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RESEARCH ARTICLE

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

Julia Nowack* and Fritz Geiser

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 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. Nevertheless, 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.

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 behaviour, morphology and/or physiology. Animals can reduce thermoregulatory costs by selecting more suitable microhabitats, such as insulated nests during cold periods (Gilbert

Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale, New South Wales 2351, Australia.

*Author for correspondence (jnowack@une.edu.au)

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 area 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; Séguy 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.), which 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 (Séguy and Perret, 2005; Jefimow et al., 2011). Therefore, it 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 reproductive season that often follows the torpor season than their solitary conspecifics (e.g. Jefimow et al., 2011).

In contrast, nesting in groups can 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

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List of abbreviations

BMR	basal metabolic rate
MR	metabolic rate
T_a	ambient temperature
$T_{a,min}$	minimum ambient temperature
T_b	body temperature
TBD	torpor bout duration
$T_{b,min}$	minimum body temperature
T_{box}	nest box temperature

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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* Waterhouse 1839) 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 because of 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; F.G., unpublished observations).

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. Alternatively, some normothermic individuals could keep the ambient temperature (T_a) inside the nest higher than in completely torpid groups, thereby reducing individual energy expenditure for thermoregulation during torpor. To gain a better understanding of the interrelationships between torpor use and huddling in mixed groups, we studied two groups of sugar gliders consisting of four individuals each under different trophic conditions in outside enclosures during winter.

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

Capture and housing
We retrieved eight sugar gliders from wooden nest boxes near Dorrigo (30°22′S, 152°34′E) and within Imbota Nature Reserve (30°35′S, 151°45′E) (four 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, USA). 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 (3.6×1.8×2 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 0.1°C before being implanted intraperitoneally under oxygen/isoflurane anaesthesia using a small abdominal incision (Rojas et al., 2010). Individuals weighed 117.6±21.8 g at the date of implantation and were weighed again after the experiments (see Results).

Measurement of T_b 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 3 days before the start of experiments. T_b was obtained at 10 min intervals using a multi-channel receiver/data logger placed outside of the aviary (for a 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 at which 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^{-1}. The number of normothermic individuals at the time of arousal was defined as the number of individuals with a T_b above 30°C; the number of torpid 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; 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 (80 g of protein mixture plus fruits) before the protocol was repeated. This 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, approximately 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 means±1 s.d.; *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 the 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 χ^2 test. For this test we assumed the expected probability that an individual of any of the two groups is torpid to be 50%, and the probability that individuals from both groups are torpid on the same day to be 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 ($T_{b,min}$) and TBD, as well as between $T_{b,min}$ 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 whether group composition affects TBD, $T_{b,min}$, cooling rates and rewarming rates (lme in library nlme; Pinheiro et al., 2014). Because other studies have indicated that food availability and T_a influence torpor patterns, our models included three fixed effects: minimum T_a ($T_{a,min}$), food availability (0%, 50%, 75%, 100%; arcsine transformed) and the number of torpid individuals per group ($n=1-4$; used for TBD and $T_{b,min}$) 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 (AIC; 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 for group 1, 7 for 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 for two females of group 1, and 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 study period (-8.9 ± 1.0 g, $n=3$), whereas torpor-prone individuals gained body mass (19.9 ± 15.7 g, $n=3$) and individuals with intermediate torpor use held their initial body mass (1.1 ± 1.8 g, $n=2$). Mean mass of all eight individuals slightly increased during the experimental period (from 117.6 ± 21.8 to 123.3 ± 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
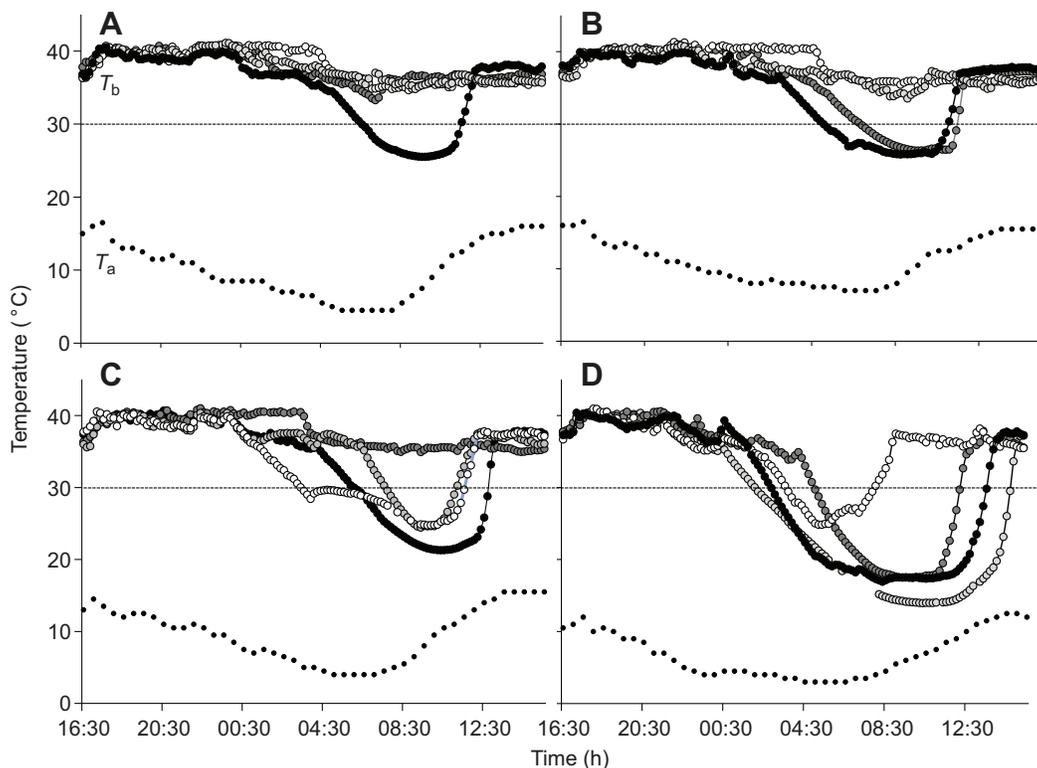

Fig. 1. Examples of huddling groups with (A) one, (B) two, (C) three and (D) four torpid sugar gliders per group. Individual traces of body temperature (T_b; 10 min intervals) for all individuals per group are shown in relation to ambient temperature (T_a). The synchronized rewarming of two torpid individuals is depicted in B–D. The dashed line indicates the torpor threshold of 30°C.

Table 1. The five best-fit models to explain the patterns observed in torpor bout duration (TBD), minimum body temperature ($T_{b,min}$), and rewarming and cooling rates

	Model	AIC	ΔAIC
TBD	**Torpid/group×food+torpid/group×$T_{a,min}$+food×$T_{a,min}$**	**989.4427**	**0**
	Torpid/group×food+food×$T_{a,min}$	996.3637	6.921
	Torpid/group×$T_{a,min}$+food×$T_{a,min}$	997.1667	7.724
	Torpid/group×food+torpid/group×$T_{a,min}$	997.7016	8.2589
	Torpid/group×food+$T_{a,min}$	1002.072	12.6293
$T_{b,min}$	**Torpid/group×food+$T_{a,min}$**	**406.4546**	**0**
	Torpid/group×food	409.3358	2.8812
	Torpid/group×food+torpid/group×$T_{a,min}$	409.5366	3.082
	Torpid/group	411.4430	4.9884
	Torpid/group×food+torpid/group×$T_{a,min}$+food×$T_{a,min}$	412.4502	5.9956
Rewarming rate	**$T_{a,min}$**	**−197.2142**	**0**
	Food	−195.6548	1.5594
	Normothermic/group[a]	−195.4812	1.733
	$T_{a,min}$+food	−189.2970	7.9172
	$T_{a,min}$+normothermic/group[a]	−187.8018	9.4124
Cooling rate	**Torpid/group[a]**	**−477.6354**	**0**
	Torpid/group[a]+$T_{a,min}$	−472.1559	5.4795
	$T_{a,min}$	−470.1356	7.4998
	Torpid/group[a]+food	−464.7737	12.8617
	Torpid/group[a]×$T_{a,min}$	−457.9257	19.7097

We tested *a priori* regression-based linear mixed-effect models including three fixed effects that were likely to affect those parameters: minimum ambient temperature ($T_{a,min}$), food availability (0%, 50%, 75%, 100%; arcsine transformed) and the number of torpid individuals per group (used for TBD and $T_{b,min}$) or the number of animals that had a body temperature above (normothermic/group; rewarming 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 in bold.
[a]The number of animals that had a body temperature above/below 30°C.

only showed torpor when food was withheld. Of the three different levels of food reduction (100%, 50% and 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; χ^2=10.09, d.f.=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 (four times in group 1; three times in group 2) and torpor in all four individuals three times (once in group 1; twice in group 2). 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 in only two of the seven observations.

Influence of group composition on torpor characteristics
Animals entered torpor between 22:00 and 06:40 h, with a peak for torpor entries between 03:00 and 06:00 h. The earliest rewarming from torpor occurred at 04:00 h, the latest at 17:30 h. Most arousals occurred between 12:00 and 14:00 h (see Fig. 1 for examples).
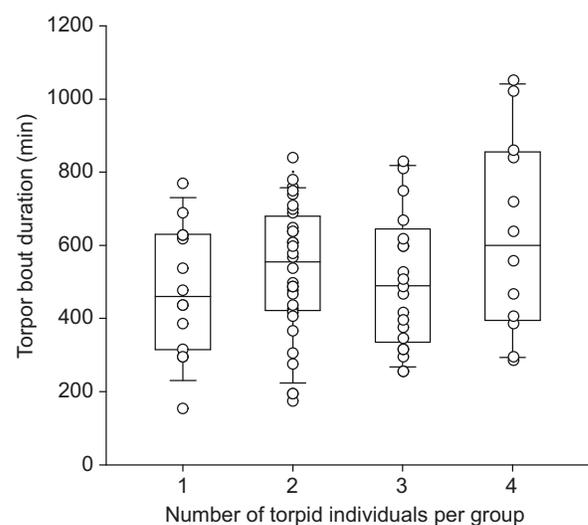
Table 2. Mean (±s.d.) minimum body temperature ($T_{b,min}$) during torpor in relation to the number of torpid individuals per group

Number of torpid individuals	$T_{b,min}$ (°C)	N
1/4	24.9±2.9	14
2/4	23.1±3.4	16
3/4	22.9±3.5	7
4/4	20.3±5.2	3

N refers to the number of observations for the particular group composition.

TBD varied between 160 and 1050 min (mean 532±198 min, N=79) and was related to $T_{b,min}$ (lme; $F_{1,70}$=106.4, P<0.001; TBD= −39.886×$T_{b,min}$+1414.771); $T_{b,min}$ varied between 14.0 and 29.9°C. In addition to $T_{a,min}$ and food availability, TBD and $T_{b,min}$ 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 one group went into torpor, one individual usually aroused from

Fig. 2. Torpor bout duration in relation to the number of torpid individuals per group. The middle line represents the median, whereas the bottom of the box is the 25th percentile and the top is the 75th percentile. The lower whisker represents the 5th percentile and the upper whisker the 95th percentile (N=79, n=8).
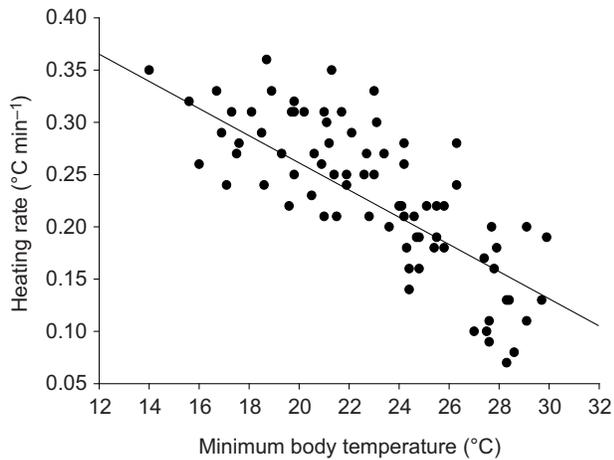
Fig. 3. Relationship between average heating rates for the complete arousal from torpor and the minimum body temperature of the individuals during torpor. Average rewarming rates were negatively correlated with minimum body temperature ($N=79$, $n=8$; lme, accounting for repeated measures; $F_{1,70}=105.3$, $P<0.001$).

torpor before the other group members reached their $T_{b,min}$ (see example in Fig. 1), thus raising the mean T_b.

The maximum individual cooling rate was 0.18°C min^{-1} for a period of 10 min (average for the entire torpor entry: 0.04±0.01°C min^{-1}, $N=79$). Although one would assume that $T_{a,min}$ and food availability both affect cooling rates, only the number of torpid animals ($T_b<30$°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^{-1}). The maximum individual rewarming rate was 0.44°C min^{-1} for a period of 10 min (average for the entire arousal: 0.28±0.07°C min^{-1}, $N=79$). Average rewarming rates were negatively correlated with $T_{b,min}$ (lme; $F_{1,70}=105.3$, $P<0.001$; Fig. 3), and were influenced by $T_{a,min}$ (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; ΔAIC<2; Table 1).
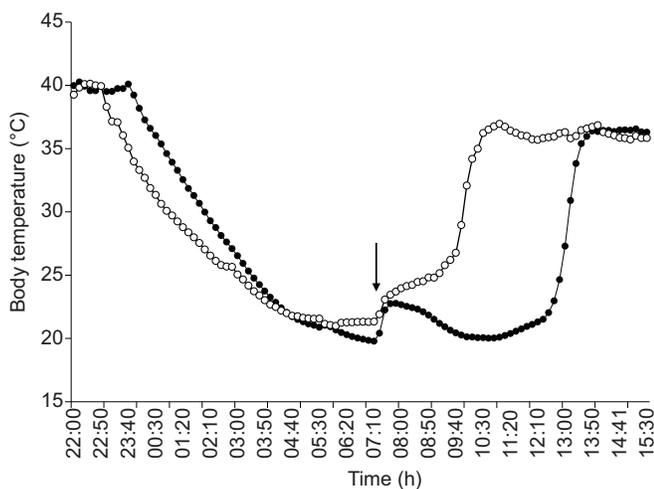

Fig. 4. Example of an arousing animal disturbing a nest mate. Individual trace of body temperature (10 min intervals) for two individuals of one group. The arrow marks the point at which animal 1 (filled circles) started rewarming and disturbed the torpor bout of animal 2 (open circles).

Influence of group composition on T_{box}

Inside the occupied nest box, minimum T_{box} was 6.6±2.4°C ($N=20$) and never fell below 2.0°C, although nightly $T_{a,min}$ during the study period fell to −5.0°C (range: −5.0 to 9.0°C; daily maxima: 6.5 to 23.0°C). The daily difference between the lowest T_{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_{box} was correlated with the number of torpid animals in the group ($N=20$; $T_{box}-T_a$ at the time of the overall $T_{b,min}$ of the group; $r^2=0.339$, d.f.=18, $P=0.007$; $T_{box}-T_a= -0.9015\times$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 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±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 the two arousals: 38±15 min; Fig. 1), but synchronized arousals were never observed for more than two individuals.

Whether an arousal led to a second individual arousing closely afterwards was dependent on the time of day. Arousals between 04:00 and 08:00 h ($N=10$) never resulted in an 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 (e.g. Fig. 4). However, the likelihood of a second arousal increased between 09:00 and 13:00 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 ($T_{b,min}\geq24$°C) and aroused in the early morning (between 04:20 and 09:40 h); the other two or three animals displaying deep torpor ($T_{b,min}<20$°C) started their arousal usually between 10:40 and 14:00 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 that sugar gliders huddle regularly during torpor, and that 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 because 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, thus lowering 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 the T_b of other animals. As many species arouse from torpor around midday, synchronized arousals might 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 $T_{b,min}$ 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.

Nevertheless, torpid individuals might benefit from their normothermic nest mates on cold days, as normothermic gliders might keep T_{box} above the threshold for thermoregulation during torpor. During entry into torpor, the hypothalamic set-point for T_b is downregulated and metabolic heat production is only used to maintain T_b at or above this $T_{b,min}$ (Florant and Heller, 1977). Hibernating species have a very low set-point for $T_{b,min}$ (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 $T_{b,min}$ 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 nest temperature is lower than $T_{b,min}$. The presence of normothermic individuals should therefore lead to decreased energy expenditure for sugar gliders because gliders increase MR during torpor at T_a values below 16°C (Fleming, 1980). The correlation between T_{box} and the number of torpid individuals per nest box clearly shows that T_{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 unknown. Normothermic thermoregulation during harsh conditions is obviously energetically costly. This is emphasized by the fact that torpor-reluctant individuals lost body mass over the study period, whereas torpor-prone individuals gained body mass. 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, because all gliders had access to the same food, this explanation for reluctant torpor use of some individuals seems rather unlikely for our study groups. As body mass 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) and 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 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 to nest solitarily. Another reason why normothermic individuals are found nesting together with torpid individuals could be social contact. 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).

Conclusions

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 entered 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.

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