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Threshold evolution in exotic populations of a polyphenic beetle

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ABSTRACT

Polyphenic development is thought to play an important role in the evolution of phenotypic diversity and morphological novelties, yet the evolution of polyphenisms has rarely been documented in natural populations. Here we compare the morphologies of male dung beetles (*Onthophagus taurus*; Coleoptera: Scarabaeidae) from populations introduced to Australia and the eastern United States. Males in this species express two alternative morphologies in response to larval feeding conditions. Males encountering favourable conditions grow larger than a threshold body size and develop a pair of horns on their heads, whereas males that encounter poor conditions do not reach this threshold size and remain hornless. Australian and US populations did not differ in overall body size ranges, but exhibited significant differences in the location of the critical body size threshold that separates alternative male morphs. Australian males remained hornless at much larger body sizes than males in US populations, resulting in substantial and significant differences in the average body size–horn length allometry between exotic populations, as well as significant differences in morph ratios. The phenotypic divergence observed between field populations was maintained in laboratory populations after two generations under identical environmental conditions, suggesting a genetic basis to allometric divergence in these populations. Divergence between exotic *O. taurus* populations was of a magnitude and kind typically observed between species. We use our results to examine potential causes of allometric divergence in onthophagine beetles, and discuss the evolutionary potential of threshold traits and polyphenic development in the origin of morphological and behavioural diversity.

Keywords: adaptive phenotypic plasticity, alternative tactics, developmental threshold, exotic species, horn polyphenism, *Onthophagus*, status-dependent selection, threshold evolution.

INTRODUCTION

Organisms commonly adjust their phenotype to suit current or future environmental conditions, a phenomenon referred to as adaptive phenotypic plasticity. An extreme yet common case of adaptive phenotypic plasticity is polyphenism: the existence of discrete

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morphological variants within populations, expressed facultatively in response to the internal or external environment experienced by an individual. Examples of polyphenisms include predator-induced polyphenisms (e.g. *Daphnia*: Grant and Bayly, 1981; barnacles: Lively, 1986a,b), seasonal polyphenisms (e.g. Lepidoptera: Shapiro, 1976; Koch and Bückmann, 1987; Kingsolver, 1995), dispersal polyphenisms in a wide range of insects (Zera and Denno, 1997), caste polyphenisms in social Hymenoptera (e.g. Weaver, 1957; Wheeler and Nijhout, 1983) and alternative male morphologies in many arthropods (e.g. thrips: Crespi, 1988; acarid mites: Radwan, 1993; beetles: Moczek and Emlen, 1999). Polyphenic development is thought to play a pivotal role in speciation and the evolution of morphological and behavioural novelties (e.g. West-Eberhard, 1989, 1992).

The proximate factors that determine which phenotype is produced are known for many polyphenisms (Velthius, 1976; Smith, 1978; Hazel and West, 1979; de Wilde and Beetsma, 1982; Denno *et al.*, 1986; Lively, 1986a,b; Wheeler, 1986; Harris, 1987; Grayson and Edmunds, 1989; Greene, 1989, 1996; Zera and Tiebel, 1989; Pfennig, 1990; Denver, 1997). Furthermore, the developmental and endocrine mechanisms that adjust developmental pathways to environmental conditions are at least in part understood for some poly-phenisms (e.g. Okkut-Kotber, 1980; Wheeler and Nijhout, 1983; Endo and Funatsu, 1985; Hardie, 1987; Koch and Bückmann, 1987; Zera and Tobe, 1990; Pener, 1991; Wheeler, 1991; Nijhout, 1994, 1999; Rountree and Nijhout, 1995; Zera and Denno, 1997; Emlen and Nijhout, 1999; Starnecker and Hazel, 1999). How these mechanisms evolve in natural populations is, however, still poorly understood (Moczek and Nijhout, in press). Several theoretical models characterize evolution of threshold traits (Lively, 1986b; Hazel *et al.*, 1990; Moran, 1992; Hazel and Smock, 1993; Roff, 1994; Gross, 1996; Gross and Repka, 1998), and geographic comparisons and breeding experiments illustrate that thresholds often vary heritably among populations (Tauber and Tauber, 1972, 1982; Harrison, 1979; Hazel and West, 1982; Semlitsch and Wilbur, 1989; Semlitsch *et al.*, 1990; Denno *et al.*, 1996; Emlen, 1996; Ahlroth *et al.*, 1999). However, the ecological factors that may shape the evolution of polyphenism in natural populations are largely unexplored, as are the consequences of such evolutionary modifications for patterns of morphological diversity.

An interesting example of polyphenic trait expression involves the development of horns in a number of beetle species, in which large 'major' males produce horns, whereas smaller 'minor' males remain hornless (Paulian, 1935; Eberhard, 1982; Cook, 1987; Eberhard and Gutierrez, 1991; Emlen, 1994; Rasmussen, 1994; Kawano, 1995; Hunt and Simmons, 1997; Moczek and Emlen, 1999). Recent experiments on a subset of species demonstrated that male adult body size is primarily determined by larval feeding conditions and that only males that exceed a critical threshold body size develop horns, whereas males below this threshold remain hornless (Emlen, 1994; Hunt and Simmons, 1997, 1998; Moczek, 1998, in press; Emlen and Nijhout, 1999; Moczek and Emlen, 1999). As a consequence of this threshold action, natural populations of these species are generally composed of two relatively discrete male shapes (Emlen, 1994; Hunt and Simmons, 1997, 1998; Moczek and Emlen, 1999).

Male horn dimorphism is widespread, yet closely related species often differ in the scaling relationship between body size and horn length, especially the critical threshold body size that separates horned and hornless male phenotypes (Emlen, 1996). Although horn length was found to exhibit no significant heritable variation in natural populations (Emlen, 1994; Moczek and Emlen, 1999), one study demonstrated that the critical threshold body

size can respond rapidly to artificial selection (Emlen, 1996). Hence, novel scaling relationships between body size and horn length may evolve through modification of the critical threshold body size that separates alternate morphs.

Here, we document a case of threshold divergence in two exotic populations of the horn dimorphic beetle *Onthophagus taurus* Schreber (Coleoptera: Scarabaeidae). *Onthophagus taurus* originally exhibited a Mediterranean distribution (Balthasar, 1963). In the early 1970s, *O. taurus* was introduced accidentally to North Carolina and, as part of a biocontrol programme, to Western Australia (Fincher and Woodruff, 1975; Tyndale-Biscoe, 1996). We show that these exotic populations have diverged in the critical threshold body size required for horn expression. Using a common garden rearing protocol, we then estimate the extent to which phenotypic differences between exotic populations are due to genetic differentiation in the critical threshold body size. We explore possible mechanisms that may have contributed to the evolution of divergent scaling relationships in these populations, and use our findings to discuss the origin of allometric diversity in onthophagine beetles.

MATERIALS AND METHODS

Collection of beetles

Onthophagus taurus is common throughout both North Carolina (NC) and Western Australia (WA). North Carolinian populations were sampled in 1996 (A.P.M.) near Bahama (Durham County) and in 1997 near Mt. Sinai Road (Orange County). Populations in Western Australia were sampled in 1997 at Margaret River and in 1998 near Busselton (J.H.). Beetles were collected using whole dung pad samples. Beetles were either frozen and stored in ethanol for morphometric measurements or brought to the laboratory for breeding experiments. About 2000 beetles collected near Busselton (WA) and 1500 beetles collected at Mt. Sinai Road (NC) were used to found two laboratory colonies for common garden rearing.

Rearing protocol

Both laboratory colonies were kept in the same insectary at Duke University at 26°C and 60% relative humidity under a 16:8 light:dark cycle. Beetles were bred (A.P.M.) in plastic containers (25 cm tall, 20 cm in diameter) filled 3:4 with a moist sand/soil mixture. Five pairs of beetles were added to each container (eight containers per colony and week) and provided with ~0.5 l of homogenized dung. Six days later, beetles were recaptured and brood balls were collected and placed in separate containers until emergence. To minimize inbreeding, individual adult beetles were allowed to produce brood balls only once and were then removed from the colony. Different generations were kept in separate containers. Over 1000 individuals were reared each generation for each strain. Great care was taken to provide both laboratory colonies with the exact same treatment and breeding set-up.

Morphometric measurements

All male beetles collected in NC in 1996 ($n = 143$) and WA in 1997 ($n = 472$), a randomly selected subset of beetles collected in NC in 1997 ($n = 171$) and WA in 1998 ($n = 172$), and a

randomly selected subset of beetles bred in the laboratory (NC: $n = 233$; WA: $n = 369$) were used to collect morphometric data. All individuals were measured by A.P.M. using a standard two-dimensional image analysis set-up at the Duke University Morphometrics Laboratory (for details, see Moczek and Emlen, 1999). We used thorax width as an estimate for body size (for justification, see Emlen, 1994; Moczek and Emlen, 1999).

Statistical analysis

To describe the average scaling relationship between horn length and body size in field and laboratory samples, we used a four-parameter non-linear regression model of the form

$$\text{horn length} = y_0 + \frac{a\,(\text{body size})^b}{c^b + (\text{body size})^b} \tag{1}$$

where y_0 specifies minimum horn length, a describes the range of horn lengths in the sample, b specifies a slope coefficient and c represents the body size at the point of inflection of the sigmoid. Parameter values were obtained using Sigma Plot™ curve fitting procedures. We used c, or the inflection point of the sigmoid, as an estimate of the average body size threshold at which males switch from the hornless to the horned phenotype. To compare two samples, we first applied the above regression model to both samples combined (=simple model) and determined the parameter values that maximized the likelihood L of our data given this model using the likelihood function:

$$L(\sigma^2, a, b, c, y_0; x) = \frac{1}{(2\pi\,\sigma^2)^{n/2}} \exp\left\{ -\frac{1}{2\,\sigma^2} \sum_{i=1}^{n} (y_i - \hat{y}\,(a, b, c, y_0; x_i)^2 \right\} \tag{2}$$

where x_i = body size of male i, σ^2 = the variance of the data about the fitted values, n = the number of beetles in the combined sample and

$$\hat{y}_i(a, b, c, y_0; x) = y_0 + \frac{ax^b}{c^b + ax_i^b} \tag{3}$$

We then repeated this analysis for each sample separately (complex model). We obtained a P-value by comparing the test statistic

$$T = 2 \ln (\text{likelihood of the complex model/likelihood of the simple model}) \tag{4}$$

to a χ^2 distribution with degrees of freedom equal to the difference in the number of parameters between the two models (Edwards, 1972; Weir, 1990). If significant differences were indicated, we used repeated Welch's t-tests to examine the extent to which differences in particular regression parameters, such as the inflection point or slope, explained allometric differences between samples (Sachs, 1992; Sokal and Rohlf, 1995).

Male body size was analysed using standard analysis of variance (ANOVA) and repeated t-tests for pairwise contrasts. Morph ratios were obtained by counting males on both sides of the inflection point of the sigmoidal regression generated for each sample and compared using multiple χ^2-tests. All significance levels were corrected for multiple comparisons using sequential Bonferroni correction procedures (Sachs, 1992; Sokal and Rohlf, 1995). Unless otherwise noted, all data are presented as the mean ± standard error.

RESULTS

Field samples

In all samples obtained from both NC and WA populations, only males above a critical body size expressed horns, whereas males below this critical threshold remained hornless, resulting in similarly shaped horn length–body size allometries in all samples (Fig. 1). However, populations differed significantly – in some cases dramatically – in the average scaling relationship between horn length and body size, largely due to significant differences in the exact location of the critical body size threshold that separates alternative male morphs (Table 1). Both NC populations began to express the horned male phenotype at thorax widths of approximately 4.8 mm (mean inflection point: 5.00 ± 0.011 mm), whereas WA populations continued to produce only the hornless phenotype at this range and began to switch to the horned male phenotype only once beetles exceeded a thorax width of approximately 5.2 mm (mean inflection point: 5.31 ± 0.027 mm; Fig. 1). Differences in inflection points remained significant when samples collected in different years were compared, suggesting that allometric differences persist in the field across generations (Fig. 1).

While the NC populations did not differ significantly in any model parameters when compared to each other, the two WA populations differed slightly in threshold body size ($T_{172} = 2.83$; $P < 0.01$, non-significant after correction for multiple comparisons) as well as in slope ($T_{172} = 2.62$; $P < 0.01$, non-significant after correction for multiple comparisons), suggesting the existence of subtle local or seasonal variation in horn length–body size allometries among WA populations. We also detected small differences in slope in one other pairwise comparison (Mt. Sinai, NC, 1997 *vs* Busselton, WA, 1998; $T_{171} = 3.19$, $P < 0.01$), which, however, also became non-significant after corrections for multiple comparisons were applied. We found no significant differences between any field-collected samples for amplitude or minimum horn length.

Mean male body sizes differed slightly but significantly between samples ($F_{3,954} = 5.78$; $P < 0.001$). However, these differences did not appear to be correlated with the origin of the respective populations, as the two WA population samples accounted for both the highest and lowest mean male body size (Table 1). North Carolinian and WA populations also exhibited significant differences in morph ratios. Both WA populations exhibited substantially higher relative frequencies of hornless males than their North Carolinian counterparts (Table 1).

Beetles reared in a common environment

A considerable portion of the phenotypic differences observed between field collected individuals was maintained after rearing beetle colonies for two generations in the laboratory under identical conditions ($T_{233} = 14.92$; $P < 0.01$; Fig. 2). Laboratory colonies descended from NC and WA populations did not differ significantly in any of the model parameters when compared to NC and WA field populations, respectively (Table 1). Instead, both laboratory colonies maintained a mean difference in inflection points (0.345 mm) similar to mean differences observed between field-collected animals (0.318 ± 0.0167 mm). Combined, these findings suggest a strong genetic component to differences in scaling relationships between NC and WA populations. Interestingly, both laboratory colonies exhibited significantly smaller mean male body sizes after two generations than field-collected individuals

a)

b)
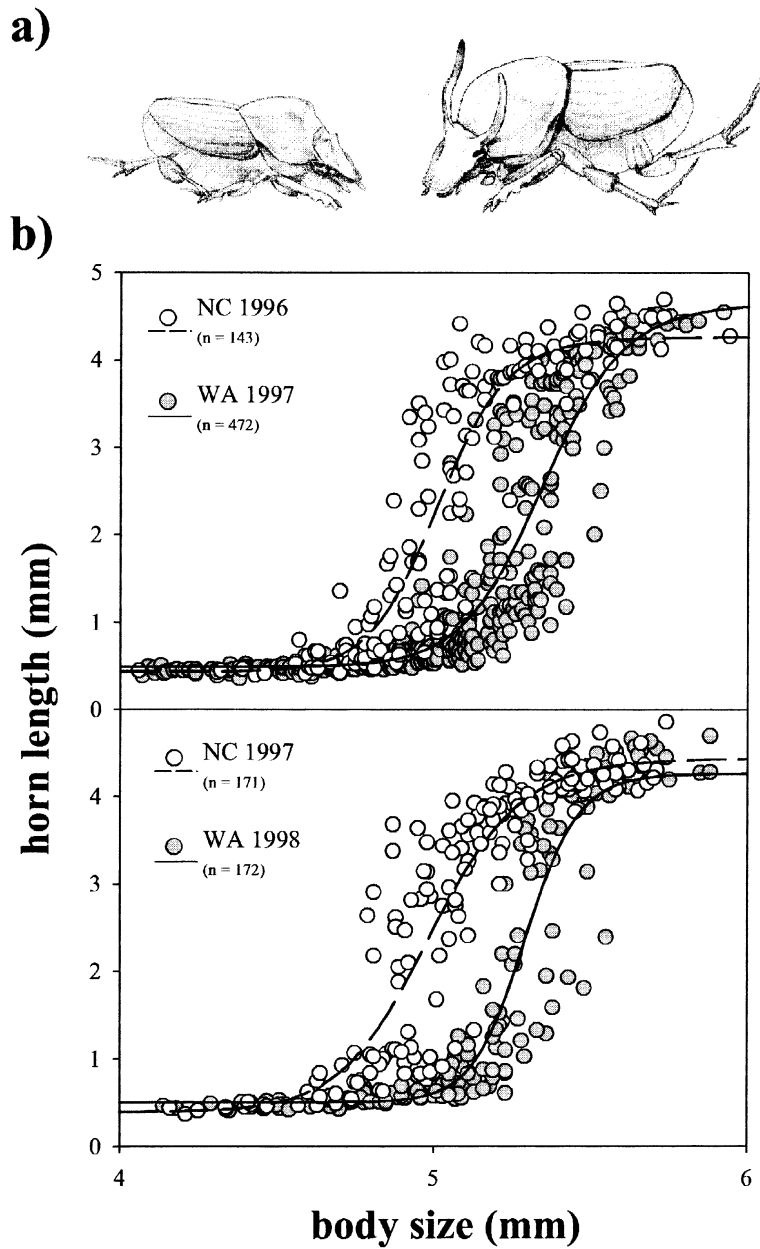
Fig. 1. (a) Typical morphology of hornless and horned male *O. taurus* (drawings by Shane Richards). (b) Scaling relationship of horn length and body size of male *O. taurus* collected in two different years and locations in North Carolina (open dots and dashed line) and Western Australia (solid dots and lines), respectively. Lines represent best-fit non-linear regressions (see text for details and Table 1 for parameter values).

Table 1. Male body size (mean ± standard error), allometric parameter values (mean ± standard error) and morph ratios in field samples and laboratory populations

Population	Body size	Regression parameters				Morph ratio horned:hornless	n
		a	b	c	y_0		
Field							
Bahama, NC, 1996	5.03 ± 0.028[a,b,c]	3.828 ± 0.024[a]	45.69 ± 6.923[a]	5.013 ± 0.017[a]	0.435 ± 0.157[a]	$1:1.01$[a,c]	143
Mt. Sinai, NC, 1997	5.09 ± 0.027[a,c]	4.04 ± 0.243[a]	34.75 ± 4.507[a]	4.99 ± 0.02[a]	0.392 ± 0.168[a]	$1:0.51$[a]	171
Margaret River, WA, 1997	4.99 ± 0.017[b]	4.16 ± 0.188[a]	41.23 ± 3.261[a]	5.346 ± 0.014[b]	0.49 ± 0.042[a]	$1:3.97$[b]	472
Busselton, WA, 1998	5.10 ± 0.028[c]	3.754 ± 0.163[a]	62.72 ± 7.517[a]	5.293 ± 0.012[b]	0.503 ± 0.07[a]	$1:2.19$[b,c]	172
Laboratory							
NC F2	4.75 ± 0.025[d]	3.649 ± 0.126[a]	45.71 ± 3.93[a]	4.953 ± 0.011[a]	0.475 ± 0.05[a]	$1:2.15$[b,c]	233
WA F2	4.76 ± 0.02[d]	4.164 ± 0.288[a]	41.15 ± 3.124[a]	5.298 ± 0.021[b]	0.473 ± 0.025[a]	$1:11.72$[d]	369

Note: a specifies the range of horn lengths within a sample (amplitude), b specifies a slope coefficient, c represents the body size at the point of inflection of the sigmoid and y_0 specifies minimum horn length. Samples that do not share a letter in the exponent are significantly different ($P < 0.05$; body size and model parameters: multiple t-tests; morph ratios: multiple χ^2 tests). All test results were corrected for multiple comparisons using sequential Bonferroni correction procedures.
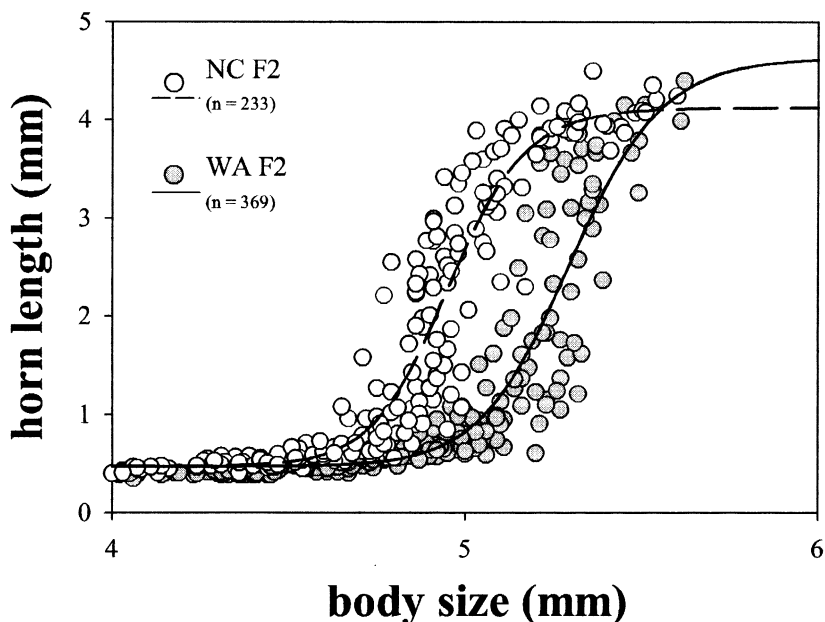
Fig. 2. Scaling relationship of horn length and body size of male *O. taurus* derived from field populations in North Carolina (open dots and dashed line) and Western Australia (solid dots and line) after beetles were reared for two generations in the laboratory under identical conditions. Lines represent best-fit non-linear regressions (see text for details and Table 1 for parameter values).

($P < 0.01$ for each comparison; Table 1). However, morph ratios remained significantly different between both strains, with a substantially higher frequency of hornless males in the WA colony (χ^2-test, $P < 0.05$; Table 1).

DISCUSSION

The significance of threshold characters in the evolution of phenotypic diversity has received much attention (Schmalhausen, 1949; West-Eberhard, 1989, 1992; Roff, 1996). However, surprisingly little is known about the extent to which developmental thresholds evolve in natural populations and the consequences of such evolution for patterns of morphological diversity (Moczek and Nijhout, in press). Here, we document a case of evolutionary divergence in body size thresholds in recently established populations of the polyphenic dung beetle *O. taurus*. North Carolinian and Western Australian populations differed significantly, and heritably, in the location of the threshold body size that separates alternative horned and hornless male phenotypes, resulting in substantial differences in the average scaling relationship between horn length and body size in these populations.

Horn polyphenism is common in the genus *Onthophagus*, and many species express similar horned and hornless male phenotypes and exhibit similar horn length–body size allometries. However, congeners often differ distinctly in the location of the threshold body size (Emlen, 1996), a pattern also observed in other beetle taxa (e.g. Kawano, 1995). This suggests that one major avenue of beetle horn evolution involves shifts in the threshold

employed in the polyphenic development of horns. The threshold divergence between NC and WA populations documented in the present study is of a magnitude similar to some of the differences observed between species (Emlen, 1996) and sister species (A.P. Moczek and H.F. Nijhout, unpublished). These data, therefore, raise the possibility that substantial allometric differentiation can evolve rapidly in geographically isolated populations, and may well precede the subsequent evolution of reproductive isolation. However, the evolutionary mechanisms that may have caused exotic *O. taurus* populations to diverge in their allometries are unclear.

In the case of exotic populations founded by an accidental introduction, such as the introduction of *O. taurus* to North Carolina, random genetic drift appears to be a particularly likely contributor to allometric divergence. Even though the introduction of *O. taurus* to Western Australia was deliberate and involved at least 36 releases between 1969 and 1983 consisting of 500–1800 individuals per release (Tyndale-Biscoe, 1996), it is still possible that genetic drift could have played an important role in the evolution of new body size thresholds. For example, knowledge of the exact habitat requirements of *O. taurus* at the time of introduction was limited and several releases were conducted in regions or at times during the season where it would have been difficult for this species to establish itself (Tyndale-Biscoe, 1996; J. Feehan and T. Weir, personal communication). Genetic drift due to local extinctions may also, therefore, have contributed to threshold divergences in Western Australian populations. If this is correct, then present-day allometries in North Carolinian and Western Australian populations should reflect pre-existing allometric variation in the native range of this species. To test this notion, we have begun to explore patterns of allometric variation in the native, circum-mediterranean range of *O. taurus*.

Alternatively, allometric differentiation between NC and WA populations could have been a response to divergent selective environments. Male horn polyphenism in *O. taurus* plays an important role in male reproductive behaviour, as the two male morphs use distinctly different alternative reproductive tactics to secure breeding opportunities (Moczek and Emlen, 2000). Large, horned males rely exclusively on aggressive fighting behaviours involving the use of horns as weapons. Although body size is the main determinant of fighting success, the possession of long horns confers an additional advantage to males that engage in fights (Emlen, 1997; Moczek and Emlen, 1999). In contrast, smaller, hornless males rely on non-aggressive sneaking behaviours to circumvent larger, horned males, and horn possession appears detrimental to the performance of small males that engage in sneaking behaviours (Emlen, 1997; Moczek and Emlen, 2000). Under such conditions, only males large enough to succeed in fights would benefit from developing horns. Smaller males may gain higher fitness by engaging in sneaking rather than fighting behaviours and should, therefore, remain hornless. Such a selection environment would favour genotypes that match the morphological switch from no to complete horn expression to the body size at which the fitness gained from sneaking becomes outweighed by the fitness gained from engaging in fights (Emlen, 1997; Moczek and Emlen, 1999, and references therein).

However, the optimal body size at which to switch from sneaking to fighting behaviours may vary as a function of external conditions. For example, changes in the average body size of competing males would change the composition of males with which a given male has to compete. Changes in size distribution may, therefore, favour corresponding shifts in the threshold for producing horns (Emlen, 1997; Moczek, in press). Alternatively, changes in the frequencies of encounters between competing males via changes in local densities may alter the relative profitability of each tactic. For example, an increase in the density of

competing males may allow only but the very largest males to benefit from engaging in fights. Consequently, sneaking behaviour would become profitable over a wider range of body sizes, which, in turn, would favour a corresponding shift of the threshold for horn production to larger body sizes. Differences in ecological or demographic conditions may, therefore, result in the evolution of divergent threshold body sizes in geographically isolated populations of onthophagine beetles. Comparative sampling of eastern US and Western Australian populations has so far shown no evidence for differences in body size ranges, but indicates substantial and consistent differences in population densities (Moczek, 2002). We are currently exploring the extent to which differences in these factors indeed select for different threshold locations.

The evolutionary potential of polyphenisms

Evolutionary changes in all morphological traits ultimately result from genetic modifications of the developmental mechanisms that produce them (West-Eberhard, 1989, 1992; Moran, 1992; Schlichting and Pigliucci, 1998). This is particularly obvious in phenotypically plastic traits. As the phenotype depends in part on the environment, plastic traits generally have very low heritabilities (Roff, 1996). Evolution of these traits may, therefore, proceed primarily via genetic changes of components of the developmental machinery that produces the plastic trait. However, these mechanisms often remain obscure and it is generally difficult to link specific changes in a regulatory mechanism to observed evolutionary modifications of a phenotype.

   Polyphenic development provides an exception to this rule. Polyphenisms are a common extreme of phenotypically plastic trait expression and rely on the existence of threshold responses to produce several discrete phenotypes, as opposed to a graded range of forms (Stearns, 1989; Nijhout, 1994; Roff, 1996). Threshold responses, such as those implemented in polyphenic development, are essential components of most physiological and developmental processes, yet have only relatively recently regained attention from evolutionary biologists (e.g. Schmalhausen, 1949; Hazel and West, 1982; West-Eberhard, 1989, 1992; Kingsolver, 1995; Emlen, 1996, 2000; Roff, 1996; Zera and Denno, 1997; Hazel *et al.*, 1998; Schlichting and Pigliucci, 1998; Lively *et al.*, 1999; Nijhout, 1999; Tomkins, 1999). Although few polyphenisms are understood well from an evolutionary perspective, it is clear that the developmental machinery that underlies them has the potential to provide ample opportunities for evolutionary modifications, and hence needs to be recognized as an important avenue of phenotype evolution (Zera and Tiebel, 1989; Zera and Tobe, 1990; Rountree and Nijhout, 1995; Gu and Zera, 1995; Zera and Zhang, 1995; Zera *et al.*, 1996; Zera and Tanaka, 1996; Roff *et al.*, 1997; Emlen, 2000; Moczek and Nijhout, in press). Furthermore, even relatively minor evolutionary changes in the control mechanisms underlying polyphenic trait expression have the potential to cause major morphological or life-history divergences between populations. For example, lacewings, *Chrysopa carnea* (Neuroptera), incorporate a threshold sensitivity to changes in daylength that regulates the polyphenic switch between direct development and overwintering diapause (Tauber and Tauber, 1970). Surveys of natural lacewing populations spanning a range of latitudes and climates revealed large-scale differences among populations in the critical daylength at which developing lacewings initiated diapause. These population differences persisted in a common garden experiment, suggesting evolutionary divergence between populations with respect to this developmental threshold (Tauber and Tauber, 1972, 1982). Tomkins (1999)

found differences in the scaling relationship between forceps length and body size that generated differences in the ratio of brachylabic to macrolabic morphs between two island populations of the earwig *Forficula auricularia*, and these differences also persisted in common garden rearing experiments. Furthermore, many reptiles incorporate a threshold temperature into a polyphenic mechanism of sex determination (e.g. Crews *et al.*, 1994) and, in snapping turtles, there is heritable variation in the critical temperature for switching between female and male development (Bobyn and Brooks, 1994). Our present comparison of Australian and US populations of the horn-polyphenic beetle *O. taurus* adds another example, and illustrates that the threshold response underlying the expression of alternative male morphologies evolves in natural (or at least introduced) conditions and has the potential to generate highly divergent scaling relationships between populations. Since polyphenic development is a central component in the production of a great diversity of phenotypes in a much wider range of taxa than currently under study, we believe that we are only now beginning to appreciate its role in the genesis of morphological diversity.

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