

RESEARCH ARTICLE

Static allometries do not reflect evolutionary allometry in exaggerated weaponry of male New Zealand sheetweb spiders (*Cambridgea* spp.)

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Abstract

Across the animal kingdom, exaggerated weaponry is frequently used by one sex to contest access for potential mates. Within species, if disproportionate investment in weaponry confers an advantage to larger individuals, this may result in positive static allometry. It is predicted that the same selective pressures may also lead to positive evolutionary allometry, where larger species bear disproportionately large weapons on average, compared with smaller species. Furthermore, in species with stronger sexual selection, the static allometries of those weapons are expected to steepen. All adult males across the New Zealand sheetweb spider genus *Cambridgea* bear exaggerated chelicerae, which are used to compete for control of females' webs. Here, we characterize the distribution of chelicera lengths within each sex of 12 *Cambridgea* species to show that chelicerae almost always exhibit positive static allometry in males while female chelicera lengths are consistently isometric. We use comparative phylogenetic methods to demonstrate that the slopes of static allometries steepen in males of larger species but that the ratio of average chelicera length to cephalothorax width is tightly conserved across taxa, leading to an isometric evolutionary allometry. While static allometries indeed steepen in larger species, possibly due to stronger sexual selection, this conservation of relative trait size suggests that chelicera length is subject to other stabilizing selective pressures. Changes to species body plans might be constrained, while still allowing for disproportionate investment in weapon traits in the upper range of intraspecific body sizes.

KEYWORDS

animal weapons, arachnology, morphology, phylogenetic least squares, sexual selection

1 | INTRODUCTION

Sexually selected weaponry is prevalent in a wide range of animal species and encompasses a spectacular array of body structures expressed with different degrees of exaggeration (Emlen, 2008;

Rico-Guevara & Hurme, 2019). Sexually selected weapons (hereafter: weapons) evolve via selection resulting from intrasexual competition over mates or resources important to mates. The majority of studies investigating the use of sexually selected weaponry have focused on males competing for access to females, which is common in

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insects (dung beetles, *Onthophagus taurus*, Moczek & Emlen, 2000; potter wasps, *Synagris cornuta*, Longair, 2004; giraffe weevils, *Lasioryhynchus barbicornis*, Painting & Holwell, 2013, cave wētā, *Pachyrhamma waitomoensis*, Fea & Holwell, 2018), spiders (jumping spiders, *Lyssomanes viridis*, Tedore & Johnsen, 2012; sheetweb spiders, *Cambridgea foliata*, Walker & Holwell, 2018), crustaceans (shore crabs, *Carcinus maenas*, Sneddon et al., 1997; fiddler crabs, *Uca* spp., Swanson et al., 2013) and mammals (bighorn sheep, *Ovis canadensis*, Coltman et al., 2002), among other animals. However, females are also known to compete for mates with sex-specific weaponry, such as occurs in jacanas (Berglund, 2013; Jenni & Collier, 1972).

Weapon morphology can vary widely in size and shape not only across species but among individuals of the same species. Commonly, the relative expression of weapons covaries with body size across closely related species and between individuals. Patterns of traits' covariation with body size—allometries—occur across species (evolutionary allometries), within species (static allometries) and within individuals across different developmental stages (ontogenetic allometries) and reflect the interaction of species-specific developmental and selective processes. The allometric scaling relationship is expressed as the power function:

$$y = ax^b.$$

In this function, y is the measure of the trait of interest, a is a normalization constant or the y -intercept, x is the measure of body size and b is the allometric or scaling exponent (Gould, 1966; Huxley, 1932; Thompson, 1917). If the allometric exponent is 1, it implies that the trait of interest scales proportionally with body size and this is described as isometry. In contrast, positive allometry occurs when the scaling exponent is greater than one and negative allometry when the scaling exponent is less than one.

Within species, positive static allometries, in which large individuals of a species possess disproportionately large weapons, have received substantial attention (Eberhard et al., 2018; Kodric-Brown et al., 2006; O'Brien et al., 2018; Petrie, 1988) and can result from a range of selective environments (Bonduriansky, 2007). In part, this diversity of origins results from the different (and sometimes multiple) biomechanical and behavioural functions that weapons can have (Eberhard et al., 2018). While some weapons are used to contact and exert force against an opponent, others allow combatants to assess each other's fighting ability ('threat signals'). Larger weapons may be beneficial because they provide a biomechanical advantage in contests. Alternatively, when individuals use trait size to assess each other's fighting ability, a greater disparity in weapon size is required for accurate assessment as individuals and their weapons become larger (Weber's Law). This makes it beneficial for larger individuals to further invest in enlarging their weapons (Eberhard et al., 2018). In both cases, positive static allometries for weapons can result provided that large individuals receive fitness gains from investing disproportionately in weaponry (Bonduriansky & Day, 2003; Eberhard et al., 2018; Emlen, 2008; Petrie, 1988). Simultaneously, the expression of exaggerated weaponry may be unnecessarily costly for small males who, therefore, invest less (Taborsky & Brockmann, 2010).

A positive evolutionary allometry will also result if larger species have, on average, larger weapons (e.g. Bovidae: Bro-Jørgensen, 2007; Tidière et al., 2017; porcelain crabs, *Petrolisthes*: Baeza & Asorey, 2012). This may occur if sexual selection on weapon size is stronger in larger species and/or selection for larger weaponry creates a concomitant increase in body size (Summers & Ord, 2022). However, how static and evolutionary allometries interrelate among closely related species remains relatively unexplored despite the two relationships most likely sharing the same developmental properties (Gould, 1966; Pélabon et al., 2014). Within species, a heritable scaling relationship has been proposed as a plausible mechanism generating observed covariation of body and weapon size. In this case, differential trait expression of the same genotype is conditional on environmental variables such as food availability (Emlen & Nijhout, 2000). The insulin-like growth factor (IGF) signalling pathway in rhinoceros beetles (*Trypoxylus dichotomus*) is one such example of a mechanism in which horn tissues have heightened sensitivity to the physiological correlates of foraging success, producing large male morphs when a certain threshold for the physiological correlate, relating to juvenile nutrition, is exceeded (Emlen et al., 2012). Similar mechanisms have been implicated in a range of sexually selected characters in both holometabolous and hemimetabolous invertebrates (Nijhout & McKenna, 2018) and may be applicable to some vertebrates as well (Mahr et al., 2020). By their nature, we would expect that the heritable scaling relationships of ancestors must impact the allometries of descendants. That is, if a positive static allometry in a common ancestor is inherited, we would expect an overall positive evolutionary allometry for the trait across its multiple descendent species with larger species exhibiting heightened expression of weapon traits (Lande, 1979, 1985).

However, because these mechanisms are themselves under selection, we must, therefore, expect that static allometries should themselves evolve in intercept, slope and shape between closely related species. In some taxa, static allometries are steeper in species exhibiting evidence of stronger sexual selection (e.g. cervids, Clutton-Brock et al., 1980, Plard et al., 2011; earwigs, Simmons & Tomkins, 1996; stalk-eyed flies, Diopsidae, Voje & Hansen, 2013). By contrast, if natural selection through predation strongly selects against cumbersome weapons in already larger and more visible individuals, we may expect the opposite with shallower, isometric or even negative static allometries in large species.

Here we examine the evolution of weapons and their allometric relationships using a genus of sheetweb spiders endemic to New Zealand (*Cambridgea* L. Koch 1872; Desidae). With 30 extant described species (Paquin et al., 2010), males of this genus invariably bear exaggerated chelicerae, which are significantly larger than those of conspecific females. Relatively rare among spiders, males also have a similar body size to females and in some cases are slightly larger. We have previously demonstrated positive static allometries in male chelicera length for two species of this genus (*Cambridgea foliata*, Walker & Holwell, 2018; *Cambridgea plagiata*, McCambridge, Painting, et al., 2019; McCambridge, Walker, et al., 2019). We have also shown that males will lock their chelicerae together and push forward

against one another ('grappling') when fighting for access to females and that larger males are more likely to win contests (McCambridge et al., 2021; Walker & Holwell, 2018). Contests usually end when one male retreats and departs the web. Injuries are infrequent but, when they do occur, are the result of one male stabbing a fang into his opponent's cephalothorax during grappling. We have proposed that positive static allometry in *Cambridgea* spp. is driven by the fact that only the largest males escalate contests to grappling and, therefore, use their chelicerae while earlier contests phases consist of using only their anterior legs to tap at each other (Walker & Holwell, 2018).

This study aims to understand how chelicera length and static allometries for chelicera have evolved across this genus and to disentangle the potential roles of sexual and natural selection in this process. To achieve this, we use morphological data of 12 species of *Cambridgea* to (1) examine intraspecific variation in chelicera length, calculating static allometries for each sex and species and estimates of sexual size dimorphism; (2) compare average species traits for chelicera length and body size across species and sexes to estimate the evolutionary allometries for males and females of this genus; (3) compare how static allometries vary across the genus, using phylogenetic comparative method.

If positive static allometries are common within this genus, then we predict positive evolutionary allometry with disproportionately larger chelicerae in the largest *Cambridgea* species. If stronger sexual selection results in benefits to weapon exaggeration for larger individuals relative to other forms of selection, we also predict that static allometries steepen in larger species and species that have male-biased sexual size dimorphism. Sexual size dimorphism is commonly treated as an index for the strength of sexual selection (see: Macedo et al., 2013; Schütz & Taborsky, 2011). However, among *Cambridgea* species, SDI does not generally appear to be heavily male-biased. Therefore, we predict that, if sexual selection drives steeper male weapon allometries, those species with either larger absolute male size or larger size relative to females will exhibit steeper static allometries.

2 | MATERIALS AND METHODS

2.1 | Measurements

We measured chelicera length and cephalothorax width (used as a measure of body size for spiders) of 1087 spiders ($N_{\text{female}} = 490$; $N_{\text{male}} = 597$) using live specimens from the field and preserved specimens from Aotearoa, New Zealand's major natural history collections between November 2014 and May 2017. The collections we accessed include the Entomology Research museum, Lincoln University (LUNZ); the Museum of New Zealand Te Papa Tongarewa, Wellington (MONZ); the New Zealand Arthropod Collection, Landcare research (NZAC); Auckland War Memorial Museum, Auckland (AMNZ); and Otago Museum (OMNZ).

The 12 taxa sampled in this study were *Cambridgea ambigua* Blest & Vink, 2000; *Cambridgea annulata* Dalmis 1917; *Cambridgea antipodiana* (White, 1849); *Cambridgea arboricola* (Urquhart, 1891);

Cambridgea fasciata L. Koch; *Cambridgea foliata* (L. Koch, 1872); *Cambridgea obscura* Blest & Vink, 2000; *Cambridgea pallidula* Blest & Vink, 2000; *Cambridgea peelensis* Blest & Vink, 2000; *Cambridgea plagiata* Forster & Wilton, 1973; *Cambridgea quadromaculata* Blest & Taylor, 1995; and *Cambridgea reinga* Forster & Wilton, 1973.

We measured 43 specimens twice to conduct a repeatability test. Measurements had high repeatability for both chelicera length (0.985) and cephalothorax width (0.962) (Whitlock & Schluter, 2015). All measurements were made using hand callipers accurate to 0.01 mm.

2.2 | Species traits and static allometries of chelicera length

2.2.1 | Species trait estimates

We calculated arithmetic means of cephalothorax width and chelicera length for males and females of each species. We calculated a sexual size dimorphism index (SDI) for both chelicera length and cephalothorax width using the method outlined by Lovich et al. (2014) in which:

$$\text{SDI} = (\text{female body size} / \text{male body size}) - 1.$$

For this index, negative values indicate male-biased sexual size dimorphism and positive values indicate female-biased sexual size dimorphism. This index has been used in a range of studies including those on nephilid spiders (Kuntner & Cheng, 2016), tree frogs (*Scinax fuscovarius*, Goldberg et al., 2018) and slider turtles (*Trachemys scripta*, Gibbons & Lovich, 1990).

2.2.2 | Static allometries

We estimated the allometric relationship between the logs of cephalothorax width and chelicera length for each sex of each species using ordinary least squares regression and tested whether the allometric slope differed from isometry (Kilmer & Rodríguez, 2017). We conducted analyses in R 3.4.1. (R Core Team, 2017) using the *slope.test* function in the package *smatr* to test the correlation, *r*, between residual and fitted values and determine if slopes were significantly different to 1 (Warton et al., 2012). Due to the small number of individuals available for *C. reinga* and *C. pallidula* we excluded them from any analyses involving allometric relationships.

2.3 | Evolutionary allometry of species' chelicera length

2.3.1 | Variation in average species traits

To examine how traits covary across closely related species, we conducted Phylogenetic Generalized Least Squares (PGLS) regressions using average measures of species' traits for each sex with the analysis weighted based on the degree of relatedness between

species (Garamszegi, 2014). This process involves estimating the degree to which trait values are affected by relatedness (because lability of traits vary) using Pagel's λ , which is the most commonly used index (Blomberg et al., 2003; Münkemüller et al., 2012). We adopted the species tree built by Walker et al. (2019) (Figure 1) using branch lengths to weight our analyses. We used PGLS to examine how weapon size covaried with body size in males and females and cephalothorax SDI. We analysed covariation of weapon size using both absolute chelicera length and relative chelicerae size (average chelicera length/average cephalothorax width). Whenever we compared species' traits, we used averages of our measurements for those species.

Due to the limited number of species available for analyses (<20 species) PGLS would most likely underestimate phylogenetic signal (in our case, λ). For this reason, in addition to using the maximum likelihood method of estimating phylogenetic signal with the *comparative.data* function in the R package *caper* (Orme et al., 2013), we also conducted the analyses using a fixed value of phylogenetic signal, $\lambda = 1$, which is indicative of strong phylogenetic signal or a Brownian motion model of evolution with changes accruing solely as the result of genetic drift. In this latter scenario, the residuals of closely related species are similar because those species share a recent common ancestor, and this autocorrelation is accounted for when estimating model parameters (Symonds & Blomberg, 2014). As predicted, nearly all maximum likelihood estimates of phylogenetic signal returned an estimate of $\lambda = 0$. If we were to treat this estimate as correct, it would suggest that body size and chelicerae length have evolved independently in each species and that similarities in these traits are no more expected among closely related species than distantly related ones. This seems unlikely given that body size in other species, and morphological traits in general, usually exhibit a high degree of phylogenetic signal (Blomberg et al., 2003). When we conducted PGLS using this maximum likelihood estimate, similar results were produced as when we ran regressions using $\lambda = 1$. Therefore, we present only the results of PGLS using $\lambda = 1$.

2.3.2 | Variation in static allometries

To study how static allometries vary between *Cambridgea* species, we used PGLS to examine the covariation of static allometric slopes

(β_1) and intercepts (β_0) with average cephalothorax width for males and for females; and with SDI of cephalothorax width. We were not able to collect enough measurements to calculate static allometries for *Cambridgea reinga* and *Cambridgea pallidula*. Therefore, we used a modified tree with these species removed when conducting analyses involving estimates of static allometries.

3 | RESULTS

3.1 | Species traits and static allometries of chelicera length

3.1.1 | Species traits

The *Cambridgea* sampled for this study ranged in cephalothorax width from 2.43–5.96 mm while chelicera length varied from between 1.89–5.91 mm. *C. foliata* and *C. plagiata* were the largest of the taxa sampled while *C. reinga* was the smallest, irrespective of sex. Sexual dimorphism was generally very minor with respect to cephalothorax width (average SDI = -0.0261 ± 0.0468 SD). By contrast, male chelicerae were consistently about 25% larger than those of conspecific females (average SDI = -0.253 ± 0.060 SD; Table 1, Figures 2 and 3). This is further reflected in the relative chelicera sizes for each sex with male chelicera length demonstrating an almost 1:1 relationship with male cephalothorax width on average for each species. Meanwhile, for females, average chelicera length was generally about 70% that of cephalothorax width.

3.1.2 | Static allometries of chelicera length

Males of all but two species had positively allometric chelicerae while all females possessed weakly negatively allometric chelicerae or allometries, which were not significantly different to a slope of 1 (Table 2; Figure 4). Of the species studied, *C. plagiata* had the steepest male allometric slope ($\beta_1 = 1.49$, 95% CI = 1.31, 1.68). We did not find evidence that allometric slopes for male *C. ambigua* and

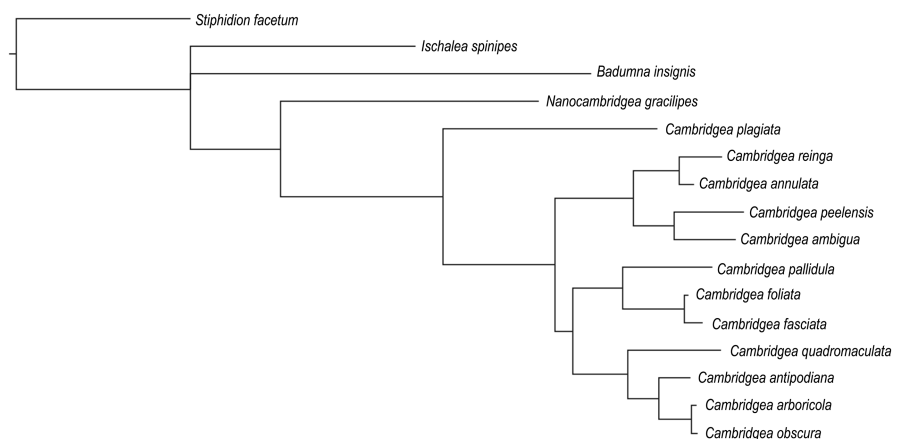


FIGURE 1 Bayesian species tree adopted from Walker et al. (2019).

TABLE 1 Descriptive statistics for male and female chelicera lengths and cephalothorax widths for 12 species of *Cambridgea* included in molecular phylogeny

Species	Chelicera length (mm)		Cephalothorax width (mm)		Relative chelicerae size (Chl/CW)		SDI		
	Female	Male	Female	Male	Female	Male	Chelicera	Cephalothorax	
<i>Cambridgea ambigua</i>	$n_m = 16$ $n_f = 12$	2.94 (0.483)	4.39 (0.614)	3.85 (0.732)	4.21 (0.421)	0.769 (0.053)	1.043 (0.097)	-0.330	-0.086
<i>Cambridgea annulata</i>	$n_m = 117$ $n_f = 63$	3.65 (0.666)	4.43 (1.27)	4.56 (0.771)	4.25 (0.869)	0.800 (0.059)	1.028 (0.132)	-0.175	0.074
<i>Cambridgea antipodiana</i>	$n_m = 56$ $n_f = 89$	3.20 (0.774)	4.44 (1.38)	4.17 (0.940)	4.30 (0.908)	0.767 (0.060)	1.019 (0.149)	-0.278	-0.030
<i>Cambridgea arboricola</i>	$n_m = 23$ $n_f = 35$	3.25 (0.523)	4.57 (1.31)	4.29 (0.617)	4.58 (0.938)	0.758 (0.044)	0.983 (0.121)	-0.287	-0.064
<i>Cambridgea fasciata</i>	$n_m = 32$ $n_f = 21$	2.50 (0.489)	3.62 (0.772)	3.22 (0.565)	3.55 (0.629)	0.775 (0.070)	1.017 (0.114)	-0.310	-0.093
<i>Cambridgea foliata</i>	$n_m = 152$ $n_f = 98$	4.41 (0.605)	5.91 (1.20)	5.73 (0.599)	5.72 (0.847)	0.771 (0.072)	1.025 (0.099)	-0.253	0.001
<i>Cambridgea obscura</i>	$n_m = 11$ $n_f = 20$	3.63 (0.453)	4.82 (1.41)	4.69 (0.557)	4.71 (0.906)	0.774 (0.047)	1.004 (0.125)	-0.245	-0.004
<i>Cambridgea pallidula</i>	$n_m = 5$ $n_f = 19$	2.45 (0.281)	2.82 (0.846)	3.08 (0.267)	3.03 (0.365)	0.795 (0.052)	0.918 (0.169)	-0.132	0.0164
<i>Cambridgea peenlensis</i>	$n_m = 12$ $n_f = 15$	3.54 (0.601)	4.52 (1.09)	4.43 (0.575)	4.80 (0.828)	0.797 (0.059)	1.000 (0.073)	-0.217	-0.078
<i>Cambridgea plagiata</i>	$n_m = 130$ $n_f = 49$	4.67 (0.707)	5.88 (1.38)	5.96 (0.815)	5.93 (0.841)	0.777 (0.101)	0.983 (0.153)	-0.206	0.004
<i>Cambridgea quadromaculata</i>	$n_m = 29$ $n_f = 56$	3.34 (0.410)	4.50 (1.00)	4.24 (0.537)	4.31 (0.697)	0.792 (0.069)	1.040 (0.109)	-0.257	-0.018
<i>Cambridgea reinga</i>	$n_m = 10$ $n_f = 3$	1.89 (0.320)	2.89 (0.927)	2.43 (0.439)	2.52 (0.456)	0.780 (0.009)	1.123 (0.239)	-0.345	-0.036

Note: Species averages presented with standard deviations in parentheses where applicable. n_m and n_f indicate number of male and female specimens measured, respectively. Chl refers to chelicera length, CW refers to cephalothorax width, and SDI refers to sexual size dimorphism index, which was calculated according to the method outlined by Lovich et al. (2014). Values range from -1 to 1 with negative values indicating degree of male bias while positive values indicate degree of female bias.

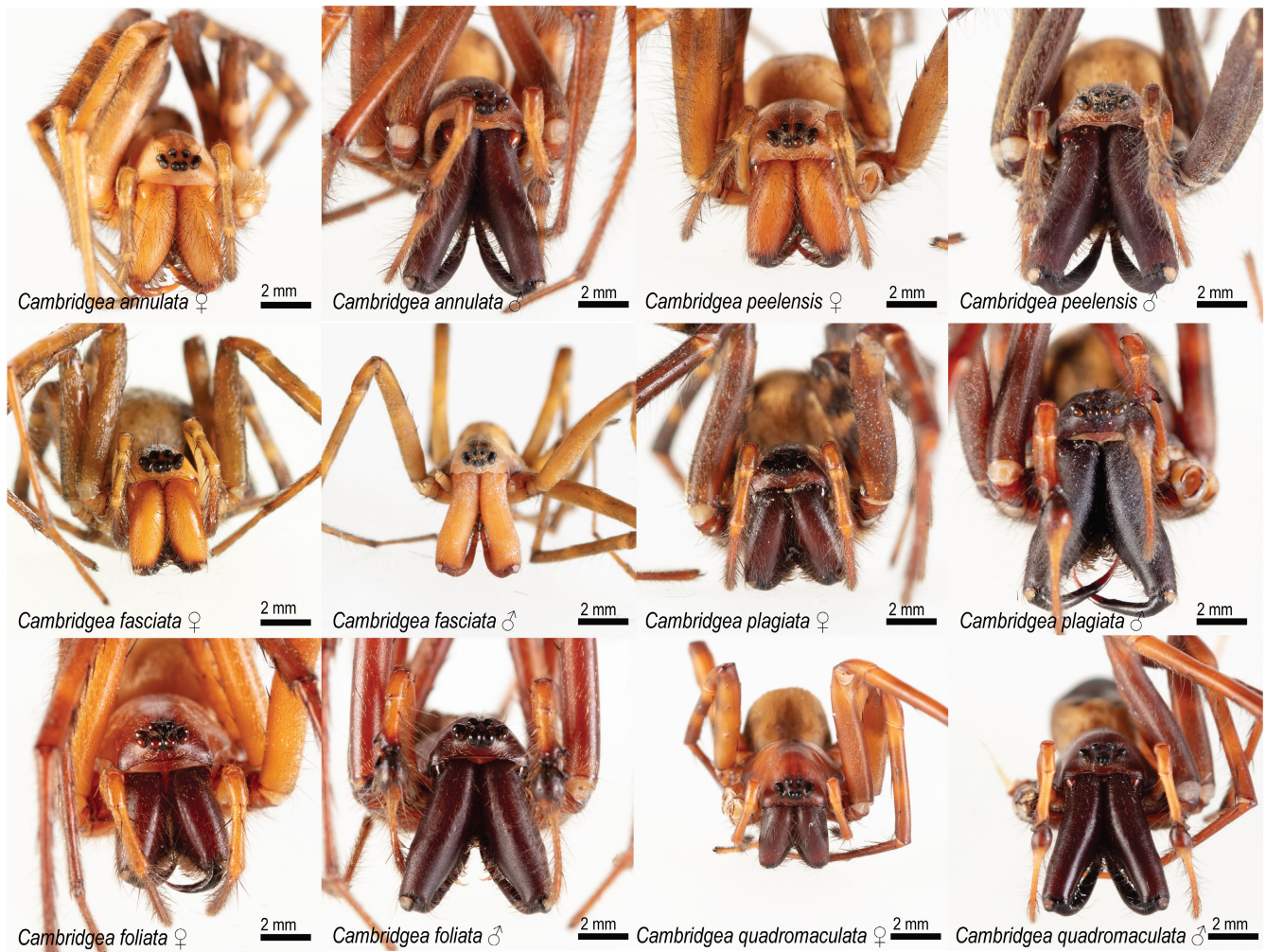


FIGURE 2 Chelicerae of male and female *Cambridgea* for six of the sampled taxa. All images © Auckland museum CC BY. Including specimens: *C. annulata*, AMNZ154199, AMNZ154201; *C. fasciata*, AMNZ154198; *C. peelensis*, AMNZ154194, AMNZ154197; *C. plagiata*, AMNZ154195, AMNZ154196; *C. quadromaculata*, AMNZ154193, AMNZ154200.

C. fasciata were significantly different to 1 (*C. ambigua*: $r_{14} = -0.0861$, $p = 0.749$; *C. fasciata*: $r_{32} = 0.114$, $p = 0.533$).

3.2 | Evolutionary allometry of species' chelicera length

3.2.1 | Do larger species have disproportionately larger male weapons?

We did not find evidence that male chelicerae are disproportionately larger in larger species; male chelicera length scales isometrically with cephalothorax width (Figure 5; $\beta_0 = 0.0416$, $\beta_1 = 0.978$, $SE = 0.0491$, $p < 0.0001$, $F_{1,10} = 396.6$, adjusted- $R^2 = 0.973$) with no evidence that the estimated slope differs significantly from 1 ($r_s = 0.318$, $p = 0.340$). Therefore, we did not find evidence for positive evolutionary allometry in male weapon size.

We similarly found that average chelicera length scaled isometrically with average cephalothorax width in females (Figure 5;

$\beta_0 = -0.261$, $\beta_1 = 1.01$, $SE = 0.0179$, $p < 0.0001$, $F_{1,10} = 318.5$, adjusted- $R^2 = 0.997$). The higher regression intercept for males relative to females reflects that adult males have proportionally larger chelicerae across all species, as shown in Figures 2 and 3.

We found that, among larger species, sexual dimorphism in body size became slightly more female-biased ($\beta_0 = -0.260$, $\beta_1 = 0.161$, $SE = 0.0587$, $p = 0.0209$, $F_{1,10} = 7.50$, adjusted- $R^2 = 0.371$). However, body size dimorphism was consistently low in this genus (between 9.3% male-biased and 7.4% female-biased; Table 1).

3.3 | Variation in static allometries

3.3.1 | Do larger species exhibit steeper chelicerae allometries in males?

We found evidence that the static allometries of male chelicera became steeper in larger species (Figure 6; $\beta_0 = 0.462$, $\beta_1 = 0.558$, $SE = 0.220$, $p = 0.035$, $F_{1,10} = 6.44$, adjusted- $R^2 = 0.377$).

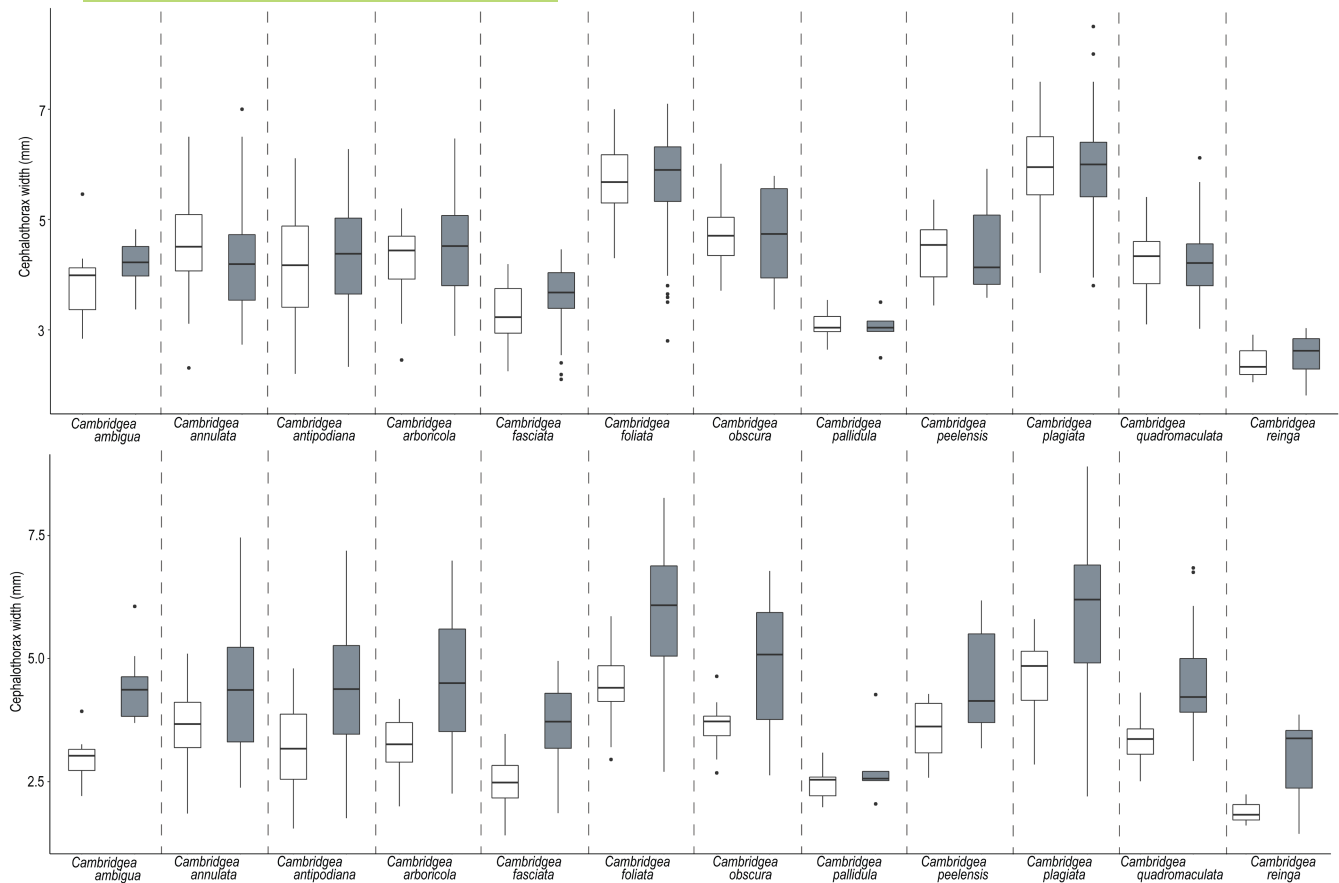


FIGURE 3 Boxplots showing the distributions of cephalothorax widths (top) and chelicera lengths (bottom) for males (filled) and females (unfilled) of 12 species of *Cambridgea*.

Simultaneously, allometric intercepts decrease in larger species (Figure 6; $\beta_0 = 0.453$, $\beta_1 = 0.0443$, SE = 0.492, $p = 0.0143$, $F_{1,8} = 9.73$, adjusted- $R^2 = 0.492$). This was expected as steeper allometric slopes commonly result in lower intercepts.

While female allometric slopes seem to reduce and even become slightly negatively allometric in larger species, this relationship was not statistically significant ($\beta_0 = 1.18$, $\beta_1 = -0.152$, SE = 0.127, $p = 0.266$, $F_{1,8} = 1.43$, adjusted- $R^2 = 0.0456$), and we found no evidence that the females' allometric intercept changes with average body size ($\beta_0 = -0.0321$, $\beta_1 = -0.0123$, SE = 0.204, $p = 0.954$, $F_{1,8} = 0.00362$, adjusted- $R^2 = -0.125$).

3.3.2 | Does SDI correlate with chelicerae allometry?

We found that static allometric slopes steepened in species with female-biased sexual size dimorphism (SDI > 0; $\beta_0 = 1.38$, $\beta_1 = 2.47$, SE = 0.526, $p = 0.00155$, $F_{1,8} = 22.07$, adjusted- $R^2 = 0.701$). This result likely reflects the fact that the species exhibiting female-biased sexual size dimorphism were generally also larger in absolute terms (Table 1). By contrast, there was a non-significant, negative relationship between female allometric slope and SDI ($\beta_0 = 0.931$, $\beta_1 = -0.719$, SE = 0.523, $p = 0.206$, $F_{1,8} = 1.89$, adjusted- $R^2 = 0.0900$).

4 | DISCUSSION

We found that male chelicera length exhibits positive static allometries in nearly every species of *Cambridgea* sampled. There was very little sexual dimorphism in body size, and a high degree of overlap in the variance among males and females, suggesting that SDI would be a poor measure of the strength of sexual selection among *Cambridgea* species. However, as predicted, static allometries for male chelicerae length were steeper in larger-bodied species. Positive static weapon allometries are selected for when increasing weapon size grants net benefits in contests above and beyond an increase in body size (Bonduriansky & Day, 2003). The steeper allometries exhibited by males of larger *Cambridgea* species, therefore, suggest that the fitness gains for large males are greatest among the larger species but nevertheless exist to some extent across the sampled taxa. A heritable scaling relationship such as has been identified in other systems, inherited from a common ancestor, could be a parsimonious explanation for this near ubiquity.

The mostly positive static allometries in male chelicerae suggests that these traits are used in similar ways to resolve contests across the genus. For both *C. foliata* (Walker & Holwell, 2018) and *C. plagiata* (McCambridge et al., 2021), contests are divided into pre- and post-contact phases and size is a significant predictor for both contest outcome and whether the contest escalates. As with other

TABLE 2 Estimated allometric slopes and intercept estimates for males and females, respectively, and slope test results for based on log-transformed chelicera lengths and cephalothorax widths (formula: $\log(y) = \log(\beta_0) + \beta_1 \log(x)$)

Species	$n_m = 16, n_f = 12$	$n_m = 117, n_f = 63$	$n_m = 56, n_f = 89$	$n_m = 23, n_f = 35$	$n_m = 32, n_f = 21$	$n_m = 152, n_f = 98$	$n_m = 11, n_f = 20$	$n_m = 12, n_f = 15$	$n_m = 130, n_f = 49$	$n_m = 29, n_f = 56$
<i>Cambridgea ambigua</i>	0.920 (0.397, 1.44)	1.34 (1.24, 1.44)	1.4 (1.25, 1.55)	1.38 (1.17, 1.60)	1.07 (0.849, 1.29)	1.31 (1.22, 1.39)	1.56 (1.29, 1.83)	1.31 (1.11, 1.50)	1.49 (1.31, 1.68)	1.24 (0.988, 1.49)
	0.826 (0.610, 1.04)	1.01 (0.899, 1.11)	1.03 (0.961, 1.10)	1.01 (0.881, 1.14)	1.03 (0.786, 1.28)	0.938 (0.770, 1.11)	0.964 (0.717, 1.21)	0.24 (0.942, 1.53)	0.894 (0.667, 1.12)	0.748 (0.581, 0.915)
	0.066 (-0.261, 0.393)	-0.204 (-0.267, -0.141)	-0.246 (-0.341, -0.151)	-0.261 (-0.404, -0.117)	-0.0319 (-0.152, 0.0879)	-0.222 (-0.287, -0.157)	-0.376 (-0.557, 0.195)	-0.198 (-0.326, -0.0690)	-0.391 (-0.535, -0.248)	-0.136 (-0.294, 0.0216)
	Female intercept, β_{0f} (95% CI)	Male intercept, β_{0m} (95% CI)	Female slope, β_{1f} (95% CI)	Male slope, β_{1m} (95% CI)	Female intercept, β_{0f} (95% CI)	Male slope test	Female slope test			
	-0.0145 (-0.141, 0.112)	-0.102 (-0.172, -0.0320)	-0.136 (-0.179, -0.0922)	0.127 (-0.209, -0.0461)	-0.13 (-0.255, -0.00414)	-0.0657 (-1.93, 0.0614)	-0.088 (-0.254, 0.0778)	-0.252 (-0.443, -0.0619)	-0.0259 (-0.202, 0.150)	0.0541 (-0.0504, 0.159)
	$r_{14} = -0.0861, p = 0.749$	$r_{115} = 0.530, p < 0.0001$	$r_{53} = 0.594, p < 0.0001$	$r_{21} = 0.624, p = 0.001$	$r_{30} = 0.114, p = 0.533$	$r_{150} = 0.499, p < 0.0001$	$r_9 = 0.844, p = 0.001$	$r_{10} = 0.735, p = 0.00647$	$r_{128} = 0.419, p < 0.0001$	$r_{27} = 0.353, p = 0.0608$
	$r_{10} = -0.493, p = 0.103$	$r_{61} = 0.0139, p = 0.914$	$r_{87} = -0.0935, p = 0.383$	$r_{33} = 0.0283, p = 0.872$	$r_{19} = 0.0651, p = 0.779$	$r_{95} = -0.0751, p = 0.464$	$r_{18} = -0.0712, p = 0.766$	$r_{13} = 0.435, p = 0.106$	$r_{47} = -0.136, p = 0.353$	$r_{54} = -0.381, p = 0.00380$

Note: n_m and n_f indicate sample size for males and females, respectively, and slope tests refer to whether male or female static allometry slopes differed from isometry. Slope test statistic, r , indicates correlation between residual and fitted values with significant results indicated in bold.

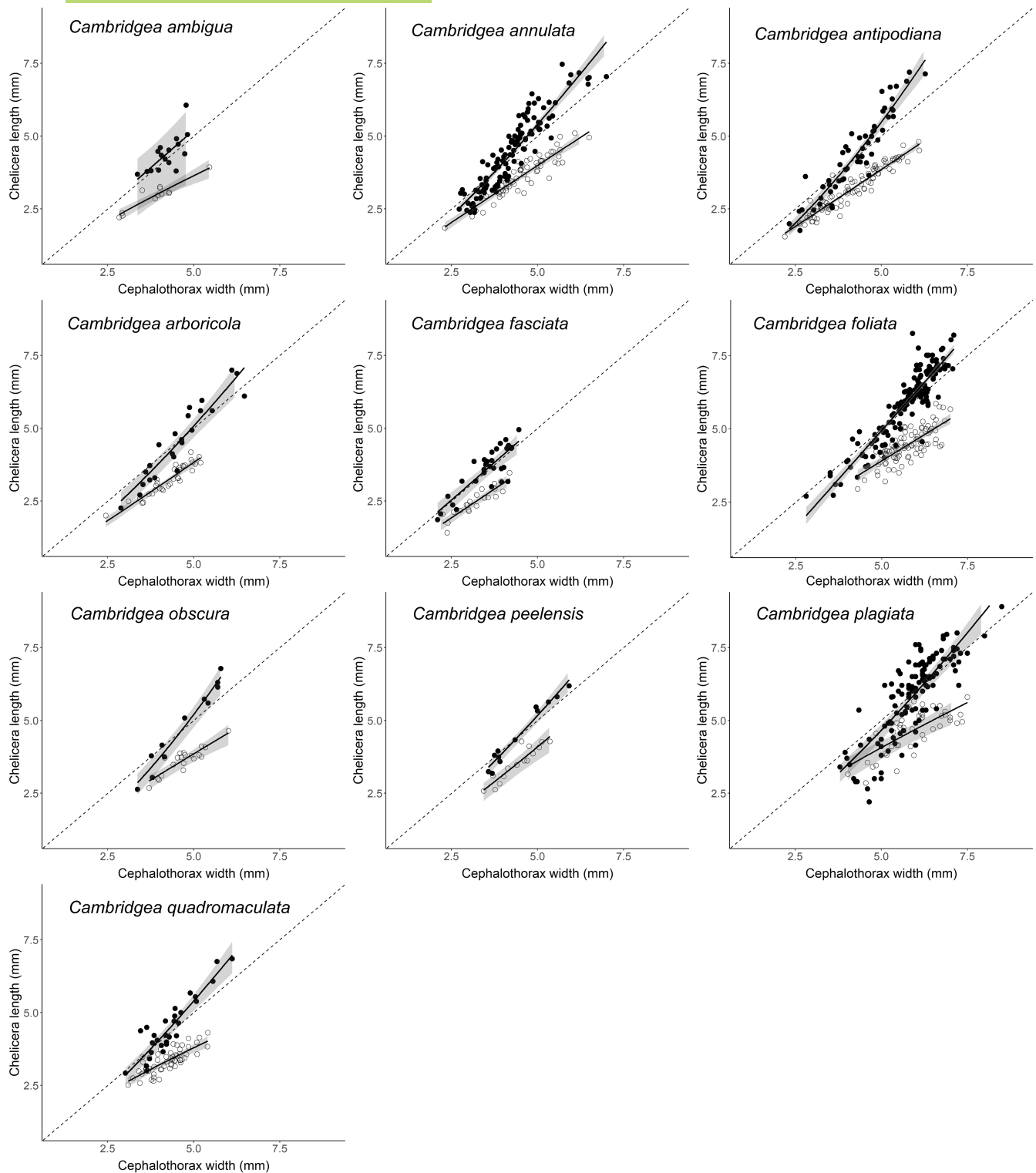


FIGURE 4 Static allometries ($\pm 95\%$ confidence intervals) of chelicera length and cephalothorax width for males (filled circles) and females (open circles) of 10 *Cambridgea* species. Linear models were fit on log-transformed data (for parameters see [Table 2](#)) so models and confidence intervals have been back-transformed (formula: $Y = ax^b$; Huxley, 1932) to fit untransformed axes and data.

spiders (e.g. jumping spiders, *Servaea incana*, McGinley et al., 2015; *Lyssomanes viridis*, Tedore & Johnsen, 2012), males of *C. foliata* and *C. plagiata* only make contact with each other in the most escalated contests. Therefore, investing in exaggerated chelicerae may only

be beneficial to males that are larger and, therefore, more likely to engage in escalated contests, resulting in positive static allometries (Arnott & Elwood, 2009; Bonduriansky & Day, 2003; McCambridge et al., 2021; Palaoro & Briffa, 2017; Walker & Holwell, 2018).

Behavioural observations of other *Cambridgea* species would confirm whether this holds true across the genus.

In general, we expected static allometries to steepen in species experiencing stronger sexual selection, as measured by sexual size dimorphism index and average male body size. In testing both measures, we found that static allometries were steepest in species that were slightly female-biased in size and in species that had larger males in absolute terms. The former result is against expectations but also less useful as *Cambridgea* appear to be largely monomorphic with limited differences (<9%) in even the most female- and male-biased species. We also found that our most female-biased species

were incidentally our largest ones. Therefore, because larger absolute male body and weapon size is a good predictor of contest success in at least two *Cambridgea* species (McCambridge, Walker, et al., 2019; Walker & Holwell, 2018), absolute male body size may be a better indicator of the strength of sexual selection.

Across the genus, in support of this possibility, we did find that larger species exhibited steeper male allometric slopes and lower intercepts. Our results, therefore, also suggest that males of smaller species of *Cambridgea* may be under weaker sexual selection. Differences in allometric slope and intercept across species, likely result from selection acting to differing degrees upon the characteristics of each species' scaling relationships (Eberhard et al., 2018; Rico-Guevara & Hurme, 2019) rather than on absolute trait sizes, resulting in changes in slope, intercept and shape (Perl et al., 2017). Indeed, changes in scaling relationships can occur over a small number of generations as demonstrated by artificially selecting for specific ratios of trait to body size in fruit flies (*Drosophila melanogaster*, Weber, 1990), stalk-eyed flies (*Cyrtodiopsis dalmanni*, Wilkinson, 1993) and dung beetles (*Onthophagus acuminatus*, Emlen, 1996).

Our finding that steeper male static allometries occur in the largest species may also support Weber's law, recently proposed as a driver of positive static allometry for structures with a signalling function (Eberhard et al., 2018). Positive static allometry within a species may result because as the weapons of rivals become larger, their ability to assess differences between them will become less precise. This would favour greater exaggeration of weapons among the largest males in order to more reliably intimidate rivals. Intriguingly, this may also apply across species - greater disparity in weapon size may be required for more accurate assessment of rivals as species become larger, in absolute terms. This would drive the evolution of steeper allometric slopes in larger species, just as we have observed

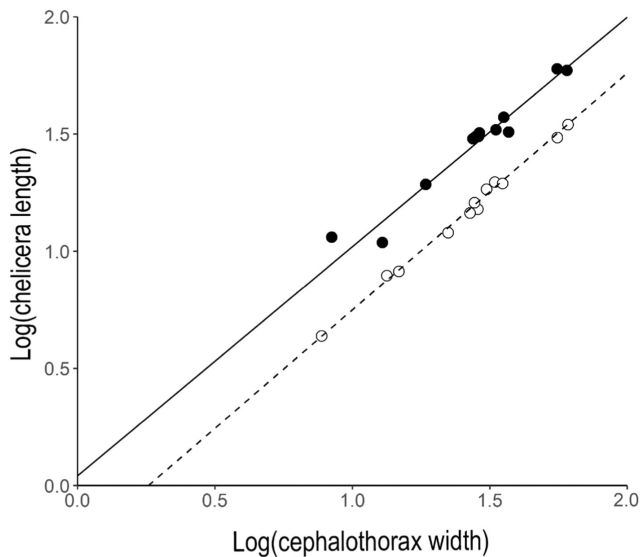


FIGURE 5 Covariation of chelicera length and cephalothorax width for males (filled circles, unbroken line) and females (unfilled circles, dotted line) using phylogenetic signal of $\lambda = 1$.

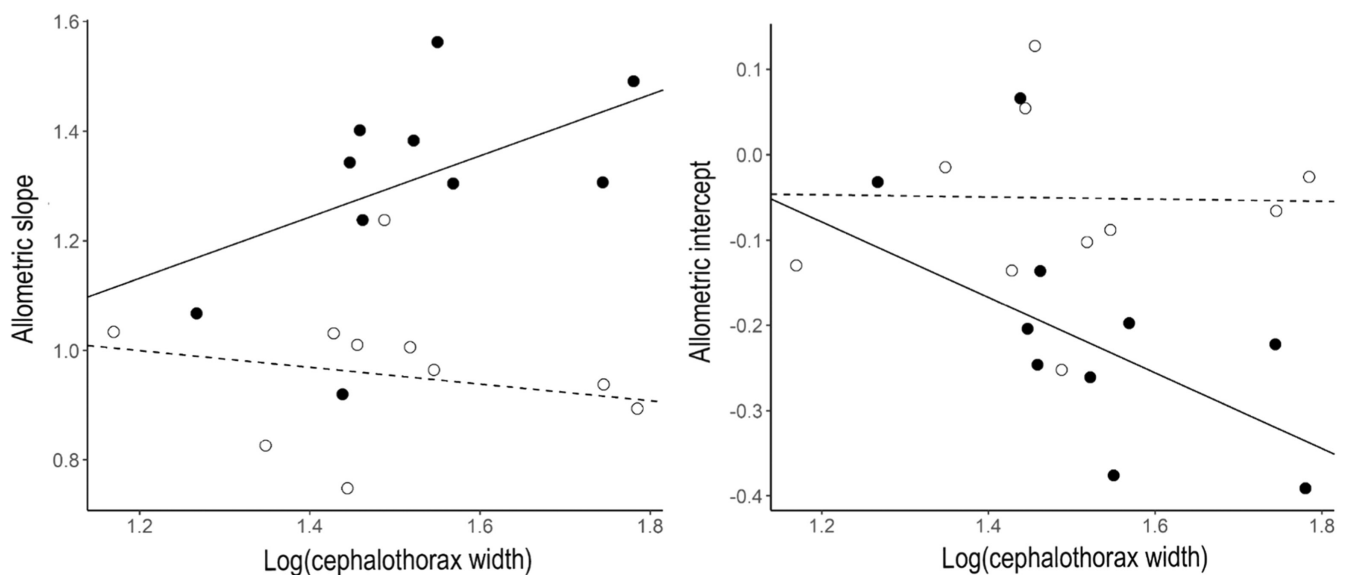


FIGURE 6 Covariation of static allometry characteristics for males (filled circles, unbroken line) and females (unfilled circles, dashed line) with cephalothorax width using phylogenetic signal of $\lambda = 1$. Changes in allometric slope shown on the left and allometric intercept on the right.

for *Cambridgea*. Once again, behavioural observations of species, especially the smaller ones, are necessary to test these hypotheses.

We predicted, given the near ubiquity of both chelicerae exaggeration and positive static allometries for males, that we would observe a positive evolutionary allometry for chelicera length. While positive evolutionary allometries in weaponry have been observed in other systems (e.g. porcelain crabs, *Petrolisthes*, Baeza & Asorey, 2012; Bovidae: Bro-Jørgensen, 2007; Tidière et al., 2017), we instead found that male chelicera length exhibits evolutionary isometry. That is, the length of chelicerae relative to body size is uniform across the genus. Consequently, while the two largest species of our sampled taxa, *C. foliata* and *C. plagiata*, have the steepest allometries, their ratios of chelicera length to body size is approximately the same as those for smaller species such as *C. fasciata* and *C. ambigua*. Chelicera length also exhibits evolutionary isometry in *Cambridgea* females although we estimated that female chelicerae may scale with a slightly negative exponent, indicating that females of larger species have slightly smaller chelicerae relative to body size.

Evolutionary isometry of male chelicera length suggests that natural selection may constrain divergence. Specifically, the conservation of male and female ratios of chelicera length to body size suggests that there is an optimal morphology for foraging that males only deviate from due to sexual selection. That is, while adult males need exaggerated chelicerae for intrasexual contests, natural selection may be limiting further increases in size, meaning the average relative length for chelicera remains relatively fixed. In some arachnids, raptorial feeding appendages can become increasingly exaggerated across both males and females provided that both species benefit from the greater length (e.g. tusked harvestmen, *Phareicranaus manauara*, Palaoro et al., 2022). However, as female *Cambridgea* have consistently smaller chelicera with consistently lower allometric slopes, it seems likely that isometry or negative allometries may be expected when only natural selection is acting on chelicerae size in this group (Pollard, 1994; Voje, 2016). Evolutionary isometry in chelicerae for both males and females suggests such constraints are at play across the genus.

The near ubiquity of positive static allometries within *Cambridgea* males are likely to result from sexual selection acting on males contesting access to females. However, that the characteristics of these static allometries vary across species while the sampled taxa overall exhibit evolutionary isometry indicates that there is likely to be stabilizing selection that influences how the benefits and costs of bearing exaggerated weaponry accrue across individuals of different species. While behavioural studies with two *Cambridgea* species indeed suggest that weapon exaggeration is selected for in contests, it is not known how larger or smaller chelicera may fare in prey capture and how foraging success by males compares to those of females, which tend to exhibit more isometric static allometries. By studying weapons at a range of scales it becomes clear that multiple selective pressures are likely to be acting in concert to produce the observed distribution of morphologies at intra- and inter-specific levels.

AUTHOR CONTRIBUTIONS

LW and GH involved in conceptualization, method design, manuscript preparation and writing. LW involved in data collection and formal data analysis.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/jeb.14100>.

DATA AVAILABILITY STATEMENT

Morphological data have been archived in Dryad at <https://doi.org/10.5061/dryad.gmsbcc2r5>. For species tree including sequence accession details see Walker et al. (2019).

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