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EVOLUTION OF SEXUAL SIZE DIMORPHISMS IN EMYDID TURTLES: ECOLOGICAL DIMORPHISM, RENSCH'S RULE, AND SYMPATRIC DIVERGENCE

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The origin of sexual size dimorphisms (SSD) has long been a central topic in evolutionary biology. However, there is little agreement as to which factors are most important in driving the evolution of SSD, and several hypotheses concerning SSD evolution have never been tested empirically. Emydid turtles include species with both male and female-biased SSD, and some emydids exhibit among the most extreme SSD in tetrapods. Here, we use a comparative phylogenetic approach in emydids to analyze the origins of SSD and test several hypotheses for the evolution of SSD, some for the first time. We test the Fairbairn–Preziosi hypothesis for the origin of Rensch's rule, and support it in lineages with male-biased SSD but not those with female-biased SSD. We also find support for the secondary ecological dimorphism hypothesis, which proposes that selection for ecological divergence between sexes exaggerates preexisting SSD. Finally, we find only equivocal support for the Bolnick–Doebeli hypothesis, which relates intersexual ecological divergence to interspecific ecological divergence. Our results also illustrate how global analyses of SSD may mislead in groups in which the factors that drive the evolution of SSD vary among clades.

KEY WORDS: Comparative methods, Emydidae, phylogeny, sexual size dimorphism.

Differences in the average or maximum body size of males and females are nearly universal among sexually reproducing organisms, and in some species one sex may be several times the size of the other (Darwin 1871; Fairbairn et al. 2007). The evolution of sexual size dimorphisms (SSD) has been a central topic in evolutionary biology since Darwin (Darwin 1871; reviews in Fairbairn 1997; Fairbairn et al. 2007). Adaptive explanations for the evolution of sexual size dimorphism (SSD) have generally fallen into three broad categories: (1) sexual selection on male body size (e.g., Berry and Shine 1980; Abouheif and Fairbairn 1997; Cox et al. 2003), (2) fecundity selection on female body size (e.g., Wiklund and Karlsson 1988; Fairbairn and Shine 1993), and (3) ecological divergence between sexes due to intraspecific competition (e.g., Preest 1994; Herrel et al. 1999; Butler et al. 2000; Bolnick and Doebeli 2003). All three hypotheses can be traced back to Darwin (1859, 1871).

Sexual selection is generally thought to favor larger males, either through increased success in behavioral interactions, such as male–male aggression and forced insemination (e.g., Darwin 1871; Ghiselin 1974; Trivers 1976; Howard 1988; Parker 1992; Shine et al. 2000), or hypoallometry with combat or display structures (e.g., Rensch 1960; Wallace 1987; Winquist and Lemon 1994). Directional selection for larger males has also been hypothesized to be related to Rensch's rule (Rensch 1960), a pattern

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observed in many groups in which the degree of SSD is positively correlated with overall body size in species that display male-biased SSD (i.e., SSD, measured as the ratio of the larger sex to the smaller sex, is larger in large species than in small species), and degree of SSD is negatively correlated with overall size in species that display female-biased SSD (reviewed in Abouheif and Fairbairn 1997). Fairbairn and Preziosi (1994) hypothesized that Rensch's rule results from a combination of the genetic correlation between male and female body size and consistent directional sexual selection for larger male body size, with the latter causing evolutionary shifts in male body size to generally be larger than evolutionary shifts in female body size (Fairbairn and Preziosi 1994; Abouheif and Fairbairn 1997; Fairbairn 1997). Thus, in lineages with female-biased SSD, evolutionary increases in overall body size tend to move male body size toward female body size, shrinking SSD. In contrast, in lineages with male-biased SSD, evolutionary increases in overall body size move male body size away from female body size, increasing SSD. This hypothesis has not yet been directly tested in a species-level comparative study, although the hypothesis was proposed to explain patterns of SSD among species by Abouheif and Fairbairn (1997). Fairbairn and Preziosi (1994) supported this hypothesis in a comparative study of populations within a species of water strider (*Aquarius remigis*), but Fairbairn (2005) rejected it in a subsequent study of the same species.

A second factor thought to be a major driver of the evolution of SSD is female fecundity selection (e.g., Darwin 1871; Williams 1966; Hughes and Hughes 1986; reviewed in Shine 1988; Fairbairn 1997). According to this hypothesis, larger females have increased reproductive potential, either through greater allocation to individual offspring (e.g., larger eggs), greater numbers of offspring (e.g., more eggs), or the ability to reproduce more frequently (e.g., more clutches per year). However, in some species female body size is inversely correlated with longevity, potentially leading to lower total lifetime reproduction (e.g., Schluter and Smith 1986; Larsson 1989). Various authors have hypothesized that the effects of fecundity selection on female body size should be directional (e.g., Darwin 1871; Williams 1966; Hughes and Hughes 1986) or stabilizing around some optimum (e.g., Lande 1980; Shine 1988; Preziosi and Fairbairn 2000).

A third hypothesis suggests that SSD may evolve through intraspecific competition between males and females (Darwin 1871; Shine 1989). In a species in which foraging is related to size (e.g., gape-limited predators) or where an allometric relationship between overall size and trophic morphology exists, SSD can be associated with males and females consuming different resources (i.e., intersexual niche partitioning), thus lessening intraspecific competition (Shine 1989). Empirical evidence for ecological dimorphism has been mixed (reviewed in Shine 1989; Fairbairn 1997), with empirical studies supporting it in some cases (e.g., Weatherhead 1980; Longland 1989; Shine 1991; Butler et al. 2007) but not others (e.g., Price 1984; Jehl and Murray 1986; Székely et al. 2000). Several authors have hypothesized that, in some cases, ecologically important dimorphisms arise first via sexual selection or fecundity selection and then subsequently are exaggerated by natural selection to reduce intraspecific competition (Shine 1989, 1991; Andersson 1994; Fairbairn 1997). Here, we define secondary ecological dimorphism as the hypothesis that ecological dimorphism can exaggerate preexisting SSD that did not evolve due to intersexual niche partitioning. Surprisingly, this intriguing hypothesis has not yet been directly tested.

Most past studies of SSD have directly considered only one or two of these three main classes of explanation (e.g., Berry and Shine 1980; Zamudio 1998; Herrel et al. 1999; Székely et al. 2000, 2004; but see Blanckenhorn et al. 1995; Hormiga et al. 2000; Cox et al. 2003), and there is little consensus as to the relative importance of these factors. For example, some authors have assumed that ecological dimorphism between sexes commonly drives the evolution of SSD (e.g., Selander 1972; Shine 1989; Butler et al. 2000), whereas others have concluded that it is likely of only minor importance in most groups (e.g., Emerson 1994; Fairbairn 1997). Two relatively recent, synthetic studies (Hormiga et al. 2000; Cox et al. 2003) did consider all three hypotheses, but did not find strong evidence for any of them. This may have been because both studies used "global" analyses that included large numbers of species from disparate clades. If the factors that drive the evolution of SSD vary among species or clades within a broad group, a global analysis of all species may either (1) obscure the effects of factors that are important in some groups but not in others, or (2) make factors that are actually only important in some groups appear to be a global explanation for patterns of SSD, even if they are invariant within the majority of groups. We illustrate both of these effects in a well-studied group of vertebrates, emydid turtles. In addition, we use a phylogenetic approach to reconstruct the specific evolutionary changes in body size in each sex that lead to the origin of SSD and to tease apart the clade-specific effects.

Recent theory suggests that another critical component in the evolution of SSD may be its relationship to the adaptive divergence of sympatric species (Bolnick and Doebeli 2003), in which this adaptive divergence may or may not be related to sympatric speciation. Given that both processes potentially involve ecological differentiation of sympatric forms to reduce competition, SSD may impede sympatric divergence of species and sympatric divergence may impede the evolution of SSD. There have been few, if any, empirical tests of this hypothesis. However, studies of *Anolis* on islands with a single species suggest that these single-species islands favor the evolution of increased SSD, as expected (Butler et al. 2007; Poe et al. 2007). We address this hypothesis here in emydid turtles.

Emydidae is a family of turtles with 12 genera (Stephens and Wiens 2003a) and approximately 43 currently recognized species (Starkey et al. 2003; Uetz 2008), and includes many common North American species such as the eastern box turtle (*Terrapene carolina*), red-eared slider (*Trachemys scripta*), and painted turtle (*Chrysemys picta*). Adult females of some emydid species are up to 158% longer in carapace length than males (Ernst et al. 1994), which is the second largest SSD known in tetrapods. Only one other species (*Kachuga tentoria*) in a closely related family (Geoemydidae), has been reported to show greater SSD (175%, Gibbons and Lovich 1990; based on a personal communication from E. Moll), and no other reptile species (even within *Kachuga*) has been reported to exhibit SSD of greater than 130% (reviewed in Cox et al. 2007). The extent of SSD in emydids is greater than the largest SSD reported in mammals (i.e., male southern elephant seals [*Mirounga leonine*] are on average 73% longer in body length than females; Weckerly 1998; Lindenfors et al. 2002), birds (i.e., the largest females moas [*Diornis* sp.] were 150% taller than the largest males; Webster 1992; Bunce et al. 2003), and amphibians (i.e., females are on average 68% longer in body length than males in one frog species; Kupfer 2007 [but which species is not reported]).

Emydids are an excellent system for studying the evolution of SSD because (1) species vary greatly in the degree of SSD, with the larger sex ranging from 1% to 158% of the smaller sex (Ernst et al. 1994), (2) various species exhibit both male-biased and female-biased SSD (Ernst et al. 1994), (3) they have been the subjects of numerous behavioral and ecological studies (reviewed in Ernst and Barbour 1989; Ernst et al. 1994) such that the data needed to test the main hypotheses concerning the origins of SSD are already available, and (4) a well-supported phylogeny is available for the group, at least at the generic level (the position of *Clemmys guttata* excepted; e.g., Stephens and Wiens 2003a, 2008).

Several previous authors have considered SSD in turtles in general (Berry and Shine 1980; Lagarde et al. 2001; Willemsen and Hailey 2003) and emydids in particular (Gibbons and Lovich 1990; Forsman and Shine 1995; Lovich et al. 1998; St. Clair 1998; Lindeman 2003; Luca Zuffi et al. 2006; Lindeman 2008). Four previous studies tested adaptive hypotheses concerning the origin or maintenance of SSD in emydids (Berry and Shine 1980; Forsman and Shine 1995; Lindeman 2003, 2008). Berry and Shine (1980) included 23 species, but considered only the sexual selection hypothesis and did not take phylogeny into account. Forsman and Shine (1995) looked at the relationship between reproductive frequency and SSD in emydids, using an earlier phylogeny (Gaffney and Meylan 1988). Lindeman (2003) tested and supported the ecological dimorphism hypothesis in a single species (*Graptemys versa*). Lindeman (2008) analyzed patterns of body-size evolution in six genera in a phylogenetic context, and provided one of the most thorough analyses of SSD evolution in emydids to date. However, that study differs from ours in that the majority of analyses were limited to *Graptemys* and SSD was not directly quantified. In this study, we use phylogenetic comparative methods to test for the effects of male sexual selection, female fecundity, and ecological dimorphism on the evolution of SSD in 32 species of emydids, representing all 12 genera, for which a nearly complete suite of behavioral and reproductive data are available. We also perform the first species-level comparative tests of the Fairbairn–Preziosi hypothesis for the origins of Rensch's rule, the secondary ecological dimorphism hypothesis, and the Bolnick–Doebeli hypothesis.

Materials and Methods

ESTIMATING EMYDID PHYLOGENY

Emydid generic-level relationships are generally well supported, but many aspects of the species-level phylogeny are uncertain. Here, emydid relationships were investigated using a combined analysis of morphological data from Stephens and Wiens (2003a), sequence data from four mitochondrial gene regions (NADH dehydrogenase subunit 4, cytochrome *b*, mitochondrial ribosomal large subunit, and control region), and sequence data from the RNA fingerprint protein 35 nuclear intron. Sequence data from the literature (Lamb et al. 1994; Bickham et al. 1996; Feldman and Parham 2002; Spinks et al. 2004; Stephens and Wiens 2008) were supplemented with additional data generated using procedures outlined in Stephens and Wiens (2008). A full description of data and GenBank accession numbers are listed in Appendix S1. Parsimony analyses (implemented in PAUP version 4.0b10; Swofford 2002) and Bayesian analyses (implemented in MrBayes version 3.1; Huelsenbeck and Ronquist 2001) were performed as described in Stephens and Wiens (2008). Eleven outgroup species from Geoemydidae (sister family to Emydidae) and two from Kinosternidae (from the clade which is the sister to Emydidae + Geoemydidae; Krenz et al. 2005) were also included.

Our study focuses on 32 species for which behavioral and morphological data are available to test hypotheses concerning SSD evolution. Our sampling includes every species of emydine emydid (i.e., *Clemmys*, *Glyptemys*, *Emydoidea*, *Emys*, *Terrapene*; sensu Stephens and Wiens 2003a), the only clade in which the direction of SSD (male biased or female biased) has shown evolutionary shifts. We also include representatives of every deirochelyine genus (i.e., *Chrysemys*, *Deirochelys*, *Graptemys*, *Malaclemys*, *Pseudemys*, *Trachemys*), and all species of *Graptemys* (the genus that exhibits the most extreme SSD in Emydidae; Ernst et al. 1994).

All comparative analyses were performed using trees from both parsimony and Bayesian analysis, as well as a third tree constrained to be consistent with the topology reported by Stephens and Wiens (2008). The results of hypothesis tests were identical with all three trees (Appendix S1). We prefer the present results from Bayesian analysis because they are based on more data and more extensive taxon sampling than Stephens and Wiens (2008) and because parsimony assumes a simple model of evolution that is rejected for our data (see Stephens and Wiens [2008] and Appendix S1 for details of model selection procedures). Phylogenetic comparative analyses were also repeated using three sets of branch lengths: (1) equal branch lengths, (2) branch lengths estimated from the Bayesian analysis of the combined data, and (3) branch lengths estimated from the ND4 and cytochrome *b* genes. Analyses using all three sets of branch lengths were similar, and only results from the combined-data Bayesian branch lengths are reported here. See Appendix S1 for the results of analyses using all three sets of branch lengths and tree topologies.

QUANTIFYING SSD

The use of ratios to quantify SSD (as opposed to residual measures) has been somewhat contentious (reviewed in Fairbairn 1997; Smith 1999; Cox et al. 2003) although the statistical properties of residual and ratio measures of SSD have rarely been directly compared. Many authors have criticized the use of ratio measures of SSD in comparative analyses of body size and SSD, based on the observation that both variables contain body size (either male or female) and thus are not mathematically independent (e.g., Ranta et al. 1994; Abouheif and Fairbairn 1997; Fairbairn 1997) and might be expected to inflate rates of type I error. However, residual measures of SSD also have distinct drawbacks. They tend to be intuitively hard to interpret, and they are not species specific because they change depending upon the species that are compared (Smith 1999; Cox et al. 2003). Smith (1999) argued from both a theoretical standpoint and from observations of empirical datasets that residual measures of SSD are inappropriate for comparisons between SSD and variables that do not vary directly with body size because their use can inflate rates of type II error.

Based on the results of Smith (1999), we used residual measures of SSD for statistical tests using variables that are significantly correlated with body size, to reduce chances of type I error. These variables included clutch size, egg volume, clutch mass (i.e., egg volume × clutch size), and female body size (Table S1). To reduce rates of type II error we used ratio measures of SSD to examine evolutionary correlations with head width dimorphism and reproductive frequency, which showed no correlation with body size (Table S1).

The two most commonly used residual measures of SSD are (1) residuals of regression of ln (female size) versus ln (male size) and (2) residuals of regression of ln (male size) – ln (female size) versus ln (female size). We used the latter measure of SSD because Smith (1999) argued that it is more appropriate least-squares regression analysis.

For our ratio measure of SSD within species, we used the Lovich–Gibbons "two step" ratio, which produces measures of SSD that are continuous around zero, directional, intuitively easy to interpret, and properly scaled among species of different overall sizes (Lovich and Gibbons 1992; Smith 1999). The ratio consists of:

$$\begin{aligned}\mathrm{SSD} = ((L/S) - 1) * 1 \text{ if female is the}\\ \text{larger sex or } * \ -1 \text{ if male is larger,}\end{aligned}$$

where L is the average size of the larger sex for that species and S is the average size of the smaller sex for that species. All percentage measures of SSD in this study refer to the Gibbons–Lovich two-step ratio.

We calculated SSD for each species based on average adult male and female carapace lengths (i.e., the length of the upper part of the shell). Carapace length is the standard size measure reported in studies of turtles and has been shown to be strongly correlated with other, less commonly reported size measures, such as mass and plastron length (reviewed in Ernst and Barbour 1989; Ernst et al. 1994). Carapace lengths were obtained from the literature for as many species as possible (21 of 32). Most literature data were from Gibbons and Lovich (1990), with additional data from Lovich et al. (1998), Litzgus and Mousseau (2004), Conner et al. (2005), and Lindeman (2007). In addition, we obtained carapace lengths from the museum specimen data of Stephens and Wiens (2003a). The number of specimens sampled generally consisted of six males and six females of each species (4 to 20 specimens per species, mean = 11.76). Estimates of carapace length or SSD from museum specimens were used only for species in which literature estimates were unavailable. For species in which both were available, estimates of SSD based on museum specimens were highly correlated with those obtained from the literature in regression analysis ($n = 21$, $r = 0.937$, $P < 0.001$).

Estimating SSD in species that that show continuous growth can be somewhat problematic because the size distribution of a sample will be correlated with its age distribution (Stamps 1993). We included only adults (not subadults or juveniles) in our analyses. Only specimens reported to be adults were included from the literature, and museums specimens were assigned to age categories based on size at which sexual maturity is reported in each species (reviewed in Ernst et al. 1994). More detailed data on the age structure of samples were unavailable, as "growth ring" methods for estimating the ages of adult turtles have been shown to be unreliable in the majority of species (Wilson et al. 2003). Analyses were repeated using maximum sizes for each species as reported in Ernst et al. (1994) and Ernst and Barbour (1989), which should represent the asymptotic size distribution of species.

The results of these analyses were similar to those reported here with respect to the strength of observed correlations and statistical significance, and were identical with respect to support (or lack of it) for hypotheses tested and are not reported.

EVOLUTION OF SSD AND BODY SIZE

To infer how changes in male and female body size contribute to the evolution of SSD, we reconstructed ancestral values of average male and female carapace length on the phylogeny. Each character was mapped using the linear-generalized least squares method (GLS) of Martins and Hansen (1997) as implemented in COMPARE version 4.6b (Martins 2004).

EVOLUTIONARY HYPOTHESIS TESTING

Sexual selection on male body size

Some emydid species exhibit male combat and forced insemination and these behaviors are thought to produce sexual selection for larger males (Berry and Shine 1980; Fairbairn et al. 2007). If sexual selection on male body size is important to the evolution of SSD in emydids, then we predict that species that exhibit these behaviors should show male-biased SSD.

To test whether sexual selection related to mating behavior has been important to the evolution of SSD in emydids, we quantified the relationship between the presence of forced insemination and male combat with SSD (measured as a ratio) and with the direction of dimorphism (male biased or female biased). Behavioral data were from the review of Berry and Shine (1980), and their data for emydids are given in Table S2, and coded as discrete characters, 1 for behavior present and 0 for behavior absent. Analysis of variance (ANOVA) (implemented in JMP version 3.2.1) was used to determine whether these behavioral characteristics were correlated with overall variation in SSD in emydids. To test for an evolutionary correlation between SSD and behavior we performed phylogenetic generalized least squares (PGLS) ANOVA (Martins and Hansen 1997; Ord and Martins 2006). Both behavioral variables were regressed against SSD using the PGLS method implemented in COMPARE, version 4.6b (Martins 2004). We assessed the statistical significance of observed correlations using a t-test for the statistical significance of r (as described in Sokal and Rohlf 1995) calculated in Microsoft Excel version 11.2.5 for Macintosh with $N - 2$ degrees of freedom, where N was the number of species included in the analysis (following Martins and Garland 1991; Pagel 1993). This method yields identical results with respect to statistical significance to looking up r in Table R of Rohlf and Sokal (1995). PGLS ANOVAs were repeated using both estimated and equal branch lengths (see Appendix S1).

To test for a significant evolutionary correlation between direction of dimorphism and behavior we performed a phylogeny-based likelihood-ratio test comparing the likelihood of a model in which behavior and direction of SSD are assumed to vary independently to one where they are assumed to vary dependently. Likelihoods were calculated using BayesDiscrete (Pagel and Meade 2006). The likelihood-ratio test statistic, LR = 2(log-likelihood[dependent model] – log-likelihood[independent model]), was calculated and assessed against the chi-square distribution with four degrees of freedom, following the recommendation of Pagel and Meade (2006).

Rensch's rule and the Fairbairn–Preziosi hypothesis

To address the Fairbairn–Preziosi (1994) hypothesis, we first demonstrated that male and female body sizes show a pattern of allometry consistent with Rensch's rule (i.e., a slope of less than 1 in a graph of ln [male body size] versus ln [female body size] or a graph of contrasts in body size; Abouheif and Fairbairn 1997; Fairbairn 1997; see Results). The Fairbairn–Preziosi hypothesis for the origins of Rensch's rule predicts three evolutionary patterns: (1) evolutionary shifts in male and female body size will be positively correlated, (2) in lineages that show male-biased SSD, evolutionary increases in SSD (i.e., the absolute value of SSD) will occur due to male body size changing more than female body size, and (3) in lineages that show female-biased SSD, evolutionary decreases in SSD will occur due to male body size changing more than female body size.

To test for the first pattern we performed regression analysis of independent contrasts in average male body size and average female body size, using the topology and branch lengths from the Bayesian analysis. To test for the second and third patterns, we reconstructed changes in male body size, female body size, and SSD on each branch (using the GLS method described above) to determine whether the predicted evolutionary shifts occurred more often than expected by chance. With respect to these three variables, every branch in a tree can fall into one of four possible categories depending on whether male or female body size changes more and whether the absolute value of SSD increases or decreases (i.e., Table 1). We constructed a table summarizing how many branches fell into each of the four categories (i.e., Table 1), counting branches that showed male-biased SSD separately from those that showed female-biased SSD. The few branches that showed shifts between male and female-biased SSD were excluded from this analysis. Comparing the magnitude of shifts in male and female body size alone is not sufficient to test the Fairbairn–Preziosi hypothesis because such a comparison does not indicate whether male and female body size are moving together or apart on a given branch (i.e., whether SSD is increasing or decreasing). For example, if male body size changes more than female body size in a lineage with male-biased SSD, then this pattern is consistent with the Fairbairn–Preziosi hypothesis if the absolute value of SSD increases but is inconsistent if SSD decreases.

Table 1. Possible combinations of shifts in male body size, female body size, and absolute value of SSD in relationship to the hypothesis of Fairbairn and Preziosi (1994) for the evolution of Rensch's rule.

	Change in female body size greater	Change in male body size greater
|SSD increases|	Inconsistent with Fairbairn–Preziosi hypothesis	Consistent with Fairbairn–Preziosi hypothesis in lineages with male-biased SSD (inconsistent when SSD is female biased)
|SSD decreases|	Inconsistent with Fairbairn–Preziosi hypothesis	Consistent with Fairbairn–Preziosi in lineages with female-biased SSD (inconsistent when SSD is male biased)

We then used a chi-square test, implemented in JMP (version 3.2.1), to determine whether a greater proportion of branches than expected by chance alone showed the combination of shifts in male body size, female body size, and SSD predicted by the second and third parts of the Fairbairn–Preziosi hypothesis. We also used a *t*-test to determine whether changes in SSD in these categories tend to be larger than changes in SSD in the other three categories. For example, in lineages with male-biased SSD, we tested whether a greater proportion of branches than expected by chance showed increases in the absolute value of SSD due to male body size increasing more than female body size. We also tested whether changes in SSD on such branches were larger than on branches in which SSD decreased or in which female body size changed more than male body size.

Female fecundity selection

If female fecundity selection is driving evolution of SSD in emydids, female body size and one or more measures of fecundity should be positively correlated with SSD. To test for the effects of female fecundity selection on SSD in emydids, we quantified the relationships between SSD and (1) female body size, (2) clutch size, (3) egg volume, (4) reproductive frequency, and (5) clutch mass (clutch size × egg volume). Data on clutch size, egg length, reproductive frequency, and egg width came from the reviews of Ernst and Barbour (1989) and Ernst et al. (1994) with additional data from Forsman and Shine (1995), and Lindeman (2007). See Table S2 for a summary of all reproductive data used in analyses.

Direct observations of egg volume are available for relatively few species of emydids, but data on egg length and width are available for nearly every species. To convert length and width measures into volume we used the formula for the volume of an ellipsoid:

$$V = 4/3\,\pi\, ab^2,$$

where "a" is the length of the long axis and "b" is the length of the short axis. Rose et al. (1996) found that this formula slightly overestimated egg volume (by an average of 2.37%), but that it yields estimates of egg volume in the emydid *Pseudemys texana* more closely correlated with the true volume than the formula for the volume of a sphere or the bicone formula of Maritz and Douglas (1994).

All five of the variables above were compared to SSD using least squares regression analyses of species averages (i.e., tips analysis) and of independent contrasts of species averages (Felsenstein 1985). Tips analyses were implemented in JMP version 3.2.1, whereas independent contrasts analyses were implemented in Mesquite version 1.12 (Maddison and Maddison 2006). Independent contrasts analyses followed the procedure of Garland et al. (1992), and were repeated using several sets of branch lengths (see Appendix S1). Before analyzing the correlation between contrasts in variables, we plotted the absolute value of standardized contrasts against their standard deviations using Mesquite to ensure that contrasts were adequately standardized by the branch lengths they were estimated from. Contrasts obtained from the majority of branch length estimates proved to be adequately standardized. However, test plots showed strong negative correlations between contrasts constructed using branch lengths estimated from cytochrome *b* and ND4 sequence data and their standard deviations (see Appendix S1), indicating that contrasts calculated from long branches were overstandardized compared to contrasts estimated from short branches. ND4 and cytochrome *b* branch lengths were therefore log transformed following the recommendations of Garland et al. (1992), and these transformed branch lengths were used to estimate new contrasts that were used for subsequent analyses.

Ecological dimorphism

Relatively few studies of emydids have reported the diets of males and females separately (review in Ernst and Barbour 1989; Ernst et al. 1994). However, in those emydids in which intersexual ecological dimorphism has been reported, head width is strongly correlated with differences in diet between sexes (Lindeman 2000; Lindeman and Sharkey 2001; Lindeman 2008), and is highly correlated with differences in diet among other emydid species (Ward 1980). If ecological dimorphism is important in driving the evolution of SSD, we would expect the difference in size-corrected head width between males and females (head width dimorphism) to be positively correlated with SSD using independent contrasts. Procedures for analysis of independent contrasts followed those given above. Head width data were from Stephens and Wiens (2003a), and were size-corrected by regression with skull length prior to estimating differences between sexes.

Secondary ecological dimorphism hypothesis

The secondary ecological dimorphism hypothesis (Shine 1989, 1991; Andersson 1994; Fairbairn 1997) states that ecological dimorphism exaggerates preexisting SSD that evolved due to fecundity selection or sexual selection. Members of the *Graptemys–Malaclemys* clade generally exhibit much greater SSD (females 54% to 158% longer than males, average 94% among species) than other emydids (SSD 1% to 72%, average 17%; Table S2). *Graptemys* and *Malaclemys* are also known to exhibit intersexual ecological dimorphism in diet (Ernst and Barbour 1989; Ernst et al. 1994).

If extreme SSD in the *Graptemys–Malaclemys* clade occurs because ecological dimorphism exaggerated preexisting SSD, we would expect several patterns. First, ecological dimorphism should be greater in the *Graptemys–Malaclemys* clade than in other emydids. We tested whether head-width dimorphism is greater in the *Graptemys–Malaclemys* clade using PGLS ANOVA (in COMPARE). Species were coded as either (0) members of the *Graptemys–Malaclemys* clade, or (1) not.

Second, we would expect that ecological dimorphism is more important to the evolution of SSD within the *Graptemys–Malaclemys* clade than in the family overall. Thus, regression of independent contrasts of head width versus SSD should be significant within the *Graptemys–Malaclemys* clade, but weak when these species are excluded.

Finally, we would expect a large increase in SSD in the *Graptemys–Malaclemys* clade and that the direction of dimorphism (i.e., male vs. female biased) would be the same as in their deirochelyine ancestors (i.e., female-biased SSD existed ancestrally in the *Graptemys–Malaclemys* clade and was then exaggerated). We evaluated this hypothesis using GLS reconstructions of male body size, female body size, and SSD described above. To investigate what factors drive the evolution of SSD in deirochelyines outside the *Graptemys–Malaclemys* clade, we repeated the analyses of fecundity variables and SSD after excluding the *Graptemys–Malaclemys* clade.

SSD versus interspecific divergence

Bolnick and Doebeli (2003) hypothesized that ecological divergence between sister species or between sexes can constitute alternate evolutionary solutions to resource competition (i.e., "two sides of the same ecological coin"). According to this hypothesis, sister species that are sympatric may diverge ecologically if they show weak sexual dimorphism. For allopatric sister species, ecological divergence between sexes may be more likely to evolve.

Many studies have shown that body size is among the most ecologically important characteristics of an organism (e.g., Wilson 1975; Calder 1984; Vezina 1985; Brown and Maurer 1986; Brashares et al. 2000; Roy et al. 2001). This is convenient for testing the Bolnick–Doebeli hypothesis because it leads to two simple predictions concerning patterns of SSD variation and body size divergence between sister-species: (1) allopatric sister species that inhabit similar environments should show less divergence in average adult body size than sympatric sister species pairs (i.e., standard character displacement), and (2) average SSD in allopatric sister-species pairs should be greater than in sympatric sister-species pairs. These predictions were tested by comparing average SSD and body size divergence in sympatric and allopatric emydid sister species, using an *F*-test (implemented in JMP). Divergence in body size of sister species was defined as the ratio of the carapace length of the larger species over that of the smaller species. Details of how sister species were identified are provided in Appendix S1.

Results

EMYDID PHYLOGNETIC RELATIONHIPS

Parsimony and Bayesian analyses of the combined data generated trees with slightly different topologies (Fig. 1, Fig. S1). Both trees also differed from the results of another recent analysis (Stephens and Wiens 2008) in which *Terrapene coahuila* appears as the sister to *T. carolina* and *T. ornata*, rather than as the sister to *T. carolina*. This small discrepancy may be due to the exclusion of *T. nelsoni* in the analysis of Stephens and Wiens (2008). Save for a minor change in the position of *Clemmys guttata*, both Stephens and Wiens (2008) and the current study and both parsimony and Bayesian analyses agree on the generic-level relationships of emydids. The results of our comparative analyses proved extremely robust to choice of tree topology and branch length estimates (Appendix S1, Tables S4, S5, S6, S7, S8, and S9; Figs. S1 and S2).

EVOLUTION OF SSD AND BODY SIZE

Mapping male and female body size onto the phylogeny shows substantial differences in the pattern of SSD between major emydid clades (Fig. 2). In emydines, SSD is generally slight and both male-biased and female-biased SSD have evolved. Most of the body-size divergence in the group is between species, with an average interspecific divergence of sister species (Fig. 2, Table 2) of 51.95% and no species showing SSD of larger than 10% (Fig. 2). In contrast, in deirochelyines, SSD is always female-biased, varies from moderate (16%) to extreme (up to 158%), and average divergence in body size between sister-species pairs is only 16.15% (Table 2).

The evolution of female-biased SSD in basal deirochelyines is associated with a substantial increase in female body size (Fig. 2). Conversely, in *Graptemys* extreme SSD seems to occur primarily through a dramatic reduction in male body size (e.g., average carapace length of male *Graptemys* = 9.91 cm, versus 18.31 cm for other deirochelyines, an 84% reduction) compared to female body size (e.g., average carapace length

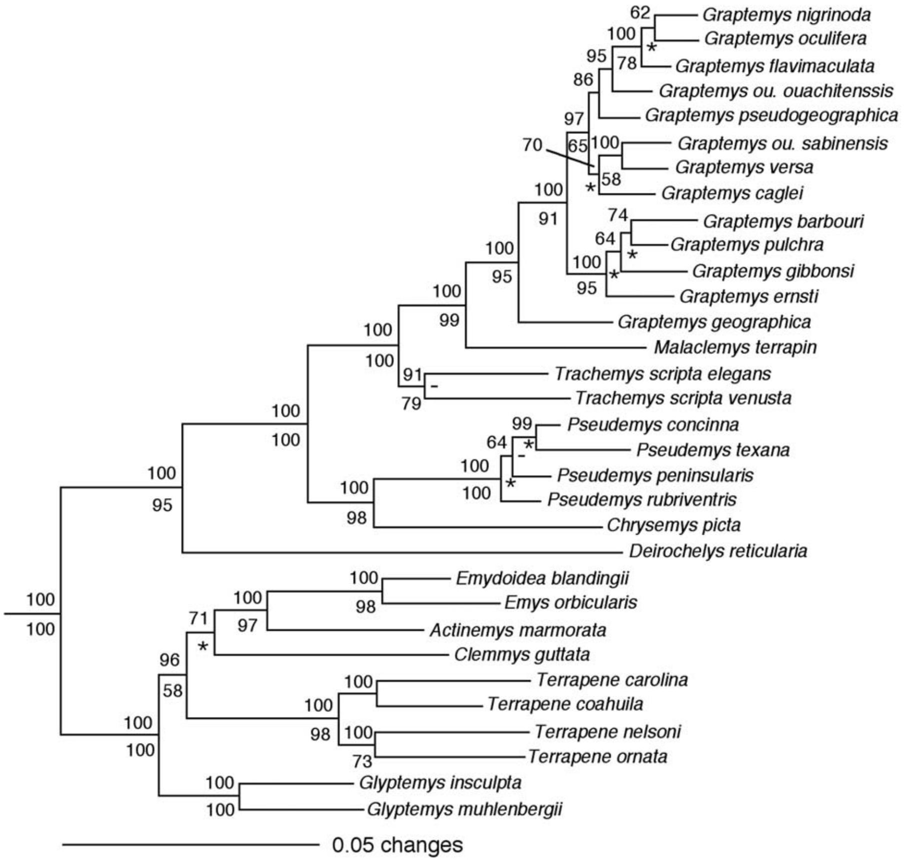

Figure 1. Phylogeny of emydid turtles based on a partitioned Bayesian analysis of the combined morphological and molecular data. Numbers above each branch indicate Bayesian posterior probabilities (×100), whereas numbers below each branch indicate bootstrap support (%) from a parsimony analysis (bootstrap percentages $\leq$ 50 are not reported). Asterisks indicate clades unique to the Bayesian analysis. Branch lengths are averages of the Bayesian branch lengths from the pooled post burn-in trees. Outgroup taxa are not shown.

of female *Graptemys* is 18.67 cm, vs. 26.67 cm for other deirochelyines, a 43% reduction).

MALE SEXUAL SELECTION AND DIRECTION OF DIMORPHISM

The presence or absence of male combat and forced insemination explained little of the overall variance in SSD in emydids (respectively, $r = 0.372$, $P = 0.073$; $r = 0.196$, $P = 0.337$). When the analysis is restricted to the Emydinae (subfamily in which direction of dimorphism varies, Fig. 2), male combat shows a significant correlation with SSD ($r = 0.797$, $P = 0.032$), but forced insemination does not ($r = 0.402$, $P = 0.324$). When the direction of dimorphism is coded as a discrete variable, male combat (likelihood-ratio test statistic = 14.76, $P = 0.005$) and forced insemination (likelihood-ratio test statistic = 14.16, $P = 0.007$) are strongly correlated with direction of SSD across the entire family.

MALE SEXUAL SELECTION AND RENSCH'S RULE

Emydids show a pattern of overall allometry in male and female body size consistent with Rensch's rule. If ln male body size (independent variable) is plotted against ln female body size (dependent variable), the slope of the regression line is significantly less than 1 (slope = 0.552, 95% CI on slope is 0.170–0.935). The slope is also less than 1 when independent contrasts in male and female body size are regressed (slope = 0.698; 95% CI = 0.439–0.956).

Independent contrasts in male and female body size were strongly positively correlated ($r = 0.802$, $P < 0.001$). When lineages with female-biased SSD are considered, fewer branches showed decreases in SSD driven by male body size increasing more than female body size than expected (Table 3; $\chi^2 = 3.507$, $P = 0.061$), in contrast to the predictions of the Fairbairn–Preziosi hypothesis. When lineages with male-biased SSD are considered, the proportion of branches showing increases in SSD due to male body size increasing more than female body size was greater than expected (Table 3; $\chi^2 = 6.533$, $P = 0.011$), consistent with the predictions of the Fairbairn–Preziosi hypothesis. There was no evidence of larger changes in SSD on branches that showed shifts consistent with the Fairbairn–Preziosi hypothesis than on branches with shifts inconsistent with the hypothesis in either

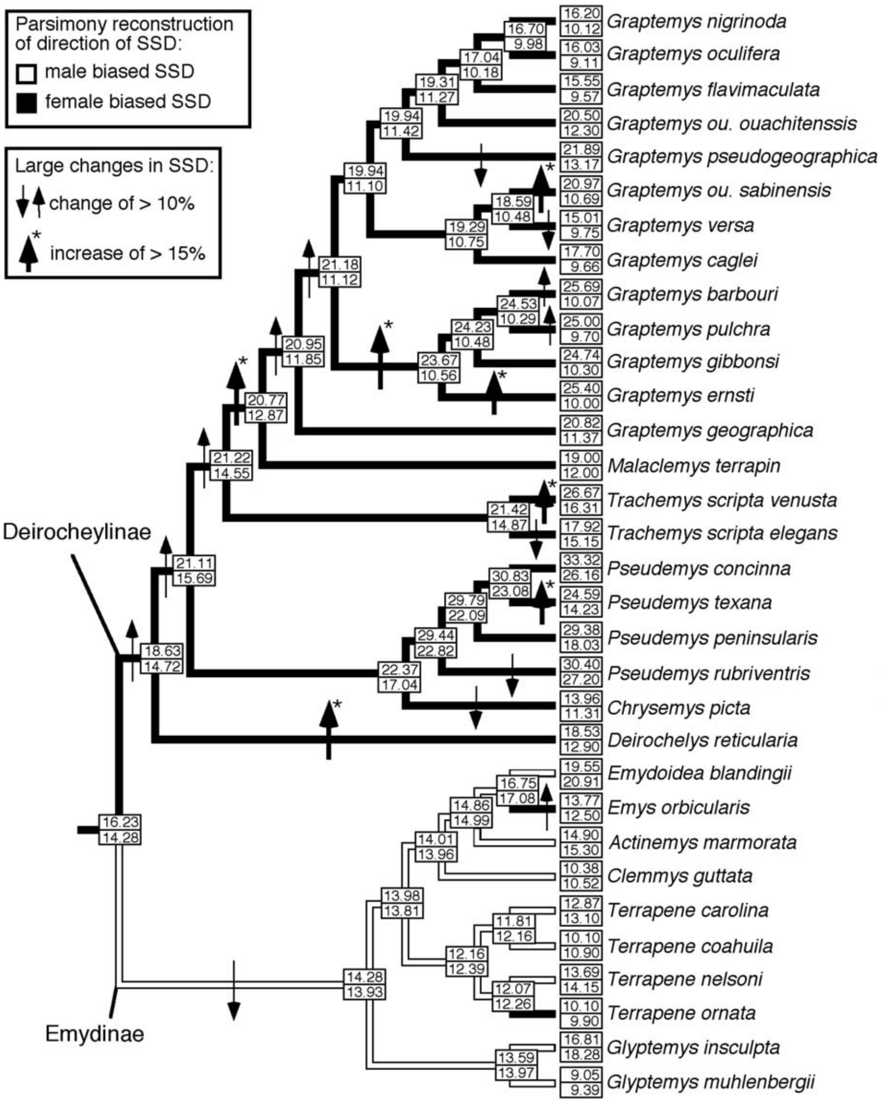

Figure 2. Body size evolution in male and female in emydid turtles based on GLS reconstructions of average male and female body size. Shading represents direction of SSD reconstructed using parsimony. The numbers in boxes are average male (lower box) and female (upper box) carapace length reconstructed using linear-generalized least squares, and species values used for reconstruction. Arrows represent reconstructed changes in SSD of greater than 10% between an ancestral and descendant node. Branch lengths here are arbitrary, but lengths from Figure 1 were used in reconstructions.

lineages with female-biased ($r = 0.137$, $P = 0.365$) or male-biased ($r = 0.275$, $P = 0.440$) SSD.

FEMALE FECUNDITY SELECTION

Independent contrasts in SSD were positively correlated with female body size ($r = 0.531$, $P = 0.002$), clutch size ($r = 0.643$, $P < 0.001$), egg volume ($r = 0.425$, $P = 0.031$), reproductive frequency ($r = 0.559$, $P = 0.020$), and clutch mass ($r = 0.594$, $P = 0.002$), supporting the female fecundity selection hypothesis.

ECOLOGICAL DIMORPHISM

Members of the *Graptemys–Malaclemys* clade showed greater head-width dimorphism than other emydids ($r = 0.437$, $P = 0.026$). Analysis of all emydids showed a correlation between contrasts in head-width dimorphism and SSD ($r = 0.548$, $P = 0.003$), but showed no relationship when the *Graptemys–Malaclemys* clade was excluded ($r = 0.127$, $P = 0.664$). The strongest correlation between head-width dimorphism and SSD was observed when the analysis was restricted to the *Graptemys–Malaclemys* clade ($r = 0.633$, $P = 0.027$), which supports the hypothesis that ecological dimorphism is important in this clade but not in emydids in general.

The phylogeny and ancestral reconstructions show female-biased SSD in the ancestor of Deirochelyinae, an increase in female-biased SSD in the ancestor of the *Graptemys–Malaclemys* clade, and further increases in female-biased SSD within this

Table 2. Sister-species pairs used to test the Bolnick–Doebeli hypothesis. Note that Figure 1 includes only 32 of the 43 currently recognized species of emydids, whereas these pairs were selected based on a more comprehensive analysis (see Appendix S1).

Sister-species pairs	Average SSD (%)	Difference in average (of male and female) adult body size (%)
Deirochelyinae		
Pseudemys nelsoni-P. rubriventris	16.6	10.3
Graptemys barbouri-G. pulchra	156.4	21.7
Graptemys ouachitensis pt*sabinensis-G. versa*	75.1	27.9
Graptemys nigrinoda-G. oculifera	68.0	4.7
Emydinae		
Emys orbicularis-Emydoidea blandingii	5.4	54.0
Terrapene carolina-T. coahuilae	4.9	23.7
Terrapene nelsoni-T. ornata	2.7	39.7
Glyptemys insculpta-G. muhlenbergii	6.3	90.4

clade (Fig. 2). When the *Graptemys–Malaclemys* clade is excluded from analyses, female body size ($r = 0.724$, $P < 0.001$), clutch size ($r = 0.633$, $P = 0.005$), egg volume ($r = 0.497$, $P = 0.036$), reproductive frequency ($r = 0.845$, $P < 0.001$), and clutch mass ($r = 0.526$, $P = 0.019$) all show similar or stronger correlations with SSD, relative to the analysis of all emydids. Taken together, these observations support the hypothesis that ecological dimorphism has exaggerated preexisting female-biased SSD within the *Graptemys–Malaclemys* clade, and suggest that female-biased SSD first arose in deirochelyines through female fecundity selection

SYMPATRIC DIVERGENCE VERSUS SSD

Allopatric species showed interspecific size divergences significantly smaller than those seen in the one sympatric species pair (Fig. 3A). However, there was no statistically significant difference in the average SSD of allopatric and sympatric species pairs (Fig. 3B).

Discussion

In this study, we present the first species-level empirical tests of three hypotheses concerning the evolution of SSD: (1) the hypothesis of Fairbairn and Preziosi (1994) for the origins of Rensch's rule, (2) the secondary ecological dimorphism hypothesis, and (3) the hypothesis of Bolnick and Doebeli (2003) relating ecological SSD to the ecological divergence of sympatric sister species. We found some support for all three hypotheses. We also found evidence for the effects of all three of the common adaptive hypotheses for the evolution of SSD in emydids (i.e., male sexual selection, female fecundity selection, and ecological dimorphism). However, each accounts for different patterns of SSD variation. Global analyses of SSD were misleading in some cases either by masking or exaggerating the importance of factors that were only correlated with SSD in some groups. Below we discuss these topics in more detail.

GLOBAL VERSUS LOCAL ANALYSES OF SSD EVOLUTION

Our results illustrate how a global analysis of SSD can be potentially misleading when the factors driving SSD vary among clades. For example, analyses of SSD as a continuous character showed no effects of male combat across emydids ($r = 0.215$, $P = 0.302$), even though male combat seems to drive male-biased SSD within Emydinae ($r = 0.851$, $P = 0.015$). Similarly, in analyses of all emydids ecological dimorphism seems to drive the evolution of female-biased SSD (i.e., a correlation between

Table 3. Summary of reconstructed changes in male body size, female body size, and SSD on each branch that were used to test the Fairbairn–Preziosi hypothesis. The top number in each cell indicates the number of branches falling into a given category, the bottom number is the average shift in percentage SSD observed among branches falling into a given category. The cells that contain bold numbers are ones in which the combination of shifts in male body size, female body size, and SSD matches the predictions of the Fairbairn–Preziosi hypothesis.

	Lineages with female-biased SSD		Lineages with male-biased SSD	
	Change in female body size greater	Change in male body size greater	Change in female body size greater	Change in male body size greater
SSD increased	10	12	3	**6**
	14.5%	13.6%	3.0%	**3.0%**
SSD decreased	19	**6**	1	1
	7.8%	**7.7%**	1.0%	0.0%

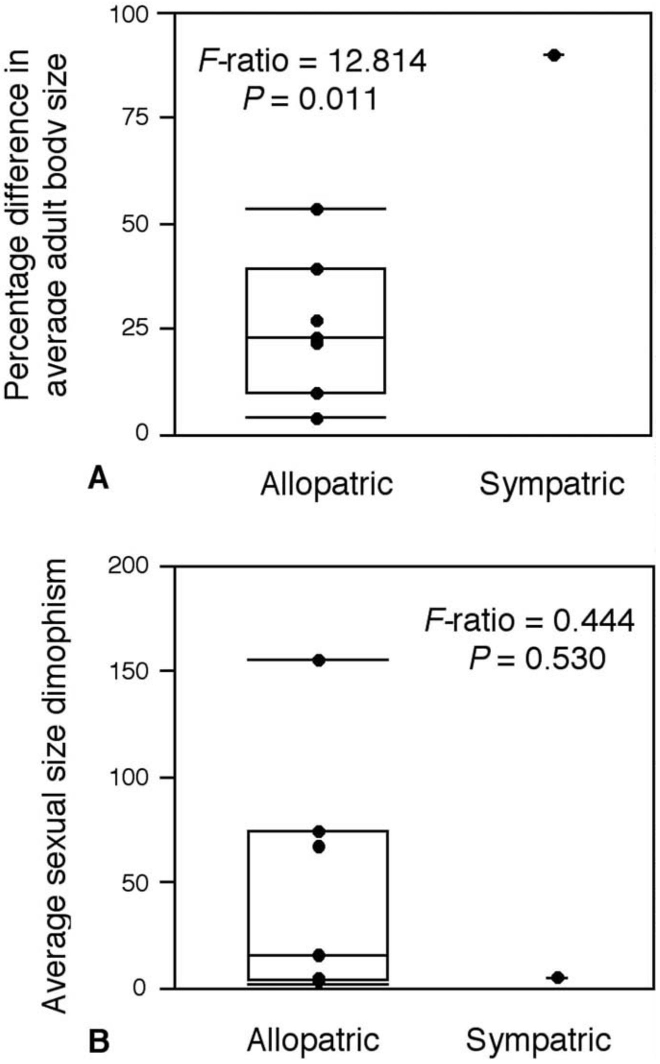

Figure 3. Quartile plots comparing (A) size divergence and (B) average SSD of sympatric and nonsympatric sister-species pairs (see Table 2).

head-width dimorphism and SSD, $r = 0.548$, $P = 0.003$). However, further analysis showed that this global result was primarily due to the *Graptemys–Malaclemys* clade. When these species were excluded, there was no evidence supporting ecological dimorphism as a cause of SSD variation in the remaining emydids ($r = 0.127$, $P = 0.664$). Because members of the *Graptemys–Malaclemys* clade show much stronger SSD than other emydids, including them in a global analysis makes it appear that head-width dimorphism is strongly correlated with patterns of SSD in all emydids, even though it varies little among most species.

Lindenfors et al. (2007) demonstrated a similar phenomenon in their study of SSD in Mammalia. Global analyses of all mammals showed a pattern of Rensch's rule allometry. However, more detailed analyses showed that only three of 12 orders follow Rensch's rule (see their Table 2.1). The failure of two major comparative studies to strongly support any hypotheses for the evolution of SSD might be due to the failure of global analyses to detect factors that were only important in some clades (Hormiga et al. 2000; Cox et al. 2003). Clearly, the results of broad-scale comparative analyses of SSD should be interpreted cautiously, particularly if the direction of SSD varies among clades (i.e., suggesting that different processes drive the evolution of SSD in different clades).

BODY SIZE EVOLUTION: RENSCH'S RULE

In this study, we tested the hypothesis of Fairbairn and Preziosi (1994) for the origins of Rensch's rule. We first showed that there is a pattern of overall allometry in emydids consistent with Rensch's rule (i.e., a slope of less than 1 in a graph of ln male body size and ln female body size; Abouheif and Fairbairn 1997; Fairbairn 1997). Fairbairn and Preziosi (1994) and Abouheif and Fairbairn (1997) hypothesized that such relationships result from a combination of genetic correlation between male and female body size and sexual selection for male body size to increase.

The Fairbairn–Preziosi hypothesis makes three predictions about macroevolutionary patterns of body size change. First, that male and female body size should be strongly correlated among species, which was confirmed in our analyses. Second, that lineages with female-biased SSD should show decreases in SSD driven by male body size changing more than female body size. However, we found no tendency for SSD to either increase or decrease in lineages with female-biased SSD, and we found that female body size rather than male body size showed larger changes on branches with female-biased SSD (Table 3; $\chi^2 = 3.507$, $P = 0.061$). Even if the evolutionary changes predicted by the Fairbairn–Preziosi hypothesis do not occur on a large proportion of branches, as long as shifts in SSD on these branches are larger than those elsewhere in the tree, it could still produce a pattern of Rensch's rule allometry. Nevertheless, we found no evidence of this in emydids with female-biased SSD ($r = 0.137$, $P = 0.365$). The branches included in this analysis were primarily from lineages in which neither male combat nor forced insemination have been documented (Berry and Shine 1980; Ernst et al. 1994), so strong sexual selection on male body size might not be expected.

Third, the Fairbairn–Preziosi hypothesis predicts that lineages with male-biased SSD will show increases in SSD driven by male body size increasing more than female body size. We found that there was a strong tendency for SSD to increase in these lineages and that male body size tended to change more than female body size, such that the proportion of branches showing the evolutionary shifts predicted by Fairbairn and Preziosi (1994) and Abouheif and Fairbairn (1997) was greater than would be expected by chance (Table 3; $\chi^2 = 6.533$, $P = 0.011$). These branches were all from emydine lineages, and the majority of emydine species have been reported to exhibit male combat (Berry and Shine 1980). In summary, the Fairbairn and Preziosi hypothesis is supported in those emydids showing male-biased SSD but not those showing female-biased SSD. These results support the speculation of Lindeman (2008), who showed that deirochelyine emydids (all of which exhibit female-biased SSD) do not conform to Rensch's rule and hypothesized that it was due to the absence of male combat.

In their reviews, Abouheif and Fairbairn (1997) and Fairbairn (1997) found that Rensch's rule was nearly universal among groups showing male-biased SSD, but frequently did not occur in groups showing female-biased SSD. They hypothesized that this was due to directional selection for larger males generally being stronger in groups with male-biased SSD than in groups with female-biased SSD, which is consistent with the patterns we observed in emydids. However, to our knowledge this is the first study to support this hypothesis in a single group in which the direction of dimorphism varies.

THE EVOLUTION OF EXTREME SSD AND SECONDARY ECOLOGICAL DIMORPHISM

In this article, we tested the hypothesis that preexisting SSD can be exaggerated by natural selection to reduce intraspecific competition (i.e., the secondary ecological dimorphism hypothesis; Shine 1989, 1991; Andersson 1994; Fairbairn 1997). Our results seem to support this hypothesis. We showed that SSD in the *Graptemys–Malaclemys* clade is in the same direction as in their deirochelyine ancestors (female-biased), and that the largest reconstructed shifts in SSD occurred in the branch leading to the *Graptemys–Malaclemys* clade, and within the clade itself (Fig. 2). When *Graptemys* and *Malaclemys* are excluded from analyses all fecundity variables still show significant correlations with SSD (see results). These results suggest that female-biased SSD was driven by fecundity selection in the ancestor of the deirochelyine emydids, and later exaggerated by ecological dimorphism in the *Graptemys–Malaclemys* clade. We found a strong relationship between SSD and head-width dimorphism in emydids that is due entirely to the *Graptemys–Malaclemys* clade. A relationship between head-width dimorphism and ecological divergence in diet is supported by previous functional and dietary studies (Ward 1980; Ernst et al. 1994; Lindeman 2000).

This analysis still leaves open the question of why secondary ecological dimorphism occurred in the *Graptemys–Malaclemys* clade and not in any other emydids. We speculate that it may be related to a shift to carnivory in the ancestors of *Graptemys* and *Malaclemys*. The majority of deirochelyines are omnivorous or herbivorous (Ernst et al. 1994), and rarely show SSD > 50%. However, we previously reconstructed a shift to strict carnivory in the ancestor of the *Graptemys–Malaclemys* clade (Stephens and Wiens 2003a), which was followed by several large increases in SSD (Fig. 2). The shift to carnivory may have reduced competition between sexes, and thus produced an opportunity for secondary ecological dimorphism.

In order for ecological dimorphism to select for exaggerated SSD, size differences between sexes would need to be tightly correlated with resource consumption. Many studies have shown that body size tends to be strongly correlated with prey size in carnivores (e.g., Brooks and Dodson 1965; Gittleman 1985; Osenberg and Mittelbach 1989). Ernst et al. (1994) reported that females of *Malaclemys* consume larger individual prey than males. Lindeman (2000, 2008) also showed that in the species of *Graptemys* with the greatest SSD males, are insectivorous whereas adult females are molluscivorous. Dietary resource partitioning has not been reported in other emydids, although it has rarely been directly tested for in species outside the *Graptemys–Malaclemys* clade (but see Lindeman 2007). If size is more strongly correlated with resource utilization in emydid carnivores than in herbivores and omnivores, the shift to carnivory in the ancestors of the *Graptemys–Malaclemys* clade could help explain the occurrence of secondary ecological dimorphism in these species.

SSD AND SYMPATRIC DIVERGENCE

Bolnick and Doebeli (2003) suggested the intriguing hypothesis that ecological divergence between sister species or between sexes can constitute alternate evolutionary solutions to resource competition. If we consider patterns of body-size variation between sexes and sister species, then their hypothesis makes two primary predictions (1) allopatric sister species pairs should show less divergence in average adult body size than sympatric sister species pairs and, (2) SSD in allopatric sister species pairs should be greater than that in sympatric sister species pairs. Emydids do show both patterns (Fig. 3), although the second pattern was not statistically significant (Table 2). By far the largest divergence in body size was in the one sympatric sister species pair examined, with adult *Glyptemys insculpta* having an average carapace length nearly twice that of its sister species *G. muhlenbergii*. As predicted, both species show only limited SSD. In general, the emydine species pairs showed limited SSD and considerable body size divergence between sister species, whereas the deirochelyine species pairs showed greater SSD and limited interspecific divergence in allopatric species pairs (Table 2). Overall, these observations support the notion that SSD and ecological divergence may be somewhat mutually exclusive, as suggested by Bolnick and Doebeli (2003). However, this result must be considered preliminary, given that our study included only one sympatric sister species pair and that this is the first empirical test of the Bolnick–Doebeli hypothesis.

CONCLUSIONS

In this study, we use a phylogenetic approach to test three hypotheses concerning the evolution of SSD, focusing on a group that shows some of the most extreme SSD in tetrapods. All of these tests involve going beyond overall regression analyses of the entire group, and require dissecting patterns on a clade-by-clade basis. The Fairbairn–Preziosi hypothesis concerns patterns of evolutionary change in three variables (male body size, female body size, and SSD) and makes different predictions for lineages with male-biased and female-biased SSD. The secondary ecological dimorphism hypothesis predicts that ancestral SSD can be exaggerated by ecological divergence between sexes, and requires considering patterns in specific clades and their ancestors. Finally, the Bolnick–Doebeli hypothesis makes different predictions about SSD in allopatric and sympatric sister-species pairs. We also demonstrated how global analyses of SSD can be somewhat misleading even when testing simple hypotheses about SSD, such as the male sexual selection hypothesis. Although global analyses of SSD across large clades may be particularly appealing due to their comprehensive nature and large sample sizes, they may be problematic when different processes occur within different subclades.

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Supporting Information

The following supporting information is available for this article:

Appendix S1. Sources of sequence data and robustness of results to choice of tree topology and branch length estimates.
Table S1. Correlations between continuous variables, male body size, female body size, and average body size.
Table S2. Raw data on SSD and reproductive variables used in analyses, "—" indicates species for which data were not available.
Table S3. Sources of sequences used in study.
Table S4. Testing for the effects of mating behavior on the evolution of SSD.
Table S5. Testing for the effects of mating behavior on direction of dimorphism in emydids.
Table S6. Testing for the effects of female fecundity on the evolution of SSD in emydids.
Table S7. Testing for the effects of female fecundity on the evolution of SSD in emydids, members of the *Graptemys–Malaclemys* clade excluded.
Table S8. The relationship between SSD and sexual dimorphism in size corrected head width.
Table S9. Average SSD and patterns of body size divergence in sister species pairs that differed between Bayesian and parsimony analysis.
Figure S1. Reconstruction of body size evolution in Emydidae based on parsimony topology and branch lengths estimated from cytochrome *b* and ND4 sequences using maximum likelihood.
Figure S2. Quartile plots comparing (A) male and (B) female body size divergence of sympatric and nonsympatric sister species pairs.

Supporting Information may be found in the online version of this article.
(This link will take you to the article abstract).

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