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RESEARCH ARTICLE

Social thermoregulation and torpor in the Siberian hamster

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SUMMARY

Social thermoregulation and huddling bring about energy benefits to animals sharing a nest because of the smaller surface-to-volume ratio of a huddle and the higher local temperature in the nest. We tested whether living in groups and huddling affect daily torpor, metabolic rate and seasonal changes in the body mass of a small heterothermic rodent, the Siberian hamster (*Phodopus sungorus*), housed under semi-natural conditions both singly and in groups of four litter-mates. We predicted that in hamsters housed in groups: (1) synchronized torpor bouts would be longer and deeper than non-synchronized ones but shallower than in solitary hamsters, (2) seasonal variations in metabolic rate would be lower than in solitary hamsters, and (3) the winter decrease in body mass would be smaller in grouped than in singly housed hamsters. We found that group housing led to a smaller decrease in body mass in winter, and affected the length and depth of daily torpor. In group-living hamsters more than 50% of all torpor episodes were synchronized and torpid animals were often found in huddles formed of all cage-mates. The longest and deepest torpor bouts in groups were recorded when all animals in a group entered torpor simultaneously. Although the minimum body temperature during torpor was higher, torpor duration was slightly longer than in solitary hamsters. We did not record significant differences in the body mass-adjusted rate of oxygen consumption between solitary and grouped animals, either in the cold or at the lower critical temperature. We conclude that social thermoregulation enables maintenance of a larger body mass, and thus a larger body fat content, which can ensure better body condition at the beginning of the reproductive season.

Key words: social thermoregulation, Siberian hamster, daily torpor, body temperature, metabolic rate, body mass.

INTRODUCTION

The survival of many animals depends on proper preparation for winter food shortage and harsh environmental conditions. In the process of acclimatization, animals undergo morphological and physiological changes that facilitate winter survival. They can increase body insulation (Cherry and Verner, 1975; Rinehart-Whitt and Pagels, 2000; Kuhlmann et al., 2003), increase or decrease body mass (m_b) (Morrison, 1960; Hoffmann, 1973; Armitage et al., 1976; Heldmaier et al., 2004), increase m_b-specific metabolic rate (Heldmaier and Steinlechner, 1981a) and increase the efficiency of heat production, especially by means of non-shivering thermogenesis (NST) (Heldmaier and Buchberger, 1985; Merritt et al., 2001; Bao et al., 2002). In winter, animals stay active or enter daily or seasonal torpor (Hoffmann, 1973; Lyman, 1982b; Körtner and Geiser, 2000; Heldmaier et al., 2004). Although heterothermy is generally considered to be an energy-saving strategy, it also entails considerable costs related to periodic arousal from torpor and interbout normothermy (Thomas et al., 1990; Dunbar and Tomasi, 2006; Wojciechowski et al., 2007; Karpovich et al., 2009). Total energy requirements in winter may be further reduced by behavioural adjustments like selection of particular thermal micro-environments, well-insulated nests or hibernacula that provide protection from the cold (Morris, 1973; Walhovd, 1976; Ferron, 1996; Schmid, 1998), postural adjustments, like a curled position during sleep or torpor (Lyman, 1982a; Geiser, 2002), and finally communal nesting and huddling (Roverud and Chappell, 1991; Arnold, 1993; Blumstein et al., 2004) (for a review, see Gilbert et al., 2010).

Animals spend winter solitarily or in groups with other conspecifics (Twente, 1955; Walhovd and Jensen, 1976; Webster and Brooks, 1981; Nowak and Paradiso, 1983; Arnold, 1988; Blumstein and Walter, 1998; Vogt and Kakooza, 1993; Ferron, 1996). Both strategies have pros and cons (Armitage et al., 1976; Armitage et al., 2003; Arnold, 1993; Arnold et al., 1991; Berteaux et al., 1996; Blumstein et al., 2004; Hwang et al., 2007) (for a review, see Gilbert et al., 2010). In huddling animals, heat loss can be reduced as a result of body contact with other group members and hence a smaller surface area-to-volume ratio, as well as increased local temperature in the nest (Hayes et al., 1992; Séguy and Perret, 2005). In groups, the total cost of torpor can be reduced by mutual passive warming through body contact or passive rewarming during arousal by gaining heat from warmer nest-mates that started to rewarm earlier (Arnold, 1993; Blumstein et al., 2004). Arnold and colleagues found that the greater the number of alpine marmots (*Marmota marmota*) sharing one burrow the longer the burrow temperature remained above 5°C, which is the temperature threshold for an increase in metabolic rate in hibernating marmots (Arnold et al., 1991). Alpine marmots hibernating solitarily also have faster cooling rates during entrance into a hibernation bout and reach lower body temperatures (T_b) closer to ambient temperature (T_a) than animals hibernating in groups (Arnold, 1988).

Huddling is enhanced by several factors: ecological (cold, food shortage), social (family groups) and morphological (small body size, weak insulation) (for a review, see Gilbert et al., 2010). It is beneficial at low T_a, especially for young animals that could not gain appropriate m_b before winter and which can lose up to

50% of their m_b during hibernation (Armitage et al., 1976). The importance of body reserves for successful hibernation is emphasized by the fact that shorter winters (i.e. shorter hibernation season) are associated with greater survival of juvenile yellow-bellied marmots (*Marmota flaviventris*) over their first hibernation (Armitage et al., 1976; Blumstein et al., 2004). For juveniles, reduced winter m_b loss due to social hibernation can make the difference between survival or death and it is not surprising that marmots' sociability correlates with the harshness of the environment [Barash (Barash, 1974) after Frase and Hoffmann (Frase and Hoffmann, 1980)].

Huddling or social thermoregulation is known in 67 mammalian species from 20 families (Gilbert et al., 2010). In tropical grey mouse lemurs (*Microcebus murinus*), nest sharing lengthens torpor bout duration but its depth is the same as in solitary animals (Séguy and Perret, 2005). Also, winter-active mammals, even those considered to be territorial and solitary in summer, like shrews or voles, may share nests with other conspecifics and benefit from huddling in winter (Webster and Brooks, 1981; Hays and Lidicker, 2000). Other benefits of nest sharing include decreased individual predation risk and development or maintenance of social relationships between individuals (Berteaux et al., 1996). However, communal nesting can also increase the risk of disease or parasite transmission and can potentially lead to depletion of resources in the vicinity of the nest (Hwang et al., 2007).

One species for which the importance of social interactions and huddling for winter survival is unknown is the Siberian hamster, *Phodopus sungorus*, a small heterothermic rodent inhabiting the Siberian steppe (Ross, 1998). Many morphological and physiological adaptations like reduced m_b, white pelage and daily torpor reduce its total energy requirements in winter (Figala et al., 1973; Hoffmann, 1973; Heldmaier and Steinlechner, 1981a; Heldmaier and Steinlechner, 1981b; Ruf and Heldmaier, 1992; Ruf et al., 1993; Kuhlmann et al., 2003). Daily torpor occurs as the last response to winter conditions, after a decrease in m_b and moulting (Heldmaier and Steinlechner, 1981a). The main cue for acclimation to winter is a short photoperiod (SP), while low T_a has a smaller effect (Ruf et al., 1993). The frequency of torpor bouts increases with the time of acclimation to SP (Heldmaier and Steinlechner, 1981b; Kirsch et al., 1991; Ruf et al., 1993; Jefimow et al., 2004b) but the timing of maximum torpor frequency, duration of torpor bouts and minimum T_b during torpor depend on T_a; in the cold, torpor occurrence is advanced, bouts are longer and minimum T_b is lower (Heldmaier and Steinlechner, 1981b; Kirsch et al., 1991; Ruf et al., 1993). The last torpor bouts are usually recorded between the 28th and 38th week of acclimation to SP, depending on T_a and the individual (Lynch and Puchalski, 1986; Kirsch et al., 1991). The mean duration of torpor episodes is 4–8 h, and the lowest T_b is usually around 14°C (Heldmaier and Steinlechner, 1981b; Ruf and Heldmaier, 1992; Ruf et al., 1991; Ruf et al., 1993; Jefimow et al., 2004b).

Apart from changes in physiology and morphology, there is also reason to suppose that Siberian hamsters rely on social thermoregulation in winter. Males and females share a nest during the breeding season and the tendency for sociality presumably increases towards winter (Wynne-Edwards, 1995). Although there is no information on their huddling behaviour in the wild, very strong synchrony in torpor occurrence was found in breeding pairs kept together under SP (Ruf et al., 1991).

Taking into account the importance of social thermoregulation for winter survival and its potential benefits for the animal energy budget, we tested the hypothesis that living in groups affects seasonal changes in m_b and torpor characteristics in winter-acclimatized Siberian hamsters. We predicted that the winter decrease in m_b would be smaller in grouped than in singly housed hamsters. We expected that in hamsters housed in groups, synchronized torpor bouts would be longer and deeper than non-synchronized ones but shallower than in animals housed singly. We also hypothesized that living in groups would affect resting metabolic rate and the ability to cope with cold. We predicted that seasonal variations in metabolic rate would be lower in grouped than in solitary individuals because of a more stable thermal environment in the nest. To test our predictions, we housed Siberian hamsters under semi-natural conditions, singly or in groups of four litter-mates, and continuously measured their T_b. In addition, five times a year (in winter, spring, summer and twice in autumn) we measured resting metabolic rate. We measured oxygen consumption of individual hamsters in the cold (10°C), to examine whether living in a group could affect their ability to cope with cold, and at the lower critical temperature (LCT; 20°C in winter, 26°C in summer and 23°C in spring and autumn), to study the effect of housing conditions on basal metabolic rate.

MATERIALS AND METHODS

Animals and housing

This study lasted for 15 months, from September 2007 to November 2008. All experiments were done at the Nicolaus Copernicus University in Toruń, Poland (53°00′N, 18°56′E). We used 24 adult female Siberian hamsters (*P. sungorus*, Pallas 1773) housed under semi-natural conditions. Hamsters originated from our breeding colony and were born between April and May 2007. The breeding colony was kept under natural photoperiod and laboratory T_a of 23±2°C. All siblings were housed together with their parents until 4 weeks of age. After 4 weeks, eight hamsters, taken from three different litters, were housed singly, and 16 others were housed in four groups of four litter-mates each.

In September 2007, all hamsters were transferred to separate outdoor enclosures located on the campus [see Jefimow et al. for description (Jefimow et al., 2004a)], which were modified to meet the needs of the present experiments. Each enclosure consisted of a wooden box (1.0×1.0×1.0 m) buried in the ground to 3/4 of the height with a plastic cage inside it. The size of the cage was 40×26×35 cm for each of the eight single hamsters and 70×40×40 cm for the grouped hamsters (four groups of four litter-mates each). Cages were filled with sawdust mixed with sand, and covered with wire netting. The area between the wooden box and plastic cage was filled with soil and sand. A transparent roof was set up about 2 m above all enclosures to protect the animals from rain, but it still ensured natural photoperiod and temperature. Animals were additionally provided with paper towel as bedding material. They had free access to water and food (standard rodent pellets and occasionally fresh vegetables or fruits). Hamsters were weighed with an electronic balance (Ohaus Scout Pro 402, Brooklyn, NY, USA) to the nearest 0.1 g before being transferred to the outdoor enclosures and then every week thereafter. During winter, weighing was done every 2 weeks to reduce disturbance to torpid animals. Hamsters living in groups were often found in one place in the cage sharing the nest and were amicable. However, in May 2008 the animals in one cage started to bite each other and had to be separated because their aggressive behaviour was recurring. Afterwards, they were housed singly until the end of the experiment. Because torpor season ended in March 2008 we could still analyse torpor bouts recorded in these animals. However, the data on m_b and metabolic rate obtained after separation were excluded from statistical analyses.

Environmental conditions in the enclosure were monitored continuously using a DataHog 2 Logger (Skye Instruments Ltd, Llandrindod Wells, Powys, UK). T_a (at the height of 2 m), soil temperature (T_s; outside the plastic cage, at a depth of about 40 cm, i.e. the bottom of the cage) and light intensity (above the enclosure) were recorded every 30 min.

Experimental procedures were approved by the Local Committee for the Ethics in Animal Research.

T_b recordings

After being transferred to outdoor enclosures, hamsters were implanted intraperitoneally with miniature data loggers (iBBat 22L, Alpha Mach Inc., Mont St-Hilaire, QC, Canada). In November 2007, we implanted six animals kept singly and 12 kept in groups (three groups of four nest-mates). Six hamsters (two single and four in one group) were implanted 7 weeks later than the others. Before implantation, loggers were pre-calibrated against a mercury-in-glass thermometer and were paraffin coated (mass with paraffin, 1.5–1.7 g). The surgery was done under ketamine (40 mg kg^{-1}; Narkamon 5%, SPOFA, Prague, Czech Republic) and xylazine (8 mg kg^{-1}; Rometar 2%, SPOFA) anaesthesia. After surgery all hamsters were kept singly in the laboratory for 3 days. Similarly, after logger replacement (surgery was repeated twice, in March and August 2008), hamsters stayed in the laboratory (under natural photoperiod) for 3 days and were then transferred back to the outdoor enclosures. With T_b being recorded every 25 min to the nearest 0.5°C, loggers (with a capacity of 8192 samples) had to be replaced every 142 days. Two data loggers failed for unknown reason and it was impossible to restore the recorded data.

Respirometry

In winter (January 2008), spring (April 2008), summer (July 2008) and twice in autumn (October and November 2008) we measured oxygen consumption rate ($\dot{V}_{O_2}$) of individual hamsters in the cold (T_a=10°C) and at LCT using flow-through respirometry. For the measurements in winter and summer we used LCT values calculated by Heldmaier and Steinlechner (Heldmaier and Steinlechner, 1981a), i.e. 20 and 26°C, respectively. For autumn and spring measurements we chose an intermediate T_a of 23°C.

$\dot{V}_{O_2}$ was measured in six solitary hamsters and in 12 animals housed in groups (three out of four from each group). All animals were always measured individually, independent of housing conditions. Each recording session lasted for approximately 6–7 h, during the light phase of the day (ρ phase). Animals were transferred from the enclosure to the laboratory in the morning. If hamsters were found torpid, they were taken to the laboratory and allowed to arouse fully before commencement of the respirometry trial. On each day three animals were measured simultaneously. Hamsters were placed individually in a transparent respirometry chamber (1.7 l) which was placed in a temperature-controlled cabinet. Air, dried with Drierite® (W. A. Hammond Drierite Co. Ltd, Xenia, OH, USA) and CO_2-scrubbed with soda lime (Dwory S. A., Oświęcim, Poland), was pumped into the chamber at a rate of ~900 ml min^{-1}. Flow rate was measured upstream of the respirometry chamber with a mass-flow meter (FlowBar-4, Sable Systems Int., Las Vegas, NV, USA). The main flow from animals was sequentially subsampled at ~100 ml min^{-1} (with RM-4 Multiplexer, Sable Systems Int.) and analysed with an integrated CO_2/O_2 analyser (Foxbox C, Sable Systems Int.). Gases were dried with magnesium perchlorate (POCh S.A., Gliwice, Poland) before CO_2 analysis and then, before O_2 analysis, CO_2 was scrubbed with soda lime and re-dried with Drierite®. Gases leaving the respirometry chambers were analysed for 10 min with 1 min reference air readings between animals. Between channel switches, recording was paused for 3 min to flush the analyser with the new gas sample. This setup resulted in each animal being measured every 54 min. All data were recorded and later analysed with ExpeData, Data Acquisition & Analysis, version 1.1.10 (Sable Systems Int.). $\dot{V}_{O_2}$ was calculated using eqn 10.1 from Lighton (Lighton, 2008).

Statistical analysis

The data were tested for normality and analysed with analysis of variance (ANOVA) followed by *post hoc* Tukey's HSD or LSD test, when appropriate. The effect of housing conditions (single *vs* grouped hamsters) on m_b was analysed with 2-way ANOVA with time of year as the repeated measures factor and housing conditions as a between-groups factor.

Daytime and night-time normothermic T_b was calculated as a monthly mean, excluding time of torpor and time of metabolic measurements. The effect of housing conditions (single *vs* grouped hamsters) on normothermic T_b was analysed with 3-way ANOVA with the time of year and time of day as the repeated measures factors and housing conditions as the between-groups factor.

Daily torpor was defined when T_b was equal to or below 32°C (Ruf and Heldmaier, 1992; Ruf et al., 1989; Ruf et al., 1993). Even when animals were interrupted because of feeding and weighing, the data were used in the computation of torpor frequency but they were excluded from calculations of torpor bout duration and depth. The timing of torpor was analysed using the Kruskal–Wallis *H*-test. Based on the T_b recordings of grouped hamsters we classified torpor bouts as synchronized if they commenced and were completed at the same time on a particular day and had a similar pattern. From all torpor bouts recorded in a particular group we calculated the number of bouts that were recorded simultaneously in four, three and two animals. For comparison of the length and depth (minimum T_b) of torpor bouts with different degrees of synchronization and for comparison between single and grouped hamsters, a *t*-test was used. As six hamsters were implanted later than the others, the frequency of torpor bout occurrence in single and grouped hamsters was compared with a *z*-test, within 6 weeks, from 1 January to 15 February (the time of maximum torpor frequency).

Resting metabolic rate (RMR) was determined as the minimum $\dot{V}_{O_2}$ during 400 s of one of the 10 min measurement periods. If a hamster entered torpor during metabolic measurements, RMR was defined as the lowest $\dot{V}_{O_2}$ when the hamster was normothermic, but not immediately before or after the torpor bout, i.e. at least 1 h before the gradual decrease in T_b and oxygen consumption or 1 h after arousal, at the earliest, respectively.

In winter, especially during measurements at 10°C, animals often entered torpor, so we were able to estimate $\dot{V}_{O_2}$ only in two normothermic hamsters. The effect of season, housing condition and temperature (10°C or LCT) on $\dot{V}_{O_2}$ was tested with multifactor analysis of covariance (ANCOVA), with m_b as a covariate. Data for $\dot{V}_{O_2}$ and m_b were log transformed before analysis and then back transformed to present the results graphically.

Differences were considered statistically significant at $P<0.05$.

RESULTS

Environmental conditions

Mean T_a (Fig. 1) during the coldest months of December, January and February was 1.7±3.7°C (minimum –7.4°C, maximum 10.5°C), 2.0±3.9°C (minimum –10.2°C, maximum 9.85°C) and 4.5±3.4°C (minimum –8.0°C, maximum 13.0°C), respectively. Temperatures below 0°C were recorded only during a few days at the end of

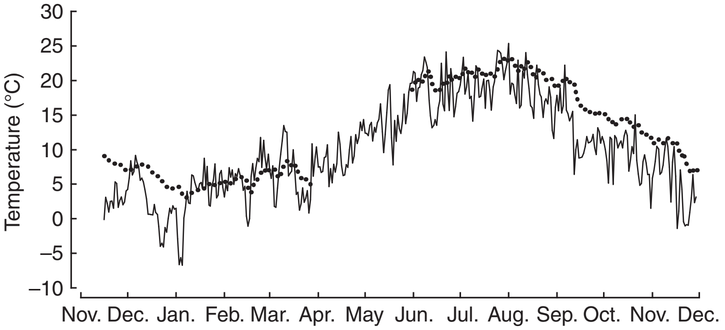

Fig. 1. Ambient (air) temperature (T_a, solid line) and soil temperature (T_s, dotted line) in the outdoor enclosure recorded during the entire study (from 15 November 2007 to 1 December 2008). Because of technical problems there are no data on T_s from 30 March to 30 May. Tick marks indicate the first of the month.

December and at the beginning of January and February. A relatively warm winter during the study period resulted in a relatively high soil temperature which, at a depth of 40 cm, never dropped below 0°C. The mean T_s was 6.4±1.3°C in December, 4.3±0.7°C in January and 5.7±0.9°C in February. In March mean T_a was similar to mean T_a in February (4.1±3.6°C) but mean T_s increased to 6.7±1.0°C.

m_b

Before being transferred to the outdoor enclosures there was no significant difference in m_b of solitary (44.5±3.5 g) *vs* grouped hamsters (46.1±4.6 g; $P>0.05$). All animals displayed seasonal changes in m_b ($F_{13,91}=15.93$; $P<0.001$), independent of housing conditions (single or grouped, $F_{13,91}=1.22$; $P=0.28$; Fig. 2). However, although initial m_b values were the same, during the entire study mean m_b of hamsters kept singly (35.0±5.2 g) was lower than that of animals kept in groups (40.0±6.0 g; $F_{1,7}=16.23$; $P<0.01$).

Normothermic T_b

In hamsters housed both singly and in groups, mean T_b changed seasonally, being lower in winter than in summer, and these differences were greater in hamsters kept in groups ($F_{12,36}=2.41$, $P<0.03$). Independent of housing conditions there were clear day–night differences in T_b ($F_{12,36}=5.17$, $P<0.001$; Fig. 3). The lowest daytime and night-time T_b values were recorded in winter, from December to February, in both single and grouped hamsters.

Torpor occurrence and its characteristics

All torpor bouts were recorded between the 10th and 25th week of acclimation to semi-natural conditions, i.e. from the beginning of December until the middle of March. The highest frequency of torpor bouts was from 1 January to 15 February, and this was similar in animals living solitarily and in groups (38.8 and 41.1% of days, respectively; $P>0.05$).

In hamsters that were housed in groups, torpor bouts were usually recorded in all individuals at the same time. As we observed during weighing, torpid hamsters were often in huddles of four, touching each other's heads with their rears pointing to the outside of the huddle (Fig. 4). In total, we recorded 23 days with torpor in group I, 34 days in group II and 45 days in group III. The synchronized episodes (all hamsters in a group in torpor) amounted to 69.6, 53.0 and 66.7% of all torpor episodes in group I, II and III, respectively (Fig. 5). Bouts that were synchronized in all four hamsters were longer and deeper than those exhibited by only one member of a group at a time (Fig. 6). The mean duration of simultaneous torpor bouts in grouped hamsters was 418.6±135.2 min with a minimum T_b of 21.5±3.4°C. Conversely, when only one hamster in a group entered torpor, the mean duration was only 125.8±88.6 min with a minimum T_b of 29.4±2.0°C ($P<0.001$).

As winter progressed, torpor bouts gradually lengthened in both single and grouped hamsters (Kruskal–Wallis test: $H_{14,156}=30.69$, $P<0.01$ for single hamsters, and $H_{14,233}=63.76$, $P<0.001$ for grouped hamsters). Lengthening of torpor bouts was not correlated with changes in ambient (air) and soil temperatures. The mean duration of torpor episodes was slightly longer in grouped than in single hamsters (5 h 36 min and 5 h, respectively, $P<0.05$). The longest episodes of torpor were recorded between the 16th and 22nd week of acclimation (10 January to 27 February) in hamsters housed singly and between the 18th and 21st week (24 January to 20 February) in hamsters housed in groups. There was a strong negative correlation between torpor bout duration and minimum T_b during torpor, in both single and grouped hamsters. However, in single hamsters this relationship was best described by a logarithmic regression ($y=-6.2232\ln x+54.571$; $R^2=0.9045$; Fig. 7) while in grouped hamsters it was best described by a linear one ($y=-0.0219x+31.154$; $R^2=0.7139$). We suspected that the general,

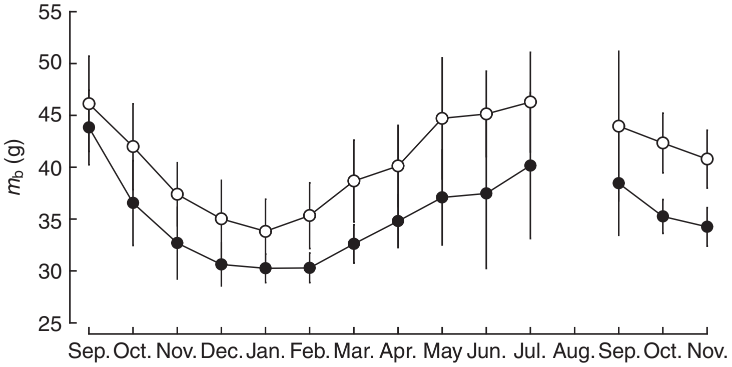

Fig. 2. The seasonal changes in body mass (m_b, means ± s.d.; from September 2007 to November 2008 but without data for August) of Siberian hamsters housed under semi-natural conditions, singly (filled circles) or in groups of four nest-mates (open circles).

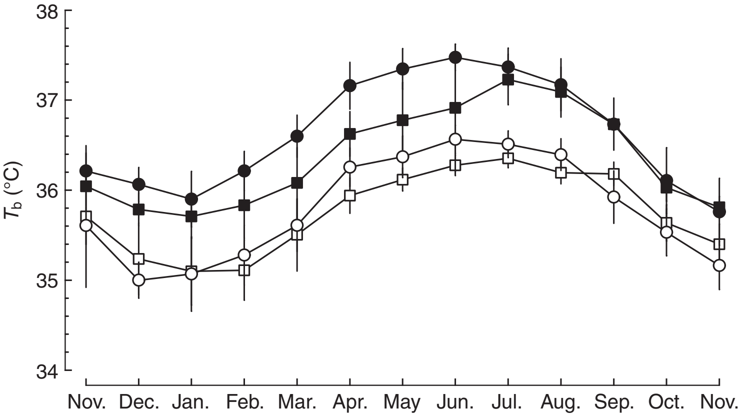

Fig. 3. Mean (±s.d.) normothermic body temperature (T_b) of Siberian hamsters housed under semi-natural conditions, solitarily (squares) or in groups of four nest-mates (circles). Filled and open symbols represent night-time and daytime T_b, respectively.

logarithmic shape of the relationship between torpor bout duration and T_b could be affected by the synchrony of some torpor events among hamsters in groups and thus appeared linear. However, when synchronous and asynchronous torpor bouts were separated, the shape remained linear in both subgroups. Thus we decided not to differentiate between synchronous and asynchronous torpor bouts.

When all recorded torpor bouts were pooled together within time categories (based on duration), significant differences between single and grouped hamsters became more evident. During torpor bouts of the same duration, hamsters housed singly had a lower minimum T_b than hamsters kept in groups (Fig. 8). The lowest T_b values (14.3±0.0°C in single and 16.4±1.0°C in grouped animals, $P<0.05$) were recorded during the longest torpor bouts, lasting more than 700 min. However, such long episodes were very rare (only three in single and four in grouped hamsters). Most torpor bouts lasted for less than 10 h.

Oxygen consumption

The m_b-adjusted rate of oxygen consumption ($\dot{V}_{O_2}$) in the cold and at the LCT depended on season ($F_{4,103}=13.13$, $P<0.001$, Fig. 9). $\dot{V}_{O_2}$ was always higher at 10°C than at LCT ($P<0.001$). In the cold, $\dot{V}_{O_2}$ in winter (January) was lower than in other seasons (April, July and October: $P<0.001$; November: $P<0.01$). At LCT, the lowest $\dot{V}_{O_2}$ was recorded in the summer (compared with spring and autumn: $P<0.001$). Additionally, $\dot{V}_{O_2}$ measured at LCT was lower in winter than in spring ($P<0.01$) and autumn ($P<0.05$). Although m_b-adjusted rates of oxygen consumption were slightly higher in hamsters housed in groups than in solitary hamsters, these differences did not reach significance ($F_{1,103}=2.89$, $P=0.09$).

Fig. 4. Four Siberian hamsters huddling in torpor.

DISCUSSION

The data presented here support our initial hypothesis that living in groups affects the winter physiology of Siberian hamsters. Starting from the autumn of 2007, we observed a gradual decrease in m_b, moulting to white fur, lowering of the set-point for normothermic T_b regulation and torpor use, in both solitary and grouped hamsters. We also recorded seasonal changes in the rate of oxygen consumption in all animals. Yet, housing in groups and hence the possibility of social thermoregulation and huddling led to a smaller decrease in winter m_b and longer but shallower daily torpor bouts than in solitary animals.

Essential to the benefits of social hibernation or, in more general terms, social thermoregulation, is behavioural and physiological synchronization between individuals in groups (Arnold, 1993; Ruf and Arnold, 2000). Synchronous patterns of hibernation among individuals in a group may result in lower m_b loss throughout winter than in groups with asynchronous entrance into or arousal from torpor (Arnold, 1993; Ruf and Arnold, 2000). In our groups of hamsters more than half of torpor bouts were synchronized (Fig. 5) and hamsters entered and aroused from torpor at the same time. All animals, independent of housing conditions, showed a winter decrease in m_b (Fig. 2). Although the time course of m_b changes was similar for all animals, there were two important findings. First, despite a similar m_b at the beginning of the experiment in autumn 2007, the mean m_b during the entire experiment was lower in solitary than in grouped hamsters. Second, m_b of solitary hamsters in summer and autumn the following year did not return to the initial level unlike in animals housed in groups. This indicates that group housing allows for the maintenance of a higher m_b during winter, and consequently a better body condition in the following spring. Higher m_b seems to be the result of huddling, possibly during both torpor and normothermy. Conversely, Bartness did not find any effect of group housing on photoperiod-induced changes in body and fat mass of Siberian hamsters but experimental conditions in his experiments were different from ours (Bartness, 1996). In his study, animals were kept singly or in groups of 10 animals under SP and a T_a of 23°C for 6 weeks. All animals showed a similar decrease in m_b that resulted from a decrease in white adipocyte diameter but that diameter was larger in animals kept in groups (Bartness, 1996). Thus, it is possible that the larger winter m_b of our group-living hamsters also resulted from larger adipocytes.

In both solitary and grouped hamsters, maximum torpor frequency was recorded in January and in the first half of February. A similar

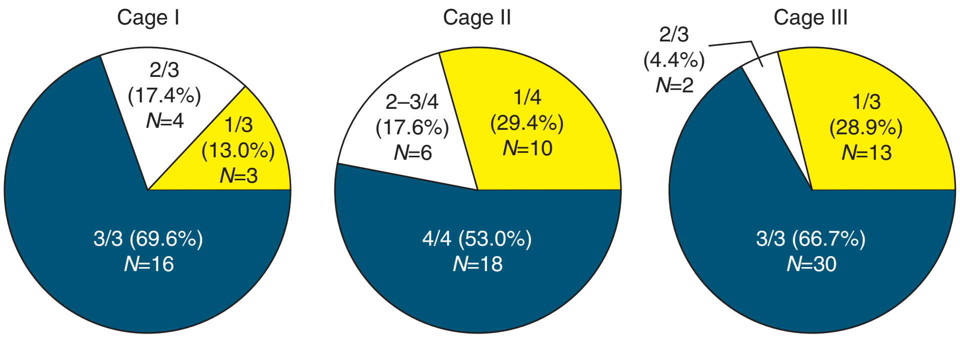

Fig. 5. Synchronization of torpor bouts in Siberian hamsters. In all groups more than half of all torpor bouts were fully synchronous. 1/3 or 1/4, one torpid hamster in a group; 2/3 or 2–3/4, two or three hamsters in torpor; 3/3 or 4/4, all hamsters in a group torpid at the same time. *N* indicates the number of observations.

timing of torpor was described in hamsters housed under natural photoperiod and T_a (50°06′N, 08°41′E) (Heldmaier and Steinlechner, 1981b). There are no data on torpor use in Siberian hamsters living in the natural environment, but taking into account the timing of reproduction, T_a and above-ground plant biomass we suspect that animals use torpor from October through to March (see Weiner, 1987).

In our study, the frequency of torpor bouts in single and grouped hamsters did not differ. Conversely, in striped skunks (*Mephitis mephitis*), huddling decreased torpor frequency and depth but grouped skunks lost much less body fat than single ones (Hwang et al., 2007). Thus, the benefit of huddling would be larger body fat reserves at emergence in spring and a better body condition at the beginning of the reproductive season (Hwang et al., 2007). It was reported previously that sufficient body fat content in spring ensures successful breeding in female Alpine marmots (Hackländer and Arnold, 1999) and Columbian ground squirrels, *Spermophilus columbianus* (King et al., 1991).

We predicted that living in groups would lead to the synchronization of torpor episodes among group members, and, indeed, in hamsters housed in groups more than 50% of all torpor episodes were synchronous (Fig. 5). However, the frequency of torpor episodes was similar in single and grouped hamsters. In accordance with our prediction, the minimum T_b during torpor was higher and torpor bouts were slightly longer in grouped than in solitary hamsters (Figs 7 and 8). This indicates that animals in a group can afford to maintain a higher minimum T_b. However, in hamsters housed in groups the minimum T_b in torpor was lowest when all animals in a group entered torpor simultaneously and were presumably huddling (Figs 4 and 6). Vogt and Kakooza suggested that huddling could increase the occurrence of torpor if animals (white-footed mice *Permomyscus leucopus noveboracensis*) sharing the nest were known to each other (Vogt and Kakooza, 1993). Our hamsters kept in groups were siblings and were housed together from birth. Although more than half of torpor bouts were synchronous, this value was still less than the 75% recorded by Ruf and colleagues in hamsters living in pairs (Ruf et al., 1991). Thus, it seems that the synchrony of torpor can be affected by group size. Based on demographic data collected over 38 years, Armitage and Woods (Armitage and Woods, 2003) concluded that group hibernation did not trigger any benefits as they did not find a significant effect of group size on winter survival in juvenile yellow-bellied marmots from the same litter hibernating together. However, the mean percentage survival for litters of three was ~60% while for litters of eight it was only ~34% (Armitage and Woods, 2003). This indicates that a larger group size can result in a less synchronized pattern of heterothermy.

Although we predicted that seasonal variations in metabolic rate would be lower in hamsters living in groups because of the more stable environment of their nests, we did not find any differences in m_b-adjusted $\dot{V}_{O_2}$ between solitary and grouped hamsters (Fig. 9). In

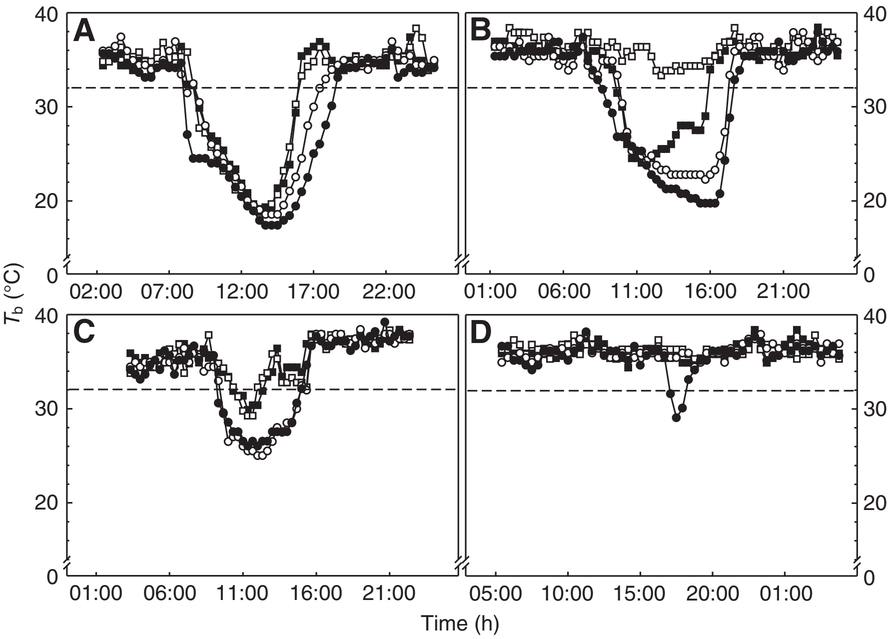

Fig. 6. Example of torpor bouts with different degrees of synchronization. (A) All four hamsters in torpor, (B) three out of four hamsters in torpor, (C) two hamsters in torpor, and (D) only one hamster in torpor while three others remain normothermic. Different symbols represent different hamsters.

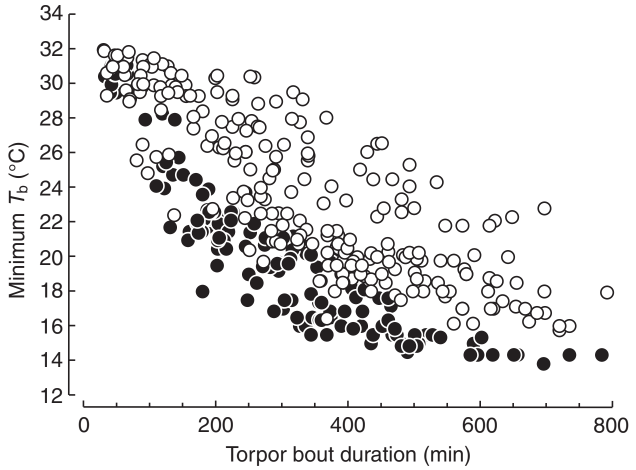

Fig. 7. In Siberian hamsters housed singly (filled circles) and in groups of four (open circles), minimum T_b during torpor depended on torpor duration (i.e. the longer the torpor bout the lower the T_b). In hamsters kept in groups we did not differentiate between synchronous and asynchronous torpor because the shape of the relationship was the same.

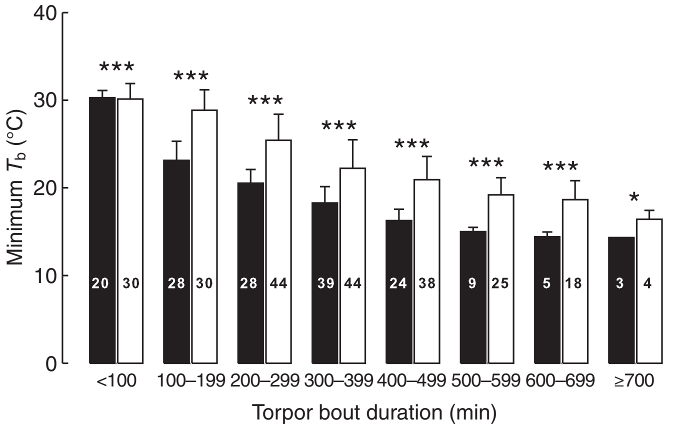

Fig. 8. Minimum body temperature (means + s.d.) during torpor bouts in Siberian hamsters housed singly (filled bars) and in groups of four littermates (open bars). Torpor bouts were pooled within eight time categories. Numbers inside bars indicate the total number of torpor bouts of that duration. ***$P<0.001$; *$P<0.05$.

all animals, m_b-adjusted oxygen consumption in the cold (10°C) was highest in summer and lowest in winter (Fig. 9). This simply indicates higher energy requirements in summer for maintaining constant T_b in the cold. In normothermic hamsters, lower energy requirements for thermoregulation in winter result from lower m_b and better insulation (Heldmaier and Steinlechner, 1981a). Independent of season, m_b-adjusted $\dot{V}_{O_2}$ was similar in single and grouped hamsters most probably because all animals were measured individually. Also Contreras reported that huddling in the nest did not affect the metabolic rate of individually tested laboratory mice (*Mus musculus*) and Mongolian gerbils (*Meriones unguiculatus*) (Contreras, 1984).

We hypothesized that living in groups affects the ability to cope with cold because huddling can decrease the capacity for NST (Himms-Hagen and Villemure, 1992; Merritt et al., 2001), the main source of heat in winter-acclimatized hamsters (Heldmaier and Buchberger, 1985). Although we did not measure NST capacity, we found that oxygen consumption at 10°C did not differ between animals housed singly and in groups, indicating the same ability to cope with cold. One of the reasons for these results could be the hamsters' activity pattern. Siberian hamsters are active on a daily basis and in winter they experience short days and low T_a every day. Another reason is that high NST capacity is a prerequisite for the development of heterothermy in the annual cycle (Jefimow et al., 2004b), in both solitary and grouped hamsters.

Social thermoregulation may reduce energy expenditure through decreased heat loss, as a result of both decreased body surface exposed to the external environment and increased local temperature in the nest (Séguy and Perret, 2005). As a consequence, the increase in metabolic rate in response to low T_a may be smaller (Gębczyński, 1969; Kenagy and Pearson, 2000; Kauffman et al., 2003; Scantlebury et al., 2006). Although we did not measure nest temperature, it is plausible that the local temperature in the nest with four animals inside was higher than that of the nest of single hamsters. According to Hayes and colleagues, local heating from metabolic heat production has a much greater effect than decreased surface area on energy savings in huddling animals (Hayes et al., 1992). Local heating increases as T_a decreases. Interestingly, changes in local nest temperature exert a more pronounced effect on metabolic rate than changes in ambient, outside temperature (Hayes et al., 1992).

One could argue that animals living in a group have a lower metabolic rate because of changes in the gas atmosphere inside the nest. Schlenker and colleagues found that increasing the level of CO_2 to 0.2% reduces the metabolic rate of mice by ~30% (Schlenker et al., 1981). Opposite results were described by Speakman and Rossi, who found that increasing the CO_2 concentration did not induce metabolic suppression in white mice although CO_2 ranged between 0.22 and 0.44% (Speakman and Rossi, 1999). However, these results should be treated with caution because before measurements mice were housed separately.

In conclusion, we found that in Siberian hamsters housed in groups the winter decrease in m_b was smaller than that in animals housed

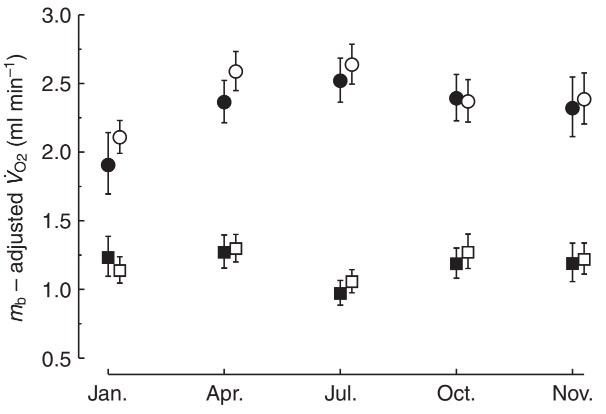

Fig. 9. The m_b-adjusted rate of oxygen consumption (least squares means with 95.0% confidence intervals) in the cold (10°C; circles) and at lower critical temperature [LCT; squares, 20°C in winter (January), 23°C in spring (April) and autumn (October and November), and 26°C in summer (July)] in Siberian hamsters housed singly (filled symbols) or in group of four littermates (open symbols). Measurements were done on individual animals (independent of housing conditions) in four different seasons (twice in autumn).

singly, and that social thermoregulation influenced the characteristics of daily torpor. Torpor bouts were slightly longer and shallower in grouped than in solitary hamsters. When torpor bouts were synchronized in all group members, minimum T_b was kept at the lowest level. Although our knowledge of the behaviour of Siberian hamsters living in the natural environment is rather limited, based on the present results we presume that social overwintering as well as social thermoregulation may also be important strategies for Siberian hamsters. We know that they are social animals that establish stable intrasexual hierarchies (Wynne-Edwards and Lisk, 1987; Wynne-Edwards and Lisk, 1988). Observations in the wild indicate that males and females can share one burrow at the end of the breeding season. However, it seems that in the middle of summer (July), sharing the nest is less common or even absent, suggesting seasonal changes in nest sharing (Wynne-Edwards, 1995). We are not aware of any data on huddling in Siberian hamsters in the wild. It is possible that not only breeding pairs but also the young from the last litter in the year share one nest during winter. Social thermoregulation could reduce energetic costs at low T_a while higher m_b and large fat reserves could ensure a better body condition for the beginning of reproduction in spring.

LIST OF ABBREVIATIONS

LCT	lower critical temperature
m_b	body mass
SP	short photoperiod
T_a	ambient temperature
T_b	body temperature
T_s	soil temperature
$\dot{V}_{O_2}$	rate of oxygen consumption

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