

A Comparative Study of the Role of Sex-Specific Condition Dependence in the Evolution of Sexually Dimorphic Traits

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ABSTRACT: Sexual selection can displace traits acting as ornaments or armaments from their viability optimum in one sex, ultimately giving rise to sexual dimorphism. The degree of dimorphism should not only mirror the strength of sexual selection but also the net viability costs of trait maintenance at equilibrium. As the ability of organisms to bear exaggerated traits will depend on their condition, more sexually dimorphic traits should also exhibit greater sex differences in condition dependence. While this has been demonstrated among traits within species, similar patterns are expected across the phylogeny. We investigated this prediction within and across 11 (sub)species of sepsid flies with varying mating systems. When estimating condition dependence for seven sexual and nonsexual traits that vary in their sexual dimorphism, we not only found a positive relationship between the sex difference in allometric slopes (our measure of condition dependence) and relative trait exaggeration within species but also across species for those traits expected to be under sexual selection. Species with more pronounced male aggression further had relatively larger and more condition-dependent male fore- and midlegs. Our comparative study suggests a common genetic/developmental basis of sexual dimorphism and sex-specific plasticity that evolves across the phylogeny—and that the evolution of size consistently alters scaling relationships and thus contributes to the allometric variation of sexual armaments or ornaments in animals.

Keywords: allometry, Sepsidae, sexual selection, sexual size dimorphism, phenotypic plasticity.

Introduction

The magnitude, type, or form of selection typically varies between sexes. Thus, directional sexual selection often drives the evolution of exaggerated male secondary sexual traits that serve as ornaments or armaments by shifting phenotypes away from their viability fitness optimum, which may differ markedly from the female optimum of the same trait

(Andersson 1994; Fairbairn et al. 2007). Reflecting the evolutionary net outcome of various sex-specific natural and sexual selection pressures, such sexually antagonistic selection ultimately gives rise to sexual dimorphism (Price 1984; Preziosi and Fairbairn 2000; Blanckenhorn 2005, 2007). If sexual selection is driving dimorphism, and assuming the between-sex genetic correlation does not impose major constraints, the displacement from the viability selection optimum reflects the net costs and benefits of (exaggerated) trait expression (which may not be the case if dimorphism is due to ecological character displacement; e.g., Shine 1989, 1991; Temeles et al. 2000). The capacity of organisms to bear particular traits typically varies to the extent that only individuals in good condition—that is, those with access to more metabolic resources (Rowe and Houle 1996)—will be able to afford expressing a certain degree of trait exaggeration that then can act as an indicator of their intrinsic quality. Traits under strong directional selection, for instance, via female choice, are therefore expected to show a heightened degree of condition dependence (Iwasa and Pomiankowski 1991, 1999). This is because condition dependence—a form of phenotypic plasticity linking an individual's genome-wide genetic quality to trait expression under a given amount of resources (Rowe and Houle 1996)—allows for a flexible trade-off of survival costs that arise through trait exaggeration with the corresponding reproductive benefits. (Think of the antlers of a male deer that regrow every year to an impressive size depending on the available extrinsic resources and the intrinsic quality—i.e., mass or size—of the individual relative to the antlers of the female). If individuals in good condition enjoy larger marginal benefits, they should show greater trait investment (Bonduriansky and Day 2003; Johnstone et al. 2009). Sexually antagonistic directional selection should hence not only drive the evolution of sexual dimorphisms but also evoke sex-specific variation in the extent of condition dependence, if only because both are driven by selection. Consequently, although formal theory to this ef-

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fect is currently lacking (but see Iwasa and Pomiankowski 1991), the sex showing phenotypic exaggeration for a given trait should also show heightened condition dependence, and sexual dimorphism itself should become dependent on condition (Bonduriansky and Day 2003; Bonduriansky and Rowe 2005; Bonduriansky 2007a, 2007b).

The predicted association between dimorphism and condition dependence for morphological traits has received great attention in vertebrate and invertebrate species with very conspicuous (sex-specific) armaments or ornaments (Cotton et al. 2004b; Tomkins et al. 2010). Such work was historically grounded in early comparative studies of solitary and social primates, ungulates, and birds attempting to understand the evolution of sexual dimorphism by their underlying developmental processes (Jarman 1983; Leigh 1992; Teather and Weatherhead 1994; Blanckenhorn et al. 2007; Bro-Jørgensen 2007). This was also of interest to developmental biologists and geneticists because sex-specific condition dependence represents a form of sex-limited epistasis, which could also resolve between-sex genetic correlations that would otherwise hamper the establishment of sexual dimorphisms (Bonduriansky 2007a, 2007b). However, many previous studies are limited to few traits, lack nonsexual control traits in the same or opposite sex, or provide data for only one sex. Studying merely a few traits not only poses difficulties in terms of statistical power but might also be unrepresentative, hence hampering evaluation of the generality of putative relationships. To fully understand and quantitatively assess the predicted covariation between dimorphism and condition dependence, multiple sexual and nonsexual traits need to be studied analogously in both sexes.

The rather few experimental studies explicitly investigating the relationship between dimorphism and sex-specific condition dependence suggest a positive correlation (Bonduriansky and Rowe 2005; Bonduriansky 2007a; Punzalan et al. 2008; Johns et al. 2014; Oudin et al. 2015; but see Cayetano and Bonduriansky 2015). Transcriptomic studies in *Drosophila melanogaster* (Wyman et al. 2010) and the dung beetle *Onthophagus taurus* (Ledón-Rettig and Moczek 2016) also suggest a link between sexual dimorphism and condition dependence. Patterns among traits within species thus appear to be consistent. However, based on the same argument, sex-specific condition dependence and sexual dimorphism are also predicted to correlate across species, provided that other selective ecological pressures are similar and intersexual genetic correlations or morphological integration do not pose major constraints (Bonduriansky 2007b). Thus, in species subjected to an increased degree of sex-specific directional selection on a given trait (e.g., following mating system evolution), sexual dimorphism should become amplified and so should the benefit of condition dependence (Rowe and Houle 1996). However, this prediction remains underexplored at the interspecific level, and the existing studies are often lim-

ited to a few traits of primarily stalk-eyed flies (Simmons and Tomkins 1996; Wilkinson and Taper 1999; Baker and Wilkinson 2001; Cotton et al. 2004a, 2004b, 2004c; Kawano 2004), hampering our understanding of whether and how the relationship between dimorphism and condition dependence can evolve.

Testing this prediction is complicated because estimating condition dependence is difficult in many organisms. This is because traits often develop over a long time and/or irregularly grow merely during specific and nonoverlapping life stages or seasons. While this is a pervasive issue in many species with indeterminate growth, such as many vertebrates or crustaceans, condition-dependent trait expression can be more readily studied in morphological traits of holometabolous insects. Holometabola develop essentially all their adult tissue during metamorphosis, with the entire energy budget determined at the onset of metamorphosis. If reared in a standardized environment where only the amount of food is manipulated, the overall size of the pupa—and, consequently, the adult—thus estimates the total available metabolic resources, that is, condition. Because different adult traits develop simultaneously and compete for resources during metamorphosis, the relationship of relative trait size to overall body size in the adult—the static allometric coefficient (Cheverud 1982; Klingenberg and Zimmermann 1992)—therefore well estimates the degree of dependency of trait expression on condition (Shingleton and Frankino 2018). This is further supported by studies of the developmental underpinnings of allometry. Proximally, variation in static allometric slopes among traits has been linked to variation in the sensitivity of various organ primordia responding to varying levels of insulin-like peptides (ILPs). Because the insulin-signaling pathway links nutrition to growth, ILP sensitivity mirrors the dependency of the growth of a specific structure to the organisms' nutritional status (Tang et al. 2011; Emlen et al. 2012; Shingleton and Frankino 2018). Therefore, static trait allometries of holometabolous insects, and likely many other organisms as well, should reflect variation in the responsiveness of trait growth to condition, that is, condition dependence, such that steeper allometries imply greater allocation of resources to a given trait with size. Note, however, that although we here use allometric slopes as a measure of condition dependence, the two concepts are not necessarily synonymous in other contexts, as the literature on allometry as well as condition dependence is complex (e.g., Johnstone et al. 2009; Hill 2011; Pelabon et al. 2013).

Black scavenger flies (Diptera: Sepsidae) are well suited for studying the relationship between sex-specific condition dependence and sexual dimorphism, as their morphology is highly plastic and traits vary strongly in their direction and degree of sexual dimorphism. Moreover, previous studies have demonstrated considerable variation in mating systems among taxa that goes hand in hand with sex-specific

directional selection and directional variation in sexual size dimorphism (SSD; Puniamoorthy et al. 2012a, 2012b; Rohner et al. 2016, 2018). Generally, scramble competition for access to mates with direct and indirect female choice tends to be associated with female-biased SSD (e.g., in *Sepsis cynipsea*; Blanckenhorn et al. 2000), whereas male-biased SSD is found in species with pronounced male-male competition (e.g., *Sepsis thoracica* or *Sepsis punctum*; Zerbe 1993; Busso and Blanckenhorn 2018b).

Taking advantage of their well-resolved phylogeny, our ability to rear multiple species under controlled laboratory conditions, and their large interspecific variation in sexual dimorphism, we here test for and quantify the relationship between sex-specific condition dependence and sexual dimorphism among traits within and across closely related sepsid species. We consider both putatively sexually and naturally selected traits to expand the extent of dimorphism and compare the degree of condition dependence between sexual and nonsexual control traits (Cotton et al. 2004b; Fairbairn 2005; Bonduriansky 2007a). We additionally investigate the effect of reversals in sexual size dimorphism, a close correlate of mating-system variation, on the relationship between sex-specific condition dependence and dimorphism. Our ultimate goal is to test for systematic relationships between sex-specific scaling relationships, indicative of condition dependence, and sexual dimorphism in sexual versus nonsexual traits across the sepsid phylogeny.

Material and Methods

Sepsids are usually associated with decaying organic matter (e.g., vertebrate dung, rotting plant material) as breeding substrate (Pont and Meier 2002). Because such habitats are typically ephemeral, variation in the amount of resources available for an individual's metabolism and development (i.e., condition) is large under natural conditions. Sepsid flies consequently exhibit strongly plastic responses to food quantity and quality, involving both development time and adult body size (adult dry weight of siblings can vary by a factor of 10; Zerbe 1993; see also Blanckenhorn 1999; Dmitriew and Blanckenhorn 2014; Rohner et al. 2018).

Most sepsid species also show pronounced sexual dimorphism in various traits other than overall body size, with its degree being highly trait specific. In the genus *Sepsis* Fallén 1810, males typically show marked modifications of their forefemur (Pont and Meier 2002). These include spines, bristles, and protrusions that are absent entirely in females (cf. fig. 1a, 1b; also see Sepsidnet, the digital reference collection for Sepsidae: <http://sepsidnet-rmbr.nus.edu.sg/>; Ang et al. 2013). This strongly modified forefemur is used to hold on to the female's wing base during copulation and is therefore believed to be under sexual selection (Eberhard 2001b; Blanckenhorn et al. 2004), although its function is likely also stimulatory and thus complex (Eberhard 2001b, 2005; Ingram et al. 2008). Other appendages are also used during cop-

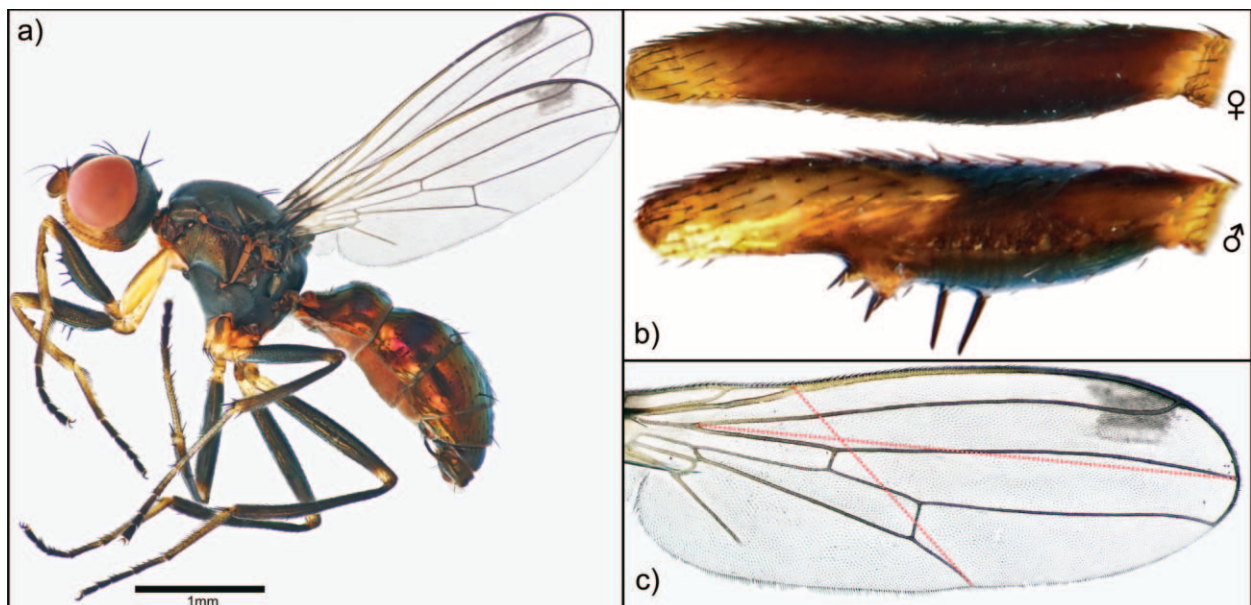


Figure 1: a, General morphology of *Sepsis cynipsea*. b, While the female forefemur (top) is bare, the male forefemur (bottom) exhibits pronounced protrusions and spines. c, Measurements for wing length and width. Images come from Sepsidnet (<http://sepsidnet-rmbr.nus.edu.sg/>), with kind permission from Dr. Yuchen Ang at the National University of Singapore.

ulatory courtship, including tactile and visual stimulation of the female with the male midlegs (Puniamorthy et al. 2009; Puniamorthy 2014) or the transmission of chemical compounds originating from the osmeterium located on the hind-leg onto the female wing (Eberhard 2001a). Yet their functions often remain elusive (Araujo et al. 2014).

Whereas the male (but not female) legs are probably sexually selected in at least some sepsid species, other traits, like the thorax or wings, likely are not. Unless involved in courtship, insect wings are typically under stabilizing natural (i.e., viability) selection, such as in *Drosophila melanogaster* (Gilchrist et al. 2000). In *Sepsis*, both females and males almost permanently wave their wings, a behavior that is therefore not specific to the mating context (Pont and Meier 2002). Similarly, the insect thorax, which primarily harbors the flight muscles, is also likely to be subject to stabilizing selection with no (or limited) function during courtship or mating.

Taxon Sampling

To quantify sexual dimorphism and condition dependence, we experimentally reared nine closely related species of black scavenger flies (table 1). As populations of *Sepsis neocynipsea* and *Sepsis punctum* evolved divergent mating systems and morphologies on different continents (Europe and North America; Puniamorthy et al. 2012a, 2012b; Rohner et al. 2016), we treated these populations as independent evolutionary lineages (hereafter referred to as taxa). All taxa were kept in large, outbred laboratory cultures (200–300 individuals) for several generations prior to any experimental procedure.

Condition Dependence

Condition dependence can be estimated in several sensible ways (e.g., Cotton et al. 2004b; Hill and Farmer 2005; Bonduriansky et al. 2015). Comparing species with very different body sizes and levels of sexual size dimorphism, however, we could not use discrete environmental treatments because similar environments (e.g., food amounts) are unlikely to have identical effects across species. We therefore used a continuous environmental treatment to estimate sex- and trait-specific static allometries, which permit standardized comparisons across species and the sexes controlling for overall body size differences. Although this is no quantitative genetic study because we used food to manipulate phenotypes in population cages, by quantifying evolved sex differences across species in a standardized way, we are indirectly addressing the evolution of sex-specific genotype-by-environment effects in the broadest sense.

We first induced variation in condition by manipulating food availability during the larval stage. To this end, we collected eggs from outbred laboratory cultures by providing adult flies with a petri dish filled with cow dung. After 1 day, the petri dish was removed, and the eggs laid were haphazardly distributed among plastic containers with varying amounts of homogenized cow dung (ranging from 10 individuals per 3 g up to 10 individuals per 30 g) and subsequently incubated at a constant 18°C. For each species, we set up 10–30 replicates. Note that, in contrast to flies reared with overabundant food, strong food limitation caused very high levels of larval mortality in all species, suggesting that we approximate the full phenotypic body size range given the temperature regime. Upon emergence and complete hardening, all individuals were frozen and stored in 70% ethanol. Once all individuals had emerged, we haphazardly selected 30–50 indi-

Table 1: Taxonomic authority, population origin, and the direction and extent of sexual size dimorphism (SSD) in the 11 taxa studied here (data from Rohner et al. 2016)

Species	Origin	SSD	SDI
<i>Saltella sphondylii</i> (Schränk, 1803)	Zurich	Female biased	.03
<i>Sepsis cynipsea</i> (Linnaeus, 1758)	Zurich	Female biased	.07
<i>Sepsis duplicata</i> Haliday, 1838	Zurich	Female biased	.12
<i>Sepsis flavimana</i> Meigen, 1826	Zurich	Female biased	.09
<i>Sepsis lateralis</i> Wiedemann, 1830	La Laguna, Spain	Male biased	−.03
<i>Sepsis neocynipsea</i> (EU) Melander & Spuler, 1917	Sörenberg, Switzerland	Female biased	.05
<i>S. neocynipsea</i> (NA) Melander & Spuler, 1917	Belgrade, MT	Male biased	−.04
<i>Sepsis orthocnemis</i> Frey, 1908	Zurich	Female biased	.07
<i>Sepsis punctum</i> (EU) (Fabricius, 1794)	Zurich	Male biased	−.07
<i>S. punctum</i> (NA) (Fabricius, 1794)	Syracuse, NY	Female biased	.03
<i>Sepsis thoracica</i> (Robineau-Desvoidy, 1830)	Zurich	Male biased	−.08

Note: The sexual size dimorphisms index (SDI), a standardized ratio (Fairbairn et al. 2007), was calculated by dividing the size of the larger sex by the smaller and subtracting 1 from this ratio. The index arbitrarily defines SDI as positive if females are larger and negative if males are larger. EU = Europe; NA = North America.

viduals per sex and species covering the full phenotypic range for morphological measurements.

The right forelegs, midlegs, and hindlegs, as well as the right wing, were removed from the thorax and mounted on a glass slide using Euparal. We subsequently took pictures of all dissected appendages as well as the thorax (lateral view) using a Leica DFC490 camera mounted on a Leica MZ12 microscope. The lengths of the forefemur, foretibia, midtibia, hindtibia, and the thorax were measured using digitized landmarks (derived from tpsDig; Rohlf 2009). We also estimated wing length and width as depicted in figure 1c.

Forefemur morphology differs strongly among species, ranging from a sheer lack of any modification (e.g., *Sepsis duplicata*) to pronounced exaggeration (e.g., *Sepsis lateralis*, *S. punctum*). As the apparent degree of exaggeration does not necessarily relate to femur length, we quantified investment in forefemur morphology by estimating its average width. We thus measured the total area of the forefemur (following Busso and Blanckenhorn 2018a) and divided it by its length.

Hindtibia length was among the traits loading most strongly on the first principal component (table S1; tables S1, S2 are available online) and was always close to isometry when calculating (sex-specific) multivariate allometric slopes (Jolicoeur 1963; fig. S1, available online); it was therefore used as our best estimate of overall body size (as in previous studies; e.g., Martin and Hosken 2004; Blanckenhorn 2007; Rohner et al. 2018). To test for taxon and sex effects on overall body shape allometry, we first used MANCOVA fitting all focal traits as a function of log hindtibia length, sex, taxon, and their interactions using type III sums of squares. Static trait- and sex-specific allometric slopes were calculated by regressing log trait size against log hindtibia length in a reduced major axis regression (RMA). We tested for intraspecific associations of the degree of trait-specific condition dependence between the sexes using Pearson's product moment correlations. We further used the logarithm of the ratio between the male and female allometric RMA slopes as an index of sex-specific condition dependence (positive if males have steeper allometries).

Sexual Dimorphism

As some taxa investigated here secondarily evolved male-biased sexual size dimorphism (Rohner et al. 2016, 2018), comparing absolute trait sizes between species does not necessarily reflect sex differences in the relative investment in a trait. To remove any variation due to overall body size, we first calculated the residual trait size derived from a regression of trait size against hindtibia length using all data (sexes were pooled). These residuals were z-scored and averaged by sex. The average difference between the sexes then

represents our size-controlled index of relative sexual dimorphism. In what follows, we refer to this measure unless specifically discussing sexual size dimorphism.

Relationship between Sex-Specific Condition Dependence and Sexual Dimorphism

To test for a relationship between sex-specific condition dependence (i.e., sex differences in allometric slopes) and relative sexual dimorphism among traits, we calculated Pearson's correlation coefficients for each species separately. To test for a general relationship independent of species and trait identity, we pooled all data and used a mixed model with species and trait as crossed random effects (using the lme4 R package; Bates et al. 2015).

Our comparative approach further allowed testing for the coevolution of sex-specific condition dependence and sexual dimorphism of each trait across the phylogeny. To this end, we used phylogenetic generalized least-squares (PGLS) models (using the R package caper; Orme et al. 2013) with the average species- and sex-specific condition dependence as response and relative sexual dimorphism as the predictor variable. To account for the phylogenetic relationships among species, we used a cropped version of the phylogeny published by Zhao et al. (2013), setting all branch lengths to unity. The branch length transformation parameter λ was estimated using maximum likelihood.

Linking Mating System Variation to Sex-Specific Scaling Relationships

Animal species in which males are the larger sex, such as most mammals, typically show male-male competition for access to females, while in species with female-biased sexual size dimorphism, males typically scramble for access to mates and females are choosier (Andersson 1994; Fairbairn 1997; Blanckenhorn 2005; Lüpold et al. 2015). Accordingly, the intensity of precopulatory sexual selection on male size correlates with the direction of sexual size dimorphism in sepsid flies (Puniamorthy et al. 2012a, 2012b; Rohner et al. 2016): in species or populations in which males are the larger sex, males show pronounced male-male competition or combat behavior that is also apparent under laboratory conditions (Zerbe 1993; Eberhard 1999, 2002; Rohner et al. 2016; Busso and Blanckenhorn 2018b). We therefore used the direction of dimorphism as a crude proxy for the mating system, that is, the presence of pronounced male-male competitive behavior. (Note that using a continuous index of sexual dimorphism shows qualitatively similar results.) To test for an association between the mating system and body shape or scaling relationships, we compared sex-specific allometric slopes and relative sexual dimorphism of taxa with male- and female-biased dimorphism using PGLS.

Results

Sex-Specific Condition Dependence

Overall body shape varied strongly with body size (MANCOVA; log hind-tibia length: $F_{7, 838} = 19,149.2$; $P < .001$; $\eta_p^2 = 0.99$), among taxa ($F_{70, 6,510} = 100.5$; $P < .001$; $\eta_p^2 = 0.48$), and between the sexes ($F_{7, 838} = 746.2$; $P < .001$; $\eta_p^2 = 0.85$). Apart from these main effects, all interactions were statistically significant: that is, allometric relationships differed between taxa (taxon \times log hind-tibia length: $F_{77, 5,908} = 9.6$; $P < .001$; $\eta_p^2 = 0.17$) and the sexes (log hind-tibia length \times sex: $F_{7, 838} = 15.1$; $P < .001$; $\eta_p^2 = 0.14$). Sex-specific allometries and sex differences in overall body shape further differed between taxa (taxon \times sex: $F_{70, 5,908} = 19.6$; $P < .001$; $\eta_p^2 = 0.18$; taxon \times log hind-tibia length \times sex: $F_{70, 5,908} = 2.4$; $P < .001$; $\eta_p^2 = 0.03$).

In both males and females, thorax length and forefemur width tended to be strongly hyperallometric (fig. 2; table S2), while wing length and wing width were hypoallometric (all relative to hind-tibia length; fig. 2; table S2). Allometric slopes were strongly correlated between the sexes (linear mixed model using trait identity and species as random effects: $F_{1, 73.8} = 59.1$; $P < .001$; $r = 0.67$ [95% confidence interval: 0.53, 0.76]; $P < .001$).

Sexual Dimorphism

Relative sexual dimorphism varied strongly among traits (fig. 3). Thorax length, wing width, and wing length were always larger in females, whereas forefemur width and length were larger in males except for *Saltella sphondylii* and *Sepsis duplicata*, both of which lack pronounced sex-specific modification of this body part (Pont and Meier 2002). Fore- and midtibia length showed more idiosyncratic patterns across species (see fig. 3).

Relationship between Sex-Specific Condition Dependence and Sexual Dimorphism

The extent of sexual dimorphism correlated positively with the sex difference in condition dependence (linear mixed model using trait and taxon as random effects: $\chi^2_{(1)} = 16.80$; $P < .001$; $r = 0.52$ [0.28, 0.68]). Hence, traits that are relatively larger in males also more strongly depend on condition in males (and vice versa). This relationship remained statistically significant when forefemur width, the most pronounced sexually dimorphic trait, was excluded from the analysis ($\chi^2_{(1)} = 5.43$; $P = .020$). Note that these relationships were not often significant when tested within species (table 2), but a strong overall pattern persisted (avg. $r = 0.66 \pm 0.04$ SE). Interestingly, this relationship among traits was stronger in taxa with pronounced male-male competition ($r = 0.75 \pm 0.02$ SE, $n = 4$) than in taxa with more

female choice ($r = 0.60 \pm 0.05$ SE, $n = 7$; PGLS: $F_{1,9} = 7.30$, $P = .024$).

We also found a positive relationship between sex-specific condition dependence and sexual dimorphism for forefemur width, foretibia length, and the length of the midtibia across species (fig. 4). Taxa that evolved increased sexual dimorphism in these traits hence also evolved increased differences in condition dependence between the sexes. The remaining traits showed much weaker and nonsignificant patterns (fig. 4).

Linking Mating System Variation to Sex-Specific Scaling Relationships

Taxa with male-biased SSD (and more male-male competition) had broader and more condition-dependent (i.e., more hyperallometric) male forefemora (relative size; PGLS: $F_{1,9} = 9.16$, $P = .014$; fig. 5a; static allometric coefficient; PGLS: $F_{1,9} = 9.65$, $P = .013$; fig. 5b). All other traits did not systematically present such differences (not shown).

Discussion

We here demonstrated that sex-specific condition dependence and sexual dimorphism consistently covary among traits within 11 sepsid taxa. Using a comparative approach, we further showed that this relationship extends to the interspecific level. Species with higher degrees of sexual dimorphism exhibit greater sex differences in their condition dependence for sexual but not necessarily for nonsexual traits: the overall correlation based on all traits and taxa was $r = 0.52$ [0.28, 0.68]. As a whole, our results support the prediction that sexually antagonistic directional selection not only mediates the evolution of sexual dimorphisms but also the establishment of sex differences in condition dependence, both within and across species. This relationship is stronger in taxa that secondarily evolved male-biased SSD with pronounced male-male competition (the derived state in this group of flies), likely driven by stronger sexual selection on overall body size and/or forefemur width in males (Dmitriew and Blanckenhorn 2012; Puniamoorthy et al. 2012a, 2012b; Rohner et al. 2016; Busso and Blanckenhorn 2018b). In what follows, we elaborate on the causes and consequences of this coevolution of sexual dimorphism and condition dependence, and discuss how mating system variation may influence the evolution of scaling relationships.

Ultimately, different male and female phenotypes are thought to evolve due to sexually divergent fitness optima, resulting from variation in the strength, shape, and direction of natural and sexual selection between the sexes (Hedrick and Temeles 1989; Shine 1989; Blanckenhorn 2005; Fairbairn et al. 2007; although the specific role of ecology

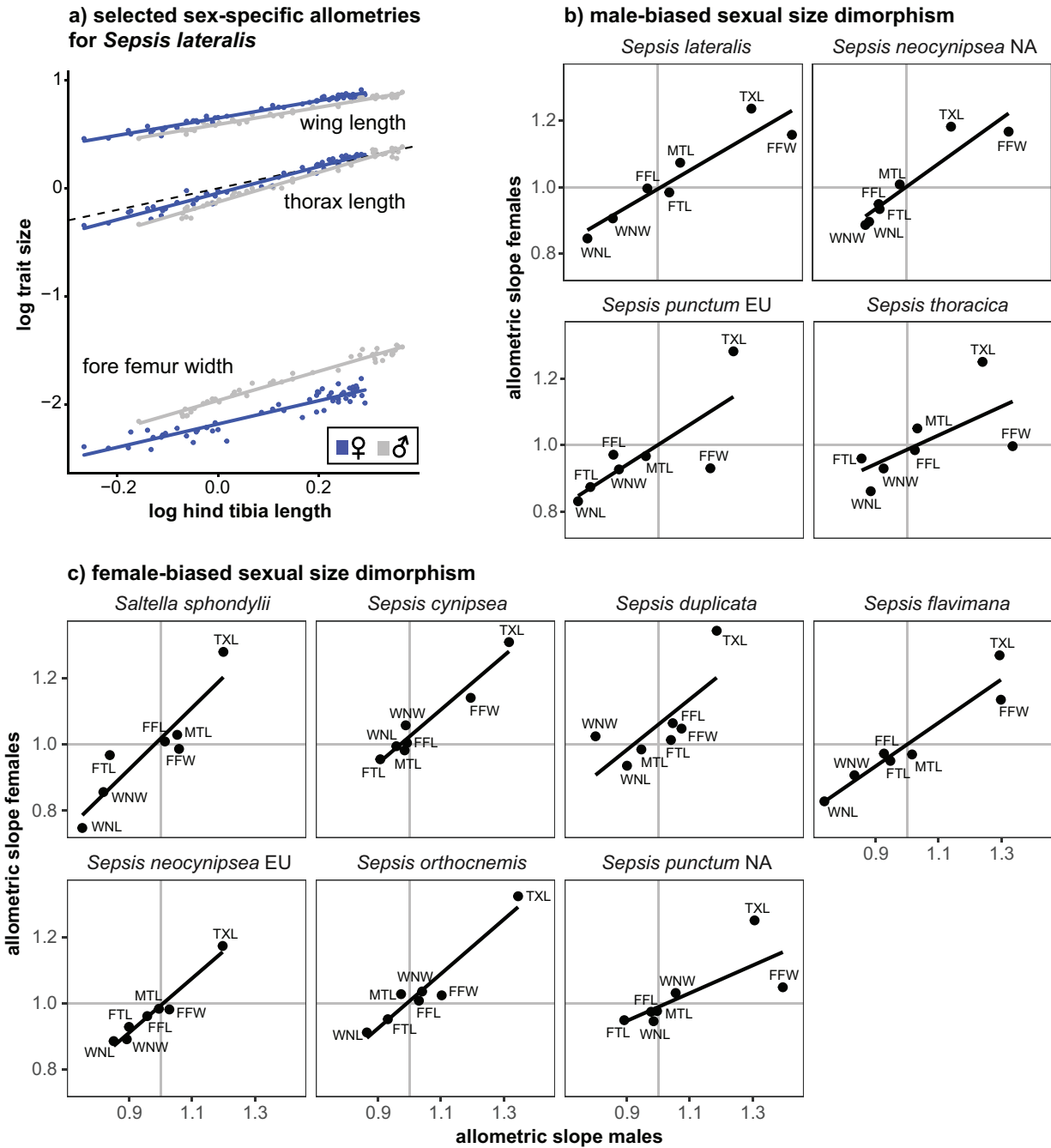


Figure 2: Static allometric (reduced major axis regression) slopes (relative to hindtibia length) differ for various traits and somewhat between species but generally correlate strongly between the sexes. Particularly, thorax length is strongly hyperallometric in all taxa, while wing length and width are hypoallometric. *a*, Sex-specific allometries for wing length, thorax length, and forefemur width as an example (the dashed line indicates isometry). *b*, Patterns in taxa with male-biased sexual size dimorphism (SSD). *c*, Patterns in taxa with female-biased SSD. FFL = forefemur length; FFW = forefemur width; FTL = foretibia length; MTL = midtibia length; TXL = thorax length; WNL = wing length, WNW = wing width. See figure 1.

in shaping sexual dimorphisms remains contentious, particularly in insects without parental provisioning [Blanckenhorn 2005]). However, even under consistent and sexually

antagonistic directional selection, the evolution of sexual dimorphism in any trait must be hampered by genetic correlations between sexes (Lande 1980). As conspecific males

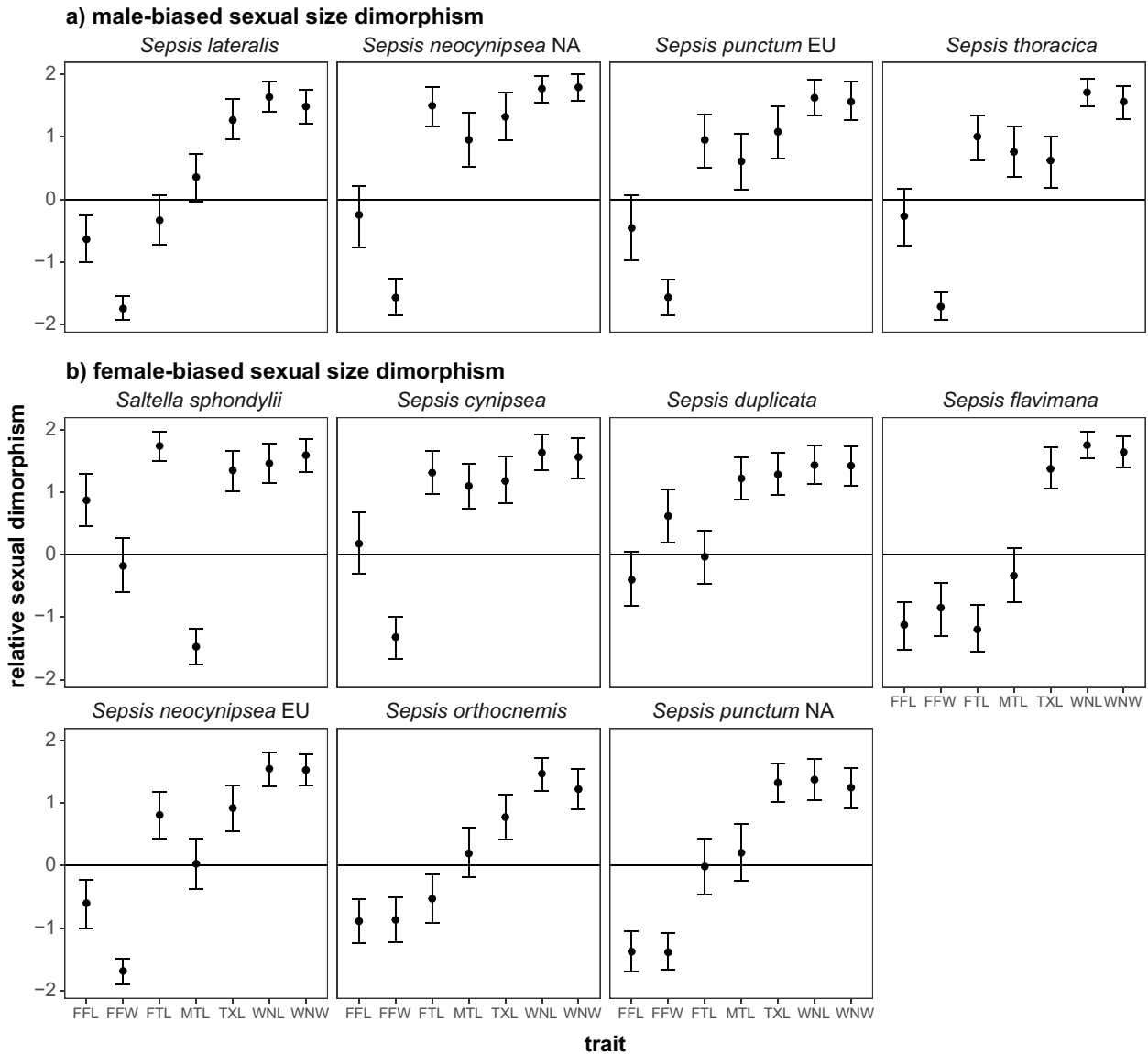


Figure 3: Relative sexual dimorphism (corrected for dimorphism in overall size, i.e., hindtibia length) varies strongly among traits within species, though patterns are rather consistent across species. Positive scores indicate bias toward males (a), and negative scores indicate female-biased dimorphism (b). Error bars represent 95% bootstrap confidence limits. FFL = forefemur length; FFW = forefemur width; FTL = foretibia length; MTL = midtibia length; TXL = thorax length; WNL = wing length; WNW = wing width. See figure 1.

and females usually share most of their genome, including genes controlling the basic parameters of growth and development (Fairbairn 1997), such between-sex correlations can be strong and must be overcome in order to reduce or resolve intersexual (ontogenetic) conflict (Rice and Chippindale 2001; Badyaev 2002). In theory, sexual conflicts can be overcome if condition dependence can evolve in a sex-specific manner (Badyaev 2002). At minimum requiring the evolution of a sex-linked locus causing condition-dependent expression in merely one sex, this would permit optimal investment in secondary sexual traits without displacing the

opposite sex from its fitness optimum—a form of sex-limited epistasis. While resolving sexual conflict, this would also establish a common genetic and developmental basis for sexual dimorphisms and condition dependence.

Such mechanisms are evident in several previously studied species, for instance, in the neriid fly *Telostylinus angusticollis*. Bonduriansky (2007a) showed that condition dependence and sexual dimorphism are tightly correlated among traits in this species, suggesting that most (if not all) sexual dimorphism in various traits is caused by differential sex-specific condition dependence, such that, empirically, the two

Table 2: Among-trait correlations between sex-specific condition dependence and sexual dimorphism for the 11 taxa investigated, here grouped by the direction of sexual size dimorphism (SSD; male or female larger)

SSD, species	<i>t</i>	df	<i>r</i> [95% CI]
Female larger:			
<i>Saltella sphondylii</i>	2.01	5	.67 [−.11, .8]
<i>Sepsis cynipsea</i>	2.92	5	.79 [.07, .87]
<i>Sepsis duplicata</i>	1.71	5	.61 [−.18, .77]
<i>Sepsis flavimana</i>	1.47	5	.55 [−.23, .75]
<i>Sepsis neocynipsea</i> (EU)	2.04	5	.67 [−.11, .8]
<i>Sepsis orthocnemis</i>	1.35	5	.52 [−.25, .73]
<i>Sepsis punctum</i> (NA)	.99	5	.40 [−.33, .69]
Average			.60 (±.05 SE)
Male larger:			
<i>Sepsis lateralis</i>	2.63	5	.76 [.01, .85]
<i>S. neocynipsea</i> (NA)	2.52	5	.75 [−.01, .84]
<i>S. punctum</i> (EU)	2.19	5	.70 [−.08, .82]
<i>Sepsis thoracica</i>	3.03	5	.80 [.09, .87]
Average			.75 (±.02 SE)

Note: Traits that are relatively larger in males tend to exhibit a corresponding increase in their allometric slope compared to females, and vice versa (global avg. correlation: 0.66 ± 0.04 SE). EU = Europe; NA = North America.

concepts are difficult to distinguish. Similarly, Ledón-Rettig and Moczek (2016) found that condition dependence and sexual dimorphism share genetic underpinnings at the transcriptome level, also suggesting a common developmental basis. Corroborating these results and extending them to the comparative level, we here found that although allometric slopes (signifying condition dependence) always correlate strongly between the sexes (fig. 2), more dimorphic traits also feature larger differences in their sex-specific condition dependence across 11 closely related taxa (table 2). This result documents a strong and consistent pattern in sepsid flies. Measuring seven traits in 11 species allowed us to estimate that sex-specific condition dependence explained merely about 30% of the variance in sexual dimorphism across species and traits. Compared to *T. angusticollis*, in which 90% of the variance in sexual dimorphism was explained by sex-specific condition dependence (Bonduriansky 2007a), sexual dimorphism in overall shape of sepsid flies thus seems far less condition dependent. Although direct comparisons between the neriids and sepsids are hampered by different traits and methodologies used, the markedly different variance components reported nonetheless suggest varying degrees of interdependence between condition dependence and sexual dimorphism across taxa (and traits), implying that this dependency can therefore evolve.

Such interspecific variation is also evident among the sepsids examined here, in that species with male-biased SSD, generally featuring more male-male competition, showed a significantly tighter relationship between trait dimorphism and sex-specific condition dependence ($r = 0.75$) than spe-

cies with female-biased SSD ($r = 0.60$). On the one hand, such directional reversals of size dimorphism might be rather recent, and in response, sex-specific condition dependence (i.e., plasticity) may be more likely to evolve than functional genetic sex differences, particularly if plasticity can better alleviate any constraints imposed by strong genetic correlations between sexes (as argued above; Lande 1980). In the long run, however, the evolution of (fixed) sex linkage might subsequently weaken such sex-specific condition dependence, as appears to be the case in the taxa with the ancestral female-biased SSD.

On the other hand, the difference between taxa exhibiting either male- or female-biased dimorphism may well relate to variation in the selective regime imposed on males. If sexual selection leads to the evolution of larger males, secondary sexual traits might acquire novel functions, or alternatively, their ancestral function may persist and be further strengthened during combat or courtship through positive selection. That is, sexual selection may promote further evolutionary amplification of the hyperallometric male slope (Gould 1966; Bonduriansky 2007c), thus strengthening the relationship between sex-specific condition dependence and sexual dimorphism of particular secondary sexual and other morphologically integrated traits. Although mostly anecdotal, observations in both the laboratory and the field suggest heightened degrees of male-male competition for access to females in those sepsids that secondarily evolved male-biased SSD. For instance, whereas males of species with female-biased SSD use their forelegs primarily to interact with the female during their elaborate precopulatory courtship displays, males of species with male-biased SSD use their modified forefemora to also fend off nearby competitors (Eberhard 1999, 2002) or attempt to vigorously dislodge males that are already mounted on females (particularly evident in North American vs. European *Sepsis punctum*; Zerbe 1993; Puniamoorthy et al. 2012a). In taxa with male-biased SSD, the armored foreleg therefore gained additional functions in male-male competition. Accelerating selection may thus have tightened the relationship between dimorphism and condition dependence (and possibly other morphologically integrated traits) in taxa with male-biased SSD. Future research will, however, be necessary to experimentally assess the underlying drivers of this variation.

We here comprehensively extended empirical microevolutionary evidence to the macroevolutionary level, a prime goal of evolutionary ecology. Aligning with the overall sex-specific body-size plasticity, which generally correlates with the degree and direction of SSD across insects (Teder and Tammaru 2005; Stillwell et al. 2010; Rohner et al. 2018), we here found trait-specific support for this pattern across species. We uncovered significant correlations between (relative) sexual dimorphism and sex differences in condition dependence only for the investigated fore- and midleg traits

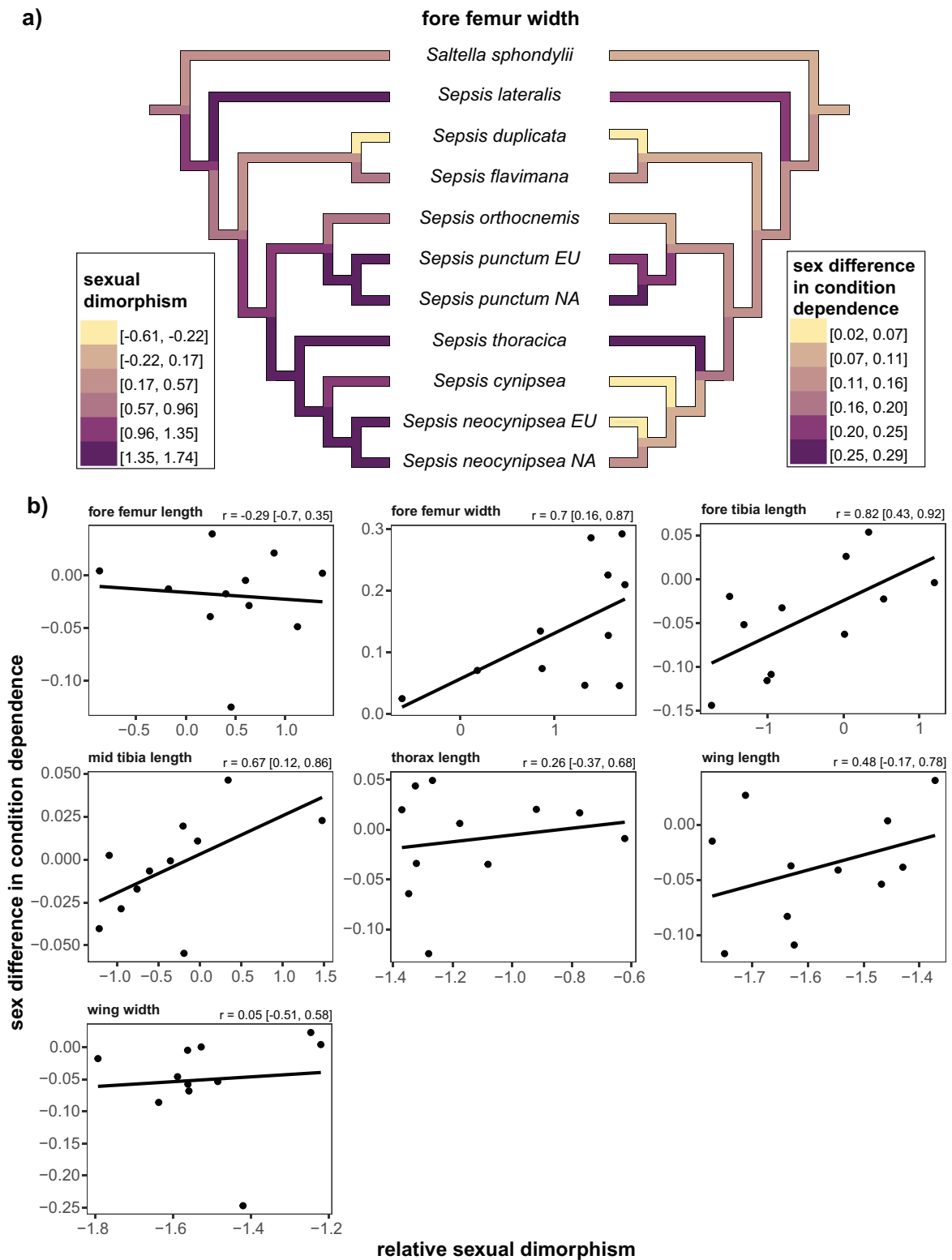


Figure 4: Sex-specific condition dependence as a function of sexual dimorphism among species. *a*, Ancestral character reconstruction for forefemur width as an example (squared-change parsimony; for illustration only). *b*, Raw, uncorrected values for all seven traits. Phylogenetically corrected correlation coefficients with corresponding 95% confidence limits are given.

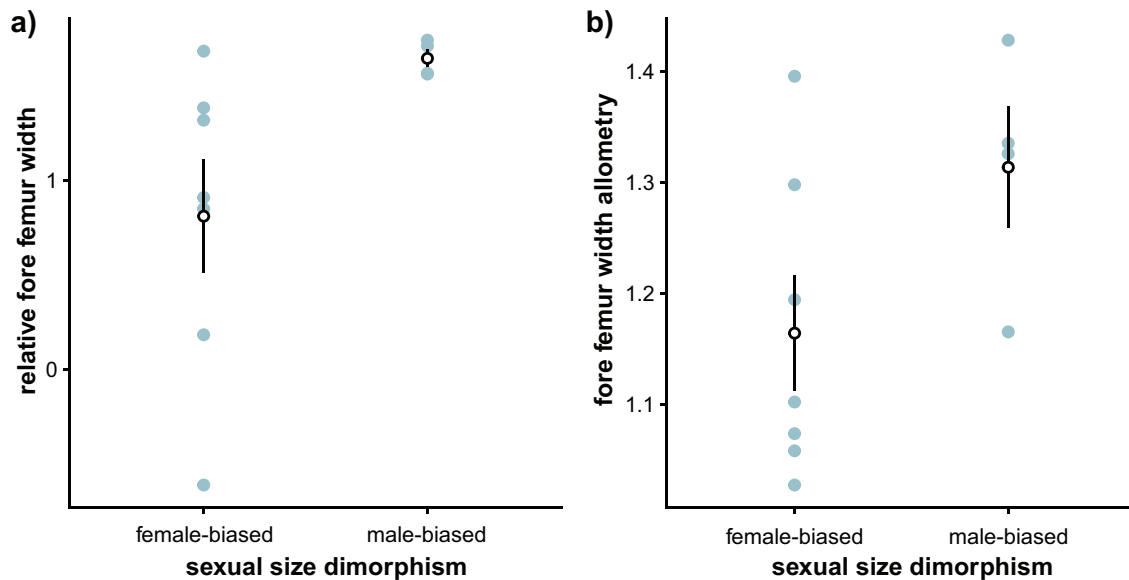


Figure 5: Taxa with male-biased sexual size dimorphism (the derived character state; cf. Rohner et al. 2016) show increased investment in relative forefemur width (*a*) and steeper allometric slopes (i.e., condition dependence; *b*) for this trait. Plots show raw, uncorrected values. Phylogenetically corrected statistics are given in the text.

(fig. 4): taxa that evolved relatively broader forefemora and longer foretibiae in males showed heightened condition dependence in males compared to females. The same applies to the length of the midtibiae. Such relationships are expected if the costs and benefits of increased trait investment in males are shared among species. Then, increased selection on trait dimorphism drives the evolution of condition dependence because large individuals benefit more from trait production and/or maintenance. This scenario apparently only applies to the forelegs, which are sexually selected in some species but not in others, and indeed appear to be costly (as indicated by more hyperallometric growth compared to females; Parker 1972; Zerbe 1993; Blanckenhorn et al. 2000; Dmitriew and Blanckenhorn 2012, 2014; Puniamoorthy et al. 2012*a*, 2012*b*; Busso and Blanckenhorn 2018*b*). The midtibia is frequently observed to be used in the transmission of chemical compounds or the stimulation of the female during copulation and thus likely also appears to be under sexual selection in males (Eberhard 2001*a*; Puniamoorthy et al. 2009; Araujo et al. 2014; Puniamoorthy 2014). In contrast, patterns were weak and nonsignificant in all those traits that do not seem to play a major role in the sexual context (e.g., thorax, wing). This observed heterogeneity among traits may thus relate to varying levels of sexual selection across species, to the extent that only traits under consistent directional selection may drive the pattern of coevolution observed. This contrasts with cases where dimorphism is associated with selection driven by ecological niche differentiation between sexes (i.e., ecological sexual dimorphism; Shine 1989, 1991; Temeles et al. 2000).

When the sexes represent different ecotypes, we expect stabilizing, and not directional, selection acting on the same trait in each sex, and condition dependence should not play a major role if dimorphism is truly ecological.

Conclusions

Across 11 closely related sepsids with varying mating systems, we found support for a relationship between sex differences in condition dependence and sexual trait dimorphisms among traits. Although these correlations were overall weaker than in some previously studied insects (Bonduriansky 2007*a*, 2007*b*, 2007*c*), this suggests a common developmental basis. Our findings reiterate that sex-specific condition dependence and sexual dimorphism are not necessarily independent biological properties, as the latter may arise through the former at least to some extent. We further found this relationship to coevolve for traits that are sexually selected in males of some but not other species (fore- and midleg morphology), particularly in species that secondarily evolved male-biased sexual size dimorphism (*Sepsis thoracica*, European *S. punctum*, *Sepsis lateralis*, North American *Sepsis neocynipsea*). Other traits assumed to be primarily under natural selection (thorax and wings) showed no such association. Although we here performed a phenotypic and not a quantitative genetic study, we systematically compared sex differences in trait plasticity of closely related species that likely share genetic mechanisms. In manipulating food availability, we thus

estimated mere environmental (V_e) as well as corresponding genotype-by-environment effects ($V_{g \times e}$), which presumably evolved due to similar selection pressures in the past. Which and how many genes are involved in regulating such sex-specific trait expression remains to be documented.

Whereas the evidence on the relationship between condition dependence and trait dimorphism presented here and elsewhere (Wilkinson and Taper 1999; Cotton et al. 2004a, 2004b; Bonduriansky 2007a, 2007b, 2007c) refers mostly to insects, we suspect it to be a general pattern in organisms where sexually antagonistic directional sexual selection drives dimorphism. After all, the underlying proximate causes of sexual size dimorphism in terms of growth and developmental mechanisms, both of which are strongly dependent on environmental conditions, are well established in many other vertebrate and invertebrate taxa (Jarman 1983; Leigh 1992; Teather and Weatherhead 1994; Blanckenhorn et al. 2007; Bro-Jørgensen 2007). Nevertheless, the causes and consequences of this phenomenon warrant further mechanistic scrutiny, particularly at the physiological and genetic levels (Tang et al. 2011; Emlen et al. 2012; Rohner et al. 2017; Shingleton and Frankino 2018).

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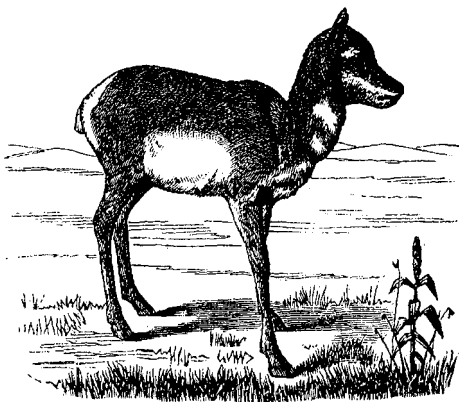
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“Kid of the prong buck, four months old.” From “The American Antelope, or Prong Buck” by J. D. Caton (*The American Naturalist*, 1876, 10:193–205).