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Does the timing of attainment of maturity influence sexual size dimorphism and adult sex ratio in turtles?

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The attainment of sexual maturity has been shown to affect measures of sexual size dimorphism (SSD) and adult sex ratios in several groups of vertebrates. Using data for turtles, we tested the model that sex ratios are expected to be male-biased when females are larger than males and female-biased when males are larger than females because of the relationship of each with the attainment of maturity. Our model is based on the premise that the earlier-maturing sex remains smaller, on average throughout life, and predominates numerically unless the sexes are strongly affected by differential mortality, differential emigration, and immigration, or biased primary sex ratios. Based on data for 24 species in seven families, SSD and sex ratios were significantly negatively correlated for most analyses, even after the effect of phylogenetic bias was removed. The analyses provide support for the model that SSD and adult sex ratios are correlated in turtles as a result of simultaneous correlation of each with sexual differences in attainment of maturity (bimaturism). Environmental sex determination provides a possible mechanism for the phenomenon in turtles and some other organisms. © 2014 The Authors. Biological Journal of the Linnean Society published by John Wiley & Sons Ltd on behalf of The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **112**, 142–149.

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INTRODUCTION

Biologists remain fascinated with two fundamental attributes of populations: differences in the mean adult size of males and females, or sexual size dimorphism (SSD), and variation in adult sex ratios. This unrelenting curiosity is fostered by the fact that, in some species, one sex can be smaller or more numerous than the opposite sex, whereas different, potentially related species exhibit the converse situation. Although some suggest that scientific thinking about sexual dimorphism is rooted in the Platonic ideal of a universally correct developmental pathway and outcome (Blackless *et al*., 2000), in reality, SSD and sex ratios exhibit a continuum of character states, thus paving the way for diverse comparative studies (Abouheif & Fairbairn, 1997).

Although a plethora of adaptive theories have been offered to explain the mechanism and evolution of SSD, there is still considerable disagreement about how it arises via sex-specific developmental pathways or evolutionary mechanisms (Hedrick & Temeles, 1989; Fairbairn, 1990; Fairbairn, 1997; Fairbairn, Blanckenhorn & Székely, 2007), or even how it should be measured (Lovich & Gibbons, 1992; Smith, 1999). Because of the different roles that the sexes play in reproduction, sexual selection is often invoked as the causative agent (Gibbons & Lovich, 1990; Shine, 1994a; Davis & Roth, 2008), even causing SSD to correlate with species size (Fairbairn, 1997; Dale *et al*., 2007). Still others invoke the role of natural selection, assuming that differential interactions of each sex with their environment result in SSD (Shine, 1989; Camilleri & Shine, 1990; Shine, 1991; Zhang

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et al., 2012). However, ecological differences may also be forced as a consequence of sexually-selected dimorphism (Shine, 1986) or vice versa (Stephens & Wiens, 2009; Scharf & Meiri, 2013). Other non-adaptive theories have been advanced for the evolution of SSD, including body-size scaling, genetic correlations between male and female body size, and phylogenetic constraints/inertia (Fairbairn, 1990; Cox, Skelly & John-Adler, 2003; Gosnell, Rivera & Blob, 2009), just as they have been for other traits (Gould & Lewontin, 1979).

A multitude of sex-determining mechanisms occur in organisms (Bull, 1983), especially turtles (Ewert & Nelson, 1991), that have the potential to affect primary sex ratios via the genetic contribution of parents to the zygote and the environmental effects on the zygote as it develops, or an interaction between the two (Quinn *et al.*, 2011). In turn, these primary sex ratios can ultimately affect adult sex ratios. Of particular interest to biologists are those that differ from the 1 : 1 ratio originally envisioned as evolutionarily stable by Fisher (1930), especially the biased sex ratios of turtles and other reptiles (Bull & Charnov, 1989). Gibbons (1990) and Lovich & Gibbons (1990) identified four demographic factors that influence adult sex ratios in turtles: (1) variation in primary or hatchling sex ratio influenced by either environmental or genetic sex determination, depending on the species (Ewert & Nelson, 1991); (2) differential mortality of the sexes; (3) differential emigration or immigration of the sexes; and (4) differential timing of maturity between the sexes, or bimaturism.

Bimaturism can result from differences in growth rate between the sexes and ultimately affects SSD through three pathways because the sexes grow at: (1) the same rate for different durations; (2) the same duration at different rates; or (3) they grow under a mix of rates and durations (O'Mara *et al.*, 2012). Asymptotic or indeterminate growth after maturity provides alternative pathways for SSD to arise (Stamps & Krishnan, 1997), although recent research suggests that indeterminate growth does not significantly affect the evolution of turtle life histories (Congdon *et al.*, 2013). Wiley (1974) may have been the first to notice a correlation between SSD and differences in the attainment of maturity between sexes. Later, Kozlowski (1989), Fairbairn (1990), Gibbons & Lovich (1990), Shine (1990), and others suggested that differences in the attainment of maturity between the sexes could ultimately be responsible for the level of SSD exhibited by a species, a theory further refined by Badyaev (2002). The basis for this hypothesis, stated simply, is that the earlier-maturing sex remains smaller (on average) than the later-maturing sex. Thus, one of the patterns to emerge from comparative studies is that SSD is not a trait *per se* but, instead, is a consequence of differential selective factors operating, more-or-less independently, on each sex (Fairbairn, 2007).

Gibbons & Lovich (1990) provide a detailed discussion of the influence of natural and sexual selection on both age and size at maturity, as well as continued growth after maturity in turtles. They concluded that SSD results from the effects of natural and sexual selection, often acting in opposition, on both size and age of maturity. In the case where there is strong sexual selection for males to mature quickly and enter the breeding population, some species forfeit delayed maturity at a larger size despite the reduced benefit larger size might otherwise confer in male-to-male combat or even decreased vulnerability to predation. Sexual selection is thus operating in opposition to natural selection because, once males reach maturity, growth slows dramatically effectively constraining the benefit of larger size and reduced susceptibility to predation. By contrast, delayed maturity at a larger size confers an advantage to females of many species because of an increased fecundity that would not be compensated by earlier maturity at a smaller size.

It is important to note that there is controversy in the literature regarding whether size or age at maturity is the target of selection. Previous research demonstrates that, in turtle species with SSD, the larger sex does indeed mature later than the smaller sex even though juvenile growth rates appear to be similar (Gibbons & Lovich, 1990; Ernst & Lovich, 2009), confirming the role of bimaturism in their life history. By contrast, Blanckenhorn *et al.* (2007) conducted a comparative study of representative insect taxa and concluded that SSD is only weakly related to bimaturism, and that the former is more often caused by differential growth rates than by developmental time differences between the sexes. However, all taxa in their analysis exhibited female-biased SSD and their results were self-acknowledged to be very different from those of vertebrate groups. Previous research on the evolution of life history traits suggests that most organisms are expected to mature along an age-size trajectory that maximizes fitness, not at a fixed age or size (Stearns & Koella, 1986). Research on well-studied turtle species demonstrates population-level variation in both age and size at maturity based on environmental conditions that differ even at small spatial scales (Gibbons *et al.*, 1981), confirming the predictions of Stearns & Koella.

Gibbons (1990) and Lovich & Gibbons (1990) also suggested that bimaturism was responsible for biased adult sex ratios in turtles. We proposed that the earlier maturing sex should predominate numerically. Our preliminary research on the diamondback terrapin (*Malaclemys terrapin*; Lovich & Gibbons, 1990), validated by data for the wood turtle (*Glyptemys* *insculpta*; Lovich, Ernst & McBreen, 1990), bog turtle (*Glyptemys muhlenbergii*; Lovich *et al.*, 1998), and the pond slider (*Trachemys scripta*; Gibbons, 1990; Gibbons & Lovich, 1990), suggested a correlation between SSD and adult sex ratios because of the relationship of each to the attainment of maturity. Integrating our hypotheses on SSD and sex ratio variation yields a model in which sex ratios are expected to be male-biased when females are larger than males and female-biased when males are larger than females. In the present study, we report the confirmation of our model through a correlation between SSD and adult sex ratios in turtles, even after controlling for phylogenetic effects, and attribute the phenomenon to differential maturity of the sexes.

MATERIAL AND METHODS

Data collection

To test our model integrating sex ratios and SSD, we used data for both variables reported by Gibbons & Lovich (1990) for turtles. As a result of the potential problems caused by sampling bias (Gibbons & Lovich, 1990), we used only population data from studies satisfying certain criteria: (1) all data were from field studies, thus excluding data based on museum specimens that might be body size-biased (Shine, 1994b); (2) when data were available from more than one population of a particular species, the most robust set (defined within these criteria) was used; (3) data were based on sexually mature adults only; and (4) studies were not used when sampling bias was suspected based on subsequent examination of the publication or communication with the author. The data set consisted of 24 species (Table 1) representing seven of the 14 living turtle families currently recognized (van Dijk *et al.*, 2012).

We used Pearson product moment correlation analysis and least squares linear regression to examine the relationship between SSD and sex ratio. For consistency in regression analyses, we defined sex ratio as the dependent variable and SSD as the independent. Validation of our integrated model relating SSD and sex ratios would require a statistically significant negative correlation between SSD and adult sex ratio. Ratios for sexual dimorphism indices (SDIs) and sex ratios were calculated using the method of Lovich & Gibbons (1992):

If females are larger or more numerous than males then,

$$\mathrm{SDI} = \left(\frac{\textit{adult female size or number}}{\textit{adult male size or number}}\right) - 1$$

If males are larger or more numerous than females then,

$$\mathrm{SDI} = -\left(\frac{\textit{adult male size or number}}{\textit{adult female size or number}}\right) + 1$$

where the value for male size or numerical superiority is a negative number. The values thus derived are symmetric around zero, the point of equal size or equal numbers of each sex, and properly scaled. For a detailed discussion of the advantages of

Table 1. Adult sex ratios and sexual dimorphism indices (SDI) of selected turtle species reported in appendix table A of Gibbons & Lovich (1990). Taxonomy generally follows van Dijk *et al.* (2012) with former nomenclature used by Gibbons & Lovich shown in parentheses. Ratios and SDIs were calculated using the method of Lovich & Gibbons (1992)

Family/species	Sex ratio	SDI
Trionychidae		
Apalone mutica (*Trionyx muticus*)	–5.83	0.57
Chelydridae		
Chelydra serpentina	6.86	–0.05
Macrochelys temminckii (*Macroclemys temminckii*)	0.32	–0.15
Cheloniidae		
Chelonia mydas	0.59	–0.03
Kinosternidae		
Kinosternon sonoriense	0.10	0.12
Kinosternon subrubrum	0.73	0.02
Sternotherus depressus	–1.43	–0.01
Sternotherus odoratus	–0.18	0.03
Emydidae		
Chrysemys picta	–0.77	0.26
Glyptemys insculpta (*Clemmys insculpta*)	0.49	–0.08
Actinemys marmorata (*Clemmys marmorata*)	–0.17	–0.03
Deirochelys reticularia	–1.79	0.63
Emydoidea blandingii	2.53	0.06
Malaclemys terrapin	–0.64	0.45
Pseudemys floridana	–0.31	0.40
Terrapene carolina	0.60	–0.06
Terrapene coahuila	0.34	–0.08
Trachemys scripta (South Carolina)	–0.83	0.38
Testudinidae		
Chersina angulata	–0.43	–0.17
Aldabrachelys gigantea (*Geochelone gigantea*)	–0.10	–0.18
Gopherus berlandieri	–1.08	–0.18
Gopherus polyphemus	–0.44	0.10
Xerobates agassizii (*Gopherus agassizii*: Utah)	–0.21	–0.04
Geomydidae		
Batagur affinis (*Batagur baska*)	–0.30	0.11

these formulae for calculating SDIs and similar ratios, see Lovich & Gibbons (1992) and Smith (1999). Statistical analyses were conducted using SYSTAT (Systat Software Inc.) and statistical significance was established at $\alpha < 0.05$.

PHYLOGENETIC CONTRAST ANALYSIS

To account for the role of phylogeny in the relationship between SSD and sex ratios, we used COMPARE 4.6b (Martins, 2004) to conduct a phylogenetic generalized least squares (PGLS) correlation analysis recognizing that patterns of SSD vary greatly among turtle clades (Halámková, Schulte & Langen, 2013). The technique follows that described by Martins & Hansen (1997), which is a supplement of the independent contrasts method of Felsenstein (1985), to test for phylogenetic contrasts between two traits (SSD and sex ratios). Correlation coefficients generated are more or less comparable to Pearson correlation coefficients and were compared with standard tables of critical values for the latter (E. Martins, pers. comm.). This method incorporates a parameter, α (estimated via a maximum-likelihood grid search), which indicates the level of selective constraint on a phenotype (Martins & Hansen, 1997; Martins, 1999). High values of α suggest that variation of taxon phenotypes is independent of phylogeny, whereas low values of α imply that the taxon phenotype is constrained by its history (Martins & Hansen, 1997). The α values tested ranged from 0 to 15.5. We used the well-supported turtle phylogeny of Thomson & Shaffer (2010), composed of a species-level tree containing two-thirds of all described turtle species, to reduce phylogenetic bias by running a PGLS analysis of all 24 species. Subsequently, we conducted an additional PGLS analysis only on the family Emydidae because this group was the most speciose in our data set (10 of 24 studied species) and another for non-emydid turtles. Divergence dates were not available in some cases, so all branch lengths were assumed to be equal and were set at 1 (Martins & Garland, 1991).

RESULTS

The use of Pearson correlation coefficient analysis for our preliminary analyses, without taking phylogeny into account, demonstrated that SSD and sex ratios were significantly negatively correlated with each other as predicted (Pearson's $r = -0.473$, $P = 0.02$) with our measure of SSD (SDI) explaining 22% of the variation in adult sex ratios (Fig. 1) using all species. Data points for *Chelydra serpentina*, *Emydoidea blandingii*, and *Apalone mutica* were treated as potential outliers in subsequent analyses because they exhibited the highest residual values (6.372, 2.497, and −3.753, respectively) after fitting the least squares linear regression model to the data. Iterative removal of potential outliers produced Pearson correlation coefficients and probabilities: (1) removal of *Chelydra* only −0.554 ($P = 0.006$); (2) removal of *Chelydra* and *Apalone*, −0.384 ($P = 0.08$); (3) removal of *Chelydra*, *Apalone*, and *Emydoidea*, −0.508 ($P = 0.019$); and (4) removal of *Chelydra* and *Emydoidea*, −0.599 ($P = 0.003$).

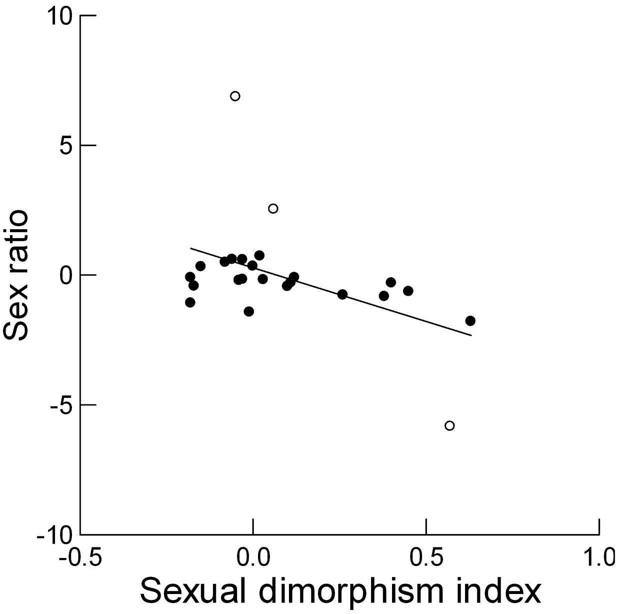

Figure 1. Plot of sexual dimorphism indices and adult sex ratios for 24 species of turtles listed in Table 1. Outliers are shown with open circles, top to bottom on *y*-axis: *Chelydra serpentina*, *Emydoidea blandingii*, and *Apalone mutica*. On both axes, values less than zero are male-biased and values greater than zero are female-biased. For computational details, see text.

Partially controlling for the effect of phylogeny, emydid turtles were analyzed separately and the relationship remained significant (Pearson's $r = -0.702$, $P = 0.024$). SSD explained 49% of the variation in adult sex ratios. Considering all non-emydid turtles, the relationship was also significant (Pearson's $r = 0.543$, $P = 0.045$). SSD explained 29% of the variation in adult sex ratios.

PHYLOGENETIC CORRELATION OF TRAITS

For the 24 species studied, the correlation of SSD on sex ratios was significant when phylogeny was considered (PGLS: $r = -0.421$; $\alpha = 2.09$; $P < 0.05$). When assessing the family Emydidae ($N = 10$) separately, the correlation of SSD on sex ratios was marginally significant (PGLS: $r = -0.599$; $\alpha = 3.29$; $0.1 > P > 0.05$).

However, when considering all non-emydid species ($N = 14$) the relationship was again significant (PGLS: $r = -0.542$; $\alpha = 15.50$; $P < 0.05$).

DISCUSSION

Turtles represent an excellent group for comparative studies of SSD because the clade is comprised of species with male-dominated SSD, female-dominated SSD, and other species with no apparent SSD (Berry & Shine, 1980; Gibbons & Lovich, 1990). The same is true for adult sex ratios because they are often biased in these reptiles (Gibbons, 1990). Phylogenetic analysis of turtle SSD suggests that the ancestral state was female-biased and that changes in SSD state are not correlated with changes in habitat preference as previously suggested (Gosnell *et al*., 2009). Although male body size and female body size were correlated with measures of fecundity, the degree of SSD was not. However, despite the value of comparative analyses in turtles, they can be problematic when different evolutionary processes occur in different subclades (Stephens & Wiens, 2009).

Most of our data sets produced statistically significant negative correlations as predicted, even when removing the effect of phylogenetic bias. It is important to note that, although data points for some species were potential outliers, their selective removal caused little difference in the degree or significance of correlation. In addition, the three outliers, taken together, conform to the overall model. If there is a linear relationship between the two variables, these outliers suggest that certain species groups may have a steeper slope. Even after controlling for phylogenetic bias, our results still supported our hypothesis, although the results for emydids were only marginally significant. Based on the general strength of association between SSD and sex ratios in turtles, we conclude that our hypothesis is supported. Analysis of more robust data sets including other turtle families will be required in future analyses.

Other studies have also noted significant negative correlations between SSD and sex ratio. For example, Crowley (2000) presented a theoretical analysis showing that the survival cost of larger body size generates a sex ratio at maturity that favours the smaller sex and that theory was consistent with empirical evidence. Georgiadis (1985) presented data for African ruminants in which male-biased sex ratios were observed in species where the female is the same weight, or heavier, than males. He suggested that males of dimorphic polygynous species experience higher mortality rates than males of monomorphic monogamous species. The difference in survival was attributed to allometric constraints affecting growth rate, metabolic rate, and longevity.

Similarly, our results are in general accord with those of Owen-Smith (1993) who examined the relationship between sex ratio and SSD in a large sample of African ungulate species. Some ungulates, such as the kudu (*Tragelaphus strepsiceros*), in which males are larger than females, exhibit higher rates of male mortality and hence have female-biased sex ratios. Possible explanations proposed for the increased male mortality included energetic expenditures in mate competition, malnutrition, increased hazards associated with smaller group sizes of males, and the fact that lions (*Panthera leo*) preferentially kill male kudus, especially large males. Owen-Smith (1993) postulated that if size dimorphism differentially influences mortality of the sexes, then SSD and sex ratios should be correlated. No correlation was observed in his full data set but, when data for the most dimorphic species with moderately female-biased sex ratios were removed, the correlation was significant. Removal of species with no SSD and sex ratios of unity rendered the correlation insignificant for the remaining species. The equivocal results were attributed to the influence of other factors on differential mortality of the sexes, possibly hunting concentrated on males. It is also worth noting that Owen-Smith (1993) did not transform sex ratios and SSD ratios to eliminate the effect of improper scaling associated with ratios of this kind (Lovich & Gibbons, 1992), and this may have influenced the results.

The degree of SSD in Norwegian moose (*Alces alces*) populations varied with ecological factors affecting body growth. Males are, on average, larger than females, although the degree of dimorphism was lowest in populations with adult female-biased sex ratios (Garel *et al*., 2006). Consistent with one of the suggestions of Owen-Smith (1993) for other ungulates, it was proposed that the decreased SSD observed was a result of a smaller proportion of adult males in those populations and its effect on mate competition during the rut.

Allometric patterns in the ecology of Australian snakes were investigated by Shine (1994b), who found that males tended to be larger than females in species with larger mean body sizes, and that snakes with larger mean body sizes tended to have male-biased adult sex ratios, even when phylogenetic biases were removed. Thus, male-biased sex ratios were observed in species with male-dominated SSD, the opposite direction of the relationship reported by us and also by Georgiadis (1985) and Owen-Smith (1993). However, all of the specimens used in the analysis were in museum collections, and Shine (1994b) acknowledged that large males are collected more often than small females or juveniles. Johansson, Crowley & Brodin (2005) predicted that sex ratios would be male-biased in dragonfly species (Odonata) with a female-biased SSD and attributed the relationship to a greater mortality of females during the foraging required to meet their greater energetic needs relative to smaller males.

Girondot & Pieau (1993) examined the influence of differential age at maturity and differential annual survival on population sex ratio. Their data showed that differential age at maturity strongly influenced sex ratio in organisms with low annual survival. By contrast, the influence of differential annual survival between the sexes on population sex ratio is important in organisms with high annual survival. Because turtles as a whole exhibit high annual adult survivorship (Iverson, 1991), Girondot & Pieau (1993) concluded that sex ratios in turtles were more sensitive to sex-specific differential survival than they were to sexual differences in the age at maturity or to biases in primary sex ratio (Girondot *et al.*, 1994).

A POSSIBLE MECHANISM FOR TURTLES

Many turtles, including several species shown in Table 1, exhibit environmental sex determination with the incubation temperature affecting the sex of hatchlings. Two patterns of environmental sex determination have been identified in turtles: Pattern Ia species are those in which males are produced at cool incubation temperatures and females are produced at warm incubation temperatures; Pattern II species are characterized by having female hatchlings produced at cool and warm incubation temperatures, whereas males are produced at intermediate temperatures (Ewert & Nelson, 1991). It was noted that Pattern Ia was found mainly in species in which adult females were larger than adult males, especially phylogenetically related species with pronounced SSD (Ewert, Jackson & Nelson, 1994). By contrast, Pattern II occurred mainly in species with adult females being slightly smaller or about the same size as adult males. Thus, the smaller sex as an adult tends to be produced at the coolest incubation temperature. The relationship between sex-determining mechanism and SSD is also supported by data for several species of crocodilians and lizards (Ewert & Nelson, 1991) and provides a possible explanation for the relationship that we observed between adult sex ratios and SSD.

Ewert and his co-authors proposed a temperature-dependent differential fitness hypothesis as a possible explanation for the relationship they observed. The hypothesis proposes that patterns of sex determination are linked to future growth potential and maturation, which are factors that affect reproductive fitness. The explanation is complicated by the fact that some turtle species (including the highly dimorphic *Apalone*; Janzen & Paukstis, 1991) (Table 1) and most other higher vertebrates do not have environmental sex determination. Alternative adaptive explanations for temperature-dependent sex determination include phylogenetic inertia, sib-avoidance by production of large proportions of unisexual clutches, and group-structured adaptation in sex ratios (Ewert & Nelson, 1991).

Our analysis provides preliminary validation of the model that SSD and adult sex ratios are correlated in turtles as a result of the simultaneous correlation of each with sexual differences in attainment of maturity. Consequently, future investigations regarding the causes of sexual dimorphism and biased sex ratios should focus on why selection favours differential ages at maturity for the sexes. Once SSD or biased sex ratios are established, selection could operate to accentuate the differences. Inclusion of robust data sets for other groups of organisms will be required to determine the generality of our turtle-based model, and the relative contributions of survival and maturity schedules, environmental sex determination, and other factors to SSD and sex ratios.

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