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Reviewed work(s):

Source: *Herpetologica*, Vol. 51, No. 4, Papers from the Savannah River Ecology Laboratory (Dec., 1995), pp. 401-411

Published by: [Herpetologists' League](#)

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MORPHOLOGICAL CHARACTERISTICS OF THE LIZARD *ANOLIS CAROLINENSIS* FROM SOUTH CAROLINA

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ABSTRACT: We report morphometric data for 721 *Anolis carolinensis* from a pine-oak community near Aiken, South Carolina. We recorded an adult male:female ratio of 1.18:1. For our sample, a sexual dimorphism of larger males was reflected in snout-vent length (SVL) and body mass, with an average 10% bias for SVL and 30% for mass. Proportioned to respective SVL, tail length, head length, and head width tended to be larger in males. However, reduced major axis analyses indicated that these sex-biased dimorphisms were isometric, primarily reflecting the same male-larger scale relationship, and not disproportionate sexual dimorphic morphologies. The percent frequency of regenerated tails was unusually low (8%) and similar for both sexes. Coefficients of body condition indicated that lizards were heaviest during the post-breeding season (August–November) and lightest during the breeding season (April–July). Comparison of data from our population in South Carolina to those from other conspecific populations and anoline species suggests that (1) the intersexual difference in SVL increases with latitude, (2) the SVL/tail length ratio of *A. carolinensis* is intermediate between anoline “jumpers” and “runners”, indicating a generalist at locomotion, and (3) at present, the sexual selection hypothesis, in contrast to the competition avoidance hypothesis or the female fecundity hypothesis, best explains the sexual size dimorphism observed in a northern latitude population of *A. carolinensis*.

Key words: *Anolis carolinensis*; Coefficient of condition; Locomotion; Morphology; Sexual dimorphism

MALES and females may differentially allocate resources to reproduction and growth, and these differences can result in differences in morphological traits (sexual dimorphism: SD) or body size (sexual size dimorphism: SSD) between the sexes (Darwin, 1871; Trivers, 1972, 1985). To explain sexual differences in organisms, the following three major hypotheses have been proposed: (1) the female fecundity hypothesis—females are larger than males because larger body size is associated with increased number or size of eggs, (2) the competition avoidance hypothesis—differences in head and mouth size and differences in microhabitat use result in decreased intersexual competition for resources, and (3) the sexual selection hypothesis—males are larger than females

because large male size is favored in male-male disputes over breeding territories (Darwin, 1871; Hedrick and Temeles, 1989; Schoener, 1977; Shine, 1989, 1990; Stamps, 1983, 1995).

The green anole (*Anolis carolinensis* Voigt) offers an opportunity to investigate SSD because it exhibits the third greatest SSD (snout-vent length) of 54 species of *Anolis* examined (Fitch, 1976). In addition, *A. carolinensis* is the most northerly distributed species of this tropical genus (Williams, 1969). It ranges from Florida to Tennessee (Conant, 1975) and geographically exhibits genotypic clines (Wilson and Echternacht, 1987), taxonomic differentiation (Christman, 1980; Wade et al., 1983; Wilson and Echternacht, 1990), and phenotypic plasticity (Michaud, 1990). *Anolis carolinensis* is exposed to a diversity of habitats across its range and to broad annual fluctuations in vegetation density, photoperiod, air temperature, and food availability, particularly in more northern populations. Thus, *A. carolinensis* provides an opportunity to examine variation in body size and morphological traits

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among populations with varying environmental conditions.

We examined data on the following characteristics of *A. carolinensis* in a population from the northern portion of its range: (1) sex ratios of adults, (2) tail break frequencies, (3) body size, (4) morphological traits, and (5) SSD. We compared data from this study to data collected on *A. carolinensis* throughout its range as well as with data on congeners. In addition, data on SSD for *A. carolinensis* were examined in relation to the hypotheses presented above.

MATERIALS AND METHODS

The study was conducted on the Savannah River Site (SRS), approximately 20 km south of Aiken, South Carolina at 33.5° latitude and 171 m elevation. The site is situated in an oak-pine community (Workman and McLeod, 1990) and experiences an annual rainfall of about 107 cm, an average daily air temperature of 17 C, and mean monthly extremes of 28 C (July) and 8 C (January; NOAA, 1992).

Morphometric measurements were made on 721 individuals during year-round censuses. The sex of lizards collected was determined from post-anal scales, and each individual was toe clipped for identification. The present data set does not include information from recaptured lizards. Some or all of the following variables were recorded from each lizard before its release at the point of capture: (1) snout-vent length (SVL) to the nearest 1.0 mm ($n = 326$ males, 395 females), (2) body mass to the nearest 0.01 g using a calibrated Pesola balance ($n = 353$ males, 354 females), (3) tail length to the nearest 1.0 mm, with tail break and regenerated portion recorded ($n = 342$ males, 346 females), and (4) head width and head length to the nearest 0.01 mm using a micrometer ($n = 34$ males, 23 females). In addition, calculated variables included (1) the coefficient of condition ($\text{body wt}^{0.33} \times 100/\text{SVL}$; Andrews et al., 1983), (2) total length (SVL + tail length), (3) ratio of SVL/total length, (4) ratio of tail length/SVL, (5) ratio of head width/SVL, and (6) ratio of head length/SVL.

Based on information from Dessauer (1955), Gordon (1956), Licht (1971, 1973), and Janssen et al. (1995), the year was divided into three seasonal periods: (1) "wintering", a period of little or no activity from December–March, (2) "breeding", a period of social and reproductive activity from April–July, and (3) "post-breeding", a period of enhanced foraging and minimal social activity from August–November.

We used nonparametric procedures (Siegel and Castellan, 1988) for comparisons when possible. Where a variable was comprised of a ratio, residuals were used for subsequent analyses (Packard and Boardman, 1987). Regression analyses followed two concepts. First, we used a conventional least squares regression, where body proportions (dependent Y variable) were regressed against SVL (independent X variable), to indicate a predicted size for the Y variable given a particular value of SVL. Second, we used a reduced major axis analysis (Sokal and Rohlf, 1995), as recommended by Harvey and Pagel (1991), Krebs (1989), and Ricker (1984), for examining isometric and allometric relationships between body proportions and for making tests of significance between groups of lizards. In the reduced major axis analysis, no variable is considered dependent or independent, and all variables are considered to be measured with an unknown amount of error. A central trend line with 95% confidence limits was generated from a functional or geometric mean regression in which the data were first transformed to natural logs (Green, 1992). In cases where the resulting slope is not significantly different from 1, an isometric relationship is suggested; where the slope significantly differs from 1, an allometric relationship is suggested. In all statistical tests, the null hypothesis was rejected at ≤ 0.05 . Statistical analyses were carried out using SAS (1985) software.

RESULTS

Sex Ratio

For 132 male and 157 female juveniles (SVL < 45 mm), the male:female ratio

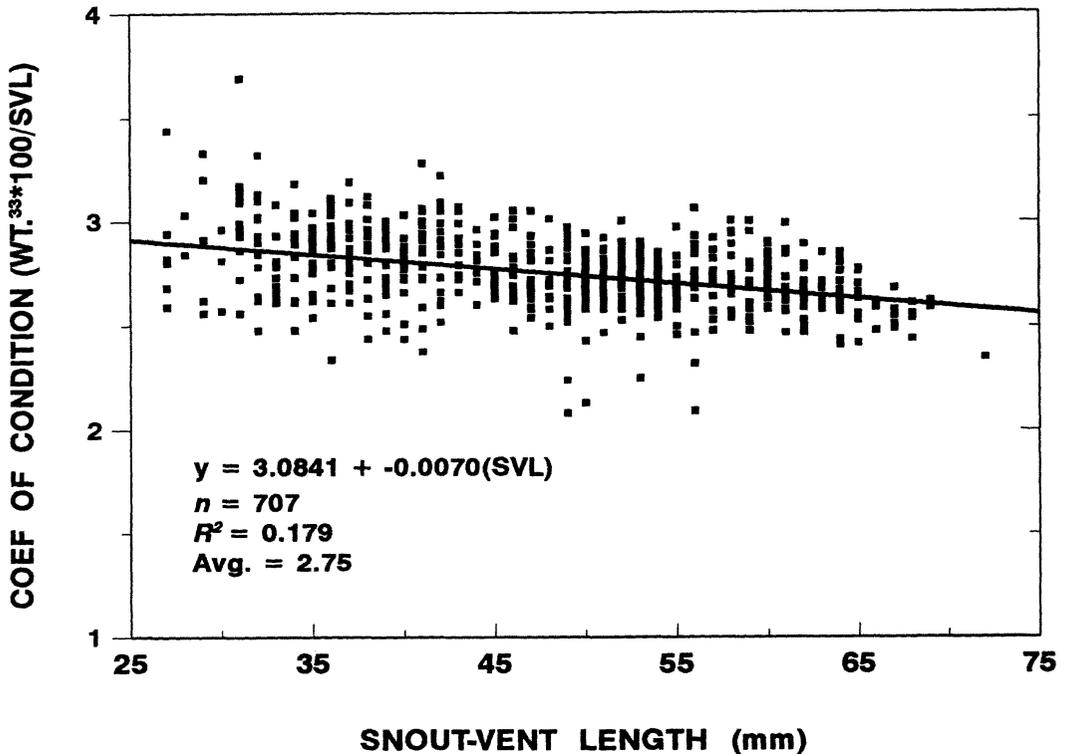


FIG. 1.—Linear regression of coefficients of condition on snout-vent length for 707 individuals of *Anolis carolinensis* from the Savannah River Site, Aiken, South Carolina.

was slightly biased toward females (0.84) but did not significantly vary from a 1:1 ratio (Chi square goodness of fit test, $\chi^2 = 2.16$, $P = 0.15$). The adult male:female ratio (1.18), derived from 248 males and 211 females, did not significantly vary from a 1:1 expectation (Chi square goodness of fit test, $\chi^2 = 2.98$, $P = 0.09$).

Tail Breaks

We recorded only 8.2% of all females ($n = 342$) and 8.4% of males ($n = 346$) as having regenerated tails. The frequency of tail breaks of males or females (Kruskal-Wallis test, $\chi^2 = 0.427$, $P > 0.81$ and $\chi^2 = 0.107$, $P > 0.95$, respectively) was not significantly different among seasons.

Body Condition

Coefficients of condition generated from juveniles and adults showed a significantly negative correlation with SVL (Fig. 1). Regressing the residuals of the coefficients of

condition on their respective SVLs, adults within each of the three seasons exhibited the same overall negative relationship seen in Fig. 1. A two-way factorial analysis, using sex and season as independent variables and the coefficient of condition as the dependent variable, found no significant effect due to sex ($F_{1,435} = 0.05$, $P = 0.818$), but did find significance due to season ($F_{1,435} = 4.45$, $P = 0.012$) with a sex/season interaction ($F_{2,435} = 3.04$, $P < 0.049$). Mean coefficients of condition for both sexes were greatest for the post-breeding period ($2.75 \pm \text{SE } 0.043$) and least during the breeding season ($2.68 \pm \text{SE } 0.007$), in spite of the fact that the breeding season sample contained gravid females.

Body Size and SSD

Male and female SVLs averaged 57.4 mm ($\text{SE} \pm 0.42$, $\text{SVL}_{\text{max}} = 72$ mm) and 52.2 mm ($\text{SE} \pm 0.22$, $\text{SVL}_{\text{max}} = 61$ mm), respectively. Adult ($\text{SVL} \geq 45$ mm: Gor-

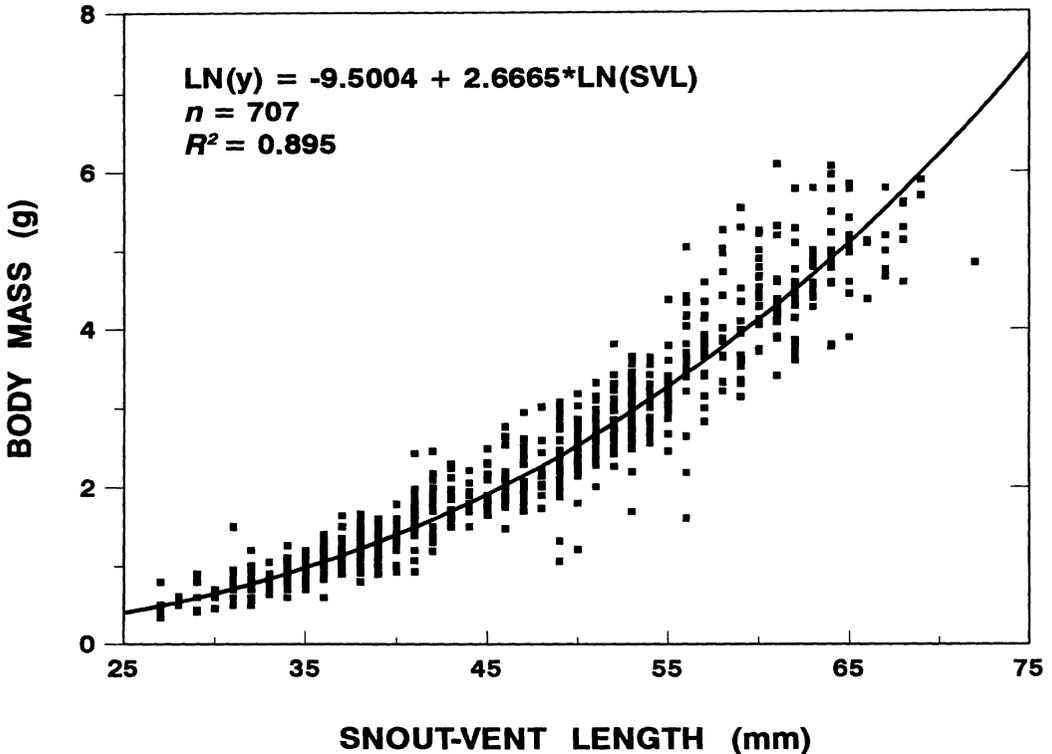


FIG. 2.—Exponential relationship of body mass on snout-vent length for 707 individuals of *Anolis carolinensis* from the Savannah River Site, Aiken, South Carolina.

don, 1956) males ($n = 248$) were larger than females ($n = 211$) and exhibited significant SSD (SVL male:female ratio of 0.909; Kruskal-Wallis test, $\chi^2 = 45.5$, $P < 0.0001$). In addition, males were approximately 24% heavier in mean body mass than were females. Body mass was exponentially correlated with SVL ($R^2 = 0.895$; Fig. 2).

Sexual Dimorphism in Morphology

We examined three body size ratios of adults: SVL/total length, head width/SVL, and head length/SVL (Table 1). For both sexes, SVL averaged 38% of the lizard's total length (Table 1). Males showed a slightly longer tail length in relationship to SVL than females, only manifesting approximately a 5% longer tail length at larger body sizes (>55 mm SVL) (Fig. 3A, B). This difference in SD, when using residuals from the tail length/SVL regressions of 346 males and 342 females, was signifi-

cant (Kruskal-Wallis test, $\chi^2 = 15.560$, $P < 0.0001$). The SSD in tail length, however, was not significant when examined by a reduced major axis analysis (Table 2). From log transformed data, the 95% confidence intervals for the male and female slopes partially overlapped, indicating non-significance by this robust test. However, the two slopes were greater than one which suggested that tail growth is allometric for both sexes.

Head width and length in proportion to a lizard's SVL also reflected borderline SSD in our sample (Fig. 4A, B; Table 1). When using the residuals of 23 male and 34 female head width and head length ratios with SVL, a significant SSD resulted, with both ratios being largest for males (Kruskal-Wallis test, $\chi^2 = 24.40$, $P < 0.0001$ and $\chi^2 = 16.46$, $P < 0.0001$, respectively). However, a reduced major axis analysis indicated that the SSD in head width and head length was an isometric relationship

TABLE 1.—Morphometric measurements and tail break frequency in *Anolis carolinensis* from the Savannah River Site, Aiken, South Carolina. Data are means, standard errors (SE), and sample sizes (n) of snout-vent length (SVL), body mass (WT), total body length (TL), and ratios using residuals involving head width (HW) and head length (HL) for adults (SVL > 44 mm).

Variable	Males			Females		
	Mean	(SE)	n	Mean	(SE)	n
SVL (mm)	57.4	(0.42)	248	52.2	(0.22)	211
WT (g)	3.79	(0.077)	234	2.89	(0.052)	207
TL (mm)	154.7	(1.59)	241	143.3	(3.57)	202
SVL/TL	0.377	(0.004)	241	0.376	(0.004)	202
HW (mm)/SVL	0.164	(0.001)	23	0.149	(0.002)	34
HL (mm)/SVL	0.269	(0.003)	23	0.239	(0.002)	34
Tail breaks (%)	8.4		346	8.2		342

(Table 2). Regressions for both sets of variables produced slopes that were not significantly different from one, and the overlap in 95% confidence intervals also indicated that there was no intersexual difference for either variable (Table 2).

DISCUSSION

Sex Ratio

Because sex ratios of both juveniles and adults on the SRS did not vary from one, it does not appear that differential mortality occurs between the sexes. Ruby (1984) also observed a sex ratio that did not differ significantly from a 1:1 ratio for a population of *A. carolinensis* from Louisiana. However, Ruby (1984) reported an average of 2.0 resident females per male territory in the latter population, and 2.8 (Jenssen et al., 1995) and 3.0 (Nunez, 1994) resident females in a population 30 km from our SRS population. Thus, the male:female sex ratio within the territories of breeding males can average 1:3. The contradictory ratios between census data and those made from longitudinal observations of marked groups of lizards suggest two inferences. The first possibility is that adult males may experience a higher mortality rate than females, but the census data are over-representing adult males due to their conspicuousness (male-biased) while under-representing the more cryptic females. The second and more likely possibility is that the adult sex ratio is unbiased, and there is a relatively large number of adult males whose home ranges have few or no inclusive females.

Tail Breaks

Regenerated tails can be interpreted as failed predator attempts that may indicate efficient anti-predator behavior or poor predator efficiency (Arnold, 1988; Congdon et al., 1974; Schoener, 1979) or ag-

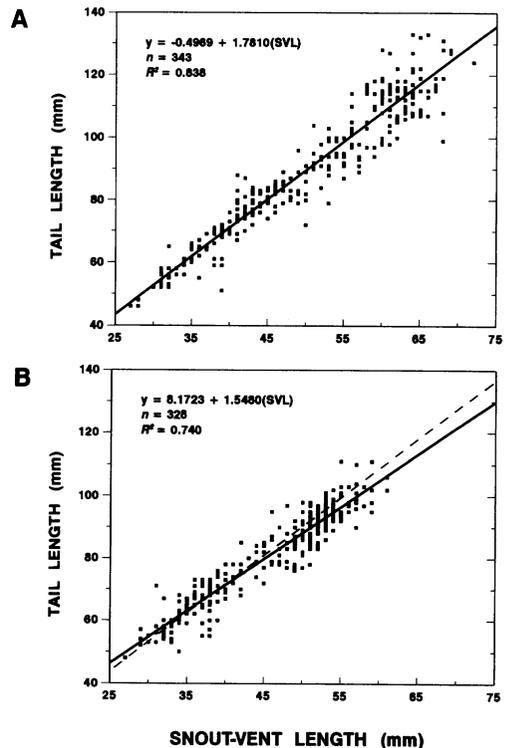


FIG. 3.—Linear regression of tail length on snout-vent length for (A) males and (B) females of *Anolis carolinensis* from the Savannah River Site, Aiken, South Carolina; dashed line represents the corresponding regression line from the data for males.

TABLE 2.—Reduced major axis analysis of morphometric variables, tail length (TL), head length (HL), and head width (HW), in which each are regressed with snout-vent length using natural log transformed data from adult males (M) and females (F) of *Anolis carolinensis* from the Savannah River Site, Aiken, South Carolina. Regression statistics are sample size (n), line intercept (INT), line slope (SLO), standard error of the line slope (SE), and lower and upper 95% confidence intervals of the line slope (LCL and UCL).

Variables	Sex	n	INT	SLO	SE	LCL	UCL
TL/SVL	M	153	-5.107	2.376	0.179	2.023	2.730
	F	198	-3.375	1.987	0.132	1.726	2.248
HL/SVL	M	23	-1.789	1.165	0.086	0.995	1.334
	F	34	-2.167	1.238	0.120	1.002	1.474
HW/SVL	M	23	-1.407	0.939	0.051	0.840	1.039
	F	34	-2.577	1.174	0.184	0.811	1.537

gressive social interactions (Jensen and Marcellini, 1986; Vitt et al., 1983, 1974, 1977). In our sample of 688 individuals, tail break frequency was about 8% for both sexes, regardless of season. The frequency of tail break is low in comparison with other anoles. For example, 40% of the adult males ($n = 502$) and 37% of the adult fe-

males ($n = 465$) of *A. opalinus* from Man-deville, Jamaica had regenerated tail segments (Jensen, unpublished data), and in the Bahamas 24% ($n = 144$) of *A. angusticeps*, 29% ($n = 847$) of *A. sagrei*, and 32% ($n = 177$) of *A. distichus* exhibited tail breakage (Schoener and Schoener, 1980). Schoener and Schoener (1980) found only a 7% ($n = 104$) tail injury frequency in the Bahamian *A. carolinensis*, a value similar to that observed for the population from South Carolina. The interpretation of tail break frequencies is difficult at best (Arnold, 1988), but the lack of different tail break frequencies between the sexes in the population at SRS suggests that aggressive interactions among males is not a factor. Schoener and Schoener (1980) have also suggested low survival rates for *A. carolinensis* as an explanation for low tail break frequency; however, tail break rates, when corrected for differential survival, were still lowest for *A. carolinensis* than for the other Bahamian congeners. The low frequency of tail break for *A. carolinensis* could suggest either weak predation pressure or efficient predators that allow few individuals to escape by tail autotomy. The nature of available demographic data for continental *A. carolinensis* (Gordon, 1956; King, 1966) and the lack of any estimate of mortality rates or predator pressure preclude more detailed interpretation for the unusually small number of tail breaks in our sample.

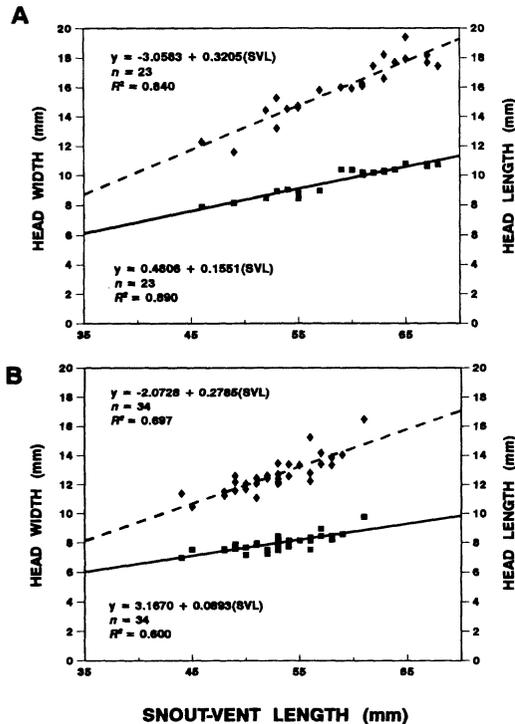


FIG. 4.—Linear regressions of head width (solid line) and head length (dashed line) on snout-vent length for (A) males and (B) females of *Anolis carolinensis* from the Savannah River Site, Aiken, South Carolina.

Body Condition

The coefficient of condition for both male and female *A. carolinensis* showed

a significant seasonal variation. Lizards were heaviest during the post-breeding period and lightest during the breeding season (significant season effect), even though some female mass included eggs during the breeding season (sex/season interaction). Ruby (1984) also recorded loss of mass for large active male *A. carolinensis* over the course of the breeding season. In contrast, both sexes of a Jamaican congener (*Anolis opalinus*) showed a positive correlation between their coefficient of condition and their reproductive condition (Jenssen and Nunez, 1994). *Anolis opalinus* is known to have a relatively constant annual food intake (Floyd and Jenssen, 1983). It may be expected that those species of *Anolis* whose food availability is distinctly altered by season (i.e., *A. carolinensis* in South Carolina) will respond with much more dramatic seasonal shifts in reproductive output, food gathering activity, energy storage, and coefficient of condition than those species for which food is more readily available throughout the year.

Body Size and SSD

Body size is a variable of interest when developing evolutionary theories because it is considered a selected character within a suite of coevolved traits that reflect an organism's life history and behavioral organization (e.g., Alcock, 1993; Stearns, 1992; Yodzis, 1989). Gibbons and Lovich (1990) discussed the causal explanations and the methodological problems with measurements of SSD and cautioned that body size of the respective sexes is the evolutionarily important consideration, not the body ratio that results. The following observations indicate that body size is an important trait in *A. carolinensis*. Michaud (1990) found that female body size, egg size, juvenile size, and growth rates increase with latitude. Adult female size on the SRS was essentially identical to Michaud's data from a population in Beaufort County, South Carolina at a similar latitude, thus fitting the proposed latitudinal gradient of increasing body size for *A. carolinensis*. For solitary insular anoles (i.e., having no congeners), body size appears

to converge toward a SVL range of ≈ 65 –80 mm for males and 40–60 for females (Schoener, 1969). Recent models based on energetics and foraging tactics support the concept of an "optimal" anoline body size (Naganuma and Roughgarden, 1990). Adults of *A. carolinensis* on the SRS represent a solitary mainland anole and their SVLs fall in the lower end of the "optimal" range for body size of solitary island anoles. The increase in body size with latitude in northern populations results in an even better fit to the predicted "optimal" body size of *Anolis* (Naganuma and Roughgarden, 1990).

Besides body size, per se, the extent of SSD in *A. carolinensis* is also important. In the comparison of 54 mainland species of *Anolis*, only two species had a more extreme "male-largest" SSD than *A. carolinensis* (Fitch, 1976; SSD presented as a ratio of female:male SVLs, so that ratios < 1 indicated a male-largest SSD and > 1 a female-largest SSD). The surveyed SSD ratios ranged from 0.74–1.25, with an average ratio of 0.789 for data collected from a variety of populations of *A. carolinensis* (Fitch, 1976). In addition, the degree of SSD also varies among populations of *A. carolinensis*. The SSDs for a Florida population (Michaud, 1990), our South Carolina population, and a population from Tennessee (Michaud, 1990) were 0.93, 0.91, and 0.86 respectively. The SSDs observed for these three populations indicate an intermediate SSD ratio for *A. carolinensis* from South Carolina and suggest a latitudinal effect, at least within the genetically grouped eastern populations (Wade et al., 1983).

Sexual Dimorphism in Morphology

The comparison of the tail length/SVL proportion of *A. carolinensis* with those found in the morphometric/locomotion analysis of seven Hispaniolan and six Costa Rican anoles (Moermond; 1979a,b; Pounds, 1988) showed the ratio for *A. carolinensis* to be intermediate between "jumpers" (proportionately long tails) and "runners" (short tails). The tail length data from our study provide an initial impression of *A. carolinensis* as a locomotory generalist.

Behavioral data also support a generalist's label. An activity profile study (Jenssen et al., 1995) documented a dramatic seasonal effect on locomotion by *A. carolinensis*. Prior to August, breeding males devoted a fourth of their day to walking, running, and jumping as they crisscrossed their territories; this pattern of rapid locomotion was replaced with creeping at the onset of the post-breeding months. Furthermore, males of *A. carolinensis* defied the usual classifications for microhabitat specialists (sensu ecomorphs: Williams, 1983), being seen from the ground to >30 m high and from tree trunks to the thin twigs of the canopy and bushes (Jenssen et al., 1995). With such a wide spectrum of gaits and microhabitat, a generalist's morphology would seem adaptive.

Sexual Dimorphism Hypotheses

The observation that males and females within a population differ in body size or morphological structures has resulted in a number of evolutionary theories and considerable speculation and debate about the causes of SSD (Darwin, 1871; Hedrick and Temeles, 1989; Schoener, 1977; Shine, 1989, 1990; Stamps, 1983, 1995). Our data on SSD are discussed in relation to the three major evolutionary SSD hypotheses presented in the introduction.

The female fecundity hypothesis does not have particular application to *A. carolinensis*, because males are larger than females. Anolines appear to be phylogenetically constrained by single egg clutches (Smith et al., 1973) and therefore cannot increase clutch size with increases in body size. There is evidence for a subtle relationship between female size and fecundity. Michaud (1990) found that northern populations of *A. carolinensis* have a larger female size and a larger egg size than do southern populations. He viewed the larger egg as an adaptation to the climate of higher latitudes because of associated shorter incubation time and larger hatchling size. Michaud indicated that an increase in size of the pelvis was required to accommodate the larger egg. In general, however, increased reproductive output for anoline females is limited to decreasing the

period between egg laying and extending the breeding season, both of which do not require an increase in body size.

The competition avoidance hypothesis is also of doubtful application, because *A. carolinensis* lacks the predicted life history and allometric characteristics. A competition avoidance effect is expected to produce intersexual shifts in morphological structures for species having (1) a monogamous mating structure, (2) similar home range sizes in males and females, (3) a distinct separation of microhabitat between the sexes, and (4) a 1:1 sex ratio (Stamps, 1983). In contrast, individuals of *A. carolinensis* are polygynous (a territorial male averages 2–3 resident females: Jenssen et al., 1995; Nunez, 1994; Ruby, 1984), have male home range volumes approximately seven fold greater than those of females (69 m³ versus 8 m³: Nunez, 1994), and exhibit broad overlap between male and female microhabitat (e.g., perch heights and diameters: Gordon, 1956; Jensen et al., 1995; King, 1966; Nunez, 1994).

Avoidance of competition could select for divergent trophic structures that decrease the overlap in prey sizes between the sexes. This being the case, Shine (1989) and Camilleri and Shine (1990) argued that a species' trunk proportion might not necessarily parallel the shift in head dimorphism (but see Cooper and Vitt, 1985*a,b*; Vial and Stewart, 1989, for a sexual selection interpretation as well). For *A. carolinensis*, the intersexual ratios for both head length and head width and the SSD ratio were all about 0.90 (Fig. 4), with no apparent differential allometry of the head dimensions. Although there are no data on food habits for *A. carolinensis* that could be used to investigate empirically prey size divergence among the sexes, it is possible that none would be found. *Anolis opalinus*, for example, has a significant SSD and SD for head width and length, and the sexes share the same range of prey sizes and morpho taxa; this remains true even when comparing adult males with juveniles (Floyd and Jenssen, 1983).

The sexual selection hypothesis best explains our data. The life history characteristics of *A. carolinensis* fit Stamps' (1983)

predictions for SD due to sexual selection. These are (1) a polygynous mating structure, (2) home ranges larger for males than females, (3) broad microhabitat overlap by the sexes, and (4) a female biased sex ratio. In addition, our SSD ratio for *A. carolinensis* conformed to another expectation when applied to Stamps' (1983:Fig. 9.3) model. Three females are predicted within an average male territory, and from a population near SRS, a mean of 2.8 and 3.0 females/male territory have been reported (Jenssen et al., 1995; Nunez, 1994).

As suggested by the sexual selection hypothesis, the increased male SVL and SSD expressed in *A. carolinensis* may be due to male-male interaction. Inter-male combat for territorial control over resident females has long been noted for *A. carolinensis* (Greenberg and Noble, 1944), with body size a prominent factor for predicting a winner (Ruby, 1984; Tokarz, 1985). Because breeding seasons should decrease in length at higher latitudes, males may be more likely to risk physical injury than to chance losing or not establishing a breeding territory before the season ends. Therefore, the frequency and intensity of prolonged aggressive interactions should increase among males in northern populations as compared to those in the southern populations (e.g., Florida), and increased aggression may be associated with increased male-biased SSD and SD expressed in the northern populations of *A. carolinensis*. Another indicator for a persistent threat of male-male contact was the difference in the SRS male:female ratio (1:1) and that derived from direct observations of breeding territories (1:3; Nunez, 1994). This differential suggests a reservoir of males with low reproductive potential. Therefore, males with females should constantly monitor their territorial boundaries for intruding males. Indeed, this seems to be the case. Jenssen et al. (1995) estimated that two-thirds of a male's daily activity was directed at boundary defense, territorial patrol, and conspecific monitoring.

Within the limits of our data, the sexual selection theory appears best to explain SD in *A. carolinensis*, but as Ruby (1984) concluded, contradictions and missing infor-

mation keep the question open. There are any number of ecological causations for SD (e.g., Gibbons and Lovich, 1990), and to discount them for the sexual selection hypothesis without more data would be premature (Shine, 1989). Even though *A. carolinensis* is widespread, common, and easily observed in the field, conclusions about the species' behavior, ecology, and physiological state have been almost exclusively based on captive subjects. There remains the need to validate the social behavior and life history of this species from natural populations.

Acknowledgments.—We thank J. Birch, K. Garrett, and J. Mays for their assistance with the statistical analyses and J. W. Gibbons, R. Howard, and S. Nunez for their review of the manuscript. Support for this study and the manuscript preparation was generously provided by the Savannah River Ecology Laboratory as a contract (DE-AC09-76SR00-819) between the United States Department of Energy and The University of Georgia's Savannah River Ecology Laboratory.

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Accepted: 17 March 1995

Associate Editor: Richard Howard