

1 **Equal temperature-size responses of the sexes are widespread in arthropod**  
2 **species**

3  
4 Andrew. G. Hirst<sup>a,b\*</sup>, Curtis R. Horne<sup>a</sup> and David Atkinson<sup>c</sup>

5  
6 \*Corresponding author: [a.g.hirst@qmul.ac.uk](mailto:a.g.hirst@qmul.ac.uk)

7  
8 <sup>a</sup>School of Biological and Chemical Sciences, Queen Mary University of London, London, E1  
9 4NS, United Kingdom.

10 <sup>b</sup>Centre for Ocean Life, National Institute for Aquatic Resources, Technical University of  
11 Denmark, Kavalergården 6, 2920, Charlottenlund, Denmark

12 <sup>c</sup>Institute of Integrative Biology, University of Liverpool, Liverpool, L69 7ZB, United Kingdom.

13

14 **Running title:** Temperature-size responses of the sexes

15 **Key words:** body size, sex, temperature, phenotypic plasticity, dimorphism

16 **Abstract:** 200 | **Main Text:** 5168 | **References:** 43 | **Figures:** 4 | **Tables:** 1

17 **Total Word Count (including abstract, references and figure legends):** 6903

18

19 **Author's Contributions**

20 AGH, CH and DA designed the study, wrote the paper and defined the statistical  
21 approaches. CH collected the data and performed the statistical analyses.

22 **Abstract**

23 Sexual size dimorphism (SSD) is often affected by environmental conditions, but the effect of  
24 temperature on SSD in ectotherms still requires rigorous investigation. We compared the  
25 plastic responses of size-at-maturity to temperature between males and females within 85  
26 diverse arthropod species, in which individuals of both sexes were reared through ontogeny  
27 under identical conditions with excess food. We find that the sexes show similar relative  
28 (proportional) temperature-body size (T-S) responses on average. The high degree of  
29 similarity occurs despite an analysis which includes a wide range in animal body sizes,  
30 variation in degree of SSD, and differences in the sign of the T-S response. We find no  
31 support for Rensch's rule, which predicts greater variation in male size, or indeed the  
32 reverse, greater female size variation. SSD shows no systematic temperature dependence  
33 in any of the 17 arthropod orders examined, 5 of which (Diptera, Orthoptera, Lepidoptera,  
34 Coleoptera and Calanoida) include  $\geq 6$  thermal responses. We suggest that the same  
35 proportional T-S response may generally have equivalent fitness costs and benefits in both  
36 sexes. This contrasts with effects of juvenile density, and food quantity/quality, which  
37 commonly result in greater size plasticity in females, suggesting these variables have  
38 different adaptive effects on SSD.

39

40 **Introduction**

41 Difference in body size between males and females within a species is termed sexual size  
42 dimorphism (SSD), and is widely observed throughout the plant and animal kingdoms [1].  
43 Male-biased SSD, where males are the larger sex, is common among endothermic  
44 vertebrates, and may in part relate to males competing for mates [2,3]. By contrast, female-  
45 biased SSD tends to predominate in ectothermic invertebrates and vertebrates [4,5]. The  
46 dimorphic niche hypothesis (reproductive role hypothesis) states that the differential  
47 reproductive roles of the sexes are associated with differential energetic costs [6] leading to  
48 different size optima [7,8], hence SSD. In most invertebrate species, there is considered to  
49 be selection for larger females, because this favours larger clutch size and / or offspring size.  
50 Males may benefit indirectly from a smaller body size associated with earlier adult  
51 emergence (protandry) because this may increase their chance to reach maturity (important  
52 when they rove for females and suffer high mortality risk), while in populations with discrete  
53 generations this may increase the potential of males to be ready to fertilize females that  
54 reach sexual maturity later [9-11].

55

56 Although SSD has at times been assumed to be rather invariant within a species, studies  
57 have found this to change as a consequence of significantly greater variation in size of  
58 males [12] or females [13]. A variety of rules and theories have been formulated to explain  
59 variation in SSD, both between and within species [14-16]. Rensch's rule (RR) states that  
60 male body size varies more than female body size, irrespective of which sex is larger. RR  
61 was originally formulated to describe the pattern seen across species within a related clade,  
62 but has since been tested within species to see if similar drivers exist at the intra-specific  
63 level [13,17]. Within a species it predicts an increase in SSD with increasing body size in  
64 species where males are the larger sex, and a decrease in SSD with body size in species  
65 where females are larger [14,16]. One prominent general hypothesis (i.e. evolutionary  
66 mechanism) potentially generating RR is when, over evolutionary time, directional (primarily

67 sexual) selection for large male size is overall stronger than directional (primarily fecundity)  
68 selection for large female size [4]. Additionally, the fitness consequences of large versus  
69 small body size can differ between the sexes under different ecological and environmental  
70 conditions because the sexes differ in the degree of plasticity they exhibit in response to  
71 climatic or ecological variables [17-19].

72

73 Variation in size at maturity has been widely documented for ectothermic species  
74 experiencing different thermal regimes during ontogeny [20-23]. This intra-specific  
75 phenotypically plastic response commonly leads to a reduction in size-at-stage with  
76 warming, and has been called the Temperature-Size Rule (TSR) [20]. Given the ubiquity of  
77 the TSR in taxonomic groups as diverse as bacteria, protists and metazoans [22,24,25], the  
78 proximate and ultimate causes have been explored in some detail [22,25-29]. The  
79 temperature-size (T-S) response has been shown to vary in magnitude in relation to species  
80 body size, voltinism, and taxonomic group, and between aquatic and terrestrial-living species  
81 [22,23]. Variation in SSD can result when males and females respond differently to their  
82 environment (differential-plasticity hypothesis [18]), and this may be an important contributor  
83 to the observed variation in SSD. Thus the degree to which different environmental factors  
84 such as juvenile density, food quality or quantity, and temperature elicit contrasting plastic  
85 body size responses between the sexes should be informative [12,19]. Here we specifically  
86 focus on sex-dependent differences in temperature-size (T-S) responses, as this may  
87 ultimately help to elucidate the underlying drivers of both SSD and T-S responses. Sex-  
88 based differences in T-S responses have been considered before; while most studies have  
89 been experimental and have considered single species, the syntheses and analyses of  
90 responses by Teder & Tammaru (2005) [13] and Stillwell *et al.* (2010) [19] on insects, have  
91 looked more broadly at differential changes in SSD with environmental conditions. We  
92 increase the amount of temperature response data considered by almost 4-fold in our  
93 analysis, and increase the range of species to include other Arthropoda. This allows greater  
94 power when testing variation in SSD with temperature. Furthermore, we explore variation in

95 *absolute* sexual size differences across temperatures, and for the first time the degree to  
96 which SSD relates to the magnitude of the T-S response.

97

98 Most analyses of variation in body size responses (and comparisons between the sexes)  
99 have expressed this change in relative terms, for example, using regressions to derive the  
100 slope of log size of one sex versus the other, or comparing SSD as a proportion (see the  
101 varied approaches in Stillwell & Fox [12]; Teder & Tammaru [13]; and Stillwell *et al.* [19]).  
102 The use of relative size responses allows for the removal of bias caused by the differences  
103 in body size of the sexes, and reduces statistical problems. Yet changes in absolute size  
104 differences between the sexes may hold important information relating to mate assessment  
105 and performance [30-32]. Consequently, although we focus our efforts mainly on exploring  
106 the thermal dependence of SSD within species using relative metrics, we also consider the  
107 implications of absolute differences in size between the sexes, and how this changes with  
108 temperature. We seek to test a range of interrelated questions using data from a diverse set  
109 of species from within the Arthropoda, specifically:

- 110 i. Do the T-S responses differ systematically between the sexes intra-specifically, and  
111 is there any evidence to support Rensch's rule?
- 112 ii. Do differences in the T-S responses of the sexes relate to the magnitude of sexual  
113 size dimorphism?
- 114 iii. How does the absolute difference in body mass between the sexes vary with  
115 temperature, and how does this differ from the relative responses?
- 116 iv. How does the effect of temperature on SSD compare with that of other environmental  
117 influences: food quantity and quality, pathogen infection, photoperiod and larval  
118 crowding and competition, as quantified by Stillwell *et al.* (2010) [19]?

119

## 120 **Methods**

121 The data compilation of Horne *et al.* [23] was revisited; this provides a single extensive set of  
122 data on the size-at-maturity responses to temperature of a wide range of arthropod species,

123 including marine, freshwater and terrestrial forms. Briefly, studies were systematically  
124 screened to include only laboratory studies where individuals were reared at a range of  
125 constant temperatures, with food concentrations at or above saturation, in order to remove  
126 the confounding impact of food limitation. Extreme, potentially stressful temperatures were  
127 excluded. Only adult size measurements were used for analysis from studies where males  
128 and females had been separated. In a small minority of cases pupal size was considered to  
129 be a reliable correlate of size at maturity. We were careful to ensure that we only included  
130 measurements when data for both sexes had been provided and the same controlled  
131 experimental conditions were used for each sex. The minimum period of acclimation for the  
132 inclusion of adult size data was set so that only individuals that were raised from egg or first  
133 larval stage were included. Adult data were collected as a variety of metrics including  
134 lengths, volumes, and dry, wet or carbon mass. These measurements were subsequently  
135 converted to dry mass (mg) using intra-specific regressions. Where these were not available,  
136 regressions for closely related species, and occasionally more general inter-specific  
137 regressions, were used. All data and conversions are detailed in our Table S1.

138

139 The sex-specific slopes of  $\log_e$  dry mass vs. temperature were used to examine thermal  
140 responses in body size for single species. This exponential form has the advantage of being  
141 a better fit than alternate transformations, as judged by Akaike weights (see Table S2 in  
142 Supplementary Information). Moreover, it has the distinct advantage of allowing examination  
143 of relative change and is largely unbiased by absolute body size. We transformed the slopes  
144 into percentage change in dry mass per  $^{\circ}\text{C}$ , using the formula,  $(\exp^{(\text{slope})} - 1) * 100 = \% \text{ change}$   
145 in mass per  $^{\circ}\text{C}$  [22]. A negative percentage indicates a decrease in size with increasing  
146 temperature (following the TSR) and a positive percentage an increase in size (converse-  
147 TSR).

148

149 Differences in body size variation can be assessed in different ways. Blanckenhorn *et al.* [17]  
150 compared latitudinal clines in body size between the sexes and obtained different results

151 depending on whether they examined clines in size ratios between the sexes (ratio-clines),  
152 or used an allometric approach plotting log body size of one sex versus that of the other.  
153 We therefore compared results derived using ratio-clines and allometric methods. Firstly, we  
154 determined the degree of difference between T-S responses of the con-specific males and  
155 females (within single studies) as:

156

$$157 \quad T-S \text{ Ratio} = (\text{larger T-S response} / \text{smaller T-S response}) - 1 \quad (1)$$

158

159 We defined the ratio as being positive when males had the greater T-S response, and  
160 negative when females had the greater response. This formulation has an advantage of  
161 providing symmetrical results around zero, regardless of which sex has the greater T-S  
162 response.

163

164 Secondly, we utilized the commonly applied method of performing an RMA regression of the  
165  $\log_{10}$  body size of one sex against the  $\log_{10}$  of the other sex, where each individual data point  
166 represents the paired size measurements at one of the experimental temperatures. This  
167 allometric slope gives a quantitative expression of how the sizes of the sexes change  
168 together. In this regression, the more size-responsive sex was represented on the y-axis and  
169 the less size-responsive on the x-axis, so the slope was always  $\geq 1$ . We subtracted 1 from  
170 the slope and again defined the value as being positive when male size was the more  
171 responsive, and negative when female size was the more responsive. This method once  
172 again ensures that results vary around zero, and there is symmetry based on equivalent  
173 differences between the sexes, regardless of which sex shows the greater response. We  
174 term this slope value the  $RMA_{Index}$ ; zero indicates isometry, i.e. equal covariation in male and  
175 female size, while increasingly positive values indicate greater male size responses  
176 (variation), and increasingly large negative values signify greater female size responses.

177

178 We quantified the absolute degree of SSD using the Sexual Dimorphic Index (*SDI*) of Lovich  
179 & Gibbons [33], where:

180

$$181 \quad SDI = (\text{mass of larger sex} / \text{mass of smaller sex}) - 1 \quad (2)$$

182

183 We followed the recent convention that the *SDI* index is given as a positive value when  
184 males are the larger sex, and as a negative value when females are larger. Mean mass  
185 values for each sex were predicted at 20°C from the T-S regressions, which in most cases  
186 did not involve any extrapolation.

187

188 In order to compare estimates of sex differences in size responses to temperature derived  
189 using the two methods, we plotted each *T-S Ratio* value against its appropriate *RMA<sub>Index</sub>*  
190 value across all 116 T-S responses and performed a Reduced Major Axis (RMA) regression  
191 (Figure 1). Additionally, we performed a paired Wilcoxon Signed-Rank test to compare *T-S*  
192 *Ratio* and *RMA<sub>Index</sub>* values. To determine whether the proportion of male and female-biased  
193 *T-S Ratio* and *RMA<sub>Index</sub>* values differed significantly from 0.5, we used a chi-squared  
194 proportionality test.

195

196 The independent effect of taxonomic order, environment type (terrestrial, freshwater, marine)  
197 and life cycle type (i.e. hemi- vs. holometaboly) on the size and sign of the *T-S Ratio* and  
198 *RMA<sub>Index</sub>* was determined using analysis of variance. Crustaceans were considered  
199 hemimetabolous, as these have direct development from larvae to juveniles to adults. *Post-*  
200 *hoc* comparisons (TukeyHSD) were used to identify any significant differences in both the *T-*  
201 *S Ratio* and *RMA<sub>Index</sub>* between taxonomic orders. Ordinary least squares (OLS) regression  
202 analysis was used to determine whether the *T-S Ratio* changes significantly with the  
203 absolute degree of sexual size dimorphism (indexed by *SDI*). All statistical analyses, with the  
204 exception of RMA analyses, were conducted using the free statistical software package *R*



205 [34]. All RMA analyses were performed using the free statistical program *RMA for JAVA*  
206 *v.1.21* [35].

207

208 To quantitatively assess the degree to which absolute sizes of males and females converge  
209 or diverge at increasing temperatures, we determined sex-specific slopes of the linear  
210 regressions of dry mass (mg) on temperature for each sex (as an estimate from what may  
211 be a somewhat curved relationship). The difference between these slopes gives the degree  
212 to which the two converge or diverge with increasing temperature; this difference was  
213 expressed as a percentage of the female size (at 20°C), hence the formula is:

214

$$215 \left( \frac{\text{[Slope for larger sex} - \text{slope for smaller sex]}}{\text{mass of the female at } 20^{\circ}\text{C}} \right) * 100 \quad (3)$$

216

217 A negative value represents convergence, and a positive value divergence with increasing  
218 temperature. Normalizing to female mass at 20°C adjusts for any considerable differences in  
219 absolute size between different taxa and the sexes. Again, we used analysis of variance to  
220 determine the effect of the absolute degree of SSD (indexed by *SDI*) and taxonomic order on  
221 change in absolute size difference with temperature, and a *post-hoc* Tukey HSD test to look  
222 for significant differences between individual taxonomic orders. In addition, a series of one-  
223 sample *t*-tests were used to identify which orders, if any, had a mean change in absolute  
224 size difference between sexes with temperature that differed significantly from zero.

225

## 226 **Results**

227 Our meta-analysis includes 116 paired male and female T-S responses [% change in dry  
228 mass (DM) °C<sup>-1</sup>] from 85 arthropod species, including representatives from 17 taxonomic  
229 orders from marine, freshwater and terrestrial environments. These responses have a  
230 negative slope in ~84% of cases, and only in 2 instances was the sign of the T-S response  
231 different between males and females within a species. There is wide variation in the strength  
232 and direction of the T-S response, ranging from -8.15%°C<sup>-1</sup> to 5.67%°C<sup>-1</sup> in females. This

233 variation across species can be largely accounted for by strong differences in responses  
234 between water-living versus air-breathing species [22,23], and, in terrestrial arthropods,  
235 between univoltine and multivoltine species [23].

236

237 In comparing the two methods used to assess which sex has the stronger size response to  
238 warming (*T-S Ratio* vs.  $RMA_{Index}$ ) (Figure 1), we typically find a close agreement between  
239 them. The  $RMA_{Index}$  suggests male body size is more responsive to temperature in 61 of 116  
240 cases, which compares with 64 cases calculated using the *T-S Ratio*. Only in 11 instances  
241 did the two disagree on which sex had the greater size response to temperature. Regressing  
242 the two metrics against one another (using RMA) (Figure 1), and excluding the two extreme  
243 values indicated in brackets, gives a slope of 1.25 (1.13 to 1.38, 95% CI range) and an  
244 intercept of 0.06 (-0.03 to 0.15, 95% CI range). This slope is significantly different from 1,  
245 while the intercept is not significantly different from zero, as inferred from the 95%  
246 confidence intervals (Figure 1). Including the two extreme values also results in a slope  
247 significantly greater than 1 (slope =2.71, 2.25 to 3.16, 95% CI range). Comparing the *T-S*  
248 *Ratio* and  $RMA_{Index}$  values using a paired Wilcoxon Signed-Rank test also reveals a  
249 significant difference between the two ( $V=3295$ ,  $p=0.01$ ). We conclude that although the two  
250 metrics produce on average very similar values, the *T-S Ratio* tends to give somewhat more  
251 extreme values than does the  $RMA_{Index}$ . Because of the very close similarity in the results  
252 between these methods, we only present the *T-S Ratio* data henceforth. However, all  
253 analyses have also been undertaken using the  $RMA_{Index}$  and are summarised in the  
254 Supplementary Information: these further support the conclusions we present here.

255

256 We observe similar body size plasticity to temperature in both the males and females of a  
257 species on average. We find a significant correlation between female and male *T-S*  
258 responses across species ( $p<0.001$ ,  $R^2=0.81$ ), with an RMA regression slope of 1.09 (1.00-  
259 1.18, 95% CI range), and with an intercept of 0.38 (0.13-0.63, 95% CI range) (Figure 2). We  
260 find that male size responds to temperature more strongly than size of con-specific females

261 in 64 of 116 cases, as assessed using the *T-S Ratio*. Hence, the null hypothesis that a  
262 stronger size response is observed equally often in each sex cannot be rejected (chi-  
263 squared proportionality test;  $\chi^2=1.24$ ,  $p=0.27$ ). This finding is further supported when size  
264 response is measured using the  $RMA_{Index}$  ( $\chi^2=0.22$ ,  $p=0.64$ ), in which male size responds  
265 more strongly than conspecific female size to temperature in 61 of 116 cases.

266

267 Our analysis highlights a close similarity in the T-S responses of both sexes within the  
268 Arthropoda, and also within orders of Arthropoda (Figure 3), although some orders have  
269 much fewer data than others in our study. Although within single taxonomic orders there is  
270 variation in the *T-S Ratio* between species, analysis of variance and *post-hoc* comparisons  
271 (Tukey HSD) show taxonomic order to have no significant effect on the size or sign of the *T-*  
272 *S Ratio* ( $F_{17,98}=0.77$ ,  $p=0.72$ ), and there appears to be no systematic patterns, such that in all  
273 orders for which we have sufficient data to make the test, the mean value does not differ  
274 significantly from zero (Figure 3). Similarly, we find no effect of environment type (marine,  
275 freshwater, terrestrial) on the thermal dependence of SSD ( $F_{2,113}=2.41$ ,  $p=0.09$ ), even though  
276 we know overall size and sign of T-S responses shown by animals relates strongly to these  
277 different environmental categories [22]. The effect of life cycle (hemi- vs. holometaboly) was  
278 also non-significant, both when testing across the entire dataset ( $F_{1,114}=0.16$ ,  $p=0.69$ ) and  
279 exclusively within insects ( $F_{1,92}=0.47$ ,  $p=0.49$ ). Although the *T-S Ratio* values for Orthoptera  
280 do not differ significantly from zero, in all 6 species considered female size responded  
281 (increased) most to warmer rearing temperatures (Figure 3).

282

283 The *T-S Ratio* does not change significantly with the degree of SSD (as indexed by *SDI*),  
284 inferred from the non-significant OLS regression between the two ( $F_{1,114}=0.28$ ,  $p=0.60$ ).  
285 Thus, across environments, orders, and for varying degrees of *SDI*, we find no evidence to  
286 suggest greater thermally induced variance in male size (i.e. no evidence to support an intra-  
287 specific version of Rensch's rule) or indeed the opposite, greater variance in female size.

288 Neither sex exhibited significantly greater relative body size response to temperature than  
289 the other on average.

290

291 Warmer rearing conditions cause male and female absolute sizes to converge in 62 cases,  
292 and diverge in 54 cases. We find a significant positive relationship between the extent of  
293 convergence/divergence in body size with warming and the strength of the female T-S  
294 response, such that species which exhibit a strong negative T-S response also show the  
295 greatest convergence in absolute body size with warming, whilst those that exhibit a strong  
296 positive T-S response show the greatest divergence in absolute body size with warming  
297 ( $F_{1,113}=98.2$ ,  $p<0.001$ ,  $r^2=0.46$ ). The corresponding regression lies predominantly within the  
298 range of values predicted given the range in *SDI* observed across our dataset, and based on  
299 an assumption that both males and females have identical proportional T-S responses (see  
300 Figures S2a and S2b in our Supplementary Information for a conceptual and quantitative  
301 examination of this). This leads us to the simple explanation that this strongly significant  
302 relationship is an outcome of similar T-S responses between males and females, which  
303 leads to greater absolute degree of size convergence and divergence the greater the relative  
304 response; an outcome expected simply from mathematics, but one with possible ecological  
305 implications. Taxonomic order has no significant effect on convergence or divergence  
306 ( $F_{16,99}=1.51$ ,  $p=0.11$ ), and the mean degree of size convergence or divergence does not  
307 differ significantly from zero, with the exception of three orders: Cyclopoida ( $-1.94\% \text{ } ^\circ\text{C}^{-1}$   
308  $\pm 1.28\text{CI}$ ;  $t_4=-4.20$ ,  $p=0.01$ ), Diptera ( $-0.24\% \text{ } ^\circ\text{C}^{-1} \pm 0.19\text{CI}$ ;  $t_{37}=-2.58$ ,  $p=0.01$ ) and Orthoptera  
309 ( $4.61\% \text{ } ^\circ\text{C}^{-1} \pm 2.47\text{CI}$ ;  $t_5=4.79$ ,  $p<0.01$ ) (Figure 4). Hence there is strong divergence in the  
310 absolute size of the sexes with warming in Orthoptera, but convergence in the Cyclopoida  
311 and Diptera.

312

### 313 **Discussion**

314 In our examination of the T-S responses of a wide range of arthropod species we find that  
315 male size responds to temperature more strongly than size of con-specific females in 64 of

316 116 cases, as assessed using the *T-S Ratio* (Figure 2). We cannot statistically reject the null  
317 hypothesis that a stronger size response is observed equally often in each sex. Indeed, this  
318 finding is also supported when size response is measured using the  $RMA_{Index}$ . Furthermore,  
319 our analysis highlights a close similarity in the T-S responses of both sexes within orders of  
320 Arthropoda (Figure 3). However, we must highlight that our conclusions are phylogenetically  
321 limited, in that only 5 orders (Diptera, Orthoptera, Lepidoptera, Coleoptera and Calanoida)  
322 included 6 or more data sets, while most orders (11 of 17) were represented by just 3 or  
323 fewer. Moreover, orders for which there are more data are still taxonomically restricted. For  
324 example, the majority of dipteran species are from just two families (Drosophilidae and  
325 Culicidae), while >50% of lepidopteran species are from two families (Lycaenidae and  
326 Nymphalidae), though these two butterfly families have the greatest number of species  
327 worldwide.

328

329 Although there is a considerable range of T-S responses, from a large increase in size with  
330 warming (especially large bodied univoltine terrestrial species), to marked reductions in size  
331 with warming (in many large-bodied aquatic species) (see Horne *et al.* [23]), we find no  
332 systematic sex-based differences in response size within arthropods. This outcome occurs  
333 despite the often radically different behaviour, physiology, life-history and body size between  
334 the sexes [36-38]. Furthermore, the average lack of sex differences in the T-S response also  
335 appear to be unaffected by the large variation in the degree of SSD, or taxonomic order.  
336 Finally, the *T-S Ratio* does not significantly correlate with the absolute degree of SSD  
337 (indexed by *SDI*), which contrasts with the findings of Teder & Tammaru [13], in which  
338 females typically showed stronger phenotypic plasticity responses with varying  
339 environmental quality when SSD was more female-biased.

340

341 Blanckenhorn *et al.* [17], in an analysis which included both vertebrates and invertebrates,  
342 examined latitudinal clines in male and female body size, and found somewhat contradictory  
343 outcomes depending upon the form of analysis used. Similar to the approach employed

344 here, they calculated both an RMA regression of the size of one sex against the other, as  
345 well as comparing the ratio of latitudinal size clines of each sex (termed slope ratio). Male  
346 size was found to vary more than female size in 66 of 98 species when examining data sets  
347 based on latitudinal-size gradients. Thus, intra-specifically the results conformed to greater  
348 male size variation (RR), suggesting a connection between Bergmann's and Rensch's rules.  
349 However, when using a conventional RMA regression, Blanckenhorn *et al.* [17] found that  
350 the size of neither sex was significantly more variable than the other (male size was found to  
351 vary more than female size in 55 of 98 species). Notably, in both their study and our own,  
352 regressing the *T-S Ratio* (or slope ratio) against the  $RMA_{Index}$  generates a slope significantly  
353 greater than 1, suggesting that the former produces the more extreme values of the two  
354 metrics. This statistical effect has not manifested itself to the same extent in our own study.  
355 We note that because the T-S response of the less variable sex can be zero (i.e. the  
356 denominator in the T-S ratio equation), the T-S Ratio can be infinite. A very low denominator  
357 value compared with the numerator will also generate very large ratios, so generating large  
358 variability, hence the apparent contradiction that can occur between the two methods.  
359 Though the different results generated by these two metrics do not alter the major outcomes  
360 and conclusions presented here, they did lead Blanckenhorn *et al.* [17] to present  
361 contrasting findings between methodologies. Unlike Blanckenhorn *et al.* [17] we find no  
362 significant differences in the body size responses of males or females, regardless of whether  
363 we use the  $RMA_{Index}$  or *T-S Ratio*. We note that whilst T-S responses are measured in  
364 controlled laboratory conditions using individuals from the same population, a great variety of  
365 influences can potentially select for changes in SSD across latitudes, which may not  
366 necessarily be linked directly with temperature. These factors may include, but are not  
367 limited to, the increased likelihood of genetic variation between populations, as well as size-  
368 dependent mortality and environmental factors such as food and season length.

369

370 The contrasting proximate mechanisms by which T-S responses are generated in organisms  
371 [39], and the extent to which the magnitude and direction of these responses correlate with

372 life history (voltinism) [23], with a possible trade-off between numbers of generations in a  
373 year and size at maturity, leads to the suggestion that these responses relate to fitness and  
374 hence are adaptive. Further, as the thermal dependence of size at maturity is so similar (in  
375 relative terms) between the sexes in individual species, then the responses may have similar  
376 fitness costs and benefits in both males and females. While it is conceivable that a very high  
377 genetic correlation between the sexes of a species may help explain the similar size  
378 response of males and females to temperature [40], this potential constraint seems to be  
379 overridden in cases of other environmental factors (e.g. changed diet or juvenile density) that  
380 generate systematic differences in size responses between males and females [19] (see  
381 Table 1).

382

383 The contrast between lack of effect of temperature on SSD observed here and the  
384 systematic effect of food quantity and also larval competition on SSD in insects [13,19],  
385 implies that there is generally a sex-dependent effect on body size caused by food resources  
386 but not by temperature (see Table 1 for a quantitative comparison of the degree of plastic  
387 variation in the sexes with changes in different environmental conditions). A useful distinction  
388 is whether food supply or quality, or increased competition, acts primarily on reducing the  
389 size of the larger sex, which is consistent with energetic restrictions acting to a greater  
390 degree on larger bodies, or whether it acts primarily on just females, even in species in  
391 which males are the larger sex (e.g. some odonates). Female size was usually affected most  
392 by food supply, but in the few species with larger males than females, no consistent sex-  
393 dependent size response was observed [13]. Thus, the relative contribution of sex versus  
394 body size to the degree of size plasticity was not clearly distinguished.

395

396 The metrics used to study the allometric scaling of SSD commonly examine relative  
397 (proportional) change in body size (e.g. Blanckenhorn *et al.* [17]). Here, we also used two  
398 methods that examine change in relative body size within species, and which account for  
399 differences in size between species. In both cases we obtained the same major conclusions.

400 In contrast to these quantitative analyses of relative size change, analyses of absolute size  
401 differences between sexes of conspecifics, and how these respond to environmental factors,  
402 has received much less attention. Yet measuring the extent to which increased rearing  
403 temperature causes absolute body sizes to converge or diverge between the sexes may be  
404 biologically informative. For example, females are very commonly the larger sex in  
405 arthropods [19,41]: yet if both sexes show similar negative T-S responses (using the metrics  
406 described herein), then their absolute body sizes will converge with increasing temperature.

407

408 We observe considerable variation in both convergence and divergence in absolute mass  
409 across species that exhibit both a normal and converse TSR (represented conceptually and  
410 quantitatively in supplementary Figures S2a and S2b respectively). Within the Orthoptera,  
411 absolute body sizes of the sexes significantly diverge with warming (Figure 4). This  
412 divergence arises partly from the fact that Orthopterans generally follow the converse TSR  
413 [23] and have larger females than males, so that a similar T-S response of males and  
414 females will cause divergence in absolute size between the sexes with warming (a similar  
415 proportional size increase in the larger sex makes the absolute difference greater). But in  
416 addition, although the mean *T-S Ratio* value for this order is not significantly different from  
417 zero (Figure 3), in all 6 orthopteran species the females have a stronger *T-S ratio* than  
418 conspecific males (Figure 3). The relatively strong variation in female body size with  
419 temperature observed in Orthoptera exerts an important influence on the mean *T-S Ratio*  
420 and  $RMA_{Index}$  of species that follow the converse TSR. Specifically, when comparing the  
421 thermal dependence of SSD between species that follow either the normal or converse TSR,  
422 we observe that females are the more variant sex in species that increase their size with  
423 warming, whilst there is no significant difference between the sexes in those that exhibit a  
424 normal T-S response. We report these observations with caution; Orthoptera account for  
425 nearly a third of positive T-S responses in our dataset, for which the sample size is already  
426 comparatively small (n=19 for positive T-S responses vs. n=97 for negative T-S responses).  
427 Indeed, we find no significant difference in body size sensitivity between the sexes in either



428 group when Orthoptera are excluded. Orthoptera have strongly positive T-S responses and  
429 strongly negative latitude-size clines, with larger species often being univoltine, and hence  
430 potentially affected by season-length constraints on size-at-maturity [23], especially in the  
431 larger sex, which typically reaches adulthood later [42,43]. If such constraints are indeed  
432 greater in the larger sex (more season-length constrained sex), warming may favour  
433 increased body size especially in females, hence the strong divergence in orthopteran  
434 absolute body sizes between the sexes at increased rearing temperatures. When there is  
435 more data available, an analysis of whether these sex-based patterns in thermal body size  
436 sensitivity extend more generally to other large univoltine species would be particularly  
437 informative.

438

439 A potential selection pressure is to reduce extreme size-divergence if it can lead to  
440 incompatibility between the sexes. Could such selection lead to very similar absolute  
441 changes in size between the sexes? In a species of Jerusalem cricket (Orthoptera:  
442 Stenopelmatinae: *Stenopelmatus*) copulatory-size incompatibility was observed even when  
443 the male was as little as 2mm longer than their conspecific female, resulting in misalignment  
444 that prolonged or completely impeded copulation [31]. The absolute difference in mass or  
445 specific body lengths between the sexes can impact many size-dependent mating and  
446 reproduction events, including courtship, mate choice, copulation, mating behaviours, and  
447 success of offspring when parental care is shared. The fact that many studies on size  
448 dimorphism focus on a single linear dimension of body size or total mass may be  
449 problematic to interpretation if critically important body dimensions do not change  
450 isomorphically to one another [18].

451

452 In conclusion, while previous comparisons of plastic body size responses of the sexes in  
453 relation to larval density and food quality in insects find greater relative variation in female  
454 size, especially when females are the larger sex [13,19], we find that plastic temperature-  
455 size responses under excess food shows no consistent inter-sex differences in size

456 response on average when examined across a wide range of arthropod orders. Indeed, our  
457 more comprehensive analysis for this variable concurs with the lack of consistent  
458 temperature effect on SSD detected by Stillwell *et al.* [19]. Consequently, we propose that in  
459 arthropods, temperature, unlike food supply, does not consistently affect optimal body size of  
460 one sex more than the other.

461

## 462 **Acknowledgments**

463 We are indebted to Wolf Blanckenhorn, Tiit Teder and an anonymous reviewer, whose  
464 comments greatly improved this work. We thank the great many authors who donated their  
465 data or clarified aspects of their studies. Axel Rossberg kindly provided statistical advice.  
466 AGH is supported by the Natural Environment Research Council and Department for  
467 Environment, Food and Rural Affairs (grant no. NE/L003279/1, Marine Ecosystems  
468 Research Programme). CH is supported by a Natural Environment Research Council  
469 Studentship NE/L501797/1. The Centre for Ocean Life is a VKR Centre of Excellence  
470 funded by the Villum Foundation.

471

472 **References**

- 473 1. Darwin C. 1874. *The Descent of Man and Selection in Relation to Sex*. New York: AL  
474 Burt.
- 475 2. Owens IPF & Hartley IR. 1998. Sexual dimorphism in birds: why are there so many  
476 different forms of dimorphism? *Proc. R. Soc. Lond. B* **265**, 397-407.  
477 (doi:10.1098/rspb.1998.0308).
- 478 3. Soulsbury CD, Kervinen M & Lebigre C. 2014. Sexual size dimorphism and the  
479 strength of sexual selection in mammals and birds. *Evol. Ecol. Res.* **16**, 63-76.
- 480 4. Fairbairn DJ. 1997. Allometry for sexual size dimorphism: pattern and process in the  
481 coevolution of body size in males and females. *Annu. Rev. Ecol. Syst.* **28**, 659-687.  
482 (doi:10.1146/annurev.ecolsys.28.1.659)
- 483 5. Blanckenhorn WU, Dixon AFG, Fairbairn DJ, Foellmer MW, Gibert P, van der Linde  
484 K, Meier R, Nylin S, Pitnick S, Schoff C *et al.* 2007. Proximate causes of Rensch's  
485 rule: Does sexual size dimorphism in arthropods result from sex differences in  
486 development time? *Am. Nat.* **169**, 245-257. (doi:10.1086/510597)
- 487 6. Savalli UM & Fox CW. 1998. Sexual selection and the fitness consequences of male  
488 body size in the seed beetle *Stator limbatus*. *Anim. Behav.* **55**, 473-483.  
489 (doi:10.1006/anbe.1997.0622)
- 490 7. Slatkin M. 1984. Ecological causes of sexual dimorphism. *Evolution* **38**, 622-630.  
491 (doi:10.2307/2408711)
- 492 8. Hedrick AV & Temeles EJ. 1989. The evolution of sexual dimorphism in animals:  
493 hypotheses and tests. *Trends Ecol. Evol.* **4**, 136-138. (doi:10.1016/0169-  
494 5347(89)90212-7)
- 495 9. Blanckenhorn WU. 2000. The evolution of body size: what keeps organisms small?  
496 *Q. Rev. Biol.* **75**, 385-407. (doi:10.1086/393620)
- 497 10. Vollrath F & Parker GA. 1992. Sexual dimorphism and distorted sex ratios in spiders.  
498 *Nature* **360**, 156-159. (doi:10.1038/360156a0)

- 499 11. Kiørboe T & Hirst AG. 2008. Optimal development time in pelagic copepods. *Mar.*  
500 *Ecol. Prog. Ser.* **367**, 15-22. (doi:10.3354/meps07572)
- 501 12. Stillwell RC & Fox CW. 2007. Environmental effects on sexual size dimorphism of a  
502 seed-feeding beetle. *Oecologia* **153**, 273-280. (doi:10.1007/s00442-007-0724-0)
- 503 13. Teder T & Tammaru T. 2005. Sexual size dimorphism within species increases with  
504 body size in insects. *Oikos* **108**, 321-334. (doi:10.1111/j.0030-1299.2005.13609.x)
- 505 14. Rensch B. 1960. *Evolution above the species level*. New York, NY: Columbia  
506 University Press.
- 507 15. Parker GA. 1992. The evolution of sexual size dimorphism in fish. *J. Fish Biol.* **41**, 1-  
508 20. (doi:10.1111/j.1095-8649.1992.tb03864.x)
- 509 16. Abouheif E & Fairbairn DJ. 1997. A comparative analysis of allometry for sexual size  
510 dimorphism: assessing Rensch's rule. *Am. Nat.* **149**, 540-562. (doi:10.1086/286004)
- 511 17. Blanckenhorn WU, Stillwell RC, Young KA, Fox CW & Ashton KG. 2006. When  
512 Rensch meets Bergmann: does sexual size dimorphism change systematically with  
513 latitude? *Evolution* **60**, 2004-2011. (doi:10.1111/j.0014-3820.2006.tb01838.x)
- 514 18. Fairbairn DJ. 2005. Allometry for sexual size dimorphism: testing two hypotheses for  
515 Rensch's rule in the water strider *Aquarius remigis*. *Am. Nat.* **166**, S69-S84.  
516 (doi:10.1086/444600)
- 517 19. Stillwell RC, Blanckenhorn WU, Teder T, Davidowitz G & Fox CW. 2010. Sex  
518 differences in phenotypic plasticity affect variation in sexual size dimorphism in  
519 insects: from physiology to evolution. *Annu. Rev. Entomol.* **55**, 227-245.  
520 (doi:10.1146/annurev-ento-112408-085500)
- 521 20. Atkinson D. 1994. Temperature and organism size - A biological law for ectotherms.  
522 *Adv. Ecol. Res.* **25**, 1-58. (doi:10.1016/S0065-2504(08)60212-3)
- 523 21. Atkinson D. 1995. Effects of temperature on the size of aquatic ectotherms -  
524 Exceptions to the general rule. *J. Therm. Biol.* **20**, 61-74. (doi: 10.1016/0306-  
525 4565(94)00028-H)

- 526 22. Forster J, Hirst AG & Atkinson D. 2012. Warming-induced reductions in body size are  
527 greater in aquatic than terrestrial species. *PNAS* **109**, 19310-19314.  
528 (doi:10.1073/pnas.1210460109)
- 529 23. Horne CR, Hirst AG & Atkinson D. 2015. Temperature-size responses match  
530 latitudinal-size clines in arthropods, revealing critical differences between aquatic and  
531 terrestrial species. *Ecol. Lett.* **18**, 327-335. (doi:10.1111/ele.12413)
- 532 24. Atkinson, D, Ciotti BJ & Montagnes DJ. 2003. Protists decrease in size linearly with  
533 temperature: ca. 2.5% C<sup>-1</sup>. *Proc. R. Soc. Lond. B* **270**, 2605-2611.  
534 (doi:10.1098/rspb.2003.2538)
- 535 25. Forster J & Hirst AG. 2012. The Temperature-size Rule emerges from ontogenetic  
536 differences between growth and development rates. *Funct. Ecol.* **26**, 483-492.  
537 (doi:10.1111/j.1365-2435.2011.01958.x)
- 538 26. Angilletta MJ, Steury TD & Sears MW. 2004. Temperature, growth rate, and body  
539 size in ectotherms: Fitting pieces of a life history puzzle. *ICB* **44**, 498-509.  
540 (doi:10.1093/icb/44.6.498)
- 541 27. Atkinson D, Morley SA & Hughes RN. 2006. From cells to colonies: at what levels of  
542 body organization does the 'temperature-size rule' apply? *Evol. Dev.* **8**, 202-214.  
543 (doi:10.1111/j.1525-142X.2006.00090.x)
- 544 28. Walters RJ & Hassall M. 2006. The temperature-size rule in ectotherms: May a  
545 general explanation exist after all? *Am. Nat.* **167**, 510-523. (doi:10.1086/501029)
- 546 29. Kingsolver JG & Huey RB. 2008. Size, temperature, and fitness: three rules. *Evol.*  
547 *Ecol. Res.* **10**, 251-268.
- 548 30. Bonduriansky R. 2001. The evolution of male mate choice in insects: a synthesis of  
549 ideas and evidence. *Biol. Rev.* **76**, 305-339. (doi:10.1017/S1464793101005693)
- 550 31. Weissman DB, Judge KA, Williams SC, Whitman DW & Lee VF. 2008. Small-male  
551 mating advantage in a species of Jerusalem cricket (Orthoptera: Stenopelmatinae:  
552 *Stenopelmatus*). *J. Orthoptera Res.* **17**, 321-332. (doi:10.1665/1082-6467-17.2.321)

- 553 32. Cator LJ, Ng'Habi KR, Hoy RR & Harrington LC. 2010. Sizing up a mate: variation in  
554 production and response to acoustic signals in *Anopheles gambiae*. *Behav. Ecol.* **21**,  
555 1033-1039. (doi:10.1093/beheco/arq087)
- 556 33. Lovich JE & Gibbons JW. 1992. A review of techniques for quantifying sexual size  
557 dimorphism. *Growth Dev. Ageing* **56**, 269-281.
- 558 34. R Core Team 2014. *R: A language and environment for statistical computing*.  
559 Vienna, Austria: R Foundation for Statistical Computing.
- 560 35. Bohonak AJ & van der Linde K. 2004. RMA: Software for Reduced Major Axis  
561 regression, Java version. Available from:  
562 <http://www.kimvdlinde.com/professional/rma.html>.
- 563 36. McElligott AG, Gammell MP, Harty HC, Pains DR, Murphy DT, Walsh JT & Hayden  
564 TJ. 2001. Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier  
565 males gain greater mating success? *Behav. Ecol. Sociobiol.* **49**, 266–272.  
566 (doi:10.1007/s002650000293)
- 567 37. Hirst AG, Bonnet D, Conway DVP & Kiørboe T. 2010. Does predation control adult  
568 sex ratios and longevities in marine pelagic copepods? *Limnol. Oceanogr.* **55**, 2193-  
569 2206. (doi:10.4319/lo.2010.55.5.2193)
- 570 38. Fairbairn DJ. 2013. *Odd couples: extraordinary differences between the sexes in the*  
571 *animal kingdom*. Princeton, New Jersey: Princeton University Press
- 572 39. Forster J, Hirst AG & Woodward G. 2011. Growth and development rates have  
573 different thermal responses. *Am. Nat.* **178**, 668-678. (doi:10.1086/662174)
- 574 40. Lande R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic  
575 characters. *Evolution* **34**, 292-305. (doi:10.2307/2407393)
- 576 41. Hirst, AG & Kiørboe T. 2014. Macroevolutionary patterns of sexual size dimorphism  
577 in copepods. *Proc. R. Soc. Lond. B* **281**, 20140739. (doi:10.1098/rspb.2014.0739)
- 578 42. Uvarov B. 1977. *Grasshoppers and Locusts: Vol. 2*. London: Centre for Overseas  
579 Pest Research.

580 43. Wedell N. 1992. Protandry and mate assessment in the wartbiter *Decticus*  
581 *verrucivorus* (Orthoptera: Tettigoniidae). *Behav. Ecol. Sociobiol.* **31**, 301-308.  
582 (doi:10.1007/BF00177770)

583 **Figure legends**

584 **Figure 1.** Comparison of two methods for estimating sex differences in body size response  
585 to rearing temperature: *T-S Ratio* [(larger response % change in body mass °C<sup>-1</sup> / smaller %  
586 change in body mass °C<sup>-1</sup>)-1] and *RMA<sub>Index</sub>* [slopes derived from the RMA regression of body  
587 mass values for the sex with the more thermally responsive body size on the y-axis (logged)  
588 versus the body size values for the less responsive sex on the x-axis (logged) minus 1] for  
589 arthropod species, where each point represents a single species in a single study. Positive  
590 values represent greater response in male size than female, negative values greater  
591 response in female size. An RMA regression through the data (excluding the two extreme  
592 ratios given in brackets) is given by the solid line, and has a slope of 1.25 (1.13-1.38, 95% CI  
593 range). The RMA slope is significantly different from 1. The diagonal dashed line indicates a  
594 1:1 relationship. The number of values falling within each of the four quadrants (*n*) is  
595 indicated.

596

597 **Figure 2.** Female versus male T-S responses (% change in body mass °C<sup>-1</sup>). Each point  
598 represents a single study of a species and is classified by taxonomic order. An RMA  
599 regression through the data is given by the solid line, and has a slope of 1.09 (1.00-1.18,  
600 95% CI range) with an intercept of 0.38 (0.13-0.63, 95% CI range), denoted in the inset  
601 panel by the black and open circles respectively. The RMA slope is not significantly different  
602 from 1. The diagonal dashed line indicates a 1:1 relationship.

603

604 **Figure 3.** A comparison of the thermal dependence of male and female size responses (*T-S*  
605 *Ratio*) within arthropod species, categorised by taxonomic order. Error bars denote 95% CI.  
606 The vertical dashed line denotes zero, i.e. no difference between male and female body size  
607 responses to temperature. Values greater than zero indicate more responsive male mass.  
608 Values less than zero indicate more responsive female mass. All order-specific *T-S Ratios*  
609 do not differ significantly from zero. The percentage of cases in which female size was the



610 more responsive is given in brackets on the left hand side of the panel after each order. The  
611 sample size ( $n$ ) of each order is given on the right hand side of the panel.

612

613 **Figure 4.** Change in the absolute mass difference between the sexes of a species with  
614 increasing temperature, expressed as a percentage of the female size (at 20°C) per degree  
615 Celsius. Data are categorized by taxonomic order. The overall effect of taxonomic order on  
616 the degree of convergence or divergence is not significant ( $F_{16,99}=1.51$ ,  $p=0.11$ ). The mean  
617 for each order does not differ significantly from zero, with the exception of Cyclopoida (-  
618 1.94% °C<sup>-1</sup> ±1.28CI;  $t_4=-4.20$ ,  $p=0.01$ ), Diptera (-0.24% °C<sup>-1</sup> ±0.19CI;  $t_{35}=-2.24$ ,  $p=0.03$ ) and  
619 Orthoptera (4.61% °C<sup>-1</sup> ±2.47CI;  $t_5=4.79$ ,  $p<0.01$ ). These orders are marked with an asterisk  
620 (\*) and + or – to indicate these have divergence or convergence respectively.

621 Table 1. Comparison of sex-specific plasticity in body mass in relation to environmental variables. We followed the methodology of Stillwell *et*  
622 *al.* (2010) [19] for the T-S data, such that  $\log_{10}$  male size is plotted on the y-axis, and  $\log_{10}$  female size on the x. Hence when the RMA slope is  
623  $<1$  females are the more size responsive sex, and when the RMA slope is  $>1$  males are more size responsive. CV is the coefficient of variation  
624 of body size across the data within each study. Asterisks denote a significant difference between the sexes, where \* gives  $p<0.05$ , and \*\* gives  
625  $p<0.01$ . Table modified from Stillwell *et al.* (2010) [19], with additions from this study.

626

627 Environmental Variable 628 (Taxonomic group)	629 Which Sex is More Plastic		630 $\chi^2$	631 Average degree of plasticity (CV among environments)			632 Source
	633 Females (No. studies with 634 RMA slope $< 1$ )	635 Males (No. studies with 636 RMA slope $> 1$ )		637 Female	638 Male	639 $t$	
632 Temperature (Arthropoda)	55 (47.4%)	61 (52.6%)	0.22	12.3%	12.1%	0.41	This Study
633 Temperature (Insecta)	46 (48.9%)	48 (51.1%)	0.01	11.6%	11.0%	1.14	This Study
634 Larval density / larval competition /							
635 diet quantity (Insecta)	18 (72.0%)	7 (28.0%)	4.84*	16.0%	12.2%	3.42**	Stillwell <i>et al.</i> (2010)
636 Pathogenic infection (Insecta)	3 (50.0%)	3 (50.0%)	0.00	6.9%	7.2%	0.34	Stillwell <i>et al.</i> (2010)
637 Photoperiod (Insecta)	1 (16.7%)	5(83.3%)	2.67	8.6%	10.7%	2.18	Stillwell <i>et al.</i> (2010)
638 Diet Quality (Insecta)	83 (61.9%)	51 (39.1%)	7.64**	12.5%	11.5%	2.47*	Stillwell <i>et al.</i> (2010)

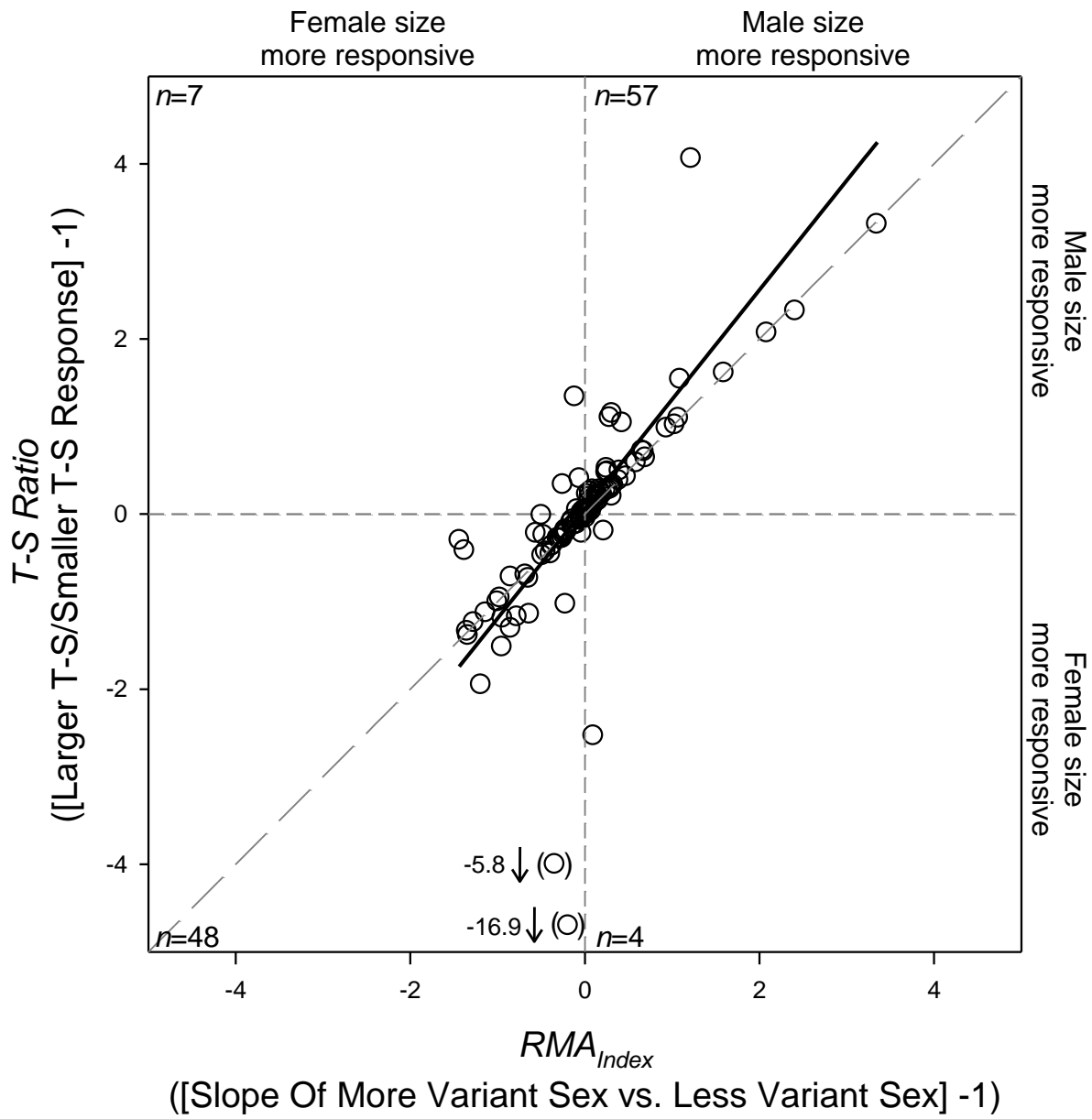


Figure 1

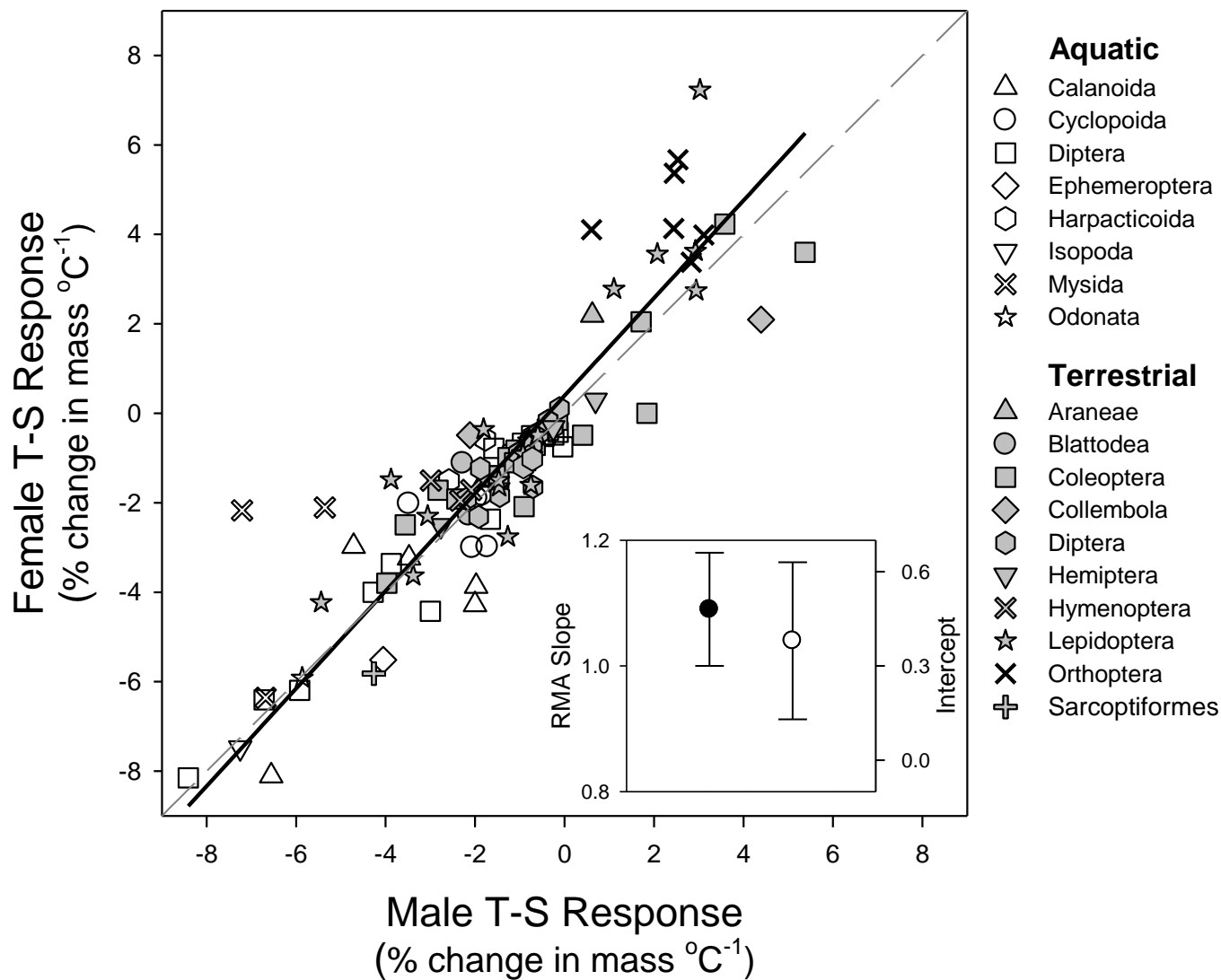


Figure 2

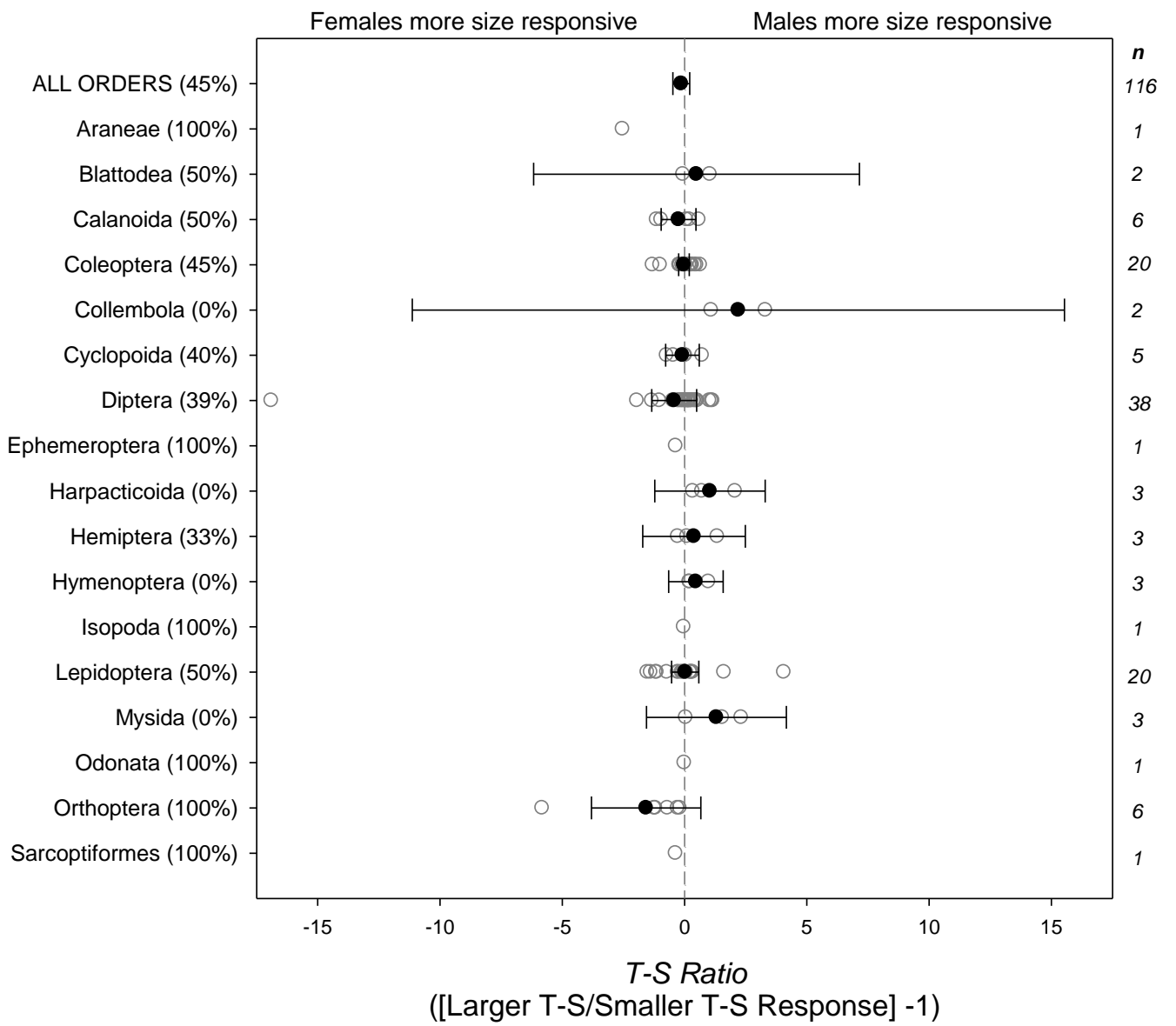


Figure 3

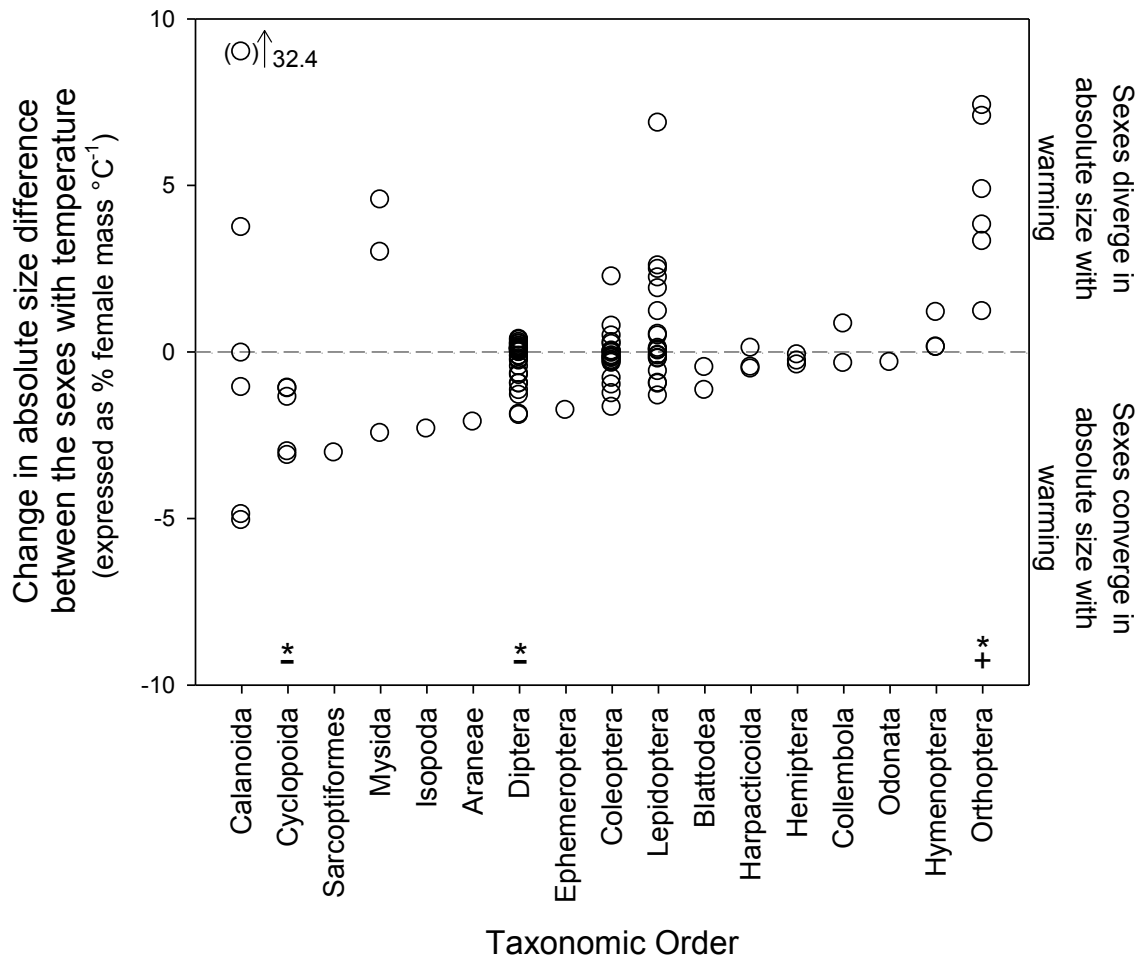


Figure 4