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Geographic Variation in Growth and Sexual Size Dimorphism of Bog Turtles (Clemmys muhlenbergii)

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ABSTRACT.—We examined sexual size dimorphism (SSD) and growth rates in samples of bog turtles (*Clemmys muhlenbergii*) from North Carolina, Pennsylvania and New Jersey. Mean carapace length (CL) of males was significantly greater than mean CL of females in all three states. However, the degree of SSD varied significantly among states. Specimens from North Carolina had the greatest SSD, the largest mean adult CL, and the largest mean hatchling CL. Growth rates were rapid until about age 6 and a CL of 80 mm. Males grew faster than females thereafter. A comparison of the three parameters estimated from von Bertalanffy growth equations showed significant differences for asymptotes between sexes and states for the North Carolina and Pennsylvania samples, but not for the growth rate constant (parameter *k*). Geographic variation in SSD appears to be a result of differences in growth related to the timing of maturity and the approach to asymptotic body size caused by indeterminate growth, or both. We suggest that male-biased SSD in this species is ultimately a consequence of the advantage conferred to larger males in male-male interactions and during mating.

INTRODUCTION

The evolution of sexual size dimorphism (SSD) is one of the most researched topics in biology and scores of papers have been published on the subject (*see* reviews by Hedrick and Temeles, 1989; Shine, 1989; Fairbairn, 1990; Gibbons and Lovich, 1990; Lovich and Gibbons, 1992). The vast majority of analyses of SSD focus on broad comparisons among species, often represented by a single estimate, with little emphasis on geographic variation or an understanding of its importance. This is surprising in that sexual dimorphism varies geographically in many species including reptiles (Iverson, 1985; Thorpe, 1989; McCoy *et al.*, 1994; Mushinsky *et al.*, 1994; Hamilton, 1995), birds (Rising, 1987), and mammals (Ralls and Harvey, 1985; Ritke and Kennedy, 1993; Gay and Best, 1995). In fact, polytypic species of reptiles show evidence of geographic variation in SSD for every species examined (Fitch, 1981). Sources of variation in the estimation of SSD can arise from several factors including sampling bias, inappropriate measures of dimorphism, improper estimates of size at maturity, geographic variation in the growth or body size of the sexes, and geographically disparate selective pressures (Gibbons and Lovich, 1990; Lovich and Gibbons, 1992).

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Adaptionist explanations for the evolution of SSD fall into two broad categories: those based on sexual selection and those based on natural selection (usually intersexual resource competition). Sexual selection itself has two fundamentally different groupings. The first, intrasexual selection, is based on the premise that individuals of one sex compete among themselves for access to members of the opposite sex (males usually compete among themselves for access to females, instead of *vice versa*) for mating opportunities. Selection favors the enhancement of anatomical features, such as large body size or weapons, that increase an individuals success in intrasexual interactions (Shine, 1979). The second, epigamic selection, assumes that members of one sex (usually females) choose members of the opposite sex for mating (Trivers, 1972; Lovich, 1996 and references therein). In this case, females may preferentially mate with larger than average males. Alternatively, larger females may be selected by males because of their ability to produce more offspring, their ability to reproduce more frequently on an annual basis (Forsman and Shiue, 1995), or their ability to provide better care for offspring. More recently, the timing of maturity, in part affected by sexual selection, has been suggested as the underlying cause of SSD (Kozłowski, 1989; Gibbons and Lovich, 1990).

Theories based on natural selection assume that SSD is a result of dissimilar interactious of each sex with their environment (*see* review in Shine, 1989; Shine, 1991). If larger individuals are able to consume larger food items than smaller individuals, then SSD may evolve to lessen competition between the sexes for a limiting dietary resource (Schoener, 1966; Selander, 1966; Fitch, 1981; Tucker *et al.*, 1995). It is important to note that ecological differences may simply be a consequence of sexually selected dimorphism (Shine, 1986).

Identification of the selective forces responsible for the evolution of SSD in a species requires the following as a minimum: (1) quantification of the degree and direction of SSD (Lovich and Gibbons, 1992); (2) identificatiou of sources of variation and their significance (Gibbons and Lovich, 1990), and (3) a detailed knowledge of sex specific growth patterns (Stamps, 1993, 1995) and maturity schedules (Kozłowski, 1989; Gibbons and Lovich, 1990; Lovich *et al.*, 1990). Our objective in this paper is to quantify and compare SSD and growth among samples of the bog turtle, *Clemmys muhlenbergii*, from Pennsylvania, North Carolina and New Jersey. The results are interpreted in light of adaptionist theories for the evolution of SSD reviewed above, specifically as they relate to evaluating the potential roles of sexual and natural selection in the evolution of SSD in *C. muhlenbergii*.

MATERIALS AND METHODS

Data were collected during previous studies of wild populatious of *Clemmys muhlenbergii* in three states; Pennsylvania, New Jersey, and North Carolina. Details of each study have been summarized previously in the followiug references: Pennsylvania—Ernst (1976, 1977), Ernst *et al.* (1989); New Jersey—Zappalorti (1976), Ernst *et al.* (1989); North Carolina—Zappalorti (1976); Lovich *et al.* (1992). Although all three studies overlapped to some degree, they were not conducted during the same time frames. Carapace and plastron lengths were measured with dial calipers accurate to 0.1 mm. Sex of turtles was determiued using characters given in Ernst *et al.* (1994), and individuals were marked for future identification by cutting notches in the marginal scutes (Ernst *et al.*, 1974). Age was determined from living specimens by counting growth annuli. Each annulus was assumed to represent 1 yr of growth, a reasonable assumption borne out in numerous studies of temperate zone turtles (Germano, 1988; Dunham and Gibbons, 1990), including *Clemmys muhlenbergii* (Ernst, 1977). Growth parameters of each sample were estimated using a von Bertalanffy equation of the form

$$CL = \alpha\ (1 - \beta e^{-k(age)})$$

where CL (carapace length) is length at an estimated age, α is the asymptote, β is a parameter related to hatchling size (Richards, 1959; Frazer *et al.,* 1990), e is the base of natural logarithms, and k is the growth rate constant (Richards, 1959) which specifies the rate of approach to asymptotic size (Stamps, 1993). Support plane confidence intervals were calculated for each parameter using the method of Schoener and Schoener (1978). These values are extremely conservative (Dunham and Gibbons, 1990) in that they define the maximum symmetrical interval wherein the true value of a parameter lies regardless of the true value of other parameters. Since *C. muhlenbergii* hatchlings rarely overwinter in the nest (Gibbons and Nelson, 1978; Bury, 1979; Ernst *et al.,* 1994), they were assigned an age of zero in growth calculations. In a previous study of growth in *C. muhlenbergii,* Ernst (1977) suggested that plastron length (PL) was a better measure of size than CL. However, a subsequent study of growth in the congeneric species *C. insculpta* shows that PL is a poor indicator of overall size because of the development of plastral concavity in males (Lovich *et al.* 1990). Thus, all measures of SSD in this paper are based on CL. Specimens that did not exhibit clearly defined secondary sexual characteristics were considered to be juveniles. Juveniles of unknown gender were included in the growth analyses for each sex based on the assumption that juvenile turtles of both sexes grow at the same rate (Dunham and Gibbons, 1990; Gibbons and Lovich, 1990). Repeated measurements were included when individual specimens were recaptured. Capture intervals span at least 2 calendar yr when repeated measures were made of the same individual. Details of this form of the von Bertalanffy model and its applicability to turtles are given in Draper and Smith (1981) and Lovich *et al.* (1990). Nonlinear estimation procedures were executed using STATGRAPHICS (STSC, 1986).

Ratios for sexual dimorphism indices (SDIs) were calculated using the method of Lovich and Gibbons (1992);

$$SDI = \left(-\frac{A}{B}\right) + 1$$

where A is the mean size of males and B is the mean size of females, when males are larger than females. The reader is referred to Lovich and Gibbons (1992) for additional discussion of the advantages of this formula for calculating SDIs.

Analyses of SSD based on CL used only specimens with a PL greater than 70 mm because this is the approximate size at which sexual maturity occurs (Ernst, 1977). Mean size differences between sexes and among localities were tested for statistical significance after the data were transformed to natural logarithms to reduce variance (Moriarty, 1977). Size differences between localities and sex were assessed using a 3 × 2 factorial design, with a significant interaction term (LOCALITY × SEX) indicating geographic variation in SSD (Thorpe, 1989; Ritke and Kennedy, 1993).

RESULTS

Males were significantly larger than females in all three geographic samples (Table 1). Sexual size dimorphism, as measured by the SDI we employed, was −0.06 for North Carolina, −0.02 for New Jersey, and −0.04 for Pennsylvania. The degree of SSD varied appreciably among samples as shown by a statistically significant interaction between sex and locality in a factorial ANOVA (Table 2). Mean male CL differed among samples as shown by a one-way ANOVA ($F = 14.51$; $df = 2, 140$; $P < 0.0001$) as did mean female CL ($F = 14.75$; $df = 2,172$; $P < 0.0001$). Mean CL of North Carolina male specimens was greater

TABLE 1.—Mean carapace length and standard deviation of male and female *Clemmys muhlenbergii* samples by state. Sample sizes are given in parentheses. Only specimens with a plastron length greater than 70 mm were used. Probabilities are based on one-tailed t-tests

State	Sex		P
	Males	Females	
North Carolina	97.6; 5.3 (62)	91.9; 4.7 (87)	<0.0001
Pennsylvania	93.5; 6.6 (20)	91.3; 5.3 (41)	0.0078
New Jersey	90.2; 4.9 (61)	87.1; 4.4 (47)	0.0411

than mean male or female CL of any state in our sample. Mean CL of New Jersey male and female specimens were less than that of either sex in Pennsylvania or North Carolina (Table 1). The largest male and female individuals in each of the three states had CL measurements as follows: Pennsylvania—males 106 mm, females 105 mm; North Carolina—males 108 mm, females 101 mm; New Jersey—males 100 mm, females 97 mm.

The mean CL of hatchlings in Pennsylvania (25.9 mm, n = 34), North Carolina (27.9 mm, n = 10), and New Jersey (26.0 mm, n = 25) was significantly different (ANOVA F = 6.94; df = 2,66; P = 0.002). Growth was rapid in both samples until about 6 yr of age and a CL of ca. 80 mm (Figs. 1 and 2). Males grew faster than females after this. Predicted growth models for the New Jersey sample provided a poor fit to observed data and the parameters had wide confidence intervals. Because of this, growth data could not be realistically compared to those for North Carolina and Pennsylvania samples (Table 3). Of the three parameters estimated, only the asymptote had nonoverlapping 95 percent support plane confidence intervals in comparisons between sex and samples in Pennsylvania and North Carolina (Table 4). Asymptotic estimates were similar in comparisons between males in Pennsylvania and North Carolina, and between females in the two states.

DISCUSSION

Recent reviews of SSD in turtles have shown that, in most species, adult females are larger than adult males (Gibbons and Lovich, 1990; Berry and Shine, 1980). Turtles of the genus *Clemmys* provide an interesting exception to this trend because males are larger than females in *C. muhlenbergii, C. marmorata* and *C. insculpta* (Gibbons and Lovich, 1990; Lovich *et al.,* 1990; Ernst *et al.,* 1994). Only *C. guttata* exhibits female-biased SSD (Gibbons and Lovich, 1990; Ernst *et al.,* 1994). This dichotomy of sexually divergent morphologies within a small and closely related (but, *see* Bickham *et al.,* 1996) taxonomic subunit is unusual in turtles, but not unreported (Germano, 1994; Lovich and Lamb, 1995).

The results of our analyses demonstrate that although the degree of sexual size dimor-

TABLE 2.—Factorial ANOVA comparing mean $\log_e$ transformed carapace length between sexually mature male and female *Clemmys muhlenbergii* from samples in Pennsylvania, North Carolina, and New Jersey (N = 318)

Source	SS	df	MS	F	P
Locality	0.174	2	0.087	26.220	<0.001
Sex	0.098	1	0.098	29.585	<0.001
Locality × Sex	0.022	2	0.011	3.304	0.038
Error	1.033	312	0.003		

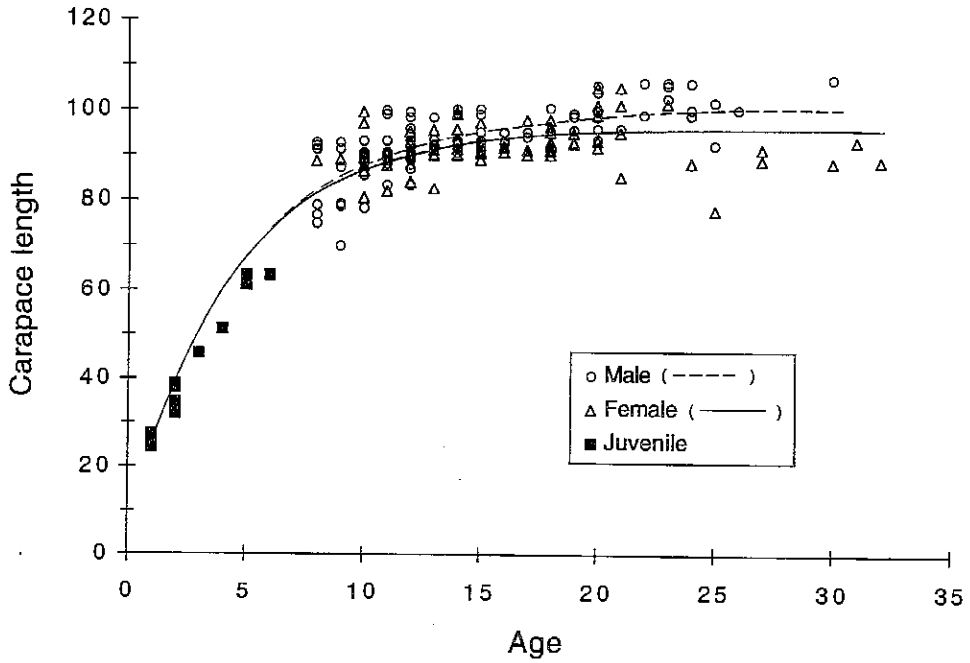

FIG. 1.—Von Bertalanffy growth curves for *Clemmys muhlenbergii* from Pennsylvania. Sample sizes are as follows: males 104, females 73, and juveniles 43

phism varies among the geographic regions (states) studied, male *Clemmys muhlenbergii* have larger mean body size than females from the same state. Geographic variation in SSD has been reported in several turtle species (Tinkle, 1961; Fitch, 1981; Iverson, 1985; Gibbons and Lovich, 1990), and in most cases involves an increase in SSD from higher to lower latitudes as seen in our data. It is of interest that the degree of SSD is greatest in North Carolina where mean body size (and hatchling size) is greatest and least in New Jersey and Pennsylvania where mean body size (and hatchling size) is least. Rowe (1995) previously demonstrated a significant positive correlation between hatchling size and maternal size in the painted turtle (*Chrysemys picta*). Since our data show that the mean CL of hatchlings is smallest in the state with the smallest mean female CL (Pennsylvania) and largest in the state with the largest female CL (North Carolina), it is tempting to speculate that such a correlation also exists in *C. muhlenbergii,* but additional study will be required for confirmation.

Other researchers have noted a correlation between body size and SSD within and among turtle species such as we observed in our study. In the turtle family Kinosternidae, SSD reportedly increases with increasing size of the species (Berry and Shine, 1980). Iverson (1985) observed that SSD was predominately male-biased in populations of *Kinosternon hirtipes*, with the greatest degree of dimorphism occurring in populations with the largest mean body size. Furthermore, he noted that SSD was positively correlated with the size of the drainage basin occupied by the population and attributed the relationship to differences in food availability. However, we have no data on food availability for the populations examined in this study. In contrast to the data of Iverson (1985), Gibbons and Lovich (1990) found little evidence to support the existence of a relationship between SSD and body size

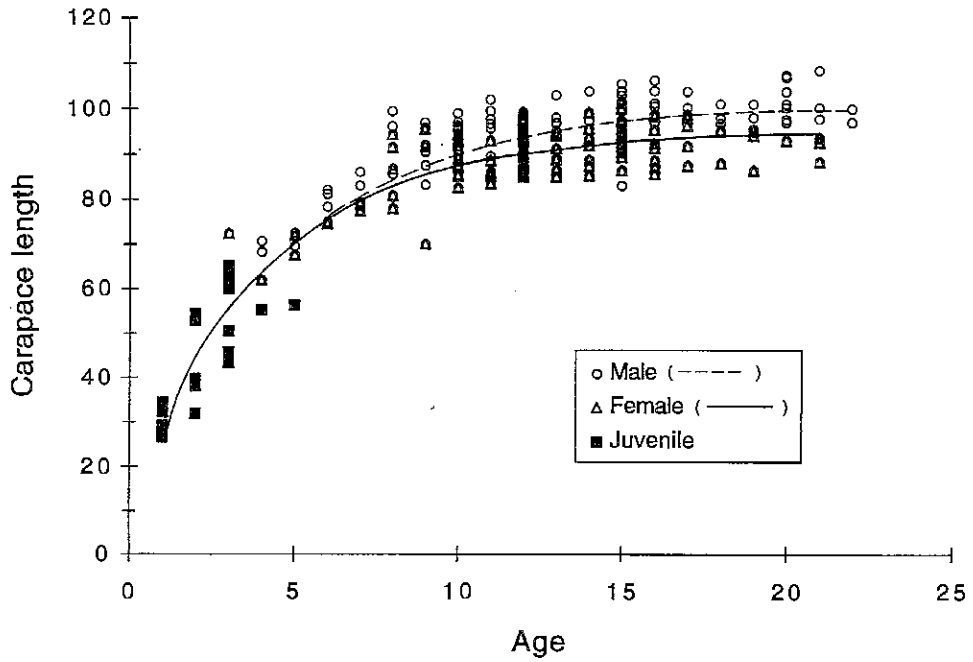

FIG. 2.—Von Bertalanffy growth curves for *Clemmys muhlenbergii* from North Carolina. Sample sizes are as follows: males 95, females 118, and juveniles 28

among turtle species or among populations of the wide-ranging turtle *Trachemys scripta*. The fact that our data show a provisional relationship between body size and SSD suggests that further work is needed on this topic.

Previously published accounts of the food habits of *Clemmys muhlenbergii* reveal no differences between the sexes (Ernst *et al.*, 1994) that would suggest the existence of resource partitioning as expected under the natural selection hypothesis. Furthermore, there are no obvious differences in the size or shape of the head between the sexes (pers. observ.) that would facilitate use of different food types or sizes. However, Shine (1986) suggested that resource partitioning may develop as a consequence of pre-existing sexually-selected differences in size. We tentatively reject the hypothesis that resonrce partitioning has driven the development of SSD in *C. muhlenbergii* but more work is needed to justify this conclusion.

TABLE 3.—Estimated parameters of the von Bertalanffy growth model for male and female *Clemmys muhlenbergii*. Standard errors of estimates are in parentheses. Sample sizes for each sex include juveniles (n = 43, Pennsylvania; n = 28, North Carolina)

Parameter estimates	Pennsylvania		North Carolina	
	Males (n = 147)	Females (n = 116)	Males (n = 123)	Females (n = 146)
α	101.743 (0.939)	95.460 (0.887)	101.596 (1.015)	94.685 (0.937)
β	0.749 (0.007)	0.735 (0.008)	0.719 (0.013)	0.696 (0.015)
k	0.185 (0.008)	0.224 (0.014)	0.227 (0.013)	0.256 (0.018)
R^2	0.981	0.978	0.952	0.934

TABLE 4.—Matrix of pairwise comparisons of 95 percent confidence intervals between sex and state for von Bertalanffy parameter estimates. Confidence intervals (CIs) that do not overlap are designated with the symbol of the parameter estimate. Comparisons are based on support plane CIs (refer to text for details). PA = Pennsylvania, NC = North Carolina, and ND = no statistically significant difference between parameters for comparison

	Pennsylvania		North Carolina	
State/sex	Males	Females	Males	Females
PA males	—	—	—	—
PA females	α	—	—	—
NC males	ND	α	—	—
NC females	α	ND	α	—

The consistent occurrence of larger males than females, on average, among the regions studied suggests that selective forces responsible for SSD operate similarly over the geographic area examined. An understanding of the significance of SSD and the selective forces that influenced its development can be enhanced by examining the mating strategy of a species (Berry and Shine, 1980). Most published accounts of the behavior of *Clemmys muhlenbergii* show that male-male competition is well developed (Ernst *et al.*, 1994). For example, Zappalorti (1976) and Holub and Bloomer (1977) noted that adult males almost always threaten or attack smaller males when they are encountered. The attacking male crawls rapidly toward the other turtle with neck extended and the mouth open or closed. Before contact, the aggressor partially withdraws the head and tilts the carapace forward by raising the hind limbs. If the threatened male responds with similar behavior, pushing and biting may ensue, leading to potential injury or even death. Larger and older males nsually prevail. Zappalorti (1976) and Holub and Bloomer (1977) also reported strong territorial behavior among some males.

Courtship is a vigorous and aggressive affair with males occasionally biting females on the head and limbs (sometimes resulting in injury and death in captivity, pers. observ.), and attempting to copulate with any female they encounter (Holub and Bloomer, 1977). Females in captivity attempt to escape the attention of courting males who often pursue them. Smaller or weaker males do not achieve copulation (Tryon and Hulsey, 1977).

The data on mating behavior of *Clemmys muhlenbergii* are consistent with predictions of the direction of SSD and reproductive strategy. Species in which male-male conflict is important in gaining access to females usually have larger males than females because body size confers an advantage in combat (Berry and Shine, 1980; Gibbons and Lovich, 1990; Shine, 1994). Furthermore, females may "discriminate" among males by subverting the efforts of smaller males to achieve copulation (Booth and Peters, 1972; Gibbons and Lovich, 1990). A fitness advantage may be conferred on the offspring of females that mate with larger males assuming that large body size is heritable, and that larger males have the ability to accrue and defend better resources, mature earlier, or grow faster as juveniles (Halliday and Verrell, 1988). Sexual selection seems to have exerted a strong and consistent influence on SSD in bog turtles. The existence of similar selective pressures and their influence on SSD has been postulated for the wide-ranging raccoon also (Ritke and Kennedy, 1993).

In a recent review of SSD, Gibbons and Lovich (1990) suggested that differences in the timing of maturity between the sexes were responsible for the degree and direction of dimorphism exhibited; a result confirmed independently by Kozłowski (1989) and later by Shine (1994). Under a model that integrates the effects of natural and sexual selection

(Gibbons and Lovich, 1990) the earlier maturing sex remains smaller, on average, throughout life, than the later maturing sex. Our data are consistent with this scenario if males mature later and at a larger size than females. Alternatively, if males and females mature at the same size as suggested by Ernst (1977), then SSD may be a consequence of faster indeterminate or asymptotic growth in males (Stamps, 1993). Indeterminate growth is known to occur in turtles, including members of the genus *Clemmys,* following attainment of maturity (Lovich *et al.,* 1990). Additional work is needed to document the attainment of sexual maturity in bog turtles using physiological criteria based on sperm or egg production.

Mushinsky *et al.* (1994) suggested that growth rate and the timing of maturity influenced the degree of SSD in populations of the gopher tortoise (*Gopherus polyphemus*). Populations living in areas with long growing seasons and high quality habitat maintained by periodic burning exhibited rapid growth and abrupt attainment of sexual maturity. The result was diminished sexual dimorphism in relation to populations living in less favorable habitats.

It is likely that differences in the degree of SSD among bog turtles are related to differences in resource availability that affect growth. The larger size attained by North Carolina *Clemmys muhlenbergii,* and perhaps their larger hatchling size, may be due to increased productivity, a longer growing season or faster growth rates relative to more northerly populations, but we found no statistically significant difference in the growth rate constant (parameter k) between samples from North Carolina and Pennsylvania, even though values for North Carolina were larger. The statistical similarity of growth rate constants is not unexpected since in most reptiles sex differences in growth occur with respect to asymptotic size, and it is common for males and females to have similar values of k (Stamps, 1995). The degree of SSD was greater in the sample from North Carolina than it was in the sample from Pennsylvania. Thus, potentially faster growth rates may produce enhanced SSD in *C. muhlenbergii,* a result that is opposite of the relationship observed by Mushinsky *et al.* (1994) for *Gopherus polyphemus.*

Our data suggest the importance of differences in the timing of maturity between the sexes in the degree and direction of SSD exhibited by populations, but faster indeterminate growth in males may be a significant factor. Previously published information on the importance of large male size in courtship and mating, and the undeviating male-biased SSD among samples suggests that sexual selection has exerted a strong and consistent influence on the evolution of SSD in *Clemmys muhlenbergii.* Geographic variation in the degree of SSD is a partial function of local differences in growth related to attainment of asymptotic body size, but potentially increased rates of growth do not necessarily result in diminished SSD as suggested previously (Mushinsky *et al.,* 1994).

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