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## MALE DIMORPHISMS IN BEETLES AND EARWIGS AND THE QUESTION OF DEVELOPMENTAL CONSTRAINTS

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**Abstract.**—Analysis of 17 species from six families indicates that male dimorphisms in weapon design may be common, at least in horned beetles. This flexibility in developmental programs constitutes evidence against the idea that the forms of these animals' weapons are the result of developmental constraints.

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Behavioral dimorphisms in males, including satellite or non-fighting tactics, have been documented in many animals (e.g., Thornhill and Alcock, 1983). In some species of insects, where an individual adult's size is relatively fixed, there are also morphological dimorphisms among males. Some body parts show alternative forms that are not simply extremes of a continuum of variation, but instead represent distinct body plans that presumably result from the expression of different developmental programs (Eberhard, 1980). A classic case of such intrasexual morphological dimorphism is provided by the major and minor morphs of certain horned beetles and earwigs: small males have reduced weapons (horns or cerci) or lack them altogether, whereas large males have oversized weapons that show a positive allometric relation to overall body size ( $\alpha > 1$  in the equation  $y = bx^\alpha$  where  $x$  = body size,  $y$  = weapon size, and  $b$  is a constant) (Huxley, 1932). The question of whether such dimorphisms are common is of general importance, because it bears on larger issues in evolutionary biology such as the importance of developmental constraints on morphology (e.g., Cheverud, 1984; Gould, 1984, 1989), and the role of phenotypic polyphenisms in evolution (West-Eberhard, 1986, 1989).

As with some other classic stories in biology, however, the data that document male dimorphisms in horns and cerci are not especially convincing when viewed at close range. Only a single earwig and a single beetle

species were originally analyzed numerically (Bateson and Brindley, 1892), the criteria in the analysis were inappropriate (below), and the earwig data were subsequently grouped (Huxley, 1927) in a misleading way. No other species of earwig has been analyzed since, and several later beetle studies have failed to find clear dimorphisms (Otte and Stayman, 1979 and Clark, 1977 on lucanids; Brown and Bartalon, 1986 on a tenebrionid; Eberhard, 1983 on a weevil). Some of these studies were based on relatively short series of museum specimens collected at a variety of times and sites, with possible collector bias for certain sizes, as well as possible geographic variation (Arrow, 1951; Otte and Stayman, 1979). Only three recent studies (Goldsmith, 1985 on the cerambycid *Dendrobias mandibularis*; Cook, 1987 on the scarabeine *Onthophagus binodis*; and Eberhard, 1987 on the dynastine *Ageopsis nigricollis*) have included statistical tests for the existence of male dimorphisms, and the first and last of these used ANCOVA analyses that assumed, possibly incorrectly, that values in both subsamples were normally distributed.

The present study aims to estimate the frequency of structural dimorphisms in male earwigs and beetles by analyzing newly collected data from large samples of each of eight additional species. In addition, data previously collected on nine other species are reanalyzed.

Data on behavior are important in understanding the significance of patterns in

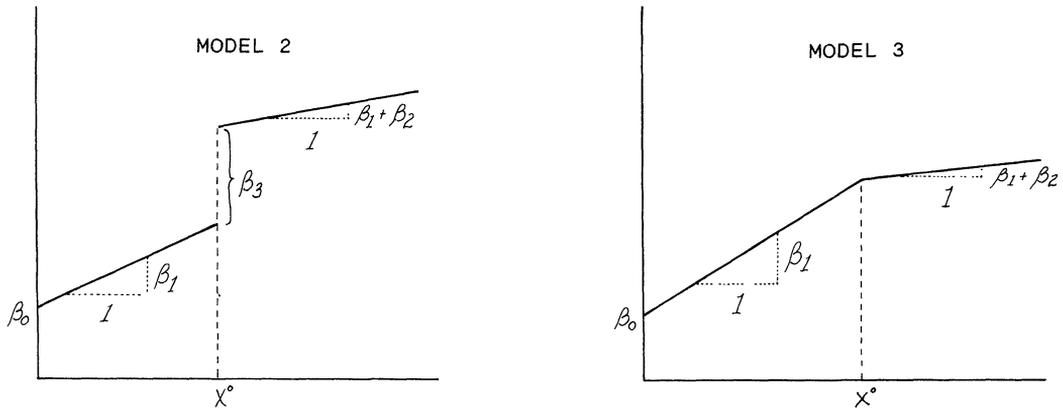


FIG. 1. Models used in statistical analyses of  $x$  (a linear measure of body size) and  $y$  (horn or cercus length). Model 2 was used to test for discontinuity at the "switch point" ( $x^\circ$ ). Model 3 was used to test for change in slope at the switch point.

morphology. In nine of the beetle species examined here behavioral observations confirm that the structures analyzed are used as weapons in intraspecific conflicts: *Ageopsis* (Eberhard, 1987); *Bolitotherus* (Pace, 1967 and pers. comm.; Brown and Bartalon, 1986); *Copris* (M. Peinador, unpubl.); *Centinaspis* (Eberhard, unpubl.); *Megasoma* (Beebe, 1944); *Dynastes* (Beebe, 1947); *Lucanus* (Darwin, 1871); *Podischnus* (Eberhard, 1979); and *Rhinostomus* (Eberhard, 1983). In the earwigs *Doru* (Briceño and Schuch, 1988), and *Metrasura* and *Paralabella* (Briceño and Eberhard, in prep.), the cerci are used both as weapons in fights between males and during courtship, and also in defense against predators. In the five other genera horn and cercus functions remain to be documented.

## MATERIALS AND METHODS

### Species

Data on previously unstudied beetle species came from measurements on a series of males collected at the following sites: 233 *Copris lugubris* B. from Santa Ana, San José Province, Costa Rica, April and May 1981 (in and under cow dung); 188 *Onthophagus incensus* Say from the same site, dates, and habitat; 129 *Centinaspis* sp. from San Antonio de Escazu, San José Province, Costa Rica, October–November 1985 (on corn plants); 183 *Xylorectes lobicollis*, 121 from Santa Maria de Dota, San José Province,

Costa Rica, April 1985, and 62 from San Ramón de Tres Rios, San José Province, Costa Rica, May and June 1984 (at lights). The following earwigs were also measured: 224 *Paralabella dorsalis* from San Antonio de Escazu, several dates in wet and dry seasons (in rotting plantain trunks in a coffee field) (135 collected in the field, 89 raised in captivity); 188 *Doru taeniatus* from near Alajuela, Alajuela Province, Costa Rica (on corn plants); and 40 *Metrasura ruficeps* from San Antonio de Escazu, October 1984–February 1985 (mostly under rotting leaves). In all cases, we attempted to collect every specimen seen in the field to avoid size biases. Two museum collections were also used: 54 *Megasoma elephas* from a variety of sites in Costa Rica (collection of the Universidad de Costa Rica); and 116 *Bolitotherus cornutus* from a variety of sites (collection of University of Michigan—data kindly provided by A. E. Pace).

The former custom of publishing raw data allowed us to analyze data on seven additional species in which appropriate statistical procedures to test for dimorphisms have not been previously performed: 177 *Cyclommatus tarandus* from various sites and dates (Dudich, 1923); 150 *Lucanus cervus* from one site (Clarke, 1977, pers. comm.); 412 *Dynastes centaurus* from one site and season (Bowden, 1959) (no linear measurement of body size was given in this species, and the cube root of wet weight was used instead); 314 *Xylotripes gideon* from

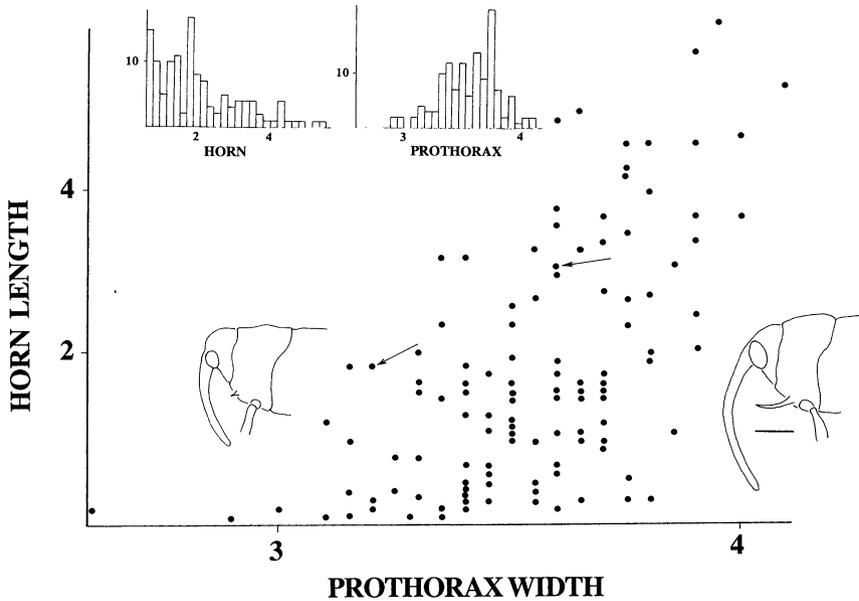


FIG. 2. Relation between maximum prothorax width and prothoracic horn length (measured from base of horn to its tip) (bar beside drawing at right) in 129 male *Centrinaspis* sp. (Curculionidae). The arrows mark the animals in the drawings.

a variety of sites (Bateson and Brindley, 1892); and 443 *Forficula auricularia* from Djakanov, 1918 in Huxley, 1927). Also included were data on 177 *Podischnus agenor* from a single season and site (Eberhard, 1982) and 46 *Rhinostomus barbirostris* from a single season and site (Eberhard, 1983).

The portions of horns and cerci that were measured are shown in Figures 2–9. All measurements were straight-line distances between two clear reference points; dimensions larger than 1 cm were measured with calipers, while others were measured with an ocular micrometer in a dissecting microscope after carefully positioning the specimen so its longitudinal and dorso-ventral axes were perpendicular to the visual axis of the ocular.

#### Analysis

Some authors (e.g., Bateson and Brindley, 1892; Huxley, 1932) have emphasized the importance of bimodal versus unimodal distributions of horn or cercus size when discussing male dimorphisms. Bimodality could result, however, from such simple and extraneous causes as different larval rearing substrates, and could be produced (or elim-

inated) by collector bias or geographic variation. Only if horn sizes are clearly bimodal and body sizes are clearly unimodal and normal are these sources of misinterpretation eliminated. Since statistical discrimination of bimodality and unimodality is difficult, this line of analysis was not used, although distributions are shown in the figures.

Data were analyzed using a combination of techniques. First a partial *F*-test (Draper and Smith, 1966) was performed by attempting to fit

$$Y^* = \alpha_0 + \alpha_1 X^* + \alpha_2 X^{*2} + \epsilon \quad (1)$$

in which  $Y^*$  is the log to base *e* of horn or cercus length;  $X^*$  is the log to base *e* of a measure of body size, such as prothorax width;  $\alpha_i$  is the regression coefficients; and  $\epsilon$  is the random component with assumed normal distribution, mean zero, and common variance.

If coefficient  $\alpha_2$  was not significantly different from zero, we concluded that further analysis was not justified and that the species showed no significant deviation from linearity.

For species with significant values of  $\alpha_2$ ,

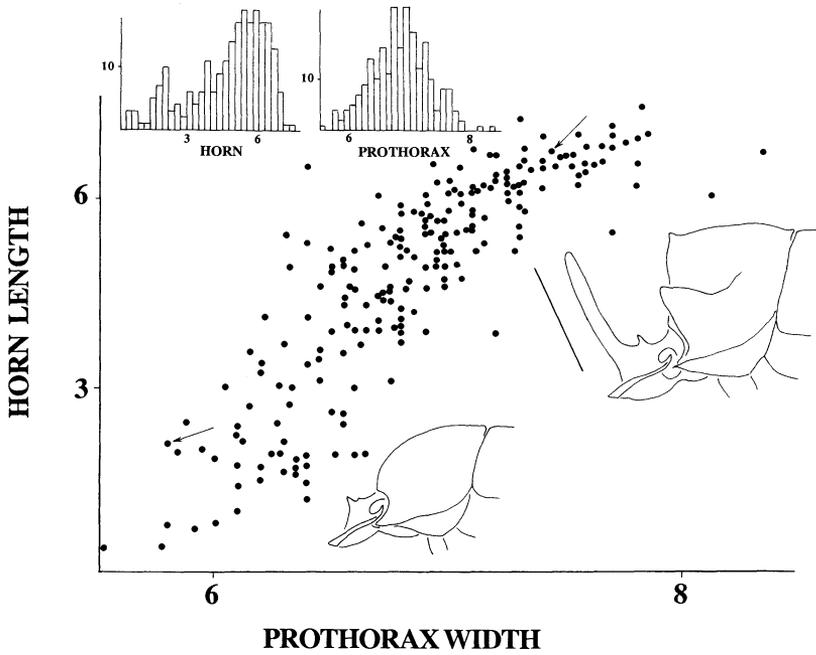


FIG. 3. Relation between maximum prothorax width and head horn length (measured from the tip of the horn to the dorsal surface of the head immediately posterior to the horn) (bar beside upper drawing) in 233 male *Copris lugubris* (Scarabeidae, Scarabeinae). The arrows to points mark the animals in the drawings.

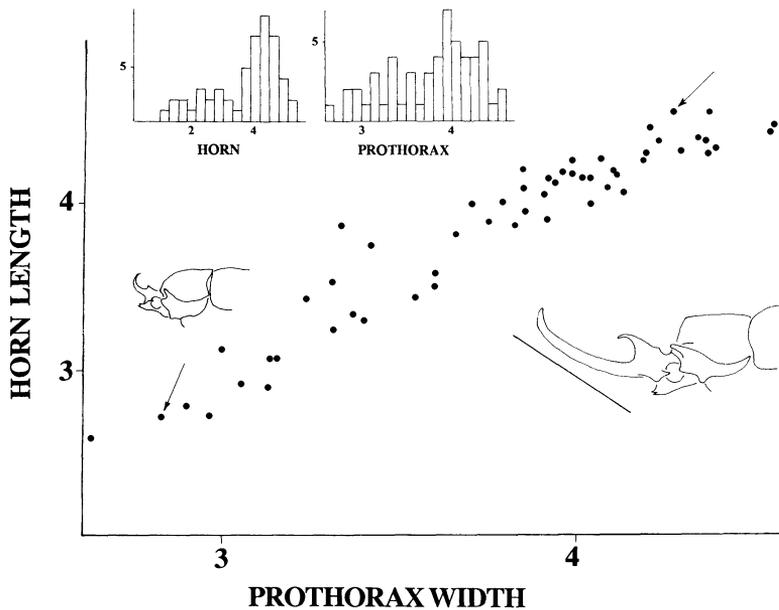


FIG. 4. Relation between maximum prothorax width and head horn length (measured from anterior-most projection of the head to the tip of the horn) (bar in figure at right) in 54 male *Megasoma elephas* (Scarabeidae, Dynastinae). The arrows mark the animals in the drawings.

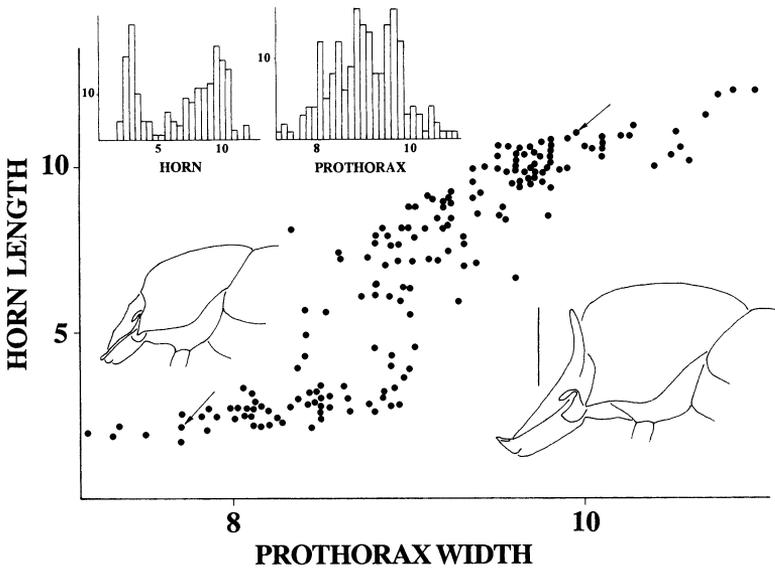


FIG. 5. Relation between maximum prothorax width and head horn length (measured from the upper margin of the eye to the tip of the horn) (bar beside figure at right) in 188 male *Onthophagus incensus* (Scarabeidae, Scarabeinae). The arrows to points mark the animals in the drawings.

a hypothesis regarding possible switching mechanisms was then tested. This hypothesis had two components: 1) the linear slope of horn or cercus ( $Y$ ) versus body size ( $X$ )

changes at some "switch point" in the range of measured body sizes; and 2) the change in  $y$  at the switch point is discontinuous rather than continuous. To test the discon-

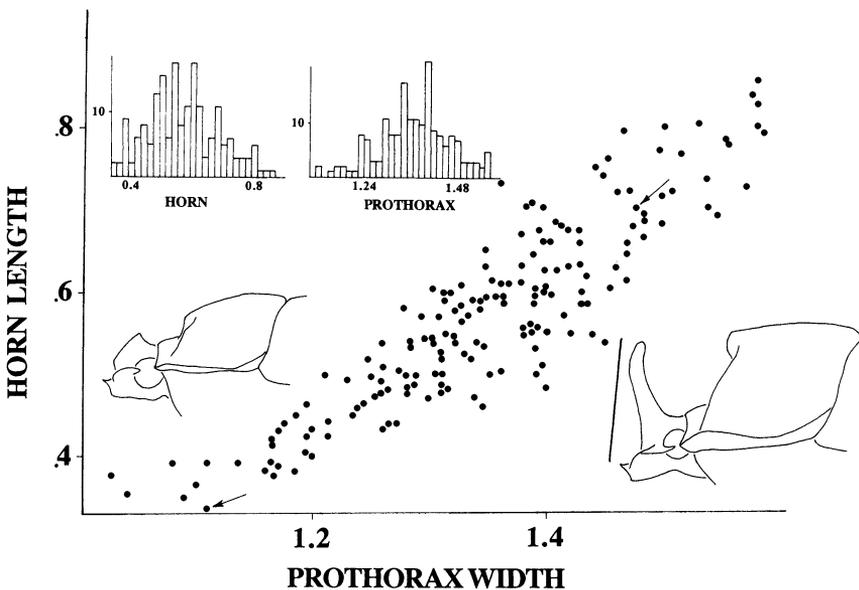


FIG. 6. Relation between maximum prothorax width and head horn length (measured from the anterior-most projection of the head to the tip of the horn) (bar beside figure at right) in 183 male *Xylorectes lobicollis* (Scarabeidae, Dynastinae). The arrows mark the animals in the drawings.

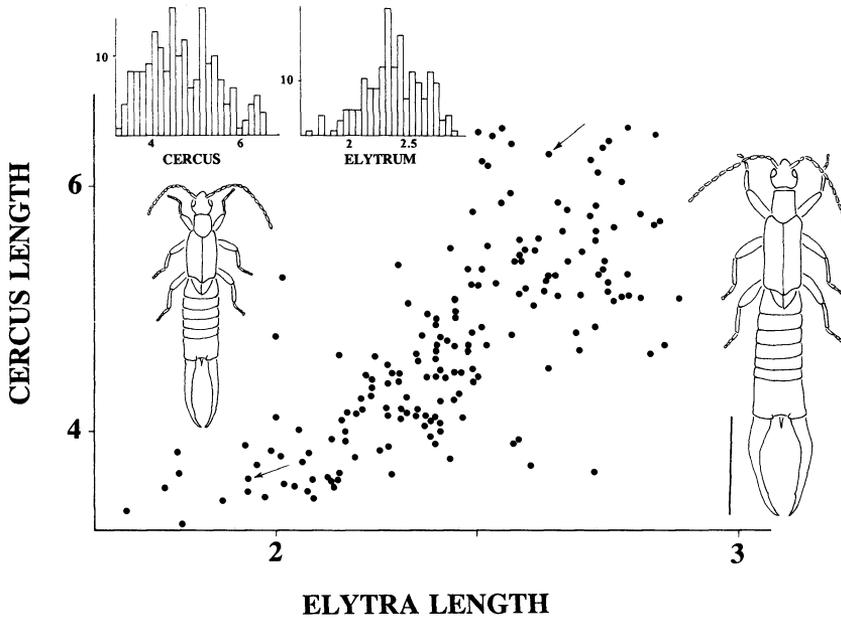


FIG. 7. Relation between elytrum length and cercus length (measured from the lateral articulation with the abdomen to the tip of the cercus) (bar beside figure at right) in 188 male *Doru taeniatus* (Forficulidae). The arrows to points mark the animals in the drawings.

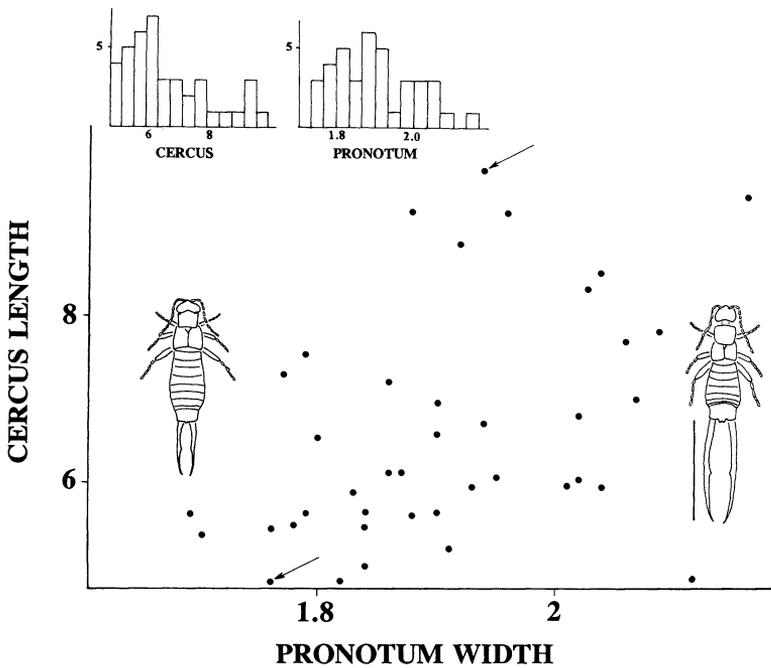


FIG. 8. Relation between maximum pronotum width and cercus length (measured from the lateral articulation with the abdomen to the tip of the cercus) (bar beside drawing at right) in 40 male *Metrasura ruficeps* (Forficulidae). The arrows mark the individuals in the drawings.

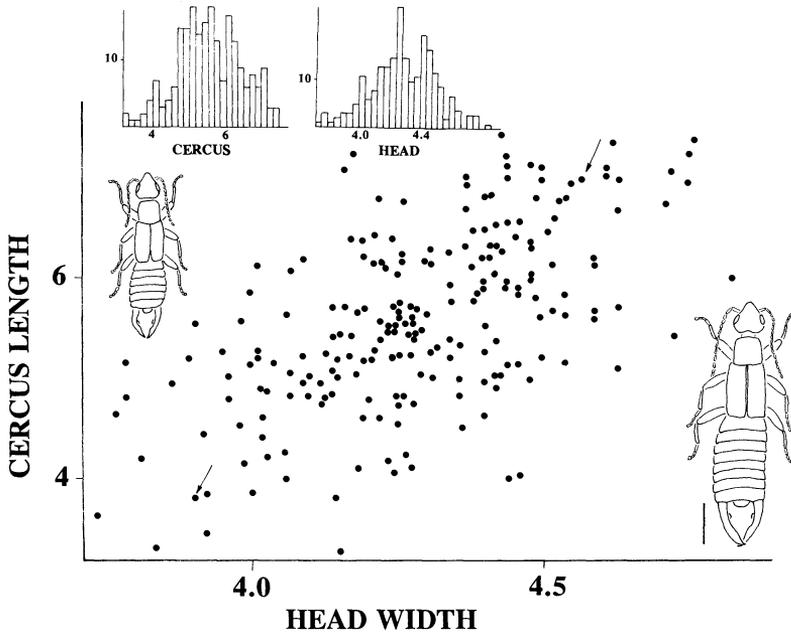


FIG. 9. Relation between maximum head width across the eyes and cercus length (measured from the lateral articulation with the abdomen to the tip of the cercus) (bar beside drawing at right) in 224 male *Paralabella dorsalis* (Labiidae). The arrows mark the individuals in the drawings.

tinuity hypothesis, the following model (Model 2 in Fig. 1) was used:

$$Y = \beta_0 + \beta_1 X + \beta_2 (X - X^0) D + \beta_3 D + \epsilon \quad (2)$$

in which  $Y$  and  $X$  are in actual measurement units;  $X^0$  is the proposed switch point;  $D$  is 0 if  $X < X^0$ ,  $D = 1$  otherwise;  $\beta_i$  is the regression coefficients;  $\epsilon$  is the random component with assumed normal distribution, mean zero, and common variance.

To determine which switch point gave the best fit, 5–10 different values of  $X^0$  (different possible switch points) were substituted in (2), and an adjusted  $R^2$  was calculated for each. The adjusted  $R^2$  values were then plotted against the possible switch points, and fitted to a fifth degree polynomial (Quasi-cubic spline); the  $X^0$  value (switch point) giving the maximum of value of adjusted  $R^2$  was determined visually.

Using this best switch value in Model 2, a hypothesis test was conducted for  $\beta_3$ . If the evidence did not justify rejection of the null hypothesis, we concluded that if a dimorphism existed, it was not discontinuous at the switch point.

To test the change of linear slope of horn or cercus versus body size at the switch point, the following model (Model 3 in Fig. 1) was used:

$$Y = \beta_0 + \beta_1 X + \beta_2 (X - X^0) D + \epsilon \quad (3)$$

in which the different terms are as defined above. Significance in the  $\beta_2$  term indicates that a “switch point” occurs.

We performed only linear tests of switch models. These represent conservative tests, since the fits of some models could undoubtedly be increased by adding higher order terms. The basic assumptions of linear regression analyses (randomness, homoscedasticity, and normality of errors) were checked in all tests using tests on the residuals. Runs tests were used for randomness, residual and normality plots for homoscedasticity, and Kolmogorov-Smirnov tests for normality.

## RESULTS

Figures 2–9 show the body size versus horn or cercus length relationships and distributions for the eight previously unstudied species, and Table 1 gives the results of par-

TABLE 1. Levels of significance for coefficient  $\alpha_2$  in Model 1 (*Dynastes* data were calculated using the cube root of wet weight).

Species	Coefficient	t-value	P-value
<b>Coleoptera</b>			
<b>Scarabeidae</b>			
<i>Ageopsis nigricollis</i>	-5.88	-6.00	<0.000
<i>Copris lugubris</i>	-25.45	-10.13	<0.000
<i>Cyclommatus tarandus</i>	-2.06	-8.94	<0.000
<i>Dynastes centaurus</i>	-3.30	-3.28	0.001
<i>Megasoma elephas</i>	-3.97	-5.94	<0.000
<i>Onthophagus incensus</i>	-6.36	-2.94	0.004
<i>Podischnus agenor</i>	-6.66	-4.91	<0.000
<i>Xylorectes lobicollis</i>	0.63	1.12	0.262 NS
<i>Xylotrupes gideon</i>	-2.26	-2.19	0.030
<b>Lucanidae</b>			
<i>Lucanus cervus</i>	1.48	4.45	<0.000
<b>Tenebrionidae</b>			
<i>Bolitotherus cornutus</i>	-14.27	-5.43	<0.000
<b>Curculionidae</b>			
<i>Centinaspis</i> sp.	6.89	1.77	0.079 NS
<i>Rhinostomus barbirostris</i>	-0.19	-1.78	0.080 NS
<b>Dermaptera</b>			
<b>Forficulidae</b>			
<i>Doru teniatus</i>	0.29	0.56	0.577 NS
<i>Forficula auricularia</i>	-1.29	-1.41	0.159 NS
<i>Metrasura ruficeps</i>	-2.99	-0.42	0.077 NS
<b>Labiidae</b>			
<i>Paralabella dorsalis</i>	-0.91	-0.34	0.730 NS

tial *F*-tests on the transformed data for all 17 species. Ten of the thirteen beetle species and none of the four earwigs showed significant values of  $\alpha_2$  in Model 1.

Of the ten beetle species that were analyzed further, five showed highly significant discontinuities (reject  $\beta_3 = 0$  in Model 2), three showed weakly significant discontinuities, and two (*Megasoma* and *Copris*) showed no significant discontinuity (Table 2). This test gave strong statistical evidence for dimorphism in *Onthophagus*, *Cyclom-*

*matus*, *Podischnus*, *Lucanus*, and *Xylotrupes*, and weaker evidence for dimorphisms in *Bolitotherus*, *Dynastes*, and *Ageopsis*). In *Cyclommatus* and *Podischnus* the coefficient for slope change was not significant, suggesting that the two morphs have similar but displaced relationships (parallel lines) between horn and body size.

Model 3 was fit to data from the species with weakly significant and non-significant  $\beta_3$  coefficients in Model 2. The change in slope was significant in all cases (Table 3), suggesting that two different patterns of allocation to weapons exist, but that the changes were gradual rather than discontinuous.

TABLE 2. Test of significance for  $H_0: \beta_3 = 0$  from Model 2. Rejection of  $H_0$  implies discontinuity.

Species	P-value
<i>Onthophagus</i>	<0.001
<i>Cyclommatus</i>	<0.001
<i>Podischnus</i>	<0.001
<i>Lucanus</i>	0.003
<i>Xylotrupes</i>	<0.001
<i>Dynastes</i>	0.027
<i>Ageopsis</i>	0.035
<i>Bolitotherus</i>	0.014
<i>Megasoma</i>	0.943 NS
<i>Copris</i>	0.853 NS

TABLE 3. Test of significance for  $H_0: \beta_2 = 0$  from Model 3. Rejection of  $H_0$  implies non-discontinuous change in body-horn relationships.

Species	P-value
<i>Copris</i>	<0.001
<i>Dynastes</i>	<0.001
<i>Ageopsis</i>	<0.000
<i>Bolitotherus</i>	<0.000
<i>Megasoma</i>	0.003

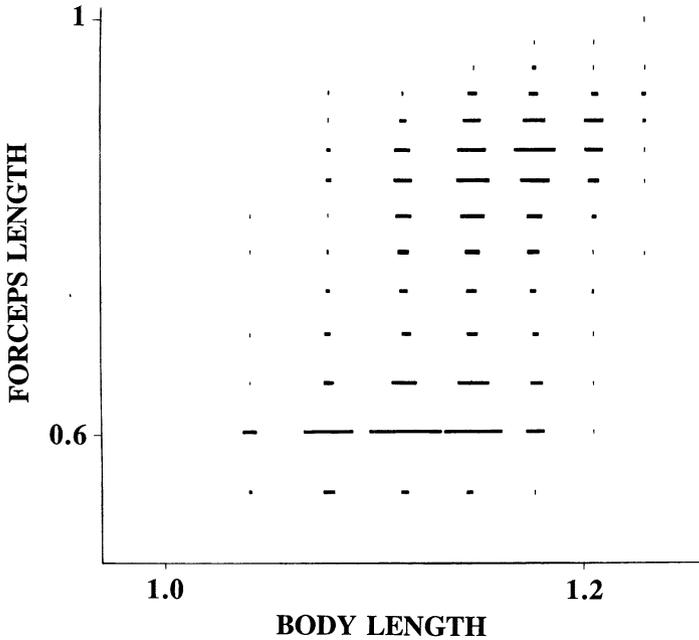


FIG. 10. Relation between body length and cercus length in 443 male *Forficula auricularia* (Forficulidae) (data from Huxley, 1932). The length of each bar is proportional to the number of individuals with each combination of values.

#### DISCUSSION

Male dimorphism was less common in earwigs (zero of four species) than in beetles (10 of 13 species). In the earwigs *Paralabella*, *Metrasura*, and *Doru*, the male cerci are used in courtship and defense against predators as well as in battles, and thus may be under more complex selective regimes in which it is not necessarily advantageous for smaller individuals to reduce relative cercus length (males of the dimorphic beetle *Lucanus cervus* also use their mandibles during interactions with females in a way which suggests courtship—W. D. Hamilton, pers. comm.). The other earwig that failed to show significant values in the partial *F*-test, *Forficula*, may have two morphs that overlap each other so broadly in body size (Fig. 10) that they failed to give significant inflection values with the models used here, which did not take into consideration the possibility of extensive overlap.

On adding the present results on beetles to published statistical analyses of other beetle species with horns or elongate mandibles (Goldsmith, 1985; Cook, 1987), the

frequency of male dimorphisms is 12 of 15 species. The two species with the smallest samples (*Rhinostomus* and *Megasoma*) failed to show highly significant dimorphisms. Sample size dependence could explain why some other studies using relatively small samples have failed to document dimorphisms (Otte and Stayman, 1979—these authors did not employ statistical tests however).

These results do not support the assumption that allometric growth patterns are relatively inflexible. They resemble similar patterns of flexibility noted in reviews of vertebrate growth patterns and body proportions: “Usually . . . the growth coefficient and the constant [b] do not remain the same in ontogeny and phylogeny . . .” (p. 141 Rensch, 1960); “evolutionary  $k$  [ $\alpha$ ] is generally not equal to ontogenetic  $k$ ” (Cock, 1966) (for recent examples see Zelditch and Carmichael, 1989; Cooper and Vitt, 1989). Thus the evidence for “allometric constraints” (sensu Gould, 1989) is not convincing.

In the context of the current debate about the relative importance of developmental

constraints versus natural selection in morphological evolution, this demonstration of flexibility in developmental rules suggests that variation in patterns of development, on which natural selection could act, may be common in these insects. Developmental rules can, like other traits, be subject to selection. "Just So Stories" that attribute such rules to developmental constraints without even attempting to test their possible selective value (e.g., Gould, 1989) are inappropriate. As noted by Lewontin (1979 p. 125) "biologists are forced to use the extreme adaptationist program," which assumes that all aspects of the phenotype are adaptive, as a point of departure in analyses "because the alternatives, although they are undoubtedly operative in many cases, are untestable in particular cases."

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#### LITERATURE CITED

- ARROW, G. 1951. Horned Beetles: A Study of the Fantastic in Nature. Dr. W. Junk, The Hague.
- BATESON, W., AND H. H. BRINDLEY. 1892. On some cases of variation in secondary sexual characters, statistically examined. Proc. Zool. Soc. Lond. 1892: 585-594.
- BEEBE, W. 1944. The function of secondary sexual characteristics in two species of Dynastinae (Coleoptera). Zool. 29:53-57.
- . 1947. Notes on the Hercules beetle, *Dynastes hercules* (Linn.) at Rancho Grande, Venezuela, with specific reference to combat behavior. Zoology 32: 109-116.
- BOWDEN, J. 1959. A note on the horn of the beetle *Dynastes centaurus* (F.). J. Entomol. Soc. South Afr. 22:78-87.
- BRICEÑO, R. D., AND W. SCHUCH. 1988. Reproductive biology and behavior of *Doru taeniatum*. Rev. Biol. Trop. 36:437-440.
- BRICEÑO, D., AND W. G. EBERHARD. In prep. The functional significance of secondary sexual characters in the cerci of males of 12 neotropical species of earwigs (Dermaptera).
- BROWN, L., AND J. BARTALON. 1986. Behavioral correlates of male morphology in a horned beetle. Am. Nat. 127:565-570.
- CHEVERUD, J. 1984. Quantitative genetics and developmental constraints on evolution by selection. J. Theor. Biol. 110:155-171.
- CLARK, J. T. 1977. Aspects of variation in the stag beetle *Lucanus cervus* (L.) (Coleoptera: Lucanidae). Syst. Zool. 2:9-16.
- COCK, A. G. 1966. Genetical aspects of metrical growth and form in animals. Q. Rev. Biol. 41:131-190.
- COOK, D. 1987. Sexual selection in dung beetles I. A multivariate study of the morphological variation in two species of *Onthophagus* (Scarabaeidae: Onthophagini). Aust. J. Zool. 35:123-132.
- COOPER, W. E., AND L. J. VITT. 1989. Sexual dimorphism of head and body sizes in an iguanid lizard: Paradoxical results. Am. Nat. 133:729-735.
- DARWIN, C. 1871. The Descent of Man and Selection in Relation to Sex. Random House, Modern Library, N.Y.
- DRAPER, N. R., AND H. SMITH. 1966. Applied Regression Analysis. Wiley, N.Y.
- DUDICH, E. 1923. Über die Variation des *Cyclommatus tarandus* Thundberg (Coleop., Lucanidae). Arch. Naturgesch. 2:62-89.
- EBERHARD, W. G. 1979. The function of horns in *Podischnus agenor* (Dynastinae), pp. 231-258. In M. Blum and N. Blum (eds.), Sexual Selection and Reproductive Competition in Insects. Academic Press, N.Y.
- . 1980. Horned beetles. Sci. Am. 242(3):166-182.
- . 1982. Beetle horn dimorphisms: Making the best of a bad lot. Am. Nat. 119:420-426.
- . 1983. Behavior of adult bottlebrush weevils (*Rhinostomus barbirostris*) (Coleoptera: Curculionidae). Rev. Biol. Trop. 31:233-244.
- . 1987. Use of horns in fights by the dimorphic males of *Ageopsis nigricollis* (Coleoptera, Scarabaeidae, Dynastinae). J. Kans. Entom. Soc. 60:504-509.
- GOLDSMITH, S. 1985. Male dimorphism in *Dendrobias mandibularis* Audinet-Serville (Coleoptera: Cerambycidae). J. Kans. Entomol. Soc. 58:534-538.
- GOULD, S. J. 1984. Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire, and Curacao: A way of studying nonadaptation. Syst. Zool. 33:217-237.
- . 1989. A developmental constraint in *Cerion*, with comments on the definition and interpretation of constraint in evolution. Evolution 43:516-539.
- HUXLEY, J. S. 1927. Studies in heteronous growth (III). Discontinuous variation and heterogeneity in *Forficula*. J. Genet. 17:309-327.
- . 1932. Problems of Relative Growth (republished 1972). Dover, N.Y.
- LEWONTIN, R. 1978. Adaptation. Sci. Am. (9):115-125.
- OTTE, D., AND STAYMEN, J. 1979. Beetle horns: Some patterns in functional morphology, pp. 259-292. In M. Blum and N. Blum (eds.), Sexual Selection and

- Reproductive Competition in Insects. Academic Press, N.Y.
- PACE, A. E. 1967. Life history and behavior of a fungus beetle, *Bolitotherus cornutus* (Tenebrionidae). Occas. Pap. Mus. Zool. Univ. Mich. 653:1-15.
- RENSCH, B. 1960. Evolution Above the Species Level. Columbia Univ. Press, N.Y.
- THORNHILL, R., AND ALCOCK, J. 1983. Evolution of Insect Mating Systems. Harvard Univ. Press, Cambridge, MA.
- WEST-EBERHARD, M. J. 1986. Alternative adaptations, speciation, and phylogeny (A review). Proc. Nat. Acad. Sci. (USA) 83:1388-1392.
- . 1989. Phenotypic plasticity and the origins of diversity. Annu. Rev. Ecol. Syst. 20:249-278.
- ZELDITCH, M. L., AND A. C. CARMICHAEL. 1989. Ontogenetic variation in patterns of developmental and functional integration of skulls of *Sigmodon fulviventer*. Evolution 43:814-824.

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