

## SEXUAL DIMORPHISM OF HEAD AND BODY SIZE IN AN IGUANID LIZARD: PARADOXICAL RESULTS

Interest in sexual size dimorphism in lizards has focused on the importance of territorial polygyny as a determinant of how sexual selection operates (Stamps 1983). Supporting data include body-size ratios between males and females as evidence of sexual dimorphism, a categorical assignment of species as territorial or nonterritorial, the sex ratio in the population, and the ratio of home-range sizes between the sexes. More-recent studies have pointed out the problems associated with attributing body-size dimorphism to sexual selection and have emphasized the importance of examining characteristics that appear important in determining the reproductive success of individuals. One such character is relative head size in species in which intrasexual aggression has been observed (Carothers 1984; Vitt and Cooper 1985, 1986; Anderson and Vitt, MS). In attempting to understand the importance of sexual selection, these and many other studies have focused on differences between the sexes rather than on relative differences among individuals within the sex. Yet differential reproductive success *among individuals* of the competing sex results in natural selection that favors hypertrophy of characters determining the outcome of social encounters.

Sexual selection, defined as selection for characters giving certain individuals an advantage over others of the same sex in obtaining successful matings (Partridge and Halliday 1984, p. 225), is a powerful evolutionary concept, which, if used cautiously in conjunction with alternative hypotheses, can explain many morphological and other secondary sexual differences. The ease with which sexual differences can be explained by a sexual-selection hypothesis has often led investigators to exclude alternative hypotheses as causes (but see Vial and Stewart 1989). A recent case involves secondary sexual differences in lizard head size. Studies on *Dipsosaurus*, an herbivorous iguanid lizard, have shown that males have larger heads than females of the same size apparently because of the importance of head size to outcomes of inter-male interactions (Carothers 1984). Similarly, extreme sexual dimorphism in head size (corrected for sexual differences in body size) has been attributed to sexual selection for nonterritorial *Eumeces* (Scincidae; Vitt and Cooper 1985, 1986) and nonterritorial *Cnemidophorus* and *Ameiva* (Teiidae; Anderson and Vitt, MS).

We present data on the territorial iguanid lizard *Sceloporus undulatus* to caution investigators against attributing differences in body and head size to sexual selection in the absence of pertinent supportive data, particularly data on reproductive success (or a correlate). *Sceloporus undulatus* is a widespread North American species in which females in most populations attain larger average and

maximum size than males (Fitch 1978). The larger size of females is generally attributed to a correlation between body size and clutch size (Tinkle and Ballinger 1972; Vinegar 1975; Ferguson et al. 1980; Tinkle and Dunham 1986). However, males are territorial and interact aggressively with each other (Vinegar 1975; Rothblum and Jenssen 1978; Cooper and Burns 1987). Thus, if male success is determined by body and/or head size relative to that of other males, selection should favor larger body and head size in males, and we might expect male body size to be as large as or larger than female body size and male head size to be larger. Because of this apparent paradox, we also examine the importance of considering differences between sexes versus considering relative differences among individuals within each sex with respect to putatively sexually dimorphic characters.

#### METHODS

The sex was determined of 329 *Sceloporus undulatus* specimens from the collection at the Museum of Natural History, University of Georgia; we then measured head width (0.1 mm) and snout-vent length (SVL, 1.0 mm). Minimum size at sexual maturity was determined for females as the SVL of the smallest female containing vitellogenic follicles or oviductal eggs. Male size at sexual maturity was arbitrarily considered identical to that for females even though males may reach sexual maturity at slightly shorter SVL (Tinkle and Dunham 1986); this was done to avoid spurious group differences. Analysis of covariance (ANCOVA) with logSVL as the covariate examined the effects of sex on head width (log-transformed) between juvenile males and juvenile females; adults of each sex versus all juveniles; all females versus all males; and adult females versus adult males. Correlation and regression statistics were computed for the relationships of the log of head width and logSVL for each age-sex category. The log-log analysis allows statistical comparisons of the allometric equation

$$HW = b(SVL)^a,$$

where HW is head width,  $b$  is a constant (the intercept of the log-log relationship), and the exponent  $a$  corresponds to the slope of the log-log relationship. Sexual comparisons of mean SVL and head width were made with the nonparametric Mann-Whitney  $U$ -test.

#### RESULTS

Minimum size at sexual maturity for females was 54 mm in snout-vent length (SVL). As expected, head width was correlated with SVL in all groups tested (table 1). ANCOVA revealed that juvenile males and females were similar to each other, adult males differed significantly from juveniles, and adult females differed significantly from both juveniles and adult males in the relationship of head width and SVL (table 2). Although head size increased with SVL in both sexes, at about the size at which sexual maturity is reached, the rate of increase in the head size of females was less than that of juveniles and adult males. The rate of increase in head size with the SVL of males was slightly greater than that of juveniles.

TABLE 1

REGRESSION STATISTICS COMPARING THE RELATIONSHIPS BETWEEN THE LOG OF HEAD WIDTH AND THE LOG OF THE SNOUT-VENT LENGTH OF *SCELOPORUS UNDULATUS*, BY AGE AND SEX

STAGE	REGRESSION MODEL				SLOPE	INTERCEPT
	$R^2$	$F$	df	$P$		
Adult males	0.71	203.5	1, 83	<0.0001	0.97	-1.42
Adult females	0.79	292.5	1, 77	<0.0001	0.82	-0.84
Juveniles	0.94	2679.2	1, 163	<0.0001	0.87	-1.03

TABLE 2

ANALYSIS OF COVARIANCE COMPARING LOG OF HEAD WIDTH AMONG AGE GROUPS AND SEXES OF *SCELOPORUS UNDULATUS*

GROUP	SLOPE TEST			INTERCEPT TEST		
	$F$	df	$P$	$F$	df	$P$
Juvenile males vs. juvenile females	0.0	1, 161	>0.75	2.3	1, 162	>0.05
Adult males vs. all juveniles	1.6	1, 246	>0.10	5.9	1, 247	<0.005
Adult females vs. all juveniles	0.9	1, 240	>0.25	5.5	1, 241	<0.005
All females vs. all males	13.0	1, 325	<0.001	39.5	1, 326	<0.001
Adult females vs. adult males	3.4	1, 160	>0.05	60.1	1, 161	<0.001

NOTE.—The log of snout-vent length is the covariate.

Mean SVL of adult females (65.43 mm  $\pm$  0.69 mm,  $n = 79$ ) was significantly greater than that of adult males (fig. 1; 62.07 mm  $\pm$  0.43,  $n = 85$ ; Mann-Whitney  $U$ -test,  $P < 0.001$ ); but mean head width of females (13.06 mm  $\pm$  0.12,  $n = 79$ ) was not significantly different from that of males (13.14 mm  $\pm$  0.10,  $n = 85$ ; Mann-Whitney  $U$ -test,  $P = 0.78$ ).

#### DISCUSSION

Similar to many other lizard species recently studied (Carothers 1984; Vitt and Cooper 1985, 1986; Anderson and Vitt, MS), sexually mature males of *Sceloporus undulatus* have larger heads than females of similar snout-vent length (SVL), except near the size at sexual maturity. In addition, and again as in other species studied, the sexual difference in head size increases with increasing SVL. In *S. undulatus*, however, the sexual dimorphism in the head size of adults is due to an apparent decrease in female head size relative to juvenile head size and an increase in the relative head size of males. Body size increases at a greater rate than head size once females reach sexual maturity. This has been reported in only one other species of lizard, *Barisia monticola*, in the family Anguillidae (Vial and Stewart 1989) but may be widespread. The present results cannot be easily attributed to sexual selection. This is somewhat paradoxical because morphological differences between the sexes in certain other lizards (Vitt and Cooper 1986; Anderson and Vitt, MS) clearly result from sexual selection. In males, head size increases more than would be expected on the basis of body-size increase alone.

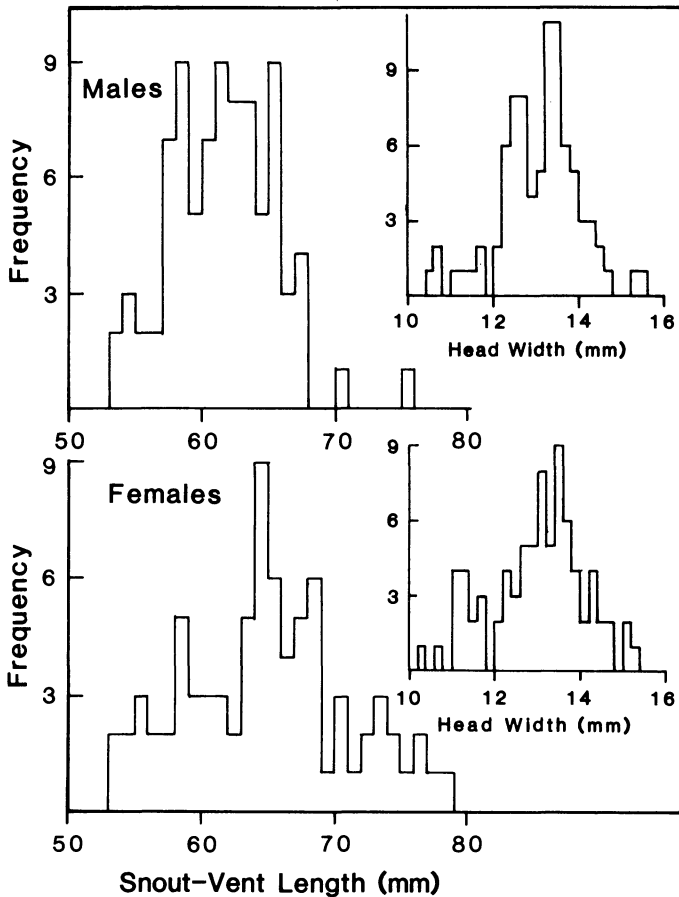


FIG. 1.—Distribution of body sizes (SVL) and head widths for male and female *Sceloporus undulatus* adults.

We can conclude for males that relative head size may be important for mate acquisition. But the fact that adult males and females have similar absolute head sizes even though body size differs could be used to argue that there is an optimal head size for adults independent of body-size differences or of sex. In contrast, it has been argued that sexual differences in the size of trophic apparatus (heads) might have evolved to reduce competition for food between the sexes (see, e.g., Schoener 1967).

The most attractive explanation for the decrease in slope of the regression of head width on SVL at sexual maturity in females is that females allocate relatively more energy to the growth of reproductively significant morphological characters after reaching maturity than to characters less directly tied to reproductive success. This is partially reflected in the greater body length attained by adult females, coincident with a reduction in the rate of head-size increase. Growth in

characters such as the head may be sacrificed for a rapid increase in SVL to realize the greater potential reproductive output associated with increased clutch size at greater SVL: in all populations of *S. undulatus* studied, clutch size increases with the SVL of females (Tinkle and Dunham 1986). The possibility that head proportions might have diverged between the sexes as a result of their importance as sex-recognition cues is unlikely. Sex identification in this species is based in part on a display of blue and black ventral coloration by males as well as on behavioral differences between the sexes (Cooper and Burns 1987).

An alternative to increasing clutch size with body size would be to increase individual egg size with body size. Although egg mass does increase significantly with mean female SVL among populations ( $F_{1,8} = 9.07$ ,  $P < 0.02$ ; data for 10 populations in Tinkle and Dunham 1986), suggesting this possibility, there is no evidence that egg mass increases with female SVL within populations of *S. undulatus*. Presumably, the interpopulational differences reflect different optimal egg sizes (Smith and Fretwell 1974), but other factors may also influence offspring size, particularly considering that female size and offspring size are correlated among populations.

We caution investigators against interpreting sexual differences in structures such as head size as direct consequences of sexual selection without proper comparisons among all age and sex groups to reveal the pattern of development of such differences and without extensive behavioral observations or experimental studies implicating the importance of a character (e.g., head size) for reproductive success. Although we cannot determine what characters are important for male reproductive success in *S. undulatus*, it is clear that male size relative to female size may not be the important comparison. It is possible that the best mating strategy for *S. undulatus* males is to invest as much energy in attaining mates as soon as possible at a cost to body growth in the face of high mortality during the first year of maturity. For example, the survival of *S. undulatus* males from spring to summer (the breeding season) is only 28.8% for an Arizona population (Tinkle and Dunham 1986), indicating that there is a cost to postponing the investment in reproductive activity. Thus, sexual selection may be operating on energy-utilization patterns of males relative to each other as well as on morphological traits such as head size.

Finally, we take this opportunity to comment on what we consider to be the relevant comparisons for drawing inferences regarding causes of sexual dimorphism in lizards. If a morphological character is suspected of being involved in mating success on the basis of field or laboratory observations, that character should be measured in a large series of individuals of both sexes covering most of the range of body sizes for the population. Comparisons of regressions of the character on SVL for adults will establish the existence of sexual dimorphism. Comparisons of regressions for each sex with their respective juvenile regressions will establish which sex is diverging in the character. Once these relationships are established, proper experiments can be designed to test the importance of the character in mating success.

We also caution against heavily weighting the sexual difference in a character in attempts to understand its origin and importance. It is necessary first to establish

the existence and nature of the sexual difference. Once the nature of the difference is established, questions about its cause should be addressed by examining intraspecific interactions. In lizard species in which relatively large head size associated with intrasexual agonistic behavior accrues a mating advantage to males, it is head size relative to that of other males that is important for understanding sexual selection, not head size of males relative to that of females. The latter indicates that males are doing something different from females, but it may reveal little about the origins of the difference.

#### SUMMARY

Sexual selection is frequently invoked to explain sexual dimorphism in characters such as the head size of lizards. For many species previously studied, it has been shown that male heads are larger than female heads at a given body size. This increased relative head size in males at sexual maturity is associated with advantages of large heads in intrasexual encounters. Males of the iguanid lizard *Sceloporus undulatus* have larger heads than females of similar size, but the difference is largely accounted for by a reduction in the rate of head growth relative to body-size growth in females rather than strictly by a relative increase in male head size. Presumably, females invest mostly in body growth and reproduction at the expense of an increase in head size once sexual maturity is reached. Consequently, we caution future investigators against attributing sexual differences in morphological characters to sexual selection unless independent data (e.g., behaviors) implicate morphological characters as determinants of differential reproductive success.

#### ACKNOWLEDGMENTS

Many individuals helped with our research, but we are particularly indebted to N. Burns, who repeated the measurements of adult lizards, and to J. Congdon, who helped her analyze the repeated data. We thank E. McGhee and the Museum of Natural History at the University of Georgia for lending specimens. This research, conducted while we were visiting faculty researchers at the Savannah River Ecology Laboratory (SREL), was supported by contract DE-AC0976SR00-810 between the U.S. Department of Energy and the University of Georgia through SREL. Support for statistical and clerical phases of this work was provided by the Departments of Biology at our respective institutions.

#### LITERATURE CITED

- Carothers, J. H. 1984. Sexual selection and sexual dimorphism in some herbivorous lizards. *Am. Nat.* 124:244-254.
- Cooper, W. E., Jr., and N. Burns. 1987. Social significance of ventrolateral colouration in the fence lizard (*Sceloporus undulatus*). *Anim. Behav.* 35:526-532.
- Ferguson, G. W., C. H. Bohlen, and H. P. Woolley. 1980. *Sceloporus undulatus*: comparative life history and regulation of a Kansas population. *Ecology* 61:313-322.
- Fitch, H. S. 1978. Sexual size differences in the genus *Sceloporus*. *Univ. Kans. Sci. Bull.* 13:441-461.

- Partridge, L., and T. Halliday. 1984. Mating patterns and mate choice. Pages 222–250 in J. R. Krebs and N. B. Davies, eds. *Behavioural ecology: an evolutionary approach*. 2d ed. Sinauer, Sunderland, Mass.
- Rothblum, L., and T. A. Janssen. 1978. Display repertoire analysis of *Sceloporus undulatus hyacinthinus* (Sauria: Iguanidae) from south-western Virginia. *Anim. Behav.* 26:130–137.
- Schoener, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* (Wash., D.C.) 155:474–477.
- Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between offspring size and number. *Am. Nat.* 108:499–506.
- Stamps, J. A. 1983. Sexual selection, sexual dimorphism, and territoriality. Pages 169–204 in R. B. Huey, E. R. Pianka, and T. W. Schoener, eds. *Lizard ecology: studies on a model organism*. Harvard University Press, Cambridge, Mass.
- Tinkle, D. W., and R. E. Ballinger. 1972. *Sceloporus undulatus*: a study of the intraspecific comparative demography of a lizard. *Ecology* 53:570–584.
- Tinkle, D. W., and A. E. Dunham. 1986. Comparative life histories of two syntopic sceloporine lizards. *Copeia* 1986:1–18.
- Vial, J. L., and J. R. Stewart. 1989. The manifestation and significance of sexual dimorphism in anguid lizards: a case study of *Barisia monticola*. *Can. J. Zool.* 67:68–72.
- Vinegar, M. B. 1975. Comparative aggression in *Sceloporus virgatus*, *S. undulatus consobrinus*, and *S. u. tristichus* (Sauria: Iguanidae). *Anim. Behav.* 23:279–286.
- Vitt, L. J., and W. E. Cooper, Jr. 1985. The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. *Can. J. Zool.* 63:995–1002.
- . 1986. Skink reproduction: *Eumeces fasciatus* in the southeastern United States, with notes on *Eumeces inexpectatus*. *J. Herpetol.* 20:65–76.

WILLIAM E. COOPER, JR.

DEPARTMENT OF BIOLOGY  
AUBURN UNIVERSITY AT MONTGOMERY  
MONTGOMERY, ALABAMA 36193-0401

LAURIE J. VITT

DEPARTMENT OF BIOLOGY  
UNIVERSITY OF CALIFORNIA  
LOS ANGELES, CALIFORNIA 90024

*Submitted April 1, 1988; Accepted October 13, 1988*