# Hypothermic abilities of migratory songbirds at a stopover site

**Claudio Carere · David Costantini · Leonida Fusani · Enrico Alleva · Massimiliano Cardinale**

**Abstract** Migratory birds use stopover sites for resting and feeding. Breaks after prolonged flights may allow cooling down the muscles and save energy through hypothermia. We measured hypothermic abilities in two long-distance migratory songbirds (garden warbler, *Sylvia borin*, and icterine warbler, *Hippolais polyglotta*) at a stopover site during spring migration selecting (1) birds just arrived after a prolonged flight (morning) (2) birds that had been resting in the vegetation for several hours (afternoon) and (3) birds caught in the late afternoon and kept overnight in standard conditions (night). In the first two samples, body temperature was measured immediately, 30 and 180 min after capture. In the night sample, it was measured at 1 a.m. in birds awake and asleep, and at 7 a.m., when all birds were awake. Morning birds showed the highest values (39.7°C), dropping of about 3°C after 180 min. In the afternoon birds (2), the time course was similar, but values (38.5°C) were lower than that of morning birds of about 1°C. At night, asleep birds had lower temperature than awake birds, reaching up to 10°C less than daytime values, but recovering in the early morning. Such remarkable plasticity in thermogenic abilities during migration could allow small migrants to economize energy in emergency situations.

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## 1 Introduction

Bird migration imposes a number of physiological and energetic challenges upon sustained
flight efforts and prolonged fasting (Gwinner 1990; McWilliams et al. 2004). To fuel long-
term flights, birds derive energy from fat and protein stores accumulated in the pre-
migratory phase as well as at certain stopover sites between prolonged flights (Pilastro and
Spina 1997; Berthold 2001). They can perform long and uninterrupted flights especially
when crossing ecological barriers, as in the case of Western Palearctic migrants that cross
the Sahara and the Mediterranean in order to move between their wintering and breeding
areas (Pilastro et al. 1998). Stopover sites are used for resting and/or feeding. External
factors such as weather conditions, predation risk and food availability, and internal factors
such as energy reserves and endogenous programs influence the decision of staying at or
leaving a stopover site (Jenni and Schaub 2003; Fusani et al. 2009).

To cope with periods of fasting two non-mutually exclusive strategies can be adopted: (1)
accumulation of large energy reserves (Klaassen and Biebach 1994; Klaassen et al. 1997), (2)
economization of resources by strategic reduction of energy expenditure (Biebach 1977;
Graf et al. 1989; Schleucher 2001). While birds of large size and good flight performance,
such as geese or shorebirds, use stopover sites primarily for feeding, thus compensating the
energy budget by increasing energy reserves and thermogenic abilities (Butler and Woakes
2001; Vézina et al. 2007), small passerines, which are usually nocturnal migrants, may use
them mainly for resting and saving energy by diurnal and/or nocturnal hypothermia. In fact,
one mechanism of energy saving, known both in nestlings and adults of some avian species in
certain situations is down-regulation of body temperature ($T_b$) (Biebach 1977; Graf et al.
1989; Schleucher 2001, 2004; McKechnie and Lovegrove 2002).

In birds, $T_b$ is higher than in mammals. It decreases with increasing body mass, and is
affected by resting phase, circannual variations, and sex. Mean levels for resting and active
phase are 38.54 ± 0.96 and 41.02 ± 1.29°C (Prinzinger et al. 1991). Both controlled
hypothermia (spontaneous decrease of $T_b$ between 35 and 25°C with maintained respon-
siveness to external stimuli) and torpor (a regulated lethargic state leading $T_b$ to 18–20°C)
have been documented in birds (Prinzinger et al. 1991). In standard conditions, $T_b$ reaches the
highest values in the afternoon and the lowest values at night, between 0200 and 0400 hours
(dove, Rashotte et al. 1995; sparrow, Binkley et al. 1971; zebra finch, Langman 1973). $T_b$
reductions below normothermic levels during the rest phase have been documented in
several avian taxa (Biebach 1977; Graf et al. 1989; Schleucher 2001; Vézina et al. 2007). It
has been also observed that reductions in $T_b$ can be associated with reductions in metabolic
rates (Daan et al. 1989; Rashotte et al. 1995). Small passerines are able to reduce metabolic
costs to save energy after increased workload (Deerenberg et al. 1998). Therefore, a hypo-
thermic state could help small migrating birds save energy after prolonged flight.

In this study, we describe the ability of two species of small migratory birds to achieve
hypothermic states. Empirical evidence for hypothermia in the context of bird migration in
small birds is mainly anecdotal. Bird ringers and ornithologists that carry out ringing
activity by mist-nets in small Mediterranean islands during spring migration (Spina et al.
1993) often report that during the bulk of migration they can distinguish "warm" and
"cold" individuals just by handling them during the catching and ringing procedures.
Experimental support for these observations comes from recent data obtained with skin

temperature loggers in blackcaps (*Sylvia atricapilla*) at a spring stopover site, which indicated marked hypothermia especially at night (Wojciechowski and Pinshow 2009). According to the "adaptive hypothermia hypothesis" (Koskimies 1948; Daan et al. 1989; Bize et al. 2007), cooling the body temporarily up to certain physiological limits could reduce metabolism and save energy. We therefore predicted that small passerines facing prolonged nocturnal flights might display rapid hypothermic responses at stopover sites, similar to those induced by experimental or natural fasting.

We specifically studied the inter- and intra-individual variability of avian $T_b$ by conducting systematic measurements in two common species of warblers at a stopover site, a Mediterranean island, during spring migration from Africa to Europe. We sampled individuals just arrived after a long flight, individuals that rested for some hours and individuals kept overnight. We predicted that birds just arrived should display the highest values or be even hyperthermic, while birds already resting from several hours and especially at night should substantially decrease their $T_b$ below normal resting levels. We have also aimed to study intra-individual variation in $T_b$ across time and thereby performed within-subjects measurements.

## 2 Materials and methods

### 2.1 Studied species

Garden warblers (*Sylvia borin*, 14–18 g) and Icterine warblers (*Hippolais polyglotta*, 10–14 g, see also Table 2) are long-distance migratory songbirds inhabiting woods and parks of central and northern Europe. In particular, the garden warbler (GW) is a well-known species in studies of migration ecology and physiology (Gwinner et al. 1985, 1988; Klaassen and Biebach 1994; Totzke et al. 1999, 2000). The winter grounds of this species are located in trans-Saharan Africa and one major pathway of migration towards Europe involves crossing the Mediterranean Sea (Grattarola et al. 1999). Seasonal fattening in GW is regulated by a circannual clock and is due to premigratory hyperphagia, to increased food utilization efficiency and to a dietary shift including several metabolic adjustments such as a lower glucose utilization rate (Bairlein 1985; Totzke et al. 1999, 2000). Both species are nocturnal migrants, being normally active during daytime, but performing migratory flights mainly at night. The physiological mechanisms underlying this transition are basically unknown, although the pineal hormone melatonin is a likely candidate for a role in this adaptation (Fusani and Gwinner 2005). Icterine warblers (IW) have not been studied specifically, though this is one of the most common species along the African–Europe migratory pathway (Spina et al. 1993; Pilastro et al. 1998).

### 2.2 Study area, sampling procedure and data collection

The study was carried out in Ponza, an island (9.87 Km$^2$) about 50 km off the Tyrrhenian coast of Italy (40° 50′ N, 12° 58′ E) during the bulk of spring migration. Birds were trapped by mist-nets, which are continuously monitored during the ringing period. The low number of recaptures (less than 5% of trapped birds, M. Cardinale personal observation across five seasons of ringing activities) at Ponza, as well as a recent radio-tracking study on GW indicate that most birds have spent a only a few hours and at maximum one night after a non-stop flight (Goymann et al. 2010). In particular, massive arrivals are concentrated in the mid-late morning (Fig. 1). Arriving birds can be observed by eye literally falling from the sky.
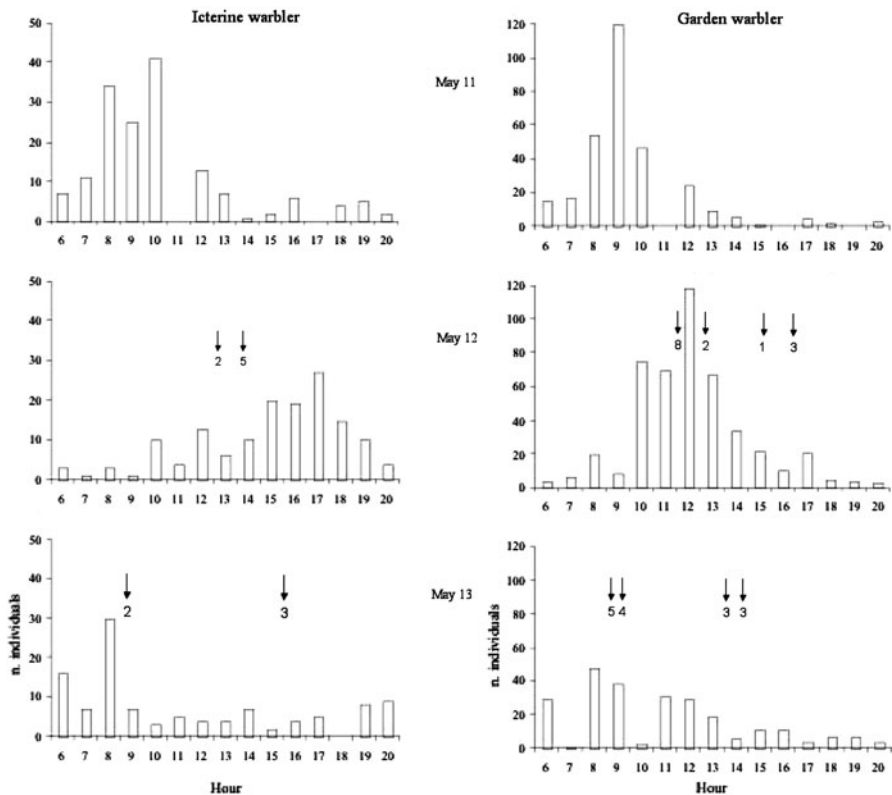
**Fig. 1** Daily patterns of capture (frequency per hour) on the days of sampling and on the previous day. The *arrows* indicate the time of capture of the sampled birds and the *numbers* indicate how many individuals were sampled for the $T_b$ daily measurements. All individuals kept overnight for the nocturnal measurements were captured at the last check of the nets before darkness (19:00) on May 12 (3 garden warblers and 5 icterine warblers) and May 13 (5 garden warblers and 6 icterine warblers)

In the morning, we waited hidden in proximity of the mist-nets located in the upper side of the ringing station where migrant birds land. We recorded (always within 3 min including a variable latency time to remove the bird from the net) only those birds that flew from high height on the upper part of the net and never flying from low height or bushes in its proximity. Therefore, the values of the morning birds should mirror the physiological status of birds that just incurred a long flight. In the afternoon, though there was no sign of clear arrivals, we only measured (always within 3 min) sampled those birds that fell in the net moving among bushes in the lower side of the ringing station. Estimates done on the neighboring Ventotene island suggest that birds had completed a 14–16 h non-stop flight with part of the final route during the day (Pilastro et al. 1995; Grattarola et al. 1999; Schwilch et al. 2002a) and that it is unlikely that refueling had taken place in North Africa, at least for GW (Grattarola et al. 1999). After the last temperature measurement, birds were ringed, weighed (0.1 g) with an electronic balance and their wing (0.5 mm) and tarsus (0.5 mm) length were measured and immediately released. This occurred 3 h upon capture for the birds sampled for daytime temperature measurements and about 12 h upon capture for the birds sampled for the

nocturnal temperature measurements. The sex of both species is undeterminable because of the lack of morphological dimorphism (Svensson 1992).

Further, fat and muscle scores were recorded. These represent two classic scores taken by bird ringers and showing high repeatability (Jenni et al. 2000). The fat score is determined by checking the visible amount of subcutaneous fat deposits between the furcula and on the abdomen (9 level score). These scores correlate well with the amount of fat extracted from whole birds (Kaiser 1993; Jenni et al. 2000). Instead, muscle scores quantify the thickness of the breast muscle (4 level score: e.g. 0 = breast muscle emaciated and its cross section shaped concavely; 3 = breast muscle bulging and shaped convexly (Kaiser 1993). Muscle scores represent an estimate of breast muscle protein mass and vary from 0 to 3 (Jenni et al. 2000).

$T_b$ was recorded on two consecutive days (May 12th and 13th, 2006) both characterized by stable and good weather conditions (atmospheric pressure: 1,011 and 1,012 mbar) in three different groups of birds (total sample: 37 GW, and 23 IW): (1) birds just arrived, morning; (2) birds that had been resting in the vegetation for several hours, afternoon; (3) birds caught in the late afternoon and kept in cotton bags for night measurements (only one night). In the first two groups, $T_b$ was measured at three time points, within 3 min ($T_0$), after 30 min ($T_1$), and at 180 min from capture ($T_2$). After $T_2$ measurement birds were subjected to morphological measurements (see above), ringed and released. In the third group, ringing and morphological measurements were taken immediately after capture, while $T_b$ was measured at 1 a.m., when we could distinguish between birds awake and birds asleep, and at 7 a.m. Birds were then immediately released. During the interval times, birds were kept in cotton bags in a calm room at ambient light and temperature and without food or water. During the sampling period, ambient temperature ranged from 24°C (daytime) to 15°C (night).

$T_b$ was measured with a thin flexible probe (about 0.5 mm Ø) connected to an analog thermometer (Physitemp Instruments Inc Model Bat 12, serial N 11187, 0.1°C resolution). The probe was inserted via the beak in the throat for 3 cm (Carere et al. 2001; Carere and van Oers 2004). For the night measurements, it was first kept in warm water (about 30°C). It took approximately 10–15 s until the value on the display became stable.

## 2.3 Data analysis

Variances were homogeneous. General linear models (GLMs) with repeated measures with group (morning; afternoon), species and day (only for the diurnal measurements) as between subjects factors were used to evaluate which variable contributed to the observed variation in $T_b$. Body condition, obtained as residuals of a regression of body mass on tarsus for the two species separately, was used as covariate. We run two separate analysis, one for the daily measurements (A) and one for the night measurements (B), in which day was not considered and the between subjects factors were species and "status" (awake vs. asleep). In both cases, after running a full model we eliminated non-significant interactions among factors. Multiple comparisons between logical sets of means were performed by Tukey test for unequal sample size for both species. The other data comparing the morning, afternoon and evening samples were analyzed by Mann–Whitney (fat and muscle scores) and by Fisher's exact test following ANOVA (body mass, and $T_b$). General linear models (GLMs) were performed with the STATISTICA package (Version 7.0, StatSoft, Inc. 2004, Tulsa, OK, USA), while the other statistics were performed with Statview.

**Table 1** Outcomes of the GLMs

| Source of variation | $F$ | $df$ | $P$ value |
|---|---|---|---|
| Day measurements | | | |
| Species | 3.80 | 1.32 | 0.06 |
| Sampling day | 3.20 | 1.32 | 0.08 |
| Morning/afternoon (M/A) | 18.10 | 1.32 | *<0.001* |
| Body condition | 1.50 | 1.32 | 0.23 |
| Sampling day × M/A | 5.20 | 1.32 | 0.03 |
| RM | 145.4 | 2.64 | *<0.001* |
| RM × Species | 0.10 | 2.64 | 0.93 |
| RM × Sampling day | 5.00 | 2.64 | *0.01* |
| RM × M/A | 0.0 | 2.64 | 0.99 |
| RM × Body condition | 0.1 | 2.64 | 0.91 |
| RM × Sampling day × M/A | 4.80 | 2.64 | 0.01 |
| Night measurements | | | |
| Species | 4.15 | 1.15 | 0.059 |
| Awake/Asleep (A/S) | 22.81 | 1.15 | *<0.001* |
| Body condition | 0.51 | 1.15 | 0.48 |
| RM | 108.8 | 1.15 | *<0.001* |
| RM × Species | 0.84 | 1.15 | 0.37 |
| RM × A/S | 41.75 | 1.15 | *<0.001* |
| RM × Body condition | 1.50 | 1.15 | 0.24 |

Significant $P$ values are shown in italics

*RM* repeated measures, *BC* body condition (obtained as residuals of a regression of body mass on tarsus)

## 3 Results

The statistical outcome for day and night measurements is reported in Table 1. In morning birds, $T_b$ did not differ between $t_0$ and $t_1$, but fell of more than 3°C at $t_2$ (Tukey posthocs $t_0$ vs. $t_2$ and $t_1$ vs. $t_2$ both $Ps < 0.001$ in both species, Fig. 2). In afternoon birds, the time course and the drop in $T_b$ was similar (Fig. 2); however, in afternoon birds $T_b$ was overall significantly lower compared to morning birds of about 1°C (Fig. 2). No species effect or interaction of species with other factors emerged. Body condition and day did not significantly explain the observed variance.

Asleep birds had lower $T_b$ than awake birds (31.4 vs. 36.0°C in GW; 29.1 vs. 34.9°C in IW, Fig. 2). The significant interaction between status and repeated measures, indicates that during the morning this difference almost disappeared. The patterns were similar in both species, but GW tended to display higher values than IW (Table 1).

In GW, the comparison of body mass, $T_b$, muscle score and fat score between the three groups (considering for $T_b$ the first measure in $T_0$ and the night measure and pooling awake and asleep individuals, Table 2) indicates that morning birds were heavier than evening GW by about 1.1 g ($F_{2,33} = 2.9$; $P = 0.07$; Fisher's PLSD $P = 0.04$), while their $T_b$ was higher than both $T_b$ of afternoon and night birds ($F_{2,33} = 54.3$, $P < 0.0001$; Fisher's PLSDs $Ps < 0.03$). Morning birds had muscle and fat scores higher than evening birds (muscle $z = -2.6$, $P = 0.009$; fat $z = -2.0$, $P = 0.04$). However, morning birds did not differ from afternoon birds in both parameters (ps > 0.42). Afternoon birds had higher muscle but not fat scores than evening birds (muscle $z = -2.2$, $P = 0.03$; $z = -1.3$, fat, $P = 0.18$). In IW, body mass did not significantly differ between the groups ($F_{2,19} = 0.98$, $P = 0.39$, Table 2). In morning birds, $T_b$ was higher than in evening birds, but not than
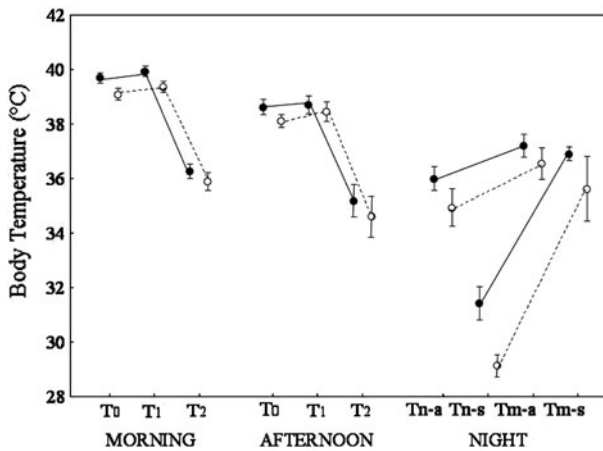
**Fig. 2** Body temperature in garden warblers (*black dots*) and icterine warblers (*white dots*) in three independent samples. The morning ($N = 19$ garden warblers; 4 icterine warblers) and afternoon ($N = 11$ garden warblers; 8 icterine warblers) samples have been recorded on two consecutive days characterized by massive arrivals of both species, while the night sample ($N = 4$ awake and 4 asleep garden warblers; 7 awake and 4 asleep icterine warblers) during the night in between them. $T_0$ three min from capture, $T_1$ 30 min after capture, $T_2$ 180 min after capture, $T_n$, night measurement (1 a.m.); $T$ = early morning measurement (7 a.m., all birds awake). *a* awake; *s* asleep. Mean ± s.e.m. are shown. See Table 2 for comparison across the three groups

afternoon birds, while evening birds had lower $T_b$ than afternoon birds ($F_{2,19} = 13.3$; $P < 0.0002$; Fisher's PLSDs morning vs. evening $P < 0.0005$; night vs. afternoon $P < 0.0005$). Morning IW had muscle but not fat scores higher than evening IW (muscle $z = -2.3$, $P = 0.02$; fat $z = -1.4$, $P = 0.17$). However, morning birds had higher fat, but not muscle score than afternoon birds (muscle $z = -1.1$, $P = 0.25$; fat $z = -2.0$, $P = 0.04$). Afternoon birds did not significantly differ from night birds (muscle $z = -1.6$, $P = 0.10$; fat $z = -1.3$; $P = 0.20$).

## 4 Discussion

Morning birds, just arrived upon a prolonged flight were normothermic. Upon capture, they decreased $T_b$ within 3 h. Afternoon birds showed a similar time course, but had overall lower values than birds just arrived. Birds kept overnight showed a more marked hypothermic state with a strong recovery in the early morning. The pattern was similar in both species suggesting an ability to achieve hypothermia during stopovers between long migratory flights. The lower temperature of afternoon birds could be due to an excess heat load from the strenuous work of long-distance flying as morning birds presumably have just arrived from a long flight. A possibility is that birds just tend to be sleepy during the day after prolonged flights thus showing values close to resting levels (Schwilch et al. 2002b).

Our data may be not representative of what happens in free ranging individuals. The observed $T_b$ reductions could be due to handling and restraint stress, however, known to elicit a rise in $T_b$ in passerine birds within at least 5 min (Carere and van Oers 2004), as well as to reduced energy intake. We took care to measure $T_b$ within 3 min after a bird felt in the net and a decreasing trend was found after 30 min of restraint in the bags. Moreover,

**Table 2** Fat scores, muscle scores (median and range), body mass and body temperature ($T_0$ morning and afternoon, $T_n$ night, mean ± s.e.m.) in the three sampled groups

| Species | Morning | | | | | Afternoon | | | | | Night | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Fat | Muscle | Weight | Body T | N | Fat | Muscle | Weight | Body T | N | Fat | Muscle | Weight | Body T | N |
| GW | 2 (med) 3 (range) | 2 (med) 1 (range) | 15.7 ± 0.3 | 39.7 ± 0.2 | 19 | 0.5 (med) 3 (range) | 2 (med) 1 (range) | 14.6 ± 0.5 | 38.5 ± 0.2 | 10 | 0 (med) 2 (range) | 1 (med) 2 (range) | 14.7 ± 0.5 | 33.7 ± 0.9 | 8 |
| IW | 1.5 (med) 3 (range) | 2 (med) 0 (range) | 12.0 ± 0.3 | 39.1 ± 0.2 | 4 | 0 (med) 0 (range) | 2 (med) 1 (range) | 11.1 ± 0.1 | 38.1 ± 0.2 | 8 | 0 (med) 2 (range) | 1 (med) 2 (range) | 11.4 ± 0.4 | 33.4 ± 1.0 | 11 |

See Sect. 3 for statistically significant values

latency to the first measurement (morning and afternoon group ranging between 39 and 121 s, average ± s.d. 90.0 ± 33.6 s, mode 88 s, median 87 s) initially taken into account as covariate in the analysis, did not contribute significantly and was removed from the model. It could be that the stress of staying in the bag for a longer period gives rise to a hypothermic, "emergency" response, explaining the decrease found after 3 h during daytime. However, night birds after the hypothermia showed a marked recovery between the lowest values at 0100 hours and the values at 0700 hours while being in the bags (Fig. 2). We cannot exclude that being restrained could have enhanced the hypothermic response, especially during daytime when the procedure could simulate a fasting period of 3 h. Nevertheless, 3 h without feeding possibility after a prolonged flight of many hours may be of little relevance. A bird with some fat reserve, as most in our sample, is still capable to metabolize it to produce ATP without necessity to feed. The mitochondria produce from a fat molecule four times more ATP than from a glucose molecule that birds could obtain in these islands feeding on nectar (Schwilch et al. 2001). A comparison of $T_b$ variation between fat and lean individuals maintained on diets different in terms of content in lipids and carbohydrates could help clarify the mechanisms underlying the observed hypothermia.

It would be interesting to investigate whether the same species show hypothermia when not migrating and whether short-distance migrants or resident species show hypothermic responses such those observed. Great tits (*Parus major*), a resident passerine of similar size, did not show any hypothermia during night in captivity conditions (active phase 40–41.5°C; night 38–38.5, Carere and van Oers 2004). Similarly, zebra finches (*Taeniopygia guttata*) and rosy finches (*Leucosticte arctoa*) kept in standard conditions and monitored with transmitters did not reach more than 2°C below daily levels at night (Langman 1973; Clemens 1989).

Zebra finches overcompensated for the increased energetic demands of activity and nocturnal energy expenditure was reduced upon experimentally elevated diurnal workload by a reduction in resting metabolic rate suggesting an extension of nocturnal compensation into inactive hours of the day (Deerenberg et al. 1998). Small sized migrants may use similar strategies after nocturnal flights, comparable to an extreme workload, and may downregulate $T_b$ further in the following night(s). Migrants could increase their energy intake as well, however, such islands may not provide sufficient resources. Furthermore, small passerines have substantially reduced digestive tract during long-distance migration and their digestive capacity is reduced (Klaassen and Biebach 1994; Klaassen et al. 1997). It is likely that birds deciding to stop at the island are borderline in terms of energy budget. In our sample, most birds had low scores of fat and muscle and we did not find any significant correlation between $T_b$ and body mass, fat or muscle score. Most birds were lean and with low fat and muscle scores. However, morning birds appeared in better condition than afternoon and evening birds (Table 2). It could be that (1) birds rapidly deplete their residual energy stores in few hours; (2) afternoon and evening birds are those in worse condition since the others move away soon. In this latter case, in the afternoon and evening rounds we may have progressively selected only lean birds, those more likely to go in hypothermia and deciding not to leave on the evening following their arrival. On the same island, we have recently shown that birds displaying nocturnal restlessness are those in better condition that would have probably left if not kept in the experimental cages (Fusani et al. 2009; Goymann et al. 2010).

It has been postulated that the adrenocortical stress response in migrants can be suppressed because the bird does not benefit from an emergency state during migration (Ramenofsky et al. 1995). Indeed, it was found that handling stress did not elicit an

increase in corticosterone in lean birds in the neighboring Ventotene island (Jenni et al. 2000). Lean migrants may inhibit the adrenal response to a stressor because there is apparently no advantage in redirecting their behavior from landing and refueling (Jenni et al. 2000). In rodents, rises in $T_b$ are accompanied by increases of plasma corticosterone and lipopolysaccharide-induced fever also elevates the amount of biologically available corticosterone (Groenink et al. 1994; Cabrera et al. 2000). Assuming that corticosterone could increase $T_b$ in birds, it is possible that birds maintain a low corticosterone reactivity to facilitate hypothermia and hence to save energy.

Migratory birds can rapidly display temporary hypothermia achieving a drop in basal metabolic rate (Schleucher 2001; McKechnie and Lovegrove 2002) and by extension in energy consumption, and to reverse it, a clear sign of phenotypic, environmentally induced plasticity. A reduction of about 4°C may allow to lower the metabolic rate and energy consumption by up to more than 50% (McKechnie and Lovegrove 2002). At night, we found levels that bring some individuals close to torpor, a phenomenon known to occur in offspring of some species, such as swifts, when parents are not provisioning the food (Koskimies 1948; Barklay et al. 2001; Bize et al. 2007). Serendipitous observations in a hummingbird suggested that birds can use torpor to conserve energy stored for later use on migration (Carpenter and Hixon 1988). More recent radio-telemetric observations on six migratory blackcaps show prolonged nocturnal drops in skin temperature to an average of 35.3°C and minimum peaks of 31.3°C (Wojciechowski and Pinshow 2009), which are in line with our data.

Since a migratory flight brings atrophy of muscles and other organs potentially involved in thermogenesis (Klaassen and Biebach 1994; Klaassen et al. 1997), the deviations from normothermy observed in those and our study could also be associated with decreased capacity for thermoregulatory heat production due to reduced organ size. The temperatures of sleeping birds at night were very low, which is consistent with saving energy during migration. Hypothermia could also have additional beneficial effects beyond that of conserving energy for the next flight. For example, hyperthermic states can be associated with increased levels of oxidative stress (Lin et al. 2006). In Ponza, we have previously found that lean birds have less plasma antioxidant capacity than fat birds (Costantini et al. 2007). Therefore, lean birds could also benefit to enter a hypothermic state because they have less antioxidants than fat birds to use to cope with oxidative stress.

The hormone melatonin, which is involved in the control of bird migration (Fusani and Gwinner 2005), is also involved in thermoregulatory processes (Saarela and Reiter 1993), can work as an antioxidant (Poeggeler et al. 1993) and affect synthesis of antioxidant enzymes (Acuna-Castroviejo et al. 2007). We suggest that future studies should look at the role that the melatonin plays in the intricate links among zugunrhue, oxidative stress, regulation of $T_b$ and body energy reserves.

In conclusion our study suggests the occurrence of hypothermia in two migratory passerines. Our data also suggest that the fat reserves could predict the ability of an individual bird to enter a hypothermic state. These thermogenic abilities during migration could allow small migrants, lean individuals in particular, to economize energy in emergency situations.

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