

SYMPOSIUM

Heterothermy, and the Energetic Consequences of Huddling in Small Migrating Passerine Birds

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From the symposium “Environment, Energetics, and Fitness: A Symposium Honoring Donald W. Thomas” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2011, at Salt Lake City, Utah.

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Synopsis The success of migration of small passerine birds depends largely on effective refueling at stopover sites. In our previous studies, we found that hypothermia facilitates accumulation of fuel at the beginning of a stopover. Later we found that blackcaps, *Sylvia atricapilla*, might further reduce their energy expenditure by huddling while at rest. Here, we report experimental results supporting our hypothesis that huddling is beneficial to small migrating passerines both from energetic and thermoregulatory points of view. To test this hypothesis we measured metabolic rates and body temperatures of seven blackcaps placed in respirometry chambers overnight, either solitarily or in groups of three or four at ambient temperatures of 5, 10, and 15°C. Concurring with our predictions, huddling blackcaps maintained higher body temperatures than did solitary birds, but had mass-specific metabolic rates lower by ~30% than those of solitary individuals. Based on our previous studies, we estimated energy savings through huddling to be comparable to energy savings through hypothermia in solitary blackcaps and suggest that huddling may be an important way of saving energy for small passerine birds resting at migratory stopovers. At the same time it might offer the additional benefit of lower risk of predation. In this light, we predict that huddling occurs frequently in nature, leading to significant savings of energy, faster accumulation of fuel, presumably lower risk of becoming a prey, more successful migration, and eventually increased fitness.

Introduction

In 2009, McGuire and Guglielmo asked the question: “What can birds tell us about the migration physiology of bats?” Indeed, much more is known about the physiology of migrating birds than about the migration physiology of bats. However, small insectivorous bats, the vast majority of which are heterothermic, can also provide insight into the physiology of small migrating birds. Here we report results of studies that were motivated by research on pre-hibernation fattening in small heterothermic bats.

From bats to birds: heterothermy at the migratory stopover site

Periodical fattening in small migrating birds is facilitated by a wide range of physiological and behavioral adjustments that include changes in digestive

physiology, dietary preferences, feeding behavior, and activity rhythms (reviewed by: Bairlein 2002; McWilliams et al. 2004). Small heterothermic bats seem to rely on thermoregulatory behavior much more than do small migrating birds. Before winter sets in they can increase body mass (m_b) by ~30% (Krzanowski 1961; Kunz et al. 1998). In order to facilitate accumulation of fat, bats change their thermal preferences and actively select roosts with low ambient temperatures (T_a) that permit deeper torpor while resting during the day. This behavior was first described by Krzanowski (1961) and later it was studied in detail by Speakman and Rowland (1999) who concluded that bats save energy necessary for surviving periods of inactivity during hibernation by proper management of energy expenditure during the pre-hibernatory period in autumn.

Although it might not be obvious at first glance, during migration small birds seem to face similar challenges to those faced by heterothermic bats before hibernation. Prior to migrating small passerine birds can store $\geq 100\%$ of their pre-migratory m_b as fuel to be used later in flight (Bairlein 2002). Migratory flight is fueled mainly by stored fat, but also some protein, whose source is the bird's internal organs, is metabolized (Klaassen and Biebach 1994; Klaassen et al. 2000). Energy stores used during the flight are replenished at stopover sites where birds forage intensely (Biebach et al. 1986, 2000; Lavee and Safriel 1989; Lavee et al. 1991; Gannes 2002). Most of the total time of the migration, and of the total energy devoted to migration, is spent at stopovers (Wikelski et al. 2003; Bowlin et al. 2005), which may last several hours to several days, depending on the bird's body condition, the quality of the stopover site, the potential quality of stopover sites further along the migration route, the direction of migration, or the distance from broad ecological barriers en route (Biebach 1996, Yosef and Wineman 2010). Birds depart when their energy reserves are sufficient to fuel the next lap of the migratory flight (Biebach et al. 1986). However, not only sufficient energy reserves, but also the entire distance of migration may be an important determinant of the duration of stopovers as well as of the success of the migration (Alerstam and Lindström 1990). Thus, in simple terms, one might say that the shorter and the more effective the process of fuel accumulation at a stopover, the greater is the chance of successful migration.

Following this logic we hypothesized that heterothermy in small migrating birds facilitates accumulation of fuel at a stopover site (Wojciechowski and Pinshow 2009). This hypothesis is supported by reports that, in hummingbirds, lowering body temperature (T_b) in torpor leads to less energy expenditure at night, thereby facilitating accumulation of fat during migratory stopover (Carpenter and Hixon 1988; Hiebert 1993). There is little evidence for the relationship between fuel accumulation and thermoregulation in small migrating passerines at stopovers. However, we found that blackcaps (*Sylvia atricapilla*, L.) indeed decrease T_b below normothermic levels and become hypothermic under simulated migratory stopover conditions (Fig. 1; Wojciechowski and Pinshow 2009).

Subsequent measurements of metabolic rate (MR) at night showed that blackcaps use $\sim 30\%$ less energy by lowering T_b by $>5^\circ\text{C}$, compared to normothermic birds. However, hypothermia was recorded only in birds of relatively low m_b (Fig. 2). In blackcaps with

m_b lower than $\sim 16\text{g}$, minimum T_b at night was strongly correlated with m_b , while in heavier ones it was not. By lowering the gradient between T_b and T_a , hypothermic blackcaps eased their gain in m_b while refueling at a stopover (Wojciechowski and Pinshow 2009). Data on the role of m_b and minimum T_b in the dynamics of changes in m_b at a stopover (Gannes 2002) suggest that heterothermy may be crucial for birds in poor body condition. The importance of heterothermy is further supported by the study of Carere et al. (2010) who found that newly arrived migrating songbirds lower their T_b by $\sim 10^\circ\text{C}$ below normothermic daytime levels when they rest at night; surprisingly, Carere and colleagues did not find any relationship between birds' body conditions and their nocturnal, resting T_b .

Thermoregulatory behavior at the stopover site

Small migrating birds may also reduce expenditure of energy at a stopover by huddling at night (Wojciechowski et al. 2008). This behavior may lead to significant savings in energy as was observed in other avian and mammalian species (Gilbert et al. 2010). Huddling is also known to facilitate conservation of energy in bats which may form huddles (or clusters) composed of several hundred individuals (Roverud and Chappell 1991; Willis and Brigham 2007; Gilbert et al. 2010). Being in a huddle brings about significant advantages, both ecological and physiological (Gilbert et al. 2010). We observed huddling in blackcaps during their spring migration in Israel while studying heterothermy in stopover birds, and again in Poland at a simulated stopover during the autumnal migration (Wojciechowski et al. 2008). These observations indicated that huddling affects thermoregulation (Wojciechowski et al. 2008). We found that night-time T_b was almost indistinguishable among individuals in a huddle. Our preliminary data also indicated that huddling blackcaps maintained higher T_b than did solitary birds (Wojciechowski et al. 2008). However, these observations did not allow us to draw solid conclusions about the thermoregulatory and energetic consequences of huddling in small migrating birds, although they were consistent with the findings of Brown and Foster (1992) and McKechnie and Lovegrove (2001) who reported that this behavior facilitated maintenance of normothermia in mousebirds (Coliidae).

In the present study, we report experimental results supporting our hypothesis that huddling is energetically beneficial for small passerines at a stopover site. Prior to our study we predicted that

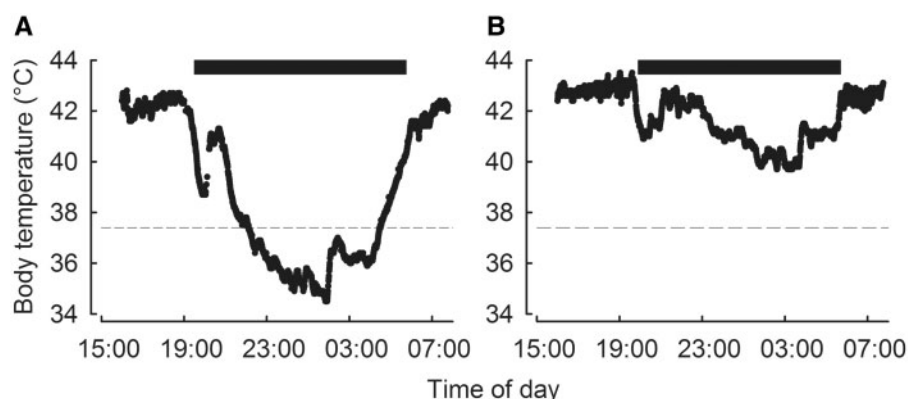


Fig. 1 Examples of body temperature (T_b) recordings of hypothermic (**A**) and normothermic (**B**) blackcaps, *Sylvia atricapilla*, under semi-natural conditions at a stopover in southern Israel. Horizontal dashed line at $T_b = 37.4^\circ\text{C}$ indicates the lower limit of normothermia. The black bar at the top of each graph indicates night. Data from Wojciechowski and Pinshow (2009).

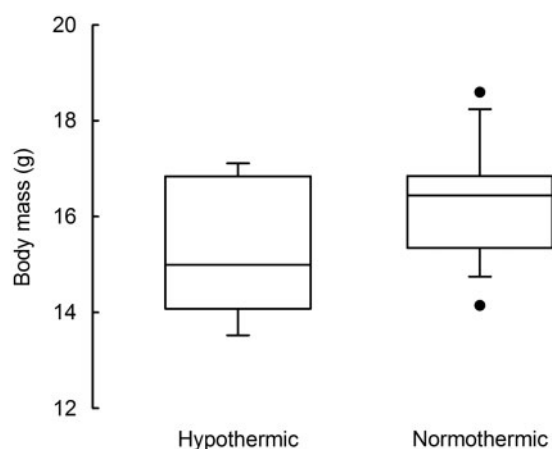


Fig. 2 Body mass of hypothermic ($n = 10$) and normothermic ($n = 22$) blackcaps, *Sylvia atricapilla*, refueling under semi-natural conditions at a stopover in southern Israel. Horizontal lines within boxes indicate medians, boxes cover the 25th to 75th percentiles, whiskers indicate the 10th and 90th percentiles, and dots indicate the 5th and 95th percentiles. Data from Wojciechowski and Pinshow (2009).

huddling blackcaps would (1) maintain a more stable and higher T_b than would solitary birds, but (2) maintain a lower mass-specific metabolic rate (MR/m_b). To test these predictions we measured T_b and MR of blackcaps placed in respirometry chambers overnight solitarily or in groups of three or four at ambient temperatures of 5, 10, and 15°C .

Materials and methods

Animals and experimental procedure

All experimental procedures were approved by the Local Committee for Ethics in Animal Research in Bydgoszcz, Poland and by the General Directorate of Environmental Protection, Poland. We used four

female and three male blackcaps that were caught with mist nets at the beginning of September 2008 in Toruń, Poland ($53^\circ00' \text{N}$; $18^\circ56' \text{E}$). Birds were transferred in cloth bags to the Institute of General and Molecular Biology where they were housed together in a large flight cage ($3.5 \times 2 \times 2 \text{ m}$) containing fresh-leaved natural branches. The seven birds' mean m_b (\bar{m}_b) at the time of capture was $18.11 \pm 1.63 \text{ g}$. For identification purposes birds were ringed with standard colored plastic rings. During the whole study, blackcaps were fed a prepared diet (see Denslow et al. 1987). Water was available to birds *ad libitum*. After one month in the aviary and 6 days before commencing the experiments, we implanted a temperature-sensitive radio transmitter (BD-2, Holohil, Canada; mass = 0.9 g) in the peritoneal cavity of each bird under ketamine (25 mg kg^{-1} ; Narkamon 5%, SPOFA, Czech Republic) and xylazine (10 mg kg^{-1} ; Rometar 2%, SPOFA, Czech Republic) anesthesia. To prevent post-surgical infection we applied an antibiotic (Penicillinum, Polfa S.A., Tarchomin, Poland) to the wound. Prior to implantation, radio-transmitters were calibrated to $\pm 0.1^\circ\text{C}$ in a water bath against a precise mercury-in-glass thermometer. After surgery birds remained indoors for 24 h in individual cages and were then returned to the aviary. Before we began the experiments, we habituated the birds to the respirometry protocol by making several respirometry measurements on each.

Each day, respirometry measurements were started $\sim 1.5 \text{ h}$ before sundown, at $\sim 16:00 \text{ CET}$. Since blackcaps were in migratory disposition and showed migratory restlessness (*Zugunruhe*) at night, we deprived them of food for $\sim 2 \text{ h}$ during the day to reduce their restlessness and facilitate rest during the nocturnal measurements, but we always replaced

food at least 3 h before measurements. Each afternoon we brought birds to the laboratory in individual cloth bags. Birds were weighed (Ohaus Scout Pro 402, USA) to ± 0.1 g before and after experiments. On each experimental night we made measurements on two birds, each placed alone in 2.5-L respirometry chambers, and on three or four birds placed together in a 10-L chamber. Birds were randomly assigned either to a group or for measurement as a solitary individual. All chambers were translucent and equipped with a single perch and were placed in a large temperature-controlled cabinet (INCUDIGIT, Selecta, Spain). Day length in the cabinet matched outdoor conditions. To observe the birds' activity behavior (active or resting, formation of a huddle) we installed a video camera with a night-vision option inside the cabinet. The camera was connected to a monitor in the laboratory and the birds' behavior during the experiment was carefully noted. All experiments were completed within 1 h after sunrise and birds were immediately returned to the aviary where food and water were available *ad libitum*.

Respirometry and body temperature

MR was measured at T_a of 5, 10, and 15°C by indirect calorimetry using an open-flow respirometry system. Air that was scrubbed of CO_2 (with soda lime, Dwory SA, Oświęcim, Poland) and desiccated (with Drierite®, WA Hammond Drierite Co. Ltd, Xenia, OH, USA) was pumped into the respirometry chambers at the rate of 1.3 (small chambers) or 5 L min^{-1} (large chambers). Flow rate was controlled with precise needle valves and measured with a mass flow meter (FlowBar 4, Sable Systems Int., Las Vegas, NV, USA or Cage Supply #1, Columbus Instruments, Columbus, OH, USA) upstream of the respirometry chambers. Air leaving the chambers was subsampled at the rate of ~ 100 mL min^{-1} . Using a computer-controlled multiplexer (MUX-4, Sable Systems Int.), we sequentially selected subsampled gas streams, dried the air with magnesium perchlorate (POCh S.A., Gliwice, Poland) and analyzed the CO_2 and O_2 concentrations using a FoxBox-C integrated CO_2 and O_2 analyzer (Sable Systems Int.). Gases leaving the respirometry chambers were analyzed for 10 min with 1-min reference-readings between animals. Between channel switching, recording was paused for 3 min while the analyzer was flushed with the new gas sample. This setup resulted in air from each animal being sampled every 52 min. Data collection, as well as instrument control, was managed using an analog-to-digital universal interface

(UI-2, Sable Systems Int.) and ExpeData software (Sable Systems Int.). Data were collected by a PC computer at 1 Hz. Air temperature within the respirometry chambers was monitored continuously with type T thermocouples connected to the computer via a thermocouple reading interface (USB-4718, Advantech Europe, Germany). The birds' T_b s were measured to $\pm 0.1^\circ\text{C}$ at ~ 1 min intervals by implanted radio-transmitters. The measurements were recorded with a logging receiver (Lotek model SRX-400 A W21AST with Event_Log® software, Newmarket, Ontario, Canada). During experiments, two transmitters failed and thus we were not able to collect T_b data from all birds (see "Results" section).

Data analysis

Rates of O_2 consumption and CO_2 production were calculated using equations 10.6 and 10.7 from Lighton (2008). Based on the calculated respiratory quotient we estimated the energy equivalent of oxygen (Lighton 2008) and then the birds' expenditure of energy. Because of limitations of the respirometry system we were unable to measure the MR of individual birds within a group. Instead, we estimated the group's mean mass-specific MR and compared this with mass-specific MRs of active and resting individual birds. Since there was no effect of group size on any of the measured variables (one-way ANCOVA with T_a as a covariate $P > 0.05$) we pooled the data from groups of three and four individuals into a single category of grouped birds. Blackcaps were considered hypothermic when their T_b was $< 37.4^\circ\text{C}$ (Wojciechowski and Pinshow 2009). Mean nocturnal T_b (740 data points) and MR (15 data points) were computed for the period from 18:30 CET (1 h after lights-off) to 04:00 (1 h before lights-on).

Statistical analyses were done using the GLM Univariate Analysis module of IBM SPSS Statistics version 19. We defined three basic activities for analysis: active, resting alone, or huddling. To analyze the effect of activity on changes in m_b and T_b , we used a mixed model with bird ID as a random factor and T_a as a covariate. Analysis of T_b data was done two ways: for all birds for which we had T_b data and after excluding two outliers, one in a huddling group, one a solitary bird. To know whether particular birds were more prone to be active or to rest at night, we tested for the interaction between bird activity and bird ID. The effect of activity on MR/m_b was analyzed using a fixed-effect model, with activity as the fixed factor and T_a as a covariate. To compare *post-hoc* mean T_b s between

solitary resting and huddling birds we used Student's *t*-test. Significance was accepted at $P \leq 0.05$. Data are presented as means \pm SD.

Results

Activity

In all cases, birds placed together in one chamber calmed down within the first hour of the experiment and started to huddle immediately after the lights were turned off. During the measurements at 5°C, blackcaps calmed down and started to form a huddle much earlier than they did at 10 or 15°C, even when the lights were still on (Fig. 3). Blackcaps in a huddle remained calm throughout the night except for occasional movements and changes of position relative to one another on the perch. In all cases birds huddled in a line on the perch, touching each other and covering their neighbors with erected contour feathers, very much resembling the huddles we observed on several nights in aviaries (Wojciechowski et al. 2008). Blackcaps that were measured solitarily either spent the night asleep (10 observations: three at 5°C, five at 10°C, and two at 15°C), or displayed migratory restlessness (six observations: three at 5°C, one at 10°C, and two at 15°C). Blackcaps that were sleeping remained so for the whole recording session, while active ones usually were calm at the beginning of the measurement and then began to be active (jumping) in the chamber within 1–2 h after lights-out. Usually they remained active for several hours, calmed down again for a short while, and recommenced activity in short bouts until the morning (Fig. 4). We found no significant interaction between bird activity and bird ID in any of our analyses.

Body mass

Body masses of the experimental birds ranged between 16.1 and 21.6 g ($\bar{m}_b = 18.43 \pm 1.41$ g). We did not find any significant effect of the analyzed factors (individual ID, T_a , or nocturnal activity) on m_b loss during the nocturnal experiments. However, birds that were active at night lost, on average, 3.43 ± 0.48 g, single resting birds lost, on average, 2.64 ± 0.41 g, while birds in huddles lost 2.27 ± 0.46 g (Fig. 5).

Body temperature

We were able to collect T_b data for 22 bird nights for huddling birds, eight for solitary resting birds and four for birds that were active during the night. Mean T_b of most huddling individuals ranged between $37.8 \pm 0.46^\circ\text{C}$ and $39.2 \pm 1.13^\circ\text{C}$, while one

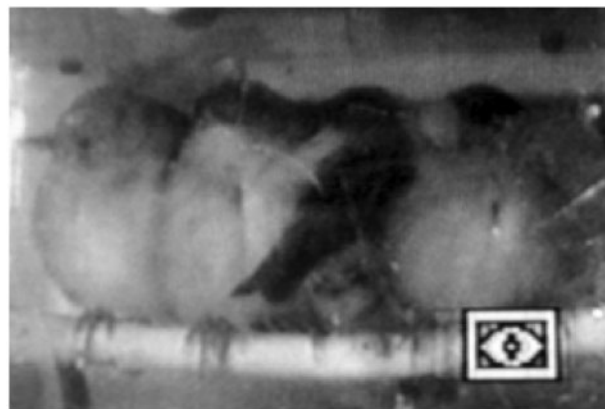


Fig. 3 Photograph of four huddling blackcaps in a respirometry chamber at 5°C.

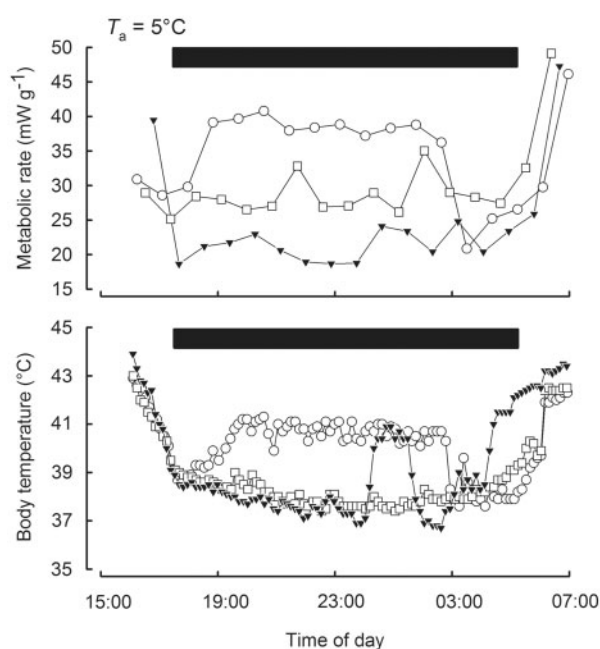


Fig. 4 Mass-specific MR (upper panel) and body temperature (lower panel) of solitary active (open circles), solitary resting (open squares), and one of three huddling (inverted filled triangles) blackcaps, *Sylvia atricapilla*, at 5°C.

individual in the huddle, for unknown reasons, became hypothermic at night and lowered its T_b to $35.4 \pm 1.45^\circ\text{C}$. Body temperature of seven out of eight resting, solitary blackcaps ranged from $37.3 \pm 0.47^\circ\text{C}$ to $38.3 \pm 0.48^\circ\text{C}$. One bird became hypothermic with a night-time mean T_b of $35.5 \pm 1.02^\circ\text{C}$. Body temperature of active birds ranged between $40.1 \pm 0.62^\circ\text{C}$ and $41.7 \pm 0.64^\circ\text{C}$. Analysis of nocturnal T_b of all birds, including outliers showed that it was affected by the birds' activity [$F_{2,20} = 5.005$, $P < 0.05$; Fig. 6] but not by T_a or individual ID. Exclusion of outliers did not change the

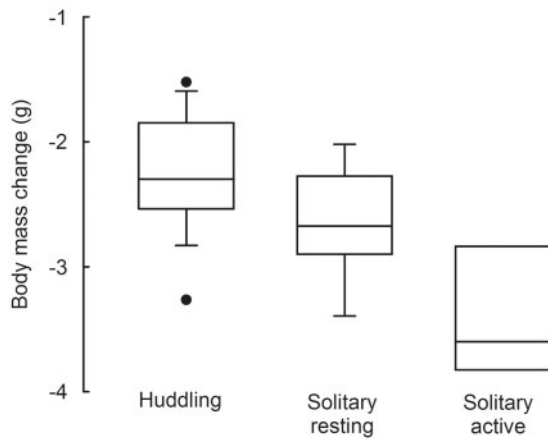


Fig. 5 Changes in body mass of solitary-active ($n=6$), solitary resting ($n=10$) and huddling ($n=28$) blackcaps, *Sylvia atricapilla*, during measurements of MR in chambers at 5, 10, and 15°C, presented as a differences between initial and final body mass. Since there was no effect of T_a , all data were pooled. Horizontal lines within boxes indicate medians, boxes cover the 25th to 75th percentiles, whiskers indicate the 10th and 90th percentiles and dots indicate 5th and 95th percentiles.

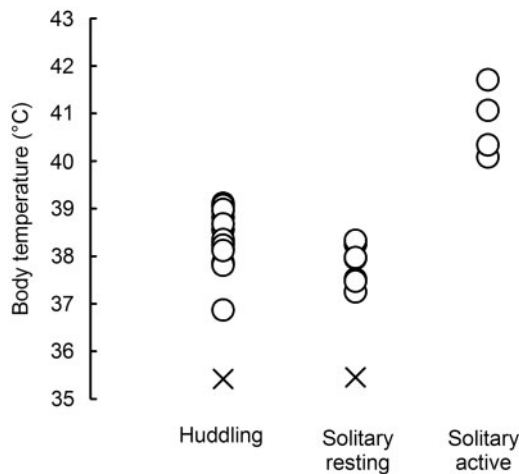


Fig. 6 Mean body temperatures (T_b) of five individual blackcaps, *Sylvia atricapilla*, during measurements of MR in chambers at 5, 10, and 15°C. Since ambient temperature did not affect T_b , all data were pooled. x symbols indicate outliers (see text for explanation). Each symbol represents an individual bird-night ($n=36$; see text for explanation).

above relationship; namely mean nocturnal T_b was affected solely by the birds' activity [$F_{2,18}=7.492$, $P<0.005$; Fig. 6]. Highest mean nocturnal T_b was recorded in active birds ($40.80 \pm 0.74^\circ\text{C}$), moderate in huddling individuals ($38.33 \pm 0.86^\circ\text{C}$ for all birds, $38.46 \pm 0.57^\circ\text{C}$ after excluding outliers) and lowest T_b recorded in solitarily resting individuals ($37.52 \pm 0.92^\circ\text{C}$ for all birds, $37.82 \pm 0.41^\circ\text{C}$ after excluding outliers). Huddling blackcaps maintained

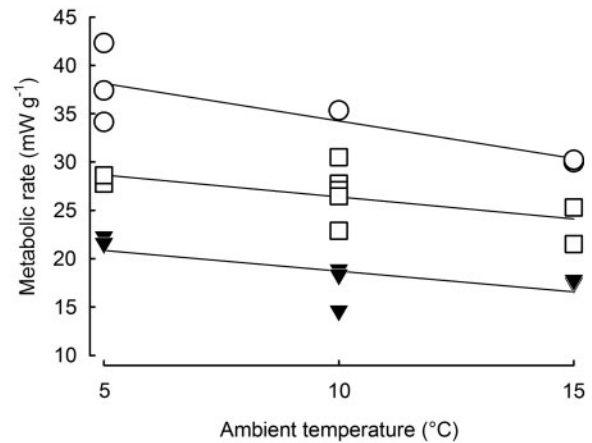


Fig. 7 Mass-specific MR of solitary active (open circles), solitary resting (open squares), and huddling (inverted filled triangles) blackcaps, *Sylvia atricapilla*, at T_a of 5, 10, and 15°C. Lines are for least-squares linear regression equations fitted to the data for each group. Each symbol represents a datum from a single measurement.

higher T_b s than did solitary, resting birds (all birds: $t_{28}=2.222$, $P<0.05$; without outliers: $t_{26}=2.725$, $P<0.05$).

Metabolic rate

We found that both nocturnal activity and T_a affected MR [$F_{2,17}=16.197$, $P<0.001$; $F(1,17)=18.079$, $P<0.001$, respectively] and there was no interaction between these two factors (Fig. 7). Independent of T_a , blackcaps huddling at night spent $\sim 30\%$ less energy than did solitary birds resting at the same T_a ($18.70 \pm 2.59 \text{ mW g}^{-1}$ and $26.61 \pm 2.71 \text{ mW g}^{-1}$, respectively).

Discussion

Our first observations of huddling behavior in migrating blackcaps under semi-natural conditions (Wojciechowski et al. 2008) suggested that this activity may affect the thermoregulation and energetics of small migrating passerines. The present study supports this notion. Huddling blackcaps maintained higher body temperature than did solitary resting birds and at the same time had lower MRs. Both huddling and solitarily resting birds had lower MR and T_b than did birds undergoing migratory restlessness.

Physiological consequences of huddling

We estimated huddling blackcaps to save $\sim 30\%$ of the energy expended by solitary, resting individuals, which is consistent with our previous estimates (Wojciechowski et al. 2008). It also concurs with

the data available for other avian species. By huddling, a group of six white-backed mousebirds (*Colius colius*) reduced their nighttime rest energy costs by as much as 50% (McKechnie and Lovegrove 2001). Huddling in red-billed woodhoopoes (*Phoeniculus purpureus*) in groups of up to five led to energy savings of between 12 and 29% compared to individuals roosting alone (Du Plessis and Williams 1994; Boix-Hinzen and Lovegrove 1998). Similarly, nine gray partridges (*Perdix perdix*) huddling at -30°C reduced their nocturnal expenditure of energy by $\sim 24\%$ (Putala et al. 1995), while huddling pairs of common bushtits (*Psaltiriparus minimus*) saved about one third of the energy spent by solitary birds at 20°C (Chaplin 1982). Probably the best known example of the energetic benefits of huddling is the emperor penguin (*Aptenodytes forsteri*), in which the males incubate eggs during the Antarctic winter in groups of several thousand individuals (Le Maho 1977). Although the energy saved by huddling is moderate ($\sim 16\%$) it is crucial for successful breeding (Pinshow et al. 1976; Ancel et al. 1997).

Surprisingly, we did not find differences in the regression coefficients relating MR/m_b to T_a in blackcaps either when they rested alone or in a huddle. Chaplin (1982) reported similar results for common bushtits. Based on the allometric scaling of MR and heat-loss coefficient with body mass (Calder 1984), one might expect that, with increasing mass of a “body” of blackcaps, namely a solitary blackcap versus a huddle, the regression coefficient would be lower for the huddling birds, as was found in speckled mousebirds (Brown and Foster 1992). The slope of the relationship between MR/m_b versus T_a for a four-mousebird huddle was significantly lower than for individual resting birds (Brown and Foster 1992). A possible explanation for this phenomenon may be the shape of the huddle, namely linear in blackcaps and bushtits, and spherical in mousebirds. The latter huddle configuration results in a larger reduction of surface area in contact with the air per individual bird. Consequently collective heat loss per unit huddle surface area is lower than that of an individual and energy expenditure is lower per individual in the huddle, especially at low T_a .

Previously, we observed huddling in normothermic or hypothermic blackcaps (Wojciechowski et al. 2008). Since huddling leads to a decrease in surface to volume ratio (Schmidt-Nielsen 1997) and reduces energy expenditure in normothermic animals, we suggest that this activity has potential for increasing energy savings in hypothermic birds. By entering rest-phase hypothermia and reducing the

$T_b - T_a$ gradient, small migrants may accelerate refueling in the initial stages of a stopover (Wojciechowski and Pinshow 2009). This may lead to overall shortening of the time spent at the stopover and reduction in the total time of migration. However, it seems that reduction of T_b does not play an important role in the later phases of gain in m_b . Just as we found in blackcaps heavier than $\sim 16\text{g}$, minimum nocturnal T_b was not related to m_b (Wojciechowski and Pinshow 2009). Our present results indicate that huddling brings about similar savings in energy as does hypothermia for individually resting birds (Wojciechowski and Pinshow 2009). Also, most hypothermic blackcaps were measured alone. In huddles of three or four individuals, only one bird became hypothermic, while the others remained normothermic. In other words, we found that huddling blackcaps maintained higher T_b than did solitary birds. Based on similar observations Brown and Foster (1992) and McKechnie and Lovegrove (2001) concluded that huddling not only results in significant savings of energy, but also facilitates the maintenance of high, stable T_b that is impossible for a solitary roosting mousebird to maintain.

Huddling behavior is also important for maintaining homeothermy in passerine chicks despite their lack of well-developed mechanisms of heat production (Clark and Balda 1981, Ricklefs 1989). This is also true for mammalian neonates (Alberts 1978; Haim et al. 1992; Gilbert et al. 2007), and naked mole rats that are unable to maintain homeothermy while solitary (Yahav and Buffenstein 1991). Huddling affects T_b regulation not only of normothermic but also of torpid animals, thereby allowing for higher T_b during torpor (Arnold 1988, Jefimov et al. 2011), or for the maintenance of high T_b , e.g., in huddling skunks (*Mephitis mephitis*) which use torpor when resting alone (Hwang et al. 2007).

Another possible benefit of huddling is less m_b loss (Hatchwell et al. 2009). It may be of particular importance for birds arriving at a stopover site with low energy reserves. In the present study birds were not deprived of food, and huddling provided sufficient savings of energy without the necessity of lowering T_b . This solution would be beneficial because higher T_b at night means a lower cost of rewarming to daytime, normothermic T_b .

Ecological consequences of huddling

From both the energetic and thermoregulatory points of view, huddling has significant ecological consequences for small migrating birds. Since

huddling may facilitate normothermia in resting blackcaps, in addition to the obvious benefit of conserving energy, it may also lessen the eventual ecological costs of hypothermia. By definition hypothermia is associated with lowered T_b that, in turn, may reduce vigilance, mobility and responsiveness of an individual, thereby leading to increased risk of predation (Choi et al. 1998, Humphries et al. 2003). Drieschke (2003) found that small passerines of m_b within the lightest 20% of the population at a migratory stopover were the most frequent prey of feral cats and raptors. Although this finding may have an alternative explanation, which is the ecological cost of the risky feeding behavior employed by lean birds (Piersma and van Gils 2011), one cannot exclude a physiological explanation. Hypothermic birds with low energy reserves are likely less responsive and would become an easier prey at migratory stopovers. Hence, huddling, through facilitation of normothermia would save energy while the birds remain responsive and so are less likely to fall prey to predators. Since huddling, in its own right, might also result in lower predation risk for an individual (Gilbert et al. 2010), this activity may be the strategy of choice for small migrating passerines at a stopover site.

Our data indicate that huddling may be an important strategy for small passerines refueling at stopover sites. However, to the best of our knowledge, except for blackcaps (Wojciechowski et al. 2008 and present study), only anecdotal information exists on huddling behavior in small migrating passerines during stopovers (Frazier and Nolan 1959). On the one hand, available data suggest that nocturnal migrants, like small passerines, usually fly singly (Gauthreaux 1972; Bruderer 1997) and therefore have limited opportunity for finding huddling partners at a stopover site. On the other hand, scarce stopover sites along the migration route may attract birds, resulting in high fidelity to these sites (Lavee and Safriel 1989; Lavee et al. 1991; Cantos and Tellería 1994).

To conclude, since food-rich habitats are attractive to migrating birds (e.g., Shochat et al. 2002), and since birds in poor body condition may congregate at food-rich patches within a stopover area (Tietz and Johnson 2007), we assume that stopover sites create opportunities for huddling in small passerines. In this light, we hypothesize that huddling occurs frequently (or more frequently than previously thought) in nature, leading to significant savings of energy, faster accumulation of fuel, lower risk of becoming a prey, more successful migration, and eventually increased fitness.

Acknowledgments

We thank Dr. Grzegorz Neubauer for his comments on the article and Dr. Jarosław Kobak for his statistical advice. Division of Comparative Physiology and Biochemistry and Division of Ecology and Evolution of the Society for Integrative and Comparative Biology and Sable Systems Int. are acknowledged for their help in organizing and funding the symposium: "Environment, Energetics, and Fitness: A Symposium Honoring Donald W. Thomas." This is publication 733 of the Mitrani Department of Desert Ecology.

Funding

The Polish Ministry of Science and Higher Education (N304 048 31/1811). While writing this article, M.S.W. and M.J. were supported by the Ministry of Science and Higher Education (3475/B/P01/2008/35) and (N N304 168739).

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