The limits of elaboration: curved allometries reveal the constraints on mandible size in stag beetles

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Many studies have demonstrated the adaptive advantage of elaborate secondary sexual traits, but few if any have shown compelling evidence for the limits to the elaboration of these traits that must exist. We describe such evidence in the exaggerated mandibles of stag beetles. In 1932, Huxley showed that the slope of the allometric relationship between mandible length and body size in some stag beetles declines in the largest males. We show that this curvature is most pronounced in species with relatively long mandibles, consistent with the hypothesis that the decrease in slope is caused by the increasing costs of large mandibles, which ultimately limit their size. Increasing depletion of resources in the prepupa and pupa by the rapidly growing mandibles is the most likely way in which these costs are manifested. The curved allometries have two components: intraspecific mandible allometry is steepest among small males of the species with the longest mandibles, but shallowest among the largest males of those same species. These patterns suggest that selection continues to favour positive allometry in species that invest relatively more in weaponry despite the limits to mandible exaggeration being reached in the largest males.

Keywords: Lucanidae; *Lucanus*; allometry; sexual selection; sexual ornaments

1. INTRODUCTION

The size of the sexual ornaments carried by male animals of many species is traditionally explained in terms of the trade-off between the benefit, in the form of increased mating success, and the costs that arise from carrying these traits (Andersson 1994). For example, diopsid flies that carry longer eyestalks have enhanced mating success (Wilkinson & Dodson 1997) but also reduced flight ability (Swallow *et al.* 2000). We use a comparative study of the allometries of sexually selected weapons to illustrate how the sizes of these characters in holometabolous insects appear to be constrained, apparently by competition for nutrients within the pupa.

Static allometry (which for the sake of brevity we shall refer to simply as 'allometry' from now on) is the relationship between the size of an individual organ and the size of a whole organism (Huxley 1932; D'Arcy Thompson 1942; Gould 1966). The allometry of secondary sexual traits has attracted particular interest (Gould 1973; Alatalo *et al.* 1988; Petrie 1988, 1992; Green 1992; Simmons & Tomkins 1996; Knell *et al.* 1999; Emlen & Nijhout 2000; Baker & Wilkinson 2001). One of the general conclusions arising from this work is that sexually selected ornaments are likely to display positive allometry, defined as a value greater than one for the exponent k in the equation relating organ size to body size, $y = bx^k$, where y is organ size and x is body size. Positive allometry means that the sexual ornaments carried by larger males will be proportionally larger than those carried by smaller males.

Evidence for positive allometry of secondary sexual ornaments comes from measurements of a variety of such ornaments, including the antlers of the extinct giant deer (Gould 1973), the tail feathers of a number of bird species (Alatalo *et al.* 1988), the facial shield of the moorhen (Petrie 1988), the crest of the great crested newt (Green 1992), the forceps of earwigs (Simmons & Tomkins 1996) and the eyestalks of diopsid flies (Wilkinson & Dodson 1997; Knell *et al.* 1999; Baker & Wilkinson 2001). This pattern is usually interpreted from an adaptationist perspective, whereby the observed relationship between ornament size and body size is regarded as a 'reaction norm', which describes how the possible phenotypes associated with a particular genotype vary according to environmental conditions. The slope of the relationship is explained in terms of the fitness advantages for the bearer and by considering trade-offs between investment in ornaments and investment in other parts of the animal (Emlen & Nijhout 2000).

Despite this interest in the allometry of sexual ornaments, one important aspect of some of these relationships has largely been ignored by recent workers (but see Nijhout 1994; Nijhout & Wheeler 1996), namely that the slopes of many such plots of sexual-ornament size versus body size actually *decrease* at the largest body sizes, giving curved, rather than straight, allometries. Huxley (1932) plotted allometric curves for the mandibles of several species of stag beetle and found clear decreases in slope in each case. Gould (1966) demonstrated a similar effect with data from another species of stag beetle, and more recently Wilkinson & Dodson (1997) commented on similar patterns found when the length of the 'antlers' carried by tephritid flies of the genus *Phytalmia* is plotted against body length. There are many other examples of similar declines in other species, including a number of horned beetles (e.g. *Copris lugubris*; Eberhard & Gutierrez 1991), and in the enlarged mandibles of the staphylinid beetle *Oxyporus stygipus* (Hanley 2001). Several authors have speculated that these curved allometries are a consequence of the increasing costs of large traits (Huxley 1932; Gould

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1966; Nijhout 1994), and in particular that the limited resources available to the rapidly growing imaginal discs that produce these traits may be the cause of these patterns (Huxley 1932; Nijhout 1994; Nijhout & Wheeler 1996), but until now there have been no empirical tests of these ideas.

We investigated the relationship between allometry and the costs and benefits associated with weapon size by comparing allometric curves for mandible length plotted against elytron length for 17 species of stag beetle from the genus *Lucanus*. These insects (family Lucanidae) are characterized by the presence of enlarged mandibles in males, which are used in intrasexual contests, during which rivals wrestle with their opponents on the logs and tree trunks where females come to oviposit (Darwin 1871; Arrow 1951; Mathieu 1969; Otte & Stayman 1979). There is considerable variation in mandible size both within and between species, making the lucanids an ideal taxon in which to study the relationship between the curvature of the allometric curve and the relative exaggeration of the secondary sexual trait. In particular, if the increasing costs of possessing larger secondary sexual traits are related to the declines in slope observed towards the upper ends of the allometric curves, we predicted that as mandibles become more exaggerated (and therefore more costly) so the deviation of the curve from linearity should become greater.

2. MATERIAL AND METHODS

The collection of *Lucanus* held in the Natural History Museum, London, was used for this study. All species with more than 10 males in the collection were measured. All males were measured except in the cases of *L. parryi* and *L. cervus*, which were very numerous. Fifty males of *L. parryi* were measured, with care being taken to ensure that a sample of males of all sizes was taken. A larger number ($n = 107$) of males of *L. cervus* were measured to determine whether the males in this collection show the dimorphism that has been reported in some populations of this species. The lengths of the left mandible and the left elytron of each male were measured using Vernier callipers. The mandibles were measured from the point of articulation with the head to the distal tip.

Species used in the analysis, sample sizes and groupings for phylogenetic analysis are: *L. laminifer* group: *L. laminifer*, $n = 25$; *L. formosanus*, $n = 37$; *L. planeti*, $n = 20$; *L. lunifer* group: *L. fryi*, $n = 11$; *L. lunifer*, $n = 42$; *L. maculifemoratus* group: *L. maculifemoratus*, $n = 54$; *L. kanoi*, $n = 33$; *L. taiwanus*, $n = 74$; *L. cervus* group: *L. tetraodon*, $n = 20$; *L. ibericus*, $n = 35$; *L. fortunei* group: *L. fortunei*, $n = 34$; *L. parryi*, $n = 50$; *L. swinhoei*, $n = 34$; *L. westermanni* group: *L. westermanni*, $n = 19$; *L. dohertyi*, $n = 13$; *L. smithi*, $n = 37$; hard to place in such a group: *L. mearsi*, $n = 29$. All groupings were by M. Zillioli (personal communication). *Lucanus cervus* was also measured but the data were not included as the allometric plot indicated a clear male dimorphism, as has been reported before for this species (Clark 1977).

The curvature of the allometric line for each species was quantified by performing a least-squares fit of a second-order polynomial ($y = ax^2 + bx + c$, $y = $ log mandible length and $x = $ log elytron length) to the data for each species. The value of a then gives an indication of the amount of curvature, with a positive value indicating an increasing slope and a negative value
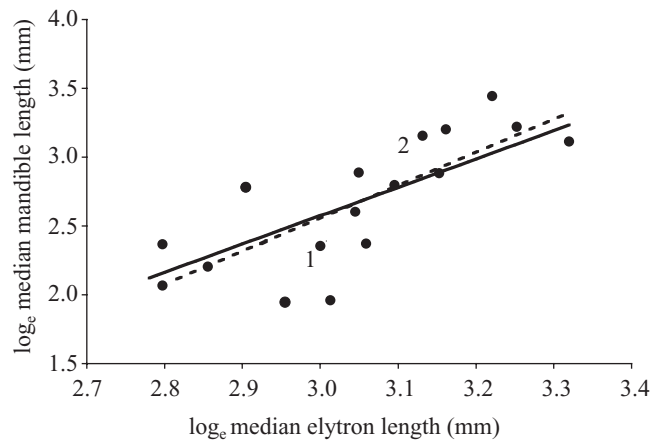
Figure 1. Interspecific allometry of mandible length in the genus *Lucanus*. Because the data are plotted on a log–log scale, the slope of the fitted line gives an estimate of the exponent k discussed in § 1. Each data point represents the median mandible length plotted against the median elytron length for an individual species. The data point marked '1' is that for *L. kanoi* and that marked '2' is that for *L. laminifer* (see figures 2 and 3). The solid line is the major-axis regression line ($y = 2.06x - 3.61$), which was used for the calculation of residuals. For comparison, the dashed line shows the least-squares regression line ($y = 2.4021x - 4.6491$).

indicating a decreasing slope, with a more pronounced decrease being indicated by a more negative value.

To control for the effects of body size on mandible size, each species was represented by its residual from the linear regression shown in figure 1. Because there is error in both the x- and y-variates in this regression, we used the major-axis regression line rather than the least-squares regression (the latter is shown on the graph for illustrative purposes; Harvey & Pagel 1991). The use of residuals in analyses such as these has recently been criticized by Garcia-Berthou (2001) and by Darlington & Smulders (2001), who recommend performing such analyses using a general linear model with the variable to be controlled for included as a covariate. This uses the least-squares estimate of the covariate, however, rather than the major-axis estimate, and statistical techniques for using more complex analytical models than a simple linear regression in conjunction with large numbers of random phylogenies (see next paragraph) have not been developed to date. For this reason we performed our analyses using residuals, and used models with body size included as a covariate whenever possible to reinforce our conclusions.

There is currently no available phylogeny for this genus, but taxonomists recognize a number of groups of species within the genus whose members are believed to be more closely related to each other than to the other members of the genus (M. Zillioli, personal communication). We used a method for analysing comparative data when the phylogeny is unknown or partly known (Martins 1996). Using COMPARE 4.4 software (Martins 2001), we generated 1000 random phylogenies with the constraint that species grouped with each other should always go together in a clade (Housworth & Martins 2001; Martins 2001). The robustness of a relationship to phylogenetic effects can then be tested using an analysis by independent contrasts for each phylogeny, and a mean least-squares regression slope calculated from all 1000 phylogenies for each analysis.
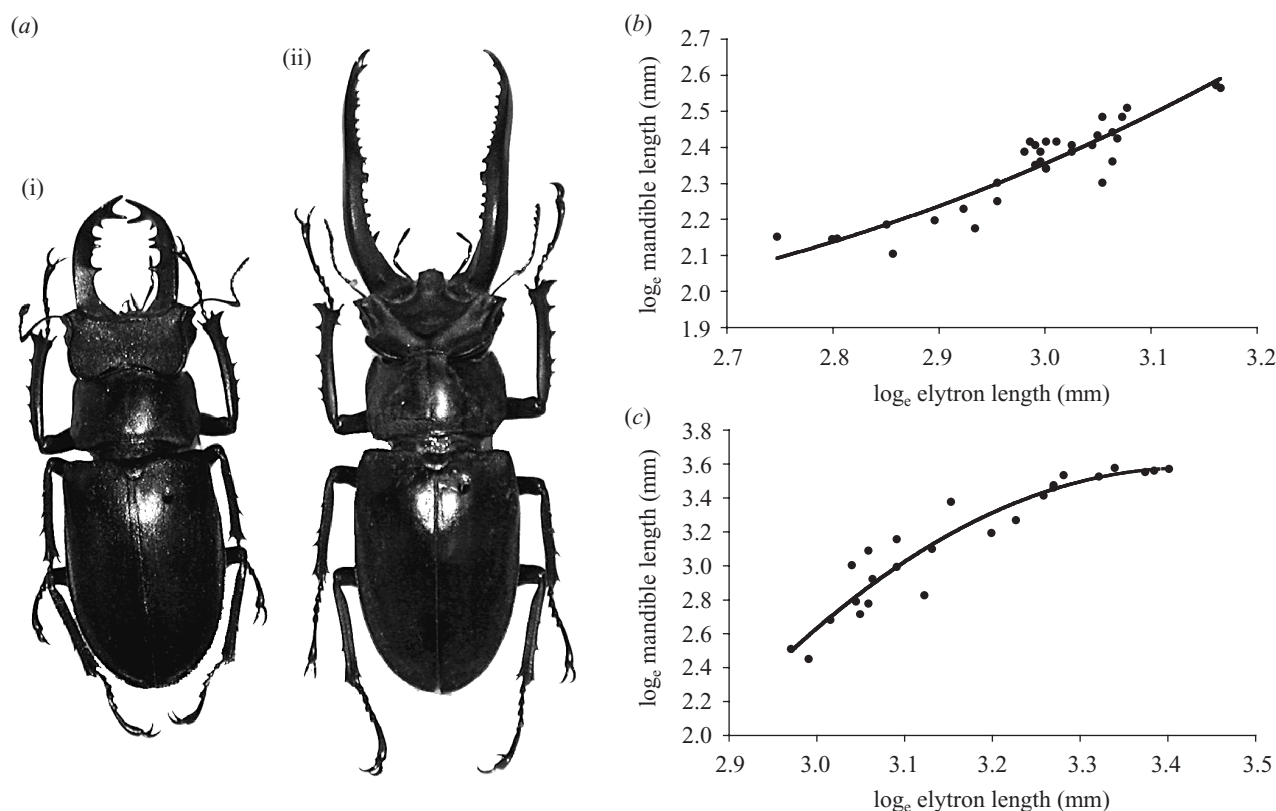
Figure 2. Variability in mandible size and allometry between lucanid species. (*a*) Examples of (i) a species with relatively small mandibles, *L. kanoi* (residual from the regression shown in figure 1 = -0.170), and (ii) a species with relatively large mandibles, *L. laminifer* (residual = 0.285). Note that these beetles were chosen to have approximately the same size elytra to emphasize the differences in mandible length. The left mandible of beetle (i) measures 11.5 mm, whereas that of beetle (ii) is 22 mm long. (*b*) Allometric curve for *L. kanoi*. The fitted polynomial is $y = 0.911x^2 - 4.197x + 6.743$. (*c*) Allometric curve for *L. laminifer*. The fitted polynomial is $y = -5.263x^2 + 36.043x - 58.127$.

3. RESULTS

Figure 1 shows the pattern of interspecific allometry found in the genus *Lucanus*. Mandible exaggeration for each species was quantified as the residual from a major-axis regression (Harvey & Pagel 1991) of log median mandible length against log median elytron length. Medians were used rather than means because the median is more robust to outliers and therefore less likely to be affected by, for example, a tendency for the collection to include more large males than is representative of the species in the wild. Figure 2 shows examples of species with large and small residual mandible lengths and their allometric curves, and figure 3 shows the relationship between residual mandible length and the curvature parameter a for each species. Residual mandible length explains 78% of the variance in curvature (linear regression: $r^2 = 0.779$, $t = 7.27$, 15 d.f., $p < 0.001$), and the relationship between curvature and relative mandible size is also significant in a general linear model with elytron length included as a covariate ($F_{1,14} = 54.91$, $p < 0.001$). This indicates that the degree of allometric curvature for mandibles depends on the amount of mandible exaggeration: beetles with relatively long mandibles for their body size have a greater decrease in the slope of the curve relating log mandible length to log elytron length than do beetles with relatively short mandibles.

Following the phylogenetic analysis described in § 2, the relationship between relative mandible size and the shape of the allometric curve remained significantly different from zero (mean regression slope from analysis by independent contrasts for 1000 random phylogenies for the relationship between curve shape and residual mandible size: -10.70, with 95% confidence limits of -16.86 to -4.53). The patterns we have found are therefore unlikely to be caused by morphologically similar species having a common phylogenetic history.

A previous comparative analysis of the allometry of earwig forceps (Simmons & Tomkins 1996) found that allometric slope increased with increasing exaggeration of the forceps. Furthermore, data from measurements of mandible length across the family Lucanidae (Otte & Stayman 1979) suggest that this may also be the case for stag beetles. Obviously simple slope comparisons are inappropriate here as many of the allometric relationships are curved, thus we calculated the slopes of the allometric curves at the smallest and largest elytron lengths from the first derivative of the fitted polynomial for each species. At the smallest body sizes the slope of the allometric curve is positively correlated with relative mandible size ($r^2 = 0.707$, $t = 6.014$, 15 d.f., $p < 0.001$), but this relationship is reversed as we move from the smallest beetles of each species to the largest, and the allometric slopes for each species at the largest body sizes are strongly negatively correlated with mandible exaggeration ($r^2 = 0.563$, $t = 4.394$, 15 d.f., $p = 0.001$). These relationships remain significant when analysed using 1000
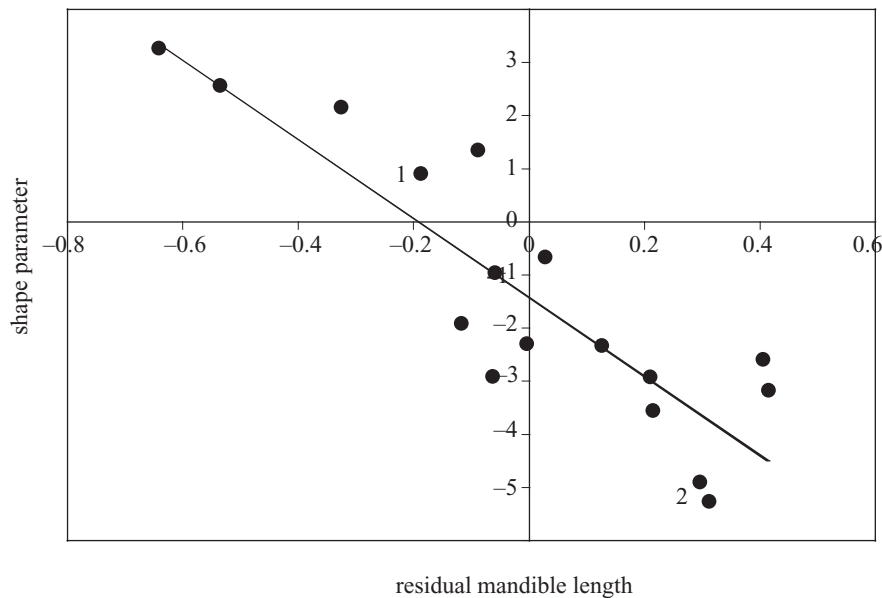
Figure 3. 'Curvature parameter' (see § 2) for each species of *Lucanus* plotted against residual mandible length (figures 1 and 2). The data point marked '1' is that for *L. kanoi* and that marked '2' is that for *L. laminifer* (see figures 1 and 2). The regression line is $y = -7.46x - 1.37$.

random phylogenies (smallest body size for each species: mean slope = 4.00, 95% confidence limits 0.518–7.490; largest body size: mean slope = −3.86, 95% confidence limits −6.50 to 1.21), and when analysed using general linear models with body size included as a covariate (smallest body size for each species: $F_{1,14} = 33.26$, $p < 0.001$; largest body size: $F_{1,14} = 28.39$, $p < 0.001$).

The sample sizes for a few of the species we used are rather small, for example *L. fryi* is represented by only 11 individuals. Reanalysis with outlying data points for these species removed or with datasets for whole species removed indicated that our conclusions are robust despite these small sample sizes.

4. DISCUSSION

Male beetles of the genus *Lucanus* that are from species with relatively large mandibles show steeper allometries at the smallest body sizes than do those from species with relatively small mandibles. The allometric curves for the beetles with relatively larger mandibles have slopes that show greater declines with body size, however, and this decline in slope is sufficient to change the direction of the relationship between relative mandible size and allometric slope at the largest body sizes, where males from species with relatively small mandibles now show the steepest allometries. This pattern is clear, and it seems unlikely that it is a consequence of common descent rather than convergent evolution.

A mechanism to account for this pattern may well be found by considering the way that the insects' mandibles develop. Beetles are holometabolous insects, and so most of the growth of the mandibles will occur from regions of the larval epidermis that behave like imaginal discs in the prepupa and pupa. The regulation of insect growth and organ size has been studied in *Drosophila* (Brogiolo *et al.* 2001; Ikeya *et al.* 2002) and in the butterfly *Precis coenia* (Nijhout & Grunert 2002). In both of these species,

growth is regulated by insulin-like peptides, acting in concert with other growth factors (imaginal-disc growth factors in *Drosophila* and the hormone ecdysone in *Precis*) that stimulate growth and mitosis. These are secreted by the central nervous system and the fat body, which appear to alter the amount of hormone released in response to haemolymph nutrient levels (Ikeya *et al.* 2002; Goberdhan & Wilson 2003; Nijhout 2003). The growth rate of the beetles' mandibles, which are derived from imaginal-disc-like epidermal tissue, is also probably dependent on hormone levels. In those species with relatively large mandibles, selection via enhanced mating success will favour beetles with, for example, more receptors for growth hormones on the cells that grow to become their mandibles, or a greater response to the growth hormones per receptor by these cells, or both. This higher growth rate of the mandibles before and during metamorphosis will give the steeper allometries seen when we analysed the slopes of the allometric curves for the smallest beetles of each species.

What of the declines in slope seen in those beetles with relatively large mandibles? The growth rate of the mandibles in the prepupa and pupa relative to that of the other parts of the animal's body is clearly important in determining their size, but their ultimate size may also be affected by the limited amount of resources available to the insect to produce the adult. Nijhout & Wheeler (1996) argue that the growth of structures during this period should be regarded as a 'miniature ecosystem', with the imaginal structures of the adult competing for a limited and diminishing pool of resources. Empirical evidence for competition between growing body parts under these circumstances comes from studies of butterflies (Lepidoptera), where removing the imaginal disc for the hindwing leads to the development of heavier forewings and other nearby structures (Nijhout & Emlen 1998; Klingenberg & Nijhout 1998), from dung beetles (Coleoptera), where large horn size correlates with

reductions in the sizes of structures close to the horns such as eyes and antennae (Nijhout & Emlen 1998; Emlen 2001), and from caddis flies (Trichoptera), in which Stevens *et al.* (2000) demonstrated trade-offs between thorax, wing and abdomen sizes. Models of the growth of imaginal discs under conditions of limited resources have shown that allometric curves with declining slopes can occur because of nutrient limitation (Nijhout & Wheeler 1996). Thus, the most obvious explanation for the patterns observed in our study is that the fast-growing mandibles of those beetles with more exaggerated characters locally deplete the resources necessary for their growth, especially when the mandibles are reaching very large sizes. In small beetles and in beetles from species with less exaggerated mandibles, the depletion of nutrients by the growing mandibles is less because they are not as large in relation to the other parts of the body, and so mandible growth is not restricted in this way.

The main cause for these curved allometries, and one of the main costs to the beetles of possessing exaggerated mandibles, therefore seems likely to be competition for resources among rapidly growing body parts in the pupa (Huxley 1932; Nijhout 1994; Nijhout & Wheeler 1996). This notion is supported by the observation that curved allometries of exaggerated traits have so far been described only in holometabolous insects, in which growth of these appendages takes place after the larva has stopped feeding (Eberhard & Gutierrez 1991; Nijhout 1994; Wilkinson & Dodson 1997; Emlen & Nijhout 2000; Hanley 2001). We are unable, however, to discount other potential costs such as the energy required to carry larger weapons, which may also contribute to these patterns (Gould 1966), and we would suggest that intraspecific tests of these ideas are necessary to complement our correlational between-species approach. Nonetheless, the observation that residual mandible size explains *ca.* 80% of the variation in the curvature of the allometric curve suggests that the increasing cost of larger mandibles is the most important factor controlling the shape of the allometric curve within this genus.

Intense directional selection, coupled with the high resource costs of these weapons, may also explain the positive interspecific allometry observed not only in this study (figure 1) but also in many other taxa, including deer (Clutton-Brock *et al.* 1980), earwigs (Simmons & Tomkins 1996) and diopsid flies (least-squares linear regression of log mean eyespan versus log mean body length using data from Baker & Wilkinson (2001): slope = 1.855, s.e. = 0.387; slope is significantly greater than 1: $t = 2.206$, 28 d.f., $p < 0.05$, major-axis slope = 2.19). A number of suggestions have been made about possible causes for this phenomenon (Clutton-Brock *et al.* 1980; Maynard Smith & Brown 1986). Most are specific to particular taxa, but Maynard Smith and Brown analysed a game-theory model of the evolution of body size when there is competition between males. They found that probable outcomes included an indefinite increase in body size, and an increase to a point where the costs of large body size became limiting and small males were able to invade, leading to cycles in body size. There are two elements of the biology of these insects that could lead to such a 'ratchet' effect driving positive interspecific allometry. First, the fitness benefit accruing to a male from possessing a sexually selected trait probably depends not on absolute trait size but on its size relative to those of conspecific males. Second, our data suggest that trait sizes are limited by their high resource costs. Males are therefore likely to become locked into an arms race whereby, as weapons reach the limits of exaggeration, only males that are larger than the average will be selected for, since they can grow larger weapons; females will become larger via genetic correlations in the genes determining body size. It should be noted here that an analysis of diopsid phylogeny and allometry (Baker & Wilkinson 2001) found evidence for decreases in allometric slope as well as increases, suggesting that such a ratchet is not necessarily unidirectional. Once again, the correlational interspecific data are suggestive, but experimental studies within species are likely to be necessary to understand these processes fully.

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