# Theses of PhD dissertation

**Factors affecting the hibernation in European ground squirrel *Spermophilus citellus* Physiological, behavioral and ecological aspects**

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## Introduction

Hibernation is one of the most mysterious behavioral patterns and a dramatic example of phenotypic plasticity in endotherms. In hibernation, animals spend a considerable amount of time well below euthermic body temperatures. This low body temperature state, called torpor is a hypothermic state which, in contrast to pathological hypothermia, is entered into voluntarily and can be terminated by the animal itself. The animal does not temporarily lose its capability for thermoregulation, rather during the state of torpor, thermoregulation and many other homeostatic regulatory processes are still functional. Ultimately, the primary function of hibernation is to save energy via substantial reduction in metabolic activity.

Torpor bouts during hibernation extend over days, weeks, or even months, but never span the entire hibernation season. All hibernators that have been studied to date, arouse from torpor at regular intervals. As metabolic rate during torpor in hibernators is extremely low, stored energy would last for very long time periods if they remained at these low levels throughout the hibernation season. Therefore, it appears counterproductive that hibernators arouse at regular intervals and use energetically wasteful endogenous heat production. Although many attempts have been made, the enigma of periodic arousals has not been resolved.

Hibernation is a behavioral and physiological adaptation to survive seasonally appearing harsh environmental conditions such as cold weather and food shortage. Hibernators mainly depend on cached fuel stores (fat or food) to sustain their overwintering for six to eight months until spring. Hibernation enhances survival by reduced energy expenditure and predation risk, but consequently hibernation takes a lot of time. The active season in many species is very short, it is just long enough to ensure reproduction and survival. Under these ecological and physiological constraints, the variability of the mating systems of hibernating mammals became rich, similarly to the mating systems of migrating birds. Therefore these species are convenient and popular subjects of studies in the fields of mammalian behavioral ecology and sociobiology.

As some properties of hibernating life style provide certain advantages for hibernating animals (enhanced survival and lifespan) over non-hibernators, the same properties make them vulnerable in a changing environment. As energetics of hibernation are in tight relationship with ambient temperature, ecological factors such as environmental temperature, or climate in a broader sense, greatly influence the life of hibernating animals.

## Aims

This thesis describes a series of investigations between 2002 and 2008, related to the physiological, behavioral and ecological aspects of hibernation in the European ground squirrel (Spermophilus citellus).

The focus of the studies on a physiological level was those inner and outer factors affecting the timing of periodic euthermy.

**a)** the role of water economy in the timing of periodic euthermy

**b)** beyond the effect of ambient temperature and the internal timing mechanism the significant effect of their interaction on the timing of periodic euthermy

**c)** the effect of the actual body mass on the timing of periodic euthermy

We investigated the effect of pre-hibernation behavior on hibernation and the effect of hibernation on reproductive behavior after hibernation, both under lab and natural conditions.

**d)** the effect of the nest constructed before the onset of hibernation on body mass loss during the hibernation

**e)** the relationships among body mass, emergence timing and mating behavior of male ground squirrels and the consequences of different mating behavior strategies in a field study

On the supra-individual organizational level, we investigated the consequences of a hibernating life style in a changing environment.

**f)** the possible effect of climate change on body mass during hibernation using computational modeling

## Materials and Methods

### a) Experimental modification of urine production during hibernation

Nine male European ground squirrels were used in this study. The experimental design was a self-controlled, randomized, two period, two way crossover study. Animals received either one dose of 0.4m/100g diuretics (Furosemide) during the treatment period or the equivalent volume of saline as a vehicle control during the control period. Body temperature fluctuations were measured indirectly via nest temperature using a computerized temperature recording system. To assess the effect of diuretic treatment, the data obtained were statistically analyzed using mixed-effects modeling.

### b) The role of ambient temperature and internal rhythms in the timing of periodic euthermy

In this experiment, groups of ground squirrels (n=5) were hibernated at three different ambient temperatures (0, 5 and 9 °C), under constant light condition. Body temperature fluctuations were also measured indirectly via nest temperature using a computerized temperature recording system. We used the mean of three arousal and torpor events in mid- and late hibernation to test our hypothesis. To assess the effect of ambient temperature and internal rhythms, the data obtained were statistically analyzed using mixed-effects modeling.

### c) The effect of body mass on the appearance of periodic euthermy

Two groups (n=9) of European ground squirrels with experimentally modified pre-hibernation body mass were used to test whether body mass has an effect on the timing of periodic euthermy during hibernation. The elevated body mass group was fed with high calorie diet, the lowered body mass group was fed with low calorie diet during the pre-hibernation period. At the start of hibernation an approximately 60g difference in average body mass was developed between the two treatment groups. Body temperature fluctuations were also measured indirectly via nest temperature using a computerized temperature recording system. To test our hypothesis, the data obtained during the entire hibernation period were used (2007/08). Data were analyzed primarily using mixed-effects modeling.

### d) The effect of nest insulation on body weight loss during hibernation

In this investigation, ten animals began their hibernation period in their self-constructed nests. Two month after the onset of hibernation the animals were firmly replaced and weighed. Physical properties of the nests were recorded (wall thickness, insulation capacity). For data analyses ANOVA and nonlinear mixed-effects modeling were used.

### e) Field observations on males' mating behavior

Our field study was conducted on a natural ground squirrel population in the Bakony mountains during the spring of 2004. Individuals were regularly trapped and weighed after their emergence. The trapped animals were permanently marked during their first capture with a subcutaneous transponder and with a commercial hair dye for facilitating visual observations. Behavioral observations and locations were carried out throughout the mating period. Home ranges were determined using Kernel–method. Data analyses were mainly done using ANOVA and logistic regression.

### f) Simulating the effect of climate change on body mass loss during hibernation

Body mass change during hibernation was determined as a function of time and environmental temperature using differential equations. Population and individual parameter estimations were carried out using population stochastic modeling and nonlinear mixed-effects modeling. We simulated the future body mass change of populations during hibernation using the obtained model and various existing climate scenarios. Model was validated on field study data.

## Results

### a) Experimental modification of urine production during hibernation

The amount of urination increased during diuretic treatment compared to vehicle control. Diuretic treatment resulted in a significant shortening of torpor bout length. Torpor bout length was significantly increased when only saline (without diuretics) was subcutaneously injected.

### b) The role of ambient temperature and internal rhythms in the timing of periodic euthermy

In this experiment, both environmental temperature and internal rhythms had a significant effect on torpor bout and arousal length. Our results showed that in spite of constant thermal conditions, an annual timing effect changed torpor bout length (TBL) at 9 °C and 5 °C but not at 0 °C. The loss in body mass was higher at higher ambient temperatures and was affected by torpor bout length and euthermic phases.

### c) The effect of body mass on the appearance of periodic euthermy

The approximately 60g difference between the average body masses of the groups at the onset of hibernation declined toward the end of hibernation. Body mass loss was significantly higher in the high calorie diet group than in the low calorie diet group. The elevated body mass significantly affected the appearance of periodic euthermy. As the frequency of periodic euthermy increased, the length of torpor bouts was decreased.

### d) The effect of nest insulation on body weight loss during hibernation

The nests constructed showed high inter-individual variability both in physical structure and insulation capacity. The insulation depended only on the wall thickness. The insulation of the nest significantly influenced body mass loss during hibernation

### e) Field observations on males' mating behavior

The timing of emergence differed among male ground squirrels by their body mass and maturity. This relationship was not observable among females. Home ranges of the males substantially overlapped. The number of females within the home ranges was in negative relationship with the timing of emergence. The earlier the male emerged the more the females were within its home range. The frequency distribution of the agonistic interactions among males peaked on the days when mass emergence of the females occurred. The body mass change of the males was in negative relationship with number of females in their home range and with number of agonistic interactions.

### f) Simulating the effect of climate change on body mass loss during hibernation

According to the results of the simulations, the body mass of the ground squirrels at their emergence will decrease with 4-6% during the 2071-2100 projected period, in comparison with the control period of 1961-1990. There was no difference in the emergence body mass after the warm and normal winter on the field. Although modeling predictions fell in body mass ranges similar to those measured on the field, the model predicted a small, but significant difference in emergence body mass between the warm and the normal winter.

## Conclusions

**a)** Results of our experiment supports the role of water economy in the appearance of periodic euthermy. Although our study did not identify the underlying mechanism, our results support the view that water economy, and water loss may play a role in the timing of periodic arousals.

**b)** Similarly to the former studies, we could show the effect of both the environmental temperature and the internal rhythms on the appearance of periodic euthermy. Nevertheless, the disappearing circannual rhythm in the timing of periodic

arousals can rather be explained by a modification in the function of the central nervous system under low temperature conditions.

**c)** The appearance of arousals directly influences body mass change during hibernation, via increasing energy requirement. Therefore, the effect of body mass on the appearance of periodic euthermy is part of a negative feed-back loop in the regulation of the torpor-arousal pattern. This feed-back loop provides an opportunity for individual optimization of the timing of arousals, on a cost-benefit ground.

**d)** Nests constructed before hibernation influence the success of hibernation. As better insulating nests allow animals to emerge with higher body mass in the spring, nest building behavior affects the mating opportunities and reproductive success, as well as overwinter survival.

**e)** Earlier timing of emergence provides advantages for males in the competition for females. The earlier timing of emergence and the competition among males cause surplus cost exhibited primarily as body mass loss. This finding can be interpreted as an example of a costly phenological strategy of the mate limited sex (male) to be present on the breeding ground when the mate limiting sex (female) appears on the ground.

**f)** Short term disturbances in the body mass cycle of hibernating animals can be compensated by the animals themselves or by the advantageous side effects of climate change (extended active period, enhanced primer production), but these perturbations, along with other disturbances by human activities, might have serious consequences on population dynamics on a longer time scale.

# Publications

## Journal articles

István Németh, Viktor Nyitrai, András Németh and Vilmos Altbäcker (2009): Diuretic treatment affects the length of torpor bouts in hibernating European ground squirrels (*Spermophilus citellus*). Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 180: 457-464
IF: 1.698 (in 2008)

István Németh, Viktor Nyitrai and Vilmos Altbäcker (2009): Ambient temperature and annual timing affect torpor bouts and euthermic phases of hibernating European ground squirrels (*Spermophilus citellus*). Canadian Journal of Zoology 87: 204 – 210
IF: 1.493 (in 2007)

Csongor Gedeon, Gábor Markó, István Németh, Viktor Nyitrai and Vilmos Altbäcker (accepted): Nest material selection affects nest insulation quality in the European ground squirrel (*Spermophilus citellus*) Journal of Mammalogy

Nyitrai Viktor, Németh István és Altbäcker Vilmos (2005): A külső hőmérséklet hatása a közönséges ürge (*Spermophilus citellus*) hibernációjára. Állattani Közlemények 90, 63-74

## Book section

Váczi Olivér, Németh István és Altbäcker Vilmos (2007): Közönséges ürge (*Spermophilus citellus*). In: Bihari Zoltán, Csorba Gábor és Heltai Miklós (ed.). A magyarországi emlősök atlasza. Kossuth Kiadó, Budapest, 140-143 pp.

## Lectures

Németh István és Altbäcker Vilmos (2009): A klímaváltozás hatása az emlősök hibernációjára. 8. Magyar Ökológus Kongresszus, Szeged

István Németh, Éva Szabó and Vilmos Altbäcker (2006): Air conditioned hibernation. Proceedings of Second European Ground Squirrel Meeting. Lynx. 39 (2) 350

Csongor. I. Gedeon, Gábor. Markó, István. Németh, Viktor Nyitrai and Vilmos Altbäcker (2008): The importance of nest material selection in nest insulation quality in the European ground squirrel (*Spermophilus citellus*). Proceedings of Second European Ground Squirrel Meeting. Lynx. 39 (2) 346-347

István Németh, Viktor Nyitrai and Vilmos Altbäcker (2006): The effect of temperature and season on the hibernation pattern. First European Ground Squirrel Meeting, Felsőtárkány, Hungary

Viktor Nyitrai, András Németh, István Németh and Vilmos Altbäcker (2006): Possible causes of periodic arousals. First European Ground Squirrel Meeting, Felsőtárkány, Hungary

Németh István, Nyitrai Viktor és Altbäcker Vilmos (2004): A külső hőmérséklet és a szezonalítás hatása a közönséges ürge hibernációjára. IX. Magyar Etológiai Kongresszus, Göd

Németh István, Váczi Olivér, Altbäcker Vilmos (2000): Ürgék időbeli aktivitásmintázatát befolyásoló környezeti tényezők VIII. Magyar Etológiai Kongresszus, Visegrád

## Poster presentations

Szövényi G., Puskás G., Orci K. M., Németh I. (2006): Két gyeplakó sáskafaj mozgásmintázata és mikrohabitat használata egy fragmentált élőhelyen. 7. Magyar Ökológus Kongresszus, Budapest

Éva Szabó, Tímea Bernáth, István Németh and Vilmos Altbäcker (2005): Condition dependent mating investment in the European ground squirrel. XXIX. International Ethological Conference, Budapest, Hungary.

Viktor Nyitrai, István Németh, and Vilmos Altbäcker (2005): The effect of season and ambient temperature on the hibernation pattern in European ground squirrel (*Spermophilus citellus*). XXIX. International Ethological Conference, Budapest, Hungary.

István Németh, Éva Szabó, Tímea Bernáth, Viktor Nyitrai & Vilmos Altbäcker (2004): Condition dependent mating investment in male European ground squirrels. 10th International Behavioral Ecology Congress, Jyväskylä, Finland

István Németh, Luis Rios, Olivér Váczi, Vilmos Altbäcker (2002): Condition dependent mating investment in male European ground squirrel. Ecology and conservation of European ground squirrel, Ecology and conservation of the European souslik, Madjarovo, Bulgaria

Ildikó J. Türke, Olivér Váczi, István Németh, Vilmos Altbäcker (2002): Can food shortage cause population density decrease in European ground squirrel? Ecology and conservation of European ground squirrel, Ecology and conservation of the European souslik, Madjarovo, Bulgaria

Németh István, Luis Rios és Altbäcker Vilmos (2002): A közönséges ürge hímek szaporodási viselkedésének vizsgálata (Spermophilus citellus) I. Magyar Természetvédelmi Biológiai Konferencia, Sopron