

Substrate Use and its Effect on Body Temperature in two Syntopic *Liolaemus* Lizards in Northwestern Argentina

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Habitat use and thermal biology are closely related, because thermal microclimates vary spatially. The use of habitat and microhabitat by different species influences many of their traits, such as their physiology, and may, therefore exert a direct effect on survival. Ectothermal animals, such as lizards, are affected by thermal and biophysical environments they inhabit, and the particular use of a given substrate reflects an overlap between thermally adequate microhabitats, and behavioral preferences. By exploiting certain microhabitats and avoiding others, many lizards tend to maintain their body temperature within a range that allows maximum performance. Here, we evaluate how two syntopic species of lizards, *Liolaemus pacha* and *L. ramirezae*, use substrates with different exposure to solar radiation. Our hypothesis is that *L. pacha* uses both soil and rock substrates indistinctly, due to being a generalist species, whereas *L. ramirezae* uses the rock substrate more frequently, due to its saxicolous habits. We expect temperatures to be different both in substrates, and in different exposures, and thermal characteristics of each species to condition their use. For example, because the body temperature range of *L. pacha* is wider, we predict that substrate use will be wider. A pre-established 100x75 m area was monitored during four Austral springs and summers between 2011 and 2015, in Los Cardones, Amaicha del Valle, Tucumán, Argentina. Species' substrate where the lizard was found (soil or rock), and exposure to solar radiation: sun, filtered shade or full shade was recorded. After capture, lizard body temperature (T_b), substrate temperature (T_s), and air temperature (T_a) were recorded in the place of the first observation of the lizard. Obtained results show that *L. pacha* and *L. ramirezae* had a more persistent use of the rock than the soil substrate, thus considering them saxicolous species. Further, they were frequently observed exposed to direct sunlight. Average body temperature was higher than environmental temperature (T_s and T_a), and significantly different in each exposure type (sun, filtered shade and full shade), and in both substrates (rock and soil). Differential use of substrate and the relationship between body temperature and microhabitat temperatures suggests that *L. pacha* and *L. ramirezae* are "active thermoregulators", using both substrate surfaces and solar radiation as heat sources.

Key words: Body temperature; *Liolaemus*; Substrate use.

The use of habitat and microhabitat by different species affects the physiology of individuals, which may have a direct effect on their survival (TRACY, 1982; TRACY & CHRISTIAN 1986; HUEY, 1991). There are different ways of

understanding habitat use. Within spatial ecology framework, the most widely accepted definition is proposed by GARSHELIS (2000), in which use / non-use is understood as the presence / absence of a given species in a given habitat, respectively. In this context, selection is understood as a synonym of use, while preference refers to a greater choice (in terms of frequency) of different resources by a certain species. Specifically, substrate preference offers another level of microhabitat selection that is likely to have strong influences on species ecology and fitness. In this study, microhabitat is used to refer to the actual substrate or perch occupied by an individual, according to the terminology used by SMITH & BALLINGER (2001).

Reptiles are appropriate models for spatial ecology studies, due to their high fidelity to specific sites of terrain, and to their low capacity of displacement in comparison to other groups of vertebrates (PIANKA, 1986; POUGH *et al.*, 1998). Among the most important drivers of displacement between sites, are resource acquisition, such as food, water, mates, sunny places to thermoregulate (or shady, when temperatures are too high), and shelter as primary drivers. There are also secondary factors that are required for their survival and / or reproduction (POUGH *et al.*, 1998). One example is vegetation structure, which determines the use of space (HUEY *et al.*, 1983; DÍAS & ROCHA, 2004). This is due to associations between external variables, such as microclimatic conditions, and presence of shelter, food, and mates associated with vegetation (ROCHA, 1991; CONVERSE &

SAVIDGE, 2003; ATTUM & EASON, 2006). Each microhabitat provides different conditions for the species. Some species show greater frequency use of certain types of sites or substrates, which depends on the needs of each individual (DIEGO-RASILLA & PÉREZ-MELLADO, 2003). Species can be generalists or specialists according to the diversity of microhabitat they select; therefore, the particular use of a substrate reflects trade-offs between microhabitats that are adequate for thermal requirements of a given species, and to its morphology, feeding and behavioral preferences (ADOLPH, 1990).

Lizards, are affected by thermal and biophysical environments where they inhabit (HUEY & STEVENSON, 1979). Body temperature of lizards varies directly with environmental temperature; therefore, access to thermal resources is one of the main limiting factors of these animals' activity (HUEY & SLATKIN, 1976). Temperature regulation is mainly through physiological (STEVENSON, 1985) or behavioral mechanisms (HUEY, 1982). The latter include variation in daily and seasonal activity period, differential use of shade and sunny patches, body flattening in relation to substrate, changes in body orientation in relation to sunlight and selection of shelters, all important for heat gain or loss (GRANT & DUNHAM, 1988; BAUWENS *et al.*, 1996; KEARNEY, 2001). Certainly, the interaction between microhabitat use and prevailing thermal conditions is an important component of behavioral thermoregulation (PAULISSEN, 1988). For instance, alternation between microhabitats with different temperatures, differential timing of activity and changes

in body posture constitute important mechanisms of thermoregulatory adjustment (BENNETT, 1980; ESPINOZA & TRACY, 1997; SMITH & BALLINGER, 2001; LABRA & VIDAL, 2003; ZUG *et al.*, 2003; LABRA *et al.*, 2008). As a result of such behaviors, species with wide thermal tolerance are able to take advantage of all possible microhabitats, although this behavior can be influenced by competition (SMITH & BALLINGER 2001; BUSTOS ZAGAL *et al.*, 2013). In this theoretical context, we investigate how two syntopic species of lizards, *Liolaemus pacha* and *L. ramirezae*, use substrates with different exposure to solar radiation, and how such use varies with body temperature.

Liolaemus is globally one of the richest and most diverse genus of iguanid lizards, with more than 260 valid species (UETZ *et al.*, 2019) that are widely distributed in many arid and semi-arid regions of South America, encompassing a wide range of climates from Peru (its most boreal distribution), to Tierra del Fuego, the southernmost one. They are found in a wide variety of habitats, with some species being arboreal, but the majority being terrestrial (CEI, 1993; ETHERIDGE, 1993; SCHULTE *et al.*, 2004). A few species are restricted to specific substrates, such as sand or rock, and exhibit morphological adaptations to such habitats, including lizards of saxicolous, arboreal and psammophile habits (ETHERIDGE, 2000; TULLI *et al.*, 2009). This variety of forms and different adaptations offer a great potential to study their use frequency of microhabitats when species are in syntopy.

Liolaemus pacha (JUÁREZ HEREDIA *et al.*, 2013), and *L. ramirezae* (LOBO & ESPINOZA,

1999) occur in northwestern Argentina, although *L. ramirezae* has a more restricted range. They are found in sympatry in the semi-arid phytogeographic region of the Prepuna (CABRERA & WILLINK, 1980), in Tucumán province, Argentina. The former belongs to the *darwinii* complex (ETHERIDGE, 1993), and the latter to the *alticolor* group (LOBO & ESPINOZA, 1999). Both species are diurnal, mainly insectivorous (HALLOY *et al.*, 2006), and oviparous (RAMÍREZ PINILLA, 1992; LOBO & ESPINOZA, 1999). ROBLES & HALLOY (2017) reported that *L. pacha* and *L. ramirezae* have an average field body temperature of 34°C and 32°C, respectively. The Tb of *L. pacha* during austral springs of 2012 and 2013 and summers of 2013 and 2014, had a range of 30 to 35°C (for *L. ramirezae* was 30 to 34°C), which was on average greater than maximum air temperatures, indicating that it can regulate its Tb during the day. Furthermore, body temperature of *L. pacha* was not affected by sex, age, snout-vent length, or weight.

Our objectives were to: 1) explore substrate use (rock or soil) in *L. pacha* and *L. ramirezae*. Our hypothesis is that, based on literature and field observations, *L. pacha* is a generalist species, we predicted to use both soil and rock indistinctly. On the other hand, *L. ramirezae* would use the rock substrate more frequently due to its saxicolous habits; 2) analyze if the body temperature (Tb) varies between species and if it is associated, to the use of the substrate, and to the different levels of exposure to solar radiation 3) analyze associated environmental temperatures: air temperature (Ta) and substrate

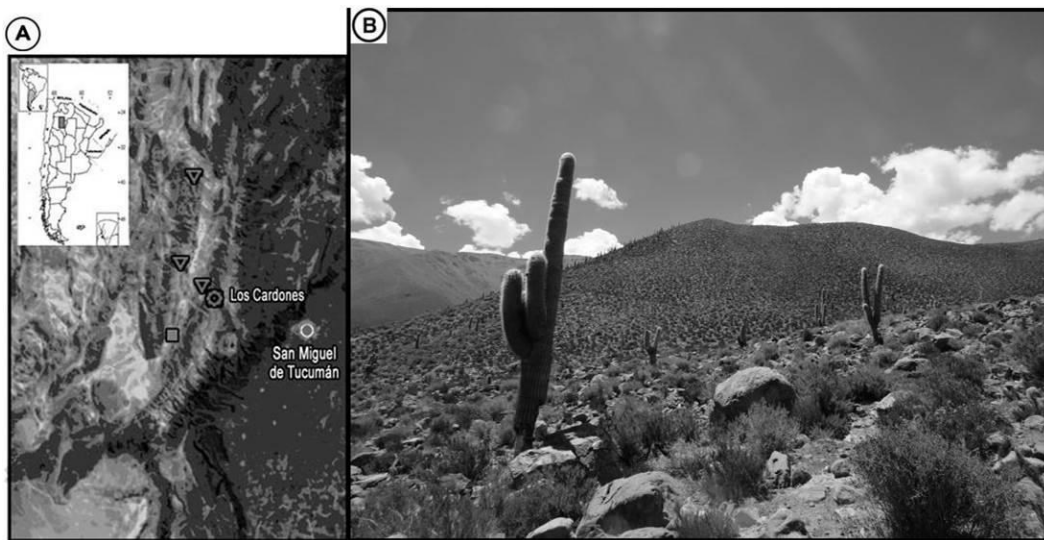


Figure 1: A) Map of Los Cardones, Km 98, Ruta Provincial 307, Tafi del Valle Department, Tucumán Province, Argentina ($26^{\circ}40'1.5''$ S, $65^{\circ}49'5.1''$ W, 2725 m). Image obtained from Google Earth Pro. B) Overview of the study site (photo: S. HALLOY)

temperature (T_s) on both substrates and exposures. We expect temperatures (T_b , T_a and T_s) to differ both in substrates and in different exposures. Hence, we anticipated that each species would have a different substrate depending their particular T_b (e.g. if T_b range is wider, we predict that substrate use will be wider), and thermal requirements.

MATERIAL AND METHODS

Study area

The study site corresponds to Los Cardones ($26^{\circ} 40' 1.5''$ S, $65^{\circ} 49' 5.1''$ W, 2700 masl) (Fig. 1A). This area is located 20 km east of Amaicha del Valle city, Tafi del Valle department, in Tucumán province, Argentina. This location is on the upper boundary between the Monte and Prepuna ecoregions (mostly Prepuna) (1600-3000 m, CABRERA & WILLINK, 1980).

The site is characterized by a coluvial substrate, scattered large rocks, and it is barely but nearly uniform vegetated with shrubs and cacti, including species belonging to *Baccharis cf grisebachii* (Compositae), *Flourenzia fiebrigii* (Compositae), *Junellia seriphioides* (Verbenaceae), *Justicia tweediana* (Acanthaceae), *Fabiana densa* (Solanaceae) and a candelabra cactus called "cardón" *Thrichocereus pasacana* (Cactaceae) (HALLOY et al., 1998) (Fig. 1B). The site corresponds to a desert climate, its average annual temperature is less than 18°C . During the summer season, the highest rainfall is recorded (90% of the annual total), with January being the rainiest month. The rains reach an annual average value of 160 mm (TORRES BRUCHMANN, 1981).

Data collection

Monthly observations were performed

during the activity period of lizards (Austral spring-summer), from December 2011 to February 2015. Each monthly expedition lasted between 2 to 3 days, summarizing 42 days of field work. In a 100 x 75 m grid established at the study site, we performed daily monitoring, using a visual encounter survey technique (HEYER *et al.*, 1994; ROBLES & HALLOY, 2008). Surveys took place in the morning (10:00 to 11:30), noon (12:00 to 13:30) and afternoon (15:00 to 17:00) with an approximate duration of 60 to 80 minutes each. When a lizard was sighted, the time, species, and substrate it was on (soil (S) or rock (R)) were recorded, assessing if it was in full sun, filtered shade (under grass), or full shade (under bush). The lizard was then captured by noose. For each individual, body temperature (T_b), substrate temperature (T_s), and air temperature (T_a) of the place where the lizard was observed, were recorded immediately. All measurements were performed using a digital thermometer with thermocouple (TES 1307 K/J precision 0.1 °C, Taiwan), which was introduced about one centimeter inside the cloaca of each individual. Substrate temperature (T_s) was taken by contacting the thermocouple with the surface where the lizard was observed. To record air temperature (T_a), the thermocouple was held one centimeter above substrate, protecting it from air currents and direct solar radiation. Subsequently, individuals were released at their capture site. The temperature data of individuals whose capture took more than one minute or occurred after it ran large distances, was discarded, to avoid the effect of greater

activity on their body temperature (MARTORI *et al.*, 2002). Individuals were held by the head to avoid heat transfer; temperature was recorded within 20 seconds of their capture (IBARGÜENGOYTÍA *et al.*, 2010). Each individual was marked with nail polish in order to avoid recapturing the same lizard during that day (VALDECANTOS, 2011). When capture was not successful, the temperature of substrate and air were still recorded.

Statistical analyses

We tested the normality assumption for residuals of our data. Because they fulfill normality and homogeneity assumptions (Kolmorov-Smirnov test), we performed parametric analyses (SIEGEL & CASTELLAN, 1988). The frequency of difference in substrate use between the two species was analyzed using the Pearson *Chi*-square. To explore the relationship among variable responses (body temperature), and different factors such as species (*L. pacha*, *L. ramirezae*), exposures to sunlight (x, y, z), and substrate (rock, soil), we performed a General Lineal Model (GLM). All tests were performed with Statistica 7.0 (StatSoft, 2004).

RESULTS

Substrate use

During the study, a total of 539 individual observations were performed (*pacha* = 434 and *L. ramirezae* = 105). Proportionally, both *L. pacha* and *L. ramirezae* had greater occupancy of rock than soil substrate. However, in spite of this, there were no statistical differences (Chi Square = 0.087, *P* = 0.77, *df* = 1) (Fig. 2).

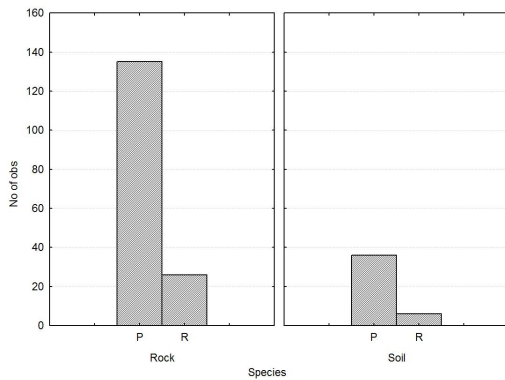


Figure 2: Number of observations of lizards *Liolaemus pacha* (P), and *L. ramirezae* (R), found on two substrates.

Body temperature, substrate and solar radiation

Considering only species factor, body temperature of *L. pacha* was different from *L. ramirezae* ($F_{(1,120)} = 11.45, P = 0.001$). The former had a higher temperature ($34^{\circ}\text{C} \pm 3,4$) than the latter ($32^{\circ}\text{C} \pm 4,8$). Regarding the type of exposure to the solar radiation (sun, filtered shade and full shade), both species were more frequently exposed to full sun, and on rocks. Body temperature was significantly lower in the individuals that were found in the shade ($F_{(2,120)} = 4.81, P = 0.01$). Considering substrates factor (rock and soil), and its interaction with species, there was no statistically significant difference ($F_{(1,120)} = 0.19, P = 0.67$).

Finally, considering the interaction among exposition, substrate and species, there was no statistically significant difference ($F_{(2,120)} = 1.17, P = 0.31$).

The associated environment temperatures of both substrates (rock and soil) were significantly different under the three exposures ($H = 27.76, P = 0.0001, n = 268$ and $H = 11.35, P = 0.01, n = 111$, respectively). Rock substrate's temperature under full sun was higher than under other exposures. Air temperature recorded over rocks showed significant differences under the different exposures ($H = 7.19, P = 0.02, n = 205, n = 52$ and $n = 13$). However, air temperature above the soil did not differ significantly between exposures ($H = 3.37, P = 0.154, n = 60, n = 44$ and $n = 7$) (Table 2).

Because of the small sample size for *L. ramirezae*, we did not analyze these data. However, the pooled values of mean body temperature reached on rock substrate was 32.53°C (1SD: $4.20^{\circ}\text{C}, n = 33$), while body temperature of individuals on soil substrate was 31.50°C (1SD: $3.20^{\circ}\text{C}, n = 6$) (Table 2)

DISCUSSION

According to field observations from previous studies at the same site, *L. pacha* was considered to be generalist in the use

	<i>L.</i>			
	<i>pacha</i>		<i>ramirezae</i>	
	Rock	Soil	Rock	Soil
sun	232 (76%)*	70 (54%)	51 (63%)*	10 (42%)
filtered shade	60 (20%)	51 (40%)	23 (28%)	11 (46%)
shade	13 (4%)	8 (6%)	7 (9%)	3 (13%)

Table 1: Number of *Liolaemus* lizards (percentage) on rock and soil, under different exposures. * $p < 0.05$.

MICROHABITAT USE AND BODY TEMPERATURE IN LIZARD SPECIES

Table 2: Body (Tb), air (Ta) and substrate temperatures (Ts) (in °C) on rock and soil in each exposure to sunlight in the two species *L. pacha* (above) and *L. ramirezae* (below). Values are presented as mean ± SD, followed by range. ** p < 0.05.

Species	Substrate	Exposition	Tb	n	Ta	Ts	n
<i>L. pacha</i>	Rock	sun	34.79 ± 3.25 ** (22.58 - 42.0)	60	26.3 ± 4.1 ** (17.1 - 41.0)	32.5 ± 4.7 ** (21.9 - 47.7)	203
		filtered shade	33.69 ± 3.41 (25.10 - 40.0)	15	25.6 ± 3.8 (18.7 - 39.0)	29.6 ± 4.5 (19.0 - 37)	52
		shade	30.55 ± 5.31 (25.0 - 40.0)	9	23.5 ± 4.9 (18.5 - 36.0)	26.0 ± 5.2 (21.0 - 38.5)	13
	Soil	sun	34.09 ± 3.34 (26.0 - 42.0)	11	26.2 ± 5.1 (16.0 - 40.0)	34.8 ± 6.8 ** (24.0 - 57.0)	60
		filtered shade	34.7 ± 2.8 (28.5 - 40.0)	7	25.9 ± 4.0 (18.3 - 37.5)	31.7 ± 5.0 (21.0 - 42.1)	44
		shade	33.14 ± 3.11 (29.0 - 36.7)	3	22.5 ± 3.9 (17.5 - 27.3)	26.0 ± 7.0 (18.0 - 38.0)	7
<i>L. ramirezae</i>	Rock	sun	33.02 ± 4.05 (24.7 - 38.0)	21	24.5 ± 3.8 (17.5 - 33.0)	31.38 ± 4.7 (22.5 - 42.4)	47
		filtered shade	33.66 ± 1.85 (30.0 - 36.0)	9	24.4 ± 2.2 (19.0 - 27.2)	30.35 ± 2.2 (25.5 - 34.5)	20
		shade	25.67 ± 4.93 (20.0 - 29.0)	3	22.6 ± 2.3 (20.3 - 27.0)	26.1 ± 5.0 (24.0 - 32.8)	7
	Soil	sun	28.0 ± 0.00 (28.0 - 28.0)	1	26.6 ± 6.6 (18.0 - 35.9)	37.39 ± 10.6 (26.5 - 51.5)	16
		filtered shade	32.75 ± 3.20 (28.0 - 35.0)	4	25.6 ± 3.9 (19.1 - 30.8)	28.45 ± 3.4 (24.0 - 34.0)	20
		shade	30.0 ± 0.0 (30.0 - 30.0)	1	23.6 ± 3.9 (21.0 - 28.1)	24.33 ± 5.1 (22.0 - 30.2)	3

of space. However, in this study the species was observed on rocks near different types of shrubs, and on open sandy soils. Thus, our results show that rock was the most used substrate by *L.*

pacha. In the case of *L. ramirezae*, literature reports that it is more restricted to rocks (saxicolous) (HALLOY & ROBLES, 2002, 2003; ROBLES & HALLOY, 2008), similarly with the results obtained in this study. The

preference for rock substrates has also been reported for other species of the genus (e.g. *L. acostai*, ABDALA & JUÁREZ HEREDIA, 2013), with a high homogeneity in the use of space, and without intrapopulation variations (sex and age group) (CÁNOVAS *et al.*, 2001, VILLAVICENCIO *et al.*, 2002). In contrast, VILLAVICENCIO *et al.* (2012) found that *Liolaemus eleodori* had a preferential use of bare soil microhabitats (completely devoid of vegetation). *Liolaemus darwini* was also frequently seen on bare soil, and among low shrubs in Mendoza, Argentina (VIDELA & PUIG, 1994). Studies carried out in Salta, Argentina with *L. chacoensis* show a preference for bare soil, in an undisturbed mature forest, whereas in a highly disturbed forest its preferred shrubs and leaf litter (PELEGRIN *et al.*, 2009). In Chile, *L. platei* used the soil while *L. nigromaculatus* used the rocks, but in this case, the observed use of habitat suggests the influence of morphology and behavior (FUENTES & CANCINO, 1979).

A preliminary analysis of soil and plant coverage at the study site shows a similar percentage of rock and bare soil coverage during the summer season (unpublished data). According to these results, we could infer a preference for rock substrate in these species of lizards. Also, from a behavioral perspective, during the reproductive season, *L. pacha* males patrol their territory from the rocks, which provide them of greater visibility of the surrounding environment (HALLOY & ROBLES, 2002, 2010). In the case of *L. ramirezae*, this behavior could be an antipredator strategy (aerial predators), due to its cryptic nature and / or the use of

crevices in the rocks as a refuge (pers. obs.). Other approach suggests that lizards use substrates with better access to prey items, as it happens in *Sceloporus undulatus* (MACLEOD *et al.*, 2018). Thereby, these substrates are suitable for important behaviors such as basking, foraging, and displaying to conspecifics.

Shifts between microhabitats of different thermal supply (HAGER, 2000), changes of body postures and of orientation to the sun for heating, and cooling control are important mechanisms of thermoregulatory behavior in lizards of temperate climates (AVERY, 1978; PIANKA, 1993; KINGSBURY, 1994). Regarding sun exposure, *L. pacha* and *L. ramirezae* showed the same pattern of exposure on both substrates. A higher percentage of individuals were recorded under the sun, followed by filtered shade and full shade on the rock, probably because mean temperature of rock under the sun is lower than mean body temperature. This type of exposure might allow species to adjust their heated body surface, thus maintaining their normal temperature activity. On the soil, both species used the three exposures, alternating mostly between sun and filtered shade. This could be because, under the sun, acquired temperature by the soil is significantly higher than acquired by rocks (34.8°C and 32.5°C respectively), thus they might select grass in search of shade, to avoid overheating. In *Tropidurus etheridgei*, CRUZ *et al.* (1998) reported a behavior pattern of alternation between sun and shade to thermoregulate, with higher shade resources used during the hottest part of the day. It could be inferred that the

variations in substrates used by *L. pacha* with different exposures to the sun (sun and filtered shade), could be a behavioral mechanism for temperature regulation, allowing the species to maintain its body temperature within its optimal range. Nevertheless, thermoregulation efficiency of these species should be determined, by measuring selected temperatures (T_{sel}), and operative temperatures (T_o), for a more reliable analysis of thermal environment (HERTZ, 1992; HERTZ *et al.*, 1993).

Mean body temperature of *L. pacha* and *L. ramirezae* recorded in this study, agrees with the results of ROBLES & HALLOY (2017). These authors consider that both species exhibit heliothermic, and tigmothermic behaviors, since the heat gained by body surface occurs through direct solar radiation, and through conduction with the substrate, allowing them to maintain the appropriate body temperature for their ecological and physiological activities. More studies are needed that include other microhabitat characteristics (plant coverage, abundance, availability, shelters, etc.). These, may help to unravel the species' preferences of use, and would allow finding the main causes of association, as well the relation with the thermal environment, and the behavioral mechanisms of these species.

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REFERENCES

- ABDALA, C.S. & JUÁREZ HEREDIA, V.I. (2013). Taxonomía y filogenia de un grupo de lagartos amenazados: el grupo de *Liolaemus anomalus* (Iguania: Liolaemidae). *Cuadernos de Herpetología* 27(2): 109-153.
- ADOLPH, S.C. (1990). Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* 71(1): 315-327.
- ATTUM, O.A. & EASON, P.K. (2006). Effects of vegetation loss on a sand lizard. *Journal of Wildlife Management* 70, 27-30.
- AVERY, R.A. (1978). *Lizards - A study in thermoregulation*. The institute of Biology's Studies in Biology. University Park Press. Baltimore N° 109.
- BAUWENS, D.; HERTZ, P.E. & CASTILLA, A.M. (1996). Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology* 1818-1830.
- BENNETT, A.F. (1980). The thermal dependence of behavioural performance of small lizards. *Animal Behaviour* 28:752-762.
- BUSTOS ZAGAL, M.G.; MANJARREZ J. & CASTRO-FRANCO, R. (2013). Uso de microhábitat y termorregulación en *Sceloporus horridus horridus* (Wiegmann

- 1939) (Sauria: Phrynosomatidae). *Acta zoológica mexicana* 29(1): 153-163.
- 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. EEUU.
- CÁNOVAS, M.G.; ACOSTA, J.C.; VILLAVICENCIO, H.J. & MARINERO, J.A. (2001). Ecología termal y uso del espacio en una población de *Liolaemus olongasta* (Squamata: Tropicuridae). San Juan. Argentina. *Acta de resúmenes IV Congreso Argentino de Herpetología*, pp: 32-33.
- CEI, J.M. (1993). *Reptiles del noroeste, nordeste y este de la Argentina*. Monografía XIV. Museo Regionali di Scienza Naturali di Torino, Italia.
- CRUZ, F.B.; SILVA, S. & SCROCCHI, G.J. (1998). Ecology of the lizard *Tropicurus etheridgei* (Squamata: Tropicuridae) from the dry Chaco of Salta, Argentina. *Herpetological Natural History* 6(1): 23-31.
- CONVERSE, S.J. & SAVIDGE, J.A. (2003). Ambient temperature, activity, and microhabitat use by ornate box turtles (*Terrapene ornata ornata*). *Journal of Herpetology* 37: 665-670.
- DÍAS, E.J.R. & ROCHA, C.F.D. (2004). Thermal ecology, activity patterns and microhabitat use by two sympatric whiptail lizards (*Cnemidophorus abietensis* and *Cnemidophorus ocellifer*) from northeastern Brazil. *Journal of Herpetology* 38: 586-588.
- DIEGO-RASILLA, F.J. & PÉREZ-MELLADO, V. (2003). Home range and habitat selection by *Podarcis hispanica* (Squamata, Lacertidae) in Western Spain. *Folia Zoology* 52(1): 87-98.
- ESPINOZA, R.E. & TRACY, C.R. (1997). Thermal biology, metabolism and hibernation. 1: 149-184, In ACKERMAN, L.J. (ed). *The Biology, Husbandry and Health Care of Reptiles*. Biology of Reptiles TFH Publications, Neptune City, N.J.
- ETHERIDGE, R.E. (1993). Lizards of the *Liolaemus darwini* complex (Squamata: Iguania: Tropicuridae) in Northern Argentina. *Bollettino del Museo Regionali di Scienza Naturali di Torino, Italia*. 11: 137-199.
- ETHERIDGE, R.E. (2000). A review of lizards of the *Liolaemus wiegmannii* group (Squamata, Iguania, Tropicuridae), and a history of morphological change in the sand-dwelling species. *Herpetological Monographs* 293-352.
- FUENTES, E.R. & CANCINO, J. (1979). Rock - ground patchiness in a simple *Liolaemus* lizard community (Reptilia, Lacertilia, Iguanidae). *Journal of Herpetology* 343-350.
- GARSHELIS, D.L. (2000). *Delusions in habitat evaluation: measuring use, selection, and importance: Controversies and Consequences*. Columbia University Press. New York, pp: 111-164.
- GRANT, B.W. & DUNHAM, A.E. (1988). Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology* 69:167-176.
- HAGER, S.B. (2000). Variation in body temperature and thermoregulatory behavior between two populations of the lesser earless lizard *Holbrookia maculata*. *Contemporary Herpetology* 1: 1-8.
- HERTZ, P.E. (1992). Evaluating thermal

- resource partitioning. By sympatric lizards *Anolis cooki* and *A. cristatellus*: a field test using null hypotheses. *Oecologia* 90: 127-136.
- HERTZ, P.E., HUEY, R.B. & STEVENSON, R. D. (1993). Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. *American Naturalist* 142: 796-818.
- HALLOY, M. & ROBLES, C. (2002). Spatial distribution in a neotropical lizard, *Liolaemus quilmes* (Liolaemidae): Site fidelity and overlapping among males and females. *Bulletin of the Maryland Herpetological Society* 38: 118-129.
- HALLOY, M. & ROBLES, C. (2003). Patrones de actividad y abundancias relativas en un lagarto del noroeste argentino, *Liolaemus quilmes*, (Iguania: Liolaemidae). *Cuadernos de Herpetología* 17: 67-73.
- HALLOY, M.; ETHERIDGE, R. & BURGHARDT, G.M. (1998). To bury in sand: Phylogenetic relationships among lizard species of the *boulengeri* group. *Liolaemus* (Reptilia: Squamata: Tropiduridae), based on behavioral characters. *Herpetological monographs* 12: 1-37.
- HALLOY, M.; ROBLES, C. & CUEZZO, F. (2006). Diet in two syntopic neotropical lizard species of *Liolaemus* (Liolaemidae): interspecific and intersexual differences. *Revista Española de Herpetología* 20: 47-56.
- HEYER, R.; MAUREEN, D.; MC. DIARMID, R.; LEE-ANN, H. & FOSTER M. (1994). *Measuring and monitoring biological diversity. Standard methods for amphibians*. Smithsonian Institution Press. Washington and London, pp: 364.
- HUEY, R.B. (1982). Temperature, physiology, and the ecology of reptiles. Volume 12, In GANS, C. & POUGH, F.H. (eds.), *Biology of the Reptilia*. Academic Press, New York, USA, pp: 25-91.
- HUEY, R.B. (1991). Physiological consequences of habitat selection. *American Naturalist* 137: 91-115.
- Huey, R.B. & Slatkin M. (1976). Cost and benefits of lizard thermoregulation. *Quarterly Review of Biology* 51 (3): 363-384.
- HUEY, R.B. & STEVENSON, R.D. (1979). Integrating thermal physiology and ecology of ectotherms. *American Zoologist* 19: 357-366.
- HUEY, R.B.; PIANKA, E.R. & SCHOENER, T.W. (1983). *Lizard Ecology: Studies of a Model Organism*. Cambridge: Harvard University Press.
- IBARGÜENGOYTÍA, N.R.; MEDINA, S.M.; FERNÁNDEZ, J.B.; GUTIÉRREZ, J.A.; TAPPARI, F. & SCOLARO, A. (2010). Thermal biology of the southernmost lizards in the world: *Liolaemus sarmiento* and *Liolaemus magellanicus* from Patagonia, Argentina. *Journal of Thermal Biology* 35(1): 21-27.
- JUÁREZ HEREDIA, V.I.; ROBLES, C. & HALLOY, M. (2013). A new species of *Liolaemus* from the darwinii group (Iguania: Liolaemidae), Tucuman province, Argentina. *Zootaxa* 3681 (5): 524-538.
- KEARNEY, M. (2001). Postural thermoregulatory behavior in the nocturnal lizards *Christinus marmoratus* and *Nephruros milii* (Gekkonidae). *Herpetological Review* 32:11-14.

- KINGSBURY, B.A. (1994). Thermal constraints and eurythermy in the lizard *Elgaria multicarinata*. *Herpetologica* 50 (3): 266-273.
- LABRA, A. & VIDAL, M. (2003). Termorregulación en reptiles: Un pasado veloz y un futuro lento, In Bozinovic, F. (ed.). *Fisiología Ecológica y Evolutiva. Teoría y casos de estudios en animales*. Universidad Católica de Chile. Santiago, Chile, pp: 207-224.
- LABRA, A.; VIDAL, M.; SOLIS, R. & PENNA, M. (2008). Ecofisiología de Anfibios y reptiles, In Vidal, M.A. & Labra, A. (eds) *Herpetología de Chile*. Science Verlag. Santiago, Chile, pp: 483-516.
- 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* 1: 122-140.
- MACLEOD, K.J.; FREIDENFELDS, N.A.; LEIGHTON, G.M. & LANGKILDE, T. (2018). Tree selection is linked to locomotor performance and associated noise production in a lizard. *Journal of Zoology*, doi:10.1111/jzo.12632.
- MARTORI R.L.; AÚN L. & ORLANDINI S. (2002). Relaciones térmicas temporales en una población de *Liolaemus koslowskyi*. *Cuadernos de Herpetología* 16 (1): 33-45.
- PAULISSEN, M.A. (1988). Ontogenetic and seasonal shifts in microhabitat use by the lizard *Cnemidophorus sexlineatus*. *Copeia* 1021-9.
- PELEGRIN, N.; CHANI, J.M.; ECHEVARRIA, A.L. & BUCHER, E.H. (2009). Effects of forest degradation on abundance and microhabitat selection by ground dwelling Chaco lizards. *Amphibia-Reptilia* 30(2): 265-271.
- PIANKA, E.R. (1986). *Ecology and natural history of desert lizards*. Princeton University Press, Princeton.
- PIANKA, E.R. (1993). The many dimensions of a lizard's ecological niche, In VOLAKOS, E.; BOHME, W.; PEREZ-MELLADO, V. & MARAGON, P. (eds.). *Lacertids of the Mediterranean region. A biological approach*, pp: 121-154, Hellenic Zoological Society, Athens.
- POUGH, F.H.; ANDREWS, R.M.; CADLE, J.E.; CRUMP, M.L.; SAVITZKY, A.H. & WELLS, K.D. (1998). *Herpetology*. Prentice Hall, New Jersey.
- RAMÍREZ PINILLA, M.P. (1992). Ciclos reproductivos y de cuerpos grasos en dos poblaciones de *Liolaemus darwini* (Reptilia: Sauria: Tropiduridae). *Acta Zoologica Lilloana* 42: 41-49.
- ROBLES, C. & HALLOY, M. (2008). Seven-year relative abundance in two syntopic neotropical lizards, *Liolaemus quilmes* and *L. ramirezae* (Liolaemidae), from Northwestern Argentina. *Cuadernos de Herpetología* 22: 73-79.
- ROBLES, C. & HALLOY, M. (2010). Core area overlap in a neotropical lizard, *Liolaemus quilmes* (Iguania: Liolaemidae): relationship with territoriality and reproductive strategy. *Herpetological Journal* 20: 243-248.
- ROBLES, C.I. & HALLOY, M. (2017). Thermal ecology of two syntopic lizard species of the genus *Liolaemus* (Iguania: Liolaemidae) in northwestern Argentina. *North-Western Journal of Zoology* 13 (1): 44-48.
- ROCHA, C.F.D. (1991). Composição do habitat e uso do espaço por *Liolaemus*

- lutzae* (Sauria: Iguanidae) em uma área de restinga. *Revista Brasileira de Biología* 51: 839–845.
- SCHULTE II, J.A.; LOSOS, J.B.; CRUZ, F.B. & NUÑEZ, H. (2004). The relationship between morphology, escape behavior and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae: Tropicuridae: Liolaemini). *Journal of Evolutionary Biology* 17: 408-420.
- SIEGEL, S.C. & CASTELLAN, J.N. (1988). *Non parametric statistics for the behavioural sciences*. 2 eds. McGraw-Hill. New York, pp: 399.
- SMITH, G.R. & BALLINGER, R.E. (2001). The ecological consequences of habitat and microhabitat use in lizards: A Review. *Contemporary Herpetology* 3.
- STATSOFT, INC. (2004), *STATISTICA* (data analysis software system), version 7. www.statsoft.com.
- STEVENSON, R.D. (1985). Body size and limits to the daily range of body temperature in terrestrial ectotherms. *American Naturalist* 125: 102–117.
- TORRES BRUCHMANN, E. (1981). *El clima de Amaicha del Valle y sus posibilidades agrícolas y ganaderas*. Publicación especial N° 14. Facultad de Agronomía y Zootecnia, Universidad Nacional de Tucumán. ISSN0325-240X.
- TRACY, C.R. (1982). *Biophysical modelling in reptilian thermal physiology and ecology*. Vol. 12. *Biology of the Reptilia*, pp: 275-321.
- TRACY, C.R. & CHRISTIAN, K.A. (1986). Ecological relations among space, time and thermal niche axes. *Ecology* 67: 609 – 615.
- TULLI, M.J.; CRUZ, F.B.; HERREL, A.; VANHOYDONCK, B. & ABDALA, V. (2009). The interplay between claw morphology and microhabitat use in neotropical iguanian lizards. *Zoology* 112: 379-392.
- UETZ, P., FREED, P., JIRÍ, H. (2019): *The Reptile Database*, <http://www.reptile-database.org>. accessed.
- VALDECANTOS, M.S. (2011). *Coexistencia entre especies: competencia, agresión o indiferencia en lagartijas de la puna del género Liolaemus (Squamata: Iguania: Liolaeminae)*. Tesis doctoral. Universidad Nacional de Córdoba, Córdoba. Argentina.
- VIDELA, F. & PUIG, S. (1994). Estructura de una comunidad de lagartos del monte. Patrones de uso espacial y temporal. *Multequina* 3: 99-112.
- VILLAVICENCIO, H.J.; ACOSTA J.C.; CÁNOVAS, M.G. & MARINERO, J.A. (2002). Patrones de actividad temporal diaria y estacional de *Liolaemus pseudoanomalus* (Squamata: Tropicuridae), en el centro-oeste de Argentina. *Multequina* 11(1): 51-60.
- VILLAVICENCIO, H.J.; ACOSTA, J.C.; BLANCO, G.M. & MARINERO, J.A. (2012). Ecología térmica de la lagartija endémica *Liolaemus eleodori* (Iguania: Liolaemidae) en el Parque Nacional San Guillermo, San Juan, Argentina. *Multequina* 21(1): 17-23.
- ZUG, G.R.; VITT, L.J. & CALDWELL, J.P. (2003). *Herpetology*. Prentice Hall, New Jersey.