



Are weapon allometries steeper in major or minor males? A meta-analysis

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Competition for mates can drive the evolution of exaggerated weaponry and male dimorphism associated with alternative reproductive tactics. In terrestrial arthropods, male dimorphism is often detected as non-linear allometries, where the scaling relationship between weapon size and body size differs in intercept and/or slope between morphs. Understanding the patterns of non-linear allometries is important as it can provide insights into threshold evolution and the strength of selection experienced by each morph. Numerous studies in male-dimorphic arthropods have reported that allometric slopes of weapons are shallower in large “major” males compared to small “minor” males. Because this pattern is common among beetles that undergo complete metamorphosis (holometabolous), researchers have hypothesized that the slope change reflects resource depletion during pupal development. However, no comprehensive survey has examined the generality of this trend. We systematically searched the literature for reports of weapon allometries in male dimorphic species and conducted a phylogenetically controlled meta-analysis to explore the factors influencing the difference in slopes between morphs. Our search identified 59 effect sizes from 19 studies, 50 species, and 5 orders of terrestrial arthropods. We found strong evidence that metamorphosis type influences the patterns of weapon allometries. Slopes were significantly steeper in minor males compared to major males in holometabolous species, but there was no difference in slopes between morphs in hemimetabolous species (i.e. those that undergo incomplete or no metamorphosis). These results support the hypothesis that holometabolous species face a resource ceiling during pupal development that limits the exaggeration of weapon size.

Key words: allometry; exaggerated traits; horns; male competition; male dimorphism; sexual selection.

Introduction

Sexually selected weapons, which are the structures used by males in physical battles over mating opportunities, are among the most exaggerated and diverse traits in the animal kingdom (Emlen 2008; Rico-Guevara and Hurme 2019). Within a given species, these structures are also among the most variable: large males produce disproportionately large weapons and small males produce disproportionately small ones (Emlen 2008; McCullough et al. 2016). In other words, sexually selected weapons often exhibit positive static allometry, meaning that the log-log regression between weapon size and body size among conspecific adults has a slope greater than 1 (Kodric-Brown et al. 2006; O'Brien et al. 2018; McCullough and O'Brien 2022). Studying the allometries of sexually selected weapons is important for understanding morphological diversity because it can provide insight into the selective pressures driving and constraining the evolution of these diverse structures (Bonduriansky and Day 2003; Tomkins et al. 2005a; Knell 2009).

Although most sexually selected weapons exhibit allometries that can be described as a single straight line, weapons can also exhibit complex, non-linear allometries (Knell 2009). Non-linear allometries are often associated with male dimorphism (or poly-

morphism), in which males develop into distinct morphs and use alternative mating tactics based on their weapon size (Knell 2009). For example, in male dimorphic species, there is typically a large-bodied “major” morph with exaggerated weapons and a small-bodied “minor” morph with small weapons or no weapons at all (Oliveira et al. 2008). Major males use their weapons to compete aggressively for mating opportunities, while minor males typically avoid fights and rely on sneaking or satellite behaviors to gain access to mates (Eberhard 1982; Emlen 1997). In some species, there are 3 or even 4 distinct male morphs (Rowland and Emlen 2009; Painting et al. 2015; Matsumoto and Knell 2017; Powell et al. 2020), but the mating tactics associated with these complex polymorphisms are largely unknown.

Despite the common assumption that larger males have disproportionately larger weapons, a recurring pattern in allometric studies of male dimorphic species is a decline in the allometric slopes of weapons between minor and major males. For example, in rhinoceros beetles (McCullough et al. 2015; Goczał et al. 2019), stag beetles (Knell et al. 2004; Chen et al. 2020), and giraffe weevils (Painting and Holwell 2013), weapons scale steeply with body size among the smallest males of a given species, but then the scaling relationship becomes shallower with continued increases

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in body size. The leading hypothesis for this decrease in slope is that large males face a resource ceiling that limits further exaggeration of weapon size (Nijhout and Wheeler 1996; Knell et al. 2004; Tomkins et al. 2005b). This hypothesis predicts that the greatest allometric declines will be found in holometabolous (i.e. complete metamorphosis) species and/or those with especially large weapons because these conditions are the most likely to exhaust available resources during weapon development (Tomkins et al. 2005a). Unlike other animals, holometabolous insects are expected to face particularly acute resource limitations because of their unique development in which adult weapons grow from a finite resource pool after the larva has stopped feeding (Nijhout and Wheeler 1996). However, other studies have found examples of the opposite pattern, in which major males have steeper weapon allometries than minor males (Tomkins and Simmons 1996), or no difference in slopes at all between morphs (Buzatto et al. 2011; Emberts et al. 2017). Unfortunately, these patterns in weapon allometries have largely been studied in individual species or groups of closely related species, so it is still unclear whether there are general trends across diverse taxa.

Here, we present the results of a phylogenetically controlled, formal meta-analysis examining the allometric slopes of sexually selected weapons in male dimorphic species across the animal kingdom. We systematically searched the literature to collect as many effect sizes as possible and then formally tested for biological and methodological factors that might influence the difference in slopes between morphs. The broad range of taxa included in our dataset allowed us to test whether a decline in allometric slopes is unique to holometabolous species, or if other factors, such as the degree of weapon exaggeration or the statistical method used in previous research to distinguish between male morphs, are better predictors of the variation in weapon allometries.

Materials and methods

We searched for relevant articles using the “Article title, Abstract, Keywords” search field across all years in the online database *Scopus*. We conducted our search on 17 January 2024, using the following keyword combinations. Numbers in parentheses indicate the number of journal articles found from each search:

- allomet* AND {sexual selection} AND dimorphism (278)
- {male dimorphism} AND allomet* (27)
- {male dimorphism} AND weapon (13)
- {male dimorphism} AND horn (20)
- {male dimorphism} AND mandible (9)
- {intrasexual selection} AND allomet* (13)
- allomet* AND major AND minor (130)
- allomet* AND alpha AND beta (71)
- allomet* AND intrasexual (64)
- allomet* AND {sexual selection} AND weapon (70)
- scaling AND {sexual selection} AND weapon (29)
- {male horn dimorphism} (8)
- {weapon morphs} (1)

Articles were included in our meta-analysis if the study met all the following criteria: (1) reported allometric data for a sexually selected weapon, (2) reported allometric data for adult males, (3) categorized the focal species as male dimorphic (or trimorphic), for example by describing males as “major” or “minor,” “alpha” or “beta,” or engaging in alternative reproductive tactics, (4) calculated separate slopes for the 2 male

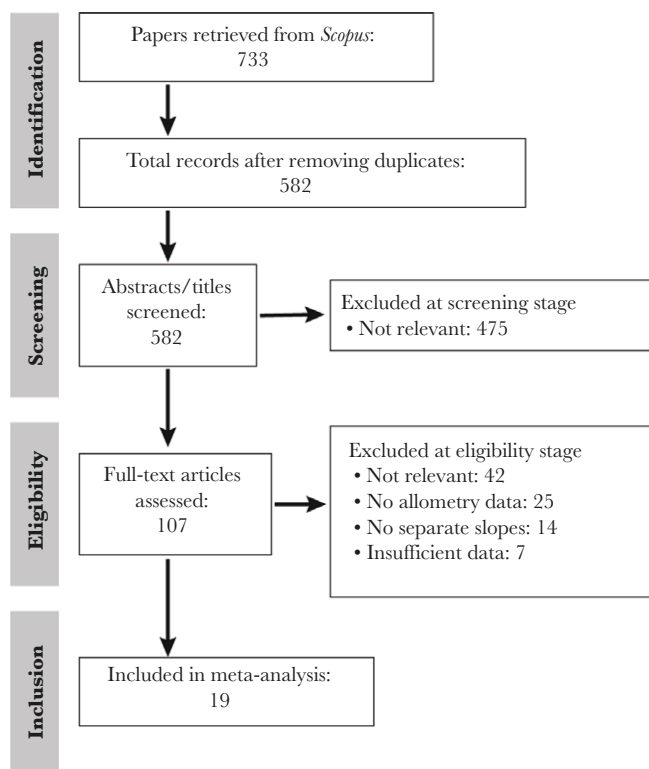


Fig. 1. PRISMA diagram showing the literature search and selection process.

morphs, and (5) provided sufficient statistical information to calculate an effect size. We summarize the literature screening process in Figure 1 and report the full list of included and excluded studies in Table S1, following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (O’Dea et al. 2021).

To compare the difference in allometric slope between major and minor males for each observation, we calculated Hedges’ g , which is a standardized measure of effect size that is commonly used to compare the difference between two groups and includes a correction for small sample sizes (Nakagawa and Santos 2012; Koricheva et al. 2013). We calculated Hedges’ g using the *mes* (means to effect size) function in the *compute.es* package in R (Del Re 2013). Our calculations were based on the allometric slopes, variances, and sample sizes for majors and minors reported in each study. If sample sizes or errors were not directly reported, we used the online tool WebPlotDigitizer (Rohatgi 2019) to manually extract the information from the figures (5 cases) or obtained the missing information by contacting the study authors or from its supplemental data (5 cases). Hedges’ g was calculated as the difference between major and minor slopes, with positive values indicating the allometric slope is steeper in minor males than major males, and negative values indicating the allometric slope is steeper in major males than minor males. Allometric slope estimates were based on log-transformed data for all observations.

We extracted all possible effect sizes from each study. In several cases, we were able to extract multiple effect sizes from the same study, either because multiple species were analyzed, or because weapon size was measured in multiple ways (e.g. weapon length and width). For 2 species (*Forficula auricularia* and *Oryctes nasicornis*), we obtained effect sizes from 2 separate studies. Two species (*Pantopsalis cheliferoideis* and *Forsteropsalis*

pureora) were described as male trimorphic, with one morph (“gamma” males) comprised of small males with reduced weaponry and 2 morphs (“alpha” and “beta” males) comprised of large males with exaggerated weaponry (Painting et al. 2015; Powell et al. 2020). In these cases, we calculated 2 separate effect sizes per weapon measurement per species: one to compare the allometric slopes between alpha and gamma males and the other to compare the allometric slopes between beta and gamma males. To control for potential non-independence arising from using multiple effect sizes from the same study or species, we included the study and species as random effects in our statistical analyses.

We created a phylogenetic tree containing all 50 species in our dataset to control for the non-independence of effect sizes due to shared evolutionary history (Koricheva et al. 2013). Because no single phylogenetic tree is available that contains all species, we constructed a supertree from phylogenetic and taxonomic information using the Open Tree of Life (OTL) database (Hinchliff et al. 2015) and the *rotl* package in R (Michonneau et al. 2016). For species not included in the latest synthetic tree (OTL version 14.9), we found a substitution that was in the OTL database from the same genus (4 cases) or family (6 cases). Species substitutions are reported in Table S2. Accurate branch lengths could not be obtained from the supertree, so all branch lengths were initially set to 1 and then made ultrametric using Grafen’s method (Grafen 1989) using the *ape* package in R (Paradis et al. 2004). The tree was then converted into a variance-covariance matrix for inclusion in the meta-analysis models (Nakagawa and Santos 2012). The final ultrametric tree used in our analyses is shown in Figure 2.

We conducted moderator analyses to test whether the difference between major and minor male slopes was influenced by 3 potential moderator (or explanatory) variables. First, we predicted that the difference in allometric slopes would depend on the degree of weapon exaggeration. We calculated the residuals from a least squares regression of log average weapon size on log average body size for major males in each species as an index of weapon exaggeration (Knell et al. 2004; McCullough et al. 2015). A positive residual indicates the species has a relatively large weapon for its body size, while a negative residual indicates the species has a relatively small weapon for its body size. If average weapon and body sizes for major males were not directly reported in the study, we calculated the averages ourselves from raw data obtained from the authors or WebPlotDigitizer. Second, we predicted that the difference in allometric slopes would be greater in species that undergo complete metamorphosis (holometabolous) compared to those that undergo incomplete metamorphosis or no metamorphosis (hereafter referred to as hemimetabolous). For brevity, we use the term hemimetabolous for all non-holometabolous species, including both hemimetabolous (e.g. earwigs) and ametabolous (e.g. harvestmen) taxa. Third, we tested whether the method used to separate male morphs influenced the difference in allometric slopes. Observations were therefore classified by their morph discrimination method: (1) a body size breakpoint in which morphs were separated based on a threshold body size (Eberhard and Gutierrez 1991); (2) a weapon size breakpoint in which morphs were separated based on a threshold weapon size (Kotiaho and Tomkins 2001); (3) a ratio breakpoint in which morphs were separated by inspecting the frequency histogram of weapon to body size ratios and identifying a threshold ratio (Cook and Bean 2006); or (4) a mixture model in which morphs were not separated according to a breakpoint “rule,” but rather through cluster analysis or finite mixture models (Rowland and Qualls

2005; Knell 2009). Our complete dataset, including the moderator variables, is available in Table S2.

We fit multi-level meta-regression models using the *rma.mv* function in the R package *metafor* (Viechtbauer 2010). To determine the overall mean effect size of the dataset, we first ran a multi-level random-effects model with study, species, phylogeny (using the variance-covariance matrix described above), and observation ID as random effects (Nakagawa and Santos 2012). Meta-analysis models require observation ID to be included as a random effect to estimate residual error (Dougherty et al. 2022). We calculated the level of heterogeneity across all effect sizes using the I^2 statistic (Higgins et al. 2003) and also partitioned total heterogeneity with respect to each of the 4 random factors using the method of Nakagawa and Santos (2012). I^2 values of 25, 50, and 75% are considered low, moderate, and high, respectively (Higgins et al. 2003).

We tested for the effect of the 3 moderator variables by adding them to the multi-level random-effects model described above. Each model still included study, species, phylogeny, and observation ID as random effects, but now also included one of the moderator variables as a categorical fixed effect (metamorphosis type and morph discrimination method) or continuous fixed effect (relative weapon size). We used the Q_M statistic to determine whether the mean effect size differed significantly between the moderator categories (Koricheva et al. 2013). For the analysis on the effect of metamorphosis type, we also ran a mixed-effect model with the intercept removed to estimate the mean effect size for each moderator category (i.e. holometabolous or hemimetabolous). The mean effect size was considered significant if the 95% confidence intervals did not overlap zero. For the analysis on the effect of weapon exaggeration, we lacked weapon and body size data for several species, so we used a slightly restricted dataset (51 effect sizes) and a pruned tree that excluded the species with missing data.

Finally, we searched for 2 signs of publication bias. First, we tested for a change in effect size over time, which could arise if studies with weak or non-significant results are less likely to be published when a research field is young (Koricheva et al. 2013). To test for a temporal trend, we ran a meta-regression with study year as a fixed effect and study, species, phylogeny, and observation ID as random effects. Second, we searched for signs of publication bias against non-significant results that could arise if effect sizes are “missing” from studies with small sample sizes or weak results (Koricheva et al. 2013). We tested for this type of publication bias using a meta-regression with inverse standard error (also known as study precision) as a fixed effect and study, species, phylogeny, and observation ID as random effects. A significant relationship between effect size and study precision was considered evidence of publication bias.

Results

Our final dataset included 59 effect sizes from 50 species, 5 orders, and 19 studies (Fig. 3). Although we did not restrict our literature search to any taxonomic group, we only identified male dimorphic weaponry and non-linear allometries among terrestrial arthropods. We are not aware of any male dimorphic weapons in a vertebrate.

Most of the effect sizes (63%) came from beetles (Coleoptera), but we also obtained multiple effect sizes for earwigs (Dermaptera) and harvestmen (Opiliones), and one effect size for a true bug (Hemiptera) and a bee (Hymenoptera). Of the 50 study species,

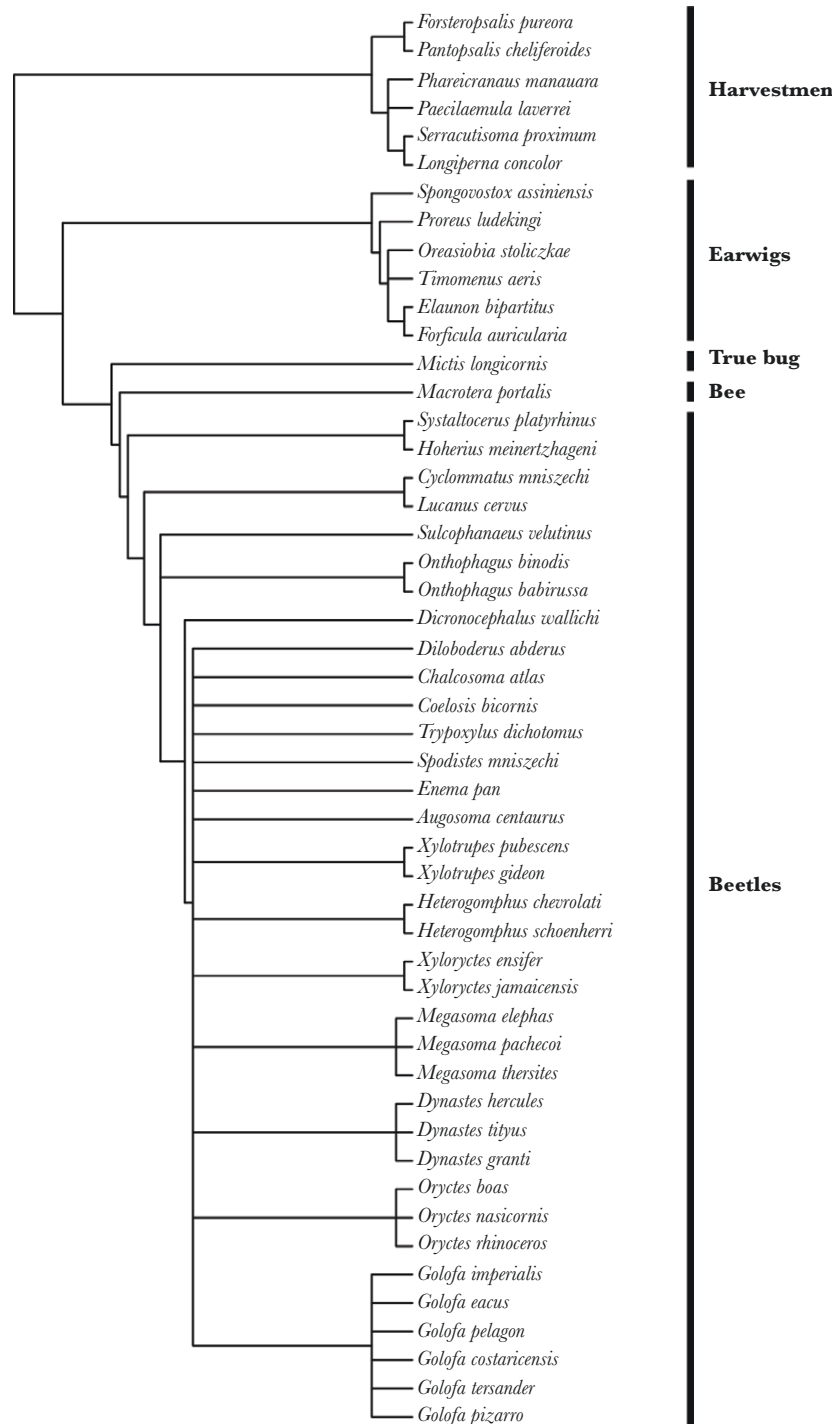


Fig. 2. Phylogenetic supertree used in the meta-analyses. Note that the branch lengths are not time calibrated. All branch lengths were set to 1 and then made ultrametric using Grafen's method.

those that belong to the orders Coleoptera and Hymenoptera are holometabolous (64% of effect sizes), and the remainder are hemimetabolous (36% of effect sizes). The full dataset was characterized by high total heterogeneity (total $I^2 = 91.9\%$), with 58.4% of the variance attributable to differences in species, 31.6% to differences in studies, 1.9% to differences in phylogenetic history, and $< 0.1\%$ to observation-level differences.

Across all observations, there was no consistent difference in allometric slopes between major and minor males (mean effect size = 0.31, 95% CI = $[-0.007, 0.64]$; Fig. 3). However, the

difference in allometric slopes was significantly influenced by metamorphosis type ($Q_M = 10.6$; $P = 0.001$; marginal $R^2 = 0.23$). In holometabolous species, minor males had significantly steeper allometries than major males (Hedges' $g > 0$), but in hemimetabolous species, there was no significant difference between major and minor allometric slopes (Fig. 4). The difference in allometric slopes was not influenced by the method used to separate male morphs ($Q_M = 0.70$; $P = 0.87$). The most commonly used method was a ratio breakpoint model ($k = 26$ or 44% of observations). Body size breakpoint models ($k = 10$ or 17%), weapon size

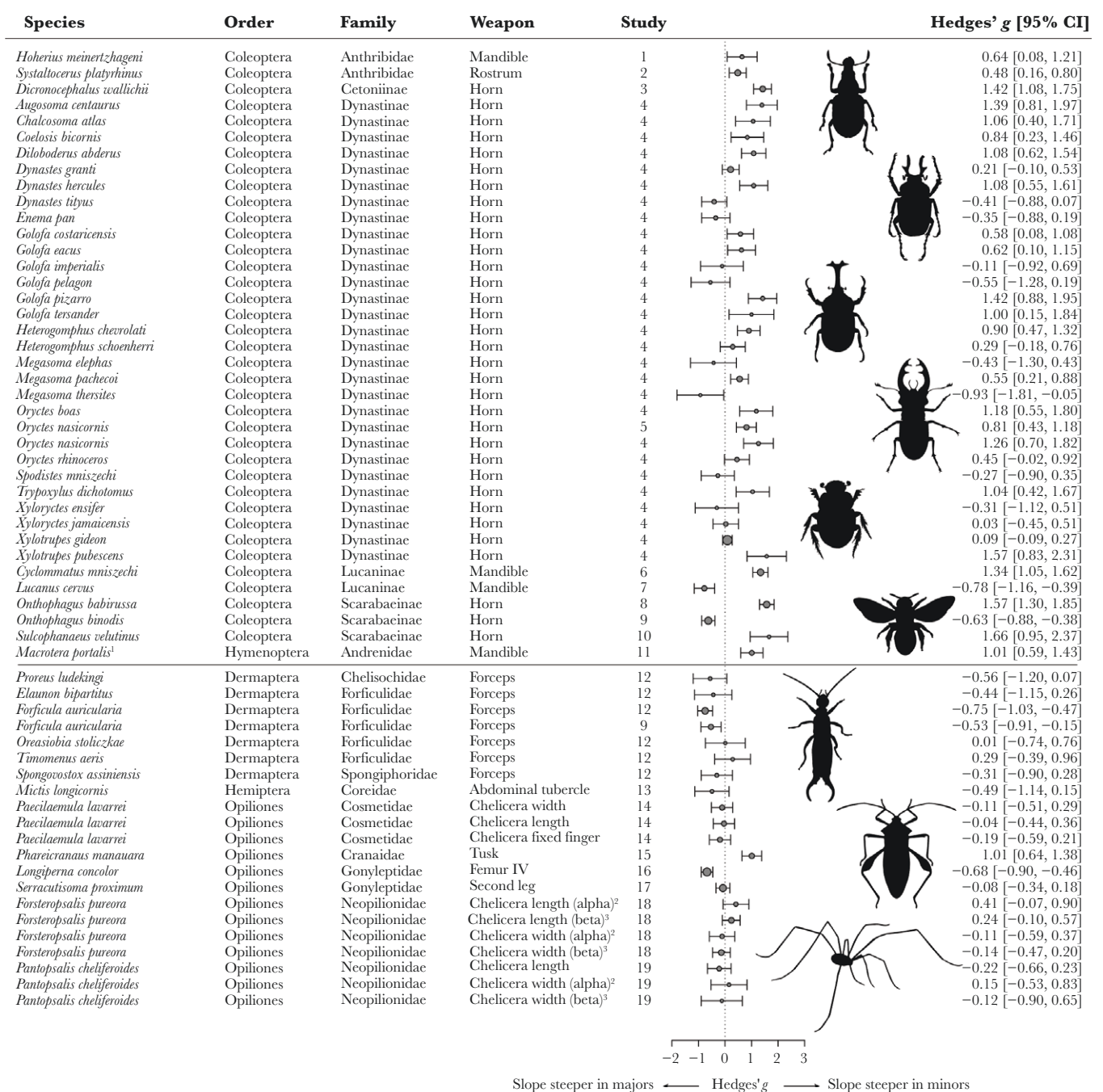


Fig. 3. Hedges' g values and 95% confidence intervals comparing the weapon allometries between major and minor males. Larger circles denote studies with larger sample sizes. The horizontal line separates holometabolous (top) and hemimetabolous (bottom) species. For the beetle family Scarabaeidae, we classified species into Subfamily to provide additional taxonomic information among this large clade. Silhouettes illustrate the organismal diversity included in our dataset (from top to bottom): fungus weevil (Anthribidae), flower beetle (Cetoniinae), rhinoceros beetle (Dynastinae), stag beetle (Lucaninae), dung beetle (Scarabaeinae), bee (Hymenoptera), earwig (Dermaptera), leaf-footed bug (Hemiptera), and harvestman (Opiliones). Study ID indicates data from the same study: 1 = Painting (2002), 2 = Mattos et al. (2014), 3 = Kojima & Lin (2017), 4 = McCullough et al. (2015), 5 = Goczał et al. (2019), 6 = Chen et al. (2020), 7 = Romiti et al. (2015), 8 = Toh et al. (2022), 9 = Tomkins et al. (2005a), 10 = Cummings et al. (2018), 11 = Danforth (1991), 12 = Tomkins and Simmons (1996), 13 = Emberts et al. (2017), 14 = Solano-Brenes et al. (2018), 15 = Palaoro et al. (2022), 16 = Zatz et al. (2011), 17 = Buzatto et al. (2011), 18 = Powell et al. (2020), 19 = Painting et al. (2015). Notes: 1 = formerly known as *Perdita portalis*; 2 = alpha vs gamma males; 3 = beta vs gamma males.

breakpoint models ($k = 10$ or 17%), and mixture models ($k = 13$ or 22%) were used at similar frequencies among the remaining observations. The difference in allometric slopes between major and minor males also was not influenced by relative weapon size ($Q_M = 1.1$; $P = 0.29$), even if we restricted the analyses to holo-metabolous species ($Q_M = 1.43$; $P = 0.23$). The restricted dataset (51 effect sizes) used in this analysis was characterized by high

total heterogeneity (total $I^2 = 91.3\%$), with 77.8% of the variance attributable to species-level differences, 13.4% to phylogenetic history, $< 0.1\%$ to study-level differences, and $< 0.1\%$ to observation-level differences.

There was a significant relationship between study year and effect size ($Q_M = 4.9$; $P = 0.03$, marginal $R^2 = 0.09$), but it was in the opposite direction than what would be expected if weak or

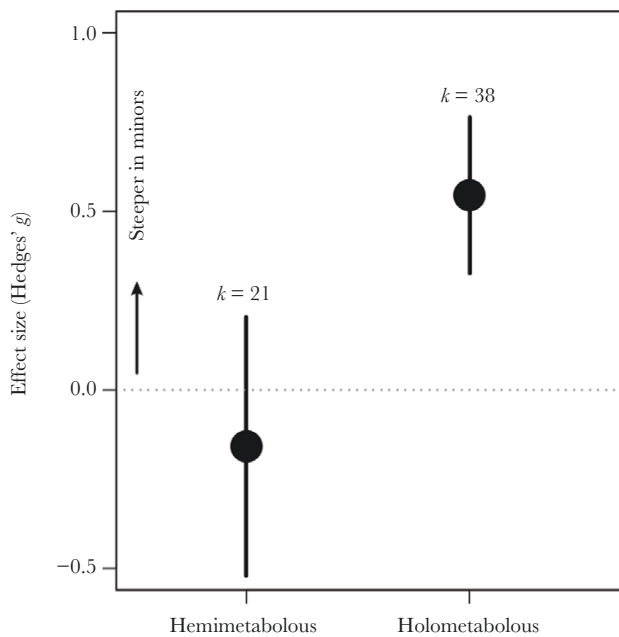


Fig. 4. Difference in weapon allometries between major and minor males (Hedges' g) for hemimetabolous and holometabolous species. Black points represent the meta-analytic mean, and black bars represent the 95% confidence intervals. k = number of effect sizes in each category.

non-significant results are less likely to be published when a research field is young. Instead, we found a significant positive relationship between effect size and publication year ($\beta = 0.03$, 95% CI = [0.003, 0.05]; Fig. 5). Despite the significant temporal trend, there was no evidence that studies with small samples and weak effect sizes were “missing” because there was no relationship between effect size and study precision ($Q_M = 1.1$; $P = 0.31$).

Discussion

Our literature search only identified male dimorphic weaponry and non-linear allometries in terrestrial arthropods, and our meta-analysis found that metamorphosis type has a significant effect on the patterns of weapon allometries in these male dimorphic species. Specifically, we found that allometric slopes were significantly steeper in minor males than in major males for holometabolous species, but there was no difference in allometric slopes between morphs for hemimetabolous species. These results are consistent with the hypothesis that resource depletion during weapon development causes a decline in allometric slope among the largest individuals because holometabolous species face stronger resource limitation than hemimetabolous species (Nijhout and Wheeler 1996; Tomkins et al. 2005b). We note that nearly all holometabolous species in our dataset are beetles, and the hemimetabolous species are mostly earwigs and harvestmen. Our results should therefore be interpreted cautiously because of taxonomic biases within the available literature.

In holometabolous species, sexually selected weapons develop from a finite resource pool after the larva has stopped feeding, so the growth of large weapons can locally deplete developmental resources during metamorphosis and ultimately limit weapon size (Knell et al. 2004; McCullough et al. 2015). By contrast, hemimetabolous species undergo minimal developmental reprogramming and no metamorphosis before the adult stage, so resource

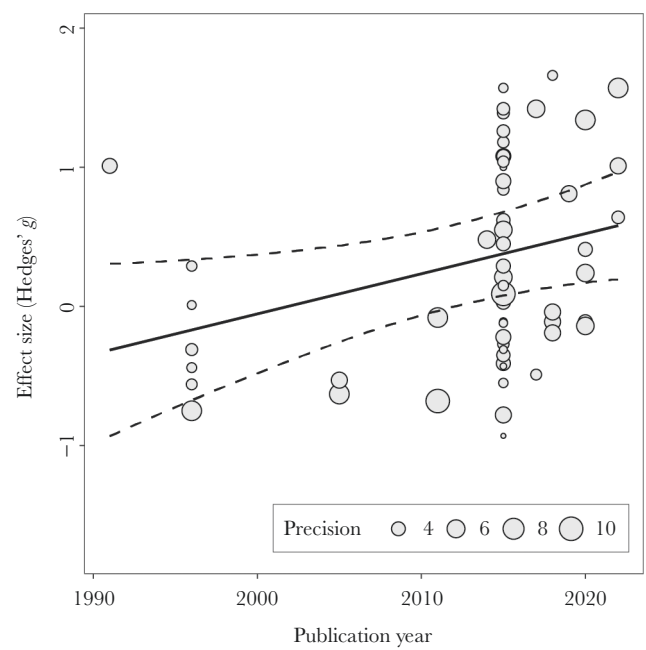


Fig. 5. Bubble plot showing the relationship between effect size (Hedges' g) and publication year. The points are scaled by the precision (inverse standard error) of each estimate. The solid line represents the predicted relationship from a meta-regression and the dashed lines represent the 95% confidence intervals.

depletion is less likely to occur (Tomkins et al. 2005b). Numerous authors have suggested that the decrease in allometric slope from minor to major males is the result of resource limitation in a closed developmental system (e.g. McCullough et al. 2015; Chen et al. 2020; Painting 2022), and our meta-analysis found that this pattern is indeed a general trend among holometabolous species. The tapered allometries of stag beetle mandibles (Knell et al. 2004) and giraffe weevil rostra (Painting and Holwell 2013) also support the hypothesis of declining allometries due to resource exhaustion, even though these species were not included in our meta-analysis because they are not distinctly male dimorphic.

Contrary to our predictions, we did not find a significant effect of weapon exaggeration on the allometric patterns between minor and major morphs. This result contrasts with a previous study on rhinoceros beetles (Coleoptera: Dynastinae) that found that species with the most exaggerated weapons exhibit the greatest decline in allometric slopes (McCullough et al. 2015). Even if we restricted our analyses to holometabolous species (which experience the most acute resource limitation), we still found no evidence that species with relatively larger weapons faced stronger constraints on continued allometric growth. The discrepancy likely arises because of the wider range of taxa included in our current study. Unlike the McCullough et al. (2015) study that had uniform measurements across all species (i.e. prothorax width for body size and head horn length for weapon size), our study included a diversity of weapon types (e.g. horns, mouthparts, legs) and body size proxies (e.g. prothorax width, elytra length, body length). A relationship between weapon exaggeration and a decline allometric slopes between male morphs may only be apparent in smaller clades with similar body shapes and the same type of weapon (e.g. Knell et al. 2004; McCullough et al. 2015).

Allometric patterns also were not influenced by the method used to separate minor and major morphs. This result was reassuring because the allometries of male dimorphic species are

highly variable, and no single method for distinguishing morphs performs best in all contexts (Knell 2009). A ratio breakpoint model was the most common method for separating male morphs in our dataset, which suggests that most species are characterized by having relatively “cryptic” male morphs that overlap in both weapon size and body size (Cook and Bean 2006; Knell 2009). We note that the mechanisms underlying threshold development remain to be tested in most species (Emlen et al. 2005; Tomkins and Moczek 2009; Buzatto et al. 2014). Future work is also needed to compare the fitness functions for weapon and body size that may favor different non-linear allometries, including sigmoidal, curvilinear, or various breakpoint allometries (Pomfret and Knell 2006).

Although the effect was statistically significant, metamorphosis type explained only 23% of the variance in effect sizes across observations. This result suggests that there are additional factors that influence allometric patterns that have yet to be identified. For example, differences in how weapons are used, or the strength of resource allocation tradeoffs may influence the optimal allometric slope in each male morph. Aggressive signaling is expected to favor weapons with steep allometries by facilitating assessment between opponents during the early stages of a fight (Eberhard et al. 2018; O'Brien et al. 2018; McCullough and O'Brien 2022). As a result, differences in the relative importance of signaling between major and minor males may contribute to variation in allometric slopes. Because minor males generally avoid male–male contests, aggressive signaling is expected to be more important for major males compared to minor males. It is therefore intriguing that major males exhibit shallower allometries than minor males in many holometabolous species. We hypothesize that the observed slopes in holometabolous species reflect opposing selection from resource limitation and weapon function (Eberhard et al. 2018; McCullough and O'Brien 2022). Weapons can also limit the growth of other body structures, such as wings, eyes, and testes, so differences in resource acquisition and allocation may influence allometric patterns between morphs (Emlen 2001; Simmons and Emlen 2006; Yamane et al. 2010; Painting and Holwell 2013).

We found evidence of publication bias in the form of a significant positive relationship between effect size and publication year. Social trends in research interests can generate a bandwagon effect where corroborative results are readily published, and the magnitude of research findings increases over time (Jennions and Møller 2002). The temporal trend observed in our dataset may therefore reflect increased interest in allometric studies, particularly in the ecological and evolutionary implications of biological scaling (Sherratt et al. 2022).

Finally, we note that the major and minor males compared in our dataset reflect discrete morphological morphs, which may or may not correspond to discrete behavioral morphs (Knell 2009). For example, in the Asian rhinoceros beetle *Trypoxylus dichotomus*, there is no evidence that major and minor males use alternative reproductive tactics: both morphs use their horns to fight with rival males, and both use sneaking behaviors to gain access to females (Hongo 2003, 2007). Similarly, in the New Zealand giraffe weevil *Lasiorhynchus barbicornis*, alternative reproductive tactics are flexible and not fixed to different morphs: small males perform sneaking behaviors but also fight with other males depending on the relative size of their opponent (Painting and Holwell 2014). Unfortunately, the reproductive behaviors of major and minor males have not been well studied in most species. Our meta-analysis reveals that metamorphosis type has a significant effect on the patterns of

weapon allometry in male dimorphic species, but more empirical work is needed to understand how behavioral differences may also contribute to the variation in scaling relationships between morphs.

Supplementary material

Supplementary material is available at *Behavioral Ecology* online.

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Author contributions

Sydney Kochensparger (Data curation [lead], Formal analysis [equal], Visualization [supporting], Writing—original draft [supporting], Writing—review & editing [supporting]), Christina Painting (Conceptualization [equal], Methodology [equal], Writing—review & editing [supporting]), Bruno Buzatto (Conceptualization [supporting], Methodology [supporting], Writing—review & editing [supporting]), and Erin McCullough (Conceptualization [equal], Methodology [equal], Data curation [supporting], Formal analysis [equal], Visualization [lead], Writing—original draft [lead], Writing—review & editing [lead])

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Conflict of interest

We declare no competing interests.

Data availability

Analyses reported in this article can be reproduced using the data and code provided by Kochensparger et al. (2024).

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