

SHORT COMMUNICATION

Pitfalls in understanding the functional significance of genital allometry

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The male genitalia of arthropods consistently show negative static allometry (the genitalia of small males of a species are disproportionately large, and those of large males are disproportionately small). We discuss relations between the 'one-size-fits-all' hypothesis to explain this allometry and the regimes of selection that may be acting on genitalia. We focus on the contrasts between directional vs. stabilizing selection, and natural vs. sexual selection. In addition, we point out some common methodological problems in studies of genital allometry. One-size-fits-all types of arguments for negative allometry imply net stabilizing selection, but the effects of stabilizing selection on allometry will be weaker when the correlation between body size and the trait size is weaker. One-size-fits-all arguments can involve natural as well as sexual selection, and negative allometry can also result from directional selection. Several practical problems make direct tests of whether directional or stabilizing selection is acting difficult. One common methodological problem in previous studies has been concentration on absolute rather than relative values of the allometric slopes of genitalia; there are many reasons to doubt the usefulness of comparing absolute slopes with the usual reference value of 1.00. Another problem has been the failure to recognize that size and shape are independent traits of genitalia; rapid divergence in the shape of genitalia is thus not paradoxical with respect to the reduced variation in their sizes that is commonly associated with negative allometric scaling.

Introduction

Static allometry (the slope of a log-log regression of the size of a structure on body size) is an intraspecific measure of the proportional size of a particular body part in individuals that are in the same ontogenetic stage but have different body sizes. Studies of the morphological evolution of sexually selected traits, such as weapons and display structures, often attempt to explain how selection has shaped them, and static allometry (henceforth 'allometry') has been a useful tool in generating hypo-

theses about selection on morphology. Discussions of allometry have traditionally emphasized adaptive interpretations (Huxley, 1932; Petrie, 1988, 1992; Green, 1992; Bonduriansky & Day, 2003; Kodric-Brown *et al.*, 2006; Bonduriansky, 2007), although a few have proposed an important role for phylogenetic inertia (Lewontin, 1978; Gould & Lewontin, 1979) or other nonadaptive explanations (Bertin & Fairbairn, 2007). Linking allometry with selection is appealing, because allometry is one way to describe morphological form, and analyses of form in terms of adaptive function have a long, extremely successful history in biology. Recent attempts to link sexual selection and allometry have emphasized the balances between the costs of different proportional sizes of structures (in terms of building and

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maintaining them), and their benefits (in terms of future offspring) (Bonduriansky & Day, 2003; Kodric-Brown *et al.*, 2006; Bonduriansky, 2007).

Several lines of evidence favour the idea that the evolution of allometry can be understood in adaptive terms. Preconditions for selection to act on allometry are met: the relative sizes of different morphological traits are often at least partially uncoupled during development (Liu *et al.*, 1996; Arnqvist & Thornhill, 1998; Macdonald & Goldstein, 1999; Shingleton *et al.*, 2005); and ample genetic variation for allometric relations exists in natural populations (summaries in Schlichting & Pigliucci, 1998; West-Eberhard, 2003; also Frankino *et al.*, 2005). When the allometric relations of structures under sexual selection were compared among closely related species, they diverged at least as rapidly as many other traits (Baker & Wilkinson, 2001; Emlen *et al.*, 2005; Shingleton *et al.*, 2007), and different geographical populations of the same species diverged very rapidly with respect to allometry (Moczek & Nijhout, 2003).

One classic pattern in allometry is that traits under sexual selection tend to show relatively steep slopes (Huxley, 1932; Petrie, 1988; Kodric-Brown *et al.*, 2006). A recent survey of sexually selected traits revealed, however, a variety of allometric values, from negative to positive (Bonduriansky, 2007), and some models predict a mix of positive and negative allometry (Bonduriansky & Day, 2003). One strikingly consistent allometric pattern is the recently discovered tendency for the male genitalia of insects and spiders to show 'negative' allometry; compared with other structures, the genitalia of small-sized individuals are disproportionately large, and those of large individuals are disproportionately small (Eberhard *et al.*, 1998; Eberhard, in press a). Because of serious problems associated with determining absolute values of allometric slopes (see below), we will use the word 'negative' here to indicate comparatively low slopes (compared with other body traits), and not an allometric slope < 1.00 as has usually been the case. The 'one-size-fits-all' hypothesis (Eberhard *et al.*, 1998) attempted to explain the adaptive significance of this pattern of low allometric slopes in genitalia. It proposed that the low slopes might be due to the advantage to a male of having genital sizes that are appropriately adjusted to the most common size of females in the population, and that such size adjustments might improve male abilities to stimulate the female and thus gain under sexual selection by female choice (Eberhard *et al.*, 1998). An additional, nonexclusive possible advantage which emphasizes the possible role of natural selection rather than sexual selection is that these adjustments may facilitate precise mechanical fits between male and female genitalia that are needed to carry out sperm transfer (House & Simmons, 2003). There has been a recent flood of publications on the allometry of genitalia which highlight some difficulties associated with these types of study (summary Eberhard, in press a). The present note

clarifies interpretations of the one-size-fits-all hypothesis, and points out what we perceive to be some common methodological problems in studies of genital allometry and tests of the one-size-fits-all hypothesis, and how to avoid them.

Stabilizing and directional selection, negative allometry and one-size-fits-all

The possible roles of stabilizing and directional selection in explaining negative allometry, and their relation to the explanation offered by the one-size-fits-all hypothesis, were not discussed carefully in the original 1998 paper, and need further clarification. Although the one-size-fits-all hypothesis made no explicit statements about the form of selection on genitalia, stabilizing selection was implied in the sense of larger genitalia being favoured in males that might otherwise have especially small genitalia (i.e. males of small body sizes), and smaller genitalia being favoured in males that might otherwise have especially large genitalia (i.e. males with large body sizes). In the first place, however, the relationship between one-size-fits-all, stabilizing selection and selection for negative allometry is not simple. Stabilizing selection can produce a gradation of intensities of selection on allometry, depending on the allometric slopes and dispersions of points around these lines (Fig. 1). At one extreme, stabilizing selection will have no effect on allometry (Fig. 1e). Detecting selection on allometric values may thus be challenging. If the allometric slope of a trait is already low because of past selection (Fig. 1c), then present-day measurements of selection may detect only weak or no selection. Experimental modifications or comparative studies may be needed to reveal the presence of selection. The possibility that allometric slopes are very low is not trivial for animal genitalia: for instance, 31 (41.3%) of 75 values for genital structures in Eberhard *et al.* (1998) did not differ significantly from 0. As the developmental coupling between genital size and body size becomes weaker, stabilizing or directional selection on genital size will have less effect on genital allometry.

Secondly, as illustrated in Fig. 2, directional selection, as well as stabilizing selection, can also result in negative allometry, and there is no intrinsic contradiction between directional selection and negative allometry. For instance, negative allometry could result from directional selection if greater relative size of a trait is more strongly favoured in small individuals than in large individuals (Fig. 2a). If differences of this sort in the intensity of selection are caused by differences in male abilities to fit with females or to stimulate them more effectively, then one-size-fits-all types of arguments could be involved. An example of the potential importance of differences in the intensity of selection is the positive relationship between the degree of polygyny and the degree of sexual dimorphism in birds (e.g. Dale *et al.*, 2007). In sum, stabilizing

Fig. 1 Relations between stabilizing selection and allometry. If stabilizing selection occurs on a trait (dotted arrows in a), it can have different effects on selection favouring negative allometry, depending on the slopes and dispersion of points (b–e). If the slope of the relation between trait and body size is steep and there is little dispersion around the line (b), stabilizing selection (dotted arrows) will strongly favour negative allometry. If the slope of the relation between trait and body size is low (c) or if there is a large amount of dispersion around the line (d), stabilizing selection (dotted arrows) will only weakly favour negative allometry. If the relation between trait and body size is very weak or nonexistent (e), stabilizing selection will not favour any particular allometric relation.

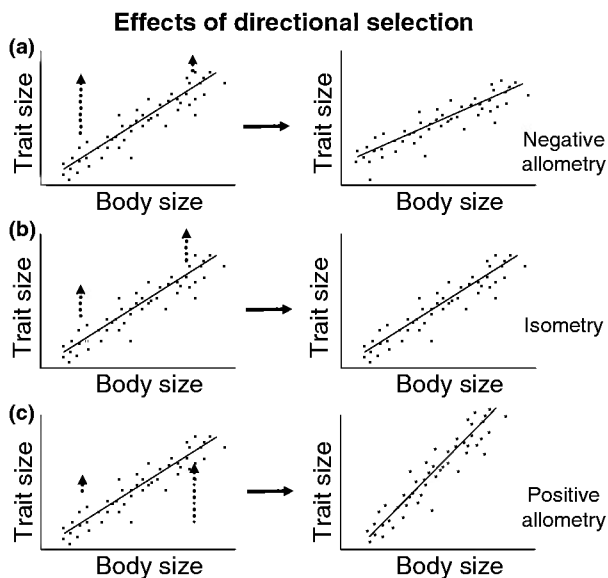
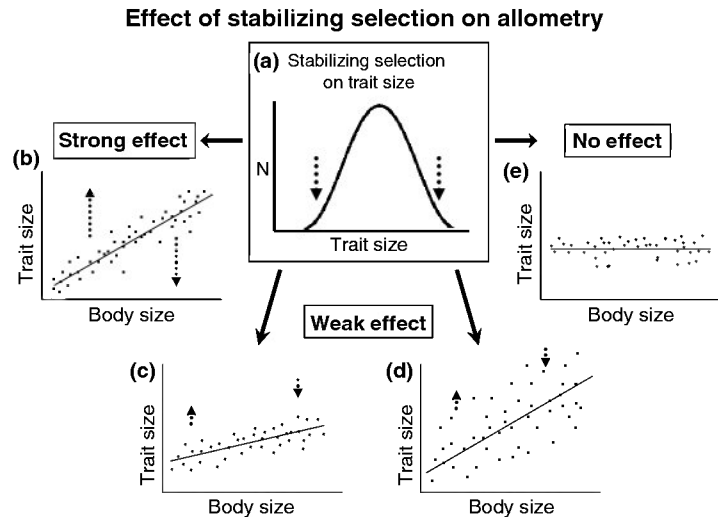


Fig. 2 Relations between directional selection and allometry. Diagrammatic representations show how variation in the intensity of directional sexual selection favouring greater trait size at different body sizes can favour the evolution of different types of allometry. The lengths of the vertical dotted arrows indicate the magnitudes of relative selective advantage enjoyed by individuals (dots in the graphs) with a relatively large size of the trait (e.g. individuals above the regression line). When the intensity of selection favouring larger trait is greater for individuals with small rather than large body sizes (a), negative allometry will be favoured; when the intensities are equal for large and small individuals (b), isometry will be favoured; and when the intensity is greater for large than small individuals (c), positive allometry will be favoured.

selection does not necessarily result in selection for negative allometry in all circumstances, more than one type of selective regime can result in any particular type

of allometry, and one-size-fits-all arguments can be extended from their original implication of stabilizing selection to include variable intensities of directional selection to explain negative allometry.

These conclusions are very different from saying that directional selection on a trait is incompatible with a one-size-fits-all explanation of negative allometry for that trait, as has been claimed (Bertin & Fairbairn, 2007). They do agree, however, with the basic point (Bonduriansky & Day, 2003; Bertin & Fairbairn, 2007) that the form of sexual selection on genitalia can be difficult to infer from observations of patterns of allometry (Bertin & Fairbairn, 2007). Nevertheless, particular patterns of allometry do predict certain forms of selection on the relative sizes of traits, and exclude other forms of selection. For example, an observation of negative allometry predicts selection of the types c, d or g mentioned in Fig. 3. Similarly, an observation of positive allometry predicts a or e, and isometry predicts either b or f.

To test for directional as opposed to stabilizing selection (e.g. c and d vs. g in Fig. 3), one could test whether an observed pattern of allometry is associated with the predicted types of selection in natural populations, or perform experimental studies focusing more specifically on the use and function of genitalia. However, there are some important methodological considerations. First, as body size-related variation in the intensity of directional selection can affect whether the expected outcome is positive allometry, negative allometry or isometry (Fig. 1), studies would need to test for body size-related variation in the intensity of selection on trait size. Simply testing for stabilizing or directional selection is not sufficient. Secondly, tests for stabilizing selection based on within-population variation may be especially likely to suffer from type II errors, i.e. there is a risk that tests will fail to detect stabilizing selection, even when it is

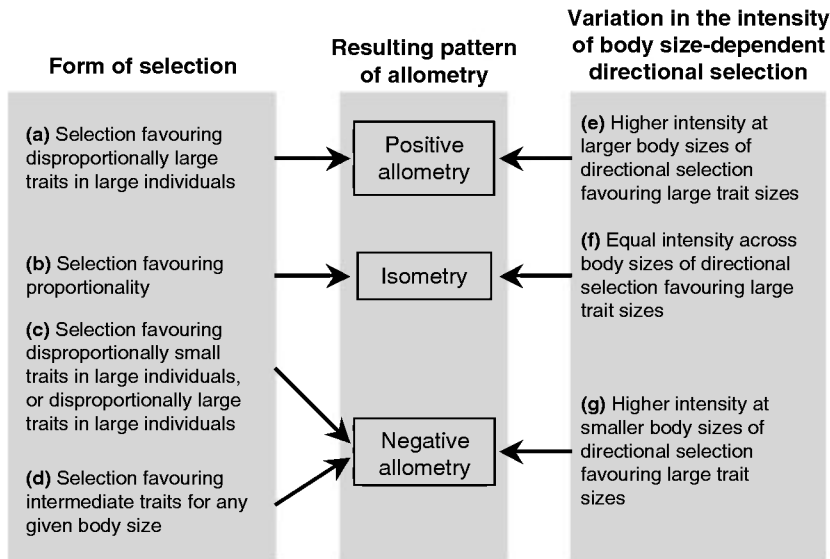


Fig. 3 Various forms of selection can lead to positive allometry, isometry or negative allometry. These include selection favouring some body designs over others (a–d on the left-hand side), or body size-dependent differences in the intensity of directional selection (e–g on the right-hand side). Observation of a particular type of allometry suggests the types of selection which may be occurring.

present. This is because the ranges of variation seen over historical as opposed to recent time scales may be quite different. If, for example, strong selection has resulted in a given range of variation in the size of a trait, a test for size effects within the current range may not reveal the strong selection that occurs outside the range of sizes that are presently available. The textbook definition of strong stabilizing selection is a case in which the change in fitness summed over the range of a trait equals zero, because the trait is at an adaptive peak (e.g. see Fuller *et al.*, 2005; Kokko *et al.*, 2006). Thus an observation that fitness is not affected over the natural range of variation in a trait could result from strong selection – and yet be interpreted as lack of selection on the trait. Experimental modifications or comparative studies may thus be needed to test for the presence of selection.

Genitalia, like many other complex traits, may often be selected as a whole, not trait-by-trait; this is especially true when the aspects of the traits that are measured are chosen on the basis of ease of measurement (as is usually the case), rather than by identification of those aspects that are the actual targets of natural and sexual selection (e.g. Ryan & Rand, 2003; Brooks *et al.*, 2005). This raises the issue of testing for multivariate stabilizing selection, which may often require extending the traditional method of testing for linear and nonlinear partial regression coefficients of fitness on measured traits to include canonical analysis of fitness surfaces (see Lande & Arnold, 1983; Phillips & Arnold, 1989; Blows & Brooks, 2003; Brooks *et al.*, 2005; Blows, 2007). Canonical exploration of fitness surfaces may be especially relevant if one is interested in demonstrating the *absence* of stabilizing selection.

There is an additional important concern for testing predictions regarding the form of selection inferred from allometric patterns. Observed patterns of allometry, such

as the widespread finding of negative allometric values for genitalia, provide information about the action of *all* sources of selection acting on genitalia. However, studies attempting to measure selection often rely on proxies for fitness, which may often reveal the action of only some sources of selection. For instance, directional sexual selection acting on male genital structures that nevertheless show low allometric slopes has been found in three insect species: the genital flagellum of the beetle *Chelymormpha alternans* (Rodriguez *et al.*, 2004); the ‘external’ genitalia of the water strider *Aquarius remigis* (Bertin & Fairbairn, 2007); and four genital sclerites in the beetle *Onthophagus taurus* (House & Simmons, 2005a). In the first two species, the directional selection that was measured favoured larger sizes; in the third it favoured larger size in two sclerites and smaller size in the others. It is possible that different intensities of directional selection in these species result in low allometric slopes (Fig. 2); but it is also possible that directional selection on genitalia may be countered by other selective pressures that favour genitalia of a particular size. For instance, House & Simmons (2003), using a natural selection version of a one-size-fits-all argument, argued that the negative genital allometry in of the beetle *O. taurus* may be the result of a balance between selective forces:

Natural selection should favour structures of an appropriate size and shape to facilitate the basic mechanics of coupling and sperm transfer. Directional sexual selection via differential fertilization success has the potential to elaborate on these basic structures, leading to variation in genital morphology, but only to the extent that the mechanics of copula are not compromised (p. 453).

Whether or not such balances in selective forces actually occur remains to be tested, but the presence of undetected sources of selection is likely when proxies for

fitness are used. For example, in the studies of paternity determination in all three species, sperm precedence was measured only with certain numbers of copulations that were separated by certain time periods (Vermette & Fairbairn, 2002; House & Simmons, 2003; Rodriguez *et al.*, 2004). Both of these factors are known to have important effects on sperm usage patterns in insects (Simmons, 2001).

Studies of *A. remigis* are particularly extensive, and have been used to support particularly strong conclusions regarding the impossibility of inferring one-size-fits-all type arguments from genital allometry (Bertin & Fairbairn, 2007). However, the data used to support these conclusions are not completely convincing. There is reason to doubt the precision of documentation of directional selection in mating success in *A. remigis* (Bertin & Fairbairn, 2005) that was said to argue against one-size-fits-all ideas (Bertin & Fairbairn, 2007). Possible post-copulatory biases in paternity on the basis of genitalia were ignored, as male 'mating success' was measured in the field as 0 for unpaired males and 1 for paired males. This binary proxy for reproductive success assumes that all matings are of equal reproductive value to a male. Although a general positive relationship has been found under certain conditions between this proxy for mating success measured this way and paternity, there is abundant reason to suppose that the assumption that all matings are of equal value is often wrong, because of sperm competition and cryptic female choice (Parker, 1970; Eberhard, 1996; Birkhead & Møller, 1998; Simmons, 2002), especially with respect to male genitalia (Eberhard, 1985, 1996; House & Simmons, 2003; Wenninger & Averill, 2006), and specifically in water strider genitalia (Arnqvist & Danielsson, 1999; Danielsson & Askenmo, 1999). Binary scores of mating success in *A. remigis* may also hide other important variation in fertilization success, as matings in this species that last under ca. 15 min do not result in sperm transfer (Rubenstein, 1989; Campbell & Fairbairn, 2001). Thus, a male collected *in copula* and scored as 1 for mating success may have been in the process of failing to transfer sperm. Selection coefficients also vary over space and time on the size of the male's body and his genitalia (Ferguson & Fairbairn, 2000), the environmental factors that determine the cause (but not the form) of selection vary (on cold days, competition between males was the main cause of variation in mating frequency, whereas on warm days male-female conflict was also important) (Sih *et al.*, 2002), and the form of selection varied when different proxies were used to estimate fitness (use of mating success suggested directional selection on male body size, whereas including prereproductive survival and reproductive longevity suggested stabilizing selection on male body size – see figs 1 and 2 in Preziosi & Fairbairn, 2000). There are still other complications for deducing the strength of sexual selection from data of this sort. The relationship between

mating length after the first 15 min and paternity may not be linear, as is assumed by this technique for estimating paternity from mating success; matings involving larger females carrying more mature eggs tend to last longer (Weigensberg & Fairbairn, 1996; Campbell & Fairbairn, 2001). Thus, a long mating may be disproportionately more profitable to a male. Also, a second male's sperm precedence increases with the ratio of the length of his mating to that of the first male's (Rubenstein, 1989).

The important general point is that it is very difficult to find biologically realistic proxies for sexual selection. Precise measurements of sexual selection in the field are extremely difficult to obtain, even in a well-studied species like *A. remigis* (and, of course, studies of sexual selection under the artificial conditions of captivity are unlikely to reveal the historical selection that resulted in current genital designs; Eberhard, in press b). It will be very difficult indeed to convincingly test the prediction of particular balances between stabilizing and direct selection on the size of genitalia that are expected under selection for negative allometry. Another general consequence of these comments for studies of genital allometry is that the relatively negative slopes that are common in genitalia are not in conflict with the possibility that the genitalia are under directional selection, even if the proxies used to measure such directional selection are adequate.

Methodological problems

The (non)significance of a slope of 1.00

A common point of departure in discussions of static allometry is that a slope of 1.00 is assumed to characterize traits under natural selection. That is, the proportion of the body dedicated to wings, legs, eyes, etc. is expected to be the same in large individuals as in small individuals. The emphasis on 1.00 is such that allometry is sometimes reported simply in terms of positive (> 1.00) and negative (< 1.00), with a slope significantly > 1.00 being used as a litmus test for sexual selection (Green, 2000; Kelly, 2004; Tasikas *et al.*, 2007). There are several reasons to think that this emphasis on the precise value 1.00 is probably misplaced.

The forms of cost and benefit curves for different designs of a structure can vary for different habitats and body sizes (Bonduriansky & Day, 2003; Dial *et al.*, 2008). For example, two species of the water strider genus *Aquarius* have larger body sizes and proportionally longer middle and hind legs (involved in locomotion) than the corresponding legs of seven species of *Gerris*; the *Aquarius* species inhabit areas with more disturbed water surfaces, where proportionally longer legs are thought to be advantageous (Klingenberg & Zimmermann, 1992). Thus the value 1.00 is not necessarily always expected, even under natural selection.

Environmental variation can also influence sexual selection, and benefit curves for genitalia can also vary with habitat differences, as in greater relative gonopod length in the poeciliid fish at sites where dangerous predators are present (Kelly *et al.*, 2000; Jennions & Kelly, 2002), or greater relative penis length in barnacles where wave action is less intense (Neufeld & Palmer, 2008). Population density could also affect benefits by altering the chances of males meeting and competing directly, or females meeting or mating with multiple males and exercising female choice (Oosthuizen & Miller, 2000); this could affect selection on genitalia (Wang *et al.*, 2008). Smaller males may have proportionally less material reserves with which to construct sexually dimorphic structures, so the construction cost curves could vary across the range of body sizes (Petrie, 1988, 1992; Green, 1992), or across different environments with different resource availability.

Benefit curves could also be affected by other aspects of the same individual's phenotype, such as behaviour. For instance, the advantage of relatively longer gonopodia in poeciliid fish would increase in smaller individuals if these individuals also had a greater propensity to execute successful sneak attack copulations (as opposed to mating attempts preceded by courtship), or if females were less likely to accede to mating attempts following courtship from smaller males; these correlations would favour lower allometric slopes for gonopod length. Behaviour can also affect biomechanical details of physical engagements, and thus the costs of structures that are able to function in these circumstances. In an example from animal weapons, the wrestling fights of antelopes produce less mechanical stress on their horns than the more forceful uses of horns in goats and sheep (Kitchener, 1985), and thus entail lower costs for effective weapons in antelopes.

Still another problem concerns interpretations based on whether or not male structures touch the female during copulation. A simple interpretation of the one-size-fits-all hypothesis would suppose that only those portions of the male genitalia that actually touch the female would be likely to be under post-copulatory sexual selection, and, conversely, that portions that do not contact the female would not be under post-copulatory sexual selection (Bertin & Fairbairn, 2007). This interpretation fails to recognize, however, that different portions of the male's body are physically and functionally interconnected. For instance, the muscles that move more distal portions of a male's genitalia often reside in more basal segments (Snodgrass, 1935; Chapman, 1998). The size of a portion of the genitalia that remains outside the female during copulation may influence both the kinds of movements made by structures that do contact her body, and the power that they exert. To a first approximation, shorter intromittent portions are likely to require smaller amounts of muscle, leading to reduced sizes of more basal, nonintromittent portions. Detailed

understanding of internal functional morphology can be necessary to make confident interpretations of some allometric patterns.

There are several additional, perhaps more important, practical reasons to de-emphasize the value 1.00. The two regression techniques most frequently used to measure allometry are ordinary least squares (OLS) and reduced major axis (RMA), which give different slopes with the same data. OLS regressions generally give lower slopes than RMA regressions; this was true, for instance, in 41 of 42 pairs of regressions in Simmons & Tomkins (1996). There is controversy regarding which technique is more appropriate, and there may not be any single answer for all cases (Eberhard *et al.*, 1999; Green, 1999; Palestini *et al.*, 2000; Cuervo & Møller, 2001; Bernstein & Bernstein, 2002; Kato & Miyashita, 2003; Ohno *et al.*, 2003; Hosken *et al.*, 2005; Warton *et al.*, 2006; Warne & Charnov, 2008), and there are strong arguments against each. It is thus not clear whether the 1.00 given by OLS or by RMA should be the point of reference.

Another problem is that the choice of the variable used to estimate body size (total body length, prothorax length or width, elytrum length and femur length have been used in different insect studies) will influence the values obtained (Kratovichil *et al.*, 2003). Perhaps the best body size indicator is some composite measure like a principal components variable that combines many different size measures (Uhl & Vollrath, 2000; Ohno *et al.*, 2003; Pizzo *et al.*, 2006), but the relative contributions of different body parts and shape will vary in different species, rendering inter-specific comparisons of absolute values difficult to interpret. Use of weight measurements is probably not a good idea, at least in some groups with large seasonal and life stage variations in weight (Miller & Burton, 2001).

Different body size indicators can give different allometric slopes. For instance, in the mosquito *Aedes aegyptii* the slopes for two different genital measures, when regressed on wing length instead of leg length, were similar but not identical: 0.31 vs. 0.34, and 0.38 vs. 0.32 (Wheeler *et al.*, 1993). Differences can occur even with a body size indicator that combines several different dimensions. Regression slopes using the centroid for elytral measures vs. the centroid for prothoracic traits as an indicator of body size in two congeneric species of beetles were 1.03 vs. 0.93 for the head and 0.44 vs. 0.35 for the genitalia in one species, and 0.33 vs. 0.27 for the head and 0.28 vs. 0.23 for the genitalia in the other (Pizzo *et al.*, 2006).

Measurement errors can also result in appreciable differences in allometric slopes. Means of allometric slopes calculated on the basis of repeated measurements of 14 different body parts in two species differed by a median of only 5.3%, but in three of the 14 they differed substantially (> 25%) (Eberhard *et al.*, 1998).

Sharp geographical variations in allometric slopes for given structures also occur in some species, providing

further reason to doubt the usefulness of absolute values of allometric slopes. For instance, slopes were measured in six different populations of the water strider *A. remigis* in California (Bertin & Fairbairn, 2007). When comparing slopes between different geographical populations of *A. remigis*, the largest slope was 214%, 178% and 198% of the smallest slope for three external genitalic traits; 167%, 180% and 193% for internal genitalic traits; and 163% and 129% for somatic traits. Two beetle species and a fish also showed substantial differences between different populations (Kelly *et al.*, 2000; Bernstein & Bernstein, 2002; Kawano, 2002). The possible significance of these tantalizing differences remains to be determined.

Finally, there is the empirical fact that some nongenital structures that are not sexually dimorphic and with no apparent relation to sex, and which would thus theoretically be expected to show allometric slopes close to 1.00, nevertheless have values quite different from 1.00 (e.g. Schulte-Hostedde & Alarie, 2006). Even the same nonsexually selected trait sometimes has quite different allometric slopes in different species. For instance, elytron length scales more steeply on pronotum width in the firefly *Photinus pyralis* (1.62) than in *P. macdermotti* (0.80), presumably because individuals of *P. pyralis* fly longer distances (Vencl, 2004). A particularly dramatic example of intraspecific variation involves the internal epipharyngeal structures of the dung beetle *O. taurus*. Seven external body traits of this species had moderate slopes in both males (0.59–0.91) and females (0.79–1.29), but four epipharyngeal traits had extremely low slopes in both males (0.05–0.30) and females (0.04–0.39) (Palestrini *et al.*, 2000). In addition, some nongenital structures that are probably not under sexual selection show positive allometry, such as the mandibular palps of some *Scathophaga* flies (Hosken *et al.*, 2005) and the middle legs of male and female *A. remigis* water striders (Bertin & Fairbairn, 2007).

Several of these problems can be avoided or ameliorated by comparing the allometric slopes of different structures of the same individuals that are and are not thought to be under sexual selection with each other, instead of executing statistical tests of differences with 1.00, as has been common (Schmitz *et al.*, 2000; Miller & Burton, 2001; Jennions & Kelly, 2002; Ohno *et al.*, 2003; Mutanen & Kaitala, 2006; Mutanen *et al.*, 2006; Bertin & Fairbairn, 2007; Kinahan *et al.*, 2007). Using the same regression technique and the same body size indicator to obtain the slopes of all structures that are compared can probably largely correct for the possible peculiarities of the variable chosen as an indicator of body size, and of the regression technique (Eberhard *et al.*, 1998, 1999; Cuervo & Møller, 2001; Bernstein & Bernstein, 2002). Comparisons of this sort should work better when many rather than only a few structures that are not thought to be under direct sexual selection are used (most studies to date are inadequate in this respect), and using median

rather than mean values of their slopes in comparisons with genital slopes. This would reduce the chances of being misled by atypical values of any particular trait. When multiple slopes have been determined for both genital and nongenital traits, their means can be compared (Uhl & Vollrath, 2000). Inclusion of alternative slopes calculated using alternative variables such as body size indicators can also help avoid possibly atypical values. Similarly, uncertainty regarding the best regression technique can be avoided by reporting values for both. In practice, conclusions based on intraspecific comparisons between genital and nongenital structures have proved to be little affected by either the regression technique or the use of different body size indicators (Eberhard *et al.*, 1999; Funke & Huber, 2005). Discussions in the literature have concentrated on absolute values of slopes, and are probably not very relevant to comparisons between slopes.

The limited usefulness of coefficients of variation

Many studies of genital allometry report the intraspecific coefficient of variation (CV) in the sizes of a genital structures (25 of 37 studies cited in W. Eberhard, unpublished data). The CV is sometimes interpreted as an indicator of the opportunity for selection to act, with the supposition that higher coefficients of variation are associated with sexual selection (Pomiankowski & Møller, 1995; House & Simmons, 2003). Unfortunately, the CV conflates two biologically different phenomena – the allometric slope and the dispersion of points around this slope. Sexual selection could act on differences in either of these variables (or both), and is not necessarily associated with steep slopes (Bonduriansky & Day, 2003; Bonduriansky, 2007). Eberhard *et al.* (1998) suggested that alternative measures of variation be used in allometry studies that specifically characterize the dispersion of points around a line. These included CV' (the coefficient of variation that y would have if x were held constant) and the standard error of estimate. Such statistics have seldom been mentioned, however, in subsequent publications (except in Palestrini *et al.*, 2000; Peretti *et al.*, 2001; Ohno *et al.*, 2003; Tatsuta *et al.*, 2007).

One-size-fits-all vs. one-shape-fits-all

Size and shape are sometimes not distinguished clearly in discussions of allometry (Bonduriansky, 2007), and some authors have puzzled over the 'paradox' of rapid interspecific divergence of genital morphology in spite of low intraspecific variation (Ramos *et al.*, 2005; Bertin & Fairbairn, 2007). Although changes in the relative size of a structure can sometimes be related to changes in its shape (Fairbairn, 1992), size and shape are two different variables that should be evaluated independently, and it

cannot be assumed that patterns of shape variation will reflect those of size. The high frequency of low size variation that has been reported for male genitalia in insects and spiders does not imply that these structures are not variable in shape. It is clear from the taxonomic literature that rapid interspecific divergence often occurs in the shapes of male genitalia rather than in their relative sizes (taxonomists seldom even mention relative size). Intraspecific analyses of size and shape led to the same conclusion in a beetle and a grasshopper (Pizzo *et al.*, 2008; Song & Wenzel, 2008). Thus, rapid divergence in the shape of genitalia is not paradoxical with respect to negative allometric scaling or reduced variation in their size.

Uncoupling between size and shape in genitalia is suggested by data on condition dependence, and quantitative trait locus analysis of genital development. Arnqvist & Thornhill (1998) assessed the effects of variations in resource availability on the size and shape of various morphological structures, including male genitalia, of the water strider *Gerris incognitus*. The effects of food stress were most pronounced for body size, whereas genital size was less affected and genital shape was not affected. In *Drosophila*, only one locus of 11 affected both size and shape of the genital lobe in a QTL analysis, suggesting independent developmental controls for these traits (Macdonald & Goldstein, 1999). Further, a study of aedeagus size and shape in two sister species of *Drosophila* found species-specificity in the relationship between size and shape (Soto *et al.*, 2007): size and shape were strongly correlated in *D. buzzatii*, but not in its sister species, *D. koepferae*. Size and shape can be analysed independently using methods such as elliptic Fourier analysis which can factor out size variation, or by evaluating the loadings of different variables in a multivariate principal components analysis.

Among studies analysing variation in both the size and shape of genitalia, some have found variation in both variables (Inger & Marx, 1962; Goulson, 1993; Miller & Burton, 2001), whereas others found evidence for variation in shape only (Garnier *et al.*, 2005; Mutanen & Kaitala, 2006; Mutanen *et al.*, 2006). There are several reasons to suggest independent selection pressures on size vs. shape of genitalia. Two studies found evidence for mosaic evolution of genitalic structures, suggesting that selection does not operate on all parts of genitalia in the same way (Song & Wenzel, 2008; Werner & Simmons, 2008). Shape and size variations of various aspects of the male genitalia are likely to have different effects on the mating processes with regard to the diverse functions attributed to the male genitalia (sperm removal, spermatophore transfer, holding the female, stimulating her, etc.). For example, detailed studies of the functional morphology and genetics of male and female genitalia in *O. taurus* found that some aedeagal sclerites function as holdfast devices whereas others work together to form

and deliver the spermatophore (Werner & Simmons, 2008); genetic correlations among the sizes of those sclerites operating as a unit to form and deliver the spermatophore were positive, whereas those associated with sclerites that operate as independent holdfast or stimulatory structures were negative (House & Simmons, 2005b). These data support the mosaic evolution of male genitalia, and suggest different possible effects of variation in size vs. variation in shape during copulatory interactions. In sum, genital size and shape are not necessarily correlated, highlighting the necessity of treating these variables independently in studies of genital evolution.

Concluding remarks

Male genitalia differ from many other sexually selected structures in often showing relatively low allometric slopes (Eberhard *et al.*, 1998; Eberhard, in press a). 'One-size-fits-all' type hypotheses, which are based on possible advantages of the male's making a precise fit with the female and can involve both natural and sexual selection, may account for this trend. Future studies to test predictions of these ideas will need to take into account the intrinsic limitations of attempts to document selection, and the importance of relative rather than absolute measures of allometric slopes. Measurements of genital structures whose probable functions are known are particularly desirable.

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