Spatial organization and habitat partitioning in a mountain lizard community of Mexico

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SUMMARY

The spatial structure of a mountain lizard community located in the Sierra Madre Occidental, N. E. Mexico, was studied from May 1979 to October 1980. The community is composed of seven species, including four Sceloporus. Analysis of microhabitat and substrate utilization by all the species in two main habitats shows that species are not specialized according to habitat but are specialized to microhabitat-substrate. Spatial niche-overlap values are very low for all paired species. The determining role of microhabitat selection in organizing this lizard community and its general ecological meanings are discussed.

KEY-WORDS: Habitat partitioning - Substrate selection - Community - México - Sierra Madre Occidental - Lizards - Sceloporus.

INTRODUCTION

The suggestion that spatial segregation may be one of the most important factors minimizing actual or potential competition between species and thus contribute to their stable coexistence was emphasized, from a theoretical point of view, by MacArthur & Pianka (1966) and supported by much empirical data reviewed by Schoener (1974). In the particular case of lizard communities, although differential food utilization may contribute to minimize ecological overlap between species (Pianka, 1973, 1975; Fuentes, 1976; Huey & Pianka, 1977; Barbault et al., 1978; Pianka et al., 1979; Maury, 1981) several workers demonstrated how important habitat partitioning may be (Pianka, 1966; Jenssen, 1973; Mellado et al., 1975;
In this study we analyse the spatial structure of a lizard community representative of the American mountain pine-oak forest. This work must be taken as a first step towards a more complete study of the ecological organization of this community. The determinant role of microhabitat selection in organizing lizard communities is discussed.

MATERIALS AND METHODS

The study was carried out at the Biosphere Reserve of La Michilia on the eastern slopes of the Sierra Madre Occidental, between 23°20' and 23°30' north, and between 104°20' and 104°07' west. The elevation of the area varies between 2,350 and 2,850 m. The mean annual temperature is between 17.4°C and 20.4°C; the annual precipitation between 525 to 609 mm, strongly concentrated in the summer (June to September). Geologically the area lies on igneous rocks of tertiary extrusions.

The plant community of the area is an oak-pine forest but the vegetation is highly diversified, including 11 distinct units of vegetation (Martinez & Saldívar, 1978). However the principal types of vegetation are the oak-pine forest (fig. 1) and the grassland (fig. 2).

The lizard community of the area consists of seven species: Sceloporus grammicus Wiegmann, 1828; the most common reptile of the area, Sceloporus virgatus Wiegmann, 1828; Sceloporus poinesis Baird & Girard, 1854; Sceloporus jarrovi Cope, 1875; Phrynosoma orbiculare (Linnaeus, 1789); Barisia imbricata (Wiegmann, 1834) and Eumeces brevirostris (Gunther, 1860).

The oak-pine forest and grassland were systematically covered in the search for lizards, between May of 1979 to October of 1980. For each lizard observed we recorded: species, sex, hour, habitat, microhabitat or substrate. Eleven kinds of microhabitat-substrate were recognized: fallen trunks, fallen branches, trees, stumps, shrubs, rocks, steep rock faces, ground, ground with grasses, ground

Fig. 1. — Aspect of the oak-pine forest (on the ground note one fallen tree trunk).
FIG. 2.—Aspect of the grassland (in the background note the oak-pine forest).

with leaf litter, ground with fallen tree trunks. Sampling included all day-light hours during the four seasons of the year, with a total of 1,650 records.

The \( \chi^2 \) goodness-of-fit test was employed to determine the statistical significance of the differences observed between distribution of species.

For the calculation of habitat niche breadth values Simpson's diversity index was used (Levins, 1968) in a standardized form (varying between 0 and 1):

\[
D_s = \left( \frac{\sum p_i^2}{N} \right)^{-1} - 1
\]

where \( p_i \) is the proportion of individuals found on the \( i \)th substrate and \( N \) the number of classes of substrate (11).

Microhabitat niche overlap values were measured using Pianka's index (1973):

\[
O_{jk} = \frac{\sum p_{ij} p_{jk}}{\sqrt{\sum p_{ij}^2 \sum p_{jk}^2}}
\]

where \( p_{ij} \) and \( p_{jk} \) are the frequency of utilization of the \( i \)th microhabitat by the \( j \)th and \( k \)th species respectively. The values obtained using this formula vary between 0 and 1.

RESULTS

Distribution of species between habitats

If we exclude the rarely seen species, *Barisia imbricata* and *Phrynosoma orbiculare*, for which there was too little data to be conclusive, all the species coexist in each habitat (table 1).

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The spectrum of species frequency appeared slightly different between the two kinds of habitat ($\chi^2$ significant at $p < 0.05$) mainly because *Sceloporus jarrovi* was scarcer in grassland than in oak-pine forest. This is because this lizard is a rock and wall dwelling species and this micro-habitat is not often found in the grassland habitat.

### Distribution of species in microhabitats or substrates

Comparing microhabitat utilization by the various species, much can be learned about the qualitative nature of ecological differences among species (table II).

*Sceloporus grammicus* is a fallen trunk dweller since most individuals were seen on fallen trees (59.6 %) and fallen branches (15.2 %). *Sceloporus scalaris* is terrestrial (89.1 % on ground), as are the three scarce species, *Phrynosoma orbiculare* (93.9 %), *Eumeces brevirostris* (100 %) and *Barisia imbricata* (77.7 %). *Sceloporus poinsetti* is mainly observed on rocks (43.6 %) but also on fallen trunks (27.7 %) and stumps (21.8 %) while the other rockdwelling species, *Sceloporus jarrovi* is generally found on steep rock faces (67.7 %) and also on big rocks (27.4 %).

All differences between paired species are statistically significant ($p < 0.01$) except between *Phrynosoma orbiculare* and *Barisia imbricata*, where there is no difference ($P > .05$).

The very low microhabitat niche breadth values found for all species ($\leq .22$, table III) indicate how very specialized these lizards are in microhabitat or substrate selection.

### Overlapping of microhabitat niche

The overlapping of microhabitat niche values between the species studied are low (table IV). If we exclude rare species such as *Phrynosoma orbiculare* and *Barisia imbricata*, the only high overlap value is between *Sceloporus poinsetti* and *Sceloporus grammicus* (0.564). However if we consider that *Sc. poinsetti* is not found on trunks with a diameter smaller than 1.0 m it is likely that the true ecological overlap value with *Sc. grammicus* is lower.

### DISCUSSION AND CONCLUSIONS

The distribution and frequency of occurrence of lizard species in the study area are mainly the result of the spatial distribution and frequency of occurrence of some of the microhabitats or substrates to which species are closely restricted.
### Table II

**Distribution of species by microhabitat (relative occurrence).**

<table>
<thead>
<tr>
<th>Species</th>
<th>Numbers</th>
<th>Fallen trunks</th>
<th>Fallen branches</th>
<th>Trees</th>
<th>Stumps</th>
<th>Shrubs (in)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sc. grammicus</em></td>
<td>886</td>
<td>0.596</td>
<td>0.152</td>
<td>0.117</td>
<td>0.099</td>
<td>0.001</td>
</tr>
<tr>
<td><em>Sc. scalaris</em></td>
<td>444</td>
<td>0.014</td>
<td>0.020</td>
<td>0</td>
<td>0.002</td>
<td>0.043</td>
</tr>
<tr>
<td><em>Sc. poinsetti</em></td>
<td>101</td>
<td>0.277</td>
<td>0</td>
<td>0.059</td>
<td>0.218</td>
<td>0</td>
</tr>
<tr>
<td><em>Sc. jarrovi</em></td>
<td>164</td>
<td>0.037</td>
<td>0</td>
<td>0.006</td>
<td>0.006</td>
<td>0</td>
</tr>
<tr>
<td><em>Ph. orbicularis</em></td>
<td>16</td>
<td>0</td>
<td>0.063</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>E. brevirostris</em></td>
<td>30</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>B. imbricata</em></td>
<td>9</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.222</td>
</tr>
</tbody>
</table>

**Numbers**

- 1,650 568 145 111 112 22

### Table III

**Microhabitat niche breadth or diversity of substrate utilized by the species.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Sc. grammicus</th>
<th>Sc. scalaris</th>
<th>Sc. poinsetti</th>
<th>Sc. jarrovi</th>
<th>Ph. orbicularis</th>
<th>E. brevirostris</th>
<th>B. imbricata</th>
<th>Dp</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.149</td>
<td>0.196</td>
<td>0.215</td>
<td>0.087</td>
<td>0.094</td>
<td>0.217</td>
<td>0.180</td>
<td></td>
</tr>
</tbody>
</table>

(1) Since these samples were small these measures are only roughly indicative.
In other words, these lizard species do not exhibit habitat specificity but they do exhibit substrate specificity. Within the area they may be found in any habitat identified by Martínez & Saldivar (1978), provided that the substrate to which they are limited is present there. Thus the ecological organization of this lizard community may be clearly depicted by a dendrogram (fig. 3) summarizing the data on similarity indices of microhabitat use between species (table IV).

![Dendrogram](image)

**Fig. 3.** — Graphical representation of the ecological structure of the lizard community.

### Table IV

<table>
<thead>
<tr>
<th></th>
<th>Sc. grammicus</th>
<th>Sc. scalaris</th>
<th>Sc. poinsetti</th>
<th>Sc. jarrovi</th>
<th>Ph. orbiculare</th>
<th>E. brevirostris</th>
<th>B. imbricata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sc. grammicus</td>
<td>0.049</td>
<td>0.564</td>
<td>0.063</td>
<td>0.029</td>
<td>0.006</td>
<td>0.013</td>
<td></td>
</tr>
<tr>
<td>Sc. scalaris</td>
<td>0.052</td>
<td>0.318</td>
<td>0.002</td>
<td>0.433</td>
<td>0.856</td>
<td>0.331</td>
<td></td>
</tr>
<tr>
<td>Sc. poinsetti</td>
<td>0.564</td>
<td>0.019</td>
<td>0.001</td>
<td>0.856</td>
<td>0.331</td>
<td>0.324</td>
<td></td>
</tr>
<tr>
<td>Sc. jarrovi</td>
<td>0.003</td>
<td>0.000</td>
<td>0.433</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td></td>
</tr>
<tr>
<td>Ph. orbiculare</td>
<td>0.006</td>
<td>0.744</td>
<td>0.013</td>
<td>0.433</td>
<td>0.331</td>
<td>0.324</td>
<td></td>
</tr>
<tr>
<td>E. brevirostris</td>
<td>0.013</td>
<td>0.300</td>
<td>0.067</td>
<td>0.305</td>
<td>0.199</td>
<td>0.324</td>
<td></td>
</tr>
<tr>
<td>B. imbricata</td>
<td>0.156</td>
<td>0.067</td>
<td>0.305</td>
<td>0.199</td>
<td>0.324</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The community appears to be composed of species specialized for substrate or microhabitat, each pertaining to a general ecological type of lizard which can also be recognized in other areas and even on other continents (Mellado et al., 1975; *Acta Ecologica/Ecologia Generalis*).
SPATIAL ORGANIZATION IN A LIZARD COMMUNITY

SAGE, 1973): there is a litter dweller species (Eumeces brevirostris), three ground dwelling species (a small one, Sceloporus scalaris, a large one Barisia imbricata (1)), and the ant-eater Phrynosoma orbiculare), a tree trunk dwelling species (Sceloporus graminicus) and two rock dwelling species (Sceloporus poinsetti and Sceloporus jarrovi).

Although the spatial niche overlap values between most paired species are very low, according to common niche theory, this does not prove that interspecific competition was the structuring force which produced the observed pattern, nor that competitive interactions are presently excluded by space segregation.

Firstly, substrate or microhabitat specialization is not necessarily, nor likely a competitively induced phenomenon. In such a case lizards may depend strongly upon close substrate adaptation to avoid predators, to thermoregulate efficiently and to be successful in mating and defending territory. Thus, substrate selection and specialization which they exhibit may be a response evolved to cope with a complex combination of various selective pressures, and not only with the pressure exerted by interspecific competition.

Secondly, when the coexisting populations are limited with respect to food it remains to be seen whether they prey on the same species in the same places, thus competing for food. Thus for instance, although remaining most of the time on tree trunks, Sceloporus graminicus may gather prey on the ground, as does the same sized species Sceloporus scalaris, and compete with it.

Although this study does not allow us to draw definite conclusions about the ecological forces involved here, it does show the importance of habitat partitioning by means of microhabitat specialization in the structuring of this mountain lizard community.

ACKNOWLEDGMENTS

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BIBLIOGRAPHY


(1) Partly a lizard predator.


