

EFFECTS OF TREE INVASION ON THE HABITAT USE OF SAND LIZARDS

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ABSTRACT: The introduction of exotic tree species may interfere with conservation efforts for natural habitats, including grasslands in coastal sand dunes. Natural plant cover is used by several species in coastal dunes of Buenos Aires, Argentina, among them the lizard *Liolaemus wiegmannii*. Here we study the habitat use and abundance of this lizard inhabiting a psammophytic grassland within this ecosystem, where *Acacia longifolia* was recently introduced. Surveys and lizard sampling were conducted along 40 transects distributed in four independent zones of 75 ha, each with a different degree of invasion impact. We measured structural and thermal features in relation to *A. longifolia* and native plants. The lizard *L. wiegmannii* was three times more abundant in zones with $\leq 25\%$ coverage of *A. longifolia*. The Jacobs selectivity index showed that all age classes selected native shrubs and avoided *A. longifolia* trees. These results were similar in greenhouse experiments. However, we found no differences in the use of any of these plants' (introduced or native) leaf litter. Structural and thermal characteristics of the habitat under the shrubs seemed to be more favorable for the physiological performance and behavior of *L. wiegmannii*, whereas the lower temperatures under *A. longifolia* might explain the lower presence of lizards in areas where this tree was introduced.

Key words: *Acacia*; Habitat selection; Invasive plants; *Liolaemus*; Lizard abundance; Psammophytic grassland

THE INTRODUCTION of exotic plant species, especially when they spread rapidly, is a serious threat to natural ecosystems worldwide (Vitousek et al., 1997). Several studies showed that invasive plants generate changes to the structure and composition in original communities, reducing species richness and abundance of native plants (Di Tomaso, 1998; Higgins et al., 1999; Ferdinands et al., 2005), invertebrates (Ellingson and Andersen, 2002; Herrera and Dudley, 2003), and vertebrates (Braithwaite et al., 1989; Wilson and Belcher, 1989; Meik et al., 2002). Introduced plants may alter the physical and chemical properties of the soil by changing the temperature; humidity; and levels of organic carbon, nitrogen, and interchangeable cations (Yelenik et al., 2004; Marchante et al., 2008). Certain traits of exotic plants, such as a large size, higher growth rate, and higher biomass production, turn these species into the dominant ground cover and affect the structural features of the natural habitat (Tomley,

1998; Yelenik et al., 2004; Valentine et al., 2007), leading to a reduction of physiognomic heterogeneity (Bateman and Ostojka, 2012).

In many places around the world Australian acacias, including *Acacia longifolia*, were planted to stabilize the dynamics of coastal sand dunes. This tree species ended up spreading into areas of native plant communities, however, leading to severe impacts on the structure of original ecosystems (Marchante, 2001; Marchante et al., 2003; Kutiel et al., 2004). In Argentina, forestation of dunes with *Acacia* began in the 1940s and the rate has grown exponentially since the 1970s, mostly over the Oriental dune barrier of the Atlantic coast of Buenos Aires (Zalba and Villamil, 2002; Faggi and Dadon, 2011).

The physical structure of vegetation is a dramatic force shaping animal communities, as observed in some species of arthropods (Samways et al., 1996; Vieira and Louzada, 2008), birds (McAdoo et al., 1989; Flanders et al., 2006), mammals (Pearson et al., 2001; Matlack et al., 2008), and herpetofauna (Martin and Murray, 2011) including lizards

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FIG. 1.—Photographs of a natural grassland (a), and a grassland modified by *Acacia longifolia* (b) in Mar Azul, Buenos Aires, Argentina.

(Nielsen, 2011; Bateman and Ostoja, 2012). Negative changes in the physical environment might produce suboptimal habitats by lowering the availability of food, increasing predation risk, or changing the environmental thermal spectrum (Märtens et al., 1996; Downes and Hofer, 2007; Valentine et al., 2007), any of which can yield diminished richness and abundance of lizard populations (Meik et al., 2002; Jellinek et al., 2004; Bateman et al., 2008). At present, there is no background information for estimating the impact of forestation with introduced plants on lizard populations in Southern Atlantic coasts. There is evidence, however, that anthropogenic disturbances negatively affect the abundance of reptiles and amphibians in this region (Rocha and Bergallo, 1992; Vega et al., 2000; Rocha et al., 2009).

Two closely related species of lizards, *Liolaemus wiegmanni* and *L. multimaculatus*, occur in sympatry along the Oriental Sand Dune Barrier of the Atlantic coast of Buenos Aires, Argentina (Ceï, 1993). These species have specialized morphological features for living in loose sand, as do the remaining nine species of the *L. wiegmanni* clade (Etheridge, 2000; Ávila et al., 2009). *Liolaemus wiegmanni* (42–64 mm snout–vent length [SVL]) is restricted to sandy substrates along the Atlantic coast of northern Argentina (Vega, 2001), but also may be found on sand or other substrates at other localities inland (Ceï, 1993; Martori et al., 1998a; Etheridge, 2000). In the coastal sand dunes of Buenos Aires, this

species may be observed near dense vegetation (Vega and Bellagamba, 1992). Despite being considered a generalist, *L. wiegmanni* abundance and thermal biology were negatively affected by the introduction of *A. longifolia* and *Populus alba* (Alberio et al., 2011; Stelletti et al., 2013). Therefore, the aims of this study are (1) to compare the abundance and the habitat use of *L. wiegmanni* in a coastal area with psammophytic grassland in original habitats and patches where *A. longifolia* was introduced; and (2) to determine if there is a selective behavior with regard to structural components of vegetation and leaf litter.

MATERIALS AND METHODS

Study Site

This study was conducted near the coastal village of Mar Azul (37°20'45.8"S, 57°03'17.9"W; datum = WGS84), Buenos Aires, Argentina. The climate is humid temperate with no dry season (Burgos and Vidal, 1995). Mean annual temperature is 14°C with a high monthly mean of 21°C in January and low monthly mean of 7.5°C in July; annual mean rainfall is 930 mm (Servicio Meteorológico Nacional). Native vegetation of coastal dunes is mainly composed of *Poa lanuginosa*, *Panicum racemosum*, and *Androtrichum trigynum* grasslands; *Cortaderia selloana* scrublands; shrublands; and mixed steppes of *Senecio crassiflorus*, *Achyrocline satureioides*, *Tessaria absinthioides*, *Baccharis*

notoserghila, and *Discaria americana* (Fig. 1a). Several areas in Mar Azul show that native vegetation was partially modified by the forestation of *A. longifolia* trees (Vervoorst, 1967; Faggi et al., 2010; Faggi and Dadon, 2011; Fig. 1b).

Field Sampling

We visited the study site twice each month from November 2009 to March 2010. Microhabitats were characterized by the substrate composition (sand without or with leaf litter) and by physiognomic plant composition (trees, shrubs, subshrubs, and herbs). Plants were identified to species level after Cabrera and Zardini (1978). Availability of microhabitats was estimated visually by measuring the relative percentage of vegetation cover. For this purpose, we used 47 quadrats (1 m²) when sampling the herbaceous layer, and 35 quadrats (25 m²) to characterize the shrubby and arboreal layers. We determined the number of sampling quadrats at each scale with the use of species accumulation curves (Gysel and Lyon, 1987; Bullock, 1996). When sampling, the location of the initial quadrat was randomly established, and subsequent samples were taken at 100-m intervals along a transect. A total of 30 individuals of each of the nine most abundant plant species were selected from the grids (Table 1), and the following parameters were measured: (1) plant height (m); (2) canopy cover (%), measured with a spherical densitometer (Lemmon, 1957); and (3) leaf litter cover (%) of the substrate under the plant, measured visually within 0.25-m² quadrats (Gysel and Lyon, 1987).

We measured the environmental temperature (*T_e*) available in the different microhabitat types (trees, shrubs, and herbs, sensu Row and Blouin-Demers, 2006) with data loggers (iButton model DS1921G, Thermochron, Sunnyvale, California, USA). Data loggers were associated with an individual plant having average structural characteristics (see Table 1), for each of the following species: *A. longifolia* (tree), *D. americana* (shrub), *T. absinthioides* (shrub), *S. crassiflorus* (subshrub), and *C. selloana* (herb). Each data logger recorded data every 12 min, over two consecutive days, starting at

TABLE 1.—Mean (± 1 standard deviation) of the structural parameters of the plants occurring at Mar Azul, Buenos Aires, Argentina. Values were compared with a Kruskal-Wallis (*H*), and Dunn post-hoc tests ($\alpha = 0.05$). Asterisks (*) indicate significant differences. *Al* = *Acacia longifolia*, *Bn* = *Baccharis notoserghila*, *Ta* = *Tessaria absinthioides*, *Da* = *Discaria americana*, *Sc* = *Senecio crassiflorus*, *As* = *Achyrocline satureioides*, *Mp* = *Mangyricarpus pinnatus*, *Cs* = *Cortaderia selloana*, *At* = *Androtrichum trigynum*.

	Trees			Shrubs			Subshrubs			Herbs			Dunn's test
	<i>Al</i>	<i>Bn</i>	<i>Ta</i>	<i>Da</i>	<i>Sc</i>	<i>As</i>	<i>Mp</i>	<i>Cs</i>	<i>At</i>	<i>H</i>	<i>P</i>	<i>df</i>	
Plant height (m)	2.50 ±	0.20 ±	0.45 ±	0.80 ±	0.20 ±	0.25 ±	0.15 ±	0.60 ±	0.50 ±	237.4	< 0.001*	8	<i>Al</i> > all; <i>Ta</i> = <i>Da</i> = <i>Cs</i> = <i>At</i> > <i>Bn</i> = <i>Sc</i> = <i>As</i> = <i>Mp</i>
Canopy cover (%)	65.00 ±	36.00 ±	35.50 ±	37.00 ±	36.50 ±	38.00 ±	44.00 ±	45.00 ±	26.00 ±	192.7	< 0.001*	8	<i>Al</i> > all; <i>At</i> < all; <i>Mp</i> = <i>Cs</i> > <i>Bn</i> = <i>Ta</i> = <i>Da</i> = <i>Sc</i> = <i>As</i>
Leaf litter cover (%)	7.35 ±	5.23 ±	5.10 ±	2.38 ±	4.85 ±	3.37 ±	3.56 ±	3.46 ±	6.13 ±	122.0	< 0.001*	8	<i>Al</i> > all; <i>Cs</i> > <i>Bn</i> = <i>Ta</i> = <i>Da</i> = <i>Sc</i> = <i>As</i> = <i>Mp</i> = <i>At</i>
	12.13 ±	7.27 ±	8.21 ±	8.15 ±	6.91 ±	4.79 ±	5.36 ±	8.42 ±	8.17 ±				

TABLE 2.—Mean (± 1 SD) of the thermal parameters of the plants under study, compared by Kruskal-Wallis and Dunn post-hoc test ($\alpha = 0.05$). Asterisks (*) indicate significant differences. *Al* = *Acacia longifolia*, *Ta* = *Tessaria absinthioides*, *Da* = *Discaria americana*, *Sc* = *Senecio crassiflorus*, *Cs* = *Cortaderia selloana*, T_e = environmental temperature.

	Shrubs					<i>H</i>	<i>P</i>	df	Dunn's test
	Trees <i>Al</i>	<i>Ta</i>	<i>Da</i>	Subshrubs <i>Sc</i>	Herbs <i>Cs</i>				
T_e in shade (°C)	31.00 ± 3.71	33.50 ± 3.42	33.50 ± 3.59	27.50 ± 1.55	28.50 ± 3.87	126.8	< 0.001*	4	<i>Ta</i> = <i>Da</i> > <i>Al</i> > <i>Cs</i> = <i>Sc</i>
T_e in filtered sunlight (°C)	31.50 ± 7.80	39.00 ± 6.30	36.00 ± 3.72	28.50 ± 1.83	32.00 ± 5.67	95.8	< 0.001*	4	<i>Ta</i> = <i>Da</i> > <i>Al</i> = <i>Sc</i> = <i>Cs</i>
T_e in total sunlight (°C)	50.75 ± 10.14	44.50 ± 7.21	57.50 ± 10.67	59.25 ± 13.89	39.75 ± 10.53	72.6	< 0.001*	4	<i>Da</i> = <i>Sc</i> > <i>Al</i> > <i>Ta</i> = <i>Cs</i>

0900 h and ending at 1730 h. Six data loggers were located under each plant species: two in shade, two in filtered sunlight, and two in full sunlight. The combination of sampling locations and duration allowed us to estimate the temperature at each microhabitat type appropriately (sensu Labra et al., 2001; Valdecantos et al., 2013), during typical summer days when lizards are highly active. The devices were painted with brown acrylic paint (Eureka, Acrylart, Buenos Aires, Argentina) to resemble the reflectance of the lizards and surroundings (Shine and Kearney, 2001; Valdecantos et al., 2013).

The study area was subdivided into four independent zones, each approximately 75 ha in size, based on the percentage of *A. longifolia* cover: 0–25%, 26–50%, 51–75%, and 76–100%. Data of lizard abundance were collected between 0900 and 1730 h (the daily activity period of this species; Vega, 2001). In order to minimize temporal sampling bias, we obtained an equal number of samples in each zone during the three daily periods (morning, midday, and afternoon). Ten transects (100 m long and 6 m wide) were established randomly in each zone; and each was surveyed only once to avoid pseudoreplication. We counted the number of lizards present in each zone, recording each subject's age class and microhabitat used (plant species and bare/covered sand). We captured each lizard and measured its SVL with digital calipers (± 0.01 mm) to assign it to an age class (hatchlings: ≤ 22 mm, yearlings: 23–41 mm, and adults: ≥ 42 mm; Martori et al., 1998a).

Laboratory Experiments

We performed two laboratory experiments to determine whether *L. wiegmanni* discrim-

inated between native plant species and the introduced tree *A. longifolia*. We captured 72 adult *L. wiegmanni* by hand or noose from sites having approximately the same proportion of *A. longifolia* and native plants. Lizards were held in captivity for 7 d to allow acclimation to laboratory conditions prior to experimental trials. The lizards were maintained under controlled air temperature (30°C) and photoperiod (12:12 h), and were fed mealworms (*Tenebrio molitor*) and crickets (*Achaeta domestica*) ad libitum. Tests were conducted in a 1.20 \times 0.40 \times 0.30-m (length \times width \times height) polyvinyl chloride terrarium with opaque walls, open on the top and filled with sand to a depth of 40 mm.

Experiment 1.—Selection of plant cover: Based on the shrubby and herbaceous plants preferred by *L. wiegmanni* in the field (Table 3), we established two different choice arenas: (1) *A. longifolia* vs. *C. selloana* (native herb) and (2) *A. longifolia* vs. *D. americana* (native shrub). In opposite ends of each arena, we positioned branches with leaves of *A. longifolia* and *C. selloana* (arena 1), or stems and branches with leaves of *A. longifolia* and *D. americana* (arena 2).

Experiment 2.—Selection of leaf litter: We established two choice arenas with the same plant species employed in Experiment 1, placing leaf litter over a 40-cm section at each end of the arena, to a depth of 10 mm. The amount of leaf litter added at each end simulated the mean coverage from each plant species observed in the field (Table 1): *A. longifolia* = 78%, *D. americana* = 25%, and *C. selloana* = 40%. Arena 1 provided a choice between *A. longifolia* vs. *C. selloana*, and arena 2 provided a choice between *A. longifolia* vs. *D. americana*.

TABLE 3.—Patterns of microhabitat availability (expressed as a proportion) and use by three age classes of *Liolaemus wiegmanni* (calculated from lizard sightings along transects) at the Mar Azul coastal dunes from November 2009 to March 2010. J = Jacobs selectivity index, BI = Bonferroni's interval. Asterisks (*) indicate significant differences between available (expected) and used (observed) ratios as determined with the use of Bonferroni's confidence intervals ($\alpha = 0.05$).

Microhabitat	Hatchlings ($n = 32$)				Yearlings ($n = 26$)			Adults ($n = 32$)		
	Available	Used	J	BI	Used	J	BI	Used	J	BI
<i>Acacia longifolia</i>	0.189	0.062	-0.558	0.080–0.297	0.000	-1.000	0.000–0.000*	0.090	-0.404	0.003–0.176*
<i>Baccharis notoserghila</i>	0.087	0.468	0.804	0.349–0.651*	0.500	0.826	0.348–0.651*	0.220	0.495	0.095–0.345*
<i>Tessaria absinthioides</i>	0.028	0.031	0.052	0.018–0.211	0.115	0.637	0.018–0.211	0.125	0.664	0.025–0.225
<i>Discaria americana</i>	0.003	0.100	0.947	0.019–0.213*	0.116	0.955	0.019–0.213*	0.098	0.946	0.008–0.188*
<i>Senecio crassiflorus</i>	0.001	0.000	-1.000	0.000–0.000*	0.000	-1.000	0.000–0.000*	0.031	0.939	-0.021–0.083
<i>Achyrocline satureoides</i>	0.006	0.093	0.888	0.005–0.180	0.000	-1.000	0.000–0.000*	0.000	-1.000	0.000–0.000*
<i>Margyricarpus pinnatus</i>	0.009	0.062	0.758	-0.003–0.157	0.077	0.803	-0.003–0.157	0.000	-1.000	0.000–0.000*
<i>Cortaderia selloana</i>	0.061	0.031	-0.340	-0.021–0.083	0.000	-1.000	0.000–0.000*	0.156	0.480	0.046–0.265
<i>Androtrichum trigynum</i>	0.098	0.093	-0.029	0.045–0.263	0.154	0.252	0.045–0.263	0.187	0.358	0.069–0.304
<i>Acacia</i> leaf litter	0.143	0.000	-1.000	0.000–0.000*	0.000	-1.000	0.000–0.000*	0.031	-0.678	-0.021–0.083*
Native leaf litter	0.070	0.030	-0.417	-0.019–0.096	0.038	-0.311	-0.019–0.095	0.062	-0.065	-0.011–0.135
Open sand	0.305	0.030	-0.868	0.000–0.000*	0.000	-1.000	0.000–0.000*	0.000	-1.000	0.000–0.000*

From the 72 collected lizards, we used 18 males and 18 females in each experimental trial. Each subject was painted at the dorsum with a different color for identification. After the 7-d acclimation period, each subject was randomly assigned to an experimental arena and released alone in the center of the arena. Lizards were allowed to roam freely within the arena for 2 d of acclimation to the experimental conditions (and to reduce the frequency of escaped behaviors; Valentine et al., 2007). Plant or leaf litter selection by each subject was then recorded at 1000 h on the third and fourth day of each trial.

Statistical Analyses

Normality and homoscedasticity were evaluated by Kolmogorov–Smirnov and Shapiro–Wilks tests, respectively (Zar, 1984). In order to fit both assumptions, data were \log_{10} transformed. Nonparametric tests were used when data did not meet assumptions (Kruskal–Wallis and Dunn's tests; Zar, 1984). The frequency of microhabitat use was analyzed by a chi-square test ($\alpha = 0.05$), assuming equal frequency among microhabitat types. When chi-square test results were significantly dif-

ferent, Bonferroni intervals were constructed to determine which of the 12 microhabitat types contributed to the difference (Neu et al., 1974; Byers et al., 1984; Garshelis, 2000). If a microhabitat component had its expected proportion included in the confidence interval for its observed proportion, that component was considered as not selected; otherwise, the analysis indicated that the component was selected, either positively (preferred) or negatively (avoided). The magnitude of selection was evaluated calculating the Jacobs selectivity index (Jacobs, 1974): $J_i = (U_i - D_i)/(U_i + D_i - 2U_iD_i)$, where U_i is the used proportion of the microhabitat resource and D_i is the availability of such resource in the habitat, which can be $J = -1$ (rejection) and $J = +1$ (selection). A chi-squared goodness-of-fit test, with Yate's correction, was used to determine habitat preference for lizards in each choice experiment (Zar, 1984).

RESULTS

Field Results

Acacia longifolia specimens are taller, and show a greater percentage of canopy and leaf

litter cover than all other native species examined (Table 1). Among native plants, shrubs and herbs were taller than subshrubs. The native *Margyricarpus pinnatus* and *Cortaderia selloana* provided a greater canopy than all the other native shrubs, subshrubs, and herbs at the study site. Additionally, *C. selloana* showed greater leaf litter cover than the other native species examined (Table 1).

When measured in the shade, the mean temperature was higher under the native shrubs than under all other plant species (Table 2). Temperatures under subshrubs and herbs were similar in both shade and filtered sunlight conditions. When measured in filtered sunlight, temperatures were higher under shrubs, whereas temperatures under *A. longifolia* canopy were similar to those found under subshrubs and herbs. Finally, temperatures recorded under full sunlight varied from 39.7 to 59.2°C, and in a pattern that was not consistent with measurements taken under other conditions (Table 2).

The abundance of *L. wiegmanni* was significantly different among the plots having different levels of acacia presence (Kruskal-Wallis: $H = 27.59$; $n = 10$; $df = 3$; $P < 0.001$). Those plots having $< 25\%$ surface coverage by *A. longifolia* had higher lizard densities than plots with higher coverage, whereas the lowest abundance of lizards was observed in plots having *A. longifolia* coverage of $\geq 76\%$ (Fig. 2).

Each age group of lizards used different microhabitats at proportions that differed from their availability (hatchlings: $\chi^2 = 112.06$, $df = 11$, $P < 0.001$, $n = 32$; yearlings: $\chi^2 = 101.78$, $df = 11$, $P < 0.001$, $n = 26$; adults: $\chi^2 = 91.45$, $df = 11$, $P < 0.001$, $n = 32$), with all age classes being observed under shrubs (particularly *D. americana* and *B. notoserigila*) more frequently than expected. Specimens from all age classes avoided areas with high cover of *A. longifolia* or its leaf litter (negative values for Jacobs selectivity index, Table 3), as well as those with open sand. Adults avoided sites under *A. saturooides* subshrubs, both hatchlings and yearlings avoided the areas under *S. crassiflorus* subshrubs, and yearling specimens avoided *A. saturooides* subshrubs and *C. selloana* herbs sites (Table 3).

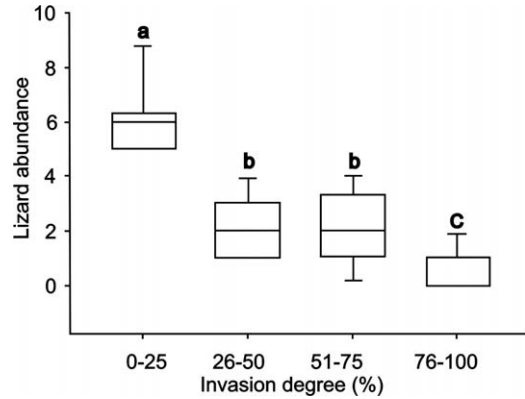


FIG. 2.—Abundance of *Liolaemus wiegmanni* (number of individuals) in zones with different degree of *Acacia longifolia* invasion ($n = 10$). Horizontal bar denotes median, vertical bar denotes range, and upper-lower boundary of boxes denotes quartile. Different letters over the bars indicate significant differences in response values (Dunn's test, $\alpha = 0.05$).

Laboratory Results

In the arenas established for Experiment 1 (selection of plant species), lizards associated more often with native plants than with *A. longifolia* on both observation days (*C. selloana* vs. *A. longifolia* $\chi^2 \geq 4.71$, $P \leq 0.029$; and *D. americana* vs. *A. longifolia* $\chi^2 \geq 6.78$, $P \leq 0.009$; Fig. 3). When offered a choice between the leaf litter of different plant species (Experiment 2), lizards did not exhibit any differences in their association with the litter from each species on either observation day (*C. selloana* vs. *A. longifolia* $\chi^2 \leq 0.11$, $P > 0.05$; *D. americana* vs. *A. longifolia* $\chi^2 = 0.11$, $P > 0.05$; Fig. 3).

DISCUSSION

The intentional planting of *Acacia longifolia* for controlling sand dunes was an important activity in the early 1960s in Argentina (Zalba and Villamil, 2002; Faggi et al., 2010; Faggi and Dadon, 2011). Variation in the coverage of *A. longifolia* appears to be influencing lizard abundance at the Mar Azul site—high densities of acacia ($\geq 76\%$) have fewer lizards, whereas greater coverage by native grassland species in dune corresponds to a greater lizard presence. This was also observed in previous studies on lizard communities in Africa (Meik et al., 2002), Australia (Valentine, 2006;

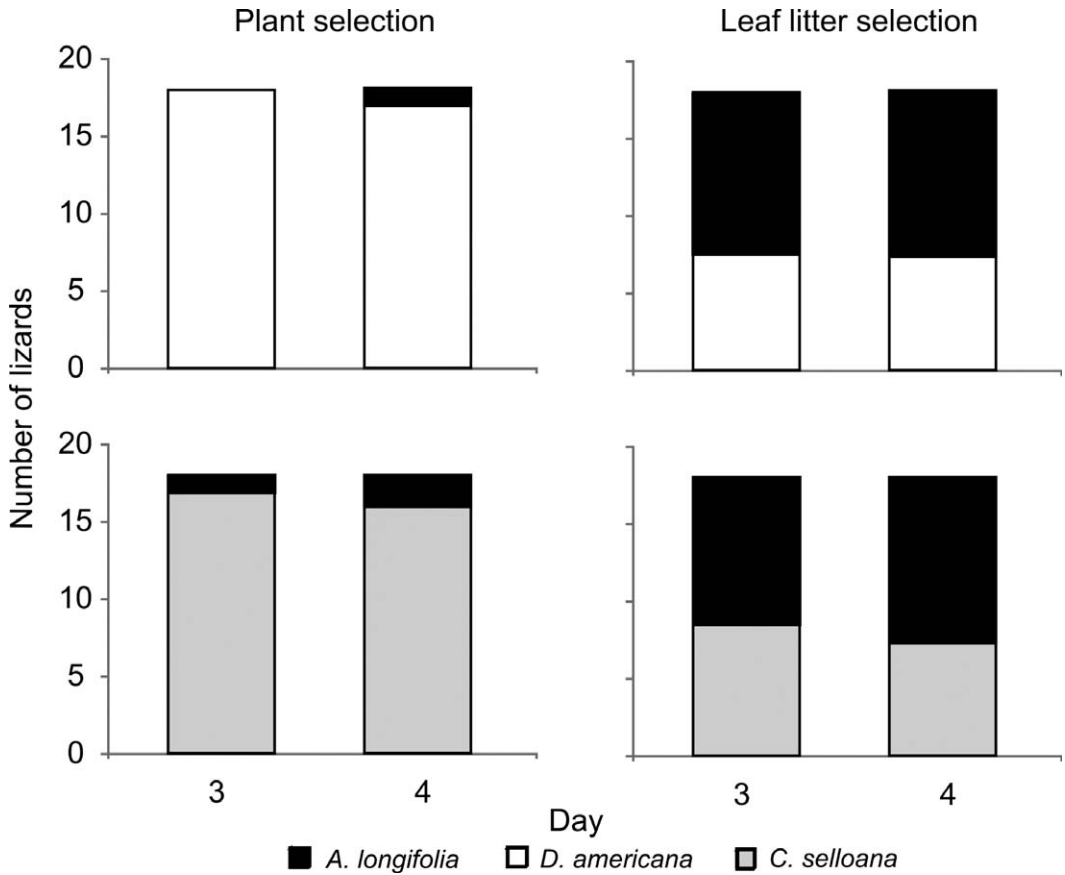


FIG. 3.—Number of *Liolaemus wiegmannii* associated with different types of plant species (Experiment 1) or leaf litter from those plants (Experiment 2). Eighteen subjects were used in each choice experiment.

Valentine et al., 2007) and the United States (Bateman et al., 2008; Bateman and Ostojka, 2012), where lizard abundance was negatively affected by exotic plants, such as *Acacia*. We do not consider other types of human activity as having had negative impacts on lizard activity at our study site, in part because the Mar Azul region has rarely been visited by tourists during the past several decades.

As observed in the field, *L. wiegmannii* of all age classes preferred native shrubs (*D. americana* and *B. notoserigila*) over other plant species, and avoided *A. longifolia*. This observation was validated in our lab experiments. Lizards used in our experiments came from sites where *A. longifolia* and native plants were equally available. Therefore, we acknowledge that any previous experience of our subjects might have influenced these

results, because reptiles are able to recall spatial information and search for known resources (Graham et al., 1996; Holtzman et al., 1999; Blouin-Demers and Weatherhead, 2001). Additionally, when individuals disperse, they tend to search for spots similar to their original habitats (Davis and Stamps, 2004). As we observed in the field, specimens from all age classes avoided leaf litter from the acacia, but not native leaf litter. In contrast, our lab experiments showed no preference for the leaf litter from any of the plant species tested. It is important to note, however, that many subjects attempted to bury themselves repeatedly under any kind of leaf litter; as such, this shelter-seeking behavior might have affected our results.

Maximizing the thermoregulatory effectiveness is crucial to achieve several physiological

and behavioral features in ectotherms (Huey, 1982; Huey and Kingsolver, 1989; Angilletta et al., 2002). In Mar Azul, the temperature range under native shrubs (33.50–39.00°C) was higher than under other types of plants, including *A. longifolia* (31.00–31.50°C). Interestingly, the range of temperatures under native shrubs encompasses the range of preferred temperatures of *L. wiegmannii* in the laboratory (36.88–39.04°C; Stellatelli et al., 2013), suggesting that temperature may be linked to microhabitat choice. Alternatively, the taller trees and the denser canopy might reduce sunlight penetration under *A. longifolia* and *C. selloana*, respectively, thereby diminishing the temperatures under them. In the case of the native *S. crassiflorus* subshrub, lower temperatures might be caused by its architecture of rooted branches leaning on the ground that decreases the incidence of solar radiation. Habitats with dense canopy produce thermal restrictions, limiting the areas for basking and thermoregulatory opportunities for ectotherms (House and Spelleberg, 1983; Sartorius et al., 1999; Román et al., 2006). Conversely, temperature ranges on substrates directly exposed to sunlight (39.75–59.25°C) not only exceeded the range of preferred body temperatures of *L. wiegmannii*, but also surpassed the critical thermal maximum registered for this genus (48.2°C; Cruz et al., 2005) and are beyond the range of temperatures for proper physiological adjustment of cellular reactions (Labra et al., 2008; Angilletta, 2009). Our results should be considered with caution, however, as our sample size to determine T_e was limited (Labra et al., 2001). Additionally, Martori et al. (1998b) reported that *L. wiegmannii* is thigmothermic, whereas Stellatelli et al. (2013) found that this species is a moderate thermoregulator. In any case, within the context of this study, *L. wiegmannii* likely faces problems when exposed to temperatures far above its thermal limits.

The establishment of acacia forests within the dune habitats along the coastal region of Argentina has reduced and homogenized avian species diversity, with habitat specialists being replaced by opportunistic and urban species of birds (Faggi et al., 2010). *Guira guira* (Cuculidae), *Milvago chimango* (Falco-

nidae), *Pitangus sulphuratus* (Tyrannidae), and *Polyborus plancus* (Falconidae), species that prey on small vertebrates, use *Acacia* trees to perch and breed (Canevari et al., 1991; Rocha and Vrcibradic, 1998; Faggi et al., 2010). This potentially affects *L. wiegmannii* survivorship at this site. Predation is also a potential factor affecting the spatial distribution of *L. wiegmannii* in Mar Azul, although further research is needed to assess this particular aspect of its ecology.

Our results indicate that habitat selection of lizards is more likely related to the physiognomic structure of the habitat and not necessarily related specifically to the nonnative plants per se, in agreement with Nielsen (2011) and Bateman and Ostoja (2012). Additionally, Valentine et al. (2007) and Hawlena et al. (2010) showed that the structural changes of the habitat associated with nonnative plants not only provide a suboptimal thermal environment for lizards, but also reduce the availability of prey and heighten the risk of predation. Based on our results, modifications of the dune habitat associated with the introduction of *A. longifolia* have manifested negative effects on the populations of *L. wiegmannii*. Should future attempts to stabilize the dune habitats in Mar Azul and other localities of the Buenos Aires involve the intentional introduction of tree species, we recommend that the deleterious consequences of this practice be considered. We also suggest the implementation of a more intensive management strategy for existing stands of *A. longifolia*, such as mechanical control in combination with litter removal, the propagation of native species, or prescribed fires to deplete the seed bank of the introduced tree (Marchante et al., 2009, 2011). If successful, these management strategies might arrest or slow the advance of *A. longifolia* and other exotic plants into the native habitats, and thus preserve the integrity of the ecosystems of coastal grasslands of Argentina.

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