Comparative demography of the high-altitude lizard, *Sceloporus grammicus* (Phrynosomatidae), on the Iztaccíhuatl Volcano, Puebla, México

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COMPARATIVE DEMOGRAPHY OF THE HIGH-ALTITUDE LIZARD, *SCELOPORUS GRAMMICUS* (PHRYNOSOMATIDAE), ON THE IZTACCHUATL VOLCANO, PUEBLA, MÉXICO

Julio A. Lemos-Espinal¹, Royce E. Ballinger², and Geoffrey R. Smith³

ABSTRACT.—Population density, reproduction, and survivorship were compared between 2 populations of *Sceoporus grammicus* occurring at different altitudes (3700 m and 4400 m) on the eastern slopes of Iztaccihuatl Volcano, Puebla, México. Lizards in both populations matured at the same age (14–15 mon) and size (39–42 mm SVL). Population density was slightly greater at high altitude (131–163 per ha) than at low altitude (52–83 per ha). Survivorship and R₀ were higher at the low-altitude area, but in general there were no significant demographic variations between altitudes that have been reported in lizard population at higher latitudes. Studies of lower-elevation populations might reveal some differences because previous studies indicate that litter size increases at lower altitudes, although they do not differ between our 3700 m and 4400 m populations.

Key words: lizard life history, demography, reproduction, altitude variation, *Sceoporus grammicus*, population density, replacement rate, survivorship.

Life histories and demographic traits of lizards can vary along elevational gradients (Ballinger 1979, Grant and Dunham 1990, Smith and Ballinger 1994a, 1994b). Altitudinal variations in life history characteristics often mimic variation observed across broader geographic ranges that can be attributed to differences in environmental conditions (e.g., Adolph and Porter 1993, 1996). In addition, some studies have shown that altitudinal variation can have at least a partial genetic basis (Smith et al. 1994, Ballinger et al. 1996), just as studies on geographic variation have shown (Ferguson and Talent 1993, Niewiarowski and Roosenburg 1993). Most of these studies have focused on lizard populations in north temperate latitudes. Understanding how life histories and demography vary in response to latitude and altitude combinations may be useful in identifying variables responsible for such changes.

In this paper we present data on demographic variation of 2 populations of *Sceoporus grammicus* (1828) at different elevations (3700 m and 4400 m) to examine whether variations in demography occur at subtropical latitudes. *Sceoporus grammicus* is a small, viviparous lizard that occurs from southern Texas, USA, to the state of Oaxaca, México (Conant and Collins 1991, Flores Villela and Gerez 1994). This species has been poorly studied and little has been published on its biology, except for studies on its reproduction (Guillette and Casas-Andreu 1980, 1981, Ortega and Barbault 1984), general population biology (Lemos-Espinal and Amaya-Elias 1986), growth (Lemos-Espinal and Ballinger 1995a), and thermal biology (Lemos-Espinal and Ballinger 1995b).

MATERIALS AND METHODS

The 2 populations we studied are located in the Campo Experimental Forestal San Juan Téta (19°10'N, 98°36'W) on the eastern slope of Iztaccihuatl Volcano, Puebla, México, at 3700 and 4400 m. On Iztaccihuatl Volcano, *S. grammicus* can be found up to 4600 m elevation. At this latitude tree line is 4000 m. The low-elevation site (hereafter designated Laguna), of approximately 4 ha, is located in a *Pinus hartwegii* forest surrounding a natural lake. Lizards were seen primarily on logs and stumps but were occasionally found under tree bark or in cracks in tree trunks. This site

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Lizards were aged according to size at first capture. Since Lemos-Espinal and Ballinger (1995a) found that lizards from both study sites show the same growth rates, we used the same size categories for both populations: size class 1 (females <39 mm SVL, males <42 mm SVL; individuals in their 1st yr), size class 2 (females 39–45 mm SVL, males 42–49 mm SVL; individuals in their 2nd yr), and size class 3 (females >45 mm SVL, males >49 mm SVL; 3 yr or older). For life table analyses we estimated age by recapture of animals marked as hatchlings or by using von Bertalanffy’s (1957) growth analyses (Lemos-Espinal and Ballinger 1995a). Survivorship was estimated for each age class as the proportion of marked animals recaptured the following year.

RESULTS

Litter size increased with female body size in both populations (Fig. 1; \( r = 0.85, n = 67, P < 0.0001 \) for Laguna, and \( r = 0.89, n = 54, \)

was studied from November 1984 to June 1988, and from September 1990 to January 1992. The high-elevation site (hereafter designated Paredon), of approximately 1 ha, is a volcanic rock formation surrounded by grassland composed primarily of *Festuca tolucensis*. Lizards at this site live under rocks and in rock crevices. We studied this site from November 1985 to June 1988, and from September 1990 to January 1992. From May 1991 to April 1992, average minimum temperatures for these 2 sites were very similar (Laguna = 2.0 ± 0.6°C [mean ± 1s]), Paredon = 2.2 ± 0.6°C); however, average maximum temperatures for Laguna were higher (13.1 ± 0.9°C) than for Paredon (5.7 ± 0.5°C; Lemos-Espinal and Ballinger 1995a).

Both populations were censused monthly. For each captured lizard we measured snout-vent length (SVL) to the nearest mm using a clear plastic ruler, and body mass (BM) to the nearest 0.01 g using a Pesola™ spring scale. We also recorded sex, tail condition (broken, regenerated, or unbroken), time of capture, and microhabitat of capture site. Each lizard was permanently marked by toe clipping. To examine reproduction, we collected females in adjacent areas more than 500 m from the 2 study sites (n = 67 for Laguna, n = 54 for Paredon) during May 1991 and dissected them to examine reproductive tracts (specimens currently in JAL’s personal collection). Size and number of yolked follicles or embryos were recorded for each female. All means are given ± 1s, unless specified otherwise.

Using Jolly’s (1965) stochastic method, which is relatively insensitive to differences in chance of capture or survival among animals (Carothers 1973), we calculated population density for each month. Although young and old lizards may have differed in capture frequency and survivorship, bias in population estimates was probably small (Smith 1981).

Litter size increased with female body size in both populations (Fig. 1; \( r = 0.85, n = 67, P < 0.0001 \) for Laguna, and \( r = 0.89, n = 54, \)
$P < 0.0001$ for Paredon). Females from Laguna had significantly larger litter sizes than did females from Paredon, after controlling for differences in body size with ANCOVA ($3.64 \pm 0.10 \, [n = 54]$ vs. $3.31 \pm 0.13 \, [n = 67]; F_{1,117} = 4.92, P < 0.03$). The interaction term was not significant. There was no indication in our study, or in that of Gullette and Casas-Andreu (1980), that females have more than 1 litter per year.

Lizards at both study sites were born at 19–20 mm SVL. Females attained sizes of approximately 39 mm SVL by 14 mon of age (Lemos-Espinal and Ballinger 1995a). The smallest reproductive female was 39 mm SVL at both Laguna and Paredon, but an SVL of approximately 40–42 mm was the typical minimum size of reproductive females (Fig 1). These data indicate that females at both study sites mature at an age of 14–15 mon (i.e., in their 2nd fall).

Annual survivorship ($l_x$) was calculated for 1985–86 and 1986–87 at Laguna, and for 1986–87 at Paredon. In general, survivorship tended to be greater at Laguna than at Paredon (Fig 2). The number of individuals per ha was greater at Paredon than at Laguna for all years of study (Table 1).

Contrast of the different age classes to age-specific fertility was similar at both study sites. Age classes 2 and 3 contributed the most (32% and 29% at Laguna, and 30% and 31% at Paredon; see Table 2). Average generation time was 3.32 yr for Laguna and 3.37 yr for Paredon. Replacement rates varied between years as did average population density (Table 2). Lower $R_0$ values in 1987 may have resulted because both study sites were sampled only 6 mon in 1988 (until June 1988); thus some lizards that survived from 1987 to 1988 may not have been registered.

**DISCUSSION**

In general, the 2 populations of *S. grammicus* studied here do not differ greatly in their biology. Survivorship estimates appear to be slightly higher in the Laguna population, but the difference is quite small. Growth rates and body temperatures also do not differ between these populations (Lemos-Espinal and Ballinger 1995a, 1995b). One of the few population differences is litter size. Females from Laguna, the low-elevation site, had slightly larger litters than did individuals from Paredon, the high-elevation site. This difference may help explain the difference in $R_0$ between these populations: Laguna’s $R_0$ suggests a growing population, whereas Paredon’s suggests a decreasing population. It is interesting to note that litter sizes of *S. grammicus* from lower-elevation populations (2000–3200 m) are even larger (mean = 5.2) than from our Laguna site (Guillette and Casas-Andreu 1980).

The lack of major differences between these 2 populations of *S. grammicus* is in contrast to several other studies of elevational variation in life history and demographic traits, such as growth (Grant and Dunham 1990, Smith and Ballinger 1994a) and survivorship (Smith and Ballinger 1994b). While it is tempting to attribute differences between the present study and other studies to geography (i.e., differences in latitude) or elevation (present study took place at higher elevations than other studies), such a conclusion is premature. Our results, taken along with those of Gullette and Casas-Andreu (1980), do suggest there may be additional elevational differences among populations of *S. grammicus* if a broader range of elevations were studied. Our results also suggest that further studies comparing populations at different elevations from a variety of latitudes would be useful in elucidating potential causes of life history and demographic variation in lizards (and other ectotherms).
TABLE 1. Average population density for 2 populations of Sceloporus grammicus from the Iztaccihuatl Volcano, Puebla, México for 5 yr. Densities are given as individuals per hectare.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Laguna</td>
<td>81</td>
<td>79</td>
<td>83</td>
<td>52</td>
<td>77</td>
</tr>
<tr>
<td>Paredon</td>
<td>—</td>
<td>155</td>
<td>163</td>
<td>131</td>
<td>135</td>
</tr>
</tbody>
</table>

Table 2. Age-specific fertility rates ($l_{mx}$ and $R_0$) for low- (Laguna) and high- (Paredon) altitude populations of Sceloporus grammicus from the Iztaccihuatl Volcano, Puebla, México. Absolute longevity is unknown, but 5-yr-old animals have been recorded. Life table was arbitrarily stopped at the end of the 6th yr.

<table>
<thead>
<tr>
<th>Age</th>
<th>Laguna 1985</th>
<th>Laguna 1986</th>
<th>Laguna 1987</th>
<th>Mean</th>
<th>Paredon 1986</th>
<th>Paredon 1987</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>0.423</td>
<td>0.439</td>
<td>0.273</td>
<td>0.378</td>
<td>0.207</td>
<td>0.181</td>
<td>0.244</td>
</tr>
<tr>
<td>2</td>
<td>0.375</td>
<td>0.308</td>
<td>0.243</td>
<td>0.338</td>
<td>0.334</td>
<td>0.170</td>
<td>0.252</td>
</tr>
<tr>
<td>3</td>
<td>0.239</td>
<td>0.259</td>
<td>0.154</td>
<td>0.217</td>
<td>0.233</td>
<td>0.089</td>
<td>0.160</td>
</tr>
<tr>
<td>4</td>
<td>0.152</td>
<td>0.169</td>
<td>0.099</td>
<td>0.140</td>
<td>0.145</td>
<td>0.056</td>
<td>0.102</td>
</tr>
<tr>
<td>5</td>
<td>0.095</td>
<td>0.107</td>
<td>0.062</td>
<td>0.089</td>
<td>0.096</td>
<td>0.030</td>
<td>0.063</td>
</tr>
</tbody>
</table>

$R_0$ = 1.284, 1.372, 0.831, 1.159, 1.108, 0.535, 0.821

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