2013

Diurnal And Nocturnal Avian Antipredator Behavior In Thermally Challenging Conditions

Jennie M. Carr
Indiana State University

Recommended Citation

Carr, Jennie M., "Diurnal And Nocturnal Avian Antipredator Behavior In Thermally Challenging Conditions" (2013). *All-Inclusive List of Electronic Theses and Dissertations*. 1916.
https://scholars.indianastate.edu/etds/1916

VITA

Jennie M. Carr

EDUCATION

2008 – 2013 Doctor of Philosophy (Biology), Indiana State University

2004 – 2008 Bachelor of Science (Biology) with minor in Psychology, Juniata College

TEACHING EXPERIENCE

2008 – 2013 Graduate Teaching Assistant, Department of Biology, Indiana State University

Courses taught: Principles of Biology Lab I/II, Human Anatomy Lab, Human Physiology Lab, General Physiology Lab

PROFESSIONAL SERVICE

Reviewer for the following peer-reviewed scientific journals:

Ethology
Israel Journal of Ecology and Evolution
PLOS ONE

HONORS AND AWARDS

2012 Outstanding Graduate Teaching Assistant. Indiana State University

2013 Research and Creativity Award. Indiana State University

SELECTED PUBLICATIONS

Carr, J. M. & Lima, S. L (submitted). Nocturnal hypothermia impairs flight ability in birds: a cost of being cool. *Proceedings of the Royal Society B*

Carr, J. M. & Lima, S. L. (submitted). Wintering birds avoid warm sunshine: predation and the costs of foraging in sunlight. *Oecologia*

Carr, J. M. & Lima, S. L. (2012). Heat-conserving postures hinder escape: a thermoregulation-predation trade-off in wintering birds. *Behavioral Ecology* **23**, 434-441.

Carr, J. M. & Lima, S. L. (2010). High wind speeds decrease the responsiveness of birds to potentially threatening moving stimuli. *Animal Behaviour* **80**, 215-220.

DIURNAL AND NOCTURNAL AVIAN ANTIPREDATOR BEHAVIOR IN THERMALLY CHALLENGING CONDITIONS

A dissertation

Presented to

The College of Graduate and Professional Studies

Department of Biology

Indiana State University

Terre Haute, Indiana

In Partial Fulfillment

of the Requirements for the Degree

Doctor of Philosophy

---

by

Jennie M. Carr

August 2013

Keywords: avian behavior, foraging, predation, thermoregulation, trade-off

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 - 1346

COMMITTEE MEMBERS

Committee Chair: Steven L. Lima, Ph. D.

Professor, Department of Biology

Indiana State University

Committee Member: George S. Bakken, Ph. D.

Professor, Department of Biology

Indiana State University

Committee Member: Diana K. Hews, Ph. D.

Professor, Department of Biology

Indiana State University

Committee Member: William A. Mitchell, Ph. D.

Associate Professor, Department of Biology

Indiana State University

Committee Member: Esteban Fernández-Juricic, Ph. D.

Associate Professor, Department of Biological Sciences

Purdue University

ABSTRACT

Diurnal avian antipredator behavior has been the focus of much past research, yet the influence of the thermal environment on such behaviors is often overlooked. Far less is known about nocturnal avian antipredator behavior, including how these behaviors are influenced by challenging thermal environments. The first portion of my research focused on how the thermal environment influences the diurnal antipredator behavior of wintering birds while (i) exposed to high wind speeds, (ii) foraging in sunlit and shaded microhabitats, and (iii) when using thermoregulatory postures to conserve body heat. In addition to increasing convective heat loss, high wind speeds increase the prevalence of background movements in the environment. My research demonstrated that wintering sparrows exposed to a moving stimulus are less likely to flush to cover on windy days than on calm days, suggesting that wind-driven visual noise may interfere with predator detection. Predator detection may also vary when feeding in sunlight and shade, and the thermal benefits of foraging in direct sunlight on cold winter days may also play an important role in dictating microhabitat choice. Regardless of the thermal benefits of foraging in sunlight, wintering sparrows preferred to feed in shaded microhabitats even at ambient temperatures well below thermoneutrality. However, these birds foraged in sunlight more frequently as ambient temperatures fell, suggesting a trade-off between thermoregulation (solar input) and predation risk. Additional evidence of such a thermoregulation-predation trade-off was evident in the use of heat-conserving thermoregulatory postures by wintering sparrows. Fluffing the feathers or standing on one foot will reduce the amount of heat lost to the environment. However, such postures slow take-off time and likely result in an increase in predation risk. As such, these risky postures were only used when feeding at relatively low ambient temperatures and when near protective cover. In general, these results indicate that characteristics of the thermal environment play an important role in dictating diurnal antipredator behavior.

To address how the thermal environment influences nocturnal avian antipredator behavior, I examined the predation-related costs of using energy-saving nocturnal hypothermia. Many species of birds reduce their nighttime body temperature, thus reducing metabolic rate and conserving energy. Such drops in body temperature may be quite substantial and likely influence a bird's ability to respond to a potential threat during the night. To examine the potential costs of hypothermia, I conducted nocturnal flight tests on hypothermic mourning doves (*Zenaida macroura*). In general, doves that cooled by more than 5 °C flew poorly or were unable to fly, but were able to fly well once re-warmed to near their normal daytime body temperatures. Thus, low body temperatures during energy-saving hypothermia likely result in an increase in the risk of nocturnal predation. Nocturnal antipredator behavior was also examined in ruby-throated hummingbirds (*Archilochus colubris*). These hummingbirds frequently use nocturnal torpor (i.e., deep hypothermia), with significant reductions in body temperature and corresponding inability to respond behaviorally to external stimuli. Although hummingbirds altered torpor use seasonally and over the course of the observation period, hummingbirds did not consistently reduce their use of torpor following an experimental increase in perceived predation risk. Thus, although hypothermia is behaviorally costly, further studies are needed to clarify the role of predation on nocturnal behavior in birds.

ACKNOWLEDGMENTS

My research was funded in part by the Department of Biology, School of Graduate and Professional Studies, and Graduate Student Association at Indiana State University. Additional financial support was also provided by Sigma Xi and the Indiana Academy of Science.

Many individuals have provided expert advice and assistance throughout my five-year tenure at Indiana State University. My dissertation advisor, Dr. Steven Lima, has provided countless hours of mentorship and has been instrumental in my development as a scientist and a professional in my field. I would also like to thank my committee members, Dr. George Bakken, Dr. Diana Hews, Dr. William Mitchell, and Dr. Esteban Fernández-Juricic for their expert advice and contributions from their respective fields. Dr. Joy O'Keefe also provided professional advice, encouragement and was, along with Kristina Hammond, instrumental in the set-up of radio-telemetry equipment. Surgical techniques for mourning dove transmitter implantations were mastered with the help of Dr. Charles Amlaner. Frequent and time-intensive surgeries were assisted by Indiana State University undergraduate Kathleen Spicer, who ever-willingly sacrificed her own study and family time to serve as "anesthesiologist". Michael Gerringer and Robert Arndt also contributed their own time to assist with animal care as needed.

Lastly, friends and family, including my parents and sister, have been an endless source of emotional support throughout my education. I would especially like to thank my husband, Joshua Carr, whose love, encouragement, and patience has been never-waning.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

HIGH WIND SPEEDS DECREASE THE RESPONSIVENESS OF BIRDS TO POTENTIALLY THREATENING MOVING STIMULI

Small foraging birds often rely on visual cues to detect the movement of potential threats. However, feeding in a high wind environment presents the challenge of interpreting the movements of many stimuli, most of which convey little information pertinent to survival. A bird that responds to each of these wind-driven movements would likely suffer the loss of much feeding time. Birds should thus become less responsive to moving stimuli at greater wind speeds. Furthermore, since inanimate objects should not move upwind, birds should generally be more responsive to upwind movements than typical downwind movements. By exposing passerine flocks to a moving, potentially threatening stimulus at various wind speeds, we found that these birds are in fact less responsive to stimulus movement (i.e., a lower tendency to flush to cover) as wind speed increases. However, birds were not more responsive to upwind movements of the stimulus. The propensity to flush was also not significantly affected by temperature or flock size. Responsiveness tended to decline over time, possibly indicating habituation to the stimulus, but the basic effect of wind speed held over the entire study. The general effect of wind on responsiveness suggests that the likelihood of responding to other stimuli or disturbances on windy days may also be reduced. [*Published:* Carr & Lima 2010, Animal Behaviour 80, 215-220]

Introduction

Wind-driven stimuli in an environment will increase in number as wind speed intensifies. As a result, an animal's response to moving stimuli is likely to vary as a function of wind speed. In a calm environment, movement is likely caused by the activities of other animals. Movement in a high-wind environment may more likely be driven by the wind itself. In many situations, an animal may filter background movements (such as moving foliage) while remaining sensitive to sudden, atypical signals (Fleishman 1992). For instance, the lizard *Amphibolurus muricatus* responded to target objects with greater accuracy when exposed to targets moving at different angular velocities as compared to prevailing background movement (Woo et al. 2009). Incorporating atypical movements into visual communicative displays has also been shown to prevent signals from being filtered alongside wind-blown vegetation movement (*Anolis sp*., Fleishman 1992). Accordingly, male *Anolis* lizards perform territorial displays with intensified signals under high levels of background vegetation movement (Ord et al. 2007; Ord & Stamps 2008). Peters and Evans (2003) similarly found that territorial displays produced by male *A. muricatus* consist of movements distinct from those of windblown vegetation. Conversely, some animals mimic readily-filtered background motions to lower the probability of being detected while moving through an environment with high wind (Watanabe & Yano 2009) or water currents (Keenleyside 1979).

Wind may also cause degradation of auditory and other signals. Some animals compensate for wind-driven noise by lengthening and intensifying calls to conspecifics (*Aptenodytes patagonicus,* Lengagne et al. 1999; *Tachycineta bicolor*, Leonard & Horn 2005; for reviews see Klump 1996; Brumm & Slabbekoorn 2005). Olfactory cues are also rapidly dispersed in an environment with high wind or water flow, a process that has been shown to alter a predator's search efficiency when foraging for prey (Finelli et al. 2000).

Increased motion in a windy environment may complicate predator detection by visually-oriented prey. Although little work has been done on this topic, movement of vegetation and debris may allow predators to approach prey more easily while remaining undetected. In other words, visual cues (and similarly auditory or olfactory cues) produced by the predator's approach may be masked by distracting visual noise (Hilton et al. 1999). Conversely, in calm environments, movements are not wind-driven and may thus carry more direct meaning. For this reason, the motion of relatively innocuous stimuli on a calm day may be viewed as threatening while movement of the same stimuli on a windy day may be perceived as much less threatening.

Winter is often a windy period in the temperate zone, thus a wintering bird must frequently deal with these wind-induced ambiguities. With wind-driven movements present in the environment, feeding birds must decide which stimuli require a response and which should be ignored, and their responsiveness to stimuli will likely change with the level of wind. As mentioned earlier, a bird foraging in a calm environment may interpret minor movements of vegetation as the approach of a threat. Such movements might thus induce escape behaviours at the cost of lost feeding opportunities. However, when feeding in an area exposed to wind, fleeing to cover after every detected movement in the environment would be very energetically costly. Therefore, on windy days, it seems likely that feeding birds would become less (immediately) responsive to moving stimuli to avoid such costs. High wind also presents many moving stimuli simultaneously. The large level of sensory input presented by a visually noisy, windy environment should also result in decreased sensitivity and a lower probability of responding to moving stimuli (Dukas 2004), lending additional support to this idea.

A variety of factors might influence a bird's responsiveness to wind-driven stimuli. For instance, during a high-wind day, any movement in the direction opposite to the prevailing wind should elicit a greater response than stimulus movement in the same direction as the wind (Woo et al. 2009). Objects moving downwind may be interpreted as wind-blown debris, while movement against the wind is clearly uncharacteristic of inanimate, innocuous stimuli. Larger flocks of feeding birds may also be less likely to flush to cover after stimulus movement. Effective "safety-in-numbers" implies that birds in larger flocks are safer due to the lower probability of being killed during an attack (Krause & Ruxton 2002; Caro 2005). For this reason, on a windy day, members of small flocks should be more responsive to a moving stimulus than those in larger flocks (e.g., Lima 1995). Finally, ambient temperature may also play a role in the responsiveness of feeding birds to moving objects. With the requirement of elevated food intake under colder conditions, feeding birds should be more likely to take greater risks and thus be less responsive to potentially threatening stimuli as temperature decreases (Pravosudov & Grubb 1995; Lima 1998; Hilton et al. 1999; Cresswell & Whitfield 2008). High wind on days with low temperatures will further increase energetic demands through convective heat loss (Bakken et al. 1991) and thus may contribute to lowered responsiveness (Grubb 1978).

We tested these ideas in flocks of small overwintering granivorous passerines by confronting them with an innocuous moving stimulus at various environmental wind speeds, as well as movement with and against the wind. The idea that responsiveness to movement should decrease with increasing wind speed was strongly supported by our results. However, the direction of stimulus movement with respect to the wind had no obvious effect on responsiveness. Responsiveness was also not affected by temperature or flock size.

Methods

Study site and species

The experiment was conducted in a harvested soy bean field (approximately 0.2 km x 0.6 km) 16 km northeast of Terre Haute, Indiana, USA (39°32'23.86"N, 87°14'6.12"W). The southern portion of the field was bordered by another large agricultural field, while the remainder of the field was bordered by mature deciduous forest. Observations at the study site were made between 17 December 2008 and 23 February 2009. Environmental conditions (temperature, wind speed and direction) were obtained from a NOAA weather station at the Terre Haute International Airport located approximately 11 km southwest of the study site. Temperatures during experimentation varied from -13 to 14 °C, and average environmental wind speed varied from 0 to 40 km/h. All observations were conducted following the Indiana State University Institutional Animal Care and Use Committee protocol #11-14-2008:SLL/JMC.

A large majority (~80%) of the birds visiting the study site were American tree sparrows *Spizella arborea* (18 g, Dunning 2007). Song sparrows (*Melospiza melodia*, 20 g), dark-eyed juncos (*Junco hyemalis*, 18.6 g) and field sparrows (*Spizella pusilla*, 12.5 g) also frequented the study site, listed in order of decreasing abundance. White-throated sparrows (*Zonotrichia albicollis*, 24.4 g), northern cardinals (*Cardinalis cardinalis*, 42.7 g) and eastern towhees (*Pipilo erythrophthalmus*, 40 g) were occasional visitors to the study site. A 9.5 x 2 m brush pile was constructed on the eastern side of the field, parallel to and 8 m from the edge of the forest (Fig. 1), to serve as protective cover and to entice birds to feed at the study site. Beginning 23 November 2008, birds were provided daily with a mixture of cornmeal and millet in a 1.2 x 1.8 m feeding area 2 m to the west of cover. The feeding area was directly exposed to wind from the south, west and north, which are the prevailing wind directions at this latitude. Days with wind from the east (blocked by forest immediately adjacent to the feeding area) were avoided.

Experimental Setup

The basic study design exposed feeding birds to the sudden movement of an experimental stimulus near the food patch. Responsiveness to the moving stimulus, defined here as the propensity to flee to protective cover, was observed over a range of low- to high-wind days. Stimulus movement was controlled from within a blind, with all experimental trials videotaped through a two-way mirror for later review. Note that our experiment focused on the effect of wind on responsiveness to movement of the experimental stimulus, not the probability of detecting stimulus movement itself (see Quinn & Cresswell 2005).

The study site set-up described in Figure 1 allowed for flexibility in dealing with daily changes in wind direction by permitting the stimulus to be moved between two appropriate wooden posts (labeled A - E). Nylon string was threaded through metal eyelets positioned 24 cm above the ground on these posts, which were 30 cm in height and 2 x 3.5 cm in cross section. Attachment at this height allowed the stimulus to move freely with wind movement while remaining close to the ground. The string was further threaded through two eyelets within the blind in a closed-circuit fashion (Fig. 1). The stimulus was moved within the blind by abruptly pulling the nylon string at a speed of approximately 3 m/s. This abrupt movement in close proximity to feeding birds is the sort that would likely elicit an immediate response (Blumstein 2003; Cresswell et al. 2009). Eyelets were attached to the blind with rubber strips to minimize the vibration (and resulting noise) produced by the string pull. Early trial runs indicated that the subject birds responded in no way to the movement of the string alone.

The experimental stimulus was four layers of heavy, flat brown paper (18 x 13 x 0.2 cm) similar in colour to dead leaves already present in the environment. The stimulus was smooth in texture and waterproofed using lightweight clear packing tape, and was suspended from the string along a trajectory that would allow movement with or against the day's wind direction (Fig. 1). This unidirectional movement mimicked the predominant movements in this open environment, which reflected blowing loose vegetative material rather than standing vegetation that swayed back and forth. This stimulus was attached to the nylon string approximately 30 min prior to the start of the day's trails. The feeding patch was established parallel to the trajectory of stimulus movement for that day, with a separation of 30 cm between the string and the closest patch edge. The stimulus moved parallel to the patch for a distance of approximately 1 m, with the degree and direction of movement as indicated by the double-headed arrow in Figure 1. However, birds feeding in the patch responded well before stimulus movement ended.

Trials

The stimulus was pulled (a "trial") during sustained wind on high-wind days and sustained relatively calm periods on low-wind days. Direct measurement of wind speeds at ground-level was impractical due to the heterogeneous and swirling nature of the wind in and around the feeding patch. We thus used average environmental wind speed (measured 3 m off the ground) as an index of the wind conditions experienced by the birds at ground level. Trials were conducted between 0900h-1630h, depending on wind conditions expected on a given day, with an equal number of trials conducted before and after noon. The stimulus was pulled to move in both upwind and downwind directions for a given sequential pair of trials, alternating between upwind and downwind initial movements throughout the course of the experiment. Two or four trials were performed during a given day, resulting in one or two paired trials. There was a minimum of 5 min (typically about 20 min) between the two stimulus movements. These paired trials served as within-day controls for the wind direction analysis. Flock size (ranging from 5 - 30 individuals) and species composition were recorded immediately before stimulus movement. A bird was determined to have responded if it flushed to cover in response to stimulus movement. Birds that did not flush upon movement of the stimulus typically ceased feeding in a crouched posture before resuming feeding, thus we focused on the more alarmed response. Performing trials on two consecutive days was avoided, but was done three times during the study due to the rarity of very calm or very windy days. A total of 62 trials were conducted over 22 experimental days.

Data analysis

The observation used for statistical analysis was the proportion of the flock that flushed to cover. In most analyses, we treated each observation (proportion flushed) as statistically independent. This is reasonable due to the large number of birds frequenting the site (well over 100), thus a given flock was comprised of only a small portion of the study site population. Furthermore, given the frequent arrival and departure of feeding birds, the flock present was a rapidly-changing subset of the birds visiting the site. Nevertheless, these observations were taken repeatedly from the same study site population, and as such, the statistical inferences made herein apply (strictly speaking) only to those birds visiting our study site and not similar populations elsewhere. However, there is no reason to believe that the study site population was unique or unusual in any way.

We first addressed the effect of movement with and against the prevailing wind direction using data derived from the paired trials. A sign test was conducted to determine responsiveness to stimulus movement in different directions by using the difference between the proportion of the flock that flushed during upwind and downwind stimulus movement. A Spearman rank correlation was then used to determine whether these differences in the proportion flushed were correlated with wind speed (N = 31 pairs). No effect of wind direction was indicated by this analysis. All subsequent analyses treated each trial as an independent observation (N = 62). The proportions of birds that flushed across trials were highly bimodal in distribution, thus logistic regression was performed to examine the effects of various factors on flock responsiveness. Included in this analysis were trial order (first or second trial in a pair), temperature, flock size, wind speed and ordinal date (with day 1 assigned to the first experimental day). We also maintained direction of stimulus movement (upwind or downwind) in the logistic model. Analyses were conducted using Statistica 6.0 (Statsoft, Tulsa, OK, U.S.A.) and SPSS 11.0 (SPSS, Inc., Chicago, IL, U.S.A.).

Results

As outlined earlier, an upwind stimulus movement should cause a greater proportion of the feeding flock to flush to cover, since free-moving inanimate objects should only move downwind. In this first analysis, each upwind and downwind stimulus movement pair was characterized as a single value by subtracting the proportion of the flock that flushed after downwind movement from the proportion flushed after upwind stimulus movement. If birds responded to directional stimulus movement as expected, then these differences in proportions should be positive. Inspection of Figure 2, however, indicates an almost equal number of positive

($N = 11$) and negative ($N = 10$) differences (sign test: $N = 31$, with 10 zero differences, $P >> 0.05$). Furthermore, there was no significant correlation between these differences and average wind speed (Spearman rank correlation: $r_s = -0.146$, $N = 31$, $P = 0.432$), indicating that birds did not flush more often when the stimulus moved upwind at higher wind speeds. These simple analyses do not suggest that the birds at the study site responded differently to stimulus movement with or against the wind.

Since inanimate objects are more likely to move during high wind conditions, we expected that birds would be less responsive to stimulus movement as average environmental wind speed increased. The results in Figure 3 clearly suggest such an effect of wind speed. Specifically, as wind speed increased, the frequency of low-response trials also increased. Flock responsiveness was also clearly bimodal, with all observations falling above 60% and below 20% of the flock responding.

Due to the strongly bimodal nature of the responses in Figure 3, logistic regression was used to examine the possible effects of wind speed, flock size, temperature, order (first or second trial in a pair), direction (up- or down-wind) and ordinal date on the proportion of the flock that responded (Tables 1, 2). Reponses were categorized as “0” when the response was < 0.2, and “1” for responses > 0.6. Wind speed had a significant effect on the tendency of birds to flush to cover in response to stimulus movement (Table 1). This decreased responsiveness was particularly apparent above average environmental wind speeds of 20 km/h, when entire flocks often failed to flush to cover. Logistic regression indicated that flock size, temperature, direction of stimulus movement and trial order had no significant effect on the proportion of birds that flushed in response to the stimulus (Table 1). Ordinal date significantly affected the proportion of the flock that flushed, indicating that birds became less responsive to stimulus movement over the course of the study (Table 1), an effect apparent in Figure 3.

The interpretation of the effect of ordinal date on flock responsiveness is complicated by a strong correlation ($r = 0.73$) between ordinal date and flock composition, as expressed by the proportion of the flock composed of tree sparrows. This correlation reflects an annual tendency for wintering tree sparrows to appear fairly late in the winter in our study area (SLL, pers. obs.). Given the strong correlation between these two variables, we chose to enter ordinal date alone into the model rather than both variables. We did, however, directly evaluate the effect of flock composition by restricting the logistic analysis to data from flocks dominated (> 60 %) by tree sparrows (36 flocks overall). The results (Table 2) were quantitatively very similar to those obtained using the full data set (Table 1), with a significant effect of both a wind speed and ordinal date. Hence the lower responsiveness seen over time probably reflected the passage of time *per se* and not changes in flock composition. We note further that flock composition was not significantly correlated with temperature (multiple regression: $P = 0.6443$; $r = 0.30$) or wind speed ($P = 0.3229$; $r = -0.19$), suggesting no complications from changes in flock composition under various environmental conditions.

Discussion

The overall results of the study indicate a clear effect of wind speed on the responsiveness of small birds to moving stimuli. The effect of wind speed is certainly sensible given that inanimate objects such as dead leaves tend to move about as wind speed increases. On days with strong wind at the study site, it was not uncommon to observe debris blowing by or through the feeding patch, sometimes coming very close to a feeding bird. Birds involved in these encounters merely stepped out of the way or ignored the debris entirely (pers. obs.). The similarly unthreatening nature of the stimulus used in this study suggests that birds would respond similarly, thus avoiding the cost of the response. However, the experimental stimulus began moving very abruptly, a characteristic not commonly observed in naturally-occurring debris. This often elicited an immediate flight response that became less frequent with increasing wind speed, lending support to previous work by Fleishman (1992) and Woo et al. (2009). The lower responsiveness on windier days might reflect the possibility of increased costs associated with flight in a high-wind environment. However, birds at the study site had no apparent difficulties taking flight from the feeding patch or landing in cover on high-wind days.

The response measure that we used addressed the most obvious response: a flush to protective cover. Non-flushing birds did, in fact, respond to stimulus movement by crouching followed by a bout of vigilance before resuming feeding. Thus, the sudden movement of the stimulus was usually seen as threatening, just less so on windy days when birds were more likely to remain at the patch to feed. We can only speculate on whether this effect of wind speed represents a learned or innate response. We suspect that much learning is involved, as wind-driven stimuli are frequently observed and thus ample opportunities for such learning are available.

Learning in the form of habituation may be the simplest explanation for the decline in responsiveness over the course of the experiment. Such habituation is perhaps to be expected in this sort of experimental design as the birds gain experience with the experimental stimulus. Nevertheless, a clear effect of wind speed on the propensity to flush was apparent throughout the course of the study (Fig. 3). Some non-habituation explanations for the decline in responsiveness over time include a possible decline in body condition over the course of the winter, which would favor the less energetically costly crouching response over the full-blown flush to cover. However, the lack of a temperature effect on responsiveness argues against this idea. A general lowering of perceived risk over time might also account for this effect, but there is no way at present to assess this possibility.

The lack of a significant effect of stimulus movement direction was surprising. Movement of the stimulus in an upwind direction on high-wind days should be interpreted as particularly alarming since innocuous stimuli should not move upwind. However, birds responded equally to stimulus movement in the upwind and downwind directions (Fig. 2; see also Table 1). Perhaps swirling debris on windy days made the differentiation of directional movement difficult. Another explanation for the lack of a directional effect lies in the immediate response to the stimulus. Birds flushed to cover immediately after the stimulus began to move, perhaps leaving little time to assess the direction of movement. Birds feeding at a greater and less dangerous distance from the moving stimulus might devote more time to assessing (relative to wind direction) whether the stimulus is indeed a threat before responding (see also Stankowich & Coss 2006). Sudden movement of the stimulus may also have obscured any underlying directional effects. A sudden increase in velocity of a potential threat may greatly increase the risk perceived by prey (Stankowich & Blumstein 2005). Therefore, the birds may have responded without considering relative wind direction due to the danger associated with sudden changes in velocity.

As temperature decreases, small wintering birds should take greater risks to obtain enough energy for survival (Lima 1998; Hilton et al. 1999; Cresswell & Whitfield 2008). However, no effect of temperature on responsiveness was observed in our study (see also Boysen et al. 2001). This result may reflect the contradictory effects of elevated foraging demands and higher attack rates by predators on cold days, as particularly dangerous predators such as sharp-shinned hawks (*Accipiter striatus*, Roth et al. 2006) must also increase food intake under colder temperatures. Furthermore, the responsiveness to stimulus movement was not significantly associated with size of the flock. Specifically, birds in larger flocks were not less responsiveness to the moving stimulus (see also Stankowich & Coss 2006, 2007). Although feeding in large flocks lowers the probability that an individual will fall victim to attack, the benefits of the dilution effect may have been negated by the sudden, explosive nature of the flight response. Such multiple sudden departures often startle flockmates, resulting in the flush of much or all of the flock (Lima 1995; Cresswell et al. 2000; Beauchamp & Ruxton 2007). Larger flocks would also have a greater probability of containing “nervous” or easily-startled individuals (see Sih et al. 2004), potentially increasing the occurrence of “false alarm” flights.

Our wind-related results have interesting implications for the dynamics of the interactions between these small birds and their predators. Lowered responsiveness of feeding birds to moving stimuli in a windy environment may decrease the probability of quickly responding to an approaching predator. Predators may thus utilize wind-blown vegetation movement to approach prey to a closer distance than under calm conditions. Previous studies have found that dangerous predators like *Accipiter* hawks often use environmental obstructions in surprise attacks (Cresswell 1993; Roth & Lima 2003; Roth et al. 2006) and these hawks may similarly use the ambiguity of movement on windy days as a sort of obstruction. Auditory signals produced by a predator’s approach may also be obscured by wind noise, further enabling an undetected approach by a predator. Further work on these topics will determine whether predators do indeed take advantage of windy conditions and whether the relative unresponsiveness of their prey translates into higher predator success rates.

Acknowledgements

Peter Scott and Diana Hews graciously allowed the use of their property over the course of this study. The Department of Biology at Indiana State University also provided much-appreciated financial support. We also thank Will Cresswell and an anonymous reviewer for providing helpful suggestions on the original manuscript.

References

Bakken, G. S., Murphy, M. T. & Erskine, D. J. 1991. The effect of wind and air temperature on metabolism and evaporative water loss rates of dark-eyed juncos, *Junco hyemalis*: a standard operative temperature scale. Physiological Zoology, **64**, 1023-1049.

Beauchamp, G. & Ruxton, G. D. 2007. False alarms and the evolution of antipredator vigilance. Animal Behaviour, **74**, 1199-1206.

Blumstein, D. T. 2003. Flight-initiation distance in birds is dependent on intruder starting distance. Journal of Wildlife Management, **67**, 852-857.

Boysen, A. F., Lima, S. L. & Bakken, G. S. 2001. Does the thermal environment influence vigilance behavior in dark-eyed juncos (*Junco hyemalis*)? An approach using standard operative temperature. Journal of Thermal Biology, **26**, 605-612.

Brumm, H. & Slabbekoorn, H. 2005. Acoustic communication in noise. Advances in the Study of Behavior, **35**, 151-209.

Caro, T. M. 2005. *Antipredator defenses in birds and mammals*. Chicago: University of Chicago Press.

Cresswell, W. 1993. Escape responses by redshanks, *Tringa totanus*, on attack by avian predators. Animal Behaviour, **46**, 609-611.

Cresswell, W., Hilton, G. M. & Ruxton, G. D. 2000. Evidence for a rule governing the avoidance of superfluous escape flights. Proceedings of the Royal Society B, **267**, 733-737.

Cresswell, W., Butler, S., Whittingham, M. J. & Quinn, J. L. 2009. Very short delays prior to escape from potential predators may function efficiently as adaptive risk-assessment periods. Behaviour, **146,** 795-813.

Cresswell, W. & Whitfield, D. P. 2008. How starvation risk in Redshanks *Tringa totanus* results in predation mortality from Sparrowhawks *Accipiter nisus*. Ibis, **150** (Suppl. 1), 209-218.

Dukas, R. 2004. Causes and consequences of limited attention. Brain Behavior and Evolution, **63**, 197-210.

Dunning, J. B. 2007. *CRC Handbook of Avian Body Masses.* 2nd edn. Boca Raton, Florida: CRC Press.

Finelli, C. M., Pentcheff, N. D., Zimmer, R. K., & Wethey, D. S. 2000. Physical constraints on ecological processes: a field test of odor-mediated foraging. Ecology, **81**, 784-797.

Fleishman, L. J. 1992. The influence of the sensory system and the environment on motion patterns in the visual-displays of anoline lizards and other vertebrates. American Naturalist, **139**, S36-S61.

Grubb, T. C. 1978. Weather-dependent foraging rates of wintering woodland birds. Auk, **95**, 370-376.

Hilton, G. M., Ruxton, G. D. & Cresswell, W. 1999. Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. Oikos, **87,** 295-302.

Keenleyside, M. H. A. 1979. *Diversity and adaptation in fish behaviour*. Berlin:Springer-Verlag.

Klump, G. M. 1996. Bird Communication in the Noisy World. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 321-338. Ithaca: Cornell University Press.

Krause, J. & Ruxton, G. 2002. *Living in groups*. New York: Oxford University Press Inc.

Lengagne, T., Aubin, T., Lauga, J. & Jouventin, P. 1999. How do king penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions?. Proceedings of the Royal Society B, **266**, 1623-1628.

Leonard, M. L. & Horn, A. G. 2005. Ambient noise and the design of begging signals. Proceedings of the Royal Society B, **272**, 651-656.

Lima, S. L. 1995. Collective detection of predatory attack by social foragers - fraught with ambiguity. Animal Behaviour, **50,** 1097-1108.

Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior, **27**, 215-290.

Ord, T. J., Peters, R. A., Clucas, B. & Stamps, J. A. 2007. Lizards speed up visual displays in noisy motion habitats. Proceedings of the Royal Society B, **274**, 1057-1062.

Ord, T. J. & Stamps, J. A. 2008. Alert signals enhance animal communication in "noisy" environments. Proceedings of the National Academy of Sciences U.S.A., **105**, 18830-18835.

Peters, R. A. & Evans, C. S. 2003. Design of the Jacky dragon visual display: signal and noise characteristics in a complex moving environment. Journal of Comparative Physiology A, **189**, 447-459.

Pravosudov, V. V. & Grubb, T. C. 1995. Vigilance in the tufted titmouse varies independently with air temperature and conspecific group size. Condor, **97**, 1064-1067.

Quinn, J. L. & Cresswell, W. 2005. Escape response delays in wintering redshank, *Tringa totanus*, flocks: perceptual limits and economic decisions. Animal Behaviour, **69**, 1285-1292.

Roth, T. C. & Lima, S. L. 2003. Hunting behavior and diet of Cooper's Hawks: An urban view of the small-bird-in-winter paradigm. Condor, **105**, 474-483.

Roth, T. C., Lima, S. L. & Vetter, W. E. 2006. Determinants of predation risk in small wintering birds: the hawk's perspective. Behavioral Ecology and Sociobiology, **60**, 195-204.

Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R.E. 2004. Behavioral syndromes: an integrative overview. The Quarterly Review of Biology, **79**, 241-277.

Stankowich, T. & Blumstein, D. T. 2005. Fear in animals: a meta-analysis and review of risk assessment. Proceedings of the Royal Society B, **272**, 2627-2634.

Stankowich, T. & Coss, R. G. 2006. Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. Behavioral Ecology, **17**, 246-254.

Stankowich, T. & Coss, R. G. 2007. Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. Behavioral Ecology, **18**, 358-367.

Watanabe, H. & Yano, E. 2009. Behavioral response of mantid *Hierodula patellifera* to wind as an antipredator strategy. Annals of the Entomological Society of America, **102**, 517-522.

Woo, K. L., Burke, D. & Peters, R. A. 2009. Motion sensitivity of the Jacky dragon, *Amphibolurus muricatus*: random-dot kinematograms reveal the importance of motion noise for signal detection. Animal Behaviour, **77**, 307-315.

Table 1. Results from the full logistic analysis of flock responsiveness to stimulus movement, using the full data set.

Variable	B	SE	χ^2	*P*-value
Wind speed	**-0.190**	**0.066**	**8.228**	**0.004**
Ordinal date	**-0.286**	**0.098**	**8.552**	**0.003**
Direction	-0.133	0.784	0.029	0.865
Order	0.016	0.783	0.000	0.983
Flock size	-0.047	0.071	0.432	0.511
Temperature	-0.004	0.053	0.006	0.938

Full model: $N = 62$, $\chi^2 = 30.614$, df = 6, Nagelkerke $R^2 = 0.564$, percent classified correctly = 80.6%, $P \ll 0.05$. Factors significantly affecting the proportion flushed are shown in bold.

Table 2. Results from the logistic analysis of flock responsiveness to stimulus movement, considering only data from flocks numerically dominated (> 60%) by American tree sparrows.

Variable	B	SE	χ^2	*P*-value
Wind speed	**-0.182**	**0.076**	**5.679**	**0.017**
Ordinal date	**-0.391**	**0.163**	**5.753**	**0.016**
Direction	-0.464	1.050	0.196	0.658
Order	-0.163	0.999	0.027	0.871
Flock size	-0.122	0.122	0.999	0.318
Temperature	0.110	0.091	0.015	0.903

Full model: $N = 36$, $\chi^2 = 22.313$, df = 6, Nagelkerke $R^2 = 0.627$, percent classified correctly = 80.6%, $P = 0.001$. Factors significantly affecting the proportion flushed are shown in bold.

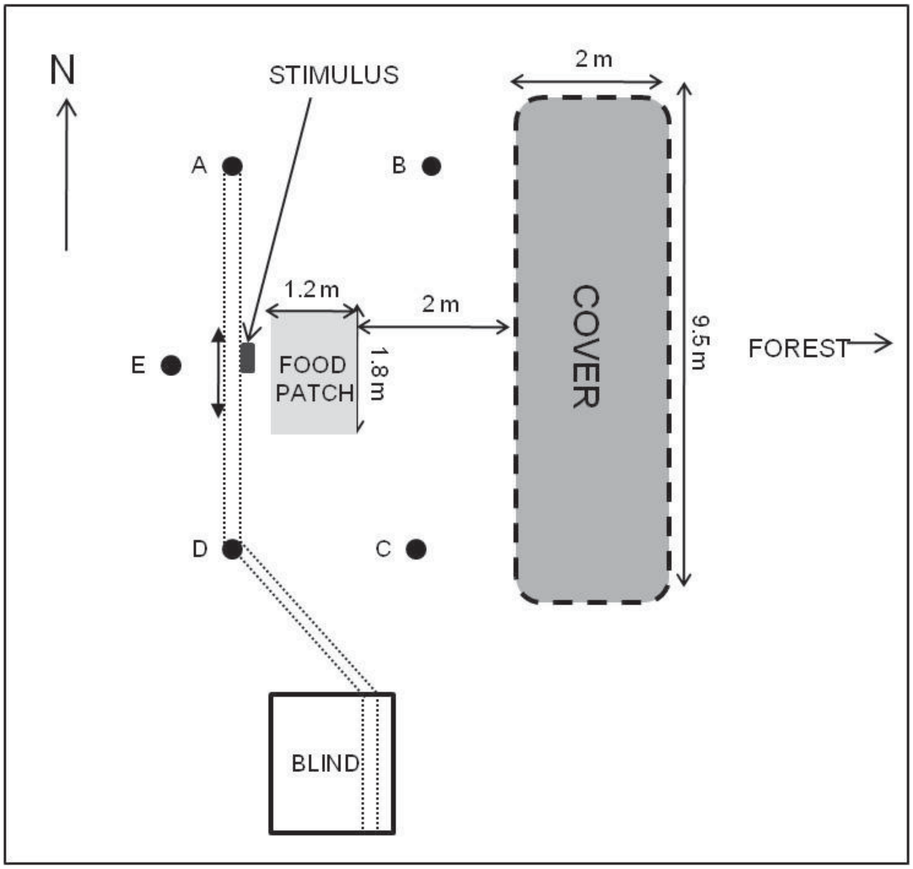


Figure 1. Study site setup. Each solid circle (A - E) indicates a short (30 cm high) wooden stake. The stimulus (four layers of 18 x 13 cm brown paper 0.2 cm in total thickness) moved between two stakes depending on wind direction. The double-headed arrow depicts stimulus movement with northerly or southerly wind direction (A - D). Stimulus movement with a northwesterly or west-northwesterly wind direction would be between A - C, etc. The food patch was established parallel to the day’s stimulus movement. The pathways A - B, B - C and D - C were never used.

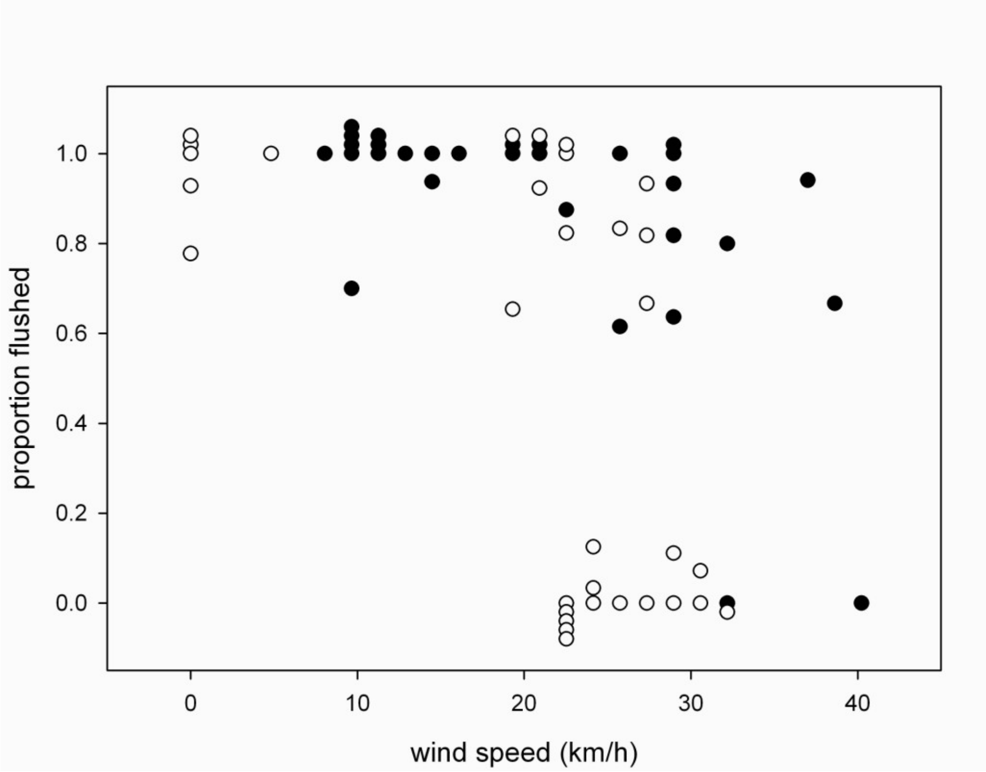


Figure 2. Difference between the proportion of the flock that flushed with upwind vs. downwind stimulus movement. Shown is the upwind-downwind difference for a given pair of trials. Wind speed indicates the average environmental wind speed over the paired trials.

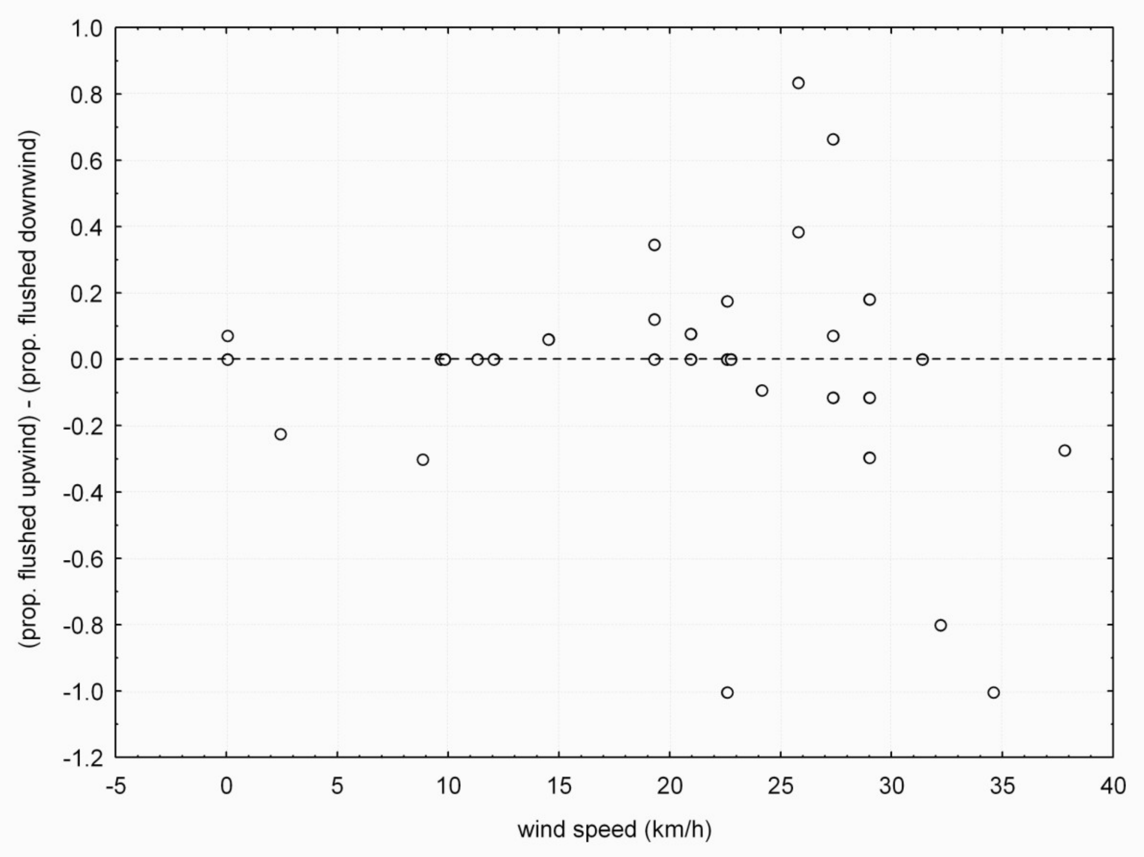


Figure 3. The proportion of birds that flushed during each trial as a function of average environmental wind speed. Solid circles (●) represent trials conducted during the first half of the experimental period; open circles (○) represent trials from the second half. Values at 0 and 1 were offset vertically below and above these values, respectively, to avoid obscuring overlapping data.

CHAPTER 2

HEAT-CONSERVING POSTURES HINDER ESCAPE: A THERMOREGULTION-PREDATION TRADE-OFF IN WINTERING BIRDS

Wintering birds may conserve body heat by adopting postures with minimal leg exposure or significant ptiloerection. However, maximally heat-conserving postures may hinder a bird's ability to escape attack, leading to a trade-off between predation risk and thermoregulation. Such a trade-off implies that birds should use the most heat-conserving postures only at very cold temperatures. Feeding in a relatively low-risk environment should also facilitate the use of such heat-conserving postures. In this experiment, we examined the effect of thermoregulatory postures on the time to initiate escape in feeding dark-eyed juncos (*Junco hyemalis*) exposed to a sudden, sharp noise. Birds using progressively more heat-conserving postures required significantly more time to initiate flight, with a 50% increase or more for certain cumbersome postures when compared to the most "flight-ready" posture. This increase in the time needed to become airborne likely leads to an increase in predation risk during an attack. Although this increase in risk could not be quantified, the delays associated with the most heat-conserving postures could allow a hawk to approach approximately 1.7 m closer to its prey during an attack. Postures that limit escape were used to a greater degree when feeding near cover and in cold conditions, lending additional support to a predation-thermoregulation trade-off. However, the effect of flock size was inconsistent and no effect of nearest neighbor distance on

thermoregulatory posture was detected. Overall, the results of this study provide insight into the seemingly intuitive observation that birds use maximally heat-conserving postures only under very cold winter conditions. [*Published:* Carr & Lima 2012, Behavioral Ecology 23, 434-441]

Introduction

Overwintering birds face many thermal challenges throughout the winter. As environmental temperatures drop below thermoneutrality, conserving body heat becomes an imperative for foraging birds (Bakken et al. 1991, Swanson and Olmstead 1999). One method of conserving body heat involves foraging in more favorable microhabitats through adjustments in foraging height or the types of trees used for roosting and feeding (Grubb 1975, Walsberg 1986, Dolby and Grubb 1999). Birds may also conserve body heat by altering their body orientation to minimize exposure to poor conditions (Fortin et al. 2000) or by gaining thermal benefits via exposure to solar radiation (Wolf and Walsberg 2000). Perhaps more generally, birds may use advantageous thermoregulatory postures when foraging in thermally-stressful conditions. Thermoregulatory postures can conserve body heat by reducing convective heat loss (Bakken 1991, Wolf and Walsberg 2000) via the covering of legs or the trapping of warm air in feathers. Ptiloerection is an important means of heat conservation in birds (see Hohtola et al. 1980). Ptiloerection reduces heat lost through the legs and feet by 20-50% (Dawson and Whittow 2000) and may increase thermal resistance by 50% (Wolf and Walsberg 2000). These sorts of behavioral responses to the thermal environment allow small birds to remain active while exposed to low temperatures or other unfavorable conditions such as high wind (Walsberg 1986, Bakken 1991, Zerba et al. 1999).

Favorable thermoregulatory postures may, however, compromise quick escape from an attacking predator. These postures may incorporate features such as ptiloerection, standing on one foot, or crouching close to the ground with feathers covering the legs and feet. These thermally-favorable postures may thus require a bird to make adjustments to posture prior to take-off, such as putting both feet on the ground and smoothing the feathers for flight. This additional adjustment time could substantially lower the probability of escape, particularly when under attack by a fast-approaching ambush predator. We thus expect that thermoregulatory postures will reflect a trade-off between heat conservation and predation risk. Accordingly, even though thermally-favorable postures would always reduce heat loss, wintering birds would be expected to use these postures only when exposed to relatively cold temperatures.

Several factors may potentially influence the posture-related predation-thermoregulation trade-off outlined above for wintering birds. Generally speaking, feeding in safer conditions should facilitate the use of more heat-conserving thermoregulatory postures. For a variety of reasons, one might expect that birds feeding in the safety of a large flock would use thermally-favorable, potentially costly postures more readily than birds in a small flock. First, feeding in a large flock lowers the probability that an individual would fall victim to an attack (Krause and Ruxton 2002, Caro 2005) and increases the probability that an attack will be detected with sufficient time to allow for escape (McNamara and Houston 1992, Lima 1995a, Roberts 1996, Beauchamp 2003). Feeding in close proximity to other foraging birds would similarly favor thermally-advantageous postures since feeding near neighbors facilitates the transfer of anti-predator information (Elgar et al. 1984, Lima and Zollner 1996, Fernández-Juricic and Kacelnik 2004). Feeding closer to protective cover would also favor thermally-advantageous postures, since the overall time required for escape would be much reduced (Lima 1993, Walther and Gosler 2001; but see Cresswell 1993).

We examined the above ideas regarding predation and avian thermoregulation in flocks of wintering emberizid sparrows. We exposed dark-eyed juncos (*Junco hyemalis*) to a sudden, alarming disturbance to determine the time required to initiate escape flight as a function of thermoregulatory posture. Postures of free-living juncos were also monitored over a range of environmental temperatures and flock sizes while experimentally manipulating distance to protective cover. The results support our expectation that the more extreme postures (i.e., postures that potentially conserve the most body heat) increase the time required to initiate flight. Birds primarily used such heat-conserving postures when feeding near cover and especially under colder conditions, supporting the idea of a thermoregulation-predation risk trade-off.

Methods

Study site and species

Our experiment was conducted 9 km southwest of Terre Haute, Indiana, USA (39°25'32.66"N, 87°29'55.43"W). Birds were observed while feeding on a ground-level 4 x 5 m concrete pad located 4 m west of a mature forest and otherwise surrounded by early successional fields. Protective cover was constructed using leafless brush held in a 5 x 1.2 x 1.2 m wooden frame placed along the eastern side of the pad. Ground corn meal was sifted to remove powdery flour and spread evenly over the pad’s surface, providing birds with enough food to avoid depletion over an entire day. This food density minimized the need to move and actively search for food, thus reducing any likely effect of posture on energy intake (Boysen et al. 2001).

The most common birds visiting the site were dark-eyed juncos (approx. 50% of birds). Other relatively common species included American tree sparrows (*Spizella arborea*), white-throated sparrows (*Zonotrichia albicollis*), song sparrows (*Melospiza melodia*) and northern cardinals (*Cardinalis cardinalis*), listed in order of decreasing abundance. Occasional visitors to the feeding pad also included white-crowned sparrows (*Zonotrichia leucophrys*), swamp sparrows (*Melospiza georgiana*), field sparrows (*Spizella pusilla*), northern flickers (*Colaptes auratus*), blue jays (*Cyanocitta cristata*) and red-bellied woodpeckers (*Melanerpes carolinus*).

Observations were made between 22 December 2008 and 10 March 2009. Behavioral observations were made from within a 1.5 x 1.2 x 1.2 m blind positioned 0.5 m from the center of the southern edge of the concrete pad. All observations were videotaped from the blind through a two-way mirror. Air temperature and wind speed were obtained from a NOAA weather station at the Terre Haute International Airport located 17 km northeast of the study site. Air temperatures ranged from -21°C to 17°C during experimental trials, with a median temperature of -5°C.

Experimental sessions

We conducted two basic types of sessions: (1) "slam sessions" when feeding birds were startled with a sharp noise (a "slam"; see below) to observe the effects of thermoregulatory posture on escape flight, and (2) "non-slam sessions" devoted only to observing postures. Observations of postures were also made between disturbances during slam sessions.

During both slam and non-slam sessions, protective cover was positioned in one of two locations; immediately adjacent to, or 4 m from, the eastern edge of the concrete pad. These are referred to as "near" and "far" treatments, respectively. Sessions were conducted by systematically cycling through the four combinations defined by slam and non-slam sessions and the two distances to cover. Only a single distance/slam combination was used during a given observation session. Sessions were conducted in a fully-crossed design with 13 near/slam, 14 far/slam, 14 near/non-slam and 13 far/non-slam sessions. The slam and non-slam sessions were generally alternated in an effort to spread-out exposure to the 80 total slam disturbances (discussed below). Three slams were usually conducted during each session with a range of 1 – 4 slams depending on prevailing conditions. Slam sessions on two consecutive days occurred 4 times, with an additional case of three consecutive slam sessions over 3 days to take advantage of brief periods of extremely cold or warm weather. All sessions were conducted between 0800 and 1130, with the exception of 2 sessions occurring between 1500 and 1700 to take advantage of unseasonably warm midwinter temperatures. Session duration ranged from 45-115 min (depending on bird activity) with a typical session length of 70 min, permitting observations of many different individuals over a range of flock sizes.

Slam sessions involved the use of a startle apparatus (the "slammer"; Fig. 4) to produce a sudden and loud, sharp noise (hereafter referred to as a "slam"). Slams were used in place of simulated attacks because slams were "jolting" and visually undetectable disturbances. The nature of the slams induced an immediate flight response with little time for decision-making that could confound our measurement of take-off time. These slams resulted in an abrupt and immediate flight to cover by feeding birds with the exception of one junco that froze in response to the slam (see below).

Behavioral observations focused on dark-eyed juncos because of their abundance at the study site. During non-slam sessions, the behavior of individual feeding juncos was videotaped when flocks were stable, defined as no birds joining or leaving the flock for approximately 15 seconds. “Focal” birds were picked at random from the flock and videotaped at high magnification for approximately 10 seconds to allow detailed analysis of behavior (see below). This process was repeated for other juncos as long as previously-unobserved juncos were present and the flock remained stable. Videotaped observations of focal birds were similarly made during slam sessions in the time between slams (minimum of 15 min, median time of 24 min). Birds returned to the concrete pad approximately 3 - 5 min post-slam and resumed normal feeding behavior.

Behavioral monitoring of slam-exposed focal juncos focused on an individual’s behavior/posture immediately prior to a slam as well as its slam-induced escape response. Prior to a slam, the experimenter focused the video camera at high magnification on a junco exhibiting a thermoregulatory posture typical for that observation session. Each slam bird was videotaped for at least 10 s to collect behavioral data (see below); that focal junco was then videotaped (at high magnification) as it prepared for flight in response to the slam. The experimenter manually reset the slammer immediately following each slam and prior to any birds returning to feed at the pad.

Posture and other behavioral measurements

Videotape analyses focused on the posture, pecking time (i.e., feeding rate) and social environment of each focal bird. We assigned a posture rank to each focal junco based on our perception of the degree to which various postures would hinder take-off during escape flights. This posture-ranking scale (Fig. 5) was devised prior to any data analysis and categorized postures from 1 - 6 based on the degree of leg exposure determined by leg position and ptiloerection, as these factors would likely have the greatest influence on take-off times. For example, the level 1 posture was characterized by sleek feathers and maximal leg exposure with visible tibiotarsus; this would presumably facilitate quick escape. Level 6 postures appeared (*a priori*) to be the most inhibitory in terms of escape ability, and featured much ptiloerection, complete foot coverage by feathers and little lateral movement, possibly with both feet held off the ground simultaneously. Note that birds using level 6 postures were not resting, but were actively feeding with regular bouts of antipredator vigilance. Intermediate posture ratings were based on the degree of leg and foot exposure (Fig. 5).

For non-slam focal juncos, a posture level was assigned based on the predominant posture during its 10 s observation period; focal birds typically maintained a single posture during this period. For focal juncos subjected to slams, posture rating was assigned based on the posture exhibited at the time of the slam itself. In addition, the head position of each slam junco was recorded at the time of the initial response to the slam, since an individual with its head down may require additional adjustments before take-off (Elgar et al. 1986, Lima 1994; but see Kaby and Lind 2003). Head position was considered “up” or “down” depending on the position of the bill above or below the horizontal plane. The time required for take-off was measured as the number of video frames from a bird’s slam-induced initial startle response (typically a sudden flinch) to when its feet were no longer in contact with the concrete pad. This total repertoire of behaviors included postural adjustments, an upward body stretch, and one flap of the wings. Since our focus was on posture and the time to initiate flight, our videotaping set-up was not devised to measure any aspects of flight *per se*, including take-off angle (Kullberg et al. 1998, Lind et al. 2002) or flight speed (Lind et al. 2010). The thermoregulatory postures used during foraging do not likely have lasting effects on flight performance following the postural adjustments associated with take-off.

For each “zoomed in” focal junco, we also recorded pecking time as the number of video frames required to complete 10 pecks (tape speed of 30 frames/sec). Flock size and nearest neighbor distance were recorded immediately prior to recording the posture and pecking times from a zoomed-out video image of the feeding area. All distance measurements were determined to the nearest 10 cm by referring to distinct reference points on the surface of the concrete pad. The proportion of non-sparrows in the flock was also recorded, since these larger birds (e.g. blue jays, cardinals, flickers) could potentially disturb or startle the smaller birds in the flock and influence their postures. However, juncos adjust their anti-predator behavior in response to heterospecific emberizid sparrows in much of the same way as they do conspecifics (Lima 1995a). Thus, we did not incorporate sparrow species composition into our analyses.

Statistical considerations

Each take-off time from a slam junco (80 over the course of the study) was considered as an independent observation. Banding for identification purposes was not practical given the fact that many postures featured legs that were completely covered with feathers, thus obscuring leg bands. However, treating each observation as independent is a reasonable assumption given the random-sampling technique used to collect observations and the large number of juncos visiting the site (ca. 200 individuals, as determined by the maximum number of juncos at the site on cold days). It is nevertheless possible that some juncos were recorded more than once. Two focal slam juncos were excluded from the analysis; one “froze” in response to the slam, and the other appeared to be extraneously startled just prior to the slam. Additionally, the focal observation period for three of the slam juncos was not long enough to determine a pecking time, leaving a total of 75 juncos for the slam-related analyses.

Our analyses of junco thermoregulatory postures (non-slam birds) focused on data from flocks ≤ 6 birds, which yielded 209 observations over 39 sessions (averaging 5.4 observations per session). Any effect of group size would be maximally detectable within this range (see Caro 2005). An overrepresentation of birds feeding in larger flocks would likely diminish our ability to detect the effects of social factors on junco behavior, as such effects diminish greatly as flock size increases (Roberts 1996, Caro 2005, Beauchamp 2008, 2010). Furthermore, frequent aggressive interactions among individuals in large flocks could alter both postures and vigilance patterns (Pravosudov and Grubb 1999; see also below). Each observation of posture was considered statistically independent due in part to the large number of juncos present and the small number of observations included per session.

A multinomial logistic regression was used (in part) to analyze which factors affect junco postures (non-slam birds) in our fully-crossed experimental design. For this analysis, posture was considered as a categorical dependent variable. We condensed the 6 posture levels in Fig. 5 to 3 categories to aid in the interpretation of resulting odds-ratios. Level 1 and 2 postures (Fig. 5) were combined into category I, as these postures all featured some degree of leg exposure. Category II included level 3 postures with legs completely covered and both feet on the ground. Posture levels 4, 5 and 6 (the latter two were fairly rare) were combined into category III, characterized by postures with one foot or both feet completely covered in feathers. Category I was used as the reference category in the analysis. Due to the large sample size required by such an analysis, only our primary variables of interest (“wind”, “temperature”, “cover position” and “flock size”) were included in the model. This analysis was conducted using the mlogit package in R (version 2.13.2).

In addition to the multinomial logistic regression, an ANCOVA was also used to help determine which factors affect the types of postures used by juncos. Unlike the multinomial regression analysis, our ANCOVA included all variables of interest as well as key interactions for all 6 posture levels. This analysis treats posture as a continuous variable, which is reasonable given that postures were defined mainly by the degree of leg coverage with coverage increasing with greater posture ratings. The exact thermal benefits associated with each change in posture level are unknown, but almost certainly increase with higher-level postures. Cover position and session type were included as fixed factors, with near and far cover position assigned a dummy code of “1” and “2” and non-slam and slam sessions coded as “0” and “1”, respectively. Remaining independent variables and interactions of interest were included as covariates. Day number was determined as the number of days following the start of the experiment, with “1” assigned to the first day of the study. The only interactions included in the model were those of biological interest, especially those involving temperature.

Unlike the posture analysis described above, an ANCOVA could not be used to analyze junco take-off times as all take-off observations were made during slam sessions. A general linear multiple regression model was thus used to analyze junco take-off times with all independent variables considered as fixed factors. Head position above or below the horizontal plane was also assigned a dummy code for this analysis (head up = 1, head down = 2). Posture and temperature were highly correlated ($r = 0.78$) and, therefore, only posture was included in the take-off time analysis. All analyses (excluding the multinomial logistic regression) were conducted using Statistica 6.0 (Statsoft, Tulsa, OK, U.S.A.)

Results

Results from the slam focal juncos (*N* = 75) support the idea that heat-conserving postures increase the time needed to initiate escape (Fig. 6). Overall, birds using higher-rated postures required significantly more time for take-off (Table 3). This result is especially clear for birds using postures 1 – 4 (see Fig. 5), with a 61% increase in the average take-off time across these postures. However, a possible decrease in the time required for full take-off (i.e., faster take-off) is apparent across the higher-rated postures, 4, 5 and 6 (Fig. 6), although there are only a small number of observations in levels 4 and above. Nevertheless, this downward trend may indicate that our posture-rating scale (developed prior to analyzing our results) did not adequately identify the most take-off limiting postures. Take-off times were not significantly related to pecking time or head position immediately prior to the slam (Table 3). Flock size, cover position, and day number also did not significantly affect take-off times. The lack of an effect of day number suggests that (i) the juncos did not habituate to the slam stimulus, and (ii) that changes in body mass did not strongly influence take-off times, since the juncos were likely increasingly lighter during the latter portions of the experiment (see Rogers and Rogers 1990, Lind et al. 2010).

Recall that we analyzed the posture of non-slam juncos using both a multinomial logistic regression and an ANCOVA. The former used only three posture categories derived from the more expansive 6 levels used in the ANCOVA (see methods). The multinomial logistic analysis indicates a strong effect of temperature on posture (see also below); categories associated with high-rated postures (i.e., categories II and III) were used more frequently as temperature dropped (Table 4), an effect that was highly significant. We also detected a nearly-significant effect of wind speed on posture, which tended to become more heat-conserving as wind speeds increased.

Higher posture categories also tended to be associated with the “near” cover position, although the effect was not significant at $\alpha = 0.05$. The multinomial logistic regression also detected a significant increase in posture category with an increase in flock size, although this effect was only significant for comparisons between category I and II (Table 4).

The ANCOVA analysis of junco postures was not as constrained by the requirement of a large sample size as was our multinomial logistic regression analysis, which allowed us to consider more posture levels, variables, and interactions. This analysis, however, similarly indicated an effect of temperature, wind speed and cover position on posture (Table 5). Thermoregulatory postures became less heat-conserving (i.e., lower posture rating, see Fig. 5) as air temperature increased (Fig. 7). Postures at or above level 3 were generally observed at air temperatures under -10°C, with level 1 and 2 postures primarily observed otherwise. Location of cover was significantly related to posture (Table 5), with birds tending to use more heat-conserving postures when feeding closer to cover (Fig. 7). Wind speed also affected junco postures (Table 5); birds used postures that conserve heat and minimize leg exposure as wind speed increased. A statistically significant wind speed-temperature interaction indicates that birds used more heat-conserving postures when cold temperatures were accompanied by higher wind speeds, which also suggests that potentially cumbersome heat-conserving postures provide thermal benefits.

Contrary to our expectations, thermoregulatory postures (ANCOVA analysis) were not significantly associated with flock size or nearest neighbor distance (NND) (Table 5). The temperature-flock size, temperature-cover and temperature-NND interactions were also not significant. Pecking time (a proxy of vigilance) and posture were not significantly associated with one another, indicating that vigilance was not strongly affected by posture. Northern cardinals and other larger birds were fairly frequent visitors to the feeding pad and sometimes caused flock disturbances during arrival and departure, but the proportion of non-sparrows in the flock did not significantly affect posture (Table 5). Day number was not significantly associated with posture, indicating that juncos did not differentially adjust their thermoregulatory postures over the experimental time period.

Discussion

Our results show that juncos used increasingly more advantageous, heat-conserving thermoregulatory postures under colder conditions. It is reasonable to assume that various posture levels provide varying thermal benefits since each posture is associated with varying coverage of areas with much potential heat loss (the legs and feet; Martineau and Larochelle 1988, Ward et al. 1999). The use of such heat-conserving postures in cold environments is as expected given the increase in metabolic rate associated with cold temperatures (Wolf and Walsberg 1996) and heat loss (Bakken 1991, Ward et al. 1999). However, this effect implies that some sort of cost is associated with the more heat-conserving postures; otherwise, such postures would be more widely used in winter conditions. In fact, the most advantageous postures were typically used only when air temperature fell well below -10°C (Fig. 7), despite the fact that a wintering junco's lower critical temperature is typically about +20°C (Bakken et al. 1991). The results from the slam focal juncos suggest that this cost reflects the increased time necessary to initiate escape when using a more advantageous posture. Hence, the tendency for birds to use increasingly heat-conserving postures under colder conditions can be viewed as a trade-off between thermoregulation and the risk of predation (see also Carrascal et al. 2001). In other words, although extreme thermoregulatory postures would always conserve much heat, birds may only resort to using such postures under very cold temperatures in which the need to conserve body heat outweighs the cost of a greater take-off time.

The observed posture-related delays in escape are seemingly small but nevertheless consequential. On average, juncos using posture 4 (Fig. 5) exhibited a 61% longer take-off time than birds using posture 1. This delay added an additional 0.12 s to take-off time as compared to the average response time of posture 1 birds. When under attack by an *Accipiter* hawk (see Roth et al. 2006), slowing escape by even a fraction of a second could mean the difference between life and death. At an *Accipiter* approach speed of about 14 m/s (Newton 1986), a delay of 0.12 s would allow a hawk to approach 1.7 m closer to a feeding bird before the latter could become airborne. We cannot say precisely how much of an increase in risk is incurred by such a delay, but it would almost certainly favor the hawk in a close ambush (see also Bednekoff 1996; but see Lind 2004). It is certainly possible that other compensatory behaviors may be used simultaneously to reduce the risk incurred in various postures (see Lind and Cresswell 2005). For instance, birds could reduce feeding rates and increase vigilance while using heat-conserving postures, but we found no such effect in our study.

The slowed take-off for birds using thermally-advantageous postures reflected the time required to prepare for flight (smoothing of feathers, putting both feet on the ground, etc.). In fact, the greatest increase in take-off time occurred at posture level 4 (Fig. 6). Birds using level 4 postures had one foot in the air at the time of the slam (Fig. 5) and had to place this foot on the ground prior to take-off. Peripheral cooling of the limbs and flight muscles may be an alternative explanation for slowed escape when feeding under cold conditions, but the observed increase in take-off time was clearly associated with postural adjustments prior to take-off rather than the ineffective muscle function that would be associated with peripheral cooling.

Furthermore, birds using higher-level postures (Fig. 5) were actively feeding and thus it is unlikely that their peripheral muscles would have cooled (if at all) to the extent of limiting mobility. Peripheral muscles were also likely still warm from the flight to the study site and frequent false alarm flights to cover (see Lima 1995b). Another alternative explanation is that longer take-off times reflected a reluctance to abandon feeding under thermally stressful conditions. However, all take-off times were brief (Fig. 6), and in no instance did birds attempt to feed (or do anything other than initiate flight) after a slam. There is thus little suggestion that a temperature-dependent decision-making process influenced take-off times. Solar heat gain and its interaction with ptiloerection can also affect a small bird's heat balance (Wolf and Walsberg 2000). However, nearly all of our observations were conducted shortly after daybreak when the sun was low in the sky and largely blocked by the forest to the east of the study site.

The juncos subject to slams probably varied in body mass over the course of the study, and this variation might have influenced the time it took for them to become airborne (take-off time). The juncos would likely have been at their heaviest early in the study, becoming progressively lighter as the winter waned (Rogers and Rogers 1990, Lind et al. 2010). Thus, an effect of body mass on the time to become airborne would likely be apparent in a significant effect of day number in our analysis, but no such effect was observed (ANCOVA analysis, Table 5). It is also not clear that an increase in body mass would lengthen the very early stage of escape (the preparation for flight) that we measured, although body mass may affect flight velocity, take-off angle and maneuverability once airborne (Witter and Cuthill 1993, Witter et al. 1994, Lind et al. 1999, Kullberg et al. 2000, Lind et al. 2010; but see Krams 2002, and also Lind et al. 2010).

Take-off times were longer with the more extreme heat-conserving postures, but the results suggest that our *a priori* posture classification system may not fully represent the limitations in take-off ability associated with each posture. The time required to take-off from the feeding pad was greatest when birds were using one-footed postures (levels 4 and 5, Fig. 5). We expected the longest escape times for birds whose feet might not have been in contact with the ground (level 6, Fig. 5). However, it was nearly impossible to determine whether such a focal junco had none, one or both feet on the ground. Hence, both feet may have been on the ground in some posture 6 birds, leading to a somewhat faster take-off than expected. In fact, the results in Fig. 6 suggest that level 6 postures may be better-positioned between levels 3 and 4. Additional data would be needed to fully resolve this issue, as we observed relatively few level 5 or 6 juncos.

Given the predation-thermoregulation trade-off outlined above, factors affecting perceived risk should affect the use of heat-conserving postures. For instance, birds should be more likely to use heat-conserving postures when feeding close to cover due to the greater probability of escape (Lima 1993, Walther and Gosler 2001, Kullberg and Lafrenz 2007). This expectation was supported by our ANCOVA analysis (Table 5, Fig. 7) and suggested by the multinomial logistic analysis (Table 4), although the effect of cover position was not as large as that of temperature. We also expected that birds would use more heat-conserving postures when feeding in larger flocks since individual predation risk would be reduced (Roberts 1996, Krause and Ruxton 2002, Caro 2005), which was partially supported by the logistic analysis, but not the more expansive ANCOVA analysis. Feeding in close proximity to flockmates should also increase safety (Fernández-Juricic et al. 2007) and thus result in the use of more heat-conserving postures, but nearest neighbor distance did not have a significant effect on the postures used by focal juncos. An ANCOVA analysis including very large flocks (up to 68 birds) detected a significant effect of flock size on posture, but one contrary to our expectations in that birds in larger flocks used slightly less heat-conserving postures (results not shown). This result appeared to reflect the greater frequency of agonistic interactions between birds in large flocks (see also Beauchamp 2009), and perhaps an increase in false-alarm flights in large flocks (e.g. Dehn 1990).

This thermoregulation-predation trade-off likely represents an important aspect of energy management in wintering birds (Pravosudov and Grubb 1997), complimenting the better-studied anti-predator trade-offs associated with vigilance (Roberts 1996, Beauchamp 2003, Caro 2005) and habitat selection (Hilton et al. 1999, Yasué et al. 2003). In fact, all of the species visiting the study site used more extreme thermoregulatory postures on very cold days (JMC and SLL, unpublished results). Heat conserved by thermoregulatory postures would also likely conserve body fat necessary for winter survival (Ekman and Hake 1990, Witter and Cuthill 1993), hence thermoregulatory postures may simultaneously reduce both the time spent foraging in harsh microclimates (Grubb 1975, Grubb 1978, Kelly et al. 2002) and exposure to predators. Predation-thermoregulation trade-offs are more obvious in ectothermic organisms that often rely directly on dangerous microhabitats for adequate thermoregulation (Downes and Shine 1998, Martín and López 1999, Amo et al. 2007, Cooper 2009), but the more subtle thermoregulation-predation trade-off examined in this study is likely widespread in birds and other endotherms.

Acknowledgements

The Department of Biology and College of Graduate and Professional Studies at Indiana State University provided financial support for this project. George Bakken and William

Mitchell also provided valuable advice throughout, and Michael Gerringer, Johan Lind and 2 anonymous reviewers provided valuable comments on the manuscript.

References

Amo L, López P, Martín J. 2007. Refuge use: A conflict between avoiding predation and losing mass in lizards. Physiol Behav. 90:334-343.

Bakken GS. 1991. Wind speed dependence of the overall thermal conductance of fur and feather insulation. J Therm Biol. 16:121-126.

Bakken GS, Murphy MT, Erskine DJ. 1991. The effect of wind and air temperature on metabolism and evaporative water loss rates of dark-eyed juncos, *Junco hyemalis*: a standard operative temperature scale. Physiol Zool. 64:1023-1049.

Beauchamp G. 2003. Group-size effects on vigilance: a search for mechanisms. Behav Process. 63:111-121.

Beauchamp G. 2008. What is the magnitude of the group-size effect on vigilance? Behav Ecol. 19:1361-1368.

Beauchamp G. 2009. How does food density influence vigilance in birds and mammals? Anim Behav. 78:223-231.

Beauchamp G. 2010. A comparative analysis of vigilance in birds. Evol Ecol. 24:1267-1276.

Bednekoff PA. 1996. Translating mass dependent flight performance into predation risk: an extension of Metcalfe & Ure. Proc R Soc Lond B. 263:887-889.

Boysen AF, Lima SL, Bakken GS. 2001. Does the thermal environment influence vigilance behavior in dark-eyed juncos (*Junco hyemalis*)? An approach using standard operative temperature. J Therm Biol. 26:605-612.

Caro TM. 2005. Antipredator Defenses in Birds and Mammals. Chicago: University of Chicago Press.

Carrascal LM, Díaz JA, Huertas DL, Mozetich I. 2001. Behavioral thermoregulation by treecreepers: trade-off between saving energy and reducing crypsis. Ecology. 82:1642-1654.

Cooper WE. 2009. Theory successfully predicts hiding time: new data for the lizard *Sceloporus virgatus* and a review. Behav Ecol. 20:585-592.

Cresswell W. 1993. Escape responses by redshanks, *Tringa totanus*, on attack by avian predators. Anim Behav. 46:609-611.

Dawson WR, Whittow GC. 2000. Regulation of body temperature. In: Whittow GC, editor. Sturkie's Avian Physiology. 5th ed. San Diego, California: Academic Press. p.343-390.

Dehn MM. 1990. Vigilance for predators: detection and dilution effects. Behav Ecol Sociobiol. 26:337-342.

Dolby AS, Grubb TC. 1999. Effects of winter weather on horizontal and vertical use of isolated forest fragments by bark-foraging birds. Condor. 101:408-412.

Downes S, Shine R. 1998. Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities. Anim Behav. 55:1387-1396.

Ekman JB, Hake MK. 1990. Monitoring starvation risk: adjustments of body reserves in greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. Behav Ecol. 1:62-67.

Elgar MA, Burren PJ, Posen M. 1984. Vigilance and perception of flock size in foraging house sparrows (*Passer domesticus* L.). Behaviour. 90:215-223.

Elgar MA, McKay H, Woon P. 1986. Scanning, pecking and alarm flights in house sparrows (*Passer domesticus* L.). Anim Behav. 34:1892-1894.

Fernández-Juricic E, Beauchamp G, Bastain B. 2007. Group-size and distance-to-neighbor effects on feeding and vigilance in brown-headed cowbirds. Anim Behav. 73:771-778.

Fernández-Juricic E, Kacelnik A. 2004. Information transfer and gain in flocks: the effects of quality and quantity of social information at different neighbour distances. Behav Ecol Sociobiol. 55:502-511.

Fortin D, Larochelle J, Gauthier G. 2000. The effect of wind, radiation and body orientation on the thermal environment of Greater Snow goose goslings. J Therm Biol. 25:227-238.

Grubb TC. 1975. Weather-dependent foraging behavior of some birds wintering in a deciduous woodland. Condor. 77:175-182.

Grubb TC. 1978. Weather-dependent foraging rates of wintering woodland birds. Auk. 95:370-376.

Hilton GM, Ruxton GD, Cresswell W. 1999. Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. Oikos. 87:295-302.

Hohtola E, Rintamäki H, Hissa R. 1980. Shivering and ptiloerection as complementary cold defense responses in the pigeon during sleep and wakefulness. J Comp Physiol B. 136:77-81.

Kaby U, Lind J. 2003. What limits predator detection in blue tits (*Parus caeruleus*): posture, task or orientation? Behav Ecol Sociobiol. 54:534-538.

Kelly JP, Warnock N, Page GW, Weathers WW. 2002. Effects of weather on daily body mass regulation in wintering dunlin. J Exp Biol. 205:109-120.

Krams I. 2002. Mass-dependent take-off ability in wintering great tits (*Parus major*): comparison of top-ranked adult males and subordinate juvenile females. Behav Ecol Sociobiol. 51:345-349.

Krause J, Ruxton GD. 2002. Living in Groups. Oxford: Oxford University Press.

Kullberg C, Jakobsson S, Fransson T. 1998. Predator-induced take-off strategy in great tits (*Parus major*). Proc R Soc Lond B. 265:1659-1664.

Kullberg C, Jakobsson S, Fransson T. 2000. High migratory fuel loads impair predator evasion in sedge warblers. Auk. 117:1034-1038.

Kullberg C, Lafrenz M. 2007. Escape take-off strategies in birds: the significance of protective cover. Behav Ecol Sociobiol. 61:1555-1560.

Lima SL. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. Wilson Bull. 105:1-47.

Lima SL. 1994. On the personal benefits of anti-predatory vigilance. Anim Behav. 48:734-736.

Lima SL. 1995a. Back to the basics of anti-predatory vigilance: the group size effect. Anim Behav. 49:11-20.

Lima SL. 1995b. Collective detection of predatory attack by social foragers: fraught with ambiguity? Anim Behav. 50:1097-1108.

Lima SL, Zollner PA. 1996. Anti-predatory vigilance and the limits to collective detection: visual and spatial separation between foragers. Behav Ecol Sociobiol. 38:355-363.

Lind J. 2004. What determines probability of surviving predator attacks in bird migration?: the relative importance of vigilance and fuel load. J Theor Biol. 231:223-227.

Lind J, Cresswell W. 2005. Determining the fitness consequences of antipredation behavior. Behav Ecol. 16:945-956.

Lind J, Fransson T, Jakobsson S, Kullberg C. 1999. Reduced take-off ability in robins due to migratory fuel load. Behav Ecol Sociobiol. 46:65-70.

Lind J, Jakobsson S, Kullberg C. 2010. Impaired predator evasion in the life history of birds: behavioral and physiological adaptations to reduced flight ability. Curr Ornithol. 17:1-30.

Lind J, Kaby U, Jakobsson S. 2002. Split-second escape decisions in blue tits (*Parus caeruleus*). Naturwissenschaften. 89:420-423.

Martín J, López P. 1999. When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. Behav Ecol. 10:487-492.

Martineau L, Larochelle J. 1988. The cooling power of pigeon legs. J Exp Biol. 136:193-208

McNamara JM, Houston A I. 1992. Evolutionarily stable levels of vigilance as a function of group size. Anim Behav. 43:641-658.

Newton I. 1986. The Sparrowhawk. Calton, UK: T. and A. D. Poyser.

Pravosudov VV, Grubb TC. 1997. Energy management in passerine birds during the nonbreeding season: a review. Curr Ornithol. 14:189-234.

Pravosudov VV, Grubb TC. 1999. Effects of dominance on vigilance in avian social groups. Auk. 116:241-246.

Roberts G. 1996. Why individual vigilance declines as group size increases. Anim Behav. 51:1077-1086.

Rogers CM, Rogers CJ. 1990. Seasonal variation in daily mass amplitude and minimum body mass: a test of a recent model. Ornis Scand. 21:105-114.

Roth TC, Lima SL, Vetter WE. 2006. Determinants of predation risk in small wintering birds: the hawk's perspective. Behav Ecol Sociobiol. 60:195-204.

Swanson DL, Olmstead KL. 1999. Evidence for a proximate influence of winter temperature on metabolism in passerine birds. Physiol Biochem Zool. 72:566-575.

Walsberg GE. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. Auk. 103:1-7.

Walther BA, Gosler AG. 2001. The effects of food availability and distance to protective cover on the winter foraging behavior of tits (Aves: Parus). Oecologia. 129:312- 320.

Ward S, Rayner JMV, Möller U, Jackson DM, Nachtigall W, Speakman JR. 1999. Heat transfer from starlings *Sturnus vulgaris* during flight. J Exp Biol. 202:1589-1602.

Witter MS, Cuthill IC. 1993. The ecological costs of avian fat storage. Philos Trans R Soc Lond B Biol Sci. 340:73-92.

Witter MS, Cuthill IC, Bonser RH. 1994. Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. Anim Behav. 48:201-222.

Wolf BO, Walsberg GE. 1996. Thermal effects of radiation and wind on a small bird and implications for microsite selection. Ecology. 77:2228-2236.

Wolf BO, Walsberg GE. 2000. The role of the plumage in heat transfer processes of birds. Amer Zool. 40:575-584.

Yasué M, Quinn JL, Cresswell W. 2003. Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in Redshanks. Funct Ecol. 17:727-736.

Zerba E, Dana AN, Lucia MA. 1999. The influence of wind and locomotor activity on surface temperature and energy expenditure of the eastern house finch (*Carpodacus mexicanus*) during cold stress. Physiol Biochem Zool. 72:265-276.

Table 3. Multiple regression analysis of take-off time in slam-startled focal juncos.

Variable	*B*	*SE*	*T*	*P*
Day number	0.025	0.015	1.669	0.100
Posture	**0.825**	**0.141**	**5.852**	**< 0.0001**
Cover position	-0.364	0.376	-0.969	0.336
Pecking time	-0.046	0.123	-0.370	0.713
Head position	0.035	0.391	0.089	0.929

Full model: $N = 75$, Adjusted $R^2 = 0.312$, $F_{5,69} = 7.7029$, $P < 0.0001$. Factors significantly affecting take-off time are shown in bold.

Table 4. Multinomial logistic regression analysis of factors affecting junco thermoregulatory postures. All significant factors are shown in bold. Posture category I includes posture levels 1 and 2 (see Fig. 5), category II includes level 3 postures and category III combines posture levels 4 – 6.

	B	*SE*	*T*	exp(*B*)	*P*
Posture category II vs. I					
Temperature	**-0.804**	**0.258**	**-3.116**	**0.448**	**0.002**
Cover position	-2.470	1.375	-1.796	0.085	0.073
Wind speed	0.322	0.178	1.815	1.380	0.069
Flock size	**0.911**	**0.452**	**2.015**	**2.487**	**0.044**
Posture category III vs. I					
Temperature	**-0.897**	**0.304**	**-2.950**	**0.408**	**0.003**
Cover position	-3.009	1.944	-1.548	0.049	0.122
Wind speed	0.259	0.208	1.243	1.296	0.214
Flock size	0.538	0.546	0.986	1.713	0.324

Table 5. ANCOVA of factors affecting junco thermoregulatory postures with all significant factors shown in bold.

Source	*df*	Mean Square	*F*	*P*
Cover position	**1**	**1.804**	**7.607**	**0.006**
Session type	1	0.320	1.350	0.247
Temperature	**1**	**1.964**	**8.283**	**0.005**
Wind speed	**1**	**2.109**	**8.893**	**0.003**
Flock size	1	0.086	0.364	0.547
Prop. non-sparrows	1	0.092	0.388	0.534
NND	1	0.005	0.023	0.880
Pecking time	1	0.002	0.010	0.921
Temperature*NND	1	0.011	0.048	0.828
Temperature*Wind	**1**	**2.173**	**9.164**	**0.003**
Temperature*Cover	1	0.142	0.601	0.439
Temperature*Flock size	1	0.268	1.132	0.289
Day number	1	0.263	1.109	0.294
Error	168	0.237		

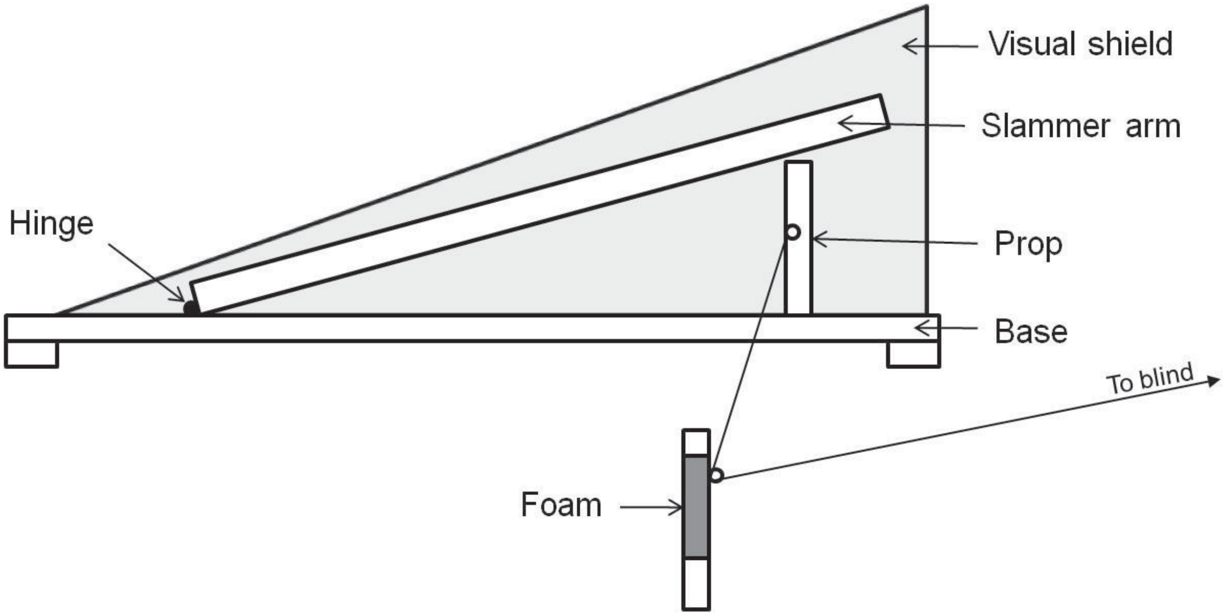


Figure 4. Schematic diagram of the “slammer” device used to create a sudden, sharp noise to startle birds into flight. The device consisted of a wooden arm (4 x 9 x 120 cm) attached at one end to a 4 x 9 x 245 cm wooden base by a flexible plastic hinge. The arm was supported by a 28 cm tall prop and could be triggered to drop onto the base by abruptly pulling a nylon string from within the blind, thereby removing the prop and creating a sudden, sharp noise. A vertically-positioned section of thin plywood (“visual shield”) concealed all moving portions of the slammer from the feeding birds, while minimally obstructing a feeding bird’s view of its surroundings. The slammer was positioned parallel and immediately adjacent to the western edge of the concrete pad with the base elevated 5 cm off the ground to maximize sound production. The string attached to the prop was threaded through an eyelet placed on a ground-level wooden stake covered with foam; the foam prevented any noise production prior to the slam from the collision with the prop.

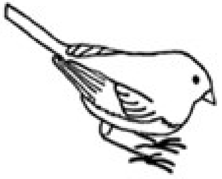
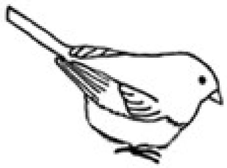
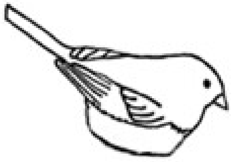
Level	Posture	Description
1		Tibiotarsus visible
2		Tibiotarsus covered; Tarsometatarsus exposed
3		Tarsometatarsus covered; both feet on ground
4		Tarsometatarsus covered; one foot on ground
5		One foot on ground; leaning towards side or tail resting on ground
6		Feathers in contact with ground; no feet visible; little lateral locomotion, but actively feeding

Figure 5. Criteria for assigning junco thermoregulatory postures to one of six levels.

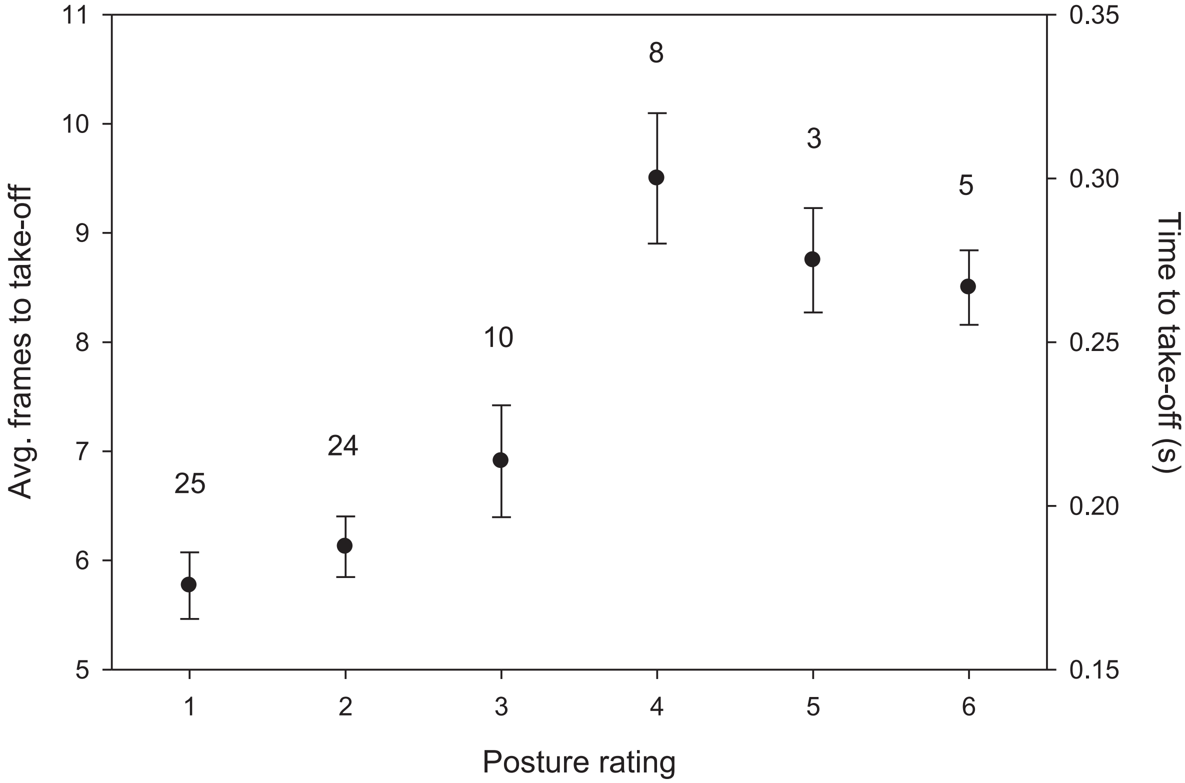


Figure 6. Average time to full take-off (± SE) of slam-exposed focal juncos for each of the six thermoregulatory postures (see Fig. 5). Both y-axes represent measures of junco take-off times; the left axis denotes the number of video frames required for a bird's toes to leave the surface of the feeding pad, and the right axis illustrates the corresponding take-off time measured in seconds. Numbers indicate sample sizes for each of the six postures.

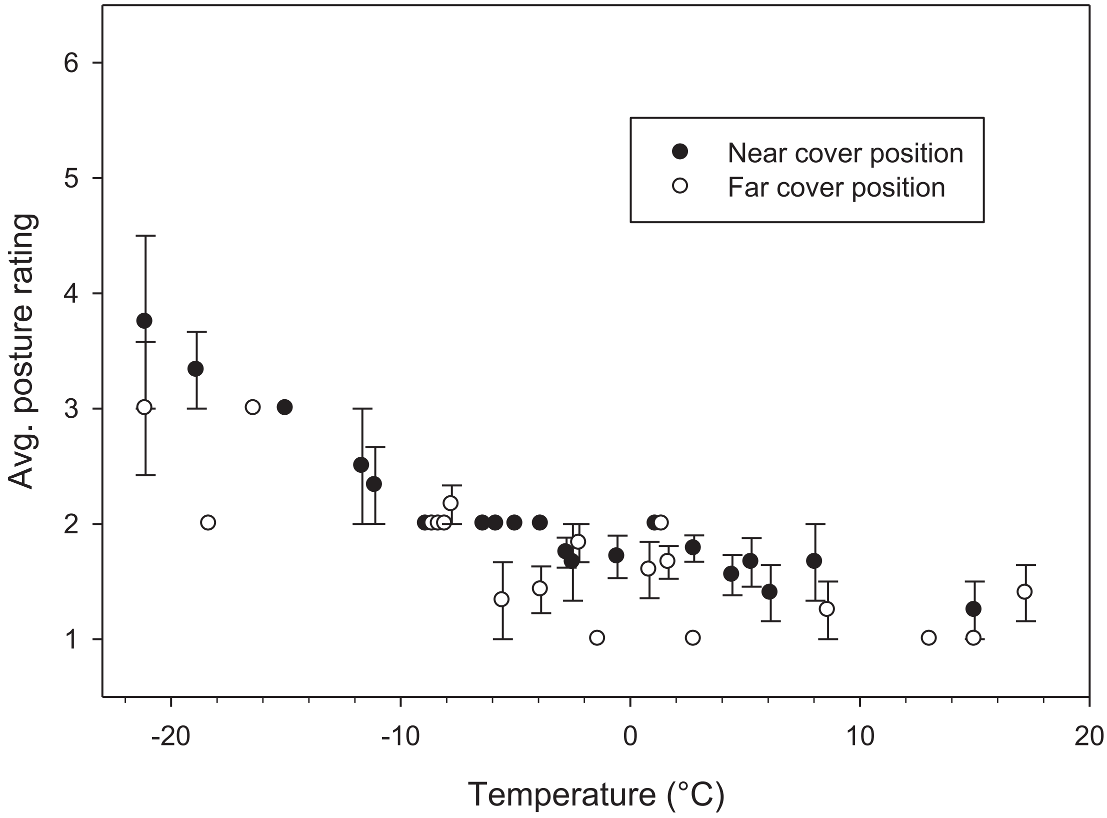


Figure 7. Average posture rating (± SE) across the range of observed air temperatures. Closed (●) and open (○) circles represent postures of birds in the near- and far-cover treatments, respectively, with observations pooled into 1°C bins. See Fig. 5 for an explanation of posture ratings.

CHAPTER 3

WINTERING BIRDS AVOID WARM SUNSHINE: PREDATION AND THE COSTS OF FORAGING IN SUNLIGHT

Wintering birds can gain significant thermal benefits by foraging in direct sunlight. However, exposure to bright sunlight might make birds easier to detect by predators and may also cause visual glare that can reduce a bird's ability to monitor the environment. Thus, birds likely experience a trade-off between the thermal benefits and predation-related costs of foraging in direct sunlight. To examine this possible thermoregulation-predation trade-off, we monitored the behavior of mixed-species flocks of wintering emberizid sparrows foraging in alternating strips of sunlight and shade. On average, these sparrows routinely preferred to forage in the shade, despite midday air temperatures as much as 30 °C below their thermoneutral zone. This preference for shade was strongest at relatively high temperatures when the thermal benefits of foraging in sunlight were reduced, suggesting a thermoregulation-predation trade-off. Glare could be reduced if birds faced away from the sun while feeding in direct sunlight, but we found that foraging birds tended to face southward (the direction of the sun). We speculate that other factors, such as the likely direction of predator approach, may explain this southerly orientation, particularly if predators use solar glare to their advantage during an attack. This interpretation is supported by the fact that birds had the weakest southerly orientation on cloudy days. Wintering birds may generally avoid foraging in direct sunlight to minimize their risk of predation.

However, given the thermal benefits of sunshine, such birds may benefit from foraging in habitats that provide a mosaic of sunlit and shaded microhabitats.

Introduction

Overwintering birds must cope with many thermal challenges that jeopardize survival. Exposure to high wind and low temperatures causes metabolic rate to increase (Webster and Weathers 1988; Wood and Lustick 1989; Bakken et al. 1991) and subsequently, birds may spend more time foraging under such conditions. However, the more time that a bird spends active and feeding, the more time it will be exposed to potential predators (Lima and Dill 1990). The depletion of energy reserves in challenging thermal environments will also increase the probability of starvation if a bird does not have enough reserves to survive periods of food unavailability (i.e., snow cover) or a cold winter night (McNamara and Houston 1990; Pravosudov and Grubb 1997).

Wintering birds may alter their behavior in a number of ways to reduce heat loss in thermally challenging environments. For instance, a bird can reduce its metabolic rate by foraging in relatively warm habitats with low wind speeds (Wachob 1996). Feeding away from wind-exposed forest edges (Dolby and Grubb 1999) and closer to the forest floor (Grubb 1975) can also reduce heat loss in cold and windy environments. Furthermore, nighttime roosts that are sheltered from the wind provide the greatest thermal benefits (Walsberg 1986). High wind speeds can also reduce thermal resistance of the feathers (Bakken 1991), thus birds can also change their orientation with respect to wind direction to minimize disruption of the thermal boundary created by the feathers (Wood and Lustick 1989; Fortin, Larochelle and Gauthier 2000). A bird’s legs and feet are also areas that contribute significantly to the loss of body heat, and efficient thermoregulatory postures can significantly reduce the amount of heat lost through these areas (Dawson and Whittow 2000). However, postures that conserve the most body heat can hinder escape and are typically used only at very low temperatures and when feeding in relatively safe conditions (Carr and Lima 2012).

Another way that birds can reduce the energetic costs of foraging in cold environments is by foraging in direct sunlight. Most habitats provide a mosaic of sunlit and shaded patches that would allow birds the opportunity to feed in sunlight. Goldstein et al. (1987) found that sunbirds prefer to feed from flowers in the sun rather than the shade, a preference attributed to the thermal benefits of feeding in sunlight. Radiative heat gain via solar radiation can lead to a significant reduction in metabolic rate (Wood and Lustick 1989; Wolf and Walsberg 1996; Walsberg et al. 1997; Wolf et al. 2000), and sunning behavior can reduce the energetic costs of foraging at low ambient temperatures (Ohmart and Lasiewski 1971; Clark and Ohmart 1985). Positioning the long axis of the body perpendicular to incoming solar radiation, and thus maximizing the amount of surface area exposed to direct sunlight, can also reduce energetic losses (Lustick et al. 1978; Fortin et al. 2000; Maloney et al. 2005; Hetem et al. 2011).

Although foraging in direct sunlight is thermally advantageous, there are also associated costs. For instance, Fernández-Juricic and Tran (2007) found that house finches (*Carpodacus mexicanus*) avoided sunlit food patches and were slower to detect predator attacks in high-light environments (see also Fernández-Juricic et al. 2012). This delayed response to predators may be explained in part by “disability glare” (Martin and Katzir 2000; Fernández-Juricic et al. 2012) caused by excess light entering the eye, thus interfering with predator detection. One way that a bird may reduce glare is by changing its orientation to minimize the amount of light entering its eyes; orienting with the sun in their blind spot (Fernández-Juricic et al. 2004) would reduce visual glare. However, no studies have addressed this matter.

A relatively bright environment might also make it easier for predators to find and attack their prey (Kacelnik 1979; Richmond et al. 2004; Meager et al. 2010). However, the thermal benefits to prey associated with foraging in sunlight may outweigh such costs when birds are exposed to cold temperatures. For instance, Carrascal et al. (2001) found that short-toed treecreepers (*Certhia brachydactyla*) spent more time vigilant and were less cryptic when they foraged in sunlight. Treecreepers preferred to forage in the shade even at environmental temperatures below their thermoneutral zone, choosing to forage in sunlit patches only at the coldest temperatures (< 4 °C). Such behavior suggests a trade-off between thermoregulation and predation risk.

In this study, we examined the microhabitat choice of overwintering emberizid sparrows foraging in a controlled environment that consisted of a large ground-level feeding pad covered in alternating strips of sunlight and shade. From a simple energetic perspective, these birds should have chosen to forage in sunlit areas. However, the birds in our experiment showed an overall preference for shade under all observed midday temperatures (as low as -12 °C). We also monitored the orientation of feeding birds with respect to the position of the sun. Birds feeding in sunlight did not tend to orient perpendicular to incoming solar radiation, which would maximize heat gain from direct sunlight (but see Bakken et al. 1985). The idea that birds should orient away from the sun to avoid disruptive glare also received little support, as birds preferred to face southward (i.e., the direction of the sun).

Materials and Methods

Study site and species

Our study site was located 9 km southwest of Terre Haute, Indiana, USA (altitude = 170 m above sea level; 39°25’32.66”N, 87°29’55.43”W). The feeding area consisted of a ground-level concrete pad (4 x 6 m). The long axis of the concrete pad was oriented north to south and was positioned parallel to and approximately 4 m west of mature forest. The pad was otherwise surrounded mainly by early successional fields. Protective, leafless brushy cover was placed in a 5 x 1.2 x 1.2 m wooden frame immediately adjacent to the eastern side of the concrete pad. The concrete pad was covered evenly with finely-ground cornmeal. Enough cornmeal was provided to serve as a food source throughout the day, but not enough to obscure the surface of the pad. This food provided a standardized feeding environment in both sunlight and shade.

Our observations were conducted on mixed-species flocks of foraging emberizid sparrows. Dark-eyed juncos (*Junco hyemalis*) and American tree sparrows (*Spizella arborea*) were the most abundant species at our study site; of the birds recorded at the site, 54% were juncos and 39% were tree sparrows. The remaining species consisted primarily of northern cardinals (*Cardinalis cardinalis*), song sparrows (*Melospiza melodia*), white-throated sparrows (*Zonotrichia albicollis*), swamp sparrows (*M. georgiana*) and field sparrows (*S. pusilla*), listed in order of decreasing abundance. Dark-eyed juncos and American tree sparrows treat one another essentially as conspecifics with regard to antipredator behaviors such as vigilance (Lima 1995). We thus considered heterospecific emberizids to be functionally equivalent throughout this study. Our qualitative results do not change if we focus our analysis on a given species.

Experimental observations were made between 23 December 2010 and 19 March 2011. All observations were made from within a blind (1.5 x 1.2 x 1.2 m) positioned 1.5 m from the center of the west side of the pad. Sessions were video-recorded from within the observation blind through a two-way mirror for later review. Measurements of air temperature, wind speed and wind direction were obtained from a National Oceanic and Atmospheric Administration weather station located 17 km northeast of the study site (altitude = 175 m above sea level) in a flat landscape of agricultural fields and forest fragments that was very similar to the landscape surrounding our study site. Past experience indicated a very close correspondence between weather variables recorded at our study site and the weather station (Boysen et al. 2001). Temperatures during the midday observation sessions (see below) ranged from -12 °C to 13 °C (mean = -0.2 °C) and wind speeds ranged from 0 to 26 km h^{-1} (mean = 13.5 km h^{-1}).

Sunlight and shade

Vertically positioned "shade boards" were placed adjacent to the south side of the pad, which generated alternating strips of sunlight and shade across the entire foraging surface. The overall shade structure was constructed using 11 long (4 m) wooden shade boards (18 cm x 5 cm in width and thickness) with 25 cm gaps between each board. The broad, wide side (18 cm) of the shade boards faced southward to maximize the amount of shade cast on the concrete pad. Shade boards were held upright by a wooden support system. This support system consisted of two 1.7 m tall 9 cm x 9 cm support posts, one located at each corner of the southern side of the concrete pad. These posts supported a 4.9 m horizontal wooden cross bar (9 cm x 9 cm in cross section) against which the shade boards rested. The shade boards were lashed to the beam with 1 cm thick rope to prevent them from falling over on windy days. Shade boards remained in place for the duration of the study, but were taken down during brief periods of very high winds and when observations were occasionally conducted with the shade boards removed (see below).

Neither the shade boards nor the support system were placed on the foraging surface, and thus did not interfere with a bird's movement while foraging on the concrete pad.

Approximately 37% of the feeding pad was covered in shade during the course of a midday observation session, as determined by the analysis of digital photos of the feeding pad. This calculation included the shade created by the vertical shade boards as well as the horizontal cross bar used to support them. These shade boards provided a glare-reduced environment for birds foraging in shade (see also Fernández-Juricic et al. 2012).

Observation sessions and video analysis

Our primary observations were conducted on sunny days when the sun was at its highest point in the sky (solar noon, ca. 1300 h local time). This time of day provided the greatest thermal benefit from feeding in sunlight. Birds were observed only under cloudless, haze-free skies to avoid conditions with diffuse light and non-distinct boundaries between shaded and sunlit strips. There were 18 such days evenly distributed over the course of the winter.

All sunny-day observation sessions lasted 1 h and were videotaped for later analysis. The video camera was panned across the entire feeding pad every minute. During these pans, we recorded each third of the concrete pad for 2 s, moving immediately to the adjacent third of the pad following each 2 s pause; each camera pan required approximately 6 s to complete. Overlapping a portion of each image when switching between thirds ensured that individual birds were not sampled twice during a given camera pan. Recording the concrete pad in short (2 s) segments reduced digital image blur and produced the clearest image of feeding birds, allowing us to accurately determine the location (foraging in sunlight or shade) and orientation (facing towards or away from the south) of each bird on the pad. A bird with at least the anterior half of its body (excluding the tail) in the shade was considered to be in the shade; all other birds were defined as foraging in sunlight (Bakken et al. 1985). Most of the birds observed during sunny-day sessions were positioned with their entire body in either sunlight or shade.

To minimize glare, and thus enhance predator detection, a bird should orient away from the sun while feeding on a sunny day. This orientation would keep the sun in the bird's blind spot, reducing the amount of light entering the eye chamber. Orientation was determined by the direction of the long axis of the body while foraging. A bird was considered to be oriented towards the south (i.e., the direction of the sun) if it was facing within 80° to the east or west of the southern cardinal direction. Birds facing the south were assigned a value of "1". Birds oriented northward (or away from the sun) had their long axis positioned within 80° to the east or west of cardinal north and were given a value of "0". Our results and conclusions are not changed by a more restrictive definition of orientation (e.g., including only birds within 45° to the east or west of cardinal south, etc.). Birds facing perpendicular to incoming sunlight on sunny days (i.e., 10° north and south of cardinal east or west) were also recorded since this orientation might allow a bird to maximize the thermal input from sunlight. In total, this definition of perpendicular orientation covered 11% (i.e., 40°) of the 360° circle used to classify orientation.

Additional supplemental observations were conducted on cloudy days when the sun was completely obscured and no shadows were visible on the concrete pad. We conducted 13 such hour-long cloudy-day observations beginning at 1300 h. Cloudy-day observations were evenly distributed throughout the winter. We also opportunistically observed birds foraging with the shade boards removed on several sunny days. These "board-down" observations ($N = 6$ sessions) were conducted during the 30 min immediately following a regular sunny day session with shade boards present. Such observations assessed the potential orientational effects of the visual obstructions produced by the shade boards, which may interfere with a bird's ability to detect predators approaching from the south (see also Roth and Lima 2003).

Bird orientation during cloudy day sessions and board-down sessions was determined as per sunny day sessions. If orientation reflects a means of glare reduction, then we expected that birds feeding on cloudy days would equally prefer a northerly or southerly orientation. The shade boards produced a visual obstruction that may reduce a bird's ability to monitor the environment and could potentially be used by a predator to conceal its approach during an attack (e.g. Roth and Lima 2003). Thus, birds may orient towards the south (i.e., towards the direction of the boards) in an attempt to better-monitor these obstructed areas. Observations conducted on sunny days with the shade boards removed allowed us to determine whether these visual obstructions influenced bird orientation on the feeding pad.

Both location (sun/shade) and orientation were recorded for each bird in the flock during a given video camera pan. These data were only recorded for birds that were feeding consistently in one location and not moving across the surface of the pad or interacting with flockmates. Flock size was also recorded at the start of each pan and all observations were collected when birds were foraging in a stable flock (i.e., no birds joined or left the pad for approximately 15 s).

Statistical considerations

Our statistical analyses were focused on average bird behavior during an observation session, although we also present raw flock-specific data as well. Each session was considered to be a statistically independent assessment of the overall behavior of the birds visiting the site.

Each day's observed birds were essentially drawn from a pool of ca. 250 individuals, as determined by the maximum number of birds at the site on very cold mornings. As such, our statistical analyses apply to the overall group of birds visiting the study site, but we have no reason to believe that this group was unusual or unique in any way.

The birds' use of shaded areas was represented by the proportion of birds foraging in the shade averaged over the course of a given sunny observation session. A multiple regression analysis was used to determine whether temperature and wind speed influenced the birds' tendency to feed in shaded areas. The presence of many birds foraging on the pad may exclude individuals from foraging in sunlight or shade, thus average flock size was also included as an independent variable in this analysis. Average flock size during a session ranged between 3.7 – 10.7 birds (mean = 6.5). Ordinal date, determined by the number of days since the start of the experiment (with day 1 assigned to the first observation day), was highly correlated with temperature over the course of the study ($r = 0.73$). Thus, ordinal date was not included in the statistical analyses.

Analysis of bird orientation with respect to the sun was also based on the average orientation of birds during an observation session. The proportion of birds facing southward (and towards the sun on sunny days) was determined by calculating the number of birds scored as facing south divided by the total number of birds with a clear preference for facing northward or southward during an observation session. We used a one-way ANOVA to determine whether the proportion of birds facing southward varied between different light conditions (sunlight, shade and cloudy days) and with the shade boards removed on sunny days. A similar ANOVA was used to compare the proportion of birds oriented eastward or westward (i.e., perpendicular to the direction of the sun) while feeding in sunlight, shade, and on cloudy days.

Multiple regressions were used to determine which factors influenced the orientation of birds when foraging in different light conditions. These analyses were also based on bird behavior averaged over a given observation session. Temperature, wind speed, average flock size, and wind direction were included as independent variables in these regressions. Wind direction during an observation session was assigned a non-compass numerical value for the purposes of this analysis. This was done to avoid the numerical discontinuities between northeasterly and northwesterly winds that would occur using standard compass wind bearings. There were no due easterly winds during observation sessions, thus the easterly cardinal direction was assigned as “0”. All other directions were assigned values based on a 360° clockwise rotation with respect to 0° at cardinal east (i.e., south = 90°, west = 180°, north = 270°). Wind directions falling between the four cardinal directions were assigned the appropriate intermediate values. All statistical analyses were conducted using STATISTICA 6.0 (Statsoft, Tulsa, OK, USA).

Results

A simple plot of the raw data (the proportion of birds in shade for each observed flock) indicated a clear preference for foraging in the shade (Fig. 8). If the birds had no preference for sunlight or shade, then we would expect that approximately 37% of each flock would be in the shade, since 37% of the foraging surface was covered in shade. Of the 556 observed flocks in the 18 observation sessions included in Fig. 8, 86% had over 37% of birds feeding in the shade. We observed very few flocks in which less than 25% of the birds were in the shade (see Fig. 8). On the other hand, we routinely observed instances where 75% or more of a flock was in the shade. Thus, even though 63% of the feeding pad was in full sunlight, the majority of most flocks was in the shade.

This preference for shade was also apparent when averaging behavior by observation session (Fig. 9). The average proportion of birds foraging in the shade during a given session ranged from 0.48 to 0.75. All means were above our null expectation of 0.37 (Fig. 9), even during our coldest observed midday temperature (-12 °C). A multiple regression indicated that temperature had a significant effect on the proportion of birds foraging in the shade, with more birds in the shade as temperature increased (Table 6, Fig. 9). There was no significant effect of wind speed or average flock size on the birds' tendency to feed in the shade (Table 6). A species-specific analysis of shade preference by dark-eyed juncos and American tree sparrows indicated that both species exhibited essentially identical preferences (results not shown).

Birds consistently tended to orient towards the south (i.e., towards the sun when visible) regardless of whether they were feeding in shade, sunlight, or under cloudy conditions (Fig. 10). Birds also faced southwards when feeding with the shade boards removed on sunny days. The average proportion of birds facing southwards during an observation session never fell below 0.5 (the value indicating no orientation preference) for any feeding condition over the course of the study (Fig. 10). However, an ANOVA indicated that there was significant variation in southward orientation ($F_{3,51} = 3.59$, $P = 0.02$), driven largely by the lower tendency to face southward during cloudy sessions. Sequential Bonferroni post-hoc comparisons (Rice 1989) indicated a significantly lower tendency to orient southward on cloudy days compared to when birds were feeding in sunlight ($P = 0.014$, adjusted $\alpha = 0.017$), shade ($P = 0.017$, adjusted $\alpha = 0.025$), and with the shade boards removed on sunny days ($P = 0.020$, adjusted $\alpha = 0.050$; see

Fig. 10). Average orientation during a given condition was not significantly influenced by any of the environmental or social factors included in the analyses (Table 7).

Birds did not tend to orient eastward or westward (i.e., perpendicular to the sun on sunny days) in order to maximize radiative heat gain. In fact, only a small proportion of the total number of birds observed during a given sunny-day session showed such an orientation (Fig. 11). If birds oriented randomly on the pad, we would expect that approximately 11% of an average flock would be oriented towards the east or west (see Methods). The average proportion of such oriented birds fell below this null expectation for all sessions on sunny days (shade and sunlight data), but not on cloudy days (Fig. 11). An ANOVA indicated that there was indeed significant variation in the proportion of perpendicular birds ($F_{2,46} = 29.67$, $P < 0.001$). Sequential Bonferroni post-hoc comparisons indicated that birds foraging under cloudy skies had a significantly greater tendency to orient eastward/westward than both shade-foraging ($P < 0.001$, adjusted $\alpha = 0.017$) and sunlight-foraging ($P < 0.001$, adjusted $\alpha = 0.025$) birds on sunny days (see Fig. 11).

Discussion

The overwintering sparrows in this study prefer to forage in shade despite the thermal advantages (e.g., Goldstein et al. 1987) associated with foraging sunlight. This preference for shade persisted throughout the study, even though air temperatures never rose above the birds' lower critical temperature (22.5 °C for wintering dark-eyed juncos; Bakken et al. 1991), and were at times 30 °C lower than this threshold. Exposure to solar radiation can lead to a significant reduction in metabolic rate when foraging in such cold environments (Wood and Lustick 1989; Wolf and Walsberg 1996; Walsberg et al. 1997). We did find that a larger proportion of birds foraged in sunlight (i.e., fewer birds were in the shade) at comparatively low ambient temperatures. The lower proportion of birds foraging in shade on colder days likely reflects a trade-off between the thermoregulatory benefits of solar radiation and the predation costs associated with feeding in sunlit areas. Our results were similar to those of Carrascal et al. (2001), who found that treecreepers preferred shaded tree trunks at relatively warm temperatures and selected sunlit trunks as temperatures dropped below 4 °C. However, the birds in our study prefer shade across the observed temperature range, down to -12 °C.

A preference for shade implies that the costs of foraging in sunlight outweigh the thermal benefits of foraging in sunlit areas. Visual glare may be one such cost of foraging in direct sunlight. For instance, house finches (Fernández-Juricic and Tran 2007) and brown-headed cowbirds (*Molothrus ater*; Fernández-Juricic et al. 2012) were slower to respond to a terrestrial predator when foraging in sunlight compared to the shade. Thus the birds in our study may have foraged in the shade to reduce glare and thus reduce predation risk while foraging. Birds foraging in sunlit patches may also be less cryptic than birds foraging in the shade; Carrascal et al. (2001) suggested that shade-seeking behavior in treecreepers reflected a trade-off between behavioral thermoregulation and enhanced crypticity.

The southerly orientation of birds at our study site suggests that visual glare alone cannot explain their orientational preferences. If the birds were primarily concerned with reducing glare while foraging, then they should have oriented away from the sun (i.e., northward). This northerly orientation should be particularly evident in birds feeding in direct sunlight where glare effects would be the most severe; birds in shade should not suffer from glare and should thus show a lesser tendency to face northward. However, both sun- and shade-feeding birds tended to orient to the south (i.e., the direction of the sun) while feeding. We nevertheless suspect that glare presents a serious problem for these birds (as per Fernández-Juricic and Tran 2007; Fernández-Juricic et al. 2012).

The southerly (sunward) orientation of birds in our study may be a response to the behavioral tactics of predators. For instance, Tucker et al. (2000) found that peregrine falcons (*Falco peregrinus*) attacked "out of the sun" during long-approach attacks, thus reducing their prey's ability to detect their approach. Common predators of our study species, such as *Accipiter* hawks, may take similar advantage of solar glare by attacking prey with the sun to their backs. Hawks may attack from the south less frequently when the sun is not visible in the sky, providing a potential explanation for why birds faced southward less often on cloudy days (Fig. 10). *Accipiter* hawks may also use the visual obstructions created by the shade boards to their advantage during an attack (Roth et al. 2006), thus our birds may have faced the boards for that reason. If visual obstructions were a primary explanation for the southerly orientation of birds in our study, then we would expect that the tendency to face southward would be reduced when the shade boards were removed. However, sunny-day birds oriented towards the south regardless of whether the shade boards were present or removed. Thus, the presence of the boards *per se* cannot explain orientation to the south. Perhaps hawks attack preferentially from the south due to the specific features and topography of the study site itself (e.g., Beauchamp and Ruxton 2008), making it advantageous to face southward regardless of the conditions in which a bird is feeding.

Characteristics of the thermal environment did not appear to influence the orientation of birds in our study. Only occasionally did birds orient eastward or westward (i.e, perpendicular to incoming solar radiation on sunny days) and they tended to do so more frequently on cloudy days. Orientation may also be influenced by the direction of the wind if birds seek to minimize disruption to the thermal boundary created by the feathers (Wood and Lustick 1989; Fortin et al. 2000). However, we did not find a significant effect of wind direction on bird orientation. The birds appeared to alter their orientation momentarily to face the direction of strong wind gusts (JMC, personal observation), but these gusts only persisted for a few seconds. Overall, consistent shade-seeking and southward orientation in our study suggest that birds were not choosing an orientation to maximize solar heat gain.

In summary, we have shown that overwintering emberizid sparrows generally choose to forage in the shade regardless of the thermal benefits of direct sunlight. Based on our work and that of others (Carrascal et al. 2001; Fernández-Juricic and Tran 2007; Fernández-Juricic et al. 2012), we believe that small wintering birds may routinely avoid feeding in sunny, thermally advantageous microhabitats. Nevertheless, the energetic benefits gained by foraging in sunlight are substantial (Wolf and Walsberg 1996) and could influence landscape-level species richness and composition (Huertas and Díaz 2001; Carrascal et al. 2012). Larger-scale habitat choice by our wintering birds is likely influenced by the avoidance of sunshine, but it seems likely that they would prefer shady spots in sun-warmed habitats over cool and deeply shaded habitats (see Carrascal and Alonso 2006). Such habitat choice should provide birds with fewer anti-predator problems in a generally warm environment.

Acknowledgements

We thank George Bakken for his expert advice and assistance throughout this study. We also thank Luis Carrascal and Sara Villén-Pérez for their helpful comments on the manuscript. The Department of Biology at Indiana State University provided financial assistance for this project. All observations were conducted under an approved Indiana State University

Institutional Animal Care and Use Committee protocol (#01-03-2011:SLL/JMC) and comply with the current laws of the United States of America.

References

Bakken GS (1991) Wind speed dependence of the overall thermal conductance of fur and feather insulation. J Therm Biol 16:121-126 doi: 10.1016/0306-4565(91)90009-Q

Bakken GS, Murphy MT, Erskine DJ (1991) The effect of wind and air temperature on metabolism and evaporative water loss rates of dark-eyed juncos, *Junco hyemalis*: a standard operative temperature scale. Physiol Zool 64:1023-1049

Bakken GS, Santee WR, Erskine DJ (1985) Operative and standard operative temperature: tools for thermal energetics studies. Am Zool 25:933-943

Beauchamp G, Ruxton GD (2008) Disentangling risk dilution and collective detection in the antipredator vigilance of semipalmated sandpipers in flocks. Anim Behav 75:1837-1842 doi: 10.1016/j.anbehav.2007.12.016

Boysen AF, Lima SL, Bakken GS (2001) Does the thermal environment influence vigilance behavior in dark-eyed juncos (*Junco hyemalis*)? An approach using standard operative temperature. J Therm Biol 26:605-612 doi: 10.1016/S0306-4565(01)00007-9

Carr JM, Lima SL (2012) Heat-conserving postures hinder escape: a thermoregulation-predation trade-off in wintering birds. Behav Ecol 23:434-441 doi: 10.1093/beheco/arr208

Carrascal LM, Alonso CL (2006) Habitat use under latent predation risk. A case study with wintering forest birds. Oikos 112:51-62 doi: 10.1111/j.0030-1299.2006.13787.x

Carrascal LM, Díaz JA, Huertas DL, Mozetich I (2001) Behavioral thermoregulation by treecreepers: trade-off between saving energy and reducing crypsis. Ecology 82:1642-1654 doi: 10.1890/0012-9658(2001)082[1642:BTBTTO]2.0.CO;2

Carrascal LM, Villén-Pérez S, Seoane J (2012) Thermal, food and vegetation effects on winter bird species richness of Mediterranean oakwoods. Ecol Res 27:293-302 doi: 10.1007/s11284-011-0900-x

Clark RG, Ohmart RD (1985) Spread-winged posture of turkey vultures: single or multiple function? Condor 87:350-355 doi: 10.2307/1367215

Dawson WR, Whittow GC (2000) Regulation of body temperature. In: Whittow GC (ed) Sturkie's avian physiology, 5th edn. Academic Press, San Diego, pp 343-390

Dolby AS, Grubb TC (1999) Effects of winter weather on horizontal and vertical use of isolated forest fragments by bark-foraging birds. Condor 101:408-412 doi: 10.2307/1370006

Fernández-Juricic E, Deisher M, Stark AC, Randolet J (2012) Predator detection is limited in microhabitats with high light intensity: an experiment with brown-headed cowbirds. Ethology 118:341-350 doi: 10.1111/j.1439-0310.2012.02020.x

Fernández-Juricic E, Erichsen JT, Kacelnik A (2004) Visual perception and social foraging in birds. Trends Ecol Evol 19:25-31 doi: 10.1016/j.tree.2003.10.003

Fernández-Juricic E, Tran E (2007) Changes in vigilance and foraging behavior with light intensity and their effects on food intake and predator detection in house finches. Anim Behav 74:1381-1390 doi: 10.1016/j.anbehav.2007.01.005

Fortin D, Larochelle J, Gauthier G (2000) The effect of wind, radiation and body orientation on the thermal environment of Greater Snow goose goslings. J Therm Biol 25:227-238 doi: 10.1016/S0306-4565(99)00028-5

Goldstein H, Verbeek NAM, Eisikowitch D, Yom-Tov Y (1987) Sunbirds prefer to feed in the sun. Ardea 75:293-295

Grubb TC (1975) Weather-dependent foraging behavior of some birds wintering in a deciduous woodland. Condor 77:175-182 doi: 10.2307/1365788

Hetem RS, Strauss WM, Heusinkveld BG, de Bie S, Prins HHT, van Wieren SE (2011) Energy advantages of orientation to solar radiation in three African ruminants. J Therm Biol 36:452-460 doi: 10.1016/j.jtherbio.2011.07.012

Huertas DL, Díaz JA (2001) Winter habitat selection by a montane forest bird assemblage: the effects of solar radiation. Can J Zool 79:279-284 doi: 10.1139/cjz-79-2-279

Kacelnik A (1979) Foraging efficiency of great tits (*Parus major* L.) in relation to light intensity. Anim Behav 27:237-241 doi: 10.1016/0003-3472(79)90143-X

Lima SL (1995) Back to the basics of anti-predatory vigilance: the group size effect. Anim Behav 49:11-20 doi: 10.1016/0003-3472(95)80149-9

Lima SL, Dill LM (1990) Behavioural decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619-640 doi: 10.1139/z90-092

Lustick S, Battersby B, Kelty M (1978) Behavioral thermoregulation: orientation toward the sun in herring gulls. Science 200:81-83

Maloney SK, Moss G, Mitchell D (2005) Orientation to solar radiation in black wildebeest (*Connochaetes gnou*). J Comp Physiol A 191:1065-1077 doi: 10.1007/s00359-005-0031-3

Martin GR, Katzir G (2000) Sun shades and eye size in birds. Brain Behav Evolut 56: 340-344 doi: 10.1159/000047218

McNamara JM, Houston AI (1990) The value of fat reserves and the trade-off between starvation and predation. Acta Biotheor 38:37-61 doi: 10.1007/BF00047272

Meager JJ, Moberg O, Strand E, Utne-Palm AC (2010) Effects of light intensity on visual prey detection by juvenile Atlantic cod (*Gadus morhua* L.). Mar Freshw Behav Phy 43:99-108 doi: 10.1080/10236241003798910

Ohmart RD, Lasiewski RC (1971) Roadrunners: energy conservation by hypothermia and absorption of sunlight. Science 172:67-69 doi: 10.1126/science.172.3978.67

Pravosudov VV, Grubb TC (1997) Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food supply. Behav Ecol 8:332-339 doi: 10.1093/beheco/8.3.332

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223-225 doi: 10.2307/2409177

Richmond HE, Hrabik TR, Mensinger AF (2004) Light intensity, prey detection and foraging mechanisms of age 0 year yellow perch. J Fish Biol 65:195-205 doi: 10.1111/j.1095-8649.2004.00444.x

Roth TC, Lima SL (2003) Hunting behavior and diet of Cooper's Hawks: an urban view of the small-bird-in-winter paradigm. Condor 105:474-483 doi: 10.1650/7219

Roth TC, Lima SL, Vetter WE (2006) Determinants of predation risk in small wintering birds: the hawk's perspective. Behav Ecol Sociobiol 60:195-204 doi: 10.1007/s00265-005-0156-y

Tucker VA, Tucker AE, Akers K, Enderson JH (2000) Curved flight paths and sideways vision in peregrine falcons (*Falco peregrinus*). J Exp Biol 203:3755-3763

Wachob DG (1996) The effect of thermal microclimate on foraging site selection by wintering mountain chickadees. Condor 98:114-122 doi: 10.2307/1369514

Walsberg GE (1986) Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. Auk 103:1-7

Walsberg GE, Tracy RL, Hoffman TCM (1997) Do metabolic responses to solar radiation scale directly with intensity of irradiance? J Exp Biol 200:2115-2121

Webster MD, Weathers WW (1988) Effect of wind and air temperature on metabolic rate in verdins, *Auriparus flaviceps*. Physiol Zool 61:543-554

Wolf BO, Walsberg GE (1996) Thermal effects of radiation and wind on a small bird and implications for microsite selection. Ecology 77:2228-2236 doi: 10.2307/2265716

Wolf BO, Wooden KM, Walsberg GE (2000) Effects of complex radiative and convective environments on the thermal biology of the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). J Exp Biol 203:803-811

Wood JT, Lustick SI (1989) The effects of artificial solar radiation on wind-stressed tufted titmice (*Parus bicolor*) and Carolina chickadees (*Parus carolinensis*) at low temperatures. Comp Biochem Phys A 92:473-477 doi: 10.1016/0300-9629(89)90351-4

Table 6. Multiple regression analysis of the factors influencing the average proportion of birds (over a session) foraging in the shade (data in Fig. 9). Statistically significant results are shown in bold.

	Beta	*SE*	*t*	*P*
Temperature	**0.694**	**0.232**	**2.994**	**0.010**
Wind speed	-0.010	0.199	-0.052	0.960
Avg. flock size	-0.073	0.216	-0.338	0.740

Full model: $N = 18$, Adjusted $R^2 = 0.436$, $F_{3,14} = 5.374$, $P = 0.011$

Table 7. Multiple regression analyses of the effects of several environmental factors on the average proportion of birds facing southward (i.e., towards the shade boards and the direction of the sun) when feeding in (A) shade, (B) sunlight or (C) on cloudy days. Three separate multiple regressions were conducted since cloudy-day observations were collected during different sessions than sunlight and shade observations.

	Beta	*SE*	*t*	*P*
A. Shade				
Temperature	0.252	0.303	0.831	0.421
Wind speed	-0.054	0.267	-0.202	0.843
Wind direction	-0.056	0.286	-0.197	0.847
Avg. flock size	-0.402	0.304	-1.320	0.210
Full model: $N = 18$, *Adjusted* $R^2 = 0.069$, $F_{4,13} = 1.317$, $P = 0.315$				
B. Sunlight				
Temperature	-0.493	0.310	-1.589	0.136
Wind speed	0.350	0.274	1.280	0.223
Wind direction	-0.018	0.293	-0.061	0.952
Avg. flock size	-0.479	0.312	-1.536	0.148
Full model: $N = 18$, *Adjusted* $R^2 = 0.024$, $F_{4,13} = 1.106$, $P = 0.395$				

Table 7. continued

	Beta	*SE*	*t*	*P*
C. Cloud				
Temperature	-0.116	0.323	-0.361	0.728
Wind speed	-0.269	0.287	-0.939	0.375
Wind direction	0.372	0.345	1.076	0.313
Avg. flock size	-0.390	0.355	-1.101	0.303
Full model: $N = 13$, *Adjusted* $R^2 = 0.233$, $F_{4,8} = 1.911$, $P = 0.202$				

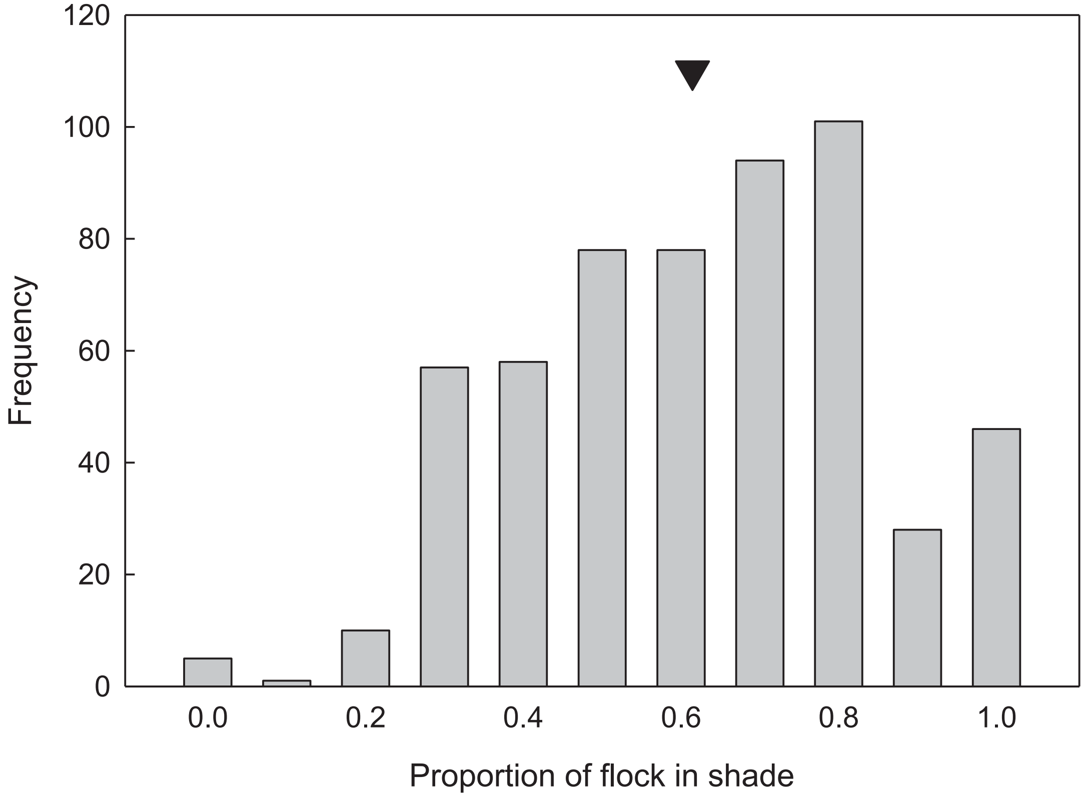


Figure 8. Frequency histogram of the proportion of birds in a flock foraging in the shade. A flock was defined as a stable group of foraging birds observed during a given sampling period in an observation session. A total of 556 flocks are represented in this figure. The black triangle represents the average proportion of birds in the shade (mean = 0.61). If birds had no preference for sunlight or shade, one would expect that approximately 37% of the birds in a flock would be located in shade since 37% of the foraging surface was shaded at any given time. Due to the inherently dichotomous nature of small flocks (for example, only 0%, 50% or 100% of birds can be in the shade for a flock of two), flocks of one and two individuals have been removed for clarity ($N = 91$). This omission has no effect on the overall conclusion. Proportions are organized into bins by rounding to the nearest 10%. For example, bin “0.2” contains observations of flocks with 15% - 24% of individuals in the shade, etc.

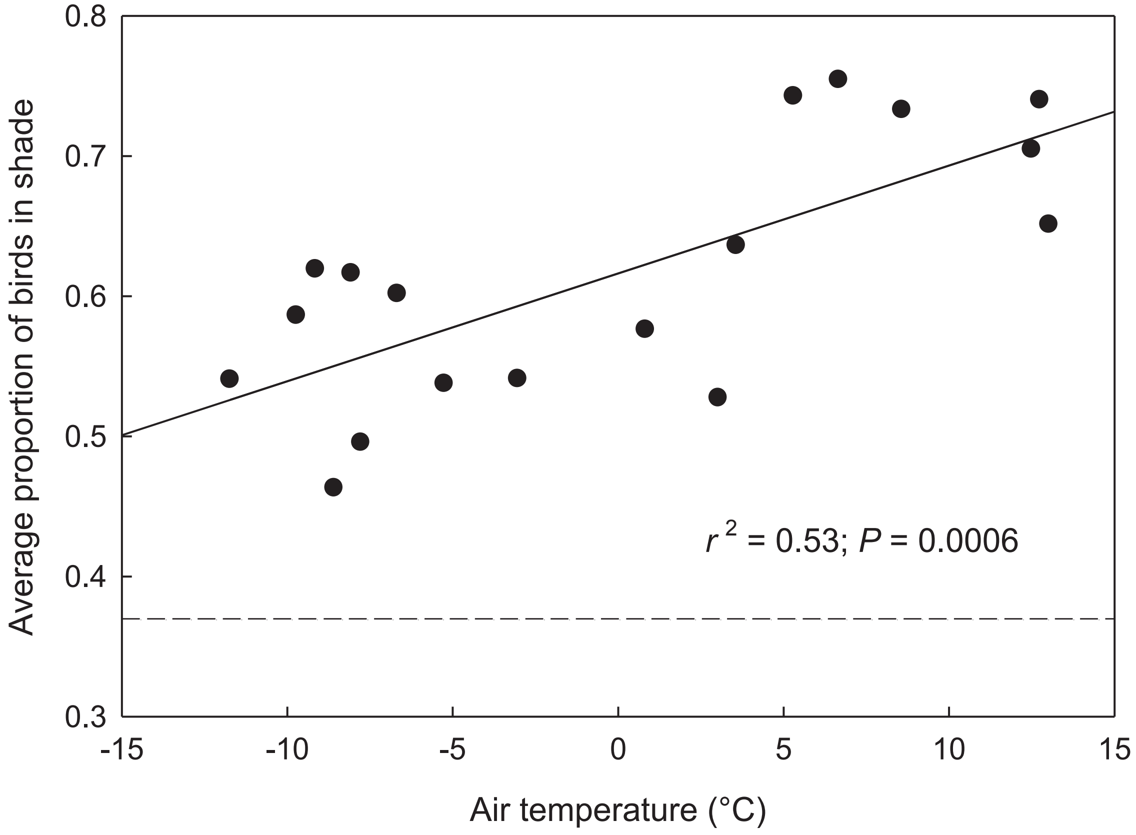


Figure 9. The average proportion of birds foraging in the shade as influenced by air temperature. Each point is an average over a given sunny-day observation session ($N = 18$). The solid line is the regression line. The dashed line indicates the expectation if birds had no preference for sunlight or shade and fed randomly with regard to these conditions (37% in shade)

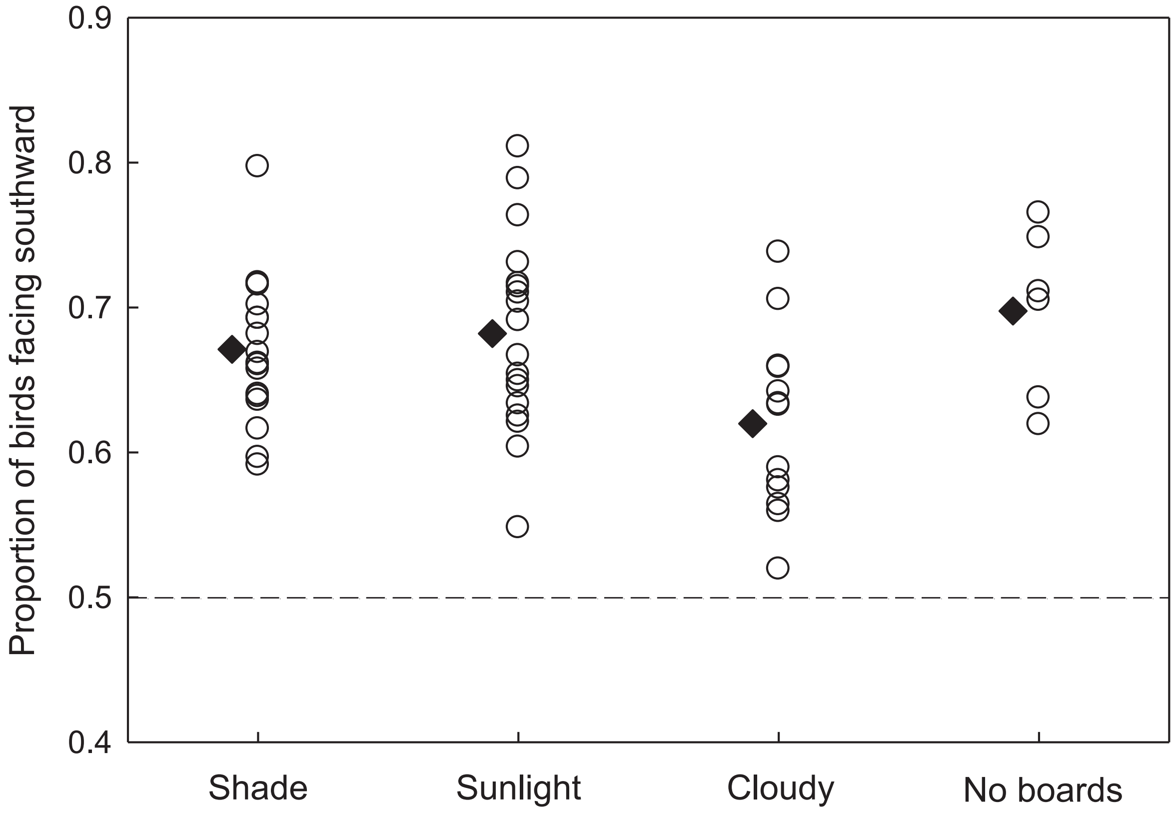


Figure 10. Orientation of birds feeding in shade, sunlight, under cloudy conditions, or with the shade boards removed on sunny days. Each point represents an average tendency to face southward for a given observation session. Black diamonds indicate the average for each condition. “Shade” and “Sunlight” indicate birds foraging in the shade or direct sunlight on sunny days. “Cloudy” indicates observations from cloudy days with no visible shadows. “No boards” indicates observations conducted from sunny days with the shade boards removed. The dashed line represents the line of no orientation preference (50%)

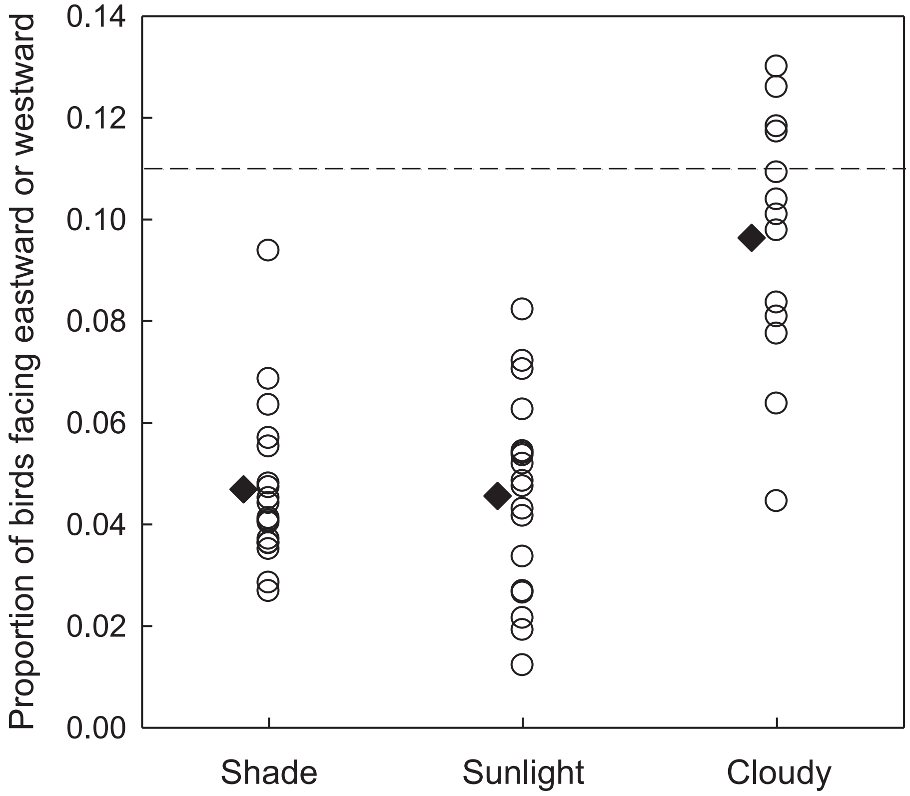


Figure 11. The proportion of birds oriented eastward or westward (perpendicular to the direction of incoming sunlight on sunny days) for birds foraging in shade, sunlight, or on cloudy days. Each point is an average over a given observation session. Black diamonds indicate the overall averages for each condition. The dashed line indicates our null expectation (11% of birds oriented eastward or westward)

CHAPTER 4

NOCTURNAL HYPOTHERMIA IMPAIRS FLIGHT ABILITY IN BIRDS: A COST OF BEING COOL

Many birds rely on a regulated drop in nighttime 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 to typical daytime T_b. Doves that were unable to fly during their first test were more hypothermic than birds that could fly, with an average T_b reduction of 5.3 °C and 3.3 °C, respectively, but a few could fly at a T_b reduction of 7 °C. 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 hypothermia and the risk of predation.

Introduction

Birds face significant energetic 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. 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.

Wintertime energy management in birds often involves the use of regulated nocturnal hypothermia (Welton et al. 2002), and many species rely on a drop in body temperature to conserve energy during periods of food restriction (McKechnie & Lovegrove 2002). Hypothermia reduces metabolic rate by lowering the differential between ambient and regulated body temperature, thus conserving energy reserves (Geiser 2004). 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 (Krüger et al. 1982, Geiser & Ruf 1995, Schleucher 2004). Torpor is most often observed in relatively small species with comparatively low energetic costs of re-warming (Geiser & Ruf 1995), and is especially pronounced in species which rely on ephemeral food sources, such as nectar or insects (McKechnie & Lovegrove 2002). Although the distinction between torpor and milder hypothermia remains unclear (Barclay et al. 2001, McKechnie & Lovegrove 2002), drops in body temperature of torpid birds generally exceed 5 °C (Schleucher 2004). Hypothermia (rather than torpor per se) is a much more prevalent and taxonomically widespread physiological response to food shortage (McKechnie & Lovegrove 2002), and even relatively small drops in body temperature can yield significant energy savings (Clark & Dukas 2000, Schleucher 2001, Ben-Hamo et al. 2010).

Although there are clear energetic benefits in hypothermia, there are also likely associated costs (Angilletta 2009). For instance, hypothermia can reduce running speed (Rojas et al. 2012), the force of muscle contraction (Holewijn & Heus 1992), and central nervous system functioning (Taltavull et al. 2003). Such limitations could easily lead to an increase in predation risk (Pravosudov & Lucas 2000), and probably underlie observations of lethargy in hypothermic animals (Graf et al. 1989, Schleucher 2001). However, few studies have directly examined the predation-related costs of hypothermia. One exception here is an experiment by Laurila and Hohtola (2005), which suggests that pigeons (*Columba livia*) reduce their depth of hypothermia in the presence of a model avian predator, indicating a trade-off between hypothermia and the risk of predation.

We examined the potential predation-related costs of nocturnal hypothermia in mourning doves (*Zenaida macroura*). Mourning doves in our study area are frequently exposed to food unavailability and high predation during winter months (Houston et al. 1998, Mazur & James 2000, Roth & Lima 2003, Livezey 2007) and thus likely experience a trade-off between thermoregulation and predation risk. Doves in general appear to use hypothermia when faced with food restriction (Graf et al. 1989, Schleucher 2001), which we also demonstrate in mourning doves. To quantify the potential predation costs of hypothermia, we food-deprived doves and measured their nocturnal flight ability while significantly hypothermic. Our results suggest that such energy-saving hypothermia is associated with an increase in predation risk through a reduction in flight ability.

Methods

Study species

All observations were conducted on wintering mourning doves captured in Vigo County, Indiana 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. All methods were approved by the Indiana State University Institutional Animal Care and Use Committee (Protocol #10-25-2010:SLL/JMC, Amendment #304728-1:SL).

Doves were housed in cages (102 x 61 x 46 cm in length, width and height) within environmental control chambers 2.5 x 2 x 2.3 m in length, width and height. Cages were constructed using 1.25 cm mesh hardware cloth framed with thin wooden boards (3.8 cm high x 2 cm wide) along the bottom edge to provide additional strength and structure. Two small doors at the top of the cage provided access for maintenance and capturing birds. The bottom of the cage was not enclosed and rested on a table lined with paper to be cleaned as necessary. Each cage was covered with a translucent white cloth to reduce stress to the doves. The environmental chambers were illuminated using two incandescent 60 W lamps placed directly over the cage and outside of the cloth cover. Each chamber was on a 10:14 h light:dark cycle and held a constant temperature of 5 °C to simulate natural winter conditions. Millet was available *ad libitum* until the start of the food deprivation period. Vitamin-supplemented water (Wild Harvest^{TM} Multi-Drops, Eight In One Pet Products) was always available to the birds. Doves could be maintained on this diet and remain healthy for several weeks. Infared-illuminators and an infared-sensitive closed-circuit television camera placed at one end of each cage allowed us to monitor bird behaviour at any point in the light:dark cycle.

A partition placed in each cage allowed us to house two of these social birds together, while allowing separate access to food. Each cage was separated into two equal-sized compartments (51 x 61 x 46 cm in length, width and height) by a hardware cloth divider. The two birds could see one another and interact through the wire mesh, reducing any stress that may have resulted from housing birds individually. Each bird had its own source of food and water. Throughout the experiment, one bird in each cage was designated as a "companion", with the other designated as a "treatment" bird to be subjected to flight tests.

Monitoring body temperature

Body temperature (T_b) was monitored using subcutaneously implanted temperature-sensitive radio transmitters. Doves were given 2 days to acclimate to laboratory conditions prior to transmitter implantation. Each bird was weighed to the nearest gram using a Pesola balance immediately prior to implantation. All surgical tools and transmitters were sterilized with 70% isopropyl alcohol prior to surgery. Birds were anesthetized using a breathing cone fitted to an isoflurane vaporizer. Anesthesia was induced under 4.0% isoflurane and 2 L/min O_2 flow rate, with surgery beginning as soon as the bird no longer responded to tactile stimulation of its feet. At this time, isoflurane was reduced to 2.0 - 3.5% to maintain anesthesia throughout the procedure.

Our transmitter implantation procedure was modified from Schulz et al. (2001). Feathers were plucked from an area approximately 20 mm long and 15 mm wide, located 30 mm posterior to the base of the dorsal side of neck (the incision site). Feathers were also plucked as needed along a 15 mm long, 3 mm wide track that ran dorsal and posterior to the incision site, forming the subcutaneous antenna track and antenna exit point. The incision site, antenna track, and exit point were then cleansed by swabbing dichlorhexane gluconate (4.0 % w/v) over the plucked areas.

The incision was made just wide enough to accommodate the width of the transmitter (transmitter dimensions: 16 x 8 x 3.5 mm in length, width and height). A subcutaneous pocket was created anterior to the incision by using a sterilized, flat microspatula (7 mm wide) to separate the skin from the underlying tissue. The temperature-sensitive transmitter (Holohil Systems, Ltd.; model BD-2T, 1.2 g) was then inserted into the pocket with the external antenna directed towards the posterior. An 18-gauge hypodermic needle was then inserted at the distal end of the antenna track (15 mm posterior to the incision), traveling subcutaneously along the antenna track with the tip of the needle exiting through the incision. The external antenna was then inserted through the needle which was then removed. The result was an external antenna that exited the body posterior to the incision point, thus placing less strain on the incision itself. The incision was closed using a 6-0 silk suture (Look; C-22, 16 mm), and antibacterial ointment was swabbed onto the incision and at the antenna exit point. Surgery duration was approximately 30 – 40 min from the initiation of anesthesia.

A backpack-style Velcro harness designed to carry additional weight during test flights (see below) was fitted to each dove immediately following transmitter implantation. Birds remained anesthetized for the duration of the backpack attachment in order to expedite backpack fitting. Backpacks were constructed using 1.6 mm polyester cord cut to a length of 40 cm. The cord was looped under each wing with an adjustable knot positioned anterior to the right wing to prevent irritation. We prevented over-tightening of the backpack by temporarily placing a wooden rod (8 mm in diameter) between the dorsal surface of the bird and the two sections of cord traveling across the bird's back (from beneath the wings). The adjustable knot was secured with super glue while the rod was in place. This precaution ensured that the backpack was secure, but not restrictive or abrasive. Any excess cord was then removed. A 15 mm wide, 25 mm long section of Velcro was attached to a 20 mm wide, 40 mm long cotton fabric strip, which was then sewn to the two parallel regions of cord running across the bird's back. The backpack attachment was completed in approximately 10 min. Thus, birds were fully anesthetized for approximately 45 min. Following backpack completion, isoflurane was turned off and birds remained in the breathing cone while exposed to an O_2 flow rate of 2.0 L/min for approximately 20 min. Birds were placed back in their home cages after they became alert and responsive.

Body temperature of implanted doves was monitored continuously from outside of the environmental chambers. A three-element Yagi antenna was connected to a datalogger (Lotek Wireless, Inc.; SRX-DL2) that recorded transmitter signals (in beats/min) every 2 s, rotating through transmitter frequencies at 10 s intervals. Transmitter signals were converted to T_b by using transmitter-specific calibration equations. During calibration, transmitters were placed in a vacuum-sealed plastic bag and submerged in a temperature-controlled circulating water bath. Transmitter pulse rate (beats/min) was recorded over a range of temperatures (25 – 45 °C) at 1 °C increments. Transmitters typically equilibrated within 30 s of a 1 °C increase in water bath temperature, with 5 min elapsed at each temperature before recording pulse rate. Calibration equations were generated by fitting a second-order polynomial to the slightly non-linear pulse rate data (R^2 values ≥ 0.996).

Inducing hypothermia

We induced nocturnal hypothermia by exposing birds to a period of food deprivation. Food deprivation began after a minimum of three days of post-surgery recovery (range = 3 - 8 d; mean = 4.7 d). The implanted (treatment) bird's food bowl was removed 2 h before the lights in the chamber turned off for the day. Each dove was food deprived for the entire following photoperiod, followed by a nighttime flight test (described below). Such food deprivation simulated a situation faced during heavy snowfall, and the majority of birds had no difficulty maintaining normal daytime T_b during the first deprivation day. Food deprivation sometimes continued 1 – 2 additional days depending on an individual bird's ability to maintain normal daytime T_b. Treatment birds were closely monitored to ensure that their daytime T_b resembled those recorded during the post-surgery recovery period with food available *ad libitum*. Any bird that was not able to maintain a normal daytime T_b was provided 2 g of millet ($N = 5$ of 25 flight-tested birds). These individuals successfully maintained normothermic daytime T_b for the remainder of the daylight hours and were included in flight tests (see below). No supplemental food was provided within 1 h of lights-off to minimize digestion-related thermogenesis during early nighttime monitoring; providing a small amount of millet earlier in the photoperiod did not have long-lasting effects on T_b (Reinertsen & Bech 1994). Seven of the 36 total implanted doves were not able to withstand the minimum 24 h deprivation period at normal daytime T_b and could not re-warm on their own after provisioning 2 g of supplemental millet (unpublished results). Such birds were provided *ad libitum* food and were not included in the study. Two birds died unexpectedly prior to the onset food deprivation and two transmitters failed. Overall, a total of 25 birds yielded nighttime flight test data while hypothermic during food deprivation.

The nature of nocturnal hypothermia in mourning doves was first examined by generating nightly T_b profiles for ten doves during Winter 2010 - 2011. The above methods for transmitter implantation and food deprivation were used for these 10 birds. However, no flight tests were conducted on hypothermia profile doves, which were left undisturbed for the duration of the deprivation period. Body temperature profiles were produced by plotting T_b for every minute of the 1 – 3 day deprivation period.

Flight tests

We conducted nighttime flight tests on hypothermic birds carrying additional weight to assess the potential predation 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 maneuverability, 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 maneuverability necessary to quickly escape a serious nocturnal attack. Note that pigeons (a somewhat larger dove) can carry up to 100 % of their weight in flight (Dial & Biewener 1993), thus a 15 % weight is not a large burden, and represents normal weight gain over the course of a day (Rogers & Rogers 1990) or the weight of a large meal.

Flight tests were conducted 3 h after "lights-off". Doves would generally maintain or approach their minimum T_b at this time. A flight test began with a quick lights-off capture of a treatment bird; no-light conditions greatly reduced attempts to flee or struggle within the cage prior to capture. The captured dove was immediately carried to a flight arena located adjacent to the environmental control chambers. Body temperature did not increase more than a fraction of a degree prior to the flight test itself.

The flight arena (7.3 x 1.2 x 2.7 m in length, width and height) was a room-temperature hallway with cream-colored walls and a single entrance that defined the near-end of the arena. The arena was illuminated with two 500 W halogen lamps suspended from a wooden crossbar placed 0.5 m from the top and 1 m from the far-end of the arena. The lamps were directed towards the adjacent walls and not at a flying bird. Illuminating the far top corner of the flight arena encouraged birds to fly the entire length and height of the arena. A white sheet was suspended 0.4 m from the far-end of the hallway, which prevented a bird from colliding with the far wall as it reached the end of the flight arena. Soft materials were placed on the floor at the far-end of the hallway to cushion any fall at the end of a bird's flight.

Additional weight was attached to the bird's backpack immediately prior to release in the flight arena. A weight consisted of a thin piece of lead of the same dimension as the Velcro strip on the bird's backpack. The amount of weight added to the backpack was 15% of the bird's starting mass recorded prior to transmitter implantation. The weight-carrying hypothermic bird was placed on the floor facing towards the illuminated end of the arena and approximately 1 m from the near end and immediately in front of the experimenter crouched near the floor. The bird was given approximately 5 s to assess its situation. If it did not attempt to fly after 5 s, the experimenter lightly tapped the base of its tail to encourage it 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.

The flight ability of hypothermic doves was scored categorically as “flight” or “no flight”. A test was considered a “flight” if the bird flew the length of the hallway at a height of half of the arena height (≥ 1.25 m). In practice, a bird that could fly the length of the hallway almost always flew in the upper half of the hallway and only one individual flew the length of the arena at approximately 0.5 m above the ground. Tests were also categorized as a “flight” if the bird flew vertically to the arena ceiling, which is a more strenuous flight task than flying to the lighted end of the arena (Dial & Biewener 1993). Trials in which birds could not fly the height or length of the arena were considered “no flight” trials. In many cases, hypothermic birds could not manage any sustained flight. Such birds struggled to fly part way down the arena at less than a meter off of the ground before landing on the floor; they could not re-launch as the experimenter approached to recapture them. All flight tests were recorded with a digital video camera.

A dove that was able to fly during their 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 and the bird was tested again the following night. Total food deprivation for such birds usually lasted for two days (with a maximum of three 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 T_b began to increase during flight tests at a rate of 0.5 °C/min (unpublished data). Both of the hypothermic flight tests were completed within the first minute of capture (with approximately 30 s between the first and second flights), thus birds remained near their minimum T_b for both flight tests. Following these two hypothermic flight tests, birds were placed in a holding bag in a well-lit room (21 °C) for approximately 20 min, during which their T_b increased to normothermic daytime levels. An additional flight test was conducted on these warmed 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.

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 maintaining hypothermic or normothermic T_b. 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.

An ANOVA was used to determine whether there was a significant difference in the extent of T_b drop for birds that could or could not fly while carrying weight during their first attempt on the first deprivation night. Body temperature drop was determined by calculating the difference between nighttime flight test T_b and daytime T_b (average T_b between 1200-1500 h the day prior to the onset of food restriction). Flight ability was included as a fixed factor in the analysis: behavioural tests scored as “no flight” and “flight” were assigned dummy codes of “0” and “1”, respectively. Starting body mass was also included as a covariate in the analysis since larger individuals with more potential energy reserves may remain less hypothermic than small individuals (but see Vuarin et al., in press). A similar ANOVA was conducted to examine the T_b drops of birds tested on the second night of food deprivation. 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 one day of food deprivation ($N = 11$) to doves that were exposed to two days without food ($N = 10$). Statistical analyses were conducted using SPSS 11.0 (SPSS, Inc., Chicago, IL, USA).

Due 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. An 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 analyzed separately. For instance, we were unable to test hypothermic but non-food-deprived birds, since significant hypothermia can only be induced by food deprivation. Similarly, food deprived birds were nearly always hypothermic, although a few birds were not very hypothermic after 1 d of deprivation (see Results). Significant hypothermia is also associated with deep sleep (Reinertsen 1996, Rashotte et al. 1998), thus we could not examine hypothermic birds that had been fully awake for a long period of time. Finally, 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 post-flight (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.

Results

Body temperature (T_b) plots show the use of energy-saving nocturnal hypothermia in food-restricted mourning doves (Fig. 12). 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 (Fig. 12). However, T_b profiles among individuals were variable. When compared to control (non-deprived) nocturnal T_b, some birds cooled relatively little during the first night of the deprivation period (Fig. 12B, D). For most birds, T_b drops during the first deprivation night were more substantial (Fig. 12A, C). The extent of further T_b reductions on subsequent deprivation nights also varied among individuals (Fig. 12A, B). On average, T_b dropped 2.2 °C (*SE*: ± 0.19) during sleep on control nights prior to food deprivation, and fell by 4.1 °C (± 0.28), 5.2 °C (± 0.63) and 6.1 °C (± 0.85) on the first, second and third day of food deprivation. Starting body mass tended to differ between birds that could withstand one or two days of food deprivation (independent samples t-test: $T = -1.947$, $P = 0.066$), although this trend was marginally non-significant. The average mass of birds able to withstand only one day of food deprivation was 123.7 ± 3.9 g (mean ± *SE*), while that of birds that could withstand two days of food deprivation was 135.3 ± 4.5 g.

Eight of the 21 flight-tested doves could not fly on the first (weighted) flight attempt during the first deprivation night. The 8 “no flight” birds were significantly more hypothermic than the 13 “flight” birds (Table 8A, Fig. 13). Given our criteria for flight, five of the eight no-flight birds could fly while hypothermic with the weight removed, although not with obvious vigor. Following the first flight test, all no-flight birds warmed up quickly, with several individuals exceeding their normal daytime T_b (Fig. 14). All 8 hypothermic no-flight birds flew strongly once re-warmed 20 min later. Starting body mass did not influence the depth of hypothermia on the first deprivation night (Table 8A).

Ten of the 13 flight birds (Fig. 13) were flown again on the second deprivation night. Three of these 13 birds were not able to withstand the second day of food deprivation, and were thus removed from the study. Four of the ten remaining doves could not fly on the first weighted attempt of the second deprivation night but were able to fly after warming up (Fig. 14)**.** Although the flight ability of all 4 no-flight birds improved when the weight was removed during hypothermia, only one dove flew given our criteria for flight. The remaining six doves were able to fly on their first attempt of the second deprivation night (Fig. 15). The ten tested birds were generally colder (more hypothermic) than during the first deprivation night (Fig. 15). Unlike the first deprivation night, there was not a clear differentiation between the T_b drop of flight and no-flight birds tested on the second night (Table 8B, Fig. 15).

Only two of the six flight birds from the second deprivation night (Fig. 15) were able to withstand three days of food deprivation. One bird was unable to fly on its first attempt (T_b drop = -5.3 °C), could not fly while hypothermic with the weight removed, but flew well when warm (Fig. 14) and carrying additional weight. The second dove was able to fly on the first attempt of the third night (T_b drop = -7.0 °C).

Discussion

We found that food-deprived hypothermic doves 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 once re-warmed to near normal daytime body temperature (T_b). The predation costs associated with the relatively moderate T_b drops observed here imply that such costs of hypothermia are likely widespread throughout avian taxa and likely play an important role in the overall energy-management strategy of small birds (Pravosudov & Grubb 1997, Clark & Dukas 2000, Pravosudov & Lucas 2000). Due to such predation-related costs of significant hypothermia, birds may limit their use of hypothermia by conserving energy through other means, such as choosing favorable microhabitats (Wachob 1996, Dolby & Grubb 1999), using effective thermoregulatory postures (Dawson and Whittow 2000, Carr & Lima 2012), and roosting with conspecifics (Hatchwell et al. 2009, Gilbert et al. 2010, Burns et al. 2013). The minor T_b reductions associated with normal sleep (e.g., Fig. 12) probably do not decrease readiness to escape in the event of a nighttime 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 all non-flying birds had adequate energy reserves to both warm up and fly. Hence, low reserves per se are not a likely reason for an inability to fly when hypothermic under food deprivation; the warming itself seemed responsible for enhanced flight. It is conceivable that some birds were incoherently "groggy" after being awakened from a deep sleep associated with food deprivation (Reinertsen 1996, Rashotte et al. 1998), and thus could fly only after becoming fully awake during the warm-up period. This seems unlikely since the birds awakened (i.e., opened their eyes) immediately upon hearing us enter the environmental chamber, and they struggled to escape once captured. They thus appeared to be very 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 Lesku et al. 2006), in which hypothermic birds would have far less time to awaken 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 (Fig. 13). Schleucher (2004) proposed that this same criterion (T_b drop ≥ 5 °C) be used to characterize torpor in birds. Perhaps hypothermic birds in our study with T_b drops exceeding 5 °C should be considered "torpid" given the observed reduction in flight performance, and the general reduction in behavioural performance associated with torpor use (Krüger et al. 1982, Geiser & Ruf 1995, Schleucher 2004). 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. For instance, larger doves tended to withstand longer food deprivation periods and may have been in better physical condition than smaller individuals. 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. (2012) 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 likely impair predator evasion. Some bat species are capable of powered flight at T_b as low as 29 °C (Choi et al. 1998, Willis & Brigham 2003; see also Lima & O'Keefe, in press), a T_b that is low enough to be categorized as "torpor" in both bats and birds. Choi et al. (1998) also found that greater tube-nosed bats (*Murina 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 move and respond to external stimuli (Speakman et al. 1991, Prinzinger et al. 1992, McKechnie & Lovegrove 2002; JMC, personal observation). Such studies and our results suggest that predation is a widespread cost of substantial hypothermia across all endotherms.

Acknowledgements

George Bakken provided expert advice throughout the course of this study and Charles Amlaner and Diana Hews provided instruction of surgical techniques. Transmitter implantations were assisted by Kathleen Spicer, and Joy O'Keefe and Kristina Hammond aided with radio telemetry. Funding was provided by the Indiana Academy of Science as well as the College of Graduate and Professional Studies and Department of Biology at Indiana State University.

References

Angilletta, M. J. 2009 *Thermal adaptation: a theoretical and empirical synthesis*. Oxford: Oxford University Press.

Barclay, R. M. R., Lausen, C. L. & Hollis, L. 2001 What's hot and what's not: defining torpor in free-ranging birds and mammals. *Can. J. Zool.* **79**, 1885-1890. (DOI 10.1139/cjz-79-10-1885)

Ben-Hamo, M., Pinshow, B., McCue, M. D., McWilliams, S. R. & Bauchinger, U. 2010 Fasting triggers hypothermia, and ambient temperature modulates its depth in Japanese quail *Coturnix japonica*. *Comp. Biochem. Phys. A* **156**, 84-91. (DOI 10.1016/j.cbpa.2009.12.020)

Burns, D. J., Ben-Hamo, M., Bauchinger, U. & Pinshow, B. 2013 Huddling house sparrows remain euthermic at night, and conserve body mass. *J. Avian Biol.* **44**, 198-202. (DOI 10.1111/j.1600-048X.2012.00018.x)

Carr, J. M. & Lima, S. L. 2012 Heat-conserving postures hinder escape: a thermoregulation-predation trade-off in wintering birds. *Behav. Ecol.* **23**, 434-441. (DOI 10.1093/beheco/arr208)

Choi, I.-H., Cho, Y., Oh, Y. K., Jung, N.-P. & Shin, H.-C. 1998 Behavior and muscle performance in heterothermic bats. *Physiol. Zool.* **71**, 257–266.

Clark, C. W. & Dukas, R. 2000 Winter survival strategies for small birds: managing energy expenditure through hypothermia. *Evol. Ecol. Res.* **2**, 473-491.

Dawson, W. R. & Whittow, G. C. 2000 Regulation of body temperature. In *Sturkie's avian physiology 5th edn* (ed. G. C. Whittow), pp. 343-390. San Diego: Academic Press.

Dial, K. P. & Biewener, A. A. 1993 Pectoralis muscle force and power output during different modes of flight in pigeons (*Columba livia*). *J. Exp. Biol.* **176**, 31-54.

Dolby, A. S. & Grubb, T. C. 1999 Effects of winter weather on horizontal and vertical use of isolated forest fragments by bark-foraging birds. *Condor* **101**, 408-412. (DOI 10.2307/1370006)

Geiser, F. & Ruf, T. 1995 Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiol. Zool.* **68**, 935-966.

Geiser, F. 2004 Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu. Rev. Physiol.* **66**, 239-274. (DOI 10.1146/annurev.physiol.66.032102.115105)

Gilbert, C., McCafferty, D., Le Maho, Y., Martrette, J., Giroud, S., Blanc, S. & Acel, A. 2010 One for all and all for one: the energetic benefits of huddling in endotherms. *Biol. Rev.* **85**, 545-569. (DOI 10.1111/j.1469-185X.2009.00115.x)

Graf, R., Krishna, S. & Heller, H. C. 1989 Regulated nocturnal hypothermia induced in pigeons by food deprivation. *Am. J. Physiol.* **256**, R733-R738.

Hatchwell, B. J., Sharp, S. P., Simeoni, M. & McGowan, A. 2009 Factors influencing overnight loss of body mass in the communal roosts of a social bird. *Funct. Ecol.* **23**, 367-372. (DOI 10.1111/j.1365-2435.2008.01511.x)

Holewijn, M. & Heus, R. 1992 Effects of temperature on electromyogram and muscle function. *Eur. J. Appl. Physiol. O.* **65**, 541-545. (DOI 10.1007/BF00602362)

Houston, C. S., Smith, D. G. & Rohner, C. 1998 Great horned owl. In *The Birds of North America* (eds. A. Poole & F. Gill). Ithaca: Cornell Laboratory of Ornithology.

Krüger, K., Prinzinger, R. & Schuchmann, K.-L. 1982 Torpor and metabolism in hummingbirds. *Comp. Biochem. Phys. A* **73**, 679-689.

Laurila, M. & Hohtola, E. 2005 The effect of ambient temperature and simulated predation risk on fasting-induced nocturnal hypothermia of pigeons in outdoor conditions. *J. Therm. Biol.* **30**, 392-399. (DOI 10.1016/j.jtherbio.2005.04.001)

Lesku, J. A., Roth, T. C., Amlaner, C. J. & Lima, S. L. 2006 A phylogenetic analysis of sleep architecture in mammals: the integration of anatomy, physiology, and ecology. *Am. Nat.* **168**, 441-453. (DOI 10.1086/506973)

Lima, S. L. & O'Keefe, J. M. In press. Do predators influence the behaviour of bats? *Biol. Rev.* (DOI 10.1111/brv.12021)

Livezey, K. B. 2007 Barred owl habitat and prey: a review and synthesis of the literature. *J. Raptor Res.* **41**, 177-201. (DOI 10.3356/0892-1016(2007)41[177:BOHAPA]2.0.CO;2)

Mazur, K. M. & James, P. C. 2000 Barred owl. In *The Birds of North America* (eds. A. Poole & F. Gill). Ithaca: Cornell Laboratory of Ornithology.

McKechnie, A. K. & Lovegrove, B. G. 2002 Avian facultative hypothermic responses: a review. *Condor* **104**, 705-724. (DOI 10.1650/0010-5422(2002)104[0705:AFHRAR]2.0.CO;2)

Pravosudov, V. V. & Grubb, T. C. 1997 Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food supply. *Behav. Ecol.* **8**, 332-339. (DOI 10.1093/beheco/8.3.332)

Pravosudov, V. V. & Lucas, J. R. 2000 The costs of being cool: a dynamic model of nocturnal hypothermia by small food-caching birds in winter. *J. Avian Biol.* **31**, 463-472. (DOI 10.1034/j.1600-048X.2000.310405.x)

Prinzinger, R., Schäfer, T. & Schuchmann, K. 1992 Energy metabolism, respiratory quotient and breathing parameters in two convergent small bird species: the fork-tailed sunbird *Aethopyga christinae* (Nectariniidae) and the Chilean hummingbird *Sephanoides sephanoides* (Trochilidae). *J. Therm. Biol.* **17**, 71–79. (DOI 10.1016/0306-4565(92)90001-V)

Rashotte, M. E., Pastukhov, I. F., Poliakov, E. L. & Henderson, R. P.1998 Vigilance states and body temperature during the circadian cycle in fed and fasted pigeons (*Columba livia*). *Am. J. Physiol. – Reg. I.* **275**, 1690-1702.

Reinertsen, R. E. 1996 Physiological and ecological aspects of hypothermia. In *Avian energetics and nutritional ecology* (ed. C. Carey), pp. 125-157. New York: Chapman and Hall.

Reinertsen, R. E. & Bech, C. 1994 Hypothermia in pigeons; relating body temperature regulation to the gastrointestinal system. *Naturwissenschaften* **81**, 133-136. (DOI 10.1007/BF01131770)

Rogers, C. M. & Rogers, C. J. 1990 Seasonal variation in daily mass amplitude and minimum body mass: a test of a recent model. *Ornis Scand.* **21**, 105-114. (DOI 10.2307/3676805)

Rojas, A. D., Körtner, G. & Geiser, F. 2012 Cool running: locomotor performance at low body temperature in mammals. *Biol. Lett.* **8**, 868-870. (DOI 10.1098/rsbl.2012.0269)

Roth, T. C. & Lima, S. L. 2003 Hunting behavior and diet of Cooper's hawks: an urban view of the small-bird-in-winter paradigm. *Condor* **105**, 474-483. (DOI 10.1650/7219)

Schleucher, E. 2001 Heterothermia in pigeons and doves reduces energetic costs. *J. Therm. Biol.* **26**, 287-293. (DOI 10.1016/S0306-4565(01)00032-8)

Schleucher, E. 2004 Torpor in birds: taxonomy, energetics, and ecology. *Physiol. Biochem. Zool.* **77**, 942-949. (DOI 10.1086/423744)

Schulz, J. H., Bermudez, A. J., Tomlinson, J. L., Firman, J. D. & He, Z. 2001 Comparison of radiotransmitter techniques using captive mourning doves. *Wildlife Soc. B.* **29**, 771-782.

Speakman, J. R., Webb, P. I. & Racey, P. A. 1991 Effects of disturbance on the energy expenditure of hibernating bats. *J. Appl. Ecol.* **28**, 1087–1104. (DOI 10.2307/2404227)

Taltavull, J. F., Chefer, V. I., Shippenberg, T. S. & Kiyatkin, E. A. 2003 Severe brain hypothermia as a factor underlying behavioral immobility during cold-water forced swim. *Brain Res.* **975**, 244-247. (DOI 10.1016/S0006-8993(03)02695-7)

Vuarin, P., Dammhahn, M. & Henry, P.-Y. In press. Individual flexibility in energy saving: body size and condition constrain torpor use. *Funct. Ecol.* (DOI 10.1111/1365-2435.12069)

Wachob, D. G. 1996 The effect of thermal microclimate on foraging site selection by wintering mountain chickadees. *Condor* **98**, 114-122. (DOI 10.2307/1369514)

Welton, N. J., Houston, A. I., Ekman, J. & McNamara, J. M. 2002 A dynamic model of hypothermia as an adaptive response by small birds to winter conditions. *Acta Biotheor.* **50**, 39-56. (DOI 10.1023/A:1014761227478)

Willis, C. K. R. & Brigham, R. M. 2003 Defining torpor in free-ranging bats: experimental evaluation of external temperature-sensitive radiotransmitters and the concept of active temperature. *J. Comp. Physiol. B.* **173**, 379-389. (DOI 10.1007/s00360-003-0343-y)

Table 8. Results of two ANOVAs comparing body temperature drop in birds that could or could not fly during their first flight test on the (A) first and (B) second night of food deprivation.

Variable	*SS*	*DF*	*MS*	*F*	*P*
A. Deprivation night #1					
Starting mass	0.648	1	0.648	0.532	0.475
Flight ability	**10.452**	**1**	**10.452**	**8.591**	**0.009**
Error	21.899	18	1.217		
Total	381.881	21			
Full model: Adjusted $R^2 = 0.429$, $F_{2,18} = 8.505$, $P = 0.003$. *Significant factors are shown in bold.*					
B. Deprivation night #2					
Starting mass	0.666	1	0.666	0.332	0.583
Flight ability	0.093	1	0.093	0.046	0.836
Error	14.059	7	2.008		
Total	268.463	10			
Full model: Adjusted $R^2 = -0.193$, $F_{2,7} = 0.272$, $P = 0.770$.					

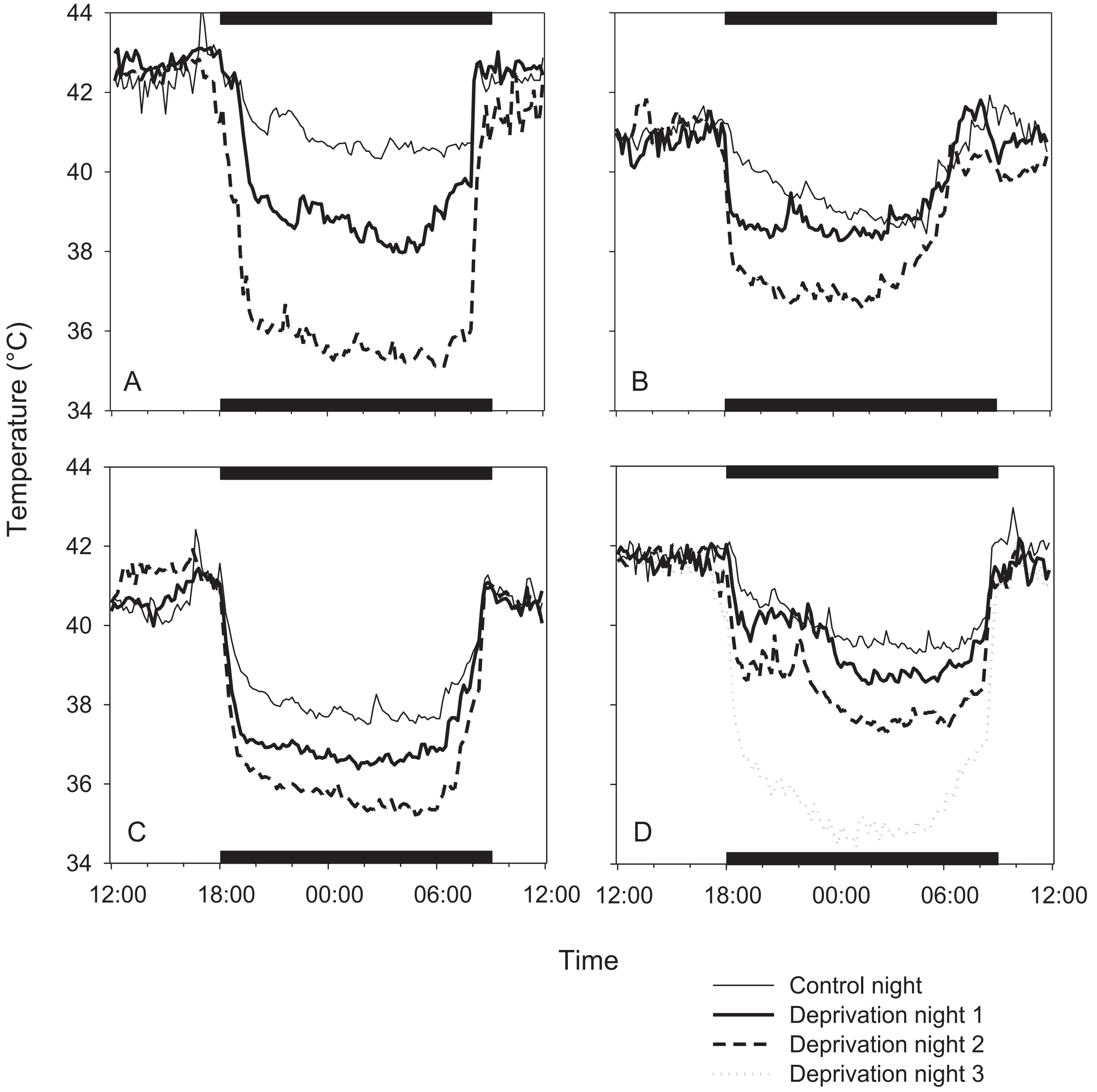


Figure 12. Examples of body temperature (T_b) profiles for four (A – D) of the 10 birds exposed to two to three days of food deprivation during Winter 2010-2011. Control nights represent the T_b of birds on a normal day with food available *ad libitum.* Black bars along the x-axis indicate periods of darkness.

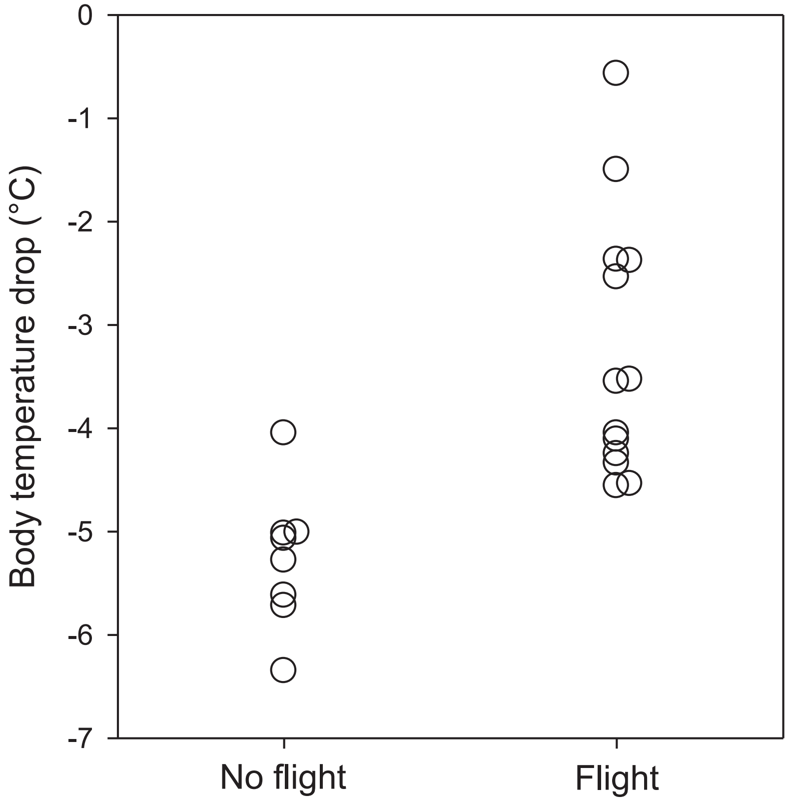


Figure 13. Body temperature (T_b) drops (compared to average daytime T_b) for birds during their first flight test when birds were hypothermic on the first night of food deprivation. All “No Flight” birds could fly when tested again while normothermic. Some points have been offset to avoid overlap.

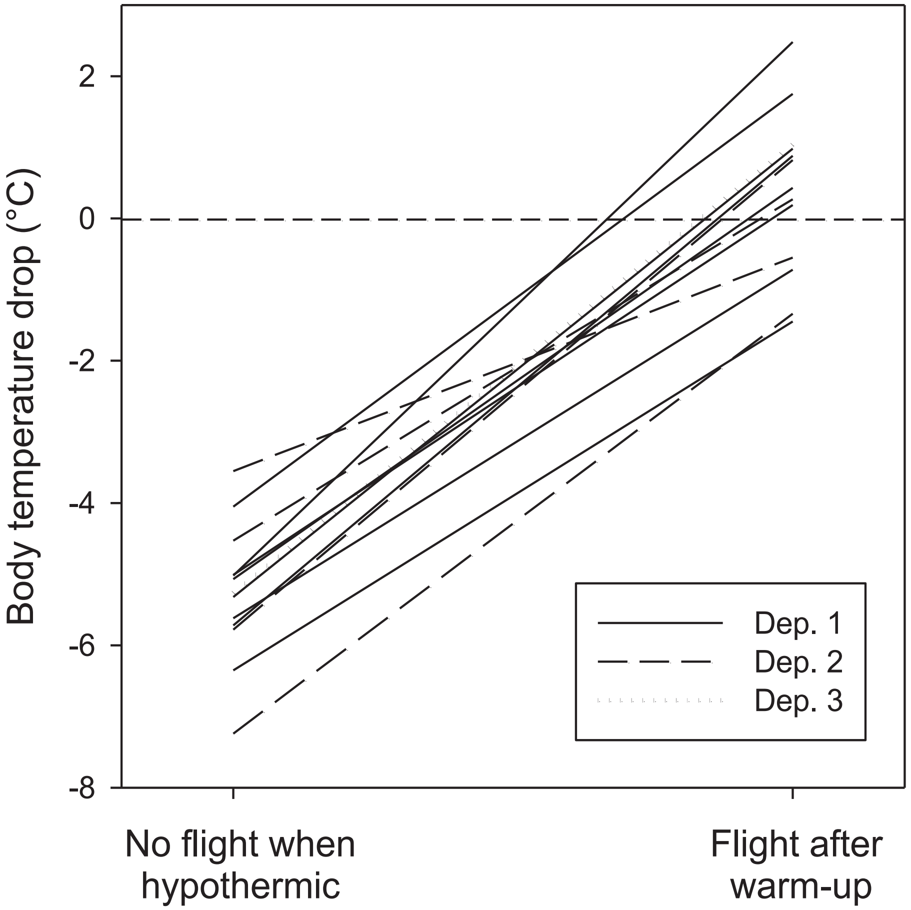


Figure 14. Body temperature (T_b) increase for no-flight birds between the first hypothermic flight attempt and a normothermic flight test conducted 20 min later. Each line on the graph represents an individual bird that could not fly during the first flight attempt of the night ($N_{\text{Dep 1}} = 8$, $N_{\text{Dep 2}} = 4$, $N_{\text{Dep 3}} = 1$). Birds that were unable to fly while hypothermic were able to fly after warming to near-normal daytime T_b, with several birds exceeding their normal daytime T_b (indicated by values that fall above "0" on the y-axis). Different line types indicate the duration of food deprivation (1 – 3 days).

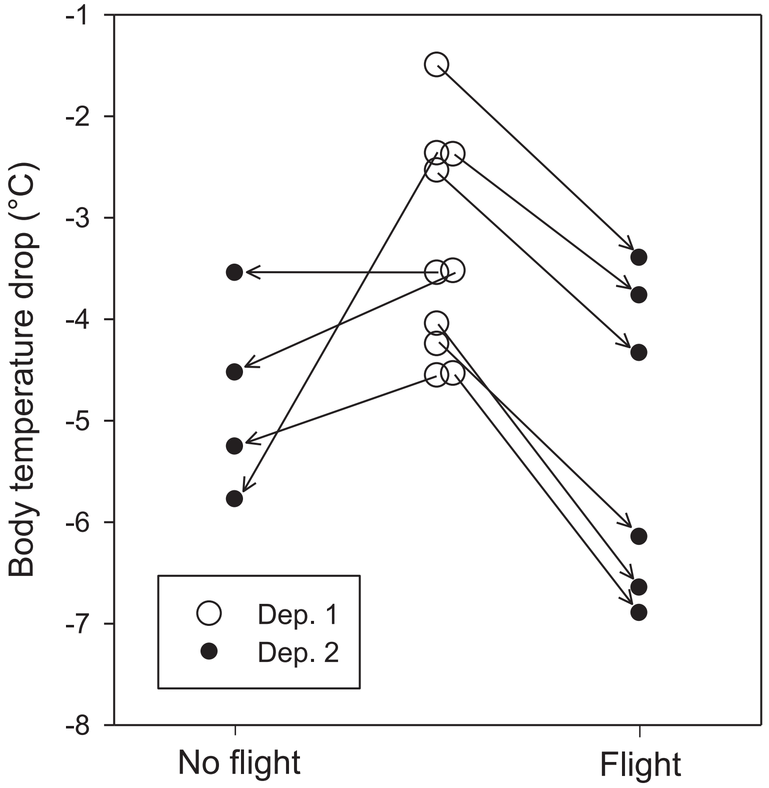


Figure 15. Body temperature (T_b) drops of 10 doves that could fly during their first attempt on the first night of food deprivation (○). Flight ability ("No flight" or "Flight") while hypothermic during the first attempt of the second deprivation night is indicated by filled circles (●). Arrows connect the T_b drops of individual doves on the first and second deprivation night.

CHAPTER 5

THE COST OF TORPOR: DO HUMMINGBIRDS STAY WARM IN HIGH-RISK CONDITIONS?

Extreme drops in nocturnal body temperature and metabolic rate during torpor allow hummingbirds to conserve energy to fuel their high metabolic requirements during the day. Such body temperature reductions often exceed 20 °C and leave torpid individuals unable to respond quickly to external stimuli. Such reduced behavioral responsiveness implies that using torpor is risky and may be used less frequently in relatively dangerous situations, but the influence of predation risk on avian torpor has not yet been examined. I monitored the use of torpor in ruby-throated hummingbirds (*Archilochus colubris*) housed in high-risk (five consecutive nights of disturbance) or low-risk (no disturbance) conditions over a period of ten days. Although disturbed hummingbirds tended to reduce their use of torpor, there was no statistically significant effect of disturbance on torpor use in either condition. In general, torpor use decreased over time regardless of disturbance regime. Food intake and Julian date were the only factors clearly associated with the degree of torpor, with greater torpor use later in the summer and following less food consumption during the previous day.

Introduction

Many avian species use torpor as a means of conserving energy during periods of food shortage and when accumulating fat reserves prior to migration. Body temperature (T_b) reductions during torpor generally exceed 5 °C, but are often much greater (McKechnie & Lovegrove 2002, Schleucher 2004). Such drops in T_b are associated with a significant reduction in both metabolic rate (Geiser 2004) and responsivness to external stimuli (Krüger et al. 1982, Geiser & Ruf 1995, Schleucher 2004). Such large reductions in nighttime energy expenditure mean that even short bouts of torpor can yield significant energy savings (Hiebert 1990). Although relatively moderate T_b drops have been observed in a diverse array of taxa, deep torpor (T_b drops exceeding 15 °C) is most often observed in relatively small species that rely on ephemeral food sources such as insects or nectar (McKechnie & Lovegrove 2002).

Torpor is particularly prevalent in hummingbirds. In addition to their small body size and reliance on nectar, hummingbirds have among the highest mass-specific metabolic rates among vertebrates (Suarez & Gass 2002) and torpid T_b reductions of 20 °C are commonplace in many species (Calder & Booser 1973, Bech et al. 1997, McKechnie & Lovegrove 2002). As such, torpor use in hummingbirds is strongly influenced by food availability; low energy reserves increase the prevalence of torpor (Hiebert 1991, Hiebert et al. 2000). However, factors such as air temperature (Hiebert et al. 2000, McKechnie & Lovegrove 2002), territoriality (Powers et al. 2003), time of year and breeding status (Hiebert 1991,1993), condition (molt or migratory) and circulating levels of stress hormone (Hiebert et al. 2000) also impact hummingbird torpor.

A torpid hummingbird also suffers a significant reduction in behavioral responsiveness (Prinzinger et al. 1992, McKechnie & Lovegrove 2002; JMC, personal observation). Thus, one might predict that predation risk would also limit the use of torpor since a torpid hummingbird would inevitably be at a greater risk of predation through their inability to respond during an attack. A potential example of how torpor might be modified in high-risk conditions can be found in bats, another taxonomic group that relies on torpor for energy conservation. Lausen and Barclay (2006) suggest that big brown bats (*Eptesicus fuscus*) reduce the depth of torpor when roosting in comparatively risky environments. However, no studies have experimentally addressed this potential trade-off between the use of energy-saving torpor and the risk of predation in birds.

In this study, I examined the use of torpor in captive ruby-throated hummingbirds (*Archilochus colubris*) exposed to different levels of perceived risk. Birds were separated into two experimental groups: (i) a treatment group exposed to nocturnal disturbance and (ii) a control group that remained undisturbed. Although treatment birds tended to reduce their use of torpor over time, I found no statistically significant difference between the proportion of the night that birds in either group spent torpid over a 10 d monitoring period. Further studies are needed to examine the potential role of predators on hummingbird torpor regulation, but these and other findings suggest that the need to conserve energy may play an overwhelming role in dictating the use of torpor in these small birds.

Methods

Ruby-throated hummingbirds were captured in Vigo County, Indiana, between 21 July 2011 and 13 September 2011. Birds were captured using a trap baited with a sugar-water feeder. These birds were routinely fed in the open trap, and thus entered it readily. Individuals were immediately transported to environmental control chambers on the Indiana State University campus. Total transport time was approximately 20 min. Methods were approved by the

Indiana State University Institutional Animal Care and Use Committee under Protocol #10-09-2009:SLL/JMC – AMEND 06-04-2010.

Birds were housed individually in 60 x 40 x 70 cm cages (length, width and height) placed in environmental control chambers. The frame of each cage was constructed using thin wooden boards 3.8 x 2 cm in cross section. White translucent fabric was wrapped around the wooden frame to create a soft roof and cage walls. Velcro attached adjacent to the front end of the cage created a fabric door for access to birds and feeders. The front (40 x 70 cm) wall was constructed using a thin, white opaque plastic sheet. This sheet transmitted thermal infared light, and thus allowed us to monitor the bird using a thermal infrared imaging camera placed 1 m in front of the cage (ThermaCAM PM 575; FLIR Systems, North Billerica, MA, USA). A 30 cm long natural stick perch approximately 5 mm in diameter was suspended 25 cm from the top of the cage. Two cages were placed immediately adjacent to one another in each chamber, allowing for the simultaneous monitoring of two birds with one thermal imager. A 60 W incandescent lamp was placed directly above each cage. The light:dark cycle was adjusted to mimic natural conditions at the time of capture. At “lights-off”, both incandescent lamps in the chamber turned off, while two 7 W incandescent night lights remained on for 30 min to simulate dusk and allow birds to find the perch if not already perched at lights-off.

Feeders were constructed using 25 mL plastic pipettes (24 cm long) for accurate measurement of food consumption. The tapered end of the pipette was heat-sealed, and a 2 mm diameter hole was drilled approximately 3 cm from the bottom tip of the pipette. A 1.5 cm long red plastic tube 8 mm in external diameter (internal diameter = 5 mm) was then sealed around the 2 mm hole to create a flower-like feeding tube. Once filled, the feeder was sealed with a rubber stopper and suspended from a hook inside the cage. All birds were fed Nektar-Plus

(*Nekton* Products, Guenter Enderle Enterprises Inc., Clearwater, FL, USA) throughout the experiment. Feeders were replaced every morning at 10:00 for consistent record of food consumption over 24 hours.

To determine whether nighttime disturbance resulted in modified torpor patterns, hummingbirds were assigned to either a treatment or control group. Birds housed in adjacent cages were assigned to the same group since it would not be possible to disturb one bird and not the other. Following a two day acclimation period at an air temperature (T_a) of 21 °C, the T_a in the environmental control chamber was reduced to 15 °C to promote the use of torpor (Hiebert et al. 2000, Schleucher 2004). Birds in the treatment group (N = 10) were disturbed for five consecutive evenings. During nights with disturbance, the experimenter entered the chamber 1 h after the nightlights in the chamber turned off (1.5 h after lights-off). No birds were torpid this early in the night. The chamber lights were turned on and the disturbance stimulus, a 4 cm in diameter aluminum foil ball at the end of a 5 mm diameter wooden dowel rod, was inserted into each of the adjacent cages through the bottom corner of the access door. This stimulus caused significant alarm and many birds took flight as soon as the stimulus entered the cage. The stimulus was slowly moved towards any bird remaining on the perch until it took flight. All birds were pursued by the stimulus at a speed of approximately 10 cm/s for 20 s. Upon conclusion of the disturbance, the stimulus was removed and the chamber lights were turned off as soon as both birds were back on their perches. The lights remained on for approximately 1 min during this sequence of disturbance events. Control birds (N = 10) in a separate chamber were not disturbed with the stimulus, but the chamber lights were timed to turn on for 1 min for five consecutive nights to control for changes in the light environment during disturbances. Following the five days of experimental disturbance, both control and treatment birds were observed while undisturbed for five additional nights to monitor for any prolonged changes in torpor use.

Birds were monitored during nighttime hours using time-lapse video recordings from the thermal imaging cameras (10 frames/s). I could not accurately measure hummingbird T_b with thermal imagery due to the insulative effect of the feathers. However, T_b fluctuations associated with the initiation, maintenance, and arousal from torpor were clearly evident via thermal imagery, and torpid birds largely “disappeared” from view as the bird appeared to cool to ambient conditions. Torpor duration was determined from the onset of torpor (when birds first began to cool) until the start of arousal (when birds exhibited the first signs of warming). Information regarding nightly torpor use could only be obtained from birds that remained perched in view of the thermal imager for the duration of the night. Birds routinely spent the night on the perch; complete data for all 10 monitoring nights were available for 13 (6 control and 7 treatment) of the 20 total birds with an average of 7.9 monitoring nights for the remaining 7 individuals (range: 5 – 9 nights).

A general linear mixed model was used to determine whether the hummingbirds modified their use of torpor during the nighttime monitoring periods. The proportion of the night spent torpid was used as the dependent variable since the duration of the night changed with natural ambient conditions over the course of the 10-week study. The 10 nights of monitoring were repeated within each individual and group identity (treatment = “1”, control = “0”), sex (male = “0”, female = “1”), day number (1-10), Julian date, and day × group and day × date interaction terms were included in the analysis. Food consumption may also influence the proportion of the night spent torpid; thus, the volume of food consumed during the previous 24 h was included as a covariate. Individual nested within the variable “group” was included as a random factor.

Birds may delay the onset of torpor instead of reducing their use of torpor in response to disturbance; thus, I also analyzed nightly data on torpor onset. A similar general linear mixed model was used, with torpor delay repeated within individual, and group identity, sex, day number, Julian date, and day × group and day × date interactions included in the analysis. Torpor delay may be influenced by the duration of torpor itself. For instance, quick torpor onset may be required in order to accommodate longer bouts of torpor. Thus, the proportion of the night spent torpid was included as a random factor along with the factor of individual nested within group. Only data for birds that used torpor during the 10-day experimental phase of the study were included in this analysis ($N = 14$ birds). Analyses were conducted using SPSS 19.0 (SPSS, Inc., Chicago, IL, USA).

Results

Ruby-throated hummingbirds routinely used torpor in the laboratory throughout the course of the study. Of the 20 total birds in the study, only three treatment birds and three control birds did not use torpor during the 10 d monitoring period (for those nights when perched in view). Two of these 6 birds did, however, use torpor during the 2 d acclimation period prior to the start of the experiment. Daily torpor duration ranged from 30 – 408 min (mean = 187 min), considering all birds. In general, birds required approximately 1 h to cool completely (i.e., to background temperature, $T_a = 15$ °C). Once in "nonregulated torpor" ($T_b = T_a$; Schleucher 2004), the bird was nearly visually indistinguishable from background colors on the thermal-imaging video recording. Birds began to warm no later than approximately 1 h before "lights-on" and were fully warmed within 30 min of "lights-on". Observations of torpid hummingbirds (in a related study, JMC personal observation) indicated that birds using nonregulated torpor were behaviorally unresponsive and could not open their eyes, although with tactile stimulation, they could slowly extend their wings, occasionally emit high frequency squeals, and immediately begin to warm.

Treatment birds (disturbed for the first 5 d of monitoring) tended to reduce the proportion of the night spent torpid over the 10 d monitoring period (Fig. 16). However, this trend was not statistically significant since group identity (“treatment” or “control”) did not significantly influence the within-individual use of torpor over time (general linear mixed model: $F = 0.052$, $P = 0.823$). The day × group interaction term was also not statistically significant ($F = 1.299$, $P = 0.243$). However, hummingbirds (as a whole) significantly reduced torpor use during the 10 d monitoring period ($F = 4.453$, $P < 0.001$; Fig. 16) and the proportion of the night spent torpid became progressively lower within individual birds over time ($F = 2.248$, $P = 0.022$). Time of year also influenced torpor use over the 10-day monitoring period: birds spent a significantly greater proportion of the night torpid as the study progressed ($F = 6.957$, $P = 0.018$), with a significant interaction between Julian date and observation day ($F = 4.102$, $P < 0.001$; Fig. 17). The amount of food consumed in the previous 24 h significantly influenced torpor use ($F = 9.697$, $P = 0.002$); individuals that consumed more food tended to use less torpor overall (Fig. 18). There was no effect of sex on the proportion of the night spent torpid ($F = 0.329$, $P = 0.574$).

Torpor delay did not vary between control and treatment birds (general linear mixed model: $F = 0.405$, $P = 0.538$; Fig. 19) and there was no significant day x group interaction ($F = 1.185$, $P = 0.323$). On average, torpor was initiated 367 min (SE: ± 62.3) after lights-off in control birds and 377 min (± 84.6) after lights-off in treatment birds. Torpor delay increased over the 10 d monitoring period both among ($F = 2.074$, $P = 0.048$) and within individuals ($F =$

6.449, $P < 0.001$). Although there was a significant day × date interaction ($F = 2.251$, $P = 0.032$), Julian date did not have a statistically significant effect on torpor delay ($F = 0.667$, $P = 0.430$). Torpor delay was also not influenced by the sex of the individual ($F = 0.931$, $P = 0.358$).

Discussion

It is reasonable to expect that torpor is influenced by predation risk given the drastic reduction in behavioral responsiveness associated with torpid T_b. Although birds (as a whole) reduced and delayed their use of torpor during the 10-day monitoring period, I found no significant effect of manipulated risk on torpor use (Fig. 16). Torpor use tended to increase over the course of the study (Fig. 17), likely reflecting the early stages of pre-migratory fattening (Hiebert 1993, Hiebert et al. 2000). I also found that greater nectar consumption reduced torpor use in hummingbirds (see also Hiebert 1991, Hiebert et al. 2000). However, the proportion of the night spent torpid was low overall (Fig. 18) and there were many nights when birds did not use torpor (90 of 185 total nights during which the use of torpor could be assessed). It is possible that the full-strength nectar used in this study provided enough nourishment that birds could minimize or forego the use of potentially risky torpor altogether. Limited food availability or increased energetic requirements (e.g., preparing for migration) will increase the need to conserve energy via torpor, thus any such trade-off between energy conservation and predation risk may be more evident under these conditions.

Hummingbirds may not have altered their torpor use if the risk of predation in nature is not a significant selective pressure (see Miller & Gass 1985). However, hummingbirds are opportunistically preyed upon by many species, including mammals (Lepczyk et al. 2003), birds (Hoyt Spofford 1976, Seutin & Apanius 1995), reptiles (Littlefield 2007), amphibians (see also

Miller & Gass 1985), and even invertebrates (Owen & Cokendolpher 2006, Lorenz 2007). Furthermore, hummingbirds do exhibit typical avian antipredator behavior when foraging during the day (Lima 1991, Blem et al. 1997). The use of daytime antipredator behavior implies that hummingbirds may also exhibit nocturnal antipredator behavior. Reports of nighttime roost locations indicate that hummingbirds tend to sleep on thin, relatively exposed branches offering little protection (Oniki et al. 2001). Although hummingbirds tend to roost high above the ground, they could remain accessible to many opportunistic predators, including small mammals. Mice are major avian nest predators (Schmidt & Ostfeld 2003), and rodents would also likely prey upon an unresponsive, torpid hummingbird if encountered during the night.

It is possible that the stimulus used here (a foil ball at the end of a wooden stick) did not elicit the same behavioral response as might a real nocturnal predator. However, all hummingbirds responded quickly and attempted to flee immediately upon presentation of the stimulus. This stimulus was also used (in a similar fashion) to examine the effect of simulated risk on unihemispheric slow-wave sleep in ruby-throated hummingbirds; this avian sleep state allows sleep and antipredator vigilance to occur simultaneously in opposite hemispheres of the brain (Rattenborg et al. 1999). The prevalence of unihemispheric slow-wave sleep in these hummingbirds increased considerably following such experimental disturbances (Carr & Lima, in prep). These findings suggest that the experimental stimulus simulated an adequate “threat” and that hummingbirds do alter their nocturnal antipredator behavior with respect to perceived risk. Since torpor and sleep fall along the same physiological continuum (Reinertsen 1996), it is likely that predation risk influences torpor as well. However, additional studies are required to further examine the likely predation-related costs of hummingbird torpor.

Acknowledgements

I would like to thank George Bakken for his instruction and assistance with the environmental control chambers and thermal imaging cameras necessary for the completion of this study. Financial support was provided by the Department of Biology at Indiana State University.

References

Bech, C., Abe, A. S., Steffensen, J. F., Berger, M. & Bicudo, J. E. P. W. (1997). Torpor in three species of Brazilian hummingbirds under semi-natural conditions. Condor **99**, 780-788.

Blem, C. R., Blem, L. B. & Cosgrove, C. C. (1997). Field studies of rufous hummingbird sucrose preference: does source height affect test results? Journal of Field Ornithology **68**, 245-252.

Calder, W. A. & Booser, J. (1973). Hypothermia of broad-tailed hummingbirds during incubation in nature with ecological correlations. Science **180**, 751-753.

Geiser, F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. Annual Review of Physiology **66**, 239-274.

Geiser, F. & Ruf, T. (1995). Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiological Zoology **68**, 935-966.

Hiebert, S. M. (1990). Energy costs of temporal organization of torpor in the rufous hummingbird (*Selasphorus rufus*). Physiological Zoology **63**, 1082-1097.

Hiebert, S. M. (1991). Seasonal differences in the response of rufous hummingbirds to food restriction: body mass and the use of torpor. Condor **93**, 526-537.

Hiebert, S. M. (1993). Seasonal changes in body mass and use of torpor in a migratory hummingbird. Auk **110**, 787-797.

Hiebert, S. M., Salvante, K. G., Ramenofsky, M. & Wingfield, J. C. (2000). Corticosterone and nocturnal torpor in the rufous hummingbird (*Selasphorus rufus*). General and Comparative Endocrinology **120**, 220-234.

Hoyt Spofford, S. (1976). Roadrunner catches hummingbird in flight. Condor **78**, 142.

Krüger, K., Prinzinger, R. & Schuchmann, K.-L. (1982). Torpor and metabolism in hummingbirds. Comparative Biochemistry and Physiology A **73**, 679-689.

Lausen, C. L. & Barclay, R. M. R. (2006). Benefits of living in a building: big brown bats (*Eptesicus fuscus*) in rocks versus buildings. Journal of Mammalogy **87**, 362-370.

Lepczyk, C. A., Mertig, A. G. & Liu, J. (2003). Landowners and cat predation across rural-to-urban landscapes. Biological Conservation **115**, 191-201.

Lima, S. L. (1991). Energy, predators and the behavior of feeding hummingbirds. Evolutionary Ecology **5**, 220-230.

Littlefield, C. D. (2007). Predation by the sonoran whipsnake on birds in southwestern New Mexico. Western Birds **38**, 232-234.

Lorenz, S. (1997). Carolina mantid (*Stagmomantis carolina*) captures and feeds on a broad-tailed hummingbird (*Selasphorus platycercus*). Bulletin of the Texas Ornithological Society **40**, 37-38.

McKechnie, A. E. & Lovegrove, B. G. (2002). Avian facultative hypothermic responses: a review. Condor **104**, 705-724.

Miller, R. S. & Gass, C. L. (1985). Survivorship in hummingbirds: is predation important? Auk **102**, 175-178.

Oniki, Y., Schuchmann, K.-L., Willis, E. O., Sigrist, T. & Baudet, G. (2001). Roosting site of the sombre hummingbird *Campylopterus cirrochloris* (Trochilidae) in southern Bahia, Brazil. Bulletin of the British Ornithologists' Club **121**, 256-257.

Owen, J. L. & Cokendolpher, J. C. (2006). Tailless whipscorpion (*Phrynus longipes*) feeds on Antillean crested hummingbird (*Orthorhyncus cristatus*). Wilson Journal of Ornithology **118**, 422-423.

Powers, D. R., Brown, A. R. & Van Hook, J. A. (2003). Influence of normal daytime fat deposition on laboratory measurements of torpor use in territorial versus nonterritorial hummingbirds. Physiological and Biochemical Zoology **76**, 389-397.

Prinzinger, R., Schäfer, T. & Schuchmann, K. (1992). Energy metabolism, respiratory quotient and breathing parameters in two convergent small bird species: the fork-tailed sunbird *Aethopyga christinae* (Nectariniidae) and the Chilean hummingbird *Sephanoides sephanoides* (Trochilidae). Journal of Thermal Biology **17**, 71–79.

Rattenborg, N. C., Lima, S. L. & Amlaner, C. J. (1999). Facultative control of avian unihemispheric sleep under the risk of predation. Behavioural Brain Research **105**, 163-172.

Reinertsen, R. E. (1996). Physiological and ecological aspects of hypothermia. In *Avian energetics and nutritional ecology* (ed. C. Carey), pp. 125-157. New York: Chapman and Hall.

Schleucher, E. (2004). Torpor in birds: Taxonomy, energetics, and ecology. Physiological and Biochemical Zoology **77**, 942-949.

Schmidt, K. A. & Ostfeld, R. S. (2003). Songbird populations in fluctuating environments: predator responses to pulsed resources. Ecology **84**, 406-415.

Seutin, G. & Apanius, V. (1995). Gray flycatcher predation on a hummingbird. Wilson Bulletin **107**, 565-567.

Suarez, R. K. & Gass, C. L. (2002). Hummingbird foraging and the relation between bioenergetics and behaviour. Comparative Biochemistry and Physiology A **133**, 335-343.

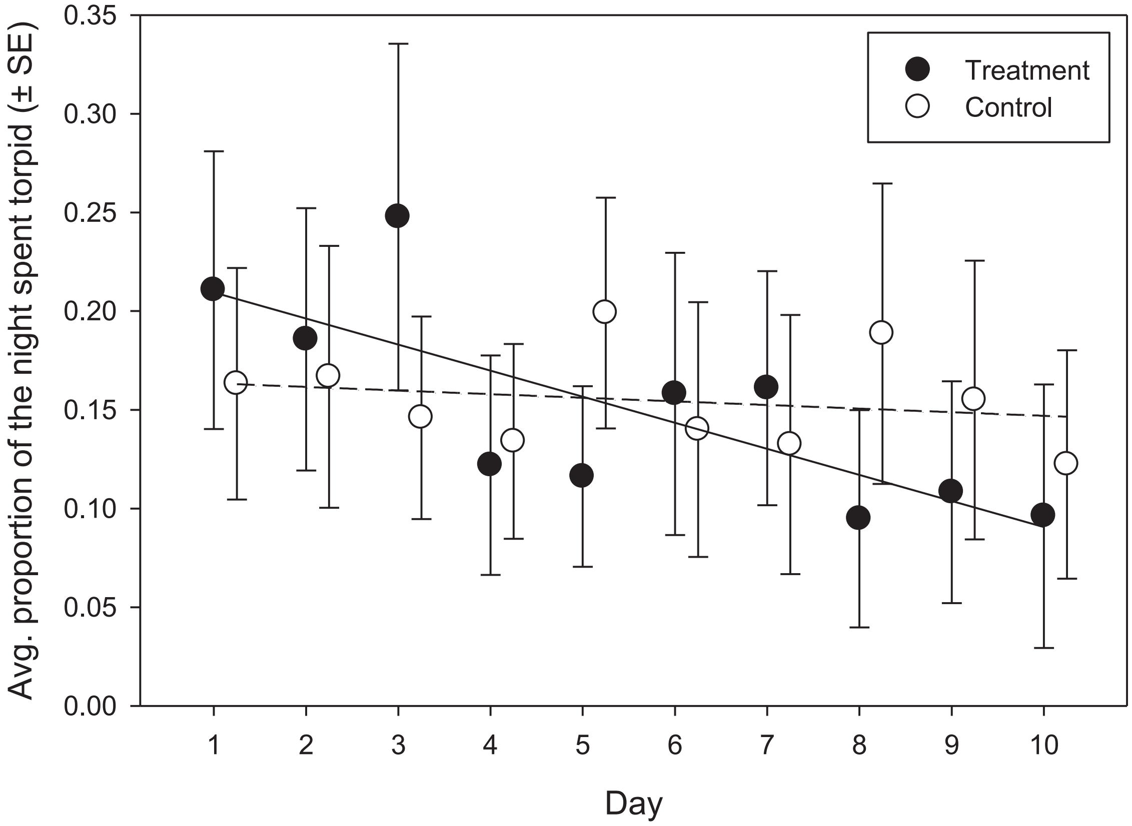


Figure 16. The average proportion of the night spent torpid (± SE) as a function observation day. Experimental disturbance occurred for 5 consecutive days (Day 1 – 5) for birds in the treatment group (●); control birds (○) were not disturbed. Treatment birds were not disrupted on days 6 – 10. The solid and dashed regression lines correspond to the treatment and control groups, respectively.

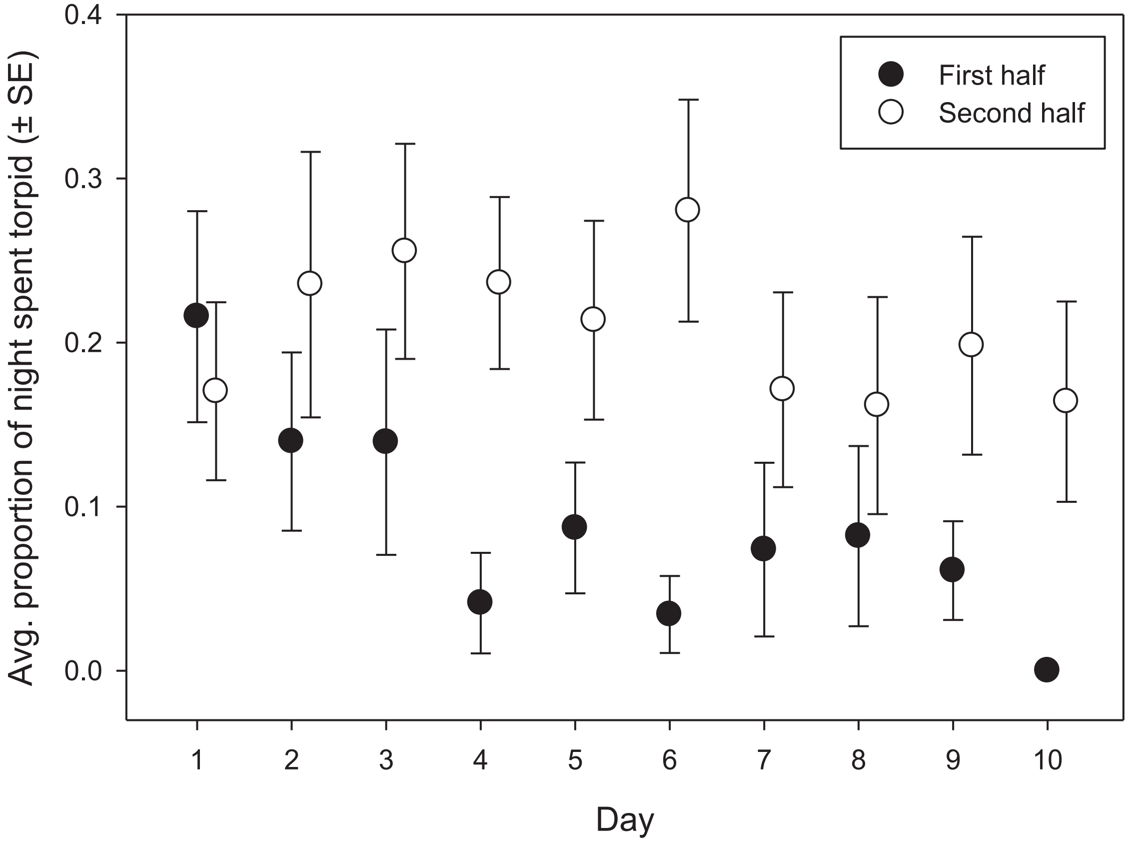


Figure 17. The average proportion of the night spent torpid (± SE) during the 10 monitoring days for the first (●) and second (○) half of the study. Nightly observations (without respect to individual or treatment group) were divided at the median date for all observations (Julian date = 235) with 90 first-half and 95 second-half observations of torpor use.

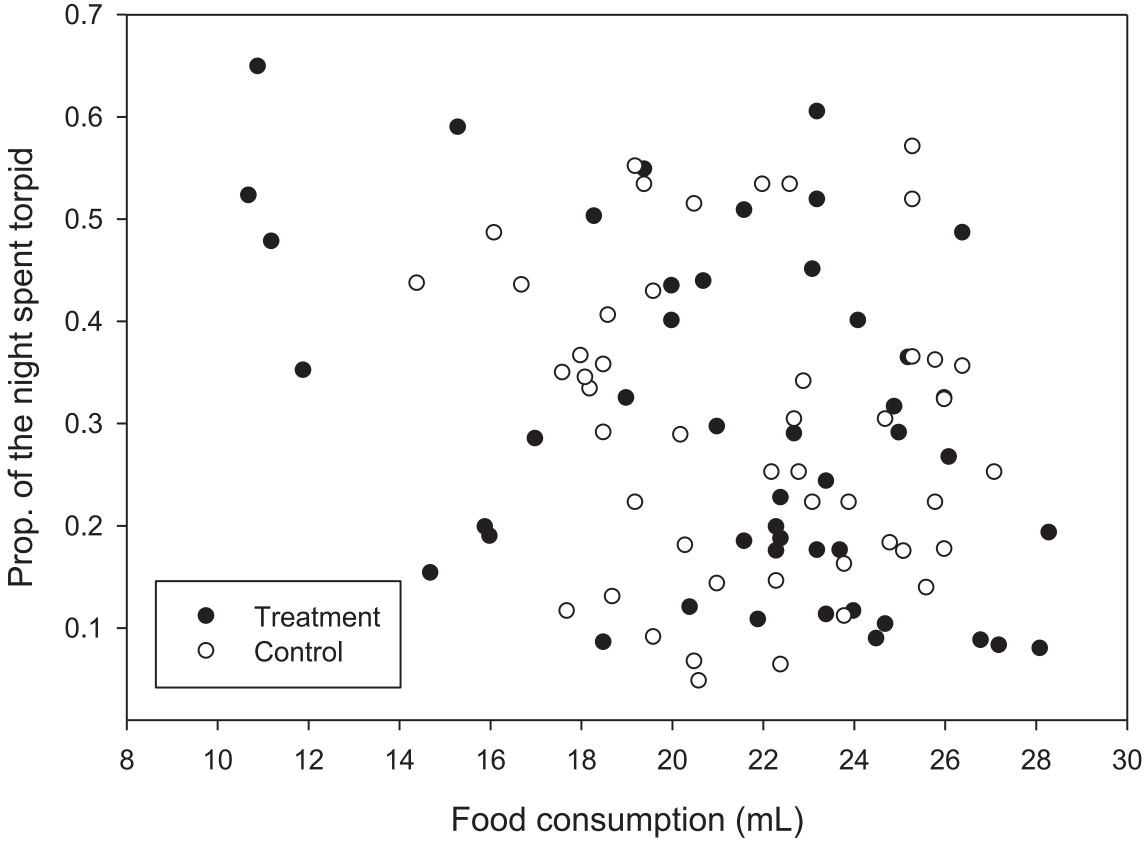


Figure 18. The proportion of the night spent torpid as a function of the volume of food consumed (in mL) for each observation night. Each point represents a night for a particular bird, but without respect to identity. Birds in the treatment and control groups are indicated by filled circles (●) and open (○) circles, respectively. Nights when birds did not use torpor were removed for clarity.