Nocturnal hypothermia impairs flight ability in birds: a cost of being cool

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Many birds use regulated drops in night-time body temperature ($T_b$) to conserve energy critical to winter survival. However, a significant degree of hypothermia may limit a bird’s ability to respond to predatory attack. Despite this likely energy-predation trade-off, the behavioural costs of avian hypothermia have yet to be examined. We thus monitored the nocturnal hypothermia of mourning doves (Zenaida macroura) in a laboratory setting in response to food deprivation. Nocturnal flight tests were used to quantify the flight ability of hypothermic doves. Many hypothermic doves (39% of tests) could not fly while carrying a small weight, but could do so after quickly warming up to typical daytime $T_b$. Doves that were unable to fly during their first test were more hypothermic than those that could fly, with average $T_b$ reductions of 5.3 ± 0.8°C and 3.3 ± 0.8°C, respectively, but there was no overall indication of a threshold $T_b$ reduction beyond which doves were consistently incapable of flight. These results suggest that energy-saving hypothermia interferes with avian antipredator behaviour via a reduction in flight ability, likely leading to a trade-off between energy-saving hypothermia and the risk of predation.

1. Introduction

Birds face significant energy challenges throughout the winter months. Exposure to low ambient temperatures increases daytime foraging demands, and many species rely on energy reserves gained during the day to survive cold winter nights [1,2]. Unpredictable winter storms can also limit or prevent access to food for an extended period of time. Thus, it is imperative that a wintering bird adequately manage its energy reserves to maximize the probability of survival during winter [3–6].

Wintertime energy management in birds often involves the use of regulated nocturnal hypothermia [7], and many species rely on a drop in body temperature (and thus metabolic rate) to conserve energy during periods of food restriction ([8,9]; see also [10]). Torpor is a more extreme form of hypothermia that is often characterized by a relatively large drop in body temperature and greatly reduced behavioural responsiveness [11–13]. Torpor is most often observed in relatively small species with comparatively low energy costs of rewarming [12] and is especially pronounced in species which rely on ephemeral food sources, such as nectar or insects [8]. Although the distinction between torpor and milder hypothermia remains unclear [8,13,14], body temperature drops in excess of 5°C could be considered torpor [13]. Hypothermia (rather than torpor per se) is a much more prevalent and taxonomically widespread physiological response to food shortage [8] and even relatively small drops in body temperature can yield significant energy savings [15–17].

Although there are clear energy benefits in hypothermia, there are also likely associated costs [18]. For instance, hypothermia can reduce running speed [19], the force of muscle contraction [20] and central nervous system functioning [21]. Such effects likely underlie observations of lethargy in hypothermic animals [16,22] and could easily lead to an increase in the risk of predation [23]. However, few studies have directly examined the predation-related costs of hypothermia. One exception here is an experiment by Laurila & Hohtola [24], which suggests that pigeons (Columba livia) reduce their depth of hypothermia in the presence of a model avian predator. On the other hand, Amo et al. [25] found that birds did not alter their night-time body temperature in response to predator odour.
We examined the potential predation-related costs of nocturnal hypothermia in mourning doves (Zenaida macroura). Mourning doves are frequently exposed to food unavailability and high predation during winter months [26–29], and thus probably experience a trade-off between thermoregulation and predation risk. Doves in general appear to use hypothermia when faced with food restriction [16,22], which we also demonstrate in mourning doves. To quantify the potential predation-related costs of hypothermia, we food-deprived doves and measured their nocturnal flight ability while significantly hypothermic. Our results suggest that such energy-saving hypothermia leads to an increase in predation via a reduction in flight ability.

2. Material and methods

All observations were conducted on wintering mourning doves captured in Vigo County, IN, USA. Birds were captured over the course of two winters, using a millet-baited trap, between 14–28 February 2012 (N = 4) and 29 December 2012–4 March 2013 (N = 32). Captured doves were immediately transported to environmental control chambers at Indiana State University. Each chamber was on a 10 L : 14 D cycle and held at a constant environmental temperature of 5°C to simulate natural winter conditions. Doves were housed in pairs in a wire mesh cage (102 × 61 × 46 cm in length, width and height) within each chamber. The birds were physically separated by a wire mesh divider that divided the cage into two equal-sized compartments, allowing these social birds to interact while maintaining separate access to food. Only one of the two birds was included in flight tests, with the other serving as a companion bird.

Dove body temperature (Tb) was monitored using subcutaneously implanted temperature-sensitive radio transmitters (Holohil Systems, Ltd; model BD-2T, 1.2 g) as detailed in the electronic supplementary material. In summary, following a 2-day acclimation period, each bird was weighed to the nearest gram and anasthetized. Transmitters were surgically implanted subcutaneously between the wings on the dorsal side of the bird. Birds remained anaesthetized following transmitter implantation, permitting us to fit a backpack-style Velcro harness designed to allow birds to carry additional weight during flight tests. Birds were placed back in their home cages once they were alert and had recovered from anaesthesia. Body temperature was monitored continuously from outside of the environmental control chambers. Transmitter signals (recorded in beats min⁻¹) were converted to Tb by using transmitter-specific calibration equations.

After a minimum of 3 days of post-surgery recovery (range = 3–8 days; mean = 4.7 days), nocturnal hypothermia was induced by exposing birds to 1–3 days of complete food deprivation, conditions similar to those experienced during heavy snow storms. The length of the food deprivation period was dependent upon the individual’s ability to maintain normothermic daytime Tb (see the electronic supplementary material). Most birds had no difficulty maintaining normal daytime Tb, although five birds required supplemental food during this period. A total of 25 birds were subjected to night-time flight tests following a minimum of 24 h of food deprivation.

The nature of nocturnal hypothermia in mourning doves was first examined by generating nightly Tb profiles for 10 doves during winter of 2010–2011. The above methods for transmitter implantation and food deprivation were used for these 10 birds. However, no flight tests were conducted on these doves, which were left undisturbed for the duration of the deprivation period. Body temperature profiles were produced by plotting Tb for every min of the deprivation period.

We conducted night-time flight tests on hypothermic birds to assess the potential predation-related costs of hypothermia. Our flight test arena was fairly large (see below) but not large enough to fully assess the flight ability of a fast bird like a mourning dove. Thus, we could not readily assess flight ability via speed or manoeuvrability, both of which are likely important in escaping a nocturnal attack from a large owl. We thus chose to assess whether or not a dove, with a small amount of backpack weight (15% of starting body mass), could fly away after being placed on the floor in front of an experimenter. A bird released close to a human should be very motivated to fly away, and we assume that a bird able to fly with this extra weight would also be able to fly with the speed and manoeuvrability necessary to quickly escape a serious nocturnal attack (see also [5,30]). Note that pigeons (a somewhat larger dove) can carry up to 100% of their weight in flight [31], thus the 15% weight is not a large burden and represents normal weight gain over the course of a day [32] or the weight of a large meal.

Flights were conducted 3 h after ‘lights-off’ when birds would be near their minimum Tb (see the supplemental material for full details). Birds were captured in their home cages and carried to a large flight arena (7.3 × 1.2 × 2.7 m in length, width and height) adjacent to the environmental control chambers. After weight addition, birds were placed on the floor in front of the experimenter facing towards the illuminated, far-end of the flight arena. Doves were given approximately 5 s to assess their environment and birds that did not attempt to fly after 5 s were lightly tapped on the tail to encourage them into the air. All birds responded to the experimenter even if they could not fly, usually attempting to run away after a failed flight attempt. Flight ability was scored as ‘flight’ if a bird flew vertically up to the ceiling or if they flew the length of the hallway at least half of the height of the arena. All other trials were scored as ‘no flight’. In practice, a bird that could fly the length of the hallway almost always flew in the upper half of the hallway; only one individual weakly flew the length of the arena at approximately 0.5 m above the ground.

A dove that was able to fly during its first trial was not tested again during the same night. We removed the weight from its backpack and immediately returned the bird to its home cage with the lights-off. Food deprivation continued (subject to a bird’s ability to maintain Tb; see the electronic supplementary material) and the bird was tested again on the following night. Total food deprivation for such birds usually lasted for 2 days (with a maximum of 3 days for two birds).

A bird that was unable to fly during the first flight test underwent two additional flight tests. First, we removed the weight and conducted another flight test immediately after the first test. This allowed us to examine the effects of weight addition on the flight ability of hypothermic birds. The bird’s Tb increased at a rate of 0.5°C min⁻¹ beginning, approximately 1 min after the start of the flight tests (J. M. Carr 2013, unpublished data). Both of the hypothermic flight tests were completed within the first minute of capture (with approx. 30 s between the first and second flights), thus birds remained near their minimum Tb for both flight tests. Following these two hypothermic flight tests, birds were placed in a translucent cloth holding bag in a well-lit room (21°C) for approximately 20 min, during which their Tb increased to normothermic daytime levels. An additional flight test was conducted on these warmed up birds (carrying the same weight) to compare their flight ability while hypothermic and normothermic. Birds were provided with ad libitum food upon the conclusion of the three consecutive flight tests. All methods were approved by the Indiana State University Institutional Animal Care and Use Committee (Protocol no. 10–25-2010:SLL/JMC, Amendment no. 304728-SLL).

(a) Statistical and related considerations

Four of the 25 flight-tested doves were not included in our analyses. Two birds appeared weak and were unable to fly.
regardless of whether or not they were carrying weight or normothermic. A third bird appeared to be stunned after it fell and missed the protective cushion at the end of the flight arena. The fourth bird exhibited the odd behaviour of flying towards and perching on the experimenter during flight tests.

A stepwise binary logistic regression was used to determine whether \( T_b \) drop or starting body mass influenced the flight ability of doves during their first attempt on the first deprivation night. Flight ability was scored as ‘no flight’ and ‘flight’, which were assigned dummy codes of 0 and 1, respectively. Body temperature drop was determined by calculating the difference between nighttime flight test \( T_b \) and daytime \( T_b \) (average \( T_b \) between 1200 and 1500 h the day prior to the onset of food restriction). Starting body mass was also included as a covariate in the analysis because larger individuals with more potential energy reserves may remain less hypothermic than small individuals (but see [33]). A binary logistic regression was also used to examine whether \( T_b \) drop influenced flight ability during the first weighted attempt of the second deprivation night. Starting body mass was not included in this analysis owing to reduced sample size on the second night of food deprivation (see Results). In addition to using relatively shallow hypothermia during the night, larger individuals may also be able to withstand a longer deprivation period in general. Thus, we also used a t-test to compare the starting body mass of doves that could withstand only 1 day of food deprivation (\( N = 11 \)) to doves that were exposed to 2 days without food (\( N = 10 \)). Statistical analyses were conducted using SPSS v. 11.0 (SPSS, Inc., Chicago, IL, USA).

Owing to the nature of regulated nocturnal hypothermia, several conceivably informative experimental tests were not possible. Our flight tests involved doves at (i) low \( T_b \), under (ii) food deprivation and (iii) just awakened from sleep. The inability to fly could be related to any of these three factors. However, these factors are inextricably linked, and thus the effects of each could not be analysed separately (see also Discussion). In addition, the only practical way to complete the sequence of flight testing over a short period of time was to conduct the hypothermic test prior to the normothermic test. Flight testing induced a period of rapid \( T_b \) increase that was often sustained for hours postflight (even with the chamber lights-off). An alternate procedure with reversed flight order (normothermic flight first) would require several hours of cool-down before the second (hypothermic) flight, with no guarantee that the birds would become significantly hypothermic after the first test.

### 3. Results

Body temperature \( (T_b) \) plots show the use of nocturnal hypothermia in food-restricted mourning doves (figure 1). Body temperature closely tracked the light : dark cycle, falling quickly at lights-off and rising approximately 1 h before lights-on. Nocturnal \( T_b \) dropped progressively lower with each day of the deprivation period (figure 1), although \( T_b \) profiles varied among individuals. On average, \( T_b \) dropped 2.2 °C (s.e.: ± 0.19; \( N = 10 \) doves) during sleep on control nights prior to food deprivation and fell by 4.1 °C (± 0.28; \( N = 10 \)), 5.2 °C (± 0.63; \( N = 10 \)) and 6.1 °C (± 0.85; \( N = 2 \)) on the first, second and third day of food deprivation, respectively.

Eight of the 21 flight-tested doves could not fly on the first (weighted) flight attempt during the first deprivation night. The logistic regression (Full model: \( \chi^2 = 18.215, N = 21 \), Nagelkerke \( R^2 = 0.789, p < 0.001 \)) indicated a statistically significant effect of \( T_b \) drop (\( \beta = 4.378, \text{s.e.} = 2.094, \text{Wald} \chi^2 = 4.373, p = 0.037; \) figure 2), but body mass did not significantly influence flight ability and was eliminated from the model (\( p = 0.148 \)). These results were supported by a supplementary ANOVA conducted to compare the \( T_b \) drops of no-flight and flight-capable doves; birds that could not fly were significantly more hypothermic than birds that were flight-capable (\( F = 8.591, d.f. = 1, 18, p = 0.009 \)) while starting mass had no effect (\( F = 0.532, d.f. = 1, 18, p = 0.475 \)). Given our criteria for flight, five of the eight no-flight birds could fly while hypothermic with the weight removed, although not with obvious vigour. Following the first flight test, all no-flight birds warmed up quickly, with several individuals exceeding their normal daytime \( T_b \) (figure 3). All eight hypothermic no-flight birds flew strongly 20 min later once rewarmed. See the electronic supplementary material, figure S1 for a description of sample size at each stage of the experiment.

**Figure 1.** Representative examples of body temperature (\( T_b \)) profiles for four (a–d) of the 10 birds exposed to 2–3 days of food deprivation during the winter of 2010–2011. Control nights represent the \( T_b \) of birds on a normal day with food available ad libitum. Black bars along the x-axis indicate periods of darkness.
Food-deprived hypothermic doves likely experience a greater risk of nocturnal predation than normothermic doves through a reduction in flight ability. Many of our hypothermic doves could not fly, but could fly a short time later once rewarmed to near-normal daytime body temperature ($T_b$). This reduction in flight ability with the relatively moderate $T_b$ drops observed here imply that such predation-related costs of hypothermia likely play an important role in the overall energy-management strategy of birds [3,15,23]. Birds may limit their use of hypothermia accordingly by conserving their first attempt of the second deprivation night (figure 4). The 10 tested birds were generally colder (more hypothermic) than they were on the first deprivation night (figure 4). Unlike the first deprivation night, the binary logistic regression model ($\chi^2 = 0.285$, $N = 10$, Nagelkerke $R^2 = 0.038$, $p = 0.594$) indicated no significant effect of $T_b$ drop ($\beta = -0.284$, s.e. = 0.540, Wald $\chi^2 = 0.277$, $p = 0.599$) on flight ability on the second deprivation night (figure 4). A supplemental t-test supported these findings; the $T_b$ drops of no-flight and flight-capable doves were not significantly different (independent samples t-test: $t = -0.95$, $p = 0.370$). Body mass tended to differ between birds that could withstand 1 or 2 days of food deprivation, but this trend was not statistically significant at $\alpha = 0.05$ (independent samples t-test: $t = -1.947$, $p = 0.066$).

Only two of the six flight-capable birds from the second deprivation night (figure 4) were able to withstand 3 days of food deprivation. One bird was unable to fly on its first attempt ($T_b$ drop = $-5.3^\circ C$) and could not fly while hypothermic with the weight removed, but flew well with the additional weight after warming up to its daytime $T_b$ (figure 3). The second dove was able to fly on the first attempt of the third night ($T_b$ drop = $-7.0^\circ C$).

4. Discussion

Food-deprived hypothermic doves likely experience a greater risk of nocturnal predation than normothermic doves through a reduction in flight ability. Many of our hypothermic doves could not fly, but could fly a short time later once rewarmed to near-normal daytime body temperature ($T_b$). This reduction in flight ability with the relatively moderate $T_b$ drops observed here imply that such predation-related costs of hypothermia likely play an important role in the overall energy-management strategy of birds [3,15,23]. Birds may limit their use of hypothermia accordingly by conserving...
energy through other means, such as choosing favourable microhabitats [34,35], using effective thermoregulatory postures [36,37] and roosting with conspecifics [38–40]. The minor $T_b$ reductions associated with sleep in non-deprived birds (figure 1) probably do not decrease the readiness to escape in the event of a night-time attack.

Given the nature of nocturnal hypothermia in birds, it was not possible to experimentally tease-apart the effects (on flight ability) of lower $T_b$, from food deprivation per se or the effects of being suddenly awakened from sleep. Food deprivation undoubtedly lowered the energy reserves available for flight in all birds, but non-flying hypothermic birds had adequate energy reserves to both warm up and then fly. Hence, low reserves per se are not a likely reason for the inability to fly when hypothermic under food deprivation. It is conceivable that some birds were incoherently ‘groggy’ after being awakened from a deep sleep associated with food deprivation [41,42], and thus could fly only after becoming fully awake during the warm-up period. This seems unlikely because the birds awakened (i.e. opened their eyes) immediately upon hearing us enter the environmental chamber (as viewed on video monitors) and they struggled to escape once captured. They thus appeared to be awake by the time that they arrived in the flight arena. Such deep sleep, however, could be a serious cost of hypothermia during natural, surprise nocturnal attacks (see also [43]), in which hypothermic birds would have far less time to awake than did our experimental doves.

Results from the first deprivation night suggest that a roughly 5°C drop in $T_b$ may be a threshold beyond which birds suffer a substantial reduction in flight ability (figure 2). Schleucher [13] proposed that this same criterion ($T_b$ drop $> 5°C$) be used to characterize torpor in birds. However, our overall results identify no clear threshold $T_b$ drop for flightlessness. In particular, some doves could fly at $T_b$ drops approaching 7°C during the second deprivation night flight tests. These findings suggest that different doves have different $T_b$ thresholds, perhaps being lower for birds in better physical condition. Variable $T_b$ thresholds for hypothermic flight may also be attributed to individual variation in muscle and nervous system anatomy and physiology, but such considerations are beyond the scope of this study.

Reductions in $T_b$ significantly limit locomotion in other endotherms. For example, Rojas et al. [19] found that three species of small marsupials were capable of directional movement while torpid (minimum $T_b = 14.8°C$), although such movements were slow and would probably impair predator evasion. Some bat species are capable of powered flight at $T_b$ as low as 29°C ([44,45]; see also [46]), a $T_b$ that is cool enough to be categorized as ‘torpor’ in both bats and birds. Choi et al. [44] also found that greater tube-nosed bats (Marina leucogaster) were able to crawl at much lower temperatures ($T_b > 8°C$). In general, endotherms in deep torpor (such as hibernating bats and torpid hummingbirds) are unable to respond quickly to external stimuli ([8,47,48]; J.M.C. 2011, personal observation). Such studies and our results suggest that predation is a widespread cost of significant hypothermia across all endotherms.

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References


