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Thermal history can affect the short-term thermal acclimation of basal metabolic rate in the passerine *Zonotrichia capensis*

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ABSTRACT

The obligatory cost of living for endotherms is measured by basal metabolic rate (BMR), a variable that is known to change after thermal acclimation. However, the relative timing between variation in ambient temperature and BMR is not well understood. In this study, we addressed this problem in the sparrow *Zonotrichia capensis*, studying whether previous thermal history affects the response of BMR to a new acclimation temperature. We found that after 4 weeks of acclimation either to 30 or 15 °C birds exhibited significant differences in BMR from pre-acclimation levels. Nevertheless, after a re-acclimation to the opposite treatment for six additional weeks, in the group previously acclimated to warm conditions the change in BMR was significantly greater than in the group previously acclimated to cold. We also found differences in the mass of the small intestine between groups but constancy in the mass of liver, kidney and heart masses at the end of the experiments. Our results indicate that the thermal history affects metabolic adjustments and highlights the importance of considering this when evaluating the plasticity of metabolic traits in small birds.

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1. Introduction

Basal metabolic rate, i.e., the metabolic rate measured in post-absorptive adults within their thermoneutral zone and during inactivity, is the standard metric of the energy cost of maintenance in endothermic animals, and is commonly used for comparing energy demands among individuals, populations, and species (Speakman et al., 1993). Although the evidence for the relationship between BMR and fitness remains elusive (Hayes and O'Connor, 1999; Boratinsky and Koteja, 2009), several comparative studies suggest that evolutionary adjustments have occurred in BMR in birds and mammals. In fact, the most important environmental factors explaining changes in BMR have been associated with temperature, primary productivity, rainfall, migration and diet (Weathers, 1979; Withers and Williams, 1990; Hinsley et al., 1993; Tieleman and Williams, 1999; Tieleman et al., 2002; Cavieres and Sabat, 2008; White et al., 2007; Jetz et al., 2008; McNab, 2009). According to McKechnie (2008), the evident variation in metabolic traits of birds could have been generated by natural selection, phenotypic plasticity or by a combination of both. Currently, the changes in BMR in response to seasonal acclimatization and acclimation in the laboratory are

profusely described in the literature (Cooper, 2002; Cooper and Swanson, 1994; Piersma et al., 1995; Swanson, 1991; Tieleman et al., 2003; Williams and Tieleman, 2000; Maldonado et al., 2009), environmental temperature being the most important factor influencing short term changes in BMR (McKechnie, 2008). This kind of response is also known as phenotypic flexibility (Piersma and Drent, 2003).

It has been proposed that physiological flexibility in energetic traits is a common feature of birds (Klaassen et al., 2004). Nevertheless, the existence of substantial inter and intraspecific variation in the response of BMR to thermal acclimation calls for more detailed studies analyzing the temporal scale of BMR changes (Swanson and Olmstead, 1999; Dawson et al., 1985; Maldonado et al., 2009). To explain the observed variability in the acclimation response, it has been proposed that the speed and magnitude of the response to thermal acclimation may vary among bird species and populations (McKechnie, 2008) and may also depend upon the acclimation temperature (McKechnie, 2008). On the other hand, it has been reported that the response to acclimation of energetic traits in birds may depend on the season in which animals were assessed (Lindsay et al., 2009a). Although it is possible that other factor such as photoperiod, diet, hormone levels and body conditions may be influencing BMR in the field (Daan et al., 1990; Chastel et al., 2003; McNab, 2009) those data suggests that the acclimation response may be affected by the thermal history, i.e., the environmental temperature to which animals were exposed before the acclimation (see also Nespolo

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and Rosemann, 1997, for an example in rodents). Thus, comparative studies addressing the response to acute thermal acclimation of a particular bird species might consider the potential effect of the acclimation span and also the temperature experienced by individuals before acclimation. To the best of our knowledge there is only one study that assessed the reversibility of BMR in response to thermal acclimation in birds (McKechnie et al., 2007). Besides, the majority of studies on phenotypic flexibility of BMR have been conducted measuring this physiological trait before and after an acclimation period (usually 2 or 3 weeks, see McKechnie, 2008 for a review). Given that the time needed to reach a new steady-state condition after thermal acclimation may be shorter than the complete acclimation period, it is difficult to get a proper estimation of the rapidity of BMR change. To address this gap, we assessed the effect of thermal history on short-term thermal acclimation in a non-migratory passerine species, *Zonotrichia capensis*. Specifically, we evaluated whether the magnitude and rapidity of the short-term thermal acclimation to contrasting temperatures depends to any extent on the initial BMR status.

2. Methods

2.1. Species and laboratory acclimations

Rufous-collared sparrows were collected from Quebrada de la Plata (33° 31' S, 70° 50' W), a region in central Chile with a Mediterranean climate. Twelve birds were captured in September 2008, in the Austral spring, weighed and brought to the laboratory in Santiago. Birds were housed individually in plastic-mesh cages (35 × 35 × 35 cm³) under a 12L:12D photoperiod at 22 ± 1 °C. After habituating birds to laboratory conditions for 1 d, each bird was assigned to one of two treatments: one group was housed in a constant temperature room at 15 ± 1 °C (cold-acclimated group, *n*=6) and the other at 30 ± 1 °C (warm-acclimated group, *n*=6). The maximum and minimum temperatures were checked daily using a max/min thermometer located inside the acclimation chambers. The photoperiod was maintained at 12L: 12D. After this first initial acclimation treatment for 4 weeks (acclimation I), birds were re-assigned to the opposite treatment (Fig. 1). Birds were acclimated to the new conditions for six additional weeks (acclimation II). During both acclimation periods the birds consumed water, seed mixture, and mealworms which were provided *ad libitum*. Hence, our experimental design contemplated two experimental treatments, the 15–30 °C (cold

to warm, CW) group and the 30–15 °C (warm to cold, WC) group (Fig. 1).

2.2. Basal metabolic rate

We measured rates of oxygen consumption (VO₂) once per week, in post absorptive, resting birds during the inactive phase (between 20:00 and 6:00 h), using standard flow-through respirometry methods. Oxygen consumption was measured using a computerized, open-flow respirometry system (FC-10a, Sable Systems, Henderson, NV, USA) calibrated with a known mix of oxygen (20%) and nitrogen (80%) that were certified by chromatography (INDURA, Chile). Measurements were made at ambient temperatures (*T_a*) of 30.0 ± 0.5 °C, which is within the thermo-neutral zone for this species (Sabat et al., 2006). We used a dark metabolic chamber (1000 ml) which received dried air at 500 ml min⁻¹ provided by a Gast pump located at the end of the system (i.e., negative pressure) and controlled by a Sierra mass-flow meter and controller (Sierra Instruments, Monterey, CA). The mass flow-meter was calibrated monthly with a volumetric (bubble) flow meter. The excurrent air passed through columns of Drierite, CO₂-absorbent granules of Baralyme, and Drierite before passing through an O₂-analyzer (model FC-10A Sable System). The complete VO₂ trial lasted 4 h. Output from the H₂O (kPa) and oxygen analyzers (%) was digitized using a Universal Interface II (Sable Systems) and recorded on a personal computer using EXPEDATA data acquisition software (Sable Systems). Our sampling interval was 5 s. Birds remained in the chamber for 4 h, which was long enough to reach steady-state conditions; this typically occurs after 3 h in *Z. capensis* (Maldonado et al., 2009). We averaged O₂ concentration of the excurrent airstream over a 20 min period after steady state was reached (following Tieleman et al., 2002). Because CO₂ was scrubbed before entering the O₂ analyzer, oxygen consumption was calculated as $VO_2 = [FR 60 (F_i O_2 - F_e O_2)] / (1 - F_i O_2)$, where FR is the flow rate in ml/min after STP correction; *F_i* and *F_e* are the fractional concentrations of O₂ entering and leaving the metabolic chamber, respectively. Body mass was measured before metabolic measurements using an electronic balance (± 0.1 g) and cloacal body temperature (*T_b*) was recorded at the end of each measurement with a Cole–Palmer copper–constantan thermocouple attached to a Digi-sense thermometer (Model 92800-15). After the end of the second acclimation period (week 10), birds were weighed, euthanized by over-exposure to CO₂, and dissected. Organs were then removed, measured (± 0.1 cm) and mass determined (± 0.005 g).

2.3. Data analyses

Changes in body mass and metabolic rate were analyzed separately through repeated-measures ANOVA (RMANOVA) using time and the experimental treatment (i.e., cold to warm and warm to cold) as factors. At least in *Z. capensis*, the allometric exponent for VO₂ is not significantly different from one (see Maldonado et al., 2009), which justifies the comparison of specific metabolic rates in mass-specific units (i.e., ml O₂ h⁻¹ g⁻¹). We performed a *a posteriori* Tukey test to search for differences between weeks. Before analyses, we tested assumptions of normality and homoscedasticity using Shapiro–Wilks *W* and Levene tests, respectively. We also compared the percent change in BMR between the experimental groups, over the first 4 weeks of acclimation II period. These rates were calculated as final BMR minus initial BMR, divided by the initial value. Then we compared these rates by means of a Mann–Withney *U*-test. All statistical analyses were performed using the Statistica (StatSoft, 2001) statistical package for Windows.

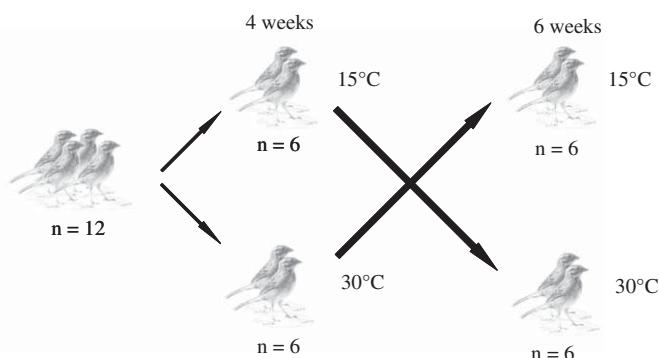


Fig. 1. Experimental design of the acclimation regimes in *Zonotrichia capensis*. Birds first were acclimated to either cold (15 °C) or warm (30 °C) conditions for 4 weeks, and then re-acclimated to the opposite temperature for six additional weeks. Basal metabolic rate was measured at the beginning and at the end of the experiment.

3. Results

Body mass of *Z. capensis* varied over time ($F_{5, 45}=26.42$, $p<0.0001$; RMANOVA), but the effect of treatment was not significant ($F_{1, 9}=0.23$, $p=0.65$; one-way ANOVA). The interaction between treatment and time was also significant ($F_{5, 45}=470$, $p=0.0016$; RMANOVA). The *post-hoc* tests showed that the change from cold to warm increased the body mass of birds until the fourth week, when asymptotic body mass was attained in the acclimation II period. On the contrary, WC birds increased their body mass only in the acclimation II period (Fig. 2). Hence, both groups increased body mass in response to cold exposure. After the complete experiment, organ masses did not differ significantly except for small intestine size, which was heavier and longer in the warm-to-cold group (see Table 1 for statistics).

Considering the entire period of acclimation, BMR was not affected by treatment ($F_{1, 9}=0.44$, $p=0.52$) or by time ($F_{5, 45}=1.69$, $p=0.16$). However an interaction between time and treatment was observed ($F_{5, 45}=6.45$, $p=0.00013$). The *post-hoc* tests showed that at the end of the acclimation I period (week 4) mass-specific BMR increased in the CW group compared to the initial value (week 0). Sparrows from the WC group also changed their mass-specific BMR significantly (Fig. 3). Accordingly, a comparison between treatments at the end of acclimation I showed a significant difference in BMR (Fig. 3) and similar rates (percent per 4 week) of BMR change (21.6 ± 10.9 and 13.4 ± 2.0 for CW and WC acclimated groups respectively; $U=17$; $p=0.93$; Mann–Whitney *U*-test). After 4 weeks of acclimation II, CW birds decreased their mass specific BMR compared to the end of acclimation I (i.e., week 4 compared to week 8), but the values after 4 or 6 weeks of acclimation II did not differ from the initial value (week 0). In turn, the WC group at the end of acclimation II period (weeks 6 and 8) showed an increase in BMR compared to the end of acclimation I, and also compared to the initial value (weeks 4 and 0 respectively). Values of BMR after 4 and 6 weeks in acclimation II period did not differ between groups. Furthermore, the percent change in BMR in the first 4 weeks of the acclimation II period was significantly greater in the WC acclimated group (28.5 ± 3.6) than in the CW acclimated group (13.17 ± 6.2 ; $U=3$; $p=0.028$). When this value is calculated for the end of the 4 weeks of acclimation body temperature did not differ among treatments ($F_{(1, 9)}=2.59$, $p=0.16$), times ($F_{(5, 45)}=0.92$, $p=0.48$) or in the

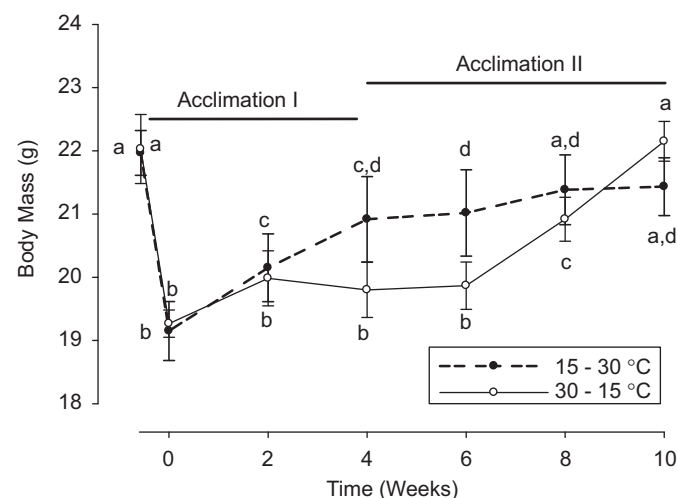


Fig. 2. Body mass profiles of *Zonotrichia capensis* acclimated to contrasting experimental temperatures. The initial value correspond to the body mass at the time of capture, one day before to the beginning of acclimations (week 0). Different letters denote significant differences between treatments by repeated measures ANOVA, at $p<0.05$. Values are means $\pm$ S.E.

Table 1

Body mass, wet mass (g) and length (cm) of internal organ in *Z. capensis* acclimated to one of two contrasting thermal regimes after the acclimation period II (week 10, see Fig. 1 for details of the experimental design).

Organs	Warm to cold (6)	Cold to warm (6)	<i>p</i>	<i>F</i> _(1,5)
Body mass (g)	22.3 $\pm$ 1.82	21.625 $\pm$ 1.41	0.93	0.19
Kidney mass (g)	0.255 $\pm$ 0.02	0.239 $\pm$ 0.02	0.75	0.11
Liver mass (g)	0.786 $\pm$ 0.05	0.747 $\pm$ 0.18	0.85	0.04
Heart mass (g)	0.261 $\pm$ 0.03	0.270 $\pm$ 0.02	0.67	0.21
Gizzard mass (g)	0.672 $\pm$ 0.09	0.569 $\pm$ 0.09	0.21	2.07
Small intestine mass (g) *	15.375 $\pm$ 1.36	12.750 $\pm$ 1.21	0.038	7.87
Small intestine length (cm) *	0.607 $\pm$ 0.06	0.410 $\pm$ 0.09	0.027	9.54
Large intestine length (cm)	2.400 $\pm$ 0.43	1.974 $\pm$ 0.22	0.20	2.19
Large intestine mass (g)	0.071 $\pm$ 0.04	0.054 $\pm$ 0.01	0.52	0.47
Cloaca length (cm)	0.500 $\pm$ 0.08	0.621 $\pm$ 0.12	0.164	2.71
Cloaca mass (g) *	0.041 $\pm$ 0.02	0.067 $\pm$ 0.01	0.04	7.65
Abdominal fat (g)	0.125 $\pm$ 0.08	0.140 $\pm$ 0.13	0.43	0.74

Sample size is in parenthesis. * Denotes significant differences between cold and warm acclimated birds after ANOVA, $p<0.05$. Values are means $\pm$ S.D.

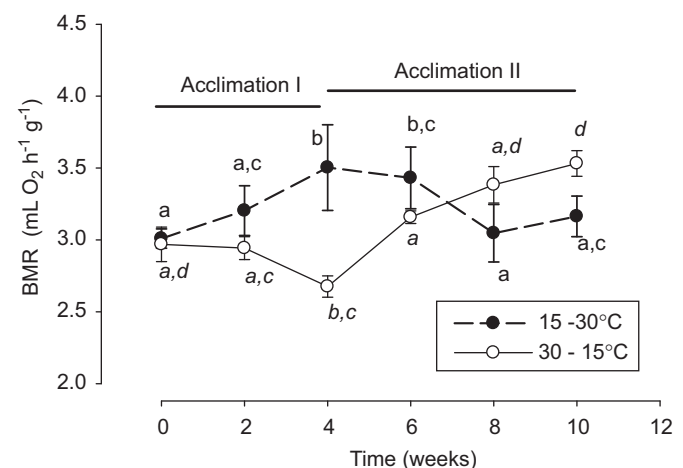


Fig. 3. Basal metabolic rate in *Zonotrichia capensis* acclimated to either cold or warm conditions for 4 weeks, and then re-acclimated to the opposite temperature for six additional weeks. Different letters denote significant differences between treatments after repeated measures ANOVA, at $p<0.05$. Values are means $\pm$ S.D.

interaction between time and treatment ($F_{(5, 45)}=1.3$, $p=0.27$). After metabolic trials all animals were normothermic, exhibiting a mean of $40.3\text{ }^{\circ}\text{C} \pm 0.84$.

4. Discussion

In this study we evaluated the reversibility of change in BMR in a passerine bird. Our results indicate that the direction of BMR change during thermal acclimation was independent of the previous thermal treatment. Thus, cold-acclimated birds tend to have higher levels of BMR compared to warm-acclimated birds. This result agrees with previous reports for this and other bird species (McKechnie et al., 2007; McKechnie, 2008; Cavieres and Sabat, 2008, but see Bush et al., 2008). However, we also found that the magnitude of short-thermal BMR acclimation depends on the previous thermal history in *Z. capensis*.

After the first 4 weeks of acclimation I, sparrows from the field modified their BMR at a similar rate when acclimated to warm or cold conditions. Birds from the CW group increased BMR by 21% whereas WC-acclimated birds decreased BMR 13.4%; however, this difference was not significant. Also, WC sparrows significantly elevated BMR by 28.5% when acclimated to cold conditions for 4

weeks. In this case final BMR values were 12% higher than the initial values. Thus, birds re-acclimated to cold conditions (WC group) reached similar values of BMR to those found in animals from the field acclimated to cold conditions. However, birds previously acclimated to cold conditions decreased BMR by only 13.2% when were re-acclimated to warmth for 4 weeks, but this BMR value was not significantly different from the initial value. In short, we found a higher rate of BMR change in the WC group than in the CW group in acclimation period II, and a trend of a higher rate of BMR change in the CW group in the acclimation period I. Thus it appears that the acclimation response of BMR to cold is faster than the acclimation to warm, and that this difference could be exacerbated when animals were previously acclimated to contrasting thermal environments (see also Nespolo and Rosemann, 1997).

Recently, Lindsay et al. (2009a,b) studied the acclimation response of metabolic rate in three populations of the Amethyst Sunbird, (*Chalcomitra amethystine*) from seasonal environments. They found that after a 6-week acclimation period to 25 °C, VO_2 values were generally higher in winter than in summer birds, especially if they came from seasonal habitats. As these authors stated, although birds can be acclimated to similar thermal conditions, underlying physiological differences can persist post-acclimation. Those results confirm that the response of birds to thermal acclimation may depend upon their previous thermal condition, both in the field and in the laboratory (this study). In this vein, it has been proposed that the magnitude of a flexible response of BMR would depend on the intensity of the environmental temperature (Swanson and Olmstead, 1999). Hence, when birds over winter in areas characterized by cold temperatures, probably they would have a higher BMR than birds overwintering in moderate climates. As a result, birds would have also a different response of BMR when reacclimated to a warm condition. Because BMR is associated with the energy cost of maintenance in endothermic animals, changes in the levels of such cost could lead to the need to satisfy those energy demands through higher food consumption. In this sense the severity of the winter areas does not only have an immediate effect on the energy expenditure through increasing the energy cost of thermoregulation, but also the associated cost of having a higher BMR.

What could be the mechanistic causes for the variation in the response to thermal acclimation between seasons and between laboratory conditions? As pointed out by McKechnie (2008), the time course of BMR adjustments in birds remains largely unknown. One possibility is that differences in the ability to modify BMR are caused by different body masses (McKechnie, 2008). However, this cause may be ruled out because sparrows exhibited similar weights in both groups after the second acclimation period. On the other hand, several authors have attempted to explain the variation in BMR in birds both at inter and interspecific levels (reviewed by McKechnie, 2008). According to the “energy demand” hypothesis for short-term adjustments (Williams and Tieleman, 2000), birds acclimated to low temperatures have higher metabolic rates coupled with a significant increase in the mass of digestive organs (probably as an effect of a substantial increase of food consumption) than warm-acclimated birds. Because of the repeated measures design used in this study, we could only measure the mass of digestive organs at the end of the complete experiment and thus no profiles of organ mass changes could be obtained. Our results, however, revealed that at the end of the 10 weeks of acclimation both groups exhibited similar organ masses, except for small intestine mass and length. Previously we have reported that *Z. capensis* exhibited differences in the mass of digestive organs and BMR both in the laboratory and in the field (Cavieses and Sabat, 2008; Maldonado et al., 2009). Those organ modifications explained some of the

variability in BMR between cold and warm acclimated birds in those studies (especially kidney, liver and heart masses). In the present study, constancy in the mass of such organs was found and only the small intestine significantly decreased its mass and length in the cold to warm group. Interestingly, liver, kidney and heart masses (organs which have been reported to have comparatively high mass-specific metabolic rates) do not follow the pattern shown by the intestine, suggesting that perhaps the synthesis of those tissues when birds were cold acclimated were faster than their regression when birds were exposed to warm conditions. Unfortunately, only a few studies have reported the temporal response of internal organs (reviewed by Karasov, 1996 and by Stark, 2005), and those studies showed that such modifications are very fast (a few days) compared to the time required for BMR acclimation in the laboratory (between 3 and 6 weeks). Besides, we cannot discard that mass changes of other organs that contributes to BMR in birds, such as the pectoralis muscle (Chappell et al., 1999), may also explain the observed differences in the rates at which BMR acclimates in *Z. capensis*.

It has been documented that variation in metabolic rates may also be associated with increase in the specific metabolic rate of different tissues, changes in the levels of respiratory enzymes, and increases in serum thyroid concentrations (Krebs, 1950; Daan et al., 1990; Williams and Tieleman, 2000; Vezina and Williams, 2005; Swanson and Thomas, 2007; Zheng et al., 2008). With regard to the specific activity of internal organs, no data on the time course of specific metabolic changes are available in birds. Thus, the possible mechanism responsible for those adjustments and their ability to show reversibility (i.e., the time course of digestive organ adjustments and enzymatic properties of specific tissues) after thermal acclimation needs further attention.

Studies on BMR flexibility in the laboratory have shown that the percentage of BMR adjustments varies greatly among species and populations in birds (Williams and Tieleman, 2000; Tieleman et al., 2003; McKechnie et al., 2007; Lindsay et al., 2009b). However, comparing the response to thermal acclimation in different bird species or populations requires that experimental approaches be comparable. As pointed by McKechnie (2008), the shapes of BMR change (i.e., the reaction norm) may be similar among bird species, but the speed of the responses may differ. In this vein, McKechnie et al. (2007) found that that BMR adjustments by thermal acclimation of the Laughing Dove (*Streptopelia senegalensis*) could be completely reversed in short time periods (3 weeks) which together with this study confirms the existence of interspecific differences in the response to thermal acclimation. Moreover, it has been hypothesized that differences in acclimation response among bird species and populations may have a genetic basis (Tieleman et al., 2003; McKechnie, 2008; Cavieses and Sabat, 2008). However our results suggest that the observed differences in the response to thermal acclimation among birds could also be explained by the exposition to different thermal regimes and it is not necessary to invoke genetic differences. Further approaches should incorporate this putative rate variation in BMR adjustments both in the field and in the laboratory when comparing the effects of temperature acclimation; otherwise such comparisons could generate misleading conclusions about the ability to modify energetic traits in birds.

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