

Microhabitat use by the sand dune lizard *Liolaemus multimaculatus* in a pampean coastal area in Argentina

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The sand dune lizard (*Liolaemus multimaculatus*) is a vulnerable species, endemic to the Pampean coasts in Argentina, yet no studies exist on its preferences for microhabitats. This work has three primary goals: 1) to assess preferences in microhabitat use in relation to their availability; 2) to evaluate differences in male, female and juvenile microhabitat use; and 3) to describe the microhabitat structure required and preferred by lizards. The study was carried out at Mar Chiquita Provincial Nature Reserve, Buenos Aires Province, Argentina. We assessed microhabitat selection and evaluated differences in microhabitat use between individual categories, by applying null models. Magnitude of selection was evaluated using Jacobs' index of selectivity. Spatial niche width and overlap were calculated using Hurlbert's measurement and Pianka's index respectively. Results showed that the sand dune lizard did not use microhabitats according to their availability, but rather that it prefers microhabitats with low to medium vegetation cover, and tends to avoid those with high or no vegetation cover. No differences between individual categories were found. Preferred microhabitats allow sand burying and rapid movements and offer refuges from predators. This study allows us to identify suitable microhabitats for this species, thus contributing to the development of conservation plans.

Key words: age differences, habitat selection, Liolaemidae, sex differences

INTRODUCTION

Knowledge of a species' habitat use and requirements is an essential element for understanding its ecology and conservation biology (Huey, 1991; Garshelis, 2000). Habitat and microhabitat use may influence several aspects, such as individual physiology (Huey, 1991), population dynamics (Holt, 1987; Pulliam & Danielson, 1991) and processes at the community level (Morris, 1988; Rosenzweig, 1991). The need to determine the selection or avoidance of one particular microhabitat in relation to its availability has been recognized as a first step towards understanding and explaining ecological interactions between organisms and their environment (Neu et al., 1974). Moreover, this understanding also provides information about natural history and selective pressures (Stark et al., 2005) and is of great importance for carrying out actions oriented to the conservation of endangered species (Manly et al., 1993; Johnson, 2000).

Lizards constitute an appropriate model for studying microhabitat use patterns because they have high site fidelity and low displacement capacity compared to other vertebrate taxa (Pianka, 1986; Pough et al., 1998). One of the main factors determining microhabitat use in lizards is vegetation structure (Huey et al., 1983; Dias & Rocha, 2004). Vegetation also represents an essential element of the microhabitat for most sand lizards (Vega, 2001; Attum & Eason, 2006). This seems to be related to microclimatic conditions, refuges, mates and food availability associated with vegetation (Rocha, 1991, 1995; Converse & Savidge, 2003; Attum & Eason, 2006). Microhabitat use can also be related to the age and sex of individuals (Butler et al., 2007).

The sand dune lizard (*Liolaemus multimaculatus*) is a small, diurnal, sand-dwelling liolaemid lizard, endemic to the pampean coasts of Buenos Aires and Río Negro provinces in Argentina (Ceí, 1993). Due to its restricted distribution, apparently low abundance and man-made disturbance of its habitat, this lizard has been categorized as a vulnerable species (Lavilla et al., 2000). Anthropogenic factors such as habitat fragmentation and loss of native plant species in coastal dunes could be reducing the natural abundance of sand lizards, promoting local species eradication (Attum & Eason, 2006; Vega et al., 2000). Currently, there are only six natural dune areas remaining in Buenos Aires Province that support populations of sand dune lizards. However, only one of these areas, Mar Chiquita Provincial Nature Reserve, efficiently protects a population of this lizard species as a result of conservation actions (Kacoliris et al., 2006).

Previous studies have postulated that habitat use in this species may be related to the structural vegetation gradient (Vega, 2001). However, no detailed studies exist of microhabitat preferences in this lizard, and neither sex nor age-related differences have previously been assessed. This information is necessary to understand key features about the spatial ecology of this lizard and would be useful for generating conservation plans based on knowledge of habitat use. The present study has three main goals: 1) to assess preferences in microhabitat use in relation to their availability; 2) to evaluate differences in microhabitat use between males, females and juveniles; and 3) to describe the microhabitat structure required and preferred by lizards. A short discussion of the amount, status and tendencies of available microhabitats for *L. multimaculatus* is also included.

METHODS

Study site

The study site comprised a 140 ha coastal dune area located within Mar Chiquita Provincial Nature Reserve (37°37'S, 57°16'W) in Buenos Aires Province, Argentina. Three different natural habitat types occur in the area:

1) Ecotone grasslands: psammophytic grassland on stable dune substrate, located between coastal dunes and pampas grasslands, with high and homogeneously spread vegetation cover.

2) Sand grasslands: psammophytic grasslands, with low to medium vegetation cover, dominated by plant species adapted to high salinity conditions, mobile substrate and low water availability.

3) Interdunes: humid lowlands with a mix of grasslands and hygrophytic plants. Sand grasslands and interdunes are distributed as patches in a matrix of active dunes with scarce or no vegetation cover (Cabrera, 1976). Exotic *Pinus* sp. and *Acacia* sp. forests also occur within the study site.

Surveys

Surveys to access *L. multimaculatus* microhabitat use were performed during January and February of 2006 and 2007, from 1100 to 1500 (peak of activity for the species), considering that lizards remain inactive during autumn and winter, and juveniles are only seen active in summer (Vega, 2001). In order to evaluate microhabitat availability, 156 control plots (of 1 m²) placed on parallel line transects ($n=8$; 1 km length) were sampled. Transects were distributed systematically in the study area. Parallel transects were separated by 160 m and plots along each transect were placed every 50 m (seven transects with 20 plots and one transect with 16 plots).

Vegetation attributes of each control plot were characterized considering: 1) type and number of plant species and 2) vegetation cover (total and specific). Vegetation cover (VC) was measured using a modified Domin–Krajina scale (Mueller-Dombois & Ellenberg, 1974). The scale used allows more discrimination among low and medium VC values, which are the most commonly used by these lizards (Kacoliris et al., 2006). The following vegetation cover categories (= microhabitats) were recognized: 1) 0%; 2) 0.5%; 3) 1–5%; 4) 6–10%; 5) 11–20%; 6) 21–30%; 7) 31–40%; 8) 41–50%; 9) 51–70%; 10) 71–100%. The number of microhabitat categories established was enough to ensure that the truly important categories were not lumped with, and thus diluted by, less important categories, while at the same time care was taken not to diminish power to discern selection by parcelling out too many categories (Garshelis, 2000). A “visual encounter survey” using a systematic line transect design, which allows all microhabitat types to be exhaustively surveyed (Crump & Scott, 1994), was used to search for lizards. Transects were 1 km long and 80 m wide ($n=13$) and were tracked by four observers separated from each other by 20 m. All surveys were performed under similar weather conditions: average temperature \pm SD of 25 \pm 3 °C; cloudless sky, moderate wind and dry sand. Total survey effort was 340 person-days. For each lizard detected, VC at-

tributes were registered in a 1 m² plot area, using the same method described for microhabitat availability above. Since visibility was not equal in all microhabitat types, efforts were increased when searching in dense vegetated microhabitats, in order to avoid bias.

Used and preferred microhabitats were described on the basis of plant species richness, types (herbs, shrubs, or trees) and percentage vegetation cover of dominant species. Sex and age were also recorded for each captured lizard. Sex was determined based on external secondary sex characters (Ceï, 1993), and age was determined based on reproductive (adults) and nonreproductive (juveniles) size (Vega, 1997), measured with dial callipers (to the nearest 0.05 mm). Three individual categories were recognized: males and females (adult individuals) and juveniles. Sex was not determined for juveniles since the small size of individuals made it difficult.

Use-availability model

Usage was measured as the number of individuals (f_r) found in each type of microhabitat, and availability was measured as the proportion of each microhabitat type (g_r). Then, Manly's alpha α_r value for n_r microhabitats was calculated. This index represents the preference of the taxon of interest for resource r , defined as:

$$\alpha_r = \frac{f_r}{g_r} / \sum_{j=1}^{n_r} \frac{f_j}{g_j}$$

For testing the existence of preferences, randomization tests and null models, rather than generalized linear models (likelihood ratio test or chi-square test) were used, because the former are more robust and appropriate (Gotelli & Graves, 1996; Manly, 1997; Pledger et al., 2007).

Manly's (1997) steps were followed in order to build a suitable randomization test. An overall test under the null hypothesis (H_0) that resource selection occurs in a random proportion, in relation to availability, with no preference shown ($\alpha=1/n_r$), was built. The test is constructed by considering the expected usage values $E(f_r)$ under the assumption of random choice (Pledger et al., 2007). If H_0 is true, the individuals are distributed over the microhabitats with an underlying process of equal frequency. The availability of each microhabitat type (g_r) is the proportional area of microhabitat r . For each microhabitat, counts were observed, and the model yielded expected counts $E(f_r)$, as follows: $E(f_r)=Fg(t)$; where F is the total number of counts in all microhabitats, and $g_{(t)}$ is the proportion of availability of microhabitat t . Due to sample size, the Bray–Curtis index of dissimilarity (BCD) was selected for comparing observed with expected values, instead of chi-square or likelihood ratio tests (Pledger et al., 2007):

$$BCD = \sum_{nr=1}^{nr} |fr - E(fr)| / 2F$$

For the overall test, an algorithm incorporating random distribution with multinomial allocation was used, as follows. 1) Expected values and BCD values were calculated under the assumption of no selection. 2) A large number of randomizations were made (10,000). Within each randomization, F individuals were independently allo-

Table 1. Microhabitat use availability analysis for the sand dune lizard *Liolaemus multimaculatus*. VC = categories of percentage vegetation cover; Av = proportion of microhabitat availability; n = number of detected lizards; α_r = Manly's alpha index; Dr = deviation between α_r and $1/n_r$; JI = Jacobs index.

VC	Av	All individuals			Females		Males		Juveniles	
		n	α_r	Dr	n	JI	n	JI	n	JI
0	0.29	5	0.004	-0.096	1	-0.96	2	-0.89	1	-0.92
0.5	0.04	5	0.026	-0.074	1	-0.68	2	-0.31	2	-1.00
1-5	0.15	98	0.146	0.046	37	0.47	24	0.38	18	0.51
6-10	0.10	61	0.137	0.037	17	0.34	16	0.35	13	0.45
11-20	0.09	58	0.149	0.049	18	0.33	15	0.38	8	0.26
21-30	0.06	65	0.259	0.159	26	0.62	20	0.68	6	0.32
31-40	0.03	22	0.197	0.097	6	0.37	3	0.18	5	0.58
41-50	0.04	11	0.066	-0.034	4	-0.18	1	-0.53	3	0.17
51-70	0.04	3	0.015	-0.085	1	-0.68	0	-1.00	0	-1.00
>71	0.15	0	0.002	-0.098	0	-1.00	0	-1.00	0	-1.00

cated to microhabitats n_1 to n_{10} with probabilities g_1 to g_{10} (a multinomial allocation). Then these pseudo-usages were applied for calculating and storing the pseudo-BCD value. A high BCD value indicates a large distance between observed and expected values. The proportion of pseudo-BCD values which exceed the observed value is the P -value (exact significance level) for our test.

Because a significant difference via the Bray-Curtis index was found, a test to determine whether each microhabitat was selected more or less than expected was carried out. The deviation of the α_r estimate from $1/n_r$, $D_r = \alpha_r - 1/n_r$, was used as a two-sided test for selection or avoidance of one microhabitat. D_r was calculated for the original data, and then at each randomization, the pseudo-value of D_r was saved. At the end, the data D_r value was compared with the null distribution of the saved pseudo-values. The P -value for resource r was calculated as the proportion of D_r pseudo-values further from zero than the data D_r value. The direction of preference was data $D_r > 0$ indicating preference, and data $D_r < 0$ indicating avoidance. Since 10 tests were performed, a sequential Bonferroni adjustment for multiple testing to the P -values was used (Holm, 1979).

Pledger et al.'s (2007) algorithm was used to compare microhabitat-specific tests of lizard categories (n_t), as follows: 1) The (estimated) α_r values for each category t and each microhabitat r were calculated. 2) BCD values between the α values for each pair of individual categories, t, t_2 were calculated and saved. BCD was calculated as:

$$BCD = 1/2 \sum_{r=1}^{n_r} |\alpha_{tr} - \alpha_{t_2r}|$$

3) The overall sum of all BCD values between all possible pairs of individual categories (D value) was saved. 4) The overall probability vector which holds if H_0 is true: $P_r = U_r / F$ for all microhabitats (U_r is the total usage of microhabitat r and F is the overall sum of the usages) was calculated. 5) 10,000 randomizations were carried out. Within each randomization, for each individual category t , F_t individuals were independently allocated to each microhabitat with probabilities p_1 to p_{10} . This gives an $n_t \times n_r$ matrix of pseudo-usages. Then, the associated $n_t \times n_r$ matrix of pseudo-alphas was calculated. The pairwise pseudo-BCD and the overall pseudo-D values were calcu-

lated and stored. 6) After the randomizations, P -values were calculated as: $P = \text{no. pseudo-D values} > \text{data D} / \text{no. of randomizations}$.

In order to evaluate the magnitude of selection of each lizard category, Jacobs' index, $JI = (p_r - g_r) / (p_r + g_r - 2p_r g_r)$, was calculated. This index works with the proportion of use (p_r) and the proportion of availability (Manly et al., 1993); an index value of -1 indicates that a particular microhabitat is completely avoided, whereas $+1$ indicates maximum preference.

Spatial niche width and overlap

Standardized Hurlbert's niche width was calculated as:

$$B' = 1 / \sum_{r=1}^{n_r} (p_r^2 / g_r)$$

(Krebs, 1998) in order to assess spatial niche width and differences among the three lizard categories. This niche measure allows the estimation of the use of resources in relation to their availability. Values range from 0 (specialist species) to 1 (generalist species). Niche overlap between males, females and juveniles was calculated using the Pianka overlap index:

$$O_{ij} = \sum_{r=1}^{n_r} p_{ij} p_{jr} / \sqrt{\sum_{r=1}^{n_r} p_{ij}^2 p_{jr}^2}$$

(Krebs, 1998), which ranges from 0 (no overlap) to 1 (complete overlap).

RESULTS

Use-availability model

Microhabitat use data for a total of 328 individuals were recorded, but only 250 of them were captured. Of those captured individuals, 111 were adult females, 83 adult males and 56 juveniles (Table 1). The use-availability model for all individuals detected, based on 10,000 randomizations, showed significant differences between use and availability ($BCD = 0.476$; $P < 0.001$).

The D_r tests for selection or avoidance of each microhabitat showed significance differences ($P < 0.001$) for microhabitats 1, 2, 3, 5, 6, 7, 9 and 10, whereas microhabitats 4 and 8 were used in accordance with their availability ($P > 0.05$). Microhabitats with a lack of VC (0-1%) and microhabitats with a higher VC (51-100%) were

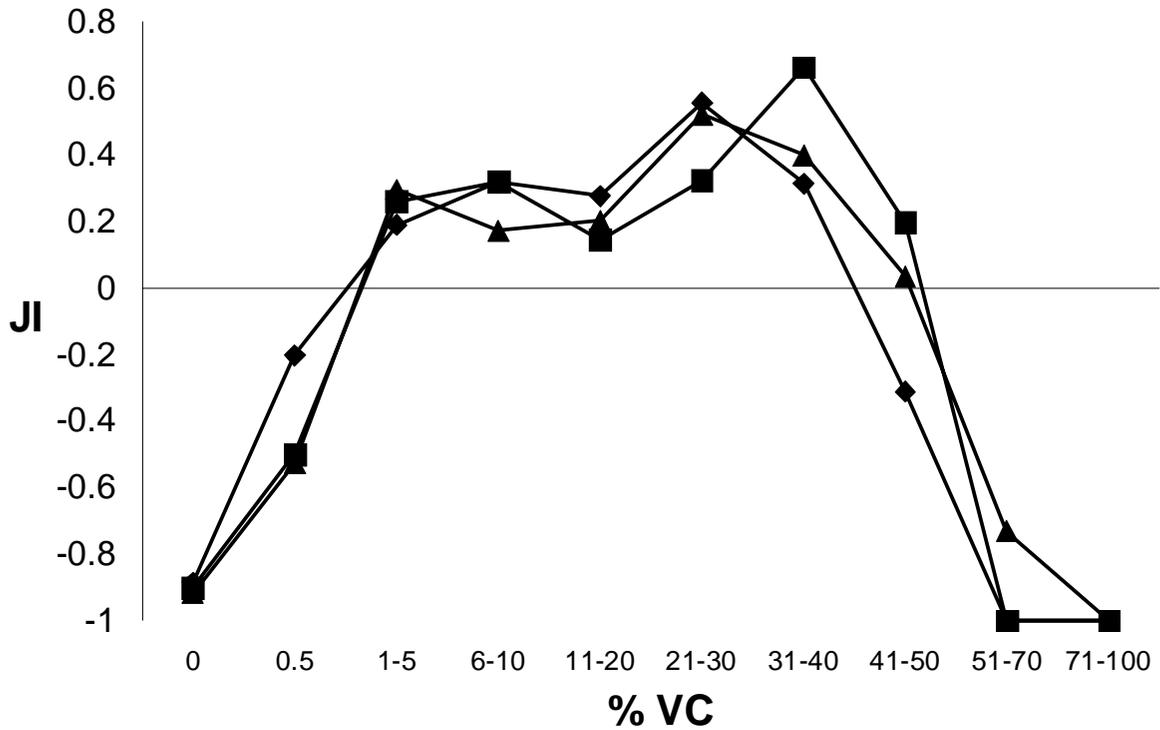


Fig. 1. Magnitude of selection in sand dune lizards *Liolaemus multimaculatus* in a pampean coastal area in Argentina. Vertical axis represents values of Jacobs Index (JI). Horizontal axis represents categories of percentage vegetation cover. Triangles= JI of females; rhombi= JI of males; squares= JI of juveniles.

avoided, while microhabitats with little to medium VC (1–40%) were preferred.

The microhabitat-specific tests of lizard categories, based on 10,000 randomizations, did not show significant differences for any pair of individual categories ($P > 0.05$; D-value = 0.593).

Jacobs' selectivity index D' showed that microhabitats with 21–30% VC (JI = 0.62–0.68) were the most preferred by males and females. Juveniles mainly preferred microhabitats with higher VC (31–40%; JI=0.58). The most avoided microhabitats in all cases were those with 0% VC (JI from –0.89 to –0.96) and microhabitats with 51–100% VC (JI from –0.68 to –1). However, the main patterns of selectivity were similar in the three categories (Fig. 1).

Spatial niche width and niche overlap

The values of Hurlbert's spatial niche width were similar in all cases. Confidence intervals (95%) of niche width ranged from 0.33 to 0.43 in males, from 0.36 to 0.53 in females and from 0.34 to 0.58 in juveniles. Niche overlaps were higher, showing values of $O = 0.99$ between males and females, $O = 0.93$ between females and juveniles and $O = 0.97$ between males and juveniles.

Microhabitat description

The analysis of availability plots ($n = 156$) showed a large amount of bare soil (VC=0%), followed by categories with 1–5% and 71–100% VC. These three categories represent 60% of total samples (Fig. 2). Sites with higher VC (51–70% and 71–100%) were mainly vegetated by an

association of *Imperata brasiliensis* (Poaceae) and *Androtrichum trigynum* (Cyperaceae), both common herbs in moist interdunes. Great richness of other associated plant species also occurred at these sites: *Cortaderia selloana*, *Hydrocotyle bonariensis*, *Achyrocline satureioides* and *Tessaria absinthioides*. The remaining categories (VC of 1–50%) were mostly represented by a great dominance of *Panicum racemosum*, a psammophytic grass more exposed to marine action such as active or semi-active frontal dunes and distal beach.

Sand dune lizards preferred microhabitats composed of 19 (70%) plant species, out of a total of 27 species recorded at the study site. The highest richness of plant species at the microhabitats used was 6 species. However, 85% of the plots were made up of only one or two associated plant species.

Of all detections, 90% occurred at sites with a cover of herbs, but when only preferred plots are considered, 96% are characterized by herb species. No lizards using plots composed only of shrubs, semi-shrubs or trees were observed.

Two main groups of plant species (with different dominant species) were recognized at the preferred microhabitats of lizards: 1) microhabitats dominated by *Panicum racemosum* in association with *Calycera crassifolia*; and 2) microhabitats dominated by *Spartina ciliata*. *Panicum racemosum* was the most frequent (83%) in used microhabitats. *Spartina ciliata* is typical of sites located near the ocean, such as frontal dunes and distal beach.

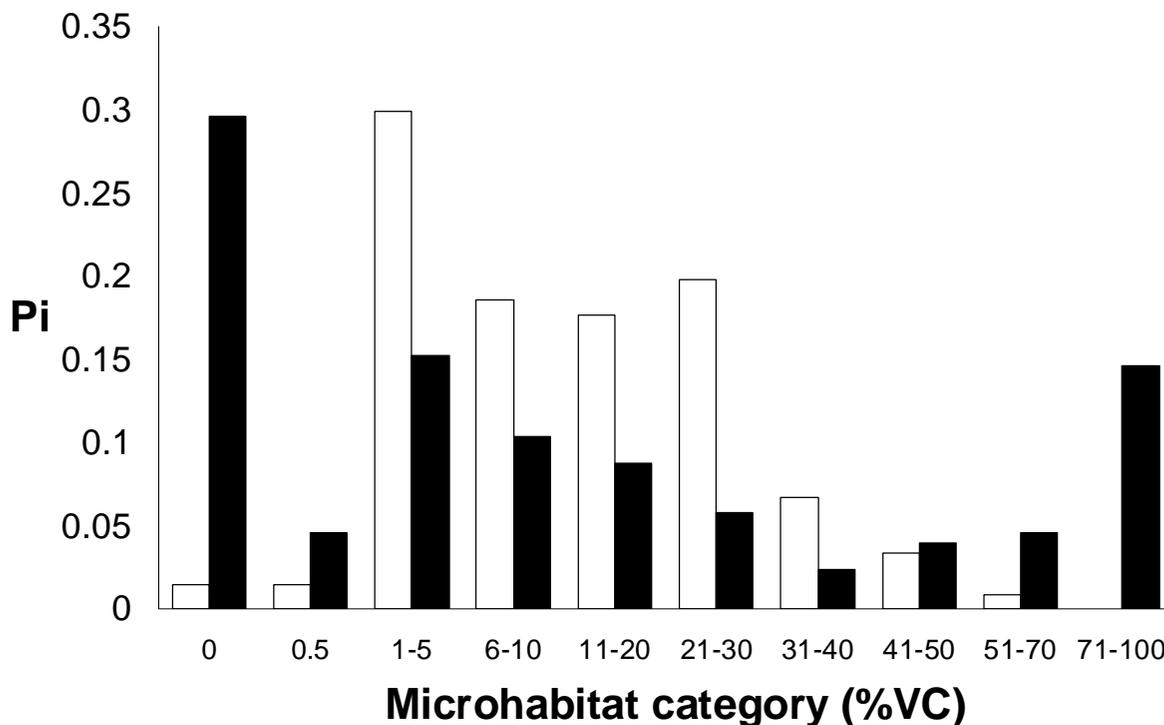


Fig. 2. Microhabitat availability (black columns) and microhabitat used by the sand dune lizard (white columns) based on data for all individuals. P_i = proportion; %VC = percentage vegetation cover.

DISCUSSION

Sand dune lizards do not use microhabitats according to their availability. *Liolaemus multimaculatus* prefers microhabitats with low to medium VC, whereas it avoids microhabitats with high or absent VC. Preferred microhabitats are mainly characterized by two dominant plant species: *Panicum racemosum* and *Spartina ciliata*. Our results showed some similarities to previous observations of a population of the same species located at Rocas Negras (approximately 100 km southwest of Mar Chiquita Provincial Nature Reserve), in Buenos Aires Province (Vega, 2001), and to other lizard species that showed selection for low to medium vegetation cover microhabitats with a high percentage of bare ground (Marcellini & Mackey, 1970; Baltrosser & Best, 1990; Green et al., 2001).

However, Vega et al.'s (2000) results were different from ours. Vega et al. (2000) observed that microhabitats comprising mainly *P. racemosum* were used less than expected. This could be related to differences between the study sites, since the availability of *P. racemosum* was lower in Rocas Negras than at our site. A summary of both studies suggests that sand dune lizards probably do not select microhabitats in relation to the type of plant association. They probably use both types (microhabitats dominated by *S. ciliata* or *P. racemosum*), depending on the availability of these plant species.

We agree with Vega (2001) that the microhabitat use of sand dune lizards could be related to their escape behav-

iour and especially to their sand burying capacity. Sand burying is critical for this lizards' survival, since it is performed in order to escape from predators (Halloy et al., 1998; Etheridge, 2000). However the ability to bury into sand depends on the degree of sand compaction which in turn depends on the degree of VC. Microhabitats with high vegetation cover, and consequently high density of roots, have higher soil compaction which probably hinders rapid burying in the presence of predators.

Furthermore, the absence of lizards in dense vegetated microhabitats could be a sampling artefact as lizards are more difficult to see in this kind of microhabitat. To avoid this problem, greater searching effort was made in high VC microhabitats. Since other related lizard species (*Liolaemus wiegmanii* and *Liolaemus gracilis*, both similar in size to sand dune lizards) were easily detected in high VC microhabitat during our surveys, we conclude that sand dune lizards were not detected in high VC microhabitat because this species avoids this kind of microhabitat.

Other recognized factors that limit microhabitat use in reptiles are thermoregulatory behaviour, foraging strategy, locomotive performance, prey availability, competition and/or predator avoidance (Huey, 1974; Huey et al., 1983; Gillis, 1991; Sanchez & Parmenter, 2002). Regarding foraging strategies, studies on the congeneric *Liolaemus lutzae* (an omnivorous lizard) in a sand dune area in Brazil showed that plant species distribution may also be an important factor affecting the lizards' use of the microhabitat. *Liolaemus lutzae* consumes only four out

of 19 plant species in its microhabitat (those that are richer in protein and water) and clearly this affects the use of some portions of the habitat (Rocha, 1991). However, in the case of *L. multimaculatus*, diet probably does not affect microhabitat selection (Vega, 2001), and this could be related to the generalist insectivorous food habits of this lizard and the high availability of insects in all dune microhabitats.

As for the avoidance of microhabitats without VC, it is important to emphasize three points: 1) a small number of lizards ($n=5$) using these microhabitats was detected, but in all cases, individuals were very close to covered microhabitats; 2) lizards ($n=12$) were also found using open sites out of the study area, but those individuals were hiding under rocks or logs; and 3) individuals that were detected in microhabitats with VC but close to open sites, ran on bare sand searching for refuges in order to escape from us. In conclusion, lizards were not frequently detected in areas lacking vegetation cover. They might use these microhabitats when plants are located nearby, when refuges such as rocks or logs were available, or to move between two refuges. Although open areas facilitate rapid movements to escape predators (Green et al., 2001), lizards are greatly exposed in these microhabitats.

The appropriate choice of a microhabitat to perch in has profound implications for the ecology of lizards. Lizards must “trade off” the costs and benefits associated with avoiding predators and competitors, and obtaining food, mates and shelter (Howard et al., 2003). Microhabitats with low to medium VC are supposedly more appropriate for *L. multimaculatus* because they allow sand burying, rapid movements and provide refuge from predators. On the other hand, open microhabitats offer better visibility (to detect competitors, prey, mates and predators) than more closed microhabitats. Microhabitats with low to medium VC also provide shade and open sites that allow efficient thermoregulation.

Our results did not show significant differences in microhabitat use and spatial niche width related to sex or age in this species. Niche overlaps among lizard classes were nearly 100% in all cases, showing no microhabitat partitioning between individual categories. Juveniles showed a slight tendency to use microhabitats with more vegetation cover than adult males and females, and this could be also associated with the fact that sand burying behaviour is less common in juveniles (Kacoliris, pers. obs.). Microhabitats with higher vegetation cover probably offer greater protection when individuals do not use sand burying behaviour frequently. Despite these slight differences in tendencies, the main patterns were similar for the three categories of lizards.

The conservation status of microhabitats used and preferred by the sand dune lizard is critical. In our study area, out of a total of 140 ha surveyed, only 66 ha (47%) represent suitable microhabitats for this species. These microhabitat types are decreasing dramatically along the remnants of dunes in Argentina. The main disturbance recorded at dune habitats is the circulation of double-traction vehicles, which reduces the availability of patches of native vegetation (Iribarne, 2001). This increase in vehicle circulation favours the appearance of

dunes lacking vegetation, which are avoided by sand dune lizards. Another factor that affects the microhabitats suitable for this species is the increasing number of forest areas dominated by the exotic invaders *Pinus* sp. and *Acacia* sp. These habitats have a high vegetation cover, and are avoided by the sand dune lizard, probably due to changes generated in sand substrate, visibility, availability of prey and predators, and sun irradiation. However, there are no studies of microhabitat use in other remaining areas of coastal dunes, nor are there studies of the effect of disturbance on sand dune lizard space use and behaviour. Future research activities should be focused on these topics in order to quantify these effects and to identify population tendencies of this vulnerable lizard across its area of distribution.

ACKNOWLEDGEMENTS

This work was funded by Rufford Small Grants, International Reptile Conservation Foundation, Neotropical Grassland Conservancy and Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina. We would like to thank E. Guerrero, J. Areta and three anonymous reviewers for their valuable suggestions on the manuscript. We would also like to thank J. Williams, R. Cañete, F. Tuñón, M. Buzato, J. Mangiarotti, A. Rafael, G. Sánchez Béliz, A. Molinari, G. Guaitoli, and M. Fernández for their assistance. Organismo Provincial de Desarrollo Sustentable gave permits for work in the study area.

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Accepted: 7 May 2009