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Matters of Scale: Positive Allometry and the Evolution of Male Dimorphisms

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ABSTRACT: The developmental independence of alternative phenotypes is key to evolutionary theories of phenotypic plasticity and the origins of diversity. Male dimorphisms associated with alternative reproductive tactics are widely cited examples of such facultative expression of divergent fitness optima. Current models for the evolution of male dimorphisms invoke a size-dependent threshold at which the phenotype is reprogrammed. We use predictions derived from allometric modeling to test for the existence of reprogramming thresholds in two species of beetle, *Onthophagus taurus* and *Onthophagus binodis*, and the European earwig *Forficula auricularia*. We also compare the allometry of a number of morphological traits to determine whether minor males suppress their secondary sexual traits. The intercept of the horn allometry was suppressed, but there was no evidence of reprogramming of horn growth in either beetle species. There was reprogramming in the earwig. In the beetles, the horn length in all males can be explained largely in terms of exponential horn growth following an extraordinarily steep power function. The asymptote in *O. taurus* can be explained by exponential growth meeting the constraint of resource exhaustion. These findings question the currently held view that beetle horn dimorphisms showcase the importance of developmental independence in the evolution of diversity.

Keywords: polyphenism, juvenile hormone, imaginal disk, condition dependence, sexual selection, trade-off.

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Alternative reproductive tactics are often accompanied by the evolution of intrasexual dimorphisms. Male dimorphisms are usually found where large males have elaborate weaponry and guard females, while small males have reduced weaponry and sneak copulations (Gross 1996). Where male dimorphisms are not determined by a simple genetic polymorphism, alternative male reproductive tactics are commonly found to fit the theoretical expectations for status-dependent alternative tactics under a conditional evolutionarily stable strategy (ESS; Gross 1996). This is particularly true in insects where variation in male body size, a prime determinant of status, often has a large environmental component (Emlen 1994; Tomkins 1999). Male dimorphisms in insects consequently have been used as examples of extreme phenotypic plasticity because small males have a radically different phenotype from large males (Emlen and Nijhout 2000; West-Eberhard 2003).

The evidence for phenotypic plasticity in male dimorphic species such as earwigs and beetles is strong; nutrient deprivation produces the small “minor” male morph, and nutrient enrichment produces larger “major” males (Emlen 1994; Hunt and Simmons 1997; Tomkins 1999). The conditional ESS with status-dependent alternative tactics predicts that the individual adopts the tactic from which it will derive the highest fitness return for its status (Gross 1996). Male dimorphisms of this nature can be thought of as threshold polyphenisms in which the developmental pathway changes radically at a particular size, producing distinct phenotypes on either side of the threshold (Nijhout 2003). The developmental “uncoupling” (Emlen and Nijhout 2000) of dimorphic structures between two alternative morphs, through the existence of a developmental threshold, is an important feature of polyphenisms because it allows the two alternative phenotypes to evolve with at least partial independence (West-Eberhard 1986, 1989, 2003). This increases the scope for the evolution of the alternative tactics, unconstrained by the phenotypic optima of the other morph.

The production of threshold traits appears to require that the developmental environment and status of the individual are monitored in order to induce the pattern of

growth required to produce the “appropriate” phenotype. Current models of the hormonal basis to the threshold polyphenism in the dung beetle *Onthophagus taurus* suggest that below the critical body size males are “reprogrammed” (Wheeler 1991; Emlen and Nijhout 2001), do not grow horns, and resemble females, while after the threshold, horn growth rapidly increases, and horns are expressed in direct proportion to body size (Emlen and Nijhout 1999, 2000, 2001; Nijhout 1999, 2003; Emlen 2000; Moczek and Nijhout 2002). These patterns of growth are thought to result in the characteristic sigmoid shape of the relationship between horn size and body size in many dung beetle species (Emlen and Nijhout 1999, 2000, 2001; Nijhout 1999, 2003; Emlen 2000; Moczek and Nijhout 2002). Hence the ESS concept of a threshold, across which fitness changes between tactics (Gross 1996), is mirrored by the existence of a developmental threshold across which phenotype changes (Emlen and Nijhout 1999, 2000, 2001; Emlen 2000).

Although the existence of a developmental threshold is intuitive, it is not the only developmental model for such a pattern. Nijhout and Wheeler (1996) developed a model under which growing structures were in competition for the resources required for growth. They modeled complex allometries both with and without size-dependent reprogramming. The patterns derived from the two alternative developmental scenarios are shown in figure 1. Figure 1A and 1C show the data on a log scale, and figure 1B and 1D are the same data but on a linear scale. Figure 1B and 1D were not presented by Nijhout and Wheeler (1996) but highlight how similar patterns of linear scaling can be derived from very different growth models. Here we re-examine the developmental model that has been invoked to explain the polyphenism in the model species, the dung beetle *O. taurus*. We compare the pattern in *O. taurus* with its congener *Onthophagus binodis* and contrast it with the hemimetabolous earwig *Forficula auricularia*. We have investigated the developmental basis of the dimorphism in these species following an allometric approach in which we examine growth rates among body parts (Nijhout and Wheeler 1996). We follow Gould (1966) in using the power function $Y = \alpha X^\beta$ to examine allometry. This method is widely recognized as the basis for understanding the significance of scaling in evolutionary biology (Wilson 1953; Gould 1966; Prothero 1986; Reiss 1989; Nijhout and Wheeler 1996; Simmons and Tomkins 1996; Bonduriansky and Day 2003; Knell et al. 2004).

We set out originally to test the hypothesis that the horns of minor males were suppressed compared to ordinary morphological traits. We predicted that “hornless males” would have allometries much lower than other morphological traits and that this suppression of condition dependence could release resources toward life-history ad-

aptations in minor males (Emlen 2001; Radwan et al. 2002; Moczek and Nijhout 2004). Using this allometric approach, we found that minor male beetles have extremely high allometric exponents for horn length, much higher than morphological traits of equivalent size, but that they are suppressed in terms of the magnitude of the intercept of the horn allometry. Furthermore, contrary to the notion of a developmental threshold, we found no evidence for a dramatic change in the rate of growth of horns between minor and major males in the two species of dung beetle. Instead, we are able to explain the sigmoid horn allometry simply in terms of exponential horn growth followed by a constraint of the type predicted by Nijhout and Wheeler (1996) and recently demonstrated by Knell et al. (2004) in stag beetles. Alternatively, we did find evidence of reprogramming of the allometry in *F. auricularia*, in which the forceps allometry cannot be explained by a simple power function. Evidence for size-dependent reprogramming in polyphenic species should be carefully considered within the context of positive allometry and constraint.

Material and Methods

The *Onthophagus taurus* beetles used in this study were a random sample of 150 males collected from the field in southwestern Western Australia. We measured their pronotum width, left and right horn length, left and right elytra length, the length of the femur, tibia, and tarsus of the left and right front leg, the femur of the left and right hind leg, the left and right wing length, and the length of the large sternite on the beetle’s abdomen. From the paired characters, we used the mean of both sides in the analysis, and in both species, we used pronotum width as a measure of body size.

The *Onthophagus binodis* beetles were first-generation laboratory-reared individuals that originated in Walpole, in southwestern Western Australia. In this sample, we measured the pronotum width, horn length, and elytra width of 277 males.

The *Forficula auricularia* earwigs were a sample of 150 collected from the island of West Wideopen in the Farne Islands group in Northumbria, United Kingdom. In this sample, we measured head width, pronotum width, right fore-femur length, right hind-femur length, right elytra length, and right forceps length.

All measurements were made using a binocular microscope and eyepiece graticule or Scion image analysis software in the case of *F. auricularia*. Each species was measured by a single person.

To compare the slopes between traits that differ in size, we used the \log_{10} transformation. Least squares regression slopes were calculated using SPSS. Allometric slopes and confidence intervals (CI) were calculated using the

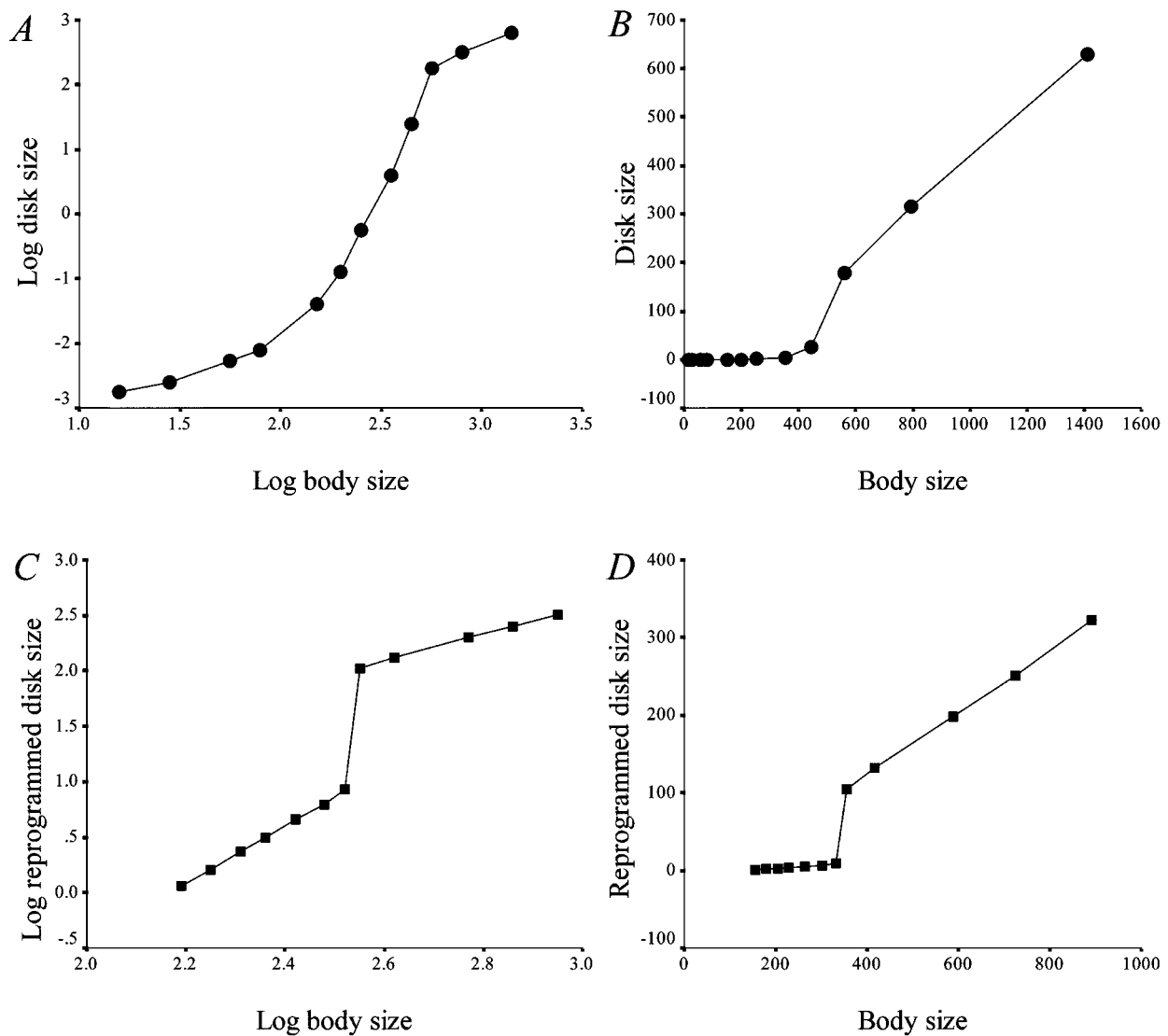


Figure 1: Plots showing the relationship between body size and the size of an imaginal disk for two growth models of Nijhout and Wheeler (1996). The points on the plot represent the end point of growth of individuals that varied in their initial size. The plots range over to two orders of magnitude, a range that is greater than is expected in a single species, and hence a species may only occupy a part of the modeled space. *A* is derived from data taken from Nijhout and Wheeler (1996 their fig. 4, lower left panel) and shows the plot where the growth parameters $S = 0.001$ and $K = 0.01$. There is no size-dependent reprogramming, and yet there are clear nonlinearities in the log-log data. *B*, Data converted to a linear scale (not presented by Nijhout and Wheeler 1996) demonstrate the existence an apparent discontinuity in disk size even though there is no size-dependent reprogramming in the model. *C*, Pattern of allometry under size-dependent reprogramming (Nijhout and Wheeler 1996, their fig. 6A). The log-log plot shows a conspicuous discontinuity, not apparent in *A*. *D*, Data from *C* on a linear scale. The patterns evident in the linear data are similar (*B*, *D*); only under log transformation (*A*, *C*) does the developmental model become evident.

(S)MATR program (Falster et al. 2003). This program calculates the standardized or reduced major axis (RMA) slope and estimates the 95% confidence intervals following Pitman (1939).

Here we only use “allometry” or “allometric” to refer to the power function with which a trait scales to body size, or to analyses performed on log-transformed vari-

ables, as the power function specifically identifies the rate at which a trait changes in size. The log transformation makes the power curve linear; the allometric slope determined from log-log regression is the same as the exponent of the power curve derived from the untransformed values of the same data. We have used the power function rather than the Gompertz growth function; the fit of the latter

is similar and good, but the interpretation of the former has more relevance to our data.

The relationship between untransformed horn or forceps length and body size in all three species is nonlinear (fig. 2). The nonlinearities in these plots provide the basis for recent interpretations of the developmental basis of these dimorphisms and also in determining the points at which one morph gives way to another. We used the modification of the Eberhard and Gutiérrez (1991) model made by Kotiaho and Tomkins (2001; see also Eberhard et al. 2000) to recognize the switch points in horn and forceps length that are apparent in these plots. We used code developed for the statistical program *R* to examine 100 possible switch points across the range of horn or forceps lengths (K. Wilson, unpublished code). We chose the switch points that maximized the r^2 of the model. The minor morph gives way to a major morph when the horn length approaches 0.29 mm in *O. taurus* ($r^2 = 0.82$) and 0.48 mm in *O. binodis* ($r^2 = 0.85$) and when forceps length approaches 3.95 mm in *F. auricularia* ($r^2 = 0.65$; fig. 1). The distributions of horn length in *O. taurus* are triphasic, having a sigmoid shape. This is less apparent in *O. binodis* and in *F. auricularia*; there is a distinct discontinuity in the distribution. The model of Kotiaho and Tomkins (2001) can also be used to detect the inflexion where the sigmoid curve begins to asymptote in *O. taurus* and *O. binodis* and between the two discontinuous sections of the forceps allometry in *F. auricularia*. We determined the upper inflexion in the horn length distributions of the three species to be at the horn or forceps length at which the β_3 term in the model was no longer significant. The β_3 term identifies the vertical displacement of the two slopes. This procedure identified a horn length of 2.70 mm for *O. taurus* and a forceps length of 5.92 mm for *F. auricularia*. For *O. binodis* there were three significant cut-off points, 0.957, 1.04, and 1.16 mm, reflecting the scarcity of the largest horned males in the sample.

We have avoided using the terms “horned” and “hornless,” but for descriptive purposes and for clarity, we categorized the majors as “majors” and “asymptotic majors.” Majors are all those above the first significant inflexion; these individuals have invested enough in horns or forceps to diverge significantly from the minor shape (determined from the untransformed scaling relationship). Asymptotic majors are those males with horns or forceps longer than the second inflexion, reflecting the asymptote or the upper part of the broken allometry.

Results

Onthophagus taurus

Despite there being an obvious nonlinearity in the relation between horn length and pronotum width in *Onthophagus*

taurus plotted on a linear scale, we found no evidence for a simple nonlinearity in the allometric exponent of log horn length on log pronotum width, evidenced by the nonsignificance of the squared term in a quadratic model ($t = 0.219$, $df = 1, 147$, $P = .83$). This suggests that a single power function is sufficient to explain most of the variation in the allometry of horn size in *O. taurus*. Consistent with this, the addition of a switch point to the model increased the model r^2 only by <1%, and the best-fitting switch point improved the model by <1% compared with the worst-fitting switch point, indicating the absence of a readily identifiable switch point. The RMA slope of horn length for all males of *O. taurus* was 15.69 (CI = 14.0–17.6), demonstrating extreme positive allometry. Figure 2B shows the power curve fitted to the untransformed data for *O. taurus*. Evidently males with the smallest horns increase their horn length with much the same allometric exponent to large males. This is further demonstrated in figure 3A in which the power curve is linearized by log-log transformation.

If minors and majors result from a reprogramming event that changes the horn growth parameters, we would expect a step function or discontinuity in the allometry of horn length on pronotum width (Nijhout and Wheeler 1996; fig. 1C). From both the power function in figure 2B and the transformed data in figure 3A, it is evident that there is no such discontinuity or step function in the allometry at the boundary between minors and majors (cf. fig. 1C, 1D). If the division between minors and majors derived from the linear data is used to discriminate male morphs, minor males have a very steep positive horn allometry of 12.2 (95% CI = 10.4–14.4); this is lower ($F = 14.1$, $df = 1, 148$, $P = .001$) but of a comparable magnitude to the allometry of all majors, 18.7 (16.2–21.5). It is evident from figure 1 that the important finding is of extreme positive allometry in the horns of minor males rather than any small differences between major and minor males in terms of the allometric slope.

The allometry of the ordinary morphological traits was also examined. There was no evidence for nonlinearity in the allometry of these traits in *O. taurus* (range of P values = .160–.929). The allometric slopes of the normal morphological traits (table 1) have a mean of 0.94 ± 0.04 (SE), close to isometry and all significantly lower than the horn length allometry.

There was a striking concordance between the allometries of the ordinary morphological traits and the upper limit of the horn lengths of major males. This suggests that the extraordinarily steep allometry cannot be sustained, and horn length in the largest males scales with size dependence. The allometry of males larger than the asymptote (asymptotic majors), as determined from untransformed data, had a horn allometry of 1.44 (95%

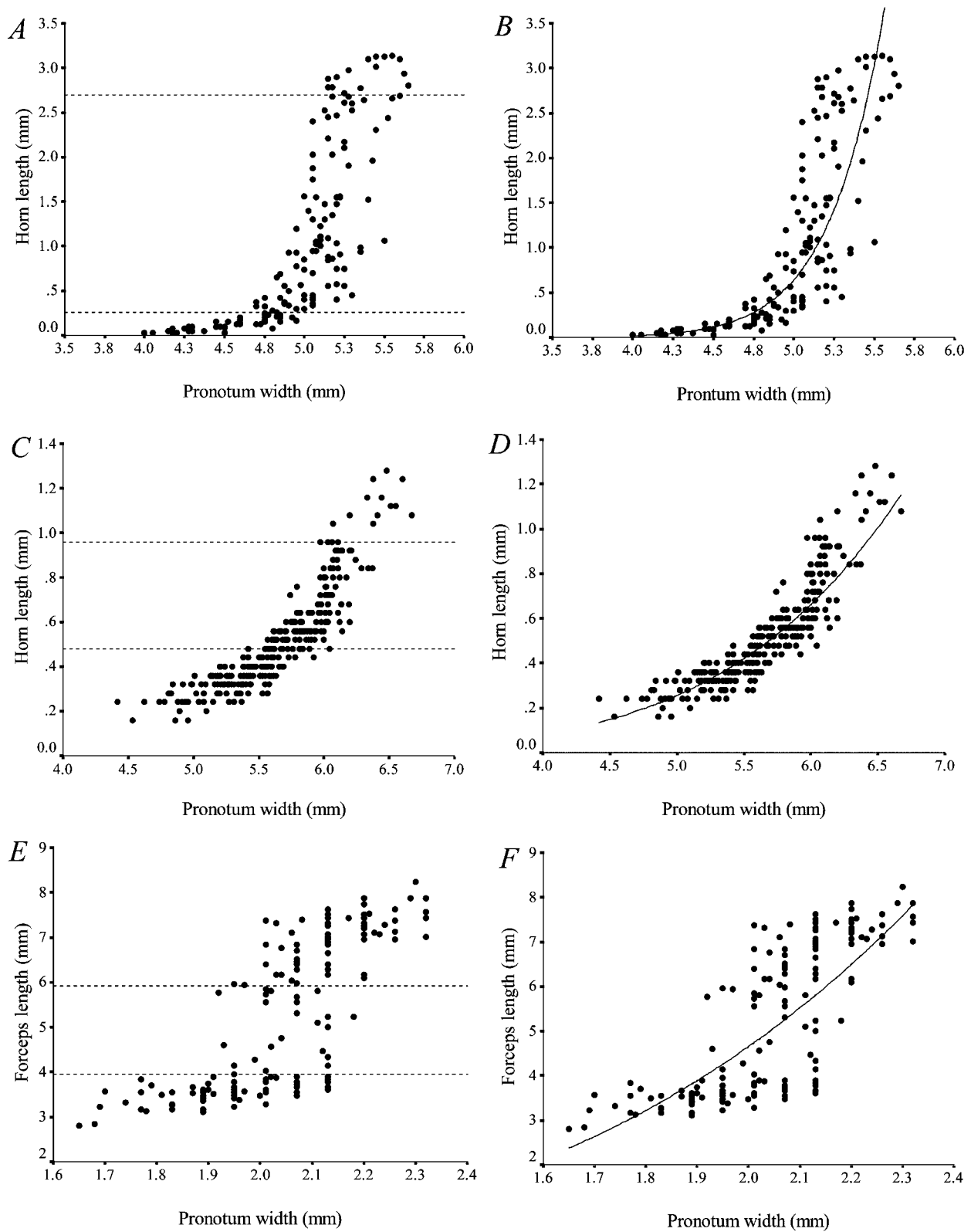
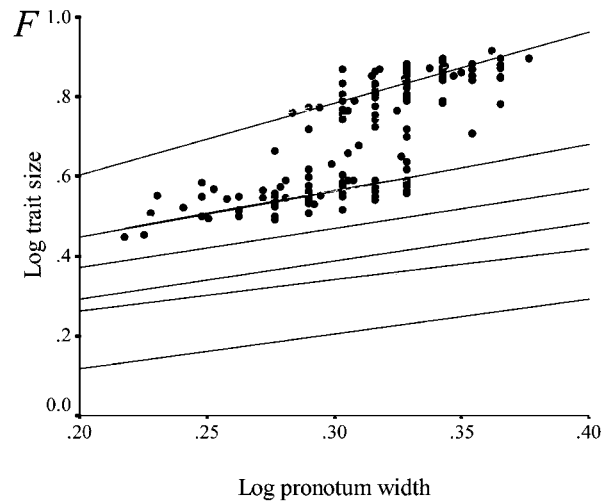
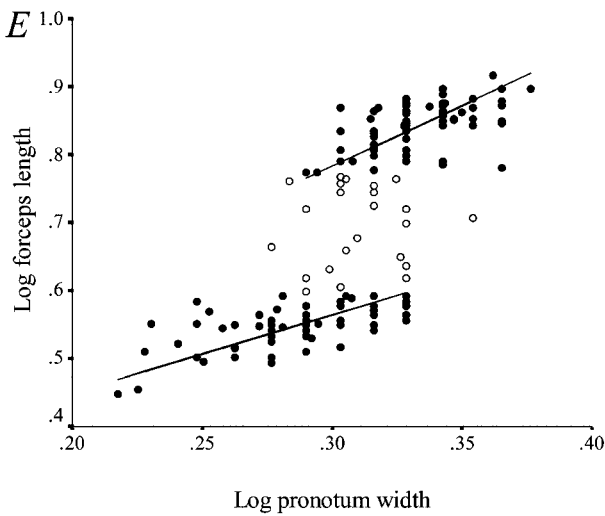
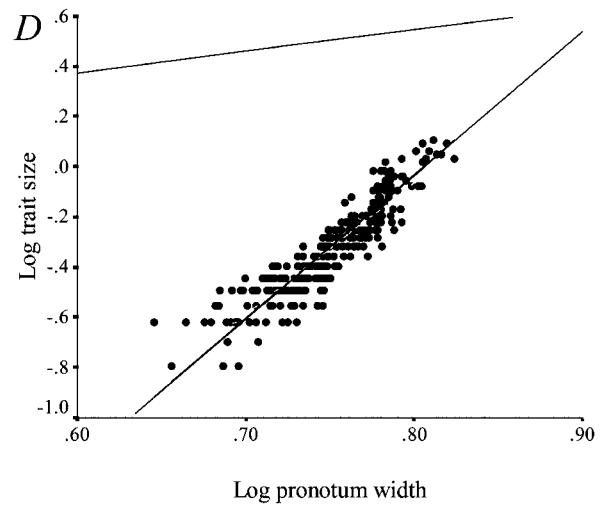
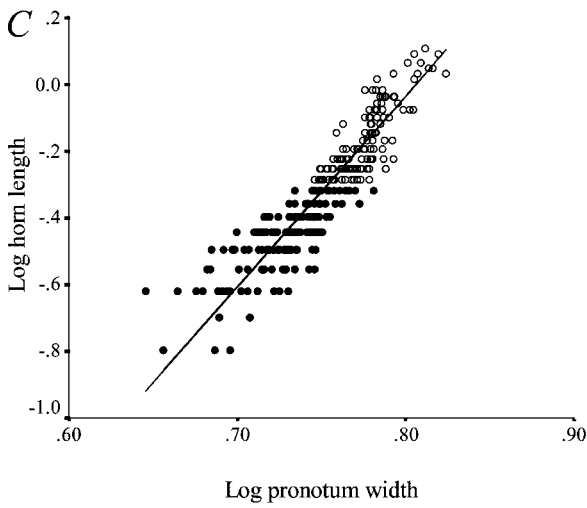
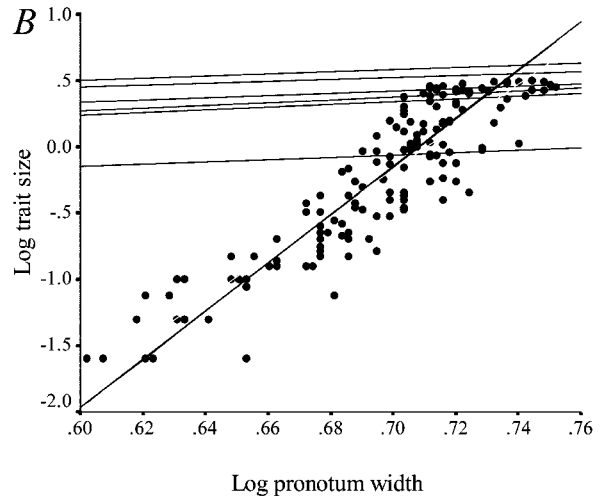
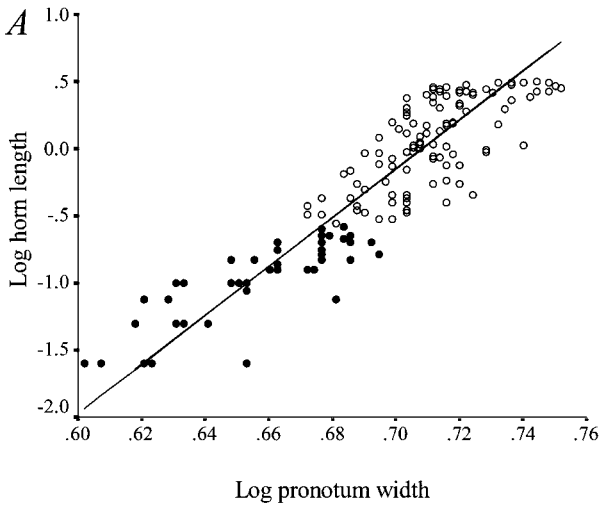


Figure 2: Distributions of horn and forceps length on body size measured as pronotum width for *Onthophagus taurus* (A, B), *Onthophagus binodis* (C, D), and *Forficula auricularia* (E, F). Lower dotted lines in A, C, and E represent the cut-off point for minor and all-major males; upper dotted lines distinguish all-majors and asymptotic majors. The power curves fitted to the untransformed data are shown in B, D, and F.



CI = 0.88–2.36) and was not significantly different from the mean allometry of normal morphological traits ($F = 3.52$, $df = 1, 14$, $P = .083$).

Onthophagus binodis

There was a significantly positive second-order term in the polynomial curve for the allometry of log horn length on log pronotum width for *Onthophagus binodis* ($r^2 = 0.85$, $t = 5.67$, $df = 2, 272$, $P < .001$). Nevertheless the raw data are fitted well by a single power function, accounting for only 2% less variance ($r^2 = 0.83$, $RMA = 5.72$, 95% CI = 5.4–6.02, $r^2 = 0.816$; fig. 2D), and there is no evidence of a step function, which might indicate reprogramming (fig. 3C). Using the morphs assigned from the nonlinearities in the raw data, we found the slope of minor males to be 4.32 (3.89–4.79) and “all-major” males to be 6.31 (5.67–7.02) and significantly different from one another ($F = 24.16$, $df = 2, 277$, $P = .001$). Elytra width scaled with isometry (table 2). We have not pursued the analysis of the asymptotic majors in this species given the ambiguity of the cut-off point and the small number of males in this size class.

Forficula auricularia

In *Forficula auricularia* there is a large overlap in the body sizes of males of putatively different morphs making the criterion of Eberhard and Gutiérrez (1991) for detecting a nonlinearity inappropriate in this species (Eberhard and Gutiérrez 1991; Tomkins 1999). The poor fit of the single power function to the data (fig. 2F) and an examination of the log-log plot of forceps length on pronotum width confirm that there is a striking difference between the allometry in *F. auricularia* and those of *O. taurus* and *O. binodis* (fig. 3A and 3C vs. 3E). The plot has the characteristics of a reprogrammed allometry in which the asymptotic majors increase in elevation (fig. 1; Nijhout and Wheeler 1996). Hence, for *F. auricularia* we reject the notion of a single power function adequately describing the data, and we use separate allometric functions for minors and asymptotic majors. The RMA slope of the forceps of the asymptotic major males was 1.78 (1.43–2.21). This is significantly greater than the average slope of other morphological traits (1.29; table 2) in majors ($F = 8.87$, $df = 1, 61$, $P = .004$) and significantly greater than the

upper 95% CI of the forceps allometry of minors (table 2; $F = 4.56$, $df = 1, 61$, $P = .03$). Hence, in addition to the increase in elevation, the majors and minors differ in the programming of the allometric slope. The slope of minor male forceps length was not significantly different from isometry (table 2; $F = 1.91$, $df = 1, 63$, $P < .170$) and no different from the average of the other morphological traits (table 2, mean = 1.21; $F = 0.24$, $df = 1, 63$, $P = .629$).

Confirming the Allometric Pattern

The surprising results for *O. taurus* prompted us to use the untransformed data to confirm the finding that the slope of horn length in minor males was unusually steep and similar to that of major males. The slopes of untransformed trait values on pronotum width cannot be used directly to test hypotheses about allometry because they are scale dependent—the variance and thus the slope increasing with the mean. This means that larger traits have steeper slopes (fig. 4). Nevertheless, the relationship between the mean size of the trait and the slope of the regression between the trait values and pronotum width for untransformed data gives us an expected value for the slope of the untransformed horn and forceps lengths. Figure 4A shows that, consistent with the data derived from the log-transformed data, the horn length on pronotum width slope derived from untransformed data for minor *O. taurus* is much steeper than expected for its mean. Data are divided between morphs in these graphs simply in order to demonstrate that the slope of minor males alone is higher than expected. Similar to minors, the slope derived from untransformed data for all-major horn length on pronotum width in male *O. taurus* is greater than expected (fig. 4B). The data points for minor and all-major male slopes both lie similar distances above the line indicating the similarity of the departure from the expected slope. The horns of asymptotic majors scale with a slope similar to what would be expected for their size and in line with the other morphological traits. In *F. auricularia*, where the log transformation indicated a slope for forceps length in minors similar to that expected for a normal morphological trait, the slopes derived from the untransformed data support this finding (fig. 4C). For all-major *F. auricularia*, the slope is steeper than expected, given the size of the forceps; this also supports the findings from

Figure 3: Log-log scatterplots showing the allometric relationships between horn length and pronotum width in *Onthophagus taurus* (A) and *Onthophagus binodis* (C) and between forceps length and pronotum width in *Forficula auricularia* (E). Minor males are represented by solid circles, and all-major males are represented by open circles, except for in *F. auricularia*, where asymptotic major males are represented by the upper cloud of solid circles. The relationship between the allometry of ordinary morphological traits (data points are reduced) and the secondary sexual traits are shown for *O. taurus* (B), *O. binodis* (D), and *F. auricularia* (F).

Table 1: Reduced major axis slopes and 95% confidence intervals (CI) between \log_{10} -transformed pronotum width and \log_{10} -transformed trait size for *Onthophagus taurus*

Trait	Common slope	95% CI
Horn length	15.69	14.0–17.6
Head width	.92	.88–.98
Elytra length	.76	.72–.80
Wing length	.84	.79–.90
Foreleg femur length	1.05	1.00–1.11
Foreleg tibia length	1.11	1.06–1.17
Foreleg tarsus length	1.05	.95–1.16
Hind leg femur length	.90	.86–.94
Sternite length	.86	.82–.91

the logged data (fig. 4D): the slope for asymptotic majors is closer to that expected from the size of the trait but lies just above the expected value.

Discussion

We have examined the allometric relationships between sexually selected traits and ordinary morphological traits in three species of male-dimorphic insect. Our results suggest that the horn dimorphism in the dung beetles studied here follow a pattern consistent with exponential growth followed by a growth constraint. In contrast, our data for the European earwig support the notion of a size-specific reprogramming event that causes a discontinuity in the forceps allometry. The data for the two onthophagines contrast with current models of horn development in which horn growth is considered to be suppressed in minor males and exponential growth to occur only in majors. This subtle change in interpretation of the growth of dimorphic structures requires a reevaluation of not only current models of dimorphic growth in these species but also the models of threshold evolution in general, the evolution of dimorphic allometries, the notion that morphs are developmentally decoupled, and the evolution of positive allometry.

We have not measured the growth rates of the epidermis that forms the horns of the beetles or the forceps of the earwigs. Instead, we are using the size of the traits in the adult as an indicator of the growth that has occurred in the preadult stage. This means that some of the differences in allometry between major and minor male morphs are likely due to small changes in shape. In distinguishing between allometries derived from continuous variation in growth parameters and variation derived from size-dependent reprogramming, the key difference is evidence of a discontinuity—a step function or “broken allometry” (Nijhout and Wheeler 1996; fig. 1). This is an important point in the interpretation of our data because even

changes to very steep allometric slopes are expected without size-dependent reprogramming (Nijhout and Wheeler 1996; fig. 1).

Current models of the evolution of the horn dimorphism in onthophagine beetles are based on the notion that there is a threshold in horn growth: larvae reaching a stable weight above a critical value go on to grow large horns, while males falling below the threshold experience a peak of ecdysone hormone and do not grow horns or grow only rudimentary horns (Emlen and Nijhout 1999, 2001). The reprogramming event is hypothesized to cause the inflexion between no horn growth and exponential growth and would be evident at a horn length of approximately 0.3 mm in our data set for *Onthophagus taurus*.

Two pieces of evidence from our data suggest that the current model for *O. taurus* requires revision. First, our data shows that the horns of minor males grow with an exponent an order of magnitude greater than other morphological traits; hence, although horns are small, they actually grow at an exponential rate. This observation itself undermines the need for a reprogramming event that has previously been invoked to explain a radical change from little or no horn growth to exponential horn growth. Second, Nijhout and Wheeler’s (1996) models have a discontinuity in the horn allometry where the reprogramming takes place (fig. 1). Our data show no such discontinuity or step function in the beetles. In both the log-log plots for the beetles (fig. 3) and where the power function is plotted against the untransformed data (fig. 2), there is a smooth transition across the point where the expected discontinuity attributable to reprogramming should lie. This smooth transition occurs because the allometric exponent in the minor males is very much steeper than expected for a trait of its size and not dissimilar to those of majors (fig. 4). These patterns contrast with those for the earwig that are consistent with size-dependent reprogramming; the power function has a poor fit to the data and minor males have a lower slope separated from majors by an obvious step function. What is evident from the modeling of Nijhout and Wheeler (1996; fig. 1A, 1B) and our data (figs. 2A, 3A) is therefore that exponential growth in horn length from the smallest minor through to the largest major has the potential to explain the principle change in the untransformed scaling relationship, that is, the sudden appearance of “horned” males along a continuum of increasing body size.

In the populations of *O. taurus* for which Emlen and Nijhout (1999, 2001) formulated the model of horn development, the asymptotic majors occur at a higher frequency than in the population studied here (Moczek et al. 2002). In Emlen and Nijhout’s model, asymptotic majors grow horns in proportion to their body size because they experience a juvenile hormone (JH) titer that is pro-

Table 2: Reduced major axis slopes with 95% confidence intervals (CI) for \log_{10} -transformed secondary sexual traits and other morphological traits on \log_{10} pronotum width in *Onthophagus binodis* and *Forficula auricularia*

Species/trait	Minor slope	95% CI	All-major slope	95% CI
<i>Onthophagus binodis</i> :				
Horn length	4.32	3.89–4.79	6.31	5.67–7.02
Elytra width	.97	.89–1.06	.97	.83–1.06
<i>Forficula auricularia</i> :				
Forceps length	1.15	.94–1.41	3.95	3.32–4.69
Forceps length (asymptotic major)	1.78	1.43–2.21
Head width	.91	.79–1.06	.98	.85–1.13
Foreleg femur length	1.37	1.14–1.64	1.28	1.06–1.56
Hind femur length	1.16	.97–1.39	1.38	1.14–1.67
Elytra length	1.39	1.13–1.72	1.52	1.28–1.82

portional to their body size and this titer determines the amount of time for which horns grow, making them linearly size dependent. We question this interpretation of the asymptote found in *O. taurus* and numerous other species of onthophagine beetle (Emlen 1996). Huxley (1932) noticed that the allometric plots of jaw length in stag beetles were curved rather than linear, showing a decreasing exponent in the largest males. Huxley's notion that this was due to the resource exhaustion in the closed system of the prepupa is supported by allometric modeling (Nijhout and Wheeler 1996) and a recent comparative study (Knell et al. 2004). An allometric exponent of 10–20 can only be sustainable when the trait is extremely small (cf. Knell et al. 2004). We suggest that the asymptotic majors have linear size-dependent horn expression not because of size-dependent hormone titers but rather due to resource limitation in the closed system of the prepupa.

Nijhout and Wheeler (1996) have modeled the effects of resource depletion on allometry. One prediction is that when resources become limited, allometry will become linear; data sets with more asymptotic majors than we have might support this prediction. A second prediction comes from the log-log plots for two imaginal disks, one reprogrammed and one not, against body size (Nijhout and Wheeler 1996, their fig. 6). In these plots, at the point at which the reprogrammed disk shifts to elevated expression, the sudden depletion in resources available to the competing, nonreprogrammed disk is revealed by a sharp change in allometry. The horn length allometry of *O. taurus* shows a sudden change consistent with Nijhout and Wheeler's prediction for the competing nonreprogrammed disk. The epithelial cells that produce the horn are not in competition with other reprogrammed tissue, but a similar effect is likely to be created by their own sudden exhaustion of the local resources. We might expect isometric scaling in a trait produced from nutrient-exhausted epithelia if resources for growth are directly proportional to the size

of the beetle. The allometry of the asymptotic majors in our data set was not significantly different from unity or the other morphological traits, as predicted by this interpretation of the constraint hypothesis.

Our data suggest that the sigmoid horn allometry in *O. taurus* is a consequence of exponential growth followed by constraint. Emlen and Nijhout (1999) propose that juvenile hormone titer determines the period of growth for the developing horns and that JH titer is likely to be size dependent, taking longer to clear from the bodies of large individuals. Size dependence in either the duration or rate of exponential growth would account for the positive allometry that generates the lower part of the sigmoid curve. Because this growth occurs at an unsustainable rate, it will exhaust the available resources and growth will cease before the maximum body size is reached, accounting for the asymptote in the sigmoid.

The revision of the horn development model presented here is compatible with the observations accounted for by the previous model. For example, there is a trade-off between horns and traits derived from the same region of the animal (Emlen 2001). Under our revision, even though the horns of minor males grow with positive allometry, they are nevertheless very small. This means that the resources available to other traits will only be depleted when horns begin to exhaust the local nutrient supply, that is, only in large majors. Further support for this revised model comes from experimental manipulations of the competition for resources within the prepupa. Moczek and Nijhout (2004) removed the imaginal disks responsible for the development of the genitalia and monitored changes in growth of the horns. Their result was surprising because instead of increasing the absolute size of the horns of the asymptotic major males, the effect was instead an apparent shift in the threshold for horn growth to a smaller critical value so that males of a smaller-than-normal body size began to produce horns. If the removal of competition

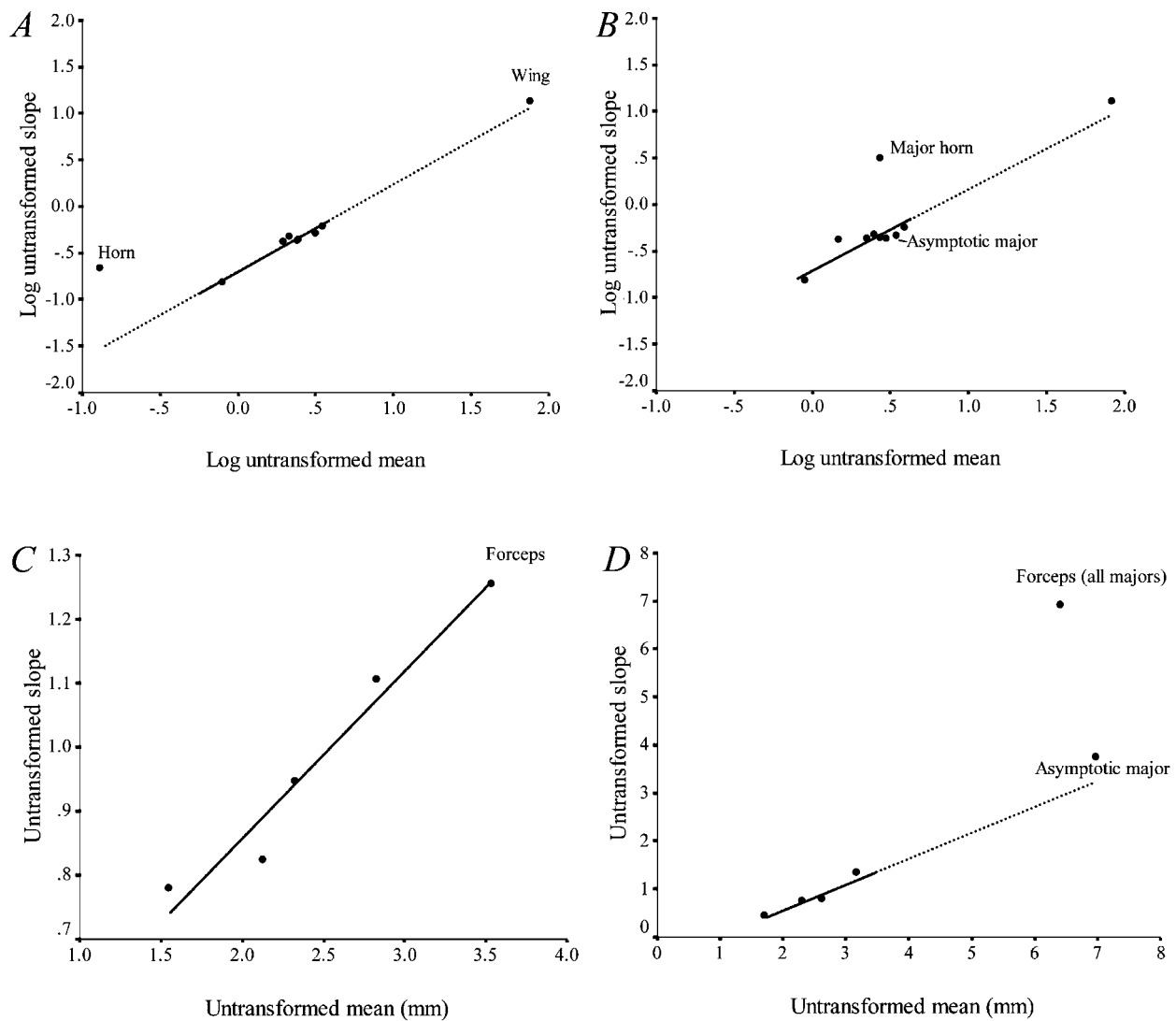


Figure 4: Relationship between \log_{10} mean trait size and the \log_{10} transformation of the slope of the untransformed trait values on untransformed pronotum width for *Onthophagus taurus* (A, B) and the relationship between mean trait size and the slope of the untransformed trait values on untransformed pronotum width for *Forficula auricularia* (C, D). The scaling relationship for both minor and major horns in *O. taurus* are highlighted (in A, B) and show how these traits have steeper slopes than expected for their size. The slope for asymptotic majors in *O. taurus* scales with a slope that is expected for the size of the trait. In *F. auricularia*, the scaling relationship for minor forceps falls along a similar line to those of other traits in that morph (C), whereas the forceps of all-majors scale with a slope greater than expected for the trait mean (D). The forceps of asymptotic majors scale slightly above the expected line. Solid lines represent least squares slopes calculated from the clustered data to avoid the influence of the outlying points (performed without using any horn or major forceps traits). Dashed lines demonstrate the expected slope derived from the clustered data.

from the genital imaginal disks prolongs the period of growth or increases the rate of horn growth in manipulated males, this would increase the horn length of males yet to reach disk exhaustion, causing an apparent shift in switch point. Consistent with the observed pattern (Moczek and Nijhout 2004), the manipulation would not be expected to increase the horn length of asymptotic majors under

the revised model because these males already grow horns for long enough or fast enough to exhaust the available resources.

Further evidence for a role of JH in determining horn size comes from topical applications of the JH analogue methoprene. Such applications have been shown to induce horn growth in putative minor males. This effect was in-

terpreted as evidence for JH sensitivity mediating a switch in morphology from hornless to horned (Emlen and Nijhout 1999). Under the revised model, the effect could be attributable to a longer period of exponential growth or a faster rate of growth in the same period, resulting in the increased length of horns at body sizes below the asymptote rather than there being any need to invoke a developmental switch. As far as we are aware, the only evidence to suggest that there is a difference in the hormonal profile between male morphs is a pulse of ecdysone found in minor males and females during the feeding stage of the larva. However, the pulse of steroid is only slightly different between the morphs and is not reported with statistics (Emlen and Nijhout 1999). The proposed effect of the ecdysone peak is to retard the growth of the horns of the minor males, but currently there is no evidence for this effect. Contrary to the notion that the ecdysone peak turns off horn growth, our data show that minors, indeed all males, have horns that have grown extremely fast.

One characteristic of dimorphisms is the bimodality in the dimorphic trait such as horns or forceps length. This characteristic invites us to believe that there is a reprogramming of trait size and that intermediate-sized individuals are selected against (Emlen and Nijhout 2000). However, intermediates are likely to be rare in species like *O. taurus* simply because the power curve becomes extraordinarily steep, and consequently trait sizes change so rapidly that few individuals fall into this size class. In the revised model, the higher mode is formed by individuals that experienced enough exponential growth to exhaust the local resources. Across species, the magnitude of the allometric exponent will determine how abruptly the transition to the asymptote occurs and also the degree of bimodality observed in the distribution of horn lengths. Species such as *Onthophagus binodis* with a relatively small allometric exponent will show low bimodality and only a gradual transition (if any) toward an asymptote as seen in our sample.

There is ample evidence that dimorphic allometries can (Emlen 1996; Roff 1996) and do evolve relatively rapidly (Roff and Fairbairn 2000; Moczek and Nijhout 2003; Unrug et al. 2004). Under the revised model, threshold evolution could occur very simply through genetic variation in the relationship between growth rates and body size. The constant α in the power function, or its transformation—the intercept in the log-log relationship—is equivalent to the number of dividing cells from which growth is initiated. Increasing α will cause the apparent threshold to shift to smaller body sizes; decreasing α will shift the apparent threshold to larger body sizes. Changes in β , the rate of growth, will similarly affect the apparent threshold. Hence, simple between-population variation in baseline growth or sensitivity to growth promoters is all

that is required to produce divergence in the apparent threshold. Whether the population variation in threshold that is known to occur in other *O. taurus* populations conforms to these patterns remains to be determined. Nevertheless, variation in JH sensitivity consistent with our expectations has already been shown (Moczek and Nijhout 2002).

Where positive allometry accounts for dimorphic variation, between-species differences in dimorphism can also arise as simple changes in the allometric parameters. For example, in *O. binodis*, although the scatter of the untransformed horn length on pronotum width is not as dramatic as *O. taurus*, the same patterns are apparent: a single power function can explain the nonlinearity, and the diphasic allometry in *O. binodis* and the triphasic allometry in *O. taurus* are therefore related simply by the magnitude of the allometric parameters. The transition from completely monomorphic species with an isometric horn, through diphasic to triphasic horn scaling, can be achieved simply through changes in the allometric properties of the curve. The more complex growth functions modeled by Nijhout and Wheeler (1996) extend this range of possibilities. Formal comparative analysis is required to confirm these patterns.

The forceps length allometry of *Forficula auricularia* is clearly very different from those of the two beetle species. The pattern conforms to one in which one morph is reprogrammed in its growth (Nijhout and Wheeler 1996; fig. 1C). In *F. auricularia*, it is the major males that appear to be reprogrammed because majors and minors are indistinguishable at the penultimate instar, but majors increase their forceps length relatively more in the molt to the adult (J. L. Tomkins, unpublished data). The discontinuous pattern of the allometry found in *F. auricularia* is by no means confined to hemimetabolous insects, being particularly common in the dimorphic wood-boring beetles such as the atlas beetle (*Chalcosoma atlas*; Kawano 1995). One mathematical reality of the power function is that where the smallest individuals have relatively large traits (i.e., α is large), it is probably impossible for the allometric exponent (β) to be large because the trait will exceed the realms of biological possibility after only a tiny increase in body size (Gould 1966). Where the smallest individuals bear a sizable trait (e.g., *C. atlas* and *F. auricularia*), it is probable that positive allometry can at best produce a gentle curve within the body size range of the organism. Hence, if selection favors two alternative tactics but both are selected (or phylogenetically constrained) to have some expression of the trait, any dimorphism is likely to be the result of reprogrammed allometries rather than a sigmoid derived from a single power function.

If a single power function explains the growth from the smallest minor to the point when the majors exhaust their

resources for growth, selection on either end of the body size distribution seems likely to have effects elsewhere. Current models for the evolution of positive allometry have not considered correlational selection in the form of selection for small horns in small males and large horns in large males (Bonduriansky and Day 2003). Correlational selection acting on different parameters of the horn allometry, for example, to reduce α and increase β , would be the form of selection expected to produce small horned minors and large horned majors. For example, selection against horns in small males is associated with a reduction in α . However, because there is still selection for large horns in large males, in order for large males to continue to express large horns, the reduction in α must be accompanied by an increase in β (fig. 5). Hence horns are suppressed, but this is because of a reduction in α that increases β . This suggests that to some extent, change in one allometric parameter (α or β) might be compensated for by change in the other. Hence, the absence of a threshold and size-dependent reprogramming weakens the possibility for selection to hone alternative phenotypes independently at either end of the size distribution (West-Eberhard 2003). If there is no developmental threshold in the male dimorphism in these beetles, the dimorphism no longer fits the description of a polyphenism as defined by Nijhout (2003) but rather is a continuous reaction norm.

Behavioral differences between morphs that appear to

correspond well to the switch in morphology apparent in the untransformed plots of horn length on pronotum width (Hunt and Simmons 1998, 2000; Hunt et al. 1999) remain to be explained if our revision is correct. It may be that despite the continuous developmental transition between morphs, behavioral adaptations to sneaking and guarding remain largely discontinuous. In this case, other adaptations (Hunt et al. 1999; Simmons et al. 1999; Hunt and Simmons 2000; Tomkins and Simmons 2000) may still be relevant. Indeed, even though the differences between morphs are not delimited by abrupt developmental boundaries, the allometry still partitions the population into distinct classes of males upon which selection for alternative behavior and investment will act.

Onthophagus taurus and dung beetles in general are a much-cited example of size-dependent reprogramming as a developmental mechanism for achieving complex phenotypes (Emlen and Nijhout 1999, 2000, 2001; Nijhout 1999, 2003; Emlen 2000; Moczek and Nijhout 2002) upon which selection can act independently, fueling the evolution of diversity (West-Eberhard 2003). Evidence for reprogramming should be manifest as a discontinuity in the log-log plots of horn size on pronotum width. This pattern is apparent in the earwig *F. auricularia* but is absent in *O. taurus* and *O. binodis*. The allometric data suggest that while the potential remains for size-dependent reprogramming to have some effects on the growth of horns in *O.*

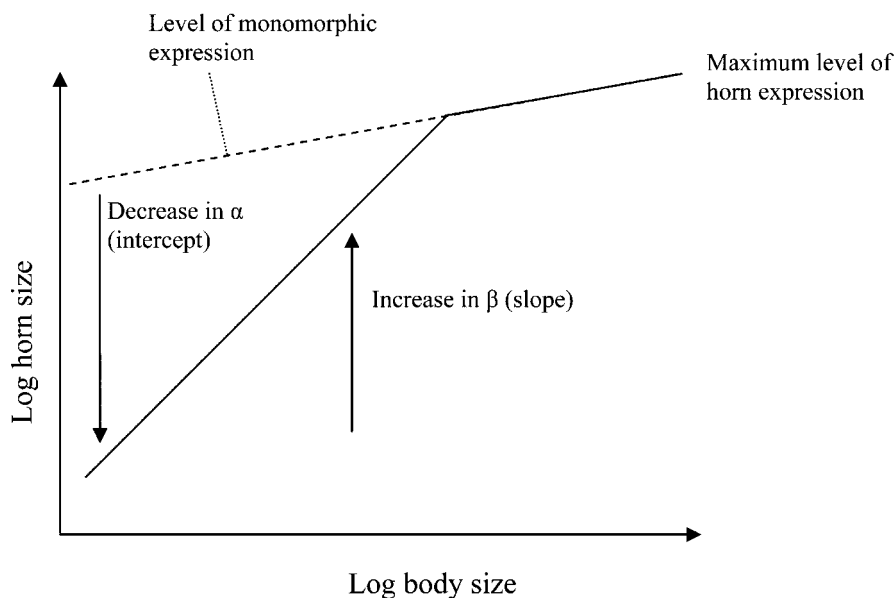


Figure 5: From a monomorphic horned ancestor in which all males express the maximum achievable horn (*dashed line*). Dimorphism (*solid line*) can arise from selection for a reduction in trait size in small males, that is, a reduction in α , the intercept of the horn allometry, accompanied by selection to maintain maximum horn expression in large males. Under this scenario, the decrease in α generates selection for an increase in β , the slope of the allometry.

taurus, these effects, if present, are far more subtle than previously modeled and can in fact be explained entirely by current models that do not include any size-dependent reprogramming events (Nijhout and Wheeler 1996). Reprogramming does occur as we have shown for *F. auricularia* and is no doubt a common feature of the allometries of many insect species. Nevertheless, our findings require the evidence for size-dependent reprogramming to be examined in the context of positive allometry and constraint.

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