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ORIGINAL PAPER

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Defining torpor in free-ranging bats: experimental evaluation of external temperature-sensitive radiotransmitters and the concept of active temperature

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Abstract A variety of definitions involving body temperature (T_b), metabolic rate and behavior have been used to define torpor in mammals and birds. This problem is confounded in some studies of free-ranging animals that employ only skin temperature (T_{sk}), a measure that approximates but may not precisely reflect T_b. We assess the accuracy of T_{sk} in the context of a recent definition for torpor called active temperature. We compared the active temperatures of individual big brown bats (*Eptesicus fuscus*), which aggregate in cavities, with solitary, foliage-roosting hoary bats (*Lasiurus cinereus*). In captive big brown bats, we compared T_{sk} and core T_b at a range of ambient temperatures for clustered and solitary roosting animals, compared T_{sk} and T_b during arousal from torpor, and quantified the effect of flight on warming from torpor. Hoary bats had significantly lower active temperatures than big brown bats despite having the same normothermic T_{sk}. T_{sk} was significantly lower than T_b during normothermia but often greater than T_b during torpor. Flight increased the rate of warming from torpor. This effect was more pronounced for T_{sk} than T_b. This suggests that bats could rely on heat generated by flight muscles to complete the final stages of arousal. Using active temperature to define torpor may underestimate torpor due to ambient cooling of external transmitters or animals leaving roosts while still torpid. Conversely, active temperature may also overestimate shallow torpor use if it is recorded during active arousal when shivering and non-shivering thermogenesis warm external transmitters. Our findings illuminate the need for laboratory studies that quantify the relationship between metabolic rate and T_{sk} over a range of ambient temperatures.

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Abbreviations *BAT* brown adipose tissue · *MR* metabolic rate · T_a ambient temperature · T_{act} active temperature · T_b body temperature · T_{sk} skin temperature

Introduction

Many mammals and some birds lower their body temperature (T_b) setpoint and metabolic rate (MR) to offset thermoregulatory costs during periods of cold ambient temperature (T_a) and or food shortage (Wang and Wolowyk 1988; Wang 1989). This heterothermy or torpor can save animals up to 99% of their daily energy requirements and, thus, is of tremendous importance for short- and long-term energy budgets (Wang 1989). Heterothermy is traditionally divided into hibernation (multi-day bouts) and daily torpor (bouts restricted to a single circadian cycle) (Geiser and Ruf 1995). In both situations, laboratory studies have revealed much about torpor patterns and associated energy savings by direct measurement of oxygen consumption or MR and T_b based on rectal temperature or using surgically implanted temperature dataloggers or temperature-sensitive radiotransmitters (e.g., Geiser et al. 1996; Geiser and Brigham 2000; Ortmann et al. 1996). However, torpor patterns may differ markedly between free-ranging and captive (Geiser et al. 2000) or captive-bred individuals (Geiser and Ferguson 2001) and metabolic rates are logistically difficult to measure in the field (although see Schmid 1996). To address questions regarding the physiological ecology of torpor, including its proximate energetic benefits and ultimate selective implications, field studies that quantify energy expenditure in free-ranging heterotherms are required. For example, how much time do animals spend torpid under different natural conditions? What is the level of energy saving associated with an individual's use of torpor in

the wild? How do inter- and intra-specific differences in biology and life history influence torpor use? These questions require an accurate measure of T_b and, more importantly, inference about MR in free-ranging animals.

For relatively large animals, dataloggers or radiotransmitters can be surgically implanted to measure T_b in the field (e.g., Barnes 1989). Body size and reception range limitations of implanted transmitters mean that studies of small heterotherms typically rely on a measure of skin temperature (T_{sk}). In free-ranging bats and birds T_{sk} is measured using external temperature-sensitive radiotransmitters affixed dorsally between the scapulae (e.g., Brigham 1992; Hamilton and Barclay 1994; Hickey and Fenton 1996; Brigham et al. 2000; Chruszcz and Barclay 2002). Few studies have rigorously evaluated T_{sk} as a measure of T_b. Audet and Thomas (1996) found that T_{sk} and T_b (measured rectally) were similar, but that T_a influenced the relationship between T_b and T_{sk} with differences as high as 6 °C even at relatively high T_a (i.e., >21 °C). Likewise, Barclay et al. (1996) demonstrated a correlation between T_{sk} and T_b but also found significant differences between T_b and T_{sk} particularly at low T_a, presumably due to ambient cooling of external transmitters. Brigham et al. (2000) reported a strong correlation between T_b and T_{sk} in Australian Owlet Nightjars (*Aegotheles cristatus*) but noted instances where T_b and T_{sk} differed by as much as 6 °C (see Fig. 1 in Brigham et al. 2000). In an analysis based on over 11,000 measurements (from one individual), T_b explained only 85% of the variation in T_{sk}.

To date, defining a reliable boundary between torpor and normothermy (i.e., periods when an endotherm's core temperature is within ±1 SD of the range associated with the species' post-absorptive, resting thermoneutral zone; IUPS Thermal Commission 2001) has proven challenging in both the laboratory and field (Barclay et al. 2001). Traditionally an arbitrary temperature or behavioral boundary is used to delineate when animals are "in" and "out" of torpor. The accuracy of such a boundary is important because initial reductions in T_b (e.g., from 35 °C to 30 °C) save animals more energy than reductions of the same increment at lower T_b (e.g., from 25 °C to 20 °C; Studier 1981). Shallow torpor is likely of greatest energetic and ecological significance but is easy to overlook. In the laboratory, MR can be measured directly and the point at which metabolism declines can be identified. However, even in laboratory studies many different definitions of torpor have been used. Some studies employ specific T_bs (e.g., 30 °C), while others rely on behavior to discriminate between torpor and normothermia (Barclay et al. 2001).

In a review of recent studies of topor in mammals and birds, Barclay et al. (2001) propose "active temperature" (T_{act}) as a standard means of defining torpor. This method generates an individual-specific definition of torpor based on T_b or T_{sk} recorded in the field. T_b or T_{sk} is recorded each day at a time when individuals are assumed to be active (e.g., within 10 min of dusk emergence). To ensure a conservative estimate of torpor use, the lowest T_{sk} at dusk for all the days a bat carries its transmitter is termed T_{act}. This temperature is then considered the threshold below which an individual is assumed to be torpid. This method helps to control for variation resulting from differences in contact between a transmitter's temperature sensor and an animal's skin, slight differences in transmitter calibration, and individual and population variation in the relationship between T_b and T_{sk} (Barclay et al. 2001).

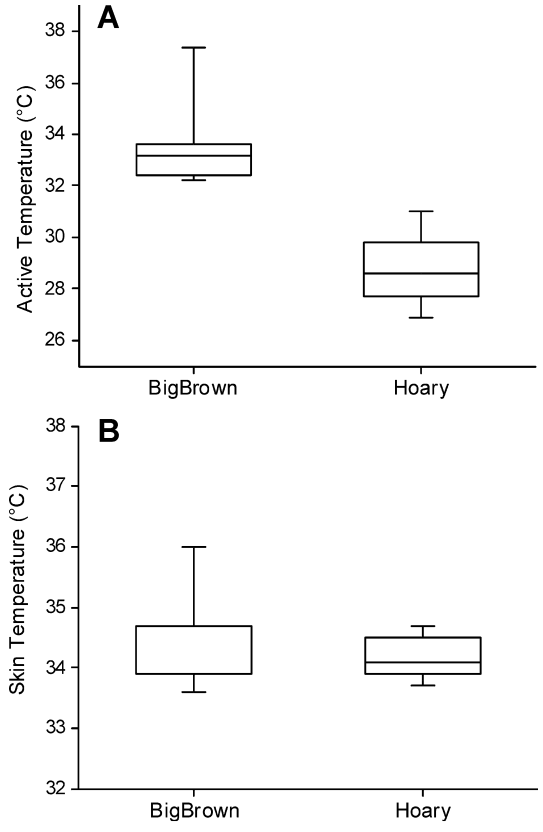

Fig. 1 **A** Box plots of hoary ($n=10$) and big brown bat ($n=8$) active temperatures recorded using temperature telemetry. *Boxes* represent quartile ranges, *whiskers* represent 5th and 95th percentiles and *lines inside the boxes* represent median values. **B** Box plots of resting normothermic T_{sk} for the same individuals

While the method of Barclay et al. (2001) is a relatively rigorous means to define torpor, it depends on a number of untested assumptions. The use of T_{act} assumes that the relationship between T_{sk} and T_b is constant; this may not be true for a number of reasons. First, decreasing air temperatures at dusk could increase ambient cooling of transmitters and thus reduce T_{act} and, therefore, the chance of detecting shallow torpor bouts. Second, transmitters must be attached to bats dorsally between the scapulae, the site of brown adipose tissue (BAT) storage (Eckert et al. 1988) and large flight muscles. During periods of active rewarming at dusk, T_{sk} could overestimate T_b because heat generated by BAT metabolism or flight muscle shivering warms the trans-

mitter. Third, differences in roost structure or roosting behavior could influence the relationship between T_b and T_{sk}, and alter the measure of T_{act}. Many mammals roost communally to reduce heat loss (e.g., Kunz 1982); thus T_{sk} recorded for an individual may be affected by its proximity to roost mates. Fourth, and most fundamentally, T_{act} assumes that animals are normothermic prior to becoming active. Some flying animals are capable of powered flight at T_bs below normothermia, as defined above (Austin and Bradley 1969; Bradley and O'Farrell 1969; this study), and motor systems of bats remain active over a wide range of T_b (Choi et al. 1998). Conceivably, bats and birds could leave roosts prior to complete rewarming and rely on heat generated by flight muscle activity to complete the final stages of warming. If this were the case, T_{act} and the use of shallow torpor bouts would be underestimated.

Our objectives were to test the above assumptions and compare T_{sk} to T_b over a range of conditions. We used captive and free-ranging big brown bats (*Eptesicus fuscus*), free-ranging hoary bats (*Lasiurus cinereus*) and temperature telemetry in the field and laboratory to address four specific questions:

1. Do active temperatures of free-ranging, solitary, foliage-roosting bats approximate those recorded for colonial, cavity-roosting bats?
2. Does T_{sk} approximate T_b over a range of T_a, during torpor, active warming from torpor, and normothermia?
3. Does clustering behavior influence the relationship between T_b and T_{sk}?
4. Are bats capable of flight at T_bs below normothermia and, if so, does flight increase the rate of rewarming?

Materials and methods

Study animals

All methods were in accordance with the Canadian Council for animal care and were approved by the University of Regina President's Committee on Animal Care. For free-ranging bats, we compared T_{act} of big brown bats to those for hoary bats. These species are well suited to this comparison because of known differences in roosting behavior. In our study area, big brown bats form maternity colonies in cavities of trembling aspen (*Populus tremuloides*; Kalcounis and Brigham 1998; Willis et al. 2003) while hoary bats roost solitarily, exposed in the open foliage of white spruce (*Picea glauca*; Willis 2003).

Active temperature

Fieldwork took place during the summers of 2000 and 2001 in the West Block of Cypress Hills Provincial Park, Saskatchewan, Canada (49°34′N, 109°53′W; see Sauchyn 1993 for description). The region is well suited to this study because it is characterized by dramatic diurnal fluctuations in T_a.

We captured bats in mist nets set at foraging areas or at roosts. Fur was clipped between the shoulders and temperature-sensitive radio-transmitters (0.7 g BD-2AT for 19.6 ± 2.6 g, range: 17.3–23.7 g big brown bats; 1.05 g BD-2T for 27.8 ± 5.84 g, range: 20.1–34.5 g hoary bats, Holohil Systems Carp, ON Canada) were affixed using surgical cement (Skin-Bond, Smith and Nephew, Largo, Fla., USA). Transmitter mass represented less than 5% of each free-ranging bat's body mass (Aldridge and Brigham 1988). We released bats within several hours of capture and followed them to roost trees on as many days as possible using hand-held telemetry receivers (R-1000, Communication Specialists, Calif., USA) and 5-element yagi antennas (AF Antronics, Urbana Ill., USA). We used datalogging radiotelemetry receivers (SRX-400, Lotek Wireless, Newmarket, ON Canada) to record inter-pulse intervals of transmitter signals every 15 min. The receivers converted inter-pulse intervals into T_{sk} values based on transmitter-specific calibration curves provided by the manufacturer, which were verified before transmitters were used.

We defined T_{act} following Barclay et al. (2001). For each bat, on as many nights as possible, we identified the T_{sk} recorded immediately prior to dusk departure and the lowest dusk departure temperature obtained during the life of a bat's transmitter was defined as T_{act}. We identified dusk departure based on the variance in signal strength recorded by the datalogging receiver. We compared T_{act} between hoary bats and big brown bats. We also compared resting T_{sk} between species based on the mean value of all T_{sk} greater than 32 °C. We selected 32 °C, because it fell between the T_{act} of the two species and because it is higher than the lower critical temperature reported in the literature for hoary bats (Genoud 1993). Hence, 32 °C likely represents a normothermic T_{sk} for this species. We only included bats in this analysis for which we recorded a dusk departure T_{sk} on at least three nights.

Effect of T_a, torpor and clustering on T_b vs. T_{sk}

To compare T_b to T_{sk} in the laboratory, we captured ten big brown bats as they emerged from a tree cavity at dusk on 9 June 2001. The bats were kept in cloth-lined wire cages at the University of Regina Biology Station, given ad lib water and handfed mealworms coated with powdered canine vitamin/iron supplement with a high essential fatty acid content (Vi-sorbits, SmithKline Beecham Animal Health, Westchester, Pa., USA). We kept cages outdoors but protected them from the elements in large, plastic containers (Rubbermaid, Wooster, Ohio, USA) with the lids elevated 20 cm above the rim on wooden stakes to increase ventilation. We attached temperature-sensitive radiotransmitters as described above (0.75 g BD-2AT, Holohil Systems). A second temperature-sensitive transmitter was surgically implanted (0.75 g BD-2ATH, Holohil Systems) into the intraperitoneal cavity of each bat under inhalant anesthesia (Isoflurane USP, Abbot Lboratories, Montreal, QC Canada). The combined mass of both transmitters represented between 6.3% and 8.7% of body mass, which exceeds Aldridge and Brigham's (1988) 5% rule for telemetry studies of flying animals. However, bats were not required to fly while in captivity and both internal and external transmitters were removed before bats were released at the end of the experiment.

We did not begin data collection until 1 week after implantation to allow bats to recover from surgery. Temperature dataloggers (iButton, Dallas Semiconductor, Dallas, Tex., USA) were used to record T_a in the cages. For the first 5 days of the experiment, all bats were housed in a single cage (clustered) and were then put in separate cages for an additional 5 days (solitary). During the clustered treatment, we did not observe bats continuously but all were found clustered with at least one other individual when they were removed for feeding each day. T_{sk} and T_b of all bats was calculated concurrently based on signals from the external and implanted transmitters, respectively, using the datalogging radiotelemetry receiver described above.

Ideally, repeated measures analyses are most appropriate for our data (Zar 1999). However, premature failure of a number of transmitters reduced the sample size and precluded this analysis. Instead, based on each bat's temperature time course, we identified bouts of steady-state normothermia and steady-state torpor and analyzed the difference between T_b and T_{sk} for each. We excluded periods of warming and cooling and defined a bout of

steady-state normothermia as any period greater or equal to 30 min duration (two sampling periods) during which a bat's T_{sk} remained above 33.6 °C (mean T_{act} for free-ranging big brown bats found in this study), and bouts of steady-state torpor as any period > 30 min duration when a bat's T_{sk} was within ± 3 °C of the minimum temperature for that bout. We chose this value based on qualitative inspection of temperature time courses, which revealed that following changes in T_{sk} greater than 3 °C, bats tended to continue warming or cooling. We calculated mean T_b, T_{sk}, and T_a values for each bout of torpor and normothermia for each bat. We removed inter-individual autocorrelation effects by calculating a group mean T_b for each treatment group. In other words we calculated four T_b values: one for all normothermic clustered bats, one for all normothermic solitary bats, one for all torpid clustered bats and one for all torpid solitary bats. An individual's T_{sk} for each bout of normothermia or torpor was then subtracted from the treatment-group-specific T_b value to obtain a measure of the difference between T_{sk} and T_b. We used one-sample Bonferroni-adjusted T-tests to determine if the difference between the treatment-group-specific T_b and individual T_{sk} differed from zero. To determine the influence of T_a, we also used a 2-factor ANCOVA, with T_a as a covariate, to compare the dependent variable (difference between treatment group T_b and individual T_{sk}) between the factors normothermia vs. torpor and clustered vs. solitary roosting.

Effect of flight on T_b vs. T_{sk}

During late August 2000, we captured four big brown bats emerging from an aspen cavity in the Cypress Hills and transported them to the laboratory at the University of Regina. In September and October, we obtained four additional big brown bats from buildings in Regina. All bats were housed for the winter in cloth-lined wire cages, fed as described above and maintained at 18 °C and 12L:12D photoperiod. Additionally they were exercised in a flight room for ca. 20 min, 3–4 times per week. Bats were always torpid when removed from cages prior to feeding and re-warmed prior to being fed. Flight experiments were not performed until all bats were able to fly continuously in the flight room.

We conducted flight experiments over a 2-week period in April 2001. Bats were placed in a refrigerator for several hours prior to flight trials to ensure they were torpid (T_{sk} < 18 °C). During the warm-up period we measured T_{sk} and T_b at 2-min intervals using a teflon coated J-type thermocouple probe and thermometer (Model 600–1040, Barnant Company, Barrington, Ill., USA). To maintain consistency with the T_{sk} data recorded using temperature telemetry in the field, we recorded T_{sk} by holding the thermocouple wire in contact with the skin between the scapulae. We used rectal temperature as our measure of T_b, following Barclay et al. (1996), by inserting the thermocouple probe 6 mm into the rectum. Each bat underwent a control trial when they were not induced to fly between sampling periods, and a flight trial when bats were dropped from a height of 1.5 m above a padded floor between each sampling period. Both control and flight trials were performed in a 21°C flight room. For each bat, we chose trial order (i.e., flight trial vs. control first) randomly. The two trials for each individual were separated by at least 4 days.

All bats underwent 2–3 practice trials 3–4 weeks prior to data recording to familiarize them with the flight trial protocol. During practice trials we devised a flight scoring system based on the ability of bats to fly in the flight room (Table 1). During experimental trials we used this system to score each flight attempt and recorded T_b and T_{sk} after each attempt. This allowed us to compare temperatures recorded when we knew that bats were capable of flying with T_{act} recorded using temperature telemetry in the field.

Statistical analysis

We report values as means ± SD unless otherwise specified. All analyses were performed using Systat Version 9 (SPSS 1998) with significance for all tests assessed at $P < 0.05$. For repeated measures analyses, conservative Greenhouse-Geiser and Huynh-Feldt adjusted P-values were equal and these are reported. All repeated measures analyses met homogeneity of slopes assumptions (Zar 1999).

Results

Active temperature

For free-ranging bats, the mean T_{act} of eight colonial, cavity-roosting big brown bats was significantly higher than that of ten solitary, foliage-roosting hoary bats (Fig. 1A; T-test, $T_{[8,10]} = 6.65$, $P < 0.001$). However, there was no difference between normothermic T_{sk} (i.e., $T_{sk} > 32$ °C; Fig. 1B; T-test, $T_{[8,10]} = 1.33$, $P = 0.21$).

Effect of T_a, torpor, and clustering on T_b vs. T_{sk}

We found a significant difference between T_b and T_{sk} for normothermic bats that was significantly influenced by T_a. We also found a significant difference between T_b and T_{sk} during active warming from torpor but found that clustering had no effect on the relationship between T_b and T_{sk}. Qualitatively, for big brown bats held in outdoor cages, T_{sk} differed from T_b, particularly at temperatures near the T_{act} of free-ranging individuals (i.e., 30–35 °C), as well as during torpor. We plotted T_{sk} vs. T_b for each bat and these relationships approximated but did not match a 1:1 relationship (Fig. 2). We did not use linear regression to analyze relationships between T_b and T_{sk} for individual big brown bats because intra-individual autocorrelation would dramatically increase the probability of Type I error. Therefore, r^2 values are not reported. A typical time course of T_b, T_{sk}, and T_a indicates the source of some of this variation (Fig. 3). T_{sk} was typically lower than T_b when bats were nor-

Table 1 Qualitative scores used to quantify flight ability of bats at different skin temperatures (T_{sk}) and body temperature (T_b)

Score	Flight characteristics
1	Dropped to the floor with no forward progress
2	Straight flight with 1–3 m forward progress
3	Flight with > 3 m forward progress and 1 turn
4	Flight with > 3 m forward progress and 2 turns
5	Flight with 3 turns before landing on "roosting site"
6	Controlled circular flight around the flight room with > 3 turns. Normal flight

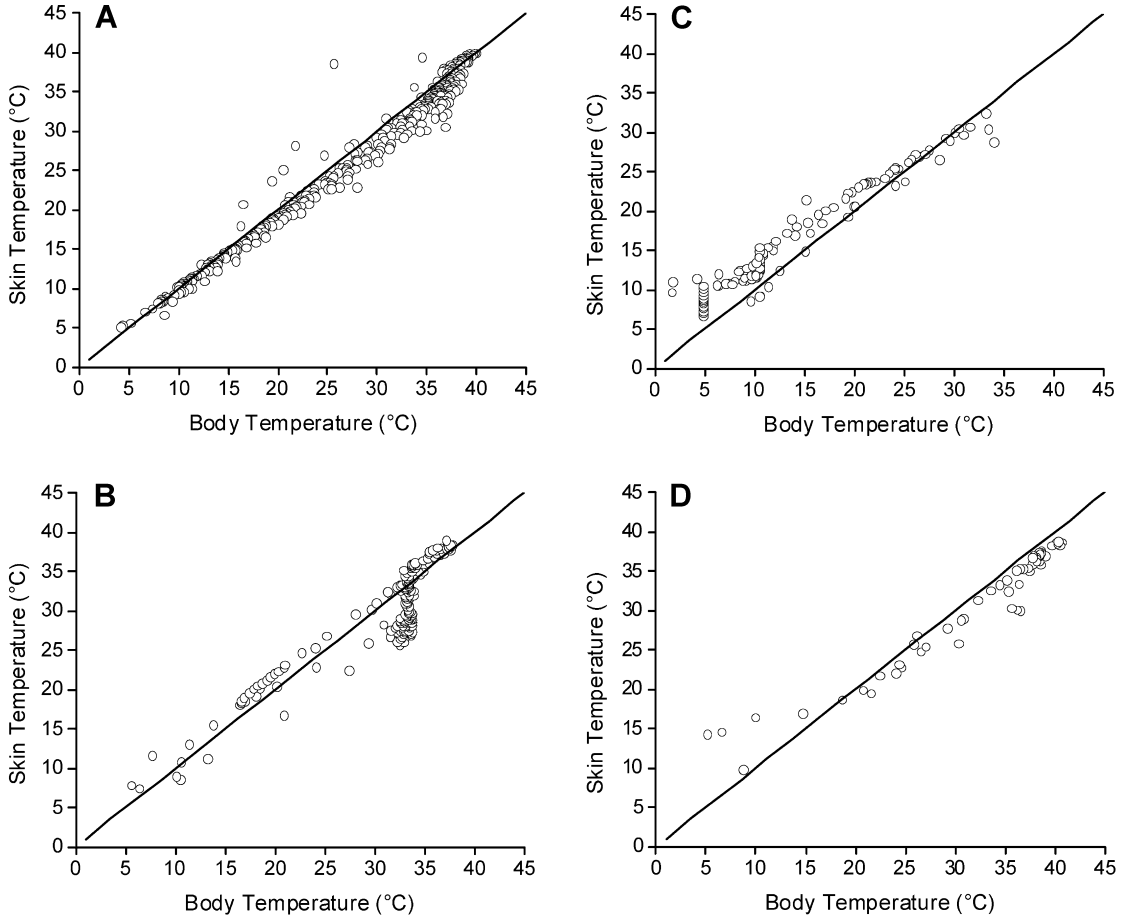

Fig. 2A–D Relationship between T_b and T_{sk} for four individual big brown bats (**A–D**) housed in outdoor cages over a range of T_a during both clustering and solitary roosting. *Diagonal lines* represent the predicted relationships if T_b and T_{sk} were equal

mothermic but usually exceeded T_b at low T_a when bats were torpid. T_{sk} also typically exceeded T_b early in periods of active warming from torpor; for example, at sunset (ca. 22:00) when bats re-warmed (Fig. 3).

In the T_b vs. T_{sk} experiment, we recorded eight bouts of spontaneous arousal from torpor by each of four individuals. All arousals were complete within three sampling periods (i.e., 45 min) or less. Overall, T_{sk} warmed significantly more slowly than T_b (Table 2; Paired T-test, $T=-2.42$, $df=7$, $P=0.046$). However, during the first 15 min of warming, T_{sk} increased significantly more rapidly than T_b (Table 2; Paired T-test, $T=2.42$, $df=7$, $P=0.046$).

We tested whether clustering and torpor affected the difference between treatment group-specific T_b and individual T_{sk} using Bonferroni-adjusted one sample T-tests. T_b was significantly greater than T_{sk} for clustered normothermic (Fig. 4; $T=3.51$, $df=18$, $P=0.01$) and solitary normothermic bats ($T=6.94$, $df=7$, $P=0.001$), but T_b and T_{sk} were not significantly different for clustered torpid ($T=-2.17$, $df=10$, $P=0.22$) or solitary torpid bats ($T=-2.54$, $df=6$, $P=0.18$). The difference between T_b and T_{sk} during torpor was highly variable, however (Fig. 4), and we recorded T_{sk} values as much as 9.5 °C higher than T_b during deep torpor at low T_a.

To test for the effect of clustering and T_a on the difference between T_b and T_{sk} we used ANCOVA, with T_a as the covariate, normothermia vs. torpor and roosting treatment (clustered vs. solitary) as factors, and the difference between treatment-group-specific T_b and individual T_{sk} as the dependent variable. The effect of T_a was highly significant ($F_{[1,40]}=17.66$, $P<0.001$) and the model was highly significant for effects of torpor vs. normothermia (Fig. 4; $F_{[1,40]}=62.12$, $n=27,18$, $P<0.001$). There was no effect of clustered vs. solitary roosting ($F_{[1,40]}=0.10$, $P=0.75$).

Effect of flight on T_b vs. T_{sk}

Captive big brown bats were capable of flight at low T_b (29.2 ± 1.1 °C) and flight significantly increased the rate of warming from torpor. To test for the influence of flight and T_{sk} vs. T_b on recorded temperature, we used a 3-factor repeated measures ANOVA with flight treatment, temperature treatment, and capture location as factors, and measured temperature as the dependent variable. The model was significant for between-subject effects of all three factors (flight treatment: $F_{[1,18]}=15.6$, $P<0.001$; temperature treatment: $F_{[1,18]}=35.4$,

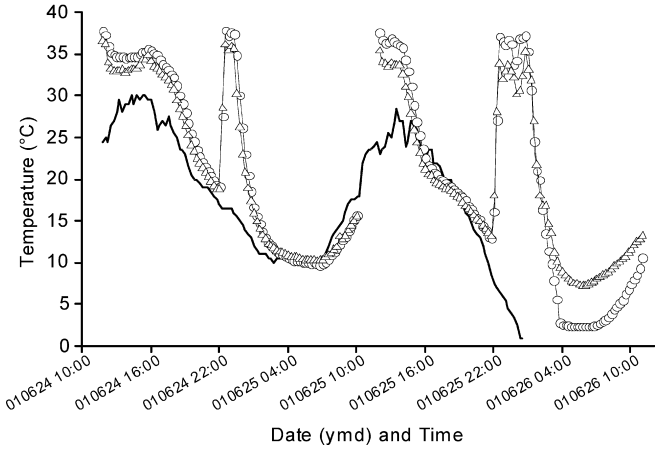

Fig. 3 Time course of T_b (*circles*), T_{sk} (*triangles*) and T_a (*solid line*) obtained over 2 days from one individual big brown bat housed in an outdoor cage. Note that T_{sk} typically exceeded T_b during active warming bouts at dusk (ca. 22:00) and during torpor at very low T_a, but that T_b exceeded T_{sk} during normothermia

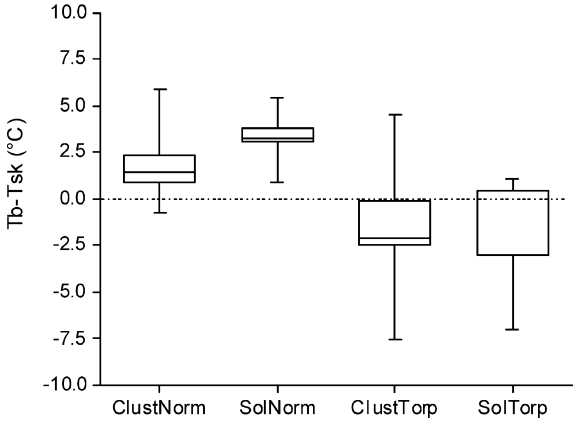

Fig. 4 Differences between treatment group T_b and individual T_{sk} for ten big brown bats. The data were divided into four groups: Clustered normothermic (*ClustNorm*, $n=19$ bouts), solitary normothermic (*SolNorm*, $n=8$ bouts), clustered torpid (*ClustTorp*, $n=11$ bouts), and solitary torpid (*SolTorp*, $n=7$ bouts). Values greater than zero (*dashed line*) indicate that T_b exceeded T_{sk} and values less than zero indicate that T_{sk} exceeded T_b

Table 2 Rates of spontaneous arousal from torpor during eight warm–up bouts by four captive big brown bats. We compared T_{sk} andT_b warm-up rates for the first 15 min of each warming bout (T_b/T_{sk}*1st 15 min*) as well as the average warm-up rate for each overall warming bout (T_b/T_{sk}*overall bout*). All values in degrees Centigrade per minute

Bat I.D.	Bout	T_b 1st 15 min	T_{sk} 1st 15 min	T_b overall bout	T_{sk} overall bout
21	1	0.56	0.65	0.62	0.58
21	2	0.22	0.32	0.54	0.46
22	1	0.05	0.15	0.71	0.49
22	2	0.92	0.80	0.53	0.45
22	3	0.20	0.37	0.50	0.40
24	1	0.37	0.41	0.43	0.34
24	2	0.09	0.18	0.56	0.47
27	1	0.09	0.21	0.24	0.34
Mean		0.31	0.39	0.52	0.44
SD		0.30	0.23	0.14	0.08

$P<0.001$; capture location: $F_{[1,18]}=14.4$, $P<0.001$). There were significant within-subject/between-subject interactions between the repeated measure (i.e., time) and flight treatment ($F_{[8,144]}=7.46$, $P<0.001$), temperature treatment ($F_{[8,144]}=10.43$, $P<0.001$), and location ($F_{[8,144]}=4.92$, $P<0.001$). This means that warming patterns of bats over the course of flight trials were influenced by all three factors (Fig. 5). We did not include body mass as a covariate in this analysis because mass was not significantly different between bats from the two study locations (Mann Whitney *U*-Test, $U=9$, $n=4,4$, $P=0.56$) and body mass did not influence arousal rates (see below).

Warm-up rates of T_b and T_{sk} for bats used in the flight experiments were greater than those recorded for bats housed in out-door cages (Table 3). We calculated the mean warm-up rate for each bout and also divided each bout in half (based on the duration of the bout) and calculated warm-up rates during the first- and second-halves of each arousal. To be conservative, we further divided these data by capture location, because of the significant difference between Cypress Hills and Regina bats. We compared mean, first-half, and second-half warm-up rates individually using two-factor blocked ANOVAs, treating each bat as a block and flight treatment (flight or control), and temperature treatment (T_{sk} vs. T_b) as factors. Flight significantly increased mean warm-up rate for bats from both locations but there were no significant differences between mean T_b and T_{sk} warm-up rates (Table 4). For the first half of rewarming bouts, flight significantly increased warm-up rate for bats from both capture locations. In contrast to mean warm-up rates, T_{sk} warmed significantly more quickly than T_b in the first half of warming bouts (Table 4). During the second half of warming, T_b warmed significantly more quickly than T_{sk} for bats from both locations (Table 4). Flight significantly increased warm-up rate for Regina bats but not for bats from the Cypress Hills during the second half of warming (Table 4). Overall, although absolute warming rates were faster for bats used in the flight experiment than for bats in the T_b vs. T_{sk} experiment, the pattern of more rapid initial warming rates for T_{sk} relative to T_b was consistent between experiments. When these analyses were repeated controlling for body mass by dividing each bat's warm-up rate by body mass, there was no change in the significance of any test. Therefore, we report analyses based on absolute and not mass-specific warm-up rates.

For flight trial data, we compared the dependent variable, measured temperature, at different flight scores using a 2-factor repeated measures ANCOVA with T_{sk} vs. T_b, and capture location (i.e., Regina vs. Cypress Hills) as factors, and flight (i.e., first and best; scores of 2 and 6 respectively) as the repeated measure. We included body mass as a covariate in this analysis because of the potential influence of mass on flight performance. There

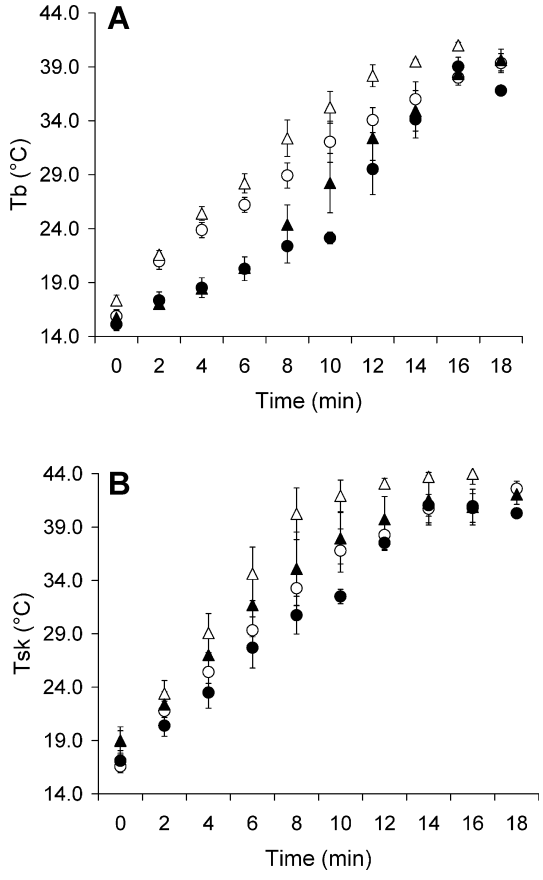

Fig. 5A–B Change in T_b (**A**) and T_{sk} (**B**) over time during flight and control trials for bats from two study locations. Flight trials shown by *open symbols* and control trials by *filled symbols*. Regina bats are represented by *triangles* and Cypress Hills bats by *circles*. Values are means ± SE

Table 3 Mean rate of temperature change T_b and T_{sk} (°C/min) during warm-up from torpor for four big brown bats from the Cypress Hills and four from Regina during flight and control trials

Cypress Hills	T_b flight	T_{sk} flight	T_b control	T_{sk} control
1st Half	1.67 ± 0.16	2.02 ± 0.22	0.95 ± 0.30	1.49 ± 0.24
2nd Half	1.41 ± 0.18	1.33 ± 0.22	1.74 ± 0.30	1.17 ± 0.24
Overall	1.55 ± 0.14	1.66 ± 0.17	1.32 ± 0.19	1.33 ± 0.30
Regina				
1st Half	1.83 ± 0.38	2.41 ± 0.50	0.93 ± 0.20	2.03 ± 0.61
2nd Half	1.61 ± 0.35	1.17 ± 0.55	1.55 ± 0.55	0.61 ± 0.25
Overall	1.71 ± 0.35	1.81 ± 0.40	1.24 ± 0.20	1.25 ± 0.17

was a significant three-way interaction between the repeated measure (flight), capture location and T_b vs. T_{sk} ($F_{[1,11]} = 7.11$, $P = 0.022$; Fig. 6). Several factors account for this interaction. First, T_{sk} was consistently greater than T_b but this effect was more pronounced at flight scores of 2 compared to scores of 6. Second, the T_b–T_{sk} differential was much greater for Regina bats than for Cypress Hills bats for flight scores of 2 but not 6. There was also a significant interaction between the repeated measure, flight, and the covariate body mass

Table 4 Results of ANOVA to compare warm-up rates of four bats from each of two capture locations (Cypress Hills and Regina, SK). Warming bouts were divided in half and the first and second halves, as well as overall warm-up rates, were compared separately. Individual bats were treated as blocks and flight and temperature (T_b vs. T_{sk}) were treated as factors

	Source	Cypress Hills			Regina		
		df	*F*	*P*	*df*	*F*	*P*
1st Half	Block	3	0.67	0.59	3	5.51	0.02
	Flight	1	13.31	0.005	1	17.34	0.002
	Temp	1	6.71	0.029	1	29.82	0.000
	Flight×Temp	1	0.35	0.57	1	2.84	0.13
	Error	9	–	–	9	–	–
2nd Half	Block	3	0.28	0.59	3	8.31	0.006
	Flight	1	0.37	0.005	1	5.47	0.044
	Temp	1	6.17	0.035	1	27.08	0.001
	Flight×Temp	1	3.38	0.099	1	3.70	0.087
	Error	9	–	–	9	–	–
Overall	Block	3	1.10	0.40	3	16.31	0.001
	Flight	1	7.09	0.026	1	59.08	0.000
	Temp	1	0.35	0.57	1	0.64	0.44
	Flight×Temp	1	0.22	0.65	1	0.38	0.55
	Error	9	–	–	9	–	–

($F_{[1,11]} = 15.23$, $P = 0.002$) but when we subdivided the data by flight score and T_b vs. T_{sk}, the only significant relationship was a positive effect of body mass on the T_b required for best flight (i.e., score = 6; Fig. 7, Linear regression, $F = 26.19$, $r^2 = 0.81$, $n = 8$, $P = 0.02$). There was no significant effect of body mass on T_{sk} at best flight (Fig. 7, $F = 2.71$, $n = 8$, $r^2 = 0.31$, $P = 0.15$), T_b at first flight ($F = 0.12$, $n = 8$, $r^2 = 0.02$, $P = 0.74$), or T_{sk} at first flight ($F = 0.82$, $n = 8$, $r^2 = 0.12$, $P = 0.40$).

We compared T_{act} of free-ranging big brown bats to the skin temperatures associated with first and best flight for captive Cypress Hills big brown bats using ANCOVA with body mass as a covariate. T_{sk} recorded when bats flew best (i.e., flight score = 6, 41.3 ± 2.1 °C) were significantly higher than T_{act} recorded in the field (33.6 ± 1.7 °C, $F_{[1,9]} = 41.70$, $P < 0.001$). The T_{sk} of bats first capable of flight (i.e., flight score = 2, 33.6 ± 2.0 °C)

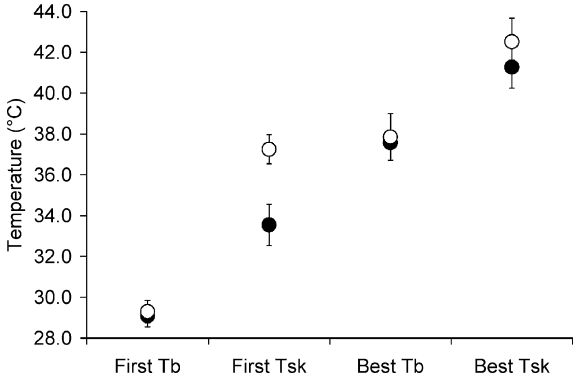

Fig. 6 T_{sk} and T_b of Regina bats (*open circles*) and Cypress Hills bats (*filled circles*) measured when bats were first capable of flight (*First*) and capable of controlled circular flight around the flight room (*Best*). Values are means ± SE

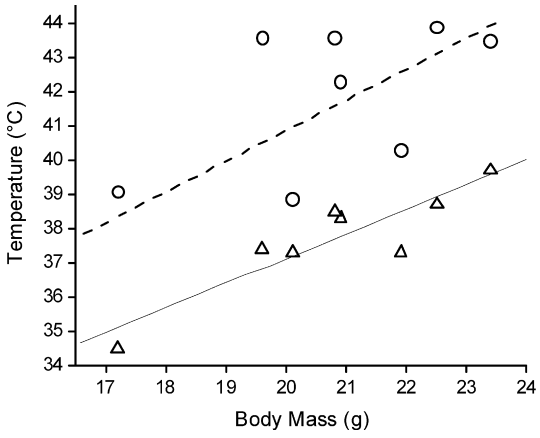

Fig. 7 Relationship between body mass and T_{sk} associated with best flight (*circles*, *dashed line*) and T_b associated with best flight (*triangles*, *solid line*)

were not significantly different from T_{act} ($F_{[1,9]} = 0.001$, $P = 0.98$).

Discussion

The objectives of our study were to evaluate assumptions about using "T_{act}" as the threshold between torpor and normothermia for free-ranging endotherms and to compare T_{sk} with T_b under a range of conditions. This is the first study to report concurrent measurements of T_{sk} and T_b in mammals, both recorded using temperature-sensitive radiotransmitters, and to report concurrent T_{sk} and T_b warm-up rates.

Active temperatures

We found that the T_{act} of free-ranging hoary bats was significantly lower than that of big brown bats despite no difference between their resting normothermic T_bs. The T_{act} of hoary bats we recorded (28.6 ± 1.5 °C) was also lower than the resting normothermic rectal temperature (34.8 °C) and lower critical temperature (31 °C) measured in laboratory trials (Genoud 1993). Low T_a at dusk could mean greater ambient cooling of external transmitters on foliage roosting, solitary hoary bats relative to cavity-roosting, clustered big brown bats. Alternatively, if hoary bats are capable of powered flight at low T_b they could be more likely to leave their roosts while still rewarming, using heat produced as a by-product of flight muscle activity to complete the final stages of warm-up. In either case, the low T_{sk} active temperatures of hoary bats clearly underestimate normothermic T_b. This has dramatic consequences for estimates of the importance of shallow torpor to overall energy budgets. For example, in a 9 g little brown bat (*Myotis lucifugus*), a reduction in T_b from 34.8 °C to 28.6 °C at $T_a = 20$ °C reduces energy expenditure by ca. 64% (ca. 0.80 kJ/h to 0.29 kJ/h; Studier 1981). Assuming similar rates for ca. 30 g hoary bats, in the absence of data from the literature, the active temperature we found could underestimate energy savings of shallow torpor by 1.70 kJ/h (2.65 kJ/h minus 0.95 kJ/h; Studier 1981). Acknowledging that hoary bat and little brown bat mass-specific metabolic rates will differ, T_{act} will nonetheless compromise our ability to accurately assess torpor in the field.

Effect of T_a, torpor and clustering on T_{sk} vs. T_b

We found that the relationship between T_b and T_{sk} differed significantly, depending on T_a and on whether or not bats were torpid. Consistent with previous research, we found that during normothermia T_{sk} underestimated T_b by up to 6 °C (Audet and Thomas 1996; Barclay et al. 1996). Our results are not surprising given that T_a was typically cooler than T_b during normothermic bouts, which likely cooled external transmitters. Such large differences present a problem for studies that employ T_{sk} to infer metabolic savings. Again using equations derived by Studier (1981) for little brown bats, underestimating T_b by 6 °C, from 30 °C to 24 °C at a T_a of 20 °C, would lead to underestimating energy expenditure by ca. 79% (0.84 vs 0.18 kJ/h) for a 20-g bat. The ambient effect is also problematic since it likely occurs at sunset when T_{act} is recorded. Underestimating T_b at sunset likely overestimates energy expenditure because it will reduce T_{act} and therefore conceal the importance of shallow torpor to the overall energy budget. T_{act} is sensitive to ambient effects because the lowest dusk departure T_{sk} or T_b is adopted as the torpor threshold. For example, using T_{act} may lead to the conclusion that, when T_a at sunset is relatively low (e.g., early in the season), bats use less shallow torpor than during the warmest months of the year, simply because of differences in ambient cooling effects.

Consistent with Barclay et al. (1996), we found that T_b and T_{sk} were not significantly different during torpor. However, for bats in deep torpor at low T_a, T_{sk} exceeded T_b by as much as 9.5 °C (Fig. 3). This could reflect two effects of metabolic heat production to defend a reduced T_b setpoint while torpid. First, brown fat metabolism could warm external transmitters. Brown fat is stored dorsally, between the shoulders in many mammals (Eckert et al. 1988), the best site for transmitter attachment. Second, also due to the position of transmitters, shivering thermogenesis of the large dorsal flight muscles could further elevate T_{sk}. This is most likely at torpid T_bs of < 20–25 °C when skeletal muscle is warm enough to shiver (Fons et al. 1997; Choi et al. 1998). Differences in the warm-up rates of T_b and T_{sk} (Table 2) support the hypothesis that brown fat and/or flight muscle shivering cause disproportionate warming of external transmitters. Over the course of individual warming bouts, T_b warmed more quickly than T_{sk}, but during the first 15 min of warming T_{sk} increased significantly more rapidly than T_b, likely due to brown fat metabolism

early in the warming bout. Overall, warm-up rates of big brown bats in our experiment were comparable to those reported for bats of similar size (e.g., *Nyctimene albiventer*, 28.8 g, 0.50 °C/min; Bartholomew et al. 1970) and are consistent with allometric predictions of warm-up rates for a ca. 20-g mammal (Stone and Purvis 1992).

T_b and T_{sk} did not differ between periods when bats were housed colonially or in isolation. Thus, for colonial species, external transmitters reliably measure T_{sk} of the individual despite the potential for clustering to influence transmitter temperature. Indeed most temperature-sensitive radiotransmitters are affixed with the temperature sensor in direct contact with the skin. This supports the use of T_{sk} as a measure of T_b when comparing thermoregulation in solitary and colonial roosting species if other sources of variation, such as ambient cooling, are controlled. This result also reinforces our comparison of T_{act} between hoary bats and big brown bats. The variation in the relationship between T_b and T_{sk}, however, suggests that considerable caution is required when defining torpor in the field based on T_{sk}, and particularly when comparing species. Comparison between mammals, which have brown fat, and birds, which do not (Eckert et al. 1988; Saarela et al. 1991), may be particularly challenging.

Effect of flight on T_b vs. T_{sk}

Comparison of overall warming rates revealed no significant difference between T_b and T_{sk}. However, this analysis concealed the fact that T_b and T_{sk} warming rates differed significantly at different stages of warm-up; T_{sk} was greater than T_b during the first half of warming while T_b was greater than T_{sk} during the second half. This corroborates our results for bats in outdoor cages and supports the hypothesis that brown fat metabolism and/or shivering thermogenesis could elevate T_{sk} early during the warming phase. It also highlights a potential source of error associated with the use of active temperature. If T_{act} is recorded during a warming bout just prior to dusk departure then T_{sk} could overestimate T_b resulting in an overestimate of T_{act} and torpor.

Flight significantly increased T_b and T_{sk} during the first half of warming bouts and for overall warming bouts. This is almost certainly due to heat released as a by-product of flight muscle activity meaning that bats could leave roosts at T_bs below normothermia. We argue that bats may exploit heat generated during flight to complete the final stages of warming. The costs of rewarming constrain total energy savings during torpor. Therefore, selection should favor mechanisms that reduce warming costs. This hypothesis is supported by the comparison of field T_{act}s with temperatures recorded during flight trials. Active temperatures of free-ranging bats were significantly lower than T_{sk}s associated with normal flight in the lab but not different than T_{sk}s associated with initial straight-line flight. Bats were capable of straight-line flights at a T_b well below most definitions for torpor (Barclay et al. 2001). Previous studies have demonstrated "good flight" by Poorwills (*Phalaenoptilus nuttalli*) at T_bs as low as 27.4 °C, weak flight at T_bs as low as 24 °C (Austin and Bradley 1969) and flight by bats at T_bs as low as 20 °C (Bradley and O'Farrell 1969). A similar pattern has been observed in non-flying mammals. Free-ranging echidnas actively forage at T_bs as low as 21 °C (Augee 1969; L. Kuchel, unpublished data). Active temperature, then, could easily be recorded while animals are technically torpid. Indeed, these findings raise questions about the use of any behavioral boundary to differentiate torpor from normothermia and demonstrate a potential conflict between temperature-based and behavior-based definitions of torpor.

Surprisingly, despite identical treatment during 6–7 months of captivity, Cypress Hills bats could fly at significantly lower T_{sk} than bats from Regina. Climate differences between the two areas could account for this apparent geographic variation. Relative to Regina, where daily summer temperatures vary by only ca. 10 °C, the Cypress Hills are characterized by dramatic diurnal fluctuations in temperature with maxima of 30–35 °C and minima of 5–10 °C common (C. Willis, unpublished observation). Bats in the Cypress Hills must regularly warm at sunset when T_a is lower than that experienced by bats in Regina. If bats do occasionally leave their roosts while still rewarming, the ability to fly with relatively cold flight muscles would represent an advantage. Intraspecific geographic variation in thermal physiology is a promising avenue for future research.

Warm-up rates we recorded during flight experiments were surprisingly high. Geiser and Baudinette (1990) and Stone and Purvis (1992) both found a negative relationship between body mass and warm-up rates for mammals. Consistent with this, the ca. 2.5-g Etruscan shrew (*Suncus etruscus*) is reported to have the highest T_b warm-up rates of any mammal (1.25 °C/min; Fons et al. 1997). However, the warm-up rates of bats in our flight experiments were greater than 1.25 °C (Table 3). T_{sk} warm-up rates were particularly high. During flight trials these approached 2–2.5 °C per min, almost two-fold greater than the shrew (Table 3). Brown fat thermogenesis and flight muscle shivering likely explain much of the difference in warm-up rates between T_b and T_{sk}, but the training protocol we employed may also have had an influence. Bats were always torpid (T_{sk}~18 °C) and re-warmed prior to being hand-fed each day for the 6-month period leading up to experiments. This daily entrainment may have altered warming ability relative to free-ranging bats. Given that captivity can influence torpor use by mammals and birds (Geiser et al. 2000), it is reasonable to postulate that it could also affect warm-up rates. Pressure to minimize energy expenditure during warming was likely relaxed for bats conditioned to regular feeding. In addition to this, bats were at $T_{sk} < 18$ °C when experiments began, below the flight room T_a of 21 °C. Thus, some ambient heating of our thermocouple may have occurred. Despite these

potential sources of variation, we contend that the patterns of warming we report (e.g., differences between T_b and T_{sk} and the effect of flight) are representative of free-ranging bats. For example, warm-up patterns we observed during the flight experiment were identical to those of bats held for short periods in outdoor cages during the T_b vs. T_{sk} experiment (i.e., T_{sk} greater than T_b early during warm-up but T_{sk} less than or equal to T_b toward the end of warm-up).

Our findings raise questions about the concept of degree-minutes or degree-hours, proposed by Barclay et al. (2001) and Lausen (2001) as a measure of energy savings associated with torpor. This metric multiplies the length of time an animal spends below T_{act} with the magnitude of T_{sk} reduction below T_{act}. The concept is problematic, first because it relies on T_{act}, which does not necessarily represent an energetically relevant definition of torpor; and second because it fails to acknowledge Q10 effects which mean that initial reductions in T_b result in greater energy savings than reductions of the same increment at lower T_b (e.g., Studier 1981). For example, 6 h at T_{sk} 10 °C below, and 12 h at T_{sk} 5 °C below a T_{act} of 34 °C, both equal 6 degree-hours of torpor. However, at a T_a of 20 °C, a 6-h reduction in T_b of 10 °C from 34 °C would save a little brown bat ca. 0.42 kJ/g while a 12-h reduction in T_b of 5 °C from 34 °C would result in a 22% greater energy savings (ca. 0.54 kJ/g; Studier 1981). The concept of degree-hours has little relevance for the energy budgets of animals in the field because it masks differences in energetic savings associated with different depths and durations of torpor.

Conclusions

Studies of the use of heterothermy by small, free-ranging endotherms have been enhanced by the use of T_{sk}-telemetry. Implanted radiotransmitters are not practical for studies of many small species and we contend that, despite its limitations, T_{sk} does provide valuable information about heterothermy. However, the limitations of T_{sk} as a measure of T_b must be addressed if we are to take these studies further and use free-ranging animals to address proximate and ultimate questions about the energetics and evolution of torpor. T_{sk} may be higher or lower than T_b depending on T_a and on whether animals are rewarming, torpid, or normothermic. Furthermore, T_{act} does not improve dramatically on arbitrary definitions of torpor. Some animals are capable of "activity" and even flight below T_bs that qualify as torpor. Indeed, our data strongly suggest that bats may leave their roosts while torpid and exploit flight muscle thermogenesis to finish rewarming. Using flight activity as a threshold for torpor obscures the energetic implications of heterothermy and is no more biologically relevant than an arbitrary T_b or T_{sk}, such as 30 °C.

We propose several measures to mitigate limitations of T_{sk} and challenges associated with defining torpor. Most importantly, field studies must assess torpor in terms of energy savings and not just reduced T_{sk} or inactivity, which are merely symptoms of torpor. As demonstrated repeatedly in the laboratory, bouts of heterothermy begin not when endotherms reach a certain T_b or when certain behaviors begin or end but when energy is saved as a result of a reduced T_b set-point. This distinction is important if field studies employing T_{sk} are to address detailed questions. The ultimate solution is to obtain a direct measure of oxygen consumption in the field. This is logistically challenging even under ideal conditions, but not impossible for some species (e.g., Schmid 1996). Another alternative is to develop species-specific models, based on laboratory data, quantifying the relationship between metabolic rate, T_b and T_{sk} over a range of T_a, during steady-state torpor, steady-state normothermia, warm-up, and cooling. These models could be used in conjunction with field T_{sk} data to infer metabolic rate and quantify energy budgets and torpor use more precisely. The resulting energy budgets could be verified in the field using doubly labeled water techniques to calculate field metabolic rates. A final and perhaps more attractive possibility, given the intraspecific variation in thermal physiology we found between bats from different study sites, would be to record T_{sk} and oxygen consumption for each study animal prior to its release. These preliminary trials, performed over a wide T_a range during normothermia, warming, cooling and torpor would, in essence, calibrate each study animal/T_{sk} combination, allowing inferences about MR to be made from T_{sk} in the field while controlling for inter-individual variation in the relationship between T_{sk} and MR. The findings of studies employing this technique could also be verified using techniques designed for estimating field metabolic rates.

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