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Why the Static Allometry of Sexually-Selected Traits Is So Variable: The Importance of Function

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Synopsis Sexually-selected traits often show positive static allometry, with large individuals bearing disproportionately large structures. But many other sexually-selected traits show isometry or even negative allometry, with trait size varying relatively little with body size. We recently proposed that the functions of these traits (as aggressive signals, weapons, courtship signals, and contact courtship devices) determine their allometries. Positive allometry is generally favored for aggressive signals because aggressive signals are selected to emphasize body size (and thus fighting prowess). In contrast, the biomechanics of force application in weapons only sometimes select for positive allometry; the content of courtship signals is even less often related to body size; and contact courtship devices are selected to be relatively invariant across body sizes. Here we summarize the arguments in favor of this "functional allometry" hypothesis and expand a comparative test of its predictions. Our results indicate that sexual traits have the allometric slopes predicted by our hypothesis, regardless of which body part bears the structure.

Introduction

The contrast between traits that have evolved under sexual versus natural selection can be summarized as extravagance as opposed to utility. Not only do sexually-selected traits tend to evolve and diverge faster, they also tend to reach greater extremes of elaboration, showiness, and relative size (Darwin 1871; Thornhill and Alcock 1983; Eberhard 1985; Andersson 1994). We focus here on the static allometry of sexually-selected traits, a measure of their size relative to the body of the bearer (sexually mature adults in this article). The allometric relation between the size of a structure (y) and the body size (x) has usually been quantified using the "Huxley power equation", $y = a + x^b$, where a is the intercept and b the slope of a log-log regression of y on x (Huxley 1932). This classic model is undoubtedly a simplification, and a more biologically realistic expression of how different structures have evolved would probably need to have a larger number of

factors to reflect the growth mechanisms involved in producing the structure (the model of Nijhout and McKenna (2017), for instance, has eight kinetic parameters). In addition, some traits show non-linear relations in such plots (Shingleton et al. 2007; Nijhout and McKenna 2017). Nevertheless, the simpler Huxley equation is useful at several other levels of analysis, such as the structure's functional properties, including its strength, mechanical advantage, and ability to stimulate sensory receptors of other animals, and the patterns of relative investments of materials in different portions of the body. These are the variables emphasized in our analyses here. An allometric slope of $b = 1$ indicates that differences in the trait between individuals are exactly proportional to the differences in their body sizes ("isometry"). A slope of $b > 1$ ("positive allometry" or "hyperallometry") indicates that the trait is disproportionately large in larger individuals (and that smaller individuals have relatively small

structures). A slope of $b < 1$ ("negative allometry" or "hypoallometry") indicates the trait size is relatively constant compared with body size; large individuals have relatively small structures, and small individuals have relatively large structures. Isometry has often been taken to be the default scaling relationship for traits under natural selection, but weak negative allometry appears to be more common (Voje 2016).

Many of the sexually-selected traits whose allometry was first analyzed showed positive allometry, and extreme positive allometry has sometimes been used as a diagnostic for sexual selection (Green 2000; Kelly 2005; Kodric-Brown et al. 2006; Tasikas et al. 2009, O'Brien et al. 2018; O'Brien 2019). But it is now known that sexually-selected traits exhibit a very wide range of variation in allometry that ranges from strongly positive to strongly negative allometry (Eberhard et al. 1998, 2009; BondI uriansky 2007; Eberhard 2009; Voje 2016). To understand the effects of sexual selection on allometry it is necessary to understand the extreme variation in the allometry: why it varies in both directions from isometry.

We recently proposed a general explanation for variation in the allometry of sexually-selected traits, and presented data supporting it (Eberhard et al. 2018). Here we summarize this explanation (including a more specific discussion of negative allometries), and subject it to further testing. We expand the analyses in Eberhard et al. (2018) with additional tests for possible developmental constraints on allometry evolution (which body part bears the structure of concern), and for potential confounding effects of variation in sample size across studies and datasets (see Methods).

We argue that, while sexual traits are often selected for extravagance and showiness of form, only a subset are selected for extreme positive allometries in size. This subset consists mostly of traits selected to function as threats that signal body size in direct confrontations between males competing for mates.

This "functional allometry" hypothesis grows out of the fact that sexual selection arises from competition for mates in two basic contexts: (1) direct male–male aggression, sometimes in the form of aggressive threat signals, and sometimes in physical combat (often with specialized weapons) and (2) male–female interactions, which include courtship by means of long-distance advertisement signals as well as short-range, contact-courtship devices (such as genitalia) that occasionally also involve physical or physiological manipulation or coercion (Darwin 1871; Thornhill and Alcock 1983; Eberhard 1985, 1996; Andersson 1994; Arnqvist and Rowe 2005;

Emlen 2008, 2014; Rosenthal 2017). We argue that structures which function as intra-sexual aggressive signals have the greatest likelihood of being selected to indicate body size and of evolving extreme positive allometries. Weapons and courtship signals are less likely to be selected to indicate body size and to show positive allometry. And contact-courtship devices are likely to evolve negative allometries.

We present our arguments in terms of "conventional" Darwinian sex roles, with males competing over access to females and their gametes. This reflects in part writing convenience, but also that males are predominantly more strongly sexually selected than females (Janicke et al. 2016). We trust that the reader can apply the logic of our arguments to cases of sex role reversal, in which female–female aggressive signals would have the greatest likelihood of evolving extreme positive allometries to indicate larger body sizes.

Why different kinds of traits evolve different allometries: limitations of previous ideas regarding male "quality"

Although developmental mechanisms may sometimes impose limits on allometries (see Discussion), selection is expected to favor an allometry for a given structure that maximizes the net payoff for individuals over the range of different body sizes that occur naturally (Bondurianansky and Day 2003; Bondurianansky 2007; Eberhard et al. 2009). Frequently, authors have supposed that all sexually-selected traits should exhibit extreme positive allometries, often based on the widespread notion that these traits generally serve as indicators of individual quality or condition, with larger size being equated with better quality or condition (Andersson 1994; Bradbury and Vehrencamp 1998, 2000; Emlen, 2014). The logic of this supposition comes from the rationale of the handicap principle (Andersson 1994): only males of high quality or in good condition could afford to invest in disproportionately large ornaments or weapons, thereby advertising their worth as mates or their prowess as fighters. In other words, only large males could obtain net positive payoffs from having disproportionately large sexual structures.

There are, however, major problems with this view. In the first place, several recent reviews and meta-analyses point out empirical findings that sexual selection is less often based on indicators of individual quality or condition than has been supposed (Prokop et al. 2012; West-Eberhard 2014; Prum 2012, 2017; Rosenthal 2017; Ryan 2018;

Patricelli et al. 2019). It is true that the message communicated by sexually-selected traits may signal individual quality or condition, but this is only one hypothesis among many, and the data do not support it consistently. The consequence for allometry studies is that it is not universally true that sexual selection favors larger males that sport disproportionately large sexual structures.

A second basic problem is the confusion that stems from the imprecision of the words "quality" and "condition." Different studies have used many different indicators of "quality," many of which are often traits thought to confer advantages under natural selection. Some examples from the long list include the following: larger size, more valuable nuptial gifts, better nutrition, greater carotenoid content of the diet, greater degree of symmetry, a less inbred ancestry, more intense beak color, a darker black breast stripe, greater longevity, superior immune function, greater resistance to parasites (of various types), better foraging ability, greater "metabolic health," better match between nuclear and mitochondrial DNA, and greater physiological efficiency (see also Andersson 1994). Some of these indicators almost certainly correlate negatively with others. For instance, a larger (and thus less agile) flycatcher would probably be less able to avoid predators with quick evasive moves, or to overcome quick evasive maneuvers of its insect prey. An increased investment in defenses against parasites would imply reductions in investment in the structures and behavior that are used to accomplish other essential functions; in fact, increased investment to defend against one type of parasite could reduce investment in defenses against others. In sum, it is not reasonable to say that all such indicators are reliable for all species. But this lack of uniform reliability means that in order to test the male quality theory, it is necessary to choose among potential indicators of that "quality." Unfortunately, biologically reasonable criteria for making such a choice are seldom if ever available, and the entire enterprise can become self-fulfilling. If the trait in question correlates with a given indicator, the trait can be said to have evolved to signal that indicator. If, on the other hand, it does not correlate with an indicator, then it can be said to have evolved to signal some other, yet to be considered indicator. For instance, the multiple cases of negative correlations between immunity and greater elaboration of courtship signals in insects (Hunt et al. 2018) can simply be chalked up to females choosing other, as yet unstudied aspects of male "condition."

In addition, the focus on natural selection neglects another key aspect of "quality" in the context of sexual selection: the ability to communicate *per se*. In human communication, the ability to present messages clearly and appealingly is highly valued, whether the message itself involves truths or falsehoods (witness the high salaries in the advertising industry and the success of politicians with especially good communication skills). It seems inevitable that similar Fisherian "salesmanship" abilities are important for males attempting to influence female reproductive decisions in nature (West-Eberhard 1983, 2014; Prum 2012, 2017; Ryan 2018). The frequently narrow focus on natural selection in biologists' discussions of animal communication runs the risk of omitting the value of salesmanship *per se*.

In sum, supposing that the messages communicated by sexually-selected traits consistently concern individual quality or condition is not defensible empirically, and can distract attention from other important (perhaps more crucial) factors. At best it gives only an incomplete view of the signals exchanged between males, and between males and females in nature.

Aggressive intra-sexual signals are likely to be selected to scale steeply on body size

Our starting point is that in physical battles between males in nature, there is a clear general rule: larger males usually win over smaller rivals (Clutton-Brock 1982; Thornhill and Alcock 1983; Andersson 1994; Emlen 2014). This asymmetry associated with male size is crucial for understanding the evolution of aggressive (threat) signals, because the function of threats is to allow males to size each other up, estimate their chances of winning a physical battle, and (for the male likely to lose) to withdraw and thus avoid an unproductive or potentially dangerous battle. Males of all sizes can benefit from an exchange of threat signals that correlate with their size: large individuals benefit from signaling their larger size and thus winning some battles by intimidating smaller males rather than by having to fight; and smaller individuals can benefit from attending to signals correlated with their opponent's size and avoiding potentially damaging and unproductive physical combat (Parker 1974; Dawkins and Krebs 1978; Hamilton 1979; Petrie 1988, 1992; Thornhill and Alcock 1983; Andersson 1994; Simmons and Tomkins 1996; Számadó 2003, 2008). When males are approximately equal in size, an individual better-able to emphasize his size may be able to intimidate the other. While subsequent physical battles can offer the opportunity to call the bluff of

dishonest advertising of body size, deceit (feigning larger size) is possible and sometimes occurs, especially with similarly-sized males (Dawkins and Krebs 1978; Thornhill and Alcock 1983; Andersson 1994; Backwell et al. 2000; Számadó 2008).

In addition, when two large males face each other, the stakes are often higher. The risk of injury is likely to be higher; in addition, their fights will tend to occur over the highest quality prizes, because larger males tend to seek out the most valuable resources. This clumping also means that a large male is more likely to interact aggressively with other relatively large males than is a smaller male. Thus, winning an interaction by using threats can be selectively more important for large males. Furthermore, judging an opponent's size is likely to be more difficult for larger males, due to Weber's Law of perception: larger differences are required to distinguish between stimuli of larger magnitude (Marks 1974; Dember and Warm 1979; Akre and Johnsen 2016). Thus, a larger male will tend to need disproportionately large signaling devices to succeed in intimidating similarly-sized rivals.

In sum, positive allometry is expected to be favored in aggressive signaling devices for several reasons. Larger males tend to compete directly over more valuable resources; to interact more often with similar-sized opponents; and to require larger signaling devices in order to intimidate their rivals.

Use as a weapon may or may not favor steep scaling on body size

The mechanical functions of animal weapons vary widely among species: their uses include striking, pushing, pinching, stabbing, wrestling, slashing, and parrying. The biomechanics of applying force in combat favor positive allometries only in some of these situations, not universally (Geist 1977; Eberhard 2002; Dennenmoser and Christy 2013; McCullough et al. 2014). It might be that, when long reach is a key to success in a battle, larger males would benefit from having disproportionately long weapons. But, for instance, if heavy sturdy weapons are favored to pinch or hammer (e.g., McCullough et al. 2014; Geist 1977) and if energy costs are limiting, shallow allometries might be favored (Mackinnon 1981; Clutton-Brock 1982; Kitchener 1985; Bonduriansky and Day 2003; Bonduriansky 2007). Even in situations in which reach has an important influence on function, naturally-selected structures (e.g., chameleon tongues) sometimes evolve isometry/negative allometry rather than positive allometry (O'Brien et al. 2018). Careful observations of the mechanical demands on weapons can be

necessary to make predictions about the expected allometry.

In addition, it is important to realize that many (and probably most) weapons are also used prior to battles as aggressive signaling devices; for instance, ungulates with horns and antlers usually perform stylized visual displays of their weapons before beginning a battle, and males sometimes cede after the display without fighting (Geist 1977; Maynard Smith and Harper 2003). In such cases, the weapon's optimal design for the two functions of signaling and fighting likely differs; in fiddler crab claws, for instance, there is a trade-off between maximizing detectability and applying force (Dennenmoser and Christy 2013). In some mating systems, the weapon function is likely to be more important (with a lower likelihood of positive allometries evolving), because males have fewer reproductive alternatives and are thus less likely to allow themselves to be intimidated (Hamilton 1979; Thornhill and Alcock 1983; Bean and Cook 2001). In others, where males can more easily find alternative mating opportunities, the signaling function may be more important, thus favoring more positive allometries.

In sum, sexually-selected weapons are less likely to consistently exhibit positive allometries than are sexually-selected aggressive signals.

Courtship signals may or may not be selected to scale steeply on body size

The message conveyed by aggressive signals is simple and predictable: I am larger than you, back off. The advantage of over-emphasizing body size via positive allometry in such signaling devices is clear. In contrast, as we noted above, courtship signals convey a much broader range of messages; some of these messages may involve aspects of naturally-selected quality or condition, but others do not (Prokop et al. 2012; Prum 2012, 2017; West-Eberhard 2014; Rosenthal 2017; Ryan 2018; Patricelli et al. 2019). Furthermore, even when ornaments do signal quality/condition, these properties are not necessarily related to body size. There is not a necessary relation between a male's body size and his immunocompetence, the health of his metabolic processes, or the match between the nuclear and mitochondrial DNA of the pair, to name but a few of the many possible dimensions of naturally-selected quality. Only when such a relation exists, or when mate choice favors large body sizes directly, would courtship signals be expected to evolve positive allometries.

Courtship signals are often also used as threats directed at other males, and in such cases the

expectations mentioned above may need to be modified because the male–male threat function would increase the likelihood of selection favoring positive allometry. Thus, to the extent that selection on the threat function dominates, courtship signals may sometimes evolve extreme, steep allometries. However, trade-offs between courtship and threat functions would likely vary in different mating systems with respect to which component is more strongly selected, leading to less consistent patterns of allometry.

Still another reason to not necessarily expect positive allometries in courtship structures is that some signals may function to identify the male's species identity (Andersson 1994).

In sum, several lines of evidence suggest that courtship signals are even less likely than weapons to exhibit positive allometries.

Contact-courtship devices may be selected to scale shallowly with body size

Some sexually-selected traits function as courtship devices that make direct contact with the body of the mating partner. Genitalia are an example. Besides sperm transfer, genitalia often serve to stimulate the mating partner in courtship designed to influence to cryptic mate choice (Eberhard 1985, 1996; Peretti and Aisenberg 2017). There are also non-genitalic structures that are sexually dimorphic and that function as contact-courtship devices that are used to rhythmically stroke, tap, squeeze, or otherwise stimulate the mating partner. The same arguments just presented for why non-contact courtship signals are not particularly likely to evolve steep allometries also apply to contact courtship traits. In addition, the physical contact that these male structures make with specific portions of the female implies that they may often be selected to mesh well with the most common or standard sizes of female bodies and their sensory structures. This could favor male trait sizes that are relatively invariant across body sizes, resulting in especially shallow, negative allometries. This "one size fits all" explanation, originally proposed to explain why genitalia tend to show negative allometries, should also apply to non-genitalic contact-courtship traits, regardless of which part of the male's body is modified to contact the female (Eberhard 1985, 2009; Eberhard et al. 1998, 2009).

Summary and predictions

In brief, we argue that sexually-selected traits evolve steep allometries mainly if they are selected to signal large body size *per se*. This is most likely to happen

with aggressive signals. Weapons and courtship signals are less likely to evolve steep allometries, and will tend to be closer to isometry, but with greater variation between species. Contact-courtship signals, in contrast, are expected to not scale with the body size of the bearer.

This functional allometry hypothesis predicts a ranking of expected steepness in allometry: aggressive signal traits should have the steepest allometries; courtship signals should have shallower allometries than aggressive signals; and contact-courtship traits should have the shallowest allometries (Eberhard et al. 2018). The predictions could ideally be tested with a "dream team" of structures with "pure functions" (i.e., that function only as aggressive signals, only as courtship signals, or only as contact-courtship devices). We therefore scoured the literature, and also measured structures in additional species to obtain a sample to test these predictions (see Methods).

Our rationale runs counter to the argument that allometric-developmental mechanisms constrain the adaptive evolution of body proportions (Gould 1974; Gould and Lewontin 1979), as well as to observations that allometric slopes are relatively harder to modify with selection than are allometric intercepts (Egset et al. 2012; Bolstad et al. 2015; Houle et al. 2019). We tested these "constraint" hypotheses against our functional allometry hypothesis by asking whether traits evolve the predicted allometric slopes regardless of where on the body they are located, or whether their placement on the body influences the allometry of traits with different functions.

Finally, we tested for potential confounding effects of sample size on the allometries detected in different studies and different datasets. This effect could take two different forms. On the one hand, studies with small sample sizes may be at risk of reporting inflated effect sizes. On the other hand, if researchers have devoted more attention or effort to species with striking structures (Bonduriansky 2007), studies with larger sample sizes might be those reporting the larger effect sizes.

Methods

We assembled datasets for "pure function" aggressive signals, courtship signals, and contact-courtship traits. We only included a structure when (1) there was clear indication, such as sexual dimorphism and species-specificity, that the structure is sexually-selected and (2) detailed behavioral information on the animals' behavior and sensory capabilities confirmed the "purity" of its function. We will give an

example of a pure threat device, and a pure courtship device (for references and other descriptions, see the appendices of Eberhard et al. (2018)). The sexually dimorphic thin, elongate legs IV of males of the harvestman *Longiperna concolor* appear to be "pure" threat devices. When males battle over territories, they position themselves rear-to-rear, extend their legs IV laterally, and align but do not intertwine them. These legs do not have teeth or other armaments, so both behavior and morphology indicate that they are not weapons. In contrast, males court females face-to-face, and the females do not touch the male's legs IV during courtship. The limited visual capabilities of these animals make it unlikely that females (or males) can assess male hind femur length visually, so they show no sign of being courtship devices. The sexually dimorphic, elongate, hair-like antennal aristae of males of the medfly *Ceratitis capitata* appear to be "pure" courtship devices. The male begins to court a female by slowly approaching her head-to-head; at close range he rotates his head rapidly from side to side so that his aristae brush repeatedly against the female's aristae. Experimental removal of either male or female aristae lowers the chances that the male will succeed in mounting the female and copulating (in most courtships that failed, the female decamped when the male attempted to mount her). The aristae are very thin, and probably not visible to other males; they do not come into play during the brief male–male aggressive interactions, which consist of short lunges to drive a rival male from a display site.

We did not include weapons because of the difficulty in ascertaining that they are not also used in aggressive signaling, and because predicting the allometry they should evolve requires detailed knowledge of the biomechanics of how they are used in applying and resisting force in different types of fighting situations.

We measured the genitalia of some of the species in the contact-courtship dataset. We excluded genitalia from the first analyses because they might force a pattern, as they are already well-known to have very shallow allometries (Eberhard et al. 1998, 2009; Eberhard 2009; Voje 2016). Furthermore, because of their key role as sperm transfer devices, genitalia do not function as pure contact-courtship traits. We did, however, include them in a final overall comparison of allometries across all types of sexually-selected trait included in this study.

For each trait, we obtained an allometric slope (b) using ordinary least squares (OLS) $\log_{10}$-$\log_{10}$ regression of a linear measurement of its size on a linear measurement of body size (Kilmer and Rodríguez

2017). We conducted all analyses with linear mixed models in JMP 11.2.0 (SAS Institute, Cary, NC, USA). In all models, the allometric slopes (b) were the dependent variable; the independent variables are outlined below.

We first compared the allometric slopes (b) of pure aggressive signals with those of pure courtship signals. Our prediction was that aggressive signal traits would have steeper allometries than courtship signal traits. This dataset included three species of arachnids, one species of fish, and four species of insects in eight genera and six families (aggressive signals); and two species of arachnids, and three species of insects in three genera and three families (courtship signals) (see Appendixes 1 and 2 in Eberhard et al. (2018) for details). The aggressive signal traits were used in male–male interactions, except in one fish species with aggressive female–female interactions.

We then compared the allometric slopes (b) of pure contact-courtship traits with those of control, non-sexual body parts in the same species. Here the prediction was for contact-courtship traits to have shallower allometries than the control, non-sexual traits. In our prior study (Eberhard et al. 2018) we found that the results were highly robust to several potentially confounding variables (how closely the measurement pin-pointed the part that makes contact with the mating partner; whether sexual contact is the trait's only function; and whether the trait has a potential lock-and-key fit with the mating partner). The only variable that made a difference was whether contact with the mating partner was forceful (slopes were steeper when the trait is used to grab and hold the mating partner during struggles). Under the rationale of the functional allometry hypothesis, traits employed in forceful sexual contacts are more weapon-like, and so the prediction is for less consistently shallow allometric slopes (Eberhard et al. 2018). We therefore compared non-forceful and forceful sexual contact traits separately with non-sexual body parts. This dataset included 6 species of arachnids, 11 species of insects, and 3 species of anurans (in 1 of which 3 populations were analyzed) in 16 genera and 13 families (the species in Appendix 3 in Eberhard et al. (2018), plus 1 wasp from Eberhard (manuscript in preparation) and 3 anurans from Schulte-Hostedde et al. (2011)). This dataset included two species for which we measured sexual contact structures in females, and we also asked whether female allometries differed from those of males.

In the two tests above, the model also included a term for the part of the body where the sexual trait was located. We categorized body parts broadly, as
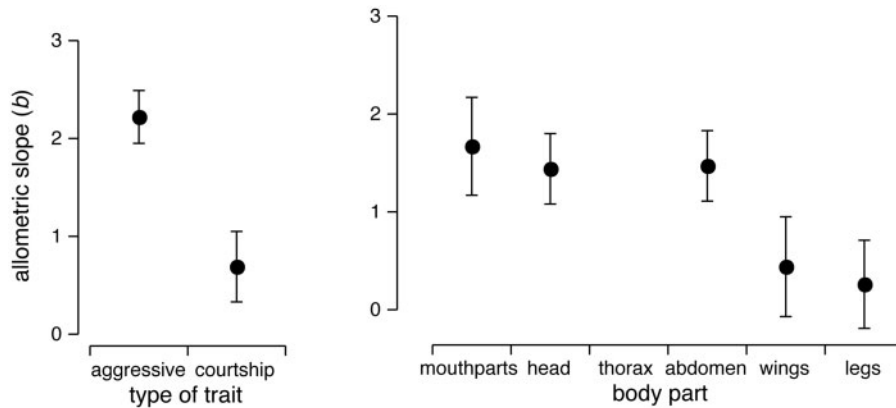
Fig. 1 Allometry of aggressive and courtship signal traits. Data are least square mean values ± 1 SE obtained from the linear mixed models (which account for the effect of the other terms in the model). The range of values in the y-axes indicates the range of variation in allometric slopes in the data. Left panel: aggressive signal traits had significantly higher allometric slopes than courtship signal traits (Table 1). Right panel: allometric slopes varied across traits on different body parts regardless of whether they were used in aggressive or courtship signals, but not significantly (Table 1).

follows: mouthparts, head (e.g., aristae or antennae), thorax, abdomen, wings, and legs. These categories are not meant to posit homologies across the species included in the analyses. However, they allow us to test in a preliminary way for possible developmental confounds on the evolution of allometry according to trait function.

To test for an effect of the sample size of each study/dataset, we calculated mean allometric slope data for each trait type for each species. We then used these mean slopes as the dependent variable in tests with trait type and sample size as the independent variables. We also tested for consistent variation in sample size across groups using a linear mixed model with broad taxa (anurans, arachnids, fish, and insects) as a fixed term and species as a random term.

Finally, we conducted one overall comparison across all four trait types (aggressive signals, courtship signals, non-forceful contact-courtship traits, genitalia) (the latter for 14 species of insects and arachnids in 11 genera and 8 families; see Appendix 3 in Eberhard et al. (2018), and Eberhard (manuscript in preparation) against one another, using the above species means per trait type.

All the above models also included species (or population, in the case of one anuran species for which three populations were sampled) as a random term fit with the Restricted Maximum Likelihood (REML) method, because some species contribute multiple data points. In the prior study we found that results did not vary according to whether we included only species as the random term, or also species nested within genus, or genus within family

Table 1 Comparison of the allometry of aggressive and courtship signals, taking into account the position of the trait on the body of the animal

Term	df	F	P
Trait type	1, 15.819	**8.57**	**0.027**
Body part	4, 6.163	2.57	0.14

Notes: We report F-ratios for the fixed terms from the linear mixed model (random species term not shown). Significant terms in bold.

(Eberhard et al. 2018). We therefore only used the species term here. In all cases, the 95% confidence intervals for the species term either overlapped zero or the term was very small. We therefore only report the F-ratio tests for the fixed terms in the models.

Results

We found strong support for all of the predictions of the functional allometry hypothesis. Traits used as aggressive signals had allometric slopes that were on average more than twice as steep as those of courtship signals (Fig. 1; Table 1). Allometric slopes varied across body parts (Fig. 1), but not significantly, and the difference between aggressive and courtship signals was robust to this variation (Table 1).

Non-forceful contact courtship traits had allometric slopes that were on average half as steep as those of non-sexual body parts, with no difference in the pattern between the sexes (Fig. 2A; Table 2). In contrast, the allometric slopes of forceful contact structures were nearly identical to those of non-sexual body parts (Fig. 2B; Table 2). Allometric slopes
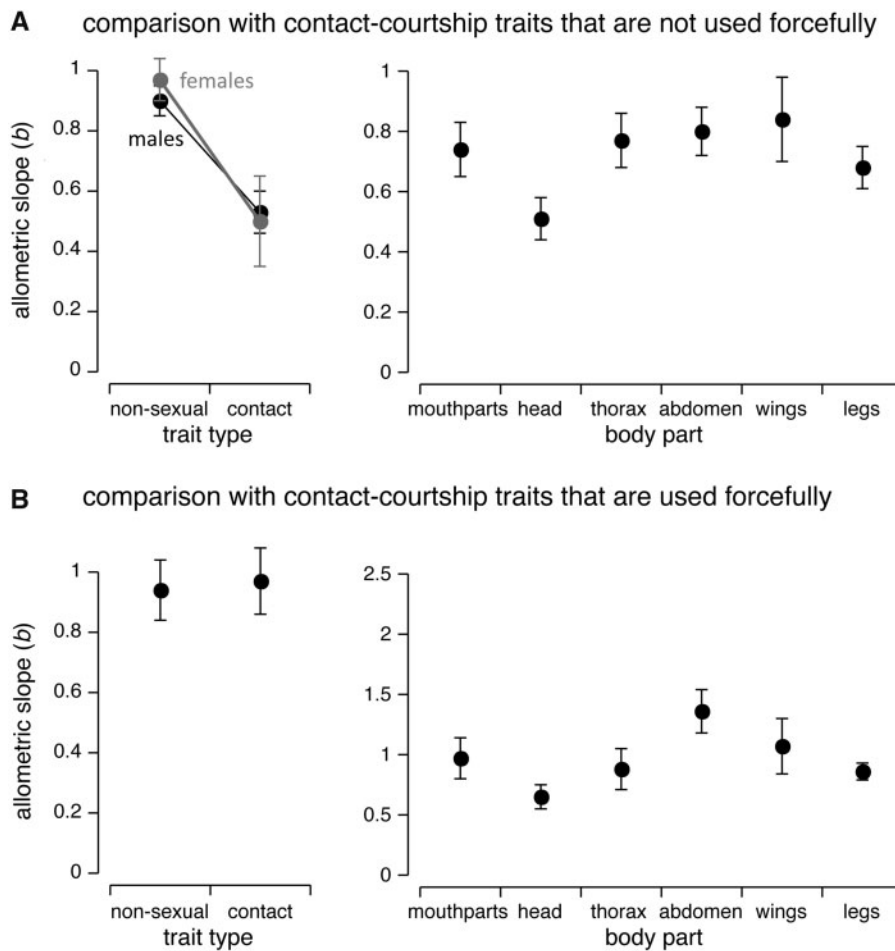
A   comparison with contact-courtship traits that are not used forcefully

B   comparison with contact-courtship traits that are used forcefully

Fig. 2 Allometry of contact courtship traits compared with non-sexual body parts. Data are least square mean values ± 1 SE obtained from the linear mixed models (which account for the effect of the other terms in the model). The range of values in the y-axes indicates the range of variation in allometric slopes in the data. (**A**) Comparison with contact courtship traits that are not used forcefully. Left panel: These contact courtship traits had significantly lower allometric slopes than control non-sexual body parts, and the pattern did not differ between the sexes (Table 2). Right panel: allometric slopes varied significantly across traits on different body parts regardless of trait type (Table 2). Note that the detected difference between contact and non-sexual traits is robust to this variation across body parts. (**B**) Comparison with contact courtship traits that are used forcefully. Left panel: These contact courtship traits had very similar allometric slopes to control non-sexual body parts (Table 2). Right panel: allometric slopes varied significantly across traits on different body parts regardless of trait type (Table 2). Note the broader range for the y-axis in this panel.

Table 2 Comparison of the allometry of contact courtship and non-sexual traits, taking into account the position of the trait on the body of the animal

Non-forcefull contact traits				Forceful contact traits			
Term	df	F	P	Term	df	F	P
Trait type	1, 120.9	**21.28**	**<0.0001**	Trait type	1, 93.1	0.0006	0.98
Sex	1, 122	0.04	0.84	Body part	5, 91.93	**3.24**	**0.0098**
Trait type × sex	1, 116.4	0.48	0.50				
Body part	5, 119.4	**3.15**	**0.010**				

Notes: Non-forceful and forceful contact traits tested separately, as the predictions differ (see text). We report F-ratios for the fixed terms from the linear mixed model (random species term not shown). Significant terms in bold.

varied significantly across body parts (Fig. 2A), but the difference between aggressive and courtship signals was robust to this variation (Table 2).

The above patterns remained when we took into account the sample size for each study/dataset (calculating mean slopes per trait type per species and

relating them to the sample size per species. In the comparison between aggressive and courtship signals, studies with larger samples detected higher slopes in both groups, but the difference between signal types remained large and significant (Fig. 3; Table 3). In the comparison between contact courtship traits and non-sexual body parts, the sample size of the study did not influence the detected slopes, and the pattern remained: non-forceful contact courtship traits had significantly lower slopes than non-sexual body parts, while forceful contact traits did not (Fig. 4; Table 4). As Figs. 3 and 4 show, sample sizes varied considerably across species and studies. However, there was no consistent difference in sample size across broad taxa (anurans, aranchids, fish, and insects; $F_{3, 28.99} = 1.67$, $P = 0.20$).

Finally, the overall comparison revealed differences in allometric slopes across all trait types (Fig. 5; Table 5). The difference remained when we removed aggressive signals (the most distinct category) from the comparison ($F_{2, 27.1} = 5.74$, $P = 0.0084$). The difference between only non-forceful contact courtship traits and genitalia was marginal ($F_{1, 21.8} = 3.37$, $P = 0.08$); however, the magnitude of the F-ratio intimates that this lack of significance may be due to low statistical power rather than lack of biological importance.

Discussion

Expanding our previous study (Eberhard et al. 2018), we tested the hypothesis that sexually-selected traits evolve different allometries according to their specific function in sexual competition. Testing across a reinforced "dream team" of sexually-selected traits that have different, clearly delimited functions, we found that traits used as "pure" aggressive signals had the steepest allometries; traits used as pure courtship signals had shallower allometries than aggressive signals; and traits used as pure contact-courtship devices had even shallower allometries (except when their function involved applying strong force to the female). These results support the two key tenets of the functional allometry hypothesis: First, only the aggressive signals subset of sexually-selected traits (which are likely to evolve body size-signaling functions) are selected to show steep positive allometries. Second, another subset of sexually-selected traits (courtship devices that must contact the mating partner in appropriate ways to bring about stimulation or mechanical fit) are selected to show shallow negative allometries. Interestingly, genitalia had marginally shallower allometries than non-genitalic contact courtship devices,
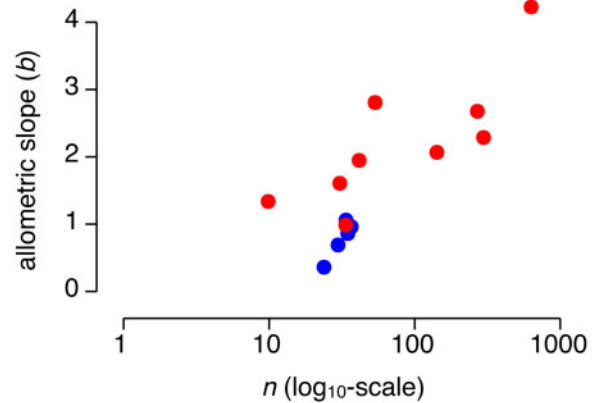

Fig. 3 Variation in the allometry of aggressive and courtship signal traits (red and blue symbols, respectively) according to the sample size (n) of the study. Data are species (study) means per trait type. The range of values in the y-axis indicates the range of variation in allometric slopes in the data. Studies with larger samples detected steeper allometric slopes, but this trend did not force the difference in the allometry of aggressive and courtship signal traits (Table 3).

Table 3 Comparison of the allometry of aggressive and courtship signal traits, taking into account variation in the sample size (n) of the different studies (see text)

Term	df	F	P
Trait type	1, 9.945	**8.55**	**0.015**
n	1, 10.1	**22.95**	**0.0007**

Notes: Data in this test are species means for each trait type. We report F-ratios for the fixed terms from the linear mixed model (random species term not shown). Significant terms in bold.

suggesting that genitalia may be even more strongly selected than non-genitalic contact courtship devices for shallow allometry. Perhaps this difference is due to more stringent requirements for adequate fit with the mating partner, either for effective courtship stimulation (e.g., if female sense organs are more localized) or for effective mechanical coupling. Another, recently compiled, larger sample of data on genitalia also showed shallow allometries (Voje 2016) (mean slopes for genitalia of insects and spiders were 0.47 and 0.45, respectively, as compared with the mean genitalia slope of 0.44 from our linear mixed model).

The results suggest that different structures have converged on different allometric patterns according to their function in sexual competition, in spite of originating in a wide variety of body parts across a broad range of animal groups (and in spite of some average differences in allometry across body parts). This contradicts expectations that allometry represents a constraint on adaptive evolution (Gould 1974; Gould and Lewontin 1979).
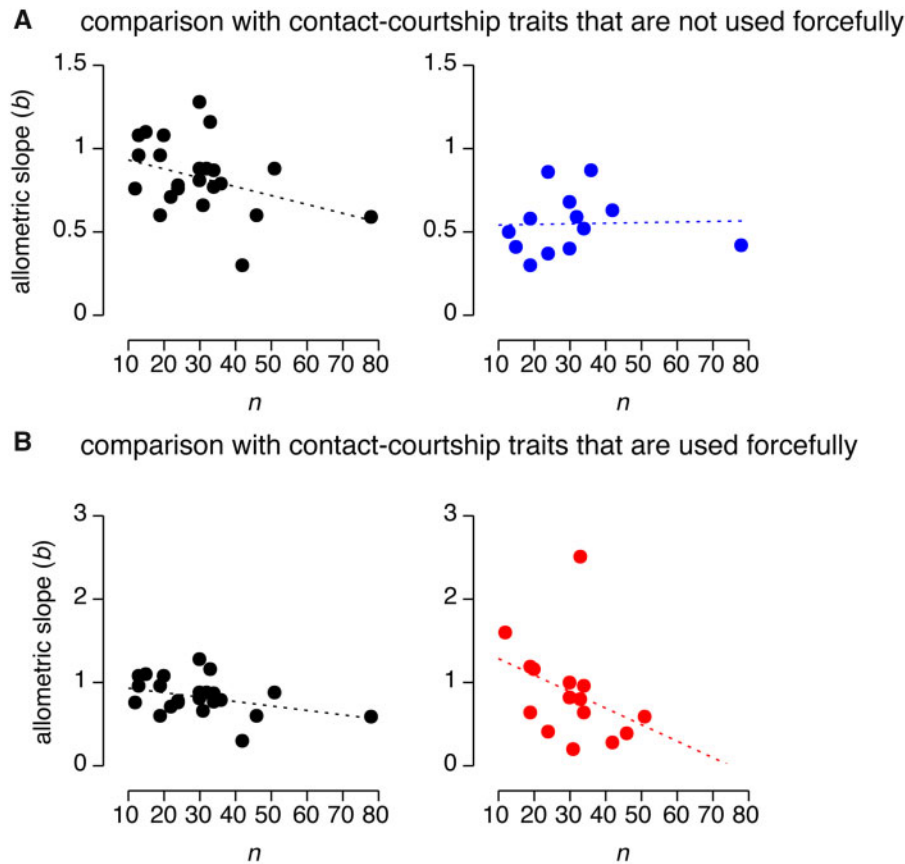
Fig. 4 Variation in the allometry of contact courtship traits (color symbols) compared with non-sexual body parts (black symbols) according to the sample size (*n*) of the study. Data are species (study) means per trait type. Dotted lines are fitted linear regressions, but note that none of them have a significant inclination (see below). The range of values in the *y*-axes indicates the range of variation in allometric slopes in the data. (**A**) Comparison between non-sexual body parts (black symbols) and contact courtship traits that are not used forcefully (blue symbols). These contact courtship traits had significantly lower allometric slopes than control non-sexual body parts, and the detected slopes did not vary with the sample size of the study (Table 4). (**B**) Comparison between non-sexual body parts (black symbols) and with contact courtship traits that are used forcefully (red symbols). These contact courtship traits did not differ significantly in allometric slope, and the detected slopes did not vary with the sample size of the study (Table 4). Note the broader range for the *y*-axes in (**B**).

Table 4 Comparison of the allometry of contact courtship and non-sexual traits, taking into account variation in the sample size (*n*) of the different studies (see text)

	forceful contact traits in data			Forceful contact traits in data			
Term	df	F	P	Term	df	F	P
Trait type	1, 21.24	**13.20**	**0.0015**	Trait type	1, 22.81	0.32	0.57
n	1, 8.732	1.58	0.24	*n*	1, 36	1.52	0.22

Notes: Data in this test are species means for each trait type. We tested non-forceful and forceful contact traits separately, as the predictions differ for them (see text). We report *F*-ratios for the fixed terms from the linear mixed model (random species term not shown). Significant terms in bold.

Although allometric scaling may be harder to modify than mean trait sizes (Egset et al. 2012; Bolstad et al. 2015; Houle et al. 2019), artificial selection, quantitative genetics, and phylogenetic studies have demonstrated sufficient standing genetic variation to permit changes over short time spans (Wilkinson 1993; Emlen 1996; Baker and Wilkinson 2001; Frankino et al. 2005; Rodríguez and Al-Wathiqui 2012; Stillwell et al. 2016; summary Nijhout and McKenna 2017). The likelihood that high numbers of growth parameters are involved in determining the allometric relationships of different structures (Nijhout and McKenna 2017), and the complexity of the mechanisms that determine the allometries of different aspects of any given structure (Hallgrimmsson et al. 2019), both imply that genetic variation on which selection can act is common.

Another possible limit to the evolution of functional allometries concerns the possibility that selection in favor of a particular allometric state is spread over many pleiotropic effects (Houle et al. 2019).
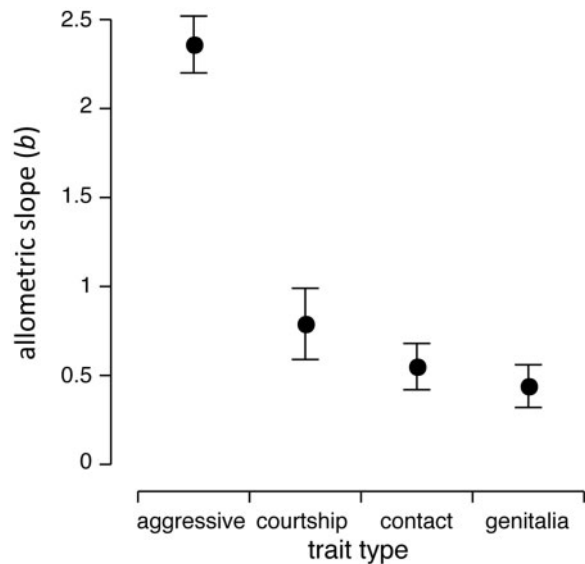
Fig. 5 Overall comparison of the allometry of traits in aggressive signals, courtship signals, non-forceful contact courtship devices, and genitalia. Data are least square mean values ± 1 SE obtained from the linear mixed model (which account for the effect of the other terms in the model).

Table 5 Overall comparison of the allometry of traits in aggressive signals, courtship signals, contact courtship devices, and genitalia

Term	df	F	P
Trait type	3, 30.27	**33.64**	**<0.0001**

Notes: We report F-ratios for the fixed terms from the linear mixed model (random species term not shown). Significant terms in bold.

The same multiplicity of growth mechanisms just mentioned, the covariance between them (Nijhout and McKenna 2017; Hallgrimmsson et al. 2019), and the apparent general importance of nutrition and insulin in various species (Shingleton et al. 2007; McKenna and Nijhout 2019; Casasa et al. 2019) imply that pleiotropy is common in the variables that control the growth of the types of structures that we have discussed above. Nevertheless, the fact that our results show that sexually selected structures with different functions show the predicted allometric patterns supports the notion that pleiotropic constraints on allometry have not been severe.

Our results imply that extreme positive allometry does not offer a diagnostic for traits under sexual selection. Indeed, it is important to recognize, as a starting point, that the extreme variation in the allometry of sexually-selected traits requires explanation. One next step will be further testing of our proposed explanation. Studies with weapons where knowledge of the biomechanics and details of

fighting behavior allow for informed predictions could be particularly illuminating. This position may not satisfy researchers when only the morphological data are available (e.g., with fossil organisms), but we believe that it is crucial to take into account the ways in which traits are used to understand their allometries.

In conclusion, theoretical considerations predicted that the allometry of structures under sexual selection will vary according to their different functions. Measurements of structures known to have different functions showed the predicted allometric relations. Careful consideration of function, which has often been lacking in previous studies of allometry, offers insights into the heretofore puzzling diversity of allometries of traits under sexual selection.

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