



Variation in allometry along the weapon-signal continuum

Erin L. McCullough¹ · Devin M. O'Brien²

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Abstract

Structures used in intrasexual competition span a continuum, with pure weapons that are used exclusively in physical fights at one extreme and pure aggressive signals that are used exclusively to assess and threaten rivals at the other. We propose this weapon-signal continuum offers a framework for understanding the variation in allometric slopes among intra-sexually selected structures. We predict allometric slopes will become steeper as the relative importance of signaling increases, because aggressive signaling will favor the evolution of hypervariable structures that facilitate the assessment of subtle differences in body size. We provide preliminary empirical support for the continuum hypothesis using species with different types of armaments and offer suggestions for how to test the weapon-signal continuum among closely related species.

Keywords Allometry · Armament · Male-male competition · Scaling · Sexual selection · Weapon

Introduction

Morphological diversity largely reflects variation in size (Huxley 1932; Thompson 1942; Gould 1966). Across species, individual body sizes, and/or developmental stages, large organisms are not simply magnified versions of small ones because they differ in the relative growth of body parts. This shape variation is especially apparent among secondary sexual structures because ornaments and armaments often scale disproportionately with body size. Specifically, the slope of the log–log regression of trait size against body size among conspecific adults is often greater than 1, indicating positive static allometry (Gould 1973; Alatalo et al. 1988; Simmons and Tomkins 1996; Kawano 1997; Baker and Wilkinson 2001; McCullough et al. 2015; O'Brien et al. 2018). Many ornaments and armaments also scale disproportionately with body size when traits are measured in the same individual across different developmental stages (e.g., Miller 1973) and among individuals from different species (e.g., Gould 1974), indicating positive ontogenetic and evolutionary allometry, respectively. Our study focuses specifically on variation in static allometry, which describes proportional trait sizes among individuals

✉ Erin L. McCullough
ErMcCullough@clarku.edu

¹ Department of Biology, Clark University, Worcester, MA 01610, USA

² Department of Natural Sciences and Mathematics, SUNY Cobleskill, Cobleskill, NY 12043, USA

from the same population and at the same developmental stage (Cheverud 1982; Klingenberg and Zimmermann 1992). Henceforth, we refer to static allometry as simply allometry.

A sufficiently large number of secondary sexual structures exhibit positive allometry that authors have concluded this pattern is “almost universal” (Kodric-Brown et al. 2006). Others have similarly argued that positive allometry can be used as a diagnostic test to evaluate whether a structure has been the target of sexual selection (Green 2000; Kelly 2005; Knell and Fortey 2005; O’Brien et al. 2018; Graham et al. 2020). But positive allometry is not a ubiquitous attribute of secondary sexual structures. Comprehensive surveys across a broad range of taxa find that ornaments and armaments can have allometric slopes less than 1 (Bonduriansky 2007; Voje 2016), and behavioral experiments find directional sexual selection does not always result in the evolution of positive allometry (Pomfret and Knell 2006; van Lieshout and Elgar 2009). Allometric slopes also exhibit a considerable degree of variation within closely related species, with slopes (calculated here using ordinary least squares regression on log-transformed data) ranging from 0.83 to 2.69 in stalk-eyed flies (Voje and Hansen 2013) and 0.52–3.50 in earwigs (Simmons and Tomkins 1996). So much variation begs an explanation.

The “functional allometry” hypothesis was recently proposed to help explain why the scaling relationships of secondary sexual structures are so variable (Eberhard et al. 2018; Rodríguez and Eberhard 2019). This hypothesis recognizes that secondary sexual structures are used in different ways and suggests the scaling relationship of a structure depends on its specific function. Aggressive signals are expected to have the steepest allometries; courtship signals are expected to have shallower allometries; and contact courtship traits are expected to have the shallowest allometries. The functional allometry hypothesis provides a valuable framework for understanding much of the observed variation among secondary sexual structures. However, the authors of the functional allometry hypothesis did not rank the expected allometry of sexually selected weapons because such predictions are complicated by the fact that weapons are often also used as aggressive signals, and their mechanical functions vary widely among species (Eberhard et al. 2018; Rodríguez and Eberhard 2019). The functional allometry hypothesis also cannot explain the variation in allometric slopes among aggressive signals (or weapons), which belong to the same functional category. The current paper aims to resolve some of this unexplained variation.

Here, we expand on the functional allometry hypothesis to make explicit predictions about the allometric slopes of sexually selected weapons and the variation observed among intra-sexually selected structures. We have previously proposed that weapons and aggressive signals should be considered as a continuum, rather than as discrete functional categories (McCullough et al. 2016). We propose that integrating this weapon-signal continuum hypothesis with allometric studies offers a comparative framework for studying the variation in allometry among species. Specifically, we suggest that the scaling relationship of structures used in intrasexual competition will be correlated with the relative importance of fighting versus signaling, allowing researchers to predict trait function based on allometric patterns (or vice versa).

The weapon-signal continuum

Intrasexual competition (typically among males) is likely the most widespread form of sexual selection (Shuker 2014) and has driven the evolution of a diverse array of morphologies that improve an individual’s chance of winning fights (Emlen 2008; Rico-Guevara and Hurme 2019). The structures used in male-male competition are often

collectively called weapons, but many are not physically engaged during fights. We previously proposed that structures used in male-male competition should be considered as part of a continuum (Fig. 1), with pure weapons that are only used in direct physical fights at one extreme and pure aggressive signals that are only used in displays to assess and threaten rivals at the other (McCullough et al. 2016). Although we did not make specific recommendations about terminology in our previous paper, we now suggest the use of “armament” as an inclusive term to refer to structures across the entire continuum. By recognizing the various ways in which armaments are used during intrasexual interactions, the weapon-signal continuum may help explain why only some armaments evolve to extreme sizes, and why only a subset scale disproportionately with body size.

The steep scaling relationships characteristic of aggressive signals are the result of selection for conspicuous, highly variable structures that advertise an individual’s fighting ability or resource holding potential. Males of all sizes benefit from exchanging aggressive signals prior to combat because it allows them to quickly and reliably assess the resource holding potential of their opponent (Parker 1974; Arnott and Elwood 2009; Hardy and Briffa 2013). Competitively superior individuals avoid wasting time and energy on fights they would easily win, and competitively weaker individuals avoid being injured in fights they would certainly lose. Intrasexual competition has therefore favored the evolution of effective and reliable signals that allow

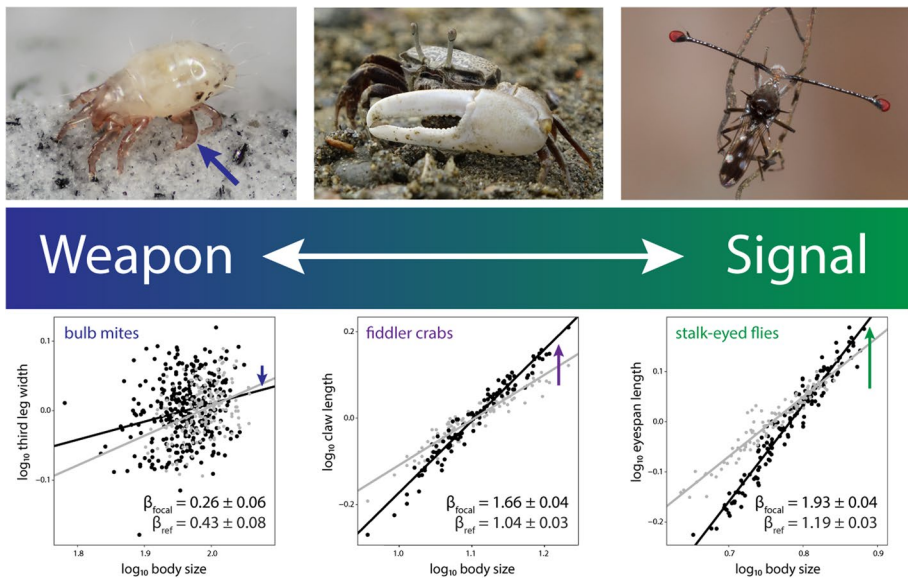


Fig. 1 Weapon-signal continuum ranging from pure weapons (left) to pure aggressive signals (right). Allometric slopes become steeper as the relative importance of signaling increases, based on comparisons of three armaments that span the weapon-signal continuum: hindlegs of bulb mites, claws of fiddler crabs, and eye-spans of stalk-eyed flies. In comparison to their reference traits, bulb mite legs (pure weapon) had the shallowest allometric slope, fiddler crab claws (dual weapon-signal) had an intermediate allometric slope, and stalk-eyed fly eye-spans (pure signal) had the steepest allometric slope. Allometric slopes (estimate ± SE) of focal traits (β_{focal} , plotted in black) and reference traits (β_{ref} , plotted in gray) are from ordinary least squares regression on \log_{10} -transformed length measurements. Figure adapted from McCullough et al. (2016). Photo credits: Jan Van Arkel (bulb mite), Daisuke Muramatsu (fiddler crab), and Jerry Wilkinson (stalk-eyed fly)

individuals to evaluate their opponents and make informed decisions on whether they should fight or retreat.

Structures that make effective and reliable aggressive signals are typically both conspicuous and hypervariable (Searcy and Nowicki 2005; Hardy and Briffa 2013). Conspicuous structures stand out by being relatively larger than other body parts. Because conspicuous structures are easily detected, they facilitate the rapid assessment of opponents during the early stages of a contest (Tazzyman et al. 2014). Hypervariable structures scale disproportionately with body size, so the structure is disproportionately large in large individuals and disproportionately small in small individuals. Because hypervariable structures amplify differences in body size, they are favored in the context of intrasexual competition by allowing males to discern otherwise subtle differences in body size and make more precise comparisons of competitive ability (Panhuis and Wilkinson 1999; Emlen 2008; O'Brien et al. 2018). Hypervariability is especially important for large individuals because differences between stimuli are more difficult to detect as the magnitude of the stimuli increases, according to Weber's Law of perception (Akre and Johnsen 2014). Larger individuals therefore need proportionally larger aggressive signals to successfully intimidate closely size-matched rivals.

While conspicuousness and hypervariability contribute to the efficacy of aggressive signals, exaggerated and highly variable structures will only be useful for pre-fight assessment if there is also a positive correlation between resource holding potential and body size (O'Brien et al. 2018). Resource holding potential is almost always associated with body size, either directly because body size is a major factor in determining contest outcome (Preston et al. 2003; Pratt et al. 2003; Reaney et al. 2011; McCullough and Simmons 2016), or indirectly because body size is tightly correlated with energetic status or other physiological predictors of fighting success (Briffa 2008). In these species, individuals benefit from assessing differences in body size before engaging in a contest, which favors the evolution of aggressive signals that amplify these differences through patterns of steep allometry (O'Brien et al. 2018).

In contrast to aggressive signals, we predict pure weapons to exhibit shallow allometries. In species with pure weapons, individuals do not assess the size or resource holding potential of their competitors before deciding to engage in a fight, so there is no selective advantage of having a structure that magnifies differences in body size (Rodríguez and Eberhard 2019). In fact, hypervariability is expected to be disfavored in the case of pure weapons because exaggerated size often limits a weapon's performance capability (Dennenmoser and Christy 2013). Once a weapon gains an additional function as an aggressive signal, however, individuals will benefit from having a more conspicuous and variable structure that is more effective in assessing and/or threatening rivals. This selective advantage will drive the evolution of steeper allometries. We therefore predict that the scaling relationships between armament and body size will vary in steepness along the length of the weapon-signal continuum, with slopes becoming steeper as the signaling function and importance of rival assessment increases. Pure weapons may also exhibit shallow allometries if males benefit from having a structure that connects well with the most common sizes of potential opponents, similar to the "one size fits all" explanation for genitalia and other contact courtship traits (Eberhard et al. 2018; Rodríguez and Eberhard 2019). Shallow allometries may therefore be a general characteristic of contact structures, regardless of whether they are used in the context of fighting or courtship.

Testing the weapon-signal hypothesis

Using different types of armaments

As a preliminary test of the weapon-signal hypothesis, we compared the allometries of three structures that spanned the weapon-signal continuum (Fig. 1): the modified hindlegs of bulb mites (Acaridae), the elongated eye-spans of stalk-eyed flies (Diopsidae), and the enlarged claws of fiddler crabs (Ocypodidae). We chose these three species because they could be confidently ranked along the weapon-signal continuum (see below). With just three species, we recognize that our analysis is just a first step in exploring the correlation between allometric slope and armament function but hope our ideas promote further study.

We hypothesize that the modified hindlegs in the aggressive “fighter” morph of bulb mites are an example of a pure weapon. Fighter males are characterized by having a thickened and sharply clawed third pair of legs that are used to puncture and kill other males (Radwan 1993, 2001; Radwan et al. 2000; Stewart et al. 2018). This strategy of lethal fighting is adaptive, particularly in small populations, because a single fighter male may be able to eliminate all of its rivals and gain exclusive reproductive access to females (Radwan 1993). Visual signaling, such as threat displays, is unlikely to be important because bulb mites are typically subterranean and therefore fight in the dark (Stewart et al. 2018).

On the other end of the continuum, the elongated eye-spans of stalk-eyed flies may represent an example of a pure signal. In sexually dimorphic diopsids, males compete for and defend access to female aggregations on exposed rootlets, and males with longer eye-spans are more successful at monopolizing these mating sites (Burkhardt and de la Motte 1987; Panhuis and Wilkinson 1999). Contests begin when two males orient face-to-face and approach with parallel eye-spans. If neither male retreats, males may perform threat displays by rising on their hindlegs and spreading their forelegs parallel to their eyestalks, potentially to emphasize the length of their eye-spans (Burkhardt and de la Motte 1987; Panhuis and Wilkinson 1999). If the contest remains unresolved, males may escalate further to intense fighting and use their forelegs to jab, hook, and upend their opponents (Panhuis and Wilkinson 1999). Eye-spans therefore should not be considered weapons because even in the most intense fights, the eye-spans are not brought into direct contact during fights (Eberhard et al. 2018). Instead, eye-spans appear to be used exclusively as visual signals to assess the overall size of opponents.

Most structures used in male-male competition are likely to have a dual function because they are used as both weapons and aggressive signals. For example, male fiddler crabs have an enlarged “major” claw that is used as a weapon in fights over ownership of breeding burrows (Hyatt and Salmon 1978; Jennions and Backwell 1996; Pratt et al. 2003) and also as a signal in waving displays to attract females and repel intruders (Backwell and Passmore 1996; Backwell et al. 1999; Pope 2000; Muramatsu 2011). The major claw can comprise nearly half the total body mass (Crane 1975) and is a fully functional weapon that can deliver a powerful pinch during fights (Levinton and Judge 1993; Dennenmoser and Christy 2013). Fiddler crabs are also visually oriented animals (Zeil and Hemmi 2006) that may spend 50% of their above-ground time performing waving displays (Hyatt 1977) and an additional 2% of their daily time budget cleaning their claws to keep them as bright as possible (Tina et al. 2016; McCullough et al. 2020). Fiddler crab claws therefore belong in the middle of the weapon-signal continuum, although the specific location may differ among species depending on the relative importance of fighting versus signaling (McCullough et al. 2016). Thus, the weapon-signal continuum offers a framework for

understanding variation in allometries both among very different types of armaments and for the same type of armament among closely related species.

We note that in our original manuscript on the weapon-signal continuum, we suggested that rhinoceros beetle horns and stag beetle mandibles were examples of pure weapons because they are used as tools to lift and lever rivals during fights but probably have little to no role in visual signaling (McCullough et al. 2016). We now realize that these armaments may play an important role in tactile and/or chemical signaling in some species (McCullough and Zinna 2013; Goyens et al. 2015), so they are probably better classified as a dual weapon-signal. Because the signaling function of armaments may occur in multiple sensory modalities, including modes that are difficult to detect for human observers, we propose that the prevalence of lethal fighting may be a better metric for ranking structures along the weapon-signal continuum.

Following the methods outlined by O'Brien et al. (2018), we compared the allometric slopes of focal (sexually selected) structures to those of reference (non-sexually selected) structures. Although allometric studies typically test for positive allometry by evaluating whether a slope is significantly greater than 1, we advocate for studies that take a more holistic approach and evaluate whether a focal trait scales more (or less) steeply than other body parts (O'Brien et al. 2018). By including reference traits as an internal control, this approach offers a more biologically relevant assessment of how sexually selected structures scale with body size. Because the analyses by O'Brien et al. (2018) focused specifically on “extreme” structures and the “positive allometry hypothesis”, our study extends their work by exploring why some weapons are relatively small, why intra-sexually selected structures exhibit a range of allometric slopes, and how such variation in allometry can provide clues about trait function.

We estimated the allometric slopes of focal (β_{focal}) and reference ($\beta_{\text{reference}}$) traits using ordinary least squares regression on \log_{10} -transformed length measurements. A summary of the estimated slopes, intercepts, and 95% confidence intervals is reported in Table 1. To facilitate slope comparisons between species, we also calculated the difference in allometric slopes between the focal and reference trait ($\Delta\beta$). For plotting purposes only, we mean centered the focal and reference traits by subtracting the individual trait values by the focal or reference trait means.

We compared the allometric slopes of bulb mite legs, stalk-eyed fly eye-spans, and fiddler crab claws using data from Pike et al. (2017), Swallow et al. (2005), and Muramatsu and Koga (2016) respectively. We chose these three datasets because they comprise large

Table 1 Summary of allometric data on focal and reference traits

Species	Trait	<i>N</i>	Intercept \pm SE	Slope \pm SE	Slope 95% CI	$\Delta\beta$
Bulb mites	Male third leg width (focal)	332	1.40 \pm 0.12	0.26 \pm 0.06	[0.14, 0.38]	−0.17
	Female third leg width (reference)	181	0.82 \pm 0.15	0.43 \pm 0.08	[0.28, 0.58]	
Fiddler crabs	Major claw length (focal)	104	−0.56 \pm 0.04	1.66 \pm 0.04	[1.58, 1.73]	0.61
	Minor claw length (reference)	104	−0.44 \pm 0.04	1.04 \pm 0.03	[0.98, 1.11]	
Stalk-eyed flies	Male eyespan (focal)	135	−0.67 \pm 0.03	1.93 \pm 0.04	[1.85, 2.00]	0.74
	Female eyespan (reference)	108	−0.20 \pm 0.03	1.19 \pm 0.03	[1.12, 1.25]	

Estimates of allometric slope and intercept are based on ordinary least squares regression on \log -transformed data (N = sample size; $\Delta\beta$ = slope of focal trait—slope of reference trait)

sample sizes ($n > 100$) and include measurements for both the focal trait and a reference trait. For bulb mites (*Rhizoglyphus echinopus*), third leg width of fighter males was the focal trait, third leg width of females was the reference trait, and anterior coxae suture length was used as a standard measure of body size (Pike et al. 2017). For stalk-eyed flies (*Teleopsis dalmanni*, formerly *Cyrtodiopsis dalmanni*), male eye-span length was the focal trait, female eye-span length was the reference trait, and body length was the measure of body size. Due to potential allometric variation among populations (Swallow et al. 2005), only individuals from the Langat population (largest sample size) were used in the analyses. For fiddler crabs (*Uca lactea*), major claw length was the focal trait, minor claw length was the reference trait, and carapace width was the measure of body size. Males with regenerated or broken claws were excluded from the analyses.

We note that for bulb mites and stalk-eyed flies, we used the homologous traits in females as the non-sexual (control) reference traits. This approach obviously is not applicable in systems where the secondary sexual structure is only present in males (e.g., horns in most rhinoceros beetles) and would not be appropriate in systems where the homologous trait in females has a female-specific function (e.g., competition for foraging sites, as in reindeer; Melnycky et al. 2013). We recognize that choosing an appropriate reference trait is likely to be challenging in most species and will require detailed knowledge about trait function. Ideally, focal and reference traits would be measured in the same individual. According to the recommendations by O'Brien et al. (2018), reference traits should be a distinct body part that is not functionally related to the focal structure and that scales proportionally with body size. Unfortunately, we are not aware of any datasets for pure weapons or pure signals that include “ideal” reference traits.

In support of the weapon-signal hypothesis, we found that the pure weapon had the shallowest allometric slope, the dual weapon-signal had an intermediate slope, and the pure signal had the steepest slope (Fig. 1). Thus, the allometric slopes of armaments become steeper as signaling becomes relatively more important (McCullough et al. 2016).

Using similar types of armaments

A more robust test of the weapon-signal continuum hypothesis would compare the allometric slopes of the same type of armament among closely related species. The continuum predicts the slopes will be steeper in species where signaling is relatively more important and shallower in species where fighting is relatively more important. Unfortunately, we are not aware of any comparative datasets that include measurements of both a focal trait and reference trait and where behavioral data is detailed enough to rank species according to the relative importance of fighting versus signaling.

One metric that could be used to rank species along the weapon-signal continuum is the percentage of fights that end in the death or serious injury of one opponent. Species that always engage in lethal fighting belong at the weapon end of the continuum. For example, in several species of Hymenoptera, there is a flightless, large-headed “aggressive” male morph that uses its enlarged mandibles to compete for females inside enclosed spaces, such as fig receptacles or subterranean nests (Hamilton 1979; Murray 1987; Danforth 1991; Bean and Cook 2001). In *Macrotera portalis* (formerly *Perdita portalis*), male-male fights always end in the death of one opponent, so the surviving male monopolizes a large number of females inside the nest and mates repeatedly with them just prior to oviposition (Danforth 1991). In support of the weapon-signal hypothesis, the allometric slope for mandibles is 72% shallower in the aggressive fighter morph than in the non-aggressive

scrambler morph, and their mandibles are also significantly less variable (Danforth 1991). Species that rarely fight to the death, on the other hand, belong closer to the signal end of the continuum. For example, only 6% of rutting red deer males are permanently injured each year (Clutton-Brock et al. 1979), and deer antlers exhibit strong positive allometry (Vanpé et al. 2007; Melnycky et al. 2013). Fatal fights are typically rare among species with the most exaggerated armaments because their effectiveness in threat displays makes it possible for males to resolve contests through assessment before escalating to a dangerous fight (Emlen 2008, 2014).

While we currently lack comparative data to compare the weapon-signal continuum among closely related species, there are several taxa that are promising candidates for future work. For example, earwig species differ in how they use their cerci during male-male interactions (Briceño and Eberhard 1995), and the allometric slopes of cerci range from significantly negative to strongly positive (Simmons and Tomkins 1996). In broad support of the continuum hypothesis, van Lieshout and Elgar (2009) found that cerci in *Euborellia brunneri* are important in resolving male-male fights, are not important in displays towards females, and exhibit a negative allometric slope. Although the authors argued that the negative slope was “unusual” for a sexually selected structure, we suggest the pattern is consistent with predictions from the weapon-signal continuum. If cerci are not favored in the context of displays towards males or females, these structures would be classified as a pure weapon and should exhibit a shallow allometric slope.

Primate canines are another system that may be informative for testing the weapon-signal continuum. Canines are used as both weapons in physical fights and signals in threat displays, and the importance of signaling should depend on a species’ social system (Plavcan and van Schaik 1992). Threat displays are predicted to be particularly important in species with large social groups and fluctuating male group membership because most males will be strangers and therefore must rely on status signals to resolve agonistic interactions (Bergman and Sheehan 2013). Consistent with these predictions, male mandrills (*Mandrillus sphinx*) are itinerant and travel in hordes with over 600 individuals (Abernethy et al. 2002) and have canines that are positively allometric (Klopp 2012) as well as bright facial coloration that may enhance canine displays (Setchell and Wickings 2005). Threat displays are predicted to be less advantageous in species that live in small social groups because there will be a much higher degree of familiarity between individuals, so aggressive signals alone will be less effective in resolving conflicts and deterring the escalation of fights (Bergman and Sheehan 2013). Intermale competition is likely to be frequent and intense, which may favor selection on canines as pure weapons (Plavcan and van Schaik 1992). Whether species with small social groups fit these predictions by having canines with shallower allometric slopes remains to be tested.

Considerations

We highlight several factors researchers must consider when testing and interpreting the weapon-signal continuum:

First, comparisons along the weapon-signal continuum will be most straightforward for armaments with linear allometries where the scaling relationship between armament and body size can be described with a single allometric slope. The continuum may be less informative for understanding variation in scaling relationships among armaments with curvilinear, sigmoidal, or other non-linear allometries (Knell 2009), including species with male dimorphism (e.g., Danforth 1991; Radwan 1993; Emlen 1997) or where depletion of developmental

resources limits armament size in the largest individuals (e.g., Knell et al. 2004; McCullough et al. 2015; see also Lemaître et al. 2014; Tidière et al. 2017). Even in these cases, however, it is possible to compare the allometric slopes among a subset of individuals, for example among just “major” males (as we did for bulb mites).

Second, aggressive signals are only expected to exhibit steep scaling relationships if resource holding potential is positively correlated with body size. In species where body size is not a reliable predictor of fight outcome (e.g., Sneddon et al. 2000; Lappin and Husak 2005; Yoshino et al. 2011), individuals will not gain information about their competitor’s fighting ability by assessing differences in body size, so intrasexual competition is not expected to favor the evolution of hypervariable armaments with steep allometries. Thus, even pure aggressive signals may exhibit relatively shallow allometries if the likelihood of winning fights does not depend on body size.

Third, variation in the biomechanics of fighting will affect the allometric slopes of pure weapons. In species where weapons are used to pinch or squeeze opponents (e.g., fiddler crab claws), individuals may not benefit from increases in weapon size because larger weapons (longer levers) have lower mechanical advantages and produce weaker closing forces (Levinton and Allen 2005). Pure pinching and squeezing weapons are therefore expected to exhibit relatively shallow allometries. In species where weapons are used to lift or strike opponents, on the other hand, selection may favor continued increases weapon size if larger weapons confer a competitive advantage due to larger strike zones or faster speeds (Maldonado et al. 1967; Loxton and Nicholls 1979; Levinton and Allen 2005). Species may also be able to compensate for mechanical constraints on weapon size by investing heavily in surrounding muscle tissue (Goyens et al. 2014; O’Brien and Boisseau 2018; O’Brien 2019), which may allow the evolution of larger weapons and steeper allometries than otherwise expected. While pure weapons are generally expected to have shallower slopes than aggressive signals, they may still exhibit a range of allometries depending on the species-specific biomechanics of how fighting forces are produced and delivered. We encourage future studies that compare the allometries of armaments with different biomechanical functions.

Lastly, structures that function as both armaments and ornaments might also exhibit a range of allometric slopes. Many armaments are used both as threat signals to deter potential rivals and as courtship signals to attract potential mates (Berglund et al. 1996). Courtship signaling may strengthen selection for steep allometries if females benefit from choosing males based on armament size by selecting higher quality mates (Berglund et al. 1996). Alternatively, courtship signaling may oppose selection on steep allometries if females do not prefer exaggerated ornaments (Wilkinson and Reillo 1994), or if exaggerated ornaments hamper a male’s ability to perform courtship displays (Byers et al. 2010). The relative importance of signaling towards males versus females may thus contribute to variation in allometric slopes.

We believe the weapon-signal hypothesis provides a valuable framework for studying variation in allometry, but further work is needed to understand its applicability across all armaments.

Conclusion

Despite decades of research on the scaling relationships of sexually selected structures, there is still debate over why their allometries are so variable (Bonduriansky 2007; Voje 2016; Eberhard et al. 2018). The weapon-signal continuum offers a framework for understanding the diversity of allometric slopes among structures used in intrasexual

competition. It predicts that as the relative importance of signaling increases (and the relative importance of physical fighting decreases), selection will favor hypervariable structures that amplify differences in body size, and thus will drive the evolution of steep allometries. Variation in allometric slopes may therefore provide important clues about armament function. More generally, the weapon-signal continuum highlights that structures used in intrasexual competition should not be lumped into a single category because weapons are different from signals. To fully understand the evolution of sexually selected traits, we must recognize their diverse and distinct functions.

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References

- Abernethy KA, White LJT, Wickings EJ (2002) Hordes of mandrills (*Mandrillus sphinx*): extreme group size and seasonal male presence. *J Zool* 258:131–137. <https://doi.org/10.1017/S0952836902001267>
- Akre KL, Johnsen S (2014) Psychophysics and the evolution of behavior. *Trends Ecol Evol* 29:291–300. <https://doi.org/10.1016/j.tree.2014.03.007>
- Alatalo RV, Hoglund J, Lundberg A (1988) Patterns of variation in tail ornament size in birds. *Biol J Linn Soc* 34:363–374. <https://doi.org/10.1111/j.1095-8312.1988.tb01969.x>
- Arnott G, Elwood RW (2009) Assessment of fighting ability in animal contests. *Anim Behav* 77:991–1004. <https://doi.org/10.1016/j.anbehav.2009.02.010>
- Backwell PRY, Passmore NI (1996) Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*. *Behav Ecol Sociobiol* 38:407–416. <https://doi.org/10.1007/s002650050258>
- Backwell PR, Christy JH, Passmore NI (1999) Female choice in the synchronously waving fiddler crab *Uca annulipes*. *Ethology* 105:415–421
- Baker RH, Wilkinson GS (2001) Phylogenetic analysis of sexual dimorphism and eye-span allometry in stalk-eyed flies (Diopsidae). *Evolution* 55:1373–1385. <https://doi.org/10.1111/j.0014-3820.2001.tb00659.x>
- Bean D, Cook JM (2001) Male mating tactics and lethal combat in the nonpollinating fig wasp *Sycoscapter australis*. *Anim Behav* 62:535–542. <https://doi.org/10.1006/anbe.2001.1779>
- Berglund A, Bisazza A, Pilastro A (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol J Linn Soc* 58:385–399
- Bergman TJ, Sheehan MJ (2013) Social knowledge and signals in primates. *Am J Primatol* 75:683–694. <https://doi.org/10.1002/ajp.22103>

- Bonduriansky R (2007) Sexual selection and allometry: a critical reappraisal of the evidence and ideas. *Evolution* 61:838–849. <https://doi.org/10.1111/j.1558-5646.2007.00081.x>
- Briceño RD, Eberhard WG (1995) The functional morphology of male cerci and associated characters in 13 species of tropical earwigs (Dermaptera: Forficulidae, Labiidae, Carcinophoridae, Pygidicranidae). *Smithsonian contributions to zoology*. Smithsonian Institution Press, Washington D.C., pp 1–63
- Briffa M (2008) Decisions during fights in the house cricket, *Acheta domestica*: mutual or self assessment of energy, weapons and size? *Anim Behav* 75:1053–1062. <https://doi.org/10.1016/j.anbehav.2007.08.016>
- Burkhardt D, de la Motte I (1987) Physiological, behavioural, and morphometric data elucidate the evolutionary significance of stalked eyes in Diopsidae (Diptera). *Entomol Gener* 12:221–233. <https://doi.org/10.1127/entom.gen/12/1987/221>
- Byers J, Hebets E, Podos J (2010) Female mate choice based upon male motor performance. *Anim Behav* 79:771–778. <https://doi.org/10.1016/j.anbehav.2010.01.009>
- Cheverud JM (1982) Relationships among ontogenetic, static, and evolutionary allometry. *Am J Phys Anthropol* 59:139–149. <https://doi.org/10.1002/ajpa.1330590204>
- Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE (1979) The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim Behav* 27:211–225. [https://doi.org/10.1016/0003-3472\(79\)90141-6](https://doi.org/10.1016/0003-3472(79)90141-6)
- Crane J (1975) *Fiddler crabs of the world: ocypodidae: genus Uca*. Princeton University Press, Princeton, NJ
- Danforth BN (1991) The morphology and behavior of dimorphic males in *Perdita portalis* (Hymenoptera: Andrenidae). *Behav Ecol Sociobiol* 29:235–247
- Dennenmoser S, Christy JH (2013) The design of a beautiful weapon: compensation for opposing sexual selection on a trait with two functions. *Evolution* 67:1181–1188. <https://doi.org/10.1111/evo.12018>
- Eberhard WG, Rodríguez RL, Huber BA et al (2018) Sexual selection and static allometry: the importance of function. *Q Rev Biol* 93:207–250
- Emlen DJ (1997) Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behav Ecol Sociobiol* 41:335–341. <https://doi.org/10.1007/s002650050393>
- Emlen DJ (2008) The evolution of animal weapons. *Annu Rev Ecol Evol Syst* 39:387–413. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173502>
- Emlen DJ (2014) *Animal weapons: the evolution of battle*. Henry Holt and Company, New York
- Gould SJ (1966) Allometry and size in ontogeny and phylogeny. *Biol Rev* 41:587–638. <https://doi.org/10.1111/j.1469-185X.1966.tb01624.x>
- Gould SJ (1973) Positive allometry of antlers in the “Irish Elk”, *Megaloceros giganteus*. *Nature* 244:375–376. <https://doi.org/10.1038/244375a0>
- Gould SJ (1974) The origin and function of “bizarre” structures: antler size and skull size in the “Irish elk” *Megaloceros giganteus*. *Evolution* 28:191–220
- Goyens J, Dirckx J, Dierick M et al (2014) Biomechanical determinants of bite force dimorphism in *Cyclommatus metallifer* stag beetles. *J Exp Biol* 217:1065–1071. <https://doi.org/10.1242/jeb.091744>
- Goyens J, Dirckx J, Aerts P (2015) Mechanoreceptor distribution in stag beetle jaws corresponds to the material stress in fights. *Arthropod Struct Dev* 44:201–208. <https://doi.org/10.1016/j.asd.2015.03.003>
- Graham ZA, Garde E, Heide-Jørgensen MP, Palaoro AV (2020) The longer the better: evidence that narwhal tusks are sexually selected. *Biol Lett* 16:20190950. <https://doi.org/10.1098/rsbl.2019.0950>
- Green AJ (2000) The scaling and selection of sexually dimorphic characters: an example using the Marbled Teal. *J Avian Biol* 31:345–350. <https://doi.org/10.1034/j.1600-048X.2000.310310.x>
- Hamilton WD (1979) Wingless and fighting males in fig wasps and other insects. In: Blum MS, Blum NA (eds) *Sexual selection and reproductive competition in insects*. Academic Press, New York, pp 167–220
- Hardy ICW, Briffa M (2013) *Animal contests*. Cambridge University Press, Cambridge, UK
- Huxley JS (1932) *Problems of relative growth*. Methuen, London
- Hyatt GW (1977) Field studies of size-dependent changes in waving display and other behavior in the fiddler crab, *Uca pugilator* (Brachyura, Ocypodidae). *Mar Behav Physiol* 4:283–292. <https://doi.org/10.1080/10236247709386960>
- Hyatt GW, Salmon M (1978) Combat in the fiddler crabs *Uca pugilator* and *U. pugnax*: a quantitative analysis. *Behaviour* 65:182–211. <https://doi.org/10.1163/156853978X00602>
- Jennions MD, Backwell PRY (1996) Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biol J Linn Soc* 57:293–306. <https://doi.org/10.1111/j.1095-8312.1996.tb01851.x>
- Kawano K (1997) Cost of evolving exaggerated mandibles in stag beetles (Coleoptera: Lucanidae). *Ann Entomol Soc Am* 90:453–461

- Kelly CD (2005) Allometry and sexual selection of male weaponry in Wellington tree weta, *Hemideina crassidens*. *Behav Ecol* 16:145–152. <https://doi.org/10.1093/beheco/arl141>
- Klingenberg CP, Zimmermann M (1992) Static, ontogenetic, and evolutionary allometry: a multivariate comparison in nine species of water striders. *Am Nat* 140:601–620. <https://doi.org/10.1086/285430>
- Klopp EB (2012) Craniodental features in male *Mandrillus* may signal size and fitness: an allometric approach. *Am J Phys Anthropol* 147:593–603. <https://doi.org/10.1002/ajpa.22017>
- Knell RJ (2009) On the analysis of non-linear allometries. *Ecol Entomol* 34:1–11. <https://doi.org/10.1111/j.1365-2311.2008.01022.x>
- Knell RJ, Fortey RA (2005) Trilobite spines and beetle horns: sexual selection in the Palaeozoic? *Biol Lett* 1:196–199. <https://doi.org/10.1098/rsbl.2005.0304>
- Knell RJ, Pomfret JC, Tomkins JL (2004) The limits of elaboration: curved allometries reveal the constraints on mandible size in stag beetles. *Proc Roy Soc B* 271:523–528. <https://doi.org/10.1098/rspb.2003.2641>
- Kodric-Brown A, Sibly RM, Brown JH (2006) The allometry of ornaments and weapons. *Proc Natl Acad Sci USA* 103:8733–8738. <https://doi.org/10.1073/pnas.0602994103>
- Lappin AK, Husak JF (2005) Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *Am Nat* 166:426–436. <https://doi.org/10.1086/432564>
- Lemaître JF, Vanpé C, Plard F, Gaillard JM (2014) The allometry between secondary sexual traits and body size is nonlinear among cervids. *Biol Lett* 10:20130869. <https://doi.org/10.1098/rsbl.2013.0869>
- Levinton JS, Allen BJ (2005) The paradox of the weakening combatant: trade-off between closing force and gripping speed in a sexually selected combat structure. *Funct Ecol* 19:159–165. <https://doi.org/10.1111/j.0269-8463.2005.00968.x>
- Levinton JS, Judge ML (1993) The relationship of closing force to body size for the major claw of *Uca pug-nax* (Decapoda: Ocypodidae). *Funct Ecol* 7:339–345. <https://doi.org/10.2307/2390214>
- Loxton RG, Nicholls I (1979) The functional morphology of the praying mantis forelimb (Dictyoptera: Mantodea). *Zool J Linn Soc* 66:185–203. <https://doi.org/10.1111/j.1096-3642.1979.tb01908.x>
- Maldonado H, Levin L, Pita JCB (1967) Hit distance and the predatory strike of the praying mantis. *Z Vgl Physiol* 56:237–257. <https://doi.org/10.1007/BF00333669>
- McCullough EL, Simmons LW (2016) Selection on male physical performance during male–male competition and female choice. *Behav Ecol* 27:1288–1295. <https://doi.org/10.1093/beheco/arw033>
- McCullough EL, Zinna RA (2013) Sensilla density corresponds to the regions of the horn most frequently used during combat in the giant rhinoceros beetle *Trypoxylus dichotomus* (Coleoptera: Scarabaeidae: Dynastinae). *Ann Entomol Soc Am* 106:518–523. <https://doi.org/10.1603/AN12155>
- McCullough EL, Ledger KJ, O'Brien DM, Emlen DJ (2015) Variation in the allometry of exaggerated rhinoceros beetle horns. *Anim Behav* 109:133–140. <https://doi.org/10.1016/j.anbehav.2015.08.013>
- McCullough EL, Miller CW, Emlen DJ (2016) Why sexually selected ornaments are not weapons. *Trends Ecol Evol* 31:742–751. <https://doi.org/10.1016/j.tree.2016.07.004>
- McCullough EL, Chou C-C, Backwell PRY (2020) Cost of an elaborate trait: a trade-off between attracting females and maintaining a clean ornament. *Behav Ecol* 31:1218–1223. <https://doi.org/10.1093/beheco/araa072>
- Melnycky NA, Weladji RB, Holand Ø, Nieminen M (2013) Scaling of antler size in reindeer (*Rangifer tarandus*): sexual dimorphism and variability in resource allocation. *J Mammal* 94:1371–1379. <https://doi.org/10.1644/12-MAMM-A-282.1>
- Miller DC (1973) Growth in *Uca*, 1. Ontogeny of asymmetry in *Uca pugilator* (Bosc) (Decapoda, Ocypodidae). *Crustaceana* 24:119–131
- Muramatsu D (2011) The function of the four types of waving display in *Uca lactea*: effects of audience, sand structure, and body size. *Ethology* 117:408–415. <https://doi.org/10.1111/j.1439-0310.2011.01884.x>
- Muramatsu D, Koga T (2016) Fighting with an unreliable weapon: opponent choice and risk avoidance in fiddler crab contests. *Behav Ecol Sociobiol* 70:713–724. <https://doi.org/10.1007/s00265-016-2094-2>
- Murray MG (1987) The closed environment of the fig receptacle and its influence on male conflict in the Old World fig wasp, *Philotrypes pilosa*. *Anim Behav* 35:488–506. [https://doi.org/10.1016/S0003-3472\(87\)80274-9](https://doi.org/10.1016/S0003-3472(87)80274-9)
- O'Brien DM (2019) Static scaling and the evolution of extreme canine size in a saber-toothed cat (*Smilodon fatalis*). *Integr Comp Biol* 59:1303–1311. <https://doi.org/10.1093/icb/icz054>
- O'Brien DM, Boisseau RP (2018) Overcoming mechanical adversity in extreme hindleg weapons. *PLoS ONE* 13:e0206997. <https://doi.org/10.1371/journal.pone.0206997>
- O'Brien DM, Allen CE, Van Kleeck MJ et al (2018) On the evolution of extreme structures: static scaling and the function of sexually selected signals. *Anim Behav* 144:95–108. <https://doi.org/10.1016/j.anbehav.2018.08.005>

- Panhuis TM, Wilkinson GS (1999) Exaggerated male eye span influences contest outcome in stalk-eyed flies (Diopsidae). *Behav Ecol Sociobiol* 46:221–227. <https://doi.org/10.1007/s002650050613>
- Parker GA (1974) Assessment strategy and the evolution of fighting behaviour. *J Theor Biol* 47:223–243. [https://doi.org/10.1016/0022-5193\(74\)90111-8](https://doi.org/10.1016/0022-5193(74)90111-8)
- Pike KN, Tomkins JL, Buzatto BA (2017) Mixed evidence for the erosion of intertactical genetic correlations through intralocus tactical conflict. *J Evol Biol* 30:1195–1204. <https://doi.org/10.1111/jeb.13093>
- Plavcan JM, van Schaik CP (1992) Intrasexual competition and canine dimorphism in anthropoid primates. *Am J Phys Anthropol* 87:461–477. <https://doi.org/10.1002/ajpa.1330870407>
- Pomfret JC, Knell RJ (2006) Sexual selection and horn allometry in the dung beetle *Euoniticellus intermedium*. *Anim Behav* 71:567–576. <https://doi.org/10.1016/j.anbehav.2005.05.023>
- Pope SD (2000) Testing function of fiddler crab claw waving by manipulating social context. *Behav Ecol Sociobiol* 47:432–437. <https://doi.org/10.1007/s002650050687>
- Pratt AE, McLain DK, Lathrop GR (2003) The assessment game in sand fiddler crab contests for breeding burrows. *Anim Behav* 65:945–955. <https://doi.org/10.1006/anbe.2003.2152>
- Preston BT, Stevenson IR, Pemberton JM et al (2003) Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. *Proc R Soc B* 270:633–640. <https://doi.org/10.1098/rspb.2002.2268>
- Radwan J (1993) The adaptive significance of male polymorphism in the acarid mite *Caloglyphus berlesii*. *Behav Ecol Sociobiol* 33:201–208. <https://doi.org/10.1007/BF00216601>
- Radwan J (2001) Male morph determination in *Rhizoglyphus echinopus* (Acaridae). *Exp Appl Acarol* 25:143–149. <https://doi.org/10.1023/A:1010688516704>
- Radwan J, Czyż M, Konior M, Kołodziejczyk M (2000) Aggressiveness in two male morphs of the bulb mite *Rhizoglyphus robini*. *Ethology* 106:53–62. <https://doi.org/10.1046/j.1439-0310.2000.00498.x>
- Reaney LT, Drayton JM, Jennions MD (2011) The role of body size and fighting experience in predicting contest behaviour in the black field cricket, *Teleogryllus commodus*. *Behav Ecol Sociobiol* 65:217–225. <https://doi.org/10.1007/s00265-010-1030-0>
- Rico-Guevara A, Hurme KJ (2019) Intrsexually selected weapons. *Biol Rev* 94:60–101. <https://doi.org/10.1111/brv.12436>
- Rodríguez RL, Eberhard WG (2019) Why the static allometry of sexually-selected traits is so variable: the importance of function. *Integr Comp Biol* 59:1290–1302. <https://doi.org/10.1093/icb/icz039>
- Searcy WA, Nowicki S (2005) The evolution of animal communication: reliability and deceptability in signaling systems. Princeton University Press, Princeton, New Jersey
- Setchell JM, Wickings EJ (2005) Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). *Ethology* 111:25–50. <https://doi.org/10.1111/j.1439-0310.2004.01054.x>
- Shuker DM (2014) Sexual selection theory. In: Shuker DM, Simmons LW (eds) The evolution of insect mating systems. Oxford University Press, Oxford, pp 20–41
- Simmons LW, Tomkins JL (1996) Sexual selection and the allometry of earwig forceps. *Evol Ecol* 10:97–104. <https://doi.org/10.1007/BF01239350>
- Sneddon LU, Huntingford FA, Taylor AC, Orr JF (2000) Weapon strength and competitive success in the fights of shore crabs (*Carcinus maenas*). *J Zool* 250:397–403
- Stewart KA, Van den Beuken TPG, Rhebergen FT et al (2018) Evidence for a third male type in a male-dimorphic model species. *Ecology* 99:1685–1687
- Swallow JG, Wallace LE, Christianson SJ et al (2005) Genetic divergence does not predict change in ornament expression among populations of stalk-eyed flies. *Mol Ecol* 14:3787–3800. <https://doi.org/10.1111/j.1365-294X.2005.02691.x>
- Tazzyman SJ, Iwasa Y, Pomiankowski A (2014) Signaling efficacy drives the evolution of larger sexual ornaments by sexual selection. *Evolution* 68:216–229. <https://doi.org/10.1111/evo.12255>
- Thompson DW (1942) On growth and form. Cambridge University Press, Cambridge, UK
- Tidière M, Lemaître JF, Pélabon C et al (2017) Evolutionary allometry reveals a shift in selection pressure on male horn size. *J Evol Biol* 30:1826–1835. <https://doi.org/10.1111/jeb.13142>
- Tina FW, Jaroensutasinee M, Jaroensutasinee K (2016) Sex and size affecting time allocations for activities in *Uca annulipes* (H. Milne Edwards, 1837). *Crustaceana* 89:759–773
- van Lieshout E, Elgar MA (2009) Armament under direct sexual selection does not exhibit positive allometry in an earwig. *Behav Ecol* 20:258–264. <https://doi.org/10.1093/beheco/arp013>
- Vanpé C, Gaillard J, Kjellander P et al (2007) Antler size provides an honest signal of male phenotypic quality in roe deer. *Am Nat* 169:481–493. <https://doi.org/10.1086/512046>
- Voje KL (2016) Scaling of morphological characters across trait type, sex, and environment: a meta-analysis of static allometries. *Am Nat* 187:89–98
- Voje KL, Hansen TF (2013) Evolution of static allometries: adaptive change in allometric slopes of eye span in stalk-eyed flies. *Evolution* 67:453–467. <https://doi.org/10.1111/j.1558-5646.2012.01777.x>

- Wilkinson GS, Reillo PR (1994) Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. *Proc Roy Soc B* 255:1–6. <https://doi.org/10.1098/rspb.1994.0001>
- Yoshino K, Koga T, Oki S (2011) Chelipeds are the real weapon: cheliped size is a more effective determinant than body size in male–male competition for mates in a hermit crab. *Behav Ecol Sociobiol* 65:1825–1832
- Zeil J, Hemmi JM (2006) The visual ecology of fiddler crabs. *J Comp Physiol A* 192:1–25. <https://doi.org/10.1007/s00359-005-0048-7>

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