

# STATIC ALLOMETRY AND ANIMAL GENITALIA

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**A survey of 117 species of arthropods and 17 species of vertebrates showed a strong trend for male genitalia to have relatively low static allometric values. This trend contrasts with the allometry of other structures under sexual selection, which usually show steep allometric slopes. The trend to low allometric genital values is less consistent in mammals than in arthropods. Data not in accord with the previous the “one-size-fits-all” explanation for low allometric slopes in genitalia, which was based on sexual selection by female choice, suggest a more general version that includes both natural selection and sexual selection, and involves both mechanical fit and stimulation. Less-complete data on the female genitalia of arthropods suggest a trend to similar low allometric slopes, and may also be explained by mechanical fit and stimulatory one-size-fits-all arguments.**

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Static allometry (the slope of an intraspecific log–log regression of the size of a structure on body size—henceforth “allometry”) is a measure of the proportional sizes of a particular body structure in a population of individuals at the same ontogenetic stage but with different body sizes. A slope (herein “allometric value” or “allometric slope”) of 1.0 (“isometry”) indicates that the structure has the same proportional size in individuals of different body sizes; a slope greater than 1.0 indicates that larger individuals have disproportionately larger structures compared with smaller individuals (“positive allometry”), and a slope of less than 1.0 (“negative allometry”) indicates that the structure is disproportionately larger in smaller individuals than in larger individuals. Many structures that are under sexual selection have allometric slopes  $> 1.0$  (Huxley 1932; Gould 1974; Petrie 1988; Kodric-Brown et al. 2006), whereas other body structures often have values that approximate 1.0. This association of sexual selection with positive allometry has been perceived to be so strong that positive allometry is sometimes used as a litmus test for sexual selection (Green 2000; Kelly 2004; Tasikas et al. 2008). The absolute value 1.0 is not an entirely reliable indicator of the existence or absence of sexual selection, however (Eberhard et al., in press), so I will use the terms “positive” and “negative” allometry in a comparative sense, to indicate slopes that are, respectively, greater than or less than the median slopes of other “control” structures of the same animals (nongenital structures that are not thought to be under sexual selection).

Although it is generally thought that male genitalia often evolve under sexual selection (Eberhard 1985, 1996, in press; Hosken and Stockley 2003), it appears that the allometric slopes of male genitalia are usually negative rather than positive. Low allometric slopes in genitalia were first noted by taxonomists (e.g., Byers 1990; Coyle 1985, 1995); the first systematic quantitative studies were by Wheeler et al. (1993), Johnson (1995), and Eberhard et al. (1998). The objective of the present article is to summarize a recent flood of data on genital allometry, to discuss possible explanations for their general patterns, and to discuss their implications for previous hypotheses to explain genital evolution.

Male genitalia in animals with internal fertilization show an unusual evolutionary pattern of sustained, rapid divergence (Eberhard 1985, in press). One commonly cited hypothesis to explain this pattern supposes that male genitalia are used as weapons in male–female battles to control copulation, sperm transfer, and sperm use that impose reproductive costs on females (Alexander et al. 1997; Arnqvist and Rowe 2005). The other most commonly cited hypothesis holds that they are often used as courtship or signaling devices (Eberhard 1985, 1996; Hosken and Stockley 2003). The allometric trends of genitalia are useful in evaluating these hypotheses, because the competing theories make different predictions. Both the theoretical reasons to expect positive allometry in weapons (Clutton-Brock 1982; Green 1992), and the extensive data documenting this trend in weapons (summaries in

Kodric-Brown et al. 2006; Kawano 2006) give reason to expect that if male genitalia were used as weapons in male–female battles, they would tend to show positive allometry. For instance, clasping the external surface of the female is one of the most common functions of insect genitalia (this was the function in 39% of 105 attributions of function in a review of the functions of genital structures in 43 species in 22 families of Diptera; Eberhard 2004). Clasping opponents is a common function of beetle horns (reviewed by Emlen in press), and they very uniformly show positive allometry (Kawano 2006). The frequent use of brute force in resolving precopulatory male–male conflicts, and the consistent advantages of large size in such contexts, indicate that it is reasonable to expect that an appreciable portion of potential male–female genital conflicts, if they exist, would be resolved by force. In sum, male–female conflict should result in at least a trend toward positive allometry in genitalia. In contrast, no trend toward positive allometry is expected under the courtship hypothesis, except if females use male genitalia to judge male size (Eberhard et al. 1998).

## Methods

A computer search based on citations of previous work (starting with Eberhard et al. 1998) was used to accumulate published data on genital allometry. Results of alternative regression techniques were noted when available (of the two most common techniques, reduced major axis slopes were consistently slightly higher than ordinary least squares slopes).

## Results

Data on 239 male genital traits in 135 species in 52 families and 15 orders are summarized in Appendix 1. Most species are arthropods (102 insects, 12 spiders, 1 scorpion, and 2 crustaceans). Different methods of summarizing these arthropod data all lead to the same clear conclusion: male genitalia have relatively low allometric slopes. A total of 196 (or 194 using RMA values rather than OLS values in those species in which both are available) of the 206 genital structures in arthropods show a lower slope than the median slope for nongenital traits of the same species that are thought not to be under sexual selection (hereafter “nongenital traits”). Analysis at the level of species yields the same trend: in 108 of 113 species the median genital slope is lower than the median nongenital slope. These analyses do not include corrections for phylogeny; the usually high evolutionary lability of genital morphology probably makes such corrections unnecessary or perhaps even counter-productive (Losos 1999).

The most dramatic exception, a scorpionfly, may “prove the rule”: the steep slopes of two genital processes (and their apparent intrasexual dimorphism) may be associated with their

very atypical use as weapons in male–male battles (Johnson 1995). Female genitalia show a similar trend to negative allometry (Appendix 2). In 10 species of insects and spiders, 16 of 16 slopes of female genital structures are lower than the median slope of nongenital structures of the same species. In all 10 species the median genital slope is lower than the median nongenital slope.

The sample of male vertebrates is small (17 species, several with only incomplete data), and the data in Appendix 1 show a mix of contrasting trends. Some have very steep slopes. Of 20 vertebrate genital structures, six have slopes higher than any of the 205 slopes measured in the male genitalia of the arthropod species. In four species the median genital slope is greater than any of the 205 slopes in arthropods. In five of six vertebrate species with sufficient data, the median genital slope is higher than the median nongenital slope, as compared with only five of 113 arthropod species ( $P = 0.0002$  with Fisher’s exact test). Thus although the sample is small, vertebrates seem to tend to have steeper genital allometries than arthropods.

This trend is not consistent, however. The slopes for mature, territorial males (males  $\geq 8$ -year old) of the cape fur seal are all  $< 0.80$  (Oosthuizen and Miller 2000). Slopes were said to be low in three rodent species: “baculum length appears to be unrelated to adult body size both among related taxa and among individuals of a single population” (Patterson and Thaler 1982, p. 5), but the allometric values calculated from data read from their graphs varied sharply (0.43, 0.94 and 1.61). Penis length in humans (not included in Appendix 1 because allometric slopes have apparently not been determined) is also apparently only weakly correlated with body size, if at all (Shah and Christopher 2002; Spyropoulos et al. 2002; Awwad et al. 2005; Orakne et al. 2006), as is typical of many arthropods with low slopes (Eberhard et al. 1998); there is some controversy, however (Ponchiatti et al. 2001, Mehraban et al. 2007, Promedu et al. 2007). No measurements of female genital allometry are available for any vertebrate species.

The only other class for which I found data is Mollusca (one species). These data are difficult to interpret, as they concern soft, internal structures, and values (even those of the same nongenital trait) vary widely (Bamminger and Haasse 2000).

Many studies (25 of 37) reported the intraspecific coefficient of variation (CV) in the sizes of genital structures. Genital CV values were usually lower than nongenital CV values in arthropods; the median genital CV was lower than the median nongenital CV in 67 of 77 arthropods and in 70 of 94 species in all. 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 and Møller 1995; House and Simmons 2003; Vencel 2004). Unfortunately, the CV conflates two biologically different phenomena—the allometric slope, and the dispersion of points around this slope (Eberhard et al. 1998); for a consistent amount of dispersion, a

steeper slope will result in a higher CV. Sexual selection could act on genetic variation that leads to differences in either of these variables (or both), and it is not necessarily associated with steep slopes (Bonduriansky and Day 2003; Bonduriansky 2007). Alternative measures of variation can be used to characterize this dispersion, such as CV' (the coefficient of variation that y would have if x were held constant), and the standard error of estimate (Eberhard et al. 1998). Such statistics were included in only a few publications, all of which concerned arthropods (Eberhard et al. 1998; Palestini et al. 2000; Peretti et al. 2001; Ohno et al. 2003; Tatsuta et al. 2007). These values do not seem to differ in genitalia as compared with nongenital structures: the median measure of dispersion of genital values around the allometric line was lower than the median measure of dispersion of nongenital values in 10 of 24 species ( $\chi^2 = 0.67$ ,  $df = 1$ ,  $P > 0.30$ ). Thus the overall trend toward lower CV values in arthropod genitalia probably results from their lower allometric slopes.

## Discussion

The most certain trend in genital allometry, with data now available for more than 100 species, is that the male genitalia of insects and spiders tend to show negative allometry. The consistency of the trend to low slopes in the genitalia of insects and spiders is especially impressive given the multiple reasons to expect variation in the absolute values of allometric slopes of genital and nongenital structures (Eberhard et al., in press), and the fact that nearly all genital structures that have been measured were chosen for ease of measurement and in ignorance of their functions. The data on vertebrates are less numerous, so their trends, which seem to be different and perhaps more mixed, are less certain. The first sections of the discussion will treat the strong, more certain trend in arthropods. Possible differences with vertebrates are discussed at the end.

### SIGNALING DEVICES: TACTILE SIGNALS AND ALLOMETRY

In contrast with signals in other modalities, the stimuli perceived by the receiving individual will be strongly influenced by the physical size of the receiver when those stimuli are tactile. The proportion of a female's body that is contacted by a tactile signaling device of a given male will be larger when the female is smaller. The original "one-size-fits-all" argument (Eberhard et al. 1998) proposed that if it is selectively advantageous for the male to contact particular portions of the female (e.g., contact certain receptors) to obtain the desired female response, or that the size of the male signaling device relative to that of the female be constant (even though particular female receptors are not consistently contacted), then some "standard" size of male stimulating device is expected. Presumably this size would usually be one that is ap-

propriate for the greatest number of females (probably females of approximately mean size). This could result in selection favoring relatively low allometric slopes in male structures that are used to deliver contact stimuli.

This peculiarity of contact displays is important for genitalia because, in contrast to many other sexually selected signaling traits, male genitalia probably usually stimulate the female by direct contact. Selection favoring a "standard" male genital size could thus favor negative genital allometry. If the exact site of male contact with the female varies, as in the male genital clasping devices of sepsid flies (Eberhard and Pereira 1996) (and perhaps many others), this argument would not apply unless the females are able to deduce the male's genital size (e.g., by sensing the distances between different points of contact) and prefer a particular male size.

### ARE THE LOW ALLOMETRIC SLOPES FOR GENITALIA COUNTER TO PREDICTIONS FOR STRUCTURES UNDER SEXUAL SELECTION?

Male structures such as weapons and signaling devices commonly show clear positive allometry (Kodric-Brown et al. 2006), but male genitalia usually show negative allometry. Male genitalia are almost never used as weapons against other males, and only very seldom as threats in male-male battles (Eberhard 1985), and are thus generally free of the selection pressures that tend to favor positive allometries in these male-male contexts (Petrie 1988; Green 1992; Petrie 1992). Male genitalia are also often relatively small, and are typically more or less hidden away except during copulation, so they are probably often relatively cheap to construct and to maintain. Thus they are likely to be poor indicators of male vigor, so females may be less likely to evolve to use them as indicators of male survival abilities. This again would reduce the likelihood of selection promoting positive allometry. In addition, genitalia likely provide tactile rather than other types of stimulation to females (Eberhard 1985), so, as just explained, they may be under selection for sizes that are appropriate for the most common sizes of females, thus favoring negative allometries. Finally, oversized male genital structures could be disadvantageous in some cases because they are less effective in transferring sperm (House and Simmons 2003) or damage the female (Sota and Kubota 1998). In sum, the lack of positive allometry in genitalia is not contrary to theoretical expectations.

It is possible that genitalia sometimes evolve under sexually antagonistic coevolution (see "Implications for Hypotheses Regarding Genital Evolution"). If so, then the obligate dependence of both males and females on successful gamete transfer may entail an additional allometric constraint that is not present in weapons in male-male battles (Eberhard 2005a). Because females need sperm to fertilize their eggs, they are expected to have only a limited tendency to escalate if they are involved in coevolutionary

struggles with males; a female that “wins” definitively, and successfully resists all males, is an evolutionary failure, as her eggs will remain unfertilized. In contrast, winning over all opponents is advantageous in male–male arms races (with possible exceptions in battles among kin). This expected limitation in female “escalation” in conflicts could tend to reduce selection favoring positive allometry in genitalia under sexually antagonistic coevolution as compared with weapons.

### IMPLICATIONS FOR HYPOTHESES REGARDING GENITAL EVOLUTION

The sexually antagonistic coevolution hypothesis for genital evolution predicts a trend toward positive allometry. The frequent use of brute force in resolving precopulatory male–male conflicts, and the consistent advantages of large size in such struggles, indicate that it is reasonable to expect that an appreciable portion of potential male–female genital conflicts, if they exist, would be resolved by force. Even though use as a weapon could sometimes be camouflaged with respect to allometric trends by counter-acting selection (see next section), and the subset of male genital structures that function inside the female’s body may be constrained in size to fit the female (above), male–female conflict should nevertheless produce at least a trend toward positive allometry in genitalia. The fact that male genitalia in arthropods show the opposite, a strong trend toward negative rather than positive allometry, is thus evidence against the sexually antagonistic coevolution hypothesis as a general explanation of genital evolution in this group. These data on allometry are in accord with similar conclusions from other large surveys (Eberhard 2004, 2005b); the sexually antagonistic coevolution hypothesis is thus unlikely to be a general explanation for rapid divergent genital evolution.

The low slopes in arthropod genitalia also argue strongly against the possibility that females use male genital size to judge overall male size and favor larger males (Eberhard et al. 1998). If females used genitalia this way, selection would favor larger males that had disproportionately large genitalia, when in fact they almost always have just the opposite design. Male genitalia are thus probably relatively poor indicators of aspects of male vigor such as size; such associations have not been found when looked for (Arnqvist and Thornhill 1998; House and Simmons 2007).

The trend toward negative genital allometry is compatible with the old lock-and-key hypothesis to explain genital evolution (now largely discredited as a general explanation of rapid divergent evolution of genitalia, largely due to the lack of female “locks” in species with species-specific male “keys”—Eberhard 1985, 1996, in press; Shapiro and Porter 1989), and with the cryptic female choice hypothesis (Eberhard 1985; Eberhard et al. 1998; but see below).

### RAPID DIVERGENCE VERSUS LOW ALLOMETRIC SLOPES IN GENITALIA: NOT A CONTRADICTION

Some authors have noted that it seems paradoxical that traits such as male genitalia, which tend to diverge relatively rapidly over evolutionary time (Eberhard 1985, in press), should be consistently more conservative in size than other traits (Ramos et al. 2005; Bertin and Fairbairn 2007). But even though relative genital size does occasionally diverge among closely related species (Lux 1961; Schuh 1984; Hormiga and Scharff 2005), the general evolutionary trend in genitalia is to diverge rapidly in shape, not in size (Eberhard et al. 1998; Eberhard et al., in press). Conservatism in proportional size does not necessarily imply conservatism in shape, and genitalic size and shape seem to be at least partially uncoupled genetically (Eberhard et al., in press). The importance of distinguishing size from shape was tested in the genitalia of a beetle by asking whether the allometries and variances of intraspecific differences in shapes show the same low values as intraspecific differences in size, as might be expected if there is conservative selection against variants in form. Instead, the shapes of both male and female genitalia showed high intraspecific variability compared with a nongenital structure (Polihronakis 2006). Future, more focused studies that compare the allometric slopes of those portions of the genitalia that are particularly distinct among closely related species with the slopes of other genital (and nongenital) structures might help unite understanding of size and shape.

### LOW SLOPES IN THE FACE OF DIRECTIONAL SELECTION

There is evidence in three insect species that directional sexual selection acts on male genital structures that nevertheless show typical low allometric slopes: the flagellum of the beetle *Chelymorpha alternans* (Rodriguez et al. 2004); the “external” genitalia of the water strider *Aquarius remigis* (Bertin and Fairbairn 2007); and four genital sclerites in the beetle *Onthophagus taurus* (House and Simmons 2003), some of which function in forming the spermatophore inside the female (Werner and Simmons 2008). In the first two species directional selection favors larger sizes; in the third it favors larger size in two of the sclerites and smaller size in two others. Bertin and Fairbairn (2007) argued that finding both directional selection and negative allometry implies that one cannot use allometric patterns to infer the pattern of sexual selection acting on male genitalia. This conclusion is not justified, however, because if directional selection on genitalia occurs at different intensities at different body sizes (e.g., positive selection on genitalia acts more intensely at lower body sizes), it can favor negative allometry (Eberhard et al., in press). In addition, as argued by House and Simmons (2003), directional selection on genitalia may be countered by other selective pressures that favor genitalia of a particular size. Counter-acting selection of this

sort could be natural selection (for instance involving efficient coupling and sperm transfer), or sexual selection. Whether such balances in selective forces actually occur, however, is not yet clear.

### PRECISE MALE-FEMALE FITS

The negative allometry in both male and female genitalia in arthropods suggests that selection favoring some sort of precise fit between males and females is likely to explain the negative allometry of male genitalia. Two nonexclusive types of selection could favor precise male-female fits. A “mechanical fit” hypothesis would be that rigid female genitalia may make it necessary for male genitalia to have a standard size in order for the male to fit or mesh with the female. In accord with this idea, for instance, pairings in the spider *Nephila edulis* between males and females that were mismatched with respect to body size resulted in lower amounts of sperm being transferred (Uhl and Vollrath 2000). A similar argument has been used to explain similarly low allometric slopes in pollen-bearing structures in an orchid that must presumably match the body size of its pollinator (Ushimaru and Nakata 2001). This idea might also explain the infrequency of negative allometry in vertebrates (in which female genitalia are relatively flexible), but it would not explain the strong positive allometries of some vertebrates. Eberhard et al. (1998) argued that this “mechanical fit” hypothesis is contradicted by the fact that in several of the arthropod species in their study with soft, yielding female genitalia, the slopes of male genitalia were as low as those in species with hard, rigid female genitalia. A precise male-female mechanical fit could be important, however, if males need to mesh precisely with flexible female structures.

A second type of evidence that has been used to argue for the importance of mechanical fit comes from the genital allometry in insect species in which some male genital structures are introduced inside the female’s body whereas others remain on her outer surface. Precise mechanical fit with the female was assumed to be more crucial for intromittent structures. As expected, male intromittent structures had lower allometric slopes in the geometrid moth *Selenia tetralunaria*, and in three species of the noctuid genus *Euxoa* (Mutanen and Kaitala 2006; Mutanen et al. 2006). The opposite trend occurs, however, in two other groups, the crambid moth *Ostrinia latissima* (Ohno et al. 2003) and the water strider *A. remigis* (Bertin and Fairbairn 2007). These two sets of data may nevertheless be compatible with mechanical fit hypotheses, because no data are available on the fine details of how male and female genitalia mesh during copulation in these species; it is possible that some internal fits are less tight than others, and that some external contacts require more precise mechanical fits than others. Better understanding of the fine details of morphological fit of intromittent and nonintromittent male structures with females is desirable for future studies of genital

allometry. One preliminary indication of the usefulness of such information is that differences in the allometry of different genital structures in a crayfish are in accord with differences in how they are used during copulation (Kato and Miyashita 2003). In sum, a “mechanical fit” version of the one-size-fits-all idea is not convincingly contradicted by the available data.

A nonexclusive alternative is the “stimulatory fit” hypothesis (the original version of the “one size fits all” hypothesis). It also supposes that a precise male-female fit is important, but that the important factor is not the mechanical fit per se, but rather the stimulation that a female receives from a male’s genitalia (Eberhard et al. 1998). As noted above, tactile stimulation is unusual in the sense that a female’s size is likely to affect the stimuli that she receives from a given male’s genitalia. Males may need to have relatively standard-sized genitalia to allow them to deliver appropriate stimulation to the most common, presumably intermediate-sized females. This “stimulatory fit” hypothesis could explain the low allometric slopes in species with soft, flexible female genitalia, if effective stimulation depends on contacting localized stretch receptors in membranes, such as those in the soft wall of the genital bursa of a butterfly (Sugawara 1979).

Stimulation and mechanical fit could operate sequentially as genitalia diverge, with each development of new male ability to stimulate the female being followed by a round of selection for stimulatory and mechanical fit. These ideas are only speculative, and need to be tested with detailed studies of male and female traits in groups with known phylogenies.

Male fit with the female could also be important for other processes, such as sperm competition via sperm removal or displacement, or quick sperm transfer (Schmitz et al. 2000). These factors seem to be ruled out, however, for some male genital structures that remain on the outside of the female with no access to sperm and that nevertheless show low slopes (Ohno et al. 2003; Bertin and Fairbairn 2007, the sepsid and tephritid flies in Eberhard et al. 1998).

The lack of an effect of female genital size on the bias that male genitalia impose on sperm precedence in the scarab beetle *O. taurus* (House and Simmons 2005) (a species with low allometric slopes in male genitalia—Palestrini et al. 2000) argues against these genital fit ideas (although if the female genitalia of this species also show negative allometry, a female effect might be difficult to document). In addition, the low male genital slopes in two species in Appendix 1 that belong to groups in which male genitalia are simple and not species-specific in form (the ichneumonid wasp *Hymenoepimecis argyraphaga* and the braconid wasp *Labania* sp.), and have thus presumably not been under sexual selection, also argues against a causal link with cryptic female choice or sperm competition. In sum, perhaps the low allometric slopes in arthropods are due to both mechanical and stimulatory versions of the one-size-fits-all hypothesis.



## ALLOMETRY OF FEMALE GENITALIA

The focus throughout this article has been on males, but the probable importance of precise male fits with females suggests important roles for females. The data from the genitalia of arthropod females, although less extensive than those for males, show the same consistent trend toward low allometric slopes. Low slopes in female genitalia are likely to have important consequences for males. If female genitalia are relatively consistent in size, then the mechanical and stimulatory advantages males would derive from having standard-sized genitalia should increase.

Why should female genitalia have low allometric values? Both natural and sexual selection could be involved. In as much as the dimensions of female genitalia are adjusted to the dimensions of their eggs, natural selection favoring a particular egg size could favor negative allometry of female genitalia. This explanation is not favored, however, in seven of the 10 species in Appendix 2, because the portions of the female genitalia that show low allometric values never interact physically with eggs. Sexual selection could also be involved if there is selection on females to favor those males whose genital sizes are more appropriate for intermediate-sized females. A female's ability to select among males could depend on her abilities to discriminate on the basis of the male's mechanical or stimulatory fit; this could result in selection favoring females that possess intermediate-sized genitalia themselves, because their sons were more likely to have appropriately sized genitalia.

## VERTEBRATES VERSUS ARTHROPODS

None of these ideas explain why the allometry of vertebrate genitalia might differ from that of the genitalia of insects and spiders. Is this another case, like "Rensch's rule" concerning male–female size dimorphisms, that shows different patterns for different taxa (Blanckenhorn et al. 2007), and if so, why? The data on vertebrates are sparse, but in at least some species their genitalia seem to have steeper slopes. The vertebrates have several possibly important peculiarities. One intuitively appealing explanation—that the female genitalia of vertebrates are less rigid than those of arthropods, and thus less demanding with respect to male fit—can be confidently discarded, because in 10 species (and probably many more) of insects in Appendix 1 have very soft female genitalia but nevertheless show clear negative allometry.

One vertebrate group, the poeciliid fish, is unusual in that one function of the male genitalia (gonopodium) is to deliver surprise stabs from a distance at the female's gonopore. Additional length seems especially likely to be useful for this function, and this could explain the relatively high allometric slopes for gonopodium length, especially if larger males are also superior stabbers for other reasons (e.g., faster swimmers). In contrast, the width of the tip of the gonopodium has a low allometric slope in *P. reticulata*; the tip is the portion of the gonopodium that shows

species-specific differences in this genus, and is the only portion that enters the female's body (Rosen and Gordon 1953). Perhaps a similar "bridging" function between male and female explains the steep slopes of bacula in some seals. Harp and hooded seals mate in the water, and baculum length shows high slopes (Miller et al. 1999; Miller and Burton 2001); cape fur seals, in contrast, mate on land and show low slopes (Oosthuizen and Miller 2000).

Another possible difference in mammals is that repeated thrusting movements of the penis generally occur during copulation. These movements may mean that the male penis need not fit especially precisely with the female, at least with respect to its length (the variable that has most often been measured in vertebrates). However, similar thrusting movements also occur in some insects, such as the beetles *Macrohaltica jamaicensis* (Eberhard and Kariko 1996) and *Pseudoxychila tarsalis* (Rodriguez 1998) that nevertheless show clear negative allometry in genital length (Eberhard et al. 1998).

Another special feature of the genitalia of vertebrates compared with those of male insects and spiders is that many continue to grow after the male reaches sexual maturity, and determining the sexual maturity of a male is sometimes difficult. Thus the slopes in Appendix 1, which generally include data from all males thought to be sexually mature, may combine static and ontogenetic allometry. If ontogenetic allometry were steeper early in maturity (if, in other words, the genitalia grow disproportionately rapidly during the early stages of sexual maturity), or if some pre-reproductive males were included in the sample, this ontogenetic effect could result in relatively steep slopes. A preliminary suggestion that ontogenetic changes may help explain at least some of the vertebrate differences comes from data of Patterson and Thaler (1982) on the mouse *Peromyscus eremicus*. The slope of data from all males (read from their graphs), including juveniles and subadults determined on the basis of pelage characters is 2.6, whereas that from only males of older age classes (2 and 3) is 0.9. The high genital slopes (1.60) in the mole rat *Bathyregus suillus* are also from a sample that may well have included subadult males; the smallest testes of these males were only 7% as long as the largest, whereas the median for similar comparisons of seven other nongenital structures was 80% (Kinahan et al. 2007). Visual inspections of the graphs for the harp seal, *Pagophilus groenlandicus*, which has the steepest genital slopes ever measured (3.4 for baculum length), and the pine marten *Martes caurina* suggest, however, that ontogenetic changes of this sort are not responsible for the high slopes in these species, as there is no obvious leveling off in mature males of larger sizes (Miller and Burton 2001; Miller and Nagorsen 2008). More work will be needed to determine whether ontogenetic changes in growth patterns contribute to the apparent differences in genital allometry between arthropods and vertebrates.

Understanding the allometry of the mammalian baculum, which is nearly the only genital structure that has been measured in mammals (and is most diverse of all vertebrate bones), is complicated by the fact that it probably has different functions. In some species the baculum appears to function only to provide mechanical support for the penis and/or protect the urethra from compression; in others it may open the vaginal orifice; in some it influences the shape of the glans or protrudes beyond the tip of the glans and may stimulate the walls of the vagina (Long and Frank 1968; Patterson 1983; Dixson 1998; Dyck et al. 2004). The distal end of the baculum is often more complex than the basal end; in some arvicoline rodents it has articulating elements that suggest a dynamic function of the tip during copulation (Dyck et al. 2004). The only allometric study of both penis and baculum length (Lüpold et al. 2004 on a bat) gave the unexpected result of positive allometry for the penis and negative allometry for the baculum. Measurements of the apparently stimulatory, claw-shaped bacula of some rodents would be interesting. The present dearth of data makes further speculation premature.

## UNSOLVED QUESTIONS

Many questions remain to be answered. The pattern of negative allometry in male arthropod genitalia is now well documented, but there are as yet no direct data concerning the process(es) by which this pattern is produced. There are numerous, varied nongenital contact courtship devices that also diverge rapidly, possibly due to sexual selection similar to that on genitalia (Eberhard 1985), but it is not clear whether they (and the portions of the female that they contact) also tend to show low allometric slopes; the high slopes of antennal clasper organ in a plant beetle (Vencel 2004), the low slope of a sternal brush in a sepsid fly (Eberhard 2002), and the mix of slopes in firefly lanterns (Vencel 2004) suggest possibly revealing variation. Are different functions of these structures during copulation (e.g., seizing as opposed to tapping or rubbing) associated with differences in their allometric slopes? Is it usual that the genitalia in different populations of the same species show different allometries, as has been found in a variety of species (Kelly et al. 2000; Bernstein and Bernstein 2002; Kawano 2002; Ohno et al. 2003; Bertin and Fairbairn 2007), and if so, why? Are there appropriately placed female sense organs in areas contacted by male genital structures with negative allometry, as expected under the stimulatory fit version of the one-size-fits-all hypothesis? Questions concerning the developmental mechanisms that determine the allometric relationships of genitalia are only beginning to be clarified; the male genitalia of *Drosophila* male respond differently to changes in insulin signaling than other tissues, but it is not known whether differences involve cell numbers or sizes (or both) (Shingleton et al. 2005). Quantitative analyses of shape (McPeck et al. 2008), especially of corresponding aspects of male and female, hold further promise. Given the strength and consistency

of allometric patterns, answers to these questions may have important implications for understanding both genital evolution and sexual selection in general.

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**Appendix 1.** Allometric slopes of male genitalia compared with slopes of other body parts ("body structures") that are thought not to be under sexual selection ("\*" indicates arthropod taxa in which the female genital structures contacted by the male structures are known to be soft and yielding).

Taxon and regression technique <sup>1</sup>	Number of species	Slope(s) gen. struct.	Slopes body struct.	Number gen. slopes < med. body slope <sup>2</sup>	Number gen. slopes < 1.00 <sup>2</sup>	Med. genit. < median nongenit. for that species <sup>2</sup>	Reference
<b>Insecta</b>							
<b>Coleoptera</b>							
<i>Cantharidae</i> O	1	0.40–0.81	0.94–1.14	1/1	1/1	1/1	Bernstein & Bernstein 2002
<i>Chauliognathus scutellaris</i> R		0.64–1.04	1.10–1.25	1/1	1/1	1/1	
<b>Cerambycidae</b>							
<i>Acrocinus longimanus</i> O	1	0.21	1.03, 1.03, 0.77	1/1	1/1	1/1	Kawano 2006
<i>Batocera rubus</i> O	1	0.40	1.28, 0.75	1/1	1/1	1/1	Kawano 2006
<i>Dorystenes walkeri</i> O	1	0.34	0.98, 1.0, 0.57 0.92	1/1	1/1	1/1	Kawano 2006
<i>Psolidognathus friendi</i> O	1	0.21	0.86, 0.98, 0.63 0.82	1/1	1/1	1/1	Kawano 2006
<i>Macrodonia cervicornis</i> O	1	0.25	1.01, 0.93, 0.95, 0.90	1/1	1/1	1/1	Kawano 2006
<i>Spondylis buprestoides</i> O	1	0.44	1.13, 0.59, 0.85, 0.67, 0.94	1/1	1/1	1/1	Kawano 2006
<b>Chrysomelidae</b>							
<i>Cerotoma salvini</i> R	1	0.72	0.70	0/1	1/1	0/1	Vencl 2004
<i>Cerotoma trifurca</i> O	1	0.54, 0.44	0.60, 0.90, 0.58	2/2	2/2	1/1	Eberhard et al. 1998
<i>Macrohaltica jamaicensis</i> * O	1	0.32, 0.30	0.74, 0.75, 0.75	2/2	2/2	1/1	Eberhard et al. 1998
<i>Chelymorphia alternans</i> O	1	–0.22, 0.21	0.72, 0.66	2/2	2/2	1/1	Eberhard et al. 1998
<i>Macropus armatus</i> * O	1	0.44	0.60, 0.83, 0.86	1/1	1/1 (0 <sup>3</sup> )	1/1	M. Losilla, unpub.
<b>Cicindellidae</b>							
<i>Pseudoxychila tarsalis</i> * O	1	0.067, 0.030	0.66, 0.85, 0.41	2/2	2/2	1/1	Eberhard et al. 1998
<b>Curculionidae</b>							
<i>E. kamerunicus</i> O	1	0.29, 0.29	0.79, 0.80	2/2	2/2	1/1	Eberhard et al. 1998
<b>Dynastidae</b>							
<i>Allomyrina dichotoma</i> O	1	0.50	1.09, 1.21, 0.87	1/1	1/1	1/1	Kawano 2006
<i>Augosoma centaurus</i> O	1	0.18	0.89, 0.96, 0.67	1/1	1/1	1/1	Kawano 2006
<i>Chalcosoma</i> spp. O	3	0.27, 0.45, 0.46	0.80–1.14	3/3	3/3	3/3	Kawano 2006
<i>Dynastes</i> spp. O	2	0.22, 0.34	0.77–1.18	2/2	2/2	2/2	Kawano 2006
<i>Eupatorius</i> spp. O	2	0.28, 0.34	0.81–1.32	2/2	2/2	2/2	Kawano 2006
<i>Megasoma janus</i> O	1	0.34	1.24, 1.12, 0.70	1/1	1/1	1/1	Kawano 2006

Continued.

Appendix 1. Continued.

Taxon and regression technique <sup>1</sup>	Number of species	Slope(s) gen. struct.	Slopes body struct.	Number gen. slopes < med. body slope <sup>2</sup>	Number gen. slopes < 1.00 <sup>2</sup>	Med. genit. < median nongenit. for that species <sup>2</sup>	Reference
<i>Pachyoryctes solidus</i> O	1	0.46	0.96, 0.89, 0.75	1/1	1/1	1/1	Kawano 2006
<i>Protaetia</i> spp. O	3	0.21, 0.24, 0.50	0.79–1.10	3/3	3/3	3/3	Kawano 2006
<i>Rhomborrhina japonica</i> O	1	0.44	0.94, 0.95, 0.99	1/1	1/1	1/1	Kawano 2006
<i>Xylotrupes gideon</i> O	1	0.25	1.12, 0.99, 0.89	1/1	1/1	1/1	Kawano 2006
Dytiscidae							
<i>Graphoderus liberus</i> ? <sup>4</sup>	1	0.061, 0.062	0.30, 0.19	1/1	1/1	1/1	Schulte-Hostedde & Alarie 2006
Euchiridae							
<i>Cheilotonus</i> spp. O	2	0.39, 0.41	0.75–.89	2/2	2/2	2/2	Kawano 2006
<i>Euchirus dupontianus</i> O	1	0.34	0.83	1/1	1/1	1/1	Kawano 2006
Gyrinidae							
<i>Dineutus nigrior</i>	1	0.51	0.83, 0.84, 0.97, 0.99	1/1	1/1	1/1	Fairm et al. 2007
Lampyridae							
<i>Lucidota punctata</i> R	1	1.0	0.83, 1.40	1/1	1/1 <sup>3</sup>	1/1	Vencl 2004
<i>Photinus</i> spp. R	2	1.02, 0.99	1.62, 0.84	0/2	1/2	0/2	Vencl 2004
Lucanidae							
<i>Cyclommatus elephas</i> O	1	0.36	1.03, 1.13, 1.08, 0.81	1/1	1/1	1/1	Kawano 2006
<i>Dorcus</i> spp. O	4	0.15, 0.21, 0.28, 0.29	0.78–1.48	4/4	4/4	4/4	Kawano 2006
<i>Lucanus maculifemoratus</i> O	1	0.25	0.73	1/1	1/1	1/1	Tatsuta et al. 2001
R		0.50	0.84	1/1	1/1	1/1	
<i>Lucanus planeti</i> O	1	0.25	1.03, 1.00, 1.06, 0.76	1/1	1/1	1/1	Kawano 2006
<i>Nigidionus parryi</i> O	1	0.76	0.67, 0.78, 0.70, 0.76	0/1	1/1	0/1	Kawano 2006
<i>Odontolabis</i> spp. O	4	0.19, 0.26, 0.27 0.38	0.81–1.30	4/4	4/4	4/4	Kawano 2006
<i>Prosopocoilus</i> spp. O	2	0.15, 0.31	0.79–1.28	2/2	2/2	2/2	Kawano 2006
<i>Prosopocoilus inclinatus</i> <sup>5</sup> O	1	0.45, 0.14, 0.23	0.61	3/3	3/3	1/1	Tatsuta et al. 2007
R		0.37, 0.15, 0.17	0.71				
Melolonthidae							
<i>Phyllophaga obsoleta</i> * O	1	0.60, 0.43, 0.40, 0.38	0.75, 0.90, 0.78, 0.85	4/4	4/4	1/1	Eberhard et al. 1998
<i>Macrodactylus silphis</i> * O	1	0.61, 0.03, 0.50, 0.63	0.74, 0.95, 0.75, 0.77, 1.36	4/4	4/4	1/1	Eberhard et al. 1998
Mordellidae							
<i>Mordellistena</i> spp. ? <sup>4</sup>	2	0.26, 0.57, 0.01, 0.08	–	–	4/4 (3 <sup>3</sup> )	–	Schmitz et al. 2000
Scarabaeidae							

Continued.

## Appendix 1. Continued.

Taxon and regression technique <sup>1</sup>	Number of species	Slope(s) gen. struct.	Slopes body struct.	Number gen. slopes < med. slope <sup>2</sup>	Number gen. slopes < 1.00 <sup>2</sup>	Med. genit. < median nongenit. for that species <sup>2</sup>	Reference
<i>Onthophagus acuminatus</i> ? <sup>4</sup>	1	γ <sup>6</sup>	γ <sup>6</sup>	1/1	?	1/1	Emlen et al. 2007
<i>O. ilyricus</i> O? <sup>7</sup>	1	0.33	1.07, 1.03	1/1	1/1	1/1	Pizzo et al. 2006
<i>O. incensus</i> O	1	0.59, 0.42, 0.29, 0.44	0.88, 0.89, 0.82	4/4	4/4	1/1	Eberhard et al. 1998
<i>O. taurus</i> * B	1	0.08, 0.15, -0.04, 0.07, 0.07, -0.01	0.78, 0.87, 0.91, 0.84, 0.59, 0.86	6/6	6/6	1/1	Palestrini et al. 2000
O <sup>7</sup> g		0.28	1.18, 0.44	1/1	1/1	1/1	Pizzo et al. 2006
R		0.50, 0.61, 0.64, 0.77, 0.90 <sup>8</sup>	0.77, 1.08 <sup>8</sup>	5/5	5/5	1/1	House and Simmons 2007
Blattodea							
Blaberidae							
<i>Nauphoeta cinerea</i> O	1	0.13	0.74–0.94	1/1	1/1	1/1	D. Hosken, W. E. Harris, J. Hunt, A. J. Moore, and P. J. Moore unpub.
R		0.44	1.54–2.45	1/1	1/1	1/1	
M		0.16		1/1	1/1	1/1	
Hemiptera							
Gerridae							
<i>Aquarius remigis</i> internal <sup>9</sup> O	1	0.82, 0.43, 0.41	1.44, 0.93	3/3	3/3 (2c)	1/1	Bertin and Fairbairn 2007
R		1.73, 0.81, 1.16	2.11, 1.21	2/3	1/3	1/1	
external <sup>9</sup> O		0.65, 0.68, 0.45	1.44, 0.93	3/3	3/3 (2c)	1/1	
R		0.97, 1.25, 1.05	2.11, 1.21	3/3	1/3	1/1	
<i>Eurygerris flavolineatus</i> (?) O	1	-0.04, 0.34, 0.43, 0.96	0.61, 0.47	3/4	4/4	1/1	W. Eberhard unpub.
Lygaeidae							
<i>Ozophora baranowskii</i> O	1	0.30, 0.25, -0.04	0.53, 0.41	3/3	3/3	1/1	Eberhard et al. 1998
Diptera							
Culicidae							
<i>Aedes aegypti</i> <sup>10</sup> O	1	0.31, 0.32	0.74, 0.83	2/2	2/2	1/1	Wheeler et al. 1993
Drosophilidae							
<i>Drosophila melanogaster</i> ? <sup>4</sup>	1	γ <sup>6</sup>	γ <sup>6</sup>	1/1	1/1	1/1	Shingleton et al. 2007
Scathophagidae							
<i>Cordilura</i> spp. O	3	0.10, 0.31, 0.93	0.48–1.13	3/3	3/3	3/3	Hosken et al. 2005
M		0.57, 0.95, 1.88	1.07–3.29	2/3	2/3	2/3	
Norellia spp. O	4	0.11, 0.11, 0.44, 0.49	0.76–1.38	4/4	4/4	4/4	Hosken et al. 2005

Continued.



Appendix 1. Continued.

Taxon and regression technique <sup>1</sup>	Number of species	Slope(s) gen. struct.	Slopes body struct.	Number gen. slopes < med. body slope <sup>2</sup>	Number gen. slopes < 1.00 <sup>2</sup>	Med. genit. < median nongenit. for that species <sup>2</sup>	Reference
M		0.14, 0.17, 0.41, 0.51	1.09–1.82	4/4	4/4	4/4	
<i>Phrosia albilabris</i> O	1	–0.001	0.83	1/1	1/1	1/1	Hosken et al. 2005
M		–0.002	1.13	1/1	1/1	1/1	
<i>Scathophaga</i> spp. O	5	–0.13–0.48	0.88–1.22	5/5	5/5	5/5	Hosken et al. 2005
M		–0.19–0.61	1.06–1.38	5/5	5/5	5/5	
Sepsidae							
<i>Archiseipsis diversiformis</i> O	1	0.35, 0.20	0.77, 0.79, 0.85	2/2	2/2	1/1	Eberhard et al. 1998
<i>Palaeosepsis dentatiformis</i> O	1	0.32	0.81, 0.93, 0.82	1/1	1/1	1/1	Eberhard 2002
Tephritidae							
<i>Ceratitis</i> spp. O	5	0.02–0.52	0.47–0.86	25/25	25/25	5/5	R. D. Briceño unpub.
Hymenoptera							
Braconidae							
<i>Labania</i> sp. O	1	0.30, 0.34, 0.36, 0.52	0.65, 0.74, 0.83	4/4	4/4	1/1	W. Eberhard, unpub.
			0.83, 0.84, 1.07				
Formicidae							
<i>Campanotus</i> sp. O	1	0.16, 0.06	0.33	2/2	2/2	1/1	Eberhard et al. 1998
Ichneumonidae							
<i>Hymenoeipimecis argyraphaga</i> O	1	0.43, 0.45, 0.55, 0.55, 0.78	0.64, 0.92, 0.92, 0.96	5/5	5/5	1/1	W. Eberhard unpub.
<i>Netelia</i> spp. O	3	0.32, 0.58, 0.60, 0.88, 0.90, 0.92	0.52–0.98	5/6	6/6	3/3	W. Eberhard unpub.
Dermaptera							
Labiidae							
<i>Paralabella dorsalis</i> * O	1	0.39, –0.23, 0.07, 0.37, 0.65	–0.09, 0.47, 0.76	4/5	5/5	1/1	Eberhard et al. 1998
Odonata							
Calopterygidae							
<i>Hetaerina fuscovittata</i> O	1	0.79, 0.14, 0.22	0.52, 0.76, 0.72	2/3	3/3	1/1	Eberhard et al. 1998
Lepidoptera							
Crambidae							
<i>Ostrinia latiniensis</i> <sup>11</sup> <i>internali</i> O	1	0.37–0.48, 0.36–0.42, 0.33–0.56, 0.01–0.39	0.94–1.13, 0.95–1.27, 1.06–1.27, 0.99–1.10, 1.04–1.33, 0.97–1.12	4/4	4/4c	1/1	Ohno et al. 2003

Continued.

## Appendix 1. Continued.

Taxon and regression technique <sup>1</sup>	Number of species	Slope(s) gen. struct.	Slopes body struct.	Number gen. slopes < med. body slope <sup>2</sup>	Number gen. slopes < 1.00 <sup>2</sup>	Med. genit. < median nongenit. for that species <sup>2</sup>	Reference
externali O		0.38–0.59	1.02–1.17, 0.88–1.04, 0.41–1.46	1/1	1/1c		
Geometridae							
<i>Selenia tetralunaria interna</i> <sup>9,12</sup> O	1	0.53 (0.34–0.84)	–	–	3/3 (1)c		Mutanen and Kaitala 2006
external <sup>9</sup> O		0.28 (–0.03–0.59)			5/5c		
Noctuidae							
<i>Euxoa spp. interna</i> <sup>9</sup> * O	3	0.14–1.30	–	–	13/15 (11c)	3/3	Mutanen et al. 2006
external <sup>9</sup> O		0.24–0.57	–	–	15/15 (10c)	3/3	Mutanen 2005
Zygaenidae							
<i>Elcysma westwoodii</i> O	1	0.41	0.64, 0.71, 0.90, 1.10	1/1	1/1	1/1	Koshio et al. 2007
M		0.49	0.78, 0.86, 1.02, 1.41	1/1	1/1	1/1	
Mecoptera							
Meropidae							
<i>Merope tuber</i> O	1	1.53, 1.68 <sup>13</sup>	–	–	0/2	–	Johnson 1995
Crustacea							
Astacidae							
<i>Pacifastacus trowbridgi</i> <sup>14</sup> O	1	0.75, 0.99	1.04	2/2	2/2	1/1	Kato and Miyashita 2003
R		0.83, 1.03	1.12	2/2	1/2	1/1	
Cambaridae							
<i>Procambarus clarkii</i> <sup>14</sup> O	1	0.94, 0.92	1.13	2/2	2/2	1/1	Kato and Miyashita 2003
R		0.97, 0.96	1.20, 1.03	2/2	2/2	1/1	
Arachnida							
Araneae							
Araneidae							
<i>Araneus expletus</i> O	1	0.56, 0.58, 0.43	1.20, 0.94, 1.23	3/3	3/3	1/1	Eberhard et al. 1998
<i>Argiope trifasciata</i> O	1	0.60, 0.48, 0.52	1.18	3/3	3/3	1/1	Eberhard et al. 1998
Dipluridae							
<i>Ischnothele annulata</i> O	1	0.58, 0.62	0.87 (0.57–1.03) <sup>15</sup>	2/2	2/2	1/1	F. Coyle, unpub.
<i>I. caudata</i> O	1	0.86, 0.85	0.83 (0.47–0.98) <sup>15</sup>	0/2	2/2	0/1	F. Coyle, unpub.
<i>I. guianensis</i> O	1	0.78, 0.94	0.82 (0.75–0.96) <sup>15</sup>	1/2	2/2	0/1	F. Coyle, unpub.
<i>I. striatipes</i> O	1	0.64, 0.30	0.83 (0.56–1.09) <sup>15</sup>	2/2	2/2	1/1	F. Coyle, unpub.
Linyphiidae							
<i>Linyphia triangularis</i> O	1	0.30, 0.25	0.61, 0.72, 0.78, 0.97	2/2	2/2	1/1	Funke & Huber 2005

Continued.

**Appendix 1. Continued.**

Taxon and regression technique <sup>1</sup>	Number of species	Slope(s) gen. struct.	Slopes body struct.	Number gen. slopes < med. body slope <sup>2</sup>	Number gen. slopes < 1.00 <sup>2</sup>	Med. genit. < median nongenit. for that species <sup>2</sup>	Reference
<b>Nephilidae</b>							
<i>Nephila edulis</i> <sup>16</sup> M	1	0.36	1.26	1/1	1/1	1/1	Uhl & Vollrath 2000
<b>Pholcidae</b>							
<i>Metagonia rica</i> <sup>a</sup> O	1	0.48, 0.38, 0.38	1.62, 1.39, 0.82	3/3	3/3	1/1	Eberhard et al. 1998
<i>Physocyclus globosus</i> <sup>*</sup> O	1	0.28, 0.35, 0.35	0.67, 0.77, 1.22 0.63, 1.10, 0.44	3/3	3/3	1/1	Eberhard et al. 1998
<b>Tetragnathidae</b>							
<i>Tetragnatha</i> sp. O	1	0.31, 0.38, 0.33, 0.36	0.87, 0.92, 0.85	4/4	4/4	1/1	Eberhard et al. 1998
<b>Uloboridae</b>							
<i>Philoponella vicina</i> O	1	0.42, 0.47, 0.55, 1.31	0.72, 0.76, 1.18	3/4	3/4	1/1	Eberhard et al. 1998
<b>Scorpiones</b>							
<b>Bothriuridae</b>							
<i>Bothriurus bonariensis</i>	1	0.421 <sup>17</sup>	1.40	1/1	1/1	1/1	Peretti et al. 2001; A. Peretti, pers. comm.
<b>Vertebrata</b>							
<b>Pisces</b>							
<b>Poeciliidae</b>							
<i>Brachyrhaphis episcopi</i> <sup>18</sup> O	1	0.89	0.76, 0.97	0/1	1/1c	0/1	Jennions & Kelly 2002
R		0.93			1/1c		
<i>Gambusia holbrooki</i> O	1	0.78	–	–	1/1	–	C. Mazzoldi, M. Rasotto, and A. Pilastro, unpubl. ms.
<i>Poecilia latipinna</i> O	1	0.64	–	–	1/1	–	C. Mazzoldi, M. Plath, I. Schlupp, and A. Pilastro, unpubl. ms.
<i>Poecilia mexicana</i> O	1	0.61	–	–	1/1	–	C. Mazzoldi, M. Plath, I. Schlupp, and A. Pilastro, unpubl. ms.
<i>Poecilia reticulata</i> R <sup>19</sup>	1	1.40 (len)	–	–	0/1	–	Kelly et al. 2000
O <sup>20</sup>		0.70 (len)	0.75	2/2	2/2	1/1	W. Eberhard unpub.
		0.36 (wid)					C. Mazzoldi, M. Berica, and A. Pilastro, unpubl. ms.
O		0.55 (len)	–	–	1/1	–	A. Pilastro, unpubl. ms.

Continued.

Appendix 1. Continued.

Taxon and regression technique <sup>1</sup>	Number of species	Slope(s) gen. struct.	Slopes body struct.	Number gen. slopes < med. body slope <sup>2</sup>	Number gen. slopes < 1.00 <sup>2</sup> median nongenit. for that species <sup>2</sup>	Med. genit. < median nongenit. for that species <sup>2</sup>	Reference
<b>Mammalia</b>							
<b>Bathyergidae</b>							
<i>Bathyergus suillus</i> R	1	1.60, 1.60	0.45, 1.34, 0.98, 0.04, 0.66, 0.69	0/2	0/2 <sup>3</sup>	0/1	Kinahan et al. 2007
<b>Cricetidae</b>							
<i>Ondatra zibethicus</i> R	1	1.40, 1.72, 3.35, 3.72	0.54, 0.66, 0.78	0/4	0/4	0/1	Tasikas et al. 2008
<i>Peromyscus eremicus</i> <sup>21</sup> O	1	0.94	—	—	1/1	—	Patterson and Thaeler 1982
<b>Geomyidae</b>							
<i>Thomomys talpoides</i> <sup>21</sup> O	1	1.61	—	—	—	—	Patterson and Thaeler 1982
<b>Mustelidae</b>							
<i>Martes caurina</i> <sup>22</sup> R	1	1.51, 2.27, 1.44	—	—	0/3	—	Miller and Nagorsen in press.
<b>Otariidae</b>							
<i>Arctocephalus pusillus</i> R	1	approx. .6 <sup>23</sup>	—	—	—	1/1	Oosthuizen and Miller 2000
<i>Eumetopias jubatus</i> <sup>24</sup> O	1	0.41	—	—	1/1	—	Miller et al. 2000
<b>Phocidae</b>							
<i>Cystophora cristata</i> O	1	0.83	—	—	1/1	—	Miller et al. 1999
R		1.23	—	—	0/1	—	
<i>Pagophilus groenlandicus</i> O(?) <sup>25</sup>	1	3.4, 4.8	0.53, 0.39, 0.79, 0.58, 0.82, 0.95	0/2	0/2 <sup>3</sup>	0/1	Miller and Burton 2001
<b>Sciuridae</b>							
<i>Eutamias cinereicollis</i> <sup>21</sup> O	1	0.43	—	—	—	—	Patterson and Thaeler 1982
<b>Vespertilionidae</b>							
<i>Nyctalus noctula</i> O	1	0.86, 0.17	0.01, 0.08, 0.09, 0.17, 0.18, 0.19, 0.21, 0.24	1/2	2/2	0/1	Lüpold et al. 2004
R		2.09	0.49, 0.57, 0.66, 0.85	0/1	0/1	0/1	
<i>N. lasiopterus</i> <sup>21</sup> O	1	1.44	—	—	0/1	—	Maeda 1978

Continued.



**Appendix 1. Continued.**

Taxon and regression technique <sup>1</sup>	Number of species	Slope(s) gen. struct.	Slopes body struct.	Number gen. slopes < med. body slope <sup>2</sup>	Number gen. slopes < 1.00 <sup>2</sup> median nongenit. for that species <sup>2</sup>	Reference
Mollusca						
Helicidae						
<i>Arianita arbustorum</i> <sup>26</sup> O	1	-0.86-1.48	0.28-0.91	15/24 (12/18)	1/1	Baminger and Haase 2000

<sup>1</sup> O, ordinary least squares; R, reduced major axis, B, Bartlett's Three Group M, major axis A.

<sup>2</sup> when more than one value was given (e.g., different populations of same species), median was used in comparisons.

<sup>3</sup> difference or equality tested statistically.

<sup>4</sup> regression technique not specified.

<sup>5</sup> regressions were broken into segments with significantly different slopes; median values are reported and were used to make comparisons. Values for head and mandibles were omitted because they are probably under sexual selection as weapons.

<sup>6</sup> regressions were presented as graphs without specifying equations; the log-log slope of genitalia was clearly lower than that of palp (*Drosophila*) or leg (*O. acuminatus*).

<sup>7</sup> no specific statement regarding regression technique; regression was performed on centroid of elytral traits as an indicator of body size.

<sup>8</sup> combined values for major and minor males raised on pasture and grain dung; genital measurements were the length of the perimeter of each of five sclerites.

<sup>9</sup> internal, inserted into female reproductive tract; external, remains on external surface of female during copulation.

<sup>10</sup> only values using leg as indicator of body size are included.

<sup>11</sup> data indicate range of values from three populations; all regressions were on PC1 from variance-covariance matrix of the raw measurements of 16 body parts.

<sup>12</sup> data are means of two morphs that differ in size, color, and season; slopes are mean and range.

<sup>13</sup> genitalia probably under sexual selection as weapons in battles between males.

<sup>14</sup> male genital structures measured remain outside female during copulation.

<sup>15</sup> median and range.

<sup>16</sup> only the mean values for regression of seven genital traits on six nongenital traits, and of six nongenital traits on six nongenital traits are given here; the means of the two groups of regressions were significantly different.

<sup>17</sup> data from the spermatophore; the spermatophore, rather than the male's genitalia, contacts the female genitalia during sperm transfer.

<sup>18</sup> mean values for 12 sites.

<sup>19</sup> study by Kelly et al. (2000) involved eight different populations; those from four populations with more predation pressure had longer gonopodia but not steeper allometric slopes. Length of gonopodium (most of which remains outside the female during copulation) does not usually include species-specific characters.

<sup>20</sup> study by Eberhard involved 25 males from a small population of unknown precedence in Costa Rica. Both length and maximum width at the tip (which is inserted into the female and which usually has the species-specific characters in this genus) were measured. The body size indicator was lens diameter (body length was not feasible due to variable damage to the tail).

<sup>21</sup> data read from graphs in publication.

<sup>22</sup> only values of older animals are used (baculum continues to grow after other parts nearly ceased to grow); body size estimated with head plus body length.

<sup>23</sup> estimated from Fig. 4A of baculum length versus body length for males more than 6-year old.

<sup>24</sup> sexually mature males only.

<sup>25</sup> "simple regression" taken to mean OLS; only data for apparently mature males (> 137 cm) are included for genital traits.

<sup>26</sup> comparing four internal traits against nongenital traits among individuals in six different populations on thorax using only male genital traits housing structures that contact the female, totals were 12/18. Closely related species in this group cannot be distinguished on the basis of the structures measured in this study.

**Appendix 2.** Allometric slopes for female genitalia in five insects, five spiders, one mammal, and one mollusc. (species in which the portion of the female genitalia that was measured probably has no direct physical interaction with eggs, and would thus not be expected to be constrained by egg size are indicated with “\*”).

Group and regression technique <sup>1</sup>	Number of species	Slope(s) gen. <sup>2</sup> struct. <sup>2</sup>	Slopes body struct. <sup>2</sup>	Number gen. slopes < med. body slope	Number gen. slopes < 1.00 median nongenit. for that species	Med. genit. < median nongenit. for that species	Reference
Insecta							
Coleoptera							
Chrysomelidae							
<i>Macropus armatus</i> O	1	0.53	0.64, 0.72, 0.72, 0.82, 0.90, 0.94	1/1	1/1	1/1	M. Losilla, unpub.
<i>Chelymophra alternans</i> * O	1	0.24	0.72, 0.76	1/1	1/1	1/1	Eberhard et al. 1998
Scarabaeidae							
<i>Onthophagus taurus</i> B	1	0.09, 0.12, 0.15, 0.21	0.79, 0.94, 0.95, 1.09, 1.11, 1.11, 1.29	4/4	4/4	1/1	Palestrini et al. 2000
Lucanidae							
<i>Prosopocoilus inclinatus</i> O	1	0.046–0.06	0.21–0.70, 0.26–0.68, 0.51–0.94, 0.39–0.88	1/1	1/1	1/1	Tatsuta et al. 2007
R	1	0.050–0.16	0.28–0.80, 0.36–0.77, 0.58–0.98, 0.41–0.93	1/1	1/1	1/1	
Diptera							
Tephritidae							
<i>Ceratitis capitata</i> O	1	0.15, 0.18, 0.41, 0.43	0.87	1/1	1/1	1/1	Eberhard et al. 1998
Lepidoptera							
Geometridae							
<i>Selenia tetralunaria</i> * external O	1	0.41 <sup>3</sup>	–	–	4/4 (2/4) <sup>4</sup>	–	Mutanen and Kaitala 2006
internal O		0.01, 0.31 <sup>3</sup>	–	–	2/2 (1/2) <sup>4</sup>	–	
Araneae							
Linyphiidae							
<i>Linyphia triangularis</i> * O	1	0.42	0.47, 0.49, 0.70, 1.08	1/1	1/1	1/1	Funke and Huber 2005; B. Huber pers. comm.
Nephilidae							
<i>Nephila edulis</i> * M	1	0.60 <sup>5</sup>	1.02 <sup>5</sup>	1/1	1/1	1/1	Uhl and Vollrath 2000
Araneidae							
<i>Argiope trifasciata</i> * O	1	0.25, 0.52, 0.52	0.85, 0.90	3/3	3/3	1/1	Eberhard et al. 1998
Uloboridae							
<i>Philoponella vicina</i> * O	1	0.12, 0.20	0.42, 0.54, 0.88	2/2	2/2	1/1	Eberhard et al. 1998
Pholcidae							
<i>Physocyclus globosus</i> * O	1	0.23, 0.72	0.80, 1.33	2/2	2/2	1/1	Eberhard et al. 1998

Continued.

Appendix 2. Continued.

Group and regression technique <sup>1</sup>		Number of species	Slope(s) gen. <sup>2</sup> struct. <sup>2</sup>	Slopes body struct. <sup>2</sup>	Number gen. slopes<med. body slope	Number gen. slopes<1.00	Med. genit.< median nongenit. for that species	Reference
Mammalia								
Bathyergidae								
<i>Bathyergus suillus</i>	R	1	>1.0 <sup>6</sup>	0.62, 1.04	0/1	0/1	0/1	Kinahan et al. 2007
Mollusca								
...								
<i>Arianita arbustorum</i> <sup>7</sup>	O	1	-0.43-1.38 0.01-1.49	0.28-0.91	3/12	6/12	0/1	Baminger and Haase 2000

<sup>1</sup> O, ordinary least squares; R, reduced major axis; B, Bartlett's Three Group; M, major axis  
<sup>2</sup> when more than one value was given (e.g., different populations of same species), median was used in comparisons.  
<sup>3</sup> median of values of two slopes for different morphs.  
<sup>4</sup> difference with 1.00 was statistically significant.  
<sup>5</sup> means for slopes of six genital and six nongenital characters.  
<sup>6</sup> authors state "positive allometry occurred for reproductive tract length with respect to body length," but give no numbers.  
<sup>7</sup> two female traits measured in six populations of these hermaphroditic animals.