SEXUAL SELECTION AND ALLOMETRY: A CRITICAL REAPPRAISAL OF THE EVIDENCE AND IDEAS

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One of the most pervasive ideas in the sexual selection literature is the belief that sexually selected traits almost universally exhibit positive static allometries (i.e., within a sample of conspecific adults, larger individuals have disproportionally larger traits). In this review, I show that this idea is contradicted by empirical evidence and theory. Although positive allometry is a typical attribute of some sexual traits in certain groups, the preponderance of positively allometric sexual traits in the empirical literature apparently results from a sampling bias reflecting a fascination with unusually exaggerated (bizarre) traits. I review empirical examples from a broad range of taxa illustrating the diversity of allometric patterns exhibited by signal, weapon, clasping and genital traits, as well as nonsexual traits. This evidence suggests that positive allometry may be the exception rather than the rule in sexual traits, that directional sexual selection does not necessarily lead to the evolution of positive allometry and, conversely, that positive allometry is not necessarily a consequence of sexual selection, and that many sexual traits exhibit sex differences in allometric intercept rather than slope. Such diversity in the allometries of secondary sexual traits is to be expected, given that optimal allometry should reflect resource allocation trade-offs, and patterns of sexual and viability selection on both trait size and body size. An unbiased empirical assessment of the relation between sexual selection and allometry is an essential step towards an understanding of this diversity.

KEY WORDS: Allometry, body shape, body size, publication bias, sampling bias, sexual selection.

Shape variation is one of the principal sources of biological diversity, and accounting for this variation is a perennial challenge for evolutionary biology (Gould 1966). The evolution of shape under sexual selection has been of particular interest because of the spectacularly exaggerated ("bizarre") sexual traits observed within some species, such as the antlers of the Irish elk, *Megaloceros giganteos* (Gould 1973, 1974). "Static" allometry reflects variation in shape among individuals of the same species and developmental stage, whereas ontogenetic allometry describes changes in relative trait size through individual development, and evolutionary allometry describes the covariation among species between mean trait size and mean body size. Although ontogenetic and evolutionary allometries of sexual traits offer fascinating puzzles in their own

right (e.g., Gould 1966; Arévalo and Heeb 2005; Blanckenhorn et al. 2006), I focus the present discussion on static allometry of adult secondary sexual traits (henceforth simply "allometry" unless indicated otherwise), because this form of allometry can be linked most clearly and directly to patterns of sexual selection operating within species.

Allometry is often described in terms of allometric slope (b), based on the equation, $Y = aX^b$, where Y and X are indices of trait size and body size. Relative trait size is constant for all body sizes when $b = 1$ ("isometry"), decreases with body size when $b < 1$ ("negative allometry"), or increases with body size when $b > 1$ ("positive allometry"). A positively allometric trait is thus relatively larger, in proportion to body size, in larger individuals.

It has been recognized for a long time that positive allometry is a typical attribute of some sexually selected traits within species belonging to certain higher-level groups. For example, nearly all of the 17 species of fiddler crabs in the genus *Uca* exhibit positive allometry of the major claw of males (Rosenberg 2002), and male mandible length is positively allometric within each of the 79 species of stag beetles examined by Kawano (1997). Extrapolating from such examples, a number of authors have hypothesized that sexual selection (or, at least, directional sexual selection) almost invariably leads to the evolution of positive allometry, and that positive allometry is a characteristic attribute of virtually all sexually selected traits (or, at least, signal and weapon traits) in all animals (e.g., Green 1992, 2000; Petrie 1992; Kodric-Brown et al. 2006). I will refer to this set of propositions as the "positive allometry hypothesis."

The positive allometry hypothesis reflects three assumptions: (1) all signal and weapon traits are under directional sexual selection, (2) body size is correlated with condition, and (3) these circumstances lead to the evolution of positive allometry (see Alatalo et al. 1988; Green 1992; Petrie 1992; Kodric-Brown et al. 2006). In other words, if secondary sexual trait size is under directional sexual selection, then increased relative trait size yields increased mating success, but viability costs limit secondary sexual trait expression in small individuals, resulting in positive allometry. It has also been suggested that positive allometry evolves to amplify differences in body size, which may be important in male–male interactions, or female assessment of male mate quality (Wallace 1987; Emlen and Nijhout 2000). Thus, whereas "honest" (or "reliable") signaling implies a correlation between secondary sexual trait size and quality (Getty 1998a,b), the positive allometry hypothesis embodies the expectation of a "super-honest" signal that increases exponentially with body size. In contrast, it is generally assumed that nonsexual traits (including female homologous of male sexual traits) almost never exhibit positive allometry (but see Green 1992; Simmons and Tomkins 1996). For example, Green (2000) has argued that static allometry can be used to discriminate sexual and nonsexual traits. It has also been suggested that genitalic traits exhibit shallower allometric slopes than other sexual traits (and many nonsexual traits), perhaps because genitalia are subject to stabilizing sexual selection (Eberhard et al. 1998). Most recently, Kodric-Brown et al. (2006) concluded that "The empirical evidence shows that the ornaments and weapons used by males to acquire mates almost universally exhibit positive allometries." Motivated by this conclusion, Kodric-Brown et al. (2006) also built a model showing how a universal pattern of positive allometry might arise in such traits.

The empirical evidence is indeed crucial because it determines the questions that need to be answered. If virtually all sexual traits are positively allometric, then theory must account for the fact that sexual selection almost invariably produces positive allometry. If sexual traits are sometimes positively allometric and sometimes not, then theory must explain why sexual selection produces a diversity of allometric patterns. If a small subset of these traits exhibits unusually large allometric slopes, then we also need to understand the special conditions that lead to extreme trait exaggeration.

Here, I undertake a critical reappraisal of the empirical literature and ideas on the evolution of static allometry in sexual traits. I argue that sampling bias—a predilection for bizarre traits—has resulted in an overrepresentation of positively allometric sexual traits in the empirical literature, giving rise to the erroneous impression that virtually all sexual traits are positively allometric. I support this conclusion by reviewing evidence from four key model systems in sexual selection research—birds, guppies (and relatives), flies, and water striders—that, like most taxa, are not universally endowed with bizarre traits. This evidence contradicts the positive allometry hypothesis, showing that many sexual traits exhibit negative or isometric scaling, whereas some nonsexual traits exhibit positive allometries. I discuss theoretical reasons why a diversity of allometric patterns may be expected to evolve, and offer more specific hypotheses and predictions for the evolution of positive allometry. I also suggest approaches to an unbiased empirical assessment of the association between sexual selection and allometry.

Bizarre Traits and the Problem of Sampling Bias

The association between sexual selection and allometry is currently confounded by a sampling bias in the empirical literature. It is clear that traits like stag beetle mandibles and fiddler crab claws become a focus of morphometric research because of their unusual degree of exaggeration, which often reflects positive allometry. Authors of studies on the allometry of sexual traits typically acknowledge this, using terms like "bizarre" (Gould 1974), "enormously oversized" (Kawano 1997), "extreme" (Rosenberg 2002), and "striking" (Zeh et al. 1992) to describe the traits they have chosen for study. As these adjectives indicate, such traits do not constitute a random sample, and are unlikely to be representative of sexually selected traits in general. Bizarre traits are, by definition, unusual. Conversely, sexual traits that are not characterized by extreme exaggeration have elicited little interest from allometricians, even in the key model species in sexual selection research. Thus, for example, I was unable to find any studies on the allometry of sexual traits (e.g., forelegs and sex combs) in *Drosophila melanogaster*. Thus, sampling bias may account for the preponderance of examples of positively allometric sexual traits in the literature. More importantly, this biased literature has been proffered as evidence of the near-universality of positive allometry in sexual traits (e.g., see Green 1992, 2000; Kodric-Brown et al. 2006).

Kodric-Brown et al. (2006) present the most extensive review of the literature on sexual trait allometries attempted thus far, comprising allometric data on one sexual trait in each of nine major taxa (rhinoceros beetle horns, stag beetle mandibles, swordtail fish tails, sailfin molly dorsal fins, newt tail crests, *Anolis* lizard dewlaps, fiddler crab claws, deer antlers, and antelope horns). Most of these traits are positively allometric, but are they representative of signal and weapon traits in general? A good reason to suspect otherwise is the conspicuous underrepresentation of the standard model organisms used in sexual selection research. If positive allometry is a near-universal attribute of signals, weapons, and other sexually selected traits, then positively allometric morphological traits should occur in most sexually reproducing species, including the standard model organisms, and species lacking bizarre traits.

Beyond Bizarre Traits: Clues From Four Key Taxa

To assess the universality of positive allometry in sexual traits, I reviewed evidence on morphological trait allometries in birds, guppies (and relatives), flies, and water striders (Table 1). I focused on these taxa because they are important models in sexual selection research, but are not universally endowed with bizarre traits (although some species within some of these taxa possess such traits). These taxa may thus provide a more representative (i.e., less biased) sample than groups in which virtually all species possess bizarre sexual traits, and that evidently became a focus of allometric analysis by virtue of possessing such traits (e.g., stag and rhinoceros beetles, fiddler crabs, etc.). This review is thus intended as a counterpoint to the review of Kodric-Brown et al. (2006), which focuses on groups characterized by bizarre sexual traits, and includes none of the taxa reviewed here. I have included studies that examined allometries of traits with clear functions in sexual competition, as well as nonsexual "control" traits (including, where possible, the homologous traits of females), and that used the allometric equation or its linearized (log-transformed) analogue to quantify allometry. Studies presenting linear slopes for untransformed data were excluded because such slopes do not describe how relative trait size changes with body size. Following convention, I define a "weapon" as an appendage brought into contact with rivals during agonistic interactions, a "signal" as a trait actively displayed in intersexual and/or intrasexual interactions, a "grasping" trait as an appendage used to cling to females during mating, and a "genital" trait as a structure directly associated with sperm transfer.

BIRDS

Birds provide some of the most striking examples of sexually selected traits (Darwin 1874). Positively allometric sexual traits have

been described in a few species: Petrie (1988) reported positive allometry of the bill "shield" in both sexes in *Gallinula chloropus*, and Alatalo et al. (1988) reported positive tail allometry in males in six other species, although they did not examine the allometries of female tails. But the most extensive overview was carried out by Cuervo and MØller (2001), who compared the allometries of male ornamental and nonornamental feathers, and homologous female traits, in 67 species of birds with sexually dimorphic plumage. They found no evidence of positive allometry in any species, and no mean difference in scaling between ornamental and nonornamental traits. However, because allometries were quantified using least-squares slopes, this study underestimates the allometries of both sexual and nonsexual traits to some degree (see below).

GUPPIES AND RELATIVES

The guppy (*Poecilia reticulata*) is a key model organism in sexual selection research. Males of this species use two distinct tactics: sigmoidal courtship displays that show off their body coloration to females, and sneak-copulations in which males attempt to inseminate unreceptive females by lunging and inserting the gonopodium (a modified pelvic fin structure used in sperm transfer) into the female gonopore. However, gonopodium length was positively allometric in few guppy populations (Kelly et al. 2000), and even fewer populations of the related species *Brachyrhaphis episcope* (Jennions and Kelly 2002). On the other hand, melanized body area (a sexual display trait) was positively allometric in all populations examined (Kelly et al. 2000).

FLIES

The true flies (Diptera) are an amazingly diverse group of animals that includes some of the most important model organisms in sexual selection research. Eberhard (2002a) examined the allometries of leg and head dimensions in two species in the drosophilid genus *Chymomyza*. In both species, males use their decorated forelegs in combat and courtship and, in one species (*Chymomyza exophthalma*), also push rivals with their heads. Although head width and virtually all leg traits were sexually dimorphic in both species, only head width and fore-tarsus length in males of *C. exophthalma* exhibited positive allometry, whereas all other leg traits in this species, and all signal and weapon traits in *C. mycopelates*, exhibited isometry or negative allometry.

Scathophaga stercoraria (Scathophagidae) is a key model species in research on sexual selection and conflict. Males fight for access to single females on dung pats, and attempt take-overs of females *in copula* (Parker 1970). Hosken et al. (2005) examined the static allometry of genital claspers (a sexual trait used by males to grasp females, and possibly to administer "copulatory courtship"), the testes, and the mandibular palp (a nonsexual sensory trait), in *S. stercoraria* and 12 other scathophagid species. They found that genital claspers were typically negatively allometric, despite

Table 1. Static allometries in birds, poeciliid fishes, flies, and water striders. Trait type distinguishes sexual traits ("S"), defined as traits directly employed in sexual competition by males, from nonsexual traits ("N"), with sexual functions (signal, weapon, grasping, or genital) indicated for the sexual traits. Static allometries are based on log-log transformed data and geometric regression (unless marked with an asterisk to indicate that ordinary least squares regression was used), and characterized as negative ($b < 1$), isometric ($b \approx 1$), or positive ($b > 1$) based on statistical tests reported in the source literature, or inspection of confidence limits for the slope.

Taxon	Trait and sexual function (if any)	Type	Static allometry		Reference
			Males	Females	
Birds					
67 species*	Ornamental feathers (signal)	S	Negative	Negative	Cuervo and Møller 2001
(various families)	Nonornamental (wing, tail) feathers	N	Negative	Negative	
Rallidae					
Gallinula chloropos	"Frontal shield" of bill	S	Positive	Positive	Petrie 1988
Poeciliid fishes					
Poecilia reticulata (guppy)	Black color area (signal)	S	Positive	–	Kelly et al. 2000
	Gonopodium length (genital)	S	Usually negative	–	
Brachyrhaphis episcope	Gonopodium length (genital)	S	Negative	–	Jennions and Kelly 2002
Flies (Diptera)					
Drosophilidae					
Chymomyza mycopelates	Head width (signal)	S	Negative	Negative	Eberhard 2002a
	Head bristle separation (signal)	S	Negative	Negative	
	Fore-femur length (signal and/or weapon)	S	Isometric	Isometric	
	Fore-tibia length (signal and/or weapon)	S	Negative	Negative	
	Hind-tibia length	N	Isometric	Isometric	
	Wings	N	Negative	Negative	
C. exophthalma	Head width (signal)	S	Positive	Isometric	Eberhard 2002a
	Head bristle separation (signal)	S	Positive	Isometric	
	Femoral spine length (weapon)	S	Positive	?	
	Femoral spine number (weapon)	S	Isometric	Positive	
	Fore-femur length (signal and/or weapon)	S	Negative	Isometric	
	Fore-tibia length (signal and/or weapon)	S	Isometric	Isometric	
	Hind-tibia length	N	Isometric	Isometric	
	Wings	N	Negative	Negative	
Scathophagidae					
13 species	Testis	S	Positive in all species	–	Hosken et al. 2005
	Genital claspers (genital, grasping)	S	Negative in nearly all species	–	
	Mandibular palp	N	Positive in most species	–	

Table 1. Continued.

Taxon	Trait and sexual function (if any)	Type	Static allometry — Males	Static allometry — Females	Reference
Diopsidae					
*Cyrtodiopsis whitei**	Eye-stalk width (signal, weapon)	S	Positive	Isometric	Burkhardt et al. 1994
Piophilidae					
Prochyliza xanthostoma	Antenna, head length, fore-leg length (signal, weapon)	S	Negative or isometric	Negative, isometric or positive	Bonduriansky 2006
	Mid- and hind-tibia, intersetal width, wing length	N	Negative or isometric	Negative or positive	
Neriidae					
Telostylinus angusticollis	Antenna, head length, fore-leg length (signal, weapon)	S	Positive	Negative	Bonduriansky 2006
	Mid- and hind-tibia, intersetal width, wing length	N	Negative or positive	Negative or isometric	
Tephritidae					
*Ceratitis capitata, C. catoirii, C. rosa, Neoceratitis cyanescens**	18 measurements of head, antenna, legs, wing	S, N	All negative	All negative	Briceño et al. 2005
Sepsidae					
Palaeosepsis dentatiformis	Head width	N	Negative	Negative	Eberhard 2002b
	Hind-tibia length (signal)	S	Negative	Isometric	
	Mid-tibia length (signal)	S	Isometric	Negative	
	Fore-tibia length (signal, weapon)	S	Negative	Negative	
	Wing length	N	Negative	Negative	
	Wing-spot length (signal)	S	Positive	Positive	
	Genital traits	S	Negative or isometric	Positive or isometric	
Water striders					
Aquarius remigis	External genitalia (grasping)	S	Isometric	–	Bertin and Fairbairn 2007
	Internal genitalia (genital)	S	Isometric	–	
	Fore-femur width, mid-femur length	N	Positive	?	
Gigantometra gigas	Fore-femur length (grasping)	S	Isometric	Isometric	Tseng and Rowe 1999
	Mid- and hind-femur length	N	Positive	Positive	
Gerris buenoi	Mid-femur length	N	Isometric	Isometric	Tseng and Rowe 1999
	Hind-femur length	N	Positive	Positive	

sexual selection on this trait (see Otronen 1998). In contrast, testis size tended to exhibit positive allometry. Curiously, mandibular palp length also exhibited positive allometry in many species.

The diopsid (stalk-eyed) flies exhibit one of the most bizarre morphologies of all animals. In *Cyrtodiopsis whitei*, male eye-stalks (used as a signal and weapon) are positively allometric, but female eye-stalks are not (Burkhardt et al. 1994). Unfortunately, only linear slopes for untransformed data have been published for other diopsid species (Wilkinson and Taper 1999; Baker and Wilkinson 2001).

In the piophilid fly *Prochyliza xanthostoma* and the neriid fly *Telostylinus angusticollis*, males have elongated heads, antennae and legs, and use these traits in sexual competition. Most sexual traits of *T. angusticollis* are positively allometric, but none of the sexual traits of *P. xanthostoma* males exhibit positive allometries, or greater allometric slopes than nonsexual male traits or homologous female traits (Bonduriansky 2006). This is despite the fact that *P. xanthostoma* is highly sexually dimorphic, and exhibits fierce male–male combat and elaborate courtship, generating sexual selection on male body shape (Bonduriansky 2003; Bonduriansky and Rowe 2003).

Briceño et al. (2005) examined the allometries of 18 morphological traits in four species of tephritid flies, including head, antenna, and foreleg traits involved in sexual competition among males. Although virtually all traits were sexually dimorphic, none exhibited positive allometry in either sex. Some traits exhibited sex differences in allometric slope, but the female slope exceeded the male slope in about half of these cases (however, all allometries were underestimated by use of least-squares regression).

Eberhard (2002b) examined the allometries of sexual and nonsexual traits in the sepsid fly *Palaeosepsis dentatiformis*. He found that male wing spots (used in male–male agonistic signaling) were positively allometric, although female wing spots (which do not appear to function in sexual competition) exhibited almost identical scaling. In contrast, neither the forelegs (used as weapons and signals), nor the mid- and hind-legs (used to elevate the body as a signal to rival males) exhibited positive allometry.

WATER STRIDERS

Several species of water striders have become a key model for research on sexual selection. Bertin and Fairbairn (2007) compared the allometries of male external genital traits (used to grasp females) that are known to be subject to directional sexual selection, internal genital traits subject to stabilizing sexual selection, and leg traits (fore-femur width and mid-femur length) subject to weak or stabilizing sexual selection, in six populations of *Aquarius remigis*. They found that both external and internal genital traits exhibited isometric scaling with body length, whereas the leg traits exhibited positive allometry. In addition, the mid legs and/or hind

legs, which appear to serve no direct sexual functions, are positively allometric in both sexes in *Gerris buenoi* and *Gigantometra gigas*, whereas the length of the forelegs (used by males to grasp females) exhibits isometric scaling in *G. gigas* (Tseng and Rowe 1999). Likewise, Klingenberg and Zimmermann (1992) found no significant differences in multivariate allometry between the sexes in nine species of water striders.

Does the Empirical Evidence Support the Positive Allometry Hypothesis?

The evidence reviewed here (Table 1) contradicts the positive allometry hypothesis in almost every respect. First, rather than a near-universal pattern of positive allometry, sexually selected traits exhibit a diversity of allometric patterns. Although the small number and limited phylogenetic range of examples preclude a meaningful quantitative meta-analysis, 10 of the 12 studies reviewed report negative allometry or isometry in some or all of the sexually selected traits examined. The positive allometry hypothesis is contradicted for signal and weapon traits (Cuervo and Møller 2001; Eberhard 2002a, b; Briceño et al. 2005; Bonduriansky 2006), as well as for grasping traits (Tseng and Rowe 1999) and genital traits (Kelly et al. 2000; Jennions and Kelly 2002; Hosken et al. 2005; Bertin and Fairbairn 2007; also see Eberhard et al. 1998). Second, even traits that are known to be under directional sexual selection do not necessarily evolve positive allometries (Bertin and Fairbairn 2007). Third, positive allometry occurs in some nonsexual traits of males (Hosken et al. 2005; also see Simmons and Tomkins 1996), and in some female homologues of male sexual traits (Petrie 1988; Tseng and Rowe 1999; Eberhard 2002b). Although nonsexual traits usually scale with negative allometry or isometry (von Bertalanffy and Pirozynski 1952; Merry et al. 2006), positive allometry may be relatively common in locomotory structures as a result of biomechanical factors (see Tseng and Rowe 1999).

Nonetheless, it is clear that positive allometry is a characteristic attribute of some sexual traits in certain taxa, and that some sexual traits exhibit extraordinarily steep allometric slopes (see Kodric-Brown et al. 2006 for examples). I am not aware of any examples of nonsexual traits with allometric coefficients that rival the most extreme positive allometries observed in sexual traits. Thus, the examples reviewed by Kodric-Brown et al. (2006) suggest that sexual selection drives the evolution of greatly elevated allometric slopes under some circumstances.

In addition, the evidence illustrates that trait "exaggeration" can involve either an increase in allometric slope, or an increase in allometric intercept (resulting in a body size independent sexual dimorphism), or both. Sexual dimorphism without positive allometry is commonplace in secondary sexual traits within the groups

included in this review (e.g., birds: Cuervo and Møller 2001; flies: Eberhard 2002a, b; Briceño et al. 2005; Bonduriansky 2006; water striders: Tseng and Rowe 1999), suggesting that sexual selection often acts on the allometric intercept rather than the allometric slope.

In summary, five conclusions can be drawn from the empirical evidence: (1) positive allometry appears to occur in a minority of sexual traits, including signals and weapons; (2) positive allometry does not necessarily evolve in response to directional sexual selection; (3) positive allometry can evolve for reasons other than sexual selection, and should not be used to infer sexual selection; (4) nonetheless, sexual selection drives extreme elevation of allometric slopes under some circumstances; (5) sexual selection sometimes increases the allometric intercept without affecting the slope.

Why do Sexual (and Nonsexual) Traits Vary in Static Allometry?

To understand why sexual selection sometimes leads to extreme exaggeration of sexual traits, but sometimes appears to have little or no effect on trait allometry, we must start with theory predicting how allometry should respond to selection. Bonduriansky and Day (2003) developed a model that predicts the optimal trait allometry under any pattern of selection on trait size and body size. The model assumes that resources are initially allocated to body growth only but, at a later stage in development, a fraction of the available resources is allocated to the growth of a secondary sexual trait. Growth is determinate, and the pool of available resources is finite, resulting in a trade-off between the final size of the secondary sexual trait and the size of the body in the adult.

The model of Bonduriansky and Day (2003) yields several relevant results. First, it suggests that any pattern of linear or sigmoidal allometry can evolve under sexual selection, a finding consistent with the allometric diversity of sexual traits (Table 1). Second, it suggests that directional selection on absolute or relative trait size will not necessarily favor positive allometry. This is because allometry reflects patterns of variation in two traits—body size and secondary sexual trait size—and the optimal allometric pattern depends on how net selection acts on each of these traits, as well as the ontogenetic resource allocation trade-off between them. Third, it shows that linear and sigmoidal scaling patterns can result from similar, continuous selection functions. Fourth, it shows that positive allometry should evolve only when the *net* advantage of an increase in relative trait size—reflecting both sexual and viability selection—is greater for large individuals than for small individuals (also see Kodric-Brown et al. 2006).

Although allometry will reflect the pattern of net selection, it is possible to identify patterns of sexual and viability selection that, all else being equal, are likely to favor positive allometry.

Below, I discuss these factors and suggest two general hypotheses and several more specific predictions for future investigations.

SEXUAL SELECTION ON TRAIT SIZE AND BODY SIZE

The model of Bonduriansky and Day (2003) suggests that, *all else being equal, positive allometry is most likely to evolve when an increase in relative trait size yields greater mating success benefits for large individuals than for small ones.* This hypothesis suggests several reasons why secondary sexual traits may vary in allometry.

It is often assumed that all signal and weapon traits are under directional sexual selection, so that larger individuals (which are less constrained by viability costs) can reap mating success benefits by expressing relatively larger traits (see Green 1992; Petrie 1992; Kodric-Brown et al. 2006). This is unlikely to be true for all signal and weapon traits, however, because the dynamics of combat and courtship are shaped to a substantial degree by body size dependent biomechanical factors (see Clutton-Brock 1982; Kitchener 1985; Hughes 2000). If performance reflects an interaction between the size of a weapon or signal trait and the ability to wield it in combat or courtship, mating success may be maximized at an intermediate trait size for any given body size. Moreover, optimal relative trait size may or may not be similar for large and small males, depending on the type of trait and how it is used. For example, if small males lack sufficient body mass or strength to wield weapons effectively, they may employ alternative tactics like scramble competition. Sexual selection may then favor relatively lower investment in weapon size by small males (positive allometry). In contrast, if larger relative trait size compensates for the competitive disadvantages of small body size, then sexual selection may favor relatively greater investment in secondary sexual traits in small individuals (negative allometry). Given that weapons are probably subject to stronger biomechanical constraints than signal (display) traits, it is also possible that sexual selection tends to favor steeper allometries in signals than in weapons, as suggested by Gould (1974).

Conversely, it has been hypothesized that genitalic traits exhibit shallower allometric slopes than other kinds of sexually selected traits because genitalic traits are under stabilizing sexual selection, reflecting their presumed roles in "copulatory courtship" and cryptic female mate choice (Eberhard et al. 1998; Bernstein and Bernstein 2002; but see Green 1999). However, this hypothesis is contradicted by evidence from the water strider Aquarius remigis, in which genitalic structures subject to directional and stabilizing sexual selection exhibit similar (isometric) scaling (Bertin and Fairbairn 2007). It thus remains unclear why genitalic structures may exhibit shallower allometries than other sexually selected traits.

Likewise, allometry may be affected by sexual selection on body size. Disruptive sexual selection on body size may result from use of different sexual tactics by large and small males (e.g.,

see above). If sexual selection favors small body size in small males but large body size in large males then, even if sexual selection on secondary sexual trait size is similar at all body sizes, large males may possess relatively smaller secondary sexual traits (negative allometry) simply because they invest relatively more in body size. Conversely, if a unit increase in body size confers greater mating success pay-offs for small males than for large individuals (i.e., mating success increases with body size, but with diminishing returns), then small males will benefit by investing relatively more in body size, and express relatively smaller secondary sexual traits (positive allometry).

Variation in static allometry might also be related to interspecific variation in body size. Mean body size may influence mating system evolution via size-dependent biomechanical or ecological factors (Webster 1992). Likewise, some groups exhibit covariation, across species, between mean body size and sexual size dimorphism (SSD). This form of evolutionary allometry, called Rench's rule (see Abouheif and Fairbairn 1997; Fairbairn 1997), may reflect a stronger response of male body size to latitudinal gradients (Blanckenhorn et al. 2006). Moreover, Gould (1966) argued that the appearance of novel body shapes as a result of body size evolution combined with conserved allometric relationships could facilitate the evolution of novel trait functions. For example, if ecological factors drive the evolution of increased body size, or increased SSD, a positively allometric nonsexual trait may become increasingly exaggerated in males and, once it exceeds a certain threshold, may become effective as a sexual clasping trait, weapon, or signal. The new vector of sexual selection on this trait may then modify the allometry. Thus, interspecific variation in mean body size (or SSD) may provide another source of variation in static allometry. It would be interesting to test for covariation among related species between mean body size or SSD and allometric slopes of homologous secondary sexual traits.

VIABILITY COSTS OF TRAIT EXAGGERATION

The model of Bonduriansky and Day (2003) also suggests that, *all else being equal, positive allometry is more likely to evolve when the viability costs of trait exaggeration are strongly body size dependent.* Because the viability costs of secondary sexual trait expression, and the scaling of these costs with body size, are likely to vary considerably between traits and species (see Kotiaho 2001), patterns of viability selection provide another key source of variation in static allometry of sexual traits.

Even if sexual selection favors similar relative trait size in large and small individuals (isometry), positive allometry may evolve when trait exaggeration is disproportionately costly for small individuals, and such costs constrain trait exaggeration at small body sizes. Conversely, if sexual selection favors positive allometry, positive allometry can evolve even if the relative viability costs of trait expression are similar for large and small

males, because the net benefit of increased relative trait size will be greater for large individuals.

Viability costs of trait exaggeration can diminish with body size if body size is correlated with condition (Alatalo et al. 1988; Green 1992; Petrie 1992), which is often the case in invertebrates (see Blanckenhorn 2000). This probably explains why positively allometric traits tend to exhibit strong condition dependence (e.g., Emlen 1997; Cotton et al. 2004; Bonduriansky 2007). Similar reasoning suggests that steep allometric slopes may be more likely to evolve in animals with indeterminate growth and long life spans (e.g., some crustaceans, fish, reptiles), where secondary sexual trait growth can continue throughout life and there is often enormous, age-dependent variation among individuals in body size and condition. Viability costs of trait exaggeration may also diminish with body size if risk of predation increases more rapidly with relative trait size in small individuals than in large individuals (e.g., because the latter are vulnerable to fewer predators), or if trait exaggeration interferes less with locomotion or other functions in larger individuals.

The genetic covariance structure within and between sexes may also affect how viability costs of trait exaggeration scale with body size. Within-sex genetic covariances may reflect resource allocation trade-offs, whereby exaggeration of a sexual trait results in reduced sizes of nonsexual traits (Nijhout and Emlen 1998; Emlen 2001; Moczek and Nijhout 2004; Tomkins et al. 2005b). The viability costs of reduced allocation to nonsexual male traits may often diminish with increasing body size because most nonsexual traits scale with negative allometry in any case (von Bertalanffy and Pirozynski 1952). Moreover, male–female genetic covariances may cause trait exaggeration in males to result in a correlated displacement of female traits from their viability-selected optima, generating intralocus sexual conflict (Lande 1980, 1987; Bonduriansky and Rowe 2005), although it is unclear whether such costs to females also tend to covary with body size.

The above reasoning suggests that viability costs of secondary sexual trait expression may diminish more rapidly with increasing body size for "dedicated" secondary sexual traits (i.e., traits that serve sexual functions only, like rhinoceros beetle horns or stag beetle mandibles) than for traits with viability-related functions and secondary roles in sexual competition (e.g., birds' tails, or fly forelegs). For example, although a beetle's horn may interfere with locomotion (Moczek and Emlen 2000), a horn of a given size probably imposes a smaller burden for a large beetle than for a smaller bettle because it constitutes a lower fraction of the large male's body mass. Likewise, although horn expression reduces the sizes of nonsexual structures like eyes through developmental resource allocation trade-offs (Emlen 2001; Moczek and Nijhout 2004), the costs of such trade-offs may often diminish with increasing body size because large individuals tend to require

relatively smaller eyes and other nonsexual traits (von Bertalanffy and Pirozynski 1952; Merry et al. 2006; also see above). In contrast, sexually selected modifications to structures with important viability-related functions may tend to impose body size independent viability costs. For example, exaggeration of a fly's foreleg or antenna length for sexual functions (see Bonduriansky 2006) is likely to interfere equally with locomotion or sensory functions in large and small individuals. This may explain why many of the available examples of positively allometric sexual traits are dedicated secondary sexual structures, such as rhino beetle horns, stag beetle mandibles, and lizard dewlaps (see Kodric-Brown et al. 2006), whereas heads, antennae, and legs with sexual functions tend to exhibit negative allometry or isometry (Table 1).

However, for traits that serve both sexual and viability-related functions, the viability costs of exaggeration may be less restrictive when the genetic architecture permits asymmetrical exaggeration of paired structures (i.e., antisymmetry). For example, many crustaceans develop a "major" claw specialized for combat or signaling functions, whereas the other claw remains optimized for feeding and other functions (e.g., see Hughes 2000). Because the exaggerated structure thus loses its viability-related functions, associated viability costs may diminish with increasing body size (see above). Antisymmetrical structures may thus exhibit positive allometry more often than symmetrical structures, and groups that have evolved the capacity to develop such structures (e.g., crustaceans) may exhibit positively allometric sexual traits more often than other groups (e.g., insects).

A strong genetic correlation between secondary sexual trait size and body size could also affect allometry. If the genetic correlation is negative as a result of resource allocation trade-offs (see above), increased secondary sexual trait expression will be associated with reduced body size. However, assuming stabilizing selection on body size, the viability costs of reduced body size would be lower for individuals that exceed the optimal body size. Such body size dependent viability costs would allow positive allometry to evolve, and the trade-off itself would accentuate the allometric slope. However, if the genetic correlation is positive as a result of pleiotropy, such that increased expression of a secondary sexual trait is genetically coupled with increased body size, isometry may result. In addition, it was once widely assumed that extreme positively allometry, like that of the "Irish elk," was a nonadaptive consequence of the evolution of increased body size combined with a conserved pattern of positive allometry (see Gould 1966, 1974 for critical discussions of this idea). However, because selection can alter genetic correlations (Archer et al. 2003) and allometries (Wilkinson 1993), nonadaptive allometries are unlikely to persist for long.

In summary, the positive allometry hypothesis provides no clear basis for the belief that the combinations of sexual and viability selection that permit the evolution of positive allometry are sufficiently pervasive to produce near-universal positive allometry in secondary sexual traits. Contrary to the assumptions of the positive allometry hypothesis (see introduction), sexual selection need not always favor greater relative secondary sexual trait size in larger individuals, and the relative viability costs of secondary sexual trait expression need not always diminish with increasing body size. The evolution of static allometry may also be subject to genetic constraints, and affected by mean body size or SSD. A similar conclusion follows if positive allometry is considered in relation to honest signaling: because positive allometry represents "super-honesty," in which trait size increases exponentially with body size, the preconditions for the evolution of positive allometry are likely to be more restrictive than the basic preconditions for the evolution of honest signaling (see Grafen 1990; Johnstone and Grafen 1993; Getty 1998a, b). The apparent diversity of secondary sexual trait allometries is thus consistent with theory.

Towards an Unbiased Empirical Assessment

Theory suggests the general conditions that favor negative, isometric, or positive allometries (see above), but we are still very far from understanding the specific factors—mechanical, behavioural, sensory, physiological, or genetic—that account for variation in static allometry among sexual traits. An essential first step is to survey this variation. For example, do some types of traits (e.g., horns, mandibles, tails, legs, color spots, antisymmetrical appendages) tend to evolve steeper allometries under sexual selection than other types of traits? Are some forms of sexual competition (e.g., combat, various modes of intersexual or intrasexual signaling, precopulatory struggles, copulatory courtship) associated with steeper trait allometries than other types? Are female sexual traits as likely to evolve steep allometries as male sexual traits? Are some taxa more likely to exhibit positively allometric sexual traits than other taxa? Does allometric slope covary with mean body size or mean SSD among species? An unbiased empirical assessment of the association between sexual selection and allometry will help to answer these questions, and to test theory.

In the past, traits have evidently been selected for allometric analysis on the basis of their exaggeration, and this appears to have resulted in an overrepresentation of positively allometric traits, and an underrepresentation of some taxonomic groups, in the empirical literature. The key to an unbiased survey is to select traits for study on the basis of their function (sexual/nonsexual) and, where possible, examine allometries of traits subject to known regimes of sexual selection, irrespective of their degree of exaggeration. One approach is to compare sexual and nonsexual traits within species. Another approach is to compare a series of sexual traits with homologous but nonsexual traits in

closely related taxa. For example, leg traits with sexual functions can be compared with homologous leg traits in a related species in which the legs play no direct role in sexual competition. This controls for trait type (e.g., forelegs can be compared with forelegs). Using nonsexual male traits as "controls" also avoids the problem of correlated evolution between sexes that may confound comparisons of sexually homologous traits. A different way to address this question is to manipulate the strength of sexual selection, and observe the evolutionary response of trait allometry.

QUANTIFYING ALLOMETRY

The techniques used to quantify allometry are very important. For allometries that can be linearized by log-transformation of the trait size and body size data, the analysis straightforward. The allometric slope, b, can be estimated using the linear analogue of the allometric equation, $\text{Ln}(Y_i) = \text{Ln}(a) + b\text{Ln}(X_i)$, and this parameter will describe how relative trait size changes as body size increases. Second, in most cases, geometric (Model II) regression such as the reduced major axis (RMA) should be used, rather than ordinary least-squares (OLS) regression (see Ricker 1984; Green 1999). OLS regression underestimates the true allometric slope because it attributes all measurement error to Y, and the degree of underestimation increases with scatter about the regression. In contrast, RMA regression assumes equal error in X and Y, and is not systematically affected by scatter. RMA should be used when measurement error in Y does not exceed measurement error in X more than threefold; otherwise, OLS regression is more appropriate (McArdle 1988). RMA slope can be calculated as the ratio of standard deviations, σ_Y/σ_X, or by dividing the OLS slope by the correlation coefficient, r. Furthermore, X and Y should have the same dimensionality (e.g., lengths, areas, volumes, masses). For example, if color patch area is regressed against a linear index of body size, areas (Y) should be square-root transformed. Lastly, the index of trait size should be chosen judiciously (see Moczek 2006).

Nonlinear allometries present much more complex analytical and conceptual problems (see Eberhard and Gutiérrez 1991; Tomkins et al. 2005a; Pomfret and Knell 2006). Such patterns cannot be described adequately by a single allometric slope because the slope covaries with body size. However, the sample can be subdivided by categories (such as "major" and "minor" males: Tomkins et al. 2005a), or the change in allometry with body size can be described by fitting a suitable nonlinear model to the entire dataset, and investigating how allometric slope changes with body size by calculating tangents to the best-fit curve (Pomfret and Knell 2006).

Conclusions

The widely held idea that virtually all sexually selected traits are positively allometric is inconsistent with empirical evidence and theory. Although positive allometry typifies some sexual traits in some taxa, the evidence reviewed here shows that many signals, weapons, and other sexual traits exhibit negative or isometric scaling, and suggests that positive allometry may characterize a minority of sexual traits. The evidence also shows that directional sexual selection is not sufficient to produce positive allometry and, conversely, that positive allometry is not necessarily indicative of sexual selection. The observed allometric diversity is consistent with the theoretical expectation that optimal allometry reflects net selection on trait size and body size, an ontogenetic resource-allocation trade-off between these traits, and genetic constraints. An unbiased empirical survey will advance our understanding of the factors-shaping static allometry.

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