




The evolution of male-biased sexual size dimorphism is associated with increased body size plasticity in males

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Abstract

1. Sexual size dimorphism (SSD) can vary drastically across environments, demonstrating pronounced sex-specific plasticity. In insects, females are usually the larger and more plastic sex. However, the shortage of taxa with male-biased SSD hampers the assessment of whether the greater plasticity in females is driven by selection on size or represents an effect of the female reproductive role. Here, we specifically address the role of sex-specific plasticity of body size in the evolution of SSD reversals to disentangle sex and size effects.
2. We first investigate sex-specific body size plasticity in *Sepsis punctum* and *Sepsis neocynipsea* as two independent cases of intraspecific SSD reversals in sepsid flies. In both species, directional variation in SSD between populations is driven by stronger sexual selection on male size. Using controlled laboratory breeding, we find evidence for sex-specific plasticity and increased condition dependence of male size in populations with male-biased SSD, but not of female size in populations with female-biased SSD.
3. To extend the comparative scope, we next estimate sex-specific body size plasticity in eight additional fly species that differ in the direction of SSD under laboratory conditions. In all species with male-biased SSD we find males to be the more plastic sex, while this was only rarely the case in species with female-biased SSD, thus suggesting a more general trend in Diptera.
4. To examine the generality of this pattern in holometabolous insects, we combine our data with data from the literature in a meta-analysis. Again, male body size tends to be more plastic than female size when males are the larger sex, though female size is now also generally more plastic when females are larger.
5. Our findings indicate that primarily selection on size, rather than the reproductive role per se, drives the evolution of sex-specific body size plasticity. However, sepsid flies, and possibly Diptera in general, show a clear sexual asymmetry with greater male than female plasticity related to SSD, likely driven by strong sexual selection on males. Although further research controlling for phylogenetic and ecological confounding effects is needed, our findings are congruent with theory in suggesting that condition dependence plays a pivotal role in the evolution of sexual size dimorphism.

KEYWORDS

adaptive canalization, condition dependence, Diptera, genic capture, Holometabola, sex-specific phenotypic plasticity, sexual size dimorphism

1 | INTRODUCTION

The strength and type of selection on body size often differ between males and females, owing to their distinct reproductive roles favouring divergent fitness optima (Blanckenhorn, 2000, 2005; Fairbairn, 2013; Fairbairn, Blanckenhorn, & Székely, 2007; Honek, 1993; Shine, 1989). Consequently, sexual size dimorphism (SSD) is widespread across animals and varies greatly among species and sometimes populations (Fairbairn, 2013; Fairbairn et al., 2007).

In insects, females are generally larger than males due to a strong size–fecundity relationship (Honek, 1993). However, despite being rare, male-biased SSD has evolved numerous times independently across the insect phylogeny, often in association with intensified sexual selection on male size and corresponding shifts in the mating system (e.g. Rohner, Blanckenhorn, & Puniamoorthy, 2016). Sexual size dimorphism can differ considerably in its extent, but rarely in its direction (i.e. males or females being the larger sex) among insect species and populations (Rohner et al., 2016; Stillwell, Morse, & Fox, 2007), and often varies strongly across environments due to pronounced sex-specific plasticity in growth and development (Fairbairn, 2005; Fischer & Fiedler, 2001; Stillwell & Fox, 2007). In species with female-biased SSD, females are generally more sensitive to environmental variation (in c. 70% of all species studied) and tend to grow disproportionately larger than males along a gradient from poor to good environmental quality, leading to an increase in SSD with body size (Stillwell, Blanckenhorn, Teder, Davidowitz, & Fox, 2010; Teder & Tammaru, 2005). The underlying evolutionary causes of this pattern are poorly understood. Whether the greater plasticity in females is the result of their reproductive role (being female) or of selection on body size (being the larger sex) remains unclear.

For instance, the sexes often differ in their nutritional requirements such that growth can be more strongly affected by nutrient limitation or quality in females than in males (Chapman, Simpson, & Douglas, 2013; Lee, 2010; Moreau, Quiring, Eveleigh, & Bauce, 2003; Stockhoff, 1993), which could cause body size to respond more strongly to environmental variation in females (Teder & Tammaru, 2005). Alternatively, the sex that has its fitness optimum at larger body size may show a stronger response to environmental variation because of greater potential fitness gains with increasing size. In insects, disentangling these alternative mechanisms and assessing whether plasticity is indirectly driven by the reproductive roles or selection on size is inherently challenging because females are the larger sex in the overwhelming majority of species. Studying sex-specific phenotypic plasticity in closely related taxa differing in the direction of SSD can, therefore, prove very useful to differentiate whether sex or size effects drive variation in sex-specific size plasticity. If female size responds more strongly to environmental quality even when females are the

smaller sex, the reproductive role is likely to account for sex-specific variation in plasticity independently of size. By contrast, if the level of sex-specific plasticity consistently co-varies with the magnitude and direction of SSD, variation in size plasticity is more likely to result from selection on size.

Sex-specific phenotypic plasticity is ultimately explained by two major alternative hypotheses. First, the adaptive canalization hypothesis (Fairbairn, 2005) predicts decreased plasticity in traits most strongly related to fitness in either sex due to increased developmental canalization by stabilizing selection (or directional selection counteracted by a constraint, Stearns & Kawecki, 1994; Stillwell et al., 2010). Alternatively, the condition dependence hypothesis posits that plasticity increases by strong directional selection for resource-use efficiency and so captures interactive genetic and environmental effects (Amend et al., 2013; Bonduriansky, 2007a; Oudin, Bonduriansky, & Rundle, 2015; Rowe & Houle, 1996). Although these two hypotheses predict opposing patterns of plasticity, differentiating between them is not straightforward. For example, female body size may be more plastic than male size due to directional selection on female size, but strong stabilizing selection on male size (or any other trait associated with body size such as growth rate or development time: Wiklund & Fagerstrom, 1977) could lead to an identical pattern. A rigorous test of these hypotheses thus requires knowledge of the selective forces driving the system, data on multiple traits, and/or comparative data that may reveal which sex evolved a heightened degree of body size plasticity.

Here, we address the role of sex-specific body size plasticity in the evolution of male-biased SSD in insects by integrating approaches at three different taxonomic levels: (1) within two species of black scavenger flies (Diptera: Sepsidae) that convergently evolved intraspecific reversals of SSD; (2) among fly species dispersed across the higher Diptera clade; and (3) in a meta-analysis across Holometabola. Sepsid flies are particularly well suited to study such patterns due to considerable SSD variation in both magnitude and direction even among closely related species and populations. Male-biased SSD evolved independently several times across the family, and the direction of SSD further varies within species. *Sepsis neocynipsea* and *Sepsis punctum* show directional variation in SSD between North American and European populations. In *S. neocynipsea*, males are larger than females in North America, while females are the larger sex in Europe (Rohner et al., 2016). In *S. punctum*, this pattern is reversed across the same continents (Dmitriew & Blanckenhorn, 2012, 2014; Puniamoorthy, Schafer, & Blanckenhorn, 2012). In both species, male-biased SSD is derived and driven by enhanced sexual selection on male size, whereas the intensity of fecundity selection on female size does not differ between male- and female-biased populations (Puniamoorthy et al., 2012; Rohner et al., 2016).

Taking advantage of these two independent microevolutionary systems with known underlying selective drivers, we conducted controlled laboratory experiments to identify which sex shows greater body size plasticity, and to test competing hypotheses based on our understanding of the underlying selective forces. If the reproductive role of females is the main driver of increased plasticity, we expected females to show greater plasticity in general, even in species with male-biased SSD. In contrast, if the larger sex is also the more plastic sex irrespective of whether males or females are larger, selection on size is likely to be a more important force. Decreased plasticity of the larger sex, in contrast, would suggest a role of adaptive canalization driven by stabilizing selection and/or directional selection, with body size otherwise being constrained at its upper limit (Fairbairn, 2005). Finally, lack of any sex-specific plasticity (i.e. constant SSD across environments) would suggest that either its evolution is constrained, or that selection pressures counterbalance and thus canalize variation in SSD across environments.

Previous research has demonstrated that different environmental variables can have disparate effects on sex-specific plasticity. Whereas sex-specific plasticity is common when food quality or quantity is manipulated (Stillwell et al., 2010; Teder & Tammaru, 2005), SSD does not seem to vary consistently with temperature across arthropods (Hirst, Horne, & Atkinson, 2015). However, in Diptera, females tend to decrease more strongly in size than males with increasing temperature (leading to a reduction in female-biased SSD with increasing temperature: Hirst et al., 2015). We, therefore, here not only manipulated food quantity, but also rearing temperature to test whether results can be generalized across multiple environmental variables.

Our second goal was to understand the evolution of sex-specific body size plasticity more broadly. To this end, we conducted a comparative study by gathering detailed data for three additional dipterans with male-biased SSD (*Sepsis lateralis*, *Drosophila prolongata*, *Scathophaga stercoraria*) and five closely related fly species with female-biased SSD (*Sepsis cynipsea*, *Sepsis fulgens*, *Drosophila melanogaster*, *Drosophila rhopaloa*, *Musca domestica*). We thus tested whether the association between sex-specific body size plasticity and SSD in *S. neocynipsea* and *S. punctum* extends to these additional flies in a more general pattern across the Diptera. Finally, we analysed published data on species with contrasting SSD in a meta-analysis to test for an even broader pattern among holometabolous insects. Integrating our results from the intraspecific case studies with the comparative Dipteran and holometabolous insect data, we discuss the general role of condition dependence, sex and body size in the evolution of sexual size dimorphism and reversals thereof.

2 | MATERIALS AND METHODS

2.1 | Intraspecific variation in sex-specific plasticity of *S. neocynipsea* and *S. punctum*

Outbred laboratory populations of *S. neocynipsea* and *S. punctum* were established using offspring of at least 10 wild-caught, gravid females of European (both species: Zurich, Switzerland) and North American

(*S. neocynipsea*: Montana, USA; *S. punctum*: Georgia, USA) origin following standard laboratory protocols (Puniamorthy et al., 2012). These populations were cultured for several generations at densities of c. 200–300 individuals.

For egg collection, each laboratory population was provided with a petri dish filled with cow dung for oviposition. After 3–4 hr, depending on the number of eggs laid, this dish was removed and incubated at 18°C for 24 hr. Thereafter, the freshly hatched first-instar larvae were retrieved from the dung by rinsing it with tap water and removing larvae using a fine brush. These larvae were then randomly assigned to different environmental treatments. To maximize environmental variation, we used a factorial design (three food treatments × two temperatures) for each population. In the unlimited food treatment, we provided 10 larvae with 6 g of standardized dung in a rectangular plastic dish. We mimicked natural food limitation by filling the lids of 1.5-ml Eppendorf tubes with dung and placing either a single larva (intermediate food limitation: 0.3 g per individual) or 10 larvae (strong food limitation: 0.03 g per individual) into it. To prevent desiccation, we placed all dishes into glass vials fitted with wet cotton. For the intermediate food treatment, we combined several Eppendorf tube lids in one glass vial, whereas in the two remaining treatments only one dish/Eppendorf lid was placed per vial. These glass vials were treated as independent experimental replicates (random effect). For each population and each food × temperature treatment, we generated at least three such replicates. When no adults emerged, we repeated the experiment to increase our sample size. The experimental procedure in these temporal blocks was identical, but we statistically accounted for this random block effect nevertheless (see below). Vials were maintained in climate chambers at either 15 or 28°C. Upon emergence, adults were sexed and frozen. To estimate body size, we removed the hind legs of each fly and mounted them on glass slides in Euparal, which were subsequently photographed and measured to determine the mean length of both hind tibiae. Note that hind tibia length correlates strongly with other measures of body size, and the sexes do not differ in the allometric relationship of tibia in relation to thorax length (Table S1). Hind tibia length thus well represents overall size. Furthermore, studies of primarily sexual selection in the close relative *S. cynipsea* (Blanckenhorn, Kraushaar, Teuschl, & Reim, 2004) show no specific morphological trait targeted by selection, but rather “overall body size.” Hind tibia length is thus unlikely to be a direct target of selection, except indirectly via body size effects.

To assess sex-specific plasticity within populations, we used linear mixed models with (mean) hind tibia length as a function of sex, temperature and food quantity, including all interactions. All non-significant interactions were discarded, except for the sex × food quantity and the sex × temperature interactions, which were our focus. We used replicates (the identity of the glass vial used for incubation) and experimental block (date on which replicates were set up) as random effects. In addition, we also formally tested whether the sexes differ in their body size response to food quantity between continents. To this end, we tested for a food quantity × population interaction for males and females of each species separately. A significant interaction term would suggest population differentiation in the sex-specific slope

of the reaction norm (body size as response to food), whereas a significant population main effect would suggest a shift in the intercept. Replicates, temporal blocks, as well as temperatures were added as random effects in these models. All analyses were conducted in R (R Core Team, 2016) using the package LME4 (Bates, Machler, Bolker, & Walker, 2015).

2.2 | Interspecific variation in sex-specific plasticity in Diptera

To examine sex-specific plasticity beyond our two focal species *S. punctum* and *S. neocynipsea*, we also lab reared several closely related dipteran species that differ in the direction of SSD. These additional species included three other *Sepsis* spp., two with female-biased SSD (*S. cynipsea* and *S. fulgens*) and one with male-biased SSD (*S. lateralis*). We further studied two other clades of Diptera showing both directions of SSD. In the *Drosophila* clade, *D. prolongata* exhibits male-biased SSD, and *D. rhopaloa* and *D. melanogaster* female-biased SSD (data for the last species derived from the literature: Miller (1964)). The second clade included two calyptate Diptera, with *M. domestica* exhibiting female-biased and *S. stercoraria* male-biased SSD (data on the latter from (Blanckenhorn, Pemberton, Bussiere, Roembke, & Floate, 2010). Given that these species dwell on various substrates and are adapted to different ecological niches, we cannot directly compare environmental treatments across species. We, therefore, did not use identical treatments across species but crossed different larval densities (1–60 individuals per container) with various amounts of food (0.3–100 g) and temperatures (15–30°C; see Table S2) separately for each species. Each species thus experienced different food and temperature treatments, mimicking a strong environmental gradient within species. Although the conditions differed between species, this did not hamper our main goal, the comparison of body size variation between the sexes within species, which were of course always reared under identical environmental conditions. *Musca domestica* and *Sepsis* spp. were reared on cow dung, *D. prolongata* and *D. rhopaloa* on standard *Drosophila* medium. As traditionally different proxies of size are used for different dipteran species, we used thorax length or log adult weight for all drosophilids and *M. domestica* but hind tibia length for all sepsids and *S. stercoraria*. We are aware that using different body size surrogates may to some extent confound the interspecific comparison. However, our research mainly focussed on between-sex comparisons within species such that the trait used to estimate body size was secondary and unlikely to greatly confound variation in SSD (because species with both male- and female-biased SSD were scored for tibia as well as thorax length).

2.3 | Data analysis

To assess sex-specific plasticity, we calculated the sex-specific mean body size for each environmental replicate (temperature × larval density) per species and regressed log(male size) against log(female size) across these replicates in reduced major-axis regressions (RMA), as is standard (Fairbairn, 2007). RMA slopes equal the ratio of the standard

deviations of the y- and x-axes. Hence, slopes deviating from unity in these regressions indicate sex-specific plasticity, with slopes >1 suggesting greater variation in male size (y-axis) across environmental conditions and slopes <1 greater female variation (x-axis). Because such ratios produce asymmetric effect-size distributions, we used the natural logarithm of the RMA slopes as index for the strength and direction of sex-specific plasticity (producing a symmetrical effect-size distribution).

We further quantified the strength and direction of SSD, either using independent datasets of our own or data retrieved from the literature (flies were raised at overabundant food in all cases), by calculating the sexual dimorphism index (SDI) as proposed by Lovich and Gibbons (1992). To this end, we divided the size of the larger sex by that of the smaller and subtracted 1 from this ratio, and arbitrarily assigned positive signs when females are the larger sex and negative ones when males are larger. To control for phylogenetic non-independence we used phylogenetic generalized linear models (PGLS) as implemented in the R-package *caper* (Orme et al., 2013), using log(RMA) as the response and SDI as the explanatory variable. Since detailed phylogenetic information was lacking, we constructed a cladogram derived from published literature (Setoguchi et al., 2014; Wiegmann et al., 2011; Zhao, Annie, Amrita, Yi, & Rudolf, 2013) and set all branch lengths to one. Note that we included our above data for North American and European *S. neocynipsea* and *S. punctum* populations in these analyses as well.

2.4 | Meta-analysis across Holometabola

To test for a general pattern in holometabolous insects, we gathered data from the literature, focussing, where possible, on closely related species pairs or triplets that differ in their direction of SSD (even if they do not represent sister species). In general, we followed the procedure of Teder and Tammaru (2005) and accepted studies in which diet, food amount, larval crowding or ant attendance (for some lycaenid butterflies) were manipulated. Further, we only considered studies presenting data for at least four environmental treatment levels for females and males separately. Adult weights at eclosion as well as pupal weights were accepted as body size estimates, although the former was preferred if both were available. The nature of environmental manipulations was very diverse, including different host species for parasitoids and herbivores, or various manipulations of food quantity or quality for other species (Table S3). Such treatments thus cannot be compared directly across species. To assess sex-specific plasticity quantitatively, we therefore again regressed species-specific log(RMA) slopes across environmental treatments (as above) against SDI. As independent body size data were lacking for most species, the mean SDI across environments was calculated for each species and used to estimate species-specific SSD. To account for the precision of RMA estimates per species, which increases with the number of independent treatment levels, our linear regression was weighted by the number of treatments within species. This approach further corrects, at least to some extent, for the different magnitudes of the environmental gradient used in different studies.

TABLE 1 Using hind tibia length as a proxy for overall body size, we found that food quantity had a pronounced effect on size in all species/populations. However, the sexes only differed in their response to food quantity in North American populations of *Sepsis neocynipsea* and European populations of *Sepsis punctum*, both of which show male-biased sexual size dimorphism (SSD). This suggests an association between SSD reversals (i.e. the evolution of male-biased SSD) and increased condition dependence in male size. Statistics are derived from general mixed models including replicate and experimental block as random effects

Effect	<i>Sepsis neocynipsea</i>						<i>Sepsis punctum</i>					
	North America male-biased SSD			Europe female-biased SSD			North America female-biased SSD			Europe male-biased SSD		
	df	F	p	df	F	p	df	F	p	df	F	p
Sex	1,103.07	4.68	.03	1,115.84	8.97	<.001	1,268.53	4.26	.04	1,154.17	17.8	<.001
Food quantity	2,41.05	86.6	<.001	2,65.14	171	<.001	2,86.68	102	<.001	2,43.64	79.9	<.001
Temperature	1,37.8	0	.99	1,74.03	11.2	<.001	1,112.55	0.32	.57	1,50.06	3.09	.08
Sex × food quantity	2,102.74	5.14	.01	2,119.22	0.11	.9	2,245.93	0.18	.83	2,150.98	6.31	<.001
Sex × temperature	1,114.64	1.48	.23	1,127.1	1.58	.21	1,248.09	5.32	.02	1,156.88	0.28	.6
Temperature × food quantity	2,38.72	5.8	.01	2,74.26	21.8	<.001						

3 | RESULTS

3.1 | Intraspecific variation in sex-specific plasticity of *S. neocynipsea* and *S. punctum*

Food quantity had a strong positive effect on hind tibia length in all populations studied (Table 1). Crucially, the effect of food quantity differed between the sexes in North American (NA) *S. neocynipsea* as well as in European (EU) *S. punctum* (sex × food quantity interaction in Table 1). In these populations, the sexes were essentially monomorphic at low food quantity but males increased more strongly in size with increasing food quantity, leading to considerable male-biased SSD under ample food conditions (Figure 1). Both independent intraspecific SSD reversals thus feature increased plasticity in males, while this pattern was absent in the sister populations with female-biased SSD (sex × food quantity interaction not significant in Table 1; Figure 1). In addition, we found no differences in the response of female body size to food quantity between continents in either *S. neocynipsea* (continent × food quantity interaction: $F_{1,39.07} = 0.68$, $p = .413$; Table S4) or *S. punctum* ($F_{1,89.80} = 2.14$, $p = .148$; Table S4). In contrast, males differed in their plastic response to food quantity between continents (continent × food quantity interaction: *S. neocynipsea*: $F_{1,17.44} = 9.49$, $p = .006$; *S. punctum*: $F_{1,46.30} = 37.13$, $p < .001$; Table S4), suggesting that the differences in sex-specific plasticity observed among populations are driven by variation in male body size plasticity alone.

The effect of food quantity on tibia length further differed between temperatures in both populations of *S. neocynipsea* (food quantity × temperature interaction; Table 1), although this did not affect SSD (because the sex × food quantity × temperature three-way interactions were non-significant throughout and hence removed; *S. neocynipsea* NA: $F_{2,83.75} = 0.45$, $p = .640$; EU: $F_{2,110.67} = 0.88$, $p = .420$; *S. punctum* NA: $F_{2,156.51} = 0.79$, $p = .460$; EU: $F_{2,14.03} = .09$, $p = .910$). The sexes differed in their reaction to temperature only in North American *S. punctum* (sex × temperature interaction in Table 1). In

this population, female tibia length increased more with decreasing temperature than in males, suggesting that female body size is more plastic in response to temperature.

3.2 | Interspecific variation in sex-specific plasticity in Diptera

Log(RMA) slopes were always steeper in taxa with male-biased SSD than in those with female-biased SSD (i.e. males are more plastic than females when they are the larger sex; Table 2). Log(RMA) slopes decreased significantly with the degree of female bias in SSD (PGLS: $F_{1,10} = 8.03$, $p = .018$, $r = -0.67$, $\lambda = 0.00$ [95% CI: 0.00–0.89], slope = -0.91 ; Figure 2a), demonstrating that taxa with relatively larger males have steeper RMA slopes. Since the reversed pattern was also observed when females were larger than males (lower right quadrant in Figure 2a), the larger sex generally seems to show heightened plasticity.

3.3 | Meta-analysis across holometabolous insects

Combining our own data with data from the literature, we obtained information on sex-specific plasticity for a total of 43 species (Coleoptera: eight species; Diptera: 16 species; Hymenoptera: four species; Lepidoptera: 15 species; see Tables S3 and S5). All these data are restricted to Holometabola, as studies of other insect groups did not fit our requirements. The number of environmental treatments per species varied from 4 to 23 (median: 7, $M \pm SD$: 7.3 ± 3.7). When averaging SDI across environments, 21 species showed female-biased SSD whereas males were the larger sex in 22 species (SDI ranging from -0.41 in *D. prolongata* to 0.32 in the cowpea seed beetle *Callosobruchus maculatus*).

Across all 43 species, log(RMA) showed a negative relationship with SDI (weighted least-squares regression: $t_{1,41} = -2.48$, $p = .017$, slope = -0.52 ; Figure 2b). Since the intercept is close to zero (estimate = -0.003 , $t_{1,41} = -0.12$, $p = .907$), males tend to be more plastic

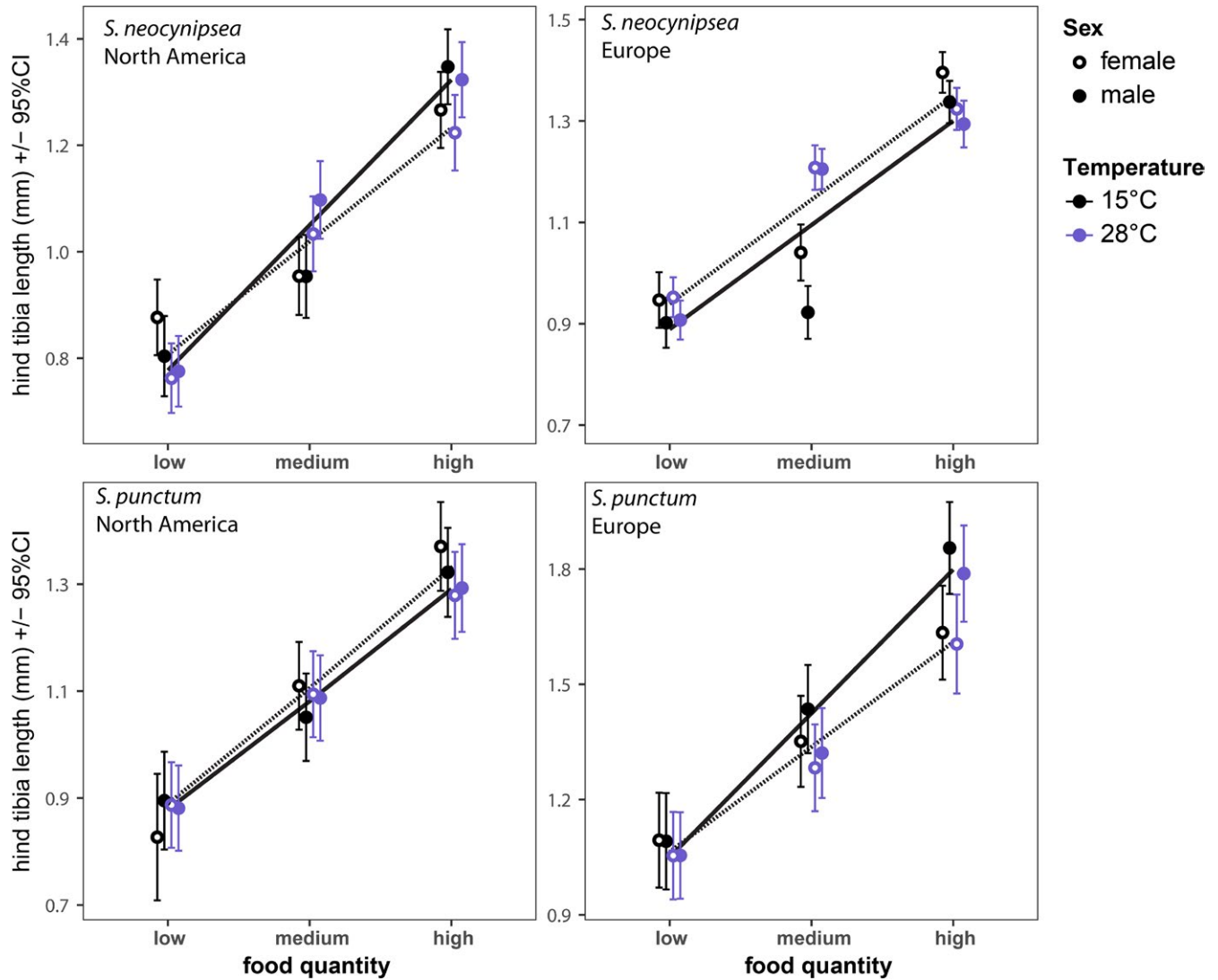


FIGURE 1 Mean hind tibia length of sepsid fly populations reared at three food (dung) quantities and two temperatures. Males increase more strongly in size with environmental quality in North American *Sepsis neocynipsea* and European *Sepsis punctum* (solid lines), the populations in which males are larger than females. In contrast, the sexes do not differ in their plastic response in populations with female-biased sexual size dimorphism (dotted lines). This pattern qualitatively holds in *S. punctum* and *S. neocynipsea*, although the latter shows a weaker sex-by-environment interaction. $M \pm SE$ estimates represent model parameters and their associated errors; random variation among blocks and replicates is thus accounted for. For simplicity, we only show average sizes across temperatures, but raw data are shown in Figure S1

than females in species with male-biased SSD, and females tend to be more plastic than males in species with female-biased SSD. When restricting the analysis to previously available data from the literature, this relationship was qualitatively similar but no longer statistically significant (weighed least-squares regression: $t_{1,29} = -1.05$, $p = .302$, slope = -0.29).

4 | DISCUSSION

Our study demonstrates an association between sex-specific body size plasticity and the strength and direction of SSD across holometabolous insects (Figure 2). In general, the larger sex tends to be more plastic in response to environmental factors, thus being more condition dependent. This result is consistent with the hypothesis

that sex-specific plasticity is driven mainly by selection on size rather than selection associated with the reproductive role (i.e. being male or female). However, at least in the sepsid flies, size plasticity is not entirely symmetrical with regard to sex. Stronger condition dependence in males is likely mediated by strong sexual selection (Bonduriansky, 2007a, 2007b; Figure 1, 2a, Table 2). We discuss potential evolutionary and ecological drivers of these patterns and their implications for the study of body size and SSD evolution.

4.1 | Intraspecific variation in sex-specific plasticity in *Sepsis*

In North American *S. neocynipsea* and European *S. punctum*, the derived male-biased SSD is associated with increased plasticity in males

TABLE 2 Reduced Major Axis (RMA) slopes of log male size against log female size with various numbers of replicates (n) reflecting a large environmental gradient. All slopes are significantly greater than unity in taxa with male-biased sexual size dimorphism (SSD), whereas for female-biased taxa slopes vary around 1. We used the sexual dimorphism index (SDI), a standardized ratio, as an estimate of the direction and strength of SSD (Lovich & Gibbons, 1992), derived from independent datasets in which flies were raised with ad libitum food at benign temperature. Means (95% CI) are given for the two SSD groups in bold italic

Taxon	Authority	n	R^2	RMA slope	p	SDI estimate
Male-biased SSD						
<i>Drosophila prolongata</i>	Singh & Gupta, 1977	17	.88	1.37	.003	-0.3
<i>Scathophaga stercoraria</i> ^a	Linnaeus, 1758	5	.99	1.2	.045	-0.25
<i>Sepsis punctum</i> EU	Fabricius, 1794	21	.85	1.24	.021	-0.07
<i>Sepsis neocynipsea</i> NA	Melander & Spuler, 1917	17	.96	1.14	.015	-0.04
<i>Sepsis lateralis</i>	Wiedemann, 1830	15	.91	1.23	.026	-0.03
				1.236 (0.074)		-0.138 (0.111)
Female-biased SSD						
<i>Sepsis punctum</i> NA	Fabricius, 1794	31	.94	0.96	.406	0.03
<i>Sepsis fulgens</i>	Meigen, 1826	30	.71	1.01	.925	0.04
<i>Sepsis neocynipsea</i> EU	Melander & Spuler, 1917	16	.83	1.09	.459	0.05
<i>Musca domestica</i>	Linnaeus, 1758	21	.81	1.06	.557	0.07
<i>Sepsis cynipsea</i>	Linnaeus, 1758	26	.97	0.87	.001	0.07
<i>Drosophila rhopaloa</i>	Bock & Wheeler, 1972	15	.79	1.14	.324	0.11
<i>Drosophila melanogaster</i> ^b	Meigen, 1830	11	.94	0.69	.001	0.13
				0.974 (0.114)		0.071 (0.027)

^aBlanckenhorn et al. (2010).

^bMiller (1964).

(significant sex-by-food quantity interaction, RMA slope >1), while conspecific female-biased populations show no sex-specific plasticity (sex-by-food quantity interaction not significant in Table 1; RMA slope not different from 1 in Table 2), a clear sexual asymmetry in condition dependence. In populations with larger males, SSD was absent in stressful environments but increased gradually with environmental quality (Figure 1). This pattern can be caused either by increased condition dependence in males or developmental canalization in females. As male body size plasticity in response to food availability differs between continents, while female plasticity does not (see Table S4), population differentiation must be caused by variation in male plasticity only, suggesting evolution of increased condition dependence in males in populations with male-biased SSD. This fits well with previous studies demonstrating that the intensity of sexual selection on male size is stronger in the male-biased populations while there is no indication for differences in fecundity selection on female size among populations (Puniamoorthy et al., 2012; Rohner et al., 2016). Hence, there is no evidence for stronger (stabilizing) selection potentially canalizing female size in male-biased populations only. We thus attribute the greater male plasticity in male-biased populations to increased directional selection on male size, consequently arguing in favour of the condition dependence hypothesis and rejecting the canalization hypothesis (Bonduriansky, 2007a; Fairbairn, 2005).

In contrast to food availability, temperature did not strongly affect sex-specific plasticity. This finding is common in insects (Hirst et al., 2015). We found a significant temperature effect on SSD only in North

American *S. punctum*, in which female size declined more strongly than male size from low to high temperature, whereas European populations responded more plastically to food (Table 1). Hirst et al. (2015) also found that in Diptera SSD unusually declines with temperature. So it is possible that the extent of sex-specific plasticity and condition dependence varies with the taxon and the environmental variable in question. According to the temperature-size rule (Atkinson, 1994; Atkinson & Sibly, 1997), low temperatures generally produce larger individuals through physiological responses. However, this size increase does not necessarily co-vary with environmental quality (Atkinson & Sibly, 1997), and it is thus unclear whether this response means increased condition (dependence), which currently hampers a functional interpretation.

Originally proposed to explain variation in ornament size via genic capture, condition dependence is predicted to link genome-wide genetic quality of an individual to the expression of its secondary sexual traits in a given environment (Rowe & Houle, 1996). This opportunistic mechanism should allow individuals to invest optimally in costly traits under resource limitation, flexibly trading fitness gains in sexual selection against viability (or any other) costs. Theory thus predicts a tight association between sexual dimorphism and condition dependence (Bonduriansky, 2007a, 2007b). In *Sepsis* and insects more generally, large size entails viability costs due to prolonged development time and/or increased growth rate (Blanckenhorn, 2000, 2009; Teder, 2014). In both sepsids and drosophilids, for example, males take longer to develop than females, possibly related to male gonad

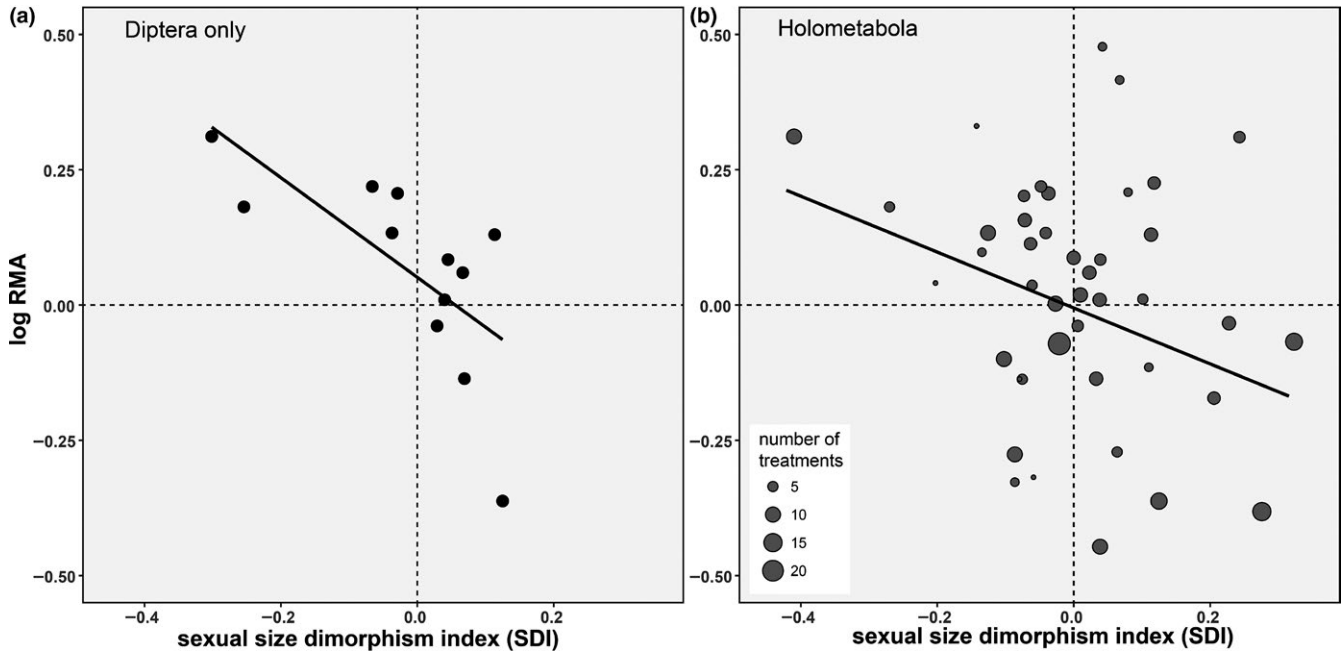


FIGURE 2 The relative plasticity of males (estimated by $\log(RMA)$ slopes) increases with the relative size of males (decreasing sexual dimorphism index [SDI]) in Diptera (a) and Holometabola in general (b). This suggests that the evolution of male-biased sexual size dimorphism (SSD) is associated with an increase in male plasticity. $\log(RMA)$ slopes larger than zero indicate that males are more responsive to environmental variation ($RMA \text{ slope} = SD(\text{males})/SD(\text{females})$), while females are more plastic if this slope is less than zero. To quantify SSD, we divided the size of the larger sex by that of the smaller and subtracted 1 from this ratio, and arbitrarily assigned positive signs when females are the larger sex and negative ones when males are larger (=SDI). While SDI of independent datasets were used in the analysis for Diptera only, we used the mean SDI across environments for the Holometabola in b). The trend line in b) gives the weighted linear regression using the number of treatments as weights (as indicated by the size of points)

or gamete development (Blanckenhorn et al., 2007; Rohner et al., 2016), so the costs of growing large at limited food are expected to be greater for males. This sex difference should be amplified if habitats are ephemeral and/or when sexual selection favouring large male size is particularly strong. When facing serious food limitation, males may therefore not be able to grow larger by prolonging growth due to severe mortality risks. Instead, they may shorten their larval development and emerge as adults earlier but at a smaller size. These small males are not favoured by sexual selection, but by reaching the adult stage they at least maintain some potential for direct fitness. Such a “bail-out” strategy in response to food limitation has been found in several dung-dwelling beetles (Shafiei, Moczek, & Nijhout, 2001) and flies (Blanckenhorn, 1999), and likely explains the evolution of greater male body size plasticity in *S. neocynipsea* and *S. punctum* populations with male-biased SSD. Selection on adult male size could thus indirectly lead to the evolution of condition dependence in larval growth rate and developmental time.

In contrast, the absence of sex-specific plasticity in populations or species with female-biased SSD is not congruent with the condition dependence hypothesis ($\text{sex} \times \text{food quantity}$ interaction not significant). When females are the larger sex, as is most common in ectotherms, it is equally reasonable to assume that females would benefit to a greater extent than males from investing in body size at limited resources, but they do not show increased plasticity in our dataset. In females, condition dependence should be driven primarily by fecundity

selection. Fecundity selection tends to be generally weaker than sexual selection on males in sepsids and other species, specifically also in the two species studied here (Puniamoorthy et al., 2012; Rohner et al., 2016), and further tends to asymptote at the largest body sizes in *S. cynipsea* (Blanckenhorn 2007). Perhaps as a consequence, female-biased SSD is relatively weak in *S. neocynipsea* and *S. punctum*, such that the absence of sex-specific plasticity here may be explained by rather weak divergent selection on body size, in which case other selective pressures may obscure any patterns (see also below). Alternatively, this lack of sex-specific plasticity might be confined to tibia length and not necessarily apply to other estimates of body size, which we, however, consider unlikely because tibia length well reflects body size in many fly species (Table S1).

4.2 | Interspecific variation in sex-specific plasticity in Diptera

In extension of the above argument, the magnitude and direction of SSD co-varied with sex-specific size plasticity among several species of flies, again suggesting that females are not inherently more responsive to environmental quality (e.g. due to their particular nutritional needs), but that the larger sex is generally more plastic. As predicted by theory (Bonduriansky, 2007a, 2007b), this suggests a pivotal role of condition dependence in the evolution of male-biased SSD, and of SSD in general.

It is important to note, however, that while RMA slopes of species with male-biased SSD are always significantly steeper than unity and often strongly so, species with female-biased SSD frequently do not show significant sex-specific size plasticity (RMA slopes not significantly shallower than unity in Table 2). As argued above, this may well be caused by the relatively weak SSD of female-biased species and the concomitant low levels of divergent selection that could be counteracted by other forms of selection. This finding corroborates the results of Teder and Tammaru (2005) showing that female size plasticity is more likely to exceed that of males as the magnitude of female-biased SSD increases. Nevertheless, irrespective of whether intra-specific RMA slopes significantly deviate from unity, the overall interspecific pattern for the Diptera covered here suggests a rather strong and sexually not entirely symmetric (inverse) relationship between condition dependence and SSD (Figure 2a).

4.3 | A general pattern in Holometabola?

Our quantitative meta-analysis adds further evidence to the notion that the larger sex tends to be more plastic (Teder & Tammaru, 2005), thus suggesting a general trend at least across the Holometabola (Figure 2). This result should be treated with some caution, however, as it was not quite statistically significant when excluding the dipterans, although the pattern itself persisted, again suggesting that Diptera are somehow different. Since our experimental rearing specifically aimed at covering extreme environments including severely limited and overabundant resource availabilities that should well cover the range experienced in nature (Blanckenhorn, 2009), our RMA slopes should adequately estimate the pattern with low biological error. The differences between Diptera and the rest of Holometabola might therefore merely be quantitative (as opposed to qualitative), with the larger sex generally being more plastic. Alternatively, however, as demonstrated by Hirst et al. (2015), patterns of sex-specific plasticity can differ among insect orders (see also Teder & Tammaru, 2005), likely caused by shared phylogenetic relatedness, life histories or habitats.

So why might sepsids, and possibly other Diptera, differ from other insects in the impact of sex-specific condition dependence on SSD expression? We can only speculate at this point. All flies studied here depend on ephemeral resources for reproduction and development. Since condition dependence is expected to be more common when resources are strongly limited, which regularly applies to the short-lived and unpredictable resources of dung flies and perhaps also *Drosophila* (Blanckenhorn, 1999, 2009), this might explain the discrepancies between Diptera and other Holometabola found here. Further data on species dwelling in other substrates are therefore required to test how common the phenomenon is, although it may not explain the sexual asymmetry in sex-specific plasticity. Alternatively, Blanckenhorn et al. (2007) also uncovered an asymmetric sex-specific pattern in that females of several insect groups, including sepsids and drosophilids but also water bugs, grow faster than males. This suggests lower viability costs for females counteracting the generally weaker fecundity selection on female size (relative to the typically stronger sexual selection on male size:

Blanckenhorn et al., 2007; Rohner et al., 2016). At least in sepsids and drosophilids, male costs are presumably exerted by the time and energy consuming production of male gonads and gametes (Blanckenhorn et al., 2007; Lupold et al., 2016), provoking stronger viability counter-selection in males. Increased investment into body and organ size thus appears generally costlier in males, but also more rewarding as sexual selection on male size tends to be stronger than fecundity selection on female size. The evolution of stronger condition dependence in males compared to females, allowing to flexibly counterbalance costs depending on environmental circumstances, thus seems to have some adaptive value (Bonduriansky, 2007a, 2007b; Rowe & Houle, 1996).

In conclusion, our study of species varying in the direction of SSD revealed that male-biased SSD is associated with increased phenotypic plasticity of males in (higher) Diptera if not all Holometabola. We corroborate theoretical predictions by demonstrating that condition dependence, particularly in males through sexual selection, plays a pivotal role in generating both quantitative and qualitative variation in sexual size dimorphism, within as well as across species. It remains yet unclear, however, whether this pattern extends to other phylogenetic clades and ecological guilds, or even beyond insects (c.f. Blanckenhorn et al., 2007). Further data for other taxonomic groups covering a wide range of different life histories and ecological adaptations will be needed to evaluate the generality of this phenomenon. Given the complex developmental patterns generating sex-specific plasticity (Stillwell & Davidowitz, 2010), particular attention should be paid to the underlying physiological and genetic mechanisms for a more comprehensive understanding of the evolution of SSD, plasticity and condition dependence (Davidowitz, 2016; Rohner, Blanckenhorn, and Schäfer, 2017).

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AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology; P.T.R., S.L. and T.T. collected the data; P.T.R. analysed the data; P.T.R. and W.U.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.f6r60> (Rohner, Teder, et al. 2017).

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