



Effect of Temperature on Activity Patterns in a Small Andean Rodent: Behavioral Plasticity and Intraspecific Variation

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Abstract

The activity rhythm of a species is ruled by internal signals as well as external factors. Among them, ambient temperature strongly influences the amount, duration, and distribution of an organism's activities throughout the day. The result is a pattern of activity that, between certain limits, can be flexible to deal with seasonal and spatial thermal heterogeneity. The range of behavioral plasticity increases with environmental variability and could be beneficial for a species' persistence under novel conditions. Thus, the goal of this study was to experimentally explore the behavioral plasticity in *Phyllotis xanthopygus*, a rodent species inhabiting an altitudinal gradient in the Central Andes Mountains of Argentina. In the laboratory, we assessed activity rate and pattern under different temperatures by comparing groups of individuals collected at different altitudes. All animals were acclimated to subsequent thermal treatments in a paired design. As expected, *P. xanthopygus* showed changes in activity under different temperatures, and animals from diverse altitudes were differently affected. In particular, animals from mid-altitudes and high altitudes reduced their activity under high temperatures. Intraspecific differences across the altitudinal gradient suggest that animals from mid-altitudes and high altitudes are less heat tolerant than those from lower sites, in spite of acclimation to equal conditions. We propose that climate ranges experienced in the field possibly promote this different response. Our results are discussed in light of recent forecasts of temperature rises in the region, which could constrain *P. xanthopygus* activity in space and time.

Introduction

The activity rhythm of a species is ruled by internal signals from the hypothalamus, and synchronized with light periodicity, through the retina via the retino-hypothalamic tract (Saarela & Reiter 1994; Reuss 1996). This rhythm is also molded by other external factors such as distribution and abundance of resources, competition, predation risk, and climate factors such as rainfall or temperature (Halle & Stenseth 2000; Körtner & Geiser 2000; Fragaszy et al. 2004). Furthermore, activity rhythms are subject to intrinsic characteristics of the animal, such as physiology, morphology, and behavior. These phenotypic traits are genetically based, and their expression is influenced

by the environment. Some of them are usually irreversible (morphology, developmental plasticity), while others can be highly flexible on short time scales. In particular, behavioral plasticity is one of the flexible manifestations of the phenotype (Pigliucci 2001). The way animals allocate time to daily activities establishes a pattern, that is, what activities they do, when, and for how long (Lehner 1996). This activity pattern is influenced by the costs and benefits of being active during certain periods, affecting time and energy budgets of animals (McNab 2002). Therefore, the general activity pattern (i.e., nocturnal, diurnal, crepuscular, ultradian, arrhythmic) is the phenotypic response to how environmental restrictions interact with endogenous rhythms (Aschoff 1964).

Ambient temperature plays a crucial role in different aspects of organisms' biology. It governs environmental conditions as well as phenotypic adjustments of individuals, such as metabolic rate variation, behavioral thermoregulation, or pelage insulation, with relevance on energy balance and ultimately on fitness (Bozinovic et al. 2011 and references therein). Therefore, the optimal amount, duration, and distribution of activities are influenced by energy availability which is strongly related to ambient temperature (Daan & Aschoff 1982; Angilletta et al. 2010). In particular, small endotherms' energy balance can be challenged by ambient temperature changes due to a relatively high surface/volume ratio and, thus, a low thermal inertia that increases energy demands for thermoregulation (McNab 2002). Maintenance of body temperature between certain limits is central to homeostasis; therefore, activity rhythms could be modified by animals to cope with ambient temperature variations in order to avoid episodes of hyper- or hypothermia.

The behavioral responses of small mammals to low temperatures may involve changes in daily activity patterns, social grouping, microhabitat selection, and nest building (Bozinovic et al. 2000; Taraborelli & Moreno 2009). Benefits of these adjustments include decreased metabolic rate (Karasov 1983; Contreras 1984; Andrews & Belknap 1986) and increased survival (Sealander 1952). On the other hand, responses to warm temperatures include decreased energy intake (Hammond et al. 2001; Sassi & Novillo 2015), depressed thermogenic capacity (Nespolo et al. 2001), lowered activity rate (Zub et al. 2009), changes in the onset and reduction of activity period (Murray & Smith 2012), and avoidance of high-temperature patches in the field (Bozinovic et al. 2000).

Behaviorally flexible responses, occurring on short time scales make a major contribution to the adaptability of animals (Pigliucci 2001). According to Komers (1997), the range of this behavioral plasticity should increase with environmental variability. From an evolutionary perspective, this could be beneficial for native species' persistence, facilitating adaptive change by initially allowing a population to persist under novel conditions. It is called 'the Baldwin effect' and is defined as the benefit obtained by animals from coping with environmental variation through behavioral plasticity (Westneat & Fox 2010). For all the above, a small mammal with a broad geographic distribution is a good model to test for phenotypic plasticity in response to temperature changes. Data from the last two centuries indicate that warming of the climate system is unequivocal, as is now evident from observations of increases in global

average air and ocean temperatures, widespread melting of snow and ice, among other signals (IPCC 2014). In view of this current climate change scenario, it is interesting to investigate the behavioral responses of a native species to changes in its thermal landscape. Particularly relevant for this study, some of the reported effects are changes in species' activity rhythms and dispersal along altitudinal gradients (Sparks et al. 2001).

Spatial heterogeneity, scarce resources, and extreme temperatures typical of arid environments offer an opportunity for determining the effect of varying ambient temperatures on activity patterns. For all this, *Phyllotis xanthopygus* seems a good model species because it is widely distributed along the Andes Mountains in southwest Argentina, north-central Chile, southwest Bolivia, and southern Peru, encompassing high environmental heterogeneity (Steppan et al. 2007). In the Central Andes of Argentina, the species has been found at altitudes between 1500 and 3300 m (Novillo & Ojeda 2014). This altitudinal range covers a broad temperature and rainfall gradient across a steep slope, implying strong environmental variations. Climate estimates indicate that *P. xanthopygus* endures markedly different conditions at diverse altitudes, with a pronounced decrease in annual mean ambient temperature and an increase in relative humidity toward higher elevations (Sassi & Novillo 2015; Table 1). The species is a mouse of medium size (body mass of adults' ca. 55 g) with large ears (length ca. 27 mm) and a tail close to the length of head and body. The overall color is grayish brown, and the pelage is long and soft. It has been described as an herbivore, but high variation in diet is reported among subspecies as well as across altitudes (Kramer et al. 1999). Particularly at this site, the species feeds on an essentially herbivorous, but seasonal, diet which in summer also includes insects and seeds (P. Sassi own data). Previous research has shown shifts from a strictly nocturnal schedule to activity bouts throughout a 24-h period, under different light intensities in the laboratory (Kramer et al. 1999). This

Table 1: Data on basic climatic variables for each site: mean annual temperature (Tmean), temperature annual range (T range), mean relative humidity (RH mean), relative humidity range (RH range)

Study site (m a.s.l.)	1700	2300	3100
Tmean (°C)	14.9	11.1	7.4
T range (min°C–max°C)	–6.8–33.7	–5.9–25.9	–7.8–20.9
RH mean (%)	45	50	56
RH range (min%–max%)	4–92	0.4–97	3.7–100

Data taken from Sassi & Novillo (2015).

suggests that the species activity pattern is flexible in response to environmental signals.

A powerful approach to explore a species' versatility is studying phenotypic trait variation along natural geographic gradients (Chown et al. 2004). Thus, the main goal of this study was to assess plasticity in the rate and pattern of activity of *P. xanthopygus* individuals from different sites along an altitudinal gradient, under the influence of different experimental temperatures. We hypothesize that, considering its broad geographic distribution, the species is plastic to cope with environmental heterogeneity, with behavioral changes (i.e., activity pattern) as a first line response. We expect animals to show changes in their rate and pattern of activity under different experimental temperatures and, given the diverse climate ranges at each origin site, we also expect the magnitude of the response to vary among animals from different altitudes. Particularly, we expect that animals from higher elevation sites will decrease their activity under warm temperatures in relation to the individuals from medium and lower elevation sites. We anticipate a decrease of activity in animals from lower elevation sites under cold temperatures in relation to the individuals from medium and higher elevation sites. And we predict that animals from different altitudes will show similar activity under mild temperatures.

Materials and Methods

Study Area

The study area is located at El Manzano Histórico Reserve, Mendoza Province, Argentina. We established sampling sites at 1700, 2300, and 3100 m elevation along an altitudinal transect (33°36'48.4''S - 69°28'42.7''W). Sites were 3 to 4 kilometers apart, encompassing gradual changes in a landscape characterized by low, sparse vegetation. The sites belong to different phytogeographic regions: sites at 1700 and 2300 m elevation correspond to the Andina ecoregion and that at 3100 m elevation to the Alto Andina ecoregion (Méndez 2011). Climate data were obtained in a previous study (Sassi & Novillo 2015) and are presented for each site in Table 1.

Animals and Acclimation

Thirty non-reproductive adult *P. xanthopygus* (ten from each site) were captured using Sherman traps between February and March 2013. All animals belonged to the same subspecies, with a sex ratio of

1/1. Based on our data set, individuals from different sites have no differences in body size (59 ± 3.76 g [1700 m a.s.l.], 60.3 ± 5.54 g [2300 m a.s.l.], and 64.3 ± 3.94 g [3100 m a.s.l.], Sassi & Novillo 2015). Genetic analyses of the individuals showed no genetic structure and high gene flow levels among sites (Ojeda et al. 2013).

In the laboratory, animals were maintained on chinchilla food pellets and water *ad libitum*. Food choice was based on previous knowledge of *P. xanthopygus*' herbivorous diet (López-Cortés et al. 2007). Individuals were housed individually in $30 \times 30 \times 40$ cm cages and maintained on 12L:12D photoperiod and at 25°C ambient temperature during 8 wks (standard laboratory conditions—Bozinovic & Nespolo 1997; Nespolo et al. 1999).

Experiment

To test for geographic-related variability, a common garden experiment (Garland & Adolph 1991) was performed; comparing individuals from different sites acclimated to common experimental conditions in the laboratory. This method is effective for detecting reversible plasticity through acclimation, while geographical effects are attributable to irreversible developmental effects, maternal effects, or genetic differences.

The experiment consisted of three trials in which rate and pattern of activity were determined on each individual under subsequent temperature treatments. Before each trial, individuals were acclimated to 25°C (trial I), 16°C (trial II), and 31°C (trial III), respectively. Variables were measured after 8 wks of acclimation to each temperature in order to detect the effect of treatments and site-related differences. The total period of acclimation for the whole experiment is equivalent to 6 mo.

Experimental temperatures were chosen based on two elements. First, preliminary field estimates evidenced a mean ambient temperature differential of 15°C between the most extreme sites along the altitudinal gradient considered. In fact, mean ambient temperatures at the time of animal captures were 24.3 ± 4.1 °C (1700 m elevation), 18.9 ± 2.3 °C (2300 m elevation), and 12.7 ± 2.3 °C (3100 m elevation), which provided preliminary information on the range of ambient temperature experienced by the species. Second, previous baseline studies on *Phyllotis darwini* and *P. xanthopygus* searching for temperature-related responses, acclimated animals to 15 and 30°C, these extremes corresponding to contrasting experimental conditions, respectively, while the typical

laboratory maintenance temperature was 25°C (Bozinovic & Nespolo 1997; Nespolo et al. 1999; Canals et al. 2009).

To determine daily activity rate and activity pattern for each individual, we used camera traps with movement sensors (DORR Boly Guard 5.0 IR.). To do the sampling, a camera was located in front of an isolated cage that housed one individual whose motion was recorded for 30 h. Animals had a plastic tube as a den, and movements were detectable every time they left it or moved within the tube. Cameras were set to detect movement and take a photograph each time, at an interval of 5 min. Each picture represented a bout of activity. Photographic records from the first 6 h were discarded to avoid influence of the experimental setting on each animal's behavior. The database was built using the hour, minutes, and seconds at which pictures were taken; therefore, number and time of movements were obtained for each individual over a 24-h period and compared among experimental treatments. Activity rate was defined as the number of movements per hour (mov/h) detected by the camera traps. Activity pattern was defined by the onset and duration of the activity period (hours).

Data Analysis

To evaluate the effect of altitude and temperature treatment on activity rate, we performed a repeated measures ANOVA, using experimental temperatures as repeated measures or levels of the factor treatment, site of origin as fixed factor and number of movements per animal/hour as the response variable.

To analyze the patterns of activity, we used circular statistics because distribution of the data throughout the day occurs on a circular scale. Reference studies on activity patterns and time partitioning have used circular statistics (e.g., Di Bitetti et al. 2009; Gerber et al. 2012). Data from circular distributions should not be analyzed using classical statistical methods due to the arbitrariness of the zero point (Zar 2010; Pewsey et al. 2013). The activity pattern is described as the smallest portion of the circle's circumference that contains all the data in the distribution. Therefore, trigonometric functions were used to obtain descriptive statistics of this data such as mean time of activity (mean vector), length of mean vector (r) that varies between 0 and 1 decreasing with the range of activity period, and other dispersal estimates such as concentration (estimating how scattered activity bouts are distributed around the mean vector), circular variance and confidence limits of the mean vector (both estimating amplitude of the activity pattern). Descriptive

estimates were obtained for the global data set (data from all mice pooled) under every treatment, and afterward for animals from each altitude separately. Similarly, circular statistical analyses were primarily made to determine the effects of temperature treatments on the activity patterns of all individuals irrespective of their origin and, further, paired comparisons were conducted among the groups of animals from each altitude to search for differences in their responses to temperature treatments.

To test whether data were randomly distributed around the day–night cycle, a Rayleigh test of uniformity (Zar 2010) was carried out using the above-mentioned descriptive statistics under each temperature treatment, comparing them against the null hypothesis that there is no mean direction of the data. A significant difference would be indicative of a non-uniform circular distribution of data, resulting in an activity pattern defined by a mean vector, a vector length different from 0, and dispersion estimates.

To assess the effect of temperature treatment on activity patterns, we performed a Moore's test for paired circular data. This is a nonparametric test which allows comparing sets of activity data among treatments and find out equivalent or different patterns. Paired comparisons between all samples exposed to each temperature treatment were performed subsequently. Afterward, the same among-treatment comparison was made separately with data from each group (i.e., 1700, 2300, and 3100 m elevation), with the objective to reveal potential intraspecific differences in the response to temperature variation.

The statistical analyses were performed using Statistica (StatSoft 2007) package for Windows and Oriana circular statistical package for Windows (version 4.0).

Results

Activity rate was significantly different among treatments ($F_{(2,50)} = 9.66$; $p < 0.01$). *Post hoc* Tukey comparisons revealed that activity rate at 16°C (mean = 3.37 mov/h; SE = 0.31) was similar to that at 25°C (mean = 3.35 mov/h; SE = 0.31) and both were significantly higher than activity rate at 31°C (mean = 2.39 mov/h; SE = 0.26). The interaction between factors was not significant ($F_{(4,50)} = 0.88$; $p = 0.48$). However, the effect of temperature treatments on the animals' activity rate was different depending on their site of origin. In fact, the reduction in activity rate observed at higher experimental temperature increases with altitude. Particularly for individuals from 2300 and 3100 m elevation, we found

that activity rate decreased significantly at 31°C compared to 16°C and 25°C. On the other hand, animals from 1700 m elevation did not show any changes in their activity rate among treatments (Fig. 1).

Regarding activity patterns, circular statistics allowed obtaining descriptive statistics for all animals under each treatment (Table 2) and for each altitudinal group in particular (Fig. 2). In general, for all altitudinal groups under all experimental conditions, activity was concentrated in the dark phase, and no activity was recorded during daylight hours. This is supported by the Rayleigh test of uniformity, which in all cases indicated that circular data were restricted to the dark phase and significantly different from uniformity ($p < 0.001$, Table 2). Moore's paired test revealed significant differences when comparing activity patterns among temperature treatments, specifically between the 31°C and 16°C treatments and between the 31°C and 25°C treatments (Table 3). In fact, at 31°C, activity peaked earlier (40 min approximately) than under the lower temperatures, as differences in mean vectors show (Table 2). In sum, the general pattern was significantly affected by experimental treatments with a reduction of activity rate and an earlier start of the activity period under 31°C. The by-group analysis recorded similar tendencies, but only the group from 2300 elevation showed a statistically significant variation in the activity pattern due to experimental temperature (Table 3). These results suggest intraspecific (i.e., altitudinal) differences in activity patterns in response to temperature variation (Fig. 2).

Discussion

The relationship between activity and ecological variables has been approached many times, recording the influence of light, temperature, food availability, and predation risk (Daly et al. 2000; Kenagy et al. 2002; Hut et al. 2011). This study reports a certain degree of behavioral plasticity in response to environmental variation, particularly in dealing with temperature changes. As expected from its heterogeneous habitat in climate terms, our model species showed changes in rate and pattern of activity under different temperature treatments. We also found that activity was concentrated at night, corroborating the nocturnal preference of the species, at least under our experimental conditions (see Kramer et al. 1999). For instance, in *Phyllotis darwini*, plastic variation in activity has also been reported in response to food restrictions, within the limits of the nocturnal phase (Rezende & Bozinovic 2001). Temperature and food resources are known determinants of energy budget (McNab 2002), so behavioral plasticity in response to these signals is not surprising. Activity rhythms may play an important role in the adjustment to different conditions, within the limits of internal rhythms. In this sense, circadian rhythm can underpin the temporal pattern of activity, but its ultimate expression is influenced by environmental factors (Aschoff 1964).

A common garden design is a powerful tool to uncover the variation in rate and pattern of activity at the intraspecific level, informing about flexibility or differentiation across the environmental gradient. The

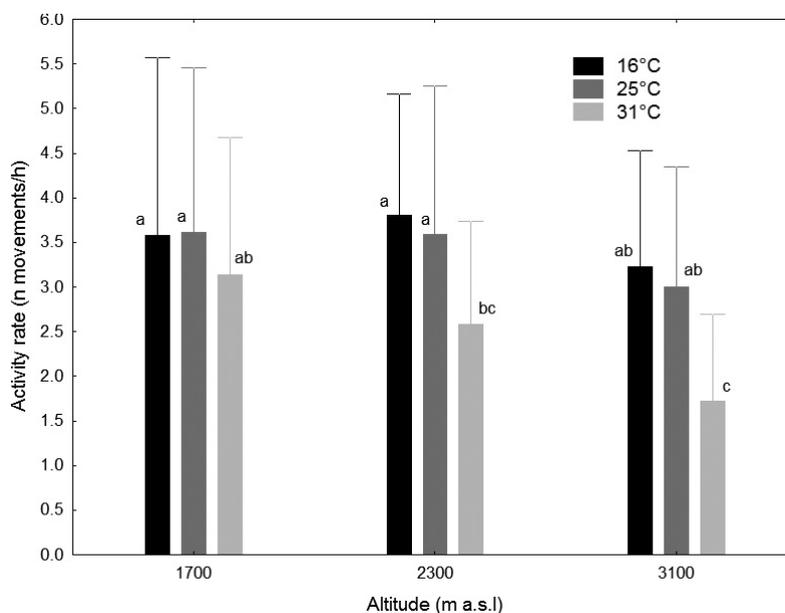


Fig. 1: Activity rate of *P. xanthopygus* estimated as the number of movements per hour, in individuals from different altitudes exposed to different temperature treatments. Vertical bars denote standard deviations. Means with different letters are significantly different at an alpha rejection rate of 0.05.

Table 2: Descriptive statistics for the data set of all mice pooled under each experimental treatment: mean time of activity (μ), length of mean vector (r), and dispersal estimates (concentration, circular variance, and confidence limits of the mean vector)

Temperature treatment	16°C	25°C	31°C
Observations (N)	28	28	28
Mean vector (μ)	00:53 a.m.	00:57 a.m.	00:17am
Length of mean vector (r)	0.94	0.97	0.96
Concentration	8.5	17.33	11.63
Circular variance	0.06	0.03	0.04
Circular standard deviation	01:21 a.m.	00:55 a.m.	01:08 a.m.
95% confidence interval (\mp) for μ	00:23 a.m. 01:23 a.m.	00:36 a.m. 01:18 a.m.	23:51 p.m. 00:42 a.m.
Rayleigh test of uniformity (p)	< 0.001	<0.001	<0.001

Rayleigh $p < 0.05$ indicates non-uniform distribution of the data.

lack of differences in activity rhythms under 16°C and 25°C treatments is probably because these temperatures fall within or close to the thermal ranges experienced by all animals in the field (Table 1). Instead, under the 31°C treatment, there is an altitudinal pattern for the behavioral response which also suggests acclimatization to the temperatures prevailing at the origin sites. As expected, individuals from 1700 m elevation, where ambient temperature in summer usually reaches 30°C, seemed unaffected by the 31°C treatment compared to animals from the highest site, where this condition is non-existent. Animals from the intermediate elevation showed a less dramatic although significant reduction in activity, which possibly mirrors its acclimatization to intermediate temperatures and thermal range (Table 1). In sum, activity rate declined under high temperatures only in individuals from 2300 and 3100 m elevation. The activity pattern was also shortened under the 31°C treatment (i.e., the timeframe spent active was reduced). The by-group analyses recorded tendencies partially consistent with the global pattern, although there were differences among animals from different elevations. All in all, intraspecific variability across the altitudinal gradient suggests that animals born at higher sites are less tolerant of high temperatures than those from lower sites, irrespective of a 6-mo period of acclimation to equal conditions in the laboratory. Among underlying mechanisms, genetic differentiation is unlikely because, as was previously mentioned, gene flow is high among sites. Differences are more likely due to maternal effects or development under distinct environments. Maternal effect is the influence of the mother's phenotype, condition, or resource status on its offspring phenotype, irrespective of the

current conditions experienced by the offspring. This is the case of the vole *Microtus arvalis* in which mothers under high ambient temperature produce low-growth rate pups, possibly through a negative effect on maternal milk production (Simons et al. 2011). Also in *Phyllotis darwini*, maternal effects are proposed to explain relatively higher capacities of thermoregulation in neonates born from mothers acclimated to cold (Canals et al. 2009). Thus, the response of a maternal individual to the environment is detected in the next generation (Mazer & Damuth 2001). Developmental plasticity refers to phenotypic variation due to environmentally induced responses throughout organisms' lifetime. Different ontogenetic trajectories can be plastic yielding differentiated adults. Examples of this are diet-induced differences in body size in the grasshopper *Melanoplus femurrubrum* or temperature-dependent sex determination in the common snapping turtle (Pigliucci 2001; and references therein). Maternal effects and developmental effects could be dissected by further studies with animals born and bred in captivity, exposed to the same thermal environment throughout their development. If geographic differences persisted, developmental effects would be ruled out. In this study, all elevation groups belong to the same population and there are no geographic barriers among them. Nevertheless, as animals from diverse elevations endure markedly different climate regimes throughout their lifetime, we tend to support that differences among them are the result of developmental plasticity. A sound mechanistic explanation for this is the reported variation in thermal conductance in *P. xanthopygus*. A recent study along the same altitudinal gradient reveals that animals from higher locations show lower heat loss rates than animals from lower sites (Sassi & Novillo 2015). This study did not investigate the mechanisms behind the variation in thermal conductance. However, previous records in southern populations of the species indicate changes in pelage thickness between animals captured in summer and winter (Kramer et al. 1999). Further studies should explore underlying heat exchange related traits, such as adipose tissue, piloerection, fur color, and posture among others. Nevertheless, the thermal resistance of the pelage (Scholander 1955) is corroborated by recent findings of strong associations of fur properties (depth) with climate (i.e., temperature; Briscoe et al. 2015). Thermal ranges experienced by our model species possibly promote the development of fixed differences in thermal conductance-related traits among individuals from each site. Considering this, we propose that thermal conductance is likely driving intraspecific

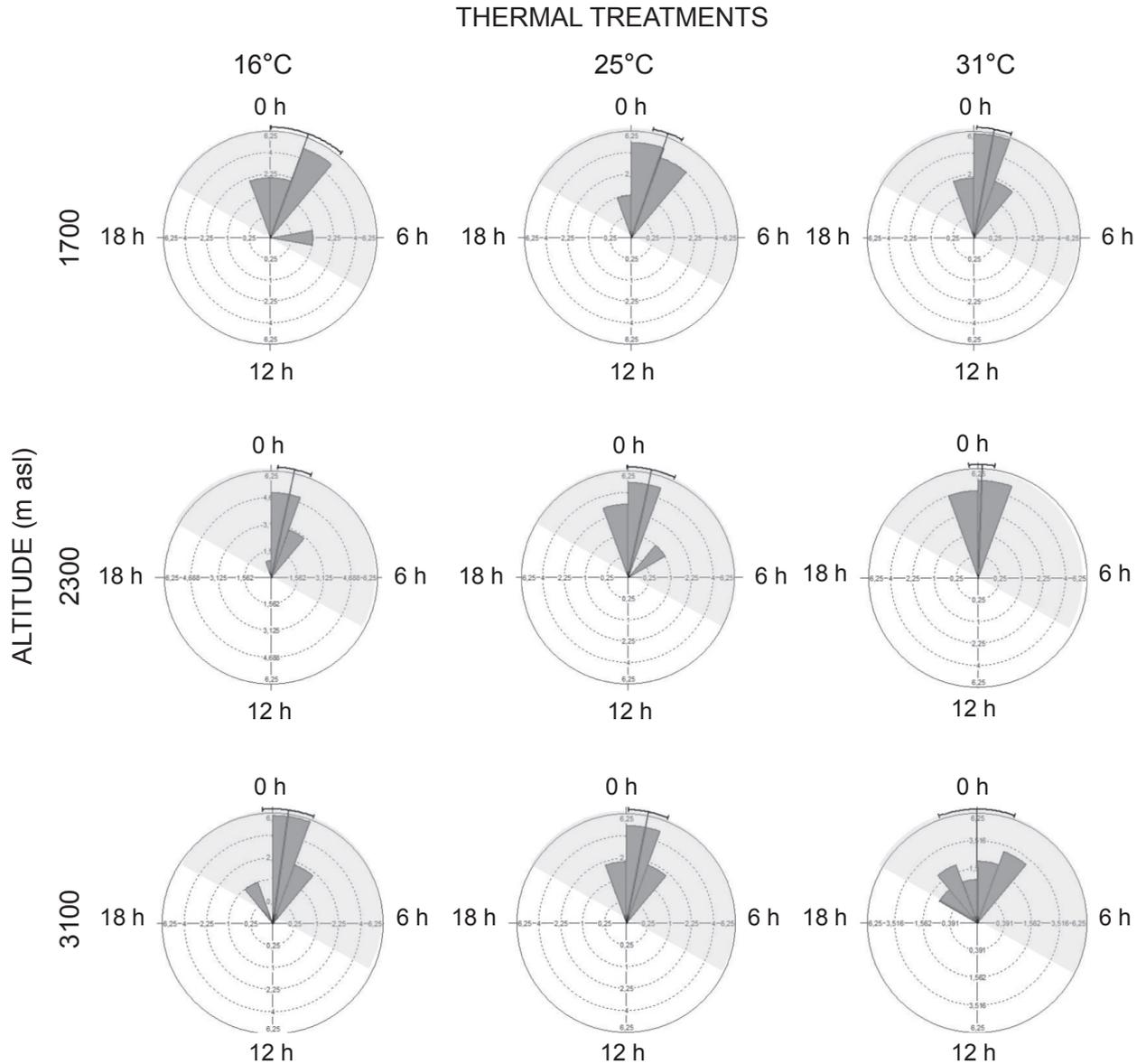


Fig. 2: Rose diagrams representing activity pattern of *P. xanthopygus* from different altitudes with different temperature treatments. Light gray shadow represents the dark phase. Dark gray polygons represent the frequency of movements in each period of time. Black lines represent mean vectors (r) and confidence intervals of 95%.

variation in the response to temperature treatments in the laboratory.

In recent years, the interest in understanding how animals deal with high temperatures has promoted a growing number of studies. Some of them found negative effects on activity (declined activity rate) in small endotherms under high ambient temperatures (Chappell & Bartholomew 1981; Lagos et al. 1995; Bozinovic et al. 2000; Murray & Smith 2012; this study). Activity in non-social small mammals can

account for a relatively high proportion of the energy metabolism (21%, Kenagy & Hoyt 1989). But in already warm conditions, heat produced by activity could be difficult to dispel. Therefore, a decrease in activity is expected in a thermal scenario that involves risk of hyperthermia. Physical activity can actually increase heat production and metabolic rate, affecting energy budgets. For example, Zub et al. (2009) showed that weasels (*Mustela nivalis*) are able to maintain a relatively constant maximum energy output by

Table 3: Paired comparisons of circular means under different temperature treatments

Altitude	Comparison treatments	Number of pairs	R	p range
All	16°C & 25°C	28	0.26	>0.9 > 0.5
All	16°C & 31°C	28	1.02	>0.1 > 0.05*
All	25°C & 31°C	28	1.12	<0.05*
1700	16°C & 25°C	10	0.63	>0.5 > 0.1
1700	16°C & 31°C	10	0.49	>0.9 > 0.5
1700	25°C & 31°C	10	0.64	>0.9 > 0.5
2300	16°C & 25°C	9	0.57	>0.5 > 0.1
2300	16°C & 31°C	9	0.97	>0.1 > 0.05*
2300	25°C & 31°C	9	0.89	>0.5 > 0.1
3100	16°C & 25°C	9	0.22	>0.9 > 0.5
3100	16°C & 31°C	9	0.53	>0.9 > 0.5
3100	25°C & 31°C	9	0.81	>0.5 > 0.1

Moore's paired tests were first performed on the global activity data set and then on each elevation group. Statistically significant differences are highlighted with asterisks (*).

adjusting activity rate to changes in temperature. They recorded a negative correlation between ambient temperature and daily expenditures, and no signs of activity above 25°C. In coincidence, the lowered activity found in *P. xanthopygus* under warm conditions could be interpreted as a strategy to reduce endogenous heat production. This is evidence of a constraint on heat dissipation rate, at least for mid-altitudes and high-altitude animals with relatively lower thermal conductance rates mentioned above.

Behavioral versatility is deemed advantageous for coping with a varying environment in the short term. However, a negative effect on activity under warming temperatures is particularly concerning as it could affect daily maintenance tasks and compromise animal performance. As proposed by Murray & Smith (2012), high temperatures impose a trade-off between remaining in a thermal safety zone vs. habitat exploitation to obtain resources. At the Central Andes, forecasts indicate a 2–4°C mean temperature increase over the next 100 yrs (Labraga & Villalba 2009). Therefore, field investigations are necessary for a complete assessment of how diverse climate parameters influence the distribution of activity in space and time in *P. xanthopygus*, and how predicted changes can affect it along its altitudinal distribution. Considering the current thermal ranges on the studied gradient, the species' variation in activity rhythms is indicative of, and possibly based on, local acclimatization. Further studies on this and other species of the assemblage should determine how behavioral plasticity integrates with physiological and morphological traits to provide comprehensive estimates for the

potential ecological implications of increasing temperatures on these fragile ecosystems.

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