

Geographic variation in life-history traits: factors shaping energy investment in reproduction in a highland dwelling rodent

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Abstract

Variation in life-history traits is shaped by intrinsic and extrinsic factors. Climate influences the availability of energy and nutrients in the environment, and thus animals' energy balance, their allocation of resources to reproduction and ultimately, fitness. Temperature is reported as a prevailing influence on animals' investment in reproduction, and diverse hypotheses propose mechanisms by which it occurs. Central and external limits to energy acquisition have been traditionally assumed. Hence, digestive limitations, periods of low food availability or demanding cold conditions would restrict this input. However, under warm conditions endotherms also face the need to dissipate heat from metabolic processes. From this perspective, a high metabolic rate process, such as lactation, would be restricted under increasing ambient temperatures (T_a). Our research addresses the variation in reproductive parameters in *Phyllotis xanthopygus*, a rodent species broadly distributed in the west highlands and southern parts of South America. Across a pronounced elevation gradient in the central Andes Mountains we found that litter size is comparatively smaller in pregnant females collected at lower elevations. This is congruent with expectations from the heat dissipation limit hypothesis. To disentangle the role of temperature on this pattern, we bred individuals under two thermal treatments. We recorded no changes in the litter size, but pups' body mass was lower at higher T_a during lactation, also in agreement with decreased metabolism. Offspring size and number are relevant to a species' fitness. The evidence suggests that in *P. xanthopygus* these traits vary geographically and are shaped by T_a in the laboratory. A species that evolved in high altitudes, inhabits cold and temperate areas and is sensitive to T_a increases in the laboratory, appears as an excellent candidate to further explore the ecophysiology-thermal landscape interface, crucial to develop accurate predictive models of biodiversity dynamics.

Introduction

The thermal biology of a species is central to its relationships with the environment. Research on this area of animal physiology has the potential to uncover the mechanisms underlying the interaction between organisms and their thermal landscape, with strong relevance to life-history traits (Antinuchi *et al.*, 2003; Bozinovic, 2003). Thus, an animal's physiology determines the way ambient temperature (T_a) will affect its ecology and evolution (Finke, 2003). Mean T_a and its variation influence body temperature (T_b) and therefore, animals' management of time and space to achieve thermal homeostasis. Hence, energy balance, critical to survival and reproductive success, is strongly tied to temperature.

According to McNab (2002), the 'Scholander and Irving model' (based on the studies by Scholander *et al.*, 1950) states

that: 'at moderate to cold temperatures, the exchange of heat between the body and the environment is mainly ruled by the thermal differential ($T_b - T_a = \Delta T$). Therefore, in order to achieve a constant T_b , all heat loss has to be replaced'. In endotherms, heat is generated mostly by metabolism, being $M = C (T_b - T_a)$, where C is thermal conductance. Yet, if the thermal differential is low and thermal conductance is limited, metabolic rate decreases to reduce endogenous heat production (McNab & Morrison, 1963). This is because in mammals thermoregulatory mechanisms are usually more effective in maintaining T_b at low T_a via increased thermogenesis, but less efficient to release heat (Nespolo, Bacigalupe & Bozinovic, 2003). As a framework for this problem, the heat dissipation limit (HDL) theory poses that the rates at which animals can use energy are limited by their capacity to dissipate the heat generated as a by-product of metabolic processes. This can

impose an upper thermal limit to diverse aspects of their performance, such as foraging behavior, activity rate and reproductive effort (Speakman & Król, 2010).

Nevertheless, the role of energy in ecological processes has been generally assumed as limiting (e.g. the Metabolic Theory of Ecology: Brown *et al.*, 2004). In other words, classical views in biology and evolution mainly consider constraints on the availability side of the energy balance equation. For instance, the central limit hypothesis postulates that metabolism is constrained by the central machinery of acquisition, processing and allocation of energy and resources (Weiner, 1992; Koteja, 1996). Therefore, energy expenditure on different activities would be limited by the energy income from the alimentary tract. Support for this has been inconclusive (Hammond & Diamond, 1992; Naya, Bozinovic & Karasov, 2008). From another perspective, environmental factors are related to primary productivity and hence nutritional quality and quantity of food, modulating energy availability. Thus, external restrictions are assumed to operate on the acquisition side of the energy balance equation. The resultant prediction is that high energy expenditures depend on the exploitation of abundant, high-quality foods (McNab, 1980; Wingfield, 2005). In contrast to both former views, the HDL theory predicts that at different spatial and temporal scales, an endotherm faces ambient temperatures that could limit its intrinsic ability to dissipate heat and hence constrain heat generating processes (Speakman & Król, 2010). All in all, separate predictions are possible from the Central Limit hypothesis, the environmental constraint idea and the HDL theory, in respect to a highly energy demanding process as reproduction in mammals.

Life-history traits such as litter size and pup size are tied to reproductive investment, and therefore to energy balance. Geographic clines in reproductive traits suggest that some environmental variables changing across the cline can account for offspring or litter size variation (Messina & Fox, 2001). Among them, gradients of T_a , salinity, length of the growing season and food abundance may influence the reproductive energy investment. In the search for physiological mechanisms underlying ecological patterns, a species occurring along an elevation gradient is an appropriate model to test the effect of thermal variation on life-history traits. Therefore, in this study we aimed to evaluate reproductive parameters in *Phyllotis xanthopygus*, a small rodent broadly distributed along the Andes Mountains at altitudes ranging from sea level in Patagonia to 5600 m a.s.l. in southern Peru (Kramer *et al.*, 1999). The species is a mouse of medium size (body mass of adults ca. 55 g) with large ears and long tail. The overall color is grayish brown and the pelage is long and soft. It has been described as an herbivore, but high variation in the diet has been reported among subspecies as well as across altitudes. It is also essentially nocturnal but changes in activity pattern have been reported in response to experimental variations in light intensities (Kramer *et al.*, 1999). The species reaches its sexual maturity at 8 weeks and litters reach seven individuals (P. Sassi, unpublished data). Collected individuals show signs of reproductive activity only during summer months (Kelt, 1994). Recent investigations performed on a population occurring along the elevation gradient in the Central Andes, report high

behavioral flexibility, physiological plasticity and diverse trophic interactions, facing great thermal and resource-related variation (Sassi & Novillo, 2015; Sassi *et al.*, 2015, 2016).

Under the framework of HDL theory, we predicted that individuals exposed to low T_a at higher altitude, would be able to invest more energy in reproduction than individuals exposed to comparatively higher T_a at lower altitude. Because annual productivity generally declines in relation to altitude as a result of shorter growing seasons and lower T_a , environmental constraints are expected. The alternative prediction, based on the assumption of limited food resources, is that individuals at higher altitudes would invest less in reproduction. Finally, if constraints on the processing capacity (i.e. digestion, absorption or milk production) are actually governing energy availability for reproduction, a limit on the overall energetic cost is expected (Hammond & Diamond, 1994). Hence, either no difference in life-history traits would exist among animals from distinct altitudes or reproductive investment would be lower at high altitude due to competing costs of thermoregulation.

Our study consisted on a first observational component to search for elevation related differences in life-history traits, followed by a second experimental component to examine variation in these traits under controlled conditions in the laboratory. Assessments were planned with the goal of disentangling the eventual role of T_a , to test predictions from the diverging theoretical views considered above.

Materials and methods

Study area

The study area was located at El Manzano Histórico Reserve, Mendoza Province, Argentina (33°36'48.4"S–69°28'42.7"W). We established sampling sites at 1700, 2300 and 3100 m elevation along an altitudinal transect. Sites were three to four kilometers apart, encompassing gradual changes in a landscape characterized by low, sparse vegetation. The area belongs to the Andean and High Andean phytogeographic provinces, but the three sites present different plant communities. The site at 1700 m a.s.l. corresponds to shrub land of *Colliguaja integerrima* and *Adesmia horrida*. The site at 2300 m a.s.l. belongs to shrub land of *Junellia scoparia*, and the site at 3100 m a.s.l. consists of *Adesmia subterranea* and *Azorella monantha* steppes (Cabrera, 1976; Méndez, 2011a). The region is characterized by low productivity and semiarid climate with increasing humidity towards the high elevations (Méndez, 2011a). The altitudinal range covers a broad gradient of T_a across a steep slope, implying strong environmental variations. Main precipitations are rainfall at low altitudes, concentrated in the summer, and snow at high altitudes during winter, where the 3100 m site is covered by snow from May to November (Méndez, 2011b). T_a and relative humidity data recorded at the selected sites are presented in Table 1.

Field and lab work (first component)

We collected 10 females at each site (total $N = 30$), using Sherman traps between February 2011 and March 2015. All

Table 1 Data on basic climatic variables for each altitudinal site (in meters above the sea level): Mean annual temperature (T mean), temperature annual range (T range), mean relative humidity (RH mean), relative humidity range (RH range). Data taken from Sassi & Novillo (2015)

Study site (m a.s.l.)	1700		2300		3100	
Season	Summer	Winter	Summer	Winter	Summer	Winter
T mean ($^{\circ}\text{C}$)	20.9	9.9	17.0	6.9	11.3	1.7
T range (min $^{\circ}\text{C}$ –max $^{\circ}\text{C}$)	7.7–32.5	–3.9–27.1	6.2–30.1	–4.2–27.0	0.6–25.3	–8.4–14.2
RH mean (%)	47.9	45.0	53.6	42.9	49.4	52.8
RH range (min%–max%)	7.3–90.4	5.0–86.4	8.7–88.5	4.5–85.3	5.8–94.0	7.7–100

animals belonged to the same subspecies. In previous work we report no genetic differences among individuals from the different sites (Ojeda *et al.*, 2013). They were weighed using a Pesola[®] Medio-Line Spring Scale.

In the laboratory, animals were maintained on chinchilla food pellets and water *ad libitum*, housed individually in $30 \times 30 \times 40$ cm cages under 12L:12D photo period, 22°C T_a and 25–35% relative humidity (RH). Cotton and wood chips bedding was provided in the cages.

Within the following 20 days we recorded any births of the collected females. Once pups were born we measured: number of pups, body mass of the pups at the age of 15 days, and body mass of the pups every fifteen days during the following 12 weeks. At day 15 pups were also sexed and at day 30 they were weaned.

Experimental work (second component)

The experiment was run with 13 adult females and four males born in captivity, from mothers belonging to the intermediate site (2300 m). It consisted of two trials at different T_a , with equal photo period 14L:10D and 20% RH, under which animals were bred. Experimental temperatures were chosen based on two factors. First, previous reference studies testing successfully for temperature-related responses on reproduction in mice (33 g) and voles (28 g), acclimated animals to 21 and 30°C , corresponding to thermal conditions below and within the thermoneutral zone (TNZ) respectively (Król & Speakman, 2003; Simons *et al.*, 2011). TNZ was recently measured on animals from our study population (Menéndez, Ruperto & Sassi, 2017), indicating that it ranges between 25°C (lower critical temperature, T_{lc}) and 38°C (upper critical temperature, T_{uc}). According to Riek & Geiser (2013) the T_{lc} in placental mammals varies negatively with body mass. Then, for *P. xanthopygus* we settled thermal treatments at 17°C and 30°C to comply with the reference studies' rationale. Second, field estimates suggest a broad thermal range of at least 10°C across the altitudinal gradient as well as within sites (Table 1). Even though both experimental treatments represent only partially the temperatures experienced in the field by our model species, the goal was to cover contrasting situations in terms of energy demands.

Approximately half of the animals were randomly assigned to each T_a treatment (17 or 30°C), and acclimated for 15 days before breeding. Following a cross-over experimental design, after the first trial, each individual was assigned to the other thermal treatment, acclimated and then bred again. Females

were weighed after acclimation and before pregnancy to control for differences due to the treatments. After parturition, we measured: number of pups, body mass of the pups at the age of 10 days, and body mass of the pups every 5 days during 12 weeks. At day 15 pups were also sexed and at day 30 they were weaned. Throughout the experiment both adults and pups after weaning were given food and water *ad libitum*.

Data analysis

To perform the comparison of reproductive parameters among female individuals collected at different elevations, we applied a Kruskal–Wallis test for determining litter size differences among altitudes. To detect changes in the development of pups among the three sites, we also performed a Repeated Measures ANOVA using altitude as the categorical variable and mean pup mass at 15, 30, 45, 60, 75 and 90 days, as the response variable. If interaction 'mean pup mass \times altitude' resulted significant, we applied *a posteriori* tests (i.e. comparing mean pup mass at each age class among altitudes).

To evaluate the effect of experimental thermal treatments, we first compared the body mass of females before pregnancy under both treatments using Wilcoxon paired test. Then, to assess reproductive parameters we applied a Wilcoxon paired test to detect differences between litter size under both temperatures. We also performed a Two-way Repeated Measures ANOVA using thermal treatments as categories and mean pup mass at different ages as response variable. When the effect of the interaction 'experiment \times age' was significant, we applied an *a posteriori* paired *t* test to determine differences between the thermal treatments at each age (i.e. comparing mean pup mass at each age class between treatments). The statistical analyses were performed using INFOSTAT 2013 version (Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina) and R 3.3.1 software (R Development Core Team, 2016).

Results

From the initial group, out of 30 collected females 18 were pregnant (six per site) and gave birth in captivity under standard conditions (22°C , 12L:12D). Litter size was significantly greater in animals from 3100 m a.s.l. compared to animals from 1700 m a.s.l. ($H = 7.07$ $P = 0.02$, d.f. = 2). Animals from 2300 m a.s.l. showed an intermediate mean value that was not significantly different from the other two sites (Fig. 1). Mean mass of the pups did not change according to the mother's origin site throughout their development (repeated

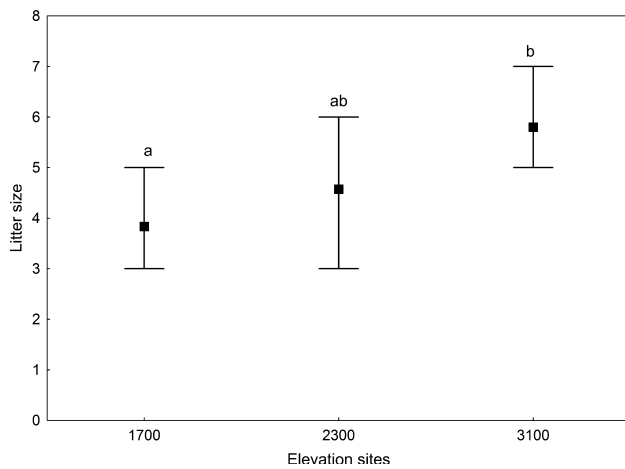


Figure 1 Litter size (mean ± sd) from pregnant females collected in the field at the three elevation sites. Different letters indicate significant differences among sites.

measures ANOVA; altitude: $F = 0.81$, $P = 0.51$, d.f. = 1; ages: $F = 60.31$, $P < 0.01$, d.f. = 5; interaction ‘mean pup mass × altitude’: $F = 0.79$; $P = 0.63$, d.f. = 10; Fig. 2).

Experimental trials were conducted with animals born in captivity from mothers belonging to the middle elevation site. We found that females’ body mass before pregnancy at 30°C was significantly higher than at 17°C (mean_{17°C} = 82.02 g, mean_{30°C} = 91.56 g, $Z = 2.19$, $P = 0.02$). T_a had no effect on litter size (mean_{17°C} = 4.54; mean_{30°C} = 4.54; $Z = 0.06$; $P = 0.95$). Nevertheless, mean pup mass varied along pup development between treatments (two-way repeated measures ANOVA; experiment: $F = 0.72$, $P = 0.40$, d.f. = 48; age: $F = 782.49$, $P < 0.01$, d.f. = 816; interaction ‘experiment × age’: $F = 2.11$, $P < 0.01$, d.f. = 816; Fig. 3). Paired comparisons for the treatments within each age revealed

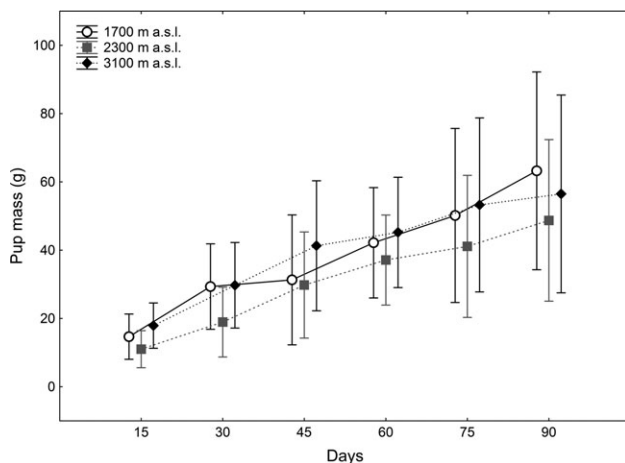


Figure 2 Mean pup body mass variation throughout their development under 22°C in the laboratory. Litters correspond to F0 mothers collected at the three elevation sites.

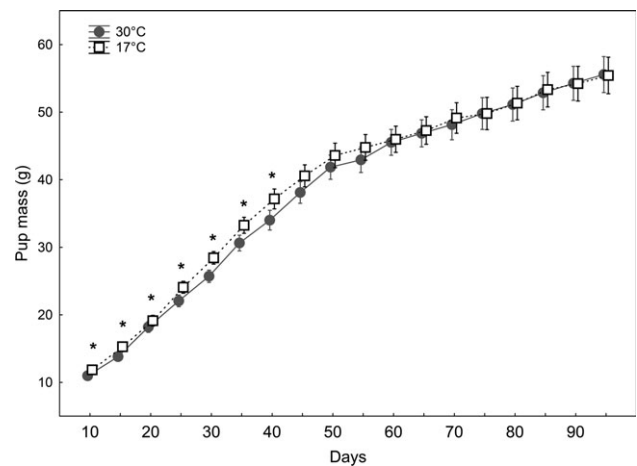


Figure 3 Mean pup body mass variation throughout their development under 17°C and 30°C treatments. Litters correspond to F1 females alternatively acclimated and bred at both temperatures. Asterisks indicate significant differences in mean pup mass between treatments within each age.

that mean pup mass was significantly higher at 17°C throughout the period from 10 to 40 days of development compared to those born at 30°C (Table 2). No significant differences were found subsequently (i.e. from 45 to 90 days old, Table 2).

Discussion

Studying the mechanisms and processes that account for energy expenditure and acquisition, especially during reproduction, is central to understand the evolutionary ecology of organisms. Temperature is an environmental variable largely invoked to explain latitudinal as well as altitudinal patterns, precisely because of its relevance to the energy balance (i.e. variation in life-history traits or physiological and morphological adjustments; Hayes & O’Connor, 1999; Hammond, Szewczak & Król, 2001; Rezende *et al.*, 2001; Speakman & Król, 2010). Other authors propose seasonality as a resource-related explanation for latitudinal and altitudinal variation in reproductive investment. The fact that resources often are unpredictable and might be limited, implies trade-offs between allocation to reproduction and all other processes (Sikes & Ylönen, 1998). This study attempted to unveil the existence of altitudinal variation in reproductive parameters and explore a possible temperature related mechanism. *P. xanthopygus* has proven to be a good model for this type of research because of its broad distribution and ecological flexibility (Nespolo *et al.*, 1999; Steppan *et al.*, 2007).

Our field data partially supports HDL predictions, as females collected at the high altitude site gave birth to larger litters than females captured at the low elevation site. Even though statistical differences are small, they are in line with greater investment where it is colder. Assuming no selective loss once captured, then the litter size they give birth to, is what they would be expecting to raise in the wild. This pattern is contrary to expectations from the environmental or central limit

Table 2 Pairwise comparisons between the pup mass (mean \pm SE) born at the two different experimental treatments. Values in bold indicate significant differences

Days of development	Mean pup mass at 17°C	Mean pup mass at 30°C	<i>P</i>	Statistic <i>t</i>	d.f.
10	11.87 \pm 0.25	10.99 \pm 0.21	<0.01	-3.26	50
15	15.31 \pm 0.28	13.84 \pm 0.24	<0.01	-3.86	50
20	19.26 \pm 0.32	18.19 \pm 0.45	<0.01	-3.01	50
25	24.15 \pm 0.37	22.08 \pm 0.48	<0.01	-3.28	50
30	28.54 \pm 0.46	25.78 \pm 0.44	<0.01	-3.08	50
35	33.23 \pm 0.54	30.68 \pm 0.61	<0.01	-2.15	50
40	37.11 \pm 0.59	34.07 \pm 0.82	0.03	-2.21	50
45	40.40 \pm 0.76	38.23 \pm 0.83	0.15	-1.47	50
50	43.83 \pm 0.91	41.83 \pm 0.87	0.39	-0.87	50
55	45.01 \pm 0.86	43.09 \pm 1.01	0.27	-1.1	50
60	46.12 \pm 0.94	45.63 \pm 0.96	0.90	0.12	50
65	47.63 \pm 1.01	46.94 \pm 1.01	0.98	0.02	50
70	49.43 \pm 1.01	48.21 \pm 1.01	0.71	-0.37	50
75	50.37 \pm 1.24	49.87 \pm 1.12	0.71	0.37	50
80	52.10 \pm 1.25	51.20 \pm 1.23	0.97	-0.04	50
85	54.07 \pm 1.29	53.00 \pm 1.30	0.97	-0.04	50
90	55.11 \pm 1.31	54.29 \pm 1.32	0.99	0.004	50

hypotheses that advise energy allocation trade-offs among processes and thermoregulation costs for a small endotherm under low T_a . Mean pup mass did not differ among sites throughout their growth. Thus, the total amount of energy allocated to a reproductive event was comparatively higher for mice derived from high altitudes than at lower ones. Although pups from all sites were raised under a uniform T_a of 22°C in the laboratory, there was no trade-off between litter size and pup mass (not in line with HDL predictions). Conversely, this result is consistent with the environmental limit hypothesis, suggesting greater investment in larger litters because in the laboratory food was unlimited and T_a was slightly under the TNZ (Menéndez *et al.*, 2017).

Litter size differences are probably reinforced by thermal ranges that consistently differ among sites throughout the year (Table 1), where increasing difference between T_b and T_a , favours relatively higher metabolic expenditures at high elevations (Rezende *et al.*, 2001). McNab (1980) suggested a correlation between metabolic rates and rates of biosynthesis, and Glazier (1985) corroborated this for milk production in five species of *Peromyscus*. In addition, hormones stimulating milk production are directly linked to the number of pups, so a female is physiologically programmed to feed them (Sikes & Ylönen, 1998). All this accounts for our tested females' ability to sustain their respective litters. Furthermore, in highly seasonal environments, a shorter favourable time window for breeding could allow a lower number of reproductive events. Females with a fixed allocation of resources will then maximize the number of surviving offspring per season (Spencer & Steinhoff, 1968; Swihart, 1984; Sikes & Ylönen, 1998). Both explanations would be consistent with our field observations, but still the underlying mechanism remains to be explored.

Thus, our goal with the laboratory experiment was to disentangle the influence of immediate T_a from that of other altitude-related factors. To discard location-specific effects we

conducted this part of the study with animals born in captivity to mothers from the middle elevation site. We found no differences in litter size between thermal treatments. Still, the data partially supported the expectations from the HDL theory, because pups raised under the 30°C treatment showed a lower mean body mass compared to those raised at the 17°C treatment, during lactation. This is consistent with the prediction of limited energy investment at low thermal difference between body and environment. On the contrary, prospects from the other hypotheses of energy restrictions under low T_a were not supported.

Litter size was in fact very similar between progeny born under both experimental temperatures and mice born to pregnant females collected at that particular location (i.e. 2300 m a.s.l.) in the field. This apparent similarity could be the result of phylogenetic inertia in litter size for the F1 generation. However, the among-site variation previously found for this parameter is unlikely to be a result of genetic differences between locations as previous analyses reported high gene flow across the elevation cline (Ojeda *et al.*, 2013). Differences might be more likely to reflect epigenetic effects at the local level, reinforced by the influence of distinctive T_a at each site. Rezende *et al.* (2001) found that *Phyllotis* species showed higher maximal metabolic rates and aerobic scope at higher altitudes. There, higher metabolism could sustain greater litters. Further studies replicating the experiments on animals from the other elevations (1700 and 3100 m a.s.l.) are necessary to unravel this issue.

As expected from HDL theory, our results showed that T_a had an effect on offspring mass in line with previous work on wild and laboratory rodents (Hammond & Diamond, 1992; Johnson & Speakman, 2001; Król & Speakman, 2003; Król, Murphy & Speakman, 2007; Simons *et al.*, 2011). These studies have also demonstrated an increased milk production in mothers exposed to relatively low T_a , and

according to Sikes & Ylönen (1998) milk availability is the main determinant of offspring growth. The lactation period is the most demanding stage in the life of mammals (Speakman & Król, 2010); it supposes an increase in the daily energy expenditure of up to 82% with respect to maintenance demands (McNab, 2012), and generates great amounts of metabolic heat. We suggest that under the 17°C treatment, milk production is probably taken to a higher level than under 30°C. In fact, our data show that pups mass was lower under the high T_a treatment only between days 10 and 40, which is consistent with a decrease in lactation at 30°C. During the following period from days 45 to 90 (after weaning, with food *ad libitum*), pups seem to compensate growth rate as differences vanished in spite of continuing under the thermal treatments. This supports the prediction that milk production and therefore offspring mass are shaped by T_a (Hammond & Diamond, 1992, 1994; Johnson, Thomson & Speakman, 2001a,b; Laurien-Kehnen & Trillmich, 2003). Offspring mass is often used as a surrogate for fitness because it is correlated with probability of survival and reproductive potential. Environmental variables affecting offspring's growth and development rates have direct impact on reproductive parameters, and indirectly rebound at the population and other organization levels (Veloso, 2003).

Previous experiments on *P. xanthopygus* have reported that high temperatures in the laboratory (30°C) result in lowered activity, decreased food intake and increased body mass in non-breeding animals (Sassi & Novillo, 2015; Sassi *et al.*, 2015). Likewise, we found here that F1 females' mass increases under the 30°C treatment, but still their pups were significantly smaller than those lactating at 17°C. Together with the results of this study, the evidence suggests that T_a triggers adjustments in *P. xanthopygus* below but also within its TNZ.

Climate change forecasts predict a relatively rapid warming in the Andes mountain ecosystems (2–4°C over the next 100 years; Labraga & Villalba, 2009). A species that evolved in high altitudes, inhabits cold and temperate areas (Steppan *et al.*, 2007) and is sensitive to T_a increases in the lab, appears as an excellent candidate to further explore the ecophysiology-thermal landscape interface, crucial to develop accurate predictive models of biodiversity dynamics.

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