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Effect of gestational and postnatal environmental temperature on metabolic rate in the altricial rodent, *Phyllotis darwini*

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ABSTRACT

1. In the altricial rodent, *Phyllotis darwini*, we found higher body temperatures and faster developmental rates of the thermoregulatory capacity in neonates born from cold- than warm-acclimated mothers.
2. This difference could be explained by maternal effects on the litter, such as high levels of catecholamines and thyroxin levels, high concentration of the uncoupled protein and larger quantity of brown adipose tissue as a consequence of cold acclimation.
3. The exposition of mothers and the maintenance of cold condition during the early development might be responsible of the high metabolism and better thermoregulatory capacity of newborns.

1. Introduction

Several species show phenotypic plasticity, which has been described as an adaptive response (Pigliucci, 2001). In contrast, some features appear to be more rigid and are rarely modified by the environment (Hughes, 1993; Sabat et al., 1998; McKechnie et al., 2007). In addition, some authors have reported phenotypic plasticity of physiology and morphology during ontogeny but an absence of response when animals are adults, i.e., an inflexible norm of reaction (Toloza and Diamond, 1990; Biviano et al., 1993; Zhao et al., 1996; Bozinovic, 1993). Thus physiological plasticity of some traits may be dependent on the ontogenetic stage at which acclimation acts (Sabat and Bozinovic, 2000).

The change from intrauterine to extrauterine life during the ontogeny of mammals is perhaps the most dramatic physiological event that individuals experience. Among the most pressing requirements after birth are the establishment of lung ventilation, the redistribution of blood between the systemic and pulmonary circulation and thermoregulation (Hull, 1973). For neonates, birth means a change from a high and stable temperature to a variable and usually low environmental temperature, which may affect dramatically the physiology of heat production and the development of the juveniles. During early postnatal development several mammals are not able to maintain a stable body temperature. For example, mink kits (*Mustela vison*) need 6 weeks to show clear thermoregulatory responses when exposed to low temperature (15 °C) and 4 weeks when exposed to high temperature (15 °C) (Tauson et al., 2006), laboratory mice exhibit poikilothermy up to 7 days after birth (Lagerspetz, 1966) and rats exposed to environmental temperatures below the lower critical limit of the thermoneutral zone show hypothermia until 11 days old (Malik and Fewell, 2003). Before birth, fetuses *in utero* also could be affected by the external environment. Low temperatures can affect gravid females, increasing catecholamines and thyroxin. This could result in a greater maturity in the metabolic machinery or a greater quantity of metabolically active tissue in the juveniles, for example a larger quantity of brown adipose tissue (BAT) at birth and an increased concentration of the uncoupling protein of the BAT (Sant Anna and Mortola, 2003). Also, a cold-induced high BAT sympathetic activity was recorded in early neonatal life of rats (Morrison et al., 2000).

Thus, cold may enhance development of metabolic machinery of juveniles during ontogeny. If plasticity exists, differential metabolic responses to warm and cold environments are expected, occurring simultaneously with the dramatic changes in the respiratory organs in early ontogeny. In this contribution we study the cold-induced developmental physiological plasticity in the metabolic response of the leaf-eared mouse (*Phyllotis darwini*) (Rodentia: Muridae), an altricial rodent which inhabits central Chile. We expected that in the altricial rodent *P. darwini*, animals exposed to high energetic thermoregulatory requirements during its gestation and developmental period, would reach higher metabolic levels and greater aerobic capacities as adults.

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2. Material and methods

2.1. Animal models and sample size

Fifteen adult males ($M_b = 54.4 \pm 17.3$ g) and 15 adult females ($M_b = 37.7 \pm 7.6$ g) of *P. darwini*, a rodent dwelling in grasslands, scrub, open forest and rocky areas, were captured in Quebrada de la Plata, Maipú in central Chile, (33°27′S, 70°42′W), between September and December, 2005. The animals were taken to the laboratory, where they were kept in pairs at room temperature with food (sunflower seeds and rabbit food Champion®) and water *ad lib*. After mating, pregnant females were maintained in individual cages ($40 \times 40 \times 20$ cm) in climatic chambers and randomly assigned to one of two temperature treatments. One group was maintained at low energetic requirements for thermoregulation at a constant temperature of 30 ± 2 °C (warm-acclimated group) and a second group maintained at high energetic requirements for thermoregulation at 15 ± 2 °C (cold-acclimated group), 10 °C below the lower critical temperature for this species (Bozinovic et al., 1988). The animals were observed daily, and were not allowed to build nests. The offspring were kept with the mother until the experimentation day or until weaning. After the offspring were born, three unrelated individuals were selected for each environmental condition at days: 1 (neonates), 7, 14, 21 and 60 (adult). The entire study period was between December 2005 and December 2007. In the newborn group at 30 °C, four individuals were analyzed. The individuals had to be killed in order to perform a structural study of lungs using CO_2, complying with the current laws of Chile and the standards of the ethical committee of the Facultad de Ciencias, Universidad de Chile, where the experiments were performed (see Canals et al., 2009). Thus, except for one group with 4 individuals, 3 independent individuals were studied for each age group and environmental condition, leading to a total sample size of $n = 31$.

2.2. Oxygen consumption

Since animals of very different ages and thermoregulatory maturity were compared, different methods were used to obtain metabolic measurements. In neonates (day 1), we studied the curve of oxygen consumption along an environmental temperature gradient from 38 to 23 °C, decreasing the temperature by 2 °C every 20 min, determining the maximum oxygen consumption ($\dot{V}_{O_2\,max}$) and the oxygen consumption at rest ($\dot{V}_{O_2}$), at each temperature (*Ta*). Body temperature was recorded at the end of each measurement period with an intra-rectal Cu-constantan thermocouple (± 0.1 °C). After each experimental trial, body temperature of individuals was recuperated by exposing them to warm, dry conditions with pre-warmed towels. The scheme was modified for individuals aged 7 days; measuring every 5 °C from 30 to 5 °C with 30 min between each experimental trial in post-absorptive individuals. The minimum $\dot{V}_{O_2}$ recorded in the thermoneutral zone was the basal metabolic rate (*BMR*). For animals of 14 days and older, only *BMR* and $\dot{V}_{O_2\,max}$ were measured.

2.3. Basal metabolic rate (BMR)

All measures of oxygen consumption ($\dot{V}_{O_2}$) were performed in an open-flow respirometer system (Sable Systems). Individual determinations of basal metabolic rate were performed in a 1 l steel chamber at a thermoneutral (30 °C) temperature. The metabolic chamber received dry air at a rate of 500 ml/min from a flow controller (Sierra Instruments), to assure an adequate air mix. CO_2 was removed and the air was dried before entering and after leaving the chamber. Oxygen was monitored every 5 s using an oxygen analyzer 1FC-1B (Sable Systems). Oxygen consumption was estimated using the equation of Whithers (1977). All measurements were made during the resting phase (08:00–18:00 h) of the species.

2.4. Maximum thermogenic oxygen consumption ($\dot{V}_{O_2\,max}$)

Beginning at 14 days, $\dot{V}_{O_2\,max}$ was determined in an atmosphere of He–O_2 (80–20%) in an open circuit respirometer. Because the high conductivity of He, this method allowed us to elicit maximum metabolism in moderate cold without changing the value of $\dot{V}_{O_2\,max}$, yielding similar values to those obtained at extreme temperatures or running in treadmills (see Rosenmann and Morrison, 1974). The metabolic chamber received dried gas mixture at 1000 mL min^{-1} from a mass flow controller and through Bev-A-Line tubing (Thermoplastic Processes Inc.) and the chamber temperature was constantly monitored (5.0 ± 0.5 °C). This flow kept the partial oxygen pressure above 150 Torr, which is considerably above the level of hypoxia. The gas mixture was passed through CO_2 and water absorbent (Baralyme and Drierite) at the entrance and exit of the chamber. To be sure that individuals reached $\dot{V}_{O_2\,max}$, measurements were stopped when the reduction of $\dot{V}_{O_2}$ was evident; hypothermia was checked with a Cole–Parmer copper–constatan thermocouple after each measurement.

2.5. Analysis

In neonates, we compared body temperature, and $\dot{V}_{O_2}$ between the two temperature-acclimated groups with an analysis of covariance, using oxygen consumption or body temperature as response variable and chamber temperature (*Ta*) as a covariate.

The body mass response, *BMR* and $\dot{V}_{O_2\,max}$ values and body temperatures at the end of maximum metabolism experiments were analyzed with a 2-way analysis of variance (ANOVA), using acclimation temperature and age groups as factors. Although the maximum values in the 1- and 7-day groups were not obtained with a He–O_2 atmosphere, we recorded the maximum oxygen consumption values before metabolic depression, which generally occurred between 25 and 23 °C in newborns and between 10 and 5 °C in the 7-day group.

3. Results

3.1. Oxygen consumption and body temperature

3.1.1. Neonates

Acclimation temperature exerted a significant effect both on oxygen consumption and body temperature. Neonates of the warm-acclimated group showed a lower oxygen consumption than the cold-acclimated group at all ambient temperatures ($F_{1,45} = 19.83$; $p < 0.001$) (Fig. 1). Offspring acclimated to 30 °C showed lower body temperatures at the end of the experiments than those acclimated to 15 °C (31.3 ± 1.86 °C and 32.31 ± 2.41 °C and for warm- and cold-acclimated groups, respectively; $F_{1,45} = 5.09$, $p = 0.029$).

3.1.2. All developmental groups

Body mass increased at a similar rate in the two acclimated groups ($F_{1,21} = 0.176$, $p > 0.05$). *BMR* were not significantly different between the warm- and cold-acclimated group ($F_{1,21} = 2.76$, $p = 0.11$) and it increased with age ($F_{4,21} = 3.05$, $p = 0.039$), with a maximum at 21 days, then decreased in the adult stage. Multiple *a posteriori* comparisons revealed only differences between

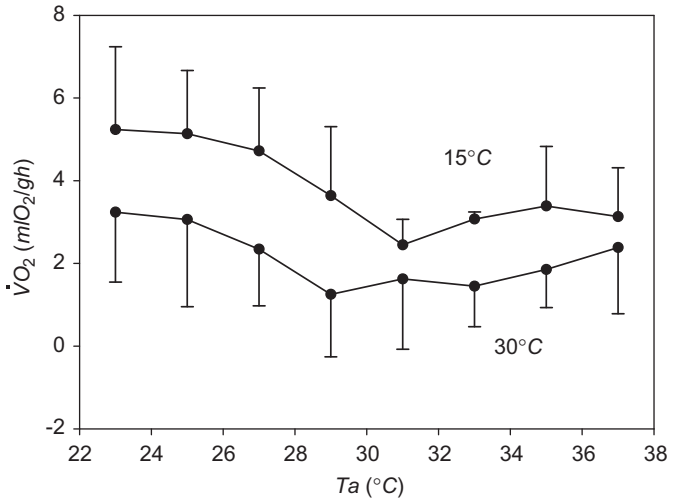

Fig. 1. Oxygen consumption ($\dot{V}_{O_2}$; ml O_2 g^{-1} h^{-1}) of neonates (1 day) born from warm-acclimated (30 °C) and cold-acclimated (15 °C) animals of the species *Phyllotis darwini*, exposed to different environmental temperatures (*Ta*).

Table 1
Body mass (M_b) and basal metabolic rate (*BMR*) of *Phyllotis darwini* during post-natal development of two acclimated groups: cold-group (15°) and warm-group (30 °C).

Age (days)	M_b (g)		*BMR* (ml O_2 g^{-1} h^{-1})	
	Cold-group	Warm-group	Cold-group	Warm-group
1	3.63±0.63	3.95±0.82	2.02±0.27	1.69±0.44*
7	9.57±0.94	8.23±1.04	2.07±0.16*	1.36±0.35*
14	14.63±0.91	11.53±2.05	2.22±0.63	2.11±0.18
21	18.43±6.31	16.73±1.15	2.21±0.24	2.42±0.81
60	38.0±8.23	41.26±1.47	1.77±0.03	1.48±0.37

Average ±1 standard deviation. Asterisks indicate significant differences within each group in Tukey test.

7-day-old individuals acclimated to 30 °C and 1- and 7-day-old individuals acclimated to 15 °C (Table 1).

The ratio between minimum oxygen consumption and that expected for an adult animal of the same body mass (based on $BMR = 3.4M_b^{0.71}$, McNab, 1988) showed the same trend, with no difference between the temperate acclimated groups ($F_{1,21} = 2.63$, $p = 0.12$). However, there was an evident difference in the age at which the curve intersects the value Observed/Expected = 1. This occurs at approximately 3.4 days in the group acclimated to 15 °C and at 10.6 days in the group acclimated to 30 °C. However, both groups reached their metabolic plateau at day 21 (Fig. 2).

Maximum oxygen consumption ($\dot{V}_{O_2\,max}$) increased with age, reaching a peak at 14 days and slowly decreasing in the older stages. However, no significant differences were found between temperature-acclimated groups ($F_{1,21} = 2.52$, $p = 0.127$), nor significant interaction between groups and age ($F_{4,21} = 0.29$, $p = 0.880$; Fig. 3).

Body temperature at the end of the experimental trials of *BMR* did not show differences for the age groups of 7, 14, 21 and 60 days ($F_{3,16} = 1.43$, $p > 0.05$), nor among temperature-acclimated groups ($F_{1,16} = 0.33$, $p > 0.05$). The mean body temperature was 37.01±1.06° for the warm group, and 36.78±0.99 °C for the cold group. However, the temperature at the end of the experimental trials for $\dot{V}_{O_2\,max}$ showed differences among age groups ($F_{3,16} = 10.85$, $p \ll 0.01$), but a similar response for temperature groups ($F_{1,16} = 0.28$, $p > 0.05$). *A posteriori* tests revealed that the differences were produced by the 7-day groups in both experimental

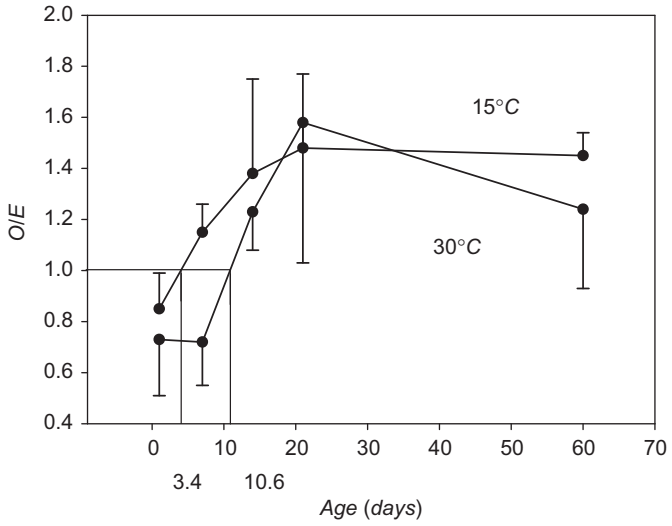

Fig. 2. Observed/expected ratio of *BMR* (O/E) of warm-acclimated animals (30 °C) and cold-acclimated animals (15 °C) of the species *Phyllotis darwini*, at different developmental stages. Expected values for the basal metabolic rate of an adult of the same body mass were obtained from $BMR = 3.4M_b^{0.71}$, McNab, 1988. Solid lines indicate where $O/E = 1$ and the days in which the metabolic curves intersect that value.

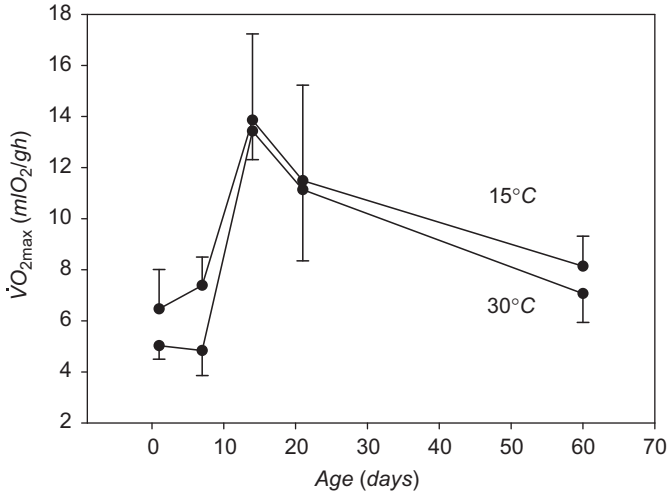

Fig. 3. Maximum metabolic rate ($\dot{V}_{O_2\,max}$) of warm-acclimated animals (30 °C) and cold-acclimated animals (15 °C) of the species *Phyllotis darwini*, at different developmental stages.

sets and the 14-day group at 30 °C compared with the groups of 21 and 60 days. We excluded from the 60-day group at 15 °C one individual who finished the experiment with extreme hypothermia of 24.5 °C (Table 2).

4. Discussion

Altricial mammals are born in a relatively defenseless state, uncoordinated and bare, having a long period of dependence on their parents; while precocial mammals are born covered with fur, with eyes open and immediate locomotor ability, quickly becoming independent from their parents. These two groups differ also in their thermoregulatory strategies after birth. Precocial animals are capable of thermoregulation based on the maturity of their metabolic machinery and the chemical energy resources provided by their mother, while altricial mammals must depend upon the resources provided by the mother and behavioral

Table 2
Body temperature at the end of $\dot{V}_{O_2\,max}$ experiments (5°) and at the end of BMR experiments of two acclimated groups: cold-group (15°) and warm-group (30 °C) of the species *Phyllotis darwini* during post-natal development.

Age (days)	$\dot{V}_{O_2\,max}$		*BMR*	
	Cold-group	Warm-group	Cold-group	Warm-group
7	25.9±4.2*	22.4±0.4*	36.9±0.5	36.1±0.8
14	30.5±4.2	28.5±4.7*	37.3±0.9	37.6±1.6
21	34.7±0.6	33.7±0.4	36.1±1.4	37.1±1.1
60	30.6±5.3	34.3±0.4	37.0±0.6	37.2±0.2

Average ±1 standard deviation. Asterisks indicate significant differences within each group in Tukey test.

thermoregulatory strategies, such as huddling with their siblings and mother, isolation in nests, etc. (Antinuchi and Busch, 2001). After birth, development of thermoregulatory abilities and respiratory structures associated with aerobic capacities has been reported in the latter group (Burri, 1974; Burri et al., 1991; McMurty, 2002; Canals et al., 2000), associated with a greater postnatal plasticity (Blanco et al., 1991; Hammond et al., 1999, 2001) than in precocial mammals (see Tenney and Remmers, 1966). The influence of climate on metabolic capacities of rodents has been well documented (Rosenmann and Morrison, 1974; Bozinovic and Rosenmann, 1989; Tieleman et al., 2002, 2003; Novoa et al., 2005).

We expected that in the altricial rodent *P. darwini*, animals exposed to high energetic thermoregulatory requirements would reach higher metabolic levels and greater aerobic capacities as adults. However, the only difference in the thermoregulatory response between the acclimation groups was manifested 1 day after being born, and at age 7 days. The cold-acclimated group showed greater metabolic rates and a greater thermoregulatory capacity at these ages than the warm-acclimated group, but this difference disappeared in 21 days old juveniles and in adults. This response is different to that reported in young mink (Mustela vison), an extreme altricial mammal, exposed to different temperatures from birth, in which animals exposed to cold took approximately 2 weeks more than animals exposed to warm temperature to reach clear thermoregulation (Tauson et al., 2006).

In our experimental setup, offspring were kept with the mother until weaning, otherwise they might have died. Nevertheless, individuals could save energy by huddling, a usual behavior in neonates at any environmental temperature, which allowed them to reduce their overall surface structure by masking out the effect of thermal stress (Canals et al., 1989, 1997, 1998). However, huddling in newborn of *P. darwini* was present in both experimental conditions even though one experimental temperature was within the thermoneutral zone (Bozinovic et al., 1988) while the other was at least 13 °C below the minimal critical temperature of the thermoneutral zone for adults of this species.

We suggest that the differences in thermoregulatory maturity must necessarily originate in maternal effects on the fetus during prenatal development, since inside the metabolic chambers behavioral mechanisms of thermoregulation were not possible.

At birth, both groups were incapable of adequate thermoregulation; this was more evident in the warm-acclimated group, which had lower temperatures at the end of the experiments and lower metabolism at the youngest ages. Development of metabolic and thermoregulatory machinery was enhanced in the cold-acclimated group. We determined this by measuring the time necessary for animals to reach the allometrically predicted metabolic rate (Fig. 2). This occurred at approximately 3.4 days in cold group and at 10.6 days in the warm group; the latter value is similar to that described for a number of altricial rodents (Malik and Fewell, 2003; Lagerspetz, 1966). Thus, the thermoregulatory maturity was advanced in the cold-acclimated group, which was evident from day 1, in which body temperatures, and metabolic rates were significantly higher than in the warm-acclimated animals. Our results are similar to the response of young rats exposed to cold. Bertin et al. (1993) found that oxygen consumption of pups reared in the cold was increased during first and second week, but similar to controls in the third week. Also, Sant Anna and Mortola (2003) found that cold-acclimated rats had mass-specific oxygen consumption higher than controls at low temperatures (5 °C).

The greater body temperature and metabolic rates in cold-acclimated group can indicate a greater maturity in the metabolic machinery or a greater quantity of metabolically active tissue, for example a larger quantity of brown adipose tissue at birth, the main oxygen-consuming organ in the body (Klaus et al., 1991; Trayhurn, 1993), or in the concentration of the uncoupling protein of BAT (UCP). Sant Anna and Mortola (2003) reported that rats exposed to cold during postnatal development showed higher concentration of UCP, and higher concentration of total proteins in the BAT than in controls. Several years ago, Lagerspetz (1966) showed that the increment in the heat production between ages of 7 and 15 days in laboratory mice was accompanied with an increase in the succinic dehydrogenase activity in the liver, probably caused by an increase in thyroid activity.

In this vein, the cold could induce a release of norepinephrine from the sympathetic nerve endings that is considered necessary for the stimulation of non-shivering thermogenesis (Jansky, 1973; Nedergaard et al., 1986; Morrison et al, 2000) and for the differentiation of fetal BAT (Casteilla et al., 1994). Morrison et al. (2000) showed that in rats, neonatal exposure to cold induces a permanent developmental alteration in the capacity for sympathetic stimulation of bat thermogenesis in rats compared with controls, due to a high BAT sympathetic activity, greater norepinephrine contents of the interscapular BAT and higher number of sympathetic ganglion cells projecting to interscapular BAT. In those reported data (Bertin et al., 1993; Morrison et al., 2000; Sant Anna and Mortola, 2003) young rats were exposed to different temperatures from birth and measured in a posterior stage. In the same way, we obtained result in concordance with these studies, but from birth. This implies that the exposition of mothers and the maintenance of cold conditions during early development are responsible for the high metabolism and better thermoregulatory capacity than controls at days 1 and 7, probably mediated by the same physiological mechanisms. This cold-induced faster thermoregulation in offspring could be and important maternal effect with consequences for the survival of the litter in cold environments.

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