

Proximate Causes of Rensch's Rule: Does Sexual Size Dimorphism in Arthropods Result from Sex Differences in Development Time?

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ABSTRACT: A prominent interspecific pattern of sexual size dimorphism (SSD) is Rensch's rule, according to which male body size is more variable or evolutionarily divergent than female body size. As-

suming equal growth rates of males and females, SSD would be entirely mediated, and Rensch's rule proximately caused, by sexual differences in development times, or sexual bimaturism (SBM), with the larger sex developing for a proportionately longer time. Only a subset of the seven arthropod groups investigated in this study exhibits Rensch's rule. Furthermore, we found only a weak positive relationship between SSD and SBM overall, suggesting that growth rate differences between the sexes are more important than development time differences in proximately mediating SSD in a wide but by no means comprehensive range of arthropod taxa. Except when protandry is of selective advantage (as in many butterflies, Hymenoptera, and spiders), male development time was equal to (in water striders and beetles) or even longer than (in drosophilid and sepsid flies) that of females. Because all taxa show female-biased SSD, this implies faster growth of females in general, a pattern markedly different from that of primates and birds (analyzed here for comparison). We discuss three potential explanations for this pattern based on life-history trade-offs and sexual selection.

Keywords: allometry, body size, development time, gonads, growth, Rensch's rule, sexual size dimorphism, sexual selection.

Sexual size dimorphism (SSD) is widespread in the animal kingdom (Hedrick and Temeles 1989; Shine 1989; Fairbairn 1997). In most ectotherms, females are larger than males (Arak 1988; Shine 1988, 1989; Fairbairn 1997), whereas in many birds and mammals, males are larger (Ralls 1977; Cabana et al. 1982; Abouheif and Fairbairn

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1997; Székely et al. 2000, 2004). However, beyond these broad generalizations, the direction and degree of SSD is highly variable within and between taxa. Rensch (1950) observed that SSD increases with body size in species where males are larger and decreases with body size in species where females are larger (recently termed Rensch's rule; Abouheif and Fairbairn 1997; Fairbairn 1997). This is equivalent to saying that male body size varies or diverges more over evolutionary time than female body size, irrespective of which sex is larger. While Rensch (1950) did not offer an explanation for this phenomenon, Fairbairn and Preziosi (1994) were the first to hypothesize that sexual selection for large male size may be the primary force driving this allometric pattern in SSD. Since then, some additional evidence for this hypothesis has been published (Abouheif and Fairbairn 1997; Fairbairn 1997; Székely et al. 2000, 2004; Kraushaar and Blanckenhorn 2002; Lindenfors et al. 2003), but more studies are clearly needed (Fairbairn 1997).

Rensch's rule thus refers to a systematic pattern of interspecific (and sometimes, by extension, analogous intraspecific, between-population) variation in SSD (e.g., Fairbairn and Preziosi 1994). For any particular species, which sex is larger depends on whether selection for (primarily fecundity selection in females and sexual selection in males) and against (primarily viability selection) large body size equilibrate differently in the two sexes (the so-called equilibrium model of SSD; Price 1984; Arak 1988; Travis 1989; Schluter et al. 1991; Andersson 1994; Fairbairn 1997; Blanckenhorn 2000). From a life-history point of view, intraspecific body size variation is proximately mediated by variation in organism growth and development (Roff 1992), which in turn are regulated by complex endocrine control mechanisms at the molecular, cellular, and physiological levels (Badyaev 2002; Nijhout 2003). Starting from first principles, there are three nonexclusive ways to achieve a larger body size: propagule (egg, seed, or offspring) size can be larger at the start, individuals can grow faster (i.e., increase growth rate), or individuals can grow for longer time (i.e., increase development time). All of these strategies presumably incur costs that can and should be demonstrated, implying trade-offs (Roff 1980, 1992; Gotthard and Nylin 1995; Abrams et al. 1996; Nylin and Gotthard 1998). Larger offspring size increases parental investment (Roff 1992). Longer development time typically incurs greater cumulative mortality before reproduction because of prolonged exposure to predators or unfavorable conditions (Roff 1980, 1992; Wiklund and Karlsson 1988; Wiklund et al. 1991). On the other hand, a faster growth rate can increase predation because of greater foraging activity (Werner and Anholt 1993; Abrams et al. 1996; Gotthard 2000; Mikolajewski et al. 2005) or starvation because of higher metabolic demands in

nutrient-limited environments (Gotthard et al. 1994; Blanckenhorn 1998). Body size, development time, and growth rate are thus intimately interconnected and traded off against each other, and they should therefore be investigated in conjunction (Nylin and Gotthard 1998).

Presuming no intraspecific sex difference in egg size, for which there is generally no evidence in arthropods (e.g., Yasuda and Dixon 2002), the SSD of any given species may consequently be proximately caused by differences between the sexes in development time and/or growth rate. There is substantial evidence in a number of taxa that both growth rate and development time can vary between the sexes and that this variation is associated with SSD (Wiklund and Fagerström 1977; Wiklund et al. 1991; Leigh 1992; Shine 1994; Teather and Weatherhead 1994; Badyaev et al. 2001*a*, 2001*b*). Leigh (1992) investigated the ontogeny of SSD in anthropoid primates and found that sex differences in both growth rate and age at maturity contribute to SSD. In insects, the relationship between development time and SSD has been discussed either in the context of protandry, that is, earlier male emergence (Wiklund and Fagerström 1977; Fagerström and Wiklund 1982), or in the context of developmental constraints, the constraint being the presumed strong correlation (or trade-off) between body size and development time mentioned above (Roff 1980, 1992; Wiklund and Karlsson 1988; Fairbairn 1990). In either case, SSD is expected to be associated with differences between the sexes in development time (Fairbairn 1990; Wiklund et al. 1991), termed sexual bimaturism (SBM) in the primatological literature (e.g., Leigh and Shea 1995), with the larger sex developing for proportionately longer time (cf. Ricklefs 1979, 1984; Teather and Weatherhead 1994).

In this study we compare the degree of interspecific SSD with the corresponding degree of SBM for seven taxonomic groups of arthropods. We thus comprehensively evaluate the relative contribution to SSD of sex differences in development time versus growth rate. Put another way, we ask whether there are interspecific patterns in SBM that are analogous to and might therefore proximately cause Rensch's rule. In so doing, we also investigate the general validity of Rensch's rule for arthropods, which so far has been documented only in very few taxa (Abouheif and Fairbairn 1997). Specifically, tephritid flies (Sivinski and Dodson 1992), odonates (Johansson et al. 2005), and water striders (Gerridae; Andersen 1994, 1997) follow Rensch's rule, whereas stick insects (Sivinski and Dodson 1992), caddis flies (Jannot and Kerans 2003), spiders (Prenter et al. 1999), and ladybird beetles (Dixon 2000; reevaluated here) do not (cf. also Baker and Wilkinson 2001). We employ a number of analytical methods because, as shall be seen, no single method captures all important aspects of variation. Additionally, we reanalyze the previously pub-

lished bird and primate data (Leigh 1992; Teather and Weatherhead 1994) using these methods for direct comparison.

Methods

Data Acquisition

We acquired data on sex-specific body size and development time for spiders (Araneae: 13 species from eight families) and five orders of insects (all listed in the appendix in the online edition of the *American Naturalist*): (1) Heteroptera (seven species of water striders), (2) Coleoptera (68 species from nine families, with a special emphasis on ladybird beetles), (3) Diptera (23 species of fruit flies and 10 species of black scavenger flies), (4) Lepidoptera (47 species from 11 families), and (5) Hymenoptera (20 species from nine families). All fly data reported here are unpublished. The data for most spiders, beetles, water striders, butterflies, and hymenopterans were gathered from published sources (see appendix). Note that although the taxonomic level varies for some of the groups examined here, all analyses were conducted within groups using paired comparisons and hence are not confounded by taxonomic scaling.

Contrary to most vertebrate taxa, there is unfortunately no standard body size measure agreed upon for arthropods, making comparative studies generally difficult. Our use of different body size measures (see appendix) posed no problem for this study, however, because we compared the sexes within groups using paired tests. To ensure that all size measures were at the same biological scale (LaBarbera 1989), we cube-root transformed all body mass measures to make them directly comparable to the linear measures.

We considered egg-to-adult (=total) development times (all in days) only of directly developing (as opposed to diapausing) individuals (cf. Wiklund and Forsberg 1991) in the laboratory; otherwise our SBM estimates could be biased and not directly comparable among species (see, e.g., Harvey and Strand 2003). In general, we aimed for a sample size of $N > 10$ individuals per sex and species to obtain reliable mean estimates for body size and development time. However, for a few species, this number was not reached, and for some, sample sizes were unknown. Because deletion of species with $N < 10$ had no significant effect on the overall results, we included all species listed in the appendix in the final analyses.

Statistical Analysis

Body size and development time allometry. We specifically wanted to compare the relationship between female

and male sizes (i.e., allometry for SSD) with the relationship between female and male development times (i.e., allometry for SBM) among species for each taxonomic group. It has become standard to analyze SSD allometry using regression plots of $\ln(\text{mean species female size})$ on $\ln(\text{mean species male size})$ or vice versa (Abouheif and Fairbairn 1997; Fairbairn 1997), thus analyzing primarily patterns of trait variance (Eberhard et al. 1998). For direct comparison we produced analogous plots for $\ln(\text{mean species development time})$. Because the y and x variables are both estimated with error and are identical, major axis (MA = model II) regression should be used instead of least squares (LS) regression (Sokal and Rohlf 1995). When male size is plotted on the X -axis, as done here, Rensch's rule becomes statistically manifest in a hypoallometric or negatively allometric slope ($b < 1$; Fairbairn and Preziosi 1994). Hypoallometry results whenever variance in y is less than that in x , and hyperallometry or positive allometry results in the opposite case. If Rensch's rule is proximately mediated by analogous variance patterns in male and female development time, we would expect the allometric slopes for body size and development time to be the same.

For comparison and generality, we calculated and present both the LS and the MA slope for SSD and SBM with their respective standard errors (SEs) based on error in y only and in x and y , respectively. MA slopes and their SEs were calculated using an Excel spreadsheet, which can be obtained upon request from W. U. Blanckenhorn. (Note that unless r^2 is very high, the MA slope is always greater than the LS slope, and the MA SE is always smaller than the LS SE.) We additionally present the reduced major axis (RMA) slopes, which can be conveniently calculated as the ratio of the standard deviations (SDs) in y and x (Sokal and Rohlf 1995). As is customary for allometric comparisons (Gould 1966; LaBarbera 1989), we \ln transformed our linear length and cube-root (body mass) measures as well as the development times. We tested both the LS and MA slopes for deviations from isometry (i.e., slope $b = 1$) using one-sample t -tests; the SSD and SBM slopes were compared using two-sample t -tests.

After analysis of the original data, we performed the same analyses with variation due to phylogenetic relatedness removed using independent contrasts (CAIC; Purvis and Rambaut 1995). Phylogenetic relationships (with branch lengths always set equal) for the Gerridae (Andersen 1997; Damgaard et al. 2000) and spiders (Coddington and Levi 1991; Griswold et al. 1999; Hormiga et al. 2000; Arnedo et al. 2004) were extracted from published sources; those for the Drosophilidae, Sepsidae, and Lepidoptera stem from our own unpublished work (K. van der Linde, R. Meier, and S. Nylin, respectively); the rest were extracted from the Tree of Life Web site, <http://>

tolweb.org/tree/phylogeny.html. The phylogenies used are available upon request from W. U. Blanckenhorn.

SSD, SBM, and growth rate indexes. For each species, we computed the percentage of body size (i.e., SSD) and development time (i.e., SBM) difference between the sexes as $100 \times (M - F) / [(M + F) / 2]$. We expected these two indexes to be the same if SSD is entirely mediated by corresponding development time differences between the sexes. SSD and SBM means could then be compared within and among groups. We further computed the correlation between these SSD and SBM indexes among species within taxonomic groups, which we expected to be strongly positive if SSD and SBM are generally congruent but vary among species. Analogously, we computed the correlation between the mean body sizes and development times of males and females combined (both \ln transformed for scaling reasons) among species within taxonomic groups. This correlation is generally expected to be positive because larger species should take longer to mature (Roff 1980, 1992).

If SSD and SBM are not congruent, SSD must be mediated instead by growth rate differences between the sexes. We therefore additionally calculated sex-specific growth rates for each species as adult body size/egg-to-adult development time (based on our various linear measures of size), assuming linear growth. These could be compared among groups as well as with the null expectation of equal growth rates of males and females. We are aware that such growth rate estimates have to be interpreted with caution because growth trajectories are typically not linear but rather sigmoid and asymptotic (see Leigh 1992 for an example). Deviation from the linearity assumption thus produces systematically biased growth estimates (probably underestimates if growth rate is strongly asymptotic), but unless the growth trajectories differ systematically in shape between the sexes, this should not strongly affect the sex comparisons undertaken here.

Results

We first present an exemplary detailed analysis of the sepsid flies to illustrate our methods. Thereafter we analyze the comparative patterns for all taxa.

Patterns within the Sepsidae

Based on the original data, the lab-reared Sepsidae were found to follow Rensch's rule, with males being larger than females only in the largest species and the interspecific allometric slope linking female and male size consequently less than 1 (fig. 1; table 1). The field-collected museum specimens, which were on average much smaller, presumably because of environmental limitations (fig. 1), equally exhibited Rensch's rule, with a slope similar to that for the

laboratory sample (LS regression equation: \ln [female size] = $0.651 \times \ln$ [male size] + 0.005; $r^2 = 0.866$; cf. table 1). In contrast to the pattern for SSD, the corresponding relationship between female and male development time is steeper, slightly hypoallometric, and marginally below 1 (fig. 1; table 1). The independent contrast data yield qualitatively equivalent results, although the body size slope is closer to and not significantly different from 1 (fig. 1; table 1).

In agreement with the results of the allometric analysis, SSD and SBM do not correlate for the Sepsidae (table 1). This occurs because the average SSD in the Sepsidae is female biased, whereas male development actually lasts a bit longer, largely independent of SSD (i.e., SBM is almost male biased on average, since its 95% confidence interval [CI] barely overlaps 0; fig. 2). Consequently, most of the SSD is explained by faster female growth (fig. 3). This lack of relationship between sex differences in body size and development time is consistent with the counterintuitive finding that body size and development time are negatively correlated among sepsid species when all are reared in the same medium (cow dung; table 1). *Sepsis cynipsea* (*cy* in fig. 1) and *Sepsis punctum* (*pu* in fig. 1) are among the largest species but have the shortest development times (fig. 1), probably reflecting their high degree of specialization to nutrient-rich fresh cow dung as used here, while other species prefer nutrient-poor, older dung (Pont and Meier 2002). Because such effects might be common, any evolutionary inferences based on the magnitude of the simple body size/development time correlation in comparative or experimental studies will be limited (cf. Roff 1992). The general lack of correspondence between SSD and SBM evident in all our analyses, including explicit phylogenetic control, suggests that phylogenetic effects are of minor importance for explaining the different patterns in SSD and SBM observed.

Comparative Patterns

Similar to the Sepsidae, the Drosophilidae and the Gerriidae (cf. Andersen 1994, 1997) were found to display body size allometry consistent with Rensch's rule (i.e., body size slope < 1 ; table 1). This implies that interspecific variance, or evolutionary divergence, in female size is less than variance in male size, which is immediately evident in the RMA ($= SD[\text{female}] / SD[\text{male}] < 1$). The Lepidoptera and the Araneae investigated here also show some tendency toward Rensch's rule in the original data (with the spiders displaying by far the greatest variation in SSD; see fig. 2), although their contrast MA slopes are clearly isometric (table 1). (Note that our lepidopteran results are largely consistent with those for the subgroups analyzed earlier by Wiklund and Forsberg [1991], and the results are also congruent for the two different body size measures in-

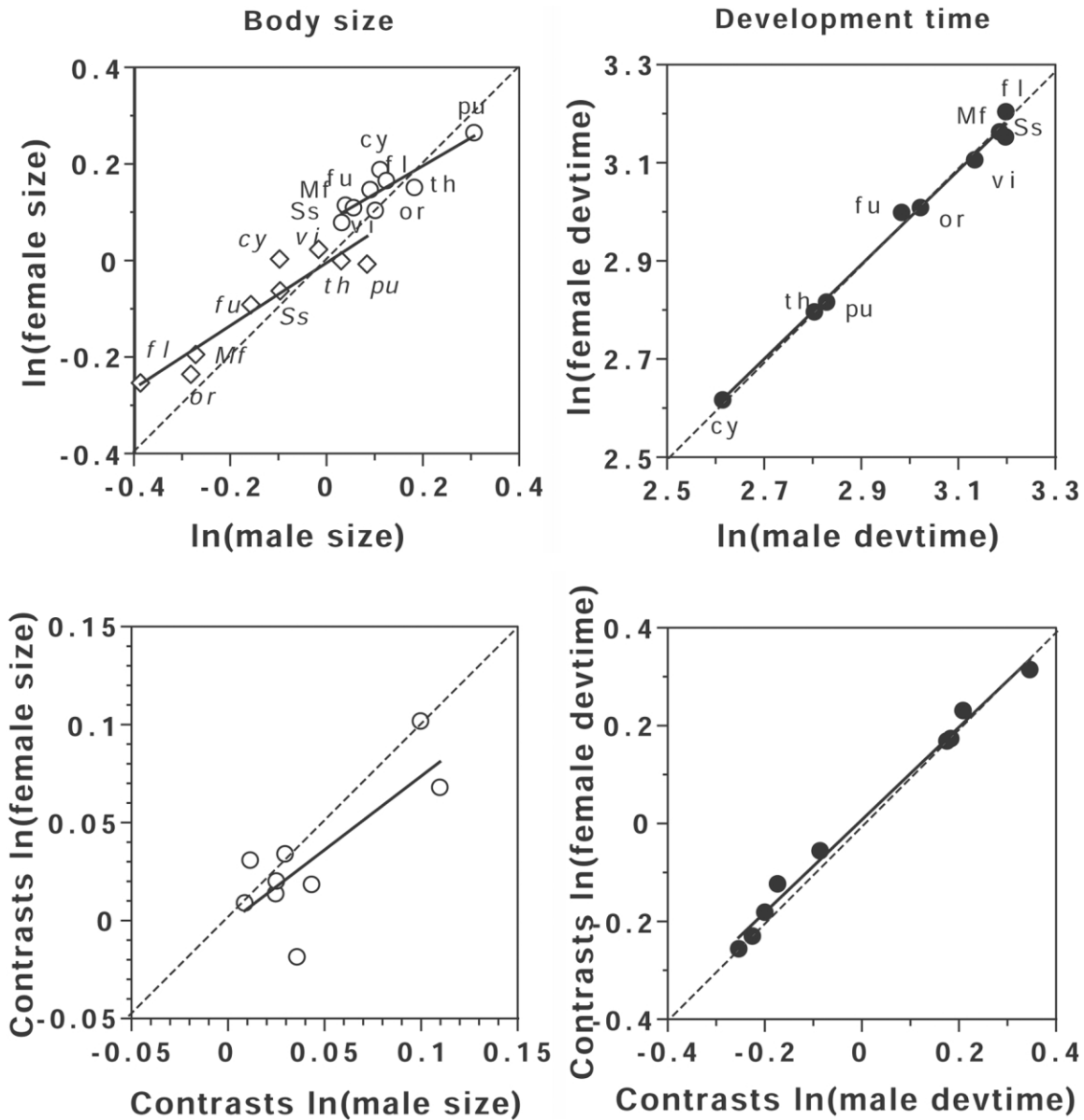


Figure 1: Original (*top*) and contrast data (*bottom*) allometric least-squares regression plots of mean female size on mean male size (*left*; estimated as \ln -transformed head width; in millimeters) and mean female on mean male development time (*right*; \ln transformed; in days) for nine species of sepsid flies (line of isometry dashed for comparison). For body size, circles show flies reared in the laboratory at standardized conditions, and diamonds show field-collected flies. Abbreviations denote species names (cf. appendix), with capital letters denoting genera other than *Sepsis*.

investigated for nine butterfly species [table 1].) In contrast, the Hymenoptera show some tendency for (contrast) slopes >1 , opposite to Rensch's rule, with variance in female size thus tending to be greater than variance in male size. This was previously also found for the full Coccinellidae (ladybird beetle) data set (Dixon 2000) included in table 1, although we found the opposite pattern here for the subset of 13 species for which both SSD and SBM

were available (table 1). All beetles together show clear isometry. Overall, therefore, Rensch's rule is not consistently supported in the arthropod groups investigated here (table 1). Similar lack of a consistent pattern is observed across vertebrates, with primates exhibiting Rensch's rule, while birds overall do not in the subsets considered here (table 1; cf. Abouheif and Fairbairn 1997 and Lindenfors et al. 2003 for larger data sets).

Table 1: Original data and independent contrast statistics for sexual size dimorphism (SSD; using $\ln[\text{linear body size}]$) allometries, SSD and sexual bimaturism (SBM) percentage correlations among species, and correlations between mean body size and development time among species (both sexes combined) for seven arthropod groups (plus some subsets) reared in the laboratory, with bird and primate data given for comparison (species-level data only)

Taxonomic group	N	LS slope	LS intercept	r^2	MA slope	MA inter- cept	RMA slope	SSD/SBM correlation	Development time/size correlation
Original data:									
Araneae	13	.662 ± .291**	.215 ± .201**	.648	.769 ± .260	.196	.821	+ .86**	+ .60**
Coleoptera	35	1.006 ± .024	.024 ± .024*	.995	1.008 ± .017	.022	1.008	+ .34**	+ .18
Coccinellidae ^a	37	<i>1.014 ± .039</i>	<i>.059 ± .036**</i>	.989	<i>1.020 ± .026</i>	<i>.054</i>	<i>1.02</i>	NA	NA
Subset ^b	13	.961 ± .031**	.085 ± .033**	.997	.959 ± .023**	.087	.962	- .02	+ .20
Other	22	<i>1.005 ± .032</i>	<i>.017 ± .028</i>	.995	<i>1.007 ± .022</i>	<i>.001</i>	<i>1.007</i>	+ .39*	+ .35
Diptera: Drosophilidae	23	.811 ± .133**	.115 ± .019**	.887	.848 ± .110**	.112	.861	- .25	+ .46**
Diptera: Sepsidae	10	.776 ± .190**	.053 ± .022**	.860	.794 ± .163**	.051	.822	- .05	- .12
Heteroptera: Gerridae	7	<i>.922 ± .076**</i>	<i>.245 ± .133**</i>	.994	.913 ± .059**	.268	.925	+ .55	+ .51
Hymenoptera	20	<i>.977 ± .033</i>	<i>.098 ± .031**</i>	.994	<i>.979 ± .025</i>	.098	.980	+ .39*	- .34
Lepidoptera	47	.903 ± .073**	.222 ± .118**	.931	.932 ± .055**	.176	.936	+ .58**	- .30**
Subset ^c	21	<i>.979 ± .076</i>	<i>.054 ± .130</i>	.976	<i>.990 ± .051</i>	<i>.037</i>	<i>.990</i>	+ .13	- .04
Wing length ^c	9	.966 ± .207	<i>.132 ± .658</i>	.942	.993 ± .147	<i>.043</i>	<i>.995</i>	+ .56	- .11
Pupal mass ^c	9	<i>.973 ± .154</i>	<i>.060 ± .483</i>	.952	<i>.987 ± .110</i>	<i>.035</i>	<i>.989</i>
Birds ^d	51	1.003 ± .036	- .009 ± .055	.984	1.012 ± .025	- .025	1.011	+ .59**	+ .92**
Primates ^e	44	.883 ± .030**	- .064 ± .026**	.987	.886 ± .023**	- .066	.889	+ .76**	+ .91**
Independent contrasts:									
Araneae	12	.413 ± .569**170	1.000 ± .478	...	1.000	+ .78**	+ .77**
Coleoptera	35	.978 ± .038999	.982 ± .027983	+ .62**	+ .09
Coccinellidae	...	NA	...	NA	NA	...	NA
Subset ^b	9	.949 ± .067*996	.947 ± .050**953	+ .10	- .03
Other	18	<i>.983 ± .050</i>990	<i>.987 ± .036</i>988	+ .69**	+ .17
Diptera: Drosophilidae	22	.825 ± .170**806	.906 ± .139919	- .44**	+ .61**
Diptera: Sepsidae	9	.752 ± .442613	.943 ± .345960	- .58*	- .36
Heteroptera: Gerridae	6	<i>.886 ± .109**</i>984	.872 ± .090**893	+ .56	+ .66
Hymenoptera	18	1.060 ± .065984	1.075 ± .043**	...	1.069	+ .45**	- .25
Lepidoptera	41	.939 ± .102886	.998 ± .077998	+ .62**	- .38**
Subset ^c	18	<i>1.018 ± .040</i>993	<i>1.023 ± .028</i>	...	<i>1.022</i>	+ .52	+ .38
Wing length ^c	8	<i>1.052 ± .409</i>737	<i>1.308 ± .312</i>	...	<i>1.225</i>	+ .83*	- .35
Pupal mass ^c	8	<i>1.011 ± .185</i>951	<i>1.043 ± .129</i>	...	<i>1.036</i>

Note: Slope and intercept data are given \pm 95% confidence intervals. Intercept and correlations were tested against 0 and slope against 1, using one-sample t -tests. Boldface indicates that SSD slope differs from SBM slope (t -test; cf. table 2). Italics indicate that the data are for a taxonomic subset. Sample size differences result from unknown or unresolved phylogenetic positions. LS = least squares; MA = major axis; RMA = reduced major axis; NA = not available.

^a Data from Dixon (2000).

^b Both SSD and SBM available.

^c Lycaenidae, Nymphalidae, Pieridae, and Satyridae (cf. Wiklund and Forsberg 1991).

^d Data from Teather and Weatherhead (1994).

^e Data from Leigh (1992).

* $P < .1$.

** $P < .05$.

In contrast to the relationship for body size, the predominant allometric relationship observed between female and male development times was isometry. The most notable exceptions to this trend were the Hymenoptera and the Coccinellidae, both of which exhibit hyperallometric slopes >1 (although isometry was found in the more comprehensive set of all Coleoptera), as well as the primates, which show a slope <1 , indicating that males vary more

than females (table 2). That is, interspecific variation in development time is generally similar for males and females in arthropods, irrespective of SSD, not generating patterns analogous to Rensch's rule. In particular, the development time slopes are generally steeper than the body size slopes, based on t -tests (tables 1, 2; note that only in primates this is reversed). These differences were significant in the Gerridae, Drosophilidae, Sepsidae, Lepidoptera,

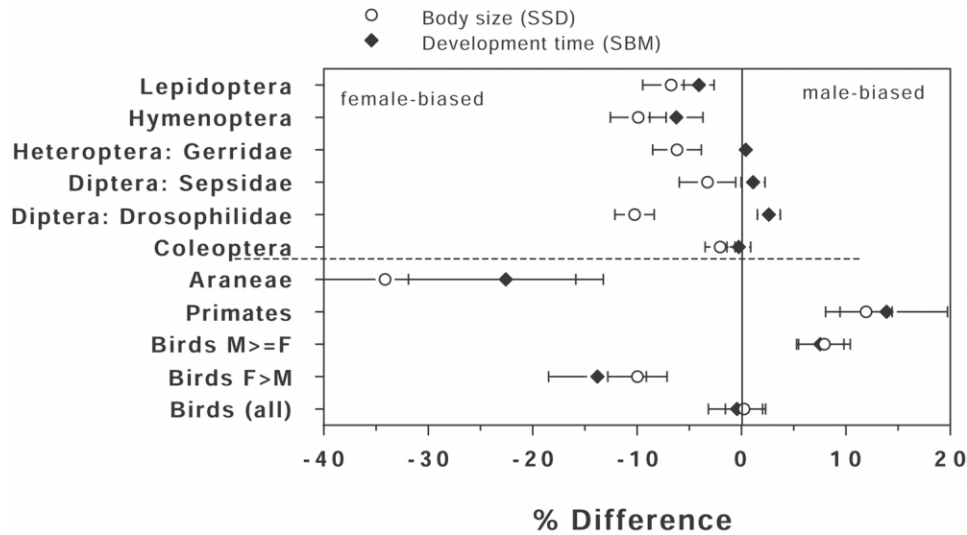


Figure 2: Paired comparison of the mean \pm 95% confidence interval body size (sexual size dimorphism; circles) and development time (sexual bimaturism; diamonds) percentage differences between the sexes (male – female) for seven arthropod groups plus birds and primates.

and the Coccinellidae subset, while the two slopes were similarly isometric in the Coleoptera and the Hymenoptera. These results suggest that Rensch's rule, where it is supported, is not or only weakly proximately caused by corresponding differences in development times. Instead, observed SSD is primarily mediated by sexual differences in growth rate, as discussed below. A triply repeated-measures ANOVA comparing the SSD versus SBM, MA versus LS, and raw versus contrast data slopes for the seven arthropod groups (with Sepsidae and Drosophilidae analyzed separately) showed that the development time slopes were indeed steeper on average than the body size slopes (0.980 ± 0.017 [95% CI] vs. 0.890 ± 0.080 ; $F = 6.83$, $df = 1, 6$, $P = .040$), whereas the MA and LS slopes (0.956 ± 0.031 vs. 0.914 ± 0.069 ; $F = 2.90$, $df = 1, 6$, $P = .139$) and raw versus contrast data slopes (0.942 ± 0.049 vs. 0.928 ± 0.047 ; $F = 2.02$, $df = 1, 6$, $P = .205$) did not differ significantly.

In all seven arthropod groups, SSD is significantly female biased (because all 95% CIs in fig. 2 do not overlap 0). At the same time, the corresponding SBM index generally revealed weaker sex differences in development time than in body size (paired t -test for the seven arthropod groups: $t = 3.76$, $df = 6$, $P = .009$; fig. 2). Specifically, three different relationships between SBM and SSD were observed: first, despite being smaller, males have development times equal to those of females (Coleoptera and Gerridae); second, despite being smaller, males have longer development times than females (Diptera: Drosophilidae and Sepsidae); and third, males have shorter development times than females, albeit not quite in proportion to the

average SSD (Araneae, Lepidoptera, and Hymenoptera; i.e., there is some degree of protandry; fig. 2). These results imply that growth rate differences between the sexes should be smallest in Araneae, Lepidoptera, and Hymenoptera, because their SSD is mediated largely by development time differences, and largest in the Drosophilidae and Sepsidae. This is roughly the case, although spiders again show great variation because of the extreme SSD of some species (fig. 3). Furthermore, in the vast majority of species with female-biased SSD, females grow faster, whereas in the few species with male-biased or no SSD, males tend to grow faster (note that this is not the case in birds; fig. 3). ANOVA (including only those taxonomic groups that display such variation, i.e., Araneae, Sepsidae, Lepidoptera, and Coleoptera) with growth rate difference as the dependent variable and SSD type and taxonomic group as fixed factors revealed this effect to be highly significant ($F = 13.17$, $df = 1, 84$, $P < .001$; fig. 3; group effect and interaction both nonsignificant).

Finally, largely in agreement with the above results, SSD and SBM tended to be positively correlated among species in those groups showing congruent sex differences in body size and development time (Araneae, Lepidoptera, Hymenoptera, and Coleoptera, the former three of which show protandry; cf. fig. 2) but uncorrelated in the other groups, where those sex differences are incongruent (Gerridae, Sepsidae, and Drosophilidae; $F = 5.26$, $df = 1, 5$, $P = .070$; repeated-measures comparison of the two subgroups using both the raw and contrast correlation coefficients given in table 1; this result remained but became nonsignificant when in the former set only the three taxa

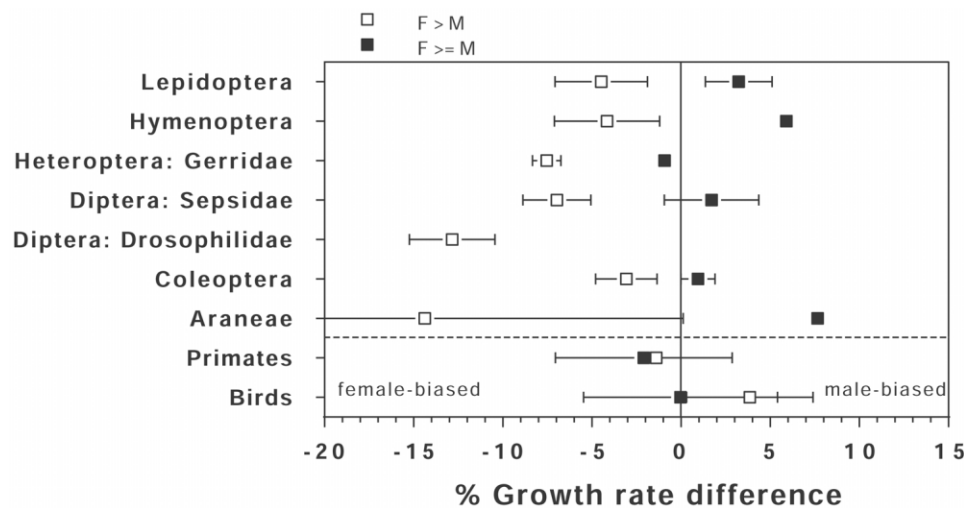


Figure 3: Paired comparison of the mean \pm 95% confidence interval difference in growth rate between the sexes (male – female) for species with female-biased sexual size dimorphism (SSD; $F > M$; open squares) and species with male-biased or no SSD ($M \geq F$; filled squares) belonging to seven arthropod groups plus birds and primates. Females grow faster in all arthropod groups unless SSD is male biased.

showing protandry were included [$F = 4.18$, $df = 1, 4$, $P = 0.111$]). The overall (mean) correlation between SSD and SBM for the seven main arthropod groups was 0.34 ± 0.28 (95% CI) for the raw and 0.29 ± 0.41 for the contrast data, demonstrating a weak correspondence between the two, while the corresponding mean correlations between body size and development time were 0.14 ± 0.29 and 0.16 ± 0.38 (i.e., nil), respectively, paired t -tests indicating in both cases that raw and contrast data did not differ significantly ($P > .2$). Note that these two correlations show no relationship ($r = 0.10$ for the raw and $r = 0.17$ for the contrast data across the seven groups investigated; $P > .7$; table 1).

Discussion

Interspecific variation in SSD consistent with Rensch's rule, that is, male body size diverging more over evolutionary time than female body size, is common in vertebrates (reviewed in Abouheif and Fairbairn 1997; Fairbairn 1997), irrespective of whether females (as in most ectotherms) or males (as in most birds and mammals) are larger. For invertebrates, the corresponding evidence so far has been scant and inconsistent (Sivinski and Dodson 1992; Andersen 1994, 1997; Abouheif and Fairbairn 1997; Fairbairn 1997; Prenter et al. 1999; Dixon 2000; Baker and Wilkinson 2001; Jannot and Kerans 2003; Johansson et al. 2005; Huey et al. 2006). Three of the seven taxa investigated here, the dipteran groups Drosophilidae and Sepsidae as well as the Gerridae (as previously shown; Fairbairn 1990; Andersen 1994, 1997), clearly exhibit Rensch's

rule for body size, that is, hypoallometry or negative allometry in plots of females versus males. In butterflies and spiders there is a slight but nonsignificant trend toward Rensch's rule, in agreement with inconsistent previous results on spiders (cf. Head 1995; Prenter et al. 1999; Hormiga et al. 2000; Huber 2005). In Hymenoptera and beetles the relationship does not differ from isometry, with possibly even a hint of a pattern opposite to Rensch's rule (cf. Dixon 2000). It is thus clear from the current and previous evidence that Rensch's rule is, at best, only weakly supported as a general macroevolutionary pattern within the Arthropoda. Why this is so remains unclear.

The main result of our analyses is that, in general, SSD is only weakly proximately mediated by development time differences between the sexes (i.e., SBM) in the wide but not comprehensive range of arthropod taxa studied here. Contrary to the predominantly hypoallometric patterns for body size, the corresponding relationship between female and male development time was largely isometric, deviating only slightly toward hypoallometry in the Sepsidae and butterflies and toward hyperallometry in the Hymenoptera and ladybird beetles. The development time relationship was almost always and overall significantly steeper than the corresponding body size relationship (cf. fig. 1). A pattern analogous to Rensch's rule therefore does not generally occur for development time. Moreover, SSD and SBM are only weakly positively correlated among species, primarily in the Araneae, Lepidoptera, Hymenoptera, and Coleoptera, with all these groups except Coleoptera regularly featuring protandry (see below). This may also relate at least in part to the lacking correlation overall

Table 2: Original data and independent contrast statistics for sexual bimaturism (SBM; $\ln[\text{development time}]$) allometries of seven arthropod groups (plus some subsets) reared in the laboratory, with bird and primate data given for comparison (species-level data only)

Taxonomic group	<i>N</i>	LS slope	LS intercept	r^2	MA slope	MA intercept	RMA slope
Original data:							
Araneae	13	.945 ± .088	1.678 ± 1.112**	.976	.953 ± .062	1.593	.957
Coleoptera	35	.999 ± .011	.011 ± .042	.999	.999 ± .008	.019	.999
Coccinellidae ^a	37	<i>1.011 ± .032</i>	<i>−.038 ± .154</i>	.995	<i>1.014 ± .022</i>	<i>−.051</i>	<i>1.013</i>
Subset ^b	13	<i>1.040 ± .032**</i>	<i>−.155 ± .157*</i>	.997	<i>1.045 ± .023**</i>	<i>−.178</i>	<i>1.041</i>
Other	22	.999 ± .014	.014 ± .097	.999	.999 ± .010	.011	.999
Diptera: Drosophilidae	23	.959 ± .068	.096 ± .116	.975	.970 ± .050	.059	.971
Diptera: Sepsidae	10	.955 ± .065	.176 ± .274	.992	.953 ± .048*	.182	.958
Heteroptera: Gerridae	7	.979 ± .064	.118 ± .178	.996	.978 ± .049	.125	.981
Hymenoptera	20	1.013 ± .015	.098 ± .107	.999	1.014 ± .010**	.091	1.013
Lepidoptera	47	.989 ± .019	.183 ± .125**	.996	.991 ± .014	.171	.991
Subset ^c	21	.978 ± .129	.238 ± .917	.982	.985 ± .095	.195	.986
Wing length ^c	9	<i>1.207 ± .173**</i>	<i>−1.183 ± .456**</i>	.974	<i>1.257 ± .099**</i>	<i>−1.491</i>	<i>1.223</i>
Birds ^d	51	1.024 ± .041	−.018 ± .133	.979	1.036 ± .029**	−.028	1.035
Primates ^e	44	.653 ± .073**	.068 ± .093	.922	.853 ± .060**	.049	.861
Independent contrasts:							
Araneae	12	.978 ± .130955	1.001 ± .093	...	1.001
Coleoptera	28	1.004 ± .012999	1.005 ± .008	...	1.004
Coccinellidae	...	NA	...	NA	NA	...	NA
Subset ^b	9	<i>1.068 ± .045**</i>996	<i>1.079 ± .031**</i>	...	<i>1.070</i>
Other	18	<i>1.001 ± .011</i>999	<i>1.002 ± .008</i>	...	<i>1.002</i>
Diptera: Drosophilidae	22	.968 ± .088960	.987 ± .063988
Diptera: Sepsidae	9	.947 ± .070990	.945 ± .052**951
Heteroptera: Gerridae	6	.962 ± .084992	.959 ± .061966
Hymenoptera	18	1.021 ± .017**999	1.023 ± .011**	...	1.022
Lepidoptera	41	.976 ± .017**997	.977 ± .013**977
Subset ^c	18	.993 ± .038994	.996 ± .027996
Wing length ^c	8	<i>1.167 ± .053**</i>997	<i>1.196 ± .035**</i>	...	<i>1.170</i>

Note: Intercept was tested against 0 and slope against 1, using *t*-tests. Italics indicate that the data are for a taxonomic subset. Sample size differences result from unknown or unresolved phylogenetic positions. LS = least squares; MA = major axis; RMA = reduced major axis; NA = not available.

^a Data from Dixon (2000).

^b Both sexual size dimorphism and SBM available.

^c Lycaenidae, Nymphalidae, Pieridae, and Satyridae (cf. Wiklund and Forsberg 1991).

^d Data from Teather and Weatherhead (1994).

^e Data from Leigh (1992).

* $P < .1$.

** $P < .05$.

between body size and development time, which is one of the major trade-offs expected by life-history theory (Roff 1980, 1992). We therefore conclude that Rensch's rule is primarily mediated by sexual differences in growth rate in the arthropod groups investigated here (discussed below).

Results from analyses treating species as independent units were qualitatively similar to those from analyses using phylogenetically independent contrasts. The lack of any substantive phylogenetic effect in our allometric analyses is perhaps not surprising, since we conducted paired tests. That is, while the empirical relationships between female and male sizes or development times may be influenced

by phylogenetic relatedness, phylogeny is unlikely to be responsible for any differences found between these two relationships because the same phylogeny underlies both. However, this does not mean that lineage-specific differences in the relationship between female and male sizes or development times are not influenced by phylogenetic relatedness.

Males were on average smaller than females in all seven arthropod taxa investigated (fig. 2), the usual SSD for arthropods (Wiklund and Karlsson 1988; Fairbairn 1997). Altogether, males were at least 2% larger than females in only nine of a total of 159 species, with another 27 species

showing no SSD (see appendix). At the same time, average development times (i.e., SBM) were the same for both sexes (in Gerridae and Coleoptera), longer for males despite their smaller size (in Diptera), or shorter for males, albeit not quite in proportion to the average SSD (in Araneae, Lepidoptera, and Hymenoptera), revealing protandry (i.e., earlier male emergence). Sexual selection has favored protandry in many butterflies (Wiklund and Fagerström 1977; Fagerström and Wiklund 1982; Wiklund and Forsberg 1991). This is consistent with the well-established life-history trade-off between body size and development time (Roff 1980), sometimes called a developmental constraint (e.g., Fairbairn 1990), that earlier emergence (of males, in this case) must come at a cost of smaller size. Protandry is thus interpreted as an adaptation to low female promiscuity, for then securing copulations with virgin females is pivotal to male reproductive success. Such conditions are expected to arise when species face seasonal time constraints, thus requiring brief, synchronized mating seasons (Wiklund and Fagerström 1977; Fagerström and Wiklund 1982; Singer 1982; Parker and Courtney 1983; Wiklund et al. 1991; Nylin et al. 1993). Our comparative results suggest that these conditions are also common in many Hymenoptera and Araneae; these two groups show SSD/SBM patterns similar to those of butterflies (figs. 2, 3). Indeed, there are several documented cases of protandry in Hymenoptera (e.g., Alcock 1997; Kawaguchi and Tanaka 1999; Teder 2005), and in spiders protandry is regularly discussed in relation to their often extreme female-biased SSD (e.g., Legrand and Morse 2000; Maklakov et al. 2004; Uhl et al. 2004). In contrast, conditions favoring protandry apparently do not generally hold for water striders, beetles, and flies (but see Jarosik and Honek 2007). Most water striders have protracted mating seasons and mate multiply (Rowe et al. 1994; Blanckenhorn and Perner 1996). The same is true for many *Drosophila* and *Sepsis*, which are of comparatively small size, develop rapidly, and hence produce many overlapping generations per year, so seasonal time constraints should not be a strong selective factor (cf. Blanckenhorn and Demont 2004).

In the absence of selection for protandry, one might expect males and females to reach adulthood at roughly the same time. This indeed occurs in beetles, water striders, and flies, although in flies the smaller males take a bit longer. Because females are generally larger, this means that they must grow faster, so SSD is proximately mediated to a large extent by growth differences between the sexes. This is true even in the groups exhibiting protandry because SBM is generally not quite proportional to SSD (fig. 2). Interestingly, in the few species with male-biased SSD, it seems that males can grow at least as fast as if not faster than females (fig. 3), a pattern that was also detected in

Signorelli's (2002) larger sample including other insect taxa. Unfortunately, there are few known cases of male-biased SSD in arthropods, so more data are needed to confirm this pattern. In any case, faster growth of females, or of the larger sex, does generally not occur in birds (Teather and Weatherhead 1994; Badyaev et al. 2001a, 2001b), reptiles (Shine 1994), or mammals (Leigh 1992; figs. 2, 3), so this seems to be peculiar to arthropods (or invertebrates).

So why can females afford to grow faster than males in most arthropods but not in mammals or birds? Or, conversely, why do males most often grow more slowly or for a longer time? Three hypotheses derived from life-history theory come to mind, which we cannot select among here. First, if the relationship between adult size and fitness is steeper for females than it is for males, there is stronger selection favoring large size in females than in males. Assuming similar risks associated with rapid growth in both sexes (and everything else being equal), females should therefore tolerate more risks by growing faster because they stand to gain more benefits. In arthropods, fecundity selection favoring large female size is indeed often strong (Honek 1993), while sexual selection favoring large male size may be weaker, a pattern that is typically reversed in birds and mammals (Andersson 1994). Second, in holometabolous insects, as in all organisms with complex life cycles, the decision to molt to adulthood entails consideration of the relative risks of surviving the two life stages in different environments. Males may benefit from remaining larvae longer if this increases their probability of survival to reproductive age, while females, if, for instance, they have to feed as adults to mature their eggs, may benefit from reaching adulthood earlier than males.

A third hypothesis derives from sexual selection theory, which posits that it is generally cheaper to produce sperm than eggs (Darwin 1871; Andersson 1994; Simmons 2001). However, it may be costlier to produce male gonads and genitalia than it is to produce female gonads and genitalia. In arthropods, development of the reproductive organs takes place primarily during the preadult (larval and/or pupal) stage, and at least in holometabolous insects, male gonads and genitals start developing and competing for resources with the soma before those of females, implying that they take longer to mature (Kerkis 1931; Reed and Beckage 1997; Dixon 2000). This can reduce the growth potential of males and may explain why males take longer to develop and/or grow more slowly (Dixon 2000, p. 51). Indeed, variation in sperm length, which can be critical to male competitive fertilization success (Parker 1970; Simmons 2001; Miller and Pitnick 2002; Snook 2005), explains much of the variation in posteclosion male maturation time among 42 *Drosophila* species (Pitnick and Markow 1994; Pitnick et al. 1995; Pitnick 1996) and thus

may also explain why development time is most strongly male biased in drosophilids (fig. 2).

In conclusion, our study shows that Rensch's rule accurately describes the macroevolutionary pattern of SSD in some arthropod lineages but not others. Our results also show only a weak positive relationship between SSD and SBM, congruence between SSD and SBM being strongest in groups for which faster male development (i.e., protandry) is of selective advantage (Lepidoptera, Hymenoptera, and Araneae, as well as mammals and birds). In the other insect groups investigated, male development time was equal to or longer than that of females. Because males are on average smaller than females in all taxa, this implies faster growth of females in the great majority of arthropod species investigated and suggests that growth rate differences between the sexes are more important than development time differences in proximately mediating SSD. This is the crucial finding that requires an explanation because it is not generally the case in vertebrates (Shine 1994; Teather and Weatherhead 1994; Leigh and Shea 1995). We discuss two potential explanations based on traditional life-history trade-offs, plus one related to sexual selection (cf. Kerkis 1931; Pitnick 1993; Dixon 2000). Unless there is strong selection favoring protandry, it seems there are few net costs associated with delayed male development, perhaps also because in insects that need to feed as adults to reproduce, males can generally reach sexual maturity sooner than females (because sperm are produced more easily than eggs) and can therefore at least partially compensate for their longer preadult development. Nevertheless, in species with larger males, the life-history costs of delayed development (or the alternative, faster growth) may eventually become prohibitive, as argued for mammals by Leigh and Shea (1995). To test this idea and investigate the generality of greater male costs of gonad development, future studies should focus on those rare arthropod species with larger males. Although we have covered a wide range of arthropod taxa here, other groups need to be investigated in this context to strengthen the generality of our conclusions.

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