Long-term effects of anthropogenic habitat disturbance on a lizard assemblage inhabiting coastal dunes in Argentina

Laura E. Vega, Patricio J. Bellagamba, and Lee A. Fitzgerald

Abstract: We studied abundance and habitat use in two species of Liolaemus (Squamata: Tropiduridae) at a coastal dune site in eastern Argentina before and 7 years after a road was built at the site. Before disturbance, lizards exhibited similar abundances and a wide segregation in microhabitat use. Liolaemus multimaculatus used flat dunes scarcely covered by Spartina ciliata, while Liolaemus gracilis used the grass Panicum racemosum as cover. After disturbance, the mean number of L. multimaculatus detected by month was significantly less than that observed in the predisturbance period, owing to a drastic reduction in S. ciliata microhabitat patches. The mean number of L. gracilis was similar to that seen during the first period. These differences were clearly linked to habitat loss at the site. We concluded that human impact on the habitat structure of foredunes induced changes in the structure of the lizard assemblage, including shifts in the relative abundance of species and the proportional use of their preferred microhabitats.


Introduction

Human activities along the northern Atlantic coast of Argentina have led to an increase in coastal erosion (Isla and Villar 1992). The major causes of “anthropogenic erosion” are urban development (Bertola et al. 1999), inadequate beach management (Isla et al. 1994), and sand mining (Farenga et al. 1992; Isla 1992). The pressure of urban development, specifically the building of roads and houses within 150 m of the high-tide mark, leads to the abrupt eradication of dunes or sets up barriers that alter the dynamic sand exchange. Inevitably, the dunes slowly waste away (Echeverría 1987; F.I. Isla and M.C. Villar2). Urban pressure, along with the cultivation of exotic plants to stabilize the dunes and the establishment of tourist facilities on the coast of Buenos Aires Province, Argentina, have led to a continuous process of habitat loss and fragmentation. This pattern has been repeated in many other coastal areas of the world (Sorensen et al. 1992).

The ecological consequences of coastal dune degradation for small vertebrates, particularly ecological interactions among arenicolous lizards, are generally unknown. Two studies have reported effects of coastal habitat alteration on the herpetofauna in South America. Gudynas (1989) described the assemblage of reptiles and amphibians in an altered site, and Rocha and Bergallo (1992) found that a gradual reduction in beach vegetation over 10 years was accompanied by a decline in the population of Liolaemus lutzae in southeastern Brazil. Dune lizard assemblages in Buenos Aires Province contain up to four species, one of which is endemic to coastal dunes. Previous work (Vega 1994) showed that these species differ in their preference for structural microhabitat characteristics and in exhibiting a high degree of spatial segregation in sympathy.

Studies on the effects of habitat disturbance on reptiles in Argentina are lacking, as are studies in which a before-and-

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after design was used to evaluate the effects of coastal dune disturbance on vertebrate communities. To properly document effects of anthropogenic disturbance on the coastal dune fauna, before-and-after data on ecology and habitat are required. Pre- and post-disturbance data constitute powerful evidence concerning how organisms may be threatened by changes in habitat (Schlesinger and Shine 1994).

In the present study, we used before-and-after comparisons to evaluate the effects of anthropogenic habitat disturbance, specifically the construction of a road through a coastal dune system, on two Liolaemus species. Each sampling period lasted 15 months, sampling was done at the same place, and identical methods were used. We were therefore able to examine directly the effects of disturbance 2 years before, 7 years after construction of the road. Our goal was to determine if and how habitat disturbance and alteration affected lizard abundance and microhabitat use and point out the implications of our findings for conservation.

Materials and methods

Study organisms

Liolaemus multimaculatus is a relatively small tropidurid lizard (70 mm snout-vent length (SVL)) endemic to coastal sand dune habitats of Buenos Aires and Rio Negro provinces in Argentina (Cei 1993). It belongs to the wiegmanni group of Liolaeminae (Etheridge 1995) and occurs only on substrates of aeolian sands (Etheridge 1993). It is insectivorous and oviparous and reproduces during the austral spring and early summer, October–December. Activity is depressed during winter months, April–July (Vega 1997). Liolaemus gracilis is a small (55 mm SVL), slender lizard belonging to the chilensis group of Liolaeminae (Etheridge 1995). It has a larger distribution than L. multimaculatus and occurs in central, southwestern, and eastern Argentina and along the Atlantic coast from Chubut to Buenos Aires provinces (Cei 1993). Liolaemus gracilis occurs on a variety of substrate types including sand (Gallardo 1977). Little is known about the ecology of L. gracilis.

Study area

The study site was an area of coastal dunes at Rocas Negras, Mar del Sud, Buenos Aires Province (38°21'S, 57°59'W). Mean annual temperature was 13.5°C with a high monthly mean of 21°C in January and low monthly mean of 7.5°C in July (Servicio Meteorológico Nacional 1988, 1998). Annual mean rainfall was >830 mm and there is no marked wet or dry season. The area consisted of 5 ha of sand and gravel beach dunes over a low ravine. The landscape became flatter away from the sea, forming a small hill bordering pampas grassland.

Habitats at the study area formed a vegetation gradient from coast to inland along the beach, foredunes, and back dunes. Foredune vegetation was dominated by Spartina ciliata ("esparrillo"), Panicum racemosum ("tupe"), and Poa barrosiana. Backdune vegetation was characterized by Aedesia incana, Poa lanuginosa, and Lagurus ovatus (Cabrera 1940). The spatial arrangement of these vegetational habitats was a mosaic of five relatively discrete patches of different plant associations in foredunes and a more homogeneous grassy area in the back dunes (Fig. 1A). It was important to describe the configuration of this habitat mosaic and the patchiness of the study area in order to test for effects of habitat disturbance.

Sampling

We visited the study site monthly from October 1984 to December 1985 (15 monthly visits). During each visit, we censused lizards visually by working our way systematically through the foredunes (600 x 80 m) and searching all habitats for lizards (Campbell and Christian 1982). Each census began at 11:00, corresponding to peak daily activity of lizards (L.E. Vega and P.J. Bellagamba, personal observation) and lasted approximately 1 h. The study area was thoroughly canvased during the censuses. Species and age-class were recorded for each lizard observed. Subadults were <45mm SVL and immature in overall appearance. Before each census we recorded air temperature 1 m above ground.

To quantify microhabitat use by individual lizards, we quantified dominant plant species and vegetation cover using Webb’s ocular estimating classes (de Vos and Mosby 1971) in a 1-m² plot around the exact location where a lizard was seen. Rock cover was quantified using the same method.

A road crossing the study site was built in 1987. Seven years post construction, from October 1994 to December 1995 (15 monthly visits), we returned to the same site to quantify the effects of road construction on the lizard assemblage. The same census and habitat-measurement protocols were followed at the same site. Because the numbers of lizards seen during censuses in 1984–1985 were positively correlated with air temperature on the census day (L. multimaculatus: r = 0.74, n = 15, p < 0.002; L. gracilis: r = 0.56, n = 15, p < 0.02), surveys in 1994–1995 were matched as closely as possible for weather conditions.

Analyses

To test the null hypothesis that abundances of the two lizard species did not differ between 1984–1985 and 1994–1995, we used Wilcoxon’s paired signed-ranks tests to compare the actual numbers of lizards seen during each census between the two time periods. We used contingency tables to test the null hypothesis that there was no difference between observed and expected frequencies of substrate use between lizard species (Zar 1984). To test the null hypothesis that there was no difference in microhabitat use by each species, we quantified the amount of each habitat available to the lizards, then calculated expected frequencies of lizards in each microhabitat according to the surface area of each microhabitat during each time period.

Results

Habitat alteration

Removal of sand and vegetation during road construction caused a drastic reduction in the original vegetation in foredunes (Fig. 1B). Use and maintenance of the road prevented accumulation of sand at this location. Progressive erosion during subsequent years exposed a slime–sand–clay soil in erosive banks. Seven years after construction, the original homogeneous sandy habitat, 14 000 m² in area and covered by S. ciliata, was reduced to two thin strips beside the road that totaled 1500 m². Although scattered clumps of S. ciliata remained, bare sand predominated. Consequently, this patch was reduced to 10% of its original area (Fig. 2). The patch of P. racemosum vegetation in hummock dunes was fragmented and finally reduced to <50% of its former area (from 1500 to 700 m²). In contrast, the patches of P. barrosiana and Poa sp. in the foredunes and the rocky patch at the beach did not change noticeably in area. Neither visible damage nor decreased vegetation cover was detected in the back dunes (Fig. 2).

Lizard abundance

The number of L. multimaculatus detected during the 15 monthly surveys in 1994–1995 (mean = 0.93, SD = 1.48, n = 15) was much lower than the number observed in 1984–1985 (mean = 7.3, SD = 12.2, n = 15) and this difference
was statistically significant (Wilcoxon’s paired signed-ranks test, \(Z = -2.81, p < 0.005, n = 15\); Fig. 3). The mean number of *L. gracilis* seen by month in 1994–1995 was 6.9 (SD = 6.5, \(n = 15\)) and was not statistically distinguishable from the number seen per month in 1984–1985 (mean = 6.7, SD = 8.9, \(n = 15\)) (Wilcoxon’s paired signed-ranks test, \(Z = -0.13, p > 0.90, n = 15\); Fig. 3).

Numbers of both species peaked during the austral spring and early summer (September–December), corresponding to recruitment of hatchlings. Age structure (the ratio of adults to juveniles) also varied with time of year and recruitment of juveniles. The age structure was 4:1 for *L. multimaculatus* in December in both 1985 and 1995. The largest number of *L. gracilis* in a census in 1985 was 33 in October. The age structure was 1:3. The largest number seen during the post-construction period was 22 in May 1995, and the age structure was also 1:3.

**Habitat use**

During 1984–1985, lizards used habitats in patches of rock along the beach and in vegetation communities in fore-dunes. Each species was statistically significantly associated with particular habitats, taking into account the surface area of each habitat available (Table 1). More *L. multimaculatus* were found than expected in *S. ciliata* and less in *P. barrostriana* and *P. racemosum* (total \(\chi^2 = 12.810, df = 3, p < 0.005\); Table 1), while *L. gracilis* was almost exclusively found in *P. racemosum* (total \(\chi^2 = 1355.66, df = 3, p < 0.0001\); Table 1). Following substantial changes in proportions of habitat available after disturbance of the dunes, the
The same pattern of habitat use was observed in 1994–1995. Numbers of *L. multimaculatus* were drastically reduced, from 110 in 1984–1985 to 14 in 1994–1995. This species remained associated with *S. ciliata* despite the reduction of this habitat from 59 to 9% of the available area (total $\chi^2 = 7.64$, df = 3, $p < 0.0542$; Table 1). It is possible that *L. multimaculatus* experienced a subtle change in the rate of habitat use during the 1994–1995 postdisturbance period. In 1994–1995, the proportion of the area consisting of rocks increased from 25 to 75%, and 8 of the 14 *L. multimaculatus* were found there. This number still was lower than expected, however, based on habitat availability. *Liolaemus gracilis* remained strictly associated with *P. racemosum* following disturbance (total $\chi^2 = 2528.86$, df = 3, $p < 0.0001$; Table 1). Habitat segregation was also very evident between the two lizard species during each sampling period, reflecting the distinct habitat associations of each species (total $\chi^2$ for either year > 187.00, df = 3, $p < 0.0001$; Table 1).

The amount of vegetation cover at microhabitat sites occupied by individual lizards differed between species during both time periods (1984–1985: total $\chi^2 = 125.59$, df = 2, $p < 0.0001$; 1994–1995: total $\chi^2 = 26.85$, df = 2, $p < 0.0001$, respectively; Table 2). More *L. multimaculatus* were sighted than expected at sites with <33% vegetation cover, while more *L. gracilis* were seen at sites with >33% vegetation cover. More *L. multimaculatus* were found than expected in 1994–1995 where substrate cover was >33% (total $\chi^2 = 21.76$, df = 2, $p < 0.0001$; Table 2), possibly because these lizards increased their use of rocks during the postdisturbance period. In contrast, the pattern of cover used by *L. gracilis* did not vary between periods (total $\chi^2 = 0.74$, df = 2, $p = 0.69$; Table 2). It appeared the *L. gracilis* were concentrated in
remaining clumps of \textit{P. racemosum} where suitable cover was available.

In summary, habitat use by these lizards can be described in terms of dune topography, type of plant association, and mean vegetation cover of sand substrate. The preferred habitat of \textit{L. multimaculatus} was \textit{S. ciliata} clumps in relatively low dunes. Individuals were detected close to the base of these grasses or running over bare sand. \textit{Liolaemus multimaculatus} were found hiding under rocks on the beach, though less frequently than in \textit{S. ciliata}. The preferred habitat of \textit{L. gracilis} was \textit{P. racemosum} in rugged dunes. \textit{Liolaemus gracilis} were detected moving under vegetation on dune slopes, and they avoided open spaces.

**Discussion**

Before the road was built, populations of both lizard species exhibited similar abundances and wide segregation in habitat use. Each species mostly used a particular part of the habitat that differed in amount of vegetative cover and in plant composition. \textit{Liolaemus multimaculatus} used open spaces in flat dunes scarcely covered by \textit{S. ciliata}. Their cryptic

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**Fig. 3.** The number of each lizard species per transect during 1984–1985 and 1994–1995.

**Table 1.** Proportions and area of habitat availability and proportions and numbers of individuals using each microhabitat during 1984–1985 and 1994–1995.

<table>
<thead>
<tr>
<th>Habitat availability</th>
<th>Proportion</th>
<th>Area (m²)</th>
<th>\textit{L. multimaculatus}</th>
<th>Proportion</th>
<th>n</th>
<th>\textit{L. gracilis}</th>
<th>Proportion</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>\textit{L. multimaculatus}</td>
<td></td>
<td></td>
<td>\textit{L. gracilis}</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Proportion</td>
<td>n</td>
<td></td>
<td>Proportion</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>1984–1985</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rocks</td>
<td>0.25</td>
<td>6 000</td>
<td>0.25</td>
<td>28</td>
<td>0.00</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.59</td>
<td>14 000</td>
<td>0.71</td>
<td>78</td>
<td>0.06</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>\textit{Spartina ciliata}</td>
<td>0.06</td>
<td>1 500</td>
<td>0.01</td>
<td>1</td>
<td>0.94</td>
<td>98</td>
<td></td>
<td></td>
</tr>
<tr>
<td>\textit{Panicum racemosum}</td>
<td>0.09</td>
<td>2 200</td>
<td>0.03</td>
<td>3</td>
<td>0.00</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>23 700</td>
<td>110</td>
<td>104</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1994–1995</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rocks</td>
<td>0.75</td>
<td>13 000</td>
<td>0.57</td>
<td>8</td>
<td>0.00</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>\textit{S. ciliata}</td>
<td>0.09</td>
<td>1 500</td>
<td>0.29</td>
<td>4</td>
<td>0.00</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>\textit{P. racemosum}</td>
<td>0.04</td>
<td>700</td>
<td>0.00</td>
<td>0</td>
<td>1.00</td>
<td>106</td>
<td></td>
<td></td>
</tr>
<tr>
<td>\textit{P. barrosiana}</td>
<td>0.13</td>
<td>2 200</td>
<td>0.14</td>
<td>2</td>
<td>0.00</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>17 400</td>
<td>14</td>
<td>106</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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coloration, specialized morphology, and behavior (Cei et al. 1975; Gallardo 1977; Halloy et al. 1998) are concordant with a lizard species highly specialized for arenicolous environments. *Liolaemus gracilis* is a generalist, occurring in a variety of habitat types throughout its range (Gallardo 1977; Cei 1993). At our study site, *L. gracilis* were found almost exclusively under clumps of *P. racemosum* and avoided open spaces. The habitat associations we observed were consistent with the pattern of habitat use documented for these species in a regional study along 350 km of coastal dunes (Vega and Bellagamba 1992).

Seven years after disturbance of dunes, the lizard populations and their habitat at Rocos Negras were clearly different. Differences included drastic changes in relative abundance, most notably the near disappearance of *L. multimaculatus*. We documented a shift in the proportional use of preferred microhabitat by *L. multimaculatus*. The 14 *L. multimaculatus* detected in 1994–1995 were found in the few remaining places with scattered clumps of *S. ciliata* and in the rocky area surrounding the *S. ciliata* patch. In the postdisturbance sampling, this lizard species showed a tendency to use open space near rocks more than *S. ciliata*. While the results of the tests were statistically significant, the pattern was difficult to interpret because so few *L. multimaculatus* were seen in 1994–1995. Rocks were more available than *S. ciliata* in 1994–1995, presumably because of progressive erosion at the site (Isla et al. 1997). It is possible the shift in habitat use occurred in relation to the changing availability of microhabitats. Relative frequencies of *L. multimaculatus* using sand among patches of *Poa* spp. were also higher during the postdisturbance period than before, but small numbers of lizards seen near *Poa* spp. in both sampling periods precluded the use of statistical tests (Table 1). While a few *L. multimaculatus* were seen in *Poa* spp., it appeared that this habitat was not preferred by *L. multimaculatus*. Importantly, the shift in habitat use by *L. multimaculatus* apparently did not compensate for the loss of preferred *Spartina* habitat in terms of recruitment. The 90% reduction in *S. ciliata* habitat was accompanied by an 87% reduction in the number of *L. multimaculatus*.

No obvious pattern of annual rainfall explained the decrease in the *L. multimaculatus* population. Annual rainfall in the region during 1981–1985 was not significantly different from that in 1991–1995 (1981–1985: mean = 802 mm, SD = 180; 1991–1995: mean = 701 mm, SD = 95; t0.05,6 = 2.45, p < 0.32) (Servicio Meteorológico Nacional 1988, 1998).

Rainfall patterns apparently had no negative effect on *L. gracilis* at our site, nor on a *L. multimaculatus* population 60 km south of the study area (Vega 1999a).

The most perceptible change at the site was the altered landscape. The road reduced and destroyed patches of vegetation and caused soil erosion. Vegetation is an essential element of most lizards’ habitat in xeric biotopes such as sand dunes. It provides thermal refugia and protection from predators, may provide nesting sites, and also provides habitat for arthropod prey consumed by lizards (Rocha 1988, 1989, 1995, 1996; Vega 1999b). Rocha and Bergallo (1992) concluded that a progressive reduction of beach vegetation over the last 10 years has reduced populations of the endemic lizard, *L. lutzei*, in Barra de Tijuca Reserve in Brazil. Considering the apparent dependency of *L. multimaculatus* on *S. ciliata*, it seems clear that the drastic reduction of this grass at our study site was the cause of the decrease in numbers of these lizards.

In spite of the 50% reduction of the *P. racemosum* area, the *L. gracilis* population was as abundant as 7 years before and exhibited a similar age structure. In contrast to the situation with *L. multimaculatus*, the decrease in area did not drive *L. gracilis* into alternative habitats. Instead, the frequency of use of remaining *P. racemosum* by *L. gracilis* increased.

Several mechanisms could account for the constant number of *L. gracilis*, but it is impossible to determine from our data which of these may have been operating. The densities of *L. gracilis* that were measured could have reflected temporary peaks and lows in a fluctuating population (Fitzgerald 1994). Additionally, the lizards were concentrated in small remnants of *P. racemosum* in 1994–1995, which may have facilitated our finding them. Alternatively, the *L. gracilis* population at this site may be limited by factors other than space, such as food availability or predation risk, that could allow relatively constant numbers to persist irrespective of density. Regardless of mechanisms governing the population dynamics of *L. gracilis*, it is clear that this species was tightly linked to *P. racemosum* cover.

Vertebrates may respond to disturbance by undergoing changes in life-history strategies, behavior, ecology, and physiology. Similar types of disturbance may produce different effects depending on the size of impacted area and the type of patch considered (Karr and Freemark 1985). For instance, if the intensity or persistence of disturbance differed among similar habitat patches, organisms using different patches might respond in different ways (Wiens 1985). This scenario is relevant in our case, since the effects of road construction varied among patches of *S. ciliata* and *P. racemosum*. The lizard species we studied showed a high degree of habitat segregation and each responded differently to habitat alteration. *Liolaemus multimaculatus* is a habitat specialist that depends on relatively open sandy substrates among patches of *S. ciliata*. In accordance with the prediction that specialists will be more sensitive to disturbance, *L. multimaculatus* showed a drastic decline.

Based on our findings we raise the following scenario for the Rocos Negras disturbance. When the road was built through the patch of *S. ciliata*, habitat used by *L. multimaculatus* was destroyed, causing the loss of many individual lizards almost immediately. The maintenance of the road and the increase in tourist activities and erosion prevented the recovery of

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**Table 2.** Proportions of two lizard species using different substrate vegetation cover classes at microhabitat sites during 1984–1985 and 1994–1995.

<table>
<thead>
<tr>
<th>Substrate cover (%)</th>
<th><em>L. multimaculatus</em></th>
<th><em>L. gracilis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1984–1985</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;33</td>
<td>0.82 (90)</td>
<td>0.06 (6)</td>
</tr>
<tr>
<td>34–66</td>
<td>0.18 (20)</td>
<td>0.89 (93)</td>
</tr>
<tr>
<td>&gt;67</td>
<td>0.00 (0)</td>
<td>0.05 (5)</td>
</tr>
<tr>
<td>1994–1995</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;33</td>
<td>0.43 (6)</td>
<td>0.04 (4)</td>
</tr>
<tr>
<td>34–66</td>
<td>0.43 (6)</td>
<td>0.89 (95)</td>
</tr>
<tr>
<td>&gt;67</td>
<td>0.14 (2)</td>
<td>0.07 (7)</td>
</tr>
</tbody>
</table>

**Note:** Numbers in parentheses are sample sizes.


Isla, F.I., Witkin, G., Bértola, G.R., and Farenga M.O. 1994. Varia-
ciones morfológicas decenales (1983–1993) de las playas de


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