SEXUAL SELECTION AND STATIC ALLOMETRY: THE IMPORTANCE OF FUNCTION

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ABSTRACT

Many spectacular cases of biological diversity are associated with sexual selection, and structures under sexual selection often show positive static allometry: they are disproportionately large for the size of the animal's body in larger individuals. Other sexually selected structures, however, show negative allometry or isometry. Theory fails to account for this variation and recent summaries do not agree regarding the frequency of positive allometry in sexually selected structures. We propose explanations for why sexually selected structures with different functions (courtship, threat signals, and weapons) should differ in allometry. Positive allometry is predicted for threat structures (including most weapons) because larger individuals tend to win fights and threat signals are used to avoid unwinnable fights with larger opponents, the reproductive payoffs for contests tend to be higher for larger males, and discriminating the sizes of relatively larger traits requires greater absolute differences due to Weber's Law of sensory physiology. Male courtship signals, in contrast, convey many types of information, much of which is not consistently related to male size, so positive allometry is expected less often. We tested these predictions empirically by comparing the allometries of male structures with relatively "pure" functions. Our predictions were confirmed, thus helping to explain differences in previous empirical surveys.

INTRODUCTION

MANY of the most spectacular cases of biological diversity are associated with sex. Well-known examples include the varied and ornate horns and antlers that male beetles and ruminant mammals use to fight each other, the train of elongate, brightly colored feathers that a male peacock raises and shakes in front of a female, and the brilliant colors of dewlaps of male lizards. One of the original purposes of sexual selection theory was to explain how such extravagant sexual traits could have evolved (Darwin 1871; Andersson 1994). Compared with traits evolving under natural selection, sexually selected traits are often disproportionately elaborate, colorful, and large. Many sexually selected traits (such as ornaments, threat devices, and weapons) are very large relative to the overall size of the animal; and they are also often disproportionately large in larger individuals of a given species. These size differences have given rise to a whole subfield of study concerning the patterns and causes of the "allometry" (the size of a part of an animal in relation to the size of the whole organism) of sexually selected traits. One problem is the fact that although many ornaments and weapons are disproportionately large, others (perhaps many others) are not. There is in fact a very wide range of variation in the allometry of sexual traits. Here we propose and test a general explanation for this variation.

In evolutionary biology, allometry is often used to quantify the relative investments that

different-sized organisms make in different body parts, and can be useful in several contexts to help understand the costs and benefits of different structures. Ontogenetic allometry refers to changes in relative sizes of structures during ontogeny, while interspecific allometry compares the relative sizes of particular structures in different species. We discuss here another type of allometry, known as "static allometry," which measures the proportional size of a particular structure in a population of conspecific individuals that have different body sizes but are at the same ontogenetic stage (sexually mature adults in this study). Static allometry (henceforth "allometry") is usually quantified as the slope of a log-log regression of the size of the structure against a standard measure of body size. An allometric slope of 1.0 ("isometry") indicates that the structure has the same proportional size in large and small individuals; a slope greater than 1.0 ("positive allometry") indicates that larger individuals have disproportionately larger structures compared with smaller individuals; and a slope of less than 1.0 ("negative allometry" indicates that the structure is disproportionately larger in smaller than in larger individuals.

Although many body parts have allometric slopes close to 1.0, structures that are under sexual selection tend to differ. Early studies found that weapons used in male-male battles (such as the horns of beetles, the antlers of ruminant mammals, and the claws of fiddler crabs) usually show positive allometry (e.g., Huxley 1972; Gould 1974; Otte and Stayman 1979). The extensive review of Kodric-Brown et al. (2006), which included the horns and mandibles of 80 species of scarabaeoid beetles, the forceps of 42 species of earwigs, the claws of 17 species of fiddler crabs, the dewlaps of 17 species of lizards, the fins of five fish and a newt, and the antlers of three cervids, found that slopes for male weapons ranged from 0.93 to 15.7, with a mode between 1.5 and 2.5 (data from Kodric-Brown et al. 2006, Figure 1 and supporting information). They concluded that positive allometry is "nearly universal." Other authors, using a somewhat different criterion that contrasted the steepness of slopes of traits under sexual selection and control traits (rather than the value 1.0), also found a positive horn allometry (Eberhard et al. 1998). In fact, positive allometry, however measured, has sometimes been used as a litmus test of the action of sexual selection on male traits (e.g., Green 2000; Kelly 2005; Tasikas et al. 2009).

There are, however, exceptions to the trend of positive allometry in sexually selected traits. Some weapons and structures used to signal other individuals (henceforth "signal traits") show negative allometry (Bonduriansky and Day 2003; Bonduriansky 2007; Pomfret and Knell 2006; Bertin and Fairbairn 2007; van Lieshout and Elgar 2009). Bonduriansky (2007) even argued that "positive allometry may be the exception rather than the rule in sexual traits" (Bonduriansky 2007:838), and that the tendency to find positive allometry in previous studies was due to a sampling bias of zoologists in favor of measuring allometry in species in which structures have "exaggerated" and "bizarre" forms. Unfortunately, neither "exaggerated" nor "bizarre" was defined quantitatively, so it is impossible to test the force of this argument directly. There is, however, an additional large group of structures under sexual selection, the genitalia of male arthropods, that clearly tend to show negative rather than positive allometry. Of 206 genital characters in 117 species surveyed, the slopes were lower than rather than greater than 1.0 in 196 or 194 (depending on the regression technique). Moreover, the median genital slope was lower than the median nongenital slope in 108 of 113 species (Eberhard 2009).

This is a puzzling mixture of results. On one hand, there is a trend to positive allometry that is so strong (at least in "exaggerated" species) that it has inspired claims that it is nearly universal. On the other hand, many clear exceptions are now known. Explaining why this variation occurs (both in the structures themselves, and in people's perceptions of the trends) is the theme of this paper.

The paper is organized into two parts. First, we set out arguments linking different functions with differences in allometry, in terms of the likely costs and benefits in the different contexts of sexual selection. Second, we test

this general prediction using empirical measurements from various animal species.

Theoretical Background

Precopulatory sexual selection on males occurs in two basic contexts: direct male-male physical interactions, and female choice (Darwin 1871; Thornhill and Alcock 1983; Andersson 1994). The first context usually involves physical coercion of rivals (or the threat of such coercion) to drive them away from sites where mating opportunities are likely to occur (e.g., near sexually receptive females). In many species, physical coercion of rivals is produced by specialized weapons (Emlen 2008, 2014). Interactions with rival males in direct male-male encounters can also often involve signaling, generally as attempts to intimidate opponents and induce them to abandon the contest. In the second, female choice context, males compete indirectly by using signals that function to induce females to accept copulation, and/or to use their sperm rather than that of other males to fertilize their eggs. There are two alternative interpretations of how selection acts in the female choice context. The classic, Darwinian view is that females gain by choosing among males. Alternatively, males may coerce females, obliging them either by physical force or use of sensory traps, to perform reproductive processes that favor the male's but not the female's reproduction (e.g., oviposit earlier, reject later males; Arnqvist and Rowe 2005).

We argue here that the sizes of sexual traits should have different allometries when they are used in these different contexts (as weapons, threat signal traits, courtship signal traits, and coercive devices) because there are differences in the likely payoffs to larger and smaller individuals from having proportionately larger or smaller structures. Throughout the history of allometry studies, however, discussions of sexually selected structures have generally lumped weapons and signaling devices (Huxley 1972; Petrie 1988, 1992; Green 1992; Bonduriansky and Day 2003; Kodric-Brown et al. 2006). We argue that this lumping has contributed to the lack of accord. In particular, the notion that sexually selected traits will consistently show positive allometries is associated with the flawed assumption that these traits serve as honest indicators of individual quality or condition (e.g., Bradbury and Vehrencamp 1998, 2000; Emlen 2014). In contrast, we propose that the magnitudes of the payoffs from different allometries vary with the contexts in which sexual selection unfolds, and that although these payoffs are predictably body size-dependent in some contexts, they are not in others. Although the sizes of many weapons and of some signal devices can be readily measured, the "sizes" of others, such as acoustic signals and color intensities, are more difficult to measure, and we will not discuss them here (see Rodríguez and Al-Wathiqui 2012; Rodríguez et al. 2015)

Allometry of Signal Devices

signals for aggressive interactions

Two general facts about aggressive interactions are crucial to understand selection on male-male signals. First, a signal will only be effective if it induces the receiver to abandon a contest. It is thus important to focus on both the information available to the receiver, and on the selection operating on the receiver's possible responses to this information. Selection on the receiver will favor abandoning a contest (instead of escalating to a physical fight) when his chances of winning are small enough that the expected payoff does not exceed the likely costs of a fight (Dawkins and Krebs 1978; Hamilton 1979; Thornhill and Alcock 1983; Andersson 1994; Számadó 2003, 2008). Second, larger males usually defeat smaller males in intraspecific contests (Clutton-Brock 1982; Thornhill and Alcock 1983; Andersson 1994; Emlen 2014). It is thus advantageous for a male to use a rival male's signals to judge the rival's size relative to his own (Parker 1974; Petrie 1988, 1992; Simmons and Tomkins 1996), and to retire from a confrontation without fighting if this information indicates that he is smaller and thus likely to lose any potentially costly contest that ensues.

A few examples among many of threat signals that are used to assess relative size in-

clude mutual leg spreading in spiders and harvestmen, and head-to-head confrontations in flies with eyestalks (Eberhard and Briceño 1985; Burkhardt and de la Motte 1987; Wilkinson and Dodson 1997; Zatz et al. 2011). Selection on signaling individuals has often favored signals that increase the male's apparent size, such as leg spreading, head elevation in diopsid flies, and hair erection in dogs (Ewer 1973; Wilkinson and Dodson 1997). In summary, sexually selected threat signals often communicate the same simple, size-dependent message: "I am larger and more powerful than you." Direct observations can confirm the possible use of prefight stimuli to determine the relative size of an opponent, when the smaller individual breaks off an interaction and leaves before coming to blows with a larger opponent.

Selection on a signaler can favor producing "dishonest" signals that increase his perceived size, and thus help to intimidate rivals that are nearly equal in size without having to engage in a physical fight. In fact, selection to increase the opponent's sensation of being smaller may have been the context in which specialized signal traits originally evolved. At the same time, selection on receivers will favor discrimination between honest and dishonest signals, and capitulation only when the probability of winning an escalated fight is low (Andersson 1994). Aggressive signals of fighting ability must at least occasionally be backed up by true fighting ability, otherwise receivers will evolve to ignore them (Dawkins and Krebs 1978; Thornhill and Alcock 1983; Andersson 1994). However, the abilities of receivers to judge their opponents' sizes are not necessarily perfect, and coevolutionary races between senders and receivers can occur (Dawkins and Krebs 1978; Maynard Smith and Harper 2003; Számadó 2008). For instance, Backwell et al. (2000) documented an especially clear case in which dishonest signals have prospered in the fiddler crab *Uca annulipes* (Ocypodidae): dishonest males simply decamped when their bluffs were called, rather than fighting. The amount of dishonesty that is feasible in a signal is determined by the magnitude of evaluation errors by receivers; only under special conditions is selection likely to favor major, systematic dishonesty in signals (Backwell et al. 2000; Számadó 2008).

A consequence of these basic facts for the evolution of allometry is that the likely benefits from a given signal are expected to vary according to the relative body size of an individual. A small male is less likely to be able to intimidate rivals prior to fighting, because fewer males in the population are smaller than he is. He is thus less likely to reap payoffs from signaling his size (Petrie 1988, 1992; Baker and Wilkinson 2001). For the same reason, the benefits of using a proportionally larger weapon in physical contests are likely to be smaller for males with smaller body sizes (Clutton-Brock 1982; Green 1992; Baker and Wilkinson 2001; Pomfret and Knell 2006). Additional factors that could favor relatively smaller investments in signaling devices in smaller males are the important effect of a male's survivorship and persistence on his overall reproductive success in some species (e.g., Christy 1980; Ryan 1985), and the likely metabolic costs of building and maintaining some relatively large signaling devices.

A second, less commonly mentioned consideration favoring relatively large signaling devices in larger males is that the benefits from winning an interaction are likely to be greater in larger males. This is because larger males often seek out and remain in especially "high-quality" situations (or places), where the likely reproductive payoffs are greatest. For instance, males seek out females in estrus, females about to lay eggs, territories in which females tend to oviposit, and females that are just about to moult to maturity or are emerging from the pupal stage and are easily mated, among others (Thornhill and Alcock 1983; Andersson 1994). The higher concentration of males at high-quality sites increases the likelihood of aggressive encounters between them; this will be especially important for males with relatively large sizes, because smaller males tend to be excluded from such sites. As a result, a male's ability to win contests over similarly sized, large rivals will tend to be especially important in determining the reproductive payoffs for larger males. In contrast, smaller males are probably often relegated to lower quality situations

in which the likely reproductive payoffs are smaller and where fewer opponents are present. In many species, the payoffs to small males are so reduced that they adopt alternative reproductive tactics with less emphasis on fighting, and tend to occur in lower quality contexts (Oliveira et al. 2008). The small males often reduce their direct contact with other males, so their likely payoffs from successful threat signals are expected to be smaller. The force of these arguments may be reduced in a few exceptional species, in which females are so concentrated in time or space that large males are unable to defend them effectively.

Two additional factors also influence the likely benefits for larger individuals having proportionally larger signaling devices. First, selection to win battles can result in a skewed distribution of body sizes toward larger males as, for instance, in the horned beetle *Podischnus agenor* (Eberhard 1982). When relatively large males are more common, exchanges of threat signals between pairs of similarly sized large males will also tend to be more common, so the benefits of more effective signals will be greater. Second is the well-established Weber's Law in sensory physiology: the magnitude of estimation error increases linearly with the magnitude of a stimulus (Marks 1974; Dember and Warm 1979). When the size of the just noticeable difference between stimuli is ΔI and the magnitude of the stimulus is I, then $\Delta I/I = K$ (a constant). As the signaling devices of rival males become larger, the males are likely to be able to judge differences between them less precisely (in absolute terms). The larger the male, the greater the difference in the size of his signaling device will need to be over that of his rival for the rival to be able to sense the difference. This sensory bias in the detectability of differences should favor positive allometry (unless males are unable to pay the costs) because Weber's Law results in a larger male needing to invest relatively more to succeed in intimidating rivals that are approximately his own size.

In summary, positive allometry is expected to be favored in aggressive signaling devices for several reasons: larger males will tend to compete directly over more valuable resources; larger males may tend to interact more often with similarly sized opponents; and scaling of receptor physiology will tend to favor proportionally larger signaling devices in larger individuals.

SIGNAL DEVICES FOR COURTSHIP INTERACTIONS

In contrast to the predictability of the messages conveyed by threat signals, the messages that are communicated in courtship interactions are probably much more varied. In some cases, as is commonly mentioned, the message may pertain to the condition or quality of the signaler as a mate (Bradbury and Vehrencamp 1998, 2000). However, the possibilities are much broader, and include various forms of partly manipulative or deceptive signals and simple signal-preference genetic correlations or purely Darwinian esthetic scenarios (Dawkins and Krebs 1978; Christy 1995; Maynard Smith and Harper 2003; Mead and Arnold 2004; Searcy and Nowicki 2005; Tazzyman et al. 2014; West-Eberhard 2014; Prum 2017). Thus, in contrast to the usual message in threat signals—"I am larger and more powerful than you"—the message of courtship signals is much more variable across species. Perhaps it can be best stated only as "I am attractive." Furthermore, even when courtship signals do indicate individual quality or condition, this quality is not necessarily expected to be related to the scaling of the signaling trait size on body size (Petrie 1988; West-Eberhard 2014; Prum 2017). In summary, selection for positive allometry in courtship signals, although not excluded, is much less likely. An interesting possible illustration of this predicted difference in the allometries of threat as opposed to courtship signal devices comes from the long-tailed manakin *Chiroxiphia linearis* (Pipridae), in which young males compete with other males for hierarchy in bands of males, but only the dominant male copulates. The tail feathers of young males show positive allometry, but the tail feathers of older males, whose displays are more likely to function to induce females to mate, show negative allometry (Arévalo and Heeb 2005).

The fact that a signal's effectiveness depends on properties of the central nervous system of the female introduces further complications in selection on allometries of courtship signal devices (Guilford and Dawkins 1991; Endler 1992). For instance, larger sizes of male signaling structures do not necessarily produce proportionally larger effects on female responses. This lack of proportionality is illustrated by the sand hoods that male *Uca terpsichores* fiddler crabs sometimes build beside their burrow entrances. The hood functions as a sensory trap, enticing females to approach the male and his burrow close enough that the male can court her (Christy 1995). Females moving across a beach tend to move toward large objects on their visual horizons as a defense against predators, and the male hoods coopt this attraction to lure females. However, the responses of females to visual stimuli from hoods do not increase above a certain hood height; it is apparently the object itself and not its size that attracts the female. Experimental increases in the hood size above about 75% of the average size of normal hoods had no effect on the tendency to approach a male's burrow when presented at the distances from the burrow at which males and females interact (Christy and Backwell 2006; the largest hoods may function to aid males in relocating their own burrows, rather than to lure females). This nonlinearity of female responses to hood size predicts a flat benefits curve for larger hood sizes and, in turn, lack of selection for positive allometry. As expected, the allometric slope of hood height on male carapace width (N = 100) was low (0.48 with ordinary least squares; Christy et al. 2001; J. Christy, unpublished data). The general point is that the properties of the female's nervous system can complicate and even remove the correlation between a signal device's size and its effectiveness.

In summary, size effects are probably much less consistently important in male-female courtship signal devices than in threat signal devices. Male signaling devices that function to stimulate females but not males are expected to display positive allometry much less often.

signals directed toward both males and females

Undoubtedly, many male signaling structures function to communicate with both males and females. It is possible that the females of some species use male-female signals to extract the same male-to-male message, "I am larger and more powerful than you"; but in other species females probably use other types of correlations with the signal that have little relation with the male's size ("I am bright red"; "I can wave this structure rapidly"; "I am a good father"). For instance, females of the leaf beetle *Diabrotica undecimpunctata howardi* favored males that stroked them more rapidly with their antennae, irrespective of the male's size (body weight; Tallamy et al. 2002). There is no obvious prediction regarding the allometric scaling of multifunctional signals. It could be that selection in the male-male context on such a multifunctional device tends to increase the chances that the traits would show positive allometry (as mentioned above, selection on receivers will favor ignoring threats that are not backed up by fighting abilities). However, female preferences might sometimes act more strongly, so it is difficult to make strong predictions.

male "quality"

A common alternative to some of the interpretations just given is that the function of messages transferred during threats and courtship is to convey information concerning male traits related to natural rather than sexual selection, such as his "quality," "condition," or to his "resource holding potential." Aspects of this sort undoubtedly correlate to some degree with the male message that we argue is crucially important in threat signals ("I am larger and more powerful than you"). However, inasmuch as they differ from this message, these factors introduce distracting and irrelevant variables. Take, for example, male resource holding potential (RHP). A given male's RHP will be influenced by his current fighting ability, by his fighting ability in future interactions, his defenses against predation, the frequency and effectiveness of his threat displays, his

ability not to be fooled by the alternative mating tactics of minor males, his persistence in guarding the resource, his nutrient reserves, his ability to obtain further nutrients, his ability to administer his metabolic resources to achieve a maximally sustained defense of the resource, his oxidative state, and his immunocompetence, among others. When a second male analyzes the signals from this male in order to decide whether or not to escalate the interaction into a physical fight, most of these factors are irrelevant; only those that correlate with the first male's fighting ability at that moment are of interest.

In addition, setting aside the profound difficulties in attempting to make biologically appropriate definitions of "quality" and "condition," there is a further problem. Many possible types of male "quality" are not necessarily associated with greater body size. This can be seen from the fact that sexually selected signals, such as color, form, song, and genitalia, are not linked to body size in many groups (e.g., Eberhard et al. 1998; Cuervo and Møller 2001). Such size-independent traits are unlikely to be useful in explaining the evolution of positive allometry, even if they are correlated with some proxy of male "quality." In fact, as noted above, the mechanisms by which make courtship signals effective vary widely, ranging from manipulative/deceptive signals (Christy 1995) to Darwinian esthetic scenarios (Maynard Smith and Harper 2003; West-Eberhard 2014; Prum 2017). Some of these mechanisms have no necessary relation to male "quality" in any context other than that of inducing the female to use the male's own gametes rather than those of other males.

ALLOMETRY OF TACTILE SIGNALS

The discussion above largely concerns visual signals. There is another category—tactile signals—that has two special characteristics that are useful in understanding the evolution of allometries. In the first instance, the perception of tactile stimuli is likely to be strongly influenced by the physical size of the receiver. For example, the proportion of a female's body that is contacted by the tactile signaling device of a given male will be larger if the female is smaller. If adequate stimulation depends on a particular portion or area of the female being contacted, then some intermediate, "standard" size of the male's stimulating device may be most effective. The optimum size in such a case could tend to be the size that fits best with the greatest number of females, usually those with approximately the mean size in the population (if larger females are more fecund, perhaps it would be somewhat above this mean). Selection to "fit" with females could result in selection favoring relatively *low* allometric slopes in male structures that are specialized to deliver contact stimuli (Eberhard et al. 1998). This "one-size-fits-all" argument could explain why male genitalia show predominantly low allometric slopes (Eberhard et al. 1998; Eberhard 2009).

A second peculiarity of contact stimulation leads to expectations of a lack of positive allometry in both male contact courtship structures and male genitalia. In contrast with many other sexually selected male signaling traits, these signals are usually directed only toward females, and not toward other males. They thus function as unusually "pure" male-female signaling devices. The ideas outlined above predict that such "pure" courtship signal traits will show lower allometric values than traits used to signal in male-male interactions.

ALLOMETRY OF WEAPONS

So far, our discussion has centered on male signaling devices, ignoring the fact that many sexually selected male structures are used as weapons. The functionality of a weapon in a physical battle is determined by behavior and biomechanics. Some properties of a weapon, such as the ability to contact rivals at a greater distance, or to pry them from the substrate with greater mechanical advantage, can favor positive allometry (Dennenmoser and Christy 2013; Emlen 2014). Behavioral data are crucial to discriminate among possible biomechanical advantages. If a weapon is used to grasp, stab, or strike an opponent at a distance, as in many

beetles, earwigs, and mammals (Beebe 1944; Geist 1966; Hamilton 1979; Briceño and Eberhard 1995), a longer weapon can be brought to bear at a distance at which a smaller opponent's weapons are ineffective. Greater length could also be advantageous when a weapon is inserted underneath the opponent to lift him from the substrate and thus reduce his ability to resist being pushed, as occurs in the horns of many beetles (Beebe 1944; Eberhard 1977, 1979; Palmer 1978; Siva-Jothy 1987; Rasmussen 1994); a longer weapon can enable a male to apply lifting forces closer to his opponent's center of gravity. Larger weapon size could also be advantageous when horns grasp the opponent laterally, nearer his center of gravity, as in some dung beetles (Moczek and Emlen 2000), or when combatants attempt to reach above, over, or around the opponent in order to strike or dislodge him, as with the front legs of *Golofa porteri* (Dynastinae) beetles (Eberhard 1977). In these cases, given sufficient muscle strength to operate the larger structures, selection would favor positive allometry.

Another common and important use of weapons is to parry and defend against blows or stabbing movements of an opponent's weapons (e.g., Geist 1966 and Clutton-Brock 1982 on mammals). Longer horns or antlers with defensive forks or tines farther from the male's own head can be more effective in stopping an opponent's weapon before it can do damage, again favoring positive allometry. It might seem that precise mutual engagements between opponents' weapons that resemble "lock-and-key" fits might favor "one-size-fits-all" selection favoring low allometric values. Nevertheless, some species that have very precise fits between male weapons during contests show high allometric values (Crane 1975 in Rosenberg 2002; Eberhard and Garcia-C. 2000; Eberhard et al. 2000).

Not all of the possible mechanical functions of weapons are expected to select for high allometric slopes (Bonduriansky 2007; Eberhard et al. 2009). A structure designed to pinch opponents with its tips, such as the mandibles of a stag beetle or the claw of a fiddler crab, will exercise reduced rather than increased force on the opponent when it is longer (Dennenmoser and Christy 2013). A weapon designed to inflict pain or produce slashing wounds may also be more effective when it is smaller (Geist 1977 on mammal weapons; see also Eberhard 2002a on possible daggers in drosophilid flies). In summary, biomechanics is expected to often favor positive allometry in weapons, but not always.

An additional complication is that many weapons (perhaps most) are also used as signaling devices, and their effectiveness as signals will be determined by the receiver's neurobiology. Visual displays of weapons to opponents, frequently employing special postures, often occur just prior to battles, and such displays are sometimes followed by one male ceding without a fight (Geist 1966; Crane 1975; Eberhard 1983; Eberhard and Marin 1996; Longair 2004). Similar mutual "sizing up" by rivals sometimes appears to occur via tactile signals at the moment when some physical contests begin: the weapons make tentative contact and then one male (usually the smaller of the two) breaks away and retires (summary in Emlen 2014; see also Geist 1966; Eberhard 1977, 1979, 1981, 1998; Clutton-Brock 1982; Miyatake 1993, 1997; Rasmussen 1994; Briceño and Eberhard 1995; Eberhard and Marin 1996; Eberhard and Garcia-C. 2000; Hongo 2003; J. Christy, pers. comm. on fiddler crabs). Probably most weapons also function as threat signals (e.g., Morina et al. 2018), although some, such as the spines on the hind legs of many gonyleptid harvestmen, may be pure weapons (Willemart et al. 2009; Appendix 1). Some previous classifications of male structures as weapons (e.g., Kodric-Brown et al. 2006) rather than signaling devices are probably oversimplifications.

Selection may not favor the same traits when a structure is used as a threat signal as when it is used as a weapon. For example, the bright colors on some fiddler crab claws or special behavior patterns like the attention-getting gaping and blinking behavior of a male baboon in displays of his canines can improve the signaling function of a structure, but they do not improve its weapon function.

Inversely, some of the internal strength traits of beetle horns that improved their effectiveness as weapons in engineering analyses (McCullough et al. 2014) may have few or no consequences for their effectiveness as threat signals. And, of course, the mechanical properties of many threat devices, such as a lizard's dewlap, make them useless as weapons.

When a structure functions as both a weapon and a threat device and the optimal designs for the two functions are not identical, selection for the weapon function is likely to have more effect. This is because threatening with a weapon that is inappropriately designed to function as a weapon is not likely to persist over evolutionary time: opponents are expected to eventually evolve to "call the bluffs" of displaying males (Williams 1966; Backwell et al. 2000). Male weapons that also function as signaling devices to threaten other males are thus predicted to have designs more appropriate for the weapon function. This prediction was confirmed for the major claws of the fiddler crabs *Uca beebei* and *U. terpsichores* (Dennenmoser and Christy 2013). Longer claws (favored by selection for signaling) remained effective weapons, despite the decreased mechanical advantage associated with their longer lever arms. This was because their mechanical disadvantage was more than compensated by increased muscle mass, and by positioning of the force-delivering tubercles close to the apex of the gape in longer claws. This implies that in studies of weapons in which the two types of selection act on different features, their allometries should be analyzed separately, considering their biomechanical properties separately from their signaling properties.

Bonduriansky and Day (2003) argued that the allometric slopes of some male-male threat signaling devices may tend to be steeper than those of weapons, because weapons may be relatively costly because they must be sturdy enough to resist the sometimes severe physical stresses of battles (Mackinnon 1981; Clutton-Brock 1982; Kitchener 1985; Bonduriansky 2007). For instance, in *Uca terpsichores* and *U. beebei* fiddler crabs, the cuticle of a male's fighting claw is sometimes perforated or damaged locally as a result of mutual claw squeezes during fights (Dennenmoser and Christy 2013). Serious damage would presumably be more common if the claw cuticle were much thinner. Indeed, the cuticle of the claws of males of 21 species of fiddler crabs was just strong enough to resist the maximum forces that claws produced in grappling fights (Swanson et al. 2013). In contrast, many signaling devices are probably not subject to such intense "quality controls," and can be flimsier (Aparicio et al. 2003). However, we do not know of comparative data on the relative costs and the relative importance of weapon and threat signal functions for the same structures to test this prediction.

Because of the different expectations regarding selection for allometry in weapons as opposed to threat devices, clarity in how to distinguish between the two is important. Bonduriansky (2007) emphasized contact per se in distinguishing a weapon ("an appendage brought into contact with rivals during agonistic interactions") from a signal device ("a trait actively displayed in intersexual and/or intrasexual interactions"; Bonduriansky 2007:840). These criteria are useful in many species, but they omit subtle yet potentially important biomechanical properties and behavioral details (Williams 1966, 1998). An example illustrates the importance of detailed behavioral observations. Bonduriansky (2007) classified the disproportionately wide heads of stalk-eyed diopsid flies as weapons, because rivals sometimes made head-to-head contact. Nevertheless, both the morphological details of the widened heads and the biomechanical consequences of details of the behavior of these flies indicate that their laterally projecting form does not function as a weapon. Fighting flies did not strike or push each other with the projecting portions of their heads (Burkhardt and de la Motte 1987). Instead, in intense agonistic interactions they carefully aligned themselves head-to-head, raised themselves as much as possible from the substrate by extending their middle and hind legs (thus *reducing* their ability to push forcefully), and then performed apparent displays in this position that included extending their front legs laterally alongside their eyestalks, vigorously shaking their bodies and abdo-

mens from side to side, spreading one or both wings, and beating their abdomens against the substrate. The eyestalks did not strike against the opponent. None of these behavioral details is appropriate to physically coerce the opponent with the projecting eyestalks. The widened heads of diopsids are thus probably not weapons, but rather signals designed to impress the rival with the signaler's size. Similar detailed analyses of behavior and biomechanics will be needed in studies of allometry (see Appendixes 1 and 2) if our hypothesis that a structure's function has important consequences for its allometry is correct.

In summary, some weapons and some signaling devices show negative allometry or isometry, so traditional ideas and models that suppose that sexually selected weapon traits will consistently show positive allometry are incorrect. Structures that function as weapons are expected to often show positive allometry, but less consistently than structures that function as threat devices, and detailed behavioral observations may be needed to distinguish functions. Many (probably most) weapons also function as threat signals; if selection on a given structure differs regarding its signal and weapon functions, the weapon function is likely to have more effect. If this argument is correct, then the long lists of positive allometries of "exaggerated" weapon/threat structures in some other studies (e.g., Kodric-Brown et al. 2006; McCullough et al. 2015) fit with the prediction here of a strong trend toward positive allometries in weapons.

signals in nonsexual contexts

Animals also sometimes emit signals in social competition for other, nonsexual resources. For instance, nestling birds display brightly colored and ornamented mouths, and vigorous calls and movements in apparent attempts to attract the attention of their parents when they arrive at the nest with food (West-Eberhard 1983). We have not searched for studies of the allometry of devices that are specialized to produce such signals, but our ideas make a clear prediction. The social selection that results from this type of competition probably resembles classic sexual selection by female choice (West-Eberhard 1983; Lyon et al. 1994), so (unless parents are attempting to feed only their larger offspring because the others are likely to die) these signals are predicted to show low allometries.

a prediction to test

A key implication of this discussion is that structures under sexual selection to function only as courtship signals should tend to show lower allometric slopes than those under selection to function only as signals in aggressive interactions. To test this hypothesis, we assembled data for suites of traits with specific sexual functions: relatively "pure" courtship traits, and relatively "pure" threat traits. We excluded weapons because most of them probably also function as threat signals, and it is difficult to distinguish functions with current behavioral data.

Methods

To test the hypothesis that structures with different signaling functions show different allometric slopes, we assembled data for suites of traits that have relatively certain sexually selected functions, and that are used either as "pure" courtship signals or as "pure" threat signals but not as weapons. First, we focused on sexually dimorphic, rapidly diverging (species-specific) nongenitalic traits that are used by the male to touch the female in order to court or hold her during copulation (hereafter, "contact courtship devices"; Eberhard 1985). These traits are likely to be "pure" male-to-female courtship signaling devices because they contact only females, never males, and are not used in visual displays. Our hypothesis therefore predicts that they will tend to exhibit negative allometries (slopes < 1.0 in absolute terms; slopes lower than those of control, nonsexual body parts in comparative terms). This prediction is weaker for contact courtship traits whose biomechanical properties and behavior during courtship and mating imply that they may be used forcefully (e.g., to physically restrain the female) because larger individuals might be selected to

have disproportionately large structures to overcome female resistance, and therefore to have steeper allometric slopes. We tested potentially forceful contact traits separately from others ("nonforceful" traits) whose biomechanical properties precluded such use.

Another criterion for inclusion in the contact courtship data set was the availability of detailed observations showing that the male structures consistently contact the female on certain portions of her body during copulation, and also that they are species-specific (Appendix 3). In all cases the consistent and sustained contact with the female's body surface would seem to guarantee that stimulation occurs. We also checked to be sure that they were unlikely to be used as threat signals in male-male interactions because they were not used in male-male interactions in natural contexts, and because of the probable difficulty that other males would have in perceiving them at a distance (see discussions in Appendix 3). We measured 16 species of insects and arachnids in 13 genera and 10 families. We also used measurements of other nonsexually modified portions of the body, as well as the genitalia in some of these species, for comparison. Vouchers are deposited in the Museo de Zoología at the Universidad de Costa Rica and the Milwaukee Public Museum (*Polistes* wasps).

Second, we compared published values for the allometric slopes of other apparently "pure" courtship signal traits with published allometric values for "pure" threat signals (all male-to-male except one case of a female signal that threatens both males and females). Structures used only to produce threat signals were predicted to have higher allometric values than those used only to produce courtship signals. The criteria for inclusion in the data set were strict: only when detailed descriptions of behavior and natural history established that the trait likely functioned as either a "pure" courtship or a "pure" threat signal was a trait included (see discussions in Appendixes 1 and 2). We excluded allometry data on species that lacked sufficiently detailed behavioral observations, and on traits that could have mixed functions. This yielded allometry data for 15 species of insects, arachnids, and fish in 13 genera and nine families.

DISTINGUISHING FUNCTIONS

In general, we supposed that a structure did not function as a weapon when it did not contact rivals during physical battles, and when no feasible mechanical advantage could result during a battle from using the aspect of the structure that was accentuated (e.g., a broadening of the head with eyestalks, the lengthening of a leg). The sensory limitations of the animals involved were also important. For example, the vision of most harvestman species is poor, and they depend largely on touch or short-range chemical stimuli for intraspecific communication (Kaestner 1968; Pinto-da-Rocha et al. 2007). Thus, observations of where the legs of other individuals make contact during courtship and aggressive interactions could be used to judge whether a given male structure could function as a signal. These topics are discussed species by species in Appendixes 1 and 2.

ANALYSES OF ALLOMETRY

Our data are allometric slopes obtained with ordinary least squares (OLS) regressions of $\log_{10}$ transformed linear trait size measurements on linear body size measurements. Figure 1 illustrates how we estimated allometric slopes and used them to test our predictions. There has been controversy in evolutionary biology regarding best regression method for estimating allometric slopes (Green 1999; Eberhard et al. 1999; Kilmer and Rodríguez 2017). However, OLS regression is indicated for studies of allometry for two main reasons: first, OLS regression describes functional scaling relationships, unlike alternative methods; and, second, although measurement error in the descriptor of body size (the *x*-axis in trait size-body size regressions) biases slope estimates downwards in OLS regressions, the bias is negligible when measurement error is low (Kilmer and Rodríguez 2017). We assume that measurement error in our data set was low

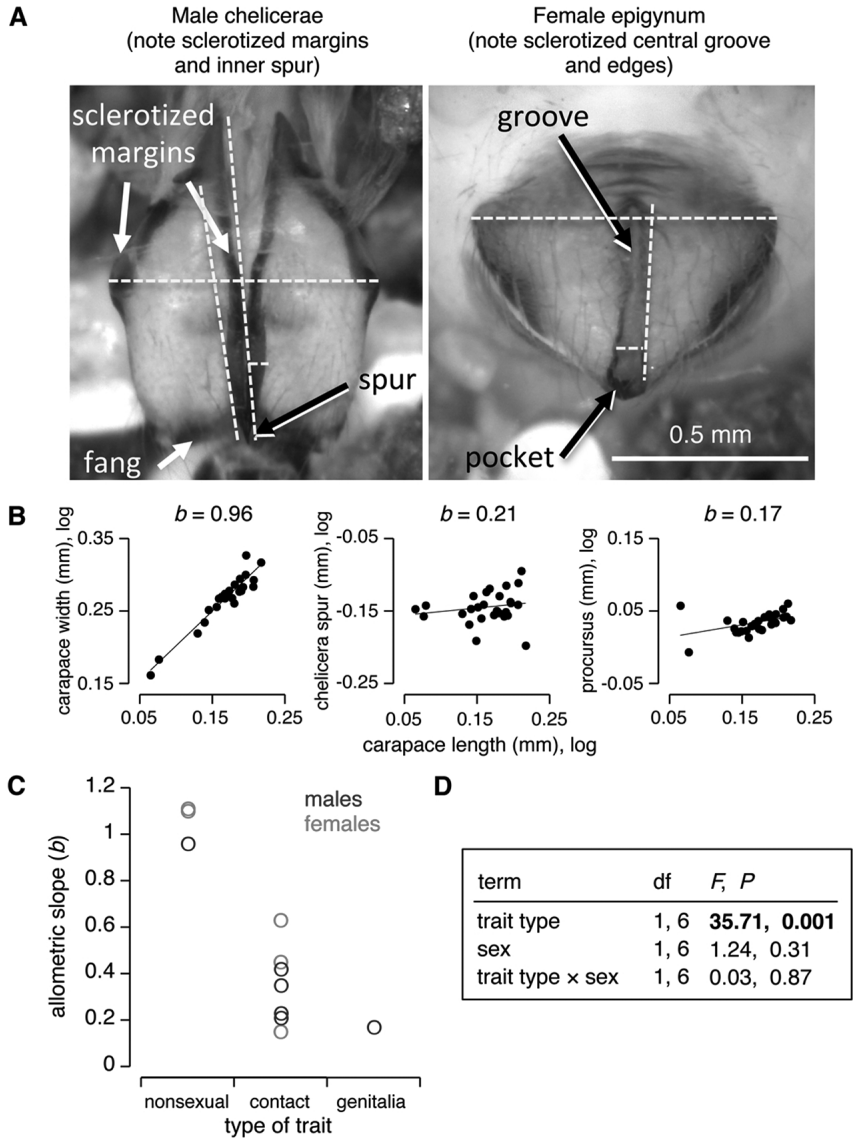

Figure 1. An Example of How We Used Allometric Slopes to Test the Predictions of Our Hypothesis

This pholcid spider, *Mesabolivar eberhardi*, is one of the 16 species that constitute the data set of contact courtship traits. A. Contact courtship traits: *M. eberhardi* males have modified chelicerae that contact the female genital plate (epigynum) during copulation (at sites separate from the site of genital intromission). The left photograph shows the male chelicerae in anterior view. The edges of the male chelicerae are sclerotized, and the tip of the heavily sclerotized inner "spur" fits into the pocket at the posterior end of the central sclerotized groove on the female epigynum (right photograph). The outer edges of the male chelicerae likely contact the sclerotized outer edges of the epigynum (Huber 1999; B. A. Huber, pers. obs.). B. We obtained allometric slopes (*b*) from regressions of trait sizes on an indicator of body size (the length of the carapace; Appendix 3). The scatter plots show examples of these traits: a nonsexual body part (carapace width—left), a contact courtship trait (length of the spur on the male chelicerae—middle), and a genitalic trait (length of the male procursus—right). *M. eberhardi* contact courtship traits had lower allometric slopes than nonsexual body parts (C, D). There were no overall differences in allometric slopes between the sexes (nonsignificant main term for sex), nor did the difference between contact courtship traits and nonsexual body parts differ between the sexes (nonsignificant trait type × sex interaction). The allometric slope of one male genital trait is included for reference.

because, in most cases, measurements were made by authors well experienced in aligning structures to focus on the landmarks defining the measurements. When the data were taken by authors new to the task, we conducted training rounds to reduce error. For example, in the data collected by Bretta Speck, the first training round had measurement repeatabilities ranging from $r = 0.810–0.996$ for different traits; the traits with lower repeatabilities were *y*-axis traits, and body size traits had high repeatabilities from the start (r = 0.990). In the second training round measurement repeatability improved to $r = 0.956–0.996$. Thus, slope underestimation after training would be at worst less than 5% (i.e., an allometric slope of 1.0 estimated as 0.95; Kilmer and Rodríguez 2017). All measurements of a given species were made by the same person. In some other cases, we obtained the data for estimating allometric slopes from published scatter plots that we digitized with the program WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/). Error was low ($r = 0.995$) in acquiring these data.

Another controversial issue has been whether allometry should be described by fitting linear models on a log scale, or power functions on an arithmetic scale (Packard 2009, 2011, 2017). We favor the first option because log transformation allows comparing allometries across traits that vary widely in magnitude (variation in the small end of the range is hidden from view using the arithmetic scale), and because it offers greater biological interpretability (Mascaro et al. 2014; Voje et al. 2014; Lemaître et al. 2015).

ALLOMETRY OF CONTACT COURTSHIP TRAITS

We measured 16 species of insects and arachnids in 13 genera and 10 families in which a sexually dimorphic, species-specific male structure consistently contacted the female during sexual interactions (mostly during copulation). In two species we also measured contact courtship traits for females (Appendix 3). For each species, we also measured reference nonsexual body parts and (in most) male genitalia (13 species in 10 genera and seven families).

ALLOMETRY OF PURE COURTSHIP AND PURE THREAT SIGNAL DEVICES

We assembled this data set from a combination of published data sets, data sets kindly provided by the authors of published behavioral descriptions, and our own measurements of species for which we had detailed observations (Appendixes 1 and 2). These include allometric slope estimates of traits used to produce pure courtship signals for five species of insects and spiders in three genera and three families, and also of traits used to produce pure threat signals for eight species in eight genera and six families of insects, harvestmen, and fish. Comparative data to determine the allometries of control body parts not involved in signaling were not available in most of these species.

STATISTICAL ANALYSES

CONTACT COURTSHIPS DEVICES

We used linear mixed models fit with JMP 7.0.1 (SAS Institute, Inc., Cary, North Carolina). The dependent variable in all models was the allometric slope estimate for each trait. The main independent variable of interest was the type of trait (contact courtship or nonsexual). We avoided using nonsexual traits that might be indirectly associated with supporting or facilitating the weapon or signal functions of the focus trait (e.g., Okada et al. 2012), although developmental integration can make this difficult (e.g., Tomkins et al. 2005). We also included an interaction term for sex and the trait type to determine whether the difference between contact and nonsexual traits varied between the sexes. There were four additional factors of potential interest that we describe below.

First, the prediction that contact courtship traits would have lower allometries than nonsexual traits was less certain for traits that are used forcefully during copulation. These traits could be stimulatory, but they could also be physically coercive, or both (coercive traits would be predicted if they were evolving under sexually antagonistic coevolution; *sensu* Arnqvist and Rowe 2005). We categorized a contact courtship trait as

potentially forceful or as not forceful whenever detailed observations were available (Appendix 3). This variable was not included in the statistical models because it only describes the contact courtship traits and was only available for a subset of them. We therefore tested its effect by running separate statistical models with data sets restricted to only nonforceful contact courtship traits, or to only potentially forceful contact courtship traits (Table 1).

A second potentially confounding factor for contact courtship traits is that a previous study showed a general trend for both sexually selected and nonsexually selected structures that are in more apical positions on the appendages of the harvestman *Leiobunum vittatum* (Sclerosomatidae; e.g., the tarsus segments that regularly contact the ground) to have negative allometries (Kilmer and Rodríguez 2017). The reason for the trend is not clear (perhaps structures that are in more apical positions on the appendages are selected to contact the environment in more precise ways). To explore the generality of this pattern, we included a term in the statistical models describing whether traits (contact courtship or nonsexual) have apical positions and contact the environment as the animal moves about.

Third, some measurements were of the precise portions of the male structure that physically contacted females, while others concerned only the general area of his body that bore contact structures (Appendix 3). We assessed whether more direct as opposed to less direct measurements influenced the outcome of our analyses by executing repeat analyses in which those contact traits that were measured less directly were excluded.

We included an estimate for each measurement of the degree to which the structure was specialized for courtship (as opposed to locomotion and prey handling, among others). The probable effect of a lack of specialization would be to reduce the expected trend of courtship structures toward lower allometric slopes, so our data would be expected to underestimate the degree of negativity resulting from sexual selection in the allometries for these structures. In line with this consideration, we were liberal in our estimations of the degree of specialization. For instance, we classified our measurement of the distance between the lateral processes at the bases of the chelicerae of *Mesabolivar eberhardi* as specialized (see Appendix 3). This was reasonable with respect to the apparent functions of the processes themselves; but our measurement also included the entire width of the bases of the chelicerae, which have the additional function of biting and manipulating food because males of this species capture and feed on prey (W. G. Eberhard, unpublished data).

Finally, a fourth factor that could offer an alternative explanation for low allometries is a "lock-and-key" function for the contact traits: male traits might function not as signals to females, but rather as "keys" to adjust to female "mechanical exclusion" devices designed to physically prevent cross-specific mating by fitting with the contact structures of conspecific males but not those of heterospecific males. We used three criteria to assign a possible a lock-and-key function: the female contact site was modified in a sexually dimorphic way; the female forms were species-specific; and the species-specific portions of the female had designs capable of mechanically rejecting cross-specific males.

Because each species contributed multiple traits to the data set in the analyses (Figure 1, Appendix 3), all models included a random term for species identity, which was fit with the restricted maximum likelihood (REML) method of JMP. We report *F*-ratio tests for the fixed terms and 95% confidence intervals for the variance component estimated for the random terms. We also report allometric slopes for genitalia for reference, but excluded them from the statistical tests. We did not test for phylogenetic inertia in our data set because our measurements involved rapidly evolving, species-specific sexual traits in which inertia seems of minor importance. In addition, we find evidence that allometries have evolved according to specialized functions (see below), and our sample spanned a broad taxonomic diversity. Nevertheless, we repeated the analyses with models having additional random terms for species nested within genus and family, and for genus nested within family. We also re-

peated the analyses with only one trait per function type (contact, nonsexual) per sex per species in order to eliminate all risk of spurious significance due to testing of correlated body parts. We retained traits blindly relative to their slopes.

In addition, we used alternative, intraspecific analyses to test the prediction that contact courtship traits will have lower allometric slopes than nonsexual traits. First, we asked whether this was the case for each species—testing for significance in the difference with a one-way analysis of variance (ANOVA) for each species. These tests had low statistical power because the sample of traits within each species was low. We then used a sign test to ask if this was the case more often than 50% of the time, summing across species. We tested species with nonforceful and potentially forceful contact traits separately. These tests had the advantage of controlling for possible effects of phylogeny and general lifestyle, but lower statistical power because of the limited number of species.

PURE COURTSHIP AND THREAT DEVICES

We used a linear mixed model fit with JMP 7.0.1. The dependent variable was the allometric slope for each trait. The independent variable was the type of signal (pure courtship versus pure threat signal). Some species contributed multiple traits to the data set, so we included a random term for species identity (REML method). We report *F*-ratio tests for the fixed terms and 95% confidence intervals for the random terms. As in the analyses of contact courtship devices, we repeated the analyses with only one trait per species to eliminate the risk of spurious significance due to testing of correlated body parts, and with models having additional random terms for species nested within genus and family, and for genus nested within family. We retained traits blindly relative to their slopes.

RESULTS

CONTACT COURTSHIPS DEVICES

We begin with a single species example to provide a sense for how we obtained data and tested predictions (Figure 1). In the spider *Mesabolivar eberhardi* (Pholcidae) the contact courtship traits are sexually dimorphic, species-specific, anteriorly directed projections on the male chelicerae that fit in a sclerotized pocket on the female genital plate (epigynum), and lateral prominences at the

TABLE 1
Comparison of the allometries of contact courtship and nonsexual traits

	Only nonforceful contact traits in data				Only forceful contact traits in data, only males			
	Term	**df num, den**	***F***	***P***	**Term**	**df num, den**	***F***	***P***
Entire data set	Trait type	1, 110.9	**16.52**	**<0.0001**	Trait type	1, 76.87	0.002	0.96
	Sex	1, 111	0.06	0.81				
	Trait type × sex	1, 105	0.67	0.42				
Strict model 1	Trait type	1, 107.9	**15.71**	**0.0001**				
	Sex	1, 105.2	0.014	0.90				
	Trait type × sex	1, 101.7	0.70	0.41				
Strict model 2	Trait type	1, 102.3	**11.98**	**0.0008**				
	Sex	1, 97.52	0.0016	0.97				
	Trait type × sex	1, 94.14	1.02	0.32				
Strict model 3	Trait type	1, 106.4	**18.24**	**<0.0001**				
	Sex	1, 102.9	0.05	0.82				
	Trait type × sex	1, 99.57	0.50	0.48				

We show separate tests with data sets including only nonforceful contact courtship traits (left column) or only potentially forceful contact courtship traits (right column). We also show tests that included those contact courtship traits for which we had high confidence that they: pinpoint the exact part that makes contact with the female (Strict model 1); are on structures with unique, specialized contact courtship functions (Strict model 2); and do not have a lock-and-key function (Strict model 3). We report F-ratios for the fixed terms from the linear mixed models with the corresponding degrees of freedom for the numerator and denominator mean squares (df num, den). In all cases, the 95% confidence intervals of the random terms for species identity overlapped zero.

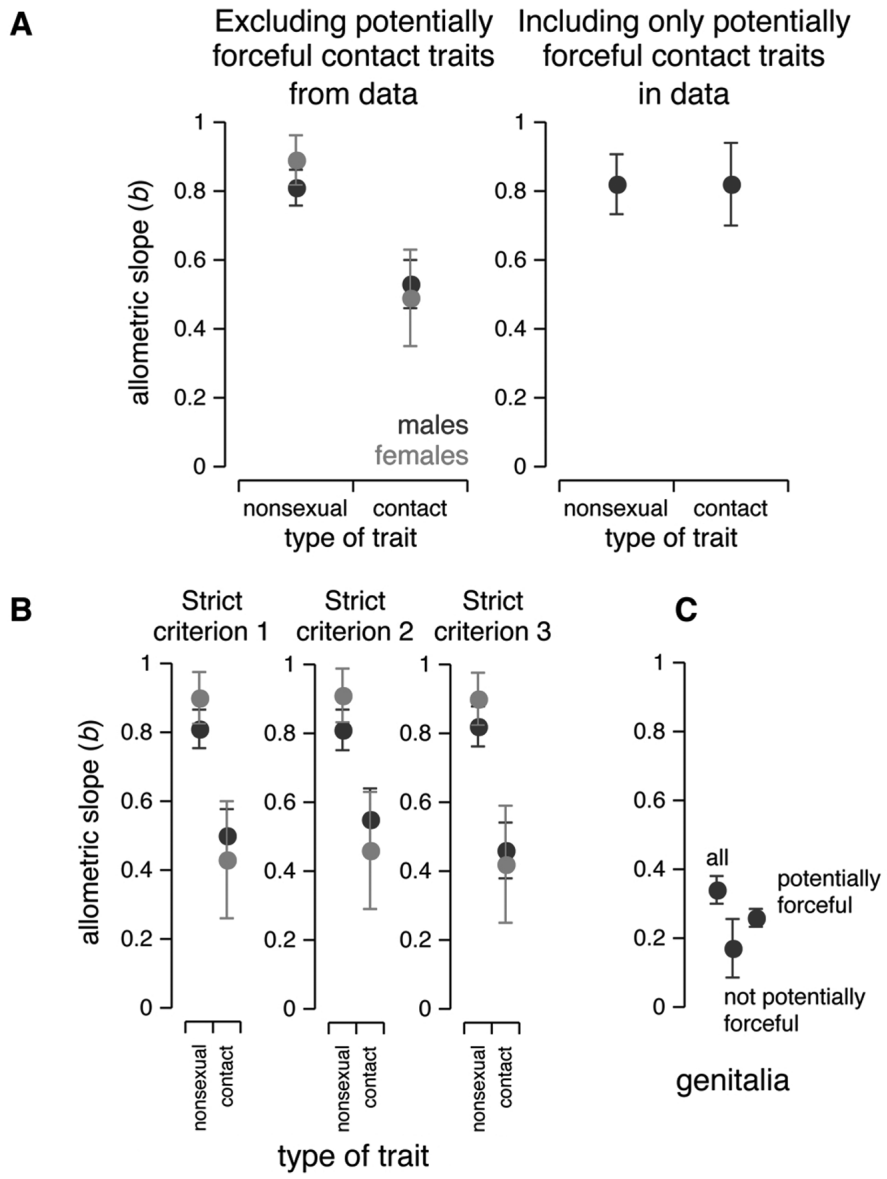

Figure 2. Allometry of Contact Courtship Traits in Comparison With Nonsexual Traits

A. We show analyses for data sets that either excluded potentially forceful contact traits (left) or included only potentially forceful contact traits (right). Contact courtship traits had significantly lower allometric slopes than nonsexual traits regardless of sex when the contact traits are not potentially used forcefully. There was no difference when male traits were capable of being used forcefully (Table 1). B. The difference between contact courtship traits and nonsexual traits became more pronounced in tests of contact courtship structures not potentially forceful when we used stricter inclusion criteria: criterion 1—only data in cases in which we were certain that the measure we took pinpointed the portion of the structure that contacts the female; criterion 2—the trait was on a structure with an exclusive contact function; criterion 3—the trait had no possibility of serving a lock-and-key function (these correspond to Strict models 1–3 in Table 1). C. Allometric slopes for genitalia: overall mean and separate means for genetic traits that are mechanically capable of being used forcefully or not. All panels except that of genitalia show least square mean values ± 1 SE obtained from the JMP models (which took into account the effect of the other terms in the model). For genitalia we calculated a mean value for each species and then a grand mean across species.

TABLE 2

Comparison of the allometry of contact courtship traits and nonsexual traits

	Species	Sex	$b_{nonsexual}$	$b_{contact\ nonforceful}$	$b_{contact\ forceful}$	$b_{contact\ nonforceful} < b_{nonsexual}$?		$b_{contact\ forceful} < b_{nonsexual}$?	
Araneae	*Mesabolivar eberhardi*	M	0.96	0.30 ± 0.05		$F_{1,3} = 34.7$, $P = 0.0098$	Y*		
		F	1.10 ± 0.01	0.41 ± 0.14		$F_{1,3} = 14.8$, $P = 0.0311$	Y*		
	Metagonia rica	M	1.28 ± 0.24	0.68 ± 0.02		$F_{1,3} = 3.70$, P = 0.15	Y		
	Physocyclus globosus	M	0.88 ± 0.18	0.59 ± 0.06		$F_{1,5} = 1.90$, $P = 0.23$	Y		
	Tetragnatha sp.	M	0.88 ± 0.02		0.82 ± 0.02			$F_{1,3} = 3.57$, $P = 0.15$	Y
	Argyrodes sp.	M	0.81	0.4			Y		
Coleoptera	*Cerotoma salvini*	M	0.30 ± 0.16	0.63	0.28 ± 0.28	$F_{1,2} = 1.12$, $P = 0.40$	N	$F_{1,3} = 0.01$, $P = 0.95$	Y
	Cerotoma sp.	M	0.60 ± 0.12	0.58 ± 0.08	0.64 ± 0.04	$F_{1,4} = 0.01$, $P = 0.93$	Y	$F_{1,4} = 0.07$, $P = 0.81$	N
	Phyllophaga obsoleta	M	0.79 ± 0.02	0.87		$F_{1,3} = 3.82$, $P = 0.15$	N		
	Phyllophaga valeriana	M	0.76 ± 0.05	0.86 ± 0.04		$F_{1,6} = 1.15$, $P = 0.33$	N		
Diptera	*Archisepsis diversiformis*	M	0.77		0.64 ± 0.14			$F_{1,2} = 0.22$, $P = 0.69$	Y
	Archisepsis pleuralis	M	0.88 ± 0.16		0.59 ± 0.12			$F_{1,4} = 2.22$, $P = 0.21$	Y
	Pseudopalaeosepsis dentatiformis	M	0.87 ± 0.04	0.52 ± 0.07	0.96	$F_{1,5} = 24.0$, $P = 0.0045$	Y*	$F_{1,4} = 0.93$, $P = 0.39$	N
		F	0.96 ± 0.04						
Hymenoptera	*Crabro* sp.	M	1.08 ± 0.25	0.50 ± 0.11		$F_{1,4} = 4.52$, $P = 0.10$	Y		
	Polistes fuscatus	M	0.66 ± 0.11		0.2			$F_{1,4} = 2.86$, $P = 0.17$	Y
		F	0.59 ± 0.04	0.42		$F_{1,4} = 2.52$, $P = 0.19$	Y		
Odonata	*Hetaerina* sp.	M	1.16 ± 0.16		2.51 ± 1.42			$F_{1,4} = 2.26$, $P = 0.21$	N
Opiliones	*Leiobunum vittatum*	M	0.60 ± 0.07		0.39 ± 0.10			$F_{1,14} = 1.75$, $P = 0.21$	Y
		F	0.71 ± 0.07						

For each species in our data set, we asked whether the mean allometric slope (b) for contact courtship traits was lower than the mean allometric slope for nonsexual traits (separating nonforceful and potentially forceful contact courtship traits). We then used a sign test to ask if this was the case more often than in 50% of the cases (sign test reported in Figure 3). Asterisks indicate statistically significant differences.

bases of the chelicerae that fit against the lateral edges of the epigynum (right in Figure 1A). These sites are separate from the site of genital intromission (the epigastric furrow, not visible in Figure 1A). Male contact traits (e.g., spur in Figure 1B) had significantly lower allometric slopes than did nonsexual body parts (e.g., carapace width in Figure 1B), as also occurred in a male genital trait (procursus in Figure 1B). Female contact traits also had low slopes (summary in Figure 1C).

In the full data set (Appendix 3), the allometric slopes of structures that were apical were significantly lower. This effect disappeared, however, when the harvestman *Leiobunum vittatum* was removed from the data set. We concluded that apical position was important in this species, but not in the others. Thus, we removed this factor from further analyses.

Contact courtship traits had lower allometric slopes than nonsexual traits, approximating those of genitalia. This was the case, however, only for contact traits that were not potentially forceful (Figure 2; Table 1). This tendency toward lower allometric slopes in nonforceful traits was strongest when the strictest criteria were used for inclusion in the analysis, i.e., with only traits for which we measured the exact portion of the structure that contacts the female (criterion 1 in Figure 2B). The pattern remained when we used another, similarly strict criterion, including only nonforceful contact traits on a derived, specialized structure that had no function other than contact courtship (criterion 2 in Figure 2B; Table 1). Finally, the pattern also remained when we used only nonforceful contact traits that were not mechanically capable of performing a lock-and-key function (criterion 3 in Figure 2B; Table 1). The models with additional random terms for species nested within genus and family, and for genus nested within family all yielded essentially the same results; e.g., in the full model for nonforceful contact traits, the main term for trait type remained significant ($F_{1,111.6} = 11.27$, $P = 0.0011$) and the terms for sex and the trait type x sex interaction remained nonsignificant. Finally, the model with only one trait per function type (contact, nonsexual) per sex per species also yielded the same result (main term for trait type: $F_{1,28} = 16.33$; $P = 0.0004$; sex and sex × trait type: $F_{1,28} \leq 0.26$; $P \geq 0.62$).

Similar trends occurred in the alternative, species-by-species tests of contact courtship traits. Nonforceful traits had lower allometric slopes than nonsexual traits in most of the species, but the trend was only marginally significant (Table 2, Figure 3). The trend was similar but weaker and nonsignificant for the allometries of potentially forceful contact traits (Table 2, Figure 3).

pure courtship and threat devices

The traits used to produce pure courtship signals (Appendix 2) had negative or nearly isometric allometric slopes, ranging from 0.26 to 1.06 in the high confidence sample (Figure 4). Moreover, the slopes of these traits were much lower than the slopes of the pure threat traits (Appendix 1), which ranged from 1.89 to 4.19 in the high confidence sample. The differences were significant in both the entire data set and when

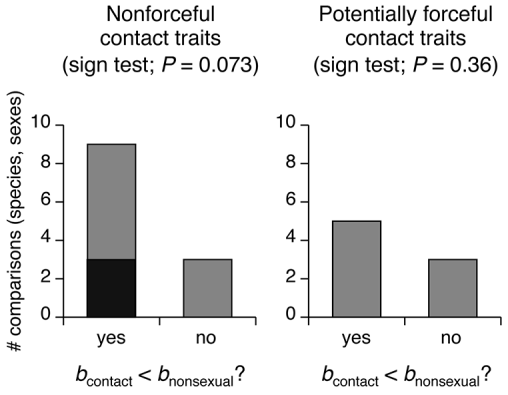

Figure 3. Comparisons of Allometric Values For Contact Courtship Traits With Those of Nonsexual Traits in the Same Species

Nonforceful contact courtship traits are on the left, and potentially forceful contact courtship traits are on the right. The *y* axis gives the numbers of species for which contact courtship traits had lower *b* values than nonsexual traits, regardless of the magnitude of the difference. Gray bars indicate lack of statistically significant differences in each species; black bar indicates significant differences. The probability values are the results of sign tests, asking whether the difference occurred more often than in 50% of the cases.

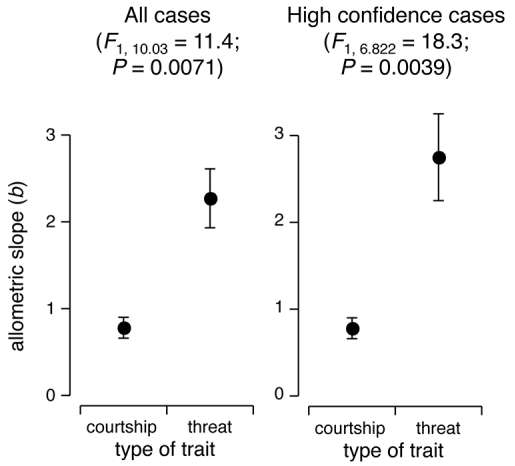

FIGURE 4. COMPARISON OF THE ALLOMETRIES OF TRAITS THAT ARE USED TO PRODUCE PURE THREAT AND PURE COURTSHIP SIGNALS

Slopes for traits used to produce pure threat signals were two-to-three times steeper than those for traits used to produce pure courtship signals in both the full data set (left), and in only those cases for which the behavioral observations gave higher confidence that the signals had pure functions (right). The *F*-ratio tests are for the fixed term for signal function from the linear mixed models (the other component in these models was a random term for species identity, for which the 95% confidence intervals overlapped zero in both cases).

only the highest confidence cases were included in the analysis (Figure 4). The difference remained significant in the model with only one trait per species ($F_{1,11}$ = 10.05; P = 0.0089), as well as in the model with additional random terms for species nested within genus and family, and for genus nested within family ($F_{1,8.038}$ = 6.06, P = 0.039).

DISCUSSION

One major pattern emerging from our measurements of contact courtship devices is that they tended to have negative allometries, both in the entire data set and when stringent criteria were imposed (Figures 1–3, Appendix 3). In this respect, as well as in their tendency to diverge especially rapidly during evolution (Eberhard 1985), contact courtship devices resemble male and female genitalia (Eberhard et al. 1998; Eberhard 2009). They are likely to be relatively "pure" male-female signaling devices, and their negative allometries are thus in accord with our prediction that sexual selection on courtship structures favors lower allometries than on threat and weapon structures. A second major pattern documented here is for other male structures that produce "pure" courtship signals to have significantly lower allometric slopes than those that produce "pure" threat signals (Figure 4, Appendixes 1 and 2). This trend also supports our hypothesis regarding the effects of sexual selection on the allometries of courtship as opposed to threat structures.

Many of the structures used in this study undoubtedly have multiple functions. The antennae of a male *Polistes* wasp, for instance, are certainly used for other functions in addition to stroking female antennae. The allometries for multifunction structures, such as weapons that are also used as display devices, likely result from balances between different selective pressures, including both natural and sexual selection. Such balances may explain the lack of difference between contact structures that do not exercise physical force on the female and those that do (Figure 2A). Perhaps forcefulness is included in the stimuli from these structures that induce cryptic female choice responses to the male. Alternatively, females may be physically forced to cooperate, as predicted under the sexually antagonistic coevolution hypothesis (SAC; *sensu* Arnqvist and Rowe 2005). The SAC hypothesis would predict, however, the existence of species-specific female resistance structures and behaviors to counteract male species-specific coercive structures. This prediction was not confirmed here, as only two and at most three of 19 traits in Appendix 3 had possible lock-and-key relationships with females (and one of these was speculative). This lack of support echoes a similar pattern seen in a larger survey of the biomechanical properties of contact courtship devices and their interactions with female morphology (Eberhard 2004).

It might be thought that the negative allometries in both genitalia and contact courtship devices are not typical for sexually selected signals in other sensory modalities such as vision, because these contact structures may be under "lock-and-key" selection

favoring precise physical fit with the female or her touch receptors (Eberhard 2009). Precise contact and fit also characterize some weapons that show strong positive allometry, such as the claws of *Uca* fiddler crabs and prothoracic horns of *Parisoschoenus expositus* weevils. Thus, a precise mechanical fit per se does not necessarily imply low allometric values. In addition, several lines of evidence (in particular, widespread divergence in species whose ranges do not overlap with those of any other closely related species, and a correlation between species-specificity and multiple mating by females) argue strongly against lock-and-key functions having been generally important in the evolution of animal genitalia (Scudder 1971; Eberhard 1985; Arnqvist 1998; contra Simmons 2014).

Why the Previous Disagreements Regarding Allometry?

The emphasis here on function helps explain previous disagreements over whether positive allometry is characteristic of sexually selected traits. The "nearly universal" positive allometry found by Kodric-Brown et al. (2006) was based nearly entirely on structures that they termed "weapons" (127 of 133 species; many of which probably also function as threat devices—see above). In contrast, the much lower allometric values found by Cuervo and Møller (2001) involved exclusively ornamental feather traits (such as tails, crests, and mustaches), none of which could function as weapons. The more eclectic survey of Bonduriansky (2007) mixed threat signals and weapons, and was also smaller (13 taxa; not counting either the Cuervo and Møller data or the data on testes, which are not necessarily either signals or weapons). The results were also intermediate, with 42% of 24 traits showing positive allometry.

A General Conclusion

Some have argued that the traditional supposition that patterns of allometry can reveal past histories of selection should be discarded (e.g., Bertin and Fairbairn 2007), but there are several reasons to question this conclusion (Wilkinson 1993; Baker and Wilkinson 2001; Frankino et al. 2005). Allometries vary intraspecifically and are influenced genetically, and are thus likely to respond to selection (Emlen 1996; Tobler and Nijhout 2010; Rodriguez and Al-Wathiqui 2012). In fact, our results show that sexually selected structures with different functions show predictable allometric patterns, supporting the notion that these patterns of investment respond differently to selection.

Thus, studies of the effect of sexual selection on allometry will benefit from greater attention to the details of behavioral contexts in which particular structures are used, as well as to the details of how they are used (see also Bonduriansky 2007). Deducing probable functions of both signals and weapons depends largely on behavioral details, with careful attention in weapons to determining the points of contact and the probable forces exerted. Most previous studies of sexual selection and allometry have emphasized mathematical regularities, and have been uncomfortably free of the complications associated with data from biomechanics, neurobiology, and behavior. The present study suggests that at least some disagreements over the allometric patterns of sexually selected male traits have been due to differences in the functions of these traits. This study also provides evidence that traits under sexual selection have repeatedly evolved the allometries predicted by their function, in spite of originating in a wide variety of body parts across a broad range of animal groups. This is strong evidence of the adaptive evolvability of allometric scaling.

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APPENDIX 1

Allometry of structures for which there is evidence that they are used exclusively as intrasexual (mostly male-to-male) threat signaling devices, and that are neither male-to-female signals nor weapons

Species	Trait	*b*	Observations that suggested that the structure functions strictly as a male-male signal	References
High confidence				
Opiliones				
Longiperna concolor (Mitobatinae, Gonyleptidae)	Femur length, leg IV	4.19	The femur of leg IV of the male is thin and elongate, and femora are dimorphic among the males ("major" and "minor" morphs). Within morphs, the allometric slopes were 3.56 (majors) and 1.71 (minors). Males perform displays back-to-back while defending territories at oviposition sites, and may have harems. When displaying, males extended and aligned their legs IV (which do not have teeth or other armaments), but kept their bodies about 1 cm apart and did not intertwine their legs. Contact was limited to metatarsal tapping. One male always left after tapping. Courtship was face-to-face, and the female did not touch or attempt to touch male coxae IV.	Zatz et al. 2011; G. Machado, pers. obs.; *b* obtained from Zatz et al. 2011
Promitobates ornatus (Mitobinae, Gonyleptidae)	Femur length, leg IV (males)[1]	2.64	Behavior was as in *Longiperna* (see previous row). For female femur length, $b = 0.49$.	G. Machado, pers. obs.; *b* from original data from G. Machado
Serracutisoma proximum (Goniosomatinae, Gonyleptidae)	Length of leg II	2.25	Leg II is elongate, and dimorphic in males ("major" and "minor" morphs); within the morphs, $b = 1.09$ (majors) and 0.86 (minors). Large males used legs II in fights in the field. Rivals aligned face-to-face, spread their legs II laterally, then touched each other repeatedly with their tips, presumably mutually assessing leg length. Males sometimes "whipped" the rival's legs, and (in majors) a row of acuminate spines on the tibia sometimes "locked" (like a zipper) with the spines on the opponent's leg II tibia (in minor males, which never fought, legs II lacked these spines). The males' weapons were their powerful, heavily armed pedipalps, which were extended anteriorly, and struck repeatedly at the other male in apparent attempts to seize his legs (generally the strikes fell short). Males very rarely touched females with their legs II; instead they tapped the female intensely with legs I. Occasionally, legs II of males and females touched, but probably only due	Buzatto and Machado 2008; Buzatto et al. 2011; B. Buzatto, pers. obs.; *b* from data in the scatter plot in Buzatto et al. 2011

continued

APPENDIX 1
Continued

Species	Trait	*b*	Observations that suggested that the structure functions strictly as a male-male signal	References
			to their common use as antennae, and not when they were in spread positions. During mate guarding, the male also occasionally touched the female dorsum and/or legs with his legs II, but again only in an apparent antennal function rather than courtship. Because of these animals' poor vision, communicative stimuli are probably mostly tactile (and chemical).	
Perciformes				
Alticus arnoldorum (Blenniidae)	Size of red area on dorsal fin (females) (Talofofo site) Size of red area on dorsal fin (females) (Tagachang site)	1.89 1.92	Females flashed the red area during threat displays against males and females when defending foraging sites.	Ord and Hsieh 2011; *b* from original data deposited at Dryad
Lower confidence				
Coleoptera				
Exechesops leucopis (Anthribidae)	Eye span Length of eye stalk	1.52 2.53	Eyes are on stalks that project laterally from the head. In battles near oviposition sites, similarly sized males aligned themselves head-to-head and each pushed forward. One then decamped (was often chased). In the most intense interactions "both individuals dropped from the substrate with excessive vigor" (Yoshitake and Kawashima 2004:79). Contact occurred in the central portion of the head, not the eyestalks, and the mechanical design of the eyestalks was not used to apply force to the rival. Courtship was not described, other than to note that "Some species of Diopsidae use the eye span also during female-male interactions, . . . but we could not observe male choice by females in *E. leucopis*" (Yoshitake and Kawashima 2004:82); visual assessment of male heads by females cannot be ruled out entirely.	Yoshitake and Kawashima 2004; Matsuo 2005

continued

APPENDIX 1
Continued

Diptera				
Pseudopalaeosepsis dentatiformis (Sepsidae)	Width of dark spot on wing (males) Width of dark spot on wing (females)	1.57 1.30	Male-male aggressive displays were face-to-face. Each male often opened his wings laterally and twisted them so the wing spots were perpendicular to his rival's line of sight, thus displaying the spot to his rival. They also briefly flicked their wings anteriorly during preliminary interactions. Physical fights involved forceful collisions, grappling, and hitting with legs and heads. Males mounted females by surprise, often from the rear with no preliminary display and the wings were mostly held over the male's body (not visible to female) while he was mounted. Opening the wings was not included in the list of male courtship movements while riding females during copulation. In one figure of precopulatory courtship with legs II, however, the male's wings were fanned anteriorly but not twisted as they were during displays to other males (the wings may have been performing a vibration display); thus female visual assessment of male wing spots cannot be ruled out completely. Their use in displays associated with female-female threats has not been observed, although females occasionally lunged briefly at other flies at feeding and oviposition sites.	Eberhard 2002b; W. G. Eberhard, unpublished data
Phytalmia alcicornis (Tephritidae, Diptera)	Span of antlers (lateral "cheek processes")	2.77	Male aggressive displays involved pushing face-to-face with their lateral cheek processes aligned. In high-intensity fights both bodies were raised high on legs II and III; contact occurred mostly with the cheek processes. In forceful resolutions, the loser was pushed over backwards. Thus the lateral extension of cheek processes was not apparently mechanically appropriate to gain advantage (the larger male won 84% of 420 contests). Experimentally increasing or reducing antler length indicated that "it appears that antlers are not required in order to win contests: the outcome is determined primarily by size. However, males without antlers expended more effort in escalated contests before the outcome was determined" (Wilkinson and Dodson 1997:317). There was no courtship display other than the male interposing himself between the female and an oviposition site. Nevertheless, the female obviously could see male cheek processes, and visual assessment cannot be ruled out. The male mounted from above and held her wing bases with his legs I (whose femora are modified for this function).	Wilkinson and Dodson 1997; *b* from data in the scatter plots in Wilkinson and Dodson 1997

continued

APPENDIX 1
Continued

Species	Trait	*b*	Observations that suggested that the structure functions strictly as a male-male signal	References
Odonata				
Hetaerina sp.[2] (Calopterygidae)	Length basal wing spot	0.95	Males flashed their sexually dimorphic bright red spots on the upper surfaces of their wings when they threatened intruders and chased them from their mating territories. In a closely related species, *H. americana*, experimental elimination of spots reduced male ability to defend territories, but did not reduce the numbers of females with which the male mated while on the territory[2].	Grether 1996; new measurements by W. G. Eberhard

We report the allometric slope (b) estimated with OLS regression (see text). We indicate our confidence that conditions for inclusion in this appendix are met, based on the level of detail available in behavioral observations.
[1]Slope for leg IV in females = 0.49.
[2]Possibly *H. macropus*; observed near San José, Costa Rica. There are no experimental observations similar to those for *H. americana*, whose basal spots are somewhat larger and more rectangular. Another source of uncertainty is the lack of evidence regarding the possibility that the spot may influence postcoupling female choice mechanisms. Data on other structures in this species are in Appendix 3.

APPENDIX 2

Allometry of male structures for which there is evidence that they are used exclusively as intersexual courtship signaling devices, and that they are neither male-to-male threat signals nor weapons

Species	Trait	*b*	Observations that suggested that the structure functions as a male-female signal	References
High confidence				
Ceratitis capitata (Tephritidae, Diptera)	Length of distal "flag" on face bristle	0.28	The two flag-like capitate supra-fronto-orbital bristles on the face of the flies differ in form and color between *C. capitata* and other congeneric species. Males engaged in brief, only moderately intense fights for individual leaves from which to call females pheromonally in leks (a loser simply moved to an adjacent leaf; the positions of leaves did not affect mating success). During courtship, the male rocked his head side to side while displaying to the female in a head-to-head position. The dark expansions at the tips of the setae make them visually obvious against the male's sexually dimorphic white frons and multicolored eyes (diffraction colors on a red background). Removal of the capitate setae resulted in lower rates of copulation.	Briceño et al. 1996, 2005; Mendez et al. 1998; Eberhard 2000; Briceño and Eberhard 2002; Shelly and Villalobos 2004
	Width of distal "flag" on face bristle	0.26		
	Length of arista of antennae	0.85	The arista is very thin and probably not visible to other males, and does not come into play during aggressive behavior. During courtship it provides tactile cues by tapping on the aristae of female when the male comes close while rocking his head. Removal of either male or female aristae lowered the chances that the male would mount the female and copulate, probably because she was less likely to approach him and stand still.	Briceño et al. 1999; Miranda 2000; Eberhard 2002b
	Number of dorsal setae in arista of antennae	0.14		
	Number of ventral setae in arista of antennae	0.28		
Paratrechalea azul (Trechaleidae, Araneae)	Frontal length of basal segment of chelicerae	0.90	Males displayed their chelicerae along with the nuptial gift of prey to the female as part of courtship. Male-male combat was never seen in either *P. azul* or *P. ornata* in extensive field observations.	Costa-Schmidt and Araújo 2008; L. E. Costa-Schmidt, pers. comm.; slopes from data in Costa-Schmidt and Araújo 2008
	Frontal width of basal segment of chelicerae	0.81		
	Lateral width of basal segment of chelicerae	0.86		

continued

APPENDIX 2
Continued

Species	Trait	*b*	Observations that suggested that the structure functions as a male-female signal	References
Paratrechalea ornata (Trechaleidae, Araneae)	Frontal length of basal segment of chelicerae	0.91		
	Frontal width of basal segment of chelicerae	1.03		
	Lateral width of basal segment of chelicerae	0.93		
Photinus pyralis (Lampyridae, Coleoptera)	Length of light-producing abdominal lantern	1.06	Males of *P. pyralis* formed "love knots" of scrambling beetles around a female who responded to the male's visual, aerial display, so male-male signals are at least remotely possible, although apparently improbable. Lack of use of light signals in male-male interactions was more certain in *P. macdermotti*.	Vencl 2004; slopes from original data provided by F. V. Vencl
	Width of light-producing abdominal lantern	1.05		
Photinus macdermotii (Lampyridae, Coleoptera)	Length of light-producing abdominal lantern	0.55		
	Width of light-producing abdominal lantern	0.82		

We report the allometric slope (b) estimated with OLS regression (see text).

APPENDIX 3

Allometry of contact courtship traits, genitalia, and nonsexual traits

Species	Sex	Trait type	Trait	*b*	Measures only part that contacts partner?	Sexual contact is trait's only function?	Contact function is potentially forceful?	Trait has apical position on appendage	Possible lock-and-key function?	References
Araneae										
Mesabolivar eberhardi (Pholcidae)	M	Nonsexual	Carapace width	0.96						Huber 1999; W. G. Eberhard, H. Miller, and R. L. Rodríguez, original data
	M	Contact	Width across chelicerae	0.42	Y	Y	N		N[a]	
	M	Contact	Chelicera spur (tip-to-tip) length	0.35	Y	Y	N		N[a]	
	M	Contact	Chelicera spur (inner margin-to-tip) length	0.21	Y	Y	N		N[a]	
	M	Contact	Chelicera spur width	0.23	Y	Y	N		N[a]	
	M	Genitalia	Pedipalp procursus length	0.17			N			
	F	Nonsexual	Carapace width	1.11						
	F	Nonsexual	Tibia III length	1.1						
	F	Contact	Epigynum width	0.63	Y	Y	N		N[a]	
	F	Contact	Length of groove on epigynum	0.45	Y	Y	N		N[a]	
	F	Contact	Width of groove on epigynum	0.15	Y	Y	N		N[a]	

continued

APPENDIX 3
Continued

Species	Sex	Trait type	Trait	*b*	Measures only part that contacts partner?	Sexual contact is trait's only function?	Contact function is potentially forceful?	Trait has apical position on appendage	Possible lock-and-key function?	References
Metagonia rica	M	Nonsexual	Eye width	0.82						B. A. Huber, original data
(Pholcidae)	M	Contact	Distance between processes on clypeus, outer margins	0.71	Y		N		N[b]	
	M	Contact	Distance between processes on clypeus, inner margins	0.66	Y		N		N[b]	
	M	Nonsexual	Tibia I length	1.62						
	M	Nonsexual	Tibia IV length	1.39						
	M	Genitalia	Genital bulb width	0.48						
	M	Genitalia	Length of process on pedipalp procursus	0.38	Y					
	M	Genitalia	Length of row of tines on process of genital bulb	0.38	Y					
Physocyclus globosus (Pholcidae)	M	Contact	Distance between tips of male cheliceral apophyses	0.46	Y	Y	N		N[c]	Huber 1996, Figure 1 measures 10 and 14; Eberhard et al. 1998; contact trait from B. A. Huber, original data
	M	Contact	Chelicerae width	0.67					N[c]	
	M	Contact	Chelicera length	0.63					N[c]	

continued

APPENDIX 3
Continued

	M	Nonsexual	Distance between outer margins of AM and AL eyes	0.77						
	M	Nonsexual	Tibia I length	1.22						
	M	Nonsexual	Tibia IV length	1.1						
	M	Nonsexual	Pedipalp tibia width	0.44						
	M	Genitalia	Pedipalp procursus length	0.28						
	M	Genitalia	Genital bulb length	0.35						
	M	Genitalia	Genital bulb width	0.35						
Tetragnatha sp.	M	Nonsexual	Carapace length	0.87						B. A. Huber,
(Tetragnathidae)	M	Contact	Basal cheliceral segment length	0.84			Y[sl]			original data
	M	Contact	Cheliceral fang length	0.81	Y		Y[sl]			
	M	Nonsexual	Tibia I length	0.92						
	M	Nonsexual	Tibia III length	0.85						
	M	Genitalia	Genital bulb length	0.31						
	M	Genitalia	Genital bulb width	0.38						
	M	Genitalia	Conductor of genital bulb length	0.33	Y					
	M	Genitalia	Conductor of genital bulb width	0.36						
Argyrodes sp.	M	Nonsexual	Carapace width	0.81						B. A. Huber,
(Theridiidae)	M	Contact	Clypeus modification width	0.4	Y	Y	N	N	N	original data

continued

APPENDIX 3
Continued

Species	Sex	Trait type	Trait	*b*	Measures only part that contacts partner?	Sexual contact is trait's only function?	Contact function is potentially forceful?	Trait has apical position on appendage	Possible lock-and-key function?	References
Coleoptera										
Cerotoma salvini	M	Nonsexual	Maximum head width	0.3						Original data provided by
(Chrysomelidae)	M	Contact	Upper head plate width	0.63					N?	F. V. Vencl
	M	Contact	Width of notch on third antennal segment clamp	0.56	Y	Y	Y		N	
	M	Contact	Maximum width of modified fourth antennal segment	−0.002	Y	Y	Y		N	
	M	Nonsexual	Fifth antennal segment length	0.03						
	M	Nonsexual	Femur leg III	0.57						
	M	Genitalia	Aedeagus length	0.32						
	M	Genitalia	Aedeagus width	−0.04						
Cerotoma sp.	M	Nonsexual	Head width	0.6						W. G. Eberhard,
(Chrysomelidae)	M	Contact	Upper head plate width	0.5	Y	Y			N?[e]	original data
	M	Contact	Distance between tips of lower and upper head plates	0.66	Y	Y			N?[e]	

continued

APPENDIX 3
Continued

	M	Contact	Width of notch on second antennal segment	0.68	Y	Y	Y		N	
	M	Contact	Maximum width of third antennal segment	0.61	Y	Y	Y		N	
	M	Nonsexual	Fourth antennal segment length	0.31						
	M	Nonsexual	Apical antennal segment length	0.58				Y		
	M	Nonsexual	Femur I length	0.9						
	M	Genitalia	Basal piece of the aedeagus length	0.54	Y	Y			?	
	M	Genitalia	Basal piece of the aedeagus width	0.44	Y	Y			?	
Phyllophaga obsoleta (Scarabaeidae)	M	Nonsexual	Distance between inner edges of eyes	0.75						Eberhard 1993; W. G. Eberhard, original data
	M	Nonsexual	Maximum width of basal segment of antennal club	0.84				Y		
	M	Nonsexual	Pygidium length	0.78						
	M	Nonsexual	Femur III length	0.78						
	M	Contact	Length of row of teeth on abdominal sclerite	0.87	Y	Y	N		N	

continued

APPENDIX 3
Continued

Species	Sex	Trait type	Trait	*b*	Measures only part that contacts partner?	Sexual contact is trait's only function?	Contact function is potentially forceful?	Trait has apical position on appendage	Possible lock-and-key function?	References
	M	Genitalia	Process of paramere length	0.35						
	M	Genitalia	Paramere width	0.6						
	M	Genitalia	Basal piece width	0.3						
	M	Genitalia	Basal piece length	0.4						
Phyllophaga valeriana	M	Nonsexual	Maximum width head	0.69						Eberhard 1993; W. G.
(Scarabaeidae)	M	Nonsexual	Penultimate segment of the antenna length	0.86				Y		Eberhard, original data
	M	Nonsexual	Femur III length	0.91						
	M	Contact	Length of the patch of tubercles on the modified abdominal sternite	0.9	Y	Y	N		N	
	M	Contact	Width of notch on posterior edge of modified abdominal sternite	0.81	Y	Y	N		Y	
	M	Nonsexual	Maximum width of the pygidium	0.81						
	M	Nonsexual	Apical segment of the maxillary palps length	0.66				Y		
	M	Nonsexual	Tarsus I length	0.64				Y		

continued

APPENDIX 3
Continued

	M	Genitalia	Basal piece of the aedeagus width	0.78	Y	Y			
	M	Genitalia	Parameres length	0.48	Y	Y			
	M	Genitalia	Basal piece of the aedeagus length	0.8	Y	Y			
Diptera									
Archisepsis diversiformis	M	Nonsexual	Head width	0.77					Eberhard and Pereira
(Sepsidae)	M	Contact	Femur I length	0.79			Y		1996; Eberhard 2002c;
	M	Contact	Bristle femur I length	0.35	Y	Y	Y	N[f]	W. G. Eberhard, original data; measurement of head width was less certain
	M	Contact	Distance between tips, major clamp processes on femur I	0.77	Y	Y	Y	N[f]	
	M	Genitalia	Hypandrium (genitalic clasper) length	0.35				N	
	M	Genitalia	Distance between the tips of the teeth on the hypandrium (genitalic clasper)	0.2				N	
Archisepsis pleuralis	M	Nonsexual	Head width	0.72					Eberhard and Pereira
(Sepsidae)	M	Contact	Femur I length	0.83			Y	N[f]	1996; W. G. Eberhard, original data
	M	Contact	Tibia I length	0.52	Y		Y	N[f]	
	M	Contact	Notch on femur I width	0.3	Y	Y	Y	N[f]	
	M	Contact	Large tooth on femur I length	0.7	Y	Y	Y	N[f]	
	M	Nonsexual	Femur II length	1.05					
	M	Genitalia	Hypandrium length	0.33		Y	Y	N	

continued

APPENDIX 3
Continued

Species	Sex	Trait type	Trait	*b*	Measures only part that contacts partner?	Sexual contact is trait's only function?	Contact function is potentially forceful?	Trait has apical position on appendage	Possible lock-and-key function?	References
	M	Genitalia	Distance between the tips of the teeth on the hypandrium	0.11	Y	Y	Y		N	
Pseudopalaeosepsis dentatiformis (Sepsidae)	M	Nonsexual	Head width	0.81						Eberhard 2002b; sternal brush moves actively, brushing on female surface
	M	Nonsexual	Tibia III length	0.93						
	M	Nonsexual	Tibia II length	0.99						
	M	Contact	Tibia I length	0.96			Y		N[f]	
	M	Nonsexual	Wing length	0.82						
	M	Genitalia	Hypandrium length	0.32	Y	Y	Y		N	
	M	Contact	Sternal brush length	0.45	Y	Y	N		N	
	M	Contact	Sternite IV length	0.58	Y	Y	N		N	
	M	Nonsexual	Sternite II length	0.80						
	F	Nonsexual	Head width	0.81						
	F	Nonsexual	Tibia III length	1.03						
	F	Nonsexual	Tibia II length	0.90						
	F	Nonsexual	Tibia I length	0.95						
	F	Nonsexual	Wing length	0.87						
	F	Nonsexual	Sternite IV length	1.15						
	F	Nonsexual	Sternite II length	1.00						

continued

APPENDIX 3
Continued

Hymenoptera									
Crabro sp. (Crabronidae)	M	Nonsexual	Head width across eyes	0.87					Low and Wcislo 1992; W. G. Eberhard, original data
	M	Nonsexual	Tibia III length	0.79					
	M	Nonsexual	Length of cell in wing	1.59					
	M	Contact	Tibial plate on leg I length	0.55	Y		N	N	
	M	Contact	Tibial plate on leg I width	0.65	Y		N	N	
	M	Contact	Pointed process on plate on tibia I length	0.29	Y		N	N	
Polistes fuscatus (Vespidae)	M	Nonsexual	Antenna scape length	0.69					West-Eberhard 1969; B. Speck, original data; the male slides his antenna along the female's; the stroking movement is more or less rearward and pulls the female's antenna rearward
	M	Nonsexual	Antenna pedicel length	0.51					
	M	Nonsexual	Antenna basal 2 flagellomeres length	0.36					
	M	Contact	Antenna apical 8 flagellomeres length	0.2		Y	Y	N	
	M	Nonsexual	Face width	0.72					
	M	Nonsexual	Tibia length	1.02					
	F	Nonsexual	Antenna scape length	0.58					
	F	Nonsexual	Antenna pedicel length	0.51					
	F	Nonsexual	Antenna basal 2 flagellomeres length	0.53					
	F	Contact	Antenna apical 8 flagellomeres length	0.42			Y		
	F	Nonsexual	Face width	0.58					
	F	Nonsexual	Tibia length	0.76					

continued

APPENDIX 3
Continued

Species	Sex	Trait type	Trait	*b*	Measures only part that contacts partner?	Sexual contact is trait's only function?	Contact function is potentially forceful?	Trait has apical position on appendage	Possible lock-and-key function?	References
Odonata										
Hetaerina sp. (Calopterygidae)	M	Nonsexual	Tibia I length	1.21						Eberhard 1986; W. G. Eberhard, original data; the measurement of the length of tibia I could have error
	M	Nonsexual	Basal segment of antenna length	0.89						
	M	Nonsexual	Pleuron I length	0.94						
	M	Contact	Length of the superior abdominal clasper (middle prominence to distal tip - dorsal view)	1.09	Y	Y	Y		Y?[g]	
	M	Contact	Length of the inferior abdominal clasper (middle to distal tooth - ventral view)	3.93	Y	Y	Y		Y?[g]	
	M	Nonsexual	Genital sclerite length	1.58						
	M	Genitalia	Penis width	0.32						
	M	Genitalia	Penis length	0.2						
Opiliones										
Leiobunum vittatum (Sclerosomatidae)	M	Genitalia	Penis length	0.40						Fowler-Finn et al. 2014; Kilmer and Rodríguez 2017
	M	Nonsexual	Diagonal length of carapace	0.59						
	M	Nonsexual	Palp patella length	1.02						
	M	Nonsexual	Palp tibia length	1.05						
	M	Contact	Palp tarsus length	0.53			Y	Y	N	
	M	Nonsexual	Leg II patella length	0.48						
	M	Nonsexual	Leg II tibia length	0.81						

continued

APPENDIX 3
Continued

M	Nonsexual	Leg II metatarsus length	0.54	Y	Y	N
M	Contact	Leg II tarsus length	0.44			
M	Nonsexual	Leg III patella length	0.29			
M	Nonsexual	Leg III tibia length	0.75			
M	Nonsexual	Leg III metatarsus length	0.54			
M	Contact	Leg III tarsus length	0.21	Y	Y	N
M	Nonsexual	Leg IV patella length	0.48			
M	Nonsexual	Leg IV tibia length	0.54			
M	Nonsexual	Leg IV metatarsus length	0.53			
M	Nonsexual	Leg IV tarsus length	0.17		Y	
F	Nonsexual	Diagonal length of carapace	0.87			
F	Nonsexual	Palp patella length	1.10			
F	Nonsexual	Palp tibia length	0.98			
F	Nonsexual	Palp tarsus length	0.90		Y	
F	Nonsexual	Leg II patella length	0.68			
F	Nonsexual	Leg II tibia length	0.89			
F	Nonsexual	Leg II metatarsus length	0.77			
F	Nonsexual	Leg II tarsus length	0.31		Y	
F	Nonsexual	Leg III patella length	0.87			
F	Nonsexual	Leg III tibia length	0.68			
F	Nonsexual	Leg III metatarsus length	0.88			
F	Nonsexual	Leg III tarsus length	0.20		Y	
F	Nonsexual	Leg IV patella length	0.41			

continued

APPENDIX 3
Continued

Species	Sex	Trait type	Trait	*b*	Measures only part that contacts partner?	Sexual contact is trait's only function?	Contact function is potentially forceful?	Trait has apical position on appendage	Possible lock-and-key function?	References
	F	Nonsexual	Leg IV tibia length	0.76						
	F	Nonsexual	Leg IV metatarsus length	0.84						
	F	Nonsexual	Leg IV tarsus length	0.20				Y		

The allometric slope (b) was estimated with ordinary least squares regressions (see text). Several variables affect the level of confidence that the contact courtship trait has a "pure" male-to-female courtship signaling function: whether or not our measure included only the portion of the male structure that makes contact with the female during copulation; whether the structure is specialized and has no other obvious function other than contact courtship (e.g., it is not on a leg or an antenna); whether the trait could potentially be used forcefully (e.g., to restrain the female); whether the trait has an apical position on an appendage such that it contacts the environment as the animal moves about; and whether the portion of the female that is contacted has a species-specific design that meshes mechanically with the male structure. A blank space indicates there is a lack of information or the question is not relevant for this variable.

[a]The male cheliceral process almost certainly fits into the groove on the female epigynum. But the cheliceral processes of the males of several dozen other species of *Mesabolivar* seem designed to also fit into epigynal grooves, so a lock-and-key function is not convincing. The possible function of the lateral margins of the epigynum as a lock that is fit only by the lateral margins of conspecific male chelicerae is even less convincing as a lock-and-key with data from other species.

[b]The female zone of contact is barely or not modified, and is not species-specific.

[c]The contact area of the female epigynum is modified and species-specific, but there is no female structure that corresponds to the male cheliceral modifications.

[d]The question of possible male force is complex. The male-female cheliceral clasp is mutual, and the female must cooperate by opening her fangs, so physical coercion by the male on an unwilling female seems unlikely (although not impossible because it is possible that the female spreads her fangs in attempting to bite the male, and he then blocks them open with his chelicerae). Once the chelicerae are locked, it is possible that the male applies twisting or prying pressure on the female.

[e]The female's mouth area, which is contacted by the male's head plate, is not obviously modified, but details of its fit with the male are lacking.

[f]The base of the female's wing is very complex, with several rounded, steep "hills" (veins) and valleys between them. The male femur and tibia fit tightly against the dorsal and ventral surface of the wings, with indentations receiving veins and processes projecting into the valleys (Eberhard 2001). There is thus a clear, tight mechanical mesh between male and female (and thus a possible lock-and-key). There are multiple chordotonal sense organs (which sense stress on cuticle) on the veins, so the female likely has sensory information regarding the male clamps. But the female morphology varies little between species, and is also not clearly sexually dimorphic in either morphological contours or in sense organs; each species of male meshes in a slightly different way with this more or less standard female design. The chordotonal organs do vary somewhat in numbers and positions between species in females, but there is no convincing intraspecific sexual dimorphism, and no clear correspondence between where the organs are and where the male contacts the female wing. The classification as "lock-and-key" is doubtful, and is included here in an attempt to be conservative.

[g]This is a conservative classification; corresponding female prothorax morphology is not known sufficiently well to be certain.