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A Review of Techniques For Quantifying Sexual Size Dimorphism

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ABSTRACT: Previous studies of sexual size dimorphism (SSD) use a variety of size dimorphism indices (SDI's) to quantify SSD. We propose that a useful SDI should meet four criteria as follows; 1) it should be properly scaled, 2) it should have high intuitive value, 3) it should produce values with one sign, (positive) when sex A is larger than sex B, and the opposite sign when sex B is larger, and 4) it should produce values that are symmetric around a central value, preferably zero. Many previously published SDI's do not meet any of these criteria, and none meet more than three. We present an alternative SDI based on the mean size of the larger sex divided by the mean size of the smaller sex with the result arbitrarily defined as positive (minus one) when females are larger and negative (plus one) in the converse case. Careful selection of a primary size variable is crucial to meaningful interpretation of sexual size differences.

KEY WORDS: Sexual size dimorphism, Size dimorphism index.

INTRODUCTION

In most species of animals adult males and females exhibit different mean body sizes. This phenomenon, known as sexual size dimorphism (SSD), has been the subject of intense study and controversy. Reviews of SSD have been published for a diverse array of taxa including invertebrates (Ridley and Thompson, 1985; Wiklund and Karlsson, 1988; Fairbairn, 1990), fish (Feduccia and Slaughter, 1974), amphibians (Shine, 1979; Woolbright, 1983; Halliday and Verrell, 1986), reptiles (Shine, 1978; Berry and Shine, 1980; Fitch, 1981; Stamps, 1983; Gibbons and Lovich, 1990), birds (Amadon, 1959; Selander, 1966; Earhart and Johnson, 1970; Sigurjónsdóttir, 1981; Payne, 1984; Price, 1984; Lewin, 1985; Mueller and Meyer, 1985; Temeles, 1985; Rising, 1987), and mammals (Clutton-Brock et al., 1977; Clutton-Brock and Harvey, 1977; Ralls, 1976; 1977; Myers, 1978; Moors, 1980; Cabana et al., 1982; Leutenegger and Cheverud, 1982; Cheverud *et al.*, 1985; Greenwood and Wheeler, 1985; Ralls and Harvey, 1985; Bondrup-Nielson and Ims, 1990). Despite the biological significance of SSD and the importance of comparisons across phylogenetic groups, a general approach for defining the degree of difference between the sexes has not been developed. Our intent in this paper is to propose a simple and universally applicable method for quantifying SSD.

Two major theories have been proposed to explain the evolution and maintenance of SSD. The first proposes that size differences between the sexes are the result of selective factors not directly related to the environment. Darwin (1871) envisioned sexual size differences as a result of sexual selection, a selective force unrelated to natural selection (Arnold, 1983), in which characters that enhance access of one sex to the opposite sex (usually of males to females) were favored. Such characters include bright coloration, hypertrophied morphological features (both unrelated to SSD), or large body size. Sexual selection can result from; 1) intrasexual competition for mates, usually in the form of male combat, or 2) epigamic selection in which females choose among males (Trivers, 1972). The sexual selection model has been invoked by numerous investigators to explain the evolution of SSD (Amadon, 1959; Moskovits, 1988; Ridley and Thompson, 1985; Shine, 1986; Trivers, 1976; Vitt, 1983; Vitt and Cooper, 1985).

The second major theory suggests that SSD is a result of ecological forces or natural selection, due to differential interactions of each sex with its environment (Camilleri and Shine, 1990; Earhart and Johnson, 1970; Feduccia and Slaughter, 1974; Mueller and Meyer, 1985; Schoener, 1966; Selander, 1966; Shine, 1989; Slatkin, 1984). Several ecological mechanisms have been proposed that could account for SSD, and they are reviewed in detail by Slatkin (1984).

The conclusions offered by most previous studies of SSD hinge ultimately on the accuracy of estimates of SSD, and the relationship between those estimates and other variables. Thus, a fundamental starting point for studies of SSD is development of a methodology to describe quantitatively the degree of size difference between the sexes for the species or population of interest. The methods that have been used to do this are almost as numerous as the publications on the topic, suggesting the need for a more general approach that is applicable to any group of organisms. In this paper we review and evaluate methods of quantifying SSD. In addition, we present a general approach that we believe leads to a meaningful interpretation of sexual size differences across all phylogenetic groups. Our discussion is supplemented with data from a recent review of SSD in turtles (Gibbons and Lovich, 1990).

DEFINITIONS

For the purpose of our discussion we define sexual size dimorphism as any statistically significant difference in the mean length or weight of sexually mature organisms from the same population during a given time interval. We define size as a measure of distance along a major morphological axis, or as body weight. Although the exact definition of "size" is controversial, our usage is consistent with that recommended by Bookstein (1989).

It is important to note that SSD can vary between populations of the same species in degree and direction (Tinkle, 1961; Iverson, 1985; Ralls and Harvey, 1985; Rising, 1987; Gibbons and Lovich, 1990) due to population-specific growth patterns, size-specific mortality, and possibly food availability. Calculations of SSD should therefore consider potential variation among populations. Gibbons and Lovich (1990) demonstrated that even local populations of the turtle *Trachemys scripta* exhibited different degrees of SSD. Estimates of SSD can also vary though time. Pizzimenti (1981) reported an increase in SSD in prairie dogs in less than 100 years as a result of human disturbance, although sampling bias may have contributed to this trend. Recognition of potential interpopulational and temporal variation in estimates of SSD is necessary in any analysis of sexual size differences.

SELECTING AN APPROPRIATE SIZE DIMORPHISM INDEX

One approach for identifying general phylogenetic patterns of SSD within a group of animals is to establish which sex, if either, is larger among a large number of taxa (e.g., amphibians - Shine, 1979; snakes - Shine, 1978; turtles - Berry and Shine, 1980; mammals - Greenwood and Wheeler, 1985; birds - Höglund, 1989). The procedure of rating species on the basis of the direction of SSD has the advantage of permitting broad phylogenetic comparisons but the disadvantage of not permitting the ranking of species on the basis of degree of dimorphism. Also it does not allow quantitative comparison of populations that can demonstrate levels of variability within a species.

The use of a size dimorphism index (SDI) has been proposed by numerous authors to quantify the degree of SSD exhibited by a species or population. However, the variation in methods of calculating the SDI has been extensive, and the diversity of methods has, in some instances, hampered comparisons

TABLE 1.
Selected list of references that used the simple ratio of size of one sex divided by size of the opposite sex. The existence of one or both directions of sexual size dimorphism among species in the taxa studied is indicated.

REFERENCE	SEX ASSIGNED TO NUMERATOR		LARGER SEX		
	M	F	M	F	BOTH
Adams and Greenwood (1983)	X				X
Bondrup-Nielson and Ims (1990)		X			X
Carothers (1984)	X				X
Clutton-Brock *et al.* (1977)	X				X
Clutton-Brock and Harvey (1977)	X				X
Dunham *et al.* (1978)	X		X		
Fairbairn (1990)		X			X
Fitch (1981)		X			X
Iverson (1985)	X				X
Moors (1980)	X		X		
Mueller and Meyer (1985)	X				X
Payne (1984)	X				X
Ralls (1976)		X		X	
Ralls and Harvey (1985)	X		X		
Ridley and Thompson (1985)	X				X
Shine (1988)		X			X
Singer (1982)		X			X
Stamps (1983)	X				X
Wiklund and Karlsson (1988)		X		X	
Woolbright (1983)		X			X

among phylogenetic groups. Methods for calculating an SDI are roughly divisible into two broad classes: those based on a ratio, and those based on a difference. We propose that a useful SDI should meet four criteria.

1) First, it should exhibit proper scaling. For example, consider the situation in which mean body size of one sex is exactly two times greater than mean body size of the opposite sex and let the SDI equal X. If mean body size of the larger sex is four times greater than mean size of the opposite sex, then the calculated SDI must equal 2X, if the SDI is properly scaled.
2) Second, the SDI should produce measures that have high intuitive value. By this we mean that a reader would be able to look at an SDI and determine the actual degree of SSD exhibited without referring to the formula used to calculate it. SDI's based on log transformations or complex formulas do not possess this property and by our definition exhibit low intuituve value. We prefer to think of SSD in terms of size superiority of the larger sex, not size inferiority of the smaller sex. Thus, the situation where mean female body size is 1.70 times larger than mean male body size should generate an SDI of 1.70, not 0.59 (the inverse of 1.70).
3) Third, a useful SDI should exhibit directionality. In other words, situations where one sex is larger than the other would have SDI's preceded by a positive sign, whereas in

the converse situation the sign would be negative, thus providing the reader with information concerning the directionality of SSD.

4) The fourth and last characteristic that we consider to be desirable in an SDI is symmetry around a central value, preferably zero, where the sexes exhibit equal mean body size. We define symmetry as follows. Consider the case where females are N times larger than males and let the SDI = X. In the case where males are N times larger than females the SDI must = -X to be symmetric. Thus, this criterion is directly related to the directionality criterion mentioned previously.

We do not consider this list of criteria to be either exhaustive or indispensable under all circumstances. Some criteria are admittedly arbitrary, but they provide at least a basis for reviewing the characteristics of each of the many published SDI's. It is important to note that the nature of the question asked by an investigator will largely determine the choice of an SDI. However, we believe that application of the criteria suggested above results in an SDI with high utility and generality.

SDI's Based On Ratios

The most common class of SDI's is based on ratios. The simplest and most widely used is the ratio of mean size of one sex divided by mean size of the opposite sex (Table 1). The assignment of sex to numerator or denominator has been inconsistent among studies but remains constant within a specific analysis. To evaluate the performance of the simple ratio based SDI, relative to our criteria for a useful SDI, we plotted SDI values against various hypothetical size dimorphism scenarios (Figure 1a). The simple ratio SDI is properly scaled for situations where the same sex is always larger than the opposite sex, and the larger sex is placed in the numerator. When taxa are considered that exhibit both directions of SSD (i.e., male size superiority in some taxonomic subunits and female size superiority in other subunits), or when the smaller sex is placed in the numerator, the relationship exhibits curvilinearity characteristic of improper scaling. Numerous references in Table 1 have analyzed data for taxa exhibiting both directions of SSD and are thus potentially biased due to scaling problems. The intuitive value of the simple ratio SDI is high for situations where one sex is always larger, but becomes somewhat lower when both directions of SSD are exhibited. The loss of intuitiveness occurs when the smaller sex is placed in the numerator. In this case, SDI's become less than one, and the SDI reflects the inverse of size superiority of the larger sex. Finally, the simple ratio SDI does not exhibit directionality and is not symmetric around a central value.

Cabana *et al.* (1982) and Gaulin and Sailor (1984) used the logarithm of the simple ratio of size of one sex over size of the opposite sex. This formula generates SDI values that are curvilinearly symmetric around zero with the desired directionality characteristic showing which sex has size superiority (Figure 1b). However, it exhibits improper scaling and has low intuitive value due to logarithmic transformation.

One SDI that gained widespread acceptance after its first use by Storer (1966) has the formula

$$SDI = 200\left(\frac{\textit{female size - male size}}{\textit{male size + female size}}\right).$$

Others that have used "Storer's Index" or a modification thereof include Earhart and Johnson (1979), Keppie and Redmond, (1988), Pleasants and Pleasants (1988), Rising (1987), and Temeles (1985). This SDI is symmetric around zero and exhibits directionality (Figure 1c). However, it exhibits improper scaling and has low intuitive value. The SDI value of 120, associated with situations in which one sex is four times larger than the other has little intuitive value. Keppie and Redmond (1988) used a modification of Storer's Index of the form

$$SDI = \frac{100\ \textit{(size of larger sex - size of smaller sex)}}{\textit{size of both sexes combined}}.$$

This SDI is affected by two of the same problems as Storer's: improper scaling and low intuitive value. Beyond that, it is not symmetric around zero and does not exhibit directionality (Figure 1d).

The most recent variation of the ratio theme was proposed by Höglund (1989) using the formula

$$SDI = \frac{\textit{male size - female size}}{\textit{female size}}.$$

This formula generates SDI values with somewhat reduced intuitive value for situations where the male is the larger sex since the SDI represents the actual magnitude of difference minus one. SDI

FIGURE 1a - 1d

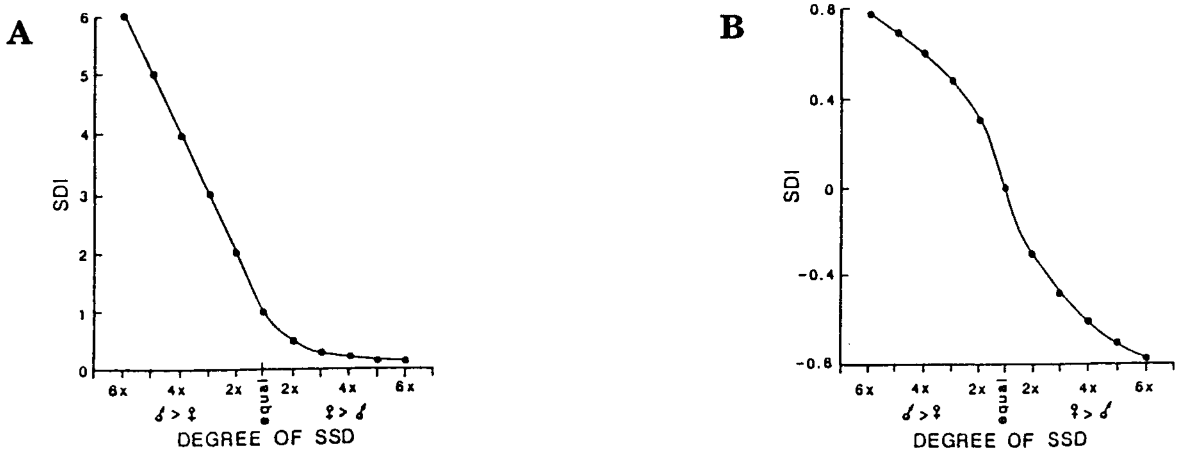

Figure 1a: The relationship between SDI values and various hypothetical sexual size dimorphism scenarios.

SDI = male size / female size.

Values to the right of "equal" on the abscissa designate situations where the female is increasingly larger than the male.

Figure 1b: The relationship between SDI values and various hypothetical sexual size dimorphism scenarios.

SDI = log (male size / female size).

Abscissa labeled as in Figure 1a.

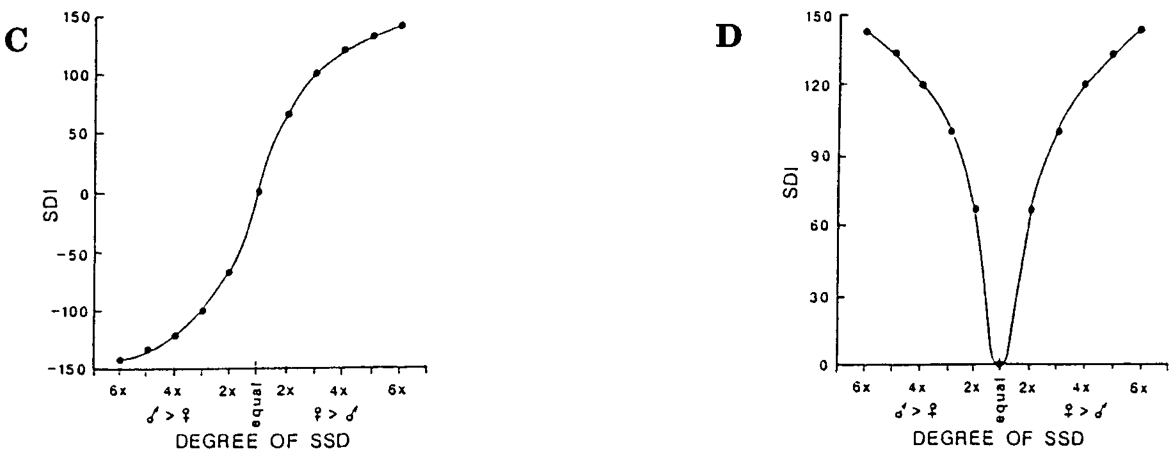

Figure 1c: The relationship between SDI values and various hypothetical sexual size dimorphism scenarios.

$$SDI = 200\,x\,\left(\frac{\text{mean female size - mean male size}}{\text{mean male size + mean female size}}\right)$$

Abscissa labeled as in Figure 1a.

Figure 1d: The relationship between SDI values and various hypothetical sexual size dimorphism scenarios.

$$SDI = \frac{100\ (\text{mean size of larger sex - means size of smaller sex})}{\text{mean size of both sexes combined}}$$

Abscissa labeled as in Figure 1a.

FIGURE 1e - 1h

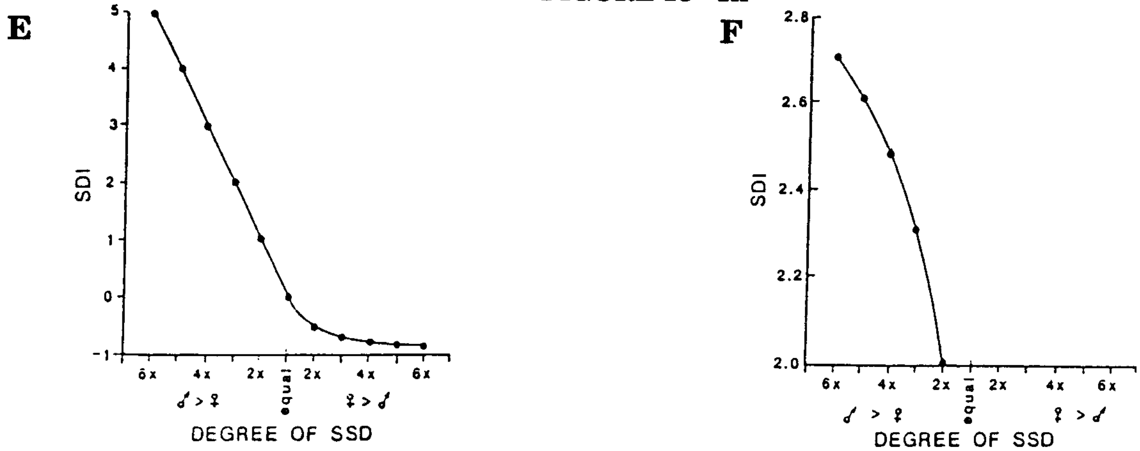

Figure 1e: The relationship between SDI values and various hypothetical sexual size dimorphism scenarios

$$SDI = \frac{male - female\ size}{female\ size}$$

Abscissa labeled as in Figure 1a.

Figure 1f: The relationship between SDI values and various hypotheical sexual size dimorphism scenarios.

$$SDI = log\ (male\ size - female\ size).$$

Abscissa labeled as in Figure 1a.

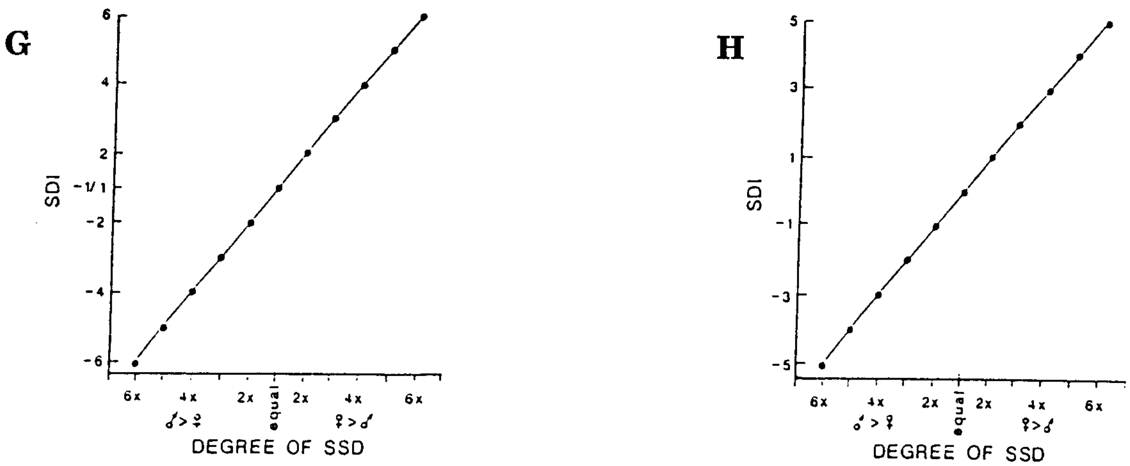

Figure 1g: The relationship between SDI values and various hypothetical sexual size dimorphism scenarios.

$$SDI = \frac{size\ of\ largest\ sex}{size\ of\ smallest\ sex};$$

Arbitrarily defined as positive when females are larger and negative in the converse situation. Abscissa labeled as in Figure 1a.

Figure 1h: The relationship between SDI values and various hypothetical sexual size dimorphism scenarios. Abscissa labeled as in Figure 1a.

$$SDI = \left(\frac{size\ of\ largest\ sex}{size\ of\ smallest\ sex}\right) + 1\ if\ males\ are\ larger\ or,$$

$$SDI = \left(\frac{size\ of\ largest\ sex}{size\ of\ smallest\ sex}\right) - 1\ if\ females\ are\ larger.$$

Arbitrarily defined as positive when females are larger and negative in the converse situation.

TABLE 2.
Variation in the degree of SSD in South Carolina populations of the slider turtle, *Trachemys scripta*, based on different size statistics. PL indicates plastron length in mm. Data from Gibbons and Lovich (1990).

			ADULT SIZE									
							Largest					
LOCATION		n	x̄ size at maturity	x̄	Median	Mode	1	3	5	10	50	100
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	353	160	186	185	175	241	238	236	220	203	188
	Male PL	570	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	354	200	234	235	238	277	275	274	263	249	235
	Male PL	760	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	58	160	190	189	189	232	229	222	217	194	-
	Male PL	63	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	328	160	195	194	188	250	246	245	231	212	196
	Male PL	653	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	78	160	211	216	206	261	256	253	248	229	-
	Male PL	185	100	136	128	110	226	220	213	190	158	135
Caper's 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	160	191	190	162	227	223	220	210	-	-
	Male PL	74	100	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	160	180	179	181	242	224	216	200	188	179
	Male PL	209	100	157	159	160	195	193	189	182	167	159

TABLE 3.
Evaluation of size dimorphism indices (SDI's) used by the references indicated to quantify sexual size dimorphism. Symbols are as follows: a plus indicates that the criterion is met, and a minus indicates that the criterion is not met. Refer to text for a discussion of criteria and computational details.

	CRITERIA				
SDI	Comment	Directionality	Intuitive value	Proper scaling	Symmetry about central value
"Ratio"	see Table 1	-	-	-	-
Cabana *et al.* (1982)		+	-	-	+
Storer (1966)		+	-	-	+
Keppie and Redmond (1988)		-	-	-	-
Leutenegger and Cheverud (1982)		-	-	-	-
Höglund (1989)		+	-	-	-
Gibbons and Lovich (1990)		+	+	+	+[1]
This study	"Compressed"	+	+[2]	+	+

[1]Symmetric around the hypothetical midpoint one and negative one simultaneously.
[2]Actual degree of sexual size dimorphism is one more than calculated when females are larger than males and one less in the converse situation.

values with low intuitive value are generated for situations where females are the larger sex (Figure 1e). Similarly, values are properly scaled when males are larger but improperly scaled when females are larger. It does exhibit directionality but is asymmetric around zero, the point of size equality.

SDI's Based On A Difference

The other major class of SDI's that has been used in the published literature is based on differences instead of ratios (Leutenegger and Cheverud, 1982; Gaulin and Sailor, 1984; Cheverud *et al.*, 1985; Ralls and Harvey, 1985; Thorpe, 1989). A potential disadvantage of this approach is that the SDI's generated do not reflect the proportional degree of size difference between the sexes. Leutenegger and Cheverud (1982) used the logarithm of the difference between male and female weights in their statistical analysis of SSD in primates, with female weight always being subtracted from male weight. The performance of this SDI is shown in Figure 1f. The curvilinear relationship shows that the SDI exhibits improper scaling. In addition, the relationship is not symmetric around a central value, does not exhibit directionality, and the associated SDI's have low intuitive value. A limitiation of this SDI stems from the fact that a logarithm cannot be taken of zero or a negative number. Thus, this technique cannot be used to calculate an SDI for situations where the sexes are equal in size. If both directions of SSD are exhibited between the sexes, one direction will generate a negative number that cannot be used to calculate an SDI. Because of this problem Leutenegger and Cheverud (1982) were forced to analyze only those primate species where males were larger than females. The correlational patterns they reported may not have been significant if species exhibiting female size superiority (n=7 in their study) had been included in the data.

Gaulin and Sailor (1984) recognized the limitations that Leutenegger and Cheverud's formula imposed and modified it by adding a small constant (c) to the difference between male and female primate body weight such that

TABLE 4.
Correlations between sexual dimorphism indices for hypothetical sexual size dimorphism scenarios (n=11) as shown on abscissas of Figures 1a-1i. SDI's are coded as follows: A=Storer (1966), B="Ratio" (Table 1), C=Keppie and Redmond (1988), D=Cabana *et al.* (1982), E="Compressed" (this study), F=Leutenegger and Cheverud (1982), G=Höglund (1989). Correlations between the SDI "F" and others are based only on situations where males are larger than females (n=5) since the formula used by Leutenegger and Cheverud (1982) is undefined for the converse situation or sexual size equality.

	SDI					
SDI	A	B	C	D	E	F
B	-0.9254					
C	0	0.3092				
D	-0.9985	0.9326	0			
E	0.9762	-0.9374	0	-0.9866		
F	-0.9998	0.9732	0.9998	0.9973	-0.9732	
G	-0.9254	1.0000	0.3092	0.9326	-0.9374	0.9732

SDI=log (male weight - female weight + c).

Given the range of body weights in their data set, addition of the constant 0.3 kilograms prevented situations that would produce a negative number prior to taking a logarithm. It is important to note that the constant c must be selected to ensure that the quantity

(male size - female size + c)

is greater than zero. In spite of their adjustment, this SDI, like Leutenegger and Cheverud's, exhibits improper scaling, is not symmetric around a central valve, and does not exhibit directionality. A far greater problem of previously published SDI's based on a difference is the fact that they produce identical values for different SSD scenarios. For example, in Table 2 of Gaulin and Sailor (1984) they show that their SDI is equal to 0.72 for the situation where male and female weights are 55 and 50 respectively, as well as for the situation where male and female weights are 10 and 5 respectively. Thus, their SDI classifies taxonomic units as equally dimorphic when the absolute difference in body weight between the sexes is equal. This condition places serious limitations on the applicability of SDI's based on the log of a difference.

Recommended SDI

Given that previously published SDI's do not meet our suggested criteria, we previously presented an alternative formulation based on the simple ratio of size of the larger sex divided by size of the smaller sex, with the result arbitrarily defined as positive when females are larger than males and negative in the converse situation (Gibbons and Lovich, 1990). A similar approach was used by Sigurjónsdóttir (1981), but without the directionality stipulation. Our previous approach produces SDI values that meet all the criteria proposed for a useful SDI except the symmetry criterion (Figure 1g).

A serious limitation of the formula proposed by Gibbons and Lovich (1990) is that values are symmetric around one and negative one simultaneously. The resulting discontinuous function presents a problem when one is attempting to use a set of bidirectional SDI's in a regression or correlation analysis since they are not continuous and are undefined for zero. For statistical purposes, the problem is solved by producing a "compressed" SDI by adding one to situations where males are larger than females and subtracting one from situations where females are larger than males. This results in a set of SDI values that are symmetric around zero (Figure 1h). There is a slight loss of intuitive value because one has to be added to or subtracted from the compressed value, depending on the direction of dimorphism, to reflect the true proportion of SSD. Despite the minor qualification, this mathematically simple and easily understandable formula is applicable to all SSD scenarios.

SELECTING AN APPROPRIATE VARIABLE

The measure of body size, whether based on 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 usually results in greater estimates of SDI than those based on linear measurements. Gibbons and Lovich (1990) examined this relationship using data from the turtle *Trachemys scripta*. We reported that 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 overall mean body mass. Cubing the plastron length measurements produces SDI's appreciably higher than those calculated from body mass. It is important to note that 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 even though the male is considered to be larger at other times based on skeletal or other measurements. The parasitic load (Rose *et al.*, 1989), osmotic condition and recent feeding history of specimens also need to be considered when using weight as a measure of body size (Iskjaer *et al.*, 1989).

Published measures of body size are usually based on some major linear component of an animal's body form. Lovich *et al.* (1990) illustrated the importance of selecting an appropriate variable to represent body size in an analysis of SSD in the wood turtle (*Clemmys insculpta*). Measures of body size in turtles are usually based on straightline length of the upper shell (carapace length=CL) or the lower shell (plastron length=PL). In the case of *C. insculpta*, mean adult male body size is significantly larger than mean adult female body size when based on CL but not when based on PL. This apparent paradox is due to differential linear growth rates of CL and PL between the sexes. Male *C. insculpta* develop pronounced plastral concavity as they mature (Ernst and Barbour, 1972), an adaptation that helps to maintain proper position during coitus. Development of this feature occurs at the expense of linear increases in PL. The result, in males, is that linear increases in CL are more rapid than linear increases in PL. This allometric situation clearly illustrates the importance of selecting an appropriate measure of body size for studies of SSD. In the case of *C. insculpta*, linear measurement of CL is a better measure of body size than PL.

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. The traditional use of the mean is reasonable since the mean body size of an organism should be a reflection of the effect of natural selection on that trait. Alternatively some authors have used some portion of the largest individuals in a sample to designate body size in a population (Soulé, 1966; Case, 1976; Berry and Shine, 1980). 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 10, 5 and 3 largest adult individuals of each sex. He concluded that for most species all ratios, except the one based on the largest individual of each sex, were close approximations of the ratio obtained from the mean sizes. However, in most populations of the turtle *Trachemys scripta* reported by Gibbons and Lovich (1990), 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 can differ substantially from those based on the mean. Use of the largest individuals of each sex can result in an interpretation of SSD that is opposite of that suggested by data based on mean body size. Lovich *et al.* (1990) concluded that male wood turtles were significantly larger than females based on mean CL. However, the largest female was larger than the largest male. Use of exceptionally large individuals provides little information on population-specific size distributions.

A STATISTICAL CAVEAT

It is important to note that ratios may violate distributional assumptions necessary for some statistical analyses (Atchley *et al.*, 1976; Albrecht, 1978). Artificially generated ratio data tend to be skewed to the right and leptokurtic with departures from normality increasing as magnitude of the denominator coefficient of variation is increased (Atchley *et al.*, 1976). For parametric analysis these departures from normality can often be corrected with an arcsine-square root transformation (Sokal and Rohlf, 1981). Alternatively, nonparametric techniques may be more appropriate. Determination of the proper analytical technique will depend largely on the characteristics of the particular data set and the questions asked by the investigator.

CONCLUSION

There has been little consistency in the use of a particular variable, statistic, or size dimorphism index in studies of sexual size dimorphism. This is due to the complexity of the problem, the nature of questions asked by an investigator, and situation specific constraints. In an effort to achieve a "common currency" we have reviewed published SDI's and evaluated their performance under a recommended set of criteria (Table 3). Few SDI's are entirely satisfactory, especially under conditions where both directions of SSD are exhibited by the taxonomic group of interest. Differences among SDI's are dramatic as shown by their pairwise correlations (Table 4) that range from 0-1. It is important to note that the main cause of inverse correlation, low correlation, or no correlation is generated by strict adherence to the computational formula used by a particular author. In other words, part of the problem is due to comparing SDI's where the sex assigned to the numerator is often different between techniques (Table 1). In many cases, the sex in the numerator could be switched with the sex in the denominator thus improving the correlation and its direction (positive vs negative relationship). However, this approach lacks generality and provides further support for the technique we propose. The "compressed" SDI we present is not intended as a global panacea. Instead, it is presented on the basis of its useful characteristics that are applicable and potentially beneficial to the majority of studies on SSD.

Quantification of SSD also requires a thorough understanding of allometric relationships between size variables. Selection of an inappropriate variable can lead to erroneous conclusions regarding SSD. In the case of data reported for the wood turtle, use of linear plastron length leads to the conclusion that the sexes attain equal mean adult body sizes (Lovich *et al.*, 1990). This is inconsistent with the fact that males do indeed achieve overall mean size superiority relative to females. Similar errors are conceivable in other taxa given the number of size variables reported. Interpretation of sexual size differences must be tempered with caution in selecting an appropriate variable and statistic.

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REFERENCES

ADAMS, J. & GREENWOOD P. J. 1983. Why are males bigger than females in pre-copula pairs of *Gammarus pulex*? *Behav. Ecol. Sociobiol.*, 13, 239-241.

ALBRECHT, G. H. 1978. Some comments on the use of ratios. *Syst. Zool.*, 27, 67-71.

AMADON, D. 1959. The significance of sexual differences in size among birds. *Proc. Am. Phil. Soc.*, 103, 531-536.

ARNOLD, S. J. 1983. Sexual selection: the interface of theory and empiricism. In: *Mate Choice* (ed. P. Bateson). pp. 67-107. Cambridge Univ. Press.

ATCHLEY, W. R., GASKINS, C. T. & ANDERSON D. 1976. Statistical properties of ratios. I. Empirical results. *Syst. Zool.*, 25, 137-148.

BERRY, J. F. & SHINE R. 1980. Sexual size dimorphism and sexual selection in turtles (Order Testudines). *Oecologia*, 44, 185-191.

BONDRUP-NIELSON, S. & IMS R. A. 1990. Reversed sexual size dimorphism in microtines: are females larger than males or are males smaller than females. *Evol. Ecol.*, 4, 261-272.

BOOKSTEIN, F. L. 1989. "Size and shape": a comment on semantics. *Syst. Zool.*, 38, 173-180.

CABANA, G., FREWIN A., PETERS R. H., & RANDALL L. 1982. The effect of sexual size dimorphism on variations in reproductive efforts of birds and mammals. *Am. Nat.*, 120, 17-25.

CAMILLERI, C. & SHINE R. 1990. Sexual dimorphism and dietary divergence: differences in trophic morphology between male and female snakes. *Copeia*, 1990, 649-658.

CAROTHERS, J. H. 1984. Sexual selection and sexual dimorphism in some herbivorous lizards. *Am. Nat.*, 124, 244-254.

CASE, T. J. 1976. Body size differences between populations of the chuckwalla, *Sauromalus obesus. Ecology*, 57, 313-323.

CHEVERUD, J. M. , DOW M. M., & LEUTENEGGER W. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution*, 39, 1335-1351.

CLUTTON-BROCK, T. H. & HARVEY P. H. 1977. Primate ecology and social organization. *J. Zool.* London, 183, 1-39.

CLUTTON-BROCK, T. H., HARVEY P. H., & RUDDER B. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature*, 269, 797-800.

DARWIN, C. 1871. The descent of man, and selection in relation to sex (2 volumes). Apppleton, New York.

DUNHAM, A. E.,. TINKLE D. W, & GIBBONS J. W. 1978. Body size in island lizards: a cautionary tale. *Ecology*, 59, 1230-1238.

EARHART, C. M. & JOHNSON N. K. 1970. Size dimorphism and food habits of North American owls. *Condor*, 72, 251-264.

ERNST, C. H. & BARBOUR R. W. 1972. Turtles of the United States. Lexington, KY: University of Kentucky Press.

FAIRBAIRN, D. J. 1990. Factors influencing sexual size dimorphism in temperate waterstriders. *Am. Nat.*, 136, 61-86.

FEDUCCIA, A. & SLAUGHTER B. H. 1974. Sexual dimporphism in skates (Rajidae) and its possible role in differential niche utilization. *Evolution*, 28, 164-168.

FITCH, H. S. 1981. Sexual size differences in reptiles. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.*, (70), 1-72.

GAULIN, S. J. C. & SAILER L. D. 1984. Sexual dimorphism in weight among primates: the relative impact of allometry and sexual selection. *Int. J. Primatol.*, 5, 515-535.

GIBBONS, J. W. & LOVICH J. E. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetological Monographs*, 4, 1-29.

GREENWOOD, P. J. & WHEELER P. 1985. The evolution of sexual size dimorphism in birds and mammals: a 'hot blooded' hypothesis. In: Evolution: Essays in Honour of John Maynard Smith (eds. P. J. Greenwood, P. H. Harvey & M. Slatkin). pp. 287-299, Cambridge. Cambridge Univ. Press.

HALLIDAY, T. R. & VERRELL P. A. 1986. Sexual selection and body size in amphibians. *Herpetological Journal*, 1, 86-92.

HÖGLUND, J. 1989. Size and plummage dimorphism in lek-breeding birds: a comparative analysis. *Am. Nat.*, 134, 72-87.

ISKJAER, C. , SLADE N. A., CHILDS J. E., GLASS G. E., & KORCH G. W. 1989. Body mass as a measure of body size in small mammals. *J. Mamm.*, 70, 662-667

IVERSON, J. B. 1985. Geographic variation in sexual dimorphism in the mud turtle *Kinosternon hirtipes. Copeia*, 1985, 388-393.

KEPPIE, D. M. & REDMOND G. W. 1988. A review of possible explanations for reverse size dimorphism of American woodcock. *Can. J. Zool.*, 66, 2390-2397.

LEUTENEGGER, W. & CHEVERUD J. 1982. Correlates of sexual dimorphism in primates: ecological and size variables. *Int. J. Primatol.*, 3, 387-402.

LEWIN, R. 1985. Why are male hawks so small? *Science*, 228, 1299-1300.

LOVICH, J. E., ERNST C. H., & McBREEN J. F. 1990. Growth, maturity and sexual dimorphism in the wood turtle, *Clemmys insculpta., Can. J. Zool.*, 68, 672-677.

MOORS, P. J. 1980. Sexual dimorphism in the body size of mustelids (Carnivora): the roles of food habits and breeding systems. *Oikos*, 34, 147-158.

MOSKOVITS, D. K. 1988. Sexual dimorphism and population estimates of the two Amazonian tortoises (*Geochelone carbonaria* and *G. denticulata*) in northwestern Brazil. Herpetologica, 44, 209-217.

MUELLER, H. C. & MEYER K. 1985. The evolution of reversed sexual dimorphism in size: a comparative analysis of the Falconiformes of the Western Palearctic. *Current Ornithol.*, 7, 65-100.

MYERS, P. 1978. Sexual dimorphism in size of vespertilionid bats. *Am. Nat.*, 112, 701-711.

PAYNE, R. B. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. *Ornithol. Monogr.*, 33, 1-52.

PIZZIMENTI, J. J. 1981. Increasing sexual dimorphism in prairie dogs: evidence for changes during the past century. *Southwestern Naturalist*, 26, 43-47.

PLEASANTS, J. M. & PLEASANTS B. Y. 1988. Reversed size dimorphism in raptors: evidence for how it evolved. *Oikos*, 52, 129-135.

PRICE, T. D. 1984. The evolution of sexual size dimorphism in Darwin's finches. *Am. Nat.*, 123, 500-518.

RALLS, K. 1976. Mammals in which females are larger than males. *Quart. Rev. Biol.*, 51, 245-276.

RALLS, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *Am. Nat.*, 111, 917-938.

RALLS, K. & HARVEY P. H. 1985. Geographic variation in size and sexual dimorphism of North American weasels. *Biol. J. Linnean Soc.*, 25, 119-167.

RIDLEY, M. & THOMPSON D. J. 1985. Sexual selection of population dynamics in aquatic crustacea. In: Behavioural Ecology: Ecological Consequences of Adaptive Behavior (eds. R. M. Sibly & R. H. Smith). pp. 409-422. Oxford. Blackwell Scien. Publ.

RISING, J.D. 1987. Geographic variation of sexual dimorphism in size of Savannah sparrows (*Passerculus sandwichensis*): a test of hypothesis. *Evolution*, 41, 514-524.

ROSE, F. L. , LONG D. R., PENCE D. B., & WADE D. 1989. Oxyurid infection of yellow mud turtles (*Kinosternon flavescens*) and correlated reductions of turtle viability. (Abst.) 65th Annual Mtg. Pennsylvania Acad. Sci. Pocono, Pennsylvania. p.58.

SCHOENER, T. W. 1966. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus., Science*, 155, 474-477.

SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor*, 68, 113-151.

SHINE, R. 1978. Sexual size dimorphism and male combat in snakes. *Oecologia*, 33, 261-268.

SHINE, R. 1979. Sexual selection and sexual dimorphism in the amphibia. *Copeia,* 1979, 297-306.

SHINE, R. 1986. Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae., Oecologia*, 69, 260-267.

SHINE, R. 1988. The evolution of large body size in females: a critique of Darwin's "fecundity advantage model." *Am. Nat.*, 131, 124-131.

SHINE, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quart. Rev. Biol.*, 64, 419-461.

SIGURJÓNSDÓTTIR, H. 1981. The evolution of sexual size dimorphism in gamebirds, waterfowl and raptors. *Ornis Scandinavica*, 12, 249-260.

SINGER, M. C. 1982. Sexual selection for small size in male butterflies., *Am. Nat.*, 119, 440-443.

SLATKIN, M. 1984. Ecological causes of sexual dimorphism., *Evolution*, 38, 622-630.

SOKAL, R. R. & ROHLF F. J. 1981. Biometry. San Francisco. W. H. Freeman and Co.

SOULÉ, M. 1966. Trends in the insular radiation of a lizard., *Am. Nat.*, 100, 47-64.

STAMPS, J. A. 1983. Sexual selection, sexual dimorphism, and territoriality. In: Lizard Ecology: Studies of a Model Organism (eds. R. B. Huey , E. R. Pianka, & T. W. Schoener). pp. 169-204. Cambridge. Harvard Univ. Press.

STORER, R. W. 1966. Sexual dimorphism and food habits of three North American accipiters. *Auk*, 83, 423-436.

TEMELES, E. J. 1985. Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. *Am. Nat.*, 125, 485-499.

THORP, R. S. 1989. Pattern and function of sexual dimorphism: a biometric study of character variation in the grass snake (*Natrix natrix*, Colubridae) due to sex and its interaction with geography. *Copeia*, 1989, 53-63.

TINKLE, D. W. 1961. Geographic variation in reproduction, size, sex ratio and maturity of *Sternothaerus odoratus* (Testudinata: Chelydridae). *Ecology*, 42, 68-76.

TRIVERS, R. L. 1972. Parental investment and sexual selection. In: Sexual Selection and the Descent of Man (ed. B. Campbell). pp. 136-179. Chicago. Aldine-Altherton.

TRIVERS, R. L. 1976. Sexual selection and resource-accruing abilities in *Anolis garmani. Evolution*, 30, 253-269.

VITT, L. J. 1983. Reproduction and sexual dimorphism in the tropical teiid lizard *Cnemidophorus ocellifer. Copeia*, 1983, 359-366.

VITT, L. J. & COOPER W. E., JR. 1985. The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. *Can. J. Zool.*, 63, 995-1002.

WIKLUND, C. & KARLSSON B. 1988. Sexual size dimorphism in relation to fecundity in some Swedish satyrid butterflies. *Am. Nat.*, 131, 132-138.

WOOLBRIGHT, L. L. 1983. Sexual selection and size dimorphism in anuran Amphibia. *Am. Nat.*, 121, 110-119.

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BOOK REVIEW

Facial Growth in the Rhesus Monkey, *A Longitudinal Cephalometric Study*, by Emet D. Schneiderman, Princeton University Press, 1992, xiii plus 217 pages, $39.50 US - Foreign £30.00, ISBN 0-691-08749-0.

This volume, derived from a 1985 doctoral thesis, has been brought up to date with literature up through 1990. Intended neither for simple reading nor for easy reference, it is a highly focussed effort directed at specialists. Schneiderman's cautious and exploratory approach and his emphasis on methodology and appropriate statistical treatment have general relevance to growth studies, but the actual results of the study will probably be of particular interest only to orthodontic researchers and others whose work concentrates on the jaws.

The longitudinal sample consists of serial head x-rays taken of 35 rhesus macaques with surgically implanted bone markers. The analysis is in the ancient tradition of cephalometric studies in that the variables are dimensions, angles and displacements considered in lateral view. Only size, growth velocities and accelerations of the elements are tracked; morphometric shape analysis is not included. However, the treatment is unconventional in its handling of the longitudinal data. Schneiderman criticizes standard growth curve analyses,which use methods from cross-sectional studies, and advocates multivariate methods derived from the work of Rao and Hills. Both his reasoning and the model study provided are convincing, and in my opinion this methodological advance is the major contribution of the book.

Although most valuable as a model for longitudinal studies, some readers will have more specific interests. Tables are included in an appendix, and these may prove useful as control data for laboratory-reared rhesus monkeys. The study provides some information on moot areas in cranial growth. Perhaps most interesting is the suggestion that growth at the mandibular condyle is more likely to be a cause than a consequence of growth rotations of the jaws.

While generally clear in writing style (except for a few awkward stacks of nouns used as adjectives), the book does not cater to the casual reader. For example, the results are presented as a series of graphs, primarily of growth velocities, beginning on p. 76, but the symbols for the graphs are not given in the captions but are buried in the text on p. 63. The frequent but minor typos feature missing or extra words and verb-subject disagreements in complicated sentences. Figures are good, but minimal. The production of the book is handsome.