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SHORT COMMUNICATION

Siberian hamsters nonresponding to short photoperiod use fasting-induced torpor

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ABSTRACT

Nonresponding Siberian hamsters (*Phodopus sungorus*) do not develop the winter phenotype of white fur, low body mass (M_b) and spontaneous torpor in response to short photoperiod. However, their thermoregulatory response to fasting remains unknown. We measured body temperature and M_b of 12 nonresponders acclimated to short photoperiod and then to cold and fasted four times for 24 h. Four individuals used torpor, and in total, we recorded 19 torpor bouts, which were shallow, short and occurred at night. Moreover, fasting increased the heterothermy index in all hamsters. Low M_b was not a prerequisite for torpor use and M_b loss did not correlate with either heterothermy index or torpor use. This is the first evidence that individuals which do not develop the winter phenotype can use torpor or increase body temperature variability to face unpredictable, adverse environmental conditions. Despite the lack of seasonal changes, thermoregulatory adjustments may increase the probability of winter survival in nonresponders.

KEY WORDS: Torpor, Fasting, Siberian hamsters, Winter phenotypes, Nonresponders

INTRODUCTION

Maintaining high body temperature (T_b), regardless of ambient conditions, can be challenging for small mammals and birds. Because of significant seasonal changes in the environment, many small endotherms face low energy availability and high energy expenditure during winter. Smaller species can be more at risk of a negative energy balance during cold exposure as they have higher surface-area-to-volume ratios to lose heat to their environments (Ruf and Geiser, 2015). To reduce energy expenditure in response to predictable (seasonal) and unpredictable (short-term) energy shortages, some endothermic species are heterothermic, i.e. use hibernation and/or daily torpor (Geiser, 2020, 2021). Although heterothermy reduces energy expenditure and allows survival in an adverse environment, torpor has also significant costs (Millesi et al., 2001; Humphries et al., 2003; Dammhahn et al., 2017), the most obvious being the energetic costs of rewarming to normothermic T_b (Tucker, 1965; Heldmaier, 1978).

The continuum of torpor responses ranges from short (<24 h) daily torpor to multi-day torpor during seasonal hibernation (Geiser and Ruf, 1995). Historically, heterothermy was considered to be a strategy to cope with energy challenges during cold winters (Willis, 2007; Ruf and Geiser, 2015), but today, a growing number of studies focus on torpor use in response to other environmental and physiological challenges (Nowack et al., 2020). Animals may use torpor in response to fasting and unpredictable phenomena like drought, fire or flood (to survive), during development (to enhance growth), before migration (to enhance fat storage) or during the reproductive season (to increase the success of offspring; reviewed in Geiser and Brigham, 2012; Nowack et al., 2017), but energy savings remain the ultimate function of torpor. Perhaps the best-studied example of torpor to avoid a negative energy balance is fasting-induced torpor (Jensen et al., 2013). It can be used by species such as mice, which never use torpor spontaneously (Hudson and Scott, 1979) and also by heterotherms that use torpor seasonally (Diedrich and Steinlechner, 2012). Fasting-induced torpor differs in its circadian, neuronal and molecular regulation from spontaneous torpor, which is induced by shortening photoperiod (Cubuk et al., 2017; Diedrich and Steinlechner, 2012). Fasting-induced torpor bouts are less frequent, shorter and shallower, and less predictable than spontaneous torpor bouts (Diedrich et al., 2015).

Interspecific variation of heterothermy is well described (Ruf and Geiser, 2015; Nowack and Turbill, 2022), but recently scientists have focused on the intraspecific variability of torpor use (Schmid and Ganzhorn, 2009; Brigham et al., 2012; Haugg et al., 2021; Spence and Tingley, 2021). One of the species with extremely variable propensity to display torpor is the Siberian hamster *Phodopus sungorus*. This is a model species for studies of both fasting-induced and spontaneous seasonal torpor (Diedrich et al., 2015). Individuals responding to shortening photoperiod (responders) develop a winter phenotype characterized by reduced body mass (M_b), regressed gonads, dense white fur and torpor use (Heldmaier and Steinlechner, 1981; Lynch et al., 1989; Gorman and Zucker, 1997). Among responders, patterns of spontaneous torpor use are profoundly variable and under the same conditions some individuals use torpor every day, while others do so sporadically throughout the winter (Haugg et al., 2021). Moreover, some hamsters do not respond to short photoperiod at all (nonresponders) and maintain the summer phenotype throughout the year (Lynch et al., 1989; Gorman and Zucker, 1997; Przybylska-Piech et al., 2021). Nonresponding individuals do not use spontaneous torpor and maintain grey fur, high body mass and active gonads during winter (Gorman and Zucker, 1997; Przybylska-Piech et al., 2021). Despite many studies comparing fasting-induced and spontaneous seasonal torpor in responding Siberian hamsters (Diedrich and Steinlechner, 2012; Diedrich et al., 2015; Cubuk et al., 2017), there are no data on the response to fasting in nonresponders. Since different mechanisms underlie fasting-induced and spontaneous torpor (Diedrich et al., 2015), we suggest that nonresponding individuals may be able to lower body temperature in response to acute food shortage, and enter torpor to reduce energy expenditure and avoid a negative energy balance. We measured the T_b of 15 nonresponding Siberian hamsters, acclimated to short-day conditions, and tested whether

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they use torpor in response to low ambient temperature (T_a) and fasting. As both seasonal and fasting-induced torpor are highly dependent on body condition (Diedrich and Steinlechner, 2012; Cubuk et al., 2017; Spence and Tingley, 2021), we also analysed changes in M_b during acclimation and fasting.

MATERIALS AND METHODS
Animals
All experimental procedures were approved by the Local Committee for Ethics in Animal Research in Bydgoszcz, Poland (decisions: 34/2020; 20/2021). We used 15 adult male Siberian hamster *Phodopus sungorus* (Pallas 1773) that did not change to the winter phenotype after 14 weeks under short photoperiod (nonresponding individuals). Animals originated from the colony maintained in the Faculty of Biological and Veterinary Sciences at the Nicolaus Copernicus University in Toruń, Poland. After birth, animals were maintained under long photoperiod (LP; 16 h light:8 h dark), at ambient temperature (T_a)=20±2°C, in standard laboratory cages (Tecniplast, 1245, Italy, 22×16.5×14 cm) with wood chips and paper tubes as bedding material. Hamsters were fed standard food for laboratory animals (Labofeed B standard, Morawski, Kcynia, Poland) and water was available *ad libitum*. At the age of ∼3 months, animals were transferred to short photoperiod (SP; 8 h light:16 h dark), but T_a and cage conditions were not changed. Animals were weighed every week to the nearest 0.1 g (Scout Pro 200, Ohaus, USA) throughout the entire acclimation period.

The phenotype of experimental animals was assessed based on M_b loss, fur colour change and torpor use. The nonresponders did not moult to white fur (stage 1 of fur colour according to the Figala scale; Figala et al., 1973), lost less than 4% of M_b and did not use spontaneous torpor after 14 weeks under short photoperiod. Body temperature was measured with miniature data loggers (model TL3-1-27; constructed by Dr Dmitry Petrovski, Russian Academy of Sciences, Novosibirsk, Russia) pre-calibrated against a mercury-in-glass thermometer traceable to NIST standards between 15°C and 45°C, and implanted intraperitoneally. Implantation was done after ∼6 weeks of acclimation to SP under 40 mg kg^{-1} ketamine (ketamine 10%, Biowet, Puławy, Poland) and 0.1 mg ml^{-1} dexmedetomidine hydrochloride (Dexdomitor, Orion Pharma, Finland) anaesthesia. The incisions were closed with absorbable sutures (Safil 5/0, Aesculap AG, Tuttlingen, Germany). Body temperature data were recorded every 15 min and downloaded wirelessly once a week. Although the threshold between torpor and normothermy can be difficult to identify and a single cut-off temperature can seldom be applied (Barclay et al., 2001; Boyles et al., 2011a), we considered an individual torpid when its body temperature dropped below 32°C for longer than 30 min. This allowed us to compare our data with previous research on Siberian hamsters (Ruf et al., 1993; Diedrich et al., 2015; Haugg et al., 2021).

Because low ambient temperature increases propensity to torpor use and moulting (Ruf et al., 1993; Ouarour et al., 1991), after 14 weeks of short-day acclimation, all individuals were transferred to cold (T_a=7±2°C) for 8 weeks. We continuously monitored changes in M_b, fur colour and torpor use. Two animals that started to moult to white fur during cold acclimation were considered to be 'late responders' (Lynch and Puchalski, 1986; Przybylska-Piech et al., 2021) and excluded from further experiments. The remaining individuals (n=13) were fasted four times for 24 h, with water available *ad libitum*. The between-fasting refeeding periods were shortened gradually, from 6 to 4 and then to 2 days in all individuals. Hamsters were weighed before and after each fasting episode. After completion of fasting experiments, hamsters remained in SP for

another week and then they were transferred back to long photoperiod and T_a=20°C.

Data analysis
Because one logger failed we obtained and analysed data from 12 individuals. Duration of torpor bout (minutes) was calculated as a time when T_b<32°C, and minimum T_b was the lowest T_b during this period. To compare the variation in T_b patterns among individuals during fasting, we quantified variability of T_b as the heterothermy index (HI; Boyles et al., 2011b). A high value of HI indicates a greater deviation of T_b from homeothermy. Heterothermy index was calculated using the following equation (Boyles et al., 2011b):

$$HI = \sqrt{\frac{\Sigma(T_{b,mod} - T_{b},i)^2}{n-1}}, \qquad (1)$$

where $T_{b,mod}$ is the modal T_b during the active phase, $T_{b,i}$ is T_b recorded at the time i, and n is the number of samples. To check whether fasting has a long-lasting effect on the variability of body temperature, we also calculated the HI on the second day after each fasting episode. We chose this time period because HI of hamsters returned to control values within 1 day after fasting (M. J. Noakes, A.S.P.-P., M. S. Wojciechowski and M.J., personal communication).

All statistical analyses were done in R version 4.0.1 (https://www.r-project.org/) using linear mixed effect models (LMM) and package lme4 (https://cran.r-project.org/package=lme4). In all models, animal identity was included as a random factor. *Post hoc* pairwise comparisons of estimated marginal means were done using the package emmeans (https://cran.r-project.org/package=emmeans). The M_b change during the whole period of SP acclimation (25 weeks; excluding the fasting episodes) and M_b changes during the four fasting episodes were analysed separately. Week of acclimation to SP (in the first analysis) or beginning and end of each fasting episode (second analysis) were included as a fixed factor. To test the effect of fasting on HI, we fitted a model with two fixed factors: the period of measurement (fasting/post fasting) and torpor use (individuals using torpor/individuals not using torpor) and the interaction between these factors. To test the effect of HI and torpor use on M_b loss during fasting, we used the model that included order of fasting episodes and torpor use as fixed factors, and HI as covariate. Results are presented as estimated marginal means and 95% confidence interval (CI) for the mean.

RESULTS AND DISCUSSION
Nonresponding Siberian hamsters did not use spontaneous torpor during the first 14 weeks of SP acclimation nor during a further 8 weeks of cold acclimation in SP. However, four out of 12 individuals used fasting-induced torpor (Table 1, Fig. 1), with similar characteristics to that recorded during fasting in LP acclimated hamsters (Diedrich et al., 2015). During all episodes of fasting, we recorded 19 torpor bouts, but 13 were from one individual. Two individuals used multiple (2 to 5) torpor bouts per day, during which one bout was usually longer (120–270 min) than the other, which lasted between 45 and 90 min (Table 1). The multiple bouts may compensate for lower energy savings during shorter and shallower episodes of torpor and are representative for fasting periods in responding Siberian hamsters (Cubuk et al., 2017). Ten out of 19 bouts occurred at night, which is the active phase of day for hamsters, and another 7 occurred partially at night. In Siberian hamsters, fasting-induced torpor seems to be

Table 1. Characteristics of torpor bouts used by four nonresponding Siberian hamsters during four consecutive, 24 h fasting episodes

Hamster ID	Total no. of torpor bouts	Minimum T_b during torpor bout (°C)	Length of torpor bout (min)	Multiple torpor bouts per day	Torpor bout during refeeding period
1232	13	22.8 (18–29.3)	125.4 (45–330)	+	+
1271	3	20.54 (18.8–22.5)	155 (120–195)	–	–
1329	2	31.05 (31.0–31.1)	60 (45–75)	+	–
1357	1	31.2	45	–	+

Hamsters 1232 and 1357 used multiple torpor bouts (from 2 to 5) per day. Results are presented as mean (range). T_b, body temperature.

independent of circadian rhythmicity, occurring mostly at night, whereas spontaneous daily torpor in winter is under circadian regulation and is used during the resting phase of the day (Ruby and Zucker, 1992; Diedrich and Steinlechner, 2012; Diedrich et al., 2015). Torpor bouts recorded in nonresponding hamsters were short (average length=118 min) and 9 of them lasted less than 100 min, whereas only 4 bouts lasted longer than 3 h (330–195 min). Depth of torpor bouts increased with the increase in bout length, and the mean minimum T_b was 23.7±4.6°C (range 18.02–31.17°C). Fasting-induced torpor bouts in long-day acclimated individuals are shorter and shallower than spontaneous torpor bouts (Diedrich et al., 2015), but bout length does not differ between fasting and non-fasting short-day acclimated responding hamsters (Cubuk et al., 2017). This suggests that the pattern of torpor is shaped directly by seasonal adaptations and this is confirmed by our results which show that SP acclimated nonresponding hamsters present a pattern of fasting-torpor similar to individuals acclimated to LP conditions (Diedrich et al., 2015; Cubuk et al., 2017). We also recorded two

torpor bouts in between fasting periods, one of which was short (45 min) and recorded at night, whereas the other was very long (330 min) and recorded partially during the light phase. However, this long bout does not seem to be a spontaneous torpor bout as this individual did not undergo other winter adjustments and did not use spontaneous torpor before or after the fasting experiments. Instead, this torpor episode could still be an effect of a negative energy balance from the previous fasting period. Since none of the hamsters used torpor after the completion of fasting experiments, we suggest that torpor was related solely to the combined effect of food deprivation and cold exposure resulting in a negative energy balance rather than an effect of the seasonal acclimation. This opportunistic heterothermy occurs in many vertebrate species in response to challenging conditions (Bech et al., 1997; Wojciechowski et al., 2007; Stawski and Geiser, 2010; Vuarin and Henry, 2014; Chi et al., 2016; Nowack and Turbill, 2022).

Although a number of seasonal heterotherms can use torpor independently of season in response to unpredictable environmental
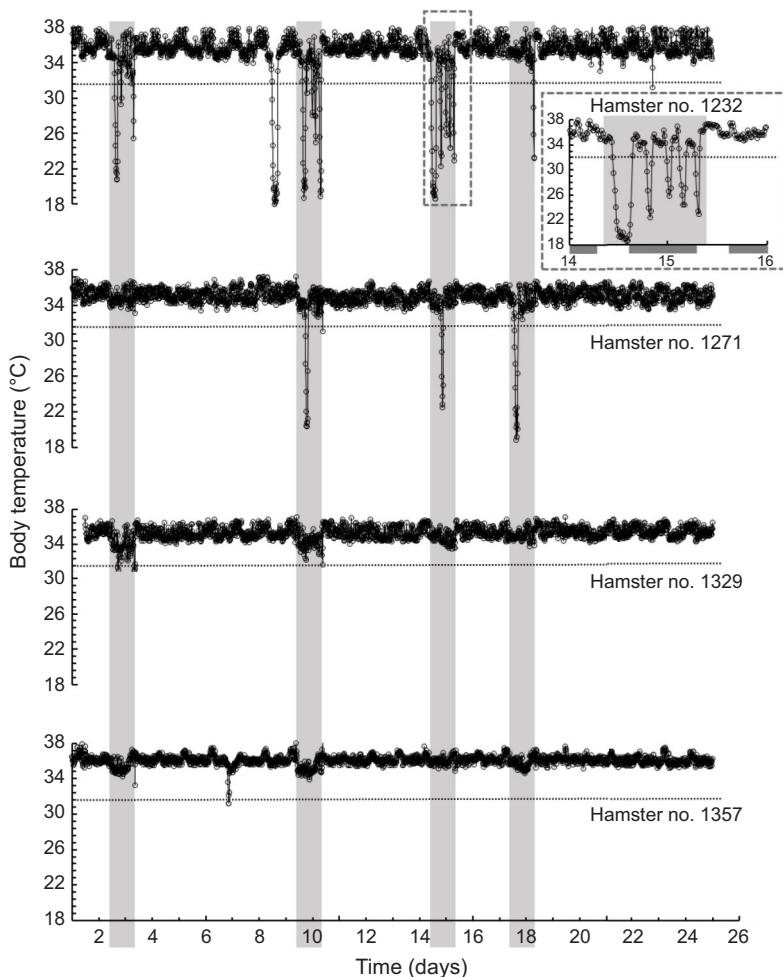

Fig. 1. Time course of body temperature of four nonresponding Siberian hamsters that used fasting-induced torpor. Fasting episodes are indicated by grey bars. The dotted horizontal line indicates the torpor threshold (32°C). Hamsters 1232 and 1329 used multiple torpor bouts per day. The insert shows one fasting period with multiple episodes of torpor; the dark grey bars below the *y*-axis represent night. In hamsters 1232 and 1357, we recorded torpor during refeeding periods.

Table 2. Body mass loss and heterothermy index (HI) during 24 h fasting episodes in nonresponding Siberian hamsters using and not using torpor

Fasting episode	Body mass loss (%)		HI (°C)	
	Using torpor (n=4)	No torpor (n=8)	Using torpor (n=4)	No torpor (n=8)
First	14.53 (11.16–17.90)	12.96 (10.58–15.30)	1.82 (0.86–2.77)	1.28 (0.60–1.95)*
Second	13.89 (10.45–17.30)	15.90 (13.45–18.40)	3.16 (2.21–4.12)	1.08 (0.41–1.76)*
Third	9.36 (5.83–12.90)	7.69 (5.28–10.01)	2.79 (1.84–3.75)	0.86 (0.18–1.53)*
Fourth	7.31 (3.91–10.70)	10.41 (8.04–12.80)	2.09 (1.14–3.05)	1.18 (0.51–1.86)*

Results are presented as mean (95% confidence interval). *P<0.05 between groups.

changes (Nowack et al., 2017), spontaneous and induced heterothermy can differ in the pattern of torpor bouts and the physiological states of individuals. In Siberian hamsters, spontaneous torpor appears as the last adjustment during acclimation to winter, after the completion of other seasonal adaptations (low M_b, regressed gonads, white fur; Heldmeier and Steinlechner, 1981; Lynch et al., 1989). The molecular base of seasonal adjustments is common for all mammals, and Siberian hamsters are not an exception. Development of winter phenotype is regulated by thyroid and steroid hormones, prolactin, leptin and growth hormone (Ouarour et al., 1991; Scherbarth and Steinlechner, 2010; Murphy et al., 2012). The lack of seasonal changes in the level of these hormones and parallel lack of physiological adjustments seems to underlie the absence of spontaneous torpor in nonresponding individuals. Fasting-induced torpor seems to be independent of seasonal changes in hormone levels because it is recorded in both long- and short-day acclimated individuals (Diedrich et al., 2015; Cubuk et al., 2017) and in responding and nonresponding individuals (present study).

Although only four out of 12 hamsters used torpor, variability of T_b (HI) increased significantly during fasting episodes in all individuals ($F_{1,82}$=7.412, P=0.008). Moreover, the HI values of the four individuals using torpor were higher than HI observed in individuals not using torpor during fasting episodes (2.47°C, CI=1.75–3.18°C and 1.10°C, CI=0.59–1.61°C, respectively; Tukey's HSD, P=0.005) but not during refeeding periods (0.70°C, CI=0.00–1.42°C and 0.58°C, CI=0.08–1.09°C, respectively; Tukey's HSD, P=0.781). However, even a slight decrease of T_b may provide energy saving under unfavourable conditions (Heldmaier et al., 1989; Przybylska et al., 2017). In contrast, the arousal from deep torpor is energy consuming. It requires a high increase of heat production which in fasted animals at low ambient temperature may even lead to death (Diedrich and Steinlechner, 2012). Since, the total cost of torpor might overbalance the cost of remaining normothermic (Tucker, 1965; Wojciechowski and Jefimow, 2006), we suggest that increasing T_b variability may be more beneficial than torpor in some scenarios. Although high variability of T_b can decrease daily energy expenditure during fasting (Przybylska et al., 2017), it was not related to the magnitude of M_b loss among individuals ($F_{1,39}$=0.097, P=0.758).

It is generally accepted that decrease of body mass is necessary to lower metabolic rate and body temperature in many species (Geiser, 1988; Mitchell et al., 2015; Spence and Tingley, 2021), including Siberian hamsters (Diedrich and Steinlechner, 2012). A low M_b after acclimation to SP and a high M_b loss throughout the SP acclimation correlates with higher spontaneous torpor frequency in this species (Haugg et al., 2021). Low body mass was also found to be necessary for the occurrence of fasting-induced torpor, both in mice (Mitchell et al., 2015) and Siberian hamsters (Ruby et al., 1993). However, we found that four individuals that used fasting-induced torpor showed different patterns of M_b changes and differed in absolute M_b. Before acclimation to SP, hamsters weighed on

average 33.1 g (CI=30.8-35.4 g) and they did not change their M_b during the first 14 weeks under SP (Tukey's HSD, P=0.441; M_b at 14 weeks=35.4 g, CI=33.2–37.7 g). During 8 weeks of further acclimation to SP and cold exposure, average M_b still did not change (Tukey's HSD, P=0.996; M_b at 22 weeks=34.2 g, CI=30.0–36.5 g). However, changes in M_b during cold acclimation differed among the four hamsters that used fasting-induced torpor. The individual that showed 13 torpor bouts (hamster no.1232, Table 1) decreased its body mass by 27%, which is approximately the value required to develop spontaneous torpor (Ruby et al., 1993). The other individual (no. 1271) with three torpor bouts recorded, reduced M_b by 11% but it still weighed above 32 g, which is much higher than the threshold M_b for the development of the winter phenotype and spontaneous torpor (Haugg et al., 2021). The remaining two individuals (no. 1329 and no. 1357) that used single, very short fasting-induced torpor bouts, did not decrease body mass throughout the entire acclimation to SP and cold and weighed 32.7 g and 38.7 g, respectively. These results indicate that low M_b is not a prerequisite for fasting-induced torpor in nonresponding hamsters.

Similarly to T_b variability, torpor use did not affect M_b loss during fasting and individuals using and not using torpor lost M_b to similar degrees ($F_{1,11}$=0.306, P=0.591; Table 2). It seems that in the face of combined cold and fasting, the increase of T_b variability or even torpor use is not enough to prevent a M_b decrease. However, animals managed to rebuild their M_b before the next fasting episodes, and M_b before the start of consecutive fasting episodes did not differ (Tukey's HSD: P>0.900). Moreover, the M_b loss during the first two fasting episodes was significantly higher than during the last two episodes ($F_{3,32}$=19.617, P<0.001; Table 2), even though the time between consecutive fasting episodes shortened. Since the ability to survive acute food deprivation depends on metabolic and physiological adjustments in animals (Jensen et al., 2013), this suggests that hamsters were able to prevent further loss of body mass during the subsequent fasting episodes and that 24 h fasting under cold does not trigger long-term changes in animal physiology.

We conclude that nonresponding Siberian hamsters are able to use fasting-induced torpor even though they do not develop the winter phenotype and do not use spontaneous torpor. Our data confirm previous statements that spontaneous torpor and heterothermy induced by environmental challenges are two different phenomena (Diedrich and Steinlechner, 2012; Diedrich et al., 2015; Nowack and Turbill, 2022). Torpor use or increased body temperature variability in fasting animals allows for energy savings in the face of adverse environmental conditions. Since climate change increases the occurrence of sudden, unpredictable environmental events, the opportunistic use of torpor might be advantageous for nonresponding individuals that do not use spontaneous torpor and maintain high M_b throughout winter. This ability may be crucial for survival and allow for the persistence of nonresponders in the natural population.

Author contributions
Conceptualization: A.S.P.-P., M.J.; Investigation: A.S.P.-P., M.J.; Data curation: A.S.P.-P., M.J.; Writing - original draft: A.S.P.-P.; Writing - review & editing: A.S.P.-P., M.J.; Funding acquisition: A.S.P.-P.

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