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AMBIENT TEMPERATURE DURING HIBERNATION AS A FACTOR CONTRIBUTING TO THE DIVERSITY OF ECOLOGICAL NICHES IN MARMOT SPECIES.

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Marmots of different species are phenotypically varied but have very similar lifestyles. Even with a range covering a vast area and varied ecological conditions, species of *Marmota* maintain nearly identical ecological and behavioral characteristics. As a result, differentiation of ecological niches in this genus is not obvious. One of the most interesting and distinctive peculiarities of marmots is their winter hibernation. They spend three to nine months every year in their burrows with their body close to ambient temperature. Variation by species in the conditions and circumstances of hibernation can potentially be studied by direct measurements inside burrows or by mathematical modeling of potentially relevant parameters, such as temperature.

The easiest way to study hibernation is to investigate the duration of hibernation and the construction of burrows where hibernation takes place. Bibikov (1989) noted that variations in the duration of hibernation were more influenced by environmental conditions than by species. The hibernation period of steppe marmot *(M. bobak)*, for instance, ranges from six to eight months in different geographical populations. Many mountain-dwelling species have different periods of hibernation depending on the elevation and orientation of the slope on which they live. Only the most northern species, such as *M. camtschatica, M. caligata,* and *M. broweri* have specifically adapted their hibernation period for survival in harsh winter conditions (Bibikov 1989).

There is no evidence of variation in the depth of hibernacula or other burrow characteristics by species. The exception is the three northernmost species mentioned above, who live where permafrost prevents the construction of deep burrows.

Thus, there are two groups of species in genus *Marmota* with differing hibernation strategies: 'species of permafrost environment' with shallow burrows situated in the thin layer of soil over the permafrost and a long-period hibernation, and 'other species'. This study explores whether there is diversity or homogeneity of hibernation behaviour within the second group of *Marmota*.

M. bobak (steppe marmot) and *M. sibirica* (Mongolian marmot), together with *M. baibacina* (the grey marmot), are joined into the *'bobak'* group of species due to their similar ecology,, external appearance, and supposed relatively recent divergence as separate species. The shared range of these three species spreads for thousands of kilometers from Ukraine in the west to Mongolia and China in the east, making this suite of species good candidate for investigating possible differences in hibernation conditions by species. There has been no observed difference in the construction of the burrows between eastern and western populations (Ryabov, 1948; Shubin, 1991; Tokarskii, 1997). The beginning and end of hibernation occurs at the same time in Ukraine, at the western edge, and in Buryatia, at the eastern edge, of the species' range; extending from the middle/end of September to the beginning of April. Populations in Kazakhstan start hibernation earlier due to the scorching of grass in the end of summer and the resulting lack of a food supply for marmots in the early autumn.

The temperature inside the burrows of two marmot species of different geographical populations was mathematically modeled. The model was based on surface temperature data from reports published by weather stations (Spravochnik po klimatu…, 1965, 1966a, 1966b, 1967) and further estimation of temperature at burrow depth by solving a standard heat equation (ссылка). Method and results have been published previously (see Nikol'skii & Savchenko, 2005; Belovezhets, 2005; Belovezhets, 2006; Nikol'skii, 2009a; Nikol'skii, 2009b; Belovezhets & Nikol'skii, 2012).

Populations of *M. bobak* are found in eastern Ukraine, through the middle Volga and southern Ural region of Russia and into central Kazakhstan. A population of *M. sibirica* occurs in the Buryatia region of Russia..

Annual patterns of temperature variation were similar across all study populations, although absolute values decreased from west to east. The degree of annual temperature variation decreased and the maximum and minimum extremes are delayed at increasing depths below the surface. The delay in temperature fluctuations can be as long as 1.5 to 2 months at the depth of marmot hibernacula (Fig.1).

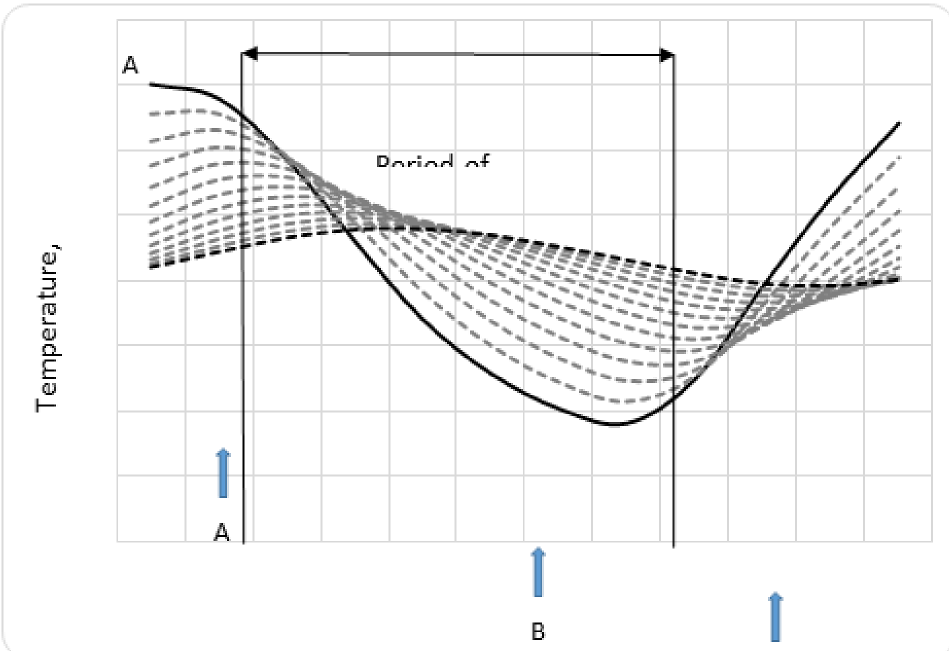

Fig. 1. *A typical pattern of temperature dynamics in the soil over marmots colonies over a year, shown is an example from Ukraine (Kharkov weather station, Spravochik… 1965). The solid line represents a depth of 2 m, the black dotted line represents a depth of 4 m, and grey dotted lines represent intermediate depths. A and B are year maxima and C and D are year minima at 2 and 4 m respectively.*

Investigations of animal physiology during hibernation show a complex and non-linear dependence of energy consumption on ambient temperature (Buck & Barnes, 1999; Armitage et al., 2003; Lee et al., 2009). There is an optimal range of temperature around 5-8°C, where energy consumption is minimized. This temperature range is typical for burrows during the hibernation of western populations of *M. bobak* from Ukraine and the Volga region. A further decrease in temperature forces marmots to spend additional energy to prevent their body temperature from dropping below freezing. Eastern populations of *M. bobak* from Southern Ural region and from Central Kazakhstan spend at least three out of seven to eight months of hibernation in conditions with temperatures lower than 5°C, and in some cases temperatures can fall below zero, especially in more shallow burrows (Fig 2).

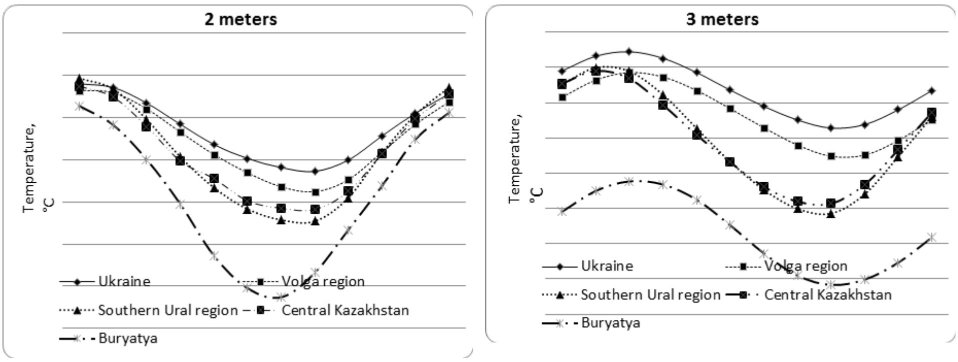

Fig.2. *Temperature in soil of marmot colonies at depths of 2 and 3 m in four populations of M. bobak (Ukraine, Volga region, Southern Ural region and Central Kazakhstan) and a population of M. sibirica from Buryatiya.*

Only the northern edge of *M. sibirica's* geographical range is within the territory of Russia. The temperature of the soil in areas with *M. sibirica* is lower than that within the range of *M. bobak*, and there can be local intrusions of permafrost. *M. sibirica* usually avoids settling in such hostile conditions, preferring more favorable and mosaic environments. Nevertheless, data from weather stations and further modeling show that soil at a depth of 3 m can be below freezing for as long as two to three months during the hibernation period. These results suggest that *M. sibirica* is capable of hibernating in burrows with negative temperatures. Moreover, unlike in populations of *M. bobak*, negative temperature in burrows of *M. sibirica* can be at any depth and animal cannot avoid them by constructing deeper burrows. We can suppose that at least northern populations of this *M. sibirica* regularly hibernate in temperature conditions below freezing.

In summary, we propose that the frequency of sub-freezing temperatures experienced by hibernating marmots potentially differentiates species and populations. . Observed populations can be divided in three groups, those whose burrow temperature:

- never falls below 0ºC (populations of *M. bobak* from Ukraine and Volga region of Russia);

- occasionally falls below 0ºC, depending on relief, burrow depth, and weather conditions (populations of *M. bobak* from Kazakhstan and Southern Ural region of Russia);
- falls below 0ºC regularly and predictably (*M. sibirica* in Buryatia).

These differences in ambient temperature conditions affect patterns of body mass loss during hibernation and fat accumulation activities prior to hibernation. The process of hibernation affects nearly every feature of marmots' lifestyle and our investigation of suggests that variation in the ambient temperature in burrows during hibernation may be one possible source of differentiation in the ecological niches of different marmot species.

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