

Proximate determination of male horn dimorphism in the beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae)

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Abstract

The existence of discrete phenotypic variation within one sex poses interesting questions regarding how such intrasexual polymorphisms are produced and modified during the course of evolution. Approaching these kinds of questions requires insights into the genetic architecture underlying a polymorphism and an understanding of the proximate mechanisms determining phenotype expression. Here we explore the genetic underpinnings and proximate factors influencing the expression of beetle horns – a dramatic sexually selected trait exhibiting intramale dimorphism in many species. Two relatively discrete male morphs are present in natural populations of the dung beetle *Onthophagus taurus* (Scarabaeidae, Onthophagini). Males exceeding a critical body size develop a pair of long, curved horns on their heads, while those smaller than this critical body size remain essentially hornless. We present results from laboratory breeding experiments designed to assess the relative importance of inherited and environmental factors as determinants of male morphology. Using father–son regressions, our findings demonstrate that horn length and body size of male progeny are not predicted from paternal morphology. Instead, natural variation in an environmental factor, the amount of food available to larvae, determined both the body sizes exhibited by males as adults and the presence or absence of horns. The nonlinear scaling relationship between the body size and horn length of males bred in the laboratory did not differ from the pattern of variation present in natural populations, suggesting that nutritional conditions account for variation in male morphology in natural populations as well. We discuss our results by extending ideas proposed to explain the evolution of conditional expression of alternative phenotypes in physically heterogeneous environments toward incorporating facultative expression of secondary sexual traits. We use this synthesis to begin characterizing the potential origin and subsequent evolution of facultative horn expression in onthophagine beetles.

Introduction

Morphological variation within species is not always continuous. In a wide variety of taxa, two or more discrete forms coexist with intermediate forms rare or absent. The existence of discontinuous phenotypic variation raises questions regarding (1) what forces generate discontinuity (i.e. do developmental processes

produce only discrete forms, or does discontinuity arise through selection against intermediates), and (2) how the resulting morphologies will be affected by selection. Answering these questions critically depends on the extent to which the proximate mechanisms leading to the production of discontinuous phenotypic variation are understood (Schlichting & Pigliucci, 1995). In this paper we begin by reviewing some of these mechanisms and their respective evolutionary repercussions. We then explore the proximate mechanisms underlying the expression of horns in male beetles (*Onthophagus taurus*) as an example of a trait exhibiting intramale dimorphism.

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Using our measures of the genetic and environmental contributions to horn length expression in *O. taurus*, as well as results from a companion study on the reproductive behaviour of these beetles, we suggest a selective regime that might have led to the evolution of the patterns of morphological variation visible today in this species.

The proximate mechanisms responsible for generating discrete variation have received considerable attention (e.g. sexual dimorphism: Charnov & Bull, 1977; seasonal dimorphism: Shapiro, 1976; Hazel & West, 1982; Greene, 1989; diapausing vs. direct developing life histories in arthropods: Tauber *et al.*, 1986; Taylor, 1986; social castes in ants: Wheeler & Nijhout, 1983, 1984; Hölldobler & Wilson, 1990; alternative reproductive tactics of males: Hamilton, 1979; Thornhill, 1981; Shuster, 1989; Shuster & Wade, 1991; see also Lively, 1986a,b; West-Eberhard, 1989; Moran, 1992) and the results from these and other studies reveal two very different determinative regimes. Discrete morphologies can result from expression of alternative alleles at one or few loci ('allelically determined polymorphism', *sensu* West-Eberhard, 1992). This appears true for alternative bill shapes in African finches (Smith, 1993), male plumage coloration in ruffs (Lank *et al.*, 1995), male tail morphologies in pigmy swordtail fish (Zimmerer & Kallman, 1989; Ryan *et al.*, 1992) and male shape in isopods (Shuster, 1989; Shuster & Wade, 1991). In these taxa, the morphology adopted by an individual depends primarily on the genotype of that individual, and only minimally on environmental conditions. Alternatively, production of different morphologies can be largely independent of the inheritance of specific alleles, and instead depend primarily on environmental conditions experienced by each individual as it develops ('environmental determination' or polyphenism). Here, each individual has the potential to develop one of several *alternative* phenotypes. Examples include alternative morphologies associated with different defence tactics of invertebrates (Harvell, 1986; Lively, 1986a,b; Greene, 1989), paedomorphic vs. metamorphic life histories in salamanders (Dent, 1968; Wilbur & Collins, 1973; Whiteman, 1994), substrate feeding vs. cannibalism in spadefoot toad tadpoles (Pfennig, 1990, 1992a,b), social castes in the hymenoptera (Wilson, 1971; Wheeler & Nijhout, 1983, 1984; Hölldobler & Wilson, 1990) and male dimorphism in some scarab beetles (Eberhard, 1982; Emlen, 1994b).

Recent theoretical work suggests that both allelically and environmentally determined polymorphisms may involve similar genetic and developmental architectures (West-Eberhard, 1992). Both types of polymorphisms may result from genetically based 'switches', which regulate the expression of morph-specific alternative sets of genes (Hazel *et al.*, 1990; West-Eberhard, 1992; Roff, 1994a,b). Determination of which phenotype will be adopted, i.e. which gene sets will be expressed, can be governed by alleles at other loci within the genome, and

hence the genotype of that individual ('allelic' determination), or by external cues correlated with a particular selective situation ('environmental' determination). Contributions from both internal (allelic) and external (environmental) factors permit a continuous range of determinative regimes (West-Eberhard, 1992).

Although allelically and environmentally determined polymorphisms may utilize similar 'switch' mechanisms, they have very different evolutionary implications. Allelic and environmental polymorphisms are predicted to occur in different selective circumstances, and the conditions required for the stable maintenance of phenotypic variation vary considerably (Dominey, 1984; Lively, 1986a; Gross, 1996). For example, if phenotypic variation is allelically determined, differential reproductive success among alternative phenotypes or genetic drift may lead to genetic fixation of one of the morphs and, hence, loss of polymorphism (Levins, 1968; Hartl, 1981; Maynard Smith, 1982).

In traits with environmentally determined polymorphisms, however, every individual has the potential to express all of the alternative phenotypes. The capacity to express multiple forms is thus transmitted to subsequent generations irrespective of the parental phenotype actually expressed (West-Eberhard, 1992). Consequently, and as has been pointed out by Schmalhausen (1949) early on, environmentally determined polymorphisms can persist over generations over a much broader range of selective circumstances (see also Lively, 1986b). Evolutionary change in this type of polymorphism may primarily result from genetic modifications of the mechanism employed to translate variation in the physical or social environment into the production of alternative phenotypes (Schmalhausen, 1949; Hazel *et al.*, 1990; Roff, 1994a,b).

Knowledge of the relative contributions of allelic and environmental factors to the production of polymorphic traits is crucial for identifying which selective forces are relevant to subsequent evolution of a polymorphism, as well as for understanding how these traits may have originated (Schlichting & Pigliucci, 1995). Here we identify the proximate forces responsible for generating dimorphic variation in male horn morphology in a species of horned beetle.

Scarab beetles provide extreme examples of both inter- and intrasexual polymorphisms. Several thousand species within the family Scarabaeidae have evolved horns or hornlike structures, resulting in arguably one of the most exuberant and at the same time most diverse classes of secondary sexual traits (Arrow, 1951). A variety of hypotheses have been proposed to explain the evolutionary significance of horns, yet most of these hypotheses have not been evaluated experimentally and are based primarily on inferences from the study of dead specimens. Originally, beetle horns were proposed to serve as indicators for male quality, to be used by females in choosing between potential mates (Darwin, 1871), or to

protect beetles against predators (Wallace, 1878). Lameere (1904) suggested that horns may have served initially as tools for digging, but eventually became coopted for fighting, while Doane (1913) hypothesized that horns enable beetles to dig, perforate or lacerate plants in order to feed on their sap. Arrow (1951) suggested that beetle horns are functionless, selectively neutral characters, and merely the incidental byproduct of selection towards larger body size. Eberhard (1979, 1982) finally demonstrated that horned beetles use their horns as weapons in intrasexual competition, a conclusion confirmed by most studies conducted thereafter (see also Eberhard, 1978, 1981, 1987; Palmer, 1978; Siva-Jothy, 1987; Otronen, 1988; Emlen, 1994b; Rasmussen, 1994).

Early scientists (e.g. Darwin, 1871; Wallace, 1878; Huxley, 1932; Arrow, 1951) were impressed with both the dramatic shapes of beetle horns and, perhaps more importantly, with the extraordinary variability of these structures. Within single populations of the same species, beetle horns can range from tiny knobs that are barely discernible to structures larger than the total length of a male's body (Arrow, 1951). These early naturalists also observed that in some horned beetle species, horns were only expressed in large males, with horns in smaller males and all females being greatly reduced or fully absent, resulting in both inter- and intrasexual horn dimorphisms (for more recent studies see for example: Siva-Jothy, 1987; Eberhard, 1991; Emlen, 1994a,b; Rasmussen, 1994; Kawano, 1995). Horns and male horn dimorphism have thus been widely appreciated for over a century. However, despite their conspicuousness and abundance, knowledge about how male horn dimorphism is produced, and how this mechanism has evolved, remains scarce.

Both allelic and environmental determination have been suggested to represent the genetic basis underlying horn polymorphisms in beetles. While Gadgil (1972) assumed that horned and hornless males in several species represent allelically determined alternatives ('genetically based alternative strategies', Gadgil, 1972), maintained by frequency-dependent selection, Eberhard (1982, 1987) and later Cook (1987, 1990) observed that length of horns was generally closely related to the body size of individuals. Since adult body size in many insects is influenced by dietary conditions experienced during preceding larval stages (Wigglesworth, 1984), Eberhard and Cook reasoned that environmental factors probably determined the presence or absence of horns in adult beetles. Emlen (1994a) and Hunt & Simmons (1997) demonstrated that artificial manipulation of larval food quantity predictably determines the development of either horned or hornless morphs irrespective of paternal phenotype.

Here we report on the determinative basis underlying male horn dimorphism in *Onthophagus taurus*. Instead of nutrition-manipulation experiments, we focus on natural variation in larval dietary conditions to examine more closely the significance of environmental factors in

determining male phenotypes. We employ father-son regressions to explore the contributions of additive genetic factors to variation in both male horn length and adult body size in this species. We then investigate the contribution of one environmental variable – the amount of food available during larval development – to this variation as well. The results presented here have general implications for the evolutionary consequences of polymorphisms, the significance of ornaments as reliable indicators for male quality in the competition over mates, and on recent theory on the mechanisms of sexual selection.

Materials and methods

Natural history of *Onthophagus taurus*

Onthophagus taurus Schreber 1759 (Scarabaeidae, Onthophagini) is a common dung beetle in North Carolina. Its abundance and eye-catching male morphology (large males bear an easily noticed pair of disproportionately long horns on their heads) probably account for the early attention given to this species (Fabre, 1899; Main, 1922; Arrow, 1951; Goidanich & Malan, 1964).

The distribution of *O. taurus* was originally limited to North Africa, Southern and Middle Europe, and Asia Minor (Balthasar, 1963). Its short generation time and ability to utilize various kinds of dung made this species suitable for artificial introduction to areas which recently had become used for horse and cattle ranching but lacked a sufficiently effective dung beetle community. *O. taurus* was successfully introduced to Australia in the 1970s (Tyndale-Biscoe, 1990). However, its introduction to the USA appears to have occurred by accident. *O. taurus* was first recorded from the USA in Santa Rosa County, Florida, in 1974 and has continuously extended its range since then (Fincher & Woodruff, 1975). In North Carolina beetles inhabit pastures from spring to autumn with varying abundance, sometimes reaching densities of up to 200 individuals per dung pad (Moczek, 1996).

O. taurus adults colonize dung pads of cattle, horses, sheep and probably other large mammalian herbivores (Fincher & Woodruff, 1975; Halfpeter & Edmonds, 1982; Hanski & Cambefort, 1991). Dung is used by both adults and larvae as a food resource. Once a dung pad is colonized, adults dig vertical tunnels through the pad into the soil (Goidanich & Malan, 1962, 1964). After a tunnel of sufficient depth has been completed, beetles form a small cavity at the blind end of the tunnel and pull dung pieces down into this cavity. Dung pieces are formed into well-compacted, ovally shaped brood balls ('brood masses' in Halfpeter & 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).

After brood ball production has finished, beetles generally seal tunnel entrances by re-filling them with the previously excavated material (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 (Fabre, 1899; Goidanich & Malan, 1962, 1964; Hallffter & Edmonds, 1982). Total development from the egg to an enclosing adult requires about 30 days in the laboratory at 28 °C (Emlen and Moczek, unpublished results).

Morphological measurements

To characterize natural variation in male morphology in *O. taurus*, a sample of 241 males was collected from a cattle farm in Durham County, North Carolina. To collect beetles, manure pads of an appropriate age and with the typical signs of colonization – tunnel entrances on the top, excavated material at the periphery – were turned over and immediately put in a plastic container, which prevented beetles from escaping into their underground tunnels. Individuals were then collected by hand, placed in a plastic bottle and either killed immediately afterwards using ethyl acetate or added to a colony maintained in the laboratory.

Horns in *O. taurus* vary in shape: short horns are straight, at intermediate lengths they are bow-shaped, and in the largest individuals they turn inwards and become U-shaped. Therefore, horn length was measured by using the outer edge of one horn, from the tip of the horn to the edge of the eye cavity, resulting in a curved instead of a straight line. Horns occasionally exhibited signs of wear, with blunt tips and rounded edges covered with scratches. Males with horns showing severe signs of wear were excluded from the analysis. Maximum thorax width was measured as an estimate for body size (Eberhard & Gutiérrez, 1991; Emlen, 1994a,b; Tomkins & Simmons, 1996).

All morphological measurements were performed using a two-dimensional image analysis set-up in the Duke Morphometrics Laboratory, Duke University, including a Wild™ stereo-dissecting microscope, a Burle™ video camera and Java™ software. Measurements of both horn length and thorax width could be obtained with high precision (thorax width: mean and standard deviation of 11 repeated measurements of the same individual: $x = 5.205$ mm, $SD = 0.0008$; horn length: mean and standard deviation of 12 repeated measurements of the same individual: $x = 1.452$ mm, $SD = 0.0108$).

Breeding design

Our experiments were designed to assess the relative contributions of genetic and environmental factors as determinants of male horn length and body size. We estimated the heritability of these traits using the

phenotypic resemblance of fathers and sons (Falconer, 1989). Because prior studies on a related species suggested that females may store sperm from multiple matings (Emlen, 1994b), only unmated females were used in this breeding experiment. One generation of beetles was reared in the laboratory prior to all experiments, and newly eclosing females were kept separate from males and fed dung until sexually mature. These females were then used for the heritability experiment.

To estimate the heritability of male horn length, each of 18 unmated females was paired randomly with a single wild-caught male of known horn length and body size and allowed to breed. Pairs were put in cylindrical buckets (30 cm in height and 8 cm in diameter), three quarters filled with a moist sand–potsoil mixture and 150 g fresh cow manure. After 4 days the sand–soil mixture was sifted, and beetles were removed. Brood balls were collected and weighed to the nearest 0.01 g using a Mettler™ balance. Each brood ball was placed in a separate container and stored in an incubator at constant 28 °C. Progeny were collected on emergence. Horn lengths and thorax widths of fathers and their sons were measured as described above.

Analyses

Parent–offspring regressions were used to predict male progeny horn length and body size, based on the measurements of these traits in their fathers (Falconer, 1989). Because siblings are more closely related to each other than to the progeny of other males, they were not considered statistically independent for these analyses. Consequently, we used family mean values of horn length and body size for estimation of the regression coefficient. Significant regressions would suggest the existence of heritable variation in these traits, with the slope of the regression being half the narrow-sense heritability (Falconer, 1989).

To look more directly at possible environmental contributions to variation in horn length and body size, we tested for effects of larval food amounts on adult morphology. We used linear regressions to estimate the effect of the amount of food available during larval development (brood ball weight) on variation in both the horn length and body size of adult males. For this analysis – since each individual fed on and developed inside a separate brood ball – we considered each progeny to be an independent estimator of the effect of brood ball mass on adult morphology. However, if large family or maternal effects on brood ball size exist, then treating all individuals as independent would artificially inflate our degrees of freedom for the regression analysis. Therefore, we also analysed these data using mean brood ball mass, mean progeny horn length and mean thorax width for each family. Significant regressions using either individual or family mean data would indicate an

environmental effect of larval food quantity (brood ball mass) on horn length and thorax width determination. We used a nonparametric test in the one instance where assumptions of the linear regression model were violated.

Results

Male dimorphism in *Onthophagus taurus*

The frequency distribution of natural variation in horn length and body size, as well as the scaling relation between these two traits, are shown in Fig. 1. Natural variation in body size did not differ significantly from a normal distribution (Kolmogoroff–Smirnov test, $P > 0.1$). However, natural variation in horn length was not normally distributed, (Kolmogoroff–Smirnov test, $P < 0.001$), and instead appeared bimodal, with few intermediate horn lengths. The scaling relationship between horn length and body size exhibited a 'broken', or sigmoidal shape characteristic of several other insect species with discrete or dimorphic variation (Wheeler & Nijhout, 1983, 1984; Eberhard & Gutiérrez, 1991; Tomkins & Simmons, 1996). In this case, substantial variation in horn lengths only occurred within a small range of body sizes (between 4.75 and 5 mm), corresponding to the inflection of the sigmoid curve (Fig. 1). Comparing the ratio of body size and horn length on both sides of this interval effectively separates males into two discrete shapes (Mann–Whitney U -test, $P < 0.001$). This result, combined with both the bimodal frequency distribution of horn length and the sigmoidal scaling

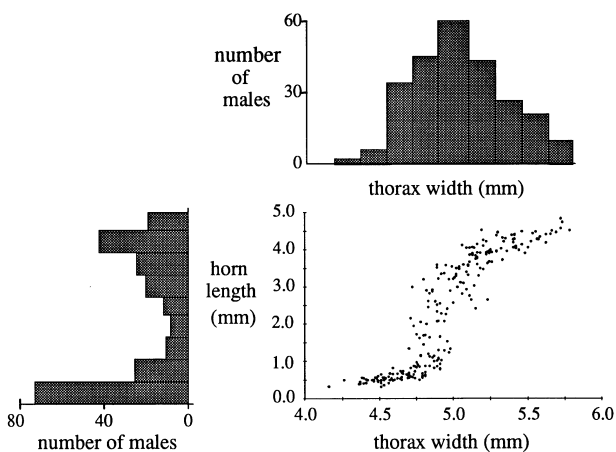


Fig. 1 Relation between horn length and body size (thorax width) for 241 male *Onthophagus taurus*, collected from Durham County, North Carolina. Bar graphs indicate the frequency distributions of natural variation in thorax widths (top) and horn lengths (left). The sigmoidal scaling relationship and the bimodal horn length frequency distribution indicate the simultaneous co-occurrence of two relatively discrete male shapes within natural populations.

relationship between horn length and body size, strongly suggests that horned *O. taurus* are not simply enlarged versions of hornless individuals. Rather than exemplifying the extremes of a continuous linear allometry, horned and hornless males represent distinct male shapes co-occurring simultaneously within populations.

Proximate determination of horn length and body size

Linear regressions of mean male progeny horn length on paternal horn length and mean male progeny body size on paternal body size were not significant, suggesting that little or no heritable variation exists for either of these traits in this population under these conditions (Fig. 2a,b; horn length: $b = -0.081$, $r^2 = 0.02$, $P = 0.59$, $n = 18$; body size: $b = -0.02$, $r^2 = 0.00$, $P = 0.92$, $n = 18$).

In contrast, the amount of food available during larval development (approximated by brood ball weight) did significantly affect both progeny horn length and body size (Fig. 2c,d; linear regression on (i) individual horn length: $b = 1.75$, $r^2 = 0.36$, $P = 0.0001$, $n = 53$; (ii) family means: $b = 1.42$, $r^2 = 0.50$, $P = 0.0031$, $n = 15$; linear regression on (i) individual thorax width: $b = 0.7$, $r^2 = 0.39$, $P = 0.0001$, $n = 53$; (ii) family means: $b = 0.69$, $r^2 = 0.51$, $P = 0.0027$, $n = 15$). Brood ball weight was positively correlated with both horn length and body size, explaining 36% and 39% of the individual progeny variation, respectively. The relationship between larval food amount and body size (individual values as well as family means) could be described best using a linear regression. Polynomial or exponential equations used to fit this relationship only marginally improved the goodness of fit, suggesting a gradual effect of food amount on body size.

The effect of larval food amount on progeny horn length, however, was not linear (Fig. 2c). Since this relationship violated the assumption of the linear regression model (Zar, 1984), the effect of larval food amount on male horn length was also analysed using nonparametric statistics, which gave similar results (Spearman's rank correlation: $r_s = 0.63$, $n = 53$, $P < 0.001$). The sigmoidal or 'broken' shape of this relationship (Fig. 2c) suggests the existence of a threshold response related to brood ball mass and/or body size, such that only males exceeding a critical threshold value produce horns. Similarly, male larvae that failed to exceed this threshold during development (by being confined to an insufficient quantity of food and the expression of small body sizes) produced only rudimentary horns or no horns at all. Combined, these results indicate that dimorphic variation manifest in natural populations is probably a consequence of developmental processes underlying horn expression, and not entirely due to later selection against intermediates.

Onthophagus taurus is the second horned beetle species in which the inheritance of variation in male morphol-

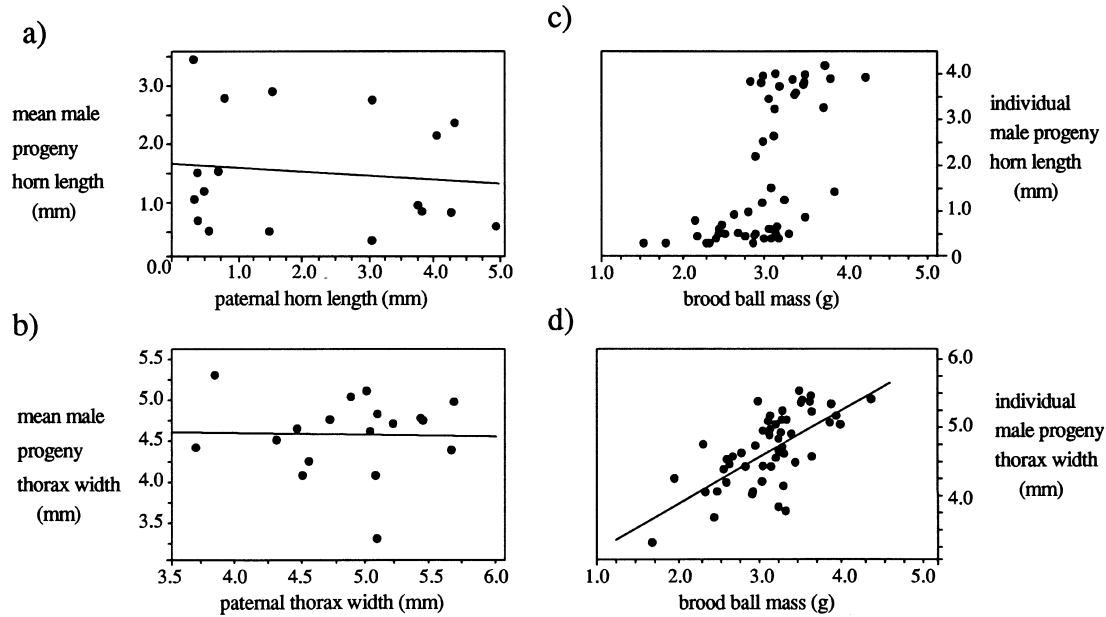


Fig. 2 Relative contributions of additive genetic (a,b) and environmental (c,d) factors to horn length and body size variation in *Onthophagus taurus*. Relations between (a) paternal horn length and the mean horn length of male progeny, and between (b) paternal body size (measured as thorax width) and mean male progeny thorax width are both shown (linear regression on horn length: $b = -0.081$, $r^2 = 0.02$, $P = 0.59$, $n = 18$; on body size: $b = -0.02$, $r^2 = 0.00$, $P = 0.92$, $n = 18$). Neither regression was significant, and none of the variation in horn length and body size appears attributable to additive genetic factors, suggesting that neither horn length nor body size are heritable in this species. (c) Horn development of individual adult male *O. taurus* expressed as a function of larval food quantity (brood ball mass). Horn length increased significantly and nonlinearly with increasing brood ball mass, demonstrating a considerable effect of the amount of food available during larval development on the later expression of horns in adult males (Spearman's rank correlation: $r_s = 0.63$, $n = 53$, $P < 0.001$). The sigmoidal shape of the horn length – brood ball mass trajectory suggests the existence of a critical food quantity required for the development of horned male phenotypes. (d) Body size in individual adult male *O. taurus* expressed as a function of larval food quantity (linear regression: $b = 0.7$, $r^2 = 0.39$, $P = 0.0001$, $n = 53$). Individual body size increased significantly and linearly with increasing brood ball mass, suggesting a continuous rather than threshold effect of food amount on growth and body size.

ogy has been explored. The related species *O. acuminatus* also exhibited pronounced effects of larval food amount on both male horn length and body size (Emlen, 1994a). However, these effects were measured using experimental manipulation of brood ball sizes, controlling for possible maternal effects on male progeny morphology. Since this design entailed augmenting or removing dung from larvae, it was not clear to what extent the nutritional effects were applicable to natural conditions. In the present study we did not manipulate larval food amounts. However, brood ball sizes still varied considerably (Fig. 2c,d), reflecting variation in female provisioning behaviour. Since no information on variation of brood ball mass in field populations is available to date, we are unable to quantify directly to what extent this variation in female provisioning behaviour observed in the laboratory is representative of conditions in the field. However, examination of the individuals reared on the brood balls produced in this study reveals a clearly sigmoidal scaling relationship between horn length and body size, resembling the natural relationship present in the wild. More importantly, the horn length body size allometry of males reared in the laboratory, including the

critical body size separating alternative morphs, fell within the range of variation observed in natural populations of *O. taurus* (Fig. 3). Combined, this suggests that results generated in this study are unlikely to be an artefact of laboratory conditions insufficiently imitating natural conditions, and that larval food amounts indeed influence the development of male morphology in the field.

Discussion

Determination of male dimorphism in *Onthophagus taurus*

The results presented in this study provide no evidence for heritable variation in either male body size or horn length. Instead, variation in the body sizes of beetles reared in our experiment was strongly influenced by environmental factors experienced during development. One measured variable – the amount of food available to larvae – strongly affected progeny body size explaining 39% of the total variation in individual size and 51% of the variation in family means, respectively.

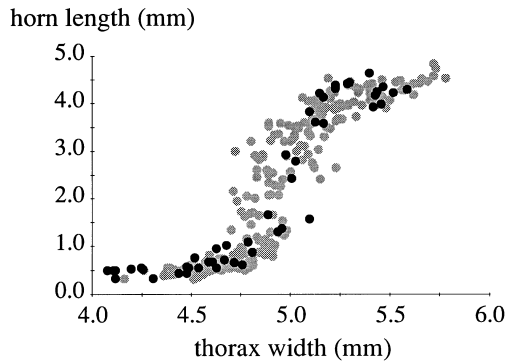


Fig. 3 Scaling relation between horn length and body size (thorax width) of male *O. taurus* reared in the laboratory (black circles), and collected from a natural population (grey circles). Despite the substantial nutritional effects on adult morphology revealed by the laboratory experiments, laboratory-reared beetles exhibited a horn length – body size scaling relationship similar to the relationship present in natural populations. This suggests that variation in the nutritional factors may also account for a substantial proportion of the variation in male morphology present in natural populations.

Male horn length was also affected by variation in larval food amount, but in a more complex fashion. Unlike body size, which showed a positive linear relationship with larval food amount (Fig. 2d), male horn length exhibited a broken, or discontinuous, response to increases in food amount (Fig. 2c). All males reared from food amounts less than 2.8 g failed to produce horns. As with the natural population, intermediate horn lengths were rare, and males went from minimal to complete horn expression abruptly, starting with food amounts of about 2.9 g. This abrupt response to increases in food amount suggests the operation of a threshold, or switch mechanism, regulating the production of male horns, with horns only expressed in males exceeding a critical level of either food amount, body size, or some as yet unidentified factor correlated with larval diet and growth. These findings are consistent with the model of developmental switch mechanisms triggered via external, environmental stimuli (Schmalhausen, 1949; Stearns, 1982; Hazel *et al.*, 1990; West-Eberhard, 1992; Roff, 1994a,b). The likely existence of a critical food amount or threshold regulating the production of alternative phenotypes suggests that horn dimorphism in *O. taurus* involves mechanisms similar to those that appear to regulate pedomorphosis in amphibians (Harris, 1987; Semlitsch & Wilbur, 1989; Semlitsch *et al.*, 1990), pupal colour dimorphisms in lepidopterans (Clarke & Sheppard, 1972; Hazel & West, 1982; Sims, 1983; Gruner & Sauer, 1988) and wing polymorphisms in orthopterans (Harrison, 1979; Roff, 1994a,b; Zera & Tanaka, 1996).

While these results demonstrate that body size and horn morphology attained by adult *O. taurus* are largely

influenced by the amount of food available during development – and hence an environmental component – several factors may influence brood ball mass itself. Initial observations in the laboratory revealed substantial variation in brood ball masses produced by females, suggesting that females may differ in the amount of food they provision for their offspring (Moczek and Emlen, unpublished data). If females vary consistently in how much they provision for their offspring, e.g. as a function of their own body size, this could add an important heritable maternal component to the determinative regime underlying morph determination in *O. taurus*. Initial experiments did reveal a tendency for large females to produce relatively large brood balls (when dung was available *ad libitum*); however, the variation within females was always very large, and typically encompassed a greater range than that observed among females (Moczek and Emlen, unpublished data). This suggests that although heritable maternal effects via female body size dependent food provisioning may exist, their contribution to the determinative regime governing morph expression in *O. taurus* is likely to be small.

Sexual selection and the evolution of morphological alternatives

Identification of the underlying mechanisms regulating the expression of male horns in *O. taurus* enables us to identify aspects of the physiological and social environment relevant to beetle horn evolution. Discrete phenotypic variation is expected to persist within populations whenever a heterogeneous environment involves the reversal of relative fitness rankings across patch types. However, organisms can respond to a heterogeneous selection environment in several ways (Lively, 1986b; Moran, 1992; Gross, 1996). Facultative expression of alternative phenotypes is predicted to be favoured over more canalized mechanisms of expression (i.e. environment-insensitive or allelically determined polymorphisms) when (1) genotypes lack the ability to select only those environments suitable for their expression (Stearns, 1982), and (2) some aspects of the environment send a reliable signal, or 'cue', to a developing individual as to which of the environments it is likely to encounter (Lively, 1986a,b; Moran, 1992). Organisms capable of detecting such a 'cue' can begin to match patterns of gene expression (and subsequent phenotypic modifications) with the environment appropriate for their expression (Lively, 1986a,b; Moran, 1992).

While these models have largely been aimed at organisms contending with spatial or temporal variation in the physical environment (Levins, 1968; Lloyd, 1984; Lively, 1986a,b; Moran, 1992), the same predictions can be applied to the conditional expression of alternative male reproductive tactics (Dominey, 1984; Gross, 1996). In this case, variation in the relative fitness of genotypes arises primarily from differential

competitive abilities of males, rather than from differences in local adaptations to the physical environment (Gross, 1996). Hazel *et al.* (1990) and Gross (1996) both recognized that the environmental factor triggering the expression of different male morphs can, in some cases, actually be an aspect of the animal's own phenotype – namely its body size. Relatively large and small males, by virtue of their different competitive abilities, often experience very different social situations and, hence, 'selective' environments. As a consequence, size-dependent expression of alternative reproductive behavioural and morphological traits is widespread (Thornhill, 1981; Shuster, 1989; Gross, 1996).

By considering an individual's body size to be a manifestation of the selective environment that an individual is likely to encounter, we can begin to apply the selective criteria predicted for the evolution and maintenance of environmentally and allelically determined polymorphisms to sexually selected traits. As before, the advantages of facultatively expressing a secondary sexual trait will depend on the extent to which a major aspect of the selective environment (in this case, body size) is unpredictable to a genotype. If natural variation in body size is highly heritable, then the evolution of allelically determined morphologies, and subsequent genetic correlations between these alleles and body size, would effectively match expression of tactic-specific traits with the appropriate body sizes. In fact, this appears to be the case in the fish genus *Xiphophorus*, where male morphs are allelically determined (Zimmerer & Kallman, 1989), body size is strongly heritable (Kallman, 1983, 1984, 1989; Ryan & Wagner, 1987) and expression of male traits is genetically correlated with body size (Ryan & Causey, 1987).

If variation in body size is influenced primarily by the environment, however, allelic determination seems less favourable. When factors external to the animal cause the final body sizes attained by developing individuals to vary, this can result in tactic-specific alleles being expressed in the wrong selective context (i.e. in animals with inappropriate body sizes). In this case, animals that couple the expression of a trait with the attainment of some critical body size may more effectively match their adult morphology with the selective conditions that they are likely to encounter.

In summary, threshold mechanisms regulating the expression of male secondary sexual traits like beetle horns are expected to be favoured by selection over alternative mechanisms of trait expression whenever: (1) large and small males utilize different reproductive behaviours or encounter different social situations, such that (2) the morphology with the highest fitness payoffs for large males differs from that of smaller males, and (3) natural variation in body size is sufficiently affected by unpredictable environmental conditions to preclude genetic specialization towards only large, or only small, male phenotypes.

Sexual selection and male dimorphism in *Onthophagus taurus*

Do these conditions apply to *Onthophagus taurus*? In this species as well as in related beetle-taxa, male competition over access to females is pervasive, often involving intense male–male combat (Siva-Jothy, 1987; Rasmussen, 1994; Moczek, 1996; Emlen, 1997). Large males in *O. taurus* employ aggressive head to head combat behaviour to gain and maintain access to females inside tunnels (Moczek, 1996). Fighting success is predominantly determined by body size (Moczek, 1996; for related taxa see: Siva-Jothy, 1989; Rasmussen, 1994; Emlen, 1997) and, within equally sized contestants, by the length of male horns (Moczek, 1996). Horns, however, may also entail high costs. Serious injury and the eventual death of contestants have been reported to result from fights between horned *Allomyrina dichotoma* males (Siva-Jothy, 1987), and horns have been shown to impede substantially male mobility inside tunnels (Emlen, 1994b; Moczek, 1996). Horn development may also prolong the time required to reach sexual maturity (Hunt & Simmons, 1997), and restrict expression of other structures such as wings in rhinoceros beetles (Kawano, 1995) or eyes in *Onthophagus taurus* (Nijhout and Emlen, in preparation).

Small male *O. taurus*, however, do not engage in extensive male–male combat. Instead, these males employ a complex set of alternative 'sneaking' behaviours, including sliding past guarding males, and utilize already established, unguarded tunnels to circumvent large males (Moczek, 1996). Results presented in Moczek (1996) and in Emlen (1994b) on the related *O. acuminatus* reveal that horns not only fail to provide any competitive advantage to small sneaking males, but may actually be detrimental to successful performance of sneaking behaviours. Combined, these findings suggest that the social and environmental conditions associated with alternative reproductive tactics adopted by fighting and sneaking male *O. taurus* represent discrete selection environments, favouring horns in males large enough to effectively guard tunnels, and hornlessness in smaller males that sneak (Emlen, 1994b; Moczek, 1996).

Here we illustrate that one major determinant of success in male–male competition – male body size – is profoundly affected by the amount of food available during larval development. External conditions affecting larval diet are likely to result in considerable variation of male body sizes in natural populations even among siblings. This should preclude genetic specialization towards a single optimal male phenotype. Instead, males able to adjust horn development relative to a given body size are likely to be favoured by selection. Using larval diet as a correlated cue may allow developing male larvae to anticipate their later adult body size, or competitive 'status' (*sensu* Gross, 1996), and to optimize the allocation

of resources during development accordingly (Nijhout and Emlen, in preparation). This mechanism would ensure that horns are only expressed when environmental conditions allow the attainment of body sizes large enough to permit the successful implementation of fighting behaviours. More generally, this indicates that condition-sensitive developmental mechanisms may be expected to be favoured by selection over strict genetic determination, whenever relevant traits within a trait complex are influenced by the environment of the developing animal.

The evolutionary consequences of facultative expression of beetle horns

The coexistence of horned and hornless morphologies among males is common in the genus *Onthophagus* (Arrow, 1951; Howden & Cartwright, 1963; Matthews, 1972). Species exhibiting male dimorphisms often differ strikingly not only in the specific morphology of the horned male morph, but also in the overall body size ranges present in their populations and in the critical body sizes separating alternative male shapes (Emlen, 1996). Both the overall body size range present in a population as well as the critical body size separating horned and hornless male shapes are likely to reflect important aspects of the selective environment in which both male phenotypes function.

Here we demonstrated that environmental conditions contribute considerably to the determination of male body size, and – by means of a threshold response – to the production of horns. Our results did not provide any evidence for heritable variation for the length of male horns. While we do not suggest that selection affecting horn morphology *per se* (provided sufficient genetic variation existed in the past) might not have contributed to the patterns of morphological variation visible today, we emphasize that modifications of the developmental mechanisms regulating horn growth may present additional major avenues for evolutionary change. For example, natural selection may favour different critical threshold values if environmental conditions cause body size ranges to vary greatly among populations. In this case, the actual target of selection, and hence the ‘character’ evolving, would be the switch point and, thus, a component of the developmental mechanism of horn expression, rather than horn morphology *per se*. Emlen (1996) recently demonstrated that the critical body size separating horned and hornless morphs in *O. acuminatus* can respond rapidly to artificial selection, confirming the potential for evolutionary change in the developmental regime associated with horn dimorphism. This is consistent with Schmalhausen’s (1949) concept of the evolution of adaptive phenotypic plasticity via modification of the mechanisms, e.g. thresholds, employed in matching the production of traits with those environments appropriate for their expression, rather than mod-

ifications of trait values *per se* (Schmalhausen, 1949; see also Schlichting & Pigliucci, 1995). Determining the extent to which selection acting on developmental aspects of male dimorphism may have contributed to the present-day patterns of morphological variation within and among species in the highly speciose genus *Onthophagus* (Balthasar, 1963) offers an intriguing field for further research and represents the focus of our current studies.

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