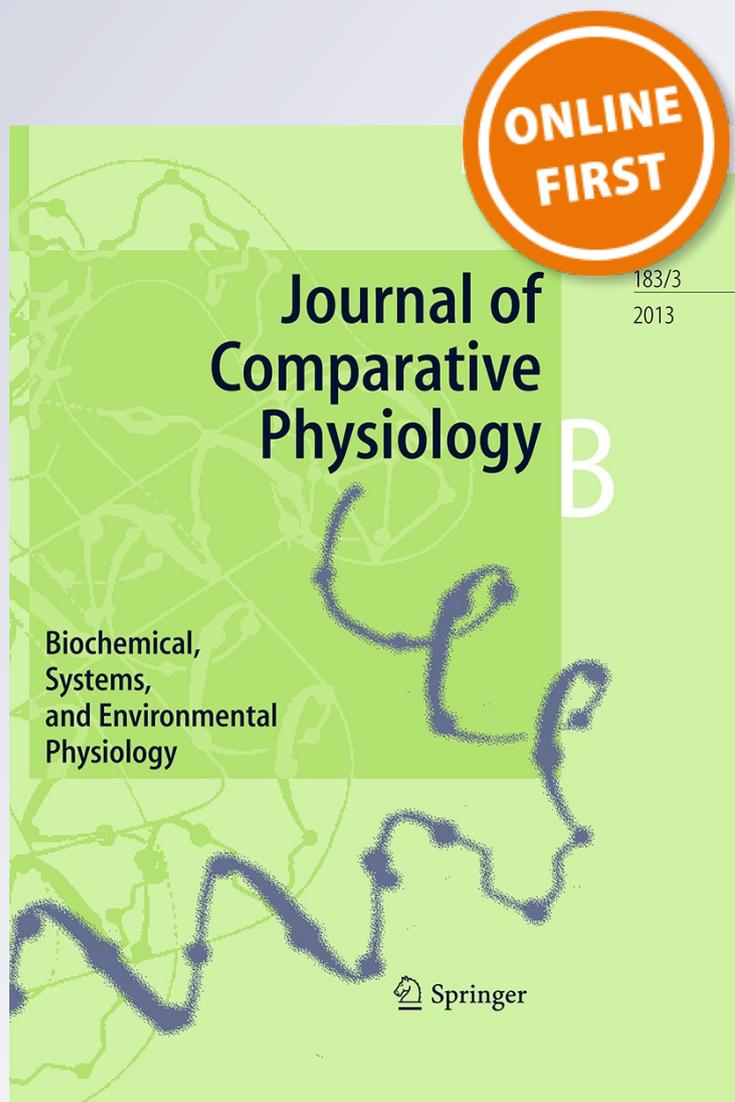# *Staying cold through dinner: cold-climate bats rewarm with conspecifics but not sunset during hibernation*

## Zenon J. Czenze, Andrew D. Park & Craig K. R. Willis

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# Staying cold through dinner: cold-climate bats rewarm with conspecifics but not sunset during hibernation

**Zenon J. Czenze · Andrew D. Park · Craig K. R. Willis**

**Abstract** For temperate endotherms (i.e., mammals and birds) energy costs are highest during winter but food availability is lowest and many mammals depend on hibernation as a result. Hibernation is made up of energy-saving torpor bouts [periods of controlled reduction in body temperature ($T_b$)], which are interrupted by brief periodic arousals to normothermic $T_b$. What triggers these arousals in free-ranging hibernators is not well understood. Some temperate bats with intermittent access to flying insects during winter synchronize arousals with sunset, which suggests that, in some species, feeding opportunities influence arousal timing. We tested whether hibernating bats from a cold climate without access to food during winter also maintain a circadian rhythm for arousals or whether cues from conspecifics in the same cluster are more important. We used temperature telemetry to monitor skin temperature ($T_{sk}$) of free-ranging little brown bats (*Myotis lucifugus*) hibernating in central Manitoba, Canada, where temperatures from 22 October to 22 March were too cold for flying insects. We found no evidence bats synchronized arousals with photoperiod but they did arouse synchronously with other bats in the same cluster. Thus, in the northern part of their range where flying insects are almost never available during winter, little brown bats exhibit no circadian pattern to arousals. Warming synchronously with others could reduce the energetic costs of arousal for individuals or could reflect disturbance of torpid bats by cluster-mates.

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## Introduction

Many temperate animals have evolved physiological and behavioural mechanisms to survive the challenging winter months. Hibernating mammals, for example, spend the majority of their time during winter in torpor, a state of controlled reduction in body temperature ($T_b$) and metabolic rate (Geiser 2004). Long-term torpor provides enormous energetic benefits (Geiser 2004), and may provide additional benefits for some species by reducing exposure to predators and extending lifespan (Wilkinson and South 2002; Stawski and Geiser 2009). However, it also appears to result in physiological and ecological costs which limit the duration of torpor bouts. For example, the inability to drink while torpid results in dehydration stress (Thomas and Cloutier 1992; Thomas and Geiser 1997) and immune responses of torpid hibernators may be suppressed increasing susceptibility to pathogens (Luis and Hudson 2006; Moore et al. 2011; Prendergast et al. 2002). Presumably as a result of these costs of torpor, all hibernators exhibit periodic arousals throughout hibernation, during which they return to a normothermic $T_b$ (e.g., Grahn et al. 1994; Jonasson and Willis 2012; Ruby et al. 2002).

Although periodic arousals are brief they account for up to 90 % of winter energy expenditure due to the high metabolic cost of thermoregulation at low ambient temperatures ($T_a$) (Geiser 2004; Thomas et al. 1990; Wang 1978). Hibernators like temperate zone bats, which cannot store a food cache, must survive exclusively on stored fat which places a limit to how many arousals they can perform (Thomas et al. 1990). As a result, they must balance

the energetic, physiological and ecological costs and benefits of torpor and arousal. Presumably, the frequency of arousals must be timed carefully to offset the risk of exhausting fat stores prematurely (Humphries et al. 2003; Jonasson and Willis 2011, 2012; Racey and Swift 1981).

The mechanism that initiates periodic arousals is still unknown but one of several hypotheses is that circadian clocks may play a role (e.g., Malan 2010). The $T_b$ of hibernating golden-mantled ground squirrels (*Callospermophilus lateralis*) fluctuates with circadian rhythms during deep torpor and individuals of this species are more likely to enter torpor at night and arouse during the day when exposed to a light/dark cycle (Grahn et al. 1994; Ruby et al. 2002). However, Ruby et al. (2002) found that the timing of entry into and arousal from torpor occurred at random times for animals housed under 24 h lights-on photoperiod. Free-ranging, cave-dwelling greater horseshoe bats (*Rhinolophus ferrumequinum*) and Natterer's bats (*Myotis nattereri*) from the United Kingdom (UK) receive little or no natural photoperiod cues in caves during winter. In spite of the lack of photoperiod, however, these species appear to maintain a circadian pattern to arousals (Hope and Jones 2012; Park et al. 2000). Hibernating bats of these species "warm up for dinner", synchronizing arousals with sunset, likely to take advantage of flying insects during occasional mild winter nights (Hope and Jones 2012; Park et al. 2000).

Greater horseshoe and Natterer's bats hibernate in relatively mild climates where temperatures during winter occasionally exceed 10 °C. This is a threshold above which aerial insect abundance can increase dramatically (Jones et al. 1995), providing opportunities to forage. Even though foraging opportunities will be less common, bats from colder environments might also synchronize arousals with sunset. To our knowledge, the maintenance costs of neural mechanisms underlying a circadian clock are unknown. However, it seems likely these costs would be small relative to the benefits of even unlikely potential foraging opportunities, especially in mid- to late-winter when fat reserves are dwindling. Thus, bats might still synchronize arousals with sunset, as selection against arousal at dusk might be relatively weak.

Another trigger of arousal, specific to communal hibernators like bats, could be cues from conspecifics. Such cues could be beneficial if groups of individuals can reduce energetic costs of arousal via social thermoregulation (Ruf and Arnold 2000). Alpine marmots (*Marmota marmota*), for example, hibernate in groups of related individuals and synchronize arousals with burrow mates to save energy. These benefits presumably increase over-winter survival, particularly for young-of-the-year (YOY), and may enhance inclusive fitness via kin selection (Ruf and Arnold 2000). On the other hand, if arousals of different

individuals are not well synchronized, disturbance by normothermic cluster-mates could be detrimental to energy balance for some animals if it induces arousals more frequently than required to offset costs of torpor. For example, in bats, males may attempt to mate with torpid females during hibernation and these mating attempts may disturb females.

In contrast to most mammalian hibernators which spend the winter in well-insulated burrows, bats hibernate in caves and mines often in large, open-air chambers. These environments may reduce the potential for bats to use metabolic heat to influence their immediate microclimate and could explain the energetically conservative hibernation patterns of little brown bats (*Myotis lucifugus*), characterized by long torpor bouts, brief arousals and the expression of shallow heterothermy in the midst of arousals (Jonasson and Willis 2012). Thus, benefits of social thermoregulation for hibernating bats may be especially important. An individual-based population model, incorporating presumed thermoregulatory benefits of clustering for little brown bats predicted that 96 % of clustering bats should survive a typical winter compared to 73 % for solitary bats (Boyles and Brack 2009). This suggests that bats from the same cluster should exploit the energetic benefits of social thermoregulation and arouse synchronously with other individuals in the cluster.

We used temperature radio-telemetry to test two hypotheses about periodic arousals in hibernating bats. First, we tested whether arousal and photoperiod are synchronized in bats from a cold climate. We predicted that arousals would remain synchronized with sunset based on the hypothesis that maintaining neural mechanisms underlying a circadian clock would be inexpensive relative to potential benefits of obtaining even an unlikely meal during winter. Second, we tested whether individual bats would take advantage of social thermoregulation to reduce arousal costs. We predicted that individuals in the same cluster would arouse from torpor at the same time and that a majority of arousals would overlap in time. Alternatively, if bats tend to arouse from torpor on a similar timetable (e.g., on roughly the same days) but not at precisely the same times, this would suggest that disturbance by conspecifics could be influencing torpor-arousal cycles. Such a pattern might be observed if, for example, bats gradually disturb each other as they rewarm, resulting in a cascade of arousal within a cluster.

## Methods

This study was conducted in Firecamp cave, near the town of Grand Rapids, in central Manitoba Canada (53°29′25″N 99°20′50″W). This cave is accessed by a sinkhole entrance

approximately 50 cm in diameter and consists of a bell-shaped chamber about 7 m deep. Between 30 and 60 bats over-winter in Firecamp cave from mid-September until mid-May. Bats in this cave all hibernate in one tight cluster within a crack 1 m long by 20 cm deep, on the ceiling of the main chamber.

All procedures were approved by the University of Winnipeg Animal Care Committee and by Manitoba Conservation Wildlife Scientific Permit WB0612. We entered the cave and handled bats during hibernation but to minimize disturbance we only entered once and limited the duration of our visit to less than 90 min. Twenty-four torpid bats were captured by hand on 20 Feb 2012, sexed, weighed to the nearest 0.01 g (Durascale-100, My Weigh, ON, Canada) and their forearm length was measured to the nearest 0.05 mm. We identified YOY based on un-fused 3rd digit metacarpal-phalangeal joints, and tapered rather than "knobby" joints following Davis and Hitchcock (1965). In many parts of their range YOY little brown bats cannot be distinguished from adults by the time hibernation begins but in our northern study area we can readily identify at least some juveniles during swarming and even into hibernation (Jonasson and Willis 2011, 2012).

For small bats, skin temperature ($T_{sk}$) provides a good approximation of $T_b$ during torpor (Audet and Thomas 1996; Barclay et al. 1996; Willis and Brigham 2003). We recorded $T_{sk}$ by attaching temperature-sensitive radio-transmitters (0.64–0.80 g, BD-2NT; Holohil Systems Ltd, Carp, Ontario) using a non-toxic, latex-based adhesive (Osto-Bond, Montreal Ostomy, Vaudreuil, QC, Canada) after clipping a small (<1 cm$^2$) patch of fur between the shoulders. Transmitters represented between 6.9 and 8.6 % of body mass, greater than the 5 % guideline suggested by Aldridge and Brigham (1988) but similar to the size which Jonasson and Willis (2012) demonstrated had no negative impact on body condition in hibernating little brown bats. We calibrated transmitters prior to use in a water bath at 5 °C increments from just above 0–45 °C against a thermometer traceable to the National Institutes of Standards and Technology. A data logging receiver (Lotek SRX600; Lotek Engineering Inc., Newmarket, Ontario, Canada) powered by a solar panel was deployed outside the cave and connected to an omnidirectional whip antenna positioned in the cave, within 60 cm of the cluster of bats. The receiver recorded $T_{sk}$ of each individual at 6-min intervals. Each bat was recorded for 15 s and a full cycle of recordings took 360 s. We recorded $T_a$ inside the cave using iButtons (DS1922L iButtons, Maxim Integrated Products, Dallas, TX, USA) coated in paraffin wax to dampen ultrasonic noise (Willis et al. 2009) and positioned at the base of the crack within 60 cm of where the bats roosted while hibernating.

We defined the phases of arousal following Jonasson and Willis (2012). Due to the large difference between normothermic $T_{sk}$ and $T_a$ in the cave, arousals were always readily obvious in the $T_{sk}$ trace. Torpor bouts were defined as periods of reduced stable $T_{sk}$ between the obvious warming and cooling phases associated with each arousal. Skin temperature measured using Holohil transmitters occasionally appears to increase slightly and gradually after initial entry into a torpor bout (e.g., Jonasson and Willis 2012). This appears to reflect an artifact of long periods at low temperature, which we could readily identify in our $T_{sk}$ traces and which did not affect our analysis.

Warming was defined by an abrupt increase in torpid $T_{sk}$ that resulted in an elevation of $T_{sk}$ until it stabilized at a normothermic steady-state. Cold $T_a$ in the cave appeared to increase ambient cooling of external transmitters, leading to slightly reduced $T_{sk}$ values during arousal (Willis and Brigham 2003). The normothermic period was defined as the time between the end of this rapid warming period and the initiation of cooling, which was in turn defined as an abrupt decline in $T_{sk}$ preceding steady-state torpor. We excluded data from the first 24 h after releasing the bats to avoid the influence of this disturbance on our results.

We recorded the date and time that arousals occurred from the $T_{sk}$ trace and converted time of arousal from minutes before or after sunset into radians. We then used Rayleigh's test for circular distributions to determine if arousal times were significantly different from a random distribution. All analyses were conducted in R version 2.10.1 (R Development Core Team 2009) and values are reported as the mean ± SD. We assessed significance at the $P < 0.05$ level.

## Results

We recorded 459 bat-days of $T_{sk}$ data from 15 individuals over 73 days following transmitter attachment and release. Average body mass at capture was 9.4 ± 1.3 g and BCI was 0.26 ± 0.04 g/mm (Table 1). All bats exhibited long bouts of torpor averaging 15.3 ± 8.9 days with the longest bout lasting 35 days, interspersed with brief periodic arousals averaging 3.3 ± 1.1 h (Fig. 1). We recorded a total of 42 discrete torpor bouts and 29 arousals before the final transmitter battery failed on May 5, 2012.

We found no evidence of a relationship between arousal times and sunset. The circular frequency distribution of differences between arousal time and sunset time, expressed in radians, was no different from a random distribution ($Z = 0.65$, $P = 0.54$, mean vector = 0.15, $N = 15$ bats, $n = 29$ arousals, Fig. 2a, b). This analysis was technically pseudoreplicated as we recorded multiple arousals from some, but not all individuals. However, we still found no

**Table 1** Sex, age class, morphometric measurements number of arousals recorded for hibernating *M. lucifugus* in Firecamp cave in Central Manitoba

| ID | Demographic | Mass (g) | Forearm (mm) | BCI (g/mm) | No. of arousals | Duration of recording (days) |
|----|-------------|----------|--------------|------------|-----------------|------------------------------|
| 1 | Female adult | 10.3 | 39.84 | 0.26 | 2 | 33 |
| 2 | Female adult | 11.0 | 37.93 | 0.29 | 1 | 25 |
| 3 | Female adult | 12.4 | 38.37 | 0.32 | 2 | 31 |
| 4 | Female adult | 11.1 | 38.26 | 0.29 | 1 | 22 |
| 5 | Female YOY | 11.5 | 38.51 | 0.30 | 6 | 52 |
| 6 | Female YOY | 10.0 | 36.57 | 0.27 | 1 | 26 |
| 7 | Female YOY | 8.7 | 36.23 | 0.24 | 1 | 23 |
| 8 | Female YOY | 11.8 | 37.30 | 0.32 | 2 | 26 |
| 9 | Male adult | 9.3 | 38.46 | 0.24 | 4 | 73 |
| 10 | Male adult | 9.5 | 37.36 | 0.25 | 2 | 31 |
| 11 | Male adult | 8.8 | 38.70 | 0.23 | 1 | 24 |
| 12 | Male adult | 8.3 | 38.01 | 0.22 | 1 | 22 |
| 13 | Male YOY | 8.9 | 37.70 | 0.24 | 2 | 25 |
| 14 | Male YOY | 8.2 | 37.69 | 0.22 | 1 | 17 |
| 15 | Male YOY | 8.2 | 38.98 | 0.21 | 2 | 29 |

Note that we did not include each bat's first arousal associated with capture in our analysis

*YOY* young-of-the-year

**Fig. 1** Skin temperature (*upper trace*) of three representative hibernating *M. lucifugus.* **a** Female adult, **b** Male young of the year, **c** female adult; *lower trace* shows the average cave temperature as measured by data loggers within 60 cm of the roosting bats
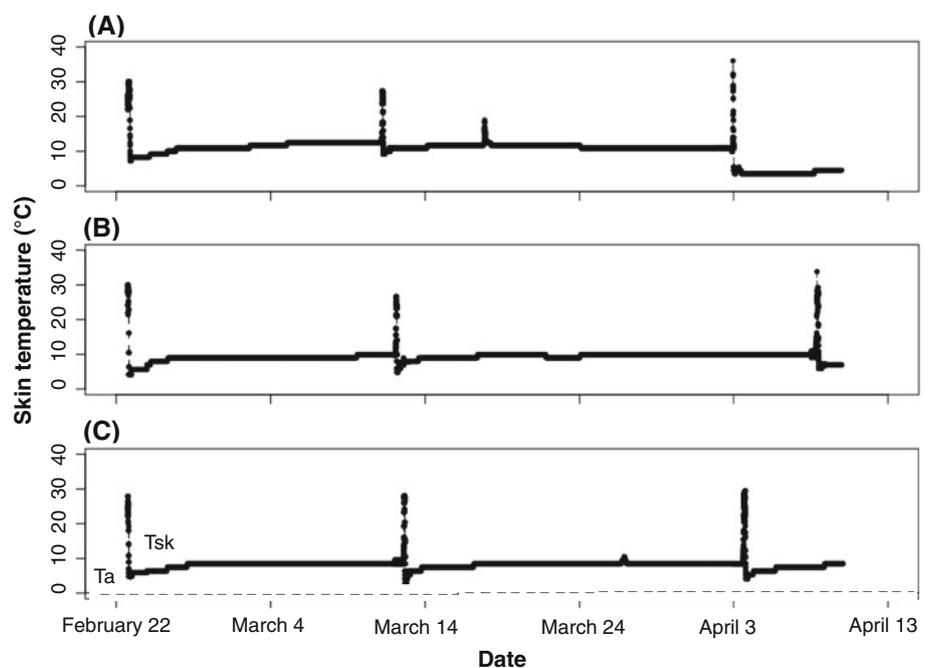


relationship between sunset and arousal time, when we limited the analysis to each individual's first arousal after capture ($Z = 1.2$, $P = 0.32$, mean vector = 0.28) or calculated the average arousal time for each individual ($Z = 0.41$, $P = 0.67$, mean vector = 0.16).

Although bats did not synchronize arousals with sunset, they did appear to synchronize arousals with each other. Twenty-one % (6/29) of all the arousals we observed occurred on only a single day (Day 17 of the study, Fig. 3) and 38 % (11/29) occurred on only 2 days. Moreover, only 38 % (11/29) of arousals occurred in isolation, on days when no other bats aroused. The distributions of days on which each individual's first arousal occurred differed from a random distribution ($Z = 3.32$, $P = 0.036$, mean vector = 0.47, $N = 15$, $n = 15$) indicating that bats were more likely than predicted by chance to arouse on the same day.

In keeping with our prediction that individuals in the same cluster should arouse from torpor at the same time, many (but not all) bats aroused on the same days although not all bats aroused at precisely the same times. For example, the six arousals we detected on Day 17 each lasted $2.9 \pm 0.9$ h and were spread out over a 14.9-h period so that some bats had already re-entered torpor before
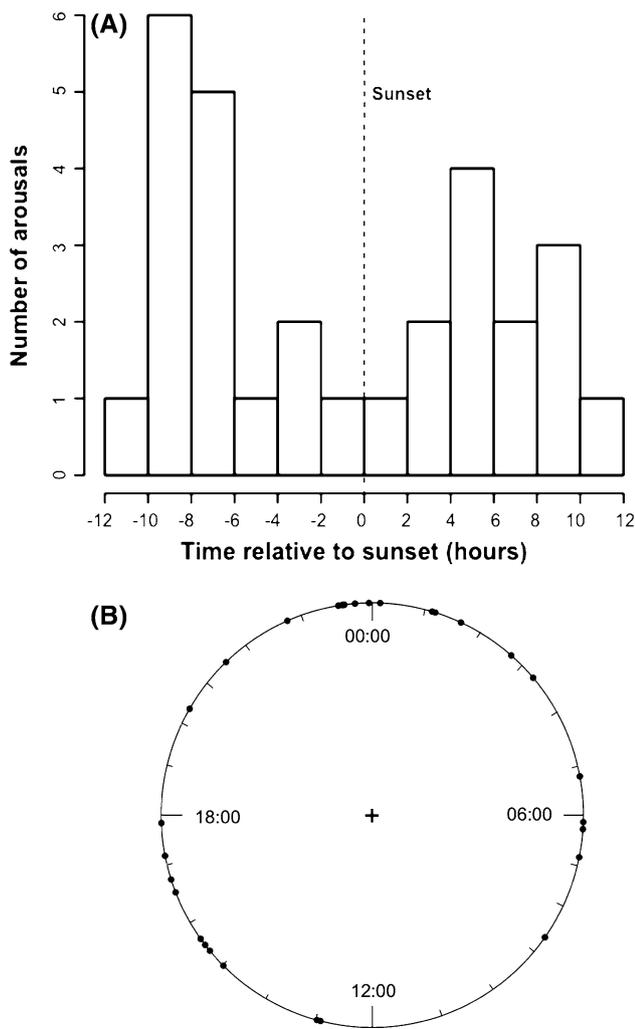
**Fig. 2 a** Histogram showing frequency of arousals from torpor versus time relative to sunset for 15 *M. lucifugus.* **b** Clock face representing the circular distribution of arousal times by individual *M. lucifugus* during hibernation. Average sunset time was 18:42 h ± 0.4 ($Z = 0.65$, $P = 0.54$, mean vector = 0.15, $N = 15$ bats, $n = 29$ arousals)

other bats rewarmed. Of all the arousals that we observed occurring on the same days as at least one other arousal, 78 % (14/18) were completely or partially overlapping with the arousals of at least one other bat (Fig. 3). In other words, bats were normothermic at the same times as other individuals in their cluster.

## Discussion

In contrast to previous studies of bats from warmer environments where winter foraging is a possibility (Park et al. 2000; Hope and Jones 2012) we found no evidence of a circadian rhythm associated with arousal. Similar to a study using bat detectors in a hibernaculum (Thomas 1993), we

found that bats did not synchronize arousals with sunset. The evidence showing that bats do arouse with sunset was obtained from the UK where $T_a$ often exceeds 10 °C during winter and flying insects are likely to be available, at least occasionally during hibernation (Park et al. 2000). Thus, the maintenance of a circadian rhythm, and the ability to synchronize arousal with a prospective foraging opportunity could by highly beneficial, allowing bats to supplement their fat reserves and take advantage of these warm nights. In central Manitoba, $T_a$ never exceeds 10 °C for 5 months of the year, and typically never exceeds freezing for at least 2–3 months (National Climate Data and Information Archive 2012). Therefore, flying insects are consistently unavailable for a much longer period during winter. Despite this limitation on foraging opportunities, we predicted that bats in our study would exhibit arousals linked with sunset because, presumably the cost of maintaining a circadian clock is relatively low and, especially as spring approaches, the potential for foraging opportunities does occasionally arise. For example, during late-winter (i.e., March) 2012, there were multiple nights during which temperatures were warm enough to support flying insects and foraging by bats (Czenze and Willis, unpublished data). However, our results suggest that, at least during mid- to late-winter in our study area, the costs of maintaining a daily rhythm appear to outweigh any possible benefits of winter foraging.

Although we found no daily pattern to arousals, we did find evidence that bats arouse synchronously with each other. We predicted that benefits of social thermoregulation would favour synchronous arousals, especially in this site as all bats in Firecamp cave hibernate exclusively in one cluster within a crack in the ceiling. Thus, in contrast to many little brown bat hibernacula, individuals in this cave have the potential to warm their local environment and presumably could also gain significant energetic benefits by arousing synchronously (Boyles et al. 2008; Boyles and Brack 2009).

Our results were consistent with the social thermoregulation hypothesis given that 78 % of all the arousals we observed overlapped with the arousals of at least one other individual and often more than one. Therefore, although bats did not appear to maximize benefits of social thermoregulation by all arousing at the same times, they almost certainly gained some energetic benefit. Mating attempts by males which occur during hibernation (Thomas et al. 1979) may also have influenced this synchrony. Interestingly, for the three sets of arousals we observed, each appeared to be initiated by a male bat, followed by multiple females. These arousals were not, however, completely synchronized. Given the tight energy budgets of hibernating bats, an interesting question for future studies is, why has selection not favoured mechanisms that allow all bats

**Fig. 3** Skin temperature (*upper trace*) of six *M. lucifugus* showing the timing of arousals on Day 17 of the study. **a** Female young of the year, **b** female young of the year, **c** male young of the year, **d** male adult, **e** female adult, **f** male adult. The *lower flat trace* shows the average cave temperature as measured by temperature data loggers within 60 cm of the roosting bats. *Dashed lines* indicate sunrise and sunset
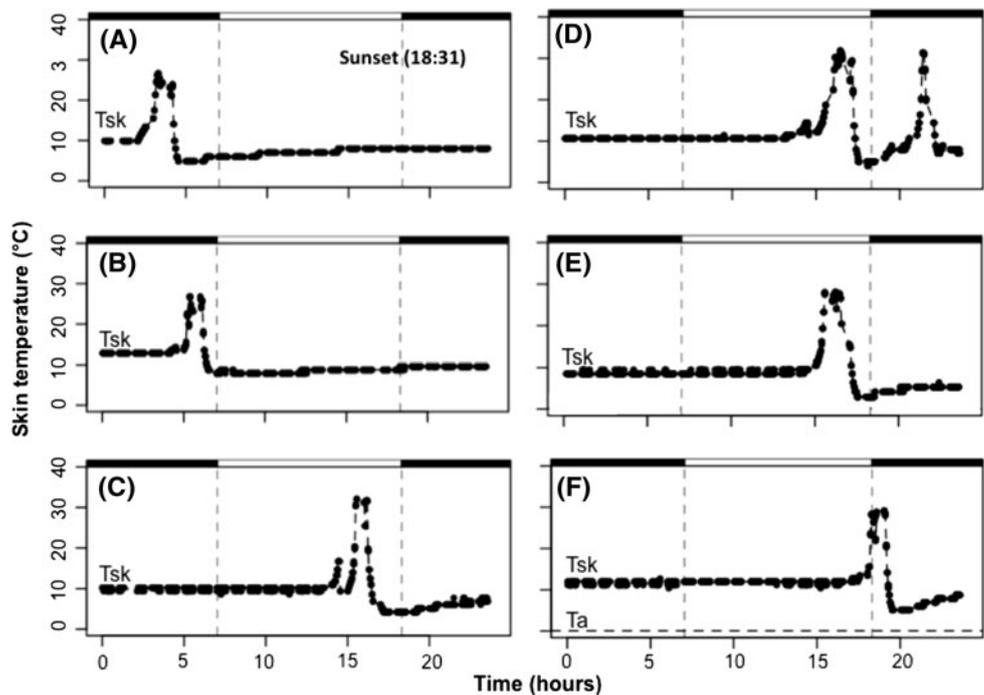


in a cluster to precisely synchronize arousals to minimize rewarming costs?

Approximately, synchronous arousals by bats in the same microclimate within a hibernaculum might be explained by multiple individuals accumulating physiological imbalance at about the same rate. They might therefore arouse at about the same time to restore homeostasis. For example, assuming evaporative water loss (EWL) influences arousal timing, bats in the same cluster in our study may have experienced similar rates of EWL during torpor (Thomas and Cloutier 1992) and, therefore, may have almost simultaneously reached a point at which arousal was necessary to re-hydrate. All radiotagged bats aroused during handling on 20 February 2012 when we attached transmitters, so it is also possible that this disturbance-induced arousal resets the mechanism underlying arousal (i.e., allowed all individuals to drink or excrete metabolic wastes) increasing the chance that their subsequent arousals would be synchronized. However, given large between-individual variation in most physiological processes, including those likely to influence arousals (e.g., metabolic rate, EWL) it seems unlikely that this is the exclusive explanation for the similar arousal times of multiple individuals in our study.

Another possible explanation for the timing of arousals we observed is that warm bats disturb torpid conspecifics. Even non-tactile disturbance by human visitors to hibernacula can stimulate arousals in bats (Thomas et al. 1990) and, it is possible that movement by other bats within a hibernaculum or within a cluster could have similar effects.

This seems unlikely given strong selection pressure for bats to remain torpid for long enough during winter to conserve energy. Such a mechanism might be important if different individuals exhibit consistent individual differences in sensitivity to disturbance. For example, mated adult females may be especially resistant to disturbance because selection appears to favour mechanisms allowing females to save fat for spring reproduction (Jonasson and Willis 2011). At the other extreme, inexperienced juvenile bats may be more prone to disturbance during torpor and, to avoid exhausting fat reserves too quickly, may need to learn how to differentiate disturbances which warrant arousing (e.g., a potential predator) from those that do not (e.g., conspecifics).

If disturbance by bats can cause arousals, this could have consequences for bats hibernating in sites affected by white-nose syndrome (WNS). WNS is caused by cutaneous infection with the fungus *Geomyces destructans* (Blehert et al. 2009; Lorch et al. 2011) and infection causes bats to arouse from torpor too frequently during hibernation and prematurely exhaust energy reserves (Boyles and Willis 2010; Reeder et al. 2012; Warnecke et al. 2012). If active bats can induce arousals in other torpid individuals, the increased arousal frequency caused by infection with *G. destructans* could result in a positive feedback of arousals, accelerating the use of fat reserves even further. More work is needed to understand the physiological signals and environmental cues that trigger arousal in hibernators, especially in bats which are highly prone to disturbance and, in North America, now facing the threat of WNS.

This is the first study to examine the timing of arousal in free-ranging little brown bats, particularly in the extreme northern part of their range and provides, to our knowledge, the first evidence that bats in northern climates synchronize their arousals with cluster-mates rather than photoperiod. Future research on northern bats should aim to examine arousal patterns of bats in caves with multiple clusters, as well as the arousal patterns of related vs. unrelated bats from the same hibernacula, to improve understanding of mechanisms underlying this critical aspect of hibernation.

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