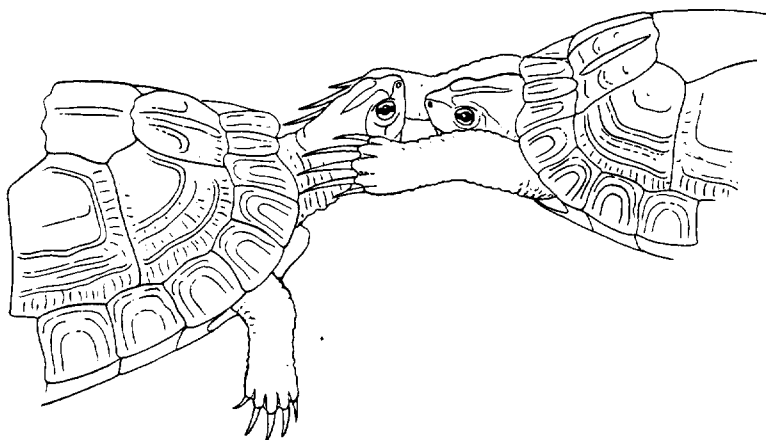


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ON THE SLIDER TURTLE (*TRACHEMYS SCRIPTA*)

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SEXUAL DIMORPHISM IN TURTLES WITH EMPHASIS ON THE SLIDER TURTLE (*TRACHEMYS SCRIPTA*)

J. WHITFIELD GIBBONS AND JEFFREY E. LOVICH

Savannah River Ecology Laboratory, Drawer E,
Aiken, SC 29801 USA

ABSTRACT: Sexual size dimorphism (SSD) in the slider turtle, *Trachemys scripta*, is pronounced; females attain larger body sizes than males in all populations for which data are available. The degree of this difference varies due to sampling biases, growth patterns, predatory pressures, population sex ratios and the size at which each sex reaches maturity. Some evidence of geographic variation is apparent. The direction and magnitude of SSD vary widely among turtle species regardless of phylogenetic relationships, but there is an overall trend toward larger females. Previously proposed relationships between SSD and mean body size were not supported; however, a relationship does appear to exist between SSD and turtle shell shape. We conclude that the size when each sex attains maturity is the underlying cause of SSD in turtles and is the critical life history trait upon which natural and sexual selection operate to determine the ultimate SSD observed, with the smaller sex maturing at a smaller size and younger age than the larger sex.

Key words: Reptilia; Testudines; Emydidae; *Trachemys scripta*; Sexual size dimorphism; Sexual selection

ADULT female slider turtles (*Trachemys scripta*) reach larger body sizes than adult males in the same population. This pattern of sexual size dimorphism (SSD) is characteristic for the species, both geographically and within regions where the size attained by individuals varies appreciably among local populations. SSD in which females are larger than males occurs in many species of turtles in several different families and is particularly prevalent among aquatic species of the family Emydidae (Berry and Shine, 1980). In other species of turtles, adult males may be larger than adult females or the sexes may be the same size. Our purposes are to document the degree and variability of SSD within *T. scripta* and to compare SSD in *T. scripta* with that observed in other species of turtles. We will also attempt to explain the evolutionary significance of the patterns observed by addressing the question of why turtle species show different patterns from one another in the degree and direction of SSD. Sexually dimorphic traits other than body size will also be considered. Turtles represent a prime group in which to examine sexual dimorphism because heterogamety is not a prerequisite for sexual size dimorphism to occur in most species (Vogt and Bull, 1982). Theoretically, two turtles could be identical genetically and yet an individual of one sex could reach an ap-

preciably larger size. The size differential must be a response to physiological or environmental differences that are peculiar to each sex.

Many interpretations of SSD appear to focus on why different-sized bodies or particular anatomical structures are to the advantage of individuals of both sexes, or the species, without adequately addressing the selective pressures that caused the differentiation initially (see review in Lewin, 1985; Mueller and Meyer, 1985). Others have suggested that SSD is a result of ecological forces or natural selection, due to differential interactions of each sex with their environment (Earhart and Johnson, 1970; Feduccia and Slaughter, 1974; Mueller and Meyer, 1985; Schoener, 1966; Selander, 1966; Slatkin, 1984). Several ecological mechanisms have been proposed that could account for SSD (Slatkin, 1984). Perhaps the most frequently invoked ecological cause of SSD is competitive displacement, a process similar to ecological character displacement as described by Brown and Wilson (1956) and Dunham et al. (1979). In the displacement model the resources used by a given sex are determined to some extent by a particular trait. For example, larger individuals or individuals with a larger feeding apparatus may be able to consume larger food items than their smaller counterparts. It is often

assumed that differences in the distribution of such a trait lessen competition between the sexes for the limiting resource. A major criticism of the natural selection model is that it is unable to predict which sex should be larger. Secondly, ecological differences may simply be consequences of sexually selected dimorphism (Shine, 1986). More recent studies found no evidence to support the niche-variation hypothesis in birds (Price, 1984; Rising, 1987).

In the only previous systematic review of sexual size dimorphism in turtles, Berry and Shine (1980) suggested that the direction and degree of SSD depended on male mating strategies. In species with male combat and/or forcible insemination, they predicted that males would be as large or larger than females. In species where female choice is important, they predicted that selection would favor small males as an adaptation to increase mobility. We agree with the general premise of Berry and Shine (1980) that sexual selection theory is a satisfactory explanation for the evolution of size differences as well as certain other sexually dimorphic traits between the sexes in turtles. However, we differ in certain interpretations of how sexual selection might work.

Sexual Selection

Sexual selection the term used by Darwin (1871) for selection that operates on individual characteristics of a particular sex to enhance an individual's probability of success, relative to other members of the same sex, in some aspect of reproduction. Thus, he distinguished between sexual selection and natural selection. Modern authors vary in their interpretations of how sexual selection operates in regards to natural selection; some consider sexual selection as a subset of the broader process of natural selection (Endler, 1986) and others hold to Darwin's view that they are distinct (Arnold, 1983). Trivers (1972) provided a succinct interpretation of sexual selection in the context of each sex's relative parental investment in the offspring. Summaries of the distinction between natural selection and sexual selection have been considered for certain amphibians (Ryan, 1985) and reptiles (Vitt and Cooper, 1985). Although sexual selection may operate in concert

with natural selection, the two processes may be in opposition.

Sexual selection can be subdivided functionally into two categories, on the basis of the trait on which selection operates: 1) intrasexual selection acts on traits that provide an individual with a competitive advantage in "intrasexual interactions" (Vitt and Cooper, 1985), and 2) intersexual selection acts on traits that make an individual more likely to be chosen by a member of the other sex, usually female choice of the male, for mating (epigamic selection). Both kinds of sexual selection are most commonly considered to operate on males of a species, although female sexual selection (i.e., male choice of females) can occur in some situations (Trivers, 1972).

Quantifying Sexual Size Dimorphism in Turtles

Although sexual dimorphism in size is a common feature of many species of turtles, a satisfactory method of quantifying the degree of difference within a population or species has not been thoroughly addressed. One approach for identifying general phylogenetic patterns within a group of animals is to establish which sex, if either, is larger among a large number of species (e.g., amphibians, Shine, 1979; snakes, Shine, 1978; turtles, Berry and Shine, 1980). This procedure of rating species on the basis of the direction of SSD has the advantage of permitting broad phylogenetic comparisons but has the disadvantage of not permitting the ranking of species on the basis of the degree of difference, nor does it allow quantitative comparison of populations that can demonstrate levels of variability within a species. A consistent scheme for determining the degree of SSD is essential if comparisons are to be made among populations or species.

The degree of difference in size between the sexes has been quantified in different ways by various authors. The ratio between the mean size of the female and the mean size of the male, or vice versa, (e.g., Ralls, 1976, for mammals; Dunham et al., 1978, Fitch, 1981, and Stamps, 1983, for reptiles) is one of the most straightforward approaches for establishing a sexual dimorphism index (SDI). The disadvantage

of this type of ratio is that the same sexes are always in the numerator and denominator so that the degree of dimorphism cannot be compared quantitatively between the sexes. For example, a reptile species with females 1.5 times as large as males would have a ratio of 1.5 whereas if males were 1.5 times as large as females the ratio would be 0.67. Another approach to quantifying the degree of sexual dimorphism in size or other individual traits was used by Storer (1966) and others (e.g., Earhart and Johnson, 1970; Rising, 1987; Temeles, 1985) who compared the degree of size difference among birds with an SDI based on mean sizes:

$$200 \times \frac{\bar{x} \text{ size of female} - \bar{x} \text{ size of male}}{\bar{x} \text{ size of male} + \bar{x} \text{ size of female}}$$

This measure of SSD has the advantage of permitting the actual degree of size difference to be compared directly regardless of the direction of the dimorphism. With this SDI, the numbers would be identical, but with different signs (larger female size would be positive). The disadvantage of this type of ratio is a scaling problem. For example, in a species with females twice as big as males the index is 66.7 whereas in one with females four times as large the index is 120.0. Using the percentage difference between mean sizes of the two sexes (e.g., Selander and Giller, 1963) has the same drawback.

The simple ratio of female size divided by male size (Ralls, 1976; Fitch, 1981) would be an effective approach to assessing the degree of SSD among species and populations when one sex is always the larger but is of lesser utility when both situations must be compared, as among turtle species. However, if the log of the resultant ratio is taken, a reverse sign improperly scaled SDI results (Cabana et al., 1982). Our approach will be to use a simple SDI

$$\frac{\text{size of larger sex}}{\text{size of smaller sex}}$$

with the result being arbitrarily defined as positive when females are larger and negative when males are. With equal size in the two sexes the SDI = 1.0. These reverse

sign SDI's eliminate the problems of scaling and imbalance resulting from the other approaches and should serve as a standard means of comparing the degree of size difference between the sexes among turtle species or other animals.

Selecting an appropriate measure of size.—The measure of body size, whether length or mass, will influence the perception of the degree of difference between the sexes and must be considered in comparisons within and among species. For example, the use of body mass results in a greater difference in SDI between the *T. scripta* in Ellenton Bay and Par Pond than does the use of plastron lengths (Table 1). No appreciable difference exists between SDI's derived from plastron length or carapace length within a population because of the high degree of linear correlation between these variables. SDI's close to those obtained from length measurements can be derived by using the means of the cube roots of body mass of each individual or using the cube roots of mean body mass. Cubing the plastron length measurements produces SDI's appreciably higher than those calculated from body mass.

Because straight-line length measurements of turtles are reported in the literature more frequently than are those of body mass, length should be the standard measurement used in calculating an SDI. If it becomes necessary to compare the degree of SSD in turtles with those of other animals for which only weight has been taken, then the cube roots of body mass would be suitable estimates in most instances. Two notes of caution are in order regarding the applicability of certain measurements. First, plastron length itself may be sexually dimorphic (relative to carapace length), as in *Gopherus polyphemus* (Goin and Goff, 1941; McRae et al., 1981), *Kinosternon sonoriense* (Hulse, 1976) and *K. subrubrum* (Iverson, 1979a; Gibbons, 1983), and may not be appropriate as a comparative measure of body size between the sexes in such species. Second, the use of body mass may adversely affect estimates of dimorphism because of the presence of eggs in females (Stamps, 1983). Amadon (1959) noted that in some species of birds the female may temporarily outweigh the male during the laying season

TABLE 1.—Comparison of SDIs using different measures of body size (PL = plastron length; CL = carapace length; BM = body mass; CR = cube roots of body mass; CRM = cube root of mean body mass; PL3 = plastron lengths cubed; PL3M = cube of mean plastron lengths) for adult *T. scripta* from South Carolina for which PL, CL, and BM was taken for each individual.

Location	n		Body size measure	x̄		SDI
	Female	Male		Female	Male	
Elleston Bay (SRP)	28	42	PL	184	136	1.35
			CL	192	148	1.30
			CR	10.3	8.0	1.29
			CRM	10.4	8.3	1.25
			BM	1117	570	1.96
			PL3	5854	2604	2.25
			PL3M	184 ³	136 ³	2.48
Par Pond (SRP)	79	193	PL	232	158	1.47
			CL	248	172	1.44
			CR	13.1	9.1	1.44
			CRM	13.3	9.4	1.41
			BM	2322	838	2.77
			PL3	12,058	4056	2.97
			PL3M	232 ³	158 ³	3.17

even though the male is considered to be larger at other times based on skeletal or other measurements.

Selecting the proper statistic.—In comparisons of the degree of SSD between species or between populations within a species, the consistent use of a statistic is imperative. For comparing the degree of SSD, the mean of the total sample of adult males and females has been used most frequently among most groups of animals, although some authors have used some portion of the largest individuals in a sample to designate body size in some reptile populations (Berry and Shine, 1980; Case, 1976; Soule, 1966). Fitch (1981) presented ratios for a variety of reptile species based not only on the sample mean, mode, median and maximum, but also on the mean of the ten, five and three largest adult individuals of each sex. He concluded that all ratios, except the one based on the largest individual of each sex, were close approximations of the ratio obtained from the mean sizes for most species. This conclusion does not hold true for *T. scripta* from the SRP (nor for the tabulated data of *T. scripta* given by Fitch). Instead, in most of the populations, a progressive increase occurs in the degree of SSD as the sample size of largest specimens is increased (Table 2). The data for several populations of *T. scripta* with large sample sizes indicate that in this species the mean and median are always close to each other

and are often identical. In contrast, the SDI's calculated from the mode generally stray further from those based on the mean.

Factors Influencing the Estimation of Sexual Size Dimorphism

Several sampling and biological factors should be considered in determining the degree of sexual size dimorphism within a population or species. The consequences of nonrandom sampling, differential mortality (Dunham, 1981) or dispersal (Gibbons, 1986) of the sexes could have a major influence on the size dimorphism in a sample.

Collecting bias.—Differential activity patterns of males and females (Blake, 1922; Gibbons, 1986; Morreale et al., 1984; Parker, 1984) coupled with age- or size-specific responses that might result in larger or smaller individuals of a particular sex being captured could be a consideration in determining SDI from a sample, especially a small sample taken over a short time span (Ream and Ream, 1966). Season or trapping method does not appear to make a major difference in the assessment of the degree of SSD in *T. scripta* populations on the SRP. For example, the SSD's of *T. scripta* caught at drift fences (1.36, $n = 485$) or aquatically (1.35, $n = 394$) or those caught in winter (1.27, $n = 25$), spring (1.35, $n = 516$), summer (1.42, $n = 268$),

TABLE 2.—Variation in the degree of SSD in South Carolina populations of the slider turtle, *T. scripta*, based on different size statistics. PL indicates plastron length in mm.

Location	n	x size at maturity	z	Median	Mode	Adult size					
						1	3	5	10	Largest	
Ellenton Bay	SDI	1.60	1.34	1.39	1.40	1.08	1.13	1.14	1.14	1.25	1.33
	Female PL	160	186	185	175	241	238	236	220	203	188
	Male PL	100	139	133	125	223	210	206	193	163	141
Par Pond	SDI	2.00	1.48	1.48	1.32	1.14	1.15	1.17	1.24	1.31	1.42
	Female PL	200	234	235	238	277	275	274	263	249	235
	Male PL	100	158	159	180	243	239	234	212	190	166
Risher Pond	SDI	1.60	1.34	1.40	1.60	1.14	1.16	1.14	1.14	1.29	—
	Female PL	160	190	189	189	232	229	222	217	194	—
	Male PL	100	142	135	118	203	197	195	191	150	—
Lost Lake System	SDI	1.60	1.34	1.33	1.31	1.19	1.19	1.21	1.26	1.30	1.34
	Female PL	160	195	194	188	250	246	245	231	212	196
	Male PL	100	146	146	144	210	206	203	183	163	146
Pond B	SDI	1.60	1.55	1.69	1.87	1.15	1.16	1.19	1.31	1.45	—
	Female PL	160	211	216	206	261	256	253	248	229	—
	Male PL	100	136	128	110	226	220	213	190	158	185
Capers Island	SDI	—	1.35	1.35	1.34	1.54	1.23	1.29	1.31	1.37	—
	Female PL	45	252	255	272	279	278	276	274	—	—
	Male PL	14	187	187	190	177	226	216	211	200	—
Kiawah Island	SDI	—	1.28	1.28	1.27	1.40	1.29	1.27	1.26	1.26	—
	Female PL	17	256	262	266	284	279	275	270	—	—
	Male PL	19	200	206	190	221	220	219	214	—	—
Cecil's Pond	SDI	1.60	1.36	1.37	1.35	1.20	1.21	1.20	1.21	—	—
	Female PL	31	191	190	162	227	223	220	210	—	—
	Male PL	74	140	139	120	189	185	182	173	—	—
McElmurray's Pond	SDI	1.60	1.15	1.13	1.13	1.24	1.16	1.14	1.10	1.13	1.13
	Female PL	106	180	179	181	242	224	216	200	188	179
	Male PL	209	157	159	160	195	193	189	182	167	159

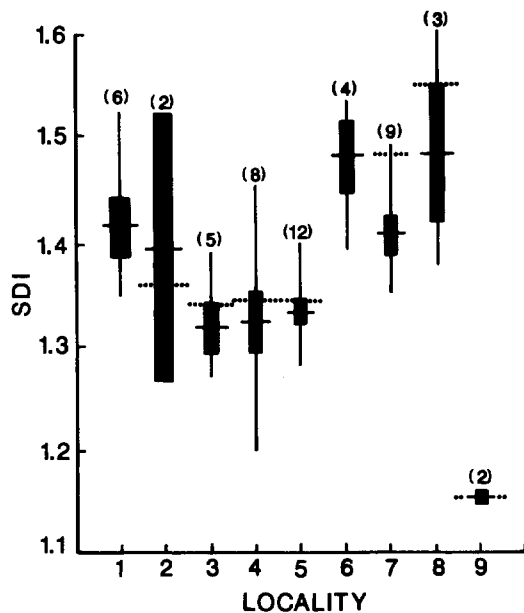


FIG. 1.—Variation in the SDI estimate in South Carolina populations of adult *T. scripta* based on samples taken in different years between 1967 and 1986. Numbers in parentheses represent sample sizes (number of different years) used to calculate means (solid horizontal lines), \pm one standard error (solid bar), and ranges (vertical line). Sample sizes for a population in a given year ranged from 20–315. We used only those years in which 10 or more adults of each sex were captured. Locality codes are as follows: 1 = Steed's Pond, 2 = Cecil's Pond, 3 = Lost Lake, 4 = Risher Pond, 5 = Ellenton Bay, 6 = Steel Creek, 7 = Par Pond, 8 = Pond B, 9 = McElmurray's Pond. The dotted horizontal lines represent overall population means from Table 2.

or fall (1.31, $n = 132$) are not appreciably different.

Sampling variability.—A measure of variation that can exist in the estimates of the SDI of a natural population can be observed in a comparison of SDIs based on samples from different years. The variance in the SDI within each of nine South Carolina populations is extensive (Fig. 1). Caution is advised in interpreting the actual magnitude of these differences because of inherent pseudoreplication in year-to-year samples (Hurlbert, 1984). An additional measure of variation in SDIs can be derived by comparing regional populations (Table 2; $\bar{x} = 1.35$, $SE = 0.04$).

Combining samples.—Another sampling consideration is whether individuals from different populations or regions have been combined. In some species, size and

age at maturity of the sexes may vary significantly between local populations [e.g., *C. picta* (Gibbons and Tinkle, 1969); *T. scripta* (Gibbons et al., 1981)] or geographic regions [e.g., *T. scripta* (Moll and Legler, 1971, Gibbons et al., 1981)]. Thus, the sexually mature part of one population may consist of individuals with different sizes and ages than those of another population. When the Ellenton Bay and Par Pond samples from the SRP are combined (Table 1, but using the Ellenton Bay size at maturity of females) the SDI is 1.38, a number intermediate between 1.35 (Ellenton Bay) and 1.47 (Par Pond). Clearly, the impact of the proportion of the sample size of each sex from each population represented would influence the SDI, but the SDI attained should be suitable for comparison with other species or among geographic regions within the species. Combining samples from different geographic regions where size differences may be more extreme could amplify this problem and should be taken into account in the use of museum specimens from widespread geographic areas.

Despite the obvious potential influence that nonrandom field sampling could have on estimating SDI's, the information available for *T. scripta* suggests that sampling bias is of minor concern with this species, and presumably with other turtles as well, and should not greatly affect the effective quantitative comparison of the degree of SSD among species or within populations of the same species.

Size at maturity.—In most populations, the SDI increases with an increase in sample size from the largest individual of each sex to the largest 100 of each sex (Table 2). Since the SDI is lowest when only the largest/oldest animals of each sex are used, males in the population either must grow faster or continue to grow for a longer period of time than do females, or large females have a higher rate of mortality than large males. Evidence from *T. scripta* at Ellenton Bay and Par Pond suggests that differential growth patterns between the sexes are responsible for a decrease in SDI's relative to time since maturity (Fig. 2) However, these trajectories should be interpreted with caution since the sexes reach maturity at different ages (see following

section). The biological significance of this observation for *T. scripta* is that, after attainment of maturity, the proportional increase in body size is greater in males than in females. Survivorship data from these two populations do not support the hypothesis that differential mortality of the sexes influences this phenomenon, although this may be an explanation in some instances (Dunham, 1981). For example, the SDI of *T. scripta* on Capers Island is best explained as a situation in which the smaller males have been disproportionately eliminated by alligator predation resulting in a change in sex ratio and in SDI (Gibbons, 1990). The preceding discussion suggests that a serious problem in quantifying the degree of SSD of a sample relates to the determination of the size at which maturity is reached in a population by individuals of each sex. As Fitch (1981) noted, "Determining the lower limit of adult size is critical," since the majority of the adult population is in the smaller size classes. Therefore, the SDI based on the mean sizes could shift considerably if a significant error is made in the estimation of size at maturity. For example, on the basis of dissections and x-ray examinations, a 200 mm plastron length was used as an approximation of the female lower limit for maturity in the Par Pond sample, compared to 160 mm for Ellenton Bay. If, instead, the 160 mm length had been used for Par Pond (as used in the combined sample noted above), the SDI would be 1.40 rather than 1.48.

In calculating the SDI, a size at maturity must be chosen for each sex with an understanding that the selected size is only an estimate based on the (usually limited) information available and also that typical biological variability will exist around the mean size at maturity for each sex. This problem may be obviated in short-lived species, such as some lizards, in which all individuals in a population reach maturity at a particular age (season) so that the adult portion of the population is easily identified. For example, Stamps (1983) observed that sexual dimorphism in size at maturity was highly correlated with sexual dimorphism based on average sizes in lizards. However, the high variability of age and size at maturity among turtle populations

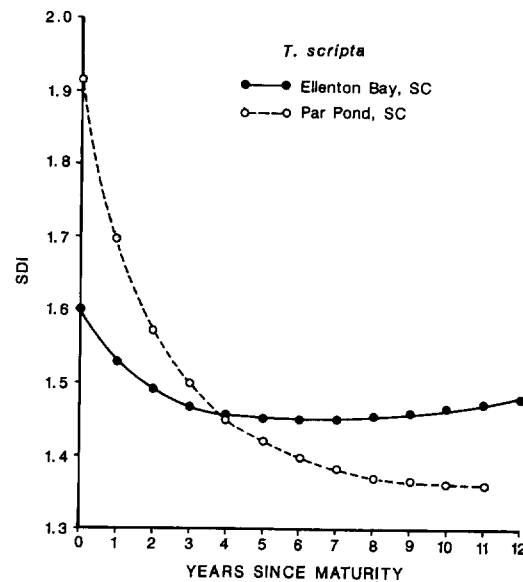


FIG. 2.—Relationship between SDI and age based on time since maturity in South Carolina populations of *T. scripta*. Sizes at each age were predicted from monomolecular growth equations generated for each sex and population. Par Pond males, $PL = 194.3 [1 - e^{-0.248(AGE)}]$; females, $PL = 265.0 [1 - e^{-0.191(AGE)}]$. Ellenton Bay males, $PL = 151.4 [1 - e^{-0.218(AGE)}]$; females, $PL = 234.0 [1 - e^{-0.128(AGE)}]$.

(Gibbons et al., 1981; Zug et al., 1986) confounds this problem considerably. Determination of age and size at maturity of both sexes as key, although difficult-to-obtain, life history statistics must become a major emphasis in the study of the natural history of turtles and other organisms.

Sex ratio, population size and age structure.—The shape of size distributions can vary considerably among different populations of the same species and affect the mean of a sample. A complication in quantifying the degree of SSD could arise from continuing changes in body size due to indeterminate growth of the adults in some species, such as *T. scripta*. For example, in a population of sexually mature turtles with limited recruitment, the SDI might change over time because of continued growth of individuals (Fig. 2).

Additional complications arise if age-specific SSD is to be determined, as suggested by Dunham (1981). In species such as slider turtles that show dramatic SSD, the males reach maturity several years before the females, so that cohort (i.e., age-specific) comparisons at certain ages would

include immature females and mature males. Thus, in species such as *T. scripta*, age-specific SSD is only meaningful after both sexes in a population have reached maturity. To determine age-specific SSD of adults within a population, not only must age and size at maturity be known, but also the actual ages of all individuals in the population. Although the determination of age-specific size dimorphism is an ideal to seek, it is not of practical applicability unless the maturation patterns of the study species are thoroughly understood.

Because of the difference between the sexes in age and size at maturity, the adult sex ratio could become important if one sex greatly outnumbers the other in older or younger cohorts. Thus, the population age and size structure can vary depending on whether smaller (younger) or larger (older) individuals have been disproportionately eliminated from the population. Also, population age structure (and, therefore, size structure) can vary as a function of the age of the population and whether it is expanding or declining in size. For example, an expanding population of *T. scripta* in which recruitment increases annually will result in a decreasing SDI over time.

Conclusion regarding SSD.—As indicated in the preceding sections, the relationship between size of the sexes can be expressed in a variety of different ways and numerous sampling and biological factors must be taken into consideration. Our recommendation is to quantify the degree of difference in sexual size dimorphism between populations of species of turtles by a simple SDI.

$$\frac{\bar{x} \text{ length of adults of larger sex}}{\bar{x} \text{ length of adults of smaller sex}}$$

The SDI is positive when females are larger and negative when males are. Mean lengths of the samples should be the standard measure of size for such comparisons since mass is a less frequently obtained measurement. This approach provides consistency in comparisons of the magnitude of the difference in size dimorphism of the sexes between different samples, populations, or species and permits the

greatest versatility in using previous literature reports.

SEXUAL SIZE DIMORPHISM IN TURTLE POPULATIONS

A comparison of the degree of sexual size dimorphism in *T. scripta* can be made using data from the Savannah River Plant populations in South Carolina (Table 2) and from those of other studies reported in the literature (Table 3). Several observations are pertinent to an understanding of sexual size dimorphism in turtles and presumably to other animals as well. The issues of variation, geographically and among local populations within a region, are of particular importance.

Variation among Populations of T. scripta

SDI's for several South Carolina populations of *T. scripta* ranged from 1.28 to 1.55. In comparing nine South Carolina populations of *T. scripta* in regard to SSD, juvenile growth rates and maturity patterns appear to dominate the final calculation. In populations of slow-growing individuals (e.g., Ellenton Bay, Gibbons et al., 1981), males reach maturity at approximately 100 mm in plastron length whereas females mature at about 160 mm. Thus, the SDI at size of maturity for the two sexes is 1.60. In contrast, Par Pond has individuals that grow significantly faster because of being thermally affected by reactor effluents (Gibbons, 1970). However, males still reach maturity at approximately 100 mm (but at a younger age), whereas females delay maturity in most instances until they attain sizes above 200 mm, reaching maturity at approximately the same ages as those at Ellenton Bay (Gibbons et al., 1981). The SDI at size of maturity in Par Pond is 2.00. Thus, the contrast between the size of the adults of both sexes is dramatically different between the two populations as a result of growth and maturity patterns. Although the size differential between the sexes is reduced in both populations (e.g., Ellenton Bay and Par Pond) as both sexes continue to grow as adults (males apparently at a faster rate than females, although this has been difficult to confirm with studies of individual growth; Fig. 2 and Table 2), the SDI's of

TABLE 3.—Geographic comparison of SDIs among slider turtle (*T. scripta*) populations based on mean plastron lengths (PL) of adults. SDIs from published studies were based on best estimates from tables, figures, text, or personal communication with the author.

Location	n		\bar{x} PL		SDI	Reference
	Male	Female	Male	Female		
South Carolina						
Ellenton Bay	570	353	139	186	1.34	This study
Par Pond	760	354	158	234	1.48	This study
Risher Pond	63	58	142	190	1.34	This study
Lost Lake System	653	328	146	195	1.34	This study
Pond B	185	78	136	211	1.55	This study
Caper's Island	14	45	187	252	1.35	This study
Kiawah Island	19	17	200	256	1.28	This study
Mississippi						
1977	76	50	132	196	1.48	Parker, 1985
1982	59	28	142	195	1.37	Parker, 1985
Illinois						
	403	441	152	189	1.24	Cagle, 1950
	12	9	183	206	1.13*	Cahn, 1937
Oklahoma	44	14	136	192	1.41	Webb, 1961
Panama			195	292	1.50	Moll and Legler, 1971
Belize	152	188	181	292	1.61	Moll, personal communication
Indiana	5	11	183	200	1.09	Minton (1972)

* Calculated from straight-line carapace length.

the two populations are closer at later sizes than at maturity.

Three populations with slow-growing individuals (Risher Pond, Lost Lake System, Cecil's Pond) are all similar in SDI to Ellenton Bay. Pond B and the two island populations (Kiawah and Capers) represent examples of possible biological situations that can arise and influence the SDI. The island population habitats allow rapid growth of juveniles and large size at maturity in females (Gibbons et al., 1979). However, juvenile recruitment on Kiawah has historically been minimal, and no juveniles (= 0 recruitment) have ever been found in the Capers Island population, presumably due to intense size-specific predation on juvenile turtles by alligators in the unusual situation of habitats with limited aquatic vegetation (Gibbons, 1990). Thus, Capers Island, isolated from the mainland by several hundred meters of open saltwater, represents a relict population of primarily or exclusively adult turtles in which the smaller size classes of adults (primarily males) have been removed. The male size curve is therefore truncated at the smaller size end so that the mean size of adult males is considerably higher than would be present in similar populations without such size-specific mortality.

Pond B is representative of a biological situation that contrasts the island populations. As a thermally affected habitat with fast-growing individuals (Christy et al., 1974), *T. scripta* in Pond B assumed the growth and maturity pattern of Par Pond. However, habitat conditions have been altered in the past several years so that Pond B is now a population of slow-growing turtles. Although males continue to mature at a size of 100 mm, their adult growth rates are considerably reduced. The population now has numerous smaller males that are mature and are proportionately more abundant than females. Thus, the female portion of the population is composed of many individuals that achieved maturity at a large size under the thermal regime that promoted rapid growth in juveniles. A major component of the male portion of the population is composed of small individuals, most of which matured under the current cooler water conditions, because of the significant earlier age at maturity of males. Thus, the abundance of small males increases the SDI.

Knowledge of the dynamics of populations is not usually available in establishing SDI's, but the above examples clearly demonstrate the potential effect. Nonetheless, it is noteworthy that, although the SDI of *T. scripta* ranged be-

tween 1.15 and 1.55 in populations with large sample sizes, the data demonstrate conclusively that *T. scripta* in South Carolina display SSD, with females being significantly larger, in all populations, regardless of growth patterns. The lack of a clear relationship between SDI and maximum size attained by individuals in a population of *T. scripta* is indicative of the importance of the population dynamics.

A slight trend is evident in the geographic variation in SDI's using a variety of populations, ranging from midtemperate to tropical areas. The tropical population studied in Panama by Moll and Legler (1971) has a high SDI, and the northernmost populations in Indiana have the lowest. However, the range in SDI's from several populations in a single geographic region in South Carolina encompasses the high value and approaches the low value (Table 3). Iverson (1985) and Tinkle (1961) reported geographic variation in the direction and magnitude of SDI in two species of kinosternids, and Fitch (1981) observed a north-to-south increase in SDI for *Chrysemys picta*. This relationship requires additional research tempered with an understanding of population dynamics and potential biases.

Our conclusion based on the available data is that SSD in *T. scripta* is a species trait in which females are characteristically larger than males but in which great variability in the degree of SSD exists among populations. This variability is explicable in terms of population dynamics and growth patterns intrinsic to a population.

Comparison of SDI in Different Species of Turtles

The degree of SSD varies widely among turtles. Examination of Appendix Table A reveals a preponderance of species in which females are larger than males. Major exceptions include chelydrids and most testudinids. SDI's range from -1.45 to 2.10 indicating that males of some species never attain the size advantage relative to females that females of other species attain relative to males. Despite the few exceptions, the facts suggest strong natural or sexual selection for large body size in females throughout the entire order.

The high variance observed in SDI among related taxa damps any inclination to provide a phylogenetic interpretation of the phenomenon. Some of this variance is undoubtedly due to sampling error or other biases, but it may also result from different selective regimes operating on each species. Alternatively, Cheverud et al. (1985) have suggested that the degree of SSD exhibited by a species is a direct reflection of ancestral dimorphism patterns. This, however, does not provide an ultimate explanation of how dimorphism occurred initially.

Relationship between SDI and Body Size

A number of researchers have implied that SDI is a function of body size. Rensch (1960; in Selander, 1966) suggested that in bird species with larger males than females, SDI increases with body size, but in the case where females are larger, SDI decreases with body size. Selander (1966) provided additional evidence for the former situation but found the correlations to be "... weak and the exceptions so numerous as to raise questions concerning the validity of the 'rule.'" Others have suggested a positive correlation between SDI and body size in mammals (Ralls, 1976; Cheverud et al., 1985; Clutton-Brock et al., 1977), frogs (Shine, 1979), and kinosternid turtles (Berry and Shine, 1980; Iverson, 1985), but Moors (1980) and Ralls and Harvey (1985) reported an inverse relationship for a similar comparison in mustelid mammals.

In order to test for the existence of a possible relationship between SSD and body size in turtles, SDI was plotted against the mean carapace length for sexually mature males and females (combined) of 63 turtle taxa representing eight families (Fig. 3). The absence of an obvious relationship casts serious doubts on the applicability of "Rensch's Rule," and we conclude that previously reported trends based on body size in turtles are the result of sampling size and error or population dynamics as discussed above. In addition, we consider that no relationship between species body size and sexual dimorphism has been convincingly demonstrated and that relationships of this kind should be examined more

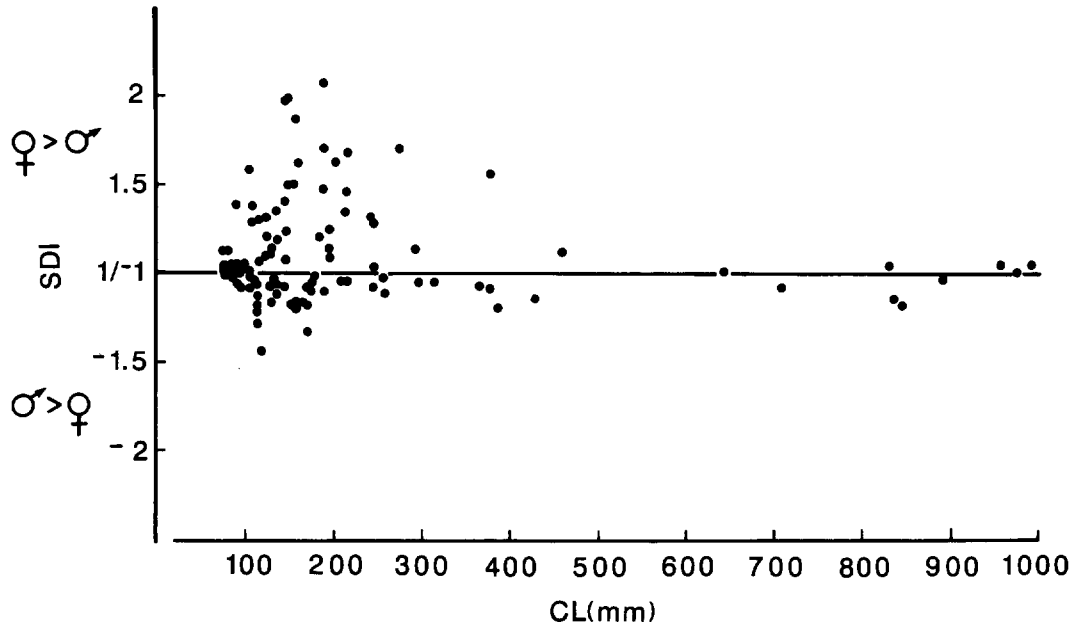


FIG. 3.—Relationship between SDI and mean body size (CL) of male and females combined for 63 turtle taxa. Data from Appendix Table A.

extensively before such implications are made.

A relationship among turtle species that may have some validity is that SDI changes as a function of shell domedness (Fig. 4). Although adequate data are not currently available to rigorously test this hypothesis, the most domed species, regardless of phylogenetic relationship, are more likely to have males that are the same size or larger than females.

Other Sexually Dimorphic Traits

In *T. scripta* at least five other traits show sexual dimorphism. One of these is the precloacal length which becomes significantly longer as males reach maturity. This lengthening of the male precloacal area is characteristic of most, probably all, species of turtles. Two other, apparently mutually exclusive, sexually dimorphic traits in *T. scripta* are lengthening of the foreclaws and elongation of the snout in adult males (Table 4). Elongated foreclaws are used during courtship and are characteristic of the subspecies of *T. scripta* in eastern North America. In contrast, most tropical subspecies of *T. scripta* have an elongated snout and short claws. Another difference apparently occurs in the weights

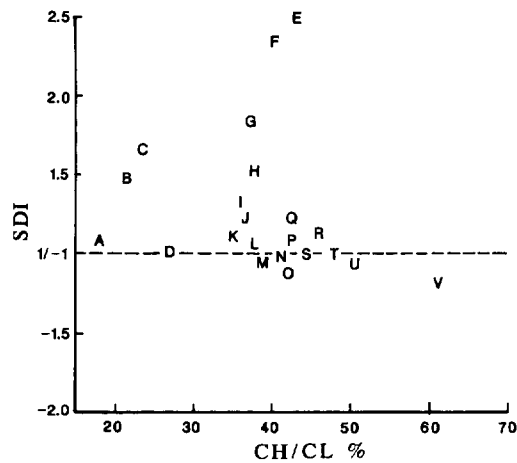


FIG. 4.—Relationship between SDI and domedness. Domedness is expressed as a percentage of mean carapace height divided by mean carapace length for males and female combined. Abbreviations are as follows: A = *Malacochersus tornieri*, B = *Trionyx muticus*, C = *Trionyx spiniferus*, D = *Platemys platycephala*, E = *Graptemys pulchra*, F = *Graptemys barbouri*, G = *Graptemys geographica*, H = *Graptemys pseudogeographica*, I = *Pseudemys concinna*, J = *Chrysemys picta*, K = *Trachemys scripta*, L = *Clemmys guttata*, M = *Emydoidea blandingii*, N = *Clemmys muhlenbergii*, O = *Chelydra serpentina*, P = *Sternotherus odoratus*, Q = *Chinemys reevesii*, R = *Batagur baska*, S = *Kinosternon subrubrum*, T = *Terrapene ornata*, U = *Terrapene carolina*, V = *Geochelone yniphora*. Data from references listed in Appendix Table A.

TABLE 4.—Claw and snout length dimorphisms exhibited by male *Trachemys scripta* and allies in relation to females.

Subspecies	Reference					
	Smith and Smith (1980)		Moll and Legler (1971)		Others	
	Claws	Snout	Claws	Snout	Claws	Snout
<i>callirostris</i>	—	—	—	—	similar	long ¹
<i>cataspila</i>	similar	—	similar	long	—	—
<i>chichiriviche</i>	—	—	—	similar	long ¹	—
<i>dorbignyi</i>	—	—	—	—	long ²	—
<i>elegans</i>	long	—	long	similar	long	similar ³
<i>gaigeae</i>	similar	—	similar	similar	—	—
<i>grayi</i>	similar	long	similar	long	—	—
<i>hiltoni</i>	similar	—	similar	long	—	—
<i>nebulosa</i>	similar	long	similar	long	—	long ⁴
<i>ornata</i>	similar	similar	similar	long	—	—
"Panamanian"	—	—	similar	long	—	—
<i>scripta</i>	long	—	long	similar	long	similar ³
<i>taylori</i>	similar	—	similar	similar	—	—
<i>troostii</i>	long	—	long	similar	long	similar ³
<i>venusta</i>	similar	similar	similar	long	—	long ⁵
<i>yaguia</i>	similar	similar	similar	long	—	—
Antillean <i>Trachemys</i>	—	—	long	long	—	—

¹ Pritchard and Trebbau (1984).² Ernst and Barbour (1989).³ Ernst and Barbour (1972).⁴ Carr (1952).⁵ Pritchard (1979).

of several brain regions. Quay (1972) found that male cerebral weights in particular were greater than those in size and weight matched females. He attributed these differences to overall differential growth rates between the sexes. A fifth trait, melanism in some adult males, is also characteristic of the species in parts of its range (Lovich et al., 1990). Numerous other forms of sexual dimorphism and sexual dichromatism are present in turtles as indicated in Appendix Table B.

MODEL FOR EVOLUTION OF SEXUAL SIZE DIMORPHISM IN TURTLES

When considering how sexual size dimorphism is developed and maintained in a species, the evolution of sexual size differences must be emphasized. The basic assumption is that ancestral populations had sexes of similar size. What traits were selected initially to cause a divergence of adult male and female sizes? And, why has a size differential been maintained in a species?

Natural selection and sexual selection have operated independently and in con-

cert to produce the ultimate sexual size dimorphism pattern characteristic of the species (Lande, 1980; Price, 1984). Among turtles, critical life history traits on which the two forms of selection operate in regard to body size are age at maturity, size at maturity, and continued growth after maturity. Natural selection should operate equally and in the same manner on both sexes while they are juveniles with similar sizes and behaviors, i.e., prior to attainment of maturity. In addition, certain factors related to body size are important to both sexes and would be acted upon by natural selection including: resource availability, predator size and intensity, thermal environment, and dehydration factors. Therefore, we must determine what features of each sex result in the differential influence of sexual selection and the resultant sexual size dimorphism observed in a species.

Larger size in females can result in more or larger eggs (Gibbons et al., 1982), whereas larger size in males may result in superiority in male-male encounters (Aufenberg, 1977; Cagle, 1950; Lardie, 1983), the potential for moving greater distances

in search of new mates, and possibly an advantage as a consequence of female choice for larger males. Either sex could benefit through sexual selection for maturity at a young age because of the competitive advantage of entering the breeding population early, thus potentially increasing the number of mating opportunities in a lifetime. It is the collective importance of these traits to reproductive performance in a species that determines the degree and direction of sexual size dimorphism. Obviously, the environmental conditions under which selection has operated will be critical in determination of the outcome.

We do not accept the concept that larger males gain a fitness advantage through physical superiority that permits forcible insemination of nonreceptive females (Berry and Shine, 1980; Tanaka and Sato, 1983). Forcible insemination as a requirement for procreation in turtles is not a believable concept to us, and we can see no means by which a male turtle can successfully achieve intromission with a recalcitrant female. Structures such as vinculae and tail spines are presumably only specializations to ensure proper apposition of the sexes when mating. Booth and Peters (1972) demonstrated that female *Chelonia mydas* are capable of using postural or behavioral mechanisms to avoid copulation. In addition, as Thornhill (1980) pointed out, the adaptive significance of heterosexual rape is difficult to demonstrate because female coyness is difficult to distinguish from apparent rape. Each of the above considerations is experimentally testable.

If juvenile turtles of both sexes grow at the same rate (Wallin and Gibbons, 1990), then a major factor that establishes sexual size dimorphism within a species may be the size at which maturity is attained. This explanation presumably applies to most turtle species, and should be considered in other groups of animals in which SSD occurs. However, the question of why one sex matures at an earlier age remains to be addressed. The positive side of early maturity is that an individual becomes part of the breeding population earlier in its life, a feature that can result in a higher probability of successful mating before

mortality (Gibbons et al., 1981). The negative side of maturing too small is that the individual is not large enough to be competitive in the breeding population, is less likely to be able to avoid or withstand attack by certain predators, or is unable to cope as effectively with some other aspect of the environment. Another negative feature of maturation at a small size can be that growth rate will diminish and the maximum size will be reduced.

Sexual Selection vs. Natural Selection in Turtles

Sexual size dimorphism in *T. scripta* is the result of sexual selection and natural selection acting in opposition on the size and age at maturity (Table 5). A male turtle is in competition with others in the timing of its entry into the breeding population. A possible reason why males do not delay maturity longer, and increase body size faster by remaining immature, is that the sexual selective advantage of becoming a competitive breeder at an early age outweighs the possible epigamic selective advantage gained through female choice of larger males. This sexual selection, however, is opposed by natural selection, because turtles reaching maturity at a young age grow slower than those remaining immature. Larger size would presumably reduce predation by some species, such as crocodilians or large fish. Therefore, natural selection operates against attainment of maturity at a young age and small size.

In South Carolina, these forces of natural selection are apparently predominant for individuals smaller than about 90–100 mm in plastron length (Gibbons et al., 1981), since maturity is seldom reached by males below this size range regardless of their age. Natural selection against turtles in size classes smaller than 90–100 mm must be very strong as it seems unlikely that such a sharp size threshold would occur otherwise, particularly when individuals grow at dramatically different rates. However, when this size is attained, male turtles will become mature. Once natural selection pressures have been relaxed (possibly because of reduced predation on turtles that have achieved the minimum size for maturity), sexual selection for maturity

TABLE 5.—Traits of turtles on which natural selection and sexual selection operate independently to cause sexual size dimorphism. NS = natural selection, SS = sexual selection.

Trait	NS		SS	
	Cost	Benefit	Cost	Benefit
Maturity at young age	—	—	—	Early entry into breeding population
Maturity at small size	Reduced growth delays attainment of large size	Fewer resources required for body maintenance	Same as for natural selection	Same as for natural selection. More resources allocated for courtship and nesting activities.
Continued growth after maturity	Additional resources required	Opportunity to achieve larger size	Additional resource acquisition required for activities	Same as for natural selection (reproductive)

at a young age becomes the dominating factor.

Once maturity is attained by a male turtle, growth apparently continues (indeterminate growth; Andrews, 1982), though at a rate greatly reduced from that of the immature form because of the partitioning of energy resources into various reproductive functions such as searching for mates and courtship exercises (Congdon et al., 1982). Sexual selection operates in concert with natural selection to favor this continued growth with the resultant increase in body size. Indeterminate growth and the rate at which it occurs in a species is a function of natural selection because of the possible inherent advantages that being larger confers on the reduction of predation, desiccation, and thermal stress. Continued growth may be a function of sexual selection because of the assumed advantages that a larger male incurs in the mating process or that a female attains through greater egg production.

If age at maturity is relatively constant in a population, then larger males could represent individuals that had demonstrated a superiority through survivorship or through more efficient utilization of resources and growth. Assuming a heritable component (Ryan, 1985; Endler, 1986) for larger size, large males would be favored

by sexual selection and the offspring of females that selected them would be favored by natural selection.

Another advantage of males achieving a larger size, i.e., selection favoring continued growth, may be that larger males are more successful in long treks overland or through aquatic habitats to seek receptive females. Male *T. scripta* and other turtles travel more extensively than females during the mating periods (Morreale et al., 1984; Gibbons, 1986). Preliminary evidence indicates that most long distance movement is by the largest males. The proposal by Berry and Shine (1980) that small male turtles are favored because of their greater "mobility" has no supportive data. Further, if small size alone were advantageous, continued growth after maturity would be maladaptive. Finally, larger males likely have a competitive advantage during male-male encounters in the presence of a female.

The issue of sexual size dimorphism among turtles is a complex one. The very fact that some species show no dramatic size dimorphism between the sexes, whereas others have much larger females than males, and still others have been reported to have slightly larger males than females, makes turtles a particularly valuable group for studying this phenomenon.

Our assessment of the situation is that the size and age at which maturity is reached are the factors on which sexual and natural selection operate to produce sexual differences in adult size. We predict that as a general rule, in species in which sexual size dimorphism occurs, the smaller sex will mature at a smaller size and at a younger age than the larger sex, and this differential size and age at maturity will correspond to the ultimate difference in size between the two sexes. Some studies (e.g., Fitch, 1960; Gibbons, 1972, with snakes) have implied that the larger sex may mature at a smaller size. However, unequivocal evidence of the exact size at which maturity is attained in each sex will be necessary to refute our contention that sexual size dimorphism in adults is a reflection of mean age and size at maturity.

Although it is difficult to simplify complex biological phenomena, the following scenario seems to apply to the evolution of sexual size dimorphism. In terrestrial habitats and situations where large size is important to avoid predation or any other environmentally induced mortality, males of many species are the same size as or larger than females. Despite Berry and Shine's (1980) conclusion that sexual selection favors larger males in terrestrial species due to an advantage in male-male combat, a different explanation seems more plausible. We propose that male turtles in terrestrial environments reach sizes as large as the females because natural selection strongly favors continued growth as rapidly as possible so that a larger size can be attained. Sexual maturity at a younger age than in females would be precluded as this would forfeit the continuation of rapid growth. The difference in cause is indeed a consequence of turtles being aquatic or terrestrial, but not for the reasons Berry and Shine (1980) propose. Instead, the difference is that terrestrial turtles are confronted with a larger array of predators from which they usually cannot escape, once they have encountered the predator, except through larger size or a protective shell covering. We conclude that a relationship between domedness and SDI will be found to exist (Fig. 4), because both domedness and large size are comparable reflections of the species' response to pre-

dition. Increased domedness and larger size operate interactively to combat predation.

Aquatic turtles, on the other hand, have a higher probability of escape in many aquatic situations because of greater effective mobility and speed compared to those in terrestrial situations. In addition, the size required of a turtle to avoid predation by aquatic predators is probably much less than that needed to deal with many terrestrial predators that can increase their predatory efficiency through increased handling time of captured prey. Also, the threats of desiccation and thermal stress are unquestionably an issue in terrestrial environments, and larger individuals have a major advantage in being able to endure environmental extremes for a longer period of time. Therefore, natural selection will favor a much larger minimum size at maturity in terrestrial turtles than in aquatic ones, thus overriding the pressure of sexual selection for male turtles to mature at a younger age and smaller size.

Finally, it is necessary to resolve the issue of why males are larger than females in some species. An explanation for why the sexes are more likely to be equivalent in size in terrestrial species has been given above. A simple extension is that sexual selection favors an additional increase in male body size due to the advantage of larger size in combat situations. This advantage would be especially true in terrestrial situations since, if two male terrestrial turtles encounter a female simultaneously, success is less dependent on speed and maneuverability, as it might be in an aquatic habitat, than on effectiveness at outcompeting the other male. Thus, a dominance hierarchical system is more likely to evolve. We do think it is important that evidence of male superiority by virtue of size be sought in aquatic species as aggressive behavior is an apparently common but seldom observed phenomenon in freshwater turtles (Lovich, 1988).

Recommendations for Future Research

The preceding discussion has revolved around a large data set on one species of

turtle and a review of previous findings and interpretations of the phenomenon of sexual size dimorphism in other species. Many of our conclusions and predictions are based on the limited data available on the subject, and they will unquestionably be improved with additional data that give consideration to certain potential biases and to the collection of more precise data on the vital life history parameters of age at maturity, size at maturity, and adult growth rates. In addition, experimental studies could serve to great advantage in resolving certain issues.

The following research would greatly improve the overall understanding and interpretation of the proximal and ultimate factors affecting sexual size dimorphism in turtles.

1. A model of the potential importance of each of the factors that varies differentially between the sexes (age and size at maturity, growth rates of juveniles and adults, size-specific emigration/immigration or mortality of adults) and that can have a proximal influence on sexual size dimorphism could be highly instructive.

2. The search for geographic trends in sexual size dimorphism could result in more definition to the issue of intraspecific variability in the phenomenon. At this time, no evidence has been presented to dismiss a conclusion that the sexual size dimorphism pattern within a turtle species varies geographically, but that differences are most closely tied to localized environmental conditions.

3. The influence of phylogenetic factors (Cheverud et al., 1985) on the pattern of sexual size dimorphism in turtles remains to be addressed. A comparison among species with consideration of phylogenetic relatedness, habitat type, domedness and other factors potentially influential on or correlated with the sexual dimorphism index could help resolve the issue.

4. An additional advantage to large male size could be that larger males are more effective at copulating with larger females because of mere physical proportions, although this has not been tested to our knowledge. In contrast to female-choice among turtles, males will presumably breed with any receptive female. However, among *T. scripta*, given a choice, a male

should theoretically select a larger female because of their probability of having a larger clutch size (Gibbons et al., 1982). Thus, this species and others with significantly larger females may represent the paradoxical situation that both female-choice and male-choice are prevalent. This hypothesis is testable in an experimental manner.

5. Forcible insemination by male turtles has been dismissed by us as an untenable concept. The null hypothesis will never be able to be dismissed entirely, but experimental studies could be conducted that either disprove it (i.e., demonstrate the occurrence of forcible insemination) or that give evidence to the contrary. Hormonal implants to stimulate male sexual activity have recently been used with success in turtles (Lovich, unpublished). A proper experimental design using nonreceptive (e.g., immature) females and stimulated males could directly address the problem.

6. Our conclusion that domedness is a response to natural selection against differential exposure to predators in terrestrial and aquatic environments can be addressed in two ways. First, the empirical data available to us could be greatly augmented by a thorough examination of other species for which both a sexual dimorphism index and carapace height/length ratio can be obtained. In addition, the phenomenon should be considered both with and without regard for phylogenetic closeness of the species used, in deference to the suggestion that phylogenetic conservatism could influence comparisons among species. Another approach with the domedness issue is to conduct experimental tests with predators to determine the relative importance of large size and domedness in predator discouragement. Also, a comparison of shell damage of terrestrial and aquatic species, or of the sexes in species in which males are strictly aquatic, may reveal a higher propensity for predator attacks on terrestrial forms. However, this type of evidence must be used with caution (Schoener, 1979).

7. Finally, a straightforward test of our prediction that the underlying cause of the pattern of sexual size dimorphism in a species will correspond to the differential age and size at maturity of the two sexes

can be completed following the compilation of robust data sets in which age and size at maturity are precisely known in the populations.

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APPENDIX

TABLE A.—Sexual size dimorphism ratios (SDI; see text for explanation) of turtle species based on mean length (plastron or carapace, mm) of adults. Ratios from published studies were based on best estimates from tables, figures, text, or personal communication with the author. South Carolina ratio for *T. scripta* is mean of the means of the seven populations in Table 3.

Taxon	Location	n		Body size measure	x size		SDI	Reference
		Fe- male	Male		Fe- male	Male		
Chelidae								
<i>Hydromedusa maximiliani</i>	Brazil	9	4	PL	112	134	-1.20	Müller (1968)
<i>Phrynops zuliae</i>	Venezuela	5	2	CL	263	191	1.38	Pritchard and Trebbau (1984)
<i>Platemys macrocephala</i>	Bolivia, Brazil	8	5	CL	196	163	1.20	Rhodin et al. (1984)
<i>Platemys platycephala</i>	S. America	50	28	CL	132	146	-1.11	Ernst and Lovich (unpublished)
<i>Rheodytes leukops</i>	Bolivia	12	15	CL	139	150	-1.08	Pritchard and Trebbau (1984)
	Australia	5	5	CL	250	246	1.02	Legler and Cann (1980)
Cheloniidae								
<i>Caretta caretta</i>	Georgia	14	8	CL	977	976	1.00	Ruckdeschel and Zug (1982)
<i>Chelonia mydas</i>	Aldabra	54	83	CL	1010	975	1.04	Frazier (1971)
	W. Samoa	9	5	CL	969	922	1.05	Witzell (1982)
	W. Indian Ocean	178	112	CL	881	904	-1.03	Hirth and Carr (1970)
<i>Eretmochelys imbricata</i>	Costa Rica	62	3	CL	831	801	1.04	Carr et al. (1966)
<i>Lepidochelys olivacea</i>	India	39	15	CL	641	640	1.00	Silas et al. (1984) in Pritchard and Trebbau (1984)
Chelydridae								
<i>Chelydra serpentina</i>	Canada	15	17	CL	235	253	-1.08	Mosimann and Bider (1960)
	Iowa	9	18	CL	255	259	-1.02	Christiansen and Burken (1979)
	Tennessee	8	14	CL	219	251	-1.15	Froese and Burghardt (1975)
	South Dakota	291	37	CL	319	335	-1.05	Hammer (1969)
	SRP, SC	21	55	PL	209	219	-1.05	This study
	Louisiana	33	25	CL	402	463	-1.15	Dobie (1971)
<i>Macrolemys temminckii</i>								
Emyidae								
<i>Batagur baska</i>	Malaysia	64	83	CL	488	438	1.11	Moll (1980)
<i>Callagur borneoensis</i>	Malaysia	107	107	CL	460	340	1.35	Moll (personal communication)
<i>Chinemys reevesii</i>	Asia	110	119	PL	111	93	1.19	Lovich and Ernst (unpublished)
	China	15	13	CL	103	75	1.37	Pope (1935)
	Taiwan	19	12	CL	146	123	1.19	Mao (1971)
<i>Chrysemys picta</i>	Marion, Illinois	14	14	PL	131	116	1.13	Cagle (1954)
	Cora, Illinois	14	17	PL	135	111	1.22	Cagle (1954)
	Herrin, Illinois	3	39	PL	125	86	1.45	Cagle (1954)
	Illinois	45	55	PL	150	114	1.32	Moll (1973)

APPENDIX
TABLE A.—Continued.

Taxon	Location	n		Body size measure	♂ size		SDI	Reference
		Fe- male	Male		Fe- male	Male		
<i>Chrysemys p. marginata</i>	Louisiana, Arkansas	37	21	PL	114	72	1.58	Moll (1973)
	Nigger Creek, Michigan	51	51	PL	139	104	1.34	Cagle (1954)
	Michigan	481	849	PL	123	98	1.26	This study
	New Mexico	54	55	PL	150	123	1.22	Christiansen et al. (1973)
	Pennsylvania	375	374	PL	117	98	1.19	Ernst (1971)
	Wisconsin	28	32	PL	153	131	1.17	Christiansen et al. (1973)
	Wisconsin	23	32	PL	157	130	1.21	Moll (1973)
	Tennessee	19	17	PL	124	97	1.28	Moll (1973)
	Illinois	6	6	CL	136	119	1.14	Cahn (1937)
	Canada	24	24	CL	136	113	1.20	Jolicoeur and Mosimann (1960)
<i>Chrysemys p. bellii</i>	Illinois	4	2	CL	161	114	1.41	Cahn (1937)
	Illinois	11	4	CL	118	86	1.37	Cahn (1937)
	Indiana	15	17	CL	103	98	1.05	Minton (1972)
	Pennsylvania	?	?	PL	90	82	1.10	Ernst (1975)
<i>Clemmys insculpta</i>	Ohio	42	21	CL	92	88	1.05	Lovich (unpublished)
	Michigan	105	86	CL	182	200	-1.10	Harding and Bloomer (1979)
<i>Clemmys muhlenbergii</i>	New Jersey	464	311	CL	165	178	-1.08	Harding and Bloomer (1979)
	Pennsylvania ¹	15	15	PL	68	73	-1.07	Ernst (1977)
	NJ, NY	4	7	CL	87	91	-1.05	Wright (1918)
<i>Clemmys marmorata</i>	USA	29	22	CL	88	90	-1.02	Barton and Price (1955)
	USA	75	82	PL	79	81	-1.03	Lovich and Ernst (unpublished)
	California	207	242	CL	149	153	-1.03	Bury (personal communication)
	Taiwan	6	7	CL	152	142	1.07	Mao (1971)
<i>Cuora flavomarginata</i>	Yaeyama Is.	?	?	CL	160	151	1.06	Tanaka and Sato (1983)
	Ellenton Bay, SC	95	265	PL	161	99	1.63	This study
<i>Deirochelys reticularia</i>	Lost Lake, SC	17	19	PL	166	108	1.56	This study
	Risher Pond, SC	11	22	PL	168	107	1.57	This study
	Steel Creek, SC	7	9	PL	159	91	1.75	This study
<i>Emydoidea blandingii</i>	Indiana	12	9	CL	172	182	-1.06	Minton (1972)
	Massachusetts	33	41	CL	204	215	-1.05	Graham and Doyle (1979)
<i>Graptemys barbouri</i> ²	Massachusetts	33	41	PL	206	206	1.00	Graham and Doyle (1979)
	Michigan	173	49	PL	187	176	1.06	Congdon (personal communication)
	Florida/Georgia	28	40	CL	248	107	2.32	This study
<i>Graptemys flavimaculata</i>	Mississippi	9	6	PL	138	81	1.70	This study

APPENDIX
TABLE A.—Continued.

Taxon	Location	n		Body size measure		x size		SDI	Reference
		Fe- male	Male	Fe- male	Male	Fe- male	Male		
<i>Graptemys geographica</i>	Indiana	11	8	CL	CL	195	105	1.86	Minton (1972)
	Illinois	6	4	CL	CL	188	117	1.61	Cahn (1937)
	Wisconsin	15	45	CL	CL	226	115	1.97	Vogt (1980)
<i>Graptemys oculifera</i>	Mississippi/Louisiana	15	8	PL	PL	144	84	1.72	This study
<i>Graptemys ouachitensis</i>	Wisconsin	265	68	CL	CL	205	123	2.07	Vogt (1980)
<i>Graptemys nigrinoda</i>	Alabama	10	39	PL	PL	177	84	2.10	Lahanas (1982)
<i>Graptemys pseudogeographica</i>	upper Missouri R.	36	36	PL	PL	197	113	1.74	Timken (1968)
	Wisconsin	109	68	CL	CL	225	133	1.69	Vogt (1980)
	Illinois	3	6	CL	CL	198	132	1.50	Cahn (1937)
	Indiana	11	4	CL	CL	164	109	1.50	Minton (1972)
<i>Graptemys pulchra</i>	Escambia R.	20	26	CL	CL	254	100	2.54	This study
	Mobile Bay Drainage System	8	30	CL	CL	250	97	2.58	This study
	Pascagoula R.	19	42	CL	CL	248	104	2.39	This study
	Pearl R.	28	41	CL	CL	247	102	2.42	This study
	India	8	9	CL	CL	44	19	2.32	Moll (personal communication)
<i>Kachuga dhongoka</i>	India	3	4	CL	CL	50	27	1.85	Moll (personal communication)
<i>Kachuga kachuga</i>	India	13	11	CL	CL	22	8	2.75	Moll (personal communication)
<i>Kachuga tentoria circumdata</i>	Kiawah I., SC	84	138	PL	PL	147	102	1.45	This study
<i>Malaclemys terrapin</i>	Europe	44	56	CL	CL	155	115	1.35	Busack and Ernst (1980)
<i>Mauremys c. caspica</i>	Europe	21	30	CL	CL	125	98	1.28	Busack and Ernst (1980)
<i>Mauremys c. rivulata</i>	Europe, Africa	38	44	CL	CL	139	105	1.32	Busack and Ernst (1980)
<i>Mauremys leprosa</i>	Taiwan	12	13	CL	CL	130	142	-1.09	Mao (1971)
<i>Mauremys mutica</i> (= <i>M. nigricans</i> , Iverson, 1986)	Taiwan	8	8	CL	CL	164	132	1.24	Mao (1971)
<i>Ocadia sinensis</i>	Illinois	2	2	CL	CL	328	216	1.52	Cahn (1937)
<i>Pseudemys concinna</i>	Indiana	4	2	CL	CL	264	209	1.29	Minton (1972)
<i>Pseudemys concinna</i> × <i>P. floridana</i>	Ellenton Bay, SC	45	59	PL	PL	223	159	1.40	This study
<i>Pseudemys floridana</i>	Risher Pond, SC	3	25	PL	PL	220	134	1.64	This study
<i>Pseudemys rubriventris</i>	Massachusetts	5	3	CL	CL	304	272	1.12	Graham (1971)
<i>Rhinoclemmys diademata</i>	Venezuela	30	11	CL	CL	203	165	1.23	Pritchard and Trebbau (1984)
<i>Terrapene carolina</i>	Illinois	9	9	CL	CL	120	116	1.03	Cahn (1937)
	Indiana	24	15	CL	CL	132	140	-1.06	Minton (1972)
<i>Terrapene coahuila</i>	Mexico	94	70	CL	CL	101	109	-1.08	Brown (1971)

APPENDIX
TABLE A.—Continued.

Taxon	Location	n		Body size measure	x size		SDI	Reference
		Fe- male	Male		Fe- male	Male		
<i>Terrapene ornata</i>	Indiana	5	8	CL	101	100	1.01	Minton (1972)
	Illinois	7	2	CL	101	98	1.03	Cahn (1937)
	Illinois	9	12	CL	206	183	1.13	Cahn (1937)
<i>Trachemys scripta</i>	Indiana	11	5	CL	200	183	1.09	Minton (1972)
	South Carolina	—	—	—	—	—	1.38	Table 3
	Illinois	441	403	PL	189	152	1.24	Cagle (1950)
	Oklahoma	14	44	PL	192	136	1.41	Webb (1961)
	Belize	152	188	PL	181	292	1.61	Moll, D. (personal communication)
	Panama	71	137	PL	292	195	1.50	Moll and Legler (1971)
<i>Trachemys terrapen</i>	Jamaica	3	2	CL	216	145	1.49	Lynn and Grant (1940)
Kinosternidae								
<i>Kinosternon flavescens</i>	Oklahoma	20	23	CL	100	103	-1.03	Mahmoud (1967)
<i>Kinosternon f. arizonense</i>	Arizona	22	7	CL	134	139	-1.04	Berry and Berry (1984)
	Arizona, Mexico	15	8	CL	124	139	-1.12	Iverson (1979b)
	Mexico	7	8	CL	120	139	-1.16	Berry and Berry (1984)
<i>Kinosternon f. durangoense</i>	Nebraska	18	18	CL	103	122	-1.18	Berry and Berry (1984)
<i>Kinosternon f. flavescens</i>	USA, Mexico	263	311	CL	108	121	-1.12	Berry and Berry (1984)
	USA, Mexico	137	158	CL	105	116	-1.10	Iverson (1979b)
<i>Kinosternon f. spooneri</i>	Illinois, Iowa, Missouri	58	60	CL	102	124	-1.22	Berry and Berry (1984)
	USA	8	16	CL	97	123	-1.27	Iverson (1979b)
	Illinois	6	9	CL	94	136	-1.45	Smith (1951)
	Mexico	33	28	PL	124	128	-1.04	Mosimann (1956)
<i>Kinosternon integrum</i>	Venezuela	9	11	CL	138	161	-1.17	Pritchard and Trebban (1984)
<i>Kinosternon scorpionoides</i>	Sycamore Creek, AZ	10	10	CL	130	118	1.10	Hulse (1976)
<i>Kinosternon sonoriense</i>	Tule Stream, AZ	90	99	CL	92	82	1.12	Hulse (1976)
	Oklahoma	20	21	CL	89	89	1.00	Mahmoud (1967)
	Arkansas	?	?	PL	92	78	1.18	Iverson (1979b)
<i>Kinosternon subrubrum</i>	Indiana	2	3	CL	97	97	1.00	Minton (1972)
	USA	576	333	CL	89	87	1.02	Gibbons (1983)
	Ellenton Bay, SC	200	268	CL	86	85	1.01	Gibbons (1983)
	SRP, SC	81	82	CL	86	87	-1.01	Gibbons (1983)
	Ellenton Bay, SC	308	405	CL	89	88	1.01	This study
	Flamingo Bay, SC	10	25	CL	86	90	-1.01	This study

APPENDIX
TABLE A.—Continued.

Taxon	Location	n		Body size measure	z size		SDI	Reference
		Fe- male	Male		Fe- male	Male		
<i>Sternotherus carinatus</i>	Risher Pond, SC	40	27	CL	89	89	1.00	This study
	Rainbow Bay, SC	76	79	CL	81	87	-1.07	This study
	Oklahoma	15	17	CL	104	103	1.01	Mahmoud (1967)
<i>Sternotherus depressus</i>	Alabama	92	224	CL	84	85	-1.01	Dodd, personal communication
	USA ¹	97	80	CL	94	93	1.01	Tinkle (1961)
<i>Sternotherus odoratus</i>	USA ²	46	43	CL	92	98	-1.07	Tinkle (1961)
	USA ³	42	40	CL	92	91	1.01	Tinkle (1961)
	USA ⁴	36	29	CL	85	83	1.02	Tinkle (1961)
	USA ⁵	83	65	CL	79	79	1.00	Tinkle (1961)
	USA ⁶	35	51	CL	80	71	1.13	Tinkle (1961)
	USA ⁷	18	18	CL	77	74	1.04	Mahmoud (1967)
	Oklahoma	5	9	CL	102	109	-1.07	Cahn (1937)
	Illinois	19	11	CL	97	95	1.02	Minton (1972)
	Indiana	80	94	CL	103	100	1.03	This study
	Ellenton Bay, SC	29	37	CL	88	84	1.05	This study
Lost Lake, SC	Risher Pond, SC	25	27	CL	75	73	1.03	This study
	Par Pond, SC	17	44	PL	101	98	1.03	This study
Steel Creek, SC	USA	28	32	PL	86	83	1.04	This study
	USA	341	310	PL	86	82	1.05	Iverson (1977)
<i>Sternotherus minor</i>								
Pelomedusidae	Peru	6	2	CL	414	266	1.56	Soini (1980) in Pritchard and Trebbau (1984)
<i>Podocnemis unifilis</i>								
	Venezuela	61	27	CL	230	171	1.35	Pritchard and Trebbau (1984)
<i>Podocnemis vogli</i>								
Testudinidae								
<i>Chersina angulata</i>	S. Africa	76	109	CL	154	180	-1.17	Branch (1984)
	Columbia	15	15	CL	289	304	-1.05	Castaño and Lugo (1981) in Pritchard and Trebbau (1984)
<i>Geochelone carbonaria</i>								
	Columbia	15	15	CL	361	394	-1.09	Castaño and Lugo (1981) in Pritchard and Trebbau (1984)
<i>Geochelone denticulata</i>								
	Venezuela	14	12	CL	310	324	-1.05	Pritchard and Trebbau (1984)

APPENDIX
TABLE A.—Continued.

Taxon	Location	n		Body size measure	\bar{x} size		SDI	Reference
		Fe- male	Male		Fe- male	Male		
<i>Geochelone gigantea</i>	Aldabra	31	30	CL	682	737	-1.08	Grubb (1971)
	Anse Mais, Aldabra	94	51	CL	794	910	-1.15	Gaymer (1968)
	Takamaka, Aldabra	73	80	CL	771	910	-1.18	Gaymer (1968)
<i>Geochelone radiata</i>	Zoo animals	5	3	CL	355	382	-1.08	Burchfield et al. (1980)
<i>Geochelone yniphora</i>	Madagascar	7	7	CL	350	419	-1.20	Juvik et al. (1980-1981)
<i>Copherus agassizii</i>	Mexico	57	69	CL	250	260	-1.04	Osorio and Bury (1982)
	Utah	50	65	CL	244	271	-1.11	Woodbury and Hardy (1948)
<i>Copherus berlandieri</i>	Hargill, Texas	8	31	CL	141	163	-1.16	Rose and Judd (1982)
	Yturria Ranch, Texas	32	36	CL	150	175	-1.17	Rose and Judd (1982)
	Laguna Atascosa, Texas	39	67	CL	170	189	-1.11	Bury and Smith (1986)
	Loma Tio Alejos, Texas	36	75	CL	141	167	-1.18	Auffenberg and Weaver (1969)
	Mesa del Gavilon, Texas	10	5	CL	167	184	-1.10	Auffenberg and Weaver (1969)
	Port Isabel Loma, Texas	8	7	CL	148	196	-1.32	Auffenberg and Weaver (1969)
<i>Copherus flavomarginatus</i>	Mexico	5	3	CL	347	277	1.25	Legler and Webb (1961)
<i>Copherus polyphemus</i>	Florida	7	12	CL	176	180	-1.02	Goin and Goff (1941)
	Georgia	54	78	CL	286	259	1.10	McRae et al. (1981)
	Africa	12	12	PL	137	121	1.13	This study
Malacocheirus tornieri								
Trionychidae								
<i>Trionyx muticus</i>	Kansas	168	1148	PL	154	98	1.57	Plummer (1977)
	Indiana	6	2	CL	229	157	1.46	Minton (1972)
<i>Trionyx sinensis</i> ³	Taiwan	5	4	CL	135	149	-1.10	Mao (1971)
<i>Trionyx spiniferus</i>	Indiana	5	8	CL	265	164	1.62	Minton (1972)
	Minnesota	98	73	CL	258	154	1.67	Breckenridge (1955)

¹ Based on specimens at least 8 years old.

² SDI using sizes at maturity reported by Sanderson (1974).

³ Maturity of specimens questionable.

⁴ Between 45-50 F isotherms.

⁵ Between 50-55 F isotherms.

⁶ Between 55-60 F isotherms.

⁷ Between 60-65 F isotherms.

⁸ Between 65-70 F isotherms.

⁹ Between 70-75 F isotherms.

TABLE B.—Sexually dichromatic and dimorphic characters other than body size in selected turtle species.

Character	Family/Species	Sexual differences	Reference
Color	Chelidae		
	<i>Phrynops dahli</i>	males retain juvenile color pattern	Medem (1966) in Pritchard and Trebbau (1984)
	<i>Phrynops zultae</i>	color of appendicular scales	Pritchard and Trebbau (1984)
	<i>Rheodytes leukops</i>	head, neck, and eye color	Legler and Cann (1980)
	Cheloniidae		
	<i>Caretta caretta</i>	head color	Deraniyagala (1939) in Pritchard and Trebbau (1984)
	Dermochelyidae		
	<i>Dermochelys coriacea</i>	females have pink occipital area ¹	Pritchard and Trebbau (1984)
	<i>Lepidochelys olivacea</i>	pigmentation	Pritchard and Trebbau (1984)
	Emyidae		
	<i>Batagur baska</i>	eye and head color	Moll (1980)
	<i>Callagur borneoensis</i>	head and shell color	Moll et al. (1981)
	<i>Chinemys reevesii</i>	melanistic males	Sachse (1975), Lovich et al. (1985)
	<i>Clemmys guttata</i>	head and jaw color; females average 15% more spots	Blake (1922), Yerkes (1905)
	<i>Cuora flavomarginata</i>	jaw color	Tanaka and Sato (1983)
	<i>Emys orbicularis</i>	color of head spots	Boulenger (1889)
	<i>Heosemys sylvatica</i>	eye and head color	Groombridge et al., 1983; Moll et al., 1986
	<i>Kachuga trivittata</i>	males have 3 dark bands on carapace	Boulenger (1889), Pritchard (1979)
	<i>Sacalia bealei</i>	females have occipital "eye spots"	Sachse (1975)
	<i>Terrapene carolina</i>	eye color, hind claw morphology	Ernst and Barbour (1972)
	<i>Trachemys scripta</i>	adult males melanistic	Cagle (1950)
	<i>Trachemys scripta chichiriquiche</i>	carapace color	Pritchard and Trebbau (1984)
	Testudinidae		
	<i>Geochelone trawancorica</i>	head color	Auffenberg (1964)
	Kinosternidae		
	<i>Kinosternon angustipons</i>	eye, jaw and plastron color	Legler (1965)
	<i>Kinosternon scortchoides</i>	head and jaw pigmentation	Pritchard and Trebbau (1984)
<i>Kinosternon sonoriense</i>	jaw color	Hulse (1976)	
Pelomedusidae			
<i>Podocnemis expansa</i>	males retain juvenile head markings	Pritchard and Trebbau (1984)	
<i>Podocnemis erythrocephala</i>	males retain juvenile head markings	Pritchard and Trebbau (1984)	
<i>Podocnemis unifilis</i>	eye and head color	Pritchard and Trebbau (1984)	
<i>Podocnemis vogli</i>	eye and head color	Pritchard and Trebbau (1984)	
<i>Peltecephalus dumerilianus</i>	head color	Pritchard and Trebbau (1984)	

TABLE B.—Continued.

Character	Family/Species	Sexual differences	Reference	
Appendages and morphology	Trionychidae	color pattern	Ernst and Barbour (1972)	
	<i>Trionyx spiniferus</i>	males have a single enlarged foreclaw	Pritchard and Trebbau (1984)	
	Cheloniidae	male forelimb and tail claw	Ernst and Barbour (1972)	
	<i>Caretta caretta</i>	males have single enlarged foreclaw	Pritchard and Trebbau (1984)	
	<i>Chelonia mydas</i>			
	<i>Lepidochelys olivacea</i>			
	Emydidae	claw length	Ernst and Barbour (1972)	
	<i>Chrysemys picta</i>	prominent foreleg scales in males	Ernst and Barbour (1972)	
	<i>Clemmys insculpta</i>	jaw width	Tanaka and Sato (1983)	
	<i>Cuora flavomarginata</i>	claw length	Lahanas (1982)	
	<i>Graptemys nigrinoda</i>	jaw width	McCauley (1945), Mount (1975)	
	<i>Malaclemys terrapin</i>	claw length	Ernst and Barbour (1972)	
	NA <i>Pseudemys/Trachemys</i>	elongated snout in males	Moll and Legler (1971)	
	Neotropical <i>Trachemys scripta</i>	vinculae and tail spines	Ernst and Barbour (1972)	
	Kinosternidae (NA)	males have heavy tail spine	Pritchard and Trebbau (1984)	
	Kinosternon <i>scorpioides</i> ²			
	Testudinidae	males have plastral callosities	Pritchard and Trebbau (1984)	
	<i>Geochelone denticulata</i>			
	Shell shape	Chelidae	jaw and interangular scute width	Pritchard and Trebbau (1984)
		<i>Phrynops zuliae</i>		
Cheloniidae		males are flatter	Pritchard and Trebbau (1984)	
<i>Chelonia mydas</i>		males have smooth shell margin	Deraniyagala (1939) in Pritchard and Trebbau (1984)	
<i>Caretta caretta</i>				
Emydidae		males are flatter; females have wider carapace	McCauley (1945); Ernst and Barbour (1972)	
<i>Clemmys muhlenbergi</i>		males are flatter	Pritchard and Trebbau (1984)	
<i>Rhinoclemmys diademata</i>				
Pelomedusidae		males have more circular carapace	Pritchard and Trebbau (1984)	
<i>Podocnemis expansa</i>				
Testudinidae		epiplastral extension in males	Ernst and Barbour (1972)	
NA <i>Gopherus</i>		epiplastral extension in males	McKeown et al. (1982)	
<i>Geochelone ymphora</i>				

¹ May be scar tissue.² Males lack vinculae.