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ORIGINAL PAPER

Coping with the cold: black-capped chickadees (*Poecile atricapillus*) use rapid facultative hypothermia to reduce fat loss overnight

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Abstract

Heat loss due to a large surface-area-to-volume ratio makes surviving periods of cold temperatures a challenge for small endothermic animals. Many temperate, non-migratory birds survive cold winter nights by increasing heat production through shivering, maintaining their body temperature at the cost of the energy provided by fat stores. An additional strategy may be the use of facultative hypothermia, allowing body temperature to decrease overnight to conserve energy rather than maintaining normothermic body temperature. In this study, we examined the relationship between overnight body temperature and fat loss under a cold temperature challenge in black-capped chickadees (*Poecile atricapillus*). To investigate this, we brought 10 wild black-capped chickadees into captivity and used quantitative magnetic resonance analysis and temperature sensitive radio transmitters to compare changes within-individual overnight fat loss and body temperature at air temperature of 20 °C versus 3 °C. Most of the black-capped chickadees showed both reduced body temperature and greater fat loss at 3 °C compared to 20 °C. Furthermore, individuals exhibiting greater decreases in body temperature showed lower overnight fat loss. Interestingly, some individuals did not drop their body temperature across the air temperature conditions. These results suggest individual variation in use of facultative hypothermia to reduce fat loss overnight and provide valuable insights into the metabolic strategies small, non-migratory birds use to survive cold nights.

Keywords Facultative hypothermia · Quantitative magnetic resonance · Cold temperature · Fat loss · Black-capped chickadee

Introduction

Endothermic animals must balance metabolic heat generation and heat exchange with the environment to maintain their body temperature for physiological function (Petit and Vézina 2014; Tattersall et al. 2012). Endothermic animals that inhabit seasonally variable regions experience substantial heat loss in cold conditions and compensate by increasing heat production at the cost of higher metabolic rate and greater energy expenditure (McKechnie and Lovegrove 2002; Tattersall et al. 2012). Thermoregulation becomes even more challenging during sleep, as animals are fasting for a prolonged period and inactivity reduces heat production (Chaplin 1974). In temperate regions, daily and seasonal changes in energy expenditure present a challenge for endothermic animals living in environments with dynamic temperature regimes.

Many animals use fat stores as energy sources to generate heat through shivering thermogenesis (Petit et al. 2017), but accumulating large fat stores can increase predation risk by impairing mobility (Walters et al. 2017), particularly in birds and other flying endotherms. While birds can compensate for compromised flight mobility by adjusting their take-off angle, flight ability becomes increasingly impaired with greater fat mass (Walters et al. 2017), limiting the viability of this strategy (Clark and Dukas 2000; Walters et al. 2017). The increased foraging time required to accumulate large fat stores may also increase predation risk during daylight hours. Further compounding the challenge of energy storage, small bird species have a higher mass-specific energy

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expenditure than that of larger birds due to the non-linear scaling of metabolic rate and a high surface-area-to-volume ratio (Chaplin 1974; McKechnie and Lovegrove 2002; Tattersall et al. 2012). A higher surface-area-to-volume ratio increases convective heat loss in small birds, requiring more energy to maintain normothermic body temperature during both day (Tattersall et al. 2012) and night (Chaplin 1974). Increased predation risk and high rate of heat loss may limit small nonmigratory birds to carrying only enough fat to sustain themselves for one to two days (Chaplin 1974).

Facultative hypothermia is an additional strategy that birds can use to lower their overnight energy expenditure (Reinertsen 1983; Tattersall et al. 2012), balance energy conservation and fat accumulation (Chaplin 1974; Clark and Dukas 2000; McKechnie and Lovegrove 2002), and reduce the energetic cost of thermoregulation (Hohtola et al. 1991; Nord et al. 2009, 2011; Tattersall et al. 2012). In the literature, shallow decreases in nocturnal body temperature have been described using various terms, including shallow torpor, daily torpor, hypothermia, controlled hypothermia, facultative hypothermia, and nocturnal hypothermia. Throughout this paper, we use the term facultative hypothermia to refer to shallow decreases in nocturnal body temperature. The term facultative hypothermia is used to distinguish this regulated, reversible reduction in body temperature from lethal hypothermia, which often implies an uncontrolled and potentially fatal decline in body temperature. Although animals metabolize fat regardless of their use of facultative hypothermia, the energetic demand for endogenous heat production is reduced, allowing them to conserve energy during sleep (Clark and Dukas 2000; Reinertsen 1983). However, facultative hypothermia also comes with the trade-off of compromised flight ability (Carr and Lima 2013). Specifically, small birds must raise their body temperature within the normal range before being able to fly, which like holding excess fat, may increase the risk of predation (Carr and Lima 2013). Furthermore, previous research suggests that facultative hypothermia can elevate nocturnal predation risk due to reduced vigilance (McKechnie et al. 2023; Pravosudov and Lucas 2000).

Use of facultative hypothermia has been widely observed across bird species, with individuals exhibiting a range of reductions in overnight body temperature (McKechnie and Lovegrove 2002). The magnitude of facultative hypothermia is influenced by environmental factors such as low ambient temperature, food predictability, and predation risk, as well as intrinsic factors including body condition, age, and plumage quality (Nord et al. 2009; Nilsson et al. 2020; Andreasson et al. 2020; Barratt et al. 2025). Facultative hypothermia becomes particularly important when energetic demands are elevated due to environmental or physiological constraints. In such cases, the energetic benefits of this strategy are achieved through suppression of metabolic rate and are considered crucial for survival under harsh conditions (Chaplin 1976; Dawson et al. 1983; Maddocks and Geiser 1997; Reinertsen 1983).

As noted, previous studies have demonstrated that many small, non-migratory birds use both fat stores and facultative hypothermia to balance thermogenesis and energy expenditure overnight (Hohtola et al. 1991; Nord et al. 2009; Reinertsen 1983), but the impact of facultative hypothermia on use of fat stores within individuals has yet to be validated. Historically, gravimetric analysis—a common technique used to quantify body composition—required sacrificing animals and processing their carcasses to assess and weigh different components (Chaplin 1974; Guglielmo et al. 2011; Ward 1969), preventing measures of overnight changes in fat stores and limiting insights on individual responses to environmental temperature changes. In addition, intermittent recordings of cloacal or body temperature have been used in previous studies to assess facultative hypothermia (Carr and Lima 2013; Chaplin 1974, 1976; Hester 2001; Wolf et al. 2020). Continuous measurements of overnight body temperature can capture both the magnitude of body temperature reduction and the duration of hypothermic bouts, thereby providing a more comprehensive understanding of hypothermia use and its effects on fat stores (Maddocks and Geiser 1997; Reinertsen & Haftorn, 1986).

To further our understanding of how small birds balance fat storage and facultative hypothermia to survive cold nights, we measured overnight fat loss and variation in skin temperature in wild caught black-capped chickadees (*Poecile atricapillus*) exposed to different overnight temperatures. Black-capped chickadees are non-migratory, food-caching songbirds inhabiting the northern United States and Canada and experience significant heat loss overnight due to their small size (10–12 g; Smith 2019). Previous studies show that black-capped chickadees rely on fat stores and facultative hypothermia to survive cold nights (Chaplin 1974, 1976; Hill et al. 1980; Nord et al. 2011; Smith 2019), however, to what degree individuals employ and balance these two strategies needs further investigation. In the current study, we compare within-individual changes in overnight fat loss and skin temperature when birds are exposed to a cold versus warm night time environmental treatments, allowing us to directly examine the relationship between overnight fat loss and change in body temperature. We predicted that black-capped chickadees will use both fat stores and facultative hypothermia to cope with the cold temperature condition, and that chickadees will show a significant decrease in fat mass and body temperature overnight in the cold environment (3 °C) compared to the warm environment (20 °C). In addition, we predicted that

individuals exhibiting greater decreases in skin temperature would exhibit lower overnight fat loss.

Methods

On December 13th and December 20th, 2024, 10 wild black-capped chickadees were captured on Western University property (43.008331, −81.282327) using temporary platform feeders baited with black oil sunflower seeds and mist nets. Upon capture, birds were weighed (g), wing length (mm) was measured, and a unique combination of plastic colour legs bands was given to each bird for identification. Birds were then placed in individual cages (46 × 46 × 46 cm) in a climate-controlled room at the Advanced Facility for Avian Research (AFAR) located on Western University campus. Birds could see and hear other chickadees while housed in the climate-controlled room. Each cage contained a cuttle bone, food dish, water dish, three perches, and a caching block. Ambient temperature was set to 20 °C during captivity and animals had *ad libitum* access to water (supplemented every other day with Oasis® Vita Drops™ for small birds) and food (shelled and unshelled black-oil sunflower seeds, mealworms [1 per day], and ground Mazuri Exotic Animal Nutrition, St. Louis, MO). Birds were maintained on a photoperiod of 10 h of light and 14 h of dark to match outdoor conditions. Following two weeks of acclimation to captivity, the experiment was conducted from December 27, 2024 – January 8, 2025. Following the conclusion of our temperature treatments (described below), we gradually adjusted the daily room temperature from 20 °C to 5 °C before releasing the birds at the original trapping site on February 10, 2025, when outside conditions were suitable. We inspected all birds to ensure they were healthy, and any missing feathers had regrown prior to release.

Cold treatment

We used temperature-sensitive radio transmitters to measure skin temperature and a quantitative magnetic resonance (QMR) analyzer to measure body composition (described below). The radio transmitters interfered with the QMR measures; therefore, we used a repeated-measures block design to obtain data from each bird in both the 3 °C and 20 °C temperature treatments (Fig. S1). Birds were randomly assigned to one of two groups, Group A ($n = 5$) or Group B ($n = 5$), and the experiment was repeated over two phases. In Phase one, Group A was equipped with temperature-sensitive radio transmitters (described below), while Group B underwent QMR analysis. In Phase two, the group treatments switched, and Group A underwent QMR analysis, while Group B was equipped with the radio transmitters. In both phases, all birds were first held at the ambient daytime and nighttime temperature of 20 °C for 3 days. Following the warm treatment, all birds were exposed to 20 °C daytime temperature and 3 °C nighttime temperature for another three nights (Fig. S1). In other words, only nighttime (1700 h to 0800 h) temperature differed between the treatment groups. We chose 3 °C because it is below black-capped chickadees lower critical temperature, which ensures that individuals experience increased heat loss, and 20 °C because it falls within the birds' thermoneutral zone (Chaplin 1974). This design also maintains a sufficient temperature difference between the two treatments to maximize the likelihood that birds would employ facultative hypothermia. To ensure birds were solely dependent on endogenous energy stores overnight, all food bowls were removed, cage trays were emptied, and paper linings were replaced to remove any cached food prior to lights-off. Room lights were programmed to turn on at 0700 h and lights off at 1700 h local time. For the cold treatment nights, the temperature was adjusted at 1600 h and had dropped to 3 °C by 1630 h. The next morning, at 0800 h the temperature was reset to 20 °C.

Temperature sensitive radio transmitters

Temperature-sensitive radio transmitters (BD-2XT, Holohil Systems Ltd., Ontario) were used to measure individual body temperature (T_b) throughout the night (Barclay et al. 1996; Williams et al. 2009). The transmitters have a temperature sensor on the underside that measures the skin temperature (T_s), which is lower than, but closely correlated to, the core T_b (Barclay et al. 1996; McGuire et al. 2012; Nord et al. 2016; Williams et al. 2009). Each transmitter emits pulses at different rate dependent on the temperature it detects; higher temperatures result in more frequent pulses. Pulse rate, expressed as beats per minute (BPM), was converted to skin temperature using a known temperature calibration curve. To affix the transmitters, a small number of feathers were removed from the back of each bird (between the shoulders) and transmitters were externally attached using a medical grade, nontoxic latex adhesive (Torbot Bonding Cement). Due to the birds' movement when the lights were on, the transmitters commonly fell off, therefore, we only used overnight recordings from the transmitters, when they were continuously attached. In cases where transmitters fell off during the day, we inspected the bird to ensure there were no injuries and reattached the transmitter 30 min–1 h prior to lights off. At the end of each Phase, transmitters were removed using REMOVE universal adhesive remover (Smith & Nephew Medical Ltd.), as needed. As directed by a Western University Veterinarian, Polysporin antibiotic ointment (Johnson & Johnson INC) was applied if birds

showed signs of irritation on the adhesive spot, however, this was rare.

Signals from the temperature sensitive transmitters were recorded using a Lotek radio receiver throughout the experiment (Lotek SRX 800, Lotek Wireless, Newmarket, ON, Canada). The radio receiver was programmed to record and log signals on the specific radio frequency of each transmitter for 30 s before switching to the next one. As a result, the pulse rate of each transmitter was recorded for 30 s every 2.5 min in a repeating cycle. To determine each bird's T_s, the recorded pulse rates were converted into temperature values using the calibration curve equations derived from each transmitter (Barclay et al. 1996; Williams et al. 2009). Prior to converting pulse rates to T_s, outliers were removed from the dataset, which included pulse rates below 25 or above 46 BPM. This step excluded inaccurate readings caused by transmitters either falsely doubling the pulse count (due to signal echo) or skipping pulses (due to poor reception).

To obtain calibration equations, the transmitters were submerged in a thermostatic water bath (Lauda Ecoline RE 106, Lauda-Brinkmann, Delran, NJ, USA), and the corresponding pulse rates were recorded between 15 °C and 40 °C at 5 °C intervals. A curve of best fit was created for each transmitter by plotting pulse interval against known water bath temperatures using a log-linear regression model. A log-linear regression provided the best fit for the data compared with square-root and linear models, as determined by the Akaike Information Criterion (AIC). The logarithmic equation derived from these curves was then used to convert the pulse rates measured during the experiment into temperature (Table S1).

Quantitative magnetic resonance

Fat and lean mass for each bird was measured using Quantitative Magnetic Resonance (QMR) (Echo-MRI-B, Echo Medical Systems, Houston, TX, USA (Guglielmo et al. 2011). QMR uses alternating magnetic fields to measure body composition, similar to magnetic resonance imaging (Guglielmo et al. 2011). This non-invasive technique allows for repeated measurements of body composition in the same bird over time (Guglielmo et al. 2011). Unlike gravimetric chemical analysis, a common method for measuring body composition, repeated measurement using QMR accounts for individual differences and allows us to determine whether an individual bird experiences fat loss overnight across treatment groups. Additionally, QMR has been shown to provide higher precision and accuracy compared to gravimetric analysis in various bird species and has been used to study fat stores (Guglielmo et al. 2011; Seewagen and Guglielmo 2011).

QMR measurements were taken from 0800 h to 0830 h and 1600 h to 1630 h each day of the experiment, one hour after lights were turned on and one hour before lights were turned off. Birds were collected from their home cages, held in cloth bags, and returned to their home cages once QMR was completed for all birds to minimize differences in handling time prior to lights off. The QMR was calibrated using a 3 g oil sample prior to measuring birds. To obtain QMR measurements, each bird was placed in a holding tube headfirst, ventral-side-down, and scanned using the 'small bird' setting of the Echo-MRI software. Each scan was conducted using the two-accumulation setting, a method shown to yield high accuracy (Guglielmo et al. 2011). A single two-accumulation scan consists of four replicate fat and lean mass measurements, which are averaged to produce the final output (Guglielmo et al. 2011). To further improve precision, each bird was scanned twice per session, and the results were averaged.

Statistical analysis

All statistical analyses were performed using R version 2024.12.1 (R Core Team 2024) and Generalized Linear Mixed Models (GLMMs) were implemented using the *glmmTMB* function from the package glmmTMB (Brooks et al. 2025). Model assumptions were checked using the function *simulateResiduals* in R package "DHARMa" (Tartig 2025). Figures were created using ggplot2 v.3.5.1 (Wickham 2016).

Skin temperature

Generalized Linear Mixed Model (GLMM) was used to test for within-individual differences in T_s of each bird at 3 °C and 20 °C. To account for the repeated measures design of our treatment, bird ID was included as a random effect. Day of each condition (first, second, and third day of 20 °C and 3 °C conditions) and group assignment (Group A and Group B) were included as fixed effects to account for acclimation to treatment condition and order effects due to the block design used. In addition, initial body mass upon capture was included in the model to account for variation in body condition in the wild, rather than body condition after acclimation to captivity.

Body composition

Individual differences in overnight fat and lean mass loss were calculated by taking the difference between fat and lean mass measured at 1600 h from fat and lean mass measured at 0800 h. To compare average fat and lean mass loss of birds under 3 °C versus 20 °C, a GLMM was used to compare the within individual fat, and lean mass loss

between temperature treatments with bird ID was included as a random effect. Group assignment (Group A and Group B) was also included as a fixed effect to account for order effects of overnight temperature treatment.

Overnight fat loss and facultative hypothermia

To quantify the degree of T_s decrease within individuals and between treatments, we calculated a facultative hypothermia index (FHI). The starting temperature of each individual at 1700 h in each condition was used as a baseline, and the area between this baseline and subsequent T_s values was calculated follow similar methods to Baloun and Guglielmo (2019). These areas were square root transformed to obtain linear scaling, and the resulting values were referred as FHI (Baloun and Guglielmo 2019). Individuals with lower T_s across the night had higher FHI values, representing a higher use of facultative hypothermia. These FHI values were then used as a predictor variable in GLMMs to test for a relationship between facultative hypothermia and overnight fat loss, lean mass loss, and total energy expenditure. In all models, FHI and temperature treatment (3 °C vs. 20 °C) were included as the fixed-effect predictors, bird ID was included as a random effect, and the response variable was either overnight fat loss, or overnight lean mass loss. Upon examining the relationship between lean mass and FHI, we detected an interaction with temperature treatment. Therefore, separate GLMMs were fitted within each condition for the lean mass analysis.

Animal care and ethics

All procedures in this study were performed under the permission of the University of Western Ontario's Animal Use and Care Committee (Protocol # 2024−113). Scientific permits for collection and banding of birds were provided by Environment and Climate Change Canada (SC-OR-2024-00096 and 10978).

Results

One bird from Group A died of unknown causes during the late experimental stage; therefore, all data obtained from that bird were excluded from statistical analysis. In addition, the room temperature was not changed to 3 °C prior to lights out on the last day of the experiment, thus the 3 °C condition data obtained from Phase 2 only consisted of two nights instead of three nights in Phase 1.

Skin temperature

Over 14 h post lights off, the mean (±standard error) overnight T_s in the 3 °C condition was 33.42±0.22 °C and 34.33±0.57 °C in the 20 °C condition. However, T_s began to stabilize around 5 h after lights off (Fig. 1) and mean T_s after this point was 31.84±0.19 °C in the 3 °C condition and 33.68±0.13 °C in the 20 °C.

Given the distribution of the data for skin temperature (T_s) (Figs. 1 and 2), we started by running a model with an interaction term between condition and hour since lights off and found a significant interaction ($\beta = -0.27$, SE=0.05, $z = -5.83$, $p<0.001$). To tease apart this interaction, we used three approaches: (1) We analyzed the two conditions in separate models, (2) We averaged T_s across the 14-hour period, and (3) We restricted the analysis to T_s 5 h following lights off, once T_s stabilized.

First, we ran separate models for each condition to assess differences between mean T_s before and after the 5th hour following lights off. We found a significant difference in the 3 °C condition ($\beta=2.68$, SE=0.26, $z=10.48$, $p<0.001$), but not in the 20 °C condition ($\beta = -0.17$, SE=0.26, $z = -0.64$, $p<0.525$). In the 3 °C condition, mean skin temperature decreased from 32.20 °C before the 5th hour to 30.94 °C after, whereas in the 20 °C condition it remained unchanged from 35.08 °C before the 5th hour to 35.20 °C after. Second, we averaged T_s across the full 14 h and found that within individual mean overnight T_s was significantly lower in the 3 °C condition compared to the 20 °C condition ($\beta = -0.72$, SE=0.21, $z = -4.25$, $p<0.0001$) (Figs. 1 and 2). Finally, when we restricted the analysis to T_s after the 5th hour, within individual mean overnight T_s was significantly lower in the 3 °C condition compared to the 20 °C condition ($\beta = -1.80$, SE=0.15, $z = -11.61$, $p<0.001$).

We did find an effect of day on T_s, such that the mean overnight T_s in the 20 °C condition (but not in the 3 °C condition) was significantly lower on the second day of treatment compared to first day of treatment ($\beta = -1.95$, SE=0.33, $z = -5.99$, $p<0.001$) and the third day of treatment compared to first day of treatment ($\beta = -2.18$, SE=0.33, $z = -6.65$, $p<0.001$; Fig. S2). Therefore, day of the treatment was included as a factor in all models. Group assignment of birds (Group A, transmitters first or Group B, QMR first) had no significant effect on overnight T_s change ($\beta=0.73$, SE=0.77, $z=0.96$, $p>0.05$). Additionally, initial body mass at capture, a proxy for body condition, had no significant effect on overnight temperature change ($\beta=0.57$, SE=0.38, $z=1.51$, $p>0.05$).

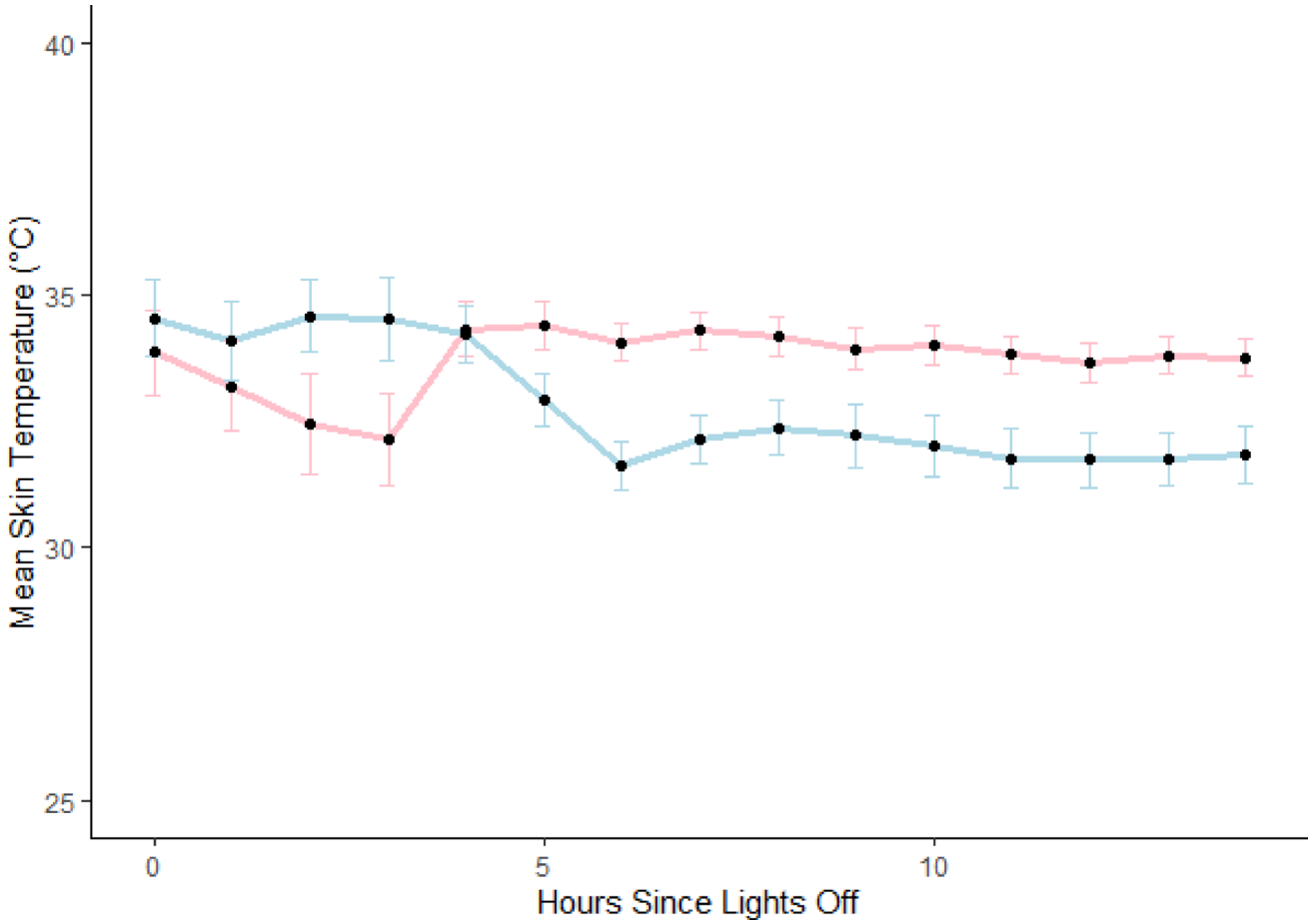

Fig. 1 Skin temperature plotted by hour for nine black-capped chickadees after lights off, at 1700 h. Black points represent mean ± SE. The pink line shows average skin temperature of birds over 14 h when the environmental temperature was 20 °C and the blue line shows average skin temperature over 14 h when the environmental temperature was 3 °C

Body composition

Overnight loss in lean mass did not differ significantly between the 3 °C and 20 °C treatment (z = −0.27, p = 0.79; Fig. 3A). However, group assignment of birds significantly affected overnight lean mass loss, with greater loss observed in birds that underwent transmitter measurements first (β = 0.14, SE = 0.06 g, z = 2.33, p = 0.020). In contrast, overnight fat loss in the 3 °C condition (0.71 ± 0.04) was significantly greater than in the 20 °C condition (0.55 ± 0.04; z = 4.348, p < 0.001; Fig. 3B) and group assignment had no significant effect on overnight fat loss (z = 1.72, p = 0.08).

Relationship between overnight mass loss and FHI

After removing one outlier from the data set, there was no significant interaction between treatment condition and use of facultative hypothermia on lean mass loss (β = −0.0058, z = −1.02, p = 0.31, Fig. 4A). The treatment condition had no significant effect on overnight lean mass loss (β = 0.033, z = −1.02, p = 0.16). However, the effect of facultative hypothermia on overnight lean mass loss approached significance (β = −0.0046, z = −1.95, p = 0.052).

Use of facultative hypothermia had a significant negative effect on overnight fat mass loss, regardless of temperature treatment (β = −0.0061, z = −4.7, p < 0.001, Fig. 4B). The model explained 38.8% of the variation in overnight fat loss (R^2 = 0.388), indicating that a greater decrease in T_s (higher FHI) was associated with less fat loss. Looking at the effect of temperature treatment on FHI and overnight fat loss, we found a significant interaction of treatment condition and FHI (β = −0.026, z = 0.−7.87, p < 0.001), therefore, we tested the effect of FHI on fat loss for each temperature condition separately. At 3 °C, there was a significant negative relationship between FHI and fat mass loss (β = −0.015, z = −2.43, p = 0.015), however, there was no significant effect of FHI on fat mass loss at 20 °C (β = 0.0014, z = 1.11, p = 0.27).

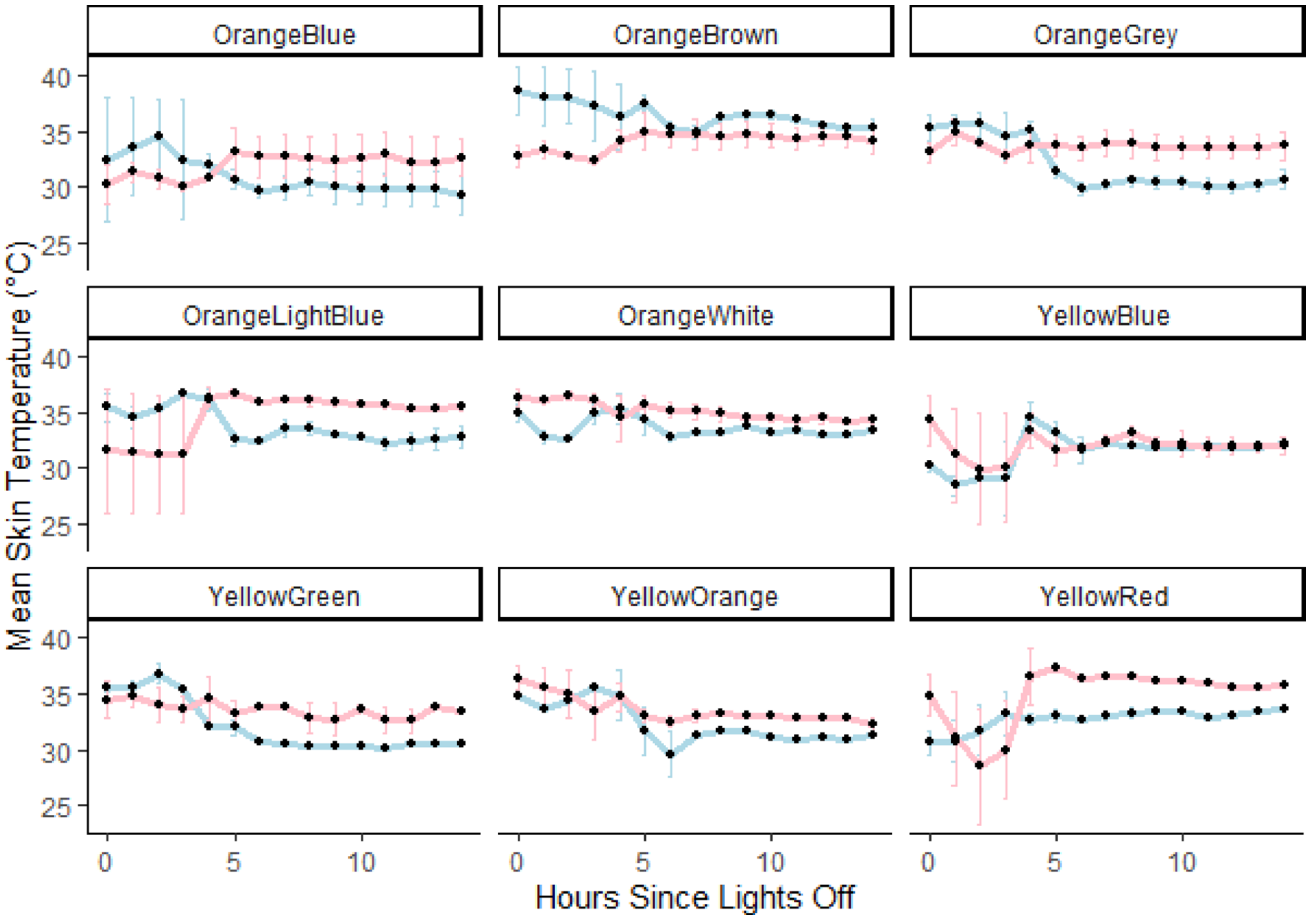

Fig. 2 Individual mean skin temperature data of nine black-capped chickadees following lights off, at 1700 h. Black points represent mean ± SE. The pink line shows average skin temperature by hour at 20 °C and the blue line shows average skin temperature by hour at 3 °C. The mean skin temperature of birds in 3 °C condition was lower than the mean skin temperature in 20 °C. Note two individuals did not show decreased skin temperature during the 3 °C treatment compared to time 0000 h (YellowRed and YellowBlue; see Fig. S3 and Table S2). Dashed lines represent the baseline temperature for each individual, used as a threshold to obtain the amount of time and temperature below baseline (T_s at lights off) and used to estimate the facultative hypothermia index

Discussion

This study aimed to assess the relationship between overnight fat mass loss and use of facultative hypothermia within individual black-capped chickadees exposed to cold versus warm environmental temperatures. Within individuals, birds showed significantly lower skin temperatures and greater overnight fat loss in the cold, 3 °C condition compared to the warm, 20 °C condition, indicating the use of facultative hypothermia in response to a drop in overnight temperature. Importantly, we found a significant negative relationship between the extent of hypothermia used and overnight fat loss, such that individuals that showed more dramatic decrease in skin temperature lost less fat overnight in the cold condition. Interestingly, while most birds dropped their skin temperature overnight in the cold condition, there were two (YellowRed, YellowBlue, see Fig. S3) that did not. These findings demonstrate individual variation in the use of facultative hypothermia to conserve fat stores and show that birds can flexibly respond according to environmental conditions and individual physiological constraints.

Overnight skin temperature of black-capped chickadees decreased in the cold temperature condition compared to the warmer condition, consistent with our predictions and previous findings that black-capped chickadees use facultative hypothermia to cope with such physiological challenges (Hill et al. 1980; McKechnie and Lovegrove 2002). Notably, in both group (Fig. 1) and individual data (Fig. 2) we see the opposite pattern of our main conclusion prior to 4 h after lights were turned off. The cold treatment group shows higher T_s compared to the warm temperature group, however, the variation in T_s prior to 4 h is much larger and there were no significant differences between the cold and warm treatment. This pattern may suggest that the birds are still active for several hours after the lights are turned off (e.g., Hawkshaw and Mathot 2026) and perhaps the first

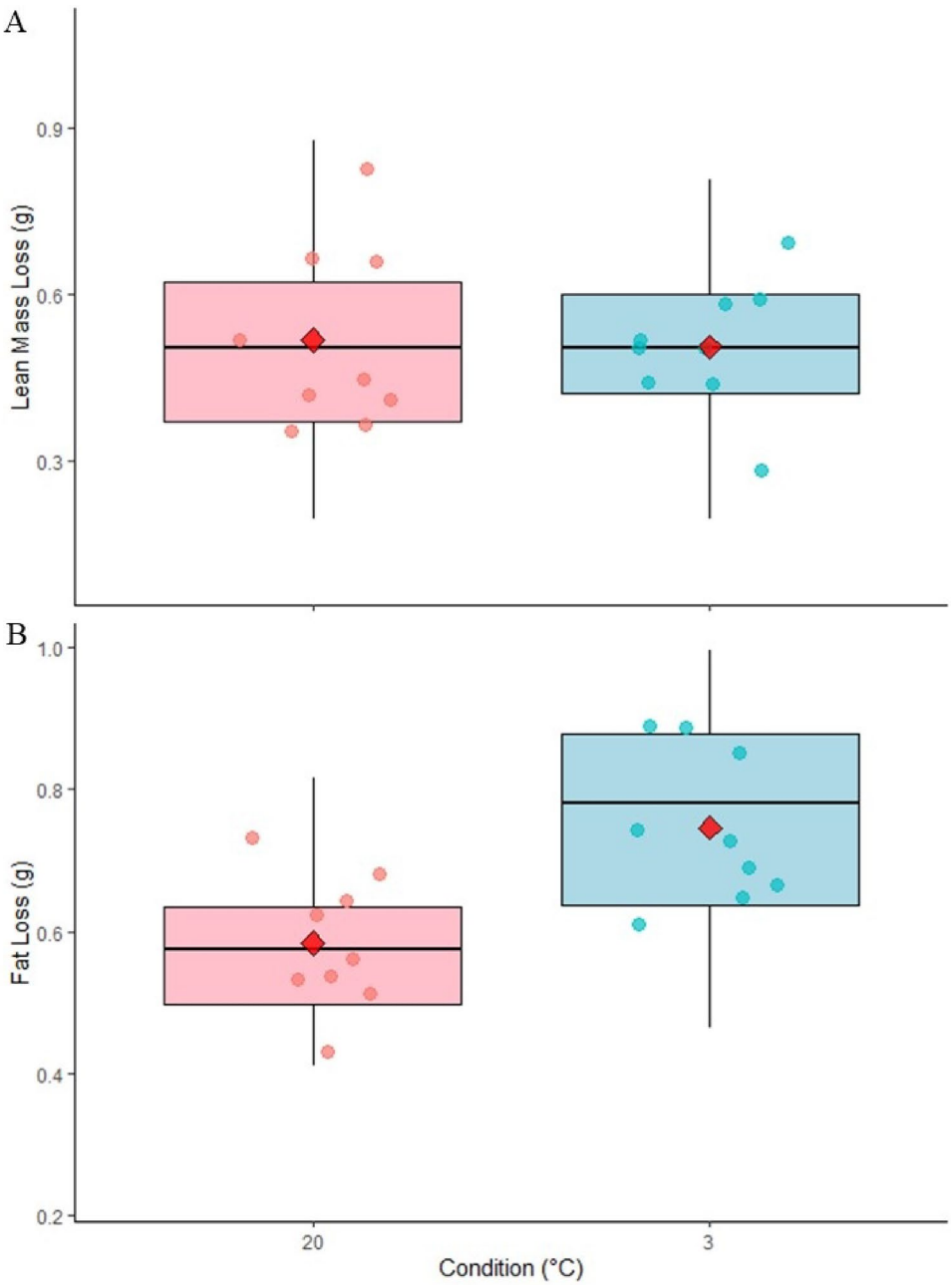

Fig. 3 Mean overnight (**A**) lean mass loss, and (**B**) fat loss in black-capped chickadees in 3 °C (blue) and 20 °C (pink) treatment conditions. (**A**) No significant difference in lean mass loss was observed between treatment groups. (**B**) Mean overnight fat mass loss was greater in 3 °C compared to 20 °C. Each points represents individual birds' data, the thick horizontal line is the median, the boxes contain the 25th and 75th percentiles, whisker lines represent maximum and minimum values and red diamonds represent the mean

4 hours are a decision time or that animals use a time sensitive threshold for facultative hypothermia. In the cold condition, birds' skin temperature decreased rapidly about 4 h after lights out and remained low for the rest of the night. This pattern of temperature decrease was consistent across most birds when they were exposed to the cold condition and suggests a potential threshold of cold exposure that triggers facultative hypothermia. Although the mean overnight difference (14 h) in T_s between cold and warm conditions was less than 1 °C, the mean decrease in T_s 5 h after lights-off differed by 1.84 °C. These temporal patterns in T_s indicate that, despite being measured on the skin, the observed differences reflect changes in body temperature rather than ambient temperature. In addition, within-individual comparisons strengthen these findings, as this experimental design accounts for variability between transmitters and identifies changes within individuals across the two temperature conditions. Importantly, the use of facultative hypothermia following a period of cold exposure warrants further investigation into the underlying cellular mechanisms, as well as the environmental and individual factors—such as food availability, predation risk, and body condition—that may influence these patterns.

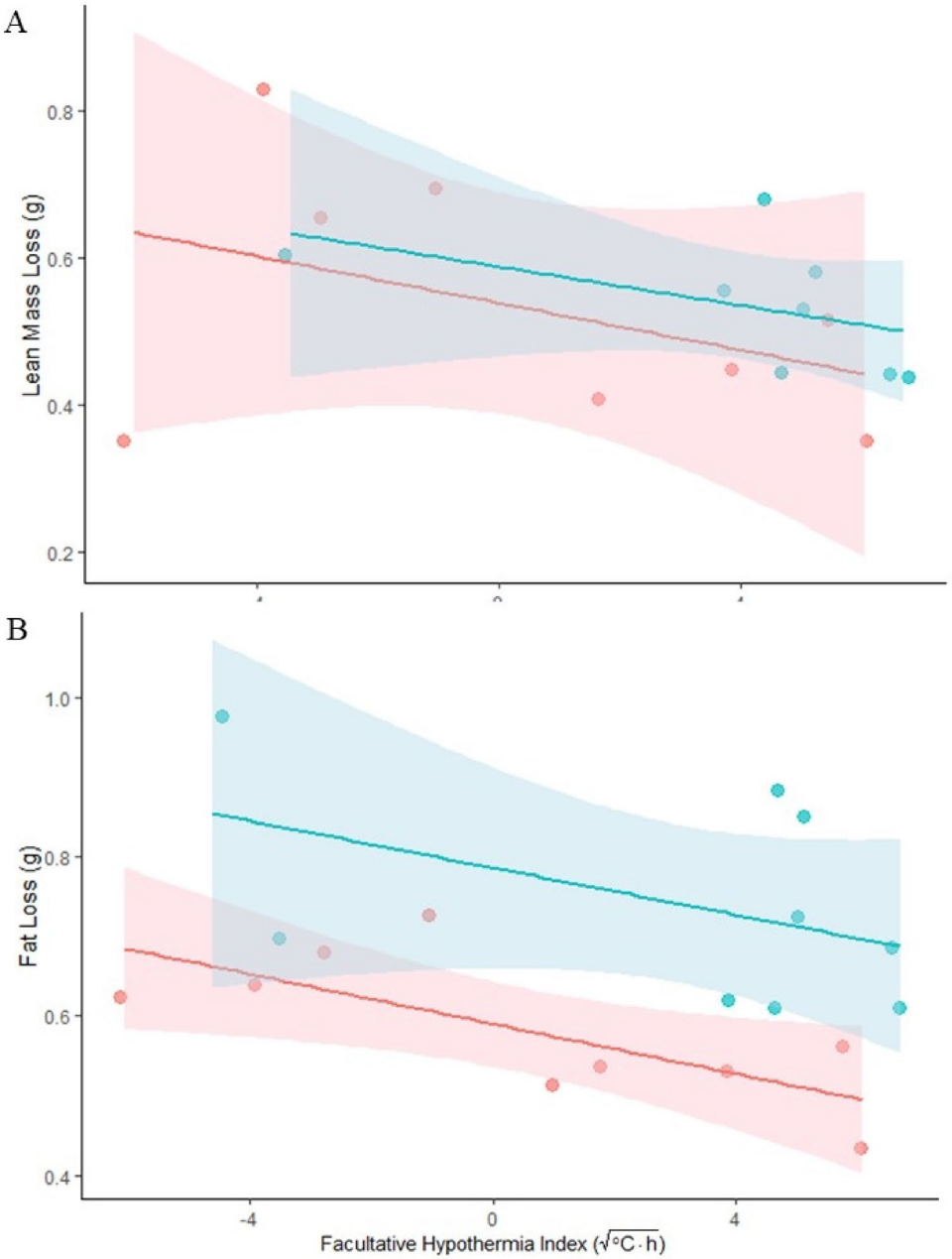

Fig. 4 Relationship between the facultative hypothermia index (FHI; √°C·h) and (**A**) lean mass loss, and (**B**) fat mass loss for each temperature treatment condition (blue = 3 °C, pink = 20 °C). Each point represents an individual bird, and solid lines represent the linear models for each condition. (**A**) Lean mass loss was positively correlated with FHI in the 3 °C condition but was not significantly correlated in the 20 °C condition, (**B**) while fat mass loss was negatively correlated with FHI in the 3 °C condition, but not the 20 °C condition

It is important to consider the validity of skin temperature as a proxy for body temperature compared with other commonly used measures. Cloacal temperature has traditionally been used because it provides a reliable estimate of core body temperature (Andreasson et al. 2023). Comparisons between skin and cloacal temperatures have shown that ambient temperature influences the relationship between these measures, with skin temperature generally being 2 °C ~ 3 °C lower than cloacal temperature under colder conditions (Andreasson et al. 2023). Although this could suggest that reductions in skin temperature simply reflect lower ambient temperatures, several lines of evidence support the use of skin temperature as an accurate indicator of facultative hypothermia. First, the thermal gradient between the body core and the skin is likely smaller in small birds like chickadee than that observed in larger avian species, resulting in skin temperature more closely reflecting core body temperature. Second, we found that greater use of facultative hypothermia was associated with reduced overnight fat use. Because all birds experienced the same experimental conditions, variation in overnight fat utilization likely reflects differences in thermoregulatory energy expenditure. As body temperature regulation is a major determinant of thermoregulatory energy expenditure, the observed relationship between skin temperature and overnight fat loss supports the use of skin temperature

as a biologically meaningful indicator of facultative hypothermia in this study.

Alongside temporal patterns in body temperature change, we observed substantial individual variation in the use of facultative hypothermia despite birds being exposed to the same ambient temperatures and housing conditions. Individuals differed in the magnitude of T_s reduction under cold conditions, and those that exhibited smaller decreases in T_s tended to lose more fat overnight. In addition, the two individuals that showed no evidence of facultative hypothermia exhibited markedly greater overnight fat loss (Fig. S3). While previous studies have linked body condition to the use of facultative hypothermia (Lewden et al. 2014; Pravosudov and Lucas 2000), body condition, measured as body mass at the time of initial capture, did not predict use of facultative hypothermia in this study.

As predicted, greater use of facultative hypothermia resulted in reduced overnight fat loss in cold conditions. This finding supports the idea that black-capped chickadees can conserve fat stores through facultative hypothermia, potentially allowing them to optimize use of these fat stores for foraging after overnight fasting (Clark and Dukas 2000; Hill et al. 1980). This energy-conserving strategy may alleviate the immediate need to forage upon waking, giving the birds more flexibility in timing their foraging activity. For instance, foraging patterns may change in response to predation risk, with peak foraging intensity delayed until later in the day if predation risk is high in the morning (Macleod et al. 2005). In such cases, facultative hypothermia can be especially advantageous, as it may allow flexible foraging timing. Consistent with this idea, the extent of facultative hypothermia has been shown to increase under elevated predation risk (Barratt et al. 2025). Overall, flexibility in foraging timing provided by facultative hypothermia may be crucial under cold, food-scarce, or high-predation winter conditions.

In this experiment, we provided each bird with similar amounts of food and deprived birds of food overnight to control for fat stores and food intake, therefore, we attribute the observed increase in overnight fat loss to changes in environmental temperature rather than differences in food availability. However, the degree of overnight fat loss observed in this study was not as pronounced as in previous studies (Chaplin 1976). This is most likely due to the difference in treatment temperature, as prior research has examined fat stores at temperatures below 0 °C (Chaplin 1974, 1976; Hill et al. 1980) and we were limited by the capabilities of our holding rooms to 3 °C. While, 3 °C does not represent the coldest conditions that chickadees may experience in winter and 20 °C does not reflect typical daytime winter temperatures, these conditions are consistent with transitional seasons like fall/spring when large swings in temperature occur. We housed birds under a corresponding photoperiod. The 3 °C lies below the lower critical temperature of black-capped chickadees and provides enough contrast from the baseline temperature (20 °C) to allow us to quantify the use of facultative hypothermia.

While acclimatization to cold environmental temperature during winter has been shown to be one of the primary drivers influencing overnight fat loss in black-capped chickadees (Cooper and Swanson 1994; Petit et al. 2017; Ward 1969), fat loss is expected during any period of fasting, which we observed under both cold and warm conditions in this experiment. Temperatures fluctuate on a day-to-day basis within a given season; thus, the ability to exhibit rapid physiological changes in response may be crucial for survival. This is especially true at higher latitudes and altitudes where weather condition can be unpredictable and change rapidly with in a day (Ohmura 2012). Considering this, the rapid responses observed in facultative hypothermia from the first day of the cold condition suggests that black-capped chickadees have the capacity to adjust their physiological responses to abrupt changes in environmental temperature (Cooper and Swanson 1994; McNamara et al. 2004).

In conclusion, the evidence suggests that black-capped chickadees rely on fat stores for overnight survival regardless of season and exhibit flexibility in the use of facultative hypothermia in response to fluctuating environmental temperatures. By using a within-individual experimental design, we found that increases in overnight fat loss under cold conditions are consistent with previous studies (Cooper and Swanson 1994; McNamara et al. 2004) and further demonstrate that variation in fat loss is driven by individual differences in the use of facultative hypothermia in response to environmental temperature changes. As the climate becomes less predictable with more extreme weather events, understanding how small birds cope with weather perturbations like overnight cold snaps can provide insights into their ability to adapt to changing environmental conditions.

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