

Seasonal and geographic variation in thermal biology of the lizard *Microlophus atacamensis* (Squamata: Tropiduridae)

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Abstract

1. We studied physiological thermal adaptation in the lizard *Microlophus atacamensis* along a latitudinal range.
2. Field body temperatures were independent from thermal environmental conditions, and show seasonal, but not geographical differences. Selected body temperature did not differ among localities and seasons, and differs from body temperature in fall, but not in spring. We found no difference among sites for heating and cooling rates.
3. Our results suggest that *M. atacamensis* compensates thermal environmental variation mainly by behavioral means.

Keywords: Heating rate; Cooling rate; Thermoregulation; Body temperature; Selected temperature

1. Introduction

Since temperature strongly influences life history traits and fitness of lizards (Grant and Dunham, 1990; Adolph and Porter, 1993), the analysis of how these organisms regulate their body temperature (T_b) and how the physical environment influences their thermal biology is a central framework in thermal ecology (e.g. Huey, 1982; Sinervo and Adolph, 1994). When biotic and abiotic factors can prevent thermoregulation, lizards may select, or may be constrained, to operate at different T_b s. As a consequence, for one species, T_b s may be variable in different populations, or within a population during different seasons (Grant and Dunham, 1990; Andrews, 1998; Catenazzi et al., 2005). Because of these constraints, field observations of T_b s alone do not reveal the thermal preferences of lizards. In this sense, the voluntary T_b that a lizard voluntarily selects in the absence of confounding variables (Licht et al., 1966), called selected body temperature (T_{sel} ;

Pough and Gans, 1982) provides a reasonable estimate of a lizard's preference of environmental constraints for thermoregulation (Hertz et al., 1993; Ibarquengoytia, 2005).

To regulate and optimize their T_b , lizards exhibit a diverse array of behavioral and physiological thermoregulatory mechanisms (Huey, 1982; Stevenson, 1985). Physiological control permits varying the rate at which these animals warm up or cool down their bodies in response to changes in environmental temperatures (Dzialowski and O'Connor, 2001). Some studies have reported that lizards living at lower temperatures show faster heating rates and slower cooling rates than populations dwelling in warmer climates (e.g. Grigg et al., 1979; O'Connor, 1999), indicating physiological control over their thermal conductance (Grigg et al., 1979). Also, intraspecific variation in heating and cooling rates has been considered as an adaptive physiological mechanism to cope with restrictions imposed on behavioral thermoregulation (Labra et al., 2001).

The genus *Microlophus* is composed of 20 lizard species distributed from Ecuador to north-central Chile, including the Galapagos archipelago. It has been divided into two monophyletic groups: *occipitalis*, composed of 10 species

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than inhabit from Ecuador to Northern Perú and the Galapagos, and *peruvianus*, also composed of 10 species ranging from northern Perú to North-central Chile (Dixon and Wright, 1975; Frost 1992). Within the *peruvianus* group two different lineages may be recognized: one lineage evolved adapted to an arid environment of inland desert and valleys, and the other evolved associated with the Pacific coast (Frost, 1992). The latter lineage is composed of two species: *Microlophus quadrivittatus* and *M. atacamensis* (Ortiz, 1980). The geographical range of *M. quadrivittatus* (from Caleta Meca, Perú 17°54'S to Antofagasta, Chile 23°3'S) lies within an area where the extreme desert reaches the coast and there is practically no precipitation during the whole year (maximum recorded = 2 mm/year; Di Castri and Hajek, 1976). In contrast, *M. atacamensis* is the southernmost species of the genus. Its range extends over 500 km into the so-called Desert Coastal area, which has a gradient of precipitation from 2 mm/year in the north (at Antofagasta) to almost 80 mm/year in the south (La Serena, 29°5'S) (Ortiz, 1980; Sepúlveda et al., 2006). The diet of *M. atacamensis* is composed of algae, crustaceans, mollusks and insects in the intertidal zone (Fariña et al., 2003), with an increasing proportion of terrestrial items in a north to south gradient (Fariña et al., 2008). The latitudinal gradient in the use of resources may in turn determine differences in the use of the thermal substrate.

The intertidal zone is an unfavorable thermal environment because lizards lose heat quickly by conduction, convection or evaporation when feeding on a wet rock substrate (Catenazzi et al., 2005). For this reason, lizards may face a trade-off between feeding and thermoregulation. Because *M. atacamensis* populations are under different thermal constraints at latitudinal, seasonal and

microhabitat scales, a temporal and geographical variability in their thermal biology is expected.

In this study we explored the physiological adjustment to environmental temperature in *M. atacamensis* by analyzing three populations along the entire geographical range of this species, from 23°S to 29°S. Considering that environmental temperature decreases as latitude increases, we specifically attempted to test the hypotheses that (1) field T_b and T_{sel} differ among populations and seasons being lower in southern populations of *M. atacamensis* and (2) that in southern populations of *M. atacamensis* heating rates should be faster and cooling rates slower than in northern populations.

2. Material and methods

2.1. Study area

The study was performed in spring 2005 (September, October), summer 2006 (January) and fall 2006 (April) (Southern Hemisphere), in three sites on the northern Chilean coast: Medano (24°37'S; 70°33'W), Zenteno (26°51'S; 70°49'W) and Arrayán (29°41'S; 71°19'W) (Fig. 1). Medano and Zenteno are under a coastal desert climatic regime, characterized by less than 2 mm of rain per year (Di Castri and Hajek, 1976). Mean air temperature (T_a) in Medano ranges from 16.8 °C in winter to 21.2 °C in summer. In Zenteno, T_a varies between 15.4 °C in winter and 20.7 °C in summer. The southernmost locality, Arrayán, falls into the semi-arid Mediterranean zone (Di Castri and Hajek, 1976). Rainfall in this site averages 60 mm/year, and mean temperatures are around 13.5 °C in winter and 18.2 °C in summer (data for the three sites were

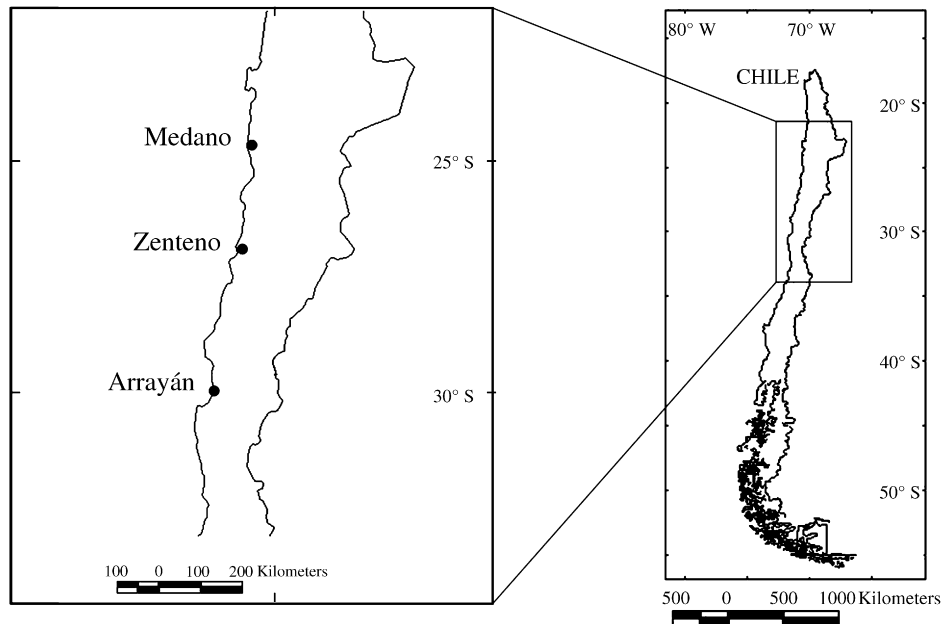


Fig. 1. Study map showing the geographic location of the collecting sites of *Microlophus atacamensis*.

obtained from the Servicio Hidrológico y Oceanográfico de the Armada de Chile).

Lizards were captured along the intertidal zone in a stretch of approximately 150–200 m. At these sites, beaches consist of flat areas of a mixture of rocks (with heights from 0.2 to 3 m), pebbles, cobblestones and sand (Vidal et al., 2002).

2.2. Field data recorded

In each season and locality we captured both active and inactive lizards. A lizard was considered as inactive when it was found under pebbles or rocks (generally early in the morning or in cool days) and exhibiting slow movements. Immediately after capture, T_b of lizards was recorded with a Digi-Sense thermocouple thermometer (accuracy 0.1 °C). We only considered the T_b of lizards that were handled less than 30 s after the capture. We manipulated them by holding their legs in order to reduce heat transfer between lizards and the observers. Date of capture, snout–vent length (SVL, ± 0.5 cm), and body mass (± 0.5 g) were registered for each individual. Additionally, substratum temperature (T_s ; in rocks or soils) and T_a (10 cm above the ground) were also recorded at the capture sites. Lizards were separated by sex and age class following Ortiz (1980). The non-parametric Kruskal–Wallis test was used to evaluate the effects of seasonality and locality on T_b of lizards because the data were not normally distributed. Active and inactive lizards were analyzed separately. Finally, T_b of active and inactive lizards was compared using a Kolmogorov–Smirnov two sample test (Sokal and Rohlf, 1995).

To establish an approximation to the thermal conditions of the habitat occupied by lizards, we placed 12 Tidbit™ temperature data loggers at randomly selected microsites for each season and locality. According to Vitt and Sartorius (1999), thermal profiles collected from the electronic devices do not differ substantially from copper lizard models exposed to the same conditions, suggesting that Tidbits may be used directly to monitor operative temperatures (T_e). To test whether this assumption was true for our model species, in the laboratory we calibrated the Tidbits measurements with those of dead lizards placed in a thermal gradient. The results showed that recorded from electronic devices are fully correlated with temperatures from dead *M. atacamensis* lizards exposed to identical thermal conditions ($r = 0.99$).

2.3. Selected temperature (T_{sel})

Experimental conditions were set to obtain T_{sel} in lizards in spring and fall. For two consecutive days, two lizards were kept in a terrarium ($73 \times 31 \times 28$ cm³) with sand-floor as substrate. Below the sand floor a thermoconductive cord was used to produce a thermal gradient from approximately 14 to 40 °C. At 8:00 each day, lizards were placed in the cool side of the terrarium to allow habituation to the

experimental conditions and left undisturbed for seven hours. Body temperature (cloacal T_b) of each lizard was obtained hourly (at 15:00, 16:00 and 17:00) using a Cu-constant thermocouple and a thermometer. Individuals were captured, and their temperatures were recorded less than 30 s after capture. We considered the central 50% of the consecutive readings of T_b as the lizard's T_{sel} (Hertz et al., 1993). One-way ANOVA was used to compare the effects of seasonality (spring and fall) and locality on T_{sel} .

2.4. Thermoregulatory ability of *M. atacamensis*

Lizards' thermoregulatory ability was estimated from the indices of thermoregulation proposed by Hertz et al. (1993): d_b , d_e and E . Indices d_b and d_e are calculated as the mean of the absolute value of the deviations of field active T_b and T_e from T_{sel} , respectively (Hertz et al., 1993; Christian and Weavers, 1996). Mean d_b represents the average to which lizards experience a T_b outside the selected temperature; d_e indicates the thermal quality of the habitat from the lizard's point of view. The index E represents the effectiveness of temperature regulation; it is defined as $E = 1 - (d_b/d_e)$. Usually, this index varies from 0 (when animals do not thermoregulate) to positive values (animals thermoregulating carefully).

For d_e estimation, we used the T_e inferred from the tidbits measurements. At all sites, T_e from the data loggers were registered every 30 min from 09:00 to 18:00 h, but because lizards in some of the sites and seasons were active over shorter time periods (Sepúlveda et al., unpublished data), we restrict our estimation of T_e to when lizards were active at a given site and season. Consequently, d_e and E provide information only on thermoregulatory periods of activity (Hertz et al., 1993). d_e data were calculated as the grand mean from daily measurements for each tidbit during the activity period of lizards (i.e., we assume that the multiple measurements on each model were statistically independent; Hertz et al., 1993). We determined the standard deviation of E by bootstrap resampling of mean d_b and d_e 1000 times, using the PopTools software. Because our small sample size data preclude effectively testing for differences among populations and seasons without violating statistical assumptions, we did not perform statistical analyses for the E index.

2.5. Heating and cooling rates

For heating and cooling rate experiments, a Cu-constant thermocouple was inserted into 1 cm into the cloaca of each experimental lizard, and was taped at its tail base to prevent it from being dislodged. Additionally, individuals were fixed with tape to a pasteboard by their extremities, to prevent movements. The thermocouple was connected to a readout which displayed the lizard's T_b to the nearest 0.1 °C.

To obtain heating rates, lizards were cooled in a refrigerator to a T_b of 14 °C. Thereafter, animals were

placed in a metabolic chamber with still air at 38 ± 0.5 °C. T_b s were recorded every 30s, beginning when T_b reached 15 °C and ended when they reached 35 °C. To obtain cooling rates, lizards were heated in a metabolic chamber to a T_b of 36 °C. They were placed in a refrigerator with still air at 8 ± 0.5 °C. T_b were recorded every 30 s, beginning when T_b reached 35 °C and ending when T_b reached 15 °C. Heating and cooling rates were transformed into thermal time constants (τ). The natural logarithm of the difference between T_b and T_a was plotted against time from the initiation of the temperature step. The thermal time constant was then calculated from the slope of a straight line fitted to the data; $b = -0.4343/\tau$ (Cossins and Bowler, 1987). Because body mass affected heating and cooling rates in a linear fashion, the effects of sex, population, and the interaction between factors upon heating and cooling rates were analyzed with a two-way ANCOVA using body mass as the covariate. All the analyses were performed in Statistica Version 6.0 (StatSoft Inc., Tulsa, OK).

3. Results

Active T_b did not show geographical differences within a season (Spring: $H_{(2,26)} = 2.55$, $P = 0.28$; Summer: $H_{(2,26)} = 1.42$, $P = 0.49$; Fall: $H_{(1,13)} = 2.54$, $P = 0.11$), but showed seasonal differences within sites. In the extreme localities (Medano and Arrayán), summer mean T_b was significantly higher than in spring and fall (Medano: $H_{(2,30)} = 6.84$, $P = 0.03$; Arrayán: $H_{(2,19)} = 8.03$, $P = 0.02$; Table 1). However, in Zenteno T_b was not significantly different between spring and summer ($H_{(1,16)} = 2.69$, $P = 0.10$). Because field T_b did not differ among sexes (Medano: $H_{(1,30)} = 0.03$, $P = 0.86$; Zenteno: $H_{(1,16)} = 0.03$, $P = 0.86$; Arrayán: $H_{(1,19)} = 0.17$, $P = 0.68$), we pooled the data to compare T_b among populations.

Regarding inactive T_b , lizards did not differ geographically in spring or fall (Spring: $H_{(2,16)} = 1.78$, $P = 0.41$; Fall: $H_{(2,24)} = 5.1$, $P = 0.08$; Table 1). Similarly, T_b of inactive lizards did not show seasonal differences within sites

(Medano: $H_{(1,14)} = 0.75$, $P = 0.39$; Zenteno: $H_{(1,17)} = 0.2$, $P = 0.66$; Arrayán: $H_{(1,9)} = 0.0$, $P = 1$).

T_b of active lizards was significantly higher than that of inactive lizards (mean $T_b = 30.89$ °C and mean $T_b = 20.46$ °C, respectively, localities and seasons combined) (Kolmogorov–Smirnov two sample test, $P < 0.001$; Table 1). In summer, lizards from the three sites were all active, when T_s was above 30 °C (Fig. 2). In spring, the proportion of active individuals in Zenteno and Arrayán were higher than in Medano, although both T_a and T_s were lower. The proportion of inactive lizards was higher in fall (excepting Medano). In Zenteno, no individuals were observed in activity in fall.

Selected temperature did not show significant differences among localities for each season (Spring: $F_{(2,5)} = 0.221$, $P = 0.809$; Fall: $F_{(1,18)} = 0.021$, $P = 0.886$), nor between seasons for Medano and Zenteno (Medano: $F_{(1,13)} = 3.056$, $P = 0.104$; Zenteno: $F_{(1,8)} = 0.245$, $P = 0.634$) (Table 1). Because T_{sel} did not differ between males and females for any season (Spring: $F_{(1,6)} = 0.408$, $P = 0.546$; Fall: $F_{(1,18)} = 0.018$, $P = 0.894$) analyses considered pooled data of both sexes.

Fig. 3 shows the indices d_b , d_e , and E for the three populations in summer and spring (fall was not compared, because we did not find active individuals in Zenteno in this season, and because in Arrayán only one individual was active). In summer, the d_b index was lower for the three populations, indicating less variation in T_b outside the T_{sel} in this season. d_e index was also lower in summer, representing a better thermal quality of the habitat, from the lizard's perspective. Thermoregulatory efficiency (E) seems to be different between seasons and sites. In Medano, and because d_b was nearly identical to d_e in both seasons, the E index was near zero, indicating that lizards from this locality are thermoconformers. In Zenteno, d_b was slightly lower than d_e , resulting in a low thermoregulatory efficiency. In Arrayán, d_b was smaller than d_e in summer. Therefore, lizards from this locality are thermoregulating in this period. However, because our data do not

Table 1
Field body temperature (T_b) and selected temperature (T_{sel}) of active and inactive *M. atacamensis* in Medano, Zenteno and Arrayán in spring, summer and fall

Season	Sex	Medano			Zenteno			Arrayán		
		Active	Inactive	T_{sel}	Active	Inactive	T_{sel}	Active	Inactive	T_{sel}
Spring	Male	30.3 ± 4.0 (4)	20.6 ± 2.2 (4)	34.6 (1)	29.1 ± 1.9 (5)	23.5 (1)	33.9 (1)	27.6 ± 4.2 (7)	24.1 (1)	–
	Female	28.3 ± 1.5 (3)	21.6 ± 1.8 (5)	33.2 ± 2.7 (3)	28 ± 1.5 (2)	18.2 ± 0.8 (2)	–	26 ± 4.9 (5)	20 ± 1.2 (3)	33.9 ± 2.9 (3)
	Both	29.4 ± 3.2 (7)	21.2 ± 1.9 (9)	33.6 ± 2.4 (4)	28.8 ± 1.7 (7)	20 ± 3.1 (3)	33.9 (1)	27 ± 4.4 (12)	18.8 ± 3.7 (4)	33.9 ± 2.9 (3)
Summer	Male	34.1 ± 2.4 (4)	–	–	30.5 ± 4.4 (6)	–	–	33.8 ± 0.6 (2)	–	–
	Female	32.4 ± 3.3 (7)	–	–	30.9 ± 5.9 (3)	–	–	32.9 ± 3 (4)	–	–
	Both	33.0 ± 3.0 (11)	–	–	30.6 ± 4.6 (9)	–	–	33.3 ± 2.4 (6)	–	–
Fall	Male	30.3 ± 2.6 (8)	24.4 ± 0.5 (3)	34.4 ± 2.2 (8)	–	19.1 ± 1.2 (6)	35.6 ± 1.6 (6)	–	19.5 ± 2.7 (2)	–
	Female	29.1 ± 3.9 (4)	19.6 ± 1.5 (2)	36.6 ± 1.8 (3)	–	20.5 ± 1.9 (8)	33.9 ± 2.6 (3)	21.8 (1)	17.6 ± 2.4 (3)	–
	Both	30.4 ± 2.5 (12)	22.5 ± 2.7 (5)	34.6 ± 2.3 (11)	–	19.9 ± 1.7 (14)	35.2 ± 2.1 (9)	21.8 (1)	18.4 ± 2.4 (5)	–

Values are expressed as mean ± SD. Number of individuals is indicated in parentheses.

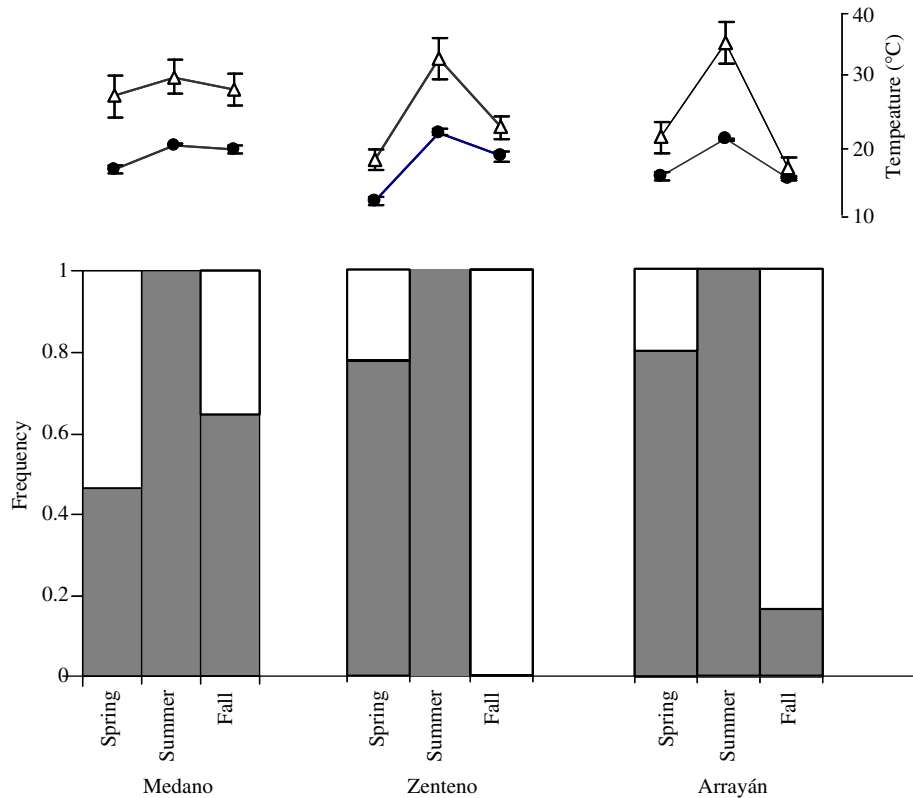


Fig. 2. Proportion of active (gray portion of the bar) and inactive (white portion) *M. atacamensis* lizards in spring, summer and fall for Medano, Zenteno and Arrayán sites. Above the figure it is indicated both T_a (black circles) and T_s (white triangles) for each season and site.

permit the use of statistical inference to test differences in the E index, its variation must be considered preliminary and is more a hypothesis than a well-established pattern.

There was a positive and significant correlation between the thermal time constant and body mass, both for heating rates ($r = 0.44$, $P < 0.01$) and cooling rates ($r = 0.89$, $P < 0.0001$) (Fig. 4). *M. atacamensis* showed no geographic or sexual variation in thermal rates. Regarding heating rates, thermal time constants did not differ among populations ($F_{(2,41)} = 1.535$, $P = 0.226$), between sexes ($F_{(1,41)} = 0.342$, $P = 0.561$), nor was the interaction between factors ($F_{(2,41)} = 0.050$, $P = 0.951$). Similarly, in cooling rates, there were no differences in thermal time constants among populations ($F_{(2,41)} = 1.711$, $P = 0.198$), between sexes ($F_{(1,41)} = 1.129$, $P = 0.334$), nor interactions ($F_{(2,41)} = 0.671$, $P = 0.517$).

4. Discussion

Our first general hypothesis was that T_b and T_{sel} differed among populations and seasons. In T_b , we found no geographical differences among populations of *M. atacamensis*. Several studies reported very little variation in field T_b among conspecific or congeneric species (e.g. Huey, 1982; Andrews, 1998; Carothers et al., 1998). Also, similar T_b has been measured in closely related taxa with different physical characteristics (e.g., body size or coloration), using different microhabitats or having different thermoregula-

tory strategies (Adolph, 1990; Carothers et al., 1998). For example, Adolph (1990) showed that T_b in two species of *Sceloporus* from southern California varied little with elevation, despite a sharp decrease in T_a s. Nevertheless, other studies demonstrated geographic variation in T_b for different populations (e.g. Grant and Dunham, 1990; Andrews, 1998), including Catenazzi et al. (2005), who found latitudinal differences in T_b between two populations of *M. peruvianus*, a species that belongs to the *M. peruvianus* group, as does *M. atacamensis*. Why might these species differ? A possible explanation might be that the maximum distance separating the Chilean populations is 500 km, whereas populations studied in Perú are separated for about 1000 km, with a consequently greater latitudinal gradient in T_a . However, due to the small sample size we have for each season, our results should be taken with caution. Differences in T_b among the studied populations should be corroborated by further observations.

Although we did not find geographical variation in T_b , seasonal differences within sites were encountered. Summer T_b was significantly higher than spring and fall T_b . A similar result was found by Catenazzi et al. (2005), who encountered that winter T_b were from 2 to 8 °C lower than summer T_b . This result suggests that both *M. peruvianus* and *M. atacamensis* lizards are under environmental constraints to thermoregulation, at least for some seasons (Vidal et al., 2002).

Microlophus atacamensis showed a lower T_b than populations of *M. peruvianus* (Huey, 1974; Catenazzi et al., 2005) and *M. quadrivittatus* (Báez and Cortés, 1990), but is higher than those reported by Vidal et al. (2002) for *M. atacamensis*, who found a T_b of around 24 °C (although, these authors captured lizards mostly in winter months). For *M. peruvianus*, Catenazzi et al. (2005) reported a mean T_b of about 36 °C in summer and 33 °C in winter. For the same species, but a northern population,

Huey (1974) reported a mean winter T_b of 35 °C. For *M. quadrivittatus*, summer and winter T_b were in the range of 36 and 34 °C, respectively (Báez and Cortés, 1990). A similar latitudinal decrease was found in T_{sel} , in which *M. atacamensis* had mean T_{sel} values of about 34 °C. However, northern species of the genus showed a mean T_{sel} of about 35.6–36 °C (Huey, 1974; Báez and Cortés, 1990; Catenazzi et al., 2005). These results confirm that T_b and T_{sel} decrease along a north to south gradient, due to a decrease in T_{as} (Catenazzi et al., 2005).

Although all the three populations were active during summer months, lizards from Medano had the lowest E index, indicating less effective temperature regulation by this population during this season. This is in accordance with the idea that northern localities offer better quality thermal conditions (Catenazzi et al., 2005), and lizards will not need to thermoregulate carefully. However, low E values, resulting from a thermal environment of high quality, may incorrectly indicate that a population (or species) is an ineffective thermoregulator (see Christian and Weavers, 1996).

For Arrayán, E value was high in summer, indicating the presence of thermoregulation. This fact implies that lizards are able to exploit the available thermal environment to the maximum extent possible, and thus maintaining a field T_b that approximates to T_{sel} (Sinervo and Adolph, 1994). However, in spring the effectiveness of thermoregulation was low and *M. atacamensis* from this locality must be active at suboptimal T_b s (Huey, 1982). Thermoregulatory indices of Zenteno were also positive (both in spring and summer), but significantly lower than from Arrayán in summer.

The indices of thermoregulation estimated suggest that *M. atacamensis*, across its geographical range, and even locally, varies from being a thermoconformer to being a thermoregulator (Huey, 1974; Hertz et al., 1993), similar to what was reported previously by Vidal et al. (2002). This thermal condition allows for this species to forage actively in the intertidal zone or close to it.

Our second hypothesis was that in southern populations of *M. atacamensis*, heating rates should be faster and

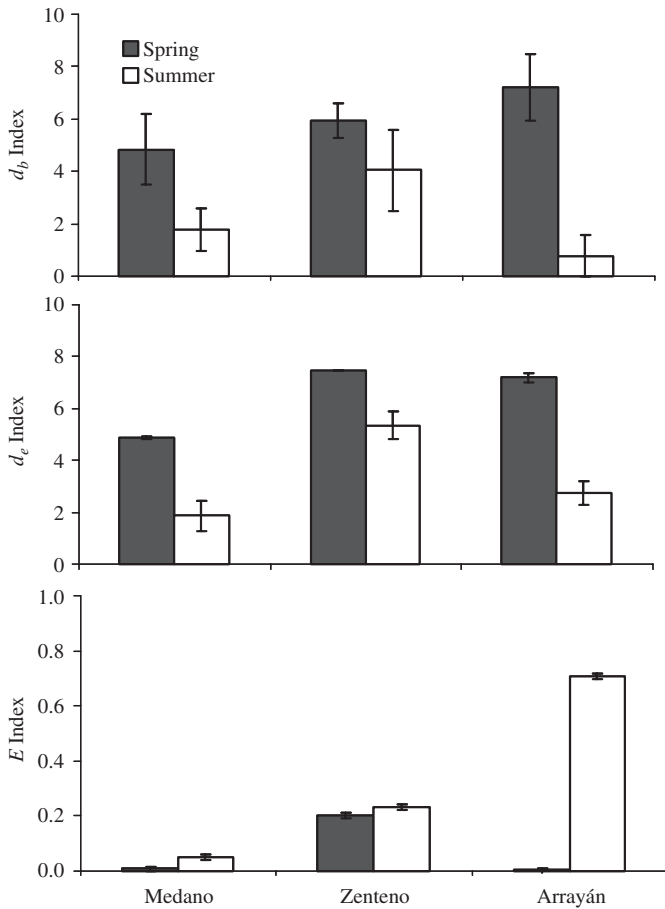


Fig. 3. Mean and standard error of d_b , d_c and E indices.

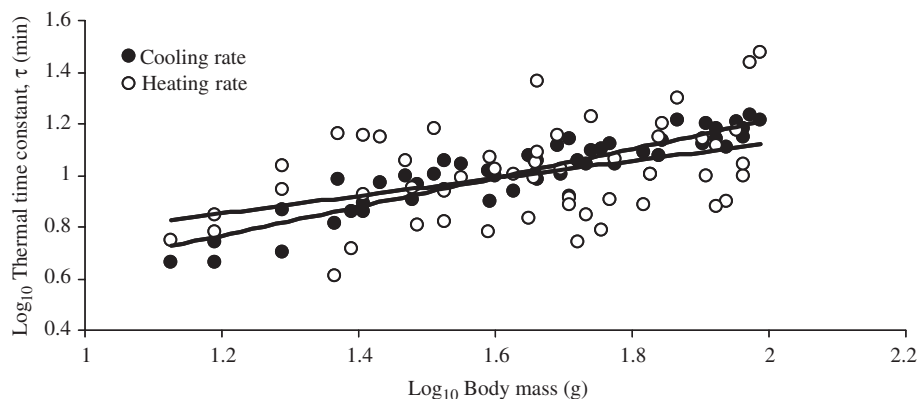


Fig. 4. Relationships between the thermal time constant (τ) and body mass of *M. atacamensis* heating and cooling rates.

cooling rates slower. Our results indicate that, similar to T_{bs} , heating and cooling rates did not vary between populations. Similar results were reached by Van Damme et al. (1990) and by Gvoždík and Castilla (2001), suggesting again that differences in thermal environment across 500 km were too small to induce physiological adjustments in this species. This result probably implies that the thermoregulation function in *M. atacamensis* is mainly behavioral (Ibargüengoytia, 2005; Rice et al., 2006). Lizards can increase physiological heating rates not only by selecting microhabitats for basking but also by changing body shape or orientating the body plane perpendicular to the sun (Gvoždík, 2002). Most behavioral adjustments serve to increase heating rates, and hence reduce basking time, not heat loss.

Although heating and cooling rates were similar among *M. atacamensis* populations, there was a correlation between thermal time constants and body size. The effect of body size on heating and cooling rates has been demonstrated in various species of lizards (Rice et al., 2006). Smaller lizards heat up more quickly and larger lizards cool down more slowly (Porter et al., 1973). This may be related to daily activity cycles in *M. atacamensis*. In fact, in all three populations, the first age class that emerges from the burrows in the morning is the juveniles. In afternoon in contrast, the last individuals to disappear are the adults (Sepúlveda et al., unpublished data).

Differences in environmental temperatures could exert significant effects on a lizard's physiology. In fact, considering a Q_{10} of near 2 to 2.5 for *M. atacamensis* (M. Sepúlveda, unpublished results), aerobic metabolism may increase from 26% and 40% when animals experience a rise of only 3 °C in environment temperature (the difference in mean maximum temperatures between the northern and southern sites). Hence, few degrees of differences may exert a significant effect on, for example, the energy budget of a lizard species. However, lack of intraspecific variation in thermal biology in *M. atacamensis* among our populations suggests that lizards may compensate adequately the variations in their thermal environment through a behavioral mechanism instead of physiological adjustment.

According to Stevenson (1985), behavioral mechanisms contribute to changes in T_b that may be four to five times greater than those provided by physiological mechanisms. This is because behavior is seemingly more plastic than physiology; conventional evolutionary wisdom asserts that an animal's first responses to a selective pressure are behavioral (Feder et al., 1987). The response of *M. atacamensis* to varying temperatures in a latitudinal gradient seems to support this idea.

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