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Responses of two sympatric sand lizards to exotic forestations in the coastal dunes of Argentina: some implications for conservation

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Abstract

Context. Exotic forestations may modify habitat quality, affecting native animal populations that require specific microhabitats to remain viable.

Aims. We determined whether abundances and body condition of the lizard species *Liolaemus wiegmannii* and *L. multimaculatus* differed between forested and non-forested dunes. We also examined what environmental attributes are important in explaining the potential differences.

Methods. We sampled six sites of 300 ha each. Three of these sites had original vegetation and three were forested with exotic *Acacia longifolia*. We traced 120 transects per site searching for lizards.

Key results. Lizards were two times more abundant in non-forested sites than in sites covered by acacia trees (even as low as a fourth of the area). Sites with high densities of acacia ($\geq$78% of coverage) had the lowest abundance of lizards. In forested sites, the snout–vent length of *L. wiegmannii* was 10% smaller and relative body mass 22% lower than in non-forested sites. We found no differences in the body size of *L. multimaculatus*.

Conclusions. The replacement of the native vegetation by *A. longifolia* has negative effects on lizard species, representing a substantial threat to *L. wiegmannii* and particularly to *L. multimaculatus*, a threatened status species. Structural and thermal characteristics of the non-forested sites seemed to be more favourable for the abundance and body condition, whereas the dense vegetation and the low temperatures on the forested sites might explain the lower presence of lizards.

Implications. We recommend that before the implementation of future forestation plans in the pampasic coastal dunes, the deleterious consequences that this practice generates on native lizard fauna must be considered. When necessary, we recommend that *A. longifolia* be planted so that the coverage does not exceed a quarter of the total area, so as to prevent the formation of continuous (or closed) forest patches and to maintain the structural heterogeneity of the habitat that these lizards need to survive. In the most affected areas, eradication and control strategies may help reduce the advancement of this exotic plant over the areas intended for conservation.

Additional keywords: dunes, exotic plants, grassland, *Liolaemus*.

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Introduction

The planting potentially invasive exotic plant species can produce serious ecological consequences for the ecosystems they are introduced to, including changes in species richness, abundance or ecosystem function (Vitousek *et al.* 1997; Grice 2004). Additionally, exotic vegetation modifies habitat quality, affecting native animal populations that require specific microhabitats to remain viable (How and Dell 2000; Brown 2001). In this way, the homogenisation of the physiognomy of the landscape generated by exotic plants negatively affects the demography of the native fauna of vertebrates such as birds (McAdoo *et al.* 1989; Flanders *et al.* 2006), mammals (Pearson *et al.* 2001; Matlack *et al.* 2008), amphibians and reptiles (Martin and Murray 2011). Reptiles use available habitat characteristics in a non-random fashion to meet their own physiological, locomotor, behavioural and ecological needs (Toft 1985; Huey 1991; Smith and Ballinger 2001; Pianka and Vitt 2003). Alteration or loss of key habitat characteristics may lead to population decline, and even local extinction of reptile populations (Brisson *et al*. 2003; Howes and Lougheed 2004).

Exotic plants may generate suboptimal habitats for lizards by lowering the availability of food, decreasing environmental temperature (Valentine *et al*. 2007; Hacking *et al*. 2014) or increasing predation (Hawlena *et al*. 2010). Many previous studies in ecosystems of Africa (Meik *et al*. 2002), Australia (Jellinek *et al*. 2004; Valentine 2006), Israel (Hawlena *et al*. 2010) and United States (Bateman *et al*. 2008; Bateman and Ostoja 2012) have shown the deleterious effect of exotic vegetation on richness and abundance of lizards, and some studies have shown subtle effects also to individuals, such as a loss of physical condition (Nielsen 2011). Body condition (a ratio between body mass and body length) is used ecologically as an estimate of the nutritional state and is a good predictor of survival and/or reproductive success in many taxa, including reptiles (Jakob *et al*. 1996; Schulte-Hostedde *et al*. 2005; Salvador *et al*. 2008). Body condition may be used to infer the response of individuals to environmental stressors such as increased predation risk (Amo *et al*. 2007*a*) or habitat degradation (Amo *et al*. 2007*b*).

Australian acacias, including *Acacia longifolia*, were planted to stabilise the dynamics of coastal sand dunes in several places around the globe. Unfortunately, these species occupied extensive areas of native plant communities, leading to severe impacts on the structure and function of several original ecosystems in Africa (Yelenik *et al*. 2004), Israel (Kutiel *et al*. 2004), Portugal (Marchante *et al*. 2003), Uruguay (Caldevilla and Quintillán 2002) and Argentina (Faggi *et al*. 2010; Alberio and Comparatore 2014). In Argentina, the sandy coast of Buenos Aires Province was planted with exotic trees since 1940s, not only to stabilise the dunes but also for decorative purposes, in an attempt to improve the attractiveness of seaside resorts (Zalba and Villamil 2002). The forestation of dunes with *Acacia* species has grown exponentially since the 1970s, mostly over the Oriental Dune Barrier of the Atlantic coast of Buenos Aires province (Faggi and Dadon 2011; Alberio and Comparatore 2014).

Two closely related species of lizards, *Liolaemus wiegmannii* and *L. multimaculatus*, occur in sympatry along the Oriental Sand Dune Barrier of the Atlantic coast of Buenos Aires, Argentina (Cei 1993; Vega 2001). These two species have specialised morphological features for living in loose sand and are included, together with nine other species, in the *L. wiegmannii* group (Etheridge 2000; Ávila *et al*. 2009). In Argentina, *L. wiegmannii* (42–64 mm snout–vent length, SVL) is restricted to sandy substrates along the Atlantic coasts of Buenos Aires and Río Negro provinces (Vega 2001), and it may also be found on sand or other substrates at many localities inland (Cei 1993; Martori *et al*. 1998; Etheridge 2000). The sand dune lizard, *L. multimaculatus* (48–70 mm SVL), is a small diurnal sand-dwelling lizard, endemic to the Pampean coasts of the provinces of Buenos Aires and Río Negro in Argentina, and was categorised as a *Vulnerable* species (Abdala *et al*. 2012). This lizard is a specialised species with respect to microhabitat selection, preferring areas with low vegetation coverage and bunch grasses as shelters (Kacoliris *et al*. 2010; Vega 2001).

Knowledge about the effects of unsuitable practices of forestation is scarce in South America, although there is evidence that anthropic disturbances reduce the abundance of lizards (Rocha and Bergallo 1992; Vega *et al*. 2000; Rocha *et al*. 2009). Additionally, recent studies have shown that the habitat use and the thermal biology of *L. wiegmannii* and *L. multimaculatus* were negatively affected by the exotic-tree forestation in the coastal dunes of Buenos Aires, Argentina (Stellatelli *et al*. 2013*a*, 2013*b*). We studied six sites where these two species of lizards occur (*L. wiegmannii* and *L. multimaculatus*); three of these sites are forested with *Acacia longifolia* and three remain non-forested. Therefore, the aims of this study were (1) to compare the abundances of *L. wiegmannii* and *L. multimaculatus* among zones with different degrees of forestation with *A. longifolia*, (2) to determine how forestation affects the body condition of lizards and (3) to analyse what environmental attributes better explain the observed differences in lizard abundances. We have conducted a natural non-manipulative experiment to test the hypothesis that in psammophytic grasslands forested with *Acacia*, the abundance of lizards is lower than in non-forested grasslands and in forested grasslands the body condition of lizards is reduced due to poor habitat quality.

Materials and methods

Study sites

The present study was conducted on six sites, each one of ~300 ha, in the coastal dunes of Buenos Aires province, Argentina (Fig. 1). Field work was carried out at three sites with native grasslands that have been partially replaced by forestations of *A. longifolia*, namely, Mar Azul (37°20′45.8″S, 057°03′17.9″W), 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), and at three sites with non-forested grasslands, including Reserva Natural Faro Querandí (37°23′51.95″S, 57°04′24.04″W), Pinar del Sol (36°55′55.7″S,

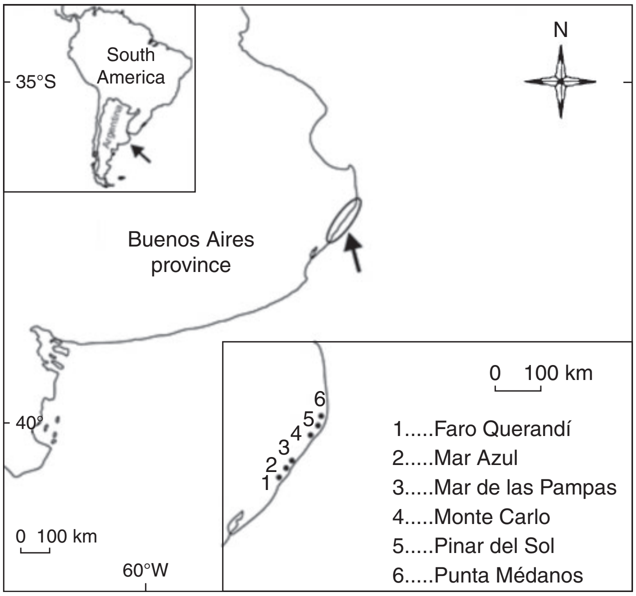

Fig. 1. Geographic location of the six study areas.

56°45′04.3″W) and Punta Médanos (36°53′30.9’’S, 56°41′20.1″W) (Fig. 1). We have attempted to control the effects of confounding variables by avoiding sites with presence of human activity, roads and urban constructions. The studied zones had landscape configurations typical of temperate coastal dunes characterised by different geomorphological zones, including upper beach, active foredunes, sand plain, active inland dunes, deflation plain, interdunal depressions and semifixed dunes. In addition, we also controlled vegetation composition of the study sites, and regardless of the presence of *Acacia*, native plant communities were similarly structured in all study sites (Wiedemann and Pickart 2004; Block 2014). Similar to temperate coastal dunes around the world, vegetation consists of edaphic communities associated with geomorphological types; native vegetation is mainly composed of *Poa lanuginosa*, *Panicum racemosum* and *Androtrichum trigynum* grasslands, *Cortaderia selloana* scrublands, shrublands and mixed steppes of *Senecio crassiflorus*, *Achyrocline satureoides*, *Tessaria absinthioides*, *Baccharis notosergila* and *Discaria americana* (Cabrera and Zardini 1978). 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).

Lizard sampling

We visited each study site twice a month from January to April 2010 and January to April 2011, corresponding to the post-reproductive period of *L. wiegmannii* and *L. multimaculatus* in the study sites (Vega 1997; Martori and Aun 1997). We used line transect, a standardised method recommended by many authors to make between-site comparison of abundances at a broad geographical scale (Díaz and Carrascal 1991; Smolensky and Fitzgerald 2011). Annually, 60 transects (100 m long and 6 m wide) were established randomly in each study site, and each transect was surveyed only one time per site to avoid pseudoreplication. Transects were at least 100 m apart each from other, taking into account the mean home ranges of *L. wiegmannii* (mean = 39 m^2) and *L. multimaculatus* (mean = 260 m^2, Block 2014). This distance was large enough to consider each transect as an independent sample. Because of landscape configuration of coastal dunes, transects in each site were also separated by different geomorphological barriers, such as patches of interdunal depressions where lizards are absent. Only lizards within 3 m of each side of the observer were considered, because preliminary samplings showed that within this distance, there was no evidence for a lack of observations at forested sites with respect to non-forested sites.

At each forested site, the 60 transects were randomly distributed among four strata with different proportions of *A. longifolia* cover, as follows: 1–25%, 26–51%, 52–77% and 78–100% (15 100 × 6 m transects per stratum). The coverage of *A. longifolia* in each stratum was estimated by line-intercept method (*sensu* Bullock 1996) by using a stretching 100-m tape (FT 100 m, Yucheng Hongri Industrial Measures Co. Ltd., Shaogang , China; ± 1 mm) to measure the length occupied by the vertical projection of the foliage. Sampling effort dedicated to find lizards was proportional to the structural complexity of each study site (more acacia, more effort) to avoid potential biases associated with variations in the detectability (i.e. conspicuity) of lizards among strata with different degrees of acacia coverage. In preliminary samplings representative of different type of transects, we estimated the effort (time) required to detect 100% of the individuals present in transects of each stratum. Time was fixed within each transect but varied among strata according to the amount of acacia cover and the difficulty of thoroughly exploring the site. We spent 10, 15, 20, 25 and 30 min per transect searching in strata with 0%, 1–25%, 26–51%, 52–77% and 78–100% of acacia coverage, respectively.

Data of lizard abundance were collected between 0900 hours and 1800 hours (based on the daily activity period of these lizards; Vega 2001). So as to minimise temporal sampling bias, we obtained an equal number of samples in each zone during the 3-day periods (morning, midday and afternoon). We counted the number of lizards present in each transect, recording each individual from each species and sex on the basis of external morphology (Cei 1993). We captured all lizards and measured their SVL with a digital caliper (SC111001, Schwyz Co, Buenos Aires, Argentina; ± 0.01 mm); body mass was measured with a digital pocket scale (CH02, Diamond Premium MR, Shenzhen Oway Technology Ltd., Shenzhen, China; ± 0.1 g). After measurement, lizards were released at the site of capture. For the analyses, we considered only adult lizards (SVL: *L. wiegmannii* >42 mm; *L. multimaculatus* ≥48 mm; Martori and Aun 1997; Vega 1997).

Environmental sampling

To analyse the lizard abundance with respect to the structural features of the habitat, we determined the microhabitat composition by taking into account the substrate composition (sand with or without leaf litter) and the physiognomic type of the plants (trees, shrubs, subshrubs and herbs) according to Cabrera and Zardini (1978). Availability of microhabitats was estimated by using line-intercept method with a stretching 100-m tape (FT 100 m, Yucheng Hongri Industrial Measures Co. Ltd., Shaogang, China; ± 1 mm) along the centreline of each lizard-sampling transect and by measuring the length occupied by the foliage of each plant type (in vertical projection), leaf litter or bare sand (Bullock 1996). Additionally, the micro-environmental temperatures were recorded at a random point from each transect, namely, substratum temperature (Ts) at 1 cm under the ground and air temperature at 1 cm above the ground (Ta) with thermocouples connected to a digital thermometer (SC133, Schwyz Co, Buenos Aires, Argentina; ± 0.01°C). The stratum complexity was quantified by measuring vegetation coverage along the centreline of each transect.

Data analyses

Because of low capture rates, we pooled lizard morphological data (SVL, body mass) over grassland type (forested vs non-forested). Normality and homoscedasticity were evaluated through Kolmogorov–Smirnov and Shapiro–Wilks tests, respectively (Zar 1984). To compare the body mass, we used two-way ANCOVA and Tukey’s *post hoc* comparison test

($\alpha = 0.05$, with SVL as the covariate) with sex and habitat type (forested, non-forested) as the factors. We used two-way ANOVA and Tukey's *post hoc* comparison test ($\alpha = 0.05$) to compare the SVL between sex and habitat type (Zar 1984).

To assess the effect of forestation on the abundance of lizards (number of individuals per transect) of each species, we used generalised linear mixed models (GLMMs) with the Poisson error structure and log function (Crawley 2007). The models were constructed with the forestation degree (0%, 1–25%, 26–51%, 52–77% and 78–100%) and year (2010, 2011) as explanatory variables (fixed factors), and the abundance of adult lizard as a response variable. Taking into account that lizard abundances in transects on the same site are likely to be more similar to each other than those obtained from different sites, we considered the transect identity as a random factor nested within site. The category 78–100% was removed from the analysis to improve the fit of the models (see Nicholls 1989), because no single *L. multimaculatus* individual was observed in sites with this degree of forestation.

To evaluate the relationship among lizard abundance and structural and thermal characteristics of the habitats, we used GLMMs with the Poisson error structure and log function (Crawley 2007). The predictor variables (fixed factors) were the habitat type (forested, non-forested), proportion of each type of microhabitat (trees, shrubs, subshrubs, herbs, sand with or without leaf litter) and the environmental temperature (*T*e) registered at each transect. We considered the transect identity as random factor nested within site. Model fitting was visually assessed by inspecting plots of standardised deviance residuals for each model. We assessed goodness of fit for all models and estimated the variance inflation factor ($\hat{c}$) as residual deviance divided by the degrees of freedom (Burnham and Anderson 1998). Considering that multicollinearity of predictors can make interpretation of alternative models difficult (Lennon 1999), we examined the correlation between substrate and air temperature for model construction and retained those with the clearest ecological meaning for each species (Stellatelli *et al.* 2013*a*).

Model selection was based on Akaike's information criterion corrected for $\hat{c}$ and small sample sizes (QAIC_c; Burnham and Anderson 2002). We used the following two measures to provide further insight into the amount of uncertainty in model selection: ΔQAIC_c (the difference in QAIC_c between the best approximating model and all other models) and Akaike weight (the probability that a given model is the best among a series of candidate models; Anderson and Burnham 1999; Burnham and Anderson 2002). 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). We assessed the degree to which 95% confidence intervals of parameter estimates overlapped zero. All statistical analyses were carried out using R software, version 2.15.0 (R Development Core Team 2012).

Results

Lizard abundance and forestation degree

Liolaemus wiegmannii was present at all six study sites, whereas *L. multimaculatus* was found only at four sites (including two forested sites, Mar de las Pampas and Monte Carlo, and two non-forested sites, Pinar del Sol and Punta Médanos). The abundance of *L. wiegmannii* was significantly different among sites with a different degree of *A. longifolia* coverage (Table 1, Fig. 2). The non-forested sites showed the highest abundance of *L. wiegmannii* (mean ± s.d. = 3.86 ± 1.92 individuals per transect, $n = 360$). The sites with 1–25% *A. longifolia* surface coverage had higher lizard abundances (mean ± s.d. = 1.94 ± 0.99 individuals per transect, $n = 90$) than did sites with a higher coverage, whereas the lowest abundance of lizards was observed at sites with *A. longifolia* coverage of

Table 1. Comparison of lizard abundances

Fixed-factor contrasts from generalised linear mixed models (GLMMs) testing the effect of the interactions between years (2010 vs 2011) and between forestation degrees on the numbers of *Liolaemus wiegmannii* and *L. multimaculatus* per transect. $\alpha = 0.05$

Parameter	*Liolaemus wiegmannii*				*Liolaemus multimaculatus*			
	Mean	s.e.	*t*-value	*P*-value	Mean	s.e.	*t*-value	*P*-value
Intercept	1.308	0.038	34.780	<0.001*	0.681	0.063	10.860	<0.001*
Year								
2010 vs 2011	–0.013	0.032	–0.404	0.686	–0.064	0.051	–1.250	0.213
Forestation degree								
0% vs 1–25%	–0.665	0.084	–7.932	<0.001*	–0.345	0.134	–2.570	0.011*
0% vs 26–51%	–1.532	0.103	–14.925	<0.001*	–1.611	0.174	–9.240	<0.001*
0% vs 52–77%	–2.249	0.130	–17.323	<0.001*	–2.428	0.228	–10.670	<0.001*
0% vs 78–100%	–4.420	0.339	–13.045	<0.001*	–	–	–	–
1–25% vs 26–51%	–0.867	0.123	–7.022	<0.001*	–1.266	0.204	–6.201	<0.001*
1–25% vs 52–77%	–1.584	0.146	–10.789	<0.001*	–2.084	0.251	–8.293	<0.001*
1–25% vs 78–100%	–3.755	0.345	–10.862	<0.001*	–	–	–	–
26–51% vs								
26–51% vs 52–77%	–0.717	0.158	–4.531	<0.001*	–0.817	0.275	–2.974	0.003*
26–51% vs 78–100%	–2.888	0.350	–8.235	<0.001*	–	–	–	–
52–77% vs 78–100%	–2.170	0.359	–6.036	<0.001*	–	–	–	–

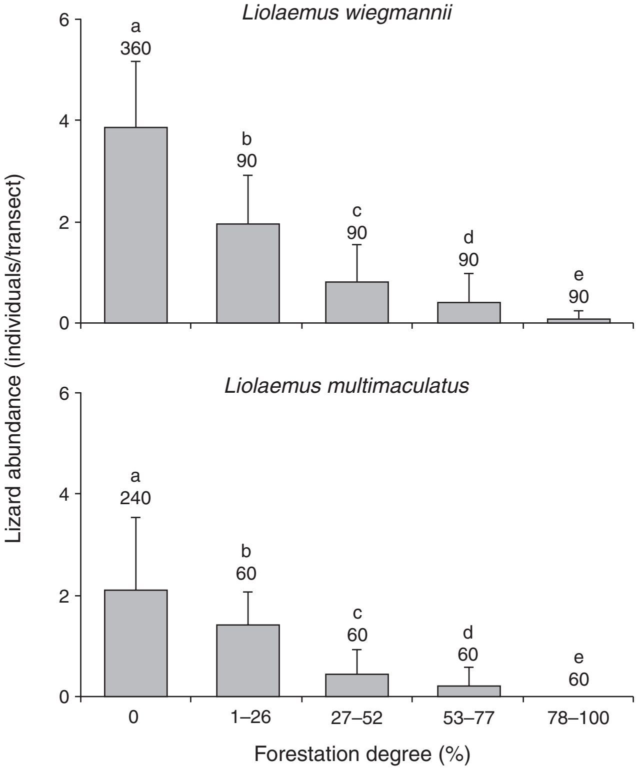

Fig. 2. Number of lizards per transect in zones with different degrees of exotic *Acacia longifolia* forestation. The different letters above the standard deviation bars indicate significant differences according to fixed-factor contrasts from generalised linear mixed model (GLMMs) analyses ($\alpha = 0.05$) and the numbers indicate the sample sizes.

≥78% (mean ± s.d. = 0.04 ± 0.20 individuals per transect, $n = 90$; Fig. 2). The abundance of *L. multimaculatus* showed a pattern similar to that observed for *L. wiegmannii*, with the non-forested sites showing the highest abundance of lizards (mean ± s.d. = 2.10 ± 1.43 individuals per transect, $n = 240$). The sites with 1–25% surface coverage by *A. longifolia* had higher *L. multimaculatus* abundances (mean ± s.d. = 1.40 ± 0.67 individuals per transect, $n = 60$) than did sites with a higher coverage, whereas no lizard was observed at sites with ≥78% *A. longifolia* coverage (Fig. 2). Additionally, we found no differences in the abundance of both species of lizards between years (Table 1).

Body condition comparison

Body mass of *L. wiegmannii* was lower in forested than in non-forested habitats (mean ± s.d., forested = 3.71 ± 1.24 g, $n = 136$; non-forested = 4.72 ± 0.94 g, $n = 148$; Fig. 3), with two-way ANCOVA showing significant differences ($F_{1,280} = 11.130$, $P < 0.001$, SVL as covariate); however, there was no effect of sex ($F_{1,280} = 0.75$, $P = 0.386$), nor was there a significant interaction between these factors ($F_{1,280} = 0.03$, $P = 0.864$). Additionally, SVL of *L. wiegmannii* was significantly different between habitats (two-way ANOVA: $F_{1,280} = 92.36$, $P < 0.001$), but no effect of sex was observed ($F_{1,280} = 0.75$, $P = 0.386$), nor was there a significant interaction between these factors ($F_{1,280} = 0.03$, $P = 0.864$). Average SVL was lower in forested than in non-forested habitats (mean ± s.d., forested = 48.56 ± 4.94 mm, $n = 136$; non-forested = 53.61 ± 3.82 mm, $n = 148$). The SVL range in forested habitats was 42.00–56.20 mm and in non-forested habitats it was 42.56–59.43 mm.

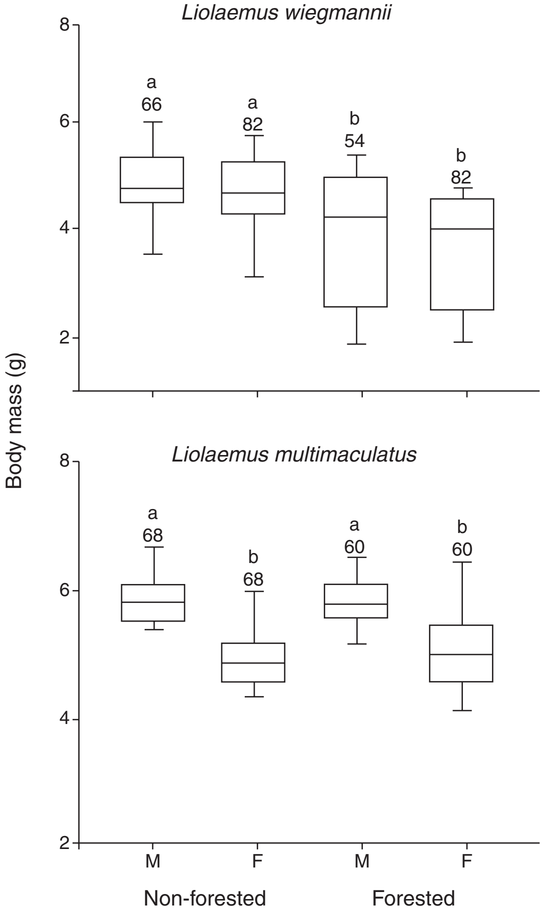

Fig. 3. Body mass of males (M) and females (F) of *Liolaemus wiegmannii* and *L. multimaculatus* in forested and non-forested habitats. Horizontal bar denotes median, vertical bar denotes range, and upper–lower boundary of boxes denotes quartile. Different letters above the bars indicate significant differences in response values (Tukey's test, $\alpha = 0.05$). Numbers above the bars indicate the sample sizes.

Body mass of *L. multimaculatus* did not vary significantly between habitats (two-way ANCOVA: $F_{1,251} = 1.672$, $P = 0.197$, SVL as covariate), but was significantly affected by sex ($F_{1,251} = 17.803$, $P < 0.01$); there was no significant interaction between these factors ($F_{1,251} = 2.258$, $P = 0.134$; Fig. 3). Additionally, SVL of *L. multimaculatus* did not differ significantly between habitats (two-way ANOVA: $F_{1,252} = 0.01$, $P = 0.949$), but there was a significant effect of sex ($F_{1,252} = 181.83$, $P < 0.001$); there was no significant interaction between these factors ($F_{1,252} = 0.11$, $P = 0.745$). Males were larger (mean ± s.d.: 59.20 ± 4.48 mm, $n = 128$) than females (mean ± s.d.: 52.51 ± 3.39 mm, $n = 128$). The SVL range was 48.00–69.00 mm for the males and 48.00–60.20 mm for the females.

Environmental variables and lizard abundance

The *A. longifolia*-forested habitats showed a significantly higher proportion of substrate covered by leaf litter, a lower proportion of bare sand and a significantly lower coverage of native plant species (shrubs, subshrubs and herbs) than did non-forested habitats (Table 2). Mean substrate and air temperatures were 3.5°C and 1.2°C, respectively, lower in forested than in non-forested habitats (Table 2). GLMMs indicated that trees, shrubs, habitat type and air temperature were the most important factors explaining the abundance of *L. wiegmannii* (Table 3). These factors were included in Model 1, which was the one with the highest support (Table 3). This model accounted for more than 75% of the variation in lizard abundance (Table 3). Trees, habitat type and substrate temperature were the most important predictors because all of them showed high likelihood parameter values and presented confidence intervals that excluded zero (Table 4). The abundance of *L. multimaculatus* was better explained by the bare sand, substrate temperature and habitat-type factors (Table 3). These variables were included in Model 1 (Table 3). This model accounted for more than 77% of the variation in lizard abundance (Table 3). Bare sand, substrate temperature and habitat type were important predictors because they all showed high likelihood parameter values and presented confidence intervals that excluded zero (Table 4).

Discussion

Forestation with *A. longifolia* in the pampasic coastal dunes of Buenos Aires, Argentina, resulted in low sand lizard abundances. Variation in the coverage of *A. longifolia* apparently influences the abundance of *L. wiegmannii* and *L. multimaculatus* populations, because lizards were two times more abundant in non-forested sites than in sites with up to a quarter of area covered by *A. longifolia*. Additionally, zones with high densities of acacia ($\geq$78% of coverage) showed the lowest abundance of *L. wiegmannii*, and *L. multimaculatus* was completely absent from these zones. Our results showed that this tendency (zones planted with exotic trees have the lowest lizard abundance) is maintained along the coastal sand dunes of Buenos Aires not

Table 2. Environmental characterisation of the habitats

Mean (±1 s.d.) values of environmental variables were measured by habitat type and compared by Student's *t*-test ($\alpha = 0.05$). Asterisks (*) indicate significant differences

	Trees (%)	Shrubs (%)	Sub-shrubs (%)	Herbs (%)	Leaf litter from trees (%)	Leaf litter from natives (%)	Bare sand (%)	Substrate temperature (°C)	Air temperature (°C)
Forested	49.48 ± 28.27	8.57 ± 10.71	0.77 ± 1.67	7.64 ± 9.20	12.46 ± 9.22	1.46 ± 2.53	19.13 ± 16.76	34.21 ± 3.41	34.14 ± 3.21
Non-forested	0.00 ± 0.00	27.99 ± 15.01	6.04 ± 7.09	17.35 ± 12.60	0.00 ± 0.00	6.73 ± 3.82	41.88 ± 9.24	37.67 ± 2.04	35.34 ± 2.17
t-value	–	–20.58	–17.83	–14.22	–	–26.45	–18.17	–15.60	–5.87
d.f.	–	718	718	718	–	718	718	718	718
P-value	–	<0.001*	<0.001*	<0.001*	–	<0.001*	<0.001*	<0.001*	<0.001*

Table 3. Selection of the explicative models

Generalised linear mixed models (GLMMs) explaining the factors affecting the abundance of *Liolaemus wiegmannii* and *L. multimaculatus.* Only models with strong support are shown (i.e. $\Delta QAIC_c < 2$). Models are listed in a decreasing order of importance for each lizard species. Bs, bare sand; Ha, habitat (forested, non-forested); He, herbs; Sh, shrubs; Ss, subshrubs; *T*e, environmental temperature (corresponding *T*s for *L. multimaculatus*, *T*a for *L. wiegmannii*); Tr, trees

Model	Explanatory variables	Deviance	R^2	$QAIC_c$	$\Delta QAIC_c$	Weight
L. wiegmannii						
1	Tr+Sh+Ha+*T*e	189.38	0.755	203.54	0.00	0.28
2	Tr+Ha+Te	193.29	0.750	205.41	1.87	0.11
3	Tr+Sh+Ha+Ss+*T*e	189.31	0.755	205.51	1.97	0.10
4	Tr+Sh+Ha+He+*T*e	189.31	0.755	205.52	1.98	0.10
Global	All variables	189.30	0.755	209.60	6.06	0.01
Null	–	771.70	0.000	777.70	574.20	0.00
L. multimaculatus						
1	Tr+Ha+Bs+*T*e	94.13	0.779	108.4	0.00	0.18
2	Ha+Bs+*T*e	96.26	0.774	108.5	0.06	0.17
3	Ha+He+Bs+*T*e	95.78	0.775	110.1	1.65	0.08
4	Tr+Ha+Ss+Bs+*T*e	93.78	0.780	110.1	1.72	0.08
5	Tr+Ha+Bs+Te	95.94	0.775	110.2	1.81	0.07
6	Tr+Sh+Ha+Bs+*T*e	94.01	0.779	110.4	1.96	0.07
Global	All variables	93.47	0.780	114.00	5.60	0.01
Null	–	425.60	0.000	431.7	323.30	0.00

Table 4. Variables affecting the abundance of lizards

Parameter estimates (±s.e.) from generalised linear mixed models (GLMMs) describing the factors affecting the abundance of *Liolaemus wiegmannii* and *L. multimaculatus*. Parameter likelihoods (PL) are QAIC_c weights 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 weights) from all models and standard errors (s.e.) are calculated from all candidate models from unconditional variances. *T*e, environmental temperature (corresponding *T*s for *Liolaemus multimaculatus*, *T*a for *Liolaemus wiegmannii*). Explanatory variables with a confidence interval (CI) excluding zero are in bold

Explanatory variable	*Liolaemus wiegmannii*			*Liolaemus multimaculatus*		
	Parameter ± s.e.	CI	PL	Parameter ± s.e.	CI	PL
Intercept	–7.440 ± 0.578	–8.570; –6.310		–15.200 ± 1.270	–17.700; –12.700	–
Trees	**–0.019 ± 0.003**	**–0.025; –0.013**	**1.00**	0.006 ± 0.008	–0.010; 0.022	0.49
Shrubs	0.002 ± 0.003	–0.003; 0.007	0.62	–0.001 ± 0.004	–0.009; 0.006	0.27
Subshrubs	–0.001 ± 0.002	–0.004; 0.003	0.23	0.001 ± 0.003	–0.005; 0.007	0.26
Herbs	0.0003 ± 0.001	–0.003; 0.002	0.26	–0.001 ± 0.003	–0.006; 0.004	0.28
Bare sand	0.0004 ± 0.001	–0.003; 0.002	0.25	**0.022 ± 0.006**	**0.011; 0.033**	**1.00**
Habitat (non-forested)	**0.888 ± 0.106**	**0.680; 1.100**	**1.00**	**0.866 ± 0.165**	**0.542; 1.190**	**1.00**
*T*e	**0.219 ± 0.015**	**0.190; 0.249**	**1.00**	**0.333 ± 0.031**	**0.273; 0.393**	**1.00**

only for *L. wiegmannii* but also for *L. multimaculatus*, the latter having a conservation status *Threatened* (Abdala *et al.* 2012).

The structural features (size, canopy) of native shrubs and herbs preferred by *L. wiegmannii* and *L. multimaculatus* provide thermally suitable sites, allowing lizards to maintain an appropriate adjustment of their vital functions (Block *et al.* 2013; Stellatelli *et al.* 2013*a*). Conversely, *A. longifolia* coverage reduces ambient temperatures by producing shade and leaf litter (Stellatelli *et al.* 2013*b*) and this could be negatively affecting the physiological performance and the reproductive success of *L. wiegmannii* and *L. multimaculatus.* In *Liolaemus* lizards, elevated and stable body temperatures are required to optimise demanding physiological functions, digestion, growth and reproduction (Vidal-Maldonado and Labra-Lillo 2008). Because temperature affects the growth, development and survival of embryos in reptiles (Dubey and Shine 2011; Michel *et al.* 2013), specific thermal-sensitivity of embryos is a key climatic factor underlying the spatial distribution of many lizards (Shine *et al.* 2002; Angilletta *et al.* 2009).

The body condition of adult *L. wiegmannii* was significantly lower in forested than in non-forested habitats. The individuals from forested habitats showed a SVL 10% shorter and a body mass 22% lower than those from non-forested habitats. In lizards, the decrease of 20% in body mass is considered as harmful by many authors because heaviest individuals may have higher fat stores or higher rates of energy acquisition, leading to higher survivorship under poor environmental conditions (Forsman 1993; Bauwens *et al.* 1995; Civantos and Forsman 2000). *A. longifolia* reduces the thermoregulatory efficiency of *L. wiegmannii* (Stellatelli *et al.* 2013*a*) that may eventually impair the fit of the cellular functions and/or the capabilities for capturing preys in detriment of the lizards' body condition. Avery (1978), Sinervo and Adolph (1989) and Adolph and Porter (1993) also found that environmental thermal fluctuations induce variations in the growth rate of lizard species of *Podarcis* and *Sceloporus* genera, where individuals exposed to low temperatures reach smaller body sizes than those inhabiting under favourable thermal conditions. Animals with better body condition have higher energy reserves and may allocate more resources for reproduction and maintenance (Van Noordwijk and de Jong 1986; Hofmann and Henle 2006; Salvador *et al.* 2008) and they are better prepared to initiate the breeding season (Naulleau and Bonnet 1996) and to fight off parasites and diseases (Amo *et al.* 2004; Garrido and Pérez-Mellado 2013). Moreover, better body condition of females usually allows the production of larger clutches (Radder and Shanbhag 2004) and/or larger offsprings (Hofmann and Henle 2006), which in turn may lead to higher juvenile survivorship (Díaz *et al.* 2005; Sinervo *et al.* 1992).

In contrast to *L. wiegmannii*, we found no differences in the body condition of *L. multimaculatus* between forested and non-forested habitats. This could be because *L. multimaculatus* uses forested habitats differently than does *L. wiegmannii*. The sand lizard (*L. multimaculatus*) is observed to be active only in those unaltered patches that retain the structural and thermal characteristics of the unmodified environment, that is, open spaces with scarce vegetation coverage, far from acacias (Vega 2001; Block *et al.* 2012; Stellatelli *et al.* 2013*a*). Then, unaltered patches in modified habitats may provide *L. multimaculatus* the appropriate resources (high thermal quality spots) to maintain good body condition.

The replacement of the native vegetation by *A. longifolia* has negative effects on lizard species and represents a substantial threat to *L. wiegmannii* and particularly to *L. multimaculatus*. The introduction of *A. longifolia* could be disadvantageous for *L. wiegmannii* and *L. multimaculatus*, decreasing the abundance of these two species of lizards and impairing the body condition of *L. wiegmannii*. In particular, the relative abundance between these types of sites (forested vs non-forested) may vary importantly in *L. multimaculatus*, presenting a lower number of lizards per unit area in the forested sites because of the almost exclusive use of unaltered remaining patches. These differences may be mainly attributed to a lack of structural and thermal requirements needed by these lizard species. Our study showed the importance of implementation of management actions for sand lizards in coastal dunes of Buenos Aires. Although *L. wiegmannii* is relatively common in a wide range of coastal and inland habitats of Argentina and is not considered a threatened species or one that needs federal protection (see Abdala *et al.* 2012), *L. multimaculatus*, in contrast, is considered *Vulnerable* in its conservation status, for it is endemic to a threatened ecosystem, the Atlantic Coastal Dunes of Argentina (Abdala *et al*. 2012).

We recommend that before implementation of future forestation plans in the coastal dunes of Buenos Aires, the deleterious consequences that this practice generates on native lizard fauna must be considered. When necessary, we propose that *A. longifolia* should be planted in a way that its coverage does not exceed a quarter of the total area, so as to prevent the formation of continuous (or closed) forests and to maintain the dune habitat that these lizards need to survive. In the most affected areas, we also suggest the execution of techniques for managing *A. longifolia*, such as mechanical control in combination with litter removal and other supplementary management actions, such as the propagation of native species or prescribed controlled fires to deplete the seed bank of invasive species (Marchante *et al*. 2009; Marchante *et al*. 2011). This eradication and control strategies may contribute to avoiding or reducing the advance of *A. longifolia* and other exotic plants over areas intended for conservation, with the aim of preserving the integrity of the ecosystems of coastal grasslands of Buenos Aires, Argentina.

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