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Thermoregulatory behavior and habitat use of  
*Liolaemus aparicioi* at two different altitudes

Frida J. L. Gustafsson

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Handledare: Karl-Olof Bergman, Linköpings universitet

Examinator: Anders Hargeby, Linköpings universitet



**Linköpings universitet**

Institutionen för fysik, kemi och biologi

Linköpings universitet

581 83 Linköping



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Thermoregulating behavior and habitat use of *Liolaemus aparicioi*

**Handledare/Supervisor** Karl-Olof Bergman  
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Författare/Author:

Jennie Frida Linn Gustafsson

Sammanfattning/Abstract:

The thermoregulation of lizards depends highly on the environment they inhabit. Thermoregulation is crucial for physiological processes and affects therefore the life history of the lizard. High altitudes are characterized by a colder climate than on lower altitudes, and these environmental factors affects the thermoregulation of lizards. Lizards can however adapt to colder climates by adjusting their physiology and/or behavior. In this study two populations of *Liolaemus aparicioi*, an endemic lizard inhabiting the valleys close to La Paz, were observed at two different altitudes to investigate any differences in behavior or habitat use that could compensate for the high altitude. The behavioral displays associated to thermoregulation and the use of habitat were recorded in order to assess how they allocated their time and how they used the habitat available. The mean values of most parameters measured indicated that the population on the high altitude do compensate for the high altitude by behavior and habitat use.

**Nyckelord/Keyword:**

Thermoregulation, Basking behavior, Lizard, Altitude, Habitat use

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## **1 Abstract**

The thermoregulation of lizards depends highly on the environment they inhabit. Thermoregulation is crucial for physiological processes and affects therefore the life history of the lizard. High altitudes are characterized by a colder climate than on lower altitudes, and these environmental factors affects the thermoregulation of lizards. Lizards can however adapt to colder climates by adjusting their physiology and/or behavior. In this study two populations of *Liolaemus aparicioi*, an endemic lizard inhabiting the valleys close to La Paz, were observed at two different altitudes to investigate any differences in behavior or habitat use that could compensate for the high altitude. The behavioral displays associated to thermoregulation and the use of habitat were recorded in order to assess how they allocated their time and how they used the habitat available. The mean values of most parameters measured indicated that the population on the high altitude do compensate for the high altitude by behavior and habitat use.

## **2 Introduction**

Lizards are ectotherms, and are therefore also sensible to the environment. The life history of lizards are affected by their ability to thermoregulate, and environmental conditions affecting temperature are especially important. Studies have shown that the body temperature of ectotherms usually are lower in colder environment (Angilletta et al. 2006, Van Damme et al. 1989). The temperature affects several physiological processes in lizards and for a lizard to function it needs to reach its optimum body temperature. The optimum body temperature is the narrow range (Castilla & Bauwens 1991) in which the lizard can perform activities such as hunting, escaping predators, or social activities (McConnachie et al 2009, Huey & Slatkin 1976). These activities affects the individual's reproduction, growth and survival, which are important for the fitness of the individual. The ability to regulate and obtain the optimum body temperature is therefore crucial for the organism's performance and life history (Van Damme et al. 1989). Lizards are able to regulate their body temperature through adaptations of behavior or physiology (Valdecantos et al 2012, Belliure & Carrascal 1996).

The abiotic and biotic conditions for lizards changes depending on which altitude they inhabit. At higher altitudes you can expect several environmental aspects to change, for example radiation, humidity, oxygen

partial pressure and temperature<sup>1</sup>. You can also expect biotic conditions to change, such as type of vegetation. Lizards can compensate for the colder and harsher climate by changes in behavior, for example by occupying more open habitats, increasing the amount of time spent on basking (Gvozdík 2002), higher basking frequencies and restricting their movements (Hertz & Huey 1981). Behavior that affects lizard life history, such as time allocated to thermoregulation, is often phenotypically plastic and varies in response to environmental factors (Adolph & Porter 1993). An increased time spent on basking may affect the fitness negatively, since that time otherwise could be spent on activities such as foraging, reproduction and avoiding predation (Huey & Slatkin 1976, Adolph & Porter, 1993, Dunham et al. 1988). Another mechanism that partially could compensate for the high altitude is the choice of microhabitats to bask in (Gvozdík 2002). Choice of microhabitat is an important tool for lizards to control their temperature, one example is shuttling between warm and cold microhabitats (Huey 1974, Castilla & Bauwens 1991, Grant & Dunham 1988). Geographical variation in habitat use could be due to differentiation in genetics and/or behavior (Adolph & Asbury 2007). Some studies suggest that the use of habitat is explained by behavioral plasticity, rather than genetics, and that lizards at higher altitudes choose sunnier basking sites than lizards at lower and warmer altitudes (Adolph & Asbury 2007).

The aim with this research was to investigate how two populations of *Liolaemus aparicioi* at different altitudes differ in their behavioral displays with regard to thermoregulation and habitat use. The endemic species *L. aparicioi*, is a small lizard (snout-vent length maximum 60 mm) that inhabits the inter-Andean dry valleys outside of La Paz (Ocampo et al. 2012). *L. aparicioi* is found from 3000 m to 4100 m asl<sup>2</sup> (Ocampo et al. 2012).

It is important to understand the ways these lizards are able to adapt their thermoregulation for the conservation of the species (Castilla & Bauwens 1991). Two of the greatest threats against biodiversity are climate change and expansion of human settlement. These two environmental threats will influence the habitat and thermoregulation of *L. aparicioi*, and therefore its

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<sup>1</sup> Miranda Calle, B. A., 2015. *Termorregulación de poblaciones de Liolaemus aparicioi* (Iguana: Lioalemidae) a diferente altitud en el valle de La Paz, s.l.: s.n.

<sup>2</sup> Miranda Calle, B. A., 2015. *Termorregulación de poblaciones de Liolaemus aparicioi* (Iguana: Lioalemidae) a diferente altitud en el valle de La Paz, s.l.: s.n.

survival as a species. It is estimated that by year the 2080 up to 39 % of local population and 20 % of all species will be extinct (Sinervo et al. 2010). The ability of lizards to adapt their thermoregulation in new environments are crucial during a global climate change. With a greater understanding of behavioral adaptations we can make better assessments of the consequences of climate change and human expansion on populations of lizards, information that is valuable for lizard conservation.

In order to define the requirements for *L. aparicioi* the following questions were asked; 1) How do they use the habitat available for their thermoregulatory behavior? 2) How do they allocate their time on basking and foraging? 3) How does the thermoregulation and habitat use differ in different altitudes?

## **2.1 Hypothesis**

The population of *Liolaemus aparicioi* at 4100 m asl will have an increased basking proportion, increased total duration of basking, decreased time spent in movement and total distance compared to the population inhabiting a site on 3000 m asl.

The population of *Liolaemus aparicioi* at 4100 m asl will chose a habitat with less shadow, bask at sites with more sunlight, and spend more time in a flat body position (position A, Figure 1) than the population at 3000 m asl.

## **3 Material and methods**

### **3.1 Study species**

*Liolaemus aparicioi* is a newly discovered species that was previously confused with *Liolaemus walker*. A description of the *Liolaemus aparicioi* was done 2012 (Ocampo et al. 2012). *Liolaemus* (Iguana: Liolaemidae) contain 257 species, which occur in many countries in South America, from the south corner of Argentina to Peru (Abdala & Quinteros 2014). In recent years several new species have been recognized in the genus *Liolaemus*, and thus the composition in the genus has grown. The species *Liolaemus aparicioi* belongs to the *Alticolor*-group (subgenera of *Chiliensis*). There is a total of 18 species of *Liolaemus* in Bolivia, and 11 of these species belongs to the *Alticolor* subgroup (Ocampo et al. 2012).

### 3.2 Study area

The research was carried out on two different location outside La Paz, Bolivia. The field sites were located at the altitude edges of the distribution of the species, from 3000 to 4100 m asl. The field site on the lowest altitude was located at Taypichullo and the size of the area was about 0.8 ha. The village of Taypichullo is located 12 km outside of La Paz, on a alluvial platform (elevation: 3000 m; 16°38'S, 68°02'W). The habitat at the alluvial platform was dry and the flora was characterized by *Aymara senna*, *Echinopsis bridgesii*, *Optunia ficus-indica*, *Iresine* sp., *Lantana balansae*, *Baccharis boliviensis*, *Bothriochloa bardinodis*, *Verbesina mandonii*, *Viguiera australis* and *Agave americana*<sup>3</sup>. The species composition of herbs varied in different parts of the area. A few trees of the species *Caesalpinia spinosa* and *Prosopis flexuosa* were scattered over the area. The weather during the field work was characterized by sunlight and warm temperatures in the morning and rain in the afternoons.

The field site at the highest altitude was located outside of the village Taucachi, approximately 38 km outside of La Paz (elevation: 4100 m; 16°42'S & 68°05'W). The size of the area was about 2.1 ha. Stone cairns were scattered through the area and the flora was characterized by low bushes and grass. The dominant flora consisted of *Tetraglichin cristatum*, *Baccharis incarum*, *Stipa* sp., *Senna aymara*, *Calceolaria* sp., and *Hedeoma mandonia*<sup>4</sup>. The climate varied strongly, with cold temperatures, fluctuating cloudiness and strong radiation during sunshine. The residents in the area generally worked with agriculture, mainly cultivation of potatoes. The residents also kept sheep and cows, which has given the results that parts of the land were overgrazed.

### 3.3 Field observation of behavioral thermoregulation and habitat use

The field observations was conducted during 13 days, between 14 of April until 9 of May in year 2015. During this period two populations of *Liolaemus aparicioi* were studied. The populations were geographically distributed at two different altitudes, 3000 m and 4100 m asl.

The field study was restricted to sunny weather, since lizards are more active during warm temperatures. Focal sampling was used as a sampling method, and the sampling started at the first sight of a lizard in the morning and continued until 30 minutes after the last lizard was seen, approximately

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<sup>3</sup> Emilia García, 7/5 - 2015

<sup>4</sup> Emilia García, 7/5 - 2015

between 09:00 – 17:00 during sunny days. There was a variation in the weather, which had the result that the sampling period was shorter some days. No sampling occurred during weather with high cloudiness or rain.

Only lizards that seemed undisturbed by my presence were sampled, and each observation had a maximum duration of 30 minutes. In those occasions that a lizard went out of sight when observed less than 30 minutes, the shorter time was accounted for in the statistical analysis. During the observations, behavioral displays associated with thermoregulation<sup>5</sup>, foraging and habitat use (Table 1-3) were recorded. Both data from juveniles (snout-to-vent length < 50 mm) and adults (snout-to-vent length > 50 mm) were collected. After each observation the lizard was captured with a noose and snout-to-vent length and sex were recorded. At the end of each observational session the habitat in a circle of 2 m in diameter, surrounding the area that the lizard primarily used, was recorded (Table 4).

To identify and describe the habitat available for the lizards, a transect of 200 m, in 4 x 50 m long segments, was laid across each field site, representing the habitat characteristics of the site. The parameters describing habitat were measured (Table 4) at each 5 m along each transect. Each sample point was a circle with a diameter of 2 meters (40 sampling units at each field site).

The temperature in each field site was measured with a HOBO U12 data logger, which was placed approximately 1 m above the ground in a place where it was protected against sunlight and wind. The data logger recorded the temperature every 5 minutes. To measure the temperature on the ground, 4 tidbit UTBI-001 data loggers were placed in three classes of sun exposures: full, filtered and shadow. Each tidbit registered the temperature every 5 minutes. In the end of a sampling period, the tidbits and the HOBO U12 data logger were collected and data extracted.

### **3.4 Data analysis**

To assess if there were any differences in thermoregulatory behavior between the populations the following parameters were compared: 1) total basking time 2) basking duration 3) mean basking duration 4) total time spent in basking position A, B and C (Figure 1). To assess if there were any differences between the populations in movement a comparison was made

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<sup>5</sup> Miranda Calle, B. A., 2014. Ethogram of *Liolaemus aparicioi* (Iguania: Liolaemidea) in Captivity.

in 1) total distance of movement, and 2) total time moving. The total time basking were compared between the age groups adults, juvenile and unknown. The habitat use during basking were compared for four different parameters (Table 3). Since the habitat available for the lizards differed strongly between the field sites, a statistical comparison were not made between the populations on the choice of basking substrate. The following parameters in basking habitat were statistically analyzed: 1) time spent basking in three classes of sun exposures full/filtered and shade 2) the percentage of vegetation cover and 3) distance to shelter. To evaluate the habitat preferences on each altitude the following parameters were used: 1) the percentage of the different types of ground substrate 2) the percentage of vegetation layers 3) the percentage of shadow 4) the percentage of shelter. The temperature in the air and on the ground was compared to assess if there were any differences in the temperatures on the two altitudes. The abundance of the population on 3000 and 4100 m asl was calculated. The number of lizards seen during the two warmest hours (approximately the two hours where they were most active) was calculated and divided with the number of hours and the size of the area.



Figure 1. Basking position A (lying flat on the substrate), B (forelimbs erected, upper body arises from the substrate) and C (lizard standing with all four limbs erected).<sup>6</sup>

Table 1. The general information that was recorded for each focal.

Parameter	Definition
Time of the day	When the observation started and ended.
Time observed	Total time observed

<sup>6</sup> Miranda Calle, B. A., 2014. Ethogram of *Liolaemus aparicioi* (Iguania: Liolaemidea) in captivity.

SVL	Snout-to-vent length. Juvenile: < 50 mm, adult: > 50 mm. If the lizard was not measured, it was recorded as "unknown".
Sex	Male or female. If the sex of the lizard was not identified, it was recorded as "unknown".

**Table 2. Parameters recorded associated with thermoregulation and locomotion of each focal.**

Parameter	Definition
Basking	The lizard was considered basking when being still in > 10 sec. (position A, A <sub>1</sub> , B, B <sub>1</sub> described in an ethogram of <i>Liolaemus aparicioi</i> <sup>7</sup> .)
Basking position	The time in which a lizard performed a specific posture (position A, B or C) were recorded. See Figure 1 for further details
Basking duration	Duration of each basking event
Time basking	The total time basking
Basking proportion	The proportion of time spent on basking relative to the total time observed.
Movement	Movement longer than 10 cm including stops < 3 sec
Distance	The distance covered by each movement
Total distance	Total distance covered by a lizard
Time	Time duration of each movement
Total time	Total time in motion for a lizard

**Table 3. Parameters recorded for each focal regarding the choice of habitat while basking.**

Parameter	Definition
Substrate	Rock, soil, grass, herb, tree, dead vegetation
Sun exposure	Sun exposure (full sun/sun filtered by vegetation/shade)
Cover of vegetation	The estimated cover of tree or bush canopy in percentage
Distance to shelter	Distance to closest shelter

<sup>7</sup> Miranda Calle, B. A., 2014. Ethogram of *Liolaemus aparicioi* (Iguania: Liolaemidea) in captivity.

Table 4. Parameters describing the habitat of lizards (2 meters in diameter, surrounding their main area of movement).

Parameter	Definition
Ground substrate	The estimated percentage of rock/soil/grass/herbs/tree/dead vegetation
Shelter	The estimated percentage of ground covered with dead vegetation, rocks or herbs that could provide shelter
Vegetation layers	The estimated percentage of vegetation layers with height < 25 cm/ 25-50 cm/ > 50 cm
Temperature on the ground	Temperature (C°) 5 cm above the ground, in full and filtered sun as well as in the shadow.
Temperature in the air	Temperature (C°) 1 meter above the ground in the shadow
Shadow from tree and bush canopy	The estimated shadow from vegetation in percentage
Type of vegetation	Dominating species of vegetation

### 3.4 Statistical analysis

An independent t-test were used to compare the means of parameters between the two different populations. A two-way ANOVA was used to evaluate whether basking behavior differed in different age groups. To analyze the preferences of habitat at each altitude a binary logistic regression with backward elimination was used. The habitats of lizards (1) or control points (0) were used as dependent parameter. The habitat parameters (ground substrate, vegetation layer, shadow from canopy and shelter) were used as explanatory variables. SPSS v.22 were used to perform the statistical analyses. A significance level of  $p < 0.05$  was used.

## 4 Results

### 4.1 Temperature and abundance

There was a difference in the temperatures between each field site during field work (Figure 1, 2). The air temperature on the altitude of 4100 m asl was about 14 °C at its highest, while the air temperature on 3000 m asl reached 20 °C. The air temperature during night was also a few degrees lower on 4100 m asl. There was only a small difference in the highest

temperatures on the ground between the altitudes. An evident difference between the altitudes is that the ground temperature on 4100 m asl was more fluctuating than on 3000 m asl. Another difference is that the temperature is rising earlier on 3000 m asl.

The difference in abundance between the two areas were 69,6 lizards/ha on 3000 m asl and 10,9 lizards/ha.

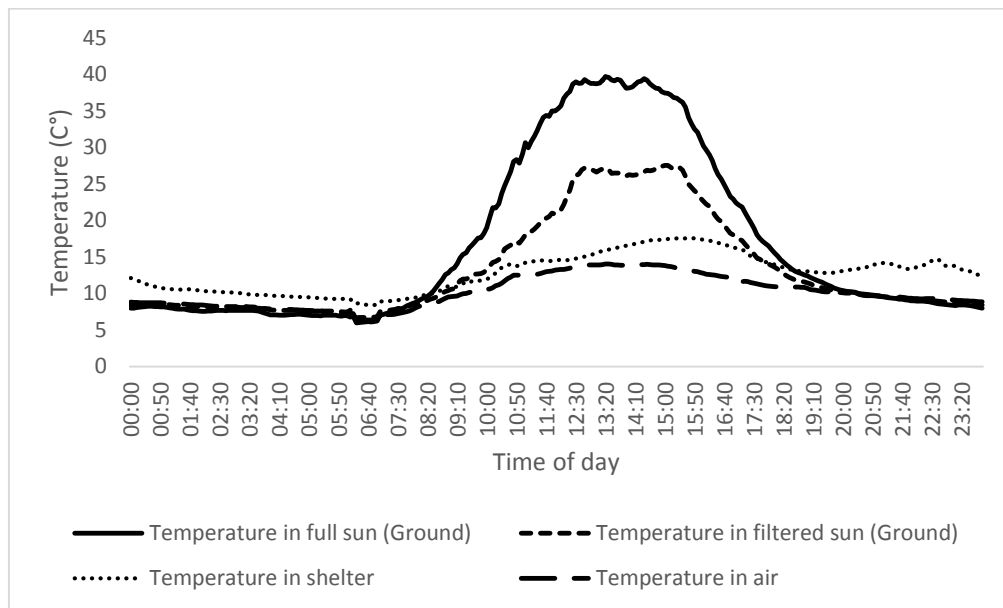


Figure 2. The mean temperature in the air and on the ground measured between 22/4 and 29/4 – 2015 on 4100 m asl.

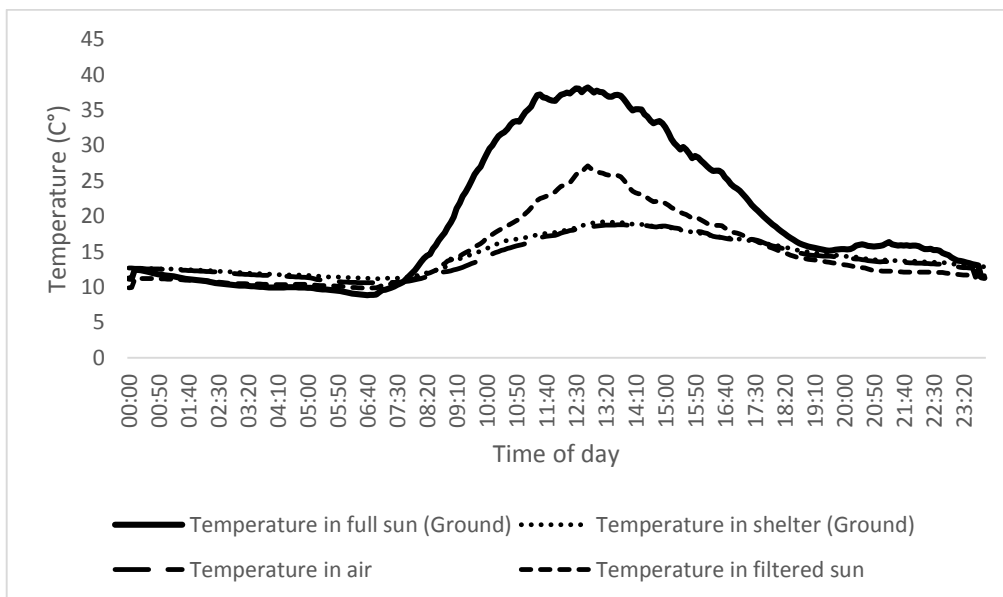


Figure 3. The mean temperature in the air and on the ground measured between 13/4 and 21/4 – 2015 on 3000 m asl.

## 4.2 Basking behavior

The lizards on 4100 m asl allocated more time to thermoregulatory behavior than lizards on 3000 m asl. The population on the higher altitude had a greater mean in basking proportion and in total basking time than the population on the lower altitude, but the difference was not significant. There were no difference in mean basking duration (basking duration for one basking period) between the populations. (Table 5).

A two way ANOVA was done to examine the effect of age and altitude on the total basking time. The test showed no significant interaction ( $F(2, 56) = 1,671, p = 0,197$ ). There was no significant difference in total basking time between the different age-groups; juvenile (mean:  $13:04 \pm 11:13$ ), adult (mean:  $12:41 \pm 10:45$ ) and unknown (mean:  $10:42 \pm 11:44$ ) ( $F(2, 56) = 0,124, p = 0,884$ ).

To further evaluate the thermoregulation behavior, a graphic comparison were made between the mean of the total basking time and basking proportion (Figure 4 & 5). The comparison of the behavior was made in different temperature intervals, instead of hours of the day. The reason for this is that the weather during field work was fluctuating, and it was therefore more accurate to compare the behavior during different temperatures than time of the day. The temperature on the ground with full exposure of sunshine was used, since that probably is of higher influence on the lizards (Bujes & Verrastro 2006). The lizards on the higher altitude did in general have longer durations of basking than the lizards on lower altitude, except in the temperature-range of 25-30 °C and 40-45 °C. The longest mean basking duration for the population on 3000 m asl was in the temperature-range between 25-30 °C, while the population on 4100 m asl had the longest basking duration in the temperatures 20-25 °C (Figure 5). The mean proportion of basking behavior was higher for the lizards on 4100 m asl between the temperatures 15 – 20 °C and 25 – 40 °C than for the lizards on 3000 m asl (Figure 4).

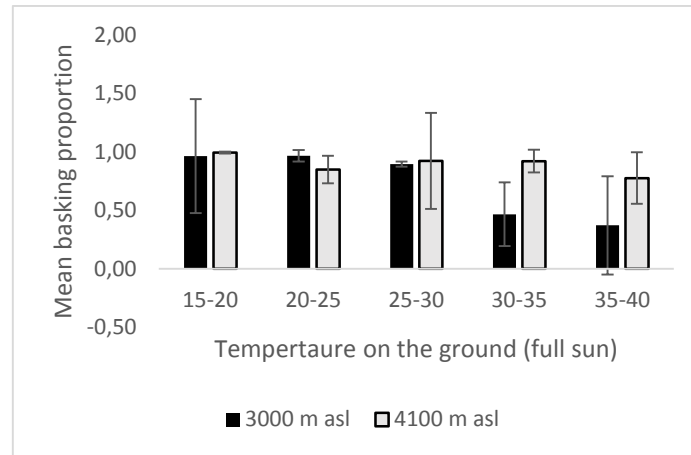


Figure 4. Mean basking proportion and std. deviation during different temperatures on the ground (in full sun exposure) by the population on 3000 (N = 33) and 4100 m asl (N = 32).

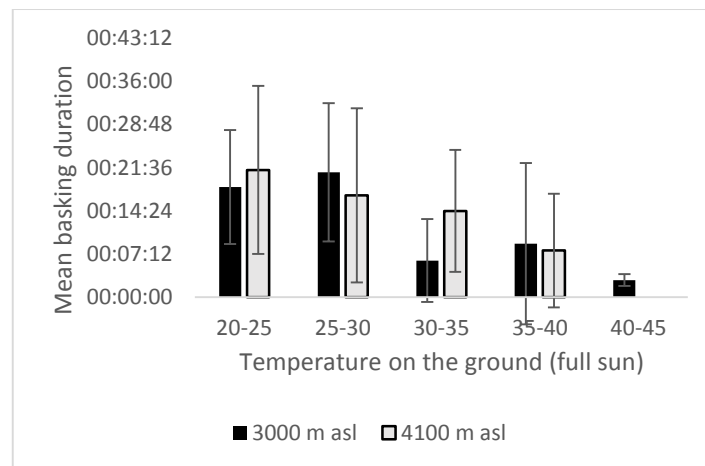


Figure 5. Mean basking duration and std. deviation during different temperatures on the ground (in full sun exposure) by the population on 3000 (N = 33) and 4100 m asl (N = 32).

The lizards on the higher altitude did in general spend more time in position A than the lizards on the lower altitude. The lizards on 3000 m asl spent more time in position B and C (Figure 6). The largest difference between the populations is the time spent in position A, the position that is dominating in the population on 4100 m asl. However, the difference was not significant between the populations regarding the mean time spent in position A, B or C (Table 5).

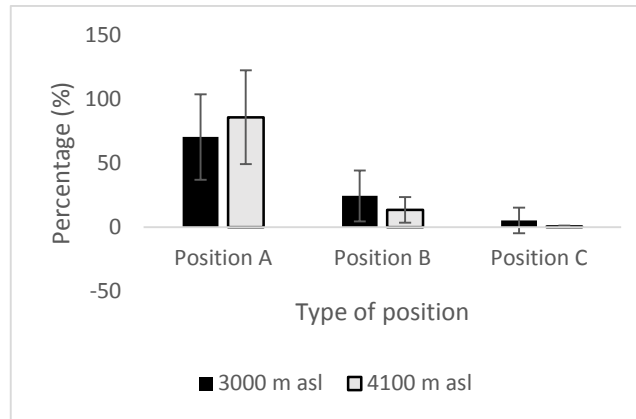


Figure 6. The percentage and std. deviation of the total basking time in basking position A, B and C by the population on 3000 (N = 33) and 4100 m asl (N = 32).

To assess if the populations differed in their time spent on foraging, a comparison was made in the total time moving and the total distance of movement. There were, however, no statistically significant difference between the two populations in the time moving or the distance of movement (Table 5).

Table 5. The results and mean values, with standard deviations (SD) in minutes, from the independent t-tests made to evaluate the differences between the population on 3000 (pop3000) and 4100 (pop4100) m asl.

Parameter	Mean value for pop3000 + SD (N = 33)	Mean value for pop4100 + SD (N = 32)	d.f.	t-value	P-value
Total basking duration	11:48 ± 10:41	12:58 ± 11:19	60	-0,485	0,629
Basking proportion	0,72 ± 0,33	0,85 ± 0,18	63	-1,929	0,058
Basking Mean duration	07:47 ± 10:09	07:06 ± 10:09	59	0,491	0,626
Total time in position A	08:26 ± 10:35	11:26 ± 11:55	55	-1,328	0,188
Total time in position B	02:55 ± 06:34	01:51 ± 03:52	55	0,143	0,887
Total time in position C	00:37 ± 0:07	00:04 ± 00:19	55	0,961	0,341
Total distance of movements	173 ± 130 cm	192 ± 170 cm	52	0,246	0,806
Total time moving	00:50 ± 01:00	00:58 ± 00:42	57	-1,863	0,068

### 4.3 Use of habitat during basking

The use of substrates during basking differed between the populations, especially the use of dead vegetation and rocks (Figure 7). The lizards on 3000 m asl mainly chose to use dead vegetation as basking substrate, but tended to use thick herbs and soil as well. Lizards on 4100 m asl used rocks as substrate during basking, and to a small fraction also dead vegetation, herbs and soil. Neither of the populations used trees as basking substrate, but it should be mentioned that there was a limited availability of trees on 3000 m asl, and at 4100 m asl there were none. The use of different substrate during basking was not compared between the populations with statistical analyses, since the habitat available for the populations differed strongly.

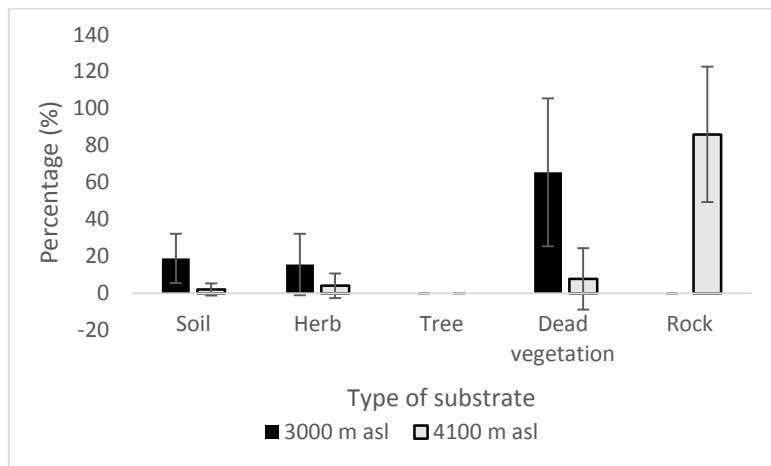


Figure 7. The percentage of time and std. deviations spent on each type of basking substrate by the population on 3000 (N = 28) and 4100 m asl (N = 31).

The lizards on 4100 m asl spent more time in full sun exposure than the population on 3000 m asl. The mean basking time in filtered sun exposure differed less between the populations than the time spent in shade, which was dominated by the lizards on 3000 m asl (Figure 8). This study could not find any significant difference between the populations, even though the means of basking time spent in different sun exposures did differ (Table 6).

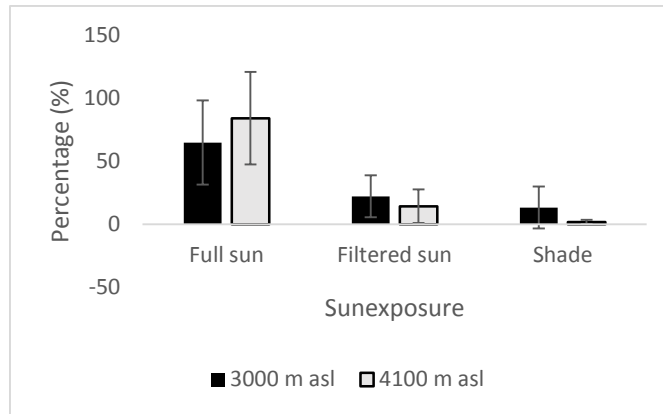


Figure 8. The percentage and std. deviations of total time spent in different types of sun exposure by the population on 3000 (N = 28) and 4100 m asl (N = 31).

A factor related to sun exposure is the cover of vegetation. The lizards on the lower altitude had a significantly higher percentage of vegetation cover than the lizards on the higher altitude (Table 6).

The lizards at 4100 m asl had, in general, a shorter distance from their basking site to the nearest shelter. The shelter from predators on 4100 m asl did mainly consist of rocks, while the lizards on 3000 m asl used dead vegetation and thick herbs. The distance to shelter was not significantly different, and only a small difference in the mean distance can be seen between the populations (Table 6).

Table 6. The results and mean values with std. deviations (SD), from the statistical analyses made to evaluate the difference between habitat use while basking between the population on 3000 (pop3000) and 4100 (pop4100) m asl.

Parameter	Mean value for pop3000 + SD (N = 28)	Mean value for pop4100 + SD (N = 31)	d.f.	t-value	P-value
Time spent basking in full sun exposure (minutes)	08:05 ± 10:07	11:12 ± 11:39	58	-1,299	0,199
Time spent basking in filtered sun exposure (minutes)	02:45 ± 05:31	01:53 ± 03:40	58	0,724	0,472
Time spent basking in shade (minutes)	01:38 ± 05:43	00:14 ± 00:45	58	1,378	0,173
Cover of vegetation (%)	32,44 ± 24,08	13,88 ± 16,02	58	3,755	0,000*
Distance to shelter (cm)	14,72 ± 13, 05	11,02 ± 1,09	58	0,925	0,359

\* Statistical significant difference

#### 4.4 Habitat use

The habitat available for lizards on 3000 m asl was characterized by herbs, soil and dead vegetation (Figure 9). Rocks and trees only occurred to a small degree in this area. The habitat use by the lizards on this altitude did mainly consist of herbs and dead vegetation (Figure 9). An important factor in the habitat was the amount of shelter (Table 7). The parameters that were kept in the backward regression model on 3000 m asl was rock, herb, tree, shelter and shadow. Rock, tree, herb and shadow were negatively related with the occurrence of lizards, while shelter were positively related. Parameters that were not kept in the regression, but had a positive relation with lizard habitat, were dead vegetation and the vegetation layers between < 25 and 25-50 cm. These parameters had a positive relationship on the probability of the occurrence of lizards, even though there were no significant differences between the lizard habitat and the control points.

The lizards on 4100 m asl had a different habitat available, with less herbs and dead vegetation, and more grass and stone cairns. The habitat use of the lizards consisted mainly of rock cairns and, to some extent, herbs (Figure 10). The parameters kept in the backward regression model were rock, dead vegetation and shelter (Table 7). These three parameters were all positively related with the occurrence of lizards.

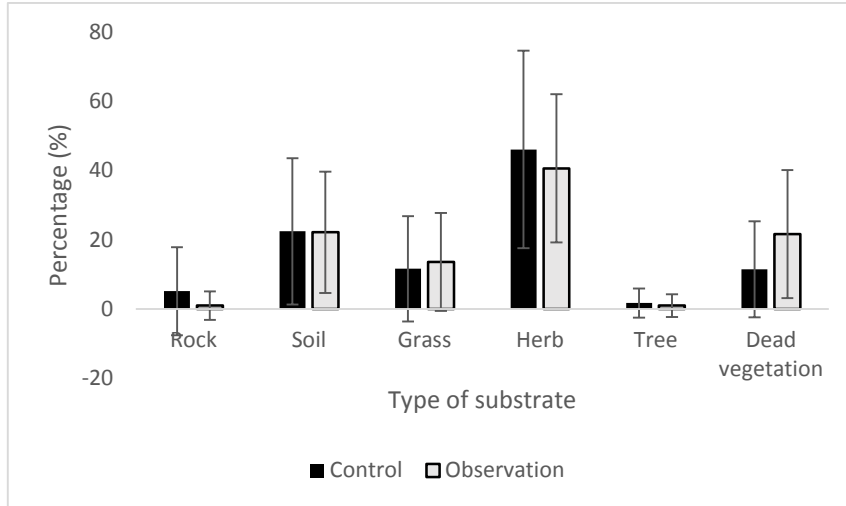


Figure 9. The percentage and std. deviations of each substrate in lizards habitat (N = 90) (2 m Ø) and control points (N =30) in the altitude of 3000 m asl.

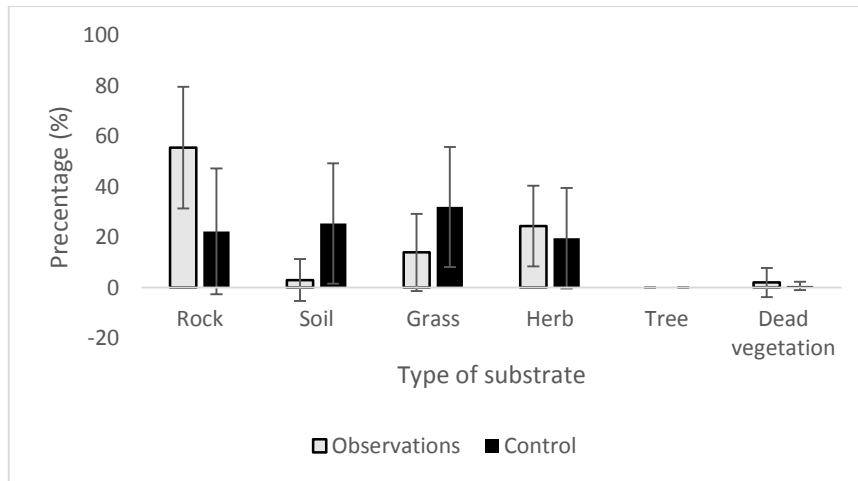


Figure 10. The percentage and std. deviations of each substrate in a lizards habitat (N = 40) (2 m Ø) and control points (N = 30) in the altitude of 4100 m asl.

Table 7. Results of the binary logistic regression analyses made on the habitation data from 3000 and 4100 m asl. Positive values in the parameters estimate indicate a positive relationship between the parameter and the probability of a lizard to occur. The odds ratio shows the strength of this relationship, where lizard habitat and control points are compared (values close to 1 indicate a weak relationship). The G-value is the test statistics for the likelihood ratio test. The p-values for the excluded parameters are those calculated when excluded. Goodness of fit of the final model on 3000 m asl: D = 25,277, d.f. = 5, P = 0,000, n = 120. Goodness of fit of the final model on 4100 m asl: D = 47,328, d.f. = 3, P = 0,000, n = 71.

Explanatory parameters	Parameter estimate $\pm$ SE	Odds ratio	G-value	P-value
<b>Parameters kept in the final model on 3000 m asl</b>				
Rock	-11,24 $\pm$ 3,94	0,000	0,001	0,004*
Herb	-4,11 $\pm$ 1,65	0,016	0,009	0,013*
Tree	-11,66 $\pm$ 6,97	0,000	0,094	0,094
Shelter	4,91 $\pm$ 1,76	135,892	0,002	0,005*
Shadow	-3,06 $\pm$ 1,50	0,047	0,040	0,041*
<b>Parameters excluded from the model on 3000 m asl</b>				
Soil	-0,19 $\pm$ 3,47	0,825	0,956	0,956
Dead vegetation	2,72 $\pm$ 1,97	15,190	0,151	0,168
Vegetation layer, < 25 cm	0,67 $\pm$ 2,22	1,946	0,763	0,764
Vegetation layer, 25-50 cm	0,33 $\pm$ 3,25	1,394	0,919	0,919
Vegetation layer, > 50 cm	-1,65 $\pm$ 1,26	0,193	0,181	0,190
<b>Parameters kept in the final model on 4100 m asl</b>				
Rock	3,44 $\pm$ 1,40	31,179	0,008	0,014*
Dead vegetation	13,09 $\pm$ 10,42	483152,997	0,084	0,192
Shelter	5,09 $\pm$ 1,80	162,462	0,002	0,000*
<b>Parameters excluded from the model on 4100 m asl</b>				
Soil	1,07 $\pm$ 4,00	2,920	0,790	0,789
Herb	0,22 $\pm$ 0,74	1,249	0,744	0,765
Tree	49,33 $\pm$ 89317,71	2,66E+21	0,114	1,000
Vegetation layer, < 25 cm	-6,09 $\pm$ 8,64	0,002	0,450	0,481
Vegetation layer, 25-50 cm	3,59 $\pm$ 5,43	36,16	0,505	0,509
Vegetation layer > 50 cm	-1,96 $\pm$ 3,71	0,140	0,605	0,597
Shadow	0,78 $\pm$ 2,74	2,182	0,776	0,776

\* Significant difference

Statistical comparisons on the use of substrate and vegetation layer were not made since the habitat available on the two altitudes differed strongly. A graphic overview of the ground substrates used by each populations were made (Figure 11), which shows that the lizards on 4100 m asl prefer a stony habitat while the lizards on 3000 m asl prefer a habitat with more herbs and dead vegetation.

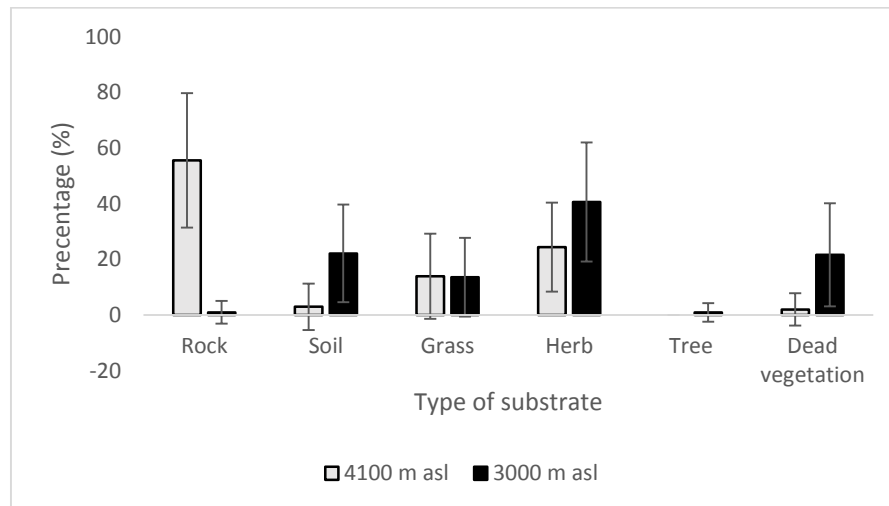


Figure 11. The percentage and std. deviations of each substrate in a lizard habitat (2 m Ø) on 3000 (N = 90) and on 4100 m asl (N = 40).

The lizards on the higher altitude tended to use a habitat with less shadow and more shelter than the lizards on the lower altitude. The study found a significant difference in the amount of shadow between the altitudes ( $t(129) = 4,166$ ,  $p = 0,000$ ), where the population on 3000 m asl ( $42,41 \pm 18,84$ ) had a greater mean than the population on 4100 m asl ( $29,87 \pm 19,28$ ). There was also a significant difference in habitat use between the two populations in shelter ( $t(130) = -4,024$ ,  $p = 0,000$ ), in which the lizards on 4100 m asl ( $56,23 \pm 22,96$ ) had a greater mean of shelter than the lizards on 3000 m asl ( $37,87 \pm 21,39$ ).

## 5 Discussion

### 5.1 Behavior

There was no statistically significant difference in any of the behavioral comparisons between the populations on 3000 and 4100 m asl. I believe that the reason for this is that the sampling size was small, and I will therefor discuss the mean values and what they indicate.

The total basking time and basking proportions showed no significant difference between the populations. But there was a difference in the means

that support the hypothesis that lizards on higher altitudes spend more time basking, at the expense of time that otherwise could have been devoted to other activities. Other studies support the theory that lizards in harsher environments behaviorally adjust their body temperature by allocating more time to basking (Gvozdík 2002, Valdecantos et al. 2012, Hertz & Huey 1981, McConnachie et al. 2009). This difference in the proportion and the time spent on basking should affect the fitness of the lizards at 4100 m asl negatively. A colder climate affects lizards by restraining the amount of time where it could be active with its preferred body temperature, which affects their ability to forage and has a negative effect on survival rate and fecundity (Adolph & Porter 1993, Dunham et al. 1988). This means that, since the population on 4100 m asl allocates a larger amount of time on basking and has shorter time during the day with a preferable temperature, the fitness of the population on 4100 m should be negatively affected. The abundance of lizards between 3000 (69.6 lizards/ha) and 4100 (10.9 lizards/ha) m asl supports this theory. Another explanation for the difference in abundance could be predation pressure and/or food availability (Díaz 1997).

There was no significant difference in total basking time found between the different age groups. Other studies have found that body size affects daily activity and thermoregulatory behavior (Castilla & Bauwens 1991, Carrascal et al. 1992, Biazquez 1996, Maia-Carneiro & Duarte Rocha 2013). Smaller (younger) lizards tend to have a faster heating- and cooling rate and therefore tend to bask shorter time periods but more frequently than larger lizards (Carrascal et al. 1992). This could have affected my data since I observed more young individuals on 3000 m asl than on 4100 m asl. The result of this should have made the mean total basking lower on 3000 m asl than on 4100 m asl, simply because I observed more young individuals and not because of environmental differences. I do not believe this is true in this case, since the mean values for the juveniles' total basking time is greater than for adults or unknown. The gender of the lizard could also affect the thermoregulatory behavior (Huey & Pianka 2007) and habitat use (Singh, et al., 2002), although this is not necessarily true (Maia-Carneiro & Duarte Rocha 2013). Pregnancy could also affect the thermoregulation of females by lowering their heating rate (Labra & Bozinovic 2002). Since my sample size was small, I did not investigate the differences between the genders.

Even though there was no significant difference in time spent in different basking positions between the populations, the means differed in a way that

supports the hypothesis that lizards on higher altitudes would use a posture that made their thermoregulation more effective (especially basking position A). By modifying their posture to get closer to the substrate, which works as a heat source (Bujes & Verrastro 2006), their thermoregulation can become more effective (McConnachie et al. 2009, Castilla & Bauwens 1991). This also means that the lizard can, by lifting its body from the substrate, remove themselves from the heat source, which is important when the substrate temperature is too high (Huey 1974). Another reason for choosing a raised body posture (position B or C) is to scan for prey while basking (McConnachie et al. 2009). Figure 6 shows that the lizards on 3000 m asl tends to use position B and C slightly more and position A less than the lizards on 4100 m asl. This indicates that the substrate together with air temperature, during some hours in the day, is getting much warmer on 3000 m asl and that they adjust their behavior according to the temperature.

There was no significant difference in time moving or total distance between the two populations. The goal with measuring this behavior was to assess if the time spent on foraging was lesser on 4100 m asl than on 3000 m asl, since the colder environment should restrict their time in thermally favorable microclimates (Grant & Dunham 1988). The locomotion of lizards are sensitive to temperature (Gunderson & Leal 2015) and plays an important role in the species fitness (Fernández et al. 2011). Lizards in colder habitats could adapt to this by either having a lower body temperature while active or be active during a shorter time (Angilletta et al. 2006). The result of movement measurements could be of great importance in order to understand how the difference in temperature affects the lizards, since it could work as an index for foraging (Bellure & Carrascal 1996). I believe that the absence of significant difference depends on the small sample size and the difficulties I had observing lizards in movement. The lizards tended to quickly disappear in vegetation during locomotion. Since there was less vegetation in the field site on 4100 m asl, the observation of movement was easier to conduct than on 3000 m asl. This is probably the main reason for fairly equal mean values in between the populations, where the lizards on 4100 m asl tend to move longer distances and spend more time in movement.

## **5.2 Habitat use during basking**

The population on 3000 m asl mainly used dead vegetation for basking. The dead vegetation was often of the plant *Opuntia ficus-indica*, which turn dark brown when dead. Dark colors gets warmer more quickly than light colors, which might be one reason why they chose dead instead of living

vegetation. Another reason could be that dead *Opuntia ficus-indica* provides shelter from predators, so the lizards could also keep a short distance to the nearest refuge by basking on dead vegetation. The population on 4100 m asl used rocks as basking substrate. Rocks provide refuge from predators, warm overnight shelters and good basking spots. Rocks have the capacity to reach high temperatures and to store heat (Sabo 2003, Biazquez 1996). The use of thermally favorable microclimates is an important tool to raise the body temperatures and activity for lizards (Grant & Dunham 1988) and I believe that the availability of stone cairns were crucial for the ability to obtain and maintain a high body temperature for the lizards on 4100 m asl. The fact that *Liolaemus aparicioi* were able to use both rock cairns and *Opuntia* (which is not an endemic species) shows of an adaptability and plasticity in behavior. It would be interesting to measure the temperature on the *Opuntia ficus-indica* to evaluate the plant's capacity to reach and store high temperatures. This is interesting since the lizards on 3000 m asl tend to favor this plant as basking site, and it is possible that it could reach as high temperatures as the rocks on 4100 m asl.

One important way of thermoregulation is the shuttling between sun and shade (Huey 1974). The lizards on the higher altitude basked in full sun exposure in a higher degree than the lizards on the lower altitude (although no significant difference). Lizards on the lower altitude chose filtered sun and shade in a higher degree, which shows a smaller need of raising their body temperature comparing to the lizards on the high altitude. Since the solar radiation is stronger on higher altitudes, basking on 4100 m asl in direct sunlight should have been even more effective in order to raise the body temperature. The effectiveness of basking is due to a lot of factors though, both environmental, physiological and behavioral, and cannot be excluded to only basking substrate and solar radiation (Hertz & Huey 1981). I believe that the combination of stronger sun radiation and rock cairns were of great importance for the thermoregulation of lizards at 4100 m asl.

The cover of vegetation could serve as a way to hide from predators and a way to obtain more shadow in the habitat. The cover of vegetation was significantly different between the populations, with greater mean percentage in the habitats of lizards on the lower altitude. This support the hypothesis that lizards in warmer environments would occupy less open habitat, a hypothesis that has been confirmed in other studies (Hertz & Huey 1981). The use of a habitat with a greater vegetation cover is probably a way to reduce body temperature. It could also be an anti-

predator behavior since it diminish the risk of predation (Castilla & Bauwens 1991). The occupation of more open habitats in the higher altitude increases the proportion of time spent in full sun, which is especially important during low air temperatures and a fluctuating weather. This should also decrease the risks and energetic costs of raising the body temperature (Huey & Slatkin 1976), which otherwise should be higher in the harsher climate of a higher altitude.

The distance to shelter differed between the populations, but they were not significantly different. The lizards on 3000 m asl had a greater mean than the lizards on 4100 m asl. A longer distance to shelter should increase the costs of basking, by increasing the time and energy used during basking. It could also increase the risk for predation and interfere with social behavior (Hertz & Huey 1981, Huey 1974). This difference in mean values could be explained by the greater vegetation cover – which leads to a smaller risk to be detected by a predator – on 3000 m asl (Castilla & Bauwens 1991). The need for a shelter close by could be smaller since the risk of getting detected is smaller. Another explanation is that the lizards on 4100 m asl only inhabited the stone cairns, which provided shelter as well as a good basking substrate. This is a habitat that is not available for the population of 3000 m asl, and it is therefore difficult to know if they would have used this shelter-rich habitat if they could. The third explanation for this differing mean value is that there could be a higher predation risk on the higher altitude, which made it even more crucial to stay close to a possible refuge. It is possible to view the shorter distance to shelter as a measure of anti-predator behavior (Carrascal et al. 1992). This, together with the fact that more time allocated to basking gives less time to avoid predators (Gvozdík 2002), indicates that the population on 4100 m asl are more careful against predators. It should be mentioned that the mean distance to shelter did not differ greatly between the populations, but that the percentage of shelter in the habitat did show a significant difference (see further down in the discussion).

### **5.3 Habitat use**

The area on 4100 m asl where characterized by a landscape of grass, short bushes and stone cairns. Lizards on 4100 m asl tended to use the rock cairns as a habitat. This tendency can be seen in the graph over ground substrate use at 4100 m asl (Figure 10) and in the outcome of the backward regression. In graph 10 one could also see that the percentage of herbs in lizard habitats is greater than in control point. The backward regression confirms that (even thou without significant difference) herbs has a positive

influence on lizards occurrence, as well as vegetation between 25-50 cm. Dead vegetation had a significant positive effect, but I find it unlikely that it had a great influence on lizard survival, since there were very little of this substrate on 4100 m asl. I believe that the reason for the lizard to be so tightly bound to the stone cairns is that they provided heat (Biazquez 1996, Castilla & Bauwens 1991), shelter from predation and night shelter. The weather on this altitude could be very fluctuating, which make the availability to a substrate with high capacity to keep heat even more important. The thermal environment affect the preference of habitat (Singh et al. 2002), and rocks could offer warmth in a cold climate. The mornings were characterized by deep cloudiness, while the afternoon could offer sunny weather with strong radiation. The air temperatures in this area were low, but the sunlight could heat the ground to similar temperatures as on 3000 m asl (see Figure 2 & 3). I believe that the stones capacity to gather and store heat were crucial for the lizards survival.

The lizards on 4100 m asl also tended to prefer herbs in their habitat. An explanation for this could be that the herbs could offer them a hunting ground that was less open and hence less exposed to predators. No lizards were found in vegetation under 25 cm, which was a very common length of grass in the area, which indicates that the vegetation had to be longer to offer protection. Herbs above a certain height should in general make it more difficult for predators to spot the lizards, while thick bushes could also provide shelter from predators.

The importance of shelter is supported by the backward regression, which shows a significant difference between the lizard habitat and control points on both 4100 and 3000 m asl. The lizards on the higher altitude had a significantly greater mean of shelter in their habitat than the lizards on the lower altitude. This is also evident in the parameter distance to shelter. To have more shelter in a habitat is an anti-predator behavior (Carrascal et al. 1992). The reasons for this should be the same as for the parameter distance to shelter, which could be a difference in the amount of predators, vegetation cover and differences in habitat availability. The longer duration spent on basking by the population on 4100 m asl also gives a higher predation risk, which partly could be compensated by being close to shelter (see the discussion about distance to shelter).

The choice of ground substrate and vegetation layer in the habitat of lizards on 3000 m asl is more diverse than on 4100 m asl (Figure 9 & 11). This field site was in general more diverse, both when it came to vegetation

layers and ground substrates. The choice of habitat is more random during warmer climates than in colder climates (Grant & Dunham 1988), which could explain the more diverse choice of habitat on 3000 m asl. Another explanation is that the lizards on this altitude could have suffered of heat-stress during the hottest hours, which made them use a more diverse habitat (Huey 1974) than the population on 4100 m asl.

Five parameters were kept in the backward regression; rock, herb, tree, shelter and shadow. The only parameter that was positively related with lizard occurrence was shelter. The backward regression did however show that lizards on 3000 m asl might have more dead vegetation and vegetation up to 50 cm in their habitat comparing to the control habitats. I believe that dead vegetation is the most important parameter of these, since it provides with night shelter, shelter from predators and good basking sites. The backward regression showed that rocks, herbs, trees and vegetation over 50 cm are less likely to occur in the lizard habitat than in the area in general. There will also be less shadow in the habitat of a lizard. I believe that herbs are an important factor for the lizards at 3000 m asl, since it provides with shelter from predators (Castilla & Bauwens 1991) and shadow during the warmest hours. The fact that a lower mean is seen in the lizard habitat compared to the control points (Figure 9) does not mean that herbs are not important and could depend on other factors. One such factor is that it could be preferable for the lizard to have a habitat with both open space and herbs to hide in. If this is true, then the herbs still are an important parameter, even though the lizards chose a habitat with less herb than was available in the area. Another possible explanation of why there were less herbs in the lizards habitat is that the lizards were more easily spotted during the field work when they inhabited a more open habitat. Even though the search for lizards was conducted over the whole area there is a chance that the lizards were too difficult to see in very high vegetation, especially since they were mostly found on the ground. In a comparison between the populations (Figure 11) one can see that the lizards on 3000 m asl used more herbs, soil and dead vegetation in their habitat than lizards on 4100 m asl. I believe that the most important factors for the population on 3000 m asl were dead vegetation and herb (especially those under 50 cm).

The percentage of shadow in the habitat was significantly different between the populations, were the lizards on 3000 m asl chose a habitat with more shadow. To choose a shadier and cooler habitat is an important thermoregulatory mechanism that have been seen in other species as well (Adolph & Asbury 2007, Huey 1974). It is difficult to exclude that the

habitat were so different in the different altitudes, that the lizards on 3000 m asl could not choose a habitat with as little shadow as on 4100 m asl. I believe that the lizards on 3000 m asl did chose a shadier habitat in order to get a cooler environment, especially during the hottest hours of the day.

#### **5.4 Climate change and lizard conservation**

Temperature has a major effect on the ecology of lizard, which makes it an important factor of the potential threats that comes with climate warming (Gunderson & Leal 2015). Lizards might survive temperature changes if they are given enough time to shift to a more favorable thermal habitat, change their behavior or adjust their physiology (Sinervo et al. 2010). Their ability to adjust their thermoregulatory behavior might buy them enough time to adjust to the new climate. The fact that *Liolaemus aparicioi* exist on two different altitudes, and that the populations differ in their thermoregulatory behavior, shows that the species have a behavioral plasticity and can to some extent adjust to temporary challenges associated with the weather. The study also shows that they are able to adapt their habitat use in order to survive in a different climate. It is very difficult to predict the responses of the lizard to climate changing. A study of how climate change affect organisms has shown that thermoregulatory behavior together with variation in topographic features can mask critical effects of climate change and that some organisms even are positively impacted by global warming (Sears et al. 2011). In order to meet the climate change and survive, it is crucial that *Liolaemus aparicioi* still has undisturbed habitat. Disturbance by human settlements might cause a decrease in population density and make the lizards more vulnerable for climate change. In the work of lizard conservation one should consider to set apart land dedicated for lizards, preferably on 3000 m asl where the population density is higher.

#### **6 Conclusion**

The result from this study do in general support the hypothesis that lizards on higher altitude compensate for a colder climate by changes in their thermoregulatory behavior and habitat use. The lizards on 4100 m asl tend to spend more time in behavior associated with thermoregulation. They also spend more time in a flat body posture and in full sun exposure than the population on the lower altitude. Lizards on 4100 m asl use rocks as basking substrate, while the lizards on 3000 m asl prefer dead vegetation. The lizards on 3000 m asl have a more diverse range of substrates in their habitat, even though they prefer dead vegetation and herbs. They also

prefer a habitat with more shadow than the population on 4100 m asl. The lizards on the higher altitude uses stone cairns as ground substrate and stay closer to shelter than the population on 3000 m asl. My conclusion of these results is that *Liolaemus aparicioi* have the ability to adjust their behavior and habitat use according to the climate and habitat available for them. The population on 3000 m asl have a climate that allow them to spend less time on thermoregulation and more time foraging than the population on 4100 m asl, and have therefore a larger population. The climate on the higher altitude is more difficult to survive in, but the stone cairns makes it possible since they provide with shelter and accumulate heat.

I think that the question of whether there are any differences in behavior or habitat use between two populations should be evaluated further. It would be interesting to collect a larger sample size that might show differences between the populations more clearly. Another important study to be made is if there are any differences between the genders, a factor that could have great influence on the results.

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