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# Stress-induced changes in body temperature of silver-haired bats (*Lasionycteris noctivagans*)

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ABSTRACT

Acute stressors such as capture and handling can elicit physiological responses in endothermic animals. One example of such a response is an increase in body temperature ($T_b$) commonly referred to as stress-induced hyperthermia (SIH). For species that employ torpor, typically an inactive state characterized by a controlled reduction in $T_b$ and metabolic rate, a rapid increase in $T_b$ could be advantageous, especially in the context of escape from predators. We quantified SIH in silver-haired bats (*Lasionycteris noctivagans*) because they readily enter torpor and often roost in exposed places where they could be vulnerable to predators. We tested the hypothesis that handling stress causes SIH in three separate contexts: a) during the nocturnal, active phase immediately following capture during flight, b) during the diurnal, inactive phase of normothermic bats, and c) during pronounced torpor immediately following exposure to cold ambient temperature. We used a standardized protocol during which $T_b$ was measured (as rectal temperature) immediately upon handling and, again, several minutes later. We found that SIH occurred for inactive, normothermic bats held at a warm temperature. Surprisingly, however, handling stress caused a reduction in $T_b$ for normothermic bats following the active, flight phase and, although in the opposite direction, this cooling rate was indistinguishable from the rate of SIH for normothermic bats during the rest phase. As expected, we observed a large change in $T_b$ during rewarming from torpor following handling. This warming rate was greater than that previously reported in the literature for any heterothermic endotherm. Rapid rewarming by silver-haired bats could reflect their tendency to roost in relatively exposed locations that may be vulnerable to predators. This study provides new information on SIH in an under-studied group of animals and illustrates the need to evaluate the hypothesis that SIH and rewarming from torpor are influenced by predation risk and activity state.

## 1. Introduction

Various stressors can activate the autonomic nervous system, and lead to an increase in body temperature ($T_b$) of endothermic animals, including introduction to novel environments [1], social defeat [2], and capture or handling stress [3, 4]. This stress-induced rise in $T_b$ has been described as an emotional fever [5], emotional hyperthermia [6] or, most commonly, stress-induced hyperthermia (SIH) [4].

There is debate in the literature about whether SIH is the result of passive, forced hyperthermia (i.e., failure in thermoregulation where heat production exceeds capacity for dissipation) or a fever (i.e., a controlled or regulated rise of in $T_b$) [7, 8]. Some evidence suggests that rises in $T_b$ can be inhibited by antipyretic drugs [9], supporting the hypothesis that SIH is a form of fever. Additionally, evidence for a regulated increase in $T_b$ includes the occurrence of shivering and peripheral vasoconstriction, as well as the lack of a relationship between SIH and ambient temperature ($T_a$) [10]. If SIH is regulated, increases in $T_b$ could be a result of an adaptive, physiological "fight or flight" stress response [7, 11] in which a stressor activates the hypothalamus leading to stimulation of the pituitary and adrenals (HPA axis). This would then allow a subsequent release of corticosterone and adrenocorticotropic hormone, which causes energy stores to be mobilized and heart rate and $T_b$ to increase (for review see [12]). Thus, SIH could be an important component of the mechanism allowing animals to either fight or flee when confronted with a critical situation (e.g., a potential predator or human disturbance).

Regardless of the mechanism, SIH has been quantified in many avian and mammalian study species including great tits (*Parus major*; [13]), silver foxes (*Vulpes vulpes*; [14]), impala (*Aepyceros melampus*; [3]) and eastern chipmunks (*Tamias striatus*; [15]). To date, studies quantifying SIH have focused on a rise in $T_b$ from a physiological perspective but have not considered differences in SIH across activity

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states, such as between the active versus inactive phases of the diurnal cycle, or across ecological contexts, such as in the context of variation in predation risk. Furthermore, SIH has not been well studied in heterothermic endotherms that regularly use torpor for energy balance and survival, despite the ubiquity of torpor expression in mammals and birds [16, 17]. Torpor is an adaptation employed by many endotherms to maintain energy balance during periods of energetic constraint ([18, 19]; see [20] for other ecological functions of torpor). During torpor, individuals drastically reduce their energy consumption by lowering both $T_b$ and metabolic rate [18]. As a result, motor reflexes and coordination are greatly reduced [21], potentially increasing vulnerability to predators, disturbance, and other acute stressors. Therefore, the capacity to rapidly generate heat in response to potential stressors may be especially important for heterothermic species due to their vulnerability while in a torpid state. This could be especially true for species that roost or nest in exposed locations as opposed to enclosed microhabitats (e.g., underground burrows, tree hollows). As well, the lower $T_b$ of torpid animals creates greater scope for potential SIH responses.

Like most temperate-zone bats, silver-haired bats (*Lasionycteris noctivagans*) are facultative heterotherms, employing torpor regularly throughout their annual cycle [22], and are also thought to hibernate in the northernmost parts of their range [23]. Unlike many other temperate bat species, however, silver-haired bats are often found roosting alone or in small groups, and inhabit a variety of roosts such as crevices, cavities under loose bark of trees [24], and, occasionally, man-made structures [25]. They also often roost in exposed locations on the surfaces of trees or in depressions in rough bark of species such as the peach-leaved willow (*Salix amygdaloides*) [26, 27]. Their tendency to roost alone in potentially exposed roosts, may leave silver-haired bats especially vulnerable to disturbance. Therefore, silver haired bats provide an ideal model to investigate ecological and behavioral drivers of variation in SIH for heterothermic species.

We used silver-haired bats to test the hypothesis that heterothermic endotherms exhibit SIH in response to an acute stressor but that this response varies with behavioral/physiological state and ecological context. We predicted: 1) that both normothermic and torpid bats would exhibit an increase in $T_b$ in response to acute handling stress; but 2) that the magnitude and rate of this increase would be greatest for torpid bats because of both the greater scope for an increase in $T_b$, and their need to regain motor control to fight or flee a potential predator.

## 2. Materials and methods

All methods were approved by the University of Winnipeg Animal Care Committee and conducted under Manitoba Conservation Wildlife Scientific Permit WB16368. Between 27 and 31 July 2014, 13 silver-haired bats were caught at Sandilands Forest Discovery Centre (49.67°N, 95.90°W) in a 12 m by 6 m mistnet set adjacent to a 10 m drop-off at the edge of the Upper Whitemouth River. We measured SIH following Van der Heyden et al. [4] and quantified SIH in three different contexts: for normothermic bats during the active phase immediately following flight, for normothermic bats during the rest phase during the day, and for torpid bats during the rest phase during the day.

To quantify SIH in the first context (hereafter the "*capture*" treatment), we checked mistnets for bats at a maximum of 10-minute intervals, although we were usually sitting within a few meters of the net and checking more frequently allowing us to observe some bats strike the net. When we observed a bat hit the net, or in the net, a stopwatch was started. The net was then lowered and within 1.46 ± 0.92 min (mean ± SD; range: 0.18–3.27 min) a 1 mm diameter thermocouple was inserted approximately 3 mm into the rectum until the reading on the digital thermometer (model 8000008, SPER Scientific LTD, Scottsdale, AZ; resolution: 0.1 °C) stabilized (hereafter $T_{b\text{-start}}$). The thermocouple thermometer was calibrated, following manufacturer instructions, against a mercury thermometer traceable to the National Institute of Standards and Technology. Rectal temperature is commonly used as a proxy for instantaneous measurement of $T_b$ in field studies of small mammals, including bats [e.g., 28, 29].

After the initial $T_b$ measurement, the bat was removed from the net and we continued gentle handling to induce/maintain a stress response (i.e., by carefully stretching out the wings and lightly blowing on the bat's fur). A second $T_b$ measurement was then taken after 4 to 5 min (exact time recorded; 4.12 ± 0.81 min; hereafter $T_{b\text{-end}}$). Variation in measurement time occurred because it often took a few seconds for $T_b$ to stabilize after inserting the thermocouple. After measurement, each bat was placed in a cloth bag, to be used for one of two other treatments (see below), while trapping continued. Nightly $T_a$ data were obtained from a meteorological station located approximately 55 km from the capture site (Station ID: 503B1ER, Environment Canada). We averaged Environment Canada $T_a$ records between 21:00 and 02:00 (i.e., the time nets were open) to provide a nightly index of $T_a$ at the time of $T_b$ measurement.

After capture, bats were transported in their cloth bags, on foot, < 1 km to our field laboratory. Sex, mass ( ± 0.1 g) and age (based on ossification of the metacarpal-phalangeal joints [30]), were recorded and bats were provided water from a disposable pipette. One subset of bats was held in individual cloth bags in a quiet holding room, under natural photoperiod and room temperature for the duration of the night (hereafter the "*warm*" treatment) while a second group was used for a concurrent respirometry study and assigned to a "*cold*" treatment (see below). The holding room was un-insulated and indoor temperature of this room and the field laboratory closely matched outdoor $T_a$. On the following day, between 13:00 and 15:30, to obtain measurements of normothermic bats, we quantified SIH following warm $T_a$ exposures (i.e., several hours at a $T_a$ approaching the likely lower critical temperature of the thermoneutral zone for silver-haired bats, Table 1). A timer was started as soon as the cloth bag was handled, the bat was immediately removed from the bag and rectal $T_{b\text{-start}}$ was recorded. The bat was then gently handled as described above (i.e. opening the wings, blowing gently on the face and fur) and, after 4 to 5 min (4.56 ± 0.24 min), a second set of rectal $T_b$ measurements ($T_{b\text{-end}}$) was recorded. After SIH measurement, each bat was given water with a disposable pipette and returned to its individual cloth bag.

As part of a concurrent respirometry study, each night, up to two bats were placed in 100 ml transparent, acrylic chambers within a temperature-controlled cabinet (i.e., the "*cold*" treatment). Cabinet temperature was well below summer thermoneutral $T_a$ for silver-haired bats (14.6 ± 0.4 °C) to encourage bats to enter torpor. The following day, between 13:00 and 22:00, immediately after each bat was removed from its respirometry chamber, we conducted the same $T_b$ measurement/handling procedure outlined above (i.e., recorded rectal $T_{b\text{-start}}$ immediately after removal and $T_{b\text{-end}}$ after approximately 4 min; 4.06 ± 0.55 min). Following these measurements, bats were, again, given water and subsequently placed in individual cloth bags in the quiet holding room until nightfall. All bats were released at the site of capture within 24 h of initial capture.

### 2.1. Statistical analysis

All statistical analyses were conducted in R [31]. In all cases we calculated the change in $T_b$ between $T_{b\text{-start}}$ and $T_{b\text{-end}}$ and the average warming rate (i.e., in °C/min). Average warming rate was our primary response variable but we also tested for differences between $T_{b\text{-start}}$ and $T_{b\text{-end}}$ within and across treatments. We captured only one adult male and one adult female, so we used one-sample *t*-tests to determine if $T_b$ and warming rate values for these individuals fell outside 95% confidence intervals for juveniles. Adult values did fall outside distributions for juveniles (see Results) so we excluded them from subsequent analysis.

While all 11 juvenile bats were included in the *capture* treatment, we subdivided these bats into the *warm* and *cold* treatments to be re-tested. In other words, all bats were subjected to two out of the three

**Table 1**
Data for *L. noctivagans* (n = 13) captured at Sandilands Forest Discovery Centre, Manitoba, Canada. Each treatment (*capture*, *warm* and *cold*) includes $T_{b\text{-start}}$, $T_{b\text{-end}}$, change in $T_b$ ($\Delta T_b$), and rate of change in $T_b$ (°C/min). $T_a$ is included for the *capture* and *warm* treatment.

| Date of capture | ID | Demographic | Body mass (g) | *Capture* treatment (°C) | | | | | *Warm* treatment (°C) | | | | | *Cold* treatment (°C) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | $T_{b\text{-start}}$ | $T_{b\text{-end}}$ | $\Delta T_b$ | Rate of $T_b$ change | $T_a$ | $T_{b\text{-start}}$ | $T_{b\text{-end}}$ | $\Delta T_b$ | Rate of $T_b$ change | $T_a$ | $T_{b\text{-start}}$ | $T_{b\text{-end}}$ | $\Delta T_b$ | Rate of $T_b$ change |
| 07/27/14 | LANO1 | Juvenile Female | 8.0 | 35.1 | 32.1 | −3.0 | −0.8 | 14.9 | – | – | – | – | – | 19.0 | 26.1 | 7.1 | 2.3 |
| 07/29/14 | LANO3 | Juvenile Male | 9.2 | 34.3 | 29.2 | −5.1 | −1.1 | 16.9 | – | – | – | – | – | 15.2 | 27.6 | 12.4 | 2.6 |
| 07/29/14 | LANO5 | Juvenile Male | 11.5 | 34.2 | 29.2 | −5.0 | −1.3 | 16.9 | – | – | – | – | – | 15.5 | 27.7 | 12.2 | 2.8 |
| 07/30/14 | LANO6 | Juvenile Male | 9.6 | 34.8 | 35.1 | 0.3 | 0.1 | 17.4 | – | – | – | – | – | 14.7 | 25.8 | 11.1 | 3.0 |
| 07/30/14 | LANO7 | Juvenile Male | 8.2 | 35.1 | 35.7 | 0.6 | 0.2 | 17.4 | – | – | – | – | – | 14.5 | 26.2 | 11.7 | 2.6 |
| 07/31/14 | LANO8 | Juvenile Male | 9.5 | 33.4 | 33.0 | −0.4 | −0.1 | 15.1 | – | – | – | – | – | 15.9 | 25.9 | 10.0 | 2.4 |
| 07/31/14 | LANO9 | Juvenile Female | 11.2 | 33.2 | 32.7 | −0.5 | −0.2 | 15.1 | 33.5 | 35.6 | 2.1 | 0.5 | 27.0 | – | – | – | – |
| 07/31/14 | LANO10 | Juvenile Female | 10.3 | 34.1 | 31.2 | −2.9 | −0.8 | 15.1 | 32.1 | 36.3 | 4.2 | 0.9 | 27.0 | – | – | – | – |
| 07/31/14 | LANO11 | Juvenile Female | 11.0 | 34.4 | 33.6 | −0.8 | −0.2 | 15.1 | 33.0 | 36.1 | 3.1 | 0.7 | 27.0 | – | – | – | – |
| 07/31/14 | LANO12 | Juvenile Female | 12.0 | 33.8 | 30.7 | −3.1 | −0.6 | 15.1 | 27.1 | 32.9 | 5.8 | 1.4 | 27.0 | – | – | – | – |
| 07/31/14 | LANO13 | Juvenile Male | 10.3 | 33.4 | 31.9 | −1.5 | −0.3 | 15.1 | – | – | – | – | – | 16.5 | 27.6 | 11.1 | 2.8 |
| 07/29/14 | LANO2 | Adult Male | 10.7 | 30.3 | 29.9 | −0.4 | −0.8 | 16.9 | 35.1 | 37.1 | 2.0 | 0.5 | 28.1 | – | – | – | – |
| 07/29/14 | LANO4 | Adult Female | 13.9 | 33.2 | 31.2 | −2.0 | −0.1 | 16.9 | 29.5 | 25.2 | −4.3 | −0.9 | 28.1 | – | – | – | – |

treatments. One subset (n = 4) was subjected to the *capture* treatment and *warm* treatments with remaining bats subjected to the *capture* and *cold* treatments (n = 7). Therefore, to account for repeated measures, we used separate paired *t*-tests to test for differences in $T_{b\text{-start}}$, $T_{b\text{-end}}$, change in $T_b$, and warming rate between *capture* and *warm* treatments and between *capture* and *cold* treatments. We also used paired *t*-tests to determine if $T_b$ increased significantly (or decreased, see Results for *capture* treatment) across the 5-min handling period. Separate bats were used for *warm* and *cold* treatments, so we used Welch's two-sample t-test (because of unequal variances) to compare change in $T_b$ and warming rate between these treatments. We used general linear models to test for effects of night-to-night variation in $T_a$ and body mass on change in $T_b$ values during each treatment. All values are reported as the mean ± SD and significance was assessed at an alpha level of 0.05.

## 3. Results

We captured 13 silver-haired bats from all four age and sex categories, but only one male adult and one lactating female adult (Table 1). One sample *t*-tests indicated that the $T_{b\text{-start}}$ measurement for the single adult male in the *capture* treatment fell outside the distribution for juveniles (Table 1; t = 98.1, df = 12, p < 0.0001) as did values for the single adult lactating female for $T_{b\text{-end}}$ and average warming rate in the *warm* treatment (Table 1; $T_{b\text{-end}}$:, t = 12.7, df = 3, p = 0.001; warming rate: t = 8.9, df = 3, p = 0.003). Therefore, we excluded the two adults from subsequent analyses.

The $T_{b\text{-start}}$ values did not differ between bats in the *capture* treatment and the *warm* treatment (Fig. 1; t = 1.6, df = 3, p = 0.20) but there was a difference in $T_{b\text{-end}}$ values for bats in these groups (Fig. 1; t = −5.0, df = 3, p = 0.02). This translated into a difference in the change of $T_b$ (t = −3.9, df = 3, p = 0.03) and warming rate (Fig. 2; t = −4.5, df = 3, p = 0.02) between the *capture* and *warm* treatments. Surprisingly, during the *capture* treatment, $T_b$ decreased significantly from 34.2 ± 0.7 °C to 32.2 ± 2.1 °C across the handling interval for a change in $T_b$ of −2.0 ± 2.0 °C (Fig. 1; t = 3.2, df = 10, p = 0.01) and a "warming" rate of −0.5 ± 0.3 °C/min. Nine of the eleven individuals showed a decline in $T_b$ during the 5 min following capture (Table 1). In the *warm* treatment, $T_{b\text{-start}}$ averaged 31.7 ± 2.9 °C for the four individuals and increased significantly to 36.3 ± 0.6 °C after 5 min for a change in $T_b$ of 3.8 ± 1.6 °C (Fig. 1; t = −4.8, df = 3, p = 0.02) or a warming rate of 0.6 ± 0.5 °C/min.

The $T_{b\text{-start}}$ for *capture* treatment bats did not differ significantly from $T_{b\text{-end}}$ for bats in the *warm* treatment (Fig. 1; t = −1.8, df = 3, p = 0.18). Likewise, the $T_{b\text{-start}}$ for bats in the *warm* treatment did not differ significantly from the $T_{b\text{-end}}$ for bats in the *capture* treatment (Fig. 1; t = 0.60, df = 3, p = 0.59).

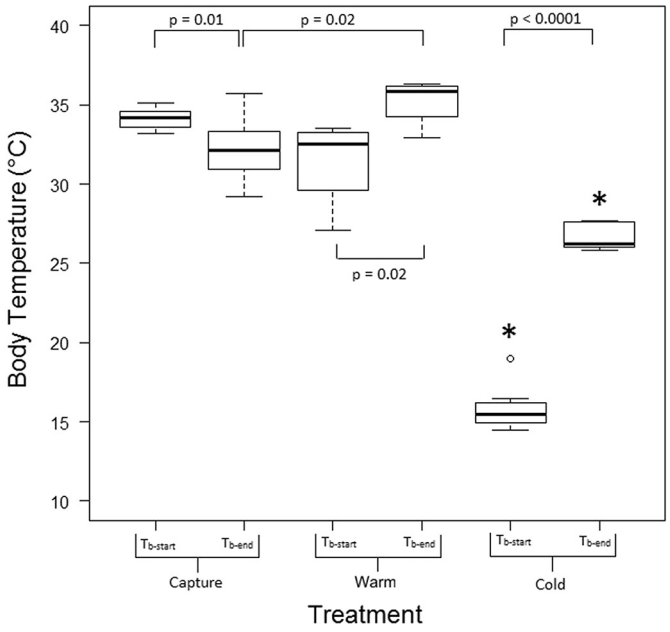


**Fig. 1.** Boxplots of $T_{b\text{-start}}$ and $T_{b\text{-end}}$ measurements in *L. noctivagans* for the *capture* (n = 11), *warm* (n = 4) and *cold* (n = 7) treatments. Significant differences between groups are shown by horizontal lines and the corresponding p-value. Asterisks above $T_{b\text{-start}}$ and $T_{b\text{-end}}$ for the *cold* treatment indicate significant differences from all other groups (p < 0.001). The median is represented by a solid horizontal line, the top and bottom of each box represents the upper and lower quartiles, respectively. Whiskers represent maximum and minimum values.

There was a difference between the *capture* treatment and the *cold* treatment for both $T_{b\text{-start}}$ (Fig. 1; t = 29.3, df = 6, p < 0.0001) and $T_{b\text{-end}}$ (Fig. 1; t = 4.5, df = 6, p = 0.004) which also resulted in a difference in the change in $T_b$ (t = −10.6, df = 6, p < 0.0001) and warming rate (Fig. 2; t = −13.6, df = 6, p < 0.0001) for these treatments. For bats in the *cold* treatment, $T_{b\text{-start}}$ averaged 15.9 ± 1.5 °C and after handling increased significantly to 26.7 ± 0.9 °C (Fig. 1; t = −32.5, df = 5, p < 0.0001), at a rapid rewarming rate of 2.6 ± 0.2 °C/min. The change in $T_b$ was greatest for bats from the *cold* treatment (10.8 ± 1.8 °C) and this value was also significantly greater than that for *warm* treatment bats ($\Delta T_b$: t = −6.7, df = 7.2, p = 0.0003; Fig. 2; warming rate: t = −8.4, df = 4.3, p = 0.0008).

$T_a$ during the capture treatment ranged from 14.9 °C to 17.4 °C on the four nights of our study but had no effect on the change in $T_b$

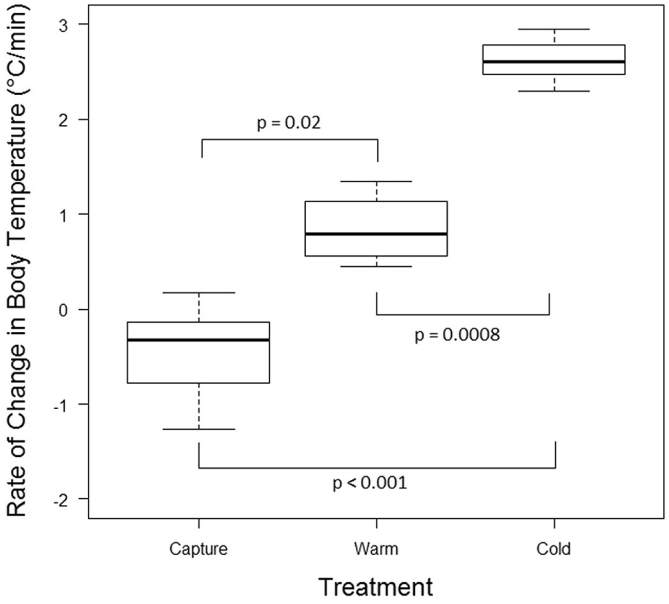


**Fig. 2.** Change in $T_b$ (°C/min) for *L. noctivagans* in the *capture* (n = 11), *warm* (n = 4), and *cold* (n = 7) treatments. Significant differences between groups are shown by horizontal lines and the corresponding p-value. The median is represented by a solid horizontal line, the top and bottom of each box represents the upper and lower quartiles, respectively. Whiskers represent maximum and minimum values.

($F_{1,9} = 0.04$, $p = 0.84$), $T_{b\text{-start}}$ ($F_{1,9} = 3.5$, $p = 0.10$) or $T_{b\text{-end}}$ ($F_{1,9} = 0.26$, $p = 0.62$). There was also no effect of body mass on change in $T_b$ during any of *capture* ($F_{1,9}$, $p = 0.51$, $r^2 = 0.57$), *warm* ($F_{1,2}$, $p = 0.59$, $r^2 = 0.24$) or *cold* treatments ($F_{1,5}$, $p = 0.22$, $r^2 = 0.14$).

## 4. Discussion

Our results suggest that juvenile silver-haired bats exhibit SIH in response to acute stressors during some, but not all, contexts, and that the rate, magnitude, and direction of this change depends on behavioral/activity state of individuals. We hypothesized that $T_b$ would increase during handling due to SIH and predicted that this increase would occur across all situations. Contrary to our prediction, however, we found that bats showed a surprising reduction in $T_b$ during post-capture handling in a mistnet during their active phase. Consistent with our predictions, we observed an increase in $T_b$ after normothermic silver-haired bats were removed from both a warm environment during their inactive phase and following exposure to a cold environment that induced torpor.

Multiple studies have documented an increase in $T_b$ due to capture stress [e.g., 3, 32, 33, 34]. Therefore, we were surprised to observe a decrease in $T_b$ for active bats in the *capture* treatment (change in $T_b = -2.0 \pm 2.0$ °C over 4 to 5 min or $-0.5 \pm 0.3$ °C/min). We did not always see bats hit the mistnet so there was potential for variation in the time between initial capture and our $T_{b\text{-start}}$ measurement. However, all *capture* treatment bats had similar $T_{b\text{-start}}$ values (Fig. 1), and there was a consistent reduction in $T_b$ between our first and second measurements for all but two individuals which slightly increased $T_b$ during handling. Moreover, the average magnitude of warming rates for these two individuals ($0.1 \pm 0.1$ °C/min) was much smaller than the average magnitude of the cooling rate for all other individuals ($-0.6 \pm 0.4$ °C/min) and also smaller than typical rates of SIH observed for other small endotherms (e.g. $0.3 \pm 0.02$ °C/min for eastern chipmunk's; [15]). To date, only one other study has reported a decrease in $T_b$ after handling, for caged great tits after capture, during their active period [13]. The authors attributed this $T_b$ decrease to the time it took them to capture the birds, by hand, from the cage, inflating their initial $T_b$ measurement. In our study, bats were captured from the wild during energetically expensive (i.e., heat-producing) flight and initial $T_b$ measurements occurred very soon after capture. This suggests to us that the decline in $T_b$ we observed for bats in the capture treatment is a biologically relevant phenomenon and not an artefact of our measurement protocol.

Two mechanisms could explain a decrease in $T_b$ during handling stress. First, it is possible that the observed $T_b$ reduction at capture could reflect the abrupt halt in activity when bats were caught in the mistnet. During flight, metabolic rate of bats is approximately 15 times greater than basal metabolic rate [35, 36] and heat produced by flight muscles would readily increase overall $T_b$. At capture, flight muscle thermogenesis likely decreased dramatically for bats in our study. Reduced heat production, coupled with high rates of heat dissipation due to vascularized flight membranes and a small body size, could explain the decrease in $T_b$. Thus, the effect we observed could simply result from passive processes associated with heat balance rather than a regulated response. Another possible mechanism could be that silver-haired bats lower their set-point in response to handling stress, which would then trigger mechanisms to increase heat loss/dissipation. This could help bats avoid the possibility of over-heating and, potentially life-threatening hyperthermia, during any struggle with a potential predator. In the case of our study, $T_{b\text{-start}}$ for bats in the *capture* treatment was surprisingly low ($34.1 \pm 0.7$ °C), likely well below the upper thermal tolerance for this species. Thus, it is unlikely they were at any risk of overheating. However, under warmer $T_a$ or during prolonged struggle with a potential predator, it is possible that overheating could be a risk. Although a decrease in $T_b$, by definition, cannot be considered SIH, if the change in $T_b$ we observed reflects a regulated adjustment in the $T_b$ set-point in response to the stressor, it could represent a similar physiological response to stress/disturbance despite the difference in the response direction.

Interestingly, and consistent with the second mechanism above, we did not observe an effect of night-to-night variation in $T_a$ on any of our $T_b$ metrics during the *capture* treatment. As previous authors have argued, the lack of an association between $T_a$ and change in $T_b$ suggests that SIH reflects a regulated adjustment in the $T_b$ setpoint [for example see 10] as opposed to a failure of thermoregulation. If the reduction in $T_b$ we observed at capture was a passive process, then the magnitude of $T_b$ decline should have correlated with $T_a$, although we concede that the range of $T_a$ during the study (2.5 °C) was small. Moreover, the reduction in $T_b$ was consistent regardless of whether bats had been sitting in the net for a few minutes or whether we observed them hit the net. If the pattern we observed was simply due to passive heat loss, bats resting in the net for up to several minutes, should already have declined in $T_b$ prior to our measurement of $T_{b\text{-start}}$ and, thus, should have exhibited an increase in $T_b$ after the stress of handling. This further suggests that the decline in $T_b$ we observed reflects a regulated reduction in the $T_b$ set-point, similar to what seems to occur for SIH. We recommend that future studies aim to quantify changes in $T_b$ immediately following capture across a wider range of $T_a$ to help understand mechanisms underlying what appears to be stress-induced reduction in $T_b$ in this species.

Bats that remained undisturbed in a holding room during the day (i.e., their inactive phase) experienced an increase in $T_b$ in response to handling as predicted. The warming rate for juvenile silver-haired bats in the *warm* treatment of our study ($0.57 \pm 0.53$ °C/min) was comparable to that of other bat species upon capture and handling [37] although was higher than that for eastern chipmunks ($\Delta T_b = 0.3 \pm 0.02$ °C; [15]). Although eastern chipmunks are relatively small-bodied mammals, they are still about 10 times larger than silver-haired bats so differences in body size, combined with a higher starting $T_b$, and, therefore, less potential scope for SIH, could explain lower rates of SIH for chipmunks. Interestingly bats in both our *warm* and *capture* treatments showed $T_{b\text{-start}}$ values that were low relative to

$T_b$ that would be considered normothermic for most endotherms (e.g., [15]). Such low $T_{b\text{-start}}$ values measured during the *capture* treatment are especially surprising given that most bats were measured within seconds to minutes of active flight. Some bat species are capable of pronounced activity and even flight at low $T_b$, even below 30 °C [38]. Thus, it is possible that silver-haired bats express relatively low $T_b$, even during activity, to save energy in the face of high rates of heat loss. Most studies of free-ranging bats employ temperature-sensitive radio-transmitters to record skin temperature as a proxy for $T_b$ but this can underestimate core $T_b$ [39]. Rectal temperature provides a better estimate of core $T_b$ than skin but may still be susceptible to ambient cooling effects and could have caused us to slightly underestimate $T_b$ [39]. We recommend additional measurements of $T_b$ for silver-haired bats across a range of circumstances to better understand natural patterns of thermoregulation in this species.

Interestingly, there was no significant difference between the final $T_b$ ($T_{b\text{-end}}$) for bats in the *warm* treatment compared to the initial $T_{b\text{-start}}$, (i.e., the "active" $T_b$) for bats in the *capture* treatment. Thus, bats in the *warm* treatment increased their $T_b$ in response to handling to a level equivalent to that of actively flying bats. This ability to drastically increase $T_b$ in response to acute stressors may be critical for survival of bats to avoid disturbance or escape predators that they may encounter while roosting during the day.

Also, interesting, $T_b$ for bats in the *capture* treatment decreased at a rate of 0.5 ± 0.5 °C/min while increasing for bats in the *warm* by 0.6 ± 0.5 °C/min. Although qualitatively higher for *warm* bats, these absolute rates were statistically indistinguishable. This may represent the "normal" rate of $T_b$ change that silver-haired bats experience when presented with an acute stressor. While the rate of $T_b$ change was consistent, the direction of change appears to be context dependant. Capture stress during the active phase may cause a reduction in set-point to avoid hyperthermia, while handling stress during the rest phase may cause an increase in set-point $T_b$ enabling an escape from predators.

Torpid bats in the *cold* treatment showed the most pronounced and rapid change in $T_b$ (10.8 ± 1.8 °C or 2.6 ± 0.2 °C/min). This rapid increase in $T_b$ (as compared to the *capture* and *warm* treatments) may reflect a combination of stress-induced rise in $T_b$ coupled with normal re-warming from torpor. Consistent with other observations of extremely rapid warming in this species [37], this rate of rewarming from torpor is the highest documented for any heterothermic endotherm by a considerable margin. The next fastest rewarming rate reported for the Chiroptera was by the hoary bat (*Lasiurus cinereus*); 2.14 °C/min [37]) and, for mammals, on the whole, was from the Estruscan shew (*Suncus etruscus*; 2.0 °C/min [40]. Importantly, rates reported for *S. etruscus* were measured for free-ranging individuals without the handling stress experienced by bats in our study. At present there are no data documenting natural rewarming rates for free-ranging silver-haired bats so comparisons to other heterothermic species should be interpreted cautiously. Nonetheless, our results suggest that silver-haired bats have a remarkable capacity to generate metabolic heat for rapid rewarming.

The roosting ecology of silver-haired bats (e.g., solitary or in small groups in thermally unstable roosts) could help explain rapid re-warming rates in this species (as for other species with similar roosting behaviour [37]). For heterotherms, rapid rates of rewarming have an overall energetic benefit; less energy is spent when rewarming occurs quickly [41, 42]. Moreover, this rapid change from torpid to active $T_b$ could be advantageous for dealing with stressors, like human disturbance or predators. Silver-haired bats commonly roost alone and often roost under tree bark, in cracks and rock crevices [26, 27], and in man-made structures [25] potentially making them more vulnerable to predation and disturbance than many bat species. While roosts provide protection from predators [43] and a thermally-stable environment for many bat species [44] the relatively exposed roosts of silver-haired bats increase the likelihood they might encounter a predator or other disturbances during torpor. Rapid increases in $T_b$ like the ones we observed in our *cold* treatment could increase the chance a torpid bat will be able to escape from, or fend off, a predator. Some bats appear capable of flight at $T_b$ approaching as low as 20 °C [38] and flying while still torpid could allow for activity-thermoregulation substitution via use of heat generated by flight muscles to finish re-warming [39]. Based on the rates we observed, juvenile silver-haired bats could rewarm from a fully torpid state to $T_b > 20$ °C, at which flight might be possible, in one or 2 min. Rapid warming rates in response to stressors could also be beneficial in the context of other sources of disturbances, such as forest fires. For example, Gould's long-eared bat (*Nyctophilus gouldii*, an Australian tree-dwelling species can respond to smoke exposure by increasing their heart and respiration rate (i.e., arousing from torpor) thereby allowing for potential escape from a fire [45]. Other heterothermic endotherms have additionally shown arousal from torpor in response to smoke (Dunnarts (*Sminthopsis crassicaudata*); [46], eastern pygmy-possums (*Cercartetus nanus*); [47]). The more rapid the physiological response to such disturbances, the more likely individuals are to escape that disturbance.

All of our results should be interpreted with caution as our sample sizes are relatively small (n = 4 to 11 individuals depending on treatment group). However, for all the comparisons we made, effect sizes were "large" to "extremely large" (Cohen's d values ranging from 0.8 to 13.3). This highlights the fact that within-treatment variation was very small relative to between group variation. It is possible that some of the differences in our response variables between treatments reflect Type 1 error, especially for comparisons to the *warm* treatment. However, the very large effect sizes and consistent patterns among individuals within treatments gives us confidence in our results. This is especially true for the most unexpected pattern we observed, of cooling during initial handling after capture, because our sample size was largest for this group. We encourage future studies to explore similar questions about response to stress using more individuals, and most species of heterothermic endotherms.

Our study is the first to examine changes in $T_b$ caused by handling and capture stress in a thermally labile heterotherm, and the first to document a reduction in $T_b$ following handling for any mammal. The patterns we observed could reflect the ability of thermally flexible heterotherms to adjust their set-point and heat production or dissipation. Inactive but normothermic bats at warm temperatures close to their thermoneutral zone exhibited a typical SIH response, similar to that of a range of mammalian species. Although the direction of $T_b$ change varied across contexts, absolute rates of change in $T_b$ were similar following both capture and inactivity at a warm temperature. Torpid bats in our study exhibited the fastest increase in $T_b$ documented to date which may reflect the ability to rewarm quickly to escape or fight potential predators. Overall, this study suggests that ecological context and activity state are important predictors of SIH in heterothermic endotherms and highlights the potential of silver-haired bats as a model for understanding $T_b$ regulation in mammals.

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