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Factors affecting the thermal behavior of the sand lizard *Liolaemus wiegmannii* in natural and modified grasslands of temperate coastal dunes from Argentina

Carolina Block*, Oscar A. Stellatelli, Germán O. García, Laura E. Vega, Juan P. Isacch

Laboratorio de Vertebrados, Departamento de Biología, Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET – Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3250 (B7602AYJ) Mar del Plata, Buenos Aires, Argentina

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ABSTRACT

The present study describes and compares the thermal behavior of individuals of *Liolaemus wiegmannii*, inhabiting patches of natural grassland and modified patches with exotic trees of *Acacia longifolia*, by analyzing the factors affecting its behavior. Thermal behavior of *L. wiegmannii* was assessed by radiotracking 22 adult individuals in a coastal dune area from Argentina. In order to account for individual responses we analyzed the factors affecting thermal behavior using Generalized Linear Mixed Models. Thermal behavior of *L. wiegmannii* was mainly affected by the time of day and the substrate temperature. The individuals basking on bare sand in the morning shifted to filtered sunlight during midday and to the shade of clump and erect stems and herbs during the afternoon. The individuals buried in sand when the substrate temperature was low and the wind speed was high. The use of sub-shrubs and shrubs could not be explained solely by thermal factors. In natural *L. wiegmannii* regulated its body temperature by shuttling between microhabitats that provided them with different levels of exposure to sunlight during the day. However, in modified patches individuals varied in the choice of plants used as shaded places to mitigate high microenvironmental temperatures and they were also more exposed to full shaded sites and less to warm sand to bask, which could have negative consequences for its thermal biology.

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1. Introduction

In lizards, as in ectotherms, the acquisition and maintenance of adequate body temperatures (T_b) depends on external heat sources (Labra et al., 2008). The notion of thermoregulation implies that organisms actively use behavioral or physiological adjustments to switch body temperatures resulting from the passive exchange of heat with the environment, and maintain body temperature within a narrow range (Castilla et al., 1999). In environments where solar radiation is available but it changes spatially (e.g. by vegetation cover or structural heterogeneity), behavior is a major contributor for achieving different body temperatures compared to physiological mechanisms, so behavioral adjustments are the primary means that ectotherms use to regulate their body temperatures (Stevenson, 1985; Bauwens et al., 1996; Cowles and Bogert, 2006). These processes influence how much radiant energy reaches the body surface of an animal (movement between shade and sun, orientation with respect to source of radiant energy, changing body contour), how much energy is absorbed and reflected (color change), and how much energy is gained or lost from the skin surface by convection, conduction, and evaporation (postural changes) (Pough et al., 1998). However, while lizards get physiological benefits from thermoregulation, they must necessarily incur costs such as the energy expenditure expended when moving between warm and cool spots (Huey, 1974, 1982; Huey and Slatkin, 1976), increased exposure to predators (Downes, 2001; Herczeg et al., 2008) and time devoted to feeding (Gvoždik, 2002) or mating (Shine et al., 2000).

Among behavioral mechanisms for achieving different body temperatures, microhabitat selection is more important than postural adjustments for controlling T_b (Stevenson, 1985). The microhabitat selected by an animal defines the environmental thermal regime it experiences (Huey, 1991). Thermoregulatory behavior and habitat selection are closely related and have an important influence on the life history and fitness of reptiles (Huey, 1991; Adolph and Porter, 1993; Bauwens et al., 1996). The structural properties of the habitat influence the capabilities of the lizard to thermoregulate efficiently, since the thermal quality can vary at a micro-scale between microhabitats within one habitat (Scheers and Van Damme, 2002). Many lizard species thermoregulate by shuttling between microhabitats where they can gain or lose heat (Huey and Pianka, 1977; Díaz, 1991; Kerr et al., 2003; Díaz and Cabezas-Díaz, 2004). In turn, thermal

* Corresponding author. Tel.: +54 223 4752426x466.
E-mail addresses: cblock@mdp.edu.ar (C. Block), os2830@gmail.com (O.A. Stellatelli), garciagerman@argentina.com (G.O. García), levega@mdp.edu.ar (L.E. Vega), jpisacch@mdp.edu.ar (J.P. Isacch).

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behavior influences greatly the spatial and temporal use of the habitat by lizards (Waldschmidt and Tracy, 1983), e.g. the daily shift in microhabitat occupation (Adolph, 1990; Castilla and Bauwens, 1991; Hager, 2000; Melville and Schulte, 2001), as well as the seasonal variation in microhabitat use (Huey and Pianka, 1977; Angert et al., 2002). Besides, sexual differences in thermoregulatory behavior have been observed, suggesting that males and females could differ in their thermal preferences (Díaz, 1991; Carretero and Llorente, 1993; Lailvaux et al., 2003; Belver et al., 2010, Maia-Carneiro and Rocha, 2013), and therefore, in the use of different microhabitats with dissimilar thermal characteristics (Singh et al., 2002; Serantes et al., 2007; Miranda et al., 2010).

The physical structure of vegetation can be a dramatic force influencing the microhabitat selection and thermoregulatory behavior in lizards (Melville and Schulte, 2001; Angert et al., 2002; Sartorius et al., 2002). In places where the physiognomic structure of the habitat is modified by exotic vegetation, the effects on thermoregulation of some reptiles can be harmful (Valentine et al., 2007; Carter, 2012; Stellatelli et al., 2013a). Certain exotic plant traits such as a larger size, higher growth rate and higher biomass production, turn them into the dominant ground cover altering markedly the structural and thermal conditions of the original habitat by promoting an attenuated light environment and a lowering of environmental temperatures (Tomley, 1998; Valentine et al., 2007; Marchante et al., 2008). In Argentina, the coastal sand dunes of the North-Eastern coast of the province of Buenos Aires have been planted with Acacia trees (*Acacia* spp) not only for stabilizing the dunes, but also for decorative purposes (Cozzo, 1976; Zalba and Villamil, 2002). As a result, in the last 70 years the structure of the vegetation of some places of coastal dunes has changed from an open to a relatively closed canopy, deteriorating the quality of the natural vegetation and affecting the dynamics of the natural ecosystem (Faggi and Dadon, 2010, 2011). The lizard *Liolaemus wiegmannii* (snout-vent length: 42–64 mm), which has specialized morphological features for living in loose sand (Etheridge, 2000) inhabits this Eastern coastal dune barrier using the vegetation cover of the semi-fixed dunes, usually far away from open spaces and beaches (Vega, 2001; Block et al., 2012). The heat source of *L. wiegmannii* can vary seasonally (Martori et al., 1998) and its body temperature and thermoregulatory efficiency are lower in habitats modified by exotic acacias than in natural sites, where there is also a closer relationship of its T_b with the substrate temperature, whereas in natural habitats there is a closer relationship between its T_b and air temperature (Stellatelli et al., 2013a). This thermal flexibility suggests that *L. wiegmannii* may adopt alternative thermal behavior in relation to the structure of the habitat, and in consequence, knowledge about how lizards behave in natural and modified habitats and which are the factors driving thermal differences, will enhance our understanding not only of the individual variations in behavior but also of its thermal biology in general. The aim of the present study is to describe the thermal behavior of *L. wiegmannii* recording individuals inhabiting patches of natural grassland and patches with *A. longifolia*, analyzing the factors affecting its behavior and microhabitat use. In most field studies on lizard thermoregulation, data are obtained through a single observation of different individuals. In this study, we used radiotelemetry methods in order to register lizard behavior without disturbing them, following the same individuals during a short period of time.

2. Materials and methods

2.1. Study area

The field study was conducted from February to April 2011 in two independent sites of approximately 160 ha of coastal dunes located between Faro Querandí Natural Reserve (S 37° 22′ 28″, W 57° 04′ 50″) and Mar de las Pampas village (S 37° 18′ 7″, W 57° 01′ 47″; Datum: WGS84) of Buenos Aires province, Argentina. The study area consists of a landscape composed of bare sand, interdune depressions and semifixed dunes with psammophytic grassland fragmented into patches of variable size interspersed among villages and forests of exotic trees. Some patches maintain the natural structure of the native plant community mainly comprising *Poa lanuginosa*, *Panicum racemosum,* and *Androtrichum trigynum*; clumps of *Cortaderia selloana*; sub-shrubs of *Senecio crassiflorus*, *Achyrocline satureioides*; and shrubs of *Discaria americana*, *Tessaria absinthioides*, and *Baccharis notosergila*. Other sites are structurally modified by the presence of exotic *A. longifolia* trees, creating patches of mixed forest and grassland with the same native plant communities. In total, we randomly selected 12 patches of natural grassland and 10 patches of grassland modified with at least 20% of the surface covered by *A. longifolia*. Each patch encompassed approximately an area of 400 m^2 and distance between patches ranged from 0.05 to 8 km.

2.2. Field survey

Thermal behavior was assessed by radiotracking 22 adult individuals of *L. wiegmannii*. One individual was captured by hand or noose per patch (natural patches: 6 females and 6 males; modified patches: 5 females and 5 males). The home range of *L. wiegmannii* is small ($\overline{X}_{♀}=29.88\pm13.91$ m^2, $n=11$; $\overline{X}_{♂}=48.82\pm19.17$ m^2, $n=11$; Stellatelli et al., unpublished data), and therefore, each patch may be considered as an independent sample. Sex determination was made based on the secondary sexual characters of the species (Cei, 1993). Each lizard was measured (snout–vent length-SVL) with a digital calipers (SC111001, Schwyz MR., Buenos Aires, Argentina, 0.01 mm), and weighed with a portable digital balance (CH02, Diamond premium MR., China, 0.01 g). We attached a 0.5 g radiotransmitter (TXB-001 G, TELENAX MR.) to the back of each individual with cyanoacrylate gel (Goodman et al., 2009). Radiotransmitters represented $<10\%$ of lizard body mass (Knapp and Abarca, 2009). After device deployment, the individuals were released at the site of capture. Radiotracking started 1 day after each individual was released using a LA12-Q portable receiver VHF (AVM Instrument Company, Ltd.) with a three-element Yagi antenna. During 3 consecutive days each lizard was relocated at every hour from 0900 to 1800h local time (-3 GMT), as the most of the lizard activity occurred during that time of day (Vega, 2001). During these days the weather conditions were fairly similar with continuous sunshine (Means $\pm$ SE: environmental $T°=22.30\pm0.37$ °C; cloudiness $=27.91\pm7.91\%$; wind speed $=22.31\pm2.14$ km/h) and with a high level of activity of lizards. Each time an individual was detected, thermoregulatory behavior was registered as one of the four a priori categories: (1) basking (when the lizard was resting fully exposed to the sun); (2) in filtered sunlight (when the lizard was still in sunlight filtered by vegetation); (3) in shade (when the lizard was still fully in shade); or (4) buried (when the lizard was still with the body wholly covered with sand) (see Huey, 1974; Adolph, 1990). Microhabitat use was registered at the site of lizard detection using five categories: shrubs, sub-shrubs, clump herbs, erect stem herbs, and bare sand. Plants were previously identified to the species level and then grouped in the above mentioned categories by physiognomic types according to Cabrera and Zardini (1978) (Table 1). Time of day [H, categorized as morning, from 0900 to 1159h (1); noon, from 1200 to 1459h (2); and afternoon from 1500 to 1800h (3)], substrate temperature (T_s, considered as a continuing variable, range: 22–47 °C), and wind speed (WS, considered as continue variable, range: 0–4.75 km/h) were also measured cautiously at

the site of lizard detection. The T_s was registered at 1 cm under the sand with a thermocouple connected to a digital thermometer (SC133, Schwyz MR., Buenos Aires, Argentina) and the WS was measured 1 cm above the sand with an anemometer (4260006, TFA ALEMANIA). To keep disturbance to lizards at a minimum, every time a radio transmitter signal began to be detected weakly we approached very quietly to the position of the lizard until the individual could be seen. We know from our previous studies on these lizards, that if individuals flee as a result of our presence, they are highly likely to return to the same place where they were originally observed, resulting in minimal or negligible influence on the subsequent behavior or sightings of these individuals.

2.3. Data analysis

To evaluate the relationship between thermoregulatory behavior and microhabitat use with the different predictor variables, we used Generalized Linear Mixed Models (GLMMs) with the Binomial error structure and log-link function (Crawley, 2007). GLMMs combine the properties of two statistical frameworks: Linear Mixed Models (which incorporate random effects) and Generalized Linear Models (which handle abnormal data by using link functions and exponential family; e.g. normal, Poisson or binomial distributions; Bolker et al., 2009). GLMMs are used to model temporal and spatial correlation structures in count data or binomial data, inherent in repeated measures designs (Breslow and Clayton, 1993; Zuur et al., 2009). The response variables considered for the models were the proportion of each observed behavior (i.e. basking, filtered sunlight, shade, and buried), and the proportion of each microhabitat used (i.e. shrubs, sub-shrubs, clump herbs, erect stem herbs, and bare sand) by lizards. The proportion of each observed behavior and microhabitat used was calculated as the number of times that an individual was observed in each behavior or using each microhabitat divided by the total number of observations within each time of day (morning, noon, and afternoon). In both analyses the predictor variables included the patch type [PT, categorized as natural grassland (Natural) o grassland with *A. longifolia* (Modified)], sex (female, male), time of day (1, 2, and 3), substrate temperature (T_s), and wind speed (WS). We considered the individual's identity as a random effect. In certain cases, some predictor variables or categories had to be removed to improve the fit of the models (see Nicholls, 1989). For the analysis of use of sub-shrubs, the patch type and category 1 for time of day were excluded from the analysis because no individual was found using sub-shrubs in modified patches or during the morning.

We used an information-theoretic approach (Burnham and Anderson, 2002) to evaluate support for models with all possible combinations of predictor variables, including a global model with all predictors and a null model without predictors. Model selection was based on Akaike's information criterion corrected for lack of independence and small sample sizes ($QAIC_c$; Burnham and Anderson, 2002). We used two measures to provide further insight into the amount of uncertainty in model selection. The first was the difference in $QAIC_c$ between the best approximating model and all the other models (Burnham and Anderson, 2002), termed $\Delta QAIC_c$. In general, a $QAIC_c$ score between 0 and 2 indicates substantial support for the model (Burnham and Anderson, 2002). The second measure calibrates models to provide relative plausibility by normalizing each model on the basis of its $\Delta QAIC_c$ value, termed "model weight" (Anderson and Burnham, 1999; Burnham and Anderson, 2002). To evaluate the support for predictor variables, parameter likelihood was estimated (Burnham and Anderson, 2002); predictor variables with good support will have high parameter likelihood values (near 1). Parameter estimates were calculated by the technique of model averaging (model-averaged inference) from $QAIC_c$ weights for all candidate models (Burnham and Anderson, 1998). Unconditional variances of those candidate models were used to calculate standard errors. To supplement evidence of important effects with parameter likelihoods, we also assessed the degree to which the 95% confidence intervals of parameter estimates overlapped zero. We calculated upper and lower confidence limits by adding or subtracting $2 \times SE$, respectively. All statistical analyses were carried out using R software, version 2.15.0 (R Development Core Team, 2012).

Table 1
Plant species used by *Liolaemus wiegmannii* in both natural and modified patches.

Patch type	Microhabitat	Status
Natural	Erect stem herbs	
	Androtrichum trigynum	Native
	Clump herbs	
	Cortaderia selloana	Native
	Sub-shrubs	
	Senecio crassiflorus	Native
	Margyricarpus pinnatus	Native
	Shrubs	
	Baccharis notosergila	Native
	Discaria americana	Endemic
	Tessaria absinthioides	Native
Modified	Erect stem herbs	
	Androtrichum tryginum	Native
	Poa sp.	Native
	Clump herbs	
	Cortaderia selloana	Native
	Shrubs	
	Baccharis notosergila	Native
	Baccharis trimera	Native
	Tessaria absinthioides	Native

3. Results

3.1. Thermoregulatory behavior

Among the four types of thermal behavior recorded for *L. wiegmannii*, the use of filtered sunlight and basking were the most frequently registered in both, natural and modified patches, but in modified patches there was an increased proportion of individuals in shade, whereas in natural patches there was an increased proportion of individuals buried (Table 2).

GLMMs indicated that sex, time of day, substrate temperature, and wind speed were the strongest factors explaining the basking behavior of lizards. We also found support for our global model

Table 2
Proportion of behavior types and microhabitat use of *Liolaemus wiegmannii* in both natural and modified patches.

	Thermal behavior				Microhabitat				
	Basking	Filtered sunlight	Shade	Buried	Shrub	Sub-shrub	Clump herbs	Erect stem herbs	Bare sand
Natural patch	0.250	0.523	0.068	0.159	0.662	0.049	0.113	0.099	0.077
Modified patch	0.368	0.404	0.132	0.096	0.482	0.000	0.412	0.079	0.026

with all effects (Table 3A). None of the models accounted for more than 22% of the variation in lizard basking proportion (Table 3A). Sex, time of day, substrate temperature and wind speed were important predictors because all showed high likelihood parameter values. Despite this, only time of day and substrate temperature presented confidence intervals that excluded zero (see Table 3B). Individuals were observed basking more frequently during the morning than during afternoon and noon, and the basking behavior increased when the substrate temperature increased (Fig. 1).

With regard to individuals using filtered sunlight, the behavior was explained mainly by the time of day, sex and substrate temperature; the selected model did not account for more than 11% of the variation (Table 3A). Time of day was the most important predictor with the highest likelihood parameter value and the confidence interval excluding zero (Table 3B). Individuals were found in filtered sunlight more frequently during the noon than afternoon and morning (Fig. 1). Although sex and substrate temperature had high likelihood parameter values, the confidence intervals encompassed zero (Table 3B).

The proportion of individuals found in shade was explained mainly by patch type, sex and time of day (Fig. 1). The best model did not account for more than 12% of the variation (Table 3A). These predictors had high likelihood parameter values and the confidence intervals did not include zero (Table 3B). The use of shade by lizards was less frequent in natural patches than in patches with exotic vegetation and in males than in females. Besides, lizards were observed more frequently in full shade during the afternoon than during the noon or morning (Table 3B).

Two variables were the most important factors explaining the lizards' burying behavior: substrate temperature and wind speed (Fig. 1). The best model including these variables did not account for more than 23% of variation (Table 3 A). Both predictors showed high likelihood parameter values and the confidence intervals of parameter estimate did not encompass zero (Table 3B). The proportion of individuals buried increased as the substrate temperature decreased and the wind speed increased (Table 3B).

Table 3A
Generalized Linear Mixed Models (GLMMs) explaining the factors affecting the thermoregulatory behavior by *Liolaemus wiegmannii* (135 observations included in the models). Number of parameters (K) in each model included the intercept, random effects and each explanatory variable. Only models with strong support are shown (i.e. $\Delta QAIC_c < 2$). Models are listed in decreasing order of importance. PT: patch type, S: sex, H: time of day; T_s: substrate temperature, WS: wind speed.

Behavior	Model	Explanatory variables	K	$\Delta QAIC_c$	$QAIC_c$ weight	R^2
Basking	1	S, H, T_s, WS	7	0.00	0.38	0.22
	Global	PT, S, H, T_s, WS	8	1.54	0.17	0.22
Filtered	1	S, H, T_s	6	0.00	0.15	0.11
Sunlight	2	S, H	5	0.10	0.14	0.09
	3	PT, S, H, T_s	7	0.39	0.12	0.12
	4	PT, S, H	6	1.74	0.06	0.10
	5	H, T_s	5	1.92	0.06	0.08
	6	T_s	4	1.93	0.06	0.07
Shade	1	PT, S, H	6	0.00	0.18	0.12
	2	PT, S	4	0.49	0.14	0.08
	3	PT, S, H, T_s	7	1.02	0.11	0.12
	4	PT, S, T_s	5	1.55	0.08	0.09
	5	PT, S, H, WS	7	1.95	0.07	0.12
Buried	1	T_s, WS	4	0.00	0.25	0.23
	2	S, T_s, WS	5	0.57	0.19	0.24
	3	PT, T_s, WS	5	1.57	0.11	0.23
	4	T_s	3	1.84	0.10	0.20

3.2. Microhabitat use

Shrubs were the microhabitat most frequently used in both natural and modified patches; however, in modified patches no individual was found using sub-shrubs and clump herbs showed a high proportion of use (Table 2).

The null models dealing with the proportion of individuals using shrubs and sub-shrubs received higher support; therefore, none of the variables considered could explain the proportion of use of these two elements (Table 4A).

Table 3B
Parameter estimates (± SE) from Generalized Linear Mixed Models (GLMMs) describing the factors affecting the thermoregulatory behavior by *Liolaemus wiegmannii*. Parameter likelihoods are $QAIC_c$ weight summed across all models that contained that parameter and are indicative of the importance of the variable. Parameter estimates are weighted averages (using $QAIC_c$ weight) from all models, and standard errors (SE) are calculated from all candidate models from unconditional variances. Confidence intervals (95%) were calculated adding or subtracting 2xSE. Explanatory variables with Confidence interval excluding zero are in bold. PT: patch type, S: sex, H: time of day; T_s: substrate temperature, WS: wind speed.

Behavior	Explanatory variable	Category	Parameter likelihood	Parameter estimate ± SE	Confidence interval
Basking	PT	Natural	0.32	−0.33 ± 0.40	−1.13; 0.46
	S	Male	0.72	−0.80 ± 0.41	−1.61; 0.01
	H	**2**	**1.00**	**−1.77 ± 0.47**	**−2.71; −0.84**
		3	**1.00**	**−1.58 ± 0.51**	**−2.59; −0.57**
	T_s		**0.99**	**0.14 ± 0.05**	**0.05; 0.23**
	WS		0.99	−0.84 ± 0.46	−1.75; 0.07
Filtered	PT	Natural	0.39	0.43 ± 0.40	−0.36; 1.23
Sunlight	S	Male	0.70	0.68 ± 0.35	−0.01; 1.38
	H	**2**	**0.92**	**1.22 ± 0.45**	**0.32; 2.11**
		3	**0.92**	**1.15 ± 0.48**	**0.19; 2.12**
	T_s		0.56	0.06 ± 0.04	−0.02; 0.14
	WS		0.28	−0.18 ± 0.37	−0.92; 0.56
Shade	**PT**	**Natural**	**0.95**	**−1.22 ± 0.45**	**−2.12; −0.33**
	S	**Male**	**0.75**	**−0.89 ± 0.44**	**−1.78; −0.01**
	H	2	0.57	0.55 ± 0.59	−0.63; 1.73
		3	**0.57**	**1.20 ± 0.58**	**0.05; 2.35**
	T_s		0.36	−0.05 ± 0.05	−0.15; 0.05
	WS		0.28	0.14 ± 0.39	−0.63; 0.92
Buried	PT	Natural	0.30	0.35 ± 0.51	−0.67; 1.38
	S	Male	0.40	0.25 ± 0.26	−0.28; 0.78
	H	2	0.17	0.50 ± 0.51	−0.51; 1.51
		3	0.17	0.10 ± 0.57	−1.04; 1.23
	T_s		**1.00**	**−0.22 ± 0.05**	**−0.32; −0.13**
	WS		**0.76**	**0.71 ± 0.35**	**0.02; 1.41**

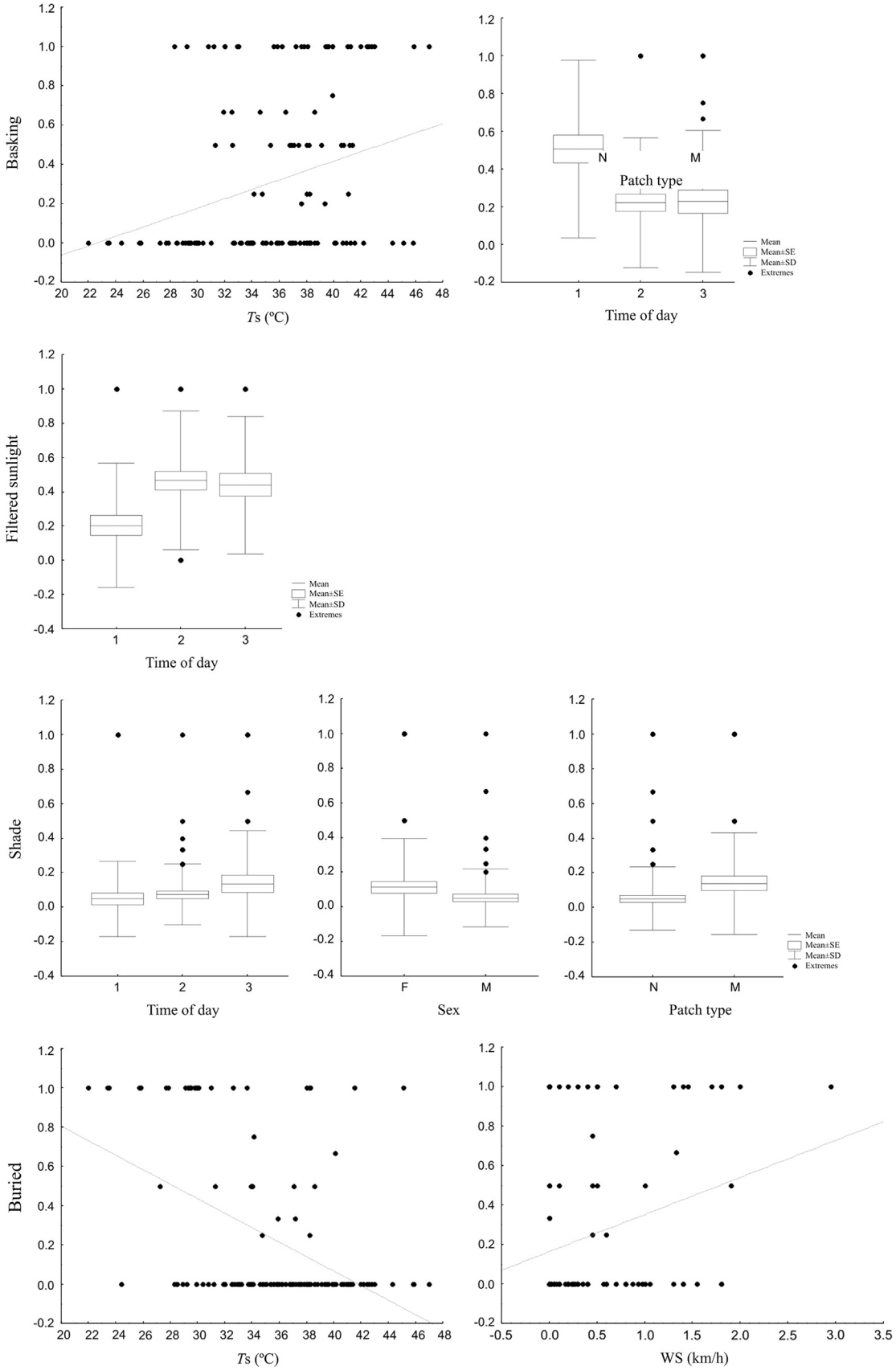

Fig. 1. Proportion of behavior types of *Liolaemus wiegmannii* (Basking, Filtered sunlight, Shade, and Buried) versus different substrate temperatures (T_s) and wind speed (WS), at different times of day [morning (1), noon (2) and afternoon (3)], between patch types [natural (N), modified (M)], and sex [female (F), male (M)]. Each behavior is shown in relation to those variables that were significant in each analysis (Table 3B).

The use of clump herbs was explained mainly by patch type, sex, time of day, and wind speed. The best model did not account for more than 22% of variation (Table 4A). All of the variables showed high likelihood parameter values, with the patch type being the most important variable followed by sex and time of day (Table 4B). Use of clump herbs by lizards was less in natural patches; males used more clump herbs than females, and the proportion of individuals was higher during afternoon than noon and morning (Fig. 2). Although wind speed showed high likelihood parameter values, the confidence interval encompassed zero (Table 4B).

The best model explaining the use of erect stem herbs included time of day, substrate temperature and wind speed. This model did not account for more than 8.8% of variation. Time of day was the most important variable and the confidence interval did not include zero (Table 4B). Individuals used this vegetation type in a major proportion during the afternoon than noon and morning (Fig. 2). Although substrate temperature and wind speed showed high likelihood parameter value, the confidence intervals encompassed zero (Table 4B).

Use of bare sand was explained mainly by patch type, sex, time of day, and substrate temperature accounting for 15.7% of the variation (Table 4A). The individuals used bare sand in a major proportion in the natural patches, and the proportion of individuals was less during the afternoon than noon and morning. The use of bare sand increased when the substrate temperature increased (Table 4B) (Fig. 2). Although sex showed a relatively high likelihood parameter value, the confidence interval encompassed zero (Table 4B).

Table 4A
Generalized Linear Mixed Models (GLMMs) explaining the factors affecting the microhabitat use by *Liolaemus wiegmannii* (138 observations included in the models). Number of parameters (K) in each model included the intercept, random effects and each explanatory variable. Only models with strong support are shown (i.e. $\Delta QAIC_c < 2$). Models are listed in decreasing order of importance. PT: patch type, S: sex, H: time of day; T_s: substrate temperature, WS: wind speed.

Microhabitat	Model	Explanatory variables	K	$\Delta QAIC_c$	$QAIC_c$ weight	R^2
Shrubs	**Null**		**2**	**0.00**	**0.14**	–
	1	S	3	0.85	0.09	0.009
	2	PT	3	1.00	0.09	0.008
	3	WS	3	1.36	0.07	0.005
	4	T_s	3	1.56	0.06	0.004
Sub-shrubs	**Null**		**2**	**0.00**	**0.17**	–
	1	H	3	0.30	0.15	0.020
	2	WS	3	0.76	0.12	0.015
	3	H, WS	4	0.96	0.11	0.035
	4	T_s	3	1.79	0.07	0.005
Clump herbs	1	PT, S, H, WS	7	0.00	0.22	0.223
	Global	PT, S, H, T_s, WS	8	0.25	0.20	0.235
	3	PT, S, WS	5	1.26	0.12	0.190
	4	PT, S, H	6	1.76	0.09	0.200
Erect stem herbs	1	H, T_s, WS	6	0.00	0.14	0.088
	2	H, WS	5	0.59	0.11	0.068
	3	H, T_s	5	0.66	0.10	0.068
	4	PT, H, T_s, WS	7	1.42	0.07	0.093
	5	H	4	1.60	0.06	0.046
	6	S, H, T_s, WS	7	1.77	0.06	0.091
	7	S, H, T_s	6	1.80	0.06	0.075
Bare sand	1	PT, S, H, T_s	7	0.00	0.39	0.157
	2	PT, H, T_s	6	1.06	0.23	0.136

4. Discussion

In natural and modified patches, thermal behavior and microhabitat use of *Liolaemus wiegmannii* were mainly affected by the time of day and the substrate temperature, since individuals basking on bare sand in the morning moved into the sunlight filtered by vegetation during midday, and to the shade of the clump and erect stem herbs during the afternoon. However, the proportion of individuals in the shade, using clump herbs and using bare sand were affected by the type of patch.

In patches modified by *Acacia longifolia* there were the greatest proportion of individuals exposed to full shade and, conversely, the least proportion of lizards using bare sand. This pattern can be interpreted in the frame of "the ecological trap" concept (Dwernychuk and Boag, 1972; Schlaepfer et al., 2002), given that lizards would be using modified patches with increased vegetation structure (i.e., by trees) as an erroneous cue of suitable habitat (Battin, 2004; Hawlena et al., 2010). Vegetation of modified patches can be recognized as a refuge against predators and by the provision of shade by lizards; however Acacia's canopy causes the enlargement of shaded areas projected, which reduce the areas for basking and limit the thermoregulatory opportunities for ectotherms (House and Spelleberg, 1983; Sartorius et al., 1999; Román et al., 2006). In the modified patches *L. wiegmannii*

Table 4B
Parameter estimates (± SE) from Generalized Linear Mixed Models (GLMMs) describing the factors affecting the microhabitat use by *Liolaemus wiegmannii*. Parameter likelihoods are $QAIC_c$ weights summed across all models that contained that parameter and are indicative of the importance of the explanatory variable. Parameter estimates are weighted averages (using $QAIC_c$ weigh) from all models, and standard errors (SE) are calculated from all candidate models from unconditional variances. Confidence intervals (95%) were calculated adding or subtracting 2xSE. Explanatory variables with Confidence interval excluding zero are in bold. PT: patch type, S: sex, H: time of day; T_s: substrate temperature, WS: wind speed.

Microhabitat	Explanatory variable	Category	Parameter likelihood	Parameter estimate ± SE	Confidence interval
Clump herbs	**PT**	**Natural**	**1.00**	**−1.89 ± 0.45**	**−2.79; −0.99**
	S	**Male**	**0.81**	**0.94 ± 0.42**	**0.11; 1.78**
	H	**2**	**0.70**	**1.07 ± 0.51**	**0.05; 2.09**
		3	**0.70**	**1.20 ± 0.54**	**0.11; 2.28**
	T_s		0.44	−0.06 ± 0.05	−0.16; 0.03
	WS		0.79	−1.16 ± 0.61	−2.38; 0.06
Erect stem herbs	PT	Natural	0.30	−0.31 ± 0.48	−1.27; 0.65
	S	Male	0.33	−0.37 ± 0.44	−1.24; 0.51
	H	2	0.88	0.92 ± 0.67	−0.42; 2.26
		3	**0.88**	**1.72 ± 0.68**	**0.36; 3.07**
	T_s		0.59	−0.08 ± 0.05	−0.17; 0.01
	WS		0.55	0.60 ± 0.36	−0.13; 1.32
Bare sand	**PT**	**Natural**	**0.96**	**1.51 ± 0.57**	**0.36; 2.65**
	S	Male	0.61	−0.80 ± 0.47	−1.74; 0.15
	H	**2**	**0.87**	**−1.10 ± 0.48**	**−2.06; −0.13**
		3	**0.87**	**−1.56 ± 0.65**	**−2.86; −0.26**
	T_s		**0.98**	**0.14 ± 0.04**	**0.05; 0.22**
	WS		0.26	0.13 ± 0.41	−0.69; 0.96

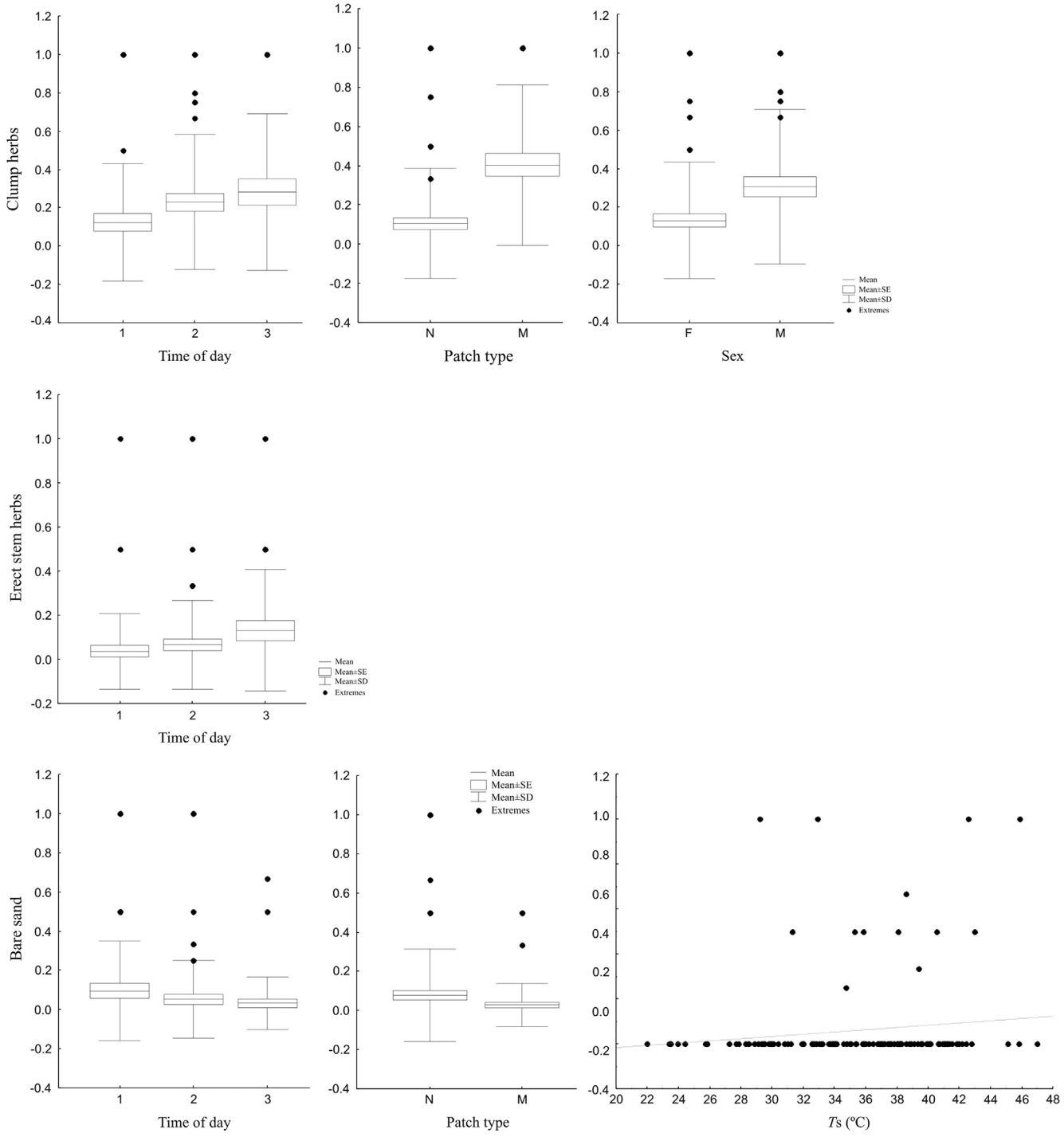

Fig. 2. Proportion of microhabitat use of *Liolaemus wiegmannii* (Clump herbs, Erect stem herbs, Bare sand) versus different substrate temperatures (T_s) and wind speed (WS), at different time of day [morning (1), noon (2) and afternoon (3)], between patch types [natural (N), modified (M)], and sex [female (F), male (M)]. Each microhabitat is shown in relation to those variables that were significant in each analysis (Table 4B).

individuals used microhabitats with lower microenvironmental temperatures perhaps due to restricted availability of thermally appropriate patches (Stellatelli et al., 2013a). In turn, the absence of individuals using shrubs and the more frequent use of clump herbs by lizards in modified patches, could be related to changes in the structure of the natural grassland induced by the acacias, which tend to replace heliophytes and shade intolerant native plants (Faggi and Dadon, 2010, 2011) and to generate a decrease in the coverage, richness and diversity of these species (Alberio and Comparatore, 2011). Interestingly, the range of operative temperatures registered in clump herbs by Stellatelli et al. (2013b) were significantly lower (28.50–39.75 °C) than those registered in native plant species used by this lizard in natural patches. In this sense, *L. wiegmannii* tended to use different microhabitat types according to the type of patch (Table 1), since those sites selected in shrubs of *Discaria americana* and in sub-shrubs, such as *Senecio crassiflorus* and *Margyricarpus pinnatus* in natural patches, were replaced by sites under clump herbs like *Cortaderia selloana,* possibly due to the scarcity or absence of the former (Block, personal observation) in modified patches.

Bare sand was the microhabitat most frequently used by lizards while basking during morning, where, due to the higher

incidence of sun rays, individuals would gain heat faster from the sand uncovered by vegetation than in other microhabitat types. However, as the superficial layers accumulate heat energy during the day (Maun, 2009) soil temperatures can rise too high during midday until becoming incompatible with life; consequently, during midday lizards tend to move to sites where the sunlight is filtered by vegetation, and during afternoon when solar radiation is still high, towards those microhabitats where sunlight is partially or completely filtered. In the study area, the temperature of bare sand at midday can reach levels up to 70.5 °C (Stellatelli et al., 2013b), exceeding not only the preferred body temperature of *L. wiegmannii* (36.88–38.12 °C, Stellatelli et al. 2013b), but also the critical temperature recorded for sand lizard species of the genus *Liolaemus* (43 °C, Cruz et al., 2005). Herbaceous plants, used in a high proportion in the afternoon, offered lower substrate temperatures than those registered in open spaces of sand at this time of day (28.50–32.00 °C, Stellatelli et al., 2013b). On the other hand, it has been stated that basking behavior helps sperm maturation in males (Halloy and Robles, 2003), and this could explain the smaller proportion of males compared to females using shaded areas at this time of the year coinciding with the recrudescence of testicular mass in this species (Martori and Aun, 1997).

The high frequency of individuals using shrubs (Table 2) and the use of sub-shrubs could not be explained by any of the variables analyzed in this study, maybe because the physiognomy of these types of plants offered a mosaic of sunlight, filtered sunlight and shade that provided lizards a wider range of temperatures than the other plants. The substrate temperature range registered under sub-shrubs and shrubs (27.50–39 °C, Stellatelli et al., 2013b), which also included the preferred body temperatures of *L. wiegmannii* (36.88–38.12 °C, Stellatelli et al., 2013a), would allow individuals to thermoregulate efficiently in the same microhabitat type without the need for moving to other places. Bauwens et al. (1996) while studying the thermal behavior of *Podarcis hispanica atrata*, also registered a spectrum of temperatures between the center and the edge of *Suaeda vera* shrubs, with the lowest and less variable in those sites under the center of the plant. However, more than one factor could be involved in the use of shrubs and sub-shrubs as they are the main refuge sites selected by *L. wiegmannii* (Etheridge, 2000; Block et al., 2012) and by other lizard species (Martín and López, 1995; Smith and Ballinger, 2001; Kerr et al., 2003). The large canopy of these plants hinders the visibility of aerial predators and allows prey movements while staring their positions. Shrubs are microhabitats of choice for ground living lizards (Bauwens et al., 1999; Díaz et al., 2005; Somaweera et al., 2012), as they provide not only suitable thermal but also safe refuge sites.

The highest proportion of buried individuals of *L. wiegmannii* was found when substrate temperatures were low at early morning and late afternoon, just after and before overnight resting behavior. Burying behavior at early hours of the morning was registered for other sand lizard species such as *Liolaemus lutzae* and *Liolaemus occipitalis* from southern coastal dunes of Brazil (Rocha, 1995; Bujes and Verrastro, 2006) and other species of the *L. wiegmanni* group (Halloy et al., 1998). Besides, the burying behavior of *L. wiegmanni* was positively correlated with the wind speed and this factor has been proposed as an important regulator of the body temperature by means of heat loss in small lizards, together with the substrate and air temperatures (Rocha, 1995; Scheers and Van Damme, 2002; Bujes and Verrastro, 2008).

In natural and modified patches, *L. wiegmannii* regulated its body temperature by shuttling between different microhabitats and substrate temperatures that varied in their exposure to sunlight at different times of the day. According to Pianka and Vitt (2003) a strong relationship exists between thermoregulatory behavior and microhabitat use when moving between sites with different levels of sun exposure through the day in many lizard species worldwide, and this is also a common behavior of *Liolaemus* species (Labra et al., 2001; Martori et al., 1998). However, in patches with *A. longifolia* individuals varied in the choice of plants used as shaded places to mitigate high microenvironmental temperatures and were more exposed to full shade sites and less to warm bare sand, for basking. Although modified habitats provide shelter against predators under the vegetation canopy of exotic acacias, similar to that observed by Block et al. (2012) in the southern dune barriers of Buenos Aires Province for the sand lizard *Liolaemus multimaculatus* using exotic shrubs of *Tamarix* sp., the potential effect of ecological trap with negative consequences for body temperatures and thermoregulatory efficiency should be considered (Stellatelli et al., 2013a). In agreement with this idea, lizard populations should be negatively affected as *A. longifolia* afforestation increases. Futures studies should assess this hypothesis by considering reproductive performance, survival and abundance of *L. wiegmannii*.

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