

## Sexual Dimorphism and Reproductive Characteristics in Five Species of *Leiocephalus* Lizards from the Dominican Republic

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**ABSTRACT.**—Although a highly visible component of the West Indian herpetofauna, few data address the biology of Curly-Tailed Lizards (*Leiocephalus*). We examined sexual dimorphism in size and head shape and reproductive life-history characteristics for five species of *Leiocephalus* from the Dominican Republic. Many hypotheses have been posited to explain head shape dimorphism in lizards. Previous studies on *Leiocephalus* lizards failed to support the niche divergence hypothesis. Consequently, we examined patterns of head shape dimorphism by measuring the scaling relationships of head dimensions of males and females for each species. Head dimensions of the sexes mostly scaled isometrically or with negative allometry, which may support the differential growth hypothesis, although patterns in one species (*Leiocephalus semilineatus*) suggest that sexual selection may be operative. Clutch sizes varied from 1–4 eggs across species, but mean clutch size generally does not differ significantly among species. Similarly, egg size varies little across species, with only the smallest of the species examined, *L. semilineatus*, differing significantly from the other species. Therefore, although maximum female snout-vent lengths differ by as much as 50 mm, reproductive characteristics are relatively static. These data are suggestive of an optimal reproductive strategy for *Leiocephalus* lizards, although detailed experimental data are necessary to examine this fully.

Lizards in the genus *Leiocephalus* are distributed across Hispaniola, Cuba, and various islands and cays in the Bahamas. Twenty extant species are currently recognized, with the highest species diversity found on Hispaniola (nine species; Schwartz and Henderson, 1991). On Hispaniola, the genus is found in a wide variety of habitats, ranging from extremely xeric sub-sea-level Cul-de-Sac/Neiba Valley, relatively mesic coastal areas dominated by karst cliffs dotted with sea grapes (*Coccoloba uvifera*), and high elevations in both Haiti and the Dominican Republic. Species in the Dominican Republic range in maximum size from approximately 48 mm in snout-vent length (SVL; *Leiocephalus semilineatus*) to about 107 mm SVL (*Leiocephalus schreibersii*; Schwartz and Henderson, 1991).

Despite a broad distribution and conspicuous behavior, few studies on the natural history and ecology of *Leiocephalus* lizards are available (diet, Schoener et al., 1982; Iverson and Smith, 2006; reproduction, Smith and Iverson, 1993; Smith and Nickel, 2002b; general natural history, Schreiber et al., 1993; Smith, 1994, 1995; Nelson et al., 2001; Micco et al., 1997). Here, we contribute data regarding sexual dimorphism in body size and head dimensions and data on reproductive characteristics of five species from the Dominican Republic (*Leiocephalus barahonensis*, *Leiocephalus lunatus*, *Leiocephalus personatus*, *L. schreibersii*, and *L. semilineatus*) by combining previously published information (Micco et al., 1997; Nelson et al., 2001; Schreiber et al., 1993) with recently collected data to provide a more comprehensive analysis of sexual dimorphism and life-history variation among species.

All species of *Leiocephalus* are sexually dimorphic in body size, with males larger than females; however, considerable variation in the degree of dimorphism exists (Schoener et al., 1982; Smith, 1992; Smith and

Nickel, 2002a). In addition, males tend to have larger heads than females (Schoener et al., 1982; Smith, 1992; Smith and Nickel, 2002a). A series of hypotheses are generally invoked to explain the evolution and maintenance of male-larger sexual dimorphism (Verwajen et al., 2002). First, differential mating success of large males over small males may favor the evolution of male-biased sexual dimorphism. This mechanism has been implicated in the evolution of sexual dimorphism in teiid lizards (e.g., Anderson and Vitt, 1990). Second, the dietary divergence hypothesis posits that sexual dimorphism results from the partitioning of food resources between the sexes and, thus, reduces intraspecific competition (Schoener, 1967; Preest, 1994; Herrel et al., 1996, 2001). A third alternative suggests that larger males, those with larger heads, or males with both characteristics have a mating advantage over small males because they have a greater copulatory biting capacity, which increases chances of successful fertilization (Herrel et al., 1996). A fourth hypothesis suggests that sexual dimorphism can result from differential growth related to ecological, physiological, and behavioral differences between the sexes (Anderson and Vitt, 1990; Cox et al., 2003, 2005; Johnson et al., 2005). For example, after maturity, females may invest less energy into somatic growth in lieu of investments in reproduction, whereas males may continue to invest energy into growth after maturity. In this case, the observed size dimorphism may simply be a result of differential growth after maturity.

Studies of Dominican *Leiocephalus* suggest that the niche divergence hypothesis can likely be rejected because, for the species studied, the sexes do not differ with respect to diet (Micco et al., 1997; Schreiber et al., 1992; Nelson et al., 2001). We examined scaling relationships of head dimensions in five species of *Leiocephalus* to begin exploring the factors influencing sexual dimorphism. We use these scaling relationships to suggest possible fruitful avenues to direct future research.

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We also report important life-history variables (clutch size and egg size) and examine whether or not these variables are correlated with female body size. We also compare these data with those for other species in the genus. In terms of clutch and egg size, we predict that female body size (SVL) will be positively correlated with clutch and egg size within species.

#### MATERIALS AND METHODS

We examined animals collected during the summers of 1995, 1999, 2004, and 2005. Specimens are in the Bobby Witcher Memorial Collection (Avila University, Kansas City, MO) and in the personal collection of MEG. For each specimen, we measured snout-vent length (SVL) from the tip of the snout to the posterior edge of the cloacal aperture, head length (HL) from the anterior edge of the auricular opening to the tip of the snout, and head width (HW) at the widest point of the head. Following measurements, females were dissected to determine the presence of enlarged ovarian follicles and eggs. Follicles and eggs were counted, removed from the body cavity, and measured. Egg measurements included maximum length and width. We also estimated egg volume for shelled eggs using the formula for a prolate spheroid ( $V = 3/4 \pi (L/2)(W/2)^2$ , where  $V$  is the volume and  $L$  and  $W$  represent the maximum length and width of the egg. Estimates of egg volume used mean egg lengths and widths for each female with fully developed eggs. The magnitude of sexual dimorphism (i.e., SSD index) was measured using the ratio of mean male SVL to mean female SVL for each species. All measurements (to the nearest 0.1 mm) were made using Mitutoyo digital calipers.

All statistical analyses used  $\log_{10}$ -transformed variables. To assess patterns of sexual dimorphism in head shape, we examined scaling relationships of head dimensions using reduced major axis regression (RMA software; Bohonak, 2002) of  $\log_{10}$ -transformed head measurements against  $\log_{10}$ -transformed SVL. We tested for significant allometry in each sex of each species by comparing the RMA slope to the null hypothesis of isometry (slope = 1) using paired  $t$ -tests (Zar, 1999). For those species in which the sexes differed in scaling of head dimensions, we tested the null hypothesis of similar slopes by examining the interaction term of an ANCOVA of head dimensions with SVL as a covariate for each case. Relationships between reproductive characteristics and female body size were examined using linear regression of clutch size (number of enlarged follicles or number of eggs) and egg size (egg lengths and egg volumes for fully developed eggs) against female SVL. Statistical analyses were conducted using JMP-IN version 5.1 (SAS Institute, Inc., Cary, NC).

#### RESULTS

*Body Size Dimorphism and Head Shape Allometry.*—Consistent with previous studies of sexual dimorphism in this genus, all species examined demonstrated male-biased sexual size dimorphism (Table 1). Males were significantly larger than females (for all species,  $F = 24.71$ – $166.72$ ,  $P < 0.0001$ ), although the degree of dimorphism varied considerably among species (Table 1). Scaling relationships of head dimen-

sions revealed positive (slope  $> 1$ ), negative (slope  $< 1$ ), and isometric (slope = 1) growth patterns, but species differed with respect to growth trajectories observed in each sex (Figs. 1, 2). In *L. barahonensis*, *L. personatus*, and *L. schreibersii*, HL scaled with negative allometry in both males and females. However, in *L. lunatus*, scaling of HL differed significantly between the sexes (ANCOVA,  $F_{1,70} = 5.78$ ,  $P = 0.019$ ); HL scaled with negative allometry in females but isometrically in males. In *L. semilineatus*, HL scaled isometrically in both males and females (Fig. 1). Head width also showed diverse patterns of growth (Fig. 2). Males and females of *L. barahonensis* and *L. lunatus* showed isometric growth trajectories for HW. Head width scaled isometrically for males and negatively for females in *L. personatus* and *L. schreibersii*, although only in *L. personatus* did the sexes differ significantly in allometric slope (ANCOVA,  $F_{1,43} = 9.48$ ,  $P = 0.004$ ). Head width scaling differed significantly between the sexes in *L. semilineatus* (ANCOVA,  $F_{1,102} = 17.22$ ,  $P = 0.00007$ ); HW scaled isometrically in females, but with positive allometry in males.

*Female Life-History Variation.*—The smallest female containing enlarged ovaries, yolked ovarian follicles, or shelled eggs represents an estimate of minimum size at maturity for each species. Based on these estimates, females of these species vary considerably in size at maturity (Table 2). Clutch sizes (number of enlarged follicles or number of eggs) differed significantly among species (Table 2; ANOVA,  $F_{4,86} = 5.17$ ,  $P = 0.0009$ ). A test for multiple comparisons indicated that mean clutch size of *L. schreibersii* was significantly larger than mean clutch sizes of *L. lunatus* and *L. semilineatus* (Tukey-Kramer HSD,  $P < 0.05$ ); no other species differed significantly from any other in clutch size (Table 2). However, after removing the effect of SVL, clutch sizes did not differ significantly among species (ANCOVA,  $F_{4,86} = 1.65$ ,  $P = 0.170$ ). Clutch size was weakly correlated with female SVL in *L. barahonensis* ( $F_{1,18} = 3.97$ ,  $b = 1.66$ ,  $r = 0.44$ ,  $P = 0.06$ ) but not any other species (*L. personatus*,  $F_{1,18} = 2.29$ ,  $b = 1.56$ ,  $r = 0.35$ ,  $P = 0.15$ ; *L. lunatus*,  $F_{1,10} = 0.85$ ,  $b = 2.08$ ,  $r = 0.31$ ,  $P = 0.39$ ; *L. schreibersii*,  $F_{1,17} = 1.94$ ,  $b = 1.50$ ,  $r = 0.34$ ,  $P = 0.18$ ; *L. semilineatus*,  $F_{1,23} = 0.101$ ,  $b = -0.43$ ,  $r = -0.07$ ,  $P = 0.75$ ).

Sample sizes for egg size measurements were much reduced relative to measurements of clutch sizes because only fully developed eggs were considered (Table 2). *Leiocephalus semilineatus* differed significantly from all other species in egg size (egg lengths, ANOVA,  $F_{4,25} = 6.03$ ,  $P = 0.002$ ; egg volumes, ANOVA,  $F_{4,25} = 8.91$ ,  $P = 0.0003$ ); no other species differed significantly from one another (Tukey-Kramer HSD, all  $P > 0.05$ ). In all species, egg lengths were not correlated with female body size (all regressions,  $P > 0.05$ ). Only in *L. barahonensis* was egg volume correlated with female SVL ( $F_{1,7} = 7.75$ ,  $b = 1.05$ ,  $r = 0.78$ ,  $P = 0.04$ ).

#### DISCUSSION

All species showed significant sexual dimorphism in both body size and head dimensions. In all cases, adult males were significantly larger than adult females. These results are consistent with previously published data for some of these species (Schreiber et al., 1992; Micco et al., 1997; Nelson et al., 2001) and for

TABLE 1. Sample size, morphometric data ( $\pm$  SD), and sexual dimorphism index (SSDI, ratio of mean male SVL to mean female SVL) for species of *Leiocephalus* measured for this study.

|                        | N  | SVL              | HL               | HW               | SSDI  |
|------------------------|----|------------------|------------------|------------------|-------|
| <i>L. barahonensis</i> |    |                  |                  |                  |       |
| Males                  | 37 | 64.66 $\pm$ 6.36 | 14.64 $\pm$ 1.25 | 11.45 $\pm$ 1.25 | 1.199 |
| Females                | 32 | 53.94 $\pm$ 4.63 | 12.12 $\pm$ 0.78 | 9.22 $\pm$ 0.73  |       |
| <i>L. lunatus</i>      |    |                  |                  |                  |       |
| Males                  | 50 | 58.64 $\pm$ 4.58 | 13.41 $\pm$ 0.98 | 10.26 $\pm$ 0.85 | 1.148 |
| Females                | 20 | 51.08 $\pm$ 3.37 | 11.67 $\pm$ 0.59 | 8.65 $\pm$ 0.49  |       |
| <i>L. personatus</i>   |    |                  |                  |                  |       |
| Males                  | 22 | 65.23 $\pm$ 5.90 | 14.78 $\pm$ 1.09 | 11.22 $\pm$ 1.01 | 1.335 |
| Females                | 21 | 48.85 $\pm$ 3.14 | 11.22 $\pm$ 0.56 | 8.19 $\pm$ 0.39  |       |
| <i>L. schreibersii</i> |    |                  |                  |                  |       |
| Males                  | 45 | 76.54 $\pm$ 7.18 | 16.73 $\pm$ 1.32 | 13.39 $\pm$ 1.20 | 1.263 |
| Females                | 54 | 60.61 $\pm$ 5.05 | 13.28 $\pm$ 0.80 | 10.44 $\pm$ 0.75 |       |
| <i>L. semilineatus</i> |    |                  |                  |                  |       |
| Males                  | 68 | 45.53 $\pm$ 2.97 | 10.91 $\pm$ 0.70 | 8.04 $\pm$ 0.63  | 1.066 |
| Females                | 34 | 42.69 $\pm$ 2.11 | 9.85 $\pm$ 0.47  | 7.08 $\pm$ 0.30  |       |

species of *Leiocephalus* in general (Schoener et al., 1982; Smith, 1992; Smith and Nickel, 2002a). This study differs from those previously published for Dominican species in that we not only considered dimorphism in body and head sizes but also scaling relationships of head dimensions. The scaling of head dimensions revealed that, in most species, sexual head-size dimorphism in adults results from differential growth after maturation (only sexually mature animals were included). In all species but *L. semilineatus*, HL and HW scaled isometrically or with negative allometry. This suggests that, after maturation, head dimensions either increase more slowly or at approximately the same rate as body size. The causes of these patterns are unclear but could result from physiological differences between the sexes (e.g., Cullum, 1998) or from selection for other characters (e.g., devotion of energy by females to reproduction rather than growth), neither of which can be discerned with these data.

In *L. semilineatus*, HL scaled isometrically in both sexes, but HW scaled with positive allometry in males and isometrically in females. These divergent patterns of growth in head dimensions between the sexes may suggest selection for larger male head size. Head size is generally related to bite force (Herrel et al., 1996, 2001). Because dietary analyses suggested that male and female *L. semilineatus* do not differ with respect to diet (Nelson et al., 2002), increased male head size may be related to intrasexual competition and mating. Male-male competition is generally associated with territorial defense or defense of critical resources like food or thermoregulatory sites. The limited data that are available regarding *Leiocephalus* behavior suggest that males are territorial (Jenssen et al., 1989). Consequently, increased head size may be related to increased bite force necessary to win male-male contests, but increased bite force (via increased head size) also may be useful in copulatory interactions. Males with higher biting capacities may be better able to subdue females during mating, which may be

particularly beneficial when the sizes of males and females are similar. *Leiocephalus semilineatus* has a sexual dimorphism index of 1.07, the lowest of any *Leiocephalus* species. Consistent with this assertion, bite force in *L. semilineatus* males scales with a slope nearly twice that observed in males of the other Dominican species (data for *L. lunatus* unavailable, MEG, unpubl. data). Bite force is correlated with both fighting capacity (Lailvaux et al., 2004) and fitness (Lappin and Husak, 2005) in some lizard species.

Empirical data regarding life-history variation in *Leiocephalus* lizards are largely limited to anecdotal observations (Schwartz and Henderson, 1991; Rodriguez-Schettino, 1999). The single exception is for *L. psammotromus* (Smith and Iverson, 1993), although Smith and Nickel (2002b) reported limited data for the Cuban species, *L. macropus*, *L. raviceps*, and *L. stictigaster*. Dominican species varied considerably in size at maturity, and these estimates appear to be associated with mean adult body size. Although Micco et al. (1997) showed differences in the timing of reproductive activity in two geographically proximate populations of *L. barahonensis* where environmental factors varied, whether transitory or cyclical differences in weather (i.e., precipitation) or habitat quality influence these life-history traits is unclear. Ideally, data would be collected over extended periods on growth and reproduction in the field, but this information is unavailable for *Leiocephalus*. Consequently, our estimates should be considered tentative until long-term data from natural populations become available.

Clutch sizes varied from 1–4 eggs across species, but mean clutch sizes generally do not. The only significant differences were between *L. schreibersii* (the largest species examined) and *L. lunatus* and *L. semilineatus* (the two smallest species). Similarly, egg sizes of *L. semilineatus* were significantly smaller than in the other species, which did not differ from one another. Therefore, *Leiocephalus* exhibit relatively low variation in clutch and egg size across species. These

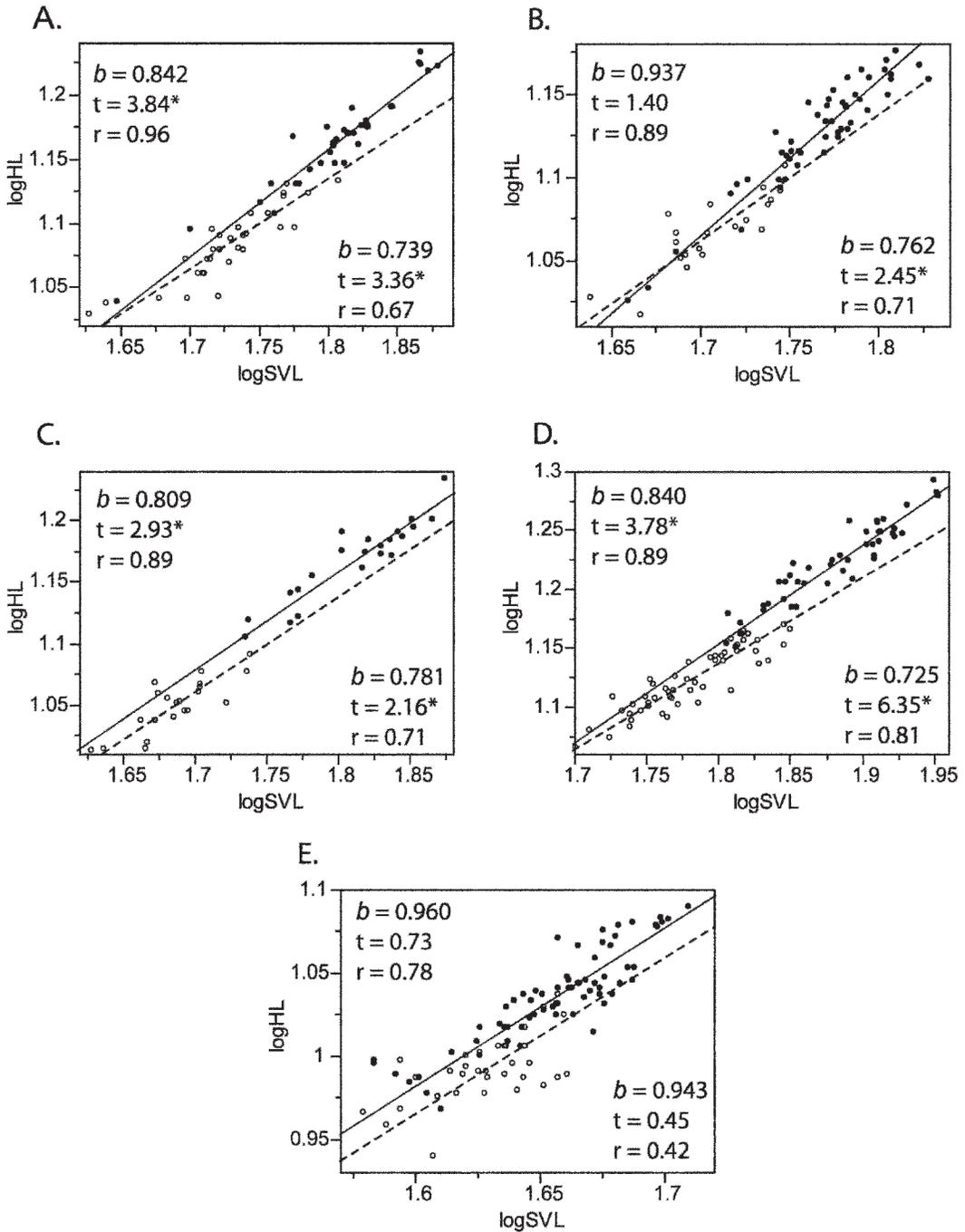


FIG. 1. Intersexual scaling relationships of log-transformed head length (HL) for five species of *Leiocephalus* lizards from the Dominican Republic. Open circles represent data for females; solid circles represent data for males. Dashed and solid lines represent RMA regression lines for females and males, respectively. The upper left portion of each plot contains the slope ( $b$ ), correlation coefficient ( $r$ ), and the absolute value of the  $t$ -statistic ( $t$ , test of the null hypothesis of isometry,  $b = 1$ ) for males. The lower right portion of each plot contains corresponding data for females. Asterisks indicate slopes that differ significantly from isometry. Each plot contains data for a different species: (A) *Leiocephalus barahonensis*; (B) *Leiocephalus lunatus*; (C) *Leiocephalus personatus*; (D) *Leiocephalus schreibersii*; and (E) *Leiocephalus semilineatus*. Note that the scaling of axes differs on some plots.

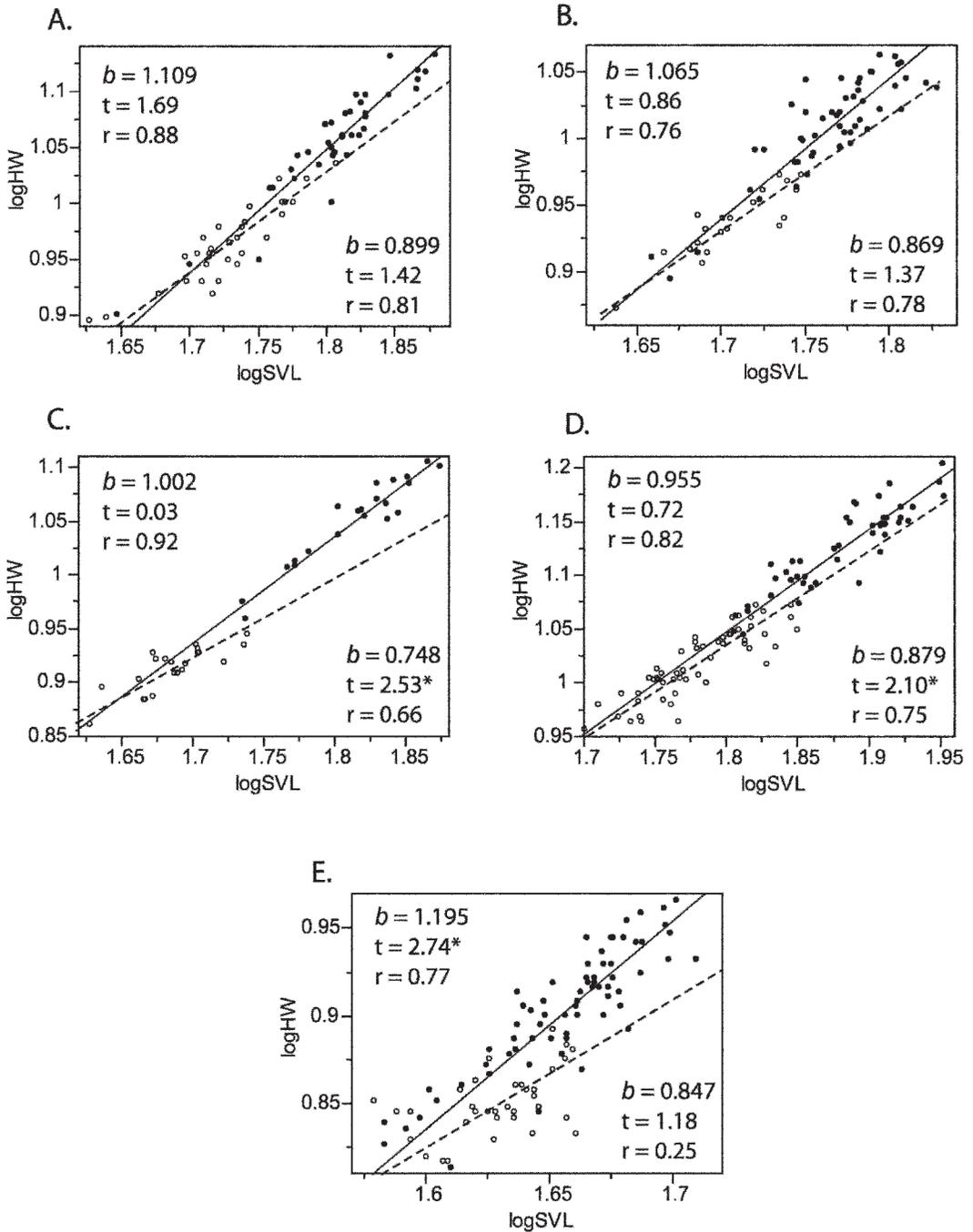


FIG. 2. Intersexual scaling relationships of log-transformed head width for five species of *Leiocephalus* lizards from the Dominican Republic. Data presentation (i.e., symbols, regression lines, etc.) are as in Figure 1.

results are consistent with the few available data for other species (Smith and Iverson, 1993; Smith and Nickel, 2002b), suggesting that, although *Leiocephalus* vary considerably in female body size (~42–90 mm SVL), mean clutch sizes are relatively constant and range from 2–3.

*Leiocephalus* has a mostly tropical distribution (only *L. carinatus* in the Northern Bahamas ranges far beyond the tropics). Clutch sizes for those northern populations are mostly unknown but tend to be higher than for the other species and populations examined to date (A. Herrel, pers. comm.; for in-

TABLE 2. Estimated female size at sexual maturity and descriptive statistics for reproductive characteristics in five species of *Leiocephalus* lizards from the Dominican Republic.

| Species                | SVL <sub>mature</sub> | Clutch size (N)  | Egg length (N)   | Egg volume (cm <sup>3</sup> ) |
|------------------------|-----------------------|------------------|------------------|-------------------------------|
| <i>L. barahonensis</i> | 47.8                  | 2.06 ± 0.54 (18) | 15.05 ± 1.22 (7) | 112.50 ± 13.64                |
| <i>L. personatus</i>   | 42.5                  | 2.0 ± 0.59 (18)  | 15.49 ± 1.35 (5) | 113.38 ± 12.54                |
| <i>L. lunatus</i>      | 46.5                  | 1.6 ± 0.52 (10)  | 13.45 (1)        | 92.45                         |
| <i>L. schreibersii</i> | 51.4                  | 2.47 ± 0.72 (17) | 16.29 ± 1.31 (4) | 117.99 ± 10.19                |
| <i>L. semilineatus</i> | 38                    | 1.78 ± 0.42 (21) | 12.89 ± 1.37 (8) | 82.84 ± 13.78                 |

roduced *L. carinatus* in Florida, see Meshaka et al., 2006). This is consistent with the hypothesis that low clutch size may evolve more commonly in less variable environments (James and Shine, 1988), which has been invoked to explain the gradient in degrees of sexual dimorphism in populations of *Leiocephalus* lizards in the Bahamas (Schoener et al., 1982).

Within-species clutch size was only weakly correlated with female body size in one of five species (*L. barahonensis*). The only other species for which these data are available is *L. psammodromus* (Smith and Iverson, 1992), in which no relationship existed between clutch size and female SVL. Thus, for the six species in which this relationship has been examined, only one shows any correlation. The relatively low variation in clutch and egg sizes among species may suggest an optimal reproductive strategy for *Leiocephalus*. Optimal egg-size theory suggests that the minimum size of an egg is constrained by the minimum offspring size necessary for survival (Brockelman, 1975). Maximum egg size, however, may be physically constrained (e.g., volume of the body cavity or energy availability). In tropical island systems, competition may be intense because of high lizard densities, suggesting that reproductive characteristics may be under energetic constraints (Tinkle et al., 1970). Tinkle et al. (1970) predicted that fast-maturing species subjected to energy constraints would produce small clutches of large eggs. Reproductive output also may be distributed among multiple annual clutches, which is likely the case in at least some populations of *Leiocephalus* (e.g., Smith and Iverson, 1993).

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