



SHORT COMMUNICATIONS

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FACULTATIVE REST-PHASE HYPOTHERMIA IN FREE-RANGING WHITE-THROATED SPARROWS

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Abstract. Shallow facultative rest-phase hypothermia has been reported in a number of passerine families, but few published data exist about its use by free-ranging birds. We used temperature-sensitive radio-transmitters to determine whether White-throated Sparrows (*Zonotrichia albicollis*) employ nocturnal hypothermia during winter. We measured skin temperatures of 24 free-ranging sparrows between 13:00 and 14:00 and between 02:00 and 03:00 for each of three days and nights per subject. The average nightly skin-temperature reduction per individual was $3.4 \pm 1.0^\circ\text{C}$ (SD). Skin temperature reductions ranged from 0.2°C to 7.0°C among all individuals. There was a significant negative correlation between the magnitude of skin temperature decline and nighttime ambient temperature. Additionally, we found a negative trend between depth of hypothermia and a body density index.

Key words: *hypothermia, thermoregulation, White-throated Sparrow, Zonotrichia albicollis.*

Fase de Reposo Hipotérmica Facultativa en Individuos de *Zonotrichia albicollis* que se Desplazan Libremente

Resumen. La fase de reposo facultativa somera ha sido mencionada para un número de familias de passeriformes, pero existen pocos datos publicados sobre su uso por parte de aves que se desplazan libremente. Usamos radio transmisores sensibles a la temperatura para determinar si *Zonotrichia albicollis* emplea hipotermia nocturna durante el invierno. Medimos la temperatura de la piel de 24 individuos que se desplazan libremente entre las 13:00 y 14:00 y entre las 02:00 y 03:00 durante tres días y tres noches por individuo. La reducción nocturna promedio de la tem-

peratura de la piel por individuo fue $3.4 \pm 1.0^\circ\text{C}$ (DE). Las reducciones de la temperatura de la piel variaron entre 0.2°C y 7.0°C considerando todos los individuos. Hubo una correlación negativa significativa entre la disminución de la magnitud de la temperatura de la piel y la temperatura ambiental nocturna. Adicionalmente, encontramos una tendencia negativa entre la profundidad de la hipotermia y el índice de densidad corporal.

Body temperature maintenance entails considerable metabolic cost for endothermic animals. When metabolic demand exceeds energy supply, some birds use facultative hypothermic responses to reduce energy expenditure (McKechnie and Lovegrove 2002). Such circumstances may arise when food supplies are insufficient or unpredictable, when weather is cold, or when foraging is inhibited for prolonged periods (Reinertsen 1996).

Avian facultative hypothermic responses occur in a broad range of depths and bout lengths, ranging from seasonal hibernation, exhibited by Common Poorwill (*Phalaenoptilus nuttallii*), to shallow rest-phase hypothermia observed in an array of avian families (McKechnie and Lovegrove 2002). They are generally most pronounced among nonpasserine nectarivores and aerial-feeding insectivores whose food sources are ephemeral and dependent upon weather (McKechnie and Lovegrove 2002). Among such taxa (e.g., Apodidae, Trochilidae, and Caprimulgidae), body temperature (T_b) reductions exceeding 10°C are common, and individuals often enter torpor (Geiser and Ruf 1995, Reinertsen 1996, Körtner et al. 2000, Barclay et al. 2001). In contrast, most passerines examined maintain nocturnal T_b within 10°C of active-phase normothermic T_b and typically do not become torpid (Reinertsen 1996, McKechnie and Lovegrove 2003). A notable exception is the nectarivorous Malachite Sunbird (*Nectarinia famosa*; Downs and Brown 2002). However, while relatively modest in depth, facultative rest-phase

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hypothermia likely affords passerines biologically significant energetic savings (Dawson and Whittow 2000).

Much about passerines' use of this energy-saving strategy remains unknown. Most research has been conducted on captive subjects (McKechnie and Lovegrove 2003), or has targeted nonpasserines (Brigham 1992, Bech et al. 1997). Our first objective was therefore to determine whether it occurs in a free-ranging temperate-zone species, the White-throated Sparrow (*Zonotrichia albicollis*).

White-throated Sparrows are winter residents of the Mid-Atlantic region of the eastern United States. They are regularly exposed to nighttime ambient temperatures (T_a) at or below those known to produce hypothermia in other passerines (Reinertson and Haftorn 1986, Clemens 1989). Furthermore, since they are primarily ground-feeding granivores (Falls and Kopachena 1994), their food supply may be periodically obscured by snow and ice, possibly subjecting them to short-term food limitation.

Another poorly understood facet of avian thermoregulation relates to the factors that produce intraspecific variability. Such factors may include both environmental and physiological variables (Reinertson 1996). A number of studies have reported relationships between T_a and the depth of hypothermia bouts, but few have examined the effects of T_a on free-ranging birds (Brigham 1992). Moreover, the effects of individuals' energetic status on the depth of hypothermia have generally been addressed via food deprivation experiments in the laboratory (Ketterson and King 1977, Graf et al. 1989, McKechnie and Lovegrove 2003). Data for individuals in the field are needed to understand the effects of energy reserves on facultative rest-phase hypothermic strategies.

Thus, our second objective was to determine whether T_a or stored energy predict the depth of facultative rest-phase hypothermia. We predicted that magnitude of skin temperature (T_{sk}) depression would be negatively correlated with both T_a and fat supply, estimated using a body density index. Additionally, we predicted that there would be an interaction between these variables.

METHODS

We conducted our study 7–21 January 2002 and from 10 January to 3 February, 2003, on the Mary Washington College grounds and adjacent residential neighborhood of Fredericksburg, Virginia (38°10'N, 77°35'W). The area contains a mixture of lawns and hedgerows, as well as unmanaged Eastern deciduous forest fragments. Bird feeders were present in the study area. During the day, we typically observed White-throated Sparrows in loosely structured social groups foraging in leaf litter. At night, sparrows most frequently roosted in broad-leaved evergreens (e.g., *Ilex opaca*, *Photinia serrulata*, and *Ligustrum lucidum*).

We mist-netted 24 adult sparrows opportunistically and weighed and measured the wing chords of each. Body masses ranged from 23.3 to 32.8 g (mean \pm SD = 27.9 \pm 2.7 g), and wing chords ranged from 65.5 to 78.0 mm (mean \pm SD = 71.6 \pm 3.0 mm). From these measurements, we calculated a body density index by dividing body mass by the cube of wing chord

length. This index is frequently used as an indicator of physical condition in birds, and variation among individuals is indicative of variation in fat supply (Pravosudov et al. 1999, Ekman and Hake 1990).

We sexed 18 individuals based on wing chord length (Piper and Wiley 1991). The wing chord lengths of six individuals were within the published range of overlap between males and females (Piper and Wiley 1991, Falls and Kopachena 1994), and consequently, we could not sex them with certainty.

Each bird was fitted with two colored leg bands to permit individual identification. We affixed a temperature-sensitive radio-transmitter (Model BD-2AT; 0.7 g; Holohil Systems Ltd., Carp, Ontario, Canada) to the interscapular apteria of each bird using Skin-Bond® latex cement (Smith & Nephew® Inc., Largo, Florida).

We measured T_{sk} of birds between 13:00 and 14:00 and between 02:00 and 03:00 during the next three consecutive days and nights by timing the interpulse interval and comparing it with the calibration curves provided by the manufacturer. We based the timing of our T_{sk} measurements on data for six individuals whose T_{sk} we measured every 3 hr also over 3 days and nights. From these pilot observations, we determined that we reliably captured maximum diurnal T_{sk} and minimum nocturnal T_{sk} during these hours. To verify that transmitters were properly attached following the third night's reading, we measured T_{sk} the next afternoon. If a transmitter detached from a bird at any time, we attached it to a new subject. We obtained six T_{sk} measurements for 12 sparrows each winter. Observations were spread as evenly as possible across calendar dates each year.

Since we were interested in measuring temperature changes only, and not absolute body temperature (T_b) values, we did not record subjects' cloacal temperatures immediately after applying transmitters. Brigham (1992) found that cloacal and interscapular T_{sk} temperatures in Common Poorwills are tightly correlated ($r^2 = 0.99$). We assumed that T_{sk} changes would reflect T_b changes in our White-throated Sparrows with a similar degree of precision. Moreover, the diurnal T_{sk} in our sample averaged 40.9 \pm 1.6°C (SD), which is within one degree of the mean T_b typical of passerines (Prinzinger et al. 1991). It is possible that T_{sk} measurements are affected by ambient cooling (Willis and Brigham 2003). However, even though the daytime T_a range was nearly equivalent to nighttime range, there was only a 0.02°C change in daytime T_{sk} measurements for every 1.0°C change in daytime T_a . Thus, it appears that T_a had little direct effect on T_{sk} measurements. We therefore feel that our use of external transmitters was a valid means of assessing T_b fluctuations.

When we measured T_{sk} , we also recorded T_a and wind speed (m sec⁻¹). T_a ranged from -7°C to 12°C (mean \pm SD = 5.0 \pm 4.3°C) during the day, and -8°C to 7°C at night (-1.6 \pm 4.7°C). T_a averages were consistent with historical T_a averages for the region. Wind speeds were negligible during both years in the vicinity of sparrows' nocturnal roost sites. Thus, we excluded wind speed from our analyses. Snow and ice cover were also insignificant during our observation period.

STATISTICAL ANALYSES

We used ANCOVA to test our predictions (SPSS 11.0 for windows). To eliminate pseudoreplication, we cal-

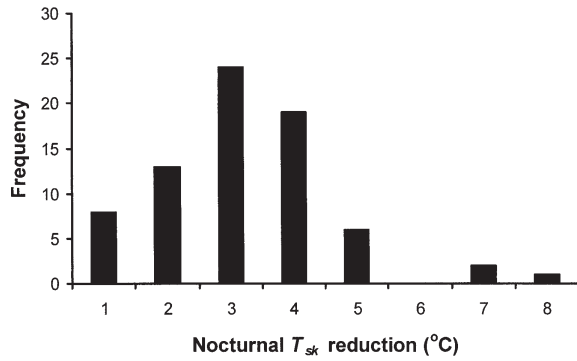


FIGURE 1. Frequency distribution of rest-phase skin temperature (T_{sk}) reduction in White-throated Sparrows ($n = 24$ individuals; three observations per subject).

culated the average nocturnal T_{sk} reduction exhibited by each individual. Our response variable, therefore, comprised the mean of the three diurnal-nocturnal T_{sk} differences recorded per individual. We also averaged the T_a for the three nights corresponding to when each subject's nocturnal T_{sk} readings were taken. Since the predicted interaction term was not significant, we removed it from our final model. We performed a separate, but identical analysis on the 18 birds that we could sex reliably. Values represent means \pm SD.

RESULTS

Overall nocturnal T_{sk} reduction ranged from 0.2°C to 7.3°C (mean 3.5 ± 1.4 °C; Fig. 1), while per-subject average T_{sk} reductions ranged between 2.2°C and 5.7°C (mean 3.4 ± 1.0 °C). Twelve of 24 sparrows exhibited mean T_{sk} decreases ≥ 3.0 °C.

We found a significant negative correlation between average per-subject T_{sk} reduction and T_a ($F_{1,21} = 4.5$, $P = 0.05$; Fig. 2). Additionally, average T_{sk} reduction tended to be negatively related to body density ($F_{1,21} = 3.9$, $P = 0.06$; Fig. 3). Both variables accounted for approximately one-third of the variation among individuals' mean nocturnal T_{sk} decline and significantly predicted the depth of hypothermia ($R^2 = 0.30$, $P = 0.02$).

In our analysis of those individuals that we could sex reliably, we found no difference in depth of hypothermia between seven males and 11 females after controlling for the effects of T_a and body density ($F_{1,14} = 1.1$, $P = 0.32$).

DISCUSSION

White-throated Sparrows in our study exhibited nocturnal T_{sk} depression that varied among individuals. Half of our 24 subjects reduced their T_{sk} by ≥ 3.0 °C, enough to suggest use of facultative rest-phase hypothermia (Prinzinger et al. 1991), likely to lessen thermoregulatory costs. To our knowledge, these data represent the first evidence of facultative rest-phase hypothermia in a free-ranging emberizid. They are consistent, however, with laboratory evidence that most passerines are capable of only modest rest-phase temperature reduction (McKechnie and Lovegrove 2002).

The average T_{sk} reduction we recorded was greater than that of well-fed captive White-crowned Sparrows (*Z. leucophrys*), a congener of equal body mass, whose

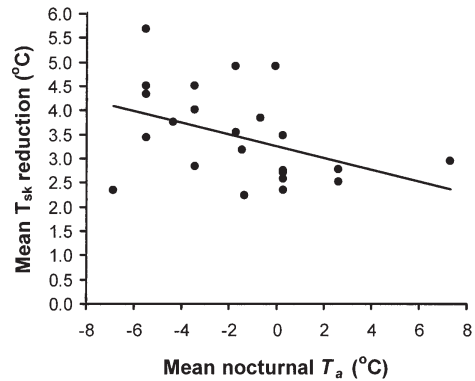


FIGURE 2. Significant negative correlation between mean rest-phase skin temperature (T_{sk}) reduction and the average nocturnal ambient temperature (T_a) in 24 White-throated Sparrows ($r = -0.42$, $P = 0.05$). Each data point represents the mean of three T_{sk} measurements of an individual.

T_b dropped by less than 1.0°C between night and day at a mean T_a of about 7.0°C (Ketterson and King 1977). In fact, the average T_{sk} decline we recorded was comparable to those of captive White-crowned Sparrows (T_b decline = 3.4°C) fasted for 56 hr, also at $T_a = 7.0$ °C, during which birds lost more than 20% of their body mass (Ketterson and King 1977).

The average nocturnal T_a in our study was nearly 9.0°C lower than in Ketterson and King's (1977) food deprivation experiment (-1.6°C versus 7.0°C). We did record 14 T_{sk} observations when the T_a was comparable (i.e., 4.0°C to 7.0°C). Under these conditions, T_{sk} reduction was still within 0.5°C (mean 3.1 ± 1.0 °C) of the T_b declines reported by Ketterson and King (1977) for severely fasted White-crowned Sparrows. Thus, our data are consistent with recent arguments that laboratory studies underestimate the amplitude of circadian T_b fluctuations typical of free-ranging birds (Geiser et al. 2000, McKechnie and Lovegrove 2002).

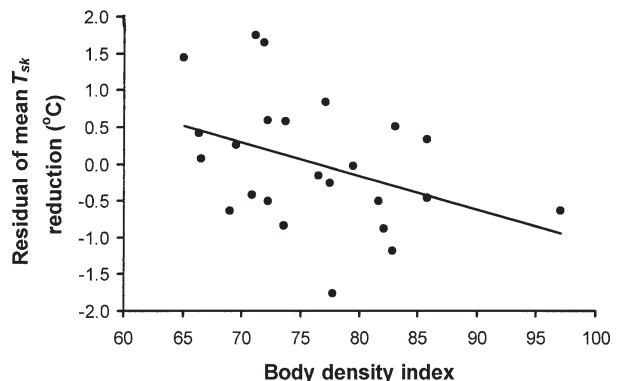


FIGURE 3. Negative relationship between rest-phase skin temperature (T_{sk}) reduction and an index of body density in White-throated Sparrows, after controlling for ambient temperature (T_a) ($r_{\text{partial}} = -0.40$, $P = 0.06$). Each data point represents the ANCOVA residual of rest-phase skin temperature (T_{sk}) reduction after we removed the effects of T_a (Fig. 2).

Variability in depth of T_{sk} reduction was at least partially explained by T_a . As T_a declines, energetic costs associated with thermoregulation should increase, creating greater need for conservation (Reinertsen and Haftorn 1983, Merola-Zwartjes 1998). The variation in nocturnal T_{sk} reduction we found was also partly explained by our body density index, although our observed negative correlation was only marginally significant. This relationship suggests that birds with lower fat reserves have greater need to reduce thermoregulatory costs.

We must interpret this trend with caution. Additional variables such as muscle mass and gut contents affect the density index. Furthermore, consistent relationships between energy limitation and depth of hypothermia have not been found in the field (Dawson and Whittow 2000). Birds that are not obviously energy limited may still enter rest-phase hypothermia or even become torpid. Brigham (1992) found that food supply did not reliably predict torpor use by free-ranging Common Poorwills. Willow Tits (*Poecile montanus*; Reinertsen and Haftorn 1983) regularly fell into hypothermia despite access to adequate food. Furthermore, the biological consequences of hypothermia for our subjects cannot be quantified based on our data.

There was no interaction between T_a and body density index, perhaps because these variables exert independent effects on subjects' thermoregulatory strategies. Alternatively, climatic conditions during our study, although typical of the region, may not have been sufficient to cause birds to thermoregulate differently depending upon their energetic status. Finally, physiological differences among individuals not captured by our body density index may have had overriding effects on thermoregulation as T_a declined.

In summary, we provide evidence that free-ranging White-throated Sparrows use facultative rest-phase hypothermia to a greater extent than would be predicted by previous laboratory work. Additional factors such as diurnal T_a , wind exposure, nocturnal predation risk, social status, and energetic quality of food consumed by birds may influence White-throated Sparrow nocturnal thermoregulation. Furthermore, much debate currently exists regarding heterothermy terminology and the physiological significance of rest-phase hypothermia (Geiser and Ruf 1995, Barclay et al. 2001, Lovegrove and Smith 2003). Nonetheless, our results reinforce the conclusion by others (McKechnie and Lovegrove 2002) that more field studies are needed to understand passerine rest-phase thermoregulation.

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YOU CAN'T JUDGE A PIGMENT BY ITS COLOR: CAROTENOID AND MELANIN CONTENT OF YELLOW AND BROWN FEATHERS IN SWALLOWS, BLUEBIRDS, PENGUINS, AND DOMESTIC CHICKENS

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Abstract. The two main pigment types in bird feathers are the red, orange, and yellow carotenoids and the black, gray, and brown melanins. Reports conflict, however, regarding the potential for melanins to produce yellow colors or for carotenoids to produce brown plumages. We used high-performance liquid chromatography to analyze carotenoids and melanins present in the yellow and brown feathers of five avian species: Eastern Bluebirds (*Sialia sialis*), Barn Swallows (*Hirundo rustica*), King Penguins (*Aptenodytes patagonicus*), Macaroni Penguins (*Eudyptes chrysolophus*), and neonatal chickens (*Gallus domesticus*). In

none of these species did we detect carotenoid pigments in feathers. Although carotenoids are reportedly contained in the ventral plumage of European Barn Swallows (*Hirundo rustica rustica*), we instead found high concentrations of both eumelanins and pheomelanins in North American Barn Swallows (*H. r. erythrogaster*). We believe we have detected a new form of plumage pigment that gives penguin and domestic-chick feathers their yellow appearance.

Key words: *Aptenodytes patagonicus*, *carotenoids*, *Eudyptes chrysolophus*, *Gallus domesticus*, *Hirundo rustica*, *melanins*, *Sialia sialis*.

No Puedes Juzgar un Pigmento por su Color: Contenido de Carotenoide y Melanina de Plumas Amarillas y Marrones en Golondrinas, Azulejos, Pingüinos y Gallinas Domésticas

Resumen. Los dos tipos principales de pigmentos que las aves incorporan en sus plumas son carotenoi-

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