

## Friends with benefits: the role of huddling in mixed groups of torpid and normothermic animals

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### Abstract

Huddling and torpor are widely used for minimizing heat loss by mammals. Despite the questionable energetic benefits from social heterothermy of mixed groups of warm normothermic and cold torpid individuals, the heterothermic Australian marsupial sugar glider (*Petaurus breviceps*) rests in such groups during the cold season. To unravel why they might do so, we examined torpor expression of two sugar glider groups of four individuals each in outside enclosures during winter. We observed 79 torpor bouts during 50 days of observation and found that torpor bouts were longer and deeper when all individuals of a group entered torpor together and therefore infer that they would have saved more energy in comparison to short and shallow solitary torpor bouts. However, all gliders of either group only expressed torpor uniformly in response to food restriction, whereas on most occasions at least one individual per group remained normothermic. On the other hand, the presence of warm gliders in mixed groups also appears to be of energetic advantage for torpid individuals, because nest box temperature was negatively correlated with the number of torpid gliders and normothermic individuals kept the nest temperature at a value closer to the threshold for thermoregulatory heat production during torpor. Our study suggests that mixed groups of torpid and normothermic individuals are observed when environmental conditions are adverse but food is available, leading to intermediate energy savings from torpor. However, under especially challenging conditions and when animals are starving, energy savings are maximized by uniform and pronounced expression of torpor.

### Summary statement

Torpor bouts are longer and deeper in uniformly torpid groups, but the presence of normothermic gliders keeps the nest temperature closer to the threshold for thermoregulatory heat production during torpor.

**Key words:** disturbance- energy saving - social thermoregulation- sugar glider

## Introduction

Small endotherms have a high surface area to volume ratio and therefore have to deal with high heat loss and thus high energetic costs when exposed to cold. These energetic costs can be difficult to meet because cold periods often coincide with the unproductive part of the year, limiting energy uptake at a time when energy demand is highest. Increasing the capacity of heat production by means of non-shivering thermogenesis (Heldmaier et al., 1982; Nowack et al., 2013a) does effectively help an animal to remain warm, but also further increases energy expenditure. To efficiently reduce energetic costs, endotherms have evolved a number of seasonal adjustments in their behavior, morphology and/or physiology. Animals can reduce thermoregulatory costs by selecting more suitable microhabitats, such as insulated nests during cold periods (Gilbert et al., 2010; Nowack et al., 2013b), via huddling with conspecifics (Nowack et al., 2013b), or by seasonal changes in body mass or pelage insulation (Scholander et al., 1950). The amount of fat, fur or feathers to increase insulation, however, is restricted by the body size of the animal and therefore is of limited use for small endotherms (Kleiber, 1947). This is not the case for huddling with other individuals, which reduces energetic costs by reducing the effective surface-to volume ratio and often increases the temperature in a nest or burrow. However, while energy savings during huddling are limited to metabolic rates (MR) that are similar to or greater than the basal metabolic rate (BMR) of an individual (Fleming, 1980; Namekata and Geiser, 2009; Gilbert et al., 2010), many small mammal and bird species further reduce their energy expenditure by using torpor, during which MR drops to a fraction of BMR (Ruf and Geiser, 2015).

Not surprisingly a few heterothermic species, such as small marsupials, bats, rodents and primates, that enter torpor during the cold and/or during periods of food shortages are known to combine both strategies and nest in groups during the torpor season (Fleming, 1980; Vogt and Lynch, 1982; Arnold, 1988; Arnold et al., 1991; Perret, 1998; Blumstein et al., 2004; Séguéy and Perret, 2005; McKechnie et al., 2006; Pretzlaff et al., 2010; Franco et al., 2012; Dausmann and Glos, 2014). Well-known examples of social hibernators are marmots (*Marmota* spp.) that have to cope with long and severely cold winter periods in their natural habitat. Several marmot species appear to benefit from social hibernation because the presence of nest mates keeps the nest temperature above the threshold for thermoregulation during torpor (Arnold et al., 1991). Moreover, the body warmth of conspecifics can reduce the costs of periodic rewarming (Arnold, 1988). Daily torpor in groups also reduces energy expenditure (Fleming, 1980; Eto et al., 2014) and animals undergoing torpor in groups often show an increased torpor bout duration (TBD) compared with solitary individuals (Séguéy and Perret, 2005; Jefimow et al., 2011). It therefore has been suggested that

huddling animals undergoing daily torpor benefit from social thermoregulation by saving more energy for survival and perhaps can maintain a better body condition for the reproduction season that often follows the torpor season, than their solitary conspecifics (e.g. Jefimow et al., 2011).

Nesting in groups can on the other hand also be detrimental for the expression of torpor. Because the air surrounding an individual is to a large extent a function of the size of the group, the cooling process during entry into torpor is slowed, the minimum body temperature ( $T_b$ ) increases and often the energy saved during torpor decreases with increasing group size (Ruf and Arnold, 2000). Furthermore, nesting in groups during torpor may result in disturbance by conspecifics that arouse for foraging or other activities, increasing the  $T_b$  and MR of torpid nest mates (Dausmann and Glos, 2014). Accordingly, yellow-bellied marmots (*Marmota flaviventris*), do not have higher energetic advantages than solitary conspecifics when hibernating in groups of three individuals (Blumstein et al., 2004) and a number of studies have shown that torpor use is more pronounced in solitary individuals than in social groups (McKechnie et al., 2006; Hwang et al., 2007).

The Australian sugar glider (*Petaurus breviceps*) is a small marsupial that commonly nests in groups that are often formed by related individuals (Klettenheimer et al., 1997). It increases group size during the winter period and can undergo daily torpor during adverse conditions (Körtner and Geiser, 2000; Christian and Geiser, 2007; Nowack et al., 2015). This small arboreal and nocturnal species is found nesting in tree hollows (Körtner and Geiser, 2000; Nowack et al., 2015) and feeds mainly on tree exudates (*Acacia* gum and *Eucalyptus* sap) and insects that undergo seasonal fluctuations and are less available during winter (Smith, 1982). It has been shown that gliders decrease their resting MR and the lower critical temperature of the thermoneutral zone via huddling (Fleming, 1980), and social thermoregulation is thought to be one of the key factors explaining why sugar gliders do not use torpor regularly during cold and unproductive winter periods (Körtner and Geiser, 2000). Furthermore, energy demands of the species are low due to good insulation (Fleming, 1980). Heterothermy has been found in gliders nesting in groups, although most of the time one animal of the group remains normothermic (Fleming, 1980); large thermally mixed groups of up to 20 individuals have been found in the wild (~50% torpid; unpubl. observ. F. Geiser).

Mixed groups consisting of torpid and normothermic individuals should have to cope with the same disadvantages that are found in groups of huddling uniformly torpid individuals, but have to deal with reduced energetic benefits. On the other hand, some normothermic individuals could keep the ambient temperature ( $T_a$ ) inside the nest higher than in completely torpid groups, therefore reducing individual energy expenditure for thermoregulation during torpor. To gain a better understanding of the interrelations between torpor use and huddling in mixed groups, we

studied two groups of sugar glider of four individuals each under different trophic conditions in outside enclosures during winter.

## Material and Methods

### *Ethical note*

Approval to conduct this study was granted by the University of New England Animal Ethics Committee and New South Wales National Parks and Wildlife Service.

### *Capture and housing*

We retrieved eight sugar gliders from wooden nest boxes near Dorriggo (30° 22'S', 152° 34') and within Imbota Nature Reserve (30° 35'S, 151° 45'E)(4 animals of one group from each location). Sugar gliders were transferred to the University of New England, weighed to the nearest 0.1 g, sexed and aged according to Suckling (1984) and micro chipped for individual recognition (PIT tags, Destron Technologies, South St. Paul, MN). The groups consisted of one adult male, two adult females and a juvenile male (group 1) and three adult females and one adult male (group 2). Animals were kept in their capture groups and housed in two outdoor enclosures (3.6 x 1.8 x 2 m), each fitted with branches, two feeding platforms and three wooden nest boxes (wall thickness: ~2.5 cm) per group. During normal holding all animal groups were fed daily with 80 g of a mixture of high protein baby cereal, egg, honey and water, to which high protein supplement (Wombaroo) was added. This food was supplemented by a dish of fresh fruits. Water was available *ad libitum*.

### *Surgeries*

We implanted all individuals with thermo-sensitive radio transmitters (2 g, Sirtrack, Havelock North, New Zealand) that allowed us to determine individual  $T_b$ . None of the females had pouch young at the time of implantation. Transmitters were waxed and calibrated in a water bath to the nearest of 0.1 °C before being implanted intraperitoneally under oxygen/isoflurane anaesthesia using a small abdominal incision (Rojas et al., 2010). Individuals weighed  $117.6 \pm 21.8$  g at date of implantation and were weighed again after the experiments (see Results).

### *Measurement of body temperature and experimental protocol*

The study was conducted for 50 days from late June to mid-August 2014. Animals were allowed to recover from surgery for three days before the start of experiments.  $T_b$  was obtained at 10-minute intervals using a multi-channel receiver/data logger placed outside of the aviary (for detailed description of the system see: Körtner and Geiser (2000)). Animals were considered to be torpid

when  $T_b$  fell below 30 °C. Entry into torpor was defined as the time when  $T_b$  began to decline continuously from above 34 °C to temperatures below 30 °C. The end point of rewarming was defined as the time when  $T_b$  reached a plateau above 30 °C. We measured average rewarming rates during rewarming from torpor from the point when rewarming rates were higher than 0.05 °C min<sup>-1</sup>. The number of normothermic individuals at time of arousal was defined as the number of individuals with a  $T_b$  above 30 °C; the number of animals during entry into torpor was defined as the number of individuals with a  $T_b$  below 30 °C.

Sugar gliders are known for their reluctant torpor use under laboratory conditions and therefore a combination of different levels of food reduction was used to induce torpor: day 1: no food (100% food reduction); day 2: 60 g of protein mixture (25% food reduction), normal amount of fruits; day 3: 40 g of protein mixture (50% of food reduction) and normal amount of fruits; followed by at least four nights of normal food supply (80g of protein mixture plus fruits) before the protocol was repeated; the above protocol was applied three times during the study period.

#### *Ambient and nest box temperature*

$T_a$  was recorded hourly within the aviaries with one data logger placed in the shade (resolution 0.5 °C; Hygrochron iButton/DS1921, Dallas Semiconductors). Nest box temperature ( $T_{box}$ ) of group 1 was recorded with data loggers every 30 min within the nest boxes, about 7.5 cm inside the nest box. We were able to collect  $T_{box}$  of occupied nest boxes for 20 days.

#### *Data analyses*

Data are presented as mean  $\pm$  1 standard deviation;  $n$  denotes the number of individuals,  $N$  the number of observations. Statistical analyses were conducted in R (R version 3.1.0; 2014-04-10, R Development Core Team, 2014). Normal distribution and homogeneity of variance were tested using Shapiro-Wilk test and Bartlett's test, respectively.

The relationship between initial body mass and torpor frequency (number of torpor bouts used by each individual) was tested via regression analyses. The synchronicity of spontaneous torpor between both groups, i.e. if torpor occurred more often on the same days in both groups than expected by chance, was tested with a Chi<sup>2</sup> test. For this test we assumed the expected probability that an individual of any of the two groups is torpid is 50 % and the probability that individuals from both groups are torpid on the same day is 25 %. The influence of weather variables on the occurrence of spontaneous torpor was tested in a binomial model, taking repeated measures into account by using "individual" as random factor (lmer in library lme4; Bates et al., 2014). The influence of the number of torpid animals per group on  $T_{box}$  was tested using regression analyses.

Linear mixed effect models that take into account repeated measures by including the individual's ID as a random effect were used to test the relationship between minimum  $T_b$  ( $T_{bmin}$ ) and TBD, as well as between  $T_{bmin}$  and rewarming rate (lme in library nlme; Pinheiro et al., 2014).

#### *A priori model-building and selection*

We built *a priori* linear-mixed effect models to explore if group composition affects TBD,  $T_{bmin}$ , cooling rates and rewarming rates (lme in library nlme; Pinheiro et al., 2014). Because other studies indicate that food availability and  $T_a$  influence torpor patterns, our models included three fixed effects: minimum  $T_a$ , food availability (0 %, 50 %, 75 %, 100 %; arcsine transformed) and the number of torpid individuals per group ( $n=1-4$ ; used for TBD and  $T_{bmin}$ ) or the number of animals that had a  $T_b$  above (heating rate)/below (cooling rates) 30°C at the time of arousal/entry. We modelled repeated measures on each individual by including the individual's ID as a random effect. We evaluated candidate models with Akaike's Information Criterion (Akaike, 1974).

## **Results**

### *Torpor occurrence*

In both groups all four gliders were found nesting together on 100 % of observation days, despite having the choice between three boxes per cage that were used in alternating order (number of changes: 10 times group 1; 7 times group 2). Torpor was observed on 24 of 50 monitored days. All eight individuals underwent bouts of daily torpor during the study period, but torpor use differed among individuals. Each group contained at least one torpor-prone individual that showed torpor on 17 to 19 of 50 days (group 1: two males; group 2: one female), whereas three individuals only displayed torpor very reluctantly (three or four times; two females of group 1, one female of group 2). Initial body mass was not related to torpor frequency (regression analyses;  $F_{1,6} = 0.16$ ,  $p > 0.05$ ;  $r^2 = -0.14$ ). Interestingly, gliders that were reluctant to use torpor lost body mass over the time of our study ( $-8.9 \pm 1.0$  g,  $n=3$ ), whereas torpor-prone individuals gained body mass ( $19.9 \pm 15.7$  g,  $n=3$ ) and individuals with intermediate torpor use held their initial weight ( $1.1 \pm 1.8$  g,  $n=2$ ). Mean mass of all eight individuals slightly increased during the experimental period (from  $117.6 \pm 21.8$  g to  $123.3 \pm 9.2$  g).

We observed a total of 79 torpor bouts, with 47 % of torpor bouts being induced (no or limited food) and 53 % occurring spontaneously (100 % food available). All individuals entered spontaneous as well as induced torpor, except one adult female that only showed torpor when food was withheld. Of the three different levels of food reduction (100 %, 50 %, 25 %), 100 % and 50 % food reduction always resulted in torpor use by some individuals, whereas 25 % food reduction only

caused torpor use on one of three occasions. Spontaneous torpor occurred significantly more often on the same days in both groups than expected by chance (at 50 % of torpor days;  $X^2=10.09$ ,  $df=2$ ,  $p<0.01$ ) and was triggered by a combination of low average  $T_a$  and the occurrence of rainfall (binomial model, interaction term:  $z=-2.15$ ,  $p=0.032$ ).

On most days when torpor was expressed, only one ( $N=15$ ) or two individuals ( $N=16$ ) per group entered torpor, whereas the other individuals remained normothermic. Torpor in three individuals of one group was only observed seven times (group 1: 4 times; group 2: 3 times) and torpor in all four individuals three times (group 1: 1 time; group 2: 2 times). Days on which all four animals of one social group underwent torpor only occurred in response to food deprivation. Torpor in three individuals was spontaneous on only two of the seven observations..

### *Influence of group composition on torpor characteristics*

Animals entered torpor between 2200 h and 0640 h with a peak for torpor entries between 0300–0600 h. The earliest rewarming from torpor occurred at 0400 h, the latest at 1730 h. Most arousals occurred between 1200 h and 1400 h (examples: Fig.1).

TBD varied between 160 min and 1050 min (mean  $532 \pm 198$  min,  $N=79$ ) and was related to  $T_{bmin}$  (lme;  $F_{1,70}=106.4$ ,  $p<0.001$ ;  $TBD=-39.886 \cdot T_{bmin}+1414.771$ );  $T_{bmin}$  varied between 14.0 °C and 29.9 °C. In addition to minimum  $T_a$  and food availability, TBD and  $T_{bmin}$  were also influenced by the number of torpid individuals per group (Table 1), with longer and deeper torpor bouts occurring when all individuals per group were torpid (Table 2, Fig. 2).

Interestingly, the mean  $T_b$  of both groups never fell below 20 °C (group 1: 20.4 °C, group 2: 22.8 °C). On days when all individuals of the group went into torpor, one individual usually aroused from torpor before the other group members reached their  $T_{bmin}$  (see example in Figure 1), therefore raising the mean  $T_b$ .

The maximum individual cooling rate was 0.18 °C min<sup>-1</sup> for a period of 10 min (average for the entire torpor entry:  $0.04 \pm 0.01$  °C min<sup>-1</sup>,  $N=79$ ). Although one would assume that minimum  $T_a$  and food availability both affect cooling rates, only the number of torpid animals ( $T_b<30^\circ\text{C}$ ) had an influence on cooling rates in the model with the best fit (Table 1), with cooling rates being faster the more individuals were torpid (range: -0.02 to -0.08 °C min<sup>-1</sup>). The maximum individual rewarming rate was 0.44 °C min<sup>-1</sup> for a period of 10 min (average for the entire arousal:  $0.28 \pm 0.07$  °C min<sup>-1</sup>,  $N=79$ ). Average rewarming rates were negatively correlated with  $T_{bmin}$  (lme;  $F_{1,70}=105.3$ ,  $p<0.001$ ; Fig. 3), and were influenced by minimum  $T_a$  (see model in Table 1), whereas food availability and the number of individuals with a  $T_b$  above 30 °C were not included in the model with the best fit (however, all three factors are theoretically equally parsimonious;  $\Delta AIC < 2$ ; Table 1).

### *Influence of group composition on nest box temperature*

Inside the occupied minimum  $T_{\text{box}}$  was  $6.6 \pm 2.4$  °C (N=20) and never fell below 2.0 °C, although nightly minimum  $T_a$  during the study period fell to -5.0 °C (range: -5.0 to 9.0 °C; daily maxima: 6.5 °C to 23.0 °C). The daily difference between the lowest  $T_{\text{box}}$  in occupied nest boxes and the lowest outside  $T_a$  at a time when all animals were normothermic was on average 3.3 °C (N=20), whereas the temperature difference in an unoccupied nest box was 1.2 °C (N=20) during the same time.  $T_{\text{box}}$  was correlated with the number of torpid animals in the group (N=20;  $T_{\text{box}}-T_a$  at the time of the overall minimum  $T_b$  of the group;  $r^2 = 0.339$ ,  $df = 18$ ,  $p = 0.007$ ;  $T_{\text{box}}-T_a$  (°C) =  $-0.9015 \times \text{number of torpid animals} + 1.9071$ ).

### *Synchronicity of entry and arousal and disruptions by other individuals*

When more than one individual of each group entered torpor, entry times varied between 0 min and 300 min among the individuals of each group. Entry times were seldom synchronized and only occurred six times within 60 min for two individuals (mean duration between two entries:  $43 \pm 12$  min, N=6 of 38). Synchronized entries for more than two individuals were only observed once for three individuals entering torpor shortly after each other (within 60 min). Arousal times among individuals differed between 0 and 490 min. In contrast to entries, arousal times were often highly synchronized for two individuals of one group (N=18 of 38; <60 min; mean duration between two arousals:  $38 \pm 15$  min, Fig. 1), but synchronized arousals were never observed for more than two individuals.

Whether or not an arousal led to a second individual arousing closely afterwards was dependent on the time of day. Arousals between 0400 h and 0800 h (N=10) never resulted in a arousal within the next 60 min and led only on two occasions to a temporary increase of the  $T_b$  of one or more torpid gliders (example: Fig. 3). However, the likelihood of a second arousal increased between 0900 h and 1300 h from 40 % (N=5) to 100 % (N=3). Furthermore, although the temperature traces show  $T_b$  increases that might be due to movements of normothermic individuals, these disturbances never led to a termination of torpor.

Interestingly, when three or four animals per nest box entered torpor, usually at least one animal displayed shallow torpor ( $T_{\text{bmin}} \geq 24$  °C) and aroused in the early morning (between 0420 and 0940 h); the other two or three animals displaying deep torpor ( $T_{\text{bmin}} < 20$  °C) started their arousal usually between 1040 and 1400 h (Fig. 1). Shallow torpor bouts were usually used by two of the three torpor-reluctant individuals, and these only used torpor on days when torpor was displayed by at least two other individuals.



## Discussion

Our data show sugar gliders huddle regularly during torpor and mixed groups of normothermic and torpid sugar gliders are the rule rather than the exception. Usually at least one individual of a group of four sugar gliders remained normothermic and uniformly torpid groups were only observed when food was withheld. This is surprising since torpor bouts were longer and deeper when all individuals expressed torpor, which would lead to higher energy savings.

Sugar gliders are known to only reluctantly enter torpor (Fleming, 1980; Körtner and Geiser, 2000; Christian and Geiser, 2007) and may remain normothermic for long periods even during winter. Social thermoregulation increases the temperature in the nests and reduces the effective surface-area to volume ratio of individuals and therefore thermoregulatory energy expenditure during normothermic phases (Fleming, 1980). However, the drawback of huddling as means of energy conservation is that it is limited to MRs near or above BMR (Fleming, 1980; Boix-Hinzen and Lovegrove, 1998; Gilbert et al., 2010). Therefore, gliders enter torpor during adverse weather conditions as well as during severe food shortage and reduce MR to a fraction of BMR (Körtner and Geiser, 2000; Christian and Geiser, 2007; Nowack et al., 2015).

In contrast to huddling during normothermia, the presence of some normothermic individuals during torpor can have negative as well as positive impacts. In most species that nest in groups during torpor, all individuals of one group undergo torpor at the same time. The few species that are known to rest in groups of normothermic and torpid individuals include sugar gliders, the feathertail glider (*Acrobates pygmaeus*), fat-tailed dunnarts (*Sminthopsis crassicaudata*), and the Japanese field mouse (*Apodemus speciosus*), all expressing mainly short bouts of torpor (Morton, 1978; Fleming, 1985; Eto et al., 2014). One reason for the generally rare occurrence of mixed groups might be that normothermic individuals or individuals that enter only short and shallow torpor bouts can disturb other individuals that undergo deep torpor. Sugar gliders usually aggregate very closely and one would assume that rewarming of one individual would increase the  $T_b$  of its nest mates. Indeed 47 % of the arousals resulted in an arousal of other gliders. However, only arousals that were closer to midday coincided with a second arousal of nest mates, whereas the rewarming of a group member in the early morning did not obviously affect  $T_b$  of other animals. As many species arouse from torpor around midday, synchronized arousals might therefore not be caused by disturbance but by circadian rhythms (Heller and Ruby, 2004; Turbill et al., 2008). However, our study also showed that cooling rates were negatively correlated with the number of warm, normothermic individuals in the group and that TBDs were shorter and  $T_{bmin}$  higher the more individuals were normothermic. Therefore, torpor use in thermally mixed huddling groups reduces energetic benefits for torpid sugar gliders, even if disturbances of nest mates are rare.

On the other hand, torpid individuals might benefit of their normothermic nest mates on cold days as normothermic gliders might keep  $T_{\text{box}}$  above the threshold for thermoregulation during torpor. During entry into torpor, the hypothalamic set point for  $T_b$  is down-regulated and metabolic heat production is only used to maintain  $T_b$  at or above this  $T_{\text{bmin}}$  (Florant and Heller, 1977). Hibernating species have a very low set point for  $T_{\text{bmin}}$  (often 0-10 °C) (Ruf and Geiser, 2015) and therefore usually only need to thermoregulate if  $T_a$  falls below these values and can thermoconform for most of the hibernation period. An increase of nest temperature due to normothermic conspecifics would therefore be counterproductive for a hibernator as its  $T_b$  and MR would be raised. In contrast, daily heterotherms, such as sugar gliders, have a minimum  $T_b$  markedly above the usual winter  $T_a$  (usually between 10 and 25°C; Ruf and Geiser, 2015). This will require thermoregulation during torpor and increase energy costs when nests temperature is lower than  $T_{\text{bmin}}$ . The presence of normothermic individuals should therefore lead to decreased energy expenditure for sugar gliders because gliders increase MR during torpor at  $T_a$ s below 16°C (Fleming, 1980). The correlation between  $T_{\text{box}}$  and the number of torpid individuals per nest box clearly shows that  $T_{\text{box}}$  is indeed warmer when more animals are normothermic and this effect is likely to increase with group size and thus affect energy expenditure. Group sizes of gliders increase towards winter (Henry and Suckling, 1984), which supports our interpretation.

Why some individuals are more reluctant to enter torpor than other individuals remains elusive. Normothermic thermoregulation during harsh conditions is obviously energetically costly. This is emphasized by the fact that torpor-reluctant individuals lost weight over the study period, whereas torpor-prone individuals gained weight. Sugar-gliders are known to use torpor as a last-resort strategy (Christian and Geiser, 2007) instead of undergoing torpor regularly and it has been argued that the digestion of some foods, such as gum, requires a high  $T_b$  (Körtner and Geiser, 2000; Nowack et al., 2013b). However, since all gliders had access to the same food, this explanation for reluctant torpor use of some individuals seems rather unlikely for our study groups. Since weight loss of torpor-reluctant individuals was not in a critical range, it is more likely that the benefits of torpor use might just not have outweighed its advantages for these individuals. Although the potential benefits of torpor use are diverse (Geiser and Brigham, 2012), torpor use also comes with costs, such as slowed reactions (Rojas et al., 2012), or increased oxidative stress (Carey et al., 2000; but see: Orr et al., 2009).

Even though it may appear counterproductive at first for a normothermic animal to share a huddle with torpid individuals, torpid animals have a  $T_b$  well above  $T_a$  and on most occasions more than one individual will stay normothermic. Therefore, it is still more advantageous to share a nest with a group of torpid individuals than nesting solitarily. Another reason why normothermic

individuals are found nesting together with torpid individuals could be social contacts. Sugar gliders are seldom found nesting solitarily and instead form groups throughout the year (e.g. Suckling, 1984). Observations of tagged gliders indicate that groups are fairly stable and if groups are divided when changing nests, they rejoin after a few days (Körtner and Geiser, 2000). This suggests that social contacts are of high importance for this species. The mating period of sugar gliders in the wild begins in winter (Suckling, 1984) and nest sharing might also be a mechanism to secure mating partners. The same mechanism has also been suggested to explain sociality during hibernation in fat-tailed dwarf lemurs (*Cheirogaleus medius*) and it has been observed in this species that when individuals change nesting sites during the mating season, the males relocate and join the female pair partners (Dausmann and Glos, 2014).

### Conclusion

In summary, our results show that sugar gliders are regular huddlers that usually nest in thermally mixed groups during winter. Even if energetic benefits for all individuals would be higher if the entire group would enter synchronized torpor, mixed groups still provide some energetic advantage for both normothermic and torpid individuals. As long as food is available torpor is only used by some gliders whereas the rest of the group remains normothermic, leading to intermediate energy savings. However, under especially harsh conditions and when animals are starving, all gliders enter torpor and energy savings are maximized.

### Abbreviations

BMR – basal metabolic rate

MR – metabolic rate

T<sub>a</sub> – ambient temperature

T<sub>b</sub> – body temperature

TBD - torpor bout duration

T<sub>bmin</sub> – minimum body temperature

T<sub>box</sub> – nest box temperature

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### **Competing Interests**

No competing interests declared.

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## Tables

**Table 1: The five best fit models to explain the patterns observed in TBD and  $T_{bmin}$ , as well as in heating and cooling rates.** We tested *a priori* regression based-linear-mixed effect models including three fixed effects that were likely affecting those parameters: minimum  $T_a$  ( $T_{amin}$ ), food availability (0%, 50%, 75%, 100%; arcsine transformed) and the number of torpid individuals per group (used for TBD and  $T_{bmin}$ ) or the number of animals that had a body temperature above (normothermic/group; heating rate) or below (torpid/group; cooling rates) 30 °C at the time of arousal/entry. We modelled repeated measures on each individual as random effects. We evaluated candidate models with Akaike's Information Criterion (AIC). The best fit model for each parameter is highlighted.

<sup>1</sup>the number of animals that had a body temperature above/below 30 °C.

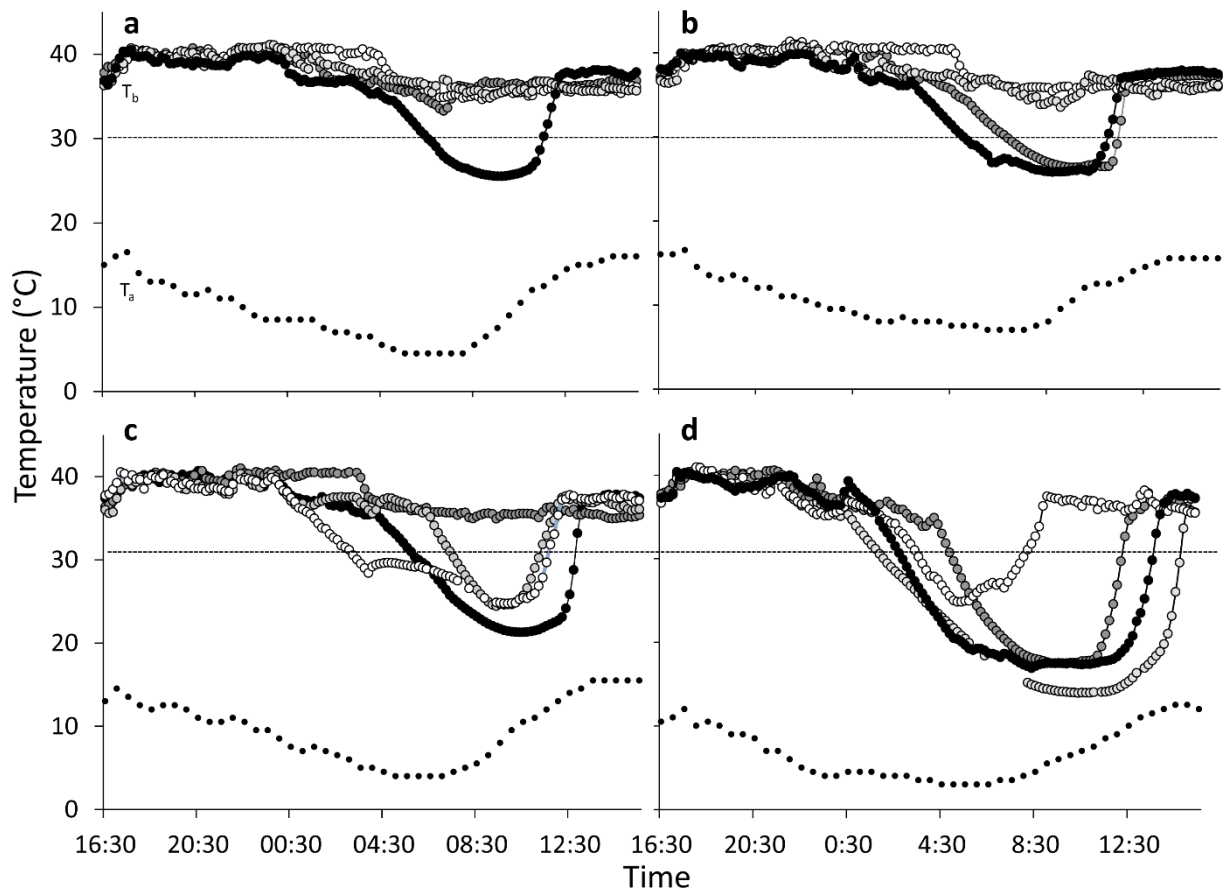
	Model	AIC	$\Delta$ AIC
<b>TBD</b>	<b>torpid/group*food + torpid/group*<math>T_{amin}</math> + food* <math>T_{amin}</math></b>	<b>989.4427</b>	<b>0</b>
	torpid/group*food + food* $T_{amin}$	996.3637	6.921
	torpid/group* $T_{amin}$ + food* $T_{amin}$	997.1667	7.724
	torpid/group*food + torpid/group* $T_{amin}$	997.7016	8.2589
	torpid/group*food + $T_{amin}$	1002.072	12.6293
<b><math>T_{bmin}</math></b>	<b>torpid/group*food + <math>T_{amin}</math></b>	<b>406.4546</b>	<b>0</b>
	torpid/group*food	409.3358	2.8812
	torpid/group*food + torpid/group* $T_{amin}$	409.5366	3.082
	Torpid/group	411.4430	4.9884
	torpid/group*food + torpid/group* $T_{amin}$ + food* $T_{amin}$	412.4502	5.9956
<b>Rewarming rate</b>	<b><math>T_{amin}</math></b>	<b>-197.2142</b>	<b>0</b>
	food	-195.6548	1.5594
	normothermic/group <sup>1</sup>	-195.4812	1.733
	$T_{amin}$ + food	-189.2970	7.9172
	$T_{amin}$ + torpid/group <sup>1</sup>	-187.8018	9.4124
<b>Cooling rate</b>	<b>torpid/group<sup>1</sup></b>	<b>-477.6354</b>	<b>0</b>
	torpid/group <sup>1</sup> + $T_{amin}$	-472.1559	5.4795
	$T_{amin}$	-470.1356	7.4998
	torpid/group <sup>1</sup> + food	-464.7737	12.8617
	torpid/group <sup>1</sup> * $T_{amin}$	-457.9257	19.7097

**Table 2: Average minimum body temperature ( $T_{\text{bmin}}$ ) during torpor in relation to the number of torpid individuals per group.** *N* refers to the number of observations for the particular group composition.

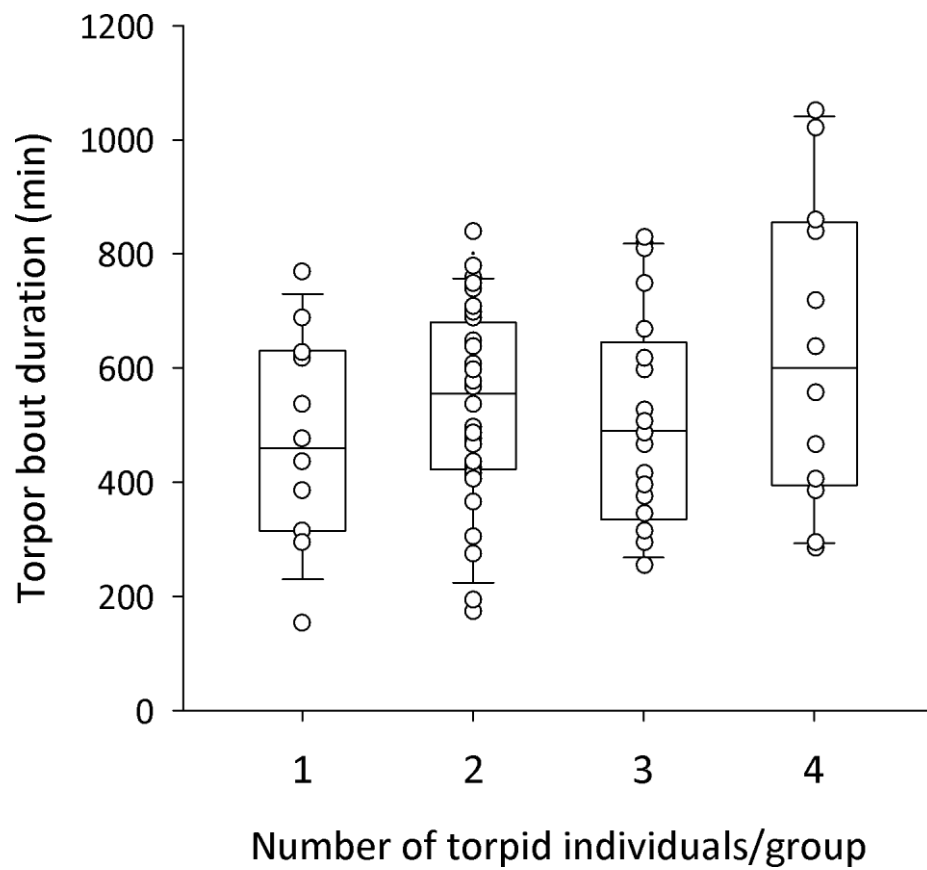
Number of torpid individuals	$T_{\text{bmin}}$
1/4	$24.9 \pm 2.9$ °C (N=14)
2/4	$23.1 \pm 3.4$ °C (N=16)
3/4	$22.9 \pm 3.5$ °C (N=7)
4/4	$20.3 \pm 5.2$ °C (N=3)



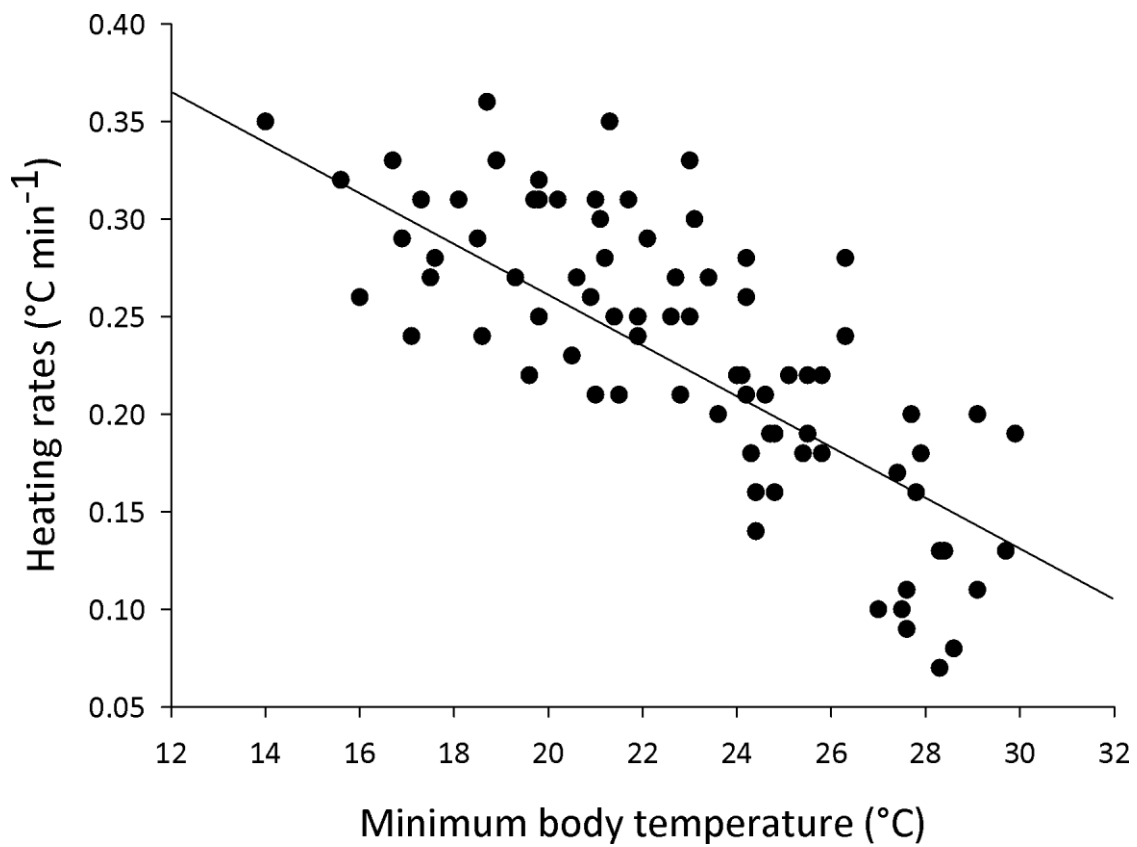
## Figures



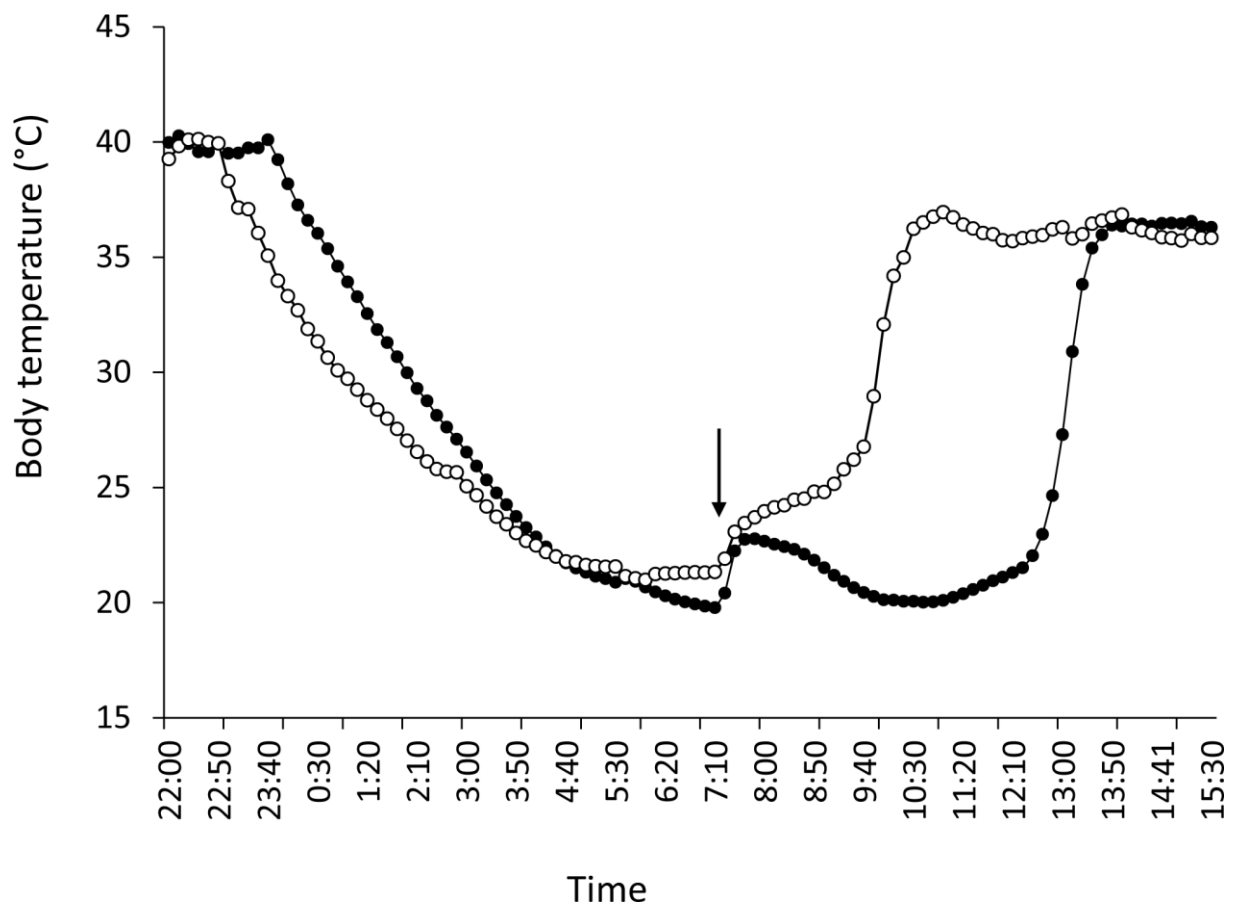
**Figure 1: Examples of huddling groups with a) one , b) two, c) three and d) four torpid individuals per group.** Individual traces of body temperature ( $T_b$ ; 10-min intervals) for all individuals per group are shown in relation to ambient temperature ( $T_a$ ). Depicted are synchronized rewarming of two torpid individuals in b, c, d, respectively. The dashed line indicates the torpor threshold of 30 °C.



**Figure 2: Torpor bout duration in relation to the number of individuals per group that were torpid.** Boxplots represent median, as well as 5-, 25-, 75- and 95-percentiles. The dots represent individual values (N=79, n=8).



**Figure 3: Relationship between average heating rates for the complete arousal from torpor and the minimum body temperature of the individuals during torpor.** Average rewarming rates were negatively correlated with minimum body temperature ( $N=79$ ,  $n=8$ ; lme, accounting for repeated measures;  $F_{1,70}=105.3$ ,  $p<0.001$ ).



**Figure 4: Example of an arousing animal disturbing a nest mate.** Individual traced of body temperature ( $T_b$ ; 10-min intervals) for two individuals of one group. The arrow marks the point where animal 1 started rewarming and disturbed the torpor bout of animal 2.