

Thermal ecology of two syntopic lizard species of the genus *Liolaemus* (Iguania: Liolaemidae) in north western Argentina

Cecilia Inés ROBLES* and Monique HALLOY

Instituto de Comportamiento Animal (ICA), Fundación Miguel Lillo, Miguel Lillo 251, San Miguel de Tucumán, Tucumán, Argentina.

*Corresponding author, C.I. Robles, E-mail: cirobles@lillo.org.ar

Received: 23. November 2015 / Accepted: 09. May 2016 / Available online: 26. June 2016 / Printed: June 2017

Abstract. Body temperature (T_b) is important in ectothermic organisms. It involves physiological and ecological mechanisms. Here we report on body temperatures in two syntopic species of the genus *Liolaemus*, from northwestern Argentina, and their relation to environmental field temperatures. We monitored an area measuring 100 x 75 m during two austral springs and summers between 2012 and 2014. *Liolaemus ramirezae* presented an average T_b that was significantly lower (32 ± 3.9 °C) than of *L. pacha* (34 ± 3 °C). This might be explained by their phylogenetic history. T_b of the two species was not affected by sex nor by morphological measurements in the case of *L. pacha*, which coincides with what has been reported in other species of the genus. T_b was correlated to microenvironmental temperatures. During the two springs and summers of the study, T_b of *L. pacha* had a range of 30 to 35 °C, which was on average greater than maximum air temperatures, indicating that it can regulate its T_b during the day. The same could not be evaluated for the other species due to low sample size. More studies are needed to better understand different aspects of thermoregulation in these species.

Key words: temperature, ectotherms, lizards, *Liolaemus*, northwestern Argentina.

Introduction

Body temperature is fundamental to the life cycle of ectothermic organisms. Physiological and ecological mechanisms play an important role, allowing an individual to obtain appropriate temperature levels (Huey & Kingsolver 1989). This is particularly important in high altitude ectotherms since in those environments, temperatures may potentially limit periods of activity (Grant & Dunham 1988, Marquet et al. 1989). According to Huey (1982) and Stevenson (1985), ectothermic organisms regulate their temperature through physiological and/or behavioral mechanisms, respectively.

Behavioral mechanisms include variations in periods of daily and seasonal activities, differential use of shaded versus sunny areas, flattening of the body on the substrate, changes in body orientation relative to sunlight, refuge selection, among others (Huey 1982, Grant & Dunham 1988, Bauwens et al. 1996, 1999, Kearney 2001). All these behavioral strategies may help gain or lose heat.

Some lizards are capable of thermoregulating, that is, they maintain a body temperature that is independent of environmental temperature. In contrast, other lizards show passive thermoregulation or thermoconformity, their body temperatures being close to that of the environment (Zug et al. 2001). In both strategies, different forms of heat

exchange may intervene, through solar radiation (heliothermy), and/or through surface temperature (thigmothermy) (Pianka & Vitt 2003), the two considered extremes within a continuum of temperatures, that occur at the level of the body surface and are affected by body size (Angilletta 2009, Cruz et al. 2011). Moreover, variations in heat rates (increase of temperature/minutes of sun exposure) between males and females of the same species have been found (Woolrich Piña et al. 2006).

Liolaemus species are found in arid and semi-arid regions of South America, with different microhabitats and climates. It is one of the most diverse iguanid lizard genera in the world, with almost 260 described species (Abdala & Quinteros 2014), including various subgroups. *Liolaemus pacha* (Juárez Heredia et al. 2013) belongs to the *L. darwini* complex within the subgenus *Eulaemus* (Etheridge 1993, 1995, Abdala 2007), whereas *L. ramirezae* belongs to the *alticolor* group within the subgenus *Liolaemus sensu stricto* (Laurent 1983). Both species are found in northwestern Argentina and in some places coexist. They occupy habitats belonging to the phytogeographic provinces of Monte and Prepuna (Cabrera & Willink 1980).

Most studies on temperature in *Liolaemus* species have focused on species from the Argentinean Patagonia or from Chile (e.g., Labra 1998, Ibarregui et al. 2010, Moreno Azócar et al. 2012,

Bonino et al. 2011). Little information on *Liolaemus* species from northwestern Argentina exists (e.g. Valdecantos et al. 2013), making this study even more relevant.

Here we present information on some aspects of the thermal ecology of two syntopic lizard species of northwestern Argentina, *Liolaemus pacha* and *L. ramirezae*. Our objectives were: 1) study the body temperatures (Tb) in the field for each species, considering sex, two age classes (for *L. pacha*), snout-vent length and weight; 2) investigate the relationship between Tb and environmental temperatures (air (Ta) and substrate (Ts) temperatures where the lizard was seen); 3) and finally, for *L. pacha*, explore the relation between Tb and minimum and maximum temperatures recorded during two austral spring and summer seasons. We did not include *L. ramirezae* because of low numbers.

Materials and methods

The study site is located at Los Cardones (26°40'1.5"S, 65°49'5.1"W, datum: WGS84, 2700 m asl), 20 km east of the city of Amaicha del Valle, Tafi del Valle Department, province of Tucumán, Argentina. The study took place during the austral springs of 2012 and 2013 and summers of 2013 and 2014, totaling 22 days of field work.

In a previously marked 100x75 m area, random walks were performed by two observers during the activity period of the lizards (approximately 10 to 17 h). When an individual was spotted, we recorded the hour, species, sex, and age (considering two age classes, adult and subadult, see further). The lizard was then captured by noose. Body temperature (Tb) was recorded using a digital thermometer with thermocouple (TES 1307 K/J precision 0.1 °C, Taiwan). Lizards were held by the head to avoid transferring heat from the observer and temperatures were recorded within 20 seconds after capture (Ibarguengoytia et al. 2010). The lizard was then marked with nail polish in order to avoid recapturing the same lizard during that day. Substrate temperature (Ts) was taken by contacting the bulb of the thermometer with the surface where the lizard was seen. Air temperature (Ta) was recorded one cm above the substrate avoiding wind and direct solar radiation.

We took the following measurements for each lizard: snout-vent length (SVL) and total length (TL) with a digital caliper (precision 0.01 mm), and weight with a digital balance (precision 0.01 gr). With this information, we assigned each lizard to an age class following categories proposed in Robles (2010): adults, SVL > 5.5 cm and weight > 5.0 gr; subadults, SVL 4.5 to 5.5 cm and weight 2.6 to 5.0 gr. Lobo & Espinosa (1999) report the size of adults of *L. ramirezae* as follow: males, mean SVL 51.8 mm (1SD: 3.0 mm); females, mean SVL 51.3 mm (1SD: 2.6 mm). Maximum and minimum temperatures for the two

springs and summers were obtained from a climate station located 3 km from the study site.

Because our data did not comply with assumptions of normality and homogeneity of variance (Shapiro-Wilks test), we performed the following analyses using non parametric statistical tests (Siegel & Castellan 1988): differences in Tb between the two species, between males and females, and between adults and subadults (the latter only for *L. pacha*) (Wilcoxon-Mann-Whitney test); relation between Tb and SVL, Tb and weight, and Tb with environmental temperatures (Ta and Ts) (simple regression analysis). All tests were calculated using Infostat program (Di Rienzo et al. 2008).

Results

Body (Tb) and, air and substrate temperatures (Ta and Ts).

We captured a total of 215 lizards of *L. pacha*,

138 adults (84 males and 54 females) and 77 subadults (26 males and 51 females). As for *L. ramirezae*, we captured a total of 38 adults (28 males and 10 females) and no subadults.

The average body temperatures during the study for the two species was: *L. pacha* 34°C (1SD: 3°C) and *L. ramirezae* 32°C (1SD: 3.9°C). Body temperature in *L. ramirezae* was significantly lower than in *L. pacha* (Mann Whitney U = 3985, $P = 0.01$, $n = 254$, Fig. 1).

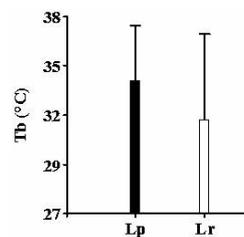


Figure 1. Mean values (bars) and standard deviations (vertical lines) of body temperatures (Tb) of *Liolaemus pacha* (Lp) and *L. ramirezae* (Lr).

In *L. pacha*, we found no significant differences in body temperatures between males and females ($W = 10971.5$; $P = 0.42$; $n = 110$, $n = 105$, respectively), nor between adults and subadults ($W = 4961.5$; $P = 0.732$; $n = 138$, $n = 77$, respectively). We therefore pooled the data in further analyses. We did not find any significant differences in Tb of *L. ramirezae* between males and females either ($W = 167.5$; $P = 0.36$; $n = 28$, $n = 10$, respectively).

Considering SVL and weight in *L. pacha*, we found no significant relation with respect to Tb ($r = 0.01$; $P = 0.17$; $r = 0.01$; $P = 0.15$, respectively). *Liolaemus ramirezae*, on the other hand, showed a significant relation between Tb and SVL

($r = 0.22; P = 0.003$), but not with respect to weight ($r = 0.06; P = 0.14$). In *L. pacha*, Tb was positively correlated to Ta and Ts ($R^2 = 0.51; R^2 = 0.55; P < 0.001$, respectively). In *L. ramirezae*, a positive significant correlation was also observed between these variables ($R^2 = 0.35; R^2 = 0.33; P < 0.001$ respectively, Fig. 2).

Body temperatures considering time of day, by season.

Because Tb in *L. pacha* was not significantly different between the two springs and between the two summers, data were pooled. The average daily Tb during these seasons stayed within the range of 30 to 35 °C. Maximum temperatures during the two springs were between 18 and 31 °C and minimum temperatures between 13 and 22 °C. Summers' maximum temperatures ranged between 17 and 30 °C and minimum temperatures between 8 and 21 °C. They followed a similar pattern both years (Fig. 3). We did not analyze data for *L. ramirezae* due to small sample size.

Discussion

Body temperatures in *L. pacha* and *L. ramirezae* were similar to those reported for other *Liolaemus* from related groups, particularly when comparing with species of the *darwinii* and *alticolor* groups respectively (e.g. Martori et al. 2002, Labra & Vidal 2003, Rodríguez Serrano et al. 2009, Moreno Azocar et al. 2013). According to Bogert (1949) and Brattstrom (1965), lizard species that are phylogenetically related tend to maintain similar body temperatures, independently of the habitat they occupy. The average body temperature of *L. ramirezae* was significantly lower than that of *L. pacha*. This could indicate that the thermal niche for these two species is different which may be due to their phylogenetic history (Vanhooydonck & Van Damme 1999) since both belong to different clades within the *Liolaemus* genus (Medina et al. 2009, Moreno Azocar et al. 2013, Valdecantos et al. 2013).

In spite of the significant result, we consider Tb cannot be explained by SVL because of the small sample size and a low r value. However further data are needed to explain this result.

The body temperature of *L. pacha* was not affected by sex, age, SVL, or weight, which is similar to what has been reported in other species belonging to this genus, e.g. *L. pictus* (Ibargüengoytia &

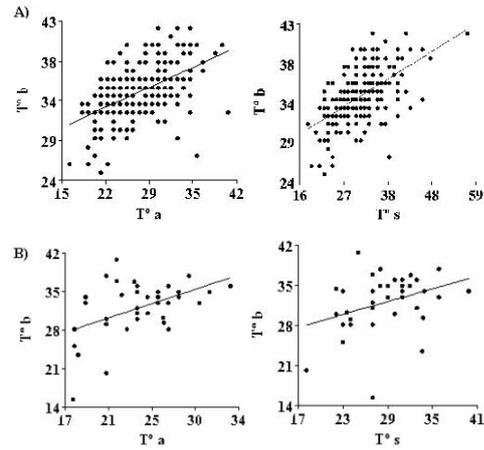


Figure 2. Relationship between body temperature (°C) and the substrate and air temperatures (°C) of *L. pacha* (A) and *L. ramirezae* (B), in Los Cardones, Tucumán, Argentina.

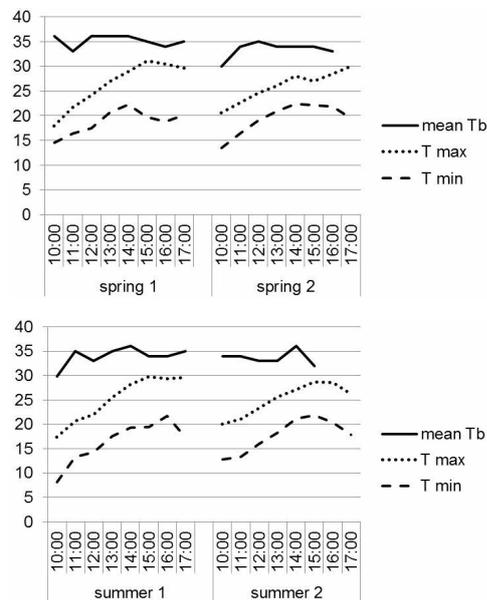


Figure 3. Mean body temperature (°C) of *Liolaemus pacha* and maximum and minimum air temperatures (°C) at different times of day in the springs (A) and summers (B) of a two year study.

Cussac 2002), *L. sanjuanensis* (Acosta et al. 2004) and *L. olongasta* (Cánovas et al. 2006). In fact, few species present intersexual differences in Tb (e.g. desert species from several different clades on three continents: Huey & Pianka 2007; *L. lutzae* Maia-Carneiro & Rocha 2013).

Some studies report the lack of a relation between Tb and SVL for lizard species of different families (e.g. Scincidae, Huey 1982; two species of *Mabuya*, Rocha & Vrcibradic 1996; *Liolaemus* species, Carothers et al. 1998; *Mabuyafrenata*, Vrcibradic & Rocha 1998; *Tropidurustorquatus*, Ribeiro et al. 2008). Maia-Carneiro and Rocha (2013) suggest that each species has an average Tb when active, appropriate to carry on different ecological and physiological activities, independently of its age or size.

In both species, Tb was related to environmental temperatures (Fig. 2). However, independence of temperature may be modulated seasonally as has been shown in *L. wiegmanni* and *L. koslowskii*, whose thermal independence is high only during the cold months (Martori et al 1998, 2002). Other non seasonal studies (e.g., *L. multi-maculatus*, *L. wiegmannii*, *L. gracilis*, Vega 1999; *L. pseudoanomalus*, Villavicencio et al. 2007), show that body temperature has a high thermal dependence, probably because measurements were taken mainly during summer, when lizards do not need to be "good thermoregulators" (Labra et al 2008). Similar results were found in *Liolaemus lutzae* (Rocha 1995).

The daily pattern seen during the spring-summer seasons of our study showed that Tb in *L. pacha* remained within a range of 30 to 35 °C and was higher than the recorded maximum temperatures. This indicates that this species is capable of modifying its Tb, behaviorally and physiologically, maintaining its Tb above environmental temperatures. Stevenson (1985) proposes that behavioral mechanisms contribute to changes in Tb and that these may be more important than those provided by physiological mechanisms, due to the fact that behavior appears to be more plastic than physiology. In the field, *L. pacha* and *L. ramirezae* were seen to be using direct solar radiation, and air and substrate temperature, as heat sources, using different body postures (pers. obs.). Martori et al. (2002) indicates the importance of this strategy as beneficial in providing caloric energy. However, more studies are needed on preferred and operational temperatures to understand the efficiency of thermoregulatory strategies in these species.

Acknowledgements. We are grateful to anonymous reviewers for their comments and suggestions, also to field assistants Luciana Vivas, Carla Cardenas and

Viviana Juarez. Wethank Recursos Naturales y Suelos of the Tucumán province (permits 936-330-2012, Resol. N° 169-13) for permission to work in the field.

References

- Abdala, C.S. (2007): Phylogeny of the *boulengeri* group (Iguania: Liolaemidae, *Liolaemus*) based on morphological and molecular characters. *Zootaxa* 1538: 1-84.
- Abdala, C., Quinteros, S. (2014): Los últimos 30 años de estudios de la familia de lagartijas más diversa de Argentina. Actualización taxonómica y sistemática de Liolaemidae. *Cuadernos de Herpetología* 28(2): 55-82.
- Acosta, J.C., Buff, R., Marinero, J.A., Gómez, P. (2004): *Liolaemus sanjuanensis* (NCN). Body temperature. *Natural History Notes. Herpetological Review* 35: 171.
- Angilletta, M.J. (2009): *Thermal adaptation: a theoretical and empirical synthesis.* Oxford University Press, Oxford.
- Bauwens, D., Hertz, P.E., Castilla, A.M. (1996): Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology* 77: 1818-1830.
- Bauwens, D., Castilla, A.M., Mouton, P., le Fras N. (1999): Field body temperatures, activity levels and opportunities for thermoregulation in an extreme microhabitat specialist, the girdled lizard (*Cordylus macropholis*). *Journal Zoology, London* 249: 11-18.
- Bogert, C.M. (1949): Thermoregulation in reptiles: a factor in evolution. *Evolution* 3: 195-211.
- Bonino, M.F., Moreno Azócar, D., Tulli, M.J., Abdala, C.S., Perotti, M.G., Cruz, F.B. (2011): Running in cold weather: morphology, thermal biology, and performance in the southernmost lizard clade in the world (*Liolaemus lineomaculatus* section: Liolaemini: Iguania). *Journal of Experimental Zoology* 315: 495-503.
- Brattstrom, B.H. (1965): Body temperatures of reptiles. *American Midland Naturalist* 73: 376-422.
- Cabrera, A.L., Willink A. (1980): *Biogeografía de América Latina.* 2a edición corregida. Monografía 13. Serie de Biología. Secretaría General de la Organización de los Estados Americanos, Washington DC, 120 pp.
- Cánovas, M.G., Acosta, J.C., Villavicencio, H.J., Marinero, J.A. (2006): *Liolaemus olongasta* (NCN). Body Temperature. *Herpetological Review* 37: 87-88.
- Carothers, J.H., Marquet, P.A., Jaksic, F.M. (1998): Thermal ecology of a *Liolaemus* lizard assemblage along an Andean altitudinal gradient in Chile. *Revista Chilena de Historia Natural* 71: 39-50.
- Cruz, F.B., Antenucci, D., Luna, F., Abdala, C.S., Vega, L.E. (2011): Energetics in *Liolaemini* lizards: implications of a small body size and ecological conservatism. *Journal of Comparative Physiology B* 181: 373-382.
- Di Rienzo J.A., Casanoves F., Balzarini M.G., Gonzalez L., Tablada M., Robledo C.W. (2008): *InfoStat, versión 2008, Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.*
- Etheridge R.E. (1993): Lizards of the *Liolaemus darwini* complex (Squamata: Iguania: Tropiduridae) in Northern Argentina. *Bolletino del Museo Regionali di Scienza Naturali di Torino, Italia* 11: 137-199.
- Etheridge R.E. (1995): Redescription of *Ctenoblepharys adspersa* Tschudi, 1845, and the taxonomy of Liolaeminae (Reptilia: Squamata: Tropiduridae). *American Museum Novitates* 3142: 1-34.
- Grant, B.W., Dunham, A.E. (1988): Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology* 69: 167-176.
- Huey, R.B. (1982): Temperature, physiology, and the ecology of reptiles. pp 25-91. In: Gans, C., Pough, F.H. (eds.), *Biology of the Reptilia.* Volume 12. Academic Press, New York, New York, USA.

- Huey, R.B., Kingsolver, J.G. (1989): Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology & Evolution* 4: 131-135.
- Huey, R.B., Pianka, E.R. (2007): Lizard thermal biology: do genders differ? *American Naturalist* 170 (3): 473-478.
- Ibargüengoytia, N.R., Cussac, V.E. (2002): Body temperatures of two viviparous *Liolaemus* lizard species, in Patagonian rain forest and steppe. *Herpetological Journal* 12: 131-134.
- Ibargüengoytia, N.R., Medina, S.M., Fernández, J.B., Gutierrez, J.A., Tappari, F., Scolari, A. (2010): Thermal biology of the southernmost lizards in the world: *Liolaemus sarmientoi* and *Liolaemus magellanicus* from Patagonia, Argentina. *Journal of Thermal Biology* 35: 21-27.
- Juárez Heredia V., Robles C., Halloy M. (2013): A new species of *Liolaemus* from the *darwini* group (Iguania: Liolaemidae), Tucumán province, Argentina. *Zootaxa* 3681(5): 524-538.
- Kearney, M. (2001): Postural thermoregulatory behaviour in the nocturnal lizards *Christinus marmoratus* and *Nephruroides* (Gekkonidae). *Herpetological Review* 32:11-14.
- Labra A. (1998): Selected body temperature of seven species of Chilean *Liolaemus* lizards. *Revista Chilena de Historia Natural* 71:349-358.
- Labra, A., Vidal, M. (2003): Termorregulación en reptiles: un pasado veloz y un futuro lento. pp.207-224. In: Bozinovic, F. (ed.), *Fisiología ecológica y evolutiva*. Ediciones Universidad Católica de Chile, Santiago.
- Labra, A., Vidal, M., Solis, R., Penna M. (2008): Ecofisiología de anfibios y reptiles. pp. 483-516. In: Vidal, M., Labra, A. (eds), *Herpetología de Chile*. Science Verlag, Santiago, Chile.
- Laurent, R.F. (1983): Contribución al conocimiento de la estructura taxonómica del género *Liolaemus* Wiegmann (Iguanidae). *Boletín de la Asociación Herpetológica Argentina* 1: 15-18.
- Lobo, F., Espinoza, R.E. (1999): Two new cryptic species of *Liolaemus* (Iguania: Tropiduridae) from Northwestern Argentina: Resolution of the purported reproductive bimodality of *Liolaemus alticolor*. *Copeia* 1999: 122-140.
- Maia Carneiro, T., Rocha, C.F.D. (2013): Influences of sex, ontogeny and body size on the thermal ecology of *Liolaemus lutzae* (Squamata, Liolaemidae) in a resting remnant in southeastern Brazil. *Journal of Thermal Biology* 38: 41-46.
- Marquet, P.A., Ortiz, J.C., Bozinovic F., Jaksic, F.M. (1989): Ecological aspects of thermoregulation at high altitudes: the case of Andean *Liolaemus* lizards in northern Chile. *Oecologia* 81:16-20.
- Martori, R., Vignolo P., Cardinale, L. (1998): Relaciones térmicas en una población de *Liolaemus wiegmannii* (Iguania: Tropiduridae). *Revista Española de Herpetología* 12: 19-26.
- Martori, R., Aun, L., Orlandini S. (2002): Relaciones térmicas temporales en una población de *Liolaemus koslowkyi*. *Cuadernos de Herpetología* 16(1): 33-45.
- Medina, M., Gutiérrez, J., Scolari, A., Ibargüengoytia, N.R. (2009): Thermal response to environmental constraints in two populations of the oviparous lizard *Liolaemus bibronii* in Patagonia, Argentina. *Journal of Thermal Biology* 34: 32-40.
- Moreno Azocar, D.L., Vanhooydonck, B., Bonino, M.F., Perotti M.G., Abdala, C.S., Schulte, J.A., Cruz, F.B. (2013): Chasing the Patagonian sun: comparative thermal biology of *Liolaemus* lizards. *Oecologia* 171: 773-788.
- Pianka, E., Vitt, L. (2003): *Lizards. Windows to the Evolution of Diversity*. University of California Press.
- Ribeiro, L.B., Gomides, S.C., Santos, A.O., Sousa, B.M. (2008): Thermoregulatory behavior of the saxicolous lizard, *Tropidurus torquatus* (Squamata, Tropiduridae), in a rocky outcrop in Minas Gerais, Brazil. *Herpetological Conservation and Biology* 3(1): 63-70.
- Robles C. (2010): Territorialidad y selección sexual en el lagarto *Liolaemus quilmes* (Liolaemidae) del Valle de Amaicha, Tucumán, Argentina. Tesis Doctoral, Universidad Nacional de Tucumán, Argentina, 121 pp.
- Rocha, C.F.D. (1995): Ecología termal de *Liolaemus lutzae* (Sauria: Tropiduridae) em uma área erestigada sudeste brasileiro. *Brazilian Journal of Biology* 55(3): 481-489.
- Rocha, C.F.D., Vrcibradic, D. (1996): Thermal ecology of two sympatric skinks (*Mabuyamacrorhincha* and *Mabuyagilis*) in a Brazilian resting habitat. *Australian Journal of Ecology* 21:110-113.
- Rodríguez Serrano, E., Navas, C.A., Bozinovic, F. (2009): The comparative field body temperature among *Liolaemus* lizards: Testing the static and the labile hypotheses. *Journal of Thermal Biology* 34: 306-309.
- Siegel, S., Castellan, N.J. (1988): *Nonparametric Statistics for the Behavioral Sciences*. McGrawHill Inc., New York, 2nd ed., 399 pp.
- Stevenson, R.D. (1985): The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *The American Naturalist* 126:102-117.
- Valdecantos, S., Martínez, V., Lobo, F., Cruz, F.B. (2013): Thermal biology of *Liolaemus* lizards from the high Andes: Being efficient despite adversity. *Journal of Thermal Biology* 38: 126-134.
- Vanhooydonck, B., Van Damme, R. (1999): Evolutionary relationships between body shape and habitat use in lacertid lizards. *Evolutionary Ecology Research* 1: 785-805.
- Vega, L.E. (1999). *Ecología de saurios arenícolas de las dunas costeras bonaerenses*. Tesis de Doctorado, Universidad Nacional de Mar del Plata, 102 pp.
- Villavicencio, H.J., Acosta, J.C., Marinero, J.A., Cánovas, M.G. (2007): Thermal ecology of a population of the lizard, *Liolaemus pseudoanomalus* in western Argentina. *Amphibia-Reptilia* 28: 163-165.
- Vrcibradic, D., Rocha, C.F.D. (1998): The ecology of the skink *Mabuyafrenata* in an area of rock outcrops in Southeastern Brazil. *Journal of Herpetology* 32(2): 229-237.
- Woolrich Piña, G.A., Lemos Espinal, J.A., Oliver López, L., Calderón Méndez, M.E., González Espinosa, J.E., Correa Sánchez, F., Montoya Ayala, R. (2006): Ecología térmica de una población de la lagartija *Sceloporus grammicus* (Iguanidae: Phrynosomatinae) que ocurre en la zona centro-oriente de la ciudad de México. *Acta Zoológica Mexicana (nueva serie)* 22: 137-150.
- Zug, G.R., Vitt, L.G. Caldwell, G.P. (2001): *Herpetology. An Introductory Biology of Amphibians & Reptiles*. 2nd Edition, Academy Press, California.