

Daily torpor in Campbell's hamster (*Phodopus campbelli* Thomas, 1905): proximate factors and ultimate fitness consequences

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ABSTRACT. In 68 pairs of Campbell's hamster (*Phodopus campbelli* Thomas, 1905) caged outdoors, under natural day length and temperature, we considered ambient temperatures, body mass and its change as proximate factors of torpor bouts. The ultimate effects of daily torpor were assessed by the mortality of animals and the number of litters born. Both sexes showed daily torpor irregularly from November 2010 to January 2011 with a maximum in December; 37% of males and 39% of females did not show any torpor at all. There was no link between torpor episodes and low ambient temperatures during the whole winter, when considering the total winter period, however, we did find a significant link between ambient temperature and torpor use in December. Daily torpor in Campbell's hamsters we studied seems not to be an obligate, strictly deterministic physiological response to critical body condition when the body reserves are close to exhaustion. Among males, we observed a tendency towards a positive correlation of the number of torpor bouts on the initial body mass in September. The body mass loss from September to December was positively correlated to September's body mass. Torpor pattern did not affect the hamsters' survival and the number of litters born. We conclude that our results do not indicate daily torpor in Campbell's hamster as an obligate life history adaptation, which should unconditionally enhance ultimate fitness consequences.

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Торпор в жизненном цикле хомячка Кэмпбелла (*Phodopus campbelli* Thomas, 1905): предпосылки возникновения и конечные характеристики приспособленности

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РЕЗЮМЕ. На 68 парах хомячков Кэмпбелла (*Phodopus campbelli* Thomas, 1905), круглогодично содержащихся на улице в условиях естественного освещения и температуры, изучали непосредственные факторы (предпосылки возникновения) и вероятные конечные эффекты торпора, имеющие отношение к отдаленным проявлениям приспособленности. В качестве непосредственных факторов рассматривали внешние температуры и внутренние ресурсы (массу тела и ее изменения). Конечные (отдаленные) эффекты торпора оценивали по смертности животных и по количеству рожденных выводков. Состояние оцепенения у животных обоих полов было нерегулярным и наблюдалось в период с ноября 2010 по январь 2011 с максимумом в декабре; 37% самцов и 39% самок вообще не демонстрировали торпор. В декабре наблюдалась отрицательная связь частоты эпизодов торпора со среднесуточными температурами, однако связь эпизодов оцепенения с низкими температурами в течение всей зимы отсутствовала. Также была обнаружена связь торпора с массой тела, изменение которой характеризует обеспеченность организма депонированными энергосубстратами. Тор-

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пор у хомячка Кэмпбелла, по-видимому, не является строго детерминированной защитной реакцией, включаемой в критическом состоянии организма, когда ресурсы близки к истощению. Среди самцов наблюдали тенденцию к положительной зависимости количества эпизодов торпора от первоначальной массы тела в сентябре. Потеря массы тела с сентября по декабрь была тем больше, чем более высокой была масса тела в сентябре. Частота случаев торпора не сказывалась на выживаемости хомячков, а также на количестве рожденных выводков. Таким образом, полученные результаты свидетельствуют о том, что торпор у хомячка Кэмпбелла не является облигатной адаптацией жизненного цикла, обеспечивающей повышение конечной приспособленности.

КЛЮЧЕВЫЕ СЛОВА: торпор, гетеротермия, хомячок Кэмпбелла, *Phodopus campbelli*, зимняя биология.

Introduction

Daily torpor is a state of decreased physiological activity in an endothermic animal (bird or mammal) associated with the lowering of body temperature, that lasts less than 24 hours. Torpor use is driven by a circadian rhythm and alternated with normothermia when the animal is active and feeding (Geiser & Ruf, 1995; Geiser & Brigham, 2012; Ruf & Geiser, 2015). In the context of classical functional explanations of seasonal hibernation (Kalabukhov, 1936; Lyman *et al.*, 1982), it was long believed that the main function of daily torpor in mammals was the necessity of saving energy and/or other resources, such as water (Geiser & Ruf, 1995). In many temperate zone mammals that exhibit circannual rhythms in physiology and behavior, the seasonality in daily torpor and hibernation is indeed driven by the need to synchronize energy balances with predictable seasonal environmental changes to maximize fitness (Scherbarth & Steinlechner, 2010; Hazlerigg, 2012). According to recent studies daily torpor appears to be a legacy of ancient primitive heterotherms, animals with imperfect thermoregulation, in which inactivity was associated with a decline in body temperature (Nowack *et al.*, 2020). This is supported by the world-wide occurrence of daily torpor among small mammals of low latitudes, where daily torpor is not related to seasonality and low ambient temperatures (Ruf & Geiser, 2015; Nowack *et al.*, 2020). Thus saving energy when food availability is scarce may not be the only short-term function of daily torpor and it may have other functions with ultimate positive effects on fitness providing better survival, or reproductive success (Geiser & Brigham, 2012; Nowack *et al.*, 2017). Functions other than short-term energy (resources) saving in conditions of food shortage have got much less attention and long-term studies are often limited (Geiser, 2021).

In this paper we provide data on daily torpor in a typical seasonal breeder, Campbell's hamsters (*Phodopus campbelli* Thomas, 1905), caged outdoor in conditions close to natural for their entire lives.

The Campbell's hamster is a small, omnivorous, polyoestral, seasonally breeding, all year round active rodent, inhabiting the dry steppes and semi-deserts of Eastern Central Asia (Flint & Golovkin, 1961; Sokolov & Orlov, 1980). In Mongolia, where our hamsters originate from, they inhabit steppe and semidesert

ecosystems (Sokolov & Orlov, 1980; Batsaikhan *et al.*, 2022) with a sharply continental climate and precipitation falling mainly in summer (Murzaev, 1952). Information about their mating system in nature is scarce, so it is safe to speak only about polygamy (Vasilieva *et al.*, 1988; Wynne-Edwards *et al.*, 1992; Surov, 2006). When a male and female share one cage, they demonstrate pronounced features of parental care including male participation in care of pups (Wynne-Edwards, 1987, 1995; Vasilieva & Khrushchova, 2010). Fragmental observations in nature also signify to the close contact of a male with the female and juveniles (Wynne-Edwards *et al.*, 1992; Sokolov & Vasilieva, 1993; Wynne-Edwards, 1995). As a non-hibernating rodent, Campbell's hamster nevertheless exhibits daily torpor in cold seasons (Khrushchova Vasilieva, 2011; Ushakova *et al.*, 2012; Müller *et al.*, 2015). However, unlike the closely related Djungarian hamster (*Phodopus sungorus*), there is not much information about torpor in Campbell's hamster (Khrushchova & Vasilieva, 2011; Ushakova *et al.*, 2012; Müller *et al.*, 2015; Khrushchova *et al.*, 2017).

We analyzed the proximate predictors (ambient temperatures and body mass) and plausible long-term effects of daily torpor which may have ultimate consequences for fitness. The ultimate (long-term) effects of daily torpor were assessed by the survival of animals and their reproductive success. We tested two hypotheses: 1) The frequency of daily torpor in male and female hamsters is influenced by ambient temperatures and by body condition (body mass and its changes); 2) Daily torpor positively affects the survival and reproductive success of Campbell's hamsters. These hypotheses were tested against the background of life history events in hamsters kept outdoors from birth to death. Therefore, we also discuss the seasonal timing of torpor episodes in their relation to individual reproductive status.

Material and methods

Animals and their keeping

The study was carried out on Campbell's hamsters originated from northeastern Mongolia and have been laboratory bred since 1980s. Hamsters used in this study were born in summer 2010 from parents caged outdoors. By September 20, 2010, 68 pairs of sexually mature

hamsters of similar age had been formed at ages varying from 4 to 18 weeks (on average, 11.0 ± 0.4 weeks).

The decision to keep hamsters in pairs was caused by the high level of sociality in Campbell's hamster discussed elsewhere (Wynne-Edwards, 1987, 1995; Vasilieva & Khrushchova, 2010). The animals lived all year round outdoors since their birth in a specially built enclosure made of metal mesh under a roof. Pairs (female and male) were kept in plastic cages $70 \times 40 \times 40$ cm with replaceable bedding (dry sawdust and technical wool as nesting material). Hamsters were exposed to natural lighting, temperature, and humidity all year round.

The period of our observations of hamsters kept outdoor coincided with sharply continental climatic conditions in Moscow region in 2010–2011. In 2010 the difference between average monthly temperature of the coldest (-14.5°C) and the warmest (26.1°C) months was 40.6°C . The winter of 2010–2011 was unusually cold with minimum temperatures in Moscow in December–March below 20°C . In April 2011, there was a sharp warming up to $+22^\circ\text{C}$. The summer 2011 was one of the hottest in the history of meteorological observations in Moscow (<https://msk.nuipogoda.ru/погода-2010>; <https://msk.nuipogoda.ru/погода-2011>).

In our study water and food (rodent chow for rats, mice and hamsters, oats with the addition of sunflower seeds, beet, cabbage, dry black bread with low-fat cottage cheese supplements) were provided *ad libitum*. In winter, the animals got water from vegetables. The animals bred freely. Litters remained with their parents until the juveniles reached 25 days of age. Then the litters were removed. In case of the death of one hamster, a new partner from the reserved stock of animals was put into the cage. In the event of the death of both founders (male and female), the cage was removed. We assessed the state of genitals, the occurrence of pregnancy (via external signs visually), the birth of a litter, its initial size, and the death of any individual, adult or juvenile, by daily inspections of all cages. Males and females were weighed monthly (at month ending). If the female was pregnant, then it was weighed after the birth of the litter. The date of the beginning of pregnancy of the female was estimated by the birthday of the brood minus 18 days (the duration of pregnancy in Campbell's hamster).

The animals continued to live outdoors until their natural death. However, long-lived females, after the fall attenuation of reproduction in 2011, no longer reproduced, with the exception of four females that gave birth to one litter each in 2012.

Daily torpor occurrence

In the winter season 2009–2010 we conducted a pilot study to verify the existence of torpor in Campbell's hamsters equipped with data-storing thermologgers (iBDL-L (DS1922L-F5) complex, LLC "NTL EIn", Moscow) implanted intraperitoneally to ten males (Khrushchova & Vasilieva, 2011). Loggers were covered by a thin layer of sterile bone wax (Ethicon W810) and implanted into the abdominal cavity under Zoletil

(Virbac, France) anesthesia. The 8–10 mm incision of the skin and abdominal wall was sutured with a sterile surgical polyamide self-absorbable Polycon thread and treated by sulphanilamide powder. Pain management was provided with novokain injections. The duration of the operation was 10–15 minutes. All surgical procedures were provided in October during several warm days, all animals were kept under regular revision until the incision's healing.

Loggers were programmed to record body temperature from 20th November to 1st May at pre-selected intervals of 30 minutes, an accuracy 0.5°C . We also surgically removed loggers from the abdominal cavity at the end of observations. All procedures were performed in according to the permission of Severtsov Institute Bioethics commission.

The analysis of thermograms allowed us to determine the most appropriate time of day to check hamsters for daily torpor visually in the main study. The preliminary study showed that two animals never showed torpor state, in other eight males all cases of deep and shallow daily torpor occurred from 8:00 to 19:30 (the mean time of torpor beginning was 10:00, the mean time of bout ending — 15:00; more than 75% of the bouts occurred from 10:00 to 16:00 (Fig. 1). The average duration of a bout in a male was 5.2 ± 0.2 hours. Therefore, to record torpor events we inspected cages between 12.00 and 15.00 every day from the day of pair formation.

The main study was conducted from the last third of September 2010 until the end of September 2011. In the beginning, we did a non-invasive study that allowed us to determine the state of daily torpor visually. Hamster in torpor is motionless, cool to the touch, breathing is slow, and the reaction to touch is absent or sluggish. Basing on these criteria we determined daily torpor on a daily basis visually by touching the motionless hamster with the finger. In this it differs easily from an active individual, including a resting one. The latter immediately becomes active when disturbed. This easy procedure allows distinguishing torpid and sleeping hamsters. When one hamster in pair was in torpor we determine the sex of an active one by anogenital distance and the size of sexually dimorphic midventral gland that is much better pronounced in males. When both hamsters were in a torpid state there was no need to handle and disturb animals.

Statistical procedures

Daily temperature and the probability of torpor — The presence of torpor for an individual was a binary variable. Thus, we performed Generalized linear mixed model (GLMM) for binomial distribution with logit link function and pair identity as a random factor using package *lme4* implemented in R 4.1.0 (R Core Development Team, 2021; Bates *et al.*, 2015). Since bouts of torpor were rare and most of them occurred in December, only the data of that month were included in the model. To analyze the effects of the date and the ambient temperature on the probability of an individual

being in torpor, we daily classified every individual as torpid (N days \times N individuals = 229) or normothermic (N days \times N individuals = 3078). The models included the presence ($n=229$) or absence ($n=3078$) of a torpor episode as the dependent variable, as well as three independent variables — date, daily average ambient temperature and sex.

Individual's body condition and the number of torpor bouts — To understand the effects of an individual's characteristics on the daily probability of torpor, we calculated for every individual all days when torpor bouts were registered in fall and winter 2010–2011. The number of torpor bouts followed a Poisson distribution, so we ran a GLMM for Poisson distribution with log link function in the library *lme4* (Bates *et al.*, 2015). To test the possible effect of initial body condition on the total number of torpor bouts per individual during the subsequent fall and winter we included September body mass (initial and maximum mean body mass) as a fixed factor in the model. Since the hamsters' minimum mean body mass was observed in December and maximum mean body mass in September, we fitted the difference in individual body mass between December and September into the model as an estimation of winter body mass loss ($\Delta = BM_{December} - BM_{September}$). Sex and age at 25.09.2010 (in days) were also included in the model as fixed effects, and pair identity was fitted as a random factor to control possible correlations between animals in pairs.

Since there was a weak negative correlation between September body mass (the beginning of observations) and the animals' age in September ($r = -0.24$, $p = 0.005$) and between relative body mass change from September through December ($\Delta_{rel} = (BM_{December} - BM_{September})/BM_{September}$) and age ($r = -0.21$, $p = 0.015$), we also used residuals from regression of body mass and its relative change on age as measures of body mass and its change for a given age in correlation analysis and graphical presentation of the data. We denoted this measure as corrected body mass.

Effects of torpor on survival probability — We investigated the effects of torpor on the probability of survival in 2010–2011 for every individual. Survival was thus a binary dependent variable and we fitted it as a response in GLMM for binomial distribution with logit link function and pair identity as a random effect. The total number of torpor bouts during the winter was included in the model as a predictor. December body mass, difference in individual body mass between December and September (winter body mass loss), sex and age at 25.09.2010 (in days) were fitted into the model as possible confounding factors.

Effects of torpor on pair reproductive success — Since males and females lived in pairs and shared cages, it was not possible to distinguish male and female reproductive success within a pair of founders. Thus, we summarized numbers of torpor bouts for male and female within pairs and averaged the age at 25.09.2010 (individual ages in pairs were similar), December body

mass and body mass loss from September within pairs. Since the number of pups we could register within the litter was influenced by prenatal death or eating of dead pups by parents, and since the correlation between annual number of offspring and annual number of litters was very high ($r=0.93$), we used only the number of litters as an estimation of annual reproductive success and did not make a separate model for number of offspring. Since N of litters fitted normal distribution, we made a linear regression model (LM) in *lme4*. We included in the analysis only those pairs in which both partners remained alive until the end of the reproductive season (until September 2011; $n=38$).

Pairs in which either partner had died before September 2011 were excluded from the analysis. Since we had data on total life span and lifetime reproductive success of females (sum of litters and pups born by the founder female) and males (sum of litters and pups born by the founder female and by the second female introduced to the male after the death of the first one), we also computed Spearman's rank correlations between the total number of individual torpor bouts we had registered in 2010–2011 and lifetime fitness characteristics separately for each sex. For all dependent variables in GLMMs and LM, we evaluated the set of candidate models with all combinations of predictors. We compared the candidate models and selected the best models using corrected Akaike information criterion (AICc; Burnham *et al.*, 2011) in the library MuMIn (Barton, 2019). We calculated AICc weights and averaged estimates with their errors for models with $\Delta AICc < 2$. We used likelihood ratio tests (LRT) to assess the significance of all effects. All quantitative predictors were standardized and the significance level was set at $p < 0.05$.

For all comparisons given in the text, we used the Kolmogorov-Smirnov test to assess normality of distributions. A Student's t -test for independent samples and Pearson's correlations were applied to compare normally distributed variables. Homogeneity of variances was assessed by the Levene's test. When deviations from normality were significant, we used the Mann-Whitney U test and Spearman's rank correlation coefficient. All tests were two-tailed, with a significance level $p < 0.05$.

For most comparisons, we used data from 68 males and 66 females. Differences in sample sizes other than those explained above were caused by the animal's accidental death or by the lack of some measurements. Sample sizes are indicated in figure captions and tables.

Statistical analyses were performed using the software packages R 4.1.0 (R Core Development Team, 2021).

Compliance with regulations when working with animals

In our study, we adhered to the recommendations given in "Principles of Laboratory Animal Care" (1996) and in legislation of the Russian Federation. All manipulations with animals in 2010–2011 complied with "Guidelines for the treatment of animals in behavioral research and teaching" (Buchanan *et al.*, 2012).

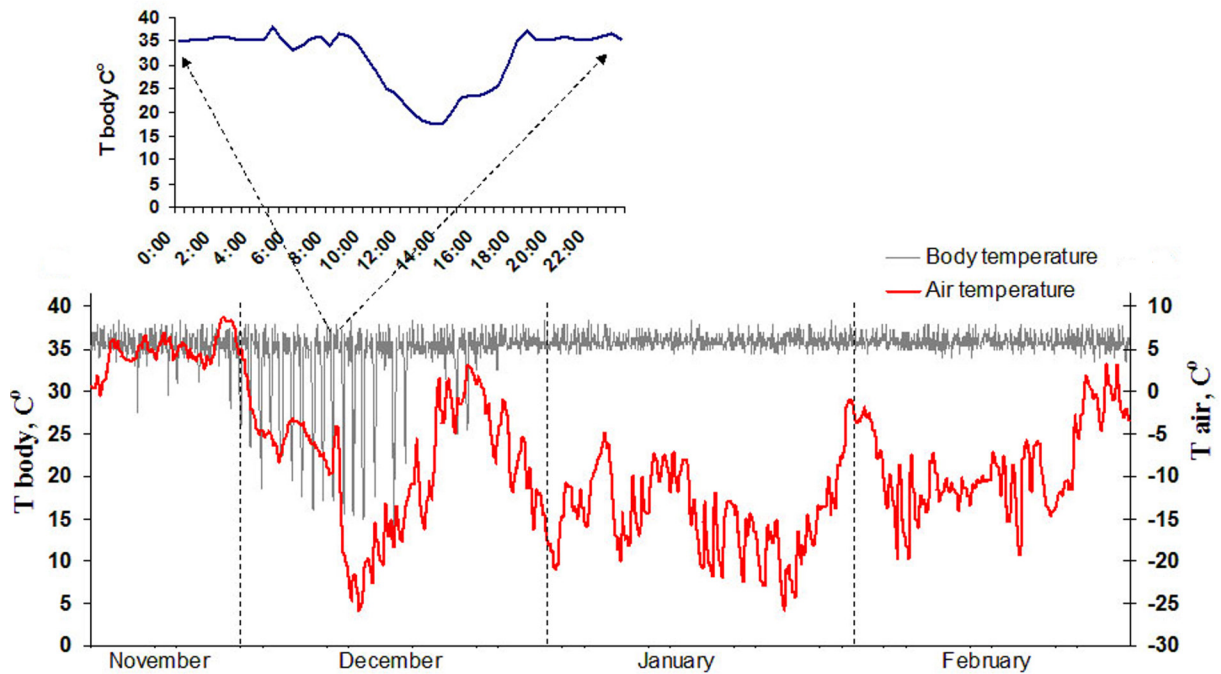


Fig. 1. Daily fluctuations in body temperature in male *Phodopus campbelli* against the background of ambient daily temperature in November 2009–February 2010.

This research scheme was approved by the Bioethics Commission of A.N. Severtsov Institute of Ecology and Evolution RAS.

Results

Proximate predictors

Ambient temperatures and torpor — Daily torpor (<24 hours) occurred in males and females from November 2010 to January 2011 only. There was no direct relationship with ambient temperatures during the whole period of cold weather. The highest total number of torpor bouts as well as the lowest daily average temperature was recorded in December 2010 (Fig. 1). The number of torpor bouts dropped sharply in January, and episodes of daily torpor were no longer observed in February in spite of very low ambient temperatures (Fig. 2). Bouts of torpor appeared irregularly among hamsters of each sex. Out of 68 males, 25 males (37%) did not show torpor during the period of observations, 19 males (28%) demonstrated torpor 1–2 times, and only four males — more than 10 times (6%). Out of 66 females, 26 females (39%) never showed torpor, 15 females (23%) 1–2 times, four females more than 10 times (6%). All three fixed effects (daily temperature, date, sex) received support in the model selection procedure for daily torpor in December and were included in the best model (GLMM with pair identity as random effect, Table 3). The daily temperature in December correlated negatively with the calendar date ($r=-0.39$, $p<0.01$). The lower the temperature

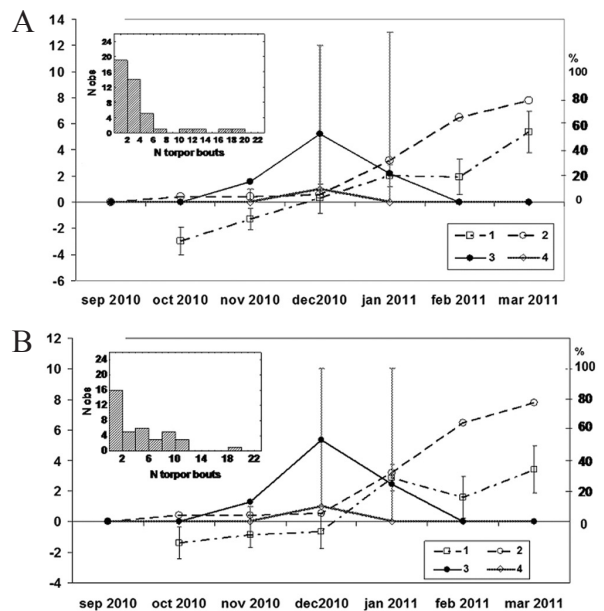


Fig. 2. Body mass, torpor and participation in reproduction of (A) males and (B) females in 2010–2011. 1 — monthly changes in body mass (mean \pm SE; negative values — mean body mass loss in the current month compared to the previous month, positive values — mean gain in body mass compared to the previous month); 2 — percentage of breeding females (pairs); 3 — percentage of hamsters in torpor; 4 — medians and range of variation in the number of torpor bouts among males and females.

and the later the date of observation, the higher was the probability of torpor (Table 1). The torpor probability was slightly higher in females than in males, but the effect was not significant (Table 1).

There was a highly significant random effect of pair identity in the model (Table 1).

Body mass and its change — A decrease in body mass in male and female hamsters occurred from September through December and was most pronounced in December. In January, the body mass of hamsters began to increase again (Fig. 2). December was the month with the highest number of torpor bouts and the lowest body mass among males and females (Fig. 2). The monthly body mass in hamsters exhibiting daily torpor was lower than the body mass of hamsters not using torpor (Fig. 3). Since there were few cases of torpor in November and January, the presence or absence of torpor was considered for the entire period, and body mass — for each of the three months. Among males, there were significant differences in body mass in December and in January, among females — in December. The number of bouts of daily torpor negatively depended on the age-corrected relative body mass change from September through December, both in males (Spearman $R = -0.55$, $n = 68$, $t = -5.38$, $p < 0.001$) and females (Spearman $R = -0.42$, $n = 66$, $t = -3.75$, $p < 0.001$) (Fig. 4). Without adjustment for age, 30.9% of males (21 out of 68) did not lose body mass from September through December. Quite the contrary, they gained in body mass,

and only six of them (28.6%) underwent daily torpor. There was no correlation of torpor with age among males which gained in body mass ($r = -0.05$, $p = 0.81$). Among females 11 out of 66 gained in body mass from September through December (16.7%); in only one female with a slight increase in body mass nine bouts of torpor were registered, and another female with increased body mass showed only one bout of daily torpor. Both females (18.2% out of 11) were not young in September (79 and 111 days from birth). The higher the age-adjusted estimates of body mass in September, the greater the age-adjusted relative (percentage) body mass loss from September through December (males: $y = 0.02 - 0.01 * x$; $r = -0.40$; $n = 68$; $p < 0.001$; females: $y = -0.025 - 0.01 * x$; $r = -0.30$; $n = 66$; $p = 0.013$) (Fig. 5).

The use of GLMM to analyze the effects of individual body condition on N of torpor bouts for every animal showed that the most parsimonious model for the total number of days with torpor included two predictors: the body mass in September and the body mass loss from September through December (Table 3). The greater the body mass loss from September through December ($\Delta = \text{BM}_{\text{December}} - \text{BM}_{\text{September}}$), the larger the number of torpor bouts during the fall–winter period (Table 1). The number of torpor bouts was higher among animals whose body mass was lower in September (Table 1). There was a strong effect of pair identity on the number of torpor bouts (Table 1). Effects of age and sex were insignificant (Table 1).

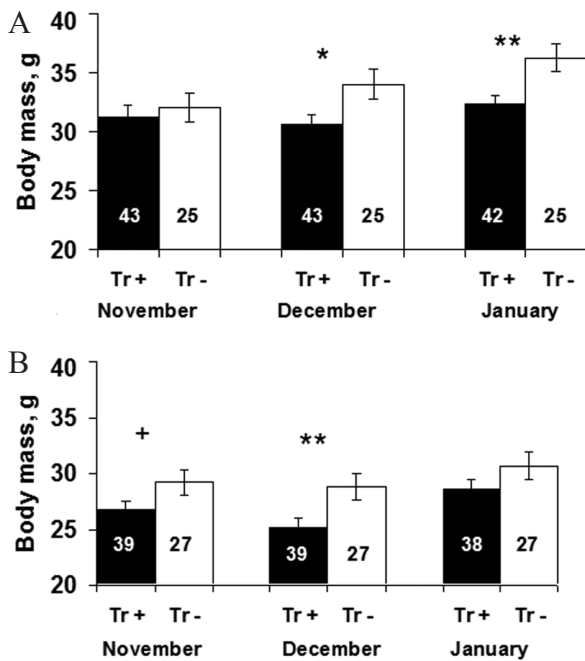


Fig. 3. Body mass (A) of males and (B) of females with (black bars) and without (white bars) torpor in November 2010 — January 2011. Since there were few cases of torpor in November and January, the presence or absence of torpor was considered for the entire period, and body mass — for each of the three months. The numbers on the bars indicate sample sizes; + $p < 0.1$, * $p < 0.05$, ** $p < 0.01$.

Reproduction and torpor

From October through December, the proportion of breeding females remained low (4–5.5%), reached 32% in January and 78% of females were involved in breeding in March. The activation of reproduction in January 2011 coincided with an increase in body mass and with a sharp decrease in the number of torpor patterns in both males and females (Fig. 2). Among females, we did not observe an overlap of pregnancy and lactation with torpor. Among males, we recorded only one bout of torpor in a male paired with a pregnant female and one bout of torpor in a male paired with a lactating female. Both cases were in January 2011. There was no difference between females who survived and died until the end 2011 in regard to the number of litters born (Student's t -test for independent samples: females: $t = -1.06$, $n_{\text{survived}} = 33$, $n_{\text{died}} = 33$, $p = 0.29$) or the total number of pups born (females: $t = -0.41$, $n_{\text{survived}} = 33$, $n_{\text{died}} = 32$, $p = 0.68$).

Ultimate effects of daily torpor

Our GLMM showed that daily torpor did not affect the probability of the hamsters' survival in 2010–2011. The best model for the survival probability included the hamster's sex only (Table 3): males lived longer than females (Table 1). Up to the end of 2011, 74.4% of males and 50% of females survived. The other effects were weak and insignificant.

The number of torpor bouts in pairs was strongly correlated ($r = 0.83$, $p < 0.0001$). There was no effect of daily torpor on the pairs' reproductive success. Effects

Table 1. Effects of temperature on daily torpor, individual characteristics on the total number of torpor bouts and the effects of torpor on the subsequent survival and reproduction in Campbell's hamster. B and SE correspond to model-averaged parameter estimates and standard errors in GLMM with binomial distribution (for the daily torpor and the survival probability model), in GLMM with Poisson distribution (for the model of the number of torpor bouts, N torpor), and in linear regression model (for number of litters in pair); χ^2 corresponds to likelihood ratio test. Pair identity (Pair ID) was introduced as a random effect in all GLMMs. Significant effects ($P < 0.05$) are marked in bold.

Model and predictors	Response and statistics
(1) Daily temperature and probability of torpor (N individuals \times N days = 4010)	Is an individual in torpor on a particular date (yes/no)
Calendar date	$B = 0.86 \pm 0.10, \chi^2 = 89.2, p < 0.0001$
Mean daily temperature	$B = -0.73 \pm 0.10, \chi^2 = 60.3, p < 0.0001$
Sex	$B = -0.15 \pm 0.17, \chi^2 = 2.8, p = 0.1$
Pair ID	$\chi^2 = 271, p < 0.0001$
(2) Individual characteristics and N torpor (N individuals = 132)	Total N torpor bouts per winter
Age in September (days)	$B = 0.10 \pm 0.14, \chi^2 = 0.5, p = 0.5$
Body mass loss from September through December (g)	$B = -0.58 \pm 0.12, \chi^2 = 24.8, p < 0.0001$
Body mass in September (g)	$B = -0.23 \pm 0.08, \chi^2 = 7.1, p = 0.008$
Sex*	$B = 0.006 \pm 0.14, \chi^2 = 0.002, p = 0.9$
Pair ID	$\chi^2 = 250, p < 0.0001$
(3) N torpor and survival (N individuals = 129)	Probability of survival during 2010–2011
Age in September (days)	$B = -0.16 \pm 0.21, \chi^2 = 0.06, p = 0.8$
Body mass loss from September through December (g)	$B = 0.29 \pm 0.25, \chi^2 = 2.1, p = 0.1$
Body mass in December (g)	$B = -0.29 \pm 0.28, \chi^2 = 1.8, p = 0.2$
N torpor bouts*	$B = -0.07 \pm 0.20, \chi^2 = 0.09, p = 0.8$
Sex	$B = 1.48 \pm 0.49, \chi^2 = 14.2, p = 0.0001$
Pair ID	$\chi^2 = 0.2, p = 0.6$
(4) N torpor and annual reproductive success (N pairs = 38)	N litters produced by the pair
Mean age in September (within pairs; days)	$B = 0.9 \pm 0.6, \chi^2 = 1.8, p = 0.2$
Mean body mass loss from September through December (g)	$B = 1.3 \pm 0.7, \chi^2 = 4.4, p = 0.04$
Mean body mass in December (g)	$B = 1.1 \pm 0.6, \chi^2 = 2.1, p = 0.2$
Total N torpor bouts in the pair	$B = 0.6 \pm 0.7, \chi^2 = 1.0, p = 0.3$

* The effects weren't included in the best models with $\Delta AIC_c < 2.0$; thus estimates from the full model were presented.

Table 2. Relationship between the total number of torpor bouts and fitness characteristics of Campbell's hamsters.

Variables	Females				Males			
	Valid N	Spearman R	$t_{(N-2)}$	p	Valid N	Spearman R	$t_{(N-2)}$	p
N torpor bouts vs. lifetime	65	0.02	0.17	0.87	68	-0.12	-0.99	0.32
N torpor bouts vs. N litters (lifetime)	65	-0.12	-0.95	0.35	68	-0.09	-0.74	0.46
N torpor bouts vs. N pups (lifetime)	65	-0.15	-1.21	0.23	67	0.06	0.47	0.64
N torpor bouts vs. N litters in 2011	65	-0.21	-1.72	0.09	68	-0.19	-1.54	0.13
N torpor bouts vs. N pups in 2011	64*	-0.21	-1.69	0.10	68	-0.07	-0.56	0.57

* Pups in one of the litters were eaten by their parents after birth.

that received support in the model selection procedure were mean body mass in December and body mass loss from September through December (Table 3). The only significant predictor that affected the number of litters

produced was body mass loss: the greater the average body mass loss in the pair, the fewer the number of litters produced during the subsequent reproductive period (Table 1).

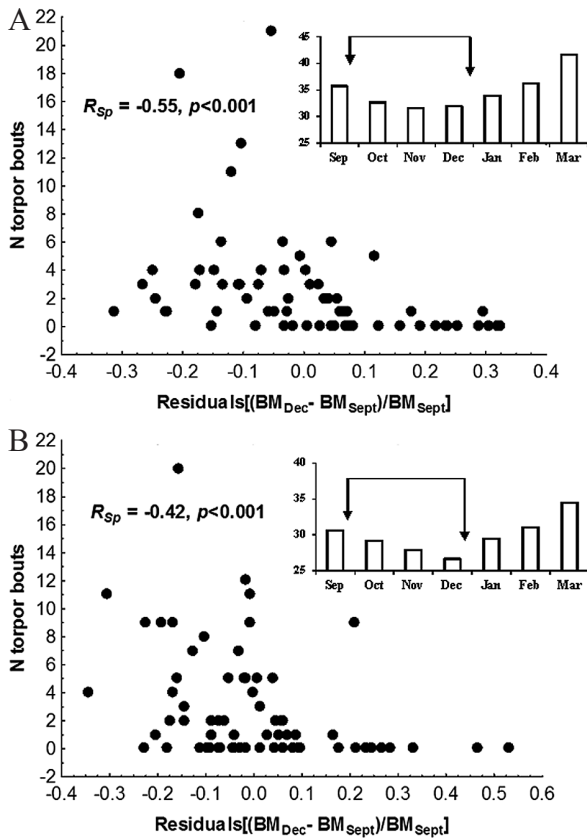


Fig. 4. Number of torpor bouts depending on the age-corrected relative body mass change from September through December 2010 among (A) males, (B) females. Insets show mean body mass change by month.

Analysis of Spearman's rank correlation coefficients provided for females and males separately also did not show statistically significant links between the total number of torpor bouts registered and fitness characteristics of these hamsters within their lifetime. There was a weak tendency towards a negative dependence of reproductive success on the number of torpor bouts in fall–winter 2010–2011 among females (Table 2).

Discussion

Torpor is observed in mammals and birds living in both temperate and tropical climates. This finding indicates that this phenomenon is not the adaptation to protect only against the cold, but in general to cope with seasonal restriction or timely limited energy supply (Heldmaier *et al.*, 2004). In many species of mammals and birds, daily torpor is observed regularly, even if there is enough food and conditions are quite favorable. It looks like a deeply genetically determined response, a result of sustained natural selection, which aimed in the short term to balance the energy budget (Geiser, 2004; Geiser & Brigham, 2012; Ruf & Geiser, 2015). In small mammals that inhabit temperate and

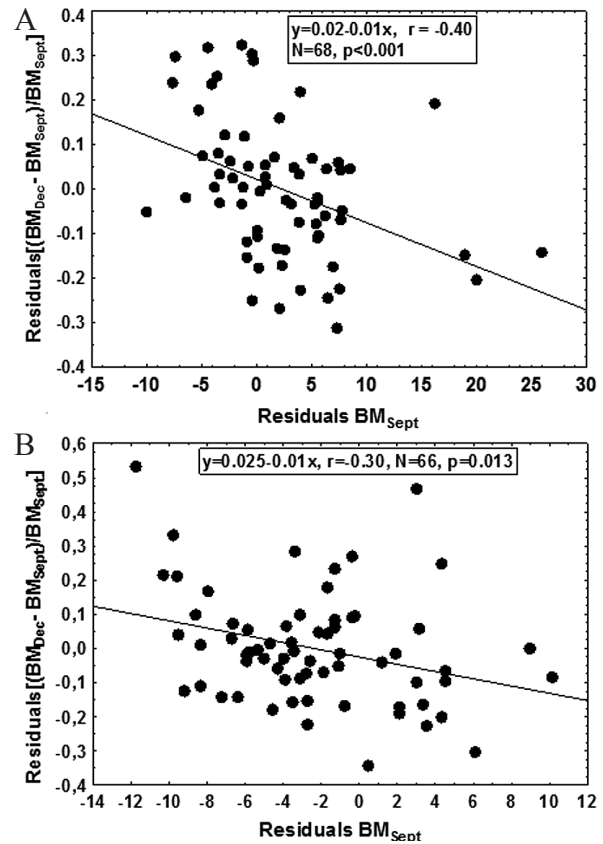


Fig. 5. Dependence of age-corrected relative body mass change from September through December 2010 on the age-corrected initial body mass in September 2010.

cold zones in the northern hemisphere, daily torpor is often a seasonal phenomenon that occurs because of climatic restrictions and reduced availability of food and is controlled by a day length change (Kortner & Geiser, 2000; Paul *et al.*, 2008; Jastroch *et al.*, 2016). In Djungarian hamster (*Phodopus sungorus*), a species closely related to Campbell's hamster, torpor is preceded by a whole complex of morphofunctional transformations triggered by a seasonal decrease in the day length (Diedrich *et al.*, 2020). In this species, daily torpor is entered spontaneously and on a day-to-day basis in animals that entered the winter morphotype (Heldmaier & Steinlechner, 1981; Ruf *et al.*, 1991, 1993; Müller *et al.*, 2015; Diedrich *et al.*, 2015; Cubuk *et al.*, 2016; Haugg *et al.*, 2021) or can appear as fasting-induced hypothermia during summer (Diedrich *et al.*, 2015). Daily torpor was also noted on winter in two other species of *Phodopus*, Campbell's hamster and the desert hamster kept outdoor (Khrushchova & Vasilieva, 2011; Ushakova *et al.*, 2012; Müller *et al.*, 2015).

In our study of Campbell's hamster, the daily torpor was also confined to the cold period of the year, and it was encountered irregularly: 37% of males and 39% of females did not show any torpor at all under *ad libitum* food availability. At the same time, there was no visible

Table 3. Model selection results describing the effects of daily temperature and individual characteristics on torpor, and effects of torpor on subsequent survival and reproductive success in Campbell's hamsters. The full names of predictors in the candidate models see in the Table 2. Pair identity was fitted as a random effect in all models for the daily torpor, the total number of torpor bouts, and the models for survival probability. k is the number of parameters estimated by the model. Only the models with $\Delta AIC_c < 2.0$ are presented; AIC_c weights calculated among models with $\Delta AIC_c < 2.0$.

Model	k	ΔAIC_c	AIC_c weights
(1) Daily temperature and probability of torpor (min $AIC_c = 1406.34$; $n=4010$)			
Date+Temperature+Sex	5	0	0.6
Date+Temperature	4	0.78	0.4
(2) Individual characteristics and N torpor (min $AIC_c = 491.46$; $n=132$)			
Body mass (September)+Weight loss	4	0	0.69
Age+ Body mass (September)+Weight loss	5	1.62	0.31
(3) N torpor and survival (min $AIC_c = 163.14$; $n=129$)			
Sex	3	0	0.33
Weight loss+Sex	4	1.17	0.18
Body mass (December)+Weight loss+Sex	5	1.24	0.18
Age+Sex	4	1.51	0.16
Body mass (December)+Sex	4	1.59	0.15
(4) N torpor and annual reproductive success (min $AIC_c = 209.10$; $n=38$)			
Mean mass (December)	3	0	0.22
Mean mass (December)+Mean weight loss	4	0.25	0.20
Mean weight loss	3	0.35	0.19
Mean age+Mean weight loss	4	0.45	0.18
Mean age+Mean mass (December)+Mean weight loss	5	1.19	0.12
Mean mass (December)+Mean weight loss+Total N torpor	5	1.98	0.08

link between torpor use and low ambient temperatures during the whole cold period, except for in December, the month with the highest number of torpor events. We also found a pronounced link between torpor use and internal body reserves, assessed through body mass. The greater the body mass loss from September through December the larger the number of torpor bouts during the fall–winter period. The percentage of body mass loss from September through December was also greater, the higher the body mass in September. However, some hamsters with a high body mass in September also showed a torpor pattern in November–January. Torpor was also registered among hamsters that gained body mass during the fall–winter period, although the proportion of torpid individuals among them was not high (28.5% among males and 18.2% among females). These facts and the pronounced irregularity of torpor may indicate the absence of a narrowly targeted, genetically determined mechanism of daily torpor in Campbell's hamster. Daily torpor in this species does not look like a strictly focused physiological response, manifested in a critical body condition, when available reserves are close to depletion (Diedrich *et al.*, 2015).

At the same time daily torpor we observed in Campbell's hamster looks similar in general to that of the Djungarian hamster, which exhibits daily torpor spontaneously during winter acclimation (Diedrich *et al.*, 2015).

In our study we kept hamsters in pairs due to high level of sociality in Campbell's hamsters that was justified by laboratory and field observations (Wynne-Ed-

wards, 1987, 1995; Vasilieva & Khrushchova, 2010). In two GLMMs, the likelihood ratio (LR) test confirmed a significant effect of pair identity (the random factor) on the number of torpor bouts demonstrated by a hamster. There was a strong correlation in the number of torpor bouts in pairs of hamsters kept in one cage. This synchronized torpor may attest to the influence of partners on each other. Synchronization of periods of heterothermy and normothermy was also noted in pairs of the Djungarian hamster (Ruf *et al.*, 1991). The employment of daily torpor can be affected by social interactions, although the simplest explanation may be related to the conditions in the nest. Torpor use in one animal likely leads to a drop in temperature in the nest, which provokes torpor in the other animal. We did not specifically test this assumption in the framework of this study.

Did the daily torpor in Campbell's hamster have long-term consequences positively affecting individual fitness within their lifetime? We did not get direct confirmation for this. Indirectly, our results support the finding of a lack of direct fitness benefits in Djungarian hamsters responding to short photoperiod by change of fur coloration and use of torpor versus non-responders (Przybylska *et al.*, 2019). It was found that despite differences in the strategy to cope with challenges of winter conditions in responders and non-responders, both phenotypes did not differ in reproductive success (Przybylska *et al.*, 2019). Relating to Campbell's hamster in nature it is possible that some thin or weakened individuals can survive by compensating for the inevitable death with a

daily torpor or by investing in reproduction the reserves saved due to torpor (Turner *et al.*, 2012). At that the ultimate fitness characteristics may not differ in torpid and non-torpid individuals. In our experiment, the animals received food ad libitum, whereas in nature the combination of low temperatures and a food shortage can act enhancing the long-term effect of daily torpor. In our study, we can only state that the daily torpor in experimental Campbell's hamsters did not positively influence their survival and reproductive success, i.e. the number of litters or pups born, as if it was an obligate, narrowly focused adaptation providing a direct increase the ultimate fitness. Based on the results we obtained, we have no reason to consider daily torpor in Campbell's hamster to be an obligate life history adaptation, directly contributing to survival or reproduction.

In our experiment, none of the females combined pregnancy and lactation with torpor episodes, while a sharp increase in the proportion of females that started breeding was accompanied by a sharp drop and complete cessation of torpor episodes in both sexes. The beginning of reproduction was accompanied by an increase in the body mass of males and females (in the latter, the weight after litter birth was used).

The negative relationship between torpor and reproduction in mammals and birds has been repeatedly noted and explained by mutually exclusive processes due to conflicting energy and hormonal demands of the body (McAllan & Geiser, 2014). Male ground squirrels with testicles in scrotum refused to hibernate (Landau & Dawe, 1960). Reproductive hormones, in particular testosterone in males, are known to suppress torpor in some hamster species (Goldman *et al.*, 1986). High concentrations of circulating testosterone positively correlate with reproductive activity, but negatively correlate with hibernation in yellow pine chipmunks (*Tamias amoenus*) (Place *et al.*, 2002), Uinta ground squirrels (*Urocitellus armatus*) (Ellis *et al.*, 1983), goldenmantled ground squirrels (*Urocitellus lateralis*) (Barnes, 1986), European ground squirrels (*Spermophilus citellus*) (Strauss *et al.*, 2008), and Mongolian hamsters (*Allocricetulus curtatus*) (Feoktistova *et al.*, 2013). Testosterone administration suppresses hibernation in male hamsters and ground squirrels (Hall & Goldman, 1980; Lee *et al.*, 1990), and the daily torpor in Djungarian hamsters (Goldman *et al.*, 1986; Ouarour *et al.*, 1991; Ruby *et al.*, 1993). Both in Djungarian and Campbell's hamsters daily torpor was observed in fall–winter period (torpor bouts started earlier in Djungarian hamster) and were associated with decreased body mass and lowered reproductive capacity (Müller *et al.*, 2015).

Despite the above facts, the known number of heterothermic species exhibiting torpor during reproduction continues to increase. According to McAllan and Geiser (McAllan & Geiser, 2014), the incompatibility of torpor and reproduction is observed mainly in rodents of high latitudes (Sciuridae, Cricetidae) living in strictly seasonal, but predictably productive habitats.

Our results do not fully agree with this opinion. As an inhabitant of the dry steppes and semi-deserts of

Central Asia with a strictly seasonal, sharply continental but rather unpredictable climate, Campbell's hamster is not associated with sustainable and productive habitats (Sokolov & Orlov, 1980; Mallon, 1985). In the context of explanations provided by McAllan and Geiser (McAllan & Geiser, 2014), animals that regularly show daily torpor during breeding must face unpredictable conditions and resources in habitats where availability of food may be reduced due to changes in weather, or such species must reproduce partially or completely in winter.

Our hamsters started breeding just after the fall–winter pause right in January. The trigger for these changes is the length of daylight hours, which changes the metabolism of hamsters from the fall–winter scenario to the spring–summer one (our unpublished data on Campbell's hamster are similar to those previously published for the desert hamster (Vasilieva *et al.*, 2020). In Djungarian hamsters this scenario is driven by decreasing day length associated with change fur, regress gonads, loss in body mass, increase in basal metabolic rate and change in locomotor activity (Heldmaier & Steinlechner, 1981; Ruf *et al.*, 1991; Scherbarth & Steinlechner, 2010). Similarly in desert hamster kept under short-day lighting at ambient temperature 23°C with food and water unlimited physiological changes included a drop in body mass, an intensification of basal metabolism, and an inhibition of reproductive activity against the background of an increased basal level of stress (Vasilieva *et al.*, 2020). Thus, the results of our study indicate the daily torpor in Campbell's hamster as a spontaneous and irregular hypometabolic state, functionally significant at short time intervals and associated with the fall–winter scenario of the organism's vital activity.

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