

Allometric plasticity in a polyphenic beetle

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Abstract. 1. Environmental conditions, such as variation in nutrition, commonly contribute to morphological variation among individuals by affecting body size and the expression of certain morphological traits; however the scaling relationship between a morphological trait and body size over a range of body sizes is generally assumed not to change in response to environmental fluctuation (allometric plasticity), but instead to be constant and diagnostic for a particular trait and species or population. The work reported here examined diet-induced allometric plasticity in the polyphenic beetle *Onthophagus taurus* Schreber (1759) (Coleoptera: Scarabaeidae).

2. Male *O. taurus* vary in body size depending on larval nutrition. Only males above a critical body size threshold express fully developed horns; males smaller than this threshold develop only rudimentary horns or no horns at all.

3. Field populations that naturally utilise two different resources for feeding larvae (horse dung vs. cow manure) exhibited significant differences in the average scaling relationship between body size and male horn length over the same range of body sizes. Males collected from cow manure populations expressed consistently longer horns for a given body size than males collected from horse dung populations.

4. Males reared in the laboratory on horse dung or cow manure also exhibited significant differences in the average scaling relationship between body size and horn length. Differences between laboratory populations reared on horse dung or cow manure were of the same kind and magnitude as differences between field populations that utilise these different resources naturally.

5. These findings suggest that between-population differences in scaling relationships between horn length and body size can be the product of differences in the quality of resources available to developing larvae. Results are discussed in the context of onthophagine mating systems and recent insights in the developmental and endocrine control of horn polyphenisms.

Key words. Adaptive phenotypic plasticity, allometric plasticity, alternative tactics, developmental threshold, horn polyphenism, *Onthophagus*, status-dependent selection, threshold evolution.

Introduction

Environmental conditions commonly affect the expression of many morphological traits, resulting in enormous phenotypic variation in some species (Schmalhausen, 1949; Shapiro, 1976; Roff, 1996; Schlichting & Pigliucci, 1998; Emlen & Nijhout, 2000). A universal environmental factor

that contributes to morphological variation is nutrition, which causes variation in overall body size and the expression of certain morphological traits in many species (e.g. head width in ants: Passera, 1974, 1985; Wheeler & Nijhout, 1983, 1984; horn length in beetles: Emlen, 1994; Moczek & Emlen, 1999; cerci length in earwigs: Tomkins, 1999). In such cases, the average scaling relationship of a morphological trait with body size within a population can be described quantitatively by means of a *static* allometry (*sensu* Cock, 1966), i.e. by plotting the relationship between body size on the *x* axis and the trait of interest on the *y* axis for a large number of individuals of the same age group or

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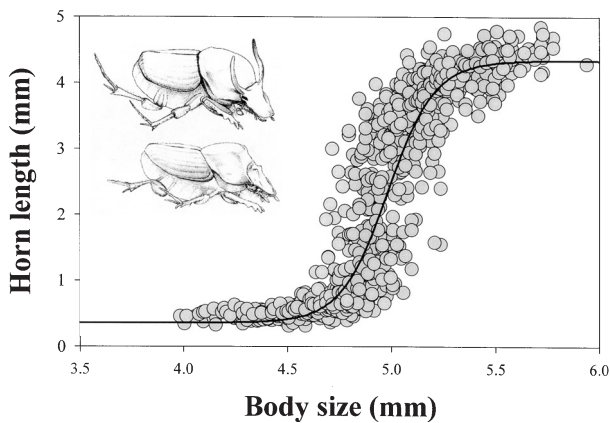


Fig. 1. Scaling relationship between horn length and body size of all field-collected males combined ($n = 821$). The combined samples were used to fit a modified logistic equation to describe the average relationship between body size and horn length (indicated by solid line; horn length = $3.974 / \{1 + \exp[-8.863 \times (\text{body size} - 4.987)]\} + 0.3596$). This reference function was used to calculate residual horn lengths for all males and to compare populations based on their residual horn length distribution (see Figs 2 and 4). Insert: Typical morphology of hornless and horned male *O. taurus* (drawings by Shane Richards).

life-history stage (Cock, 1966; Emlen & Nijhout, 2000). Static allometries are commonly used to quantify patterns of morphological variation in natural populations (Clark, 1977; Goldsmith, 1985; Wenzel, 1992; Ito *et al.*, 1994; Kawano, 1995a), to infer ecological and evolutionary processes in nature (Gould, 1973; Feener *et al.*, 1988; Petrie, 1988, 1992; Green, 1992; Kawano, 1995b, 1997; Simmons & Tomkins, 1996; Simmons *et al.*, 1999; Emlen & Nijhout, 2000; Palestini *et al.*, 2000), and for comparative taxonomic purposes (Bocquet, 1953; Kermack, 1954; Kurtén, 1954, 1964; Mitra, 1958; Bährens, 1960). While the morphological variation between individuals, on which many static allometries are based, is known to be in part due to environmental influences, certain parameters of a static allometry itself, such as its slope or the location of a switch point, are generally assumed not to depend on environmental conditions but to be constant and diagnostic for a particular species or population.

A growing number of studies, however, support the view that static allometries are not free from environmental influences but may in fact themselves respond to environmental fluctuations, such as variation in nutrition, in a plastic fashion (allometric plasticity *sensu* Emlen, 1997a; see also Wheeler & Nijhout, 1984; Knell *et al.*, 1999). The work reported here examined allometric plasticity in the horn dimorphic dung beetle *Onthophagus taurus*. Male *O. taurus* vary in body size in response to larval feeding conditions (Moczek & Emlen, 1999). Males larger than a certain critical threshold size develop a pair of disproportionately long horns on their heads, while males smaller than this threshold develop only rudimentary horns or no horns at all (Moczek, 1998; Moczek & Emlen, 1999;

Fig. 1). *Onthophagus taurus* naturally uses a wide range of resources for feeding larvae (Moczek, 1996, 1998), and previous work has established that two types of resource commonly utilised by *O. taurus* larvae (horse dung and cow manure) differ greatly in their nutritional quality and consequences for larval growth and development (Moczek, 1998). *Onthophagus taurus* therefore represents an ideal study organism to explore the effects, if any, of natural variation in larval feeding conditions on adult scaling relationships. The study examined the effects of natural variation in larval nutrition on the scaling relationship between body size and male horn length. First, natural populations that differ in the quality of resource to which they have access were compared with respect to the average scaling relationship between horn length and body size, and specifically with respect to the location of the critical threshold body size that separates alternative male morphs. A controlled laboratory rearing experiment then examined whether natural variation in larval feeding conditions can account for changes in adult scaling relationships and the location of body size thresholds. Results are discussed in the context of onthophagine mating systems. An alternative explanation for allometric plasticity based on recent insights in larval growth physiology and the developmental control of horn polyphenisms is proposed.

Materials and methods

Natural history of Onthophagus taurus

Onthophagus taurus originally exhibited a circum-Mediterranean distribution (Balthasar, 1963). In the early 1970s, *O. taurus* was introduced accidentally to the eastern United States and intentionally to several areas in Australia (Fincher & Woodruff, 1975; Tyndale-Biscoe, 1990). *Onthophagus taurus* is now the dominant onthophagine beetle in North Carolina, U.S.A., where it colonises dung pads of cattle, horses, and sheep (Moczek, 1998, and unpublished; see also Fincher & Woodruff, 1975; Halfpiter & Edmonds, 1982). Dung is used by both adults and larvae as a food resource. Once a dung pad is colonised, adults dig vertical tunnels through the pad into the soil, form a small cavity at the blind end of the tunnel, and pull dung pieces down into this cavity (Moczek, 1999). Dung pieces are formed into well-compacted, oval brood balls (*brood masses*; Halfpiter & Edmonds, 1982). At the top end of each brood ball, an egg chamber is formed, provided with a single egg, and covered with an excrement cap. Successive brood balls are formed in the same fashion, and each is separated from its neighbours by a plug of soil (Goidanich & Malan, 1962; Moczek, 1996). No further care is given to the offspring and each brood ball constitutes the total quantity of food available to a single larva. Beetles complete larval development and metamorphosis inside the brood ball (Goidanich & Malan, 1962, 1964; Halfpiter & Edmonds, 1982). Development from the egg to an enclosing adult requires ≈ 30 days in the laboratory at 26 °C (Shafiei *et al.*, 2001).

Field populations

Beetles were collected from two horse pastures and three cow pastures in Durham and Orange County, North Carolina (36°N, 79°W): Bahama (horse), Tierreich Farm (horse), Cornwallis Farm (cow), Highway 86 (cow), and Picket Farm (cow). Populations were sampled by placing entire dung pads in buckets and carefully hand-collecting all beetles that had colonised the pad. Beetles were killed immediately using ethyl acetate and stored in 70% ethanol. Individuals were sexed based on the presence of horns (expressed in males only) and pygidium morphology (Balthasar, 1963) using a WildTM dissecting microscope.

Laboratory breeding

Approximately 1200 individuals collected from Cornwallis Farm (cow) within a 2-week period were transferred to the laboratory alive and used for breeding experiments. Five pairs of beetles were placed in a plastic container 35 cm in height × 20 cm in diameter, three-quarters filled with a moist 2:1 sand:soil mixture and provided with ≈1 litre of either fresh horse or cow dung, and allowed to breed. Breeding containers were kept in an insectary at Duke University at 26°C, 60% RH, and a LD 16:8 h photoperiod. Adults and brood balls were collected after 1 week. Adults were killed and stored in ethanol. Brood balls were stored individually in plastic cups filled with a moist 2:1 sand:soil mixture at 26°C, 60% RH until emergence of adult beetles. Five breeding containers per resource per week were set up in this way for a total of 8 weeks. Emerging individuals were killed and sexed as described above.

Morphological measurements

All males collected in the field and reared in the laboratory were measured using a standard two-dimensional image analysis system in the Duke University Morphometrics Laboratory. Thorax width was used as an estimate of body size (for details see Moczek, 1996, 1998; Moczek & Emlen, 1999, 2000; for justification for using thorax width see Emlen, 1994). To avoid any personal bias in measurements, all specimen vials were made anonymous by a colleague and all specimens were measured by the author *blind*, i.e. without knowing the origin of the individuals until all measurements were complete.

Statistical analysis

Body size was not distributed normally in some samples, so a non-parametric Kruskal–Wallis *H* test was used to test for differences in body size between samples. Once significant variation was indicated, multiple Mann–Whitney *U* tests were used for pairwise comparisons (including

sequential Bonferroni corrections for multiple comparisons; see below).

In order to compare the location of the threshold body size between samples, a modified logistic equation of the form

$$\text{horn length} = \frac{a}{[1 + e^{b(\text{body size} - c)}]} + d$$

was fitted to all field-collected individuals combined ($n = 821$ males, see Fig. 1; a describes the range of horn lengths in the sample, b specifies a slope coefficient, c represents the body size at the point of inflection of the sigmoid, and d specifies minimum horn length; parameter values were obtained via iterations using Sigma PlotTM curve-fitting procedures (see the legend of Fig. 1 for actual parameter values). This reference function was then used to predict horn lengths for all males in all populations given their respective body sizes. Individual males were then characterised by the degree to which their real horn length differed from the horn length predicted by this reference function, i.e. by their *residual* horn length. Populations that differed in their scaling relationship between horn length and body size could then be recognised by consistent differences in residual horn lengths (see also Emlen, 1997a). Because horn length residuals differed significantly from normality for all populations, a non-parametric Kruskal–Wallis *H* test was used to test for significant differences between samples. Once significant variation was indicated, multiple Mann–Whitney *U* tests were used for pairwise comparisons.

Morph ratios were obtained by counting males on both sides of the inflection point of the sigmoidal reference function used to calculate horn length residuals (cut off horn length = 2.35 mm; Fig. 1) and compared using multiple χ^2 tests (Lozan, 1992). Significance levels from parametric and non-parametric tests were corrected for multiple comparisons using sequential Bonferroni correction procedures when necessary (Sachs, 1992; Sokal & Rohlf, 1995).

Results

Field populations

Pairwise comparisons between field populations showed no significant differences in body sizes, with one exception (Bahama vs. Cornwallis Farm, $Z = 2.80$, $P < 0.01$; for all other pairwise comparisons, $P > 0.5$; Table 1); however field-collected males differed significantly and consistently in their residual horn lengths depending on the resource available to the population from which they were collected (Fig. 2). Males collected from both horse dung populations in the field expressed smaller residual horn lengths (i.e. developed shorter horns for a given body size) than males collected from any of the three cow manure populations. All six pairwise comparisons between horse dung and cow

Table 1. Male median body sizes and morph ratios in field samples and laboratory populations. Different letters in the exponent indicate significantly different median male body sizes (multiple Mann–Whitney U tests including sequential Bonferroni correction for multiple comparisons, $P < 0.05$). Asterisks indicate morph ratios that are significantly different from 1:1 (multiple χ^2 tests including sequential Bonferroni correction for multiple comparisons, $P < 0.05$).

	Body size (mm)	Horned : hornless	<i>n</i>
Field			
Horse dung			
Tierreich Farm	4.995a,b	1:0.96	204
Bahama	5.01a	1:0.97	143
Cow manure			
Cornwallis Farm	4.90b,c	1:1.48*	241
Highway 86	4.95a,b,c	1:1.17	76
Pickett Road	4.96a,b,c	1:1.07	157
Laboratory			
Horse dung	4.975a,b	1:1.05	160
Cow manure	4.885c	1:1.49*	214

manure populations were significantly different if tested separately, and four comparisons remained significantly different ($P < 0.05$) after sequential Bonferroni correction procedures were applied (Fig. 2).

Laboratory populations

Males reared on cow manure in the laboratory expressed significantly smaller body sizes than males reared on horse dung ($Z = 1.97$, $P < 0.05$; Table 1) or males collected from both horse dung populations in the field ($P < 0.05$ for each comparison; Table 1). Males reared on horse dung in the laboratory expressed slightly but not significantly larger body sizes than males collected from cow dung populations in the field ($P > 0.05$; Table 1).

Laboratory-reared males also differed significantly in their residual horn lengths. Males reared on horse dung expressed significantly smaller residual horn lengths (i.e. expressed significantly shorter horns for a given body size) than males reared on cow manure or males collected from any of the three cow manure populations in the field ($P < 0.05$ for each comparison including sequential Bonferroni correction; Figs 3 and 4). Similarly, males reared on cow manure in the laboratory expressed significantly larger residual horn lengths (i.e. expressed significantly longer horns for a given body size) than males collected from both horse dung populations in the field ($P < 0.05$ for each comparison including sequential Bonferroni correction; Figs 3 and 4). Therefore, differences in residual horn lengths between populations reared in the laboratory on horse dung or cow manure were in all cases in a direction and of a magnitude similar to those observed between field populations that utilise horse dung or cow manure in nature (Figs 2 and 4). These findings suggest strongly that between-population differences in body size thresholds in nature can be the product of differences in the quality of resources available to developing larvae.

Morph ratios

Both horse dung populations exhibited morph ratios not significantly different from 1:1, as did two of the three cow manure populations (all $P > 0.1$). One cow manure population (Cornwallis Farm) exhibited a significant hornless-male bias ($\chi^2 = 4.63$, $P < 0.05$; Table 1). In the laboratory populations, both morphs emerged at approximately equal frequencies when males were reared on horse dung, whereas the hornless morph emerged at a significantly higher frequency in males reared on cow manure ($\chi^2 = 4.16$, $P < 0.05$; Table 1).

Discussion

The work reported here examined diet-induced allometric plasticity in the polyphenic dung beetle *O. taurus*. Field populations of *O. taurus* that naturally utilise horse dung or cow manure exhibited significant differences in the average scaling relationship between body size and male horn length. Males collected from cow manure populations expressed consistently longer horns for a given body size over the same body size range than males collected from horse dung populations. Furthermore, males reared in the laboratory on these two resources also exhibited significant differences in the average horn length–body size allometry. Differences observed between laboratory populations reared on horse dung or cow manure were in a direction and of a magnitude similar to the differences observed between field populations that utilise these different resources naturally. These findings suggest that between-population differences in scaling relationships and the location of threshold body sizes in this species can be the product of natural variation in the quality of resources available to developing larvae.

The results support earlier findings by Emlen (1997a) on the related horn-dimorphic species *O. acuminatus*. Emlen found that a population of *O. acuminatus* on Barro Colorado

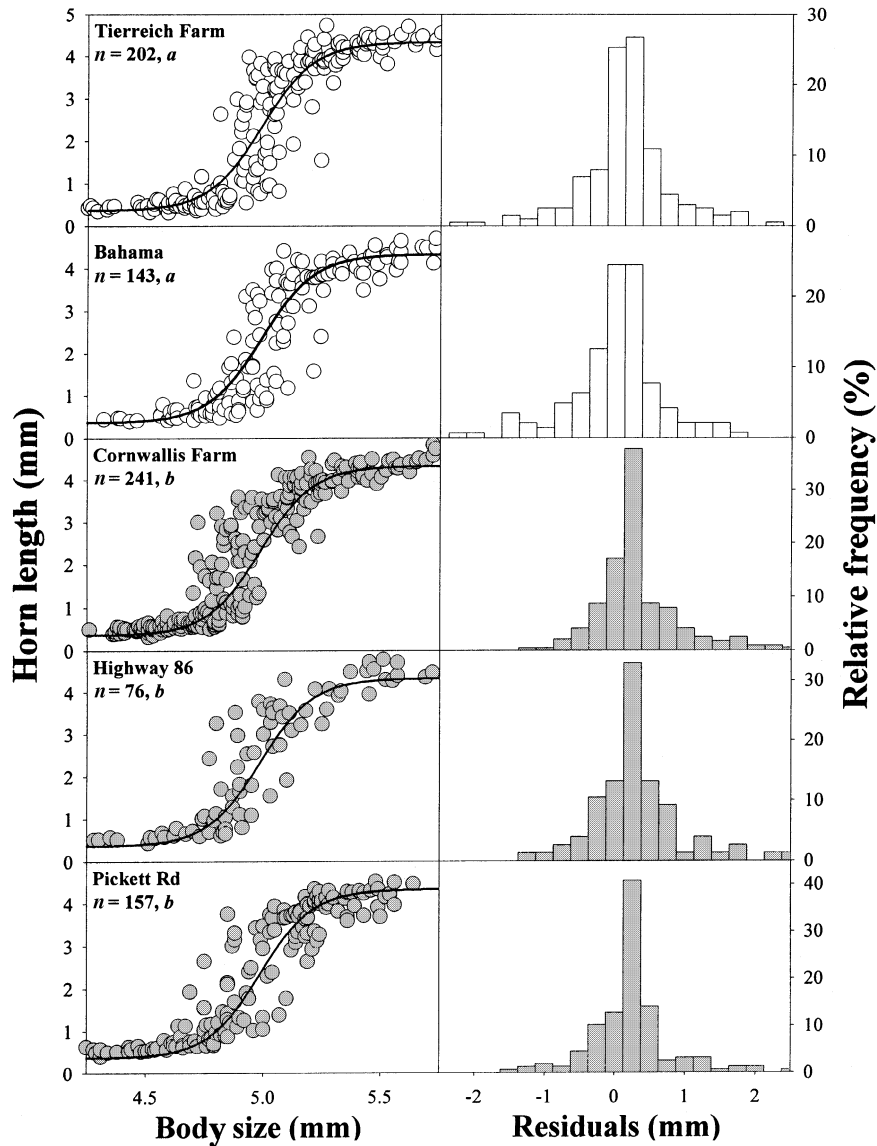


Fig. 2. Scaling relationship between body size and horn length (left) and residual horn length frequency distributions (right) of *O. taurus* males collected from two horse dung populations (open circles) and three cow manure populations (grey circles). Residuals were calculated based on the same reference function for each sample (indicated by solid line, see also Fig. 1). Samples not sharing the same letter following the sample size are significantly different ($P < 0.05$; Kruskal–Wallis H test including sequential Bonferroni correction for multiple comparisons).

Island varied seasonally in the scaling relationship between body size and horn length, resulting in changes in the threshold body size at which males switch from the hornless to the horned morph. Furthermore, threshold variation covaried partially with changes in mean body size: when mean male body size was relatively small, the threshold body size tended to shift to a smaller body size; when mean male body size was large, the threshold body size tended to shift to a larger body size. *Onthophagus acuminatus* in Barro Colorado Island feeds on howler monkey *Alouatta palliata* dung, which is likely to vary in its nutritional value depending on monkey diet, which changes with season

(Nagy & Milton, 1979; Milton *et al.*, 1980; Milton, 1982, 1991). Emlen was able to induce similar variation in switch-point locations and body sizes in the laboratory by varying larval feeding conditions using a mixture of howler monkey dung and cow manure to generate poor quality food. Therefore, he argued that the allometric variation observed in the field was a reflection of diet-induced plasticity (Emlen, 1997a).

The critical threshold body size that separates horned and hornless male morphs in *Onthophagus* beetles is thought to play a crucial role in their mating systems. Alternative male morphs in several *Onthophagus* species have been shown to

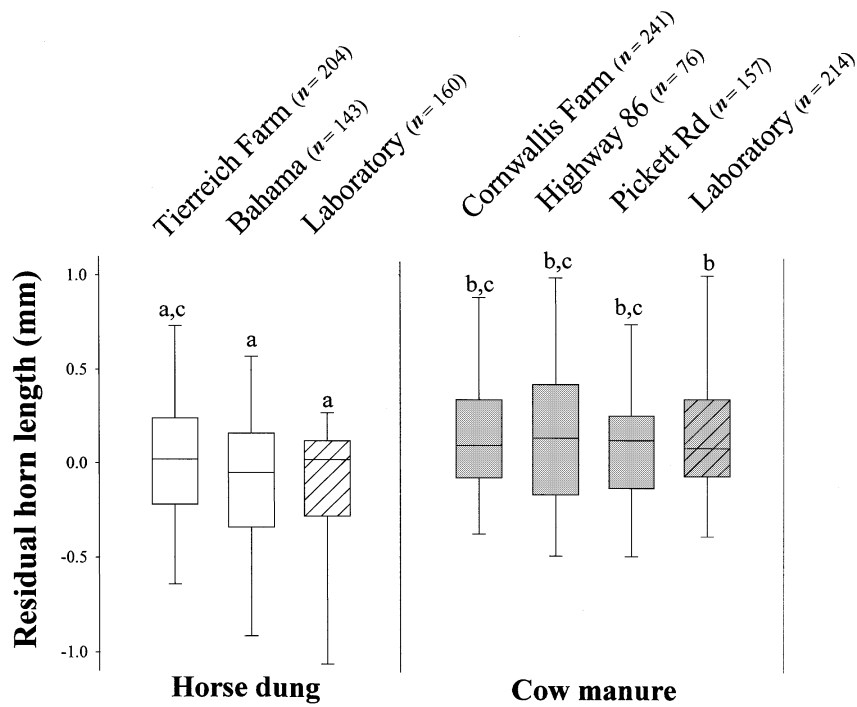


Fig. 3. Box plots of horn length residuals of males collected from horse dung populations in the field (open boxes) or reared on horse dung in the laboratory (hatched box), and males collected from cow manure populations in the field (grey boxes) or reared on cow manure in the laboratory (hatched box). Residual horn lengths were calculated based on a modified logistic equation that was fitted to the combined samples to describe the average relationship between body size and horn length (indicated by solid line in Fig. 1; horn length = $3.974 / \{1 + \exp[-8.863 \times (\text{body size} - 4.987)]\} + 0.3596$). Boxes not sharing the same letter are significantly different ($P < 0.05$; Kruskal–Wallis H test including sequential Bonferroni correction for multiple comparisons).

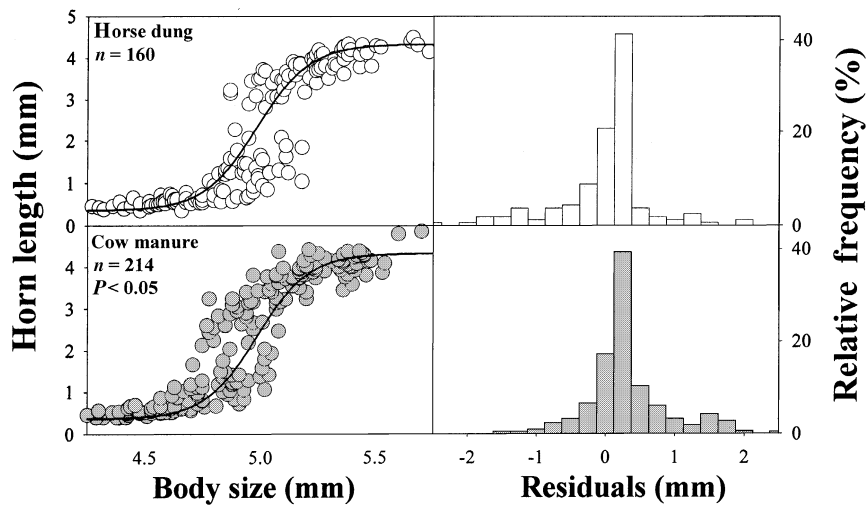


Fig. 4. Scaling relationship between body size and horn length (left) and residual horn length frequency distributions (right) of male *O. taurus* reared on horse dung (open circles) and cow manure (grey circles) in the laboratory. Residuals were calculated based on the same reference function for each sample (indicated by solid line, see also Figs 1 and 2). Both frequency distributions were highly significantly different if tested separately (Mann–Whitney U test, $P < 0.001$) and remained significantly different ($P < 0.05$) when field samples (shown in Fig. 2) were included in the analysis (Kruskal–Wallis H test including sequential Bonferroni correction for multiple comparisons).

rely on alternative reproductive tactics: horned males fight with other males over access to females using their horns as weapons, whereas hornless males sneak to gain access to breeding tunnels (Emlen, 1997b; Moczek, 1998, 1999; Moczek & Emlen, 2000). The effectiveness of horns as a

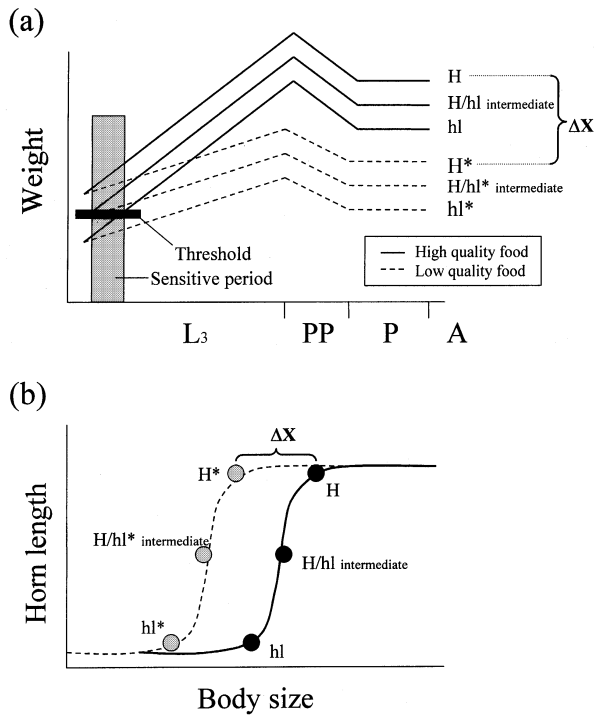


Fig. 5. Developmental model of how differences in larval nutrition can result in changes in the scaling relationship between horn length and body size. (a) Schematic larval growth trajectories during the last half of the third larval instar (L₃), the pre-pupal (PP), and pupal (P) stage to the adult (A). Larval weight is depicted on the y axis. Larvae typically feed and accumulate weight throughout most of the third instar and lose weight during the pre-pupal stage. Morph determination in males precedes the cessation of feeding. The grey bar indicates the period during which male horn morphology is specified; the black horizontal bar indicates the location of the larval weight threshold that separates incipient horned (H) and hornless (hl) morphs. Larvae that are restricted to a poor diet will gain relatively little weight after morph determination has taken place (---), whereas larvae that have access to a superior diet (—) will gain relatively more weight. Consequently, larvae reared on a poor diet but still large enough to pass the threshold for horn expression will develop horns but express smaller body sizes than larvae that had the same weight during the period of morph determination but had access to a superior diet for the remainder of the larval growth period. (b) At a population level, differences in post-morph determination weight gain (ΔX) will manifest themselves in changes in the average scaling relationship between horn length and body size and the location of the body size threshold that separates alternative male morphs. Larvae that are restricted to poor feeding conditions (which still allow a subset of larvae to pass the threshold weight for horn production) should on average express relatively longer horns for a given body size, and switch from no horn to complete horn expression at a smaller body size.

weapon depends on the body size of their bearer (Brown & Siegfried, 1983; Brown & Bartalon, 1986; Emlen, 1997b), hence males below a certain critical body size are thought to gain higher fitness by remaining hornless and engaging in sneaking behaviour instead of fighting (Eberhard, 1982; Moczek & Emlen, 2000). The exact location of this threshold body size is thought to depend on demographic and ecological conditions, e.g. the mean body size of males competing within a population (Gross, 1996; Emlen, 1997a; Moczek & Emlen, 1999). In a population where males are relatively large, males that are of medium size on an absolute scale may gain higher fitness by remaining hornless, whereas in a population where males are relatively small, the same medium-sized males may gain higher fitness by expressing horns (Moczek & Emlen, 1999). Emlen (1997a) therefore interpreted diet-induced allometric plasticity in *O. acuminatus* as an adaptation that allows males to respond to changes in population-wide body sizes and to optimise their horn length not only relative to their own body size but also relative to the mean body size of males in the population in a given season.

The results presented here are in principle congruent with Emlen's hypothesis of an adaptive plastic response that allows males to optimise relative horn length in the face of population-wide nutritional variation (Emlen, 1997a); however a companion study on the nutritive effects of dung quality on adult size, together with recent insights into the developmental and endocrine control of horn expression, suggests a simpler, non-adaptationist explanation. Earlier work has shown that horse manure is of substantially higher nutritional value to *O. taurus* larvae than is cow manure. In order to grow to a similar body size, larvae need to have access to almost twice the amount of cow manure than horse dung (Moczek, 1998), however the overall duration of larval development does not differ between horse dung and cow manure (Emlen & Nijhout, 1999; Moczek & Emlen, 1999; Shafiei *et al.*, 2001). This means that within a given amount of time and with a given amount of resource, larvae that feed on horse dung are likely to accumulate more body mass than are larvae that are restricted to cow manure. In *O. taurus*, morph determination takes place in the second half of the third and final larval instar, and appears to depend on juvenile hormone titres expressed during certain sensitive periods as a function of larval body size (Emlen & Nijhout, 1999, 2001). Both hormonal (Emlen & Nijhout, 1999, 2001) and nutritional (A. P. Moczek and H. F. Nijhout, unpublished) manipulations indicate clearly that male horn morphology is specified well before larvae stop feeding. As a consequence, male larvae will still gain mass after their future adult phenotype has already been specified. This mass gain will contribute to the final larval weight with which an individual male enters pupation, and hence will also affect adult body size, as larval weight prior to pupation explains $\approx 90\%$ of the variation in adult body size (A. P. Moczek and H. F. Nijhout, unpublished). This final weight gain after the specification of adult male horn morphology has taken place, however, should vary as a function of food quality (Fig. 5). A larva that has

access to horse dung will gain relatively more weight than a larva restricted to cow manure. If both of these larvae exceed the critical larval weight required for horn expression at the time of morph determination, they will both develop horns as adults. Because their post-horn determination weight gain is different, however, they will differ in the final weight with which they will pupate, the body size with which they will emerge as adults, and therefore the length of their horns *relative* to their body size (Fig. 5). At the level of a population, this should manifest itself in a change in the critical threshold body size that separates alternative male morphologies (Fig. 5). Larvae with access to relatively poor food should express horns at relatively small body sizes (Fig. 5).

This alternative hypothesis does not necessarily contradict the adaptive plastic response hypothesis (Emlen, 1997a). In fact, should future work support Emlen's assumptions about the adaptive nature of shifting thresholds in response to seasonal variation in larval food quality, the hypothesis outlined here may illustrate the physiological means by which this adaptive response is achieved during development. Alternatively, however, allometric plasticity in *Onthophagus* populations may simply be an emergent property of the dynamics and timing of morph determination, with little or no adaptive value in itself.

The forces and processes that determine scaling patterns of morphological traits continue to receive substantial attention (e.g. Thompson, 1942; Cock, 1966; Gould, 1966; de Wilde & Beetsma, 1982; Wheeler, 1986, 1991; Klingenberg, 1992, 1996; Emlen & Nijhout, 2000). Often, even closely related species exhibit interesting differences in static allometries, such as differences in slope or the location of switch points (Kawano, 1995a,b, 1997; Emlen, 1996), and interspecific variation in static allometries has frequently been used to make inferences about a wide array of ecological and evolutionary processes (e.g. strength of sexual selection in earwigs: Simmons & Tomkins, 1996; energetics of foraging behaviour in ants: Feener *et al.*, 1988; evolution of display traits: Green, 1992; Petrie, 1992; developmental trade-offs in stag beetles: Kawano, 1997; character displacement in rhinoceros beetles: Kawano, 1995b). Implicit in many of these studies is the assumption that the scaling relationship between body size and the morphological trait of interest is not itself plastic and influenced by environmental conditions. Consequently, it should be possible to treat certain aspects of a static allometry as species-diagnostic parameters.

The present demonstration of diet-induced allometric plasticity in a beetle adds to a growing number of studies that support the view that static allometries may themselves be influenced by environmental conditions, i.e. that certain external factors are capable of influencing not only trait expression *per se* but also how certain traits scale with body size over a range of body sizes. For example, Wheeler and Nijhout (1984) found that *Pheidole bicarinata* ants change the larval threshold weight that separates incipient worker from soldier larvae as a function of the abundance of soldiers already present in the colony. As soldier abundance

increases in a colony, larvae that would normally develop into small soldiers develop into large workers instead (Wheeler & Nijhout, 1984). Knell *et al.* (1999) showed in the stalk-eyed fly *Diasemopsis aethiopica* that adult scaling relationships change in response to larval feeding conditions. Females responded to better food by developing both larger body sizes and relatively longer eye stalks than females fed on poor food, whereas males responded by increasing only the length of the eye stalk (Knell *et al.*, 1999). The finding that static allometries themselves can be plastic and capable of short-term responses to changes in environmental conditions has important implications for their use as diagnostic and descriptive tools. Where static allometries are used to distinguish populations or species, allometric plasticity may amplify or obscure genetic differences among populations. In such cases, a common garden experiment would allow the quantification of possible contributions of divergent environmental conditions to allometric differentiation. Furthermore, making inferences about ecological or evolutionary processes based on allometric parameters derived from static allometries should be done with care, especially when allometries are based on measurements of a relatively small number of museum specimens collected from a non-representative geographic range, as allometric plasticity again may enlarge or hide real differences between species.

Acknowledgements

M. Gilchrist, C. P. Klingenberg, L. Mojonier, H. F. Nijhout, and one anonymous reviewer provided helpful comments on previous versions of this manuscript. I thank D. Emlen, K. Fiedler, H. F. Nijhout and L. Mojonier for providing helpful advice during the course of this project, and L. Mojonier for making beetle samples anonymous. I am grateful to D. Higdon and the Duke University Statistical Consulting Center for help with the statistical analyses, J. Mercer and the Duke Morphometrics Laboratory for access to equipment, and S. Richards for his outstanding drawings of *O. taurus* morphs. This work was carried out while I was supported in part by a fellowship from the German Academic Exchange Service (DAAD) and written up with financial support from the Department of Zoology, Duke University, a National Science Foundation Dissertation Improvement Grant IBN 9972567, a Sally Hughes-Schrader International Fellowship, a Duke University Grant for International Studies, a Robert R. Bryden/North Carolina Academy of Science Fellowship, and a Sigma Xi Grant-in-Aid of Research.

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Accepted 6 May 2001