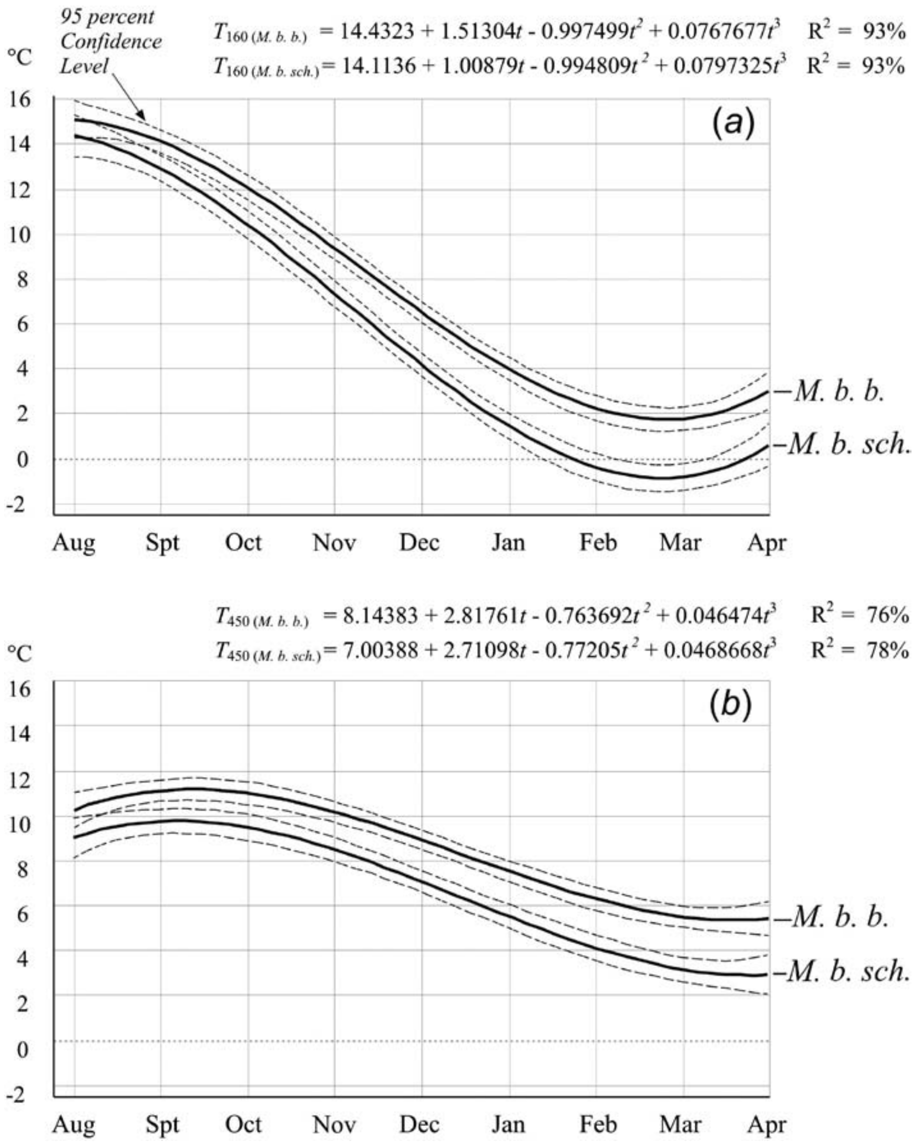

Fig. 2. — Seasonal changes in mean monthly air temperature (T_h) °C at soil depths of (h) 160 cm (*a*) and 450 cm (*b*) over the period from August to April within the range of each of the two subspecies, *M. b. bobak* and *M. b. schaganensis*.

The lines of 95% confidence intervals of each of the pairs of models rarely cross early in the hibernation season, which supports the significant differences in the hibernation temperature regime between the subspecies (Fig. 2).

At both soil depths, *M. b. bobak* hibernates at higher temperatures (by 3-4 °C), compared to *M. b. schaganensis*. Moreover, in the range of *M. b. schaganensis* the temperature of the upper layers of the soil can be below 0 °C. Other conditions being equal, eastern marmots hibernate at a lower temperature. Taking into account the soil temperatures at the level of the hibernacula and the length of the hibernation season, it can be seen that at the metapopulation level, the steppe marmot starts hibernation at a temperature of 8-16 °C, and ends hibernation when the temperature is at 2-4 °C. The maximal seasonal amplitude of the temperature in the course of hibernation within the species range is thus only 14 °C.

Some geographical differences in the soil temperature during hibernation are caused by the normal seasonal longitudinal temperature dynamics. The soil temperature is determined by two major factors — the temperature of the ambient air and the temperature of the neutral layer. The deeper is the hibernacula, the greater is the importance of the neutral layer temperature. Both factors show similar geographic trends: they decrease in an eastward direction. Sentence deleted. Of course, the steppe marmot's range is not a homogenous landscape, nor is the Obshchy Syrt Upland the absolute boundary between the subspecies. It would be unusual to find a homogeneous pattern of change in temperature from west to east, and it would be similarly unusual to expect two discrete sets of temperatures on the subspecies boundary. The selection of meteorological stations east and west of the Obshchy Syrt Upland characterizes the temperature niche of the steppe marmot, which is ideal as any model in ecology. Even under conditions of plain relief, numerous factors create considerable heterogeneity in the range space, disrupting the ideal picture of zonal climate. Although the range of the steppe marmot stretches in a narrow latitudinal strip from west to east, different sections of the range extend to 2-5°, which distort the monotonous pattern of longitudinal changes in the temperature regime.

I performed cluster analysis, where the mean monthly temperatures of the soil at a depth of 320 cm from September to March for every month were used as variables (Fig. 3). The analysis on the one hand supported the correctness of the general classification principles underlying our study, and, on the other hand, revealed some exceptions, which complicate our model. There are four "temperature disparities" in the longitudinal ranking of the 18 observations. The most noteworthy, is the location of the Uralsk meteorological station (Fig. 1, Station No. 12). This deviation is readily explained by the position of the Uralsk meteorological station above sea level (37 m). The most common elevation within the range of the steppe marmot is 150-250 m and accounts for a 1.5 °C lower air temperature compared with that at sea level. In a future study, it would be interesting to examine the geographical variability in hibernation temperature regimes for the steppe marmot based on soil temperature classification rather than by subspecies. In reality, cluster analysis revealed three groups rather than the two groups revealed by subspecies grouping.

As was noted earlier, in the eastern range of *M. b. schaganensis* the onset of hibernation is 1-1.5 months later than in the western range of *M. b. bobak*. But the end of hibernation takes place at roughly the same time throughout the entire range. To date I cannot account for the differences in the dates for the onset of hibernation in marmots. The most probable cause for the difference is the difference in air temperature, both in terms of the mean monthly and the mean monthly minimum during hibernation. During the onset of hibernation, air temperature rapidly declines, which inevitably leads to a lower burrow temperature due to convection dynamics. In the range of the Kazakhstan subspecies, both the mean monthly air temperature and the mean monthly minimum are 2-4 °C lower than those in the range of the European steppe marmot (Fig. 4). If marmots in the eastern range started hibernation in September-October, similar to their European subspecies, the temperature of the soil surrounding the burrow would still be 2-3 °C lower because of active convection. By constructing a plug long before the cold air penetrates deep into the burrow, the marmot prevents excessive cooling before the onset of hibernation.

Prevention by marmots of convective heat exchange between the outer air and the air inside the burrow appears to be of great adaptive importance. Our field observations (Nikol'skii & Savchenko 2002) have revealed that convection begins when the difference between the ground air temperature and the soil attains roughly 5 °C (under experimental conditions the depth of the burrow and the soil was about 2 m). During that time the air temperature

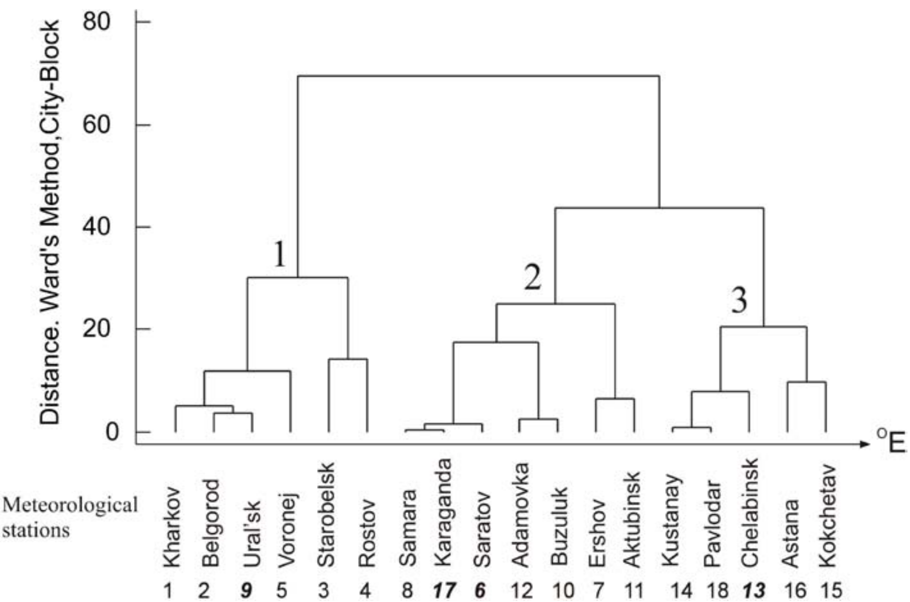

Fig. 3. — The clusters of mean monthly soil temperatures at a depth of 320 cm from September to March for the 18 meteorological stations (see Fig. 1). Stations 9, 17, 6, 13 represent a "disparity" of temperatures within the longitudinal ranking of the meteorological stations.

in the burrow starts lagging behind that of the burrow-enclosing soil. Plugging the burrows in early August, *M. b. schaganensis*, prevent its cooling. As a result, marmots can hibernate at a temperature of about 10 °C. Thus, hypothetically, in the western part of their range, a marmot starts hibernation at a relatively high temperature. Unless they plug the burrows before the end of September, the air temperature in the burrow may be lowered to 10 °C due to convection. If they plug the burrows in September, they start hibernation at about 14-15 °C, which represents actual conditions.

In the western part of the range, marmots have a longer time to remain active above ground before having to plug their burrow. This is because soil and air temperatures are relatively high when the marmots start hibernation.

After the burrow is plugged, the hibernation chamber temperature begins rising to reach that of the surrounding soil. However, the conditions for the recovery of soil temperatures in the west differ from those in the east. Assuming that in both regions marmots start hibernation in late September in burrows cooled by the outside air, it would appear that in the western range, in order to restore the "normal" burrow temperatures, the temperature would have to rise from 11 °C to 14-15 °C, whereas in the east, from 7-8 °C to 10-11 °C. That is, in both regions burrow temperatures rise by the same amount of 2-3 °C. It should be noted that 0 °C is a critical limit of extreme

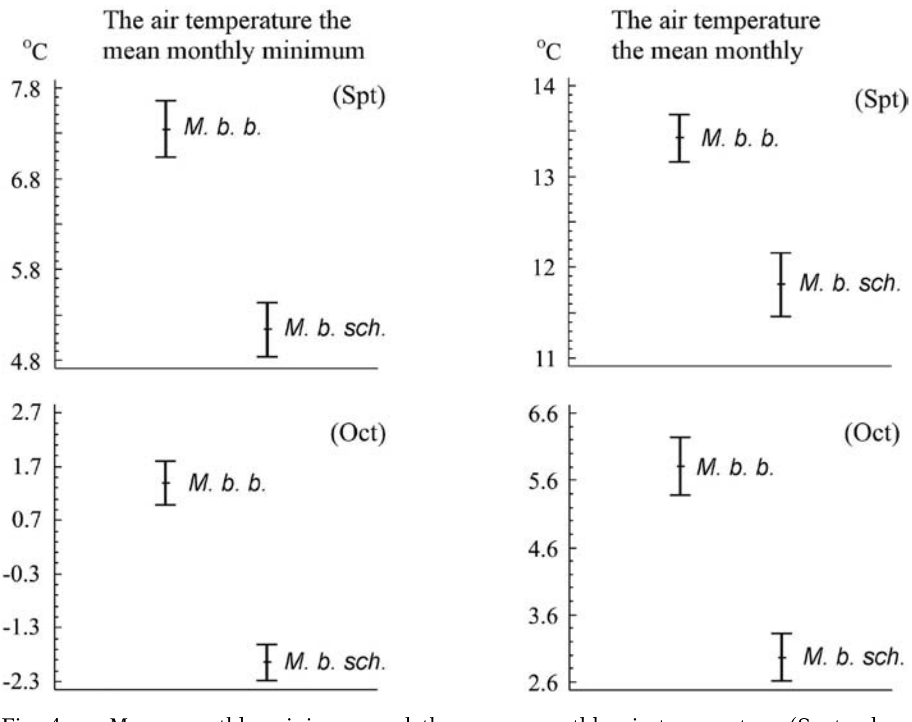

Fig. 4. — Mean monthly minimum and the mean monthly air temperature (September-October) during the onset of hibernation for the two subspecies of steppe marmots.

temperature for survival. Of course, it is can not be excluded that survival of marmots at extremely low temperature is supported by elevation of metabolic rate. For example, metabolic rates during torpor are temperature independent from about 10 ºC to about 5 ºC in *M. monax, M. marmota,* and *M. flaviventris,* but were independent to – 2 ºC in *M. camtschatica* (Armitage 2008). Below 5 ºC oxygen consumption during torpor increases markedly with decreasing ambient temperature. Similar responses occur in *M. marmota, M. monax,* and *M. camtschatica* (Armitage et al. 2003). Further investigations of oxygen consumption during hibernation in *M. bobak* are necessary as it is likely that even a small decrease of temperature below the zone of temperature independence will affect the success of hibernation significantly.

To safely survive hibernation, not only the absolute temperature, but also its dynamics from the onset of hibernation to the appearance of the marmots on the surface is of importance. In the course of 7-8 months within a small seasonal range, the soil temperature at a depth of 3-4.5 m slowly and gradually decreases at a rate of 1 °C per month. Under this temperature regime, it would not be feasible to dig deeper burrows. The gain in stabilizing the burrow temperature and its absolute value would not justify the effort needed to excavate deeper shelters. Theoretically, an ideal depth is that of 8 m. At that depth the soil temperature approaches the temperature of the neutral layer, and the annual amplitude does not exceed 1 °C (Hidrogeotermicheski 1983). However, it would be hard to imagine that there are marmots able to dig such deep burrows.

Naturally, each *local* population is characterized by long-term changes in the dates for the onset of hibernation, which may be caused by various local reasons, such as climate, relief, and soil thermal characteristics. However, those changes do not exceed interspecies differences. I believe that those differences in hibernation onset are based on the predictability of zonal climate properties, which appear to have been the major factors for selection in each subspecies and each local population.

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REFERENCES

Armitage K.B. 2008. Phylogeny and patterns of energy conservation in marmots, pp. 591-602. In: Morris S. & Vosloo A., Edits. 4th CPB meeting in Africa: Mara 2008. Molecules to migration: the pressures of life. *Bologna: Medimond Publishing*.

Armitage K.B., Blumstein D.T. & Woods B.C. 2003. Energetics of hibernating yellow-bellied marmots (*Marmota flaviventris*). *Comparative Biochemistry and Physiology (A)* 134: 101-114.

GROMOV I.M., BIBIKOV D.I., KALABUKHOV N.I. & MEIER M.N. 1965. Fauna SSSR. Mlekopitayushchie. Nazemnye belich'i (Marmotinae) [(Fauna of the Soviet Union. Mammals. Ground squirrels (Marmotinae)]. *Moscow: Nauka* (in Russian).

HIDROGEOTERMICHESKII ATLAS SSSR [Hydrogeothermal Atlas of the USSR] 1983. *Moscow: Mingeo SSSR* (in Russian).

NIKOL'SKII A.A. 2007. Temperature niche of the greater mole rat *Spalax microphtalmus* Güld. (1770). *Russian Journal of Ecology* 4: 293-298.

NIKOL'SKII A.A. & SAVCHENKO G.A. 2002. Air temperature changes in a steppe marmot burrow in the summer-autumn period. *Russian Journal of Ecology* 2: 109-114.

SHUBIN I.G., ABELENTSEV V.I. & SEMIKHATOVA S.N. 1978. Baibak/Surki. Rasprostranenie i ekologiya [Bobak/Marmots. Distribution and ecology]. *Moscow: Nauka*, pp. 10-38 (in Russian).

SLUDSKII A.A., VARSHAVSKII S.N., ISMAGILOV M.I., KAPITONOV V.I. & SHUBIN I.G. 1969. Mlekopitayushchie Kazakhstana (Mammals of Kazakhstan), Gryzuny (surki i susliki) [Rodents: Marmots and ground squirrels, Vol. 1, Part 1]. *Alma-Ata: Nauka* (in Russian).

SPRAVOCHNIK PO KLIMATU SSSR, TEMPERATURA VOZDUKHA I POCHVY [Handbook on the climate of the Soviet Union, air and soil temperatures] 1965a, 1965b, 1965c, 1965d, 1966, 1967. Issue: 9, 10, 12, 13, 18, 28. *Leningrad: Gidrometeoizdat* (in Russian).

TOKARSKII V.A. 1997. Baibak i drugie vidy roda Surki [The bobak marmot and other species of the genus *Marmota*]. *Kharkov* (in Russian).