

Nonnative Vegetation Induces Changes in Predation Pressure and Escape Behavior of Two Sand Lizards (Liolaemidae: *Liolaemus*)

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ABSTRACT: The introduction of nonnative plant species might generate habitat modifications that, in turn, increase the predation risk for animals, either by making prey species more conspicuous, limiting the availability of refuges, or by offering vantage points to potential predators. We compared predation pressure and escape behavior of two sympatric species (*Liolaemus wiegmanni* and *Liolaemus multimaculatus*) of Sand Lizards inhabiting forested and nonforested grasslands of the pampasic coastal sand dunes of Argentina. Predation pressure was evaluated by measuring the predation rate on plasticine replicas of lizards and the abundance of avian predators. We also recorded flight initiation distance (FID) of lizards in the different habitat types and the microhabitat used as refuge. Both lizard species prefer refuges in native plants but, when they are scarce, the nonnative *Acacia longifolia* is selected as alternative refuge. In forested habitats, sand-burying behavior is a complementary strategy used by *L. multimaculatus* to avoid predation. The FID of *L. wiegmanni* was greater in forested habitats than in nonforested ones. In contrast, *L. multimaculatus* exhibited a short FID in forested habitats, mostly because sand-burying behavior appears to reduce the risks typically associated with exposed areas. Plasticity in antipredatory behavior suggests that these lizards could recognize predators and develop a suitable antipredatory behavior. We conclude that increased predation pressure and structural alterations of the habitat in the presence of nonnative *A. longifolia* affect the decisions that determine how, when, and where these lizards flee.

Key words: *Acacia*; Detection; Flight initiation distance; Habitat alteration; Refuge

THE PERCEPTION of risk by prey species can vary according to the type (Amo et al. 2005) or behavior (or both) of the predator (Cooper 2003, 2009; Cooper et al. 2009); it might also vary in relation to environmental features such as habitat structure (Amo et al. 2006, 2007). Flexibility in the decision-making process is an adaptive characteristic of the escape behavior of animals (Delibes and Blázquez 1998); as such, when perceived levels of predation risk change, prey can modify their antipredatory behavior accordingly (Lima and Dill 1990; Sih et al. 1992). Among conspecific lizard populations, antipredatory behavior should vary with predation pressure, and escape tactics might diverge among sympatric species that share predators (Schall and Pianka 1980).

The optimal escape theory formulated by Ydenberg and Dill (1986) predicts that flight initiation distance increases as perception of predation risk rises, and it decreases when the cost of fleeing becomes higher. The escape responses might vary as a function of the level of perceived risk (Diego-Rasilla 2003), partially depending on the structure of the habitat (Martín and López 1995; Schulte et al. 2004). Changes in the habitat structure induced by human activities might alter the dynamics of the interactions between lizards and predators (Anderson and Burgin 2008). Lizards might begin to flee sooner, and at faster rates, in habitats where refuge quality was diminished compared to those retaining the original structure (Amo et al. 2006, 2007; Cooper et al. 2009).

The introduction of exotic plants, especially those which spread rapidly, generates changes on the structure of the original habitat (Ferdinands et al. 2005; Faggi and Dadon 2011). These habitat changes can alter the risk perception of lizards by reducing the availability of safe refuges (Valentine et al. 2007) and heightening the risk of predation (Hawlena et al. 2010). The intentional planting of exotic *Acacia*

longifolia trees for controlling movements of the pampasic coastal dunes of Argentina was an important activity in the early 1960s (Zalba and Villamil 2002; Faggi and Dadon 2011). Currently, *A. longifolia* forestations form large, dense, and continuous patches that replace native plants of psammophytic grasslands, producing zones with a relatively closed canopy (Alberio and Comparatore 2014).

Two closely related species of Sand Lizards, *Liolaemus wiegmanni* and *Liolaemus multimaculatus*, occur in sympatry along the Oriental Sand Dune Barrier near Buenos Aires, Argentina (Ceí 1993). These species are diurnal and have specialized morphological features for living in loose sand (Etheridge 2000). Typically, *L. wiegmanni* (42–64 mm snout–vent length [SVL]) occurs on sandy substrates with a relatively dense vegetation cover along the Atlantic coast of Buenos Aires (Vega 2001). Sand Dune Lizards, *L. multimaculatus* (48–70 mm SVL), are sand-dwelling specialists that occur in low vegetation cover and clump grasses (Vega 2001). This species is endemic to the Atlantic coast of the provinces of Buenos Aires and Río Negro and is of conservation concern (Abdala et al. 2012).

Both *L. wiegmanni* and *L. multimaculatus* tend to run to vegetation cover and adopt sand-burying behavior in the presence of a threat (Halloy et al. 1998; Block et al. 2012). The aim of our study was to assess the flexibility of the lizard antipredatory responses (i.e., refuge use and escaping behavior) in relation to different levels of predation pressure associated with structural changes in the habitat. We measured predation pressure in six populations of *L. wiegmanni* and *L. multimaculatus* that occupied modified (forested) and natural (nonforested) habitats. Additionally, we tested the prediction that predator avoidance behavior should vary with predation pressure. We specifically studied (1) predation pressure (number of predatory species and their abundance) experienced by lizards in both habitat types; (2) microhabitats used as refuges in each habitat type

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by each lizard species, and (3) a lizard's reaction facing an approaching predator.

MATERIALS AND METHODS

Study Site

This study was conducted at six localities, each ~300 ha in size, along the eastern Atlantic coast of Buenos Aires province, Argentina. Field work was carried out at three sites with native grasslands that have been partially replaced by intentional planting of *A. longifolia*: Mar Azul (37°20'45.8"S, 057°03'17.9"W; all datum = WGS84), 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 nonforested grassland sites: Reserva Natural Faro Querandí (37°23'51.95"S, 57°04'24.04"W), Pinar del Sol (36°55'55.7"S, 56°45'04.3"W), and Punta Médanos (36°53'30.9"S, 56°41'20.1"W). The climate at all sites 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 830 mm (Servicio Meteorológico Nacional XXXX).

Predation Pressure

To evaluate the indirect effect of predation, we recorded avian attacks (beak marks) on replicas of lizards covered with precolored, nontoxic clay (Brodie 1993; Brodie and Janzen 1995; Castilla and Labra 1998). There is evidence that many predators (such as birds) are able to visually recognize the reptiles as prey, based on their shape and color pattern, even if the reptiles remain immobile (Stuart-Fox et al. 2003; Buasso et al. 2006; Shepard 2007). A silicone mold was used to produce replicas of similar body size and shape to adult *L. wiegmanni* and *L. multimaculatus*; the replicas were painted with nontoxic acrylic paint to mimic the main color pattern of the lizards. We made a total of 100 replicas of each species of lizard. For each species, we randomly selected 10 plots of nonforested grassland and 10 plots of forested grassland, each with at least 50% of the surface covered by *A. longifolia*. Each plot encompassed an area of approximately 400 m², and distance between plots ranged from 2–6 km. We delineated a 25-m transect in each plot (positioned haphazardly) and placed one replica along it every 5 m for a total of five replicas per transect (sensu Castilla and Labra 1998; Diego-Rasilla 2003; Stuart-Fox et al. 2003). We positioned the replicas at different locations in a manner simulating basking lizards. The replicas were subsequently surveyed during two consecutive days. We only recorded whether a replica was intact or exhibited imprints independently of the number of marks because one bird might have left several marks on a single replica. A replica was considered attacked when it showed clear signs of beak marks (V- or U-shaped). We did not consider any marks of rodents (large gouges with serrations) or insects (<3 mm, bilateral, hook-like marks).

During the 2 d that the lizard replicas were deployed, we surveyed each plot for diurnal avian predators (the species and their relative abundance). Avian surveys were conducted in the morning (0900 to 1200 h) when lizards were active and, therefore, potentially available for predation. Birds were surveyed in the same 40 plots where the replicas were placed. One 100-m transect was delineated in each plot; walking along it, we counted those birds that were within

30 m of the transect (sensu Bibby et al. 1997). Only birds considered to be lizard predators were included in our counts (Canevari et al. 1991; Rocha and Vrcibradic 1998; Narosky and Yzurieta 2010).

Antipredatory Behavior

From January–April 2011 we visited each site twice per month. We walked haphazardly through each study site between 0900 and 1730 h (the daily activity period of these lizard species; Vega 2001). We retraced our path once, or until an adult (SVL: *L. wiegmanni* > 42 mm and *L. multimaculatus* > 48 mm; Martori and Aun 1997; Vega 1997) lizard was sighted, whereupon we attempted to approach it directly, thus simulating a predator attack (sensu Martín and López 1999). To avoid confounding effects that might affect subject behavior, the same person performed all approaches, walked at the same speed (40 m/min), and wore the same clothing while another person recorded subject behavior (Burger and Gochfeld 1993). Only lizards with complete tails were included in the analysis because tailless individuals might exhibit different antipredatory behavior (Martín and Salvador 1993; Capizzi et al. 2007). When a lizard was found, we recorded (1) species; (2) refuge, the microhabitat where the individual ended its flight, as either (a) under vegetation or (b) buried into the sand, and (3) flight initial distance (FID), the distance between the original location of the subject and the observer site at the moment of fleeing (Bulova 1994; Cooper 1997, 2011). Because FID is influenced by temperature (Hertz et al. 1982; Cooper 2000), we measured air temperature (T_a) with a digital thermometer ($\pm 0.1^\circ\text{C}$, a shaded bulb held 2 cm above the original subject location) immediately after each escape sequence.

Microhabitats were classified by substrate type (sand without or with leaf litter) and plant physiognomy (trees, shrubs, subshrubs, clump herbs, erect stems 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 within each site. For this purpose, we used 1-m² quadrats when sampling the herbaceous layer and 25-m² quadrats to characterize the shrubby and arboreal layers. We determined the number of sampling quadrats at each scale using species accumulation curves (Gysel and Lyon 1987; Bullock 1996). When sampling, the location of the initial quadrat was randomly established and subsequent quadrats were placed at 100-m intervals.

Statistical Analyses

Normality and homoscedasticity of our data were evaluated by Kolmogorov–Smirnov and Shapiro–Wilks tests, respectively (Zar 1984). Values for percent of microhabitat cover were arcsine square root transformed to conform to the assumptions of normality and homogeneity of variance. Then, the proportions of available microhabitats in forested and nonforested sites were compared using Student *t*-tests ($\alpha = 0.05$ in all comparisons). We used a *G*-test with Yates' correction for continuity to evaluate frequency of predation on plasticine replicas and a Mann–Whitney *U*-test to compare bird abundance between forested and nonforested habitats. The pattern of microhabitat use by lizards was analyzed by a chi-square (χ^2) test to compare observed

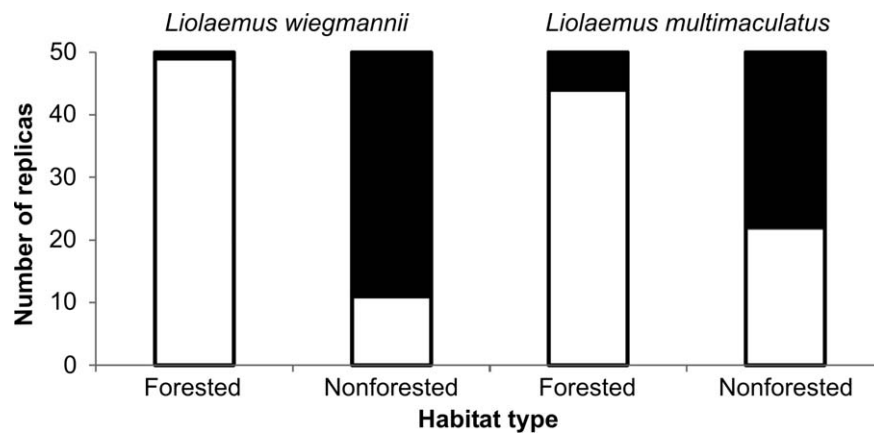


FIG. 1.—Number of lizard replicas that had been attacked (open portion of bar) and that did not show any mark (filled portion of bar) for each of two species of *Liolaemus* in two types of coastal dune habitat.

frequencies (use) to expected frequencies (availability) of each type of microhabitat. When χ^2 results were significant, Bonferroni intervals were constructed to determine which of the seven microhabitat types contributed to the difference (Neu et al. 1974; Byers et al. 1984; Garshelis 2000). We used two-way analyses of variance (ANOVA) with lizard species and habitat type as the factors and Tukey's post hoc comparisons to detect differences in FID. To examine the relationship between FID and air temperature, we calculated Pearson's product moment correlation coefficients (Zar 1984). Response variables are reported as means \pm 1 SD.

RESULTS

Predation Pressure

Frequency of predation on *L. wiegmanni* replicas was higher in forested sites than in nonforested ones (G -test; $G = 70.50$, $df = 1$, $P < 0.001$, $n = 50$). Most of the *L. wiegmanni* replicas (98%) were attacked in forested sites while only 22% were attacked in nonforested sites (Fig. 1). Frequency of predation on *L. multimaculatus* was also higher in forested sites than in nonforested ones ($G = 22.51$, $df = 1$, $P < 0.001$, $n = 50$); 88% of the *L. multimaculatus* replicas were attacked in forested sites whereas 44% showed evidence of attack in nonforested sites (Fig. 1).

During the 2 d that the plasticine replicas were deployed in each plot, we recorded 66 individuals representing seven species of birds that are potential predators of lizards in both habitats. The number of predatory birds observed in forested sites (6 species and 50 individuals) was greater than in nonforested ones (2 species and 16 individuals; $U = 72.00$, $P = 0.002$, $n = 40$). Chimango Caracaras (*Milvago chimango*) were the most-common bird species in both habitat types,

accounting for 58% and 94% of all birds recorded in forested and nonforested sites, respectively.

Antipredatory Behavior

The habitats forested with *A. longifolia* contained more leaf litter, but a lesser coverage of native plants and bare sand, than did the nonforested ones ($t > 14.64$, $P < 0.001$; Table 1, Fig. 2). The microhabitats that each lizard species used as refuges differed between habitat types (Table 2). In both forested and nonforested habitats, *L. wiegmanni* sought refuge in native shrubs, subshrubs, and clump herbs more frequently than expected (>60% of the total observations; Fig. 2, Appendix). Refuges at the base of *A. longifolia* were also preferred by *L. wiegmanni* in forested habitats. In contrast, *L. wiegmanni* avoided bare sand and leaf litter as refuges in both habitat types (Fig. 2; Appendix). In forested habitats *L. multimaculatus* preferentially sought refuge under native subshrubs, *A. longifolia*, or buried in bare sand; they avoided clump herbs, erect-stem herbs, and leaf litter. In nonforested habitats *L. multimaculatus* preferred refuges under clump herbs but avoided bare sand, leaf litter, and sites under shrubs, subshrubs, or erect-stem herbs (Fig. 2; Appendix).

The FID was not correlated with air temperature in either *L. wiegmanni* (forested $r = 0.07$, $n = 227$, $P = 0.30$; nonforested $r = 0.05$, $n = 408$, $P = 0.34$) or *L. multimaculatus* (forested $r = 0.16$, $n = 103$, $P = 0.10$; nonforested $r = 0.04$, $n = 105$, $P = 0.70$). Thus our ANOVA of FID did not include T_a as a covariate. The FID differed between lizard species ($F_{1,839} = 345.74$, $P < 0.001$) and habitat type ($F_{1,839} = 14.26$, $P < 0.001$), and an interaction between these factors ($F_{1,839} = 132.28$, $P = 0.001$). Values for FID were shorter in *L. wiegmanni* (204.44 ± 100.33 cm,

TABLE 1.—Mean values (\pm 1 SD) of the proportion of each microhabitat in forested and nonforested habitats ($n = 100$) compared using Student's t -test ($\alpha = 0.05$).

Microhabitat	Forested	Nonforested	t	df	P
<i>Acacia longifolia</i>	0.21 \pm 0.01	0.00 \pm 0.00	—	—	—
Shrubs	0.11 \pm 0.02	0.27 \pm 0.02	-49.41	198	<0.001
Subshrubs	0.02 \pm 0.01	0.08 \pm 0.02	-26.64	198	<0.001
Clump herbs	0.04 \pm 0.01	0.06 \pm 0.01	-14.64	198	<0.001
Erect-stem herbs	0.08 \pm 0.01	0.12 \pm 0.002	-20.98	198	<0.001
Leaf litter	0.18 \pm 0.01	0.08 \pm 0.04	41.72	198	<0.001
Bare sand	0.35 \pm 0.08	0.40 \pm 0.09	-4.03	198	<0.001

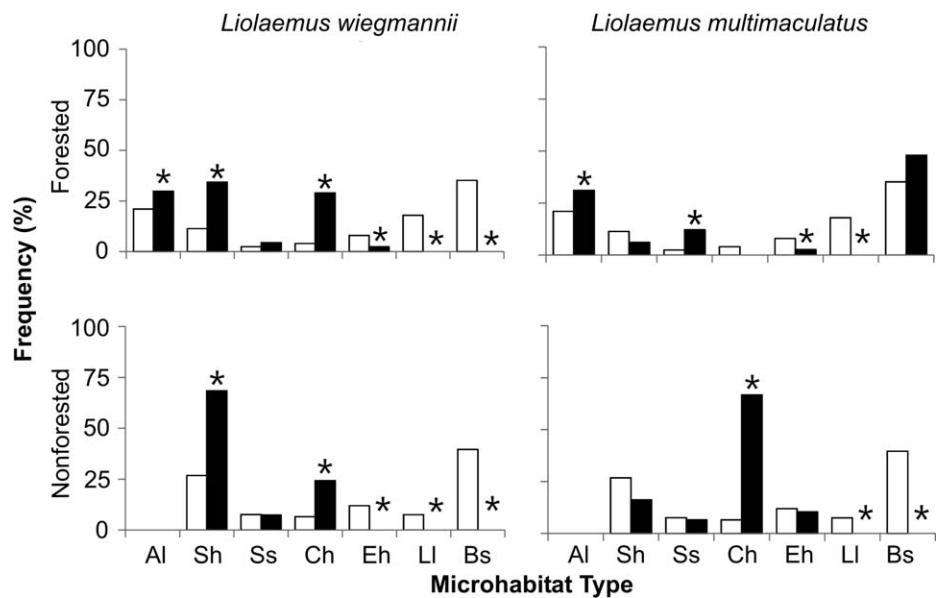


FIG. 2.—Percent of microhabitat available (open bars, $n = 100$) and that were used as a refuge (filled bars) by *Liolaemus wiegmanni* (forested, $n = 227$; nonforested, $n = 408$) and *L. multimaculatus* (forested, $n = 103$; nonforested, $n = 105$). Abbreviations: Al = *Acacia longifolia*; Sh = shrubs; Ss = subshrubs; Ch = Clump herbs; Eh = erect-stem herbs; LI = leaf litter; Bs = bare sand. Asterisks (*) indicate differences between proportions available and used, as determined using Bonferroni's confidence intervals.

$n = 635$) than in *L. multimaculatus* (365.91 ± 131.69 cm, $n = 208$; $P < 0.001$). In *L. wiegmanni*, the FID was greater in forested (244.98 ± 105.40 cm, $n = 227$) than in nonforested sites (181.88 ± 89.92 cm; $n = 408$; $P < 0.001$; Fig. 3). Conversely, the FID of *L. multimaculatus* was shorter in forested (302.92 ± 117.24 cm, $n = 103$) than in nonforested sites (427.71 ± 115.08 cm, $n = 105$; $P < 0.001$; Fig. 3).

DISCUSSION

Our data from avian surveys and attack rates on lizard models indicate that the introduction of *Acacia longifolia* in the coastal sand dunes of Argentina likely contributes to an increased frequency of bird predation upon the Sand Lizards *Liolaemus wiegmanni* and *L. multimaculatus*. Intentional forestation, such as that using *A. longifolia* to stabilize dune habitat, offers perch sites that facilitate prey detection by visually oriented predators (Denno et al. 2005). At our sites, such avian predators include *Milvago chimango* (Falconidae), the most abundant, along with other falcons (*Caracara plancus*), hawks and kites (*Buteo magnirostris* and *Elanus leucurus*; Accipitridae, respectively), gulls (*Chroicocephalus maculipennis*, Laridae) and a tyrant flycatcher (*Pitangus sulphuratus*, Tyrannidae). Increased predation pressure on the sand lizards in forested dune habitat is likely driven by an increased availability of perch sites coupled with a decreased availability of refuges in native plants available to the lizards.

Predator efficiency is often negatively correlated with habitat complexity because dense vegetation may hinder the detection and pursuit of prey (Warfe and Barmuta 2004).

The reduced coverage of native herbs and shrubs, as occurs in forested dunes, might increase the ability of predatory birds to detect plasticine models (Shepard 2007). The low profile provided by much of the native vegetation not only reduces the conspicuousness of lizards but also provides an important source of refuge microhabitat. Our results are consistent with Castilla and Labra (1998), who attributed increasing intensity of predation by gulls on *Podarcis hispanica* to the greater conspicuousness of lizards when vegetative cover was diminished. Our results also explain the reduction in the abundance of *L. wiegmanni* and *L. multimaculatus* in forested sites and a related shift in their thermal ecology (Stellatelli et al. 2013a, Stellatelli 2014).

Liolaemus wiegmanni and *L. multimaculatus* escape from predators by fleeing to microhabitats having relatively dense canopy (either among native plants or at the base of *A. longifolia*). Stellatelli et al. (2013b) reported that these Sand Lizards avoid perching on *A. longifolia* because these trees did not offer sites suitable for thermoregulation. The use of acacias as refuges, however, supports the idea that *L. wiegmanni* and *L. multimaculatus* (like other small lizards) accept the associated costs of fleeing to a nonnative tree (i.e., loss of body temperature), a choice apparently less relevant in high-risk situations (Martín 2001). We observed that refuges under low-profile native plants not only provide physical protection from predators but also allow lizards to blend in with filtered sunlight projecting through the vegetation (Block et al. 2012). In contrast, acacia trees are higher-profile plants whose branches rarely have direct

TABLE 2.—Chi-square (χ^2) tests ($\alpha = 0.05$) for microhabitat usage by two species of *Liolaemus* in coastal dunes of the Buenos Aires province of Argentina.

	Forestedused versus available				Nonforestedused versus available			
	χ^2	df	P	n	χ^2	df	P	n
<i>L. wiegmanni</i>	262.67	6	<0.001	227	268.56	5	<0.001	408
<i>L. multimaculatus</i>	74.91	6	<0.001	103	605.10	5	<0.001	105

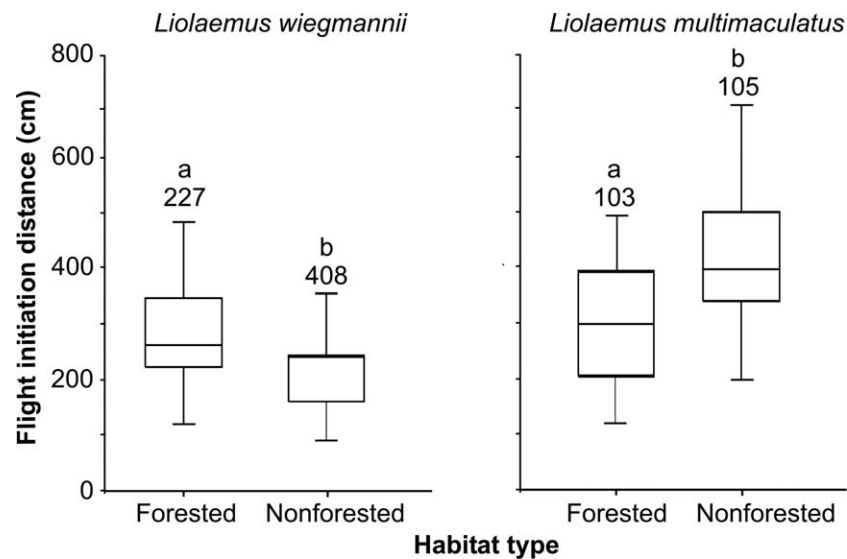


FIG. 3.—Flight initiation distance (cm) of *Liolaemus wiegmanni* and *L. multimaculatus* in forested and nonforested habitats. Horizontal bar denotes median, vertical bar denotes range, and upper–lower boundary of boxes denotes quartile. Different letters over the bars indicate differences in response values (Tukey's test; $P < 0.05$), and the numbers indicate sample sizes.

contact with the substrate (Stellatelli et al. 2013b). The use of refuges under *A. longifolia* by the *Liolaemus* species examined in our study is best explained by lizards choosing abundant, but relatively unsafe, refuges instead of reaching the safest refuge (Martín and López 2000).

In forested habitats, where predation risk is presumably high, lizards tend to compensate for this disadvantage in different ways. As predicted by the theoretical model of Ydenberg and Dill (1986), the habitat generalist *L. wiegmanni* behaves more cautiously when threatened by a potential predator in forested sites by increasing its FID by 26% with respect to nonforested sites. This increase in the FID may be explained by the fact that *L. wiegmanni* reduces its speed by 7% in substrates with an excess of leaf litter (e.g., forested habitat) compared to locomotory performance on bare sand substrates (C. Iribarren, personal communication). Because predatory success is affected by the distance that a prey permits a predator to approach (Murray et al. 1995), individuals of *L. wiegmanni* from forested sites could compensate for impairments in their sprint speed by starting to flee earlier. Therefore, there is a trade-off between FID and speed of escape.

Compared to nonforested habitats, the FID of *L. multimaculatus* decreased 29% in forested habitats, allowing a closer predator to approach before initiating an escape. We also found that, when threatened by a predator, individual *L. multimaculatus* in forested dunes buried themselves in bare sand more frequently (47.6%) than in nonforested habitats (0.1%). This reflects a difference in the escape behavior of the two lizard species, as *L. multimaculatus* is more likely to dive into the sand than it is to flee (compared to *L. wiegmanni*). Depending on vegetation height (e.g., tall acacias vs. short shrubs), *L. multimaculatus* might choose to run or dive and, if choosing to flee, FID will be greater than that for *L. wiegmanni*. Our conclusion is consistent with that of Attum et al. (2007), who suggested that traditional models of escape behavior might not apply to specialist sand lizards (such as *Liolaemus*) whose sand-burying behavior reduces the risks typically associated with occupying exposed areas.

We suggest that changes in environmental structure and predation pressure promote intra- and interspecific differences in the antipredatory behavior of *L. wiegmanni* and *L. multimaculatus*, based on the different degree of habitat specialization of both species of lizards. The replacement of native vegetation by *A. longifolia* in the pampasic coastal dunes of Argentina bears consequences for the susceptibility of these species in different ways. Given that the availability of natural refuges contributes to prey species assessment of their predation risk, deteriorated areas (in our case, forested habitats) might convey a higher perception of predation risk (Martín and López 2000; Amo et al. 2007). The patterns identified in our study allow us to conclude that predation pressure and structural alteration to the habitat generated by *A. longifolia* affect decisions that determine how, when, and where *L. wiegmanni* and *L. multimaculatus* seek refuge from predators. According to Blázquez et al. (1997), plasticity in antipredatory behavior among different populations of lizards might be a short-term result of natural selection or a direct consequence of individual experience. That is, a lizard that survives an attack could learn to recognize a threat and develop a suitable antipredatory response that factors in its immediate surroundings.

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LITERATURE CITED

- Abdala, C.S., J.L. Acosta, J.C. Acosta..., and S.M. Zalba. 2012. Categorización del estado de conservación de las lagartijas y anfisbenas de la República Argentina. Cuadernos de Herpetología 26:215–247.
- Alberio, C., and V. Comparatore. 2014. Patterns of woody plant invasion in Argentinean coastal grassland. Acta Oecologica 54:65–71.
- Amo, L., P. López, and J. Martín. 2005. Flexibility in antipredatory behavior allows wall lizards to cope with multiple types of predators. Annales Zoologici Fennici 42:109–121.

- Amo, L., P. López, and P. Martín. 2006. Refuge use: A conflict between avoiding predation and losing mass in lizards. *Physiology and Behavior* 90:334–343.
- Amo, L., P. López, and J. Martín. 2007. Habitat deterioration affects body condition of lizards: A behavioral approach with *Iberolacerta cyreni* lizards inhabiting ski resorts. *Biological Conservation* 135:77–85.
- Anderson, L., and S. Burgin. 2008. Patterns of bird predation on reptiles in small woodland remnant edges in peri-urban northwestern Sydney, Australia. *Landscape Ecology* 23:1039–1047.
- Attum, O., P. Eason, and G. Cobbs. 2007. Morphology, niche segregation, and escape tactics in a sand dune lizard community. *Journal of Arid Environments* 68:564–573.
- Bibby, C.J., N.D. Burgess, and D. Hill. 1997. *Bird Census Techniques*. Academic Press, UK.
- Blázquez, M.C., R. Rodríguez-Estrella, and M. Delibes. 1997. Escape behaviour and predation risk of mainland and island spiny-tailed iguanas (*Ctenosaura hemilopha*). *Ethology* 103:990–998.
- Block, C., L. Vega, and O. Stellatelli. 2012. Vegetation refuges of a sand lizard assemblage. *Journal of Herpetology* 46:608–613.
- Brodie, E.D., III. 1993. Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution* 47:227–235.
- Brodie, E.D., III, and F.J. Janzen. 1995. Experimental studies of coral snake mimicry: Generalized avoidance of ringed snake patterns by free-ranging avian predators. *Functional Ecology* 9:186–190.
- Buasso, C.M., G.C. Leynaud, and F.B. Cruz. 2006. Predation on snakes of Argentina: Effects of coloration and ring pattern on coral and false coral snakes. *Studies on Neotropical Fauna and Environment* 41:183–188.
- Bullock, J.M. 1996. Plant competition and community dynamics. Pp. 69–100 in *The Ecology and Management of Grazing Systems*, A. Illius and J. Hodgson (Eds.). CAB International, UK.
- Bulova, S.J. 1994. Ecological correlates of population and individual variation in antipredatory behavior of two species of desert lizards. *Copeia* 1994:980–992.
- Burger, J., and M. Gochfeld. 1993. The importance of the human face in risk perception by black iguanas, *Ctenosaura similis*. *Journal of Herpetology* 27:426–430.
- Burgos, J.J., and A.L. Vidal. 1995. Los climas de la República Argentina según la nueva clasificación de Thornthwaite. *Meteoros* 1:3–32.
- Byers, C.R., R.K. Steinhorst, and P.R. Krausman. 1984. Clarification of the technique for analysis of utilization-availability data. *Journal of Wildlife Management* 48:1050–1053.
- Cabrera, A., and E. Zardini. 1978. *Manual de la Flora de los Alrededores de Buenos Aires*, 2nd ed. ACME, Argentina.
- Canevari, M., P. Canevari, G.R. Carrizo, J. Rodríguez Mata, and R.J. Stranek. 1991. *Nueva Guía de las Aves Argentinas*, Tomo II. Fundación Acindar, Argentina.
- Capizzi, D., L. Luiselli, and L. Vignoli. 2007. Flight initiation distance in relation to substratum type, sex, reproductive status and tail condition in two lacertids with contrasting habits. *Amphibia-Reptilia* 28:403–407.
- Castilla, A.M., and A. Labra. 1998. Predation and spatial distribution of the lizard *Podarcis hispanica atrata*: An experimental approach. *Acta Oecologica* 19:107–114.
- Cei, J.M. 1993. Reptiles del noroeste, noreste y este de la Argentina. Museo Regionali di Scienze di Torino, Italy.
- Cooper, W.E., Jr. 1997. Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Canadian Journal of Zoology* 75:943–947.
- Cooper, W.E., Jr. 2000. Effect of temperature on escape behaviour by an ectothermic vertebrate, the keeled earless lizard (*Holbrookia propinqua*). *Behaviour* 137:1299–1315.
- Cooper, W.E., Jr. 2003. Risk factors affecting escape behavior by the desert iguana, *Dipsosaurus dorsalis*: Speed and directness of predator approach, degree of cover, direction of turning by a predator, and temperature. *Canadian Journal of Zoology* 81:979–984.
- Cooper, W.E., Jr. 2009. Optimal escape theory predicts escape behaviors beyond flight initiation distance: Risk assessment and escape by striped plateau lizard (*Sceloporus virgatus*). *Current Zoology* 55:123–131.
- Cooper, W.E., Jr. 2011. Influence of some potential predation risk factors and interaction between predation risk and cost of fleeing on escape by the lizard *Sceloporus virgatus*. *Ethology* 117:620–629.
- Cooper, W.E., Jr., D. Hawlena, and V. Pérez-Mellado. 2009. Islet tameness: Escape behavior and refuge use in populations of the Balearic lizard (*Podarcis lilfordi*) exposed to differing predation pressure. *Canadian Journal of Zoology* 87:912–919.
- Delibes, M., and M.C. Blázquez. 1998. Tameness of insular lizards and loss of biological diversity. *Conservation Biology* 12:1142–1143.
- Denno, R.F., D.L. Finke, and G.A. Langellotto. 2005. Direct and indirect effects of vegetation structure and habitat complexity on predator–prey and predator–predator interactions. Pp. 211–239 in *Ecology of Predator–Prey Interactions*, P. Barbosa and I. Castellanos (Eds.). Oxford University Press, UK.
- Diego-Rasilla, F.J. 2003. Influence of predation pressure on the escape behaviour of *Podarcis muralis* lizards. *Behavioural Processes* 63:1–7.
- Etheridge, R. 2000. A review of lizards of the *L. wiegmannii* group (Squamata, Iguania, Tropiduridae) and a history of morphological change in the sand-dwelling species. *Herpetological Monographs* 14:293–352.
- Faggi, A., and J. Dadon. 2011. Temporal and spatial changes in plant dune diversity in urban resorts. *Journal of Coastal Conservation* 4:585–594.
- Ferdinands, K., K. Beggs, and P.J. Whitehead. 2005. Biodiversity and invasive grass species: Multiple-use or monoculture? *Wildlife Research* 32:447–457.
- Garshelis, D.L. 2000. Delusions in habitat evaluation: Measuring use, selection, and importance. Pp. 111–164 in *Research Techniques in Animal Ecology: Controversies and Consequences*, L.I. Boitani and K. Fuller (Eds.). Columbia University Press, USA.
- Gysel, L.W., and L.J. Lyon. 1987. Análisis y evaluación del hábitat. Pp. 331–334 in *Manual de Técnicas de Gestión de Vida Silvestre*, R. Rodríguez-Tarrés (Ed.). The Wildlife Society, USA.
- Halloy, M., R. Etheridge, and G.M. Burghardt. 1998. To bury in sand: Phylogenetic relationships among lizard species of the *boulengeri* group, *Liolaemus* (Reptilia: Squamata: Tropiduridae), based on behavioral characters. *Herpetological Monographs* 12:1–37.
- Hawlena, D., D. Saltz, Z. Abramsky, and A. Bouskila. 2010. Ecological trap for desert lizards caused by anthropogenic changes in habitat structure that favor predator activity. *Conservation Biology* 24:803–809.
- Hertz, P.E., R.B. Huey, and E. Nevo. 1982. Fight versus flight: Body temperature influences defensive responses of lizards. *Animal Behaviour* 30:676–679.
- Lima, S.L., and L.M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Martín, J. 2001. When hiding from predators is costly: Optimization of refuge use in lizards. *Etología* 9:9–13.
- Martín, J., and P. López. 1995. Influence of habitat structure on escape tactics of *Psammodromus algirus* lizards. *Canadian Journal of Zoology* 73:129–132.
- Martín, J., and P. López. 1999. Nuptial coloration and mate guarding affect escape decisions of male lizards *Psammodromus algirus*. *Ethology* 105:439–447.
- Martín, J., and P. López. 2000. Fleeing to unsafe refuges: Effects of conspicuousness and refuge safety on the escape decisions of the lizard *Psammodromus algirus*. *Canadian Journal of Zoology* 78:265–270.
- Martín, J., and A. Salvador. 1993. Thermoregulatory behaviour of rock-lizards in response to tail loss. *Behaviour* 124:123–136.
- Martori, R., and L. Aun. 1997. Reproductive and fat body cycle of *Liolaemus wiegmannii* in Central Argentina. *Journal of Herpetology* 31:578–581.
- Murray, D.L., S. Boutin, M. O'Donoghue, and V.O. Nams. 1995. Hunting behavior of a sympatric felid and canid in relation to vegetative cover. *Animal Behaviour* 50:1203–1210.
- Narosky, T., and D. Izurieta. 2010. *Guía para la identificación de las aves de Argentina y Uruguay*. Vazquez-Mazini Editores, Argentina.
- Neu, C.W., C.R. Byers, and J.M. Peek. 1974. A technique for analysis of utilization availability data. *Journal of Wildlife Management* 38:541–545.
- Rocha, C.F.D., and D. Vrcibradic. 1998. Reptiles as predators of vertebrates and as preys in a restinga habitat of southeastern Brazil. *Ciência & Cultura* 50:364–368.
- Schall, J.J., and E.R. Pianka. 1980. Evolution of escape behavior diversity. *American Naturalist* 115:551–566.
- Schulte, J.A., J.B. Losos, F.B. Cruz, and H. Núñez. 2004. The relationship between morphology, escape behavior and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae, Tropidurinae, Liolaemini). *Journal of Evolutionary Biology* 17:408–420.
- Servicio Meteorológico Nacional. XXXX.
- Shepard, D.B. 2007. Habitat but not body shape affects predator attack frequency on lizard models in the Brazilian Cerrado. *Herpetologica* 63:193–202.
- Sih, A., L.B. Kats, and R.D. Moore. 1992. Effects of predatory sunfish on the density drift and refuge use of stream salamander larvae. *Ecology* 73:1418–1430.
- Stellatelli, O.A. 2014. *Ecología de lagartijas arenícolas en hábitats modificados de los médanos costeros bonaerenses*. Ph.D. dissertation, Universidad Nacional de Mar del Plata, Argentina.

- Stellatelli, O.A., L.E. Vega, C. Block, and F.B. Cruz. 2013a. Effects on the thermoregulatory efficiency of two native lizards as a consequence of the habitat modification by the introduction of the exotic tree *Acacia longifolia*. *Journal of Thermal Biology* 38:135–142.
- Stellatelli, O.A., L.E. Vega, C. Block, and F.B. Cruz. 2013b. Effects of tree invasion on the habitat use of sand lizards. *Herpetologica* 69:455–465.
- Stuart-Fox, D.M., A. Moussallia, N.J. Marshall, and P.F. Owens. 2003. Conspicuous males suffer higher predation risk: Visual modeling and experimental evidence from lizards. *Animal Behaviour* 66:541–550.
- Valentine, L.E., B. Roberts, and L. Schwarzkopf. 2007. Mechanisms driving avoidance of non-native plants by lizards. *Journal of Applied Ecology* 44:228–237.
- Vega, L.E. 1997. Reproductive activity and sexual dimorphism of *Liolaemus multimaculatus* (Sauria: Tropiduridae). *Herpetological Journal* 7:49–53.
- Vega, L.E. 2001. Herpetofauna: Diversidad, ecología e historia natural. Pp. 213–226 in *Reserva de Biosfera Mar Chiquita: Características Físicas, Biológicas y Ecológicas*. O. Iribarne (Ed.). Editorial Martín, Argentina.
- Warfe, D.M., and L.A. Barmuta. 2004. Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia* 141:171–178.
- Ydenberg, R.C., and L.M. Dill. 1986. The economics of fleeing from predators. *Advances in the Study of Behavior* 16:229–249.
- Zalba, S.M., and C.B. Villamil. 2002. Woody plant invasion in relictual grasslands. *Biological Invasions* 4:55–72.
- Zar, J.H. 1984. *Biostatistical Analysis*. Prentice Hall, USA.

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APPENDIX

Proportions of microhabitats available and those used by sand lizards (*Liolaemus wiegmanni* and *L. multimaculatus*), based on sightings along transects in coastal dunes of the Buenos Aires province, Argentina. Asterisks (*) denote differences ($P < 0.05$) between available (expected) and used (observed) ratios as determined using Bonferroni confidence intervals (BI); n = sample size.

	Available	<i>L. wiegmanni</i>		<i>L. multimaculatus</i>	
		Used	BI	Used	BI
Forested	$n = 100$	$n = 245$		$n = 103$	
<i>A. longifolia</i>	0.210	0.298*	0.218–0.375	0.310*	0.212–0.447
Shrubs	0.113	0.342*	0.260–0.423	0.061	0.000–0.119
Subshrubs	0.024	0.045	0.008–0.079	0.121*	0.038–0.201
Clump herbs	0.040	0.289*	0.211–0.366	0.000*	0.000–0.000
Erect-stem herbs	0.080	0.024*	–0.002–0.050	0.026*	–0.011–0.079
Leaf litter	0.179	0.000*	0.000–0.000	0.000*	0.000–0.000
Bare sand	0.351	0.000*	0.000–0.000	0.480	0.325–0.574
Nonforested	$n = 100$	$n = 408$		$n = 105$	
Shrubs	0.268	0.683*	0.619–0.740	0.160*	0.066–0.255
Subshrubs	0.076	0.073	0.039–0.106	0.066	0.002–0.129
Clump herbs	0.065	0.242*	0.186–0.297	0.666*	0.538–0.781
Erect-stem herbs	0.119	0.000*	0.000–0.000	0.104*	0.025–0.182
Leaf litter	0.075	0.000*	0.000–0.000	0.000*	0.000–0.000
Bare sand	0.396	0.000*	0.000–0.000	0.001*	0.000–0.000

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