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Effects on the thermoregulatory efficiency of two native lizards as a consequence of the habitat modification by the introduction of the exotic tree *Acacia longifolia*

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ABSTRACT

Habitat modification alters several aspects of the original fauna, among them the opportunity for thermoregulation. Here, we studied the thermal biology of sympatric populations of two lizard species (*Liolaemus multimaculatus* and *Liolaemus wiegmannii*) in two different situations; a grassland without trees (natural habitat) and in a grassland plus the exotic tree *Acacia longifolia* (modified habitat), aiming to assess whether the structural alteration of native Pampean coastal grasslands of Argentina affects the thermal biology of these lizards. Field body temperatures, laboratory preferred temperatures, micro-environmental temperatures, operative temperatures, thermoregulatory efficiency and spatial distribution of each species were analyzed in both habitats. Environmental operative temperature was 0.64 °C lower in the modified habitat ($T_e=38.39$ °C) than in the natural ($T_e=39.03$ °C). Thermoregulatory efficiency (E) of *L. wiegmannii* was lower in modified sites ($E=0.58$) than in natural sites ($E=0.70$). This difference may be because this lizard occupied shaded microhabitats under acacias, with suboptimal thermal features. In contrast, *L. multimaculatus* in the modified habitat restricted its activity to open microenvironments that retained a similar structure to that of the native habitat, while maintaining high thermoregulatory efficiency in both habitat types ($E_{\text{modified}}=0.92$; $E_{\text{natural}}=0.96$). Although these two lizard species are phylogenetically close, they respond differently to human-induced changes in their thermal environments. The introduction of *A. longifolia* into coastal grasslands for *L. wiegmannii* in particular, this introduction converts its native habitat into a suboptimal thermal environment.

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1. Introduction

Lizards as ectotherms need to thermoregulate to achieve their activities. Thermoregulation depends on extrinsic factors, such as the availability of thermal resources, elevation, vegetation structure, degree of exposure to wind (Bujes and Verrastro, 2006), social interactions (Labra, 1995) and predation risk (Downes and Shine, 1998). It also may depend on intrinsic factors, such as sex (Sievert and Hutchison, 1989; Huey and Pianka, 2007) and reproductive condition (Núñez, 1996; Iburgüengoytia and Cussac, 2002). In environments where solar radiation is available, behavior is a major contributor for achieving different body temperatures (T_b) compared to physiological mechanisms. Behavioral adjustments are the primary

means that ectotherms use to regulate their body temperatures. Microhabitat selection is more important than postural adjustments for controlling T_b (Stevenson, 1985). However, thermoregulatory behaviors not only bring costs such as the energy expenditure expended when moving between warm and cool spots (Huey, 1974, 1982; Huey and Slatkin, 1976) but also increased exposure to predators (Downes, 2001; Herczeg et al., 2008). Also, time devoted to thermoregulation may compromise feeding (Gvoždik, 2002) or mating opportunities (Shine et al., 2000).

Ectotherms can reduce thermoregulatory costs by inhabiting environments with operative temperatures that are similar to their preferred body temperatures (Angilletta, 2009). However, if ectotherms occupy environments with most operative temperatures outside their preferred range, they can experience substantial thermoregulatory costs (House and Spelleberg, 1983; Sartorius et al., 1999; Román et al., 2006). For example, in places where plant communities were modified by exotic vegetation, the effects on thermoregulation of some reptiles were negative (Valentine et al., 2007; Carter, 2012). Certain exotic plant traits

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such as a larger size, higher growth rate and higher biomass production, turn them into the dominant ground cover markedly altering the structural and thermal conditions of the original habitat promoting an attenuated light environment and a lowering of environmental temperatures (Tomley, 1998; Valentine et al., 2007; Marchante et al., 2008).

In many places around the world, Australian acacias, including *Acacia longifolia*, were planted to stabilize the dynamics of coastal sand dunes. Unfortunately, they invaded extensive areas of native plant communities leading to severe impacts on the structure and function of several original ecosystems of Africa (Yelenik et al., 2004), Israel (Kutiel et al., 2004), Portugal (Marchante, 2001; Marchante et al., 2003) and Uruguay (Caldevilla and Quintillán, 2002). In Argentina, the coastal sand dunes of the North-Eastern coast of the province of Buenos Aires have been planted with specimens of *Acacia*, *Pinus*, *Eucalyptus*, *Populus* and *Tamarix* not only for stabilizing the dunes but also for decorative purposes, in an attempt to improve the attractiveness of seaside resorts (Cozzo, 1976; Zalba and Villamil, 2002). Two species of lizards of the genus *Liolaemus* coexist in sympatry in these dune barriers. These species have specialized morphological features for living in loose sand and are included together with other nine species in the *wiegmannii* group (Etheridge, 2000; Avila et al., 2009). One of the species, *Liolaemus multimaculatus* (snout-vent length: 48–70 mm), is endemic to the coastal sand dune ecosystem of Buenos Aires and Río Negro provinces and its conservation status is considered vulnerable (Lavilla et al., 2000). The other species, *Liolaemus wiegmanni* (snout-vent length: 42–64 mm), is largely restricted to sandy soils of a vast region of Argentina and Uruguay (Gallardo, 1977; Cei, 1993; Martori et al., 1998a; Avila et al., 2009). Both species are spatially segregated in the coastal dunes. The first species, *L. multimaculatus*, occurs on wide open spaces of loose sand and low vegetation cover, while *L. wiegmanni* is frequently observed near more dense vegetation (Vega and Bellagamba, 1994; Vega, 1994, 1999; Kacolis et al., 2010).

Exotic trees, such as *A. longifolia*, not only change the structural characteristics of the habitat by changing shading and leaf litter accumulation but also change the thermal properties of these habitats (Yelenik et al., 2004; Tomley, 1998; Valentine et al., 2007; Marchante et al., 2008). These structural and thermal changes can potentially affect the lizards living in these habitats. Accordingly, the aim was to assess the thermal biology of the sand lizards *L. multimaculatus* and *L. wiegmanni* in habitats modified by *A. longifolia* and in natural habitats of the province of Buenos Aires, Argentina. For this purpose, we specifically addressed the following questions: (i) are there any differences between the environmental temperatures of each habitat type? (ii) are the thermoregulatory capabilities of the lizards affected by *Acacia*? and finally (iii) are the lizards randomly distributed with respect to the structural features of the habitats? Considering the differences between the species described above, we predict that (i) exotic *Acacia* trees increase shading and thus should reduce environmental temperatures below those of natural grasslands. (ii) Because *L. wiegmanni* is able to survive in habitats shaded by acacias, we predict that these lizards will have lower T_b and reduce thermoregulatory efficiency in such habitats relative to native grasslands, (iii) *L. multimaculatus* avoids microhabitats influenced by acacias, we expect that this lizard will have similar T_b s and thermoregulatory efficiency in such natural habitats relative to those in native grasslands, (iv) *L. wiegmanni* occurs in patches with relatively dense vegetation, this lizard is expected to be tolerant of acacias; and finally (v) *L. multimaculatus* restricts its activity to open sites with low vegetation cover, this lizard is expected to avoid altered patches restricting its activity to unaltered spots.

2. Materials and methods

2.1. Study area

Field work was carried out from January to April 2010 at two locations with natural psammophytic grasslands: Pinar del sol (36° 55'55.7"S, 56° 45'03.04"W) and Punta Médanos (36°53'30.9"S, 56°41'20.1"W) and in two sites with grasslands that had been modified by introduced *A. longifolia*, Mar de Las Pampas (37°18'13.4"S, 57°01'29.4"W) and Monte Carlo (37°01'47.3"S, 56°49'23.6"W), Buenos Aires, Argentina. The native vegetation of coastal dunes is composed mainly of *Poa lanuginosa*, *Panicum racemosum* and *Androtrichum trigynum* grasslands; *Cortaderia selloana* scrublands; shrublands and mixed steppes of *Senecio crassiflorus*, *Achyrocline satureioides*, *Tessaria absinthioides*, *Baccharis notoserigila* and *Discaria americana*. The region is located in a mid-latitude climate, with an average summer maximum temperature of 21 °C, a winter minimum of 7.5 °C and a mean annual precipitation of 830 mm (Servicio Meteorológico Nacional, 1920–1980; Burgos and Vidal, 1995).

2.2. Data recorded

We captured 164 individuals of *L. wiegmanni* and 64 *L. multimaculatus* by hand or by noose between 0900 and 1800 h, corresponding to the entire daily activity period of this species (Vega 1999). In order to avoid bias related to daily lizard activity we sampled during the three daily periods (morning, midday and afternoon) equally. We measured lizards' body temperature (T_b , sensu Pough and Gans, 1982) with an ultra-thin thermocouple introduced 1 cm inside the vent. We measured body temperature in the field only from active lizards. Individuals were handled by the head to avoid heat transfer and temperature was recorded within 20 s after capture. The micro-environmental temperatures were recorded at capture sites: substratum temperature (T_s) at 1 cm under the ground and air temperature at 1 cm above the ground (T_a) by thermocouples connected to a digital thermometer (SC133, Schwyz MR., Buenos Aires, Argentina). We measured operative temperatures (T_e , sensu Hertz et al., 1993) in the field using 12 regular data loggers (DS1921G, iButton Sunnyvale, CA, USA) placed directly on the substrate, temperature was captured every 12 min between 0900 and 1800 h for 2 consecutive days set at 12 random sites within the habitat of each species of lizard (sensu Vitt and Sartorius, 1999). Mean temperatures were recorded from each data logger and used to obtain the T_e of each habitat type (modified and natural).

2.3. Laboratory protocol and determination of preferred body temperature

We obtained the preferred body temperature (T_{sel}) from nine *L. wiegmanni* and 13 *L. multimaculatus* at the lab in Mar del Plata (38°00'18.32"S, 57°37'17.21"W). Previously to T_{sel} trials, lizards were kept in glass terraria (0.35 × 0.20 × 0.20 m), fed (*Tenebrio molitor* and *Achaeta domestica*) and water was offered *ad libitum*, photoperiod was 12L:12D. After that, lizards were placed individually in open-top terraria (1.50 × 0.30 × 0.18 m) with a 0.03 m sand layer on the bottom to prevent overheating. The thermal gradient was produced by a line of four overhead infrared lamps (one of 150 W, two of 100 W and one of 75 W) set at 0.10, 0.40, 0.70 and 1.00 m, respectively, from one end of the terrarium. The lamps were adjusted to different heights above the soil to make a linear substratum gradient from 18 to 65 °C. We measured body temperatures with an ultra-thin (1 mm) thermocouple fixed in place with adhesive tape approximately 1 cm inside the vent. The thermocouple was connected to a digital thermometer

(SC133, Schwyz MR., Buenos Aires, Argentina). The temperature of each lizard was recorded during two consecutive days between 0900 to 1600 h, recording data every 15 min. For each individual, we calculated the mean T_{sel} and the set-point range (lower T_{set} and upper T_{set} , considered as the temperatures within the interquartile range that include 50% of the observations, following the protocol of Hertz et al. (1993). We calculated the indexes: de , the thermal quality of the habitat; db , the accuracy of thermoregulation; and E , the effectiveness of thermoregulation (sensu Hertz et al., 1993). These indexes were developed from the use of three independent data types: (i) the distribution of T_e , (ii) field body temperature (T_b), and (iii) preferred body temperature obtained in the laboratory (T_{sel}). E is an estimate of thermoregulatory effectiveness, i.e. how close is T_b from T_{sel} for the null distribution of temperature (T_e). A given value of E results from a variety of different combinations of db and de ; then, when E is close to 1 the organism is considered as an efficient thermoregulator, conversely E value close to 0 means that the organism is a thermoformer and when E is close to 0.50 it is considered as a moderately thermoregulator (Hertz et al., 1993; Bauwens et al., 1996; Medina et al., 2009). Because we found no significant differences in any of the variables (T_b , T_s , T_a) between the two sites of the same type of habitat (natural and modified; see Appendix A), the data were grouped by habitat type, thus from now on they are called “modified habitat” (Mar de las Pampas+Monte Carlo) and “natural habitat” (Pinar del Sol+Punta Médanos).

2.4. Lizards distribution with respect to the structural features of the habitats

To analyze the spatial distribution of the lizards we determined the structural composition of the patches used by the lizards, by taking into account the stratus composition (sand with or without leaf litter) and the physiognomic type of the plants (trees, shrubs, sub-shrubs and herbs) according to Cabrera and Zardini (1978). The availability of microhabitats was estimated visually by measuring the relative percentage of coverage using 25 m² grids following Gysel and Lyon (1987). Once a lizard was detected, we placed a grid of 25 m² where central point was the initial site of the sighting. We set 124 grids for *L. wiegmanni* and 64 for *L. multimaculatus*. In addition, for structural characterization of each habitat type we

set 63 grids of 25 m² in the modified habitat and 61 in the natural habitat. Grids were placed at intervals of at least 50 m apart from each other and the number of replicates was calculated by using species accumulation curves (Gysel and Lyon, 1987).

2.5. Statistical analysis

Previously to the analyses, normality and homoscedasticity of the data set were evaluated by Kolmogorov–Smirnov and Shapiro–Wilk tests, respectively. Non-parametric tests were used when data did not meet the parametric assumptions. Thus, Mann Whitney U test ($\alpha=0.05$) was used to compare operative temperatures (T_e), microenvironmental temperatures (T_s and T_a) and field body temperature (T_b), between the modified and the natural habitat for each species of lizard. We calculated the indexes of the thermal quality of the habitat (db), accuracy of thermoregulation (de) and effectiveness of thermoregulation (E) for each habitat type. For this purpose, we used bootstrapping method, with 1000 iterations on the data matrix (Hertz et al., 1993) and then, they were compared using Mann Whitney U test ($\alpha=0.05$). We also used multiple linear regressions to explore possible associations between T_b and micro-environmental temperatures (T_s and T_a). Finally, we used discriminant-function analysis (DFA) to determine whether microsites used by *L. wiegmanni* and *L. multimaculatus* differed from randomly sampled microsites based on structural features. This analysis also allowed us to evaluate interspecific differences in habitat use and determine possible mechanisms for habitat and resource partitioning. Functions created by DFA of the original variables maximize separation between groups and indicate which variables contribute most to group separation where groups are preselected as microhabitat sites by lizards or randomly sampled sites (Zar, 1984).

3. Results

3.1. Thermal characterization of the habitats

The operative temperature was significantly lower in the modified habitat than in the natural habitat, with a difference of 0.64 °C (Table 1; Fig. 1). At *L. wiegmanni* capture sites, T_s was significantly lower in the modified habitat than in the natural one,

Table 1

Mean values \pm standard deviations and sample numbers (in brackets) of operative temperature (T_e), substrate and air temperatures (T_s and T_a) and body temperature (T_b), in modified and natural habitats for both species of lizards. References: (db) deviation on T_b from T_{sel} (de) thermal index of habitat quality, (E) thermoregulatory effectiveness (T_{sel}) mean preferred body temperature, and (T_{set}) set-point range of preferred body temperature. U =Mann Whitney statistic ($\alpha= 0.05$), P =probability value, * statistically significant differences.

| Lizard species/ habitat type | T_e (°C) | T_s (°C) | T_a (°C) | T_b (°C) | db | de | E | T_{sel} (°C) | $T_{set-lower}$ (°C) | $T_{set-upper}$ (°C) |
|---------------------------------|----------------------------|--------------------------|--------------------------|--------------------------|---------------------------|---------------------------|----------------|--------------------------|--------------------------|--------------------------|
| <i>L. multimaculatus</i> | | | | | | | | | | |
| Natural | 39.03 \pm 9.10 (1000) | 39.26 \pm 6.80 (65) | 34.40 \pm 4.38 (65) | 36.46 \pm 3.16 (65) | 1.82 \pm 0.19 (1000) | 6.13 \pm 0.50 (1000) | 0.70 (1000) | 38.12 \pm 0.83 (9) | 36.88 \pm 0.90 (9) | 39.42 \pm 0.89 (9) |
| Modified | 38.39 \pm 8.51 (1000) | 35.72 \pm 4.86 (59) | 33.99 \pm 3.27 (59) | 34.67 \pm 2.92 (59) | 2.48 \pm 0.22 (1000) | 5.94 \pm 0.41 (1000) | 0.58 (1000) | | | |
| U | 591,627 | 2465.5 | 2020.5 | 2454.5 | 35801 | 562,465 | 201,938 | | | |
| P | < 0.001* | 0.006* | 0.608 | 0.007* | < 0.001* | < 0.001* | < 0.001* | | | |
| <i>L. multimaculatus</i> | | | | | | | | | | |
| Natural | 39.03 \pm 9.10 (1000) | 39.60 \pm 1.35 (34) | 33.04 \pm 2.84 (34) | 36.28 \pm 1.41 (34) | 0.24 \pm 0.08 (1000) | 6.21 \pm 0.57 (1000) | 0.96 (1000) | 35.37 \pm 1.41 (13) | 34.05 \pm 1.76 (13) | 37.13 \pm 1.70 (13) |
| Modified | 38.39 \pm 8.51 (1000) | 39.15 \pm 3.33 (30) | 32.59 \pm 2.97 (30) | 36.21 \pm 1.78 (30) | 0.47 \pm 0.12 (1000) | 5.83 \pm 0.47 (1000) | 0.92 (1000) | | | |
| U | 591,627 | 606 | 528 | 538 | 486,590 | 477,592 | 490,946 | | | |
| P | < 0.001* | 0.198 | 0.814 | 0.711 | 0.869 | 0.83 | 0.894 | | | |

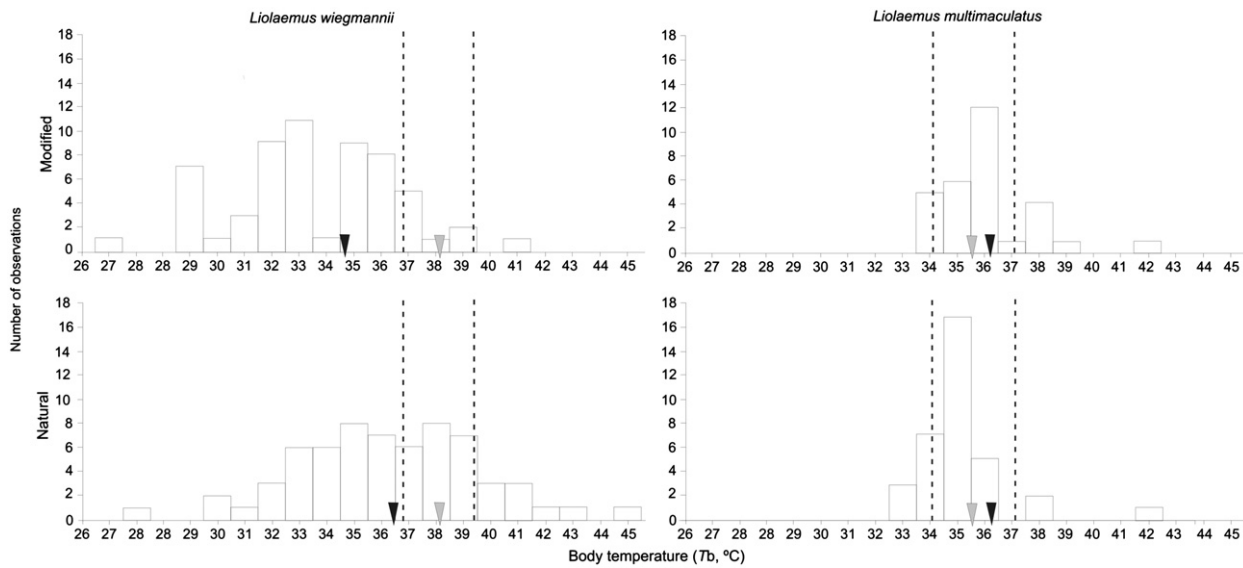


Fig. 1. Frequency of T_b in the field (bars) of *L. wiegmanni* and *L. multimaculatus* in the two habitat types. The black arrows indicate the median T_b , gray arrows the median T_{sel} and vertical dashed lines the set-point range of preferred body temperature (T_{set}).

whereas T_a was not different between habitats (Table 1). Both, T_a and T_s at *L. multimaculatus* capture sites were similar between modified and natural habitats (Table 1).

3.2. Relationship between micro-environmental and body temperatures

In the modified habitat, T_b of *L. wiegmanni* showed a significant and positive relationship with T_s but not with T_a (multiple linear regression: $r^2=0.230$, $F_{2, 59}=9.642$, $P<0.001$; partial correlation $T_b-T_s=0.497$ $P<0.001$, partial correlation $T_b-T_a=-0.155$, $P=0.245$). Conversely, in the natural habitat, T_b of *L. wiegmanni* showed a significant and positive relationship with T_a but not with T_s (multiple linear regression: $r^2=0.231$, $F_{2, 65}=10.324$, $P<0.001$; partial correlation $T_b-T_s=0.199$, $P=0.121$, partial correlation $T_b-T_a=0.357$, $P=0.004$).

In the case of *L. multimaculatus* at both habitat types, we observed significant and positive relationships between lizards' T_b and T_s but not between T_b and T_a (multiple linear regression: modified: $r^2=0.748$, $F_{2, 30}=44.131$, $P<0.001$; partial correlation $T_b-T_s=0.781$, $P<0.001$; partial correlation $T_b-T_a=-0.117$, $P=0.544$; natural: $r^2=0.912$, $F_{2, 34}=171.556$, $P<0.001$; partial correlation $T_b-T_s=0.953$ $P<0.001$; partial correlation $T_b-T_a=0.225$, $P=0.206$).

3.3. Field body temperature, preferred body temperature and thermoregulatory effectiveness

The mean T_b of *L. wiegmanni* was significantly lower in the modified than in the natural habitat (Table 1). Thermal preference data of *L. wiegmanni* are summarized in Table 1, from these data it is observed that in the modified habitat, 87.70% ($n=52$) of the T_b s were lower than the minimum T_{sets} , while in the natural habitat 70.00% ($n=44$) of T_b s was not included between the upper and lower set point ranges (Fig. 1). The accuracy and effectiveness of thermoregulation of *L. wiegmanni* were lower in the modified than in the natural habitat ($db_{modified}=2.48$, $E_{modified}=0.58$; $db_{natural}=1.82$, $E_{natural}=0.70$). The index de was higher than zero and similar between both habitat types ($de_{modified}=5.84$, $de_{natural}=6.13$), demonstrating that the T_{es} of both habitats show low thermal quality (Table 1; Fig. 1).

Table 2

Summary statistics of discriminant functions and linear correlations (r) between original variables and discriminant functions. *The largest absolute correlation between the variable and any discriminant function.

| Statistic | Discriminant function | |
|--------------------|-----------------------|---------|
| | 1 | 2 |
| Eigenvalue | 2.917 | 0.231 |
| X^2 | 479.937 | 63.452 |
| df | 14 | 6 |
| P | < 0.001 | < 0.001 |
| Percent variance | 0.926 | 0.073 |
| Linear correlation | | |
| Leaf litter | 0.330 | 0.600* |
| Open sand | -0.912* | 0.068 |
| Trees | 0.064 | 0.360 |
| Shrubs | 0.267* | -0.433* |
| Sub-shrubs | 0.129 | 0.138 |
| Clump herbs | 0.099 | -0.382 |

There were no significant differences in the T_b values between *L. multimaculatus* from the modified and those from the natural habitats (Table 1). In both habitat types, more than 70% ($n_{modified}=21$; $n_{natural}=24$) proportion of T_b s was included within the T_{set} range (Fig. 1). The low values of db ($db_{modified}=0.47$, $db_{natural}=0.24$) and E greater than 0.90 in both environmental conditions show that this species has a high thermoregulatory accuracy and effectiveness, despite the low thermal quality of the habitats indicated by the high values of de ($de_{modified}=5.83$, $de_{natural}=6.21$; Table 1).

In the modified habitat, the T_b of *L. wiegmanni* was lower than the T_b of *L. multimaculatus* ($U=634.50$, $P=0.03$), while in the natural habitat the T_b s of the two lizards were not significantly different ($U=1097.50$, $P=0.959$; Table 1).

3.4. Lizards distribution with respect to the structural features of the habitats

L. multimaculatus used more open sand habitats than *L. wiegmanni*, while *L. wiegmanni* was associated with shrubs and leaf litter cover. The DFA indicated that the first two discriminant functions were statistically significant (Table 2). The first discriminant function accounted for 92.65% of the total

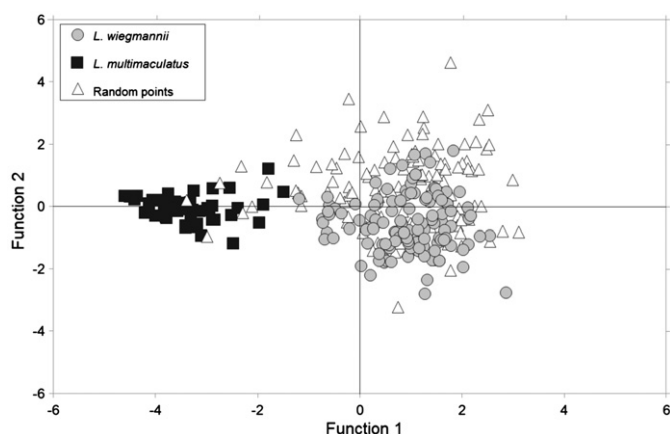


Fig. 2. Functions 1 and 2 from the discriminant functions analysis (DFA) performed on the habitat use data for *L. wiegmanni* and *L. multimaculatus*, as well as on data from randomly chosen points.

Table 3

Classification results. The numbers in parentheses are percentages of cases that were grouped correctly. The percentage of grouped cases correctly classified was 72.34%.

| Group | n | Predicted group membership | | |
|--------------------------|-----|----------------------------|--------------------------|---------------|
| | | <i>L. wiegmanni</i> | <i>L. multimaculatus</i> | Random points |
| <i>L. wiegmanni</i> | 124 | 87 (70.16) | 0 | 37 (29.84) |
| <i>L. multimaculatus</i> | 64 | 0 | 64 (100) | 0 |
| Random points | 124 | 42 (33.88) | 7 (5.64) | 75 (60.48) |

variance, this function was significantly correlated with the variables open sand and shrubs (Table 2; Fig. 2). The second discriminant function was significantly correlated with the percentage of leaf litter and shrubs (Table 2; Fig. 2). Based on both discriminant functions, the variables shrubs, open sand and leaf litter contributed significantly to separate each group centroids (Table 2; Fig. 2). This shows that our analysis was able to identify interspecific differences in microsites based on structural elements; Table 3 indicates that the three groups (i.e. *L. wiegmanni*, *L. multimaculatus* and random points) were each correctly classified with 72.34% accuracy. All individuals of *L. multimaculatus* were correctly classified by the model, its spatial distribution was restricted almost exclusively to those patches where the structure remains in the original state retaining the thermal characteristics of the natural habitats. Conversely, about 30% of individuals of *L. wiegmanni* was incorrectly classified as random points, indicating that this species has a relatively wide spatial distribution and may be observed in microhabitats with *Acacia*. This result shows that *L. multimaculatus* had a greater specificity to microhabitat than *L. wiegmanni*.

4. Discussion

The environmental temperature in the habitat modified by *Acacia* introduction was slightly lower than in the natural habitat that resembles the original landscape. At sites where *L. wiegmanni* was captured, substrate temperatures were significantly lower in the modified habitat than in the natural one, whereas air temperature did not vary despite the modification. Microenvironmental temperatures (T_a and T_s) at *L. multimaculatus* capture sites were similar in modified and natural habitats. The decrease in environmental temperatures in the modified habitat may be the result of shading by high and dense canopy and the accumulation

of leaf litter in the basal area of *A. longifolia* respect to native plant species, causing an attenuated light environment generating lower temperatures (Faggi and Dadon, 2010; Stelletti et al., unpublished data). Habitats with a dense canopy produce thermal restrictions, since they reduce the areas for basking and limit the thermoregulatory opportunities for ectotherms (House and Spelleberg, 1983; Sartorius et al., 1999; Román et al., 2006). Apparently in the modified habitat because of restricted availability of thermally appropriate patches, *L. wiegmanni* individuals use microhabitats with lower microenvironmental temperatures (T_s). On the other hand, as a consequence of the advance of *A. longifolia*, the spatial distribution of *L. multimaculatus* was restricted almost exclusively to those patches that retained microenvironmental temperatures (T_s and T_a) similar to those of natural habitat, probably because this species is a microhabitat specialist (Vega et al., 2000).

Previous studies found that there is a strong phylogenetic effect in the preferred (selected) body temperature of *Liolaemus* species (Labra et al., 2009; Moreno Azócar et al., 2012). However it is also true that this variable may be related to local temperature and climate (Labra et al., 2008, 2009). Here we found that T_{sel} of *L. wiegmanni* (38.12 ± 0.83 °C) was different and higher than *L. multimaculatus* (35.70 ± 1.41 °C), despite both species being closely related. According to the labile hypothesis of thermal biology (Hertz et al., 1983; Van Berkum, 1986), our results suggest that there is a physiological adjustment through the evolution of these species, in accordance with Rodríguez-Serrano et al. (2009) who found that thermal biology of the genus *Liolaemus* may change from site to site.

Interestingly, mean body temperatures obtained for *L. wiegmanni* and *L. multimaculatus* obtained in the present study were higher than those previously recorded (Martori et al., 1998b; Vega, 1999), also in agreement with the labile thermal hypothesis (Hertz et al., 1983; Van Berkum, 1986; Rodríguez-Serrano et al., 2009). These results show that environment models body temperatures in this lizard genus as reported before (Moreno Azócar et al., 2012). Despite everything, the T_b s of both species were within the range of body temperatures recorded for the genus at the moment (24.4 °C–37 °C; Labra et al., 2008, 2009; Moreno Azócar et al., 2012) that shows that *Liolaemus* species respond to the diverse environmental temperatures across its wide geographic distribution.

The intra and interspecific body temperatures observed in the present study highlight the versatility of the thermal biology of *Liolaemus* species that may vary up to 5 °C in their average body temperature between different populations of the same species (Labra et al., 2001; Rodríguez-Serrano et al., 2009). This is the case of *L. wiegmanni* that in the modified habitat T_b was about 2 °C lower than that in the natural habitat. On the other hand, the T_b s of *L. multimaculatus* did not differ significantly between both habitats. The greater thermal flexibility observed in *L. wiegmanni* is probably related to the wider range distribution, conversely *L. multimaculatus* is strictly psammophytic and endemic to the coastal dunes of the provinces of Buenos Aires and Río Negro (Ceí, 1993; Avila et al., 2009; Kacolis et al., 2009). These results are in agreement with those obtained by Andrews et al. (1999), who mentioned that some *Sceloporus* possessing a relatively wide geographic distribution have a variable range of mean body temperature according to the different opportunities for thermoregulation offered by each type of habitat.

The data obtained in this study suggest that *L. wiegmanni* has alternative thermal strategies in relation to the structure of the habitat. For example, in the modified habitat we observed a closer relationship of T_b with substrate temperature, while in the natural habitat we observed a closer relationship between T_b and air temperature. In contrast, *L. multimaculatus* showed a

T_b related to substrate temperature in both situations. It seems to be clear that *L. wiegmanni* interact with the thermal environment in relation with what source of heat is available to them, as our results and those from Martori et al. (1998b) and Vega (1999) show. In the case of *L. multimaculatus* our results contrast to those of Vega (1999) who proposed that this species showed a closer relationship between T_b and T_a. It is possible that these species use air or substrate temperatures as a source of heat temporally dependent on the environmental conditions experienced. This variability in the relationship between T_b and environmental temperatures is also present in other members of the *L. wiegmanni* clade (Etheridge, 2000; Avila et al., 2009), for example, *Liolaemus lutzae* (Rocha, 1995) and *Liolaemus occipitalis* (Bujes and Verrastro, 2006). However, T_a and T_s are not the only heat sources for achieving T_b, in reality this relationship is far more complex (Porter et al., 1973; Stevenson, 1985) because it may depend on interactions with other environmental variables, such as radiation, wind speed, on heat-transfer processes (radiation, convection, conduction, and evaporation), and on properties of the lizard (size, color, and shape).

According to Hertz et al. (1993), the quality of a habitat from a thermal perspective implies that the need for thermoregulation is small in environments where temperatures are nearly optimal (i.e., the mean operative environmental temperature is near or within the range of preferred body temperatures). In this study we observed that the natural habitat is thermally better than the modified habitat since the deviation of T_e from T_{sel} (de) is lower. On the other hand, both in natural and modified habitats of the study area, the T_bs of *L. wiegmanni* and *L. multimaculatus* were closer to their T_sels than to T_e. However, in the modified habitat, *L. wiegmanni* had a relatively low thermoregulatory accuracy and a moderate thermoregulatory efficiency, probably because of the differences in thermal quality between both types of habitats. To this respect, we consider that *Acacia* trees reduce thermal habitat quality by producing shade and leaf litter. Now, it is interesting that *L. multimaculatus* showed similar thermoregulatory efficiency values in both types of habitats; this is probably because *L. multimaculatus* was observed exclusively in microhabitats structurally similar to those occupied in natural habitats, with sparse vegetation cover (< 20%) avoiding the *Acacia* influence.

L. multimaculatus showed to be more specific in microhabitat use than *L. wiegmanni* because, despite the advance of *A. longifolia*, its spatial distribution was restricted almost exclusively to those patches that retained structural and thermal characteristics similar to those of natural habitats. Therefore, the availability of appropriate patches is restricted. In contrast, *L. wiegmanni* is able to use "thermally suboptimal" microhabitats. Thus, the spatial distribution of these two species may be, at least in part, the result of a selection of microhabitats based both on the thermal and structural characteristics, coinciding with the findings of Melville and Schulte (2001), Angert et al. (2002) and Sartorius et al. (2002) for lizard assemblages of Australia and the United States.

A. longifolia currently covers almost one quarter of the habitat available for the species studied. As a result of that, *L. wiegmanni* functions at suboptimal temperatures and *L. multimaculatus* is restricted to be active in patches unaltered retaining the thermal characteristics of the unmodified environment. Because of this and, paradoxically, despite being a more efficient thermoregulator *L. multimaculatus* is threatened by the loss of available habitat, meanwhile *L. wiegmanni* will coexist with altered suboptimal thermal habitats (*Acacia* modified habitats). Vega et al. (2000) showed that the structural changes in the habitat induced by other disturbances of anthropic origin affect the structure of the assemblages of lizards, altering the spatial distribution and drastically reducing the abundance of *L. multimaculatus* in other

coastal towns of Argentina. Similar situations have also been described by Meik et al. (2002) and Valentine (2006) for other lizard assemblages in the southern hemisphere where generalist species are able to remain in structurally modified sites, while specialist species tend to reduce their abundance or even disappear.

The conservation of the species of lizards in the sand dunes of the coast of Argentina should seriously consider the conservation of native grasslands and the reduction or elimination of the impact by exotic vegetation on these environments. At the same time, additional studies on some population parameters (abundance, survival, growth, etc.) of these species of lizards in modified and natural habitats may contribute to design management strategies to preserve the ecosystems of the coastal grasslands of Argentina. Paradoxically, in context of global warming, including the risk of reduction of lizard diversity as a consequence of overheating (Sinervo et al., 2010), sand dune lizards are in a challenging situation because the introduction of *A. longifolia* is generating patches with lower temperatures. This situation requires lizards to function under suboptimal thermal conditions (tolerable for *L. wiegmanni*, but unpredictable for *L. multimaculatus*) or to be established in the remaining and restricted natural microhabitats where they are specialists (*L. multimaculatus*), besides the natural habitat may be subject to a continuous process of degradation leading to undesirable consequences.

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Table A1

| Lizard species/habitat type | T _b (°C) | T _s (°C) | T _a (°C) |
|-----------------------------|---------------------|---------------------|---------------------|
| <i>L. wiegmanni</i> | | | |
| Modified | | | |
| Mar de las Pampas (n=32) | 34.65 ± 3.16 | 35.39 ± 4.82 | 34.08 ± 3.11 |
| Monte Carlo (n=27) | 34.70 ± 2.73 | 36.11 ± 3.77 | 33.88 ± 3.55 |
| Comparisons | U=428.00 | U=361.50 | U=444.50 |
| | P=0.958 | P=0.287 | P=0.855 |
| Natural | | | |
| Pinar del Sol (n=31) | 36.69 ± 3.07 | 38.85 ± 4.63 | 34.48 ± 3.87 |
| Punta Médanos (n=33) | 36.28 ± 3.22 | 39.63 ± 8.28 | 34.32 ± 4.81 |
| Comparisons | U=453.00 | U=484.50 | U=505.00 |
| | P=0.568 | P=0.891 | P=0.896 |
| <i>L. multimaculatus</i> | | | |
| Modified | | | |
| Mar de las Pampas (n=14) | 36.47 ± 1.26 | 39.55 ± 1.74 | 32.59 ± 2.39 |
| Monte Carlo (n=16) | 36.16 ± 2.15 | 38.80 ± 4.59 | 32.63 ± 3.59 |
| Comparisons | U=92.00 | U=86.00 | U=120.00 |
| | P=0.416 | P=0.288 | P=755.00 |
| Natural | | | |
| Pinar del Sol (n=15) | 36.38 ± 1.86 | 39.88 ± 1.76 | 33.33 ± 4.03 |
| Punta Médanos (n=19) | 36.19 ± 0.98 | 39.37 ± 0.91 | 32.80 ± 1.44 |
| Comparisons | U=155.50 | U=127.00 | U=171.00 |
| | P=0.664 | P=0.602 | P=0.331 |

Appendix A

Comparisons (Mann Whitney test) of snout-vent length (SVL), body mass (W), body temperature (T_b), substrate and air temperatures (T_s and T_a) between Mar de las Pampas and Monte Carlo (modified habitats) and between Pinar del Sol and Punta Médanos (natural habitats) for both species of lizards. Values represent means \pm standard deviations. References: n =sample number, U =Mann Whitney statistic (α = 0.05), P =probability value.

See Appendix Table A1.

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