

# **NATURAL HISTORY OF *LEIOCEPHALUS SEMILINEATUS* IN ASSOCIATION WITH SYMPATRIC *LEIOCEPHALUS SCHREIBERSII* AND *AMEIVA LINEOLATA***

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*Abstract.* We examined diet, habitat use, and behavior (focal animal observations of intraspecific interactions, escape behavior, and activity period) of *Leiocephalus semilineatus* from near Puerto Alejandro, Provincia de Barahona, República Dominicana, and compared some parameters to similar data collected at a site near Baní, Provincia de Peravia. *Leiocephalus semilineatus* is found in sympatry in dry scrub forests at both sites with *Ameiva lineolata*, an active-foraging teiid of approximately the same size, and at the Puerto Alejandro site with a larger congener, *L. schreibersii*. *Leiocephalus semilineatus* and *L. schreibersii* from Puerto Alejandro exhibited sexual size dimorphism, whereas *L. semilineatus* from the Baní site and *A. lineolata* did not. *Leiocephalus semilineatus* spent most of the time motionless; other observed activities were interactions with conspecifics, movement, and feeding. Lizards were active from shortly after sunrise to sundown, although activity peaked in late morning. Mean cloacal temperatures of *L. semilineatus* did not differ significantly from those of the other two species, but were significantly above ambient temperatures. Reproductive condition of collected specimens was examined and no correlation was found between snout-vent length and egg, follicle, or testis size. Clutch size was 1–2. Diets consisted primarily of invertebrates and did not differ significantly between the three species.

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Members of the iguanian lizard genus *Leiocephalus* are ground-dwelling, sit-and-wait foragers endemic to the West Indies (Pregill, 1992). Ten of the 23 currently recognized species are found on Hispaniola (Powell et al., 1996). *Leiocephalus semilineatus* ([Figure 1](#)), a Hispaniolan endemic, inhabits dry lowland habitats in the Cul-de-Sac Plain in Haiti and the Valle de Neiba and the Llanos de Azua in the República Dominicana, but may be absent from the eastern Valle de Neiba. This species has been found in dry and spiny scrub forest, open rocky terrain, along arroyos, and around garbage dumps. It is found primarily on the ground, usually perched on rocks, but sometimes in vegetation including dead agaves and small shrubs.

Several members of the genus *Leiocephalus* have been subjects of natural history studies, including *Leiocephalus carinatus* (Schoener et al., 1982), *L. psammodomus* (Smith, 1992, 1994, 1995; Smith and Iverson, 1993), *L. schreibersii* (Schreiber et al., 1993), and *L. barahonensis* (Micco et al., 1997), but little is known about the basic biology of *L. semilineatus*. Schwartz and Henderson (1991) described *L. semilineatus* as a xerophile associated with gravelly or rocky areas. In at least some parts of its range, *Leiocephalus semilineatus* is found in sympatry with the teiid *Ameiva lineolata*, an active forager of approximately the same body size, and with its larger congener, *L. schreibersii*. Because these areas of sympatry are ideal for studying niche partitioning, we examined aspects of the natural history of *L. semilineatus* and compared them to those of sympatric *L. schreibersii* and *A. lineolata* in order to evaluate the extent to which size of individual and foraging mode affect potentially competitive interactions.

## METHODS

### Study Site

The study was conducted from 29 May–14 June 1999 at a xeric site ([Figure 2](#)) between 1.7 and 3.0 km east of Canoa on the Puerto Alejandro road, Provincia de Barahona, República Dominicana. The site is in the rainshadow of the Sierra de Martín García, rendering it particularly dry. Bimodal rainfall is characteristic of the area with a minor peak in late spring and a larger peak in late summer or fall (Salcedo et al., 1983). Weather fluctuates greatly during “rainy seasons” and occasional deviations from the expected hot, dry climate are linked to variations in the numbers and behaviors of animals encountered (e.g., Powell et al., 1996). *Leiocephalus schreibersii* is common in the area, most often seen in very open, sparsely vegetated sites. *Ameiva lineolata* was more rarely encountered, usually moving in scrubby areas.

We established eight 144 m<sup>2</sup> plots for population estimates and used a 280 m section of road to observe activity and behavior. The section was generally bordered by berms of rocks and dirt, with intervening areas of variable habitats. The intervening areas included a sparsely vegetated flood plain bordered by rocky relief (to heights of about 10 m), xeric clearings, and spiny scrub forest. Prominent vegetation included cholla (*Opuntia caribaea*), melon cactus (*Melocactus communis*), *Cercus* sp., *Agave* sp., and bunch grass (*Danthonia domingensis*). In slightly less xeric sections, such as along

arroyos, trees such as mesquite (*Prosopis juliflora*), acacia (*Acacia macracantha*), and catalpa (*Catalpa longissima*) were common.

To compare diets in relation to foraging mode, we included data on *Leiocephalus semilineatus* and *Ameiva lineolata* that were collected on six previous trips to a xeric site near Baní, Provincia de Peravia (Powell et al., 1996), where *L. schreibersii* is not present. Post-preservation snout-vent lengths (SVLs) of all animals were measured to the nearest millimeter and used to calculate sexual size dimorphism (SSD) indices.

### Population Size Estimates

To estimate population sizes of *Leiocephalus semilineatus* and *L. schreibersii*, we visited study plots for 20 min/d between 0900 and 1200 for three consecutive days (Heckel and Roughgarden, 1979). We chose eight plots representing four abundant habitats: elevated rocky terrain, semi-vegetated rocky ground, rock pile and vegetation-edged road, and shady arroyos. These were situated at least 200 m apart to minimize the likelihood of site-to-site migration. *Leiocephalus* are sit-and-wait foragers, are territorial, and have small home ranges (Jenssen et al., 1989). Paint guns (Heckel and Roughgarden, 1979) were used to mark all animals found within a plot boundary, using a different color each day. To eliminate the influence of differing activity periods for the species encountered, survey times were rotated throughout the morning. First time markings and re-markings were counted and used to calculate population size (Heckel and Roughgarden, 1979). The Schnabel (1938) method was used to confirm estimates.

### Activity Period

To assess activity of *Leiocephalus semilineatus*, the same two individuals walked a 280 m transect hourly from 0645 and 1745. This procedure was similar to those used in several other studies (e.g., Rand, 1964; Smith, 1994). Rand (1964) discussed potential biases of this method. To address these issues, data were collected on three non-consecutive days. The transect was located along a road where lizards were often seen perched on rocks or foraging in the brush. The area was similar to two of the eight sampling plots, but not fully representative of the entire study site, as it included dirt and rock berms, spiny scrub, and ditches.

### Escape Behavior

To assess approach distances and responses (Regalado, 1998), we approached individual lizards at a steady rate and recorded reactions in one of three categories: retreat into a burrow or crevice, movement to another perch, or movement into vegetation. If the lizard was still visible after an initial response, a secondary response upon subsequent approach was also noted. In each instance, we marked our exact location when the lizard reacted and measured the distance to the location of the lizard before it moved.

## Focal Animal Observations

Two or more observers recorded behavior (Altmann, 1974; Schreiber et al., 1993; Durtsche et al., 1997) from a distance of 2–6 m at the same time for 10 min intervals. Only when we prematurely lost sight of a lizard were observation periods shorter. We made focal observations only of animals that did not react to our presence.

We observed 37 *Leiocephalus semilineatus* for a total of 364 min. We conducted focal observations from 0850 to 1430, with the majority of observations (53%) between 1130 and 1300. Behavior was quantified by calculating the percent time spent motionless (perching), moving, interacting, and feeding. Perching included stillness and all non-display movements, such as tail movements, head tilting, body shifting, and substrate-licking (activities that may have involved thermoregulation or surveys for the presence of potential competition, mates, or prey). Time spent moving included active foraging and shuttling between perches. We categorized display behaviors such as headbobs, pushups, and tail motions in response to the presence of other lizards as interactions. Feeding included only eating but not foraging, as the latter was often indiscernible from other movements.

## Temperature

Following focal observations and estimates of population sizes, we collected *Leiocephalus semilineatus* and *L. schreibersii* by noosing or shooting with rubber bands. We took cloacal temperatures of animals immediately after capture with Fluke 50 Series thermometers with K type thermocouples (Fluke Corp. Everett, Washington). We also recorded substrate and air temperatures at points of capture. Animals were killed by lethal injection and preserved for later analyses of diet and reproductive condition. Specimens were deposited in the Bobby Witcher Memorial Collection (BWMC 6474–78, 6487–91, 6505–17), Avila College, Kansas City, Missouri.

## Reproduction

We determined reproductive maturity of *Leiocephalus semilineatus* and *L. schreibersii* by the presence of enlarged testes in males and yolked ovarian follicles or oviductal eggs in females. We measured maximum lengths of these structures to the nearest 0.1 mm using calipers.

## Diet

We excised stomachs from *Leiocephalus semilineatus* and *L. schreibersii* from the Puerto Alejandro site and from *L. semilineatus* and *Ameiva lineolata* from the Baní site. We categorized contents as invertebrate prey (identified to order or to family in the case of ants), plant material, or grit. We counted food items, determined their volume by fluid displacement (Milstead, 1957), and noted the frequency of occurrence to calculate importance values for each item (Powell et al., 1990; Howard et al., 1999). We used importance values to calculate niche breadths (Levins, 1968),

standardized as in Hurlbert (1978), and dietary niche overlaps between species and among males, females, and juveniles within species (Pianka, 1973).

We used StatView II™ (Abacus Concepts, Inc., Berkeley, California) for statistical analyses. Means are presented  $\pm$  one SE (except population size estimates, which are presented  $\pm$  one SD). For all statistical tests,  $\alpha = 0.05$ .

## RESULTS AND DISCUSSION

### Body Size

We collected 23 *Leiocephalus semilineatus* at the Puerto Alejandro site: ten adult females, eight adult males, and five juveniles/subadults. Mean adult male SVL was  $45.8 \pm 1.2$  mm (40–52 mm) and that of adult females was  $41.1 \pm 0.8$  mm (36–44 mm). Mean juvenile/subadult SVL was  $33.6 \pm 0.9$  mm (31–36 mm). Female and male SVL differed significantly (Mann-Whitney U,  $Z = -2.86$ ,  $p = 0.004$ ). According to these data, *L. semilineatus* exhibits SSD. The SSD index was 1.11 when based on mean sizes and 1.18 when based on maximum sizes (Roughgarden, 1995). We collected 40 *L. semilineatus* at the Baní site: 16 adult females, 16 adult males, and eight juveniles/subadults. Mean adult male SVL was  $44.8 \pm 0.7$  mm ( $n = 16$ , 39–49 mm), that of adult females was  $43.3 \pm 0.5$  ( $n = 16$ , 40–48 mm), and that of juveniles/subadults was  $28.4 \pm 1.6$  ( $n = 8$ , 22–34 mm). Male and female SVL did not differ significantly ( $Z = -1.44$ ,  $p = 0.15$ ). These data indicate a lack of SSD (indices = 1.03, means; 1.02, maxima).

We collected 37 *Ameiva lineolata*: ten adult females, 14 adult males, and 13 juveniles/subadults. Mean adult male SVL was  $48.2 \pm 0.8$  ( $n = 14$ , 44–52 mm), that of adult females was  $46.9 \pm 0.8$  ( $n = 10$ , 44–51 mm), and that of juveniles/subadults was  $37.3 \pm 1.3$  ( $n = 13$ , 28–42 mm). Male and female SVL did not differ significantly ( $Z = -1.06$ ,  $p = 0.29$ ); no SSD is evident (SSD indices = 1.03, means; 1.02, maxima).

We collected 19 *Leiocephalus schreibersii*: 10 adult females, two adult males, and nine juveniles/subadults. Because we were interested in comparing diets of similarly sized animals, we collected primarily female and juvenile/subadult *L. schreibersii*, as they are most similar in size to *L. semilineatus*. Mean adult female SVL was  $55.5 \pm 0.7$  mm ( $n = 10$ , 52–59 mm), that of adult males was  $68.5 \pm 2.5$  mm ( $n = 2$ , 66–71 mm), and that of juveniles/subadults was  $35.9 \pm 1.5$  mm ( $n = 9$ , 31–43 mm). The SVL of male and female *L. schreibersii* differed significantly ( $Z = -2.16$ ,  $p = 0.031$ ). Indices of SSD (1.23, means; 1.20, maxima) were as documented by Schreiber et al. (1993).

In order to place the varying SSD indices in the two populations of *Leiocephalus semilineatus* and the greater value for *L. schreibersii* into a broader context, we calculated SSD indices for all species of *Leiocephalus* presented by Schwartz and Henderson (1991) for which both male and female SVL were available. Within the genus, SSD indices were positively correlated with size (Spearman test,  $n = 21$ ,  $Z = 2.34$ ,  $p = 0.019$ ). As a relatively large species, *L. schreibersii* has a high SSD index

compared to *L. semilineatus*, a small member of the genus. We cannot explain why this would more important in larger species, and drawing conclusions from data applicable to only one population can be misleading (see data for *L. semilineatus* above or comments in Micco et al., 1997). We hypothesize that SSD in the genus *Leiocephalus* usually is the product of intrasexual competition among males for mates (Darwin, 1871; Hendrick and Temeles, 1989). Because diets did not differ significantly between sexes in this study, the competitive niche hypothesis (Selander, 1966; Schoener, 1967) probably can be discounted. However, the degree of SSD in other species of *Leiocephalus* varies geographically, at least in the Bahamian Archipelago (e.g., Smith, 1992), and intraspecific niche divergence (*sensu* Shine, 1989) may be responsible in some instances (see also Censky, 1996).

### Population Size

At the Puerto Alejandro site, population size estimates (Heckel and Roughgarden, 1979) of our eight plots (1152 m<sup>2</sup> total area) were  $25.0 \pm 3.7$  for *Leiocephalus semilineatus* and  $5.3 \pm 1.0$  for *L. schreibersii*, indicating that the two species were sympatric at approximately a 5:1 ratio. Using the Schnabel method, we estimated a 3:1 ratio ( $26.0 \pm 0.2$  for *L. semilineatus* and  $8.3 \pm 0.4$  for *L. schreibersii*). The microhabitat of the eight plots appeared to be more suitable for *L. semilineatus* than for *L. schreibersii*, as none included the more open, treeless areas of the study site where the latter species was observed most frequently. In contrast, we saw the most *L. semilineatus* in the plots along the road and in partially vegetated rocky areas. Only one *L. semilineatus* and one *L. schreibersii* were encountered in the elevated rocky plots that received intense sunlight and had little cover.

### Activity Period

Observations while working the study plots indicated that activity began at about 0730, peaked at about 1000, and declined throughout the remainder of the day until dark. However, data collected along the transect did not correspond with this pattern. Some of the discrepancies may be attributed to the fact that we conducted several surveys of the transect on relatively cool, overcast days, during which lizards seemed less inclined to retreat into refugia. Powell et al. (1996) encountered a similar situation where abnormally high numbers of lizards were seen on cloudy days. In the current study, 79 lizards were encountered on 15 walks of the survey transect, with the greatest number of lizards found during a walk begun at 1245 ([Figure 3](#)). Activity began at about 0830, increased until early afternoon, then declined through the afternoon. The latest sightings were at 1645. Our single activity peak contrasted with the bimodal pattern observed by Smith (1994) in *Leiocephalus psammodromus* on a small cay in the Caicos Islands.

### Escape Behavior

For *L. semilineatus* the mean primary and secondary response distances were  $201 \pm 41$  cm ( $n = 20$ , 45–520 cm) and  $102 \pm 16$  cm ( $n = 10$ , 20–160 cm), respectively. For *L.*

*schreibersii* the mean primary and secondary response distances were  $385 \pm 105$  cm ( $n = 5$ , 270–595 cm) and 150 cm ( $n = 1$ ), respectively. These did not differ significantly from those of *L. semilineatus* (Mann-Whitney U,  $Z = -0.7$ ,  $p = 0.51$ ). Individuals of both species moved to other perches, in which case they were approached again, or into cover (including vegetation such as bunch grass, dead agaves, and shrubs, cracks in rocks, and burrows). On many occasions, *L. schreibersii* seemed more difficult to approach than *L. semilineatus*. The former was more frequently found in open areas and had to run considerable distances to find shelter, whereas *L. semilineatus* frequently perched on rocks under which lizards could quickly retreat. Secondary approach distances were shorter than primaries (Mann-Whitney U,  $Z = -2.4$ ,  $p = 0.015$ ). Regalado (1998) noted similar responses in Cuban *Anolis*.

### Focal Observations

We observed most animals originally perched on rocks, twigs, tree stumps, or garbage. Others were seen under brush or on dirt berms. When lizards were approached closely, they frequently responded with head bobs and/or pushups directed at the observer.

*Leiocephalus semilineatus* spent the largest percentage of time perching (mean =  $75.1 \pm 5.9\%$ , 0–100%), a qualitatively categorized “behavior” that undoubtedly including sit-and-wait foraging. Perches were almost always elevated above the surrounding substrate. Lizards used rocks more frequently than any other perches (82 of 134 recorded observations, 61.1%). Most rocks used as perches were isolated from one another but, when in piles, lizards almost always used the highest rock. We observed 32 lizards (23.9%) on sticks and debris (including trash), 14 (10.4%) on earthen berms along roads, four (3.0%) on living vegetation, and only two (1.5%) on level ground. Smith (1995) found *L. psammodomus* on litter (38.6%), trees (22.8%), bare sand (18.5%), and rocks (11.4%). Whether these differences reflect different preferences by the lizards or the availability of different perches is unknown.

The mean percentage of time spent interacting with conspecifics was  $19.3 \pm 5.9\%$  (0–100%), time spent moving was  $5.6 \pm 2.5\%$  (0–80%), and time spent feeding was  $0.006 \pm 0.005\%$  (0–0.17%). No correlation was found between time of day and percentage of time spent engaged in any of the four behavioral categories (Spearman test;  $p > 0.05$ ).

Because we made observations at different times of day, with most observations made within an hour of noon, the data may have inaccurately represented the behavior of lizards throughout an entire day. We noticed lizards basked at fully insolated sites in the morning, but moved to shaded sites or were under cover in the afternoon. During the hours when most observations were made (1130–1300 h), feeding was infrequent, possibly because the animals feed primarily at other times. Distinguishing between feeding and substrate-licking was sometimes difficult.

Interactions with other lizards constituted the second most frequently observed behavior, and primarily involved adult male-to-male and male-to-female

interactions. Juvenile/subadult lizards were most often disregarded by adults, even when moving or basking in close proximity. Males demonstrated both moderate (headbobs and pushups) and aggressive (chasing and stealing perches) behavior toward other males. On three different occasions, different individuals that appeared to be “highly agitated” followed headbobs with a wavelike raising and lowering of the body and tail. Because we failed to observe this behavior in most interactions, we believe it is limited to circumstances involving considerable stress. A similar behavior was seen in *Leiocephalus barahonensis* (R.A. Sosa, pers. obs.). Male-to-female interactions were usually not aggressive and consisted primarily of headbobs, pushups, and occasional lateral wavelike movements by females. Copulation was not observed during focal studies, but mounting was seen once during an elaborate series of displays involving two males and one female.

## Temperature

Mean cloacal temperatures of *Leiocephalus semilineatus* and *L. schreibersii* ([Figure 4](#)) did not differ significantly between species or among males, females, and juveniles/subadults within species, although body temperatures of females were higher than those of males and juveniles/subadults in both species. We also found no significant differences between environmental temperatures where specimens of the two species were collected. The mean difference between cloacal and substrate temperatures for *L. semilineatus* was  $2.90 \pm 0.4$  °C ( $n = 21$ , 0.2–6.1 °C) and between cloacal and air temperatures was  $2.61 \pm 0.32$  °C ( $n = 21$ , 0.1–6.3 °C). The mean difference between cloacal and substrate temperatures for *L. schreibersii* was  $7.0 \pm 1.5$  °C ( $n = 14$ , 1.1–19.5 °C) and between cloacal and air temperatures  $4.3 \pm 0.7$  °C ( $n = 14$ , 0.3–8.5 °C). Differences between *L. semilineatus* and *L. schreibersii* cloacal-substrate temperatures (Mann-Whitney U,  $Z = -2.54$ ,  $p = 0.01$ ) and cloacal-air temperatures ( $Z = -1.99$ ,  $p = 0.047$ ) were significant, indicating that *L. semilineatus* maintained median body temperature closer to ambient temperature than did *L. schreibersii*.

## Reproduction

Based on the presence of oviductal eggs or yolked ovarian follicles, clutch size of *Leiocephalus semilineatus* was 1–2. Mean oviductal egg length in *L. semilineatus* was  $11.0 \pm 3.2$  mm ( $n = 5$ , 6.9–14.5 mm), mean yolked ovarian follicle length was  $3.4 \pm 2.57$  mm ( $n = 3$ , 1.9–6.4 mm), and mean testis length was  $2.3 \pm 0.4$  mm ( $n = 8$ , 1.5–2.7 mm). Of the eleven adult *L. schreibersii* examined, only one female had an oviductal egg (21 mm). Two females had enlarged oviducts but had neither eggs nor yolked ovarian follicles, suggesting that eggs had been deposited recently. Mean follicle length was  $3.7 \pm 2.0$  mm ( $n = 6$ , 2.0–7.0 mm) and mean testis length  $5.0 \pm 1.4$  mm ( $n = 2$ , 4–6 mm). No correlation was found between SVL and egg, follicle, or testis length in either species (Spearman test, *L. semilineatus*: SVL-egg,  $Z = -0.10$ ,  $p = 0.92$ ; SVL-follicle,  $Z = 0.71$ ,  $p = 0.48$ ; SVL-testis,  $Z = 0.96$ ,  $p = 0.34$ ; *L. schreibersii*: SVL-follicle,  $Z = 1.81$ ,  $p = 0.07$ ; SVL-testis,  $Z = 1.00$ ,  $p = 0.32$ ).



## Diet

Food item numbers, volumes, frequencies, and importance values for all species are summarized in [Table 1](#). Twenty types of prey items were identified in *Leiocephalus semilineatus* from the Puerto Alejandro site and 18 in *L. schreibersii*. In both species, ants were the food type present in the highest numbers, volumes, and frequency. In *L. semilineatus*, coleopteran larvae ranked second in each category. In *L. schreibersii*, miscellaneous hymenopterans ranked second in volume, and coleopteran larvae ranked second in numbers and frequency. The largest single prey item in *L. semilineatus* was a millipede with a displacement of 0.04 ml found in an adult male. In *L. schreibersii*, the largest single prey item was a spider with a displacement of 0.04 ml, found in an adult female.

At the Baní site, spiders had the highest importance value in the diet of *Ameiva lineolata* and ants were most important in the diet of *Leiocephalus semilineatus*. The largest prey item in *A. lineolata* was an orthopteran with a volume of 0.35 ml found in an adult female. In *L. semilineatus*, the largest prey item was an orthopteran with a displacement of 0.70 ml found in an adult male.

We found no significant differences in total diet (based on importance values) between *Leiocephalus semilineatus* and *L. schreibersii* at Puerto Alejandro (Mann-Whitney U,  $Z = -0.21$ ,  $p = 0.83$ ); between *A. lineolata* and *L. semilineatus* at the Baní site ( $Z = -0.37$ ,  $p = 0.71$ ); between *L. semilineatus* from the Puerto Alejandro and Baní sites ( $Z = -1.08$ ,  $p = 0.28$ ); or between males, females, and juveniles within a species (Friedman test, Puerto Alejandro *L. semilineatus*,  $df = 2$ ,  $c^2 = 0.58$ ,  $p = 0.75$ ; *L. schreibersii*,  $df = 2$ ,  $c^2 = 2.03$ ,  $p = 0.36$ ; Baní *L. semilineatus*,  $df = 2$ ,  $c^2 = 0.46$ ,  $p = 0.80$ ; *A. lineolata*,  $df = 2$ ,  $c^2 = 1.00$ ,  $p = 0.61$ ).

Standardized niche breadths (B) for *Leiocephalus semilineatus* from the Puerto Alejandro site were 0.19 (females, 0.26; males, 0.33; juveniles/subadults, 0.30), for *L. schreibersii* 0.20 (females, 0.24; males, 0.16; juveniles/subadults, 0.48), for *L. semilineatus* from the Baní site 0.32 (females, 0.32; males, 0.25; juveniles/subadults, 0.41), and for *Ameiva lineolata* 0.31 (females, 0.34; males, 0.75; juveniles/subadults, 0.50). Decreasing values indicate increasing specialization; with its relatively low niche breadth value, *L. semilineatus* should be considered a specialist. However, we believe the lizards are opportunistic feeders, feeding primarily on ants only because of their abundance in the area. Schoener et al. (1982) described *Leiocephalus* from the Bahamas as “very catholic” based on the diversity of food taken. However, they also noted a correlation between increasing body size and herbivory. This could explain the paucity of plant material taken by *L. semilineatus*, but contradicts the complete absence of plants in the stomach contents of *L. schreibersii*.

Dietary niche overlap values between species and sites are summarized in [Table 2](#). Groups with high overlap values share resources, whereas groups with little overlap have different feeding habits. In *Leiocephalus schreibersii*, diets of individuals of similar size (females and juveniles) had higher overlap values than those of individuals

dissimilar in size (males to females and males to juveniles) whose diets presumably differed because of size-related feeding differences. The overlap between *L. semilineatus* and *A. lineolata* at Puerto Alejandro was low, probably a consequence of differing foraging modes. In contrast, overlap between *L. semilineatus* and our sample of *L. schreibersii* at Puerto Alejandro was high, indicating that individuals of the former species competed with smaller individuals of the latter species for many of the same food resources.

## Resource Partitioning

The ratio of *Leiocephalus schreibersii* to *L. semilineatus* seemed constant throughout the day, indicating that the two species did not partition resources temporally. We also did not find consistent evidence of prey partitioning. However, spatial partitioning occurred. *Leiocephalus schreibersii* was more common in open areas and *L. semilineatus* in rocky, vegetated areas. In addition, burrows of *L. semilineatus* were almost exclusively on slopes, whereas those of *L. schreibersii* were more common on level ground.

## SUMMARY

Although *Leiocephalus semilineatus* is the smallest member of the genus, it is relatively representative. It uses the sit-and-wait foraging strategy typical of *Leiocephalus*. Although SSD varies geographically, its absence in one population is consistent with a trend within the genus for smaller species to exhibit less SSD than larger forms. The diet of this species qualifies as “catholic,” but we found little evidence of herbivory. Again, species of *Leiocephalus* typically consume a variety of food, and the larger species are more likely to consume plants. *Leiocephalus semilineatus* frequently perches on rocks, sticks, or debris, either in isolation or in piles. This association provides some basis for habitat partitioning with sympatric *L. schreibersii*, which seemed to prefer more open areas, and with *Ameiva lineolata*. The latter is commonly seen in the same areas as *L. semilineatus*, but it rarely utilizes elevated perches and forages actively on the ground around and under the rocks and debris from which *L. semilineatus* surveys its surroundings. Daily activity peaked around midday, in contrast with bimodal patterns observed in congeners, but this may merely reflect local conditions and may vary geographically, even within species.

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