

RESEARCH ARTICLE

Slowing down the metabolic engine: impact of early-life corticosterone exposure on adult metabolism in house sparrows (*Passer domesticus*)

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ABSTRACT

Whole-organism metabolism is an integrative process that determines not only the energy cost of living but also the energy output that is available for behavioral and physiological processes during the life cycle. Developmental challenge is known to affect growth, development of several organs, and several physiological mechanisms (such as HPA responsiveness, oxidative stress or immunity), which may altogether affect adult metabolism. All of these developmental effects are likely to be mediated by glucocorticoids, but the impact of developmental glucocorticoid exposure on adult metabolism has rarely been studied and the results are equivocal. In this study, we examined the impact of developmental exposure to corticosterone (CORT, the main avian glucocorticoid hormone) on resting metabolic rate (RMR, measured in thermoneutrality, 25°C) and thermoregulatory metabolic rate (TMR, measured in cold challenge conditions, 5°C) in the house sparrow. Following experimental administration of CORT at the nestling stage, house sparrows were kept in captivity until adulthood, when their metabolism was measured. We found that post-natal CORT exposure decreased both RMR and TMR in adult sparrows. This CORT-mediated reduction of metabolism was also associated with a reduced overnight body mass loss. Therefore, our results suggest that developmental CORT exposure can orient the phenotype towards an energy-saving strategy, which may be beneficial in a constraining environmental context.

KEY WORDS: Early-life stress, Glucocorticoids, Energy expenditure, Metabolic rate

INTRODUCTION

Whole-organism metabolism is an integrative process that determines not only the energy cost of self-maintenance (Daan et al., 1990; Bryant, 1997; McNab, 2002) but also the energy output that is available for individual behavioral and physiological processes during the life cycle (Biro and Stamps, 2010; Careau et al., 2011). Resting metabolic rate (RMR) is often referred to as the energetic cost of the organism's self-maintenance (McNab, 1997; Speakman et al., 2004). For example, RMR is often positively correlated with the size of the organs of an organism (e.g. heart, liver, kidneys and intestines; Burness et al., 1998; Chappell et al.,

1999, 2007; Petit et al., 2014; Piersma et al., 1996). Importantly, RMR can also be positively associated with the expression of specific energy-demanding behaviors (reviewed in Biro and Stamps, 2010; Careau et al., 2011), suggesting that a high RMR is required to sustain high aerobic capacity and an active lifestyle (i.e. the 'performance model'; Careau et al., 2008). In contrast, a low RMR may be associated with an energy-saving strategy, which may be beneficial especially during demanding life-history stages such as growth (e.g. Moe, 2004; Moe et al., 2005) or periods of poor food availability (Mathot et al., 2009). Recently, several studies have shown that RMR can be related to reproductive performance and survival in wild vertebrates, although these results are context and species dependent (Auer et al., 2015; Blackmer et al., 2005; Boratyński and Koteja, 2010; Bouwhuis et al., 2014; Burton et al., 2011; Rønning et al., 2016).

Within a given species, there is often a high inter-individual variation in RMR, which cannot be explained by multiple traits including body mass, sex, age, environmental conditions or reproductive status (Broggi et al., 2007; Burton et al., 2011; Careau et al., 2008; Konarzewski and Książek, 2013; Speakman et al., 2004). There is good evidence that metabolic rate is at least partly heritable (e.g. Nilsson et al., 2009; Rønning et al., 2007; Sadowska et al., 2005) and repeatable, sometimes over long periods, within individuals (e.g. Bech et al., 1999; Bouwhuis et al., 2011; Broggi et al., 2009; Rønning et al., 2005). In other words, some individuals consistently have a higher RMR than others. This suggests that individuals differ in their energetic cost of living, and potentially in their ability to sustain the high energy requirements of specific behavioral or physiological processes and life-history stages (Nilsson, 2002; Careau et al., 2008). Despite the importance of RMR in determining energy budget (e.g. Moe et al., 2005; Vézina et al., 2006) and potentially performance (e.g. Larivée et al., 2010; Rønning et al., 2016), little is known regarding the origin of inter-individual variation in RMR (Speakman et al., 2004; Vézina et al., 2006; Careau et al., 2008; Burton et al., 2011).

Developmental conditions can affect growth, development of several organs, and several physiological mechanisms [such as hypothalamic–pituitary–adrenal (HPA) axis responsiveness, oxidative stress or immunity efficiency], which together, are known to affect metabolism (Moe, 2004; Vézina et al., 2009; Burton et al., 2011; Schmidt et al., 2012). For example, there is convincing evidence that developmental food restriction will induce a short-term metabolic compensation with a reduction in RMR in birds (Moe, 2004; Moe et al., 2005; Rønning et al., 2009). Similarly, developmental conditions have been shown to impact adult metabolism (Burton et al., 2011). For example, high postnatal brood competition and low-quality postnatal diet are associated with higher adult RMR in zebra finches (*Taeniopygia guttata*) (Burness et al., 2000; Careau et al., 2014; Criscuolo et al., 2008; Verhulst

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et al., 2006), while developmental exposure to chronic traffic noise is associated with reduced RMR in adult house sparrows (*Passer domesticus*) (Brischoux et al., 2017). In the zebra finch, there is also evidence that maternal effects, such as the deposition of maternal testosterone in eggs, have short- (Tobler et al., 2007) and long-term impacts on RMR in offspring (Nilsson et al., 2011).

Hormones are thought to be the main mediators of prenatal and postnatal effects of developmental conditions on adult phenotype (Groothuis et al., 2008). Among endocrine mechanisms, glucocorticoids are probably among the best candidates to mediate the impact of developmental conditions on adult metabolism. Glucocorticoids are classically secreted in response to a disruption of homeostasis (McEwen and Wingfield, 2003; Romero et al., 2009) and work to restore homeostasis by mediating morphological, physiological and behavioral changes in vertebrates (Angelier and Wingfield, 2013; Wingfield et al., 1998). In birds, elevated levels of corticosterone (CORT; the main glucocorticoid secreted in birds) are associated with multiple physiological processes, which are not necessarily related to stress responses (MacDougall-Shackleton et al., 2019). CORT action and regulation are associated with many complex cascade effects, which are derived from the activation of several types of CORT receptors (Romero, 2004; Landys et al., 2006; MacDougall-Shackleton et al., 2019). In growing chicks, exposure to exogenous CORT increases begging rates, thereby increasing parental effort to help chicks survive this short-term challenge (Kitaysky et al., 2001; Loiseau et al., 2008). Developmental glucocorticoid exposure is also known to have long-term impacts on morphology (e.g. organ size and body composition; Searcy et al., 2004; reviewed in Schoech et al., 2011) and physiology (e.g. immunity and several hormonal pathways; De Coster et al., 2011; Marasco et al., 2016; Zito et al., 2017; reviewed in Spencer, 2017). For example, developmental glucocorticoid exposure is known to affect the functioning of the HPA axis and to result in either an increased or a decreased sensitivity of this endocrine axis during adulthood (reviewed in Schoech et al., 2011; Love and Williams, 2008; Marasco et al., 2012; Schmidt et al., 2014). In addition, glucocorticoids are known to be closely linked to metabolism and energy expenditure (Astheimer et al., 1992; Jimeno et al., 2017, 2018; Landys et al., 2006). For example, an increase in circulating glucocorticoid levels is known to promote lipid and glucose mobilization (Sapolsky et al., 2000) and to increase locomotor activity (Astheimer et al., 1992; Lynn et al., 2003). Accordingly, post-developmental glucocorticoid exposure may affect metabolism through its influence on the functioning of the HPA axis. Surprisingly, the impact of developmental glucocorticoid exposure on adult metabolism has been examined in only two studies and the results are somewhat equivocal. Schmidt et al. (2012) found that developmental exposure to CORT resulted in increased RMR in female but not in male song sparrows (*Melospiza melodia*). In the zebra finch, Spencer and Verhulst (2008) found that developmental CORT exposure did not impact RMR during adulthood. Most studies on developmental glucocorticoid exposure have focused on RMR while neglecting metabolic rate under constraining conditions (e.g. thermal challenge conditions, which reflect realistic environmental variations) despite its ecological importance (Biro and Stamps, 2010; Burton et al., 2011; Careau et al., 2008).

In this study, we examined the impact of developmental exposure to CORT on metabolism in the house sparrow. Following experimental administration of CORT at the nestling stage, house sparrows were kept in captivity until adulthood (see Grace et al., 2017a,b), when their metabolism was measured. We specifically

measured their RMR (thermoneutrality, 25°C) and thermoregulatory metabolic rate (TMR, when they were exposed to challenging, cold thermal conditions, 5°C). To better assess the consequences of a potential effect of developmental CORT exposure on metabolism, we also monitored overnight body mass loss in CORT-treated and control house sparrows at 25°C and 5°C. Wild birds cannot forage at night, and thus, during the winter must maintain homeostasis while fasting under cold temperatures. In that context, their ability to maintain their body mass overnight may be a crucial determinant of overnight survival (Burns et al., 2013; Lima, 1986) and/or of the foraging activity the next morning (Bednekoff and Houston, 1994; McNamara et al., 1994; Moiron et al., 2018; Pitera et al., 2018). The effect of a developmental challenge on adult metabolism remains controversial in the literature, and several studies have found contradictory patterns (e.g. Verhulst et al., 2006; Spencer and Verhulst, 2008; Schmidt et al., 2012; Careau et al., 2014; Brischoux et al., 2017). Therefore, it is difficult to establish a directional prediction. Because we logically expect that a high metabolism will be associated with the use of body reserves, notably when food is absent (e.g. at night) or limited, we predict that the potential effect of developmental CORT exposure on RMR or TMR may translate into an effect on overnight body mass loss.

MATERIALS AND METHODS

Post-natal corticosterone treatment

This study focused on thirty-four 2-year-old house sparrows, *Passer domesticus* (Linnaeus 1758) (21 females and 13 males), which were exposed to CORT during their development (CORT-fed group, $N_{\text{female}}=10$; $N_{\text{male}}=7$) or not (control group, $N_{\text{female}}=11$; $N_{\text{male}}=6$). Briefly, all of these sparrows were born in artificial and accessible nest boxes from a free-living population. They were fed four times during their development (once at 8 and 9 days post-hatching, respectively, and twice at 11 days post-hatching) with mealworms containing either CORT dissolved in dimethyl sulfoxide (DMSO, CORT-fed group) or DMSO only (control group; see Grace et al., 2017b for details). This ingestion of CORT-treated mealworm resulted in transient increased circulating CORT level (8.6-fold) in house sparrow chicks (Grace et al., 2017a). Previous work conducted on house sparrows found similar circulating CORT levels during a standardized capture–restraint test (Angelier et al., 2016), demonstrating that our CORT level manipulation was within physiological range. At fledging, all birds were captured, raised in individual cages (45.5×35.5×51 cm) and kept in semi-captivity (outdoor aviaries 5×5×2 m) with food (commercial seed mixture) and water *ad libitum*, salt/mineral blocks and millet on the stalk. We previously tested the impact of this post-hatching CORT exposure on growth, morphology, behavior and survival (see Dupont et al., 2019; Grace et al., 2017a,b). Briefly, CORT-fed individuals were smaller as nestlings but were able to compensate for this bad start and there was no impact of the post-natal CORT treatment on body size or body condition at juvenile and adult stages (Grace et al., 2017b). In addition, we found that CORT-fed house sparrows had lower antipredator skills and had smaller visual ornaments than controls. In the present study, we specifically measured our variables of interest (RMR, TMR and overnight body mass loss) in 17 of these CORT-fed (10 females and 7 males) and in 15 of these control (10 females and 5 males) sparrows.

Metabolic measurements

Metabolic rate was measured using multichannel flow-through respirometry (RM8 Multiplexer, Sable Systems International, Las Vegas, NV, USA). All our measurements were conducted between

10 and 27 January 2017 (winter night temperature, range: from -5°C to 10°C) and followed the protocols previously described (see Dupoué et al., 2015; Powolny et al., 2016). On the day of metabolic measurement, birds (2-year-olds) were captured at 15:00 h from the outdoor aviaries and their tarsus length and wing length were measured with a sliding caliper or a graduated ruler, respectively. Tarsus and wing length did not differ between CORT-fed and control groups (ANOVAs, tarsus length: $F_{1,32}=0.059$, $P=0.810$, wing length: $F_{1,32}<0.001$, $P=0.759$). Before 16:00 h, all birds were placed in individual cages, similar to those used during the rearing period, in a designated room with food and water *ad libitum*. At 18:00 h, food was removed from cages to ensure that individuals were fasting during subsequent metabolic measurements. At 20:00 h, birds were weighed with an electronic scale and immediately placed in a dark hermetic box with a perch (glass box, internal volume=3000 ml) that was placed in walk-in chamber already adjusted to the testing temperature (25°C or 5°C). We measured metabolic rates of seven individuals per session because our multichannel open-circuit respirometry unit (Sables Systems) is composed of eight analyzer chambers, one of which remained empty as a control. Outside air was provided at a constant flow ($\sim 450\text{ ml min}^{-1}$) to each box through an air pump (Bioblock Scientific 551) and a mass flow controller (FlowBar-8, Sable Systems). Then, sequential samples were taken from expelled air of each box via a gas flow switcher (RM-Multiplexer, Sable Systems). Before water was stripped from the air using Drierite (W. A. Hammond, Drierite, Xenia, OH, USA), expelled air passed through a hygrometer (RH 300, Sable Systems). Then, dried air samples were sent to the CO_2 analyzer (CA10A, Sable Systems) and then to the O_2 analyzer (FC10A, Sable Systems). All the hardware outputs were simultaneously recorded (UI-2, Sable Systems). At 06:00 h (the following day), all birds were removed from the metabolic chambers and immediately weighed. Because air and water analysis were achieved one chamber at a time, the eight chambers were sequentially sampled during 15 min periods (see Brischoux et al., 2017). Each individual was tested at two temperatures [25°C and 5°C , which correspond, respectively, to the lower limit of this species' thermoneutral zone (defined as the lowest nocturnal metabolic rate measured according to the calorimetric chamber temperature; Hudson and Kimzey, 1966) and to a mildly challenging temperature (birds faced a minimum temperature ranging from -5°C to 10°C during that period of the year at the study site) to determine RMR and TMR for each individual. Half of the individuals were first tested at 25°C , and 1 week later at 5°C . The other half was first tested at 5°C , and 1 week later at 25°C .

Respiratory values of O_2 and CO_2 concentrations were extracted from stable resting periods. This extraction was blinded to the group allocation of each individual. We then calculated mean overnight flow rate and individual's and baseline's respiratory values of O_2 and CO_2 for each thermal condition (25°C and 5°C). Sparrow oxygen consumption rates (\dot{V}_{O_2} , ml min^{-1}) were calculated at each studied temperature using respirometric equations derived from Lighton (2008):

$$\dot{V}_{\text{O}_2} = f \times \frac{(F_{\text{IO}_2} - F_{\text{EO}_2}) - F_{\text{EO}_2} \times (F_{\text{ECO}_2} - F_{\text{ICO}_2})}{1 - F_{\text{EO}_2}}, \quad (1)$$

where f is flow rate, F_{EO_2} is the mean fractional proportion of O_2 entering the chamber, F_{IO_2} is the mean fractional proportion of O_2 exiting the chamber, F_{ECO_2} is the mean fractional proportion of CO_2

entering the chamber, and F_{ICO_2} is the mean fractional proportion of CO_2 exiting the chamber.

Water density was extracted blindly from stable resting periods. We then calculated mean overnight flow rate and individual's and baseline water density for each thermal condition (25°C and 5°C). Mean overnight total evaporative water loss (EWL, ml min^{-1}) was calculated at each studied temperature using the equation derived from Withers (1977):

$$\text{EWL} = f \times (D_{\text{chamber}} - D_{\text{baseline}}) \times 1.44, \quad (2)$$

where D_{chamber} is the mean overnight water density in the chamber containing a bird and D_{baseline} is the mean overnight water density in the empty chamber.

Overnight mass loss

Overnight body mass loss (ΔM_b ; %) was calculated at each studied temperature using the following equation:

$$\Delta M_b = 100 \times \frac{M_{b,\text{initial}} - M_{b,\text{final}}}{M_{b,\text{initial}}}, \quad (3)$$

where $M_{b,\text{initial}}$ is the initial body mass the day before metabolism measurements, taken at 20:00 h, and $M_{b,\text{final}}$ is the final body mass taken at 06:00 h the following morning.

A full dataset is available as Dataset 1.

Statistical analysis

All statistical analyses were performed with R.3.1.1 (<https://www.r-project.org/>). Firstly, we ran linear mixed-effect models (LMEMs) with a normal error distribution to test the influence of the post-natal CORT treatment on (1) oxygen consumption, (2) evaporative water loss and (3) body mass loss. For each model, we tested the effect of post-natal CORT treatment, thermal condition, initial body mass and sex. We also tested the following interactions: post-natal CORT treatment \times thermal condition, post-natal CORT treatment \times sex and thermal condition \times sex. For all models, we included individual identity as a random effect because each bird was tested twice (25°C and 5°C). Secondly, we ran two linear models (LMs) according to our two thermal conditions (25°C and 5°C) with a normal error distribution to test the influence of oxygen consumption on overnight body mass loss. We ran one model per thermal condition because oxygen consumption was strongly affected by thermal conditions and these two explanatory variables could not be included simultaneously in the model (Graham, 2003). For these two models, sex and the interaction oxygen consumption \times sex were also included as explanatory variables. In addition, we ran two LMEMs according to our two post-natal treatments (CORT-fed and control individuals) with a normal error distribution to determine the influence of thermal condition on overnight body mass loss. We ran one model per post-natal treatment because body mass loss strongly differed between post-natal treatments. In these models, we included individual identity as a random effect. Best-fitting models were selected via an information-theoretic approach using the Akaike information criterion corrected for small sample sizes (AICc), and applying the principle of parsimony (Burnham and Anderson, 2002). Parameter estimates (\pm s.e.), t -values and P -values of fixed effects are given for the best models.

Ethics statement

Permissions to capture, sample and hold house sparrows in captivity were issued by the French government (DREAL, Poitou-Charentes, permit delivered to F.A.) and by the Muséum National d'Histoires

Naturelles. All experimental procedures were approved by the French government (R45GRETA1-10) and Centre National de la Recherche Scientifique, and conform to guidelines set forth by the French Ministry of Higher Education and Research and Ministry of Agriculture and Fisheries.

RESULTS

Oxygen consumption

Oxygen consumption was significantly lower in CORT-fed individuals compared with controls (Table 1, Fig. 1). In addition, individuals consumed significantly more oxygen at 5°C compared with at 25°C (Table 1, Fig. 1), indicating that TMR was significantly higher than RMR. There was a positive effect of initial body mass on oxygen consumption (Table 1, Fig. 1). However, there was no significant effect of sex or any interaction term on oxygen consumption (Table 1), suggesting that CORT-fed individuals consumed less oxygen than controls at both 25°C and 5°C. Body

mass did not differ between CORT-fed individuals and controls (LM, post-natal CORT treatment, $F_{1,32}=1.90$, $P=0.177$; sex, $F_{1,31}=0.076$, $P=0.785$; interaction, $F_{1,30}=0.455$, $P=0.505$).

Evaporative water loss

EWL was significantly higher in the thermoneutral condition rather than in the cold challenge condition (Table S1, Fig. S1). However, there was no significant effect of post-natal CORT treatment, sex or any interaction on EWL (Table S1).

Body mass loss

Body mass loss was significantly lower in CORT-fed individuals compared with controls (Table 1, Fig. 2). Surprisingly, we found that overnight body mass loss was not higher when the birds were maintained at 5°C relative to 25°C (Table 1). In addition, there was no significant effect of sex or any interaction term on body mass loss (Table 1, Fig. 2).

Table 1. Linear mixed model selection table based on the Akaike information criterion (AICc) to determine the best models explaining oxygen consumption and body mass loss

Models	K	log(L)	AICc	Δ AICc	w_i	Parameter	Estimate \pm s.e.	t	P
Oxygen consumption									
1. Initial body mass, Thermal condition, Post-natal CORT treatment	6	13.0	-12.7	0.00	0.33	Intercept	0.931 \pm 0.517	1.80	0.072
2. Initial body mass, Thermal condition, Post-natal CORT treatment, Sex	7	13.4	-10.9	1.87	0.13	Initial body mass	0.056 \pm 0.020	2.85	0.004
3. Initial body mass, Thermal condition, Post-natal CORT treatment, Thermal condition \times Post-natal CORT treatment	7	13.2	-10.5	2.20	0.11	Thermal condition (25°C) ^a	-0.771 \pm 0.043	-17.7	<0.001
4. Initial body condition, Thermal condition	5	10.7	-10.4	2.29	0.10	Treatment (CORT-fed) ^a	-0.124 \pm 0.055	-2.26	0.024
5. Initial body mass, Thermal condition, Post-natal CORT treatment, Sex, Thermal condition \times Sex	8	13.8	-9.2	3.51	0.06				
6. NULL	3	-42.4	91.2	104.0	0.00				
Body mass loss									
1. Initial body mass, Post-natal CORT treatment	5	12.8	-14.7	0.00	0.39	Intercept	-0.640 \pm 0.483	-1.33	0.185
2. Initial body mass, Post-natal CORT treatment, Sex	6	13.4	-13.4	1.32	0.20	Initial body mass	0.068 \pm 0.018	3.66	<0.001
3. Initial body mass, Thermal condition, Post-natal CORT treatment	6	12.9	-12.4	2.36	0.12	Treatment (CORT-fed) ^a	-0.192 \pm 0.051	-3.76	<0.001
4. Initial body condition, Post-natal CORT treatment, Sex, Post-natal CORT treatment \times Sex	7	13.9	-12.0	2.77	0.10				
5. Initial body mass, Thermal condition, Post-natal CORT treatment, Sex	7	13.4	-11.0	3.76	0.06				
6. NULL	3	-0.37	7.1	21.8	0.00				
Body mass loss – Thermoneutral condition (25°C)									
1. Oxygen consumption	3	4.05	-1.3	0.00	0.700	Intercept	-0.066 \pm 0.357	-0.187	0.853
2. Oxygen consumption, Sex	4	4.06	1.3	2.56	0.194	O ₂ consumption	0.689 \pm 0.230	3.00	0.005
3. Oxygen consumption, Sex, Oxygen consumption \times Sex	5	4.21	3.7	5.03	0.057				
4. NULL	2	-0.162	4.7	6.01	0.035				
Body mass loss – Cold challenging condition (5°C)									
1. Oxygen consumption	3	6.69	-6.6	0.00	0.695	Intercept	-0.276 \pm 0.297	-0.929	0.359
2. Oxygen consumption, Sex	4	6.93	-4.5	2.11	0.242	O ₂ consumption	0.557 \pm 0.127	4.38	<0.001
3. Oxygen consumption, Sex, Oxygen consumption \times Sex	5	6.94	-1.7	4.86	0.061				
4. NULL	2	-1.30	7.0	13.6	0.001				

K represents the number of parameters and log(L) is the log likelihood value for each model. AICc computations and relative variable importance (weight, w_i) are indicated for the five best models and the null model. Best models are shown in bold and ranked from lowest to highest AICc values. Parameter estimates are presented for the best models.

^aFor fixed factors, the non-reference factor is indicated in parentheses.

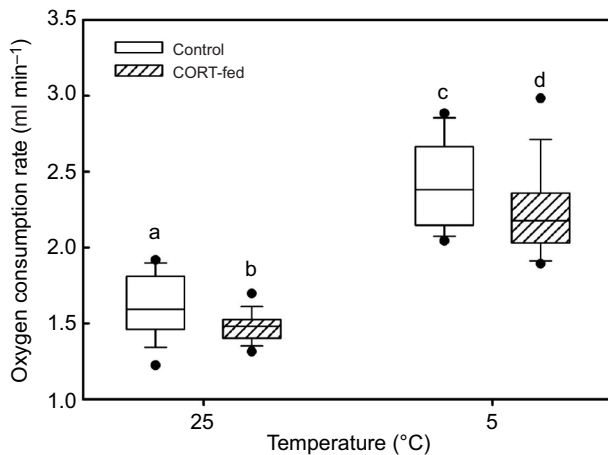


Fig. 1. Difference in oxygen consumption [resting (RMR) and thermoregulatory metabolic rate (TMR)] between the two thermal conditions (25°C and 5°C) in 34 adult house sparrows exposed to corticosterone (CORT-fed, $N=17$) or not (control, $N=17$) during their development. Hatched boxplots represent CORT-fed individuals. White boxplots represent control individuals. Box-and-whisker plots represent the data: the top and bottom of the boxes represent the top and bottom quartiles, respectively; the line across the box represents the mean. The ends of the whiskers represent the 5th and 95th percentiles, and the circles represent outliers. Different letters denote significant differences between two groups (linear mixed-effect model, $P<0.05$).

Body mass loss and oxygen consumption

Both at 25°C and 5°C, body mass loss was significantly and positively explained by oxygen consumption (25°C: $P=0.005$, $r^2=0.219$; 5°C: $P<0.001$, $r^2=0.375$; Table 1, Fig. 3A). There was no significant effect of sex or the interaction sex \times oxygen consumption on body mass loss (Table 1). Body mass loss did not differ between thermal conditions (25°C versus 5°C) for CORT-fed or control sparrows (LMER, CORT-fed: $P=0.789$; control: $P=0.744$; Fig. 3B).

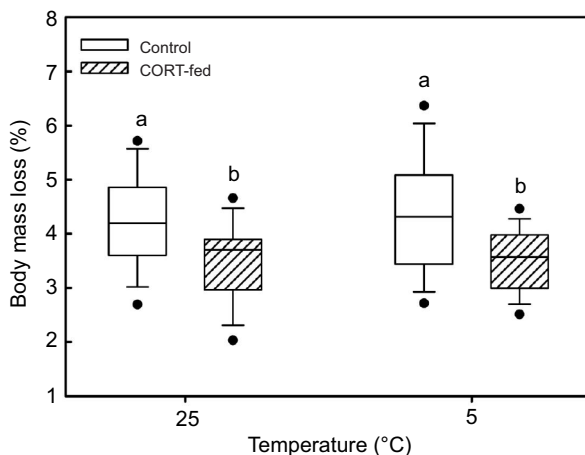


Fig. 2. Difference in overnight body mass loss between the thermal conditions (25°C and 5°C) in 34 adult house sparrows exposed to corticosterone (CORT-fed, $N=17$) or not (control, $N=17$) during their development. Hatched boxplots represent CORT-fed individuals. White boxplots represent control individuals. Box-and-whisker plots represent the data: the top and bottom of the boxes represent the top and bottom quartiles, respectively; the line across the box represents the mean. The ends of the whiskers represent the 5th and 95th percentiles, and the circles represent outliers. Different letters denote significant differences between two groups (linear mixed-effect model, $P<0.05$).

DISCUSSION

In this study, we experimentally demonstrated for the first time that developmental CORT exposure can reduce metabolism later in life in a wild vertebrate species. Accordingly, we demonstrated that post-natal CORT exposure decreased both RMR and TMR during adulthood. In line with these results, we found that house sparrows that were exposed to CORT as nestlings had lower overnight body mass loss as adults at both normal and low temperatures. Therefore, our results suggest that developmental CORT exposure can slow down metabolic rate during adulthood, potentially through a direct effect on metabolism or an indirect CORT-mediated effect on metabolism if the HPA axis of CORT-fed individuals is downregulated. This CORT-mediated metabolic response may be an adaptive response to developmental constraints through alteration of the individual's somatic state (somatic state-based adaptive developmental plasticity *sensu* Nettle and Bateson, 2015) and/or it could orient the phenotype towards an energy-saving strategy, which might be beneficial later in life if the environmental context remains constraining (e.g. low food availability, 'the environmental matching hypothesis'; Monaghan, 2008; informational developmental plasticity *sensu* Nettle and Bateson, 2015). Alternatively, this reduced metabolism could entail costs (survival cost or reproductive costs), especially if it is associated with a lower maximal metabolic rate, as previously found in other studies (Hayes and O'Connor, 1999; Petit et al., 2017).

Impact of developmental CORT exposure on RMR and TMR

In this experimental study, we found that post-natal CORT exposure was associated with lower adult metabolic rate in a wild bird species. Additionally, and according to our expectation, we found that house sparrows had a higher metabolic rate when exposed to a challenging temperature (see also Carleton and Del Rio, 2005; Vézina et al., 2006; Nzama et al., 2010). Our experimental CORT manipulation was associated not only with a reduced RMR (i.e. measured at thermoneutrality) but also a reduced TMR (i.e. measured when the individuals were held at 5°C). These results provide convincing evidence that developmental CORT exposure slows down the metabolic setup under both favorable and challenging temperature conditions in our study species.

Our metabolic results are somewhat surprising because developmental nutritional constraints have been associated with an increased adult RMR in another passerine species, captive zebra finches (Careau et al., 2014; Criscuolo et al., 2008; Verhulst et al., 2006). However, Spencer and Verhulst (2008) did not find any evidence that developmental CORT exposure affects RMR during adulthood in this same species. Additionally, developmental constraints are associated with decreased RMR in several other bird species (Brzęk and Konarzewski, 2001; Moe, 2004; Brisoux et al., 2017), and can have sex-specific effects on metabolism within a species (Schmidt et al., 2012). Together, these studies suggest that the impact of developmental conditions on metabolism probably depends on the context, timing and duration of stressor experience, sex and species. Overall, our study demonstrates that developmental conditions and, more specifically, developmental CORT exposure can shape the metabolic phenotype at adult stages through direct effects. In addition, developmental CORT exposure may have acted on metabolism through an indirect effect on endocrine systems (e.g. functioning of the HPA axis, modifications of tissue-specific CORT receptor density, or change in corticosterone binding globulin regulation). For instance, the HPA axis of CORT-fed birds could be downregulated in comparison to control birds. Consequently, they could have lower circulating CORT levels than controls when

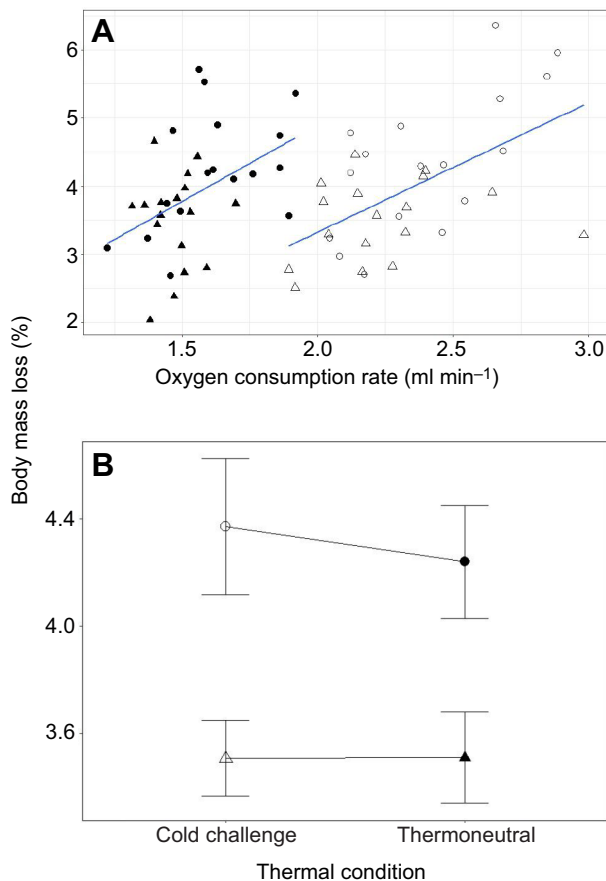


Fig. 3. Difference in body mass loss between the two thermal conditions (25°C and 5°C) in 34 adult house sparrows exposed to corticosterone (CORT-fed, $N=17$) or not (control, $N=17$). Relationship between overnight body mass loss and (A) oxygen consumption (RMR and TMR) and (B) thermal condition in 17 CORT-fed and 17 control adult house sparrows, held at either 25°C (black symbols) or 5°C (white symbols). Triangles and circles represent CORT-fed and control individuals, respectively. The lines represent the relationship between individual body mass loss and (A) oxygen consumption in thermoneutral conditions (25°C; linear mixed-effect model: $P=0.005$) and in a mildly challenging condition (5°C; linear mixed-effect model: $P<0.001$) for CORT-fed and control adults, combined.

transferred to the metabolic chambers and this could be associated with a lower metabolic rate because CORT is known to increase metabolism in birds. However, this hypothesis seems to be unlikely because all individuals were maintained in individual cages for a long period before the experiment and they were therefore habituated to these captive conditions (Grace et al., 2017a,b). In addition, they stayed in these cages for several hours before the actual metabolic measurements. Importantly, developmental constraints (e.g. nutritional deficit) and developmental CORT exposure may not always have the same effect on metabolism, especially because natural constraints, such as food constraints, may affect metabolism independently of CORT. This may indeed explain the discrepancy between our results and those from previous studies, which manipulated nutritional conditions (Verhulst et al., 2006; Schmidt et al., 2012; Careau et al., 2014), and found that nutritional constraints could be associated with no change or an increase in RMR. However, our study emphasizes that elevated physiological doses of CORT during the developmental period (within the natural range of the species; Angelier et al., 2016) affect metabolism. Therefore, natural developmental constraints

(e.g. food restriction) could affect metabolism through an effect of increased CORT levels on metabolism or other physiological mechanisms related to metabolism, as previously suggested in the zebra finch (Schmidt et al., 2012).

In birds, metabolism is mainly determined by organ size and body composition because all organs do not have the same energy need to function properly (reviewed in Burton et al., 2011). For instance, organ sizes can significantly contribute to whole-organism metabolic rate in laboratory mice, especially the sizes of energy-demanding organs such as liver, kidneys, heart, muscles and intestines (Konarzewski and Diamond, 1995; reviewed in Swanson et al., 2017). Similarly, specific organs may play a key role in explaining the differences in RMR and TMR that we reported in this study (Salin et al., 2016; reviewed in Norin and Metcalfe, 2019). In a previous study, we found that exposure to developmental CORT was associated with a delayed growth (Grace et al., 2017b), which may have affected the development of specific organs. Supporting this possibility, developmental CORT exposure has been reported to alter organ morphology and function in endotherms (reviewed in Rinaudo and Wang, 2012; Careau et al., 2014). Although CORT-treated and control nestlings had similar body size and body mass at adulthood (present study; Grace et al., 2017b), they may differ in organ size or function. Therefore, our results suggest that developmental CORT exposure may be associated with a mass-independent change in tissue metabolic activity (Vézina et al., 2006). Further studies are now necessary to assess body composition and organ mass to test this hypothesis.

Developmental CORT exposure may also have affected some endocrine pathways, which are known or suspected to regulate metabolism in vertebrates [e.g. the hypothalamic–pituitary–thyroid (HPT) axis: McNabb, 2006; and the HPA axis: Jimeno et al., 2017; Landys et al., 2006]. Several studies have shown that these two axes and circulating levels of CORT and thyroid hormones are positively correlated with RMR, activity and energy expenditure in vertebrates (corticosterone: Asheimer et al., 1992; Jimeno et al., 2017, 2018; thyroid hormones: Chastel et al., 2003; Vézina et al., 2009; Elliott et al., 2013; Welcker et al., 2013). Others have reported that developmental constraints or developmental CORT exposure can downregulate the HPA axis later in life with a potential negative effect on metabolism (reviewed in Schoech et al., 2011). Similarly, developmental food restriction was associated with a concomitant reduction of metabolism and circulating levels of thyroid hormones in Japanese quails (Rønning et al., 2009). However, further studies are necessary to test this functional hypothesis in our study species and it would be relevant to measure CORT and thyroid hormone concentrations in addition to metabolism and energy expenditures.

Body mass loss, metabolism and potential fitness consequences

Surprisingly, we found that overnight body mass loss was not higher when the birds were maintained at 5°C relative to thermoneutrality (i.e. 25°C). This result appears puzzling because TMR was much higher than RMR in our study, suggesting that house sparrows were expending more energy when held at 5°C relative to thermoneutrality. This result is supported by another study, which reported important differences in metabolism between two groups of house sparrows, but no difference in their overnight body mass loss (Nzama et al., 2010). This pattern probably results from differences in EWL between the two thermal conditions. In our study, EWL was much more important when sparrows were held at 25°C relative to 5°C (see Fig. S1 and Table S1), suggesting that sparrows were losing more water but less body reserves at 25°C than at 5°C.

Developmental CORT exposure was associated with a lower overnight body mass loss in adult house sparrows in our study. In other words, CORT-fed birds lost less mass relative to controls after a night of fasting regardless of the ambient temperature (25°C or 5°C). This difference in body mass loss between CORT-fed and control sparrows appears to result from their differences in metabolism, because metabolism is associated with energy expenditure and body reserve catabolism in fasting animals (McNab, 2002; Speakman et al., 2004; Swanson, 2010). Indeed, we found a positive and significant relationship between metabolism and overnight body mass loss at both 25°C and 5°C. Reduced overnight metabolism and body mass loss may be adaptive by allowing house sparrows to save their energy under unfavorable environmental conditions, such as low food availability or inclement weather (Reinertsen and Haftorn, 1986). This may be especially important in winter because overnight fasting is particularly energetically constraining for wild birds during that period (low temperature, longer nights and prolonged fasting; Krams et al., 2010, 2013; Burns et al., 2013). Supporting this interpretation, a few studies have reported that reduced metabolism can be associated with higher overwintering survival in mammals and birds (e.g. red squirrels, *Tamiasciurus hudsonicus*: Larivée et al., 2010; blue tits, *Cyanistes caeruleus*: Nilsson and Nilsson, 2016).

Yet, other studies have reported reduced survival associated with lower RMR (e.g. Nilsson and Nilsson, 2016; Scholer et al., 2019). Thermogenesis requires a high RMR (Vézina et al., 2006), a process that is critical to birds such as sparrows that elevate body temperature primarily by shivering (a process dependent on the size of pectoral muscles; O'Connor, 1995a,b; Dawson and O'Connor, 1996; Swanson, 2001; Hohtola, 2004). Therefore, although CORT-fed sparrows may benefit from a lower metabolic rate by conserving energy in the short-term, they may be less able to tolerate prolonged periods of cold compared with control birds with higher metabolic rates. In this study, we did not measure body temperature, and CORT-fed sparrows could therefore have a lower metabolism because of a reduced body temperature. At the ultimate level, a lower body temperature is usually associated with reduced performance (especially in term of maintenance), suggesting that CORT-fed individuals could have a lower survival, especially when cold conditions occur. We have also previously found that sparrows fed with CORT as nestlings had depressed adult evasive behavior (i.e. were easier to catch), suggesting that they may have reduced flight and/or neuromuscular abilities compared with controls (Grace et al., 2017a). In addition, in late winter, a low RMR has been associated with reduced reproductive performance in the study species (i.e. delayed laying date; Chastel et al., 2003). Altogether, these results and interpretations also suggest that a reduced RMR could be associated with costs in CORT-fed sparrows. Interestingly, the relative costs and benefits of a reduced metabolism are likely to depend on the environmental context, which may explain why several studies have failed to find consistent relationships between metabolism and fitness in vertebrates (Burton et al., 2011; Nilsson and Nilsson, 2016; Rønning et al., 2016). Further studies focusing on fitness metrics (survival and reproduction) are now required to fully assess the fitness costs and benefits of this CORT-mediated effect of developmental conditions on metabolism.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: S.M.D., J.K.G., F.A.; Methodology: S.M.D., J.K.G., O.L., F.A.; Validation: O.L.; Formal analysis: S.M.D., J.K.G., F.A.; Data curation: O.L.; Writing - original draft: S.M.D., J.K.G., F.A.; Writing - review & editing: O.L., F.B.; Supervision: F.A.; Project administration: F.A.; Funding acquisition: F.A.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.211771.supplemental>

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