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# Seasonal and diurnal variability of the body temperature in the northern white-breasted hedgehog (*Erinaceus roumanicus*) in normothermia

**Marina V. Rutovskaya* & Michail E. Diatroptov**

ABSTRACT. Both during hibernation at normothermia and while the animals are active in summer the body temperature of hedgehogs fluctuates significantly in the range from 26 to 38°C. Seasonal variability in body temperature is related to reproduction and ambient temperature. During the breeding season in May and June, the body temperature of hedgehogs is significantly higher in both males and females comparing to other seasons. This is probably due to the period of active reproduction and seasonal variability in the hormones' content in blood. The average daily body temperature in hedgehogs correlates with the ambient temperature in the summer months — May and June, when the night air temperatures do not differ much from those during daytime one and are of the optimal range for hedgehogs. In spring, at the end of summer, and in autumn, the ambient temperature may drop significantly, being out of the optimal range, and the animal body temperature does not always follow the ambient temperature changes, so no reliable correlation between them are observed. The body temperature of hedgehogs during the day is not constant: during the daytime rest in summer period, most hedgehogs have a lower body temperature, which probably saves energy. During the non-hibernation period, females usually have a higher body temperature comparing to males, which may be associated with physiological features and, in particular, with a higher metabolism. The photoperiod affects the duration of activity of hedgehogs and, accordingly, the time during which the body temperature of hedgehogs is elevated at night. During normothermia at the hibernation period, ultradian rhythms are observed for the animal body temperature with periods of 4.0–4.3 h; apparently, they are masked by the influence of other factors during the period of activity of hedgehogs.

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# Сезонная и суточная изменчивость температуры тела белогрудого ежа *Erinaceus roumanicus* в нормотермии

**М.В. Рутовская*, М.Е. Диатроптов**

РЕЗЮМЕ. Как при гибернации во время нормотермии, так и в активное летнее время, температура тела ежей значительно колеблется в диапазоне от 26 до 38°С. Сезонная изменчивость температуры тела связана с размножением и температурой окружающей среды. В период размножения в мае и июне температура тела ежей достоверно выше и у самцов, и у самок, чем в другие месяцы. Вероятно, это связано с периодом активного размножения и сезонной изменчивости концентрации гормонов в крови. Среднесуточная температура ежей имеет корреляцию с температурой окружающей среды в летние месяцы — май, июнь, когда ночная температура воздуха не сильно отличается от дневной и держится в оптимальном для ежей диапазоне. В весенние месяцы и в конце лета, осенью температура среды может сильно понижаться, выходя из оптимального диапазона температура тела ежей не всегда может следовать за изменениями температуры среды и достоверной корреляции между ними мы не получили. Температура тела ежей в течение суток не постоянна: в летний период во время дневного сна у большинства особей температура тела понижена, что вероятно экономит энергию на ее поддер-

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жание. При этом самки, как правило, имеют более высокую температуру тела, что может быть связано с особенностями физиологии и в частности с более высоким обменом веществ. Фотопериод влияет на продолжительность активности ежей и соответственно времени, в течение которого температура тела ежей в ночное время повышена. Во время нормотермии в период спячки мы выявили ультрадианные ритмы температуры тела ежей с периодами 4.0–4.3 часа, которые, видимо, маскируются влиянием других факторов в период активности ежей летом.

КЛЮЧЕВЫЕ СЛОВА: насекомоядные, белогрудый еж, температура тела, циркадный ритм, ультрадианный ритм.

## Introduction

The northern white-breasted hedgehog (*Erinaceus roumanicus* Barrett-Hamilton, 1900) is an insectivorous animal with pronounced heterothermy due to the rigid annual physiological cycle. Hedgehogs hibernate during cold season, which begins in September-November, depending on the latitude, weather conditions, and the fat reserves (Tembotova, 1997; Kucheruk & Karaseva, 1980). Cold season ends in March–April, depending on the snow melting. In the Moscow Oblast northern white-breasted hedgehogs usually wake up in the first or second decade April, when the stable positive average daily temperatures reach +10…+12°C; the exact dates fluctuate from year to year (Kucheruk & Karaseva, 1980). During hibernation, the body temperature of hedgehogs drops to ambient temperature, but not lower than –1.5°C (Rutovskaya *et al*., 2019a, b); this lowering alternates with the periods of normothermia, lasting for several hours.

As the hibernation ends, the rut begins; the last is characterized by high activity of hedgehogs, for example, the longest track of male exceeds 3.7 km (Kucheruk & Karaseva, 1980; Reeve, 1982). The readiness for reproduction in males and females is non-simultaneous, but the reproductive system of males is ready for copulation earlier. In areas with mild winters (e.g. France), this occurs already at the end of the hibernation period, and the peak of hormone secretion is observed in April. In May–June, the activity of the testes decreases slightly, sexual potency persists until the end of August, and in September, a sharp degeneration of the testes is noted (Saboureau *et al*., 1979). During hibernation, hedgehogs stop spermatogenesis, which resumes sometime after awakening (Kalabukhov, 1985). Therefore, males are ready for breeding in early spring, while females are sexually active later, when all the necessary conditions for breeding are present. In the European part of Russia, the hedgehog rut begins immediately after the hibernation ends, usually in the first decade of April (Kucheruk & Karaseva, 1980). The males do not take any part in the offspring rearing, and the pair breaks up immediately after mating (Reeve, 1994).

Pregnancy in females lasts up to 56 days, more often 4–6 cubs are born; they start independent life at the age of 40–45 days (Morris, 1997). Broods are born at the beginning of summer, however, if the brood is lost, the female can return to estrus and is able to copulate (Ognev, 1928). However, the survival rate of late broods in the northern latitudes may be low, since they must have time to gain the necessary weight and fat reserves for successful hibernation (Karaseva *et al*., 1979). In southwestern France, two successful litters per year that is common (Saboureau & Castaing, 1985).

Hedgehogs are nocturnal animals. Outside the breeding period, the main part of activity time is spent for the search for food; after saturation, the hedgehog returns to the nest before sunrise. During the day, one can observe either sick animals that did not manage to get to their shelter, or individuals that did not have time to get enough during the night, i.e. pregnant females in the spring-summer period or young individuals actively gaining weight for hibernation (Morris, 1997). It is believed that when moving, hedgehogs rely mainly on hearing and smell. When searching for food, hedgehogs demonstrate two types of movement, “searching” and “fattening”. The “fattening” type is characterized by slow movements of the animal with frequent stops and frequent changes in direction. In this case, the hedgehog moves at a pace, from very slow to more or less fast, often listens and sniffs the ground on both sides of the route. This type of movement is directly related to foraging. During “searching” type, hedgehogs run, stopping only for a short time. Apparently, this type of movement is associated with the search for unevenly distributed food objects and the survey of the territory (Filchagov, 1988). In search for food, hedgehogs move at an average speed of 3.7 m per minute (males) and 2.19 m per minute (females), although short runs at speeds of up to 120 m per minute are noted. The distance traveled per night depends on the sex, the amount of food, and the time of year, averaging ~900 m for males and ~600 m for females in wooded areas, while in open areas, the total track may reach 1.5 km for males and 1.0 km for females.

All of the cited works were carried out for the European hedgehog *Erinaceus europaeus* Linnaeus, 1758. The northern white-breasted hedgehog is close by phylogeny to the European hedgehog, so these two species are able to form hybrids (Bannikova *et al*., 2003; Bogdanov *et al*., 2009). The northern white-breasted hedgehog actively spreads to the north, replacing the European hedgehog; the northern margin of the northern white-breasted hedgehog’s range adjoined previously the southern margin of the European hedgehog range (Ognev, 1928). Later, the range of the northern white-breasted hedgehog expanded to the northern borders of the Republic of Belarus, spread to the Kostroma and Kirov Oblasts of Russian Federation (Gureev, 1979), and then protruded both to the west, forming two zones of sympatry (Bolfikova & Hulva, 2012), and to the east (Andreychev *et al.*, 2010). In the XX century, only *E. europaeus* was recorded in the Moscow Oblast, but now the northern white-breasted hedgehog (Bannikova *et al*., 2010) and its hybrids with *E. europaeus* have spread over most of this region (Zolotareva *et al*., 2021).

Heterothermia of hedgehogs refers not only to the period of hibernation, when the body temperature of animals varies from –1.5 to 37°C (Rutovskaya *et al*., 2019a, b), but also during normothermia. Little is known about the variability of body temperature in hedgehogs during the active period with normothermia. In summer activity, the body temperature of hedgehogs fluctuates significantly, when it is higher at night between 20:00 and 4:00 comparing to the period of 8:00 and 16:00; however, such variability has not been found during hibernation (Fowler & Racey, 1990). From April through August, the variations in daily body temperature are closely related to the photoperiod (Fowler & Racey, 1990).

Lactating females of the European hedgehog maintain a higher and more stable temperature during these periods than non-lactating females, but no differences in the body temperature and its fluctuations in pregnant and non-pregnant females have been found (Fowler, 1988).

In addition to diurnal and circadian rhythms, many living organisms have a whole spectrum of rhythmic changes, including ultradian (with a period of less than a day) and infradian (with a period from 28 hours to 30 days). Ultradian rhythms with a 1–6-hour period are found in the body temperature dynamics in different species (Blessing & Ootsuka, 2016; Blum *et al*., 2014; Bourguignon & Storch, 2017). Nothing is known about infradian cycles of body temperature, although infradian rhythms are observed in the motor activity of animals (Diatroptov *et al*., 2017) and in the dynamics of the hormones concentration in the blood serum, such as melatonin (Zeman *et al*., 2005), testosterone (Pronina, 1992; Diatroptov, 2011), thyroxine (Li *et al*., 2000), glucocorticoids and catecholamines (Maschke *et al*., 2003; Jozsa *et al*., 2005). Probably, infradian rhythms of body temperature may be manifested to a greater extent in heterothermal animals.

The study aims to search for the regularities and the factors preconditioning the season and daily variability of the body temperature of the northern white-breasted hedgehog during active period and during normothermia while hibernation.

## Materials and methods

The work was carried out in 2017–2020 at the Resource Sharing Center «Collection of live mammals», Chernogolovka Biological Station of A.N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences (Moscow Region, Russia). In total, 39 specimens of the northern white-breasted hedgehog were tested (19 females and 20 males). Data were not obtained for all individuals throughout the year, therefore, in different analyzes, the sample for hedgehogs differed. The hedgehogs were caught in the Spassky District of the Ryazan Oblast (Russia). Hedgehogs were kept in an outdoor enclosure with a total area of 80 m$^2$ with grass and shrub undergrowth and with deepened nests with hay as nesting material. Every day, hedgehogs received raw chicken meat cranked with bones with the addition of raw chicken eggs. Water was always available. In winter, hedgehogs were hibernating either in the outdoor enclosures, where the nests were insulated with spruce paws and snow, or indoors (1-m$^2$ compartments, with sawdust as bedding and hay as a nesting material). The ambient temperature was controlled indoors, always keeping above –2°C.

The programmed thermal sensors Petrovsky DTN3-28 (EMBI RESERCH, Novosibirsk) were implanted intraperitoneally (Petrovsky *et al.*, 2008); the body temperature was measured every 20 minutes. The sensors were implanted in one month prior the hibernation started. Zoletil (Virbac Sante Animale) was used as an anesthetic (intramuscularly, 15 mg/kg body weight). Control over the temperature of the environment was carried out with series of iButton thermal accumulators of the DS 1921 and Petrovsky, installed both in an artificial burrow without an animal, and in the vivarium; the ambient temperature was automatically checked every 30 min.

The daily temperature of hedgehogs was considered separately during the active period and at normothermia during the hibernation period. The period of hibernation was considered as the time from the moment when the hedgehog lowered the temperature below 25°C for the first time and until the animal came out from the last bout of hibernation. In autumn and spring, there could be long periods of normothermia up to 10 days between hibernation bouts. The beginning of normothermia between bouts was considered as the moment when a steady increase in body temperature at a rate of at least 0.05°C per 20 min was replaced by temperature fluctuations. The end of the normothermia period was considered as the moment when the body temperature began to steadily decrease by at least 0.05°C per 20 min. The hedgehogs did not leave the nests at normothermia during hibernation (Rutovskaya *et al*., 2019a). The hibernation period started in September–November and ended in March–April.

The monthly average body temperature was calculated for each individual in order to track seasonal changes; from these average values, a sample was formed to analyze seasonal changes in the body temperature of hedgehogs of both sexes. The average hourly temperature for each individual was used to assess the daily variation of the body temperature for different months. The average temperature for all individuals of each sex was then calculated using this average values for each individual.

Statistical data processing was performed using the Statistica Ultimate Academic 13 for Windows software package. The descriptive statistics applied mean ± error of the mean. Pairwise comparisons were made by Student's *t*-test for samples with normal distribution. Comparisons were made by one-way analysis of variance

(ANOVA Repeated Measures Analysis of Variance) or nested-design ANOVA with post-hoc Tukey HSD test analysis. Correlations were calculated using Spearman's nonparametric test. Differences were considered significant at $p < 0.05$.

The rhythmic changes in body temperature dynamics were identified by the method of cosinor analysis in the Cosinor-Analysis 2.4 for Excel 2000/XP package and the autocorrelation method, applicable for large- and medium-size data sets. The time of extremes of pronounced increases (by more than 0.5°C per 20 min) in body temperature were recorded in order to identify the time of day, at which sharp increases in body temperature were observed at short intervals of normothermia. The statistical significance of the likelihood of such sharp increases in body temperature at a certain time of the day compared with average values was determined using the *z*-test allowing to analyze two different sampling rates (SigmaStat).

The work with animals was carried out in accordance with the recommendations of the National Standard of the Principles of Good Laboratory Practice of the Russian Federation (GOST Z 53434-2009) and with a permission of the Ethical Committee of the IPEE RAS (no. 14 dated January 15, 2018).

## Results

### Active period (spring–autumn)

The body temperature of northern white-breasted hedgehogs during this period may vary in the range from 26 to 38°C; the average body temperature of females is 35.1 ± 0.1°C ($n = 9$ — the number of individuals), males — 35.0 ± 0.1°C ($n = 20$).

*Seasonal variability* — The average daily body temperature of hedgehogs depends both on the season ($F_{(12, 115)} = 5.8$; $p < 0.001$) and on sex ($F_{(1, 126)} = 19.8$; $p < 0.001$, Nested ANOVA) (Fig. 1). In March, the mean daily temperature of males and females does not differ significantly ($F_{(1, 26)} = 0.1$; $p = 0.819$, ANOVA Repeated). Later on season, the average daily body temperature of females is significantly higher than the same of males: in April ($F_{(1, 26)} = 4.3$; $p = 0.048$), May ($F_{(1, 26)} = 22.4$; $p = 0.001$), June ($F_{(1, 26)} = 28.0$; $p = 0.001$), July ($F_{(1,26)} = 36.6$; $p = 0.001$), and August ($F_{(1, 26)} = 39.7$; $p = 0.001$). In September, the body temperature of females drops and does not differ from that of males ($F_{(1, 26)} = 1.66$; $p = 0.209$).

The body temperature in both females and males is significantly higher in May comparing with annual average ($p = 0.0198$ and $p = 0.0006$, Student's *t*-test); on the contrary, the body temperature of males is significantly lower in July and September ($p = 0.0002$ and $p = 0.0215$). In October, body temperature is also below annual average; due to the small number of individuals (3 females and 2 males) remaining active in October, no significant differences are found. By this time, most of the animals were already hibernating.

*Variability throughout the month* — The average daily body temperature also fluctuates quite strongly, in some months the difference may be up to 10°C (Tab. 1). Changes in body temperature on different days are probably associated with the temperature of the external environment. However, for females, this pattern is not reliably traced. No any reliable infradian rhythms in the dynamics of the body temperature of hedgehogs are found (Fig. 2).

Spearman's correlation coefficient between the body temperature in male hedgehogs and evening air temperature for the entire period of May–June is R = 0.21, $p = 0.005$, $n = 175$, number of measurements over three years (Fig. 3A). Omitting the days when average daily temperature of the environment was above +13°C, the pattern changes (R = 0.46, $p = 0.0006$). The lowest body temperatures in male hedgehogs are observed at the environmental temperature range of 13–17°C, whereas such decreases (down to 34.2–34.7°C) were not recorded at lower ambient temperatures (3–12°C). The highest correlation coefficient is observed when omitting the data obtained at an ambient temperature below 13°C. Consequently, ambient temperature below 13°C in May–June does not cause lowering of the body temperature in male hedgehogs. No correlation between body temperature in female hedgehogs and the temperature of the environment is found for May–June (R = 0.02, $p = 0.851$, $n = 119$, number of measurements over three years) (Fig. 3B). In September–October, there is a significant correlation between body temperature and ambient temperature both in males (R = 0.56, $p < 0.0001$) and females (R = 0.51, $p < 0.0001$) (Fig. 3C, D).

*Circadian variability* — The body temperature of hedgehogs changes during the day. There is a general pattern for males and females, when the body temperature of hedgehogs drops by more than 1°C by morning, and the hedgehogs again warm up to 35.5–35.7°C by 20:00–21:00 (Fig. 3). In males, the body temperature between 8:00 and 15:00 is significantly lower than that from 20:00 to 5:00; in females, the body temperature between 12:00 and 13:00 significantly differs from body temperature for the period from 21:00 to 4:00 next day.

**Table 1.** The range of fluctuations in the average daily body temperature during the month in males and females of the northern white-breasted hedgehog.

| | | Body temperature variability, °C | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | March | April | May | June | July | August | September | October |
| Females, $n = 9$ | min | 32.7 | 32.4 | 32.6 | 31.5 | 33.0 | 33.1 | 28.0 | 25.8 |
| | max | 35.8 | 37.0 | 37.6 | 37.4 | 36.8 | 36.8 | 36.6 | 37.0 |
| Males, $n = 20$ | min | 33.4 | 29.8 | 32.0 | 30.4 | 27.9 | 28.6 | 26.4 | 28.7 |
| | max | 36.8 | 36.9 | 37.2 | 37.6 | 37.2 | 36.7 | 36.8 | 36.7 |

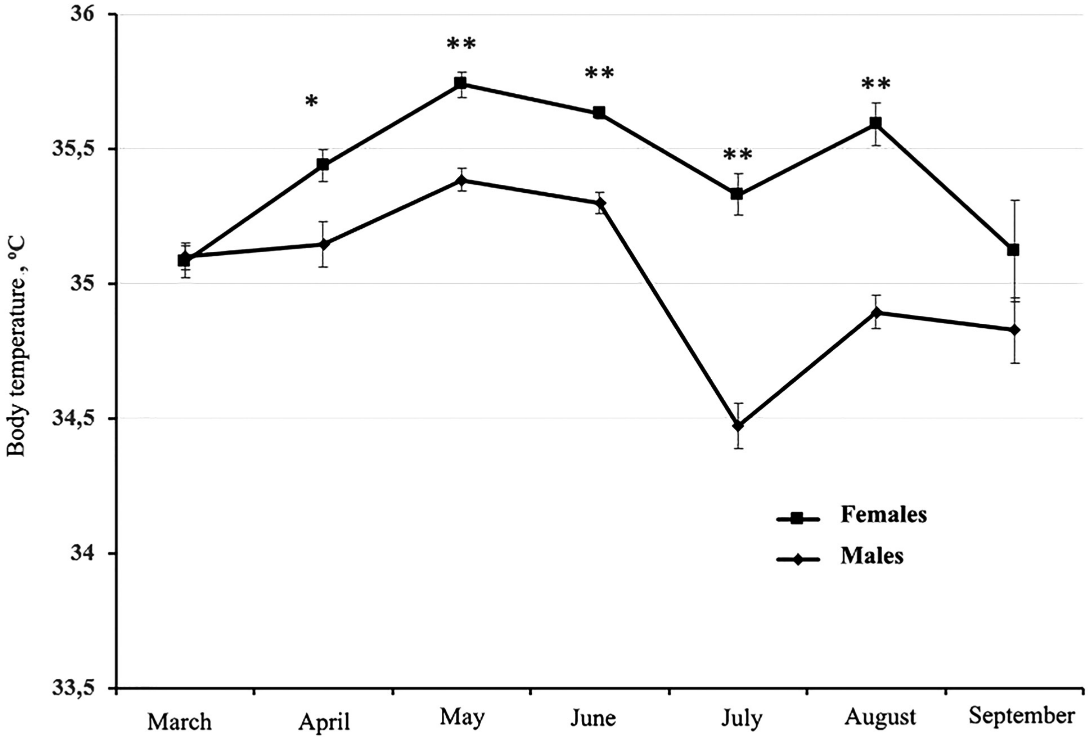


**Fig. 1.** The average body temperature of active males and females of the northern white-breasted hedgehog from March to October. Asterisks indicate significance of differences between the body temperature of males and females in a particular month as * referring to $p < 0.05$; ** — $p < 0.001$.

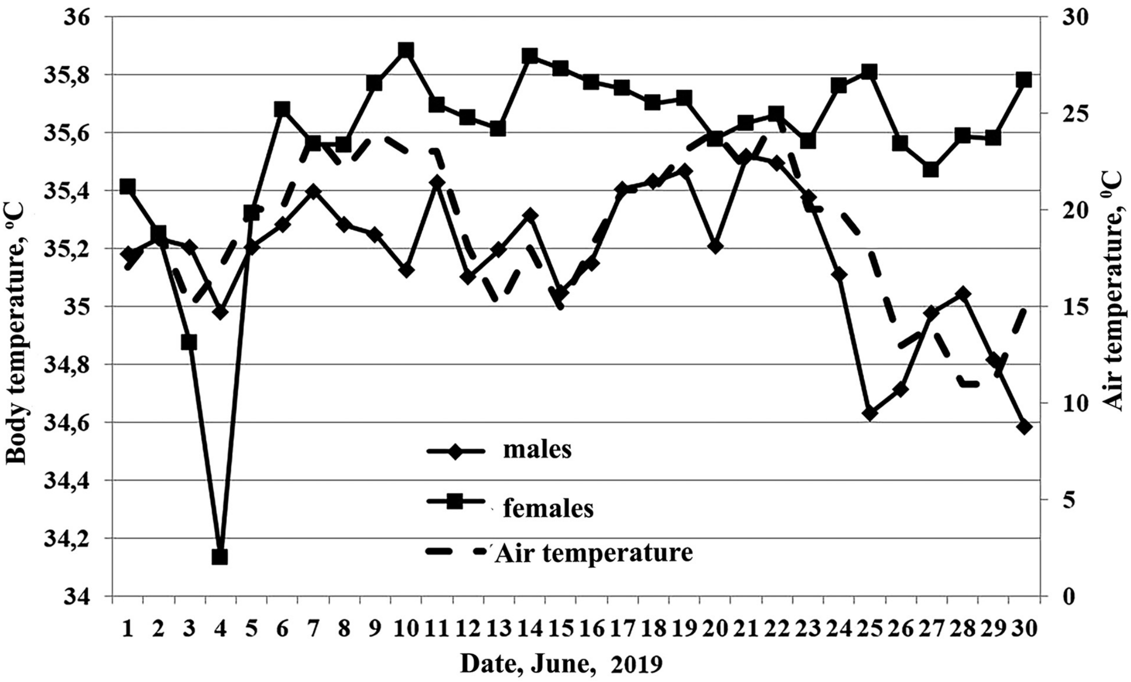


**Fig. 2.** An example of changes in the average daily temperature of northern white-breasted hedgehogs and the ambient temperature in June 2019 (evening air temperature for Chernogolovka according to Gismeteo, www.gismeteo.ru). The correlation between the ambient temperature and the body temperature is R = 0.755, $p = 0.001$ for males, R = 0.205, $p = 0.278$ for females (Spearman's nonparametric criterion).

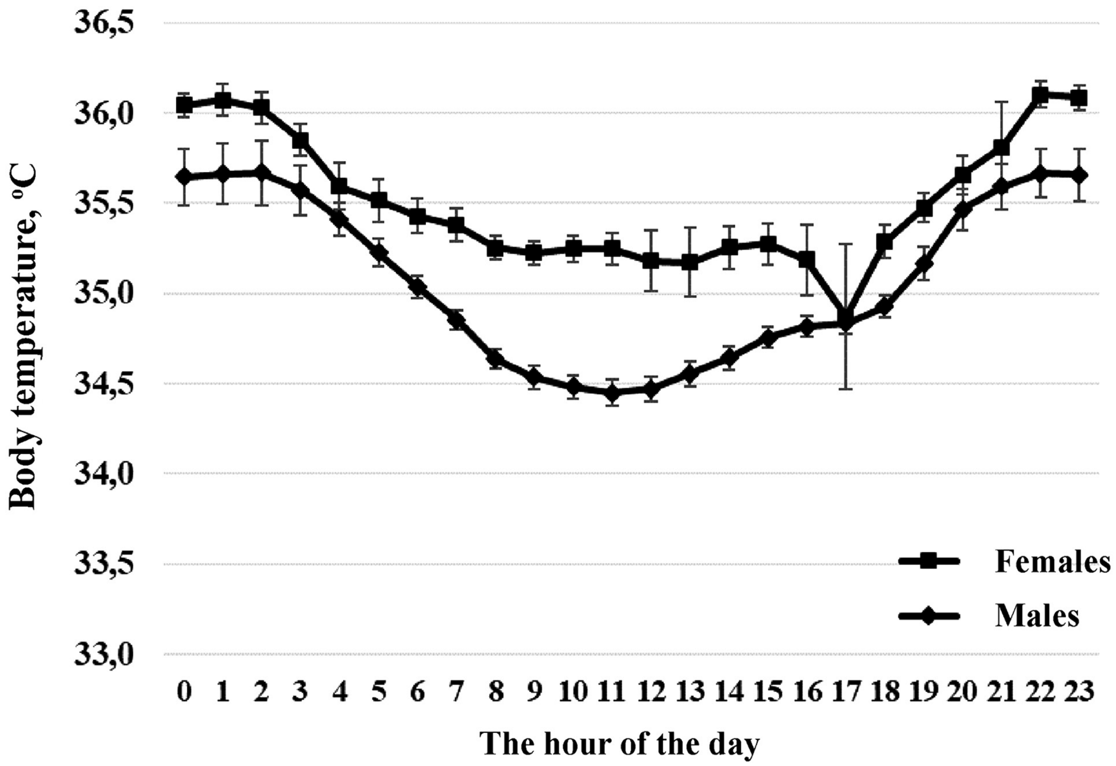


**Fig. 3.** Daily fluctuations in body temperature of non-hibernating males and females of the northern white-breasted hedgehog (5 females, 13 males).

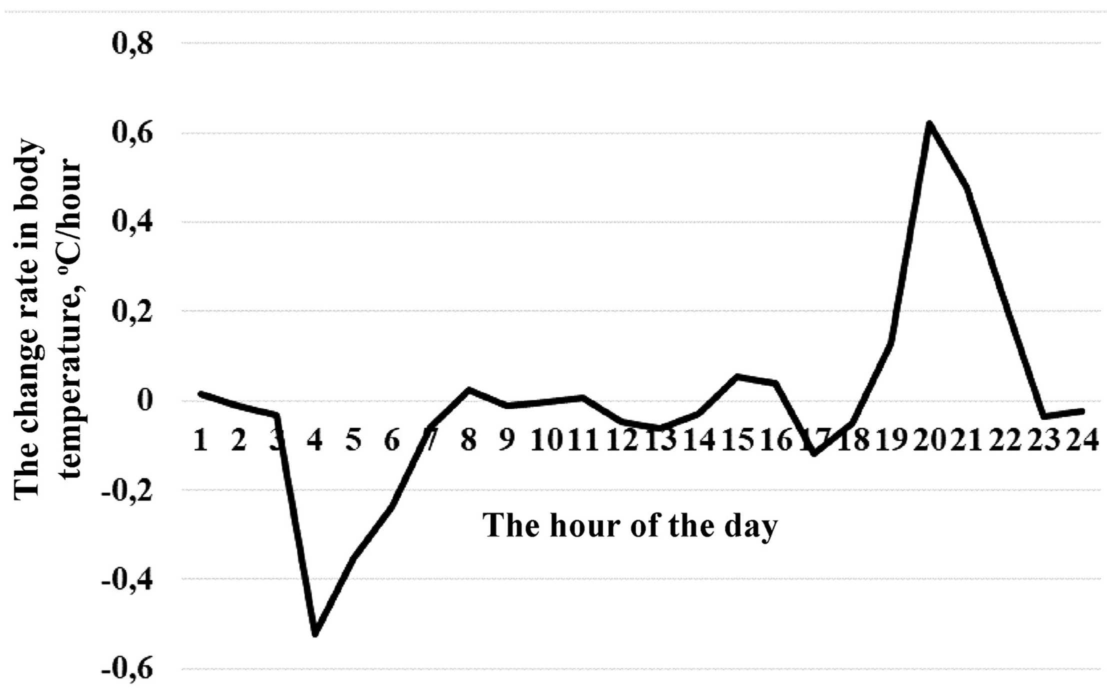


**Fig. 4.** An example of the average changing rate in body temperature of male no.21 during the day in May 2020.

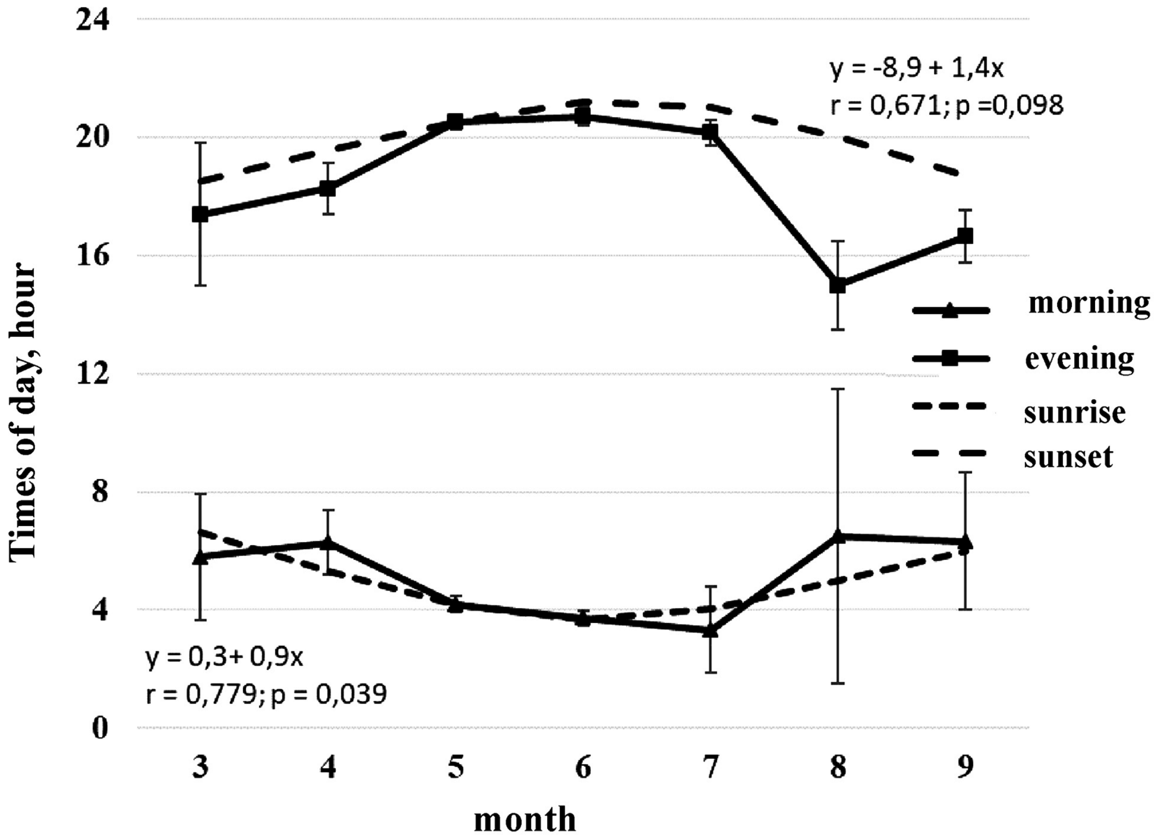


**Fig. 5.** Seasonal shifts of the time of day (Y-axis) characterized by a pronounced changing the hedgehog body temperature, referring to morning and evening time in different months (X-axis).

**Table 2.** Duration of normothermia (hours) during hibernation in the northern white-breasted hedgehog ($n$ = 13).

| September | October | November | December | January | February | March | April |
|---|---|---|---|---|---|---|---|
| 42.7±13.1 | 20.6±4.6 | 6.4±1.2 | 5.9±1.1 | 5.3±0.3 | 10.2±1.6 | 33.7±10.3 | 50.8±14.6 |

The rate of change of the body temperature, considered as the difference between the body temperature of the next hour and the previous one, has two peaks when the temperature drops and, conversely, when it starts to rise (Fig. 4). Such pronounced peaks in the rate of temperature change are found for most hedgehogs under the study (87.5%, $n$ = 16). We have checked if this peak is tied to a certain hour in different months. No significant differences are found for males and females ($F_{(10.37)}$ = 1.48, $p$ = 0.185), so the data are pooled. For this dataset, there are significant differences between the time of the beginning of the morning peak ($F_{(6.42)}$ = 2.39, $p$ < 0.044) and the evening peak ($F_{(6.42)}$ = 2.96, $p$ = 0.016) in different months. From May through July, the body temperature of hedgehogs decreases 1–2 hours earlier in the morning and increases 2–3 hours later comparing to the period of early spring and late summer–autumn (Fig. 5).

## Hibernation (autumn–spring)

*Seasonal variability* — Periods of normothermia during hedgehog hibernation last for different time; at the beginning of hibernation and at the end of this period, they are longer and vary from 5 to 50 hours in different months (Tab. 2), but the duration of normothermia periods does not differ in females and males ($F_{(1.80)}$ = 0.98, $p$ = 0.324).

The body temperature of northern white-breasted hedgehogs at normothermia during hibernation varies as 31.7–35.8°C; moreover, the body temperature of hedgehogs does not depend on the month ($F_{(14.257)}$ = 1.60, $p$ = 0.078), averaging 34.7 ± 0.1°C ($n$ = 273, the number of measurements of the average body temperature of hedgehogs in the months from October to April in different individuals during hibernation. There are 29 individuals in total, but in different months there were different numbers of sleeping animals. Data are presented for 3 years (Fig. 6).

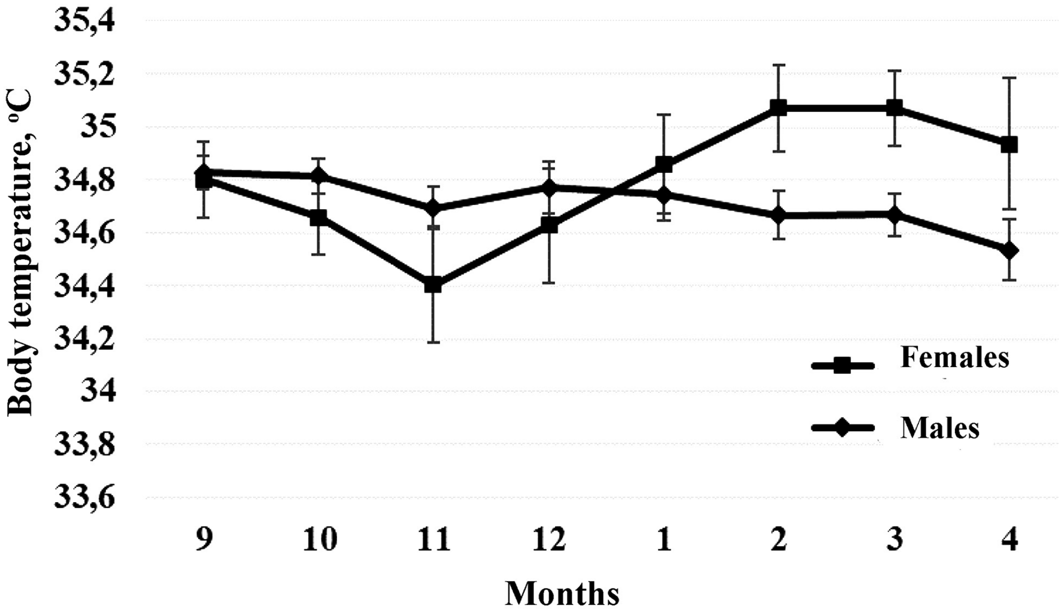


**Fig. 6.** The body temperature of the northern white-breasted hedgehog at normothermia during hibernation (25 males and 11 females).

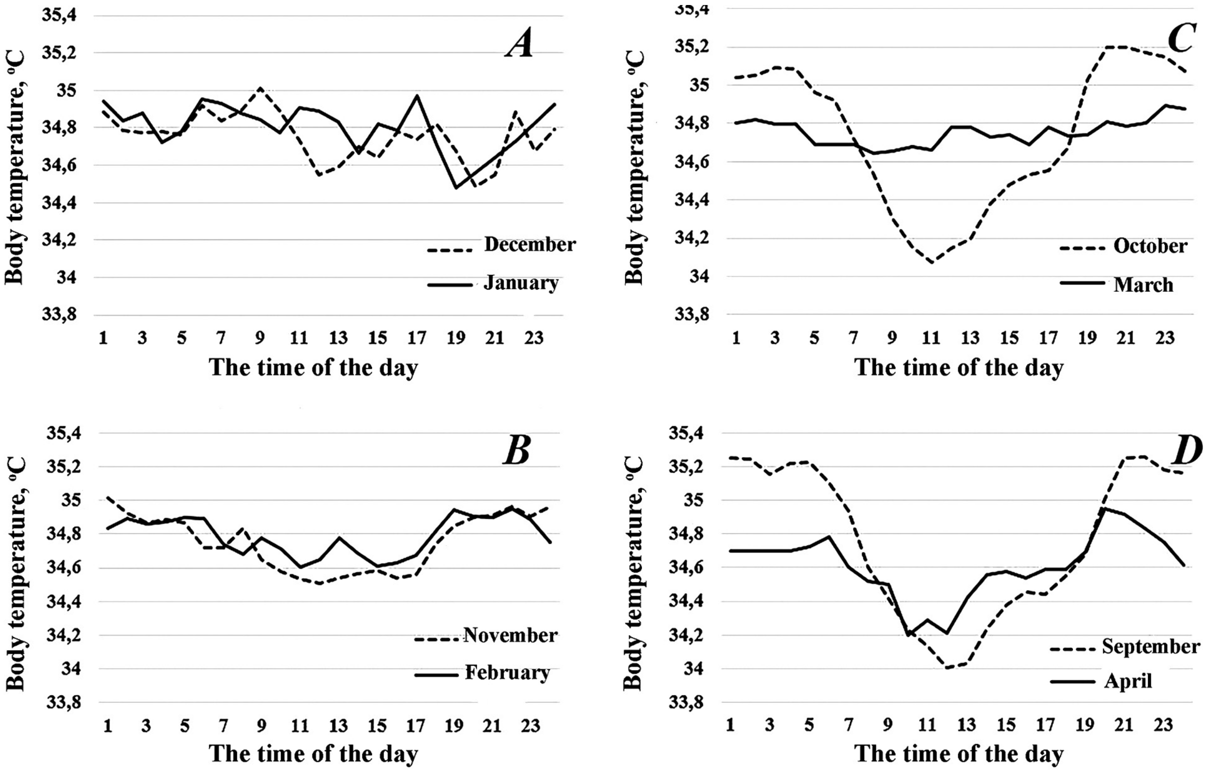


**Fig. 7.** Changes in the average body temperature of the northern white-breasted hedgehog during the day in different months. The observations were performed for 29 individuals.

*Circadian periodicity* — In hibernating animals, the circadian periodicity (characteristic of the active period of hedgehogs) gradually smooths out, exhibiting ultradian rhythm. November is the last month when the dynamics of the hedgehog's body temperature follows diurnal rhythm. The amplitude of the diurnal rhythm of body temperature is significantly reduced in November (Fig. 7B), compared to September and October (Fig. 7C, D). In spring, circadian rhythm appears only in April (Fig. 7D).

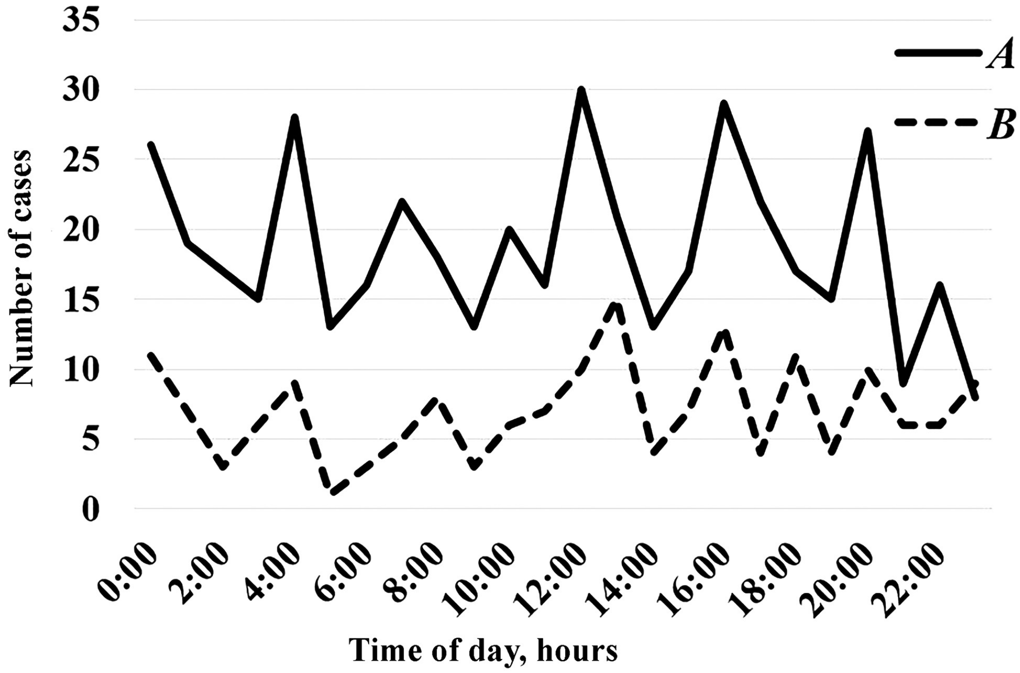


**Fig. 8.** Time distribution of the extremes of pronounced increases (more than 0.5°C) of body temperature in hedgehogs ($n$ = 15) for the period of February 1–March 10, 2020 (A) and November 1–30, 2019 (B).

*Ultradian rhythm* — In December–January, the duration of the periods of normothermia is short, which makes it impossible to analyze the distribution of pronounced peaks of body temperature. However, the maximum body temperature values are observed at midnight, 5:00–8:00, and 17:00 in December, and at midnight and at about 4:00, 8:00–10:00, and 16:00 (to a much lesser extent) in January (Fig. 7A).

Three months have been analyzed in order to search for ultradian cycles: November (autumn) and February–March (spring). September–mid-October and April are omitted for such purpose, despite the long periods of observed normothermia, because hedgehogs may leave their shelters during normothermia. Unlike these months, hedgehogs did not leave the nest at normothermia during hibernation from November to March, and the length of daylight hours cannot affect their rhythms.

In February–March, the average daily body temperature of hedgehogs is 34.8 ± 0.1°C ($n$ = 29, the number of individuals). At the same time, at normothermia, the body temperature has pronounced ultradian fluctuations (1.5–2.0°C). The daily dynamics of sharp increases (by more than 0.5°C per 20 min) of body temperature during this period evidences on the maximum number of such cases observed for the periods of 00:00–01:00, 04:00–5:00, 08:00–09:00, 12:00–13:00, 16:00–17:00, and 20:00–21:00 (Fig. 8A). In November, pronounced increases in body temperature are also observed at the indicated hours and have an approximately 4-h rhythmicity (Fig. 8B). Applying autocorrelation method makes it possible to identify an ultradian rhythm with a period of 4.0–4.3 h. Applying this 4-h period for the time of the day indicated above, the number of cases are significantly higher comparing to the remaining hours (Chi-square test $\chi^2$ = 98.01, df = 3, $p$ = 0.001, $n$ = 615, number of measurements; together for both periods, February–March and November).

## Discussion

The study of the body temperature at different periods allows us to identify a number of factors that affect the temperature regime of adult hedgehogs. Hedgehogs spend hibernation period in the nests, most of the time under a snow cover, so photoperiod cannot affect the physiological rhythms, and the ambient temperature conditions are more stable comparing to other seasons. During hibernation and at normothermia, hedgehogs are not very active (Rutovskaya *et al.*, 2019a). In present study, ultradian rhythms of the hedgehog's body temperature are found; apparently, they have been masked by other factors during the summer period of animal activity. The duration of the circadian rhythm increases up to 24.5–25.5 h and its amplitude decreases in laboratory rats kept under constant light (Diatroptov *et al.*, 2019a), the intraday dynamics of body temperature also exhibits 4-hour rhythms, and the acrophase timing coincides with that observed in hedgehogs. The rodents (order Rodentia) and insectivores (order Eulipotyphla) include the family Erinaceidae (hedgehogs) are very distant phylogenetic groups (Upham *et al.*, 2019), in which ultradian rhythms of body temperature are similar.

This indicates common mechanism for the ultradian rhythm formation for all mammals and the existence of an external synchronizer not associated with the light regime and the body circadian system.

During hibernation, no circadian rhythm in the hedgehog body temperature has been detected, similarly to that observed for the European hedgehog (Fowler & Racey, 1990). This is consistent with the literature data that the biological system of circadian rhythms does not function during hibernation. During this period, the content of circadian rhythm proteins (PER1, PER2, and BMAL1) does not change in obligate hibernators, such as Arctic ground squirrels *Urocitellus parryii* (Richardson, 1825) (Ikeno *et al*., 2017). Circadian rhythms have not been found in the dynamics of intra-abdominal body temperature during hibernation of this species. As the hibernation ends, it takes about two weeks for the circadian rhythm of body temperature to recover if the Arctic ground squirrels stay inside the burrows with no sunlight (Williams *et al.*, 2017).

The maximum body temperature of hedgehogs was noted at a certain time, namely, during short awakenings in December–January. The intraday dynamics of the awakening of hedgehogs may be named as one of the reason; during hibernation, a 4-hour rhythm has been observed, when the maximum number of episodes of the body temperature recovery has been recorded at 00:00–01:00, 04:00–5:00, 08:00–09:00, 12:00–13:00, 16:00–17:00, and 20:00–21:00 (Diatroptov *et al.*, 2019b). Probably, the revealed peak values of body temperature in hedgehogs within this study fit well the daily dynamics of the other physiological processes.

During the non-hibernation period, a number of factors affect the body temperature regime in hedgehogs. Circadian temperature dynamics in most hedgehog individuals are apparently associated with the daily activity. Hedgehogs are active throughout the night, waking up at dusk and falling asleep after dawn (Saboureau *et al.*, 1979; Morris, 1997). At night, the body temperature of hedgehogs is higher than during daytime rest, which probably has an adaptive value, i.e. saving resources when resting. An increase in body temperature at night is a result of active muscular activity of individuals. Body temperature changes abruptly (Fig. 5); the period of higher body temperature within a day is longer in May–July, compared to the early spring and late summer–autumn periods (Fig. 7). The timing of abrupt body temperature decrease correlates with the time of dawn in a particular month; however, no similar correlation of the body temperature increase at sunset has been found. In August, the body temperature increase is observed much earlier than sunset. Probably, this is due to the active preparation for the winter season, when the animals have to be active for a longer time for gaining enough fat reserves. Therefore, the photoperiod plays an important role in the circadian dynamics of the hedgehog body temperature, associated primarily with the activity of individuals, which is closely synchronized with sunrise and sunset. Such synchronization has been shown for the European hedgehog as well (Saboureau *et al*., 1979). From April through August, the variations in daily body temperature are closely related to the photoperiod (Fowler & Racey, 1990).

Lowering body temperature during daytime rest is important for hedgehogs as it probably saves energy, but not all hedgehogs exhibit this circadian pattern. In our study, about 12% of hedgehogs do not have a clearly pronounced decrease in body temperature during daytime rest, probably, due to specific physiological requirements. Pregnant and lactating females of the European hedgehog maintain a higher and more stable temperature during these periods than non-lactating females, but no differences in the body temperature and its fluctuations in pregnant and non-pregnant females have been found (Fowler, 1988). The increased body temperature in lactating females may be related to the need for abundant milk production to ensure a high growth rate of the offspring (Fowler, 1988). It is known that animals with a low metabolic rate, including hedgehogs (Krol, 1994), are able to increase the metabolic rate by 75% (Nicoll & Thompson, 1987). As a rule, females have a higher body temperature during the non-hibernation period, which may be associated with certain physiological features and, in particular, with a higher metabolism.

The average daily temperature of hedgehogs at each month correlates with the ambient temperature; significant correlations are observed in the summer months (May and June), when the night air temperature does not differ much from that during the daytime, falling within the optimal range for hedgehogs. During this period, temperature regulation in hedgehogs is similar to that in homoeothermic animals; at low ambient temperatures, they increase heat production, increasing oxygen consumption; at high ambient temperatures, they increase sweating, helping to maintain temperatures below ambient, although their body temperature rises (Shkolnik & Schmidt-Nielsen, 1976). Heterothermia allows hedgehogs to pursue a cost-effective strategy in energy use (Gnaiger, 1987).

During the spring and late summer--autumn, the environment temperature may decrease out of the optimal range for maintaining body temperature, which occurs mainly due to muscle activity during hedgehog movement (Krol, 1994). As the ambient temperature decreases, the metabolic rate (oxygen consumption) increases to generate the necessary heat (Shkolnik & Schmidt-Nielsen, 1976). In this case, the body temperature of hedgehog cannot always follow the changes in the temperature of the environment, so no correlation between these parameters has been observed in the present study.

During the breeding season in May and June, the body temperature of hedgehogs is significantly higher in both males and females than in other months. This is probably due to the period of active reproduction and seasonal variability in the concentration of hormones in the blood. Thermoregulation in homoeothermic animals is associated with the secretory activity of the thyroid gland (Frare *et al*., 2021), which increases proportionally with cooling. The activity of the hypothalamic-pituitary-thyroid system decreases significantly with overheating. In turn, corticosteroids, stimulating f thermogenesis, most likely affect tissue respiration indirectly by launching the activity of catecholamines and, possibly, thyroid hormones (Robu, 1982).

Our study demonstrates that hedgehogs are able to adapt their body temperature to changing environmental conditions. Higher body temperature is associated with increased activity of animals and with the reproduction period; during the active (summer) period, circadian rhythms of body temperature are apparently determined by the photoperiod. However, during hibernation, when the light regime is constant (no sunlight is available), the body temperature dynamics is controlled by the internal mechanisms.

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## References


Andreychev A.V., Kuznetsov V.A. & Lapshin A.S. 2010. [Northern white-breasted hedgehog in the mammalian fauna of Mordovia] // Ilyinskich N.N. (ed.). [Proceedings of the 2nd International Teleconference "Fundamental Sciences and Practice", Tomsk]. Vol.1. No.3. P.55 [in Russian].

Bannikova A.A., Kramerov D.A., Vasilenko V.N., Dzuev R.I. & Dolgov V.A. 2003. DNA polymorphism of *Erinaceus* hedgehogs and *E. concolor* taxon (Insectivora, Erinaceidae) // Zoologicheskii Zhurnal. Vol.82. No.1. P.70–80 [in Russian, with English summary].

Bannikova A.A., Lebedev V.S., Rutovskaya M.V., Khlyap L.A. & Rozhnov V.V. 2010. [Genetic identification and hybridization of common hedgehogs in Central Russia] // Rozhnov V.V. (ed.). [Proceedings of Conference "Integrity of the Species in Mammals: Isolating Barriers and Hybridization"]. Moscow: KMK Scientific Press. P.9 [in Russian].

Blessing W. & Ootsuka Y. 2016. Timing of activities of daily life is jaggy: how episodic ultradian changes in body and brain temperature are integrated into this process // Temperature (Austin). Vol.3. No3. P.371–383.

Blum I.D., Zhu L., Moquin L., Kokoeva M.V., Gratton A., Giros B. & Storch K.F. 2014. A highly tunable dopaminergic oscillator generates ultradian rhythms of behavioral arousal // Elife. Vol.3. DOI:10.7554/eLife.05105

Bogdanova A.S., Bannikova A.A., Pirusskii Yu.M. & Formozov N.A. 2009. The first genetic evidence of hybridization between West European and Northern white-breasted hedgehogs (*Erinaceus europaeus* and *E. roumanicus*) in Moscow Region // Biology Bulletin. Vol.36. No.6. P.647–651.

Bolfíkova B. & Hulva P. 2012. Microevolution of sympatry: landscape genetics of hedgehogs *Erinaceus europaeus* and *E. roumanicus* in Central Europe // Heredity. Vol.108. P.248–255.

Bourguignon C. & Storch K.F. 2017. Control of rest: activity by a dopaminergic ultradian oscillator and the circadian clock // Frontiers in Neurology. Vol.8. P.614.

Diatroptov M.E. 2011. Infradian fuctuations in serum testosterone levels in male laboratory rats // Bulletin of Experimental Biology and Medicine. Vol.151. P.638–641.

Diatroptov M.E., Diatroptova M.A., Kosyreva A.M., Dzhalilova D.Sh., Mkhitarov V.A., Mikhailova L.P. & Makarova O.V. 2019a. [Ultradian rhythms of body temperatures of Wistar rats under conditions of permanent lightning] // Bulletin of Experimental Biology and Medicine. Vol.167. No.6. P.690–694 [in Russian, with English summary].

Diatroptov M.E., Rutovskaya M.V., Kuznetsova E.V., Diatroptova M.A., Kosyreva A.M., Dzhalilova D.Sh., Ponomarenko E.A., Panchelyuga V.A. & Stankevich A.A. 2019b. [Infradian and ultradian rhythmicity of body temperature recovery during hibernation] // Bulletin of Experimental Biology and Medicine. Vol.168. No.8. P.250–254 [in Russian, with English summary].

Diatroptov M.E., Slesarev S.M. & Slesareva E.V. 2017. Characteristics of 4-day infradian biorhythms in mature male Wistar rats after pinealectomy // Bulletin of Experimental Biology and Medicine. Vol.163. P.109–113.

Filchagov A.V. 1988. [Daily activity and movement of common hedgehogs according to the materials of individual tracking] // Bulletin of Moscow Society of Naturalists. Biological Series. Vol.93. No.5. P.38–49 [in Russian].

Fowler P.A. 1988. Thermoregulation in the female hedgehog, *Erinaceus europaeus*, during the breeding season // Journal of Reproduction and Fertility. Vol.82. P.285–292.

Fowler P.A. & Racey P.A. 1990. Daily and seasonal cycles of body temperature and aspects of heterothermy in the hedgehog *Erinaceus europaeus* // Journal of Comparative Physiology, B. Vol.160. P.299–307.

Frare C., Williams C. & Drew K.L. 2021. Thermoregulation in hibernating mammals: The role of the "thyroid hormones system" // Molecular and Cellular Endocrinology. Vol.519. No.5. P.111054.

Gnaiger E. 1987. Optimum efficiencies of energy transformation in anoxic metabolism. The strategies of power and economy // Calow P. (ed.). Evolutionary Physiological Ecology. Cambridge: Cambridge University Press. P.7–36.

Gureev A.A. 1979. [Fauna of the USSR. Mammals, Vol.4. No.2. Insectivores]. Leningrad: Nauka. 502 p. [in Russian].

Ikeno T. Williams C.T., Buck C.L., Barnes B.M. & Yan L. 2017. Clock gene expression in the suprachiasmatic nucleus of hibernating Arctic ground squirrels // Journal of Biological Rhythms. Vol.32. No.3. P.246–256.

Jozsa R., Olah A., Cornélissen G., Csernus V., Otsuka K., Zeman M., Nagy G., Kaszaki J., Stebelova K., Csokas N., Pan W., Herold M., Bakken E.E. & Halberg F. 2005. Circadian and extracircadian exploration during day time hours of circulating corticosterone and other endocrine chronomes // Biomedicine & Pharmacotherapy. Vol.59. P.109–116.

Kalabukhov N.I. 1985. [Hibernation of Mammals]. Moscow: Nauka. 264 p. [in Russian].

Karaseva E.V., Gottfried A.B. & Dubinina N.V. 1979. [Lifestyle of common hedgehogs (*Erinaceus europaeus*) and their role in the natural focus of leptospirosis in the Yaroslavl region (according to observations of tagged individuals)] //

Zoologicheskii Zhurnal. Vol.58. No.5. P.705–715 [in Russian].

Krol E. 1994. Metabolism and thermoregulation in the eastern hedgehog *Erinaceus concolor* // Journal of Comparative Physiology, B. Vol.164. P.503–507.

Kucheruk V.V. & Karaseva E.V. 1980. [Hedgehogs] // Kucheruk V.V. (ed.). [Results of Tagging Mammals]. Moscow: Nauka. P.47–57 [in Russian].

Li J., Nguyen V., French B.A., Parlow A.F., Su G.L., Fu P., Yuan Q.X. & French S.W. 2000. Mechanism of the alcohol cyclic pattern: role of the hypothalamic-pituitary-thyroid axis // American Journal of Physiology. Gastrointestinal and Liver Physiology. Vol.279. No.1. P.118–125.

Maschke C., Harder J., Cornélissen G., Hecht K., Otsuka K. & Halberg F. 2003. Chronoecoepidemiology of “strain”: chronomics of urinary cortisol and catecholamines during nightly exposure to noise // Biomedicine & Pharmacotherapy. Vol.57. P.126–135.

Morris P.A. 1997. The Hedgehog // Shire Natural History, Vol.32. London: Bloomsbury Publishing. 24 p.

Nicoll M.E. & Thompson S.D. 1987. Basal metabolic rates and energetics of reproduction in therian mammals: marsupials and placentals compared // Symposium of the Zoological Society of London. Vol.57. P.7–27.

Ognev S.I. 1928. [Mammals of Eastern Europe and Northern Asia. Vol.1. Insectivores and Bats]. Moscow–Leningrad: Gosudarstvennoe Izdatel’stvo. 631 p. [in Russian].

Petrovsky D.V., Novikov E.A. & Moshkin M.P. 2008. [Dynamics of body temperature of the mole vole (*Ellobius talpinus*, Rodentia, Cricetidae) in winter] // Zoologicheskii Zhurnal. Vol.87. No.12. P.1504–1508 [in Russian, with English summary].

Pronina T.S. 1992. [Circadian and infradian rhythms of testosterone and aldosterone excretion in children] // Problemy Endokrinologii. Vol.38. No.5. P.38–42 [in Russian, with English summary].

Reeve N.J. 1982. The home range of the hedgehog as revealed by a radio tracking study. Telemetric studies of vertebrates // Cheeseman C.L. & Mitson R.B. (eds.). Proceedings of a Symposium held at the Zoological Society of London. London: Academic Press. Vol.49. P.207–230.

Reeve N.J. 1994. Hedgehogs. London: T. and A.D. Poyser. 313 p.

Robu A.I. 1982. [Relationship of Endocrine Complexes Under Stress]. Chisinau: Shtiintsa. 208 p. [in Russian].

Rutovskaya M.V., Diatroptov M.E., Kuznetzova E.V., Anufriev A.I., Feoktistova N. Y. & Surov A.V. 2019a. The dynamics of body temperature of the eastern European hedgehog (*Erinaceus roumanicus*) during winter hibernation // Biological Bulletin. Vol.46. No.9. P.1136–1145.

Rutovskaya M.V., Diatroptov M.E., Kuznetsova E.V., Anufriev A.I., Feoktistova N.Yu. & Surov A.V. 2019b. The phenomenon of negative body temperature in hibernating hedgehogs of the genus *Erinaceus* // Journal of Evolutionary Biochemistry and Physiology. Vol.55. No.6. P.515–516.

Saboureau M. & Castaing L. 1985. Hibernation and reproduction in the female hedgehog // Assenmacher I. & Biossin J. (eds.). Endocrine Regulations as Adaptive Mechanisms to the Environment. Paris: CNRS. P.191–208.

Saboureau M., Laurent G. & Boissin J. 1979. Daily and seasonal rhythms of locomotor activity and adrenal function in male hedgehog (*Erinaceus europaeus* L.) // Journal of Interdisciplinary Cycle Research. Vol.10. P.245–266.

Shkolnik A. & Schmidt-Nielsen K. 1976. Temperature regulation in hedgehogs from temperate and desert environments // Physiological Zoology. Vol.49. No.1. P.56–64.

Tembotova F.A. 1997. [Hedgehogs of the Caucasus]. Nalchik: Publishing House KBSC RAS. 80 p. [in Russian].

Upham N.S., Esselstyn J.A. & Jetz W. 2019. Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation // PLoS Biology. Vol.17. No.12. P.e3000494.

Williams C.T., Radonich M., Barnes B.M. & Buck C.L. 2017. Seasonal loss and resumption of circadian rhythms in hibernating arctic ground squirrels // Journal of Comparative Physiology, B. Vol.187. No.5–6. P.693–703.

Zeman M., Józsa R., Cornélissen G., Stebelova K., Bubenik G., Olah A., Poeggeler B., Huether G., Hardeland R., Nagy G., Czernus V., Pan W., Otsuka K. & Halberg F. 2005. Chronomics: circadian lead of extrapineal vs. pineal melatonin rhythms with an infradian hypothalamic exploration // Biomedicine & Pharmacotherapy. Vol.59(1). P.213–219.

Zolotareva K.I., Bannikova A.A., Belokon M.M., Belokon Y.S., Politov D.V., Rutovskaya M.V., Hlyap L.A., Starykov V.P. & Lebedev V.S. 2021. Genetic diversity and structure of the hedgehogs *Erinaceus europaeus* and *Erinaceus roumanicus*: evidence for ongoing hybridization in Eastern Europe // Biological Journal of the Linnaean Society. Vol.132. No.1. P.174–195.