



THE UNIVERSITY OF CHICAGO PRESS JOURNALS

Parthenogenetic Lizards: r-Selected Reproductive Characteristics?

Author(s): Jos. J. Schall

Source: *The American Naturalist*, Feb., 1981, Vol. 117, No. 2 (Feb., 1981), pp. 212-216

Published by: The University of Chicago Press for The American Society of Naturalists

Stable URL: <https://www.jstor.org/stable/2460503>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



The American Society of Naturalists and The University of Chicago Press are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*

JSTOR

PARTHENOGENETIC LIZARDS: *r*-SELECTED REPRODUCTIVE CHARACTERISTICS?

Because of the paucity of parthenogenesis among vertebrates, the $13 \pm$ all-female species of whiptail lizards (*Cnemidophorus*) have received considerable interest from evolutionary biologists. Wright and Lowe (1968) proposed that all-female *Cnemidophorus* are animal "weeds" adapted to disturbed, ecotonal, and/or extralimital zones not optimal for sympatric bisexual species. If so, the ecologies of "weedy" unisexual and "nonweedy" bisexual whiptail species should differ fundamentally. For example, unisexuals could have relatively *r*-selected (*sensu* Pianka 1970) reproductive traits compared to bisexual species.

Recently, two independent studies comparing reproductive tactics of bisexual and unisexual species reached opposing conclusions (Congdon et al. 1978; Schall 1978). My study (Schall 1978) presented data on five species sympatric in southwest Texas, two of which are parthenogenetic. Among my conclusions were (1) bisexual and unisexual species do not differ in static reproductive characteristics (clutch size, egg size, or clutch/body weight ratio, a crude estimate of reproductive effort), and (2) some interspecific differences in reproductive characteristics are attributable primarily to differences in body size. Congdon et al. examined four species in Arizona, two bisexual and two parthenogenetic. These were paired by size: Two were small, *C. inornatus* (bisexual) and *C. uniparens* (unisexual), and two were larger, *C. tigris* (bisexual) and *C. sonorae* (unisexual). They concluded that unisexual species have larger clutches, increase clutch size faster with body growth, have smaller eggs, and higher clutch/body calorie ratios.

A reanalysis of Congdon et al.'s data reveals errors in both choice and computation of statistical tests. Very different conclusions emerge when the correct analyses are performed.

1. *Clutch size*.—I calculated regression statistics using clutch size and body size (snout-vent length, SVL) data extracted from figure 2 in Congdon et al. Our correlation coefficients agree closely (table 1), demonstrating that data were correctly determined from graphs. Regression lines I computed for the four species closely match those presented in their figure 2. They state that both unisexual species add one egg per 7 mm body growth whereas the bisexual species add one egg per 11 mm (*C. tigris*) and 14 mm (*C. inornatus*). Thus, the unisexual species have a "relatively greater clutch size increase per unit growth time when compared with bisexual forms" (p. 511). Slopes computed from the numbers quoted above differ dramatically from both those I calculated from the data (table 1) and those which can be estimated from Congdon et al.'s own regression lines in their figure 2. Inspection of their figure 2 verifies that the values of 11 mm and 14 mm per egg given for *C. tigris* and *C. inornatus* are clearly in error.

I compared the two small species and then the two larger species by analysis of covariance (table 2). Homogeneity of residual variance was first established, then slopes compared. Slopes did not differ significantly between unisexuals and bisexuals (table 2). Lastly, elevations of the two pairs of parallel regressions were

TABLE 1

COMPARISON OF REGRESSION ANALYSES APPEARING IN CONGDON ET AL. (1978) (indicated with "C") AND A REEXAMINATION OF THE DATA (indicated with "R") FOR CLUTCH SIZE VERSUS BODY SIZE IN FOUR *Cnemidophorus* SPECIES

Species	<i>r</i> (R)	<i>r</i> (C)	slope (R)	slope (C)
<i>C. sonorae</i>76	.77	.119	.143
<i>C. tigris</i>70	.70	.130	.091
<i>C. uniparens</i>62	.62	.131	.143
<i>C. inornatus</i>60	.60	.110	.071

NOTE.—Slope (C) calculated from "mm per egg" data in text.

compared. The two small species did not differ but the large unisexual had significantly larger clutches than the large bisexual (table 2).

When mean SVL and mean clutch size (data from Congdon et al., their fig. 2) are plotted, three species (*C. inornatus*, *C. uniparens*, *C. sonorae*) fall on a straight line (fig. 1, here); larger species produce larger clutches. *Cnemidophorus tigris*, however, has a small mean clutch for its size. Likewise, in four of five species in west Texas, mean SVL and mean clutch are tightly correlated but, again, *C. tigris* produced small clutches (fig. 1). The difference between *C. tigris* and *C. sonorae* appears related to the generally small clutch size of *C. tigris*. *Cnemidophorus tigris* is probably the most xerically adapted of the seven whiptail species considered here. In west Texas it inhabits open desert flats and rocky canyons, seldom venturing into more mesic terrain where other whiptail species are more common. Clutch size of *C. tigris* and long-term precipitation are positively correlated over its North American range (Pianka 1970). The small clutch size of *C. tigris* may thus be related to its modal habitat. I conclude that although there are interspecific differences in clutch size, the observed variation is not correlated with reproductive mode.

2. *Egg size*.—Intraspecifically, egg and body size are unrelated in most *Cnemidophorus* species. Larger species, though, tend to produce larger eggs (Congdon et al. 1978; Schall 1978). Congdon et al. combined data for both parthenogenetic species and compared them with those for both bisexuals, con-

TABLE 2

ANALYSIS OF COVARIANCE COMPARING REGRESSION LINES FOR TWO LARGE AND TWO SMALL SPECIES OF *Cnemidophorus*

	SMALL SPECIES <i>C. uniparens</i> * × <i>C. inornatus</i>	LARGE SPECIES <i>C. sonorae</i> * × <i>C. tigris</i>
Residual variance	1.09 (38, 22) <i>P</i> > .05	1.03 (24, 47) <i>P</i> > .05
Slopes225 (1, 60) <i>P</i> > .05	.813 (1, 71) <i>P</i> > .05
Elevations	1.93 (1, 61) <i>P</i> > .05	15.7 (1, 72) <i>P</i> < .01

SOURCE.—Data from Congdon et al. (1978, fig. 2).

NOTE.—*F* values followed by df and *P*. Unisexual species indicated by*.

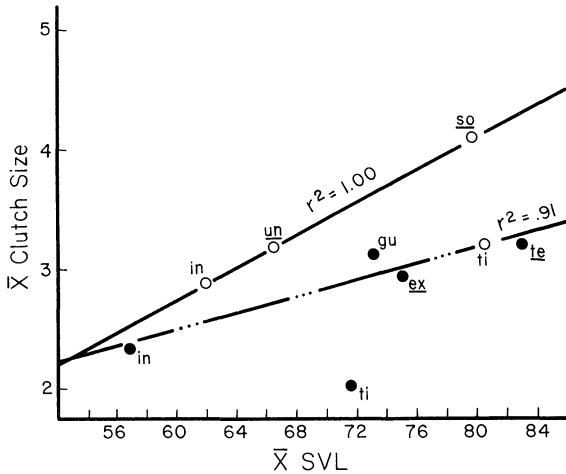


FIG. 1.—Mean SVL vs. clutch size for 4 *Cnemidophorus* species in Arizona (open dots, data from Congdon et al. 1978) and for 5 species in Texas (solid dots, data from Schall 1978). Species indicated by first two letters of specific name (see text); unisexual species' names are underlined. Regression lines are fit through the two sets of points, excluding, in both cases, the point for *C. tigris*.

cluding that sexual species produce larger eggs. However, a sample size bias exists. The “sexual” sample favors large lizards, 19 *C. tigris*, a larger species, versus only seven *C. inornatus*, a small species. (The sample size for *C. tigris* given in their paper, $N = 11$, is incorrect [L. Vitt, personal communication].) The bias is reversed for the “parthenogenetic” sample: 15 small and 12 large lizards. Large and small species pairs should be compared separately. *Cnemidophorus tigris* produces significantly larger eggs than *C. sonoriensis* but *C. uniparens* produces larger eggs than *C. inornatus* (data from their table 2; t' tests; $t' = 3.03$, $P < .05$ and $t' = 4.24$, $P < .01$, respectively). A measure which should be independent of body size is the egg size/body size ratio. This ratio can be calculated from mean calcs per egg/mean body calcs (Congdon et al. 1978, table 2 data). One unisexual species, *C. sonoriensis*, has the lowest ratio (.101) whereas the other, *C. uniparens*, has the highest (.160). These comparisons reveal no differences in egg size attributable to reproductive mode.

3. *Clutch/body ratio*.—Congdon et al. (1978, p. 513) state that this ratio “was significantly higher in unisexual species than in sexual species.” Variances between groups were heterogeneous (bisexuals vs. unisexuals, $F = 5.93$, $P < .01$); therefore, analysis of variance, which they performed, appears inappropriate. A valid statistic, the t' -test (Sokal and Rohlf 1969) reveals clutch/body ratios did not differ between either pair of species (small pair $t' = 1.92$, $P > .05$; large pair $t' = 1.16$, $P > .05$). L. Vitt has graciously provided the results of nonparametric Kruskal-Wallis tests between all pairs of species; only one of six differs significantly. Because clutch/body ratio in whiptails is not related to body size

(Schall 1978), data for both unisexuals can be compared with those of both bisexuals. Means still do not differ ($t' = 1.72$; $P > .05$).

Despite the lack of significance in these comparisons, it is suggestive that in both pairs mean clutch/body is larger in the unisexual species. Therefore, I used the method of Fisher (Sokal and Rohlf 1969, p. 621) to combine P 's. The resulting value (~ 3.5 , 4 df) is still not significant ($P > .25$).

I conclude that although variation in easily measured static reproductive characteristics (clutch size, egg weight, clutch/body ratio) exists among *Cnemidophorus* species, this variation is not attributable to reproductive mode. As egg and clutch size are correlated with body size in the genus, unisexuals appear simply to resemble one of their parental species in these traits (Schall 1978). Differences in clutch/body ratio seems related to differing habitat productivities; whiptail lizards brought into the laboratory and fed to satiation produce very heavy clutches (clutch/body ratio is above the range of field collected specimens; C. J. Cole, personal communication; Schall 1978).

Parthenogenetic species have diverged from their parental species in habitats utilized (Schall 1976; Wright and Lowe 1968) and escape behaviors (Schall and Pianka 1979). If unisexuals are "weedy" species why haven't they diverged in reproductive tactics? I suggested elsewhere (Schall 1978) that any differential selection pressures operating on whiptails' static reproductive characteristics seem overshadowed by other ecological constraints (see also Vitt and Congdon 1978). Whiptails are rapidly moving, very active, widely foraging lizards which rely on speed to elude predators. Their behavior and long thin body form may preclude major alteration in static reproductive characteristics. However, r - K -mode differences might be expressed in more dynamic aspects of reproduction such as age at first reproduction, growth rate, and clutches per season. Demographic studies are required to compare between parthenogenetic and bisexual species. Ideally, such studies would not be conducted on simply any available species but rather on a parthenogenetic species and its bisexual parental species.

ACKNOWLEDGMENTS

I thank L. Vitt and J. Congdon for additional data and analysis, C. J. Cole, B. Eisenbrey, F. Marsteller, E. R. Pianka, and J. W. Wright for their helpful comments, and R. W. Schall for drawing the figure.

LITERATURE CITED

- Congdon, J. D., L. J. Vitt, and N. F. Hadley. 1978. Parental investment: comparative reproductive energetics in bisexual and unisexual lizards, genus *Cnemidophorus*. *Am. Nat.* 112:509-521.
- Pianka, E. R. 1970. On r - and K -selection. *Am. Nat.* 104:592-597.
- . 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology* 51:703-720.
- Schall, J. J. 1976. Comparative ecology of sympatric parthenogenetic and bisexual species of *Cnemidophorus*. Ph.D. diss. University of Texas, Austin.

- . 1978. Reproductive strategies in sympatric whiptail lizards (*Cnemidophorus*): two parthenogenetic and three bisexual species. *Copeia* 1978:108–116.
- Schall, J. J., and E. R. Pianka. 1980. Evolution of escape behavior diversity. *Am. Nat.* 551–566.
- Sokal, R. R., and F. J. Rohlf. 1969. *Biometry*. Freeman, San Francisco.
- Vitt, L. J., and J. D. Congdon. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *Am. Nat.* 112:595–608.
- Wright, J. W., and C. H. Lowe. 1968. Weeds, polyploids, parthenogenesis, and the geographical and ecological distribution of all-female species of *Cnemidophorus*. *Copeia* 1968:128–138.

JOS. J. SCHALL*

DEPARTMENT OF ZOOLOGY
UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA 94720

Submitted February 9, 1979; Accepted July 10, 1979