

# Horn polyphenism in the beetle *Onthophagus taurus*: larval diet quality and plasticity in parental investment determine adult body size and male horn morphology

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In a wide range of taxa, individuals are able to express strikingly different morphologies in response to environmental conditions encountered during development. Such polyphenisms have received particular attention from evolutionary biologists because the condition-dependent expression of alternative morphologies is believed to reflect the existence of discrete sets of adaptations to heterogeneous ecological or social conditions, which preclude the evolution of a single, optimal phenotype. Correct interpretation of the adaptive significance, if any, of facultative trait development requires a solid understanding of the determinative regime governing morph expression. Here I explore the environmental variables determining male morphology in the horn-dimorphic beetle *Onthophagus taurus*. I demonstrate that natural variation in both the quantity and quality of food that larvae receive from their parents determines body size in males and females, and, by means of a threshold response, the presence or absence of horns in males. In addition, results suggest that parent beetles adjust the amount of food they provision for their offspring according to diet quality, which may help to compensate for environmental variation induced by differential resource quality in the wild. I use these results to further characterize the selective regime responsible for the evolution of male polyphenism in onthophagine beetles and discuss its significance for understanding the origin and maintenance of morphological variation in the genus *Onthophagus*. *Key words*: alternative phenotypes, facultative parental investment, *Onthophagus*, phenotypic plasticity, polyphenism. [*Behav Ecol* 9:636–641 (1998)]

Environmental factors commonly influence patterns of morphological variation within natural populations. An extreme yet common case is the existence of discrete morphological variants within populations, expressed facultatively in response to cues from the internal or external environment (Moczek and Emlen, in press; Nijhout, 1994). Examples of such polyphenisms include caste polyphenisms in ants (Nijhout and Wheeler, 1982; Wheeler and Nijhout, 1983, 1984), bees (Weaver, 1957), and termites (Lüscher, 1960; Miller, 1969), seasonal polyphenisms in butterflies (Koch and Bückmann, 1984; Shapiro, 1976) and caterpillars (Greene, 1989), predator-induced polyphenisms in *Daphnia* (e.g., Grant and Bayly, 1981), rotifers (Gilbert and Stemberger, 1984), and barnacles (Lively, 1986b), phase polyphenisms in migratory locusts (Pener, 1991; Staal, 1961) and aphids (Hardie and Lees, 1985; Tauber et al., 1986), and alternative male morphologies in many arthropods (e.g., acarid mites: Radwan, 1993; Timms et al., 1981; beetles: Emlen, 1994; Moczek and Emlen, in press; thrips: Crespi, 1988). In these cases, each individual has the potential to develop into several alternative phenotypes, but expresses a particular morphology in response to environmental conditions experienced during critical developmental periods (Nijhout, 1994).

Particular attention has been devoted to the ecological and environmental conditions required for the expression of alternative phenotypes within populations. Generally, alternative phenotypes have been construed to reflect distinct ad-

aptations to different selection regimes (Gross, 1996; Hazel et al., 1998; Levins, 1968; Lively, 1986a; Lloyd, 1984; Moran, 1992). Developing individuals are thought to be able to use reliable environmental signals or cues to anticipate the selective environment they will experience and respond by expressing the phenotype most appropriate for those conditions (e.g., Hazel and West, 1982; Hazel et al., 1990; Lively, 1986a,b). However, the developmental and ecological mechanisms governing and constraining the expression of alternative phenotypes in populations remain to be investigated for most taxa. Most studies so far have concentrated on documenting the effects of single environmental variables considered relevant to phenotype expression, such as food quantity (Emlen, 1994; Moczek and Emlen, in press), presence or absence of predators (Gilbert and Stemberger, 1984; Grant and Bayly, 1981; Lively, 1986b), or population densities (Kennedy, 1961; Timms et al., 1981). However, most species express alternative phenotypes in complex environments affected by a multitude of ecological and demographic factors (Collins and Cheek, 1983; Emlen, 1997; Hardie and Lees, 1985; Tauber et al., 1986; Wheeler and Nijhout, 1984). Thus, studies investigating only one environmental variable and its consequences for phenotype expression are likely to present an artificially narrow view of the determinative regime underlying condition-sensitive development and are prone to overlook other important sources of variation vital for our understanding of the ecological context within which polyphenic species function.

The present study explored the determinative regime underlying facultative male horn dimorphism in the beetle *Onthophagus taurus*. Male *O. taurus* larger than a critical body size develop a pair of disproportionately long horns on their heads, whereas males smaller than this critical threshold develop

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only rudimentary horns, resulting in the co-occurrence of two discrete male morphs within populations (Hunt and Simmons, 1997; Moczek, 1996; Moczek and Emlen, in press). Previous studies have shown that variation in the quantities of food provisioned for larvae by their parents is the primary determinant of adult body size, and, by means of a threshold response, the presence and absence of horns (Moczek and Emlen, in press). Here I present results from breeding experiments designed to quantify the effects of natural variation in resource quality on adult morphology. I examined the extent to which the two food resources most commonly used by natural populations of *O. taurus* differ in their effects on adult body size and male horn development. In addition, I investigated whether parental provisioning behavior exhibits plasticity as a function of the nutritional quality of the food provisioned for offspring and to what extent resource-dependent parental investment may compensate for the effects of differential resource quality in the wild. I discuss the significance of my findings in the context of the behavioral basis of male dimorphism in *O. taurus* and use this synthesis to further characterize the origin and maintenance of morphological diversity in the genus *Onthophagus*.

## MATERIALS AND METHODS

### Natural history of *Onthophagus taurus*

*Onthophagus taurus* is a common dung beetle originally limited to a circum-mediterranean distribution (Balthasar, 1963). *O. taurus* became introduced to the United States by accident probably in the late 1960s and was first recorded in Santa Rosa County, Florida, in 1974 (Fincher and Woodruff, 1975). *O. taurus* has continuously extended its range since then and now represents the dominant onthophagine species in open pastureland in North Carolina (Moczek, 1996, unpublished data). Native and exotic populations of *O. taurus* adults have repeatedly been documented to colonize various kinds of dung (including cattle, horse, sheep, swine; e.g., Fincher and Woodruff, 1975; Hanski and Cambefort, 1991; Moczek, 1996). No definite information is available on the evolutionary history of dung producers and *O. taurus* or its ancestors; however, considering *O. taurus*'s wide natural distribution (Balthasar, 1963), this species is likely to have been exposed to considerable variation in dung resources for a long time.

Dung is used as a food resource by adults and larvae (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991; Moczek, 1996). Once a dung pad is colonized, adult females (sometimes assisted by the male) dig vertical tunnels through the pad into the soil (Goidanich and Malan, 1962, 1964; Moczek, 1996). 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 multiple well-compacted, oval-shaped brood balls. At the top end of each brood ball an egg chamber is formed, provided with a single egg and covered with an excrement cap. 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 and Malan, 1962, 1964; Halffter and Edmonds, 1982; Moczek, 1996; Moczek and Emlen, in press). Total development from the egg to an eclosing adult requires about 30 days in the laboratory (Moczek, 1996).

### Adult body size and male horn development as a function of larval food quality

To test whether the two resources most commonly used by natural populations of *O. taurus* differ in how they affect lar-

val growth and development, I reared larvae in horse dung and cow dung brood balls of known mass in the laboratory. To obtain brood balls, field-collected pairs of adult *O. taurus* were placed in cylindrical plastic containers (one pair per container) filled with a moist sand-soil mixture and provided with either fresh horse or cow dung. Brood balls were collected after 6–7 days, weighed to the nearest 0.1 g using a Mettler balance, and, imbedded in moist sand, placed in individual containers until emergence of adult beetles. Pairs were only used once. Both types of dung were collected in large quantities from two pastures near Durham, North Carolina, USA. Dung of the same type was first thoroughly homogenized and then given to the beetles as appropriate. Adult beetles were killed upon emergence, and body size and horn length were measured. I measured all individuals using a standard two-dimensional image analysis setup at the Duke Morphometrics Laboratory, Duke University (for details see Moczek and Emlen, in press). Thorax width was used as an estimate for body size (for justification, see Emlen, 1994; Moczek and Emlen, in press). I used ANCOVAs to quantify the effects of diet quality on adult body size with resource type as a class variable and brood ball size (i.e., resource quantity) as a covariate. Because males and females did not differ significantly in the relationship between brood ball mass and thorax width, both sexes were combined in the analysis. I used nonparametric Mann-Whitney *U* tests to test for resource-dependent differences in the extent of male horn development.

### Parental provisioning as a function of resource quality

Parent beetles appeared to vary the amount of dung they provisioned for their offspring in response to dung quality (see below). To test more rigorously whether parents consistently and predictably adjust their provisioning behavior in response to differences in resource quality, I selected 12 pairs of wild-caught beetles (all individuals were collected from the same field population) and provided them successively with both types of resource. Six pairs were allowed to breed first on horse dung for 4 days, after which brood balls were collected and weighed. Pairs were then provided with a new breeding container and allowed to breed for additional 4 days, this time provided with cow dung. Order of treatment was reversed in the other six pairs. Because variation in brood ball weight between resources may be due to natural differences in water content, I also reweighed brood balls after they had been dried for 24 h at 70°C. Data were analyzed using a matched-pairs signed-rank test following Wilcoxon and Wilcox (1964).

## RESULTS

### Adult body size and male horn development as a function of larval food quality

The results confirmed earlier findings (Moczek, 1996; Moczek and Emlen, in press) that food availability during larval development predictably determines adult morphology. Increased weight of brood balls of either resource resulted in the development of larger adult body sizes (horse dung:  $p < .01$ ; cow dung:  $p < .05$ ; Table 1, Figure 1a) with nonsignificant differences between sexes within each resource (horse dung:  $p > .9$ ; cow dung:  $p > .5$ ). However, the resource quantity required to achieve similar developmental results differed substantially between resources ( $p < .0001$  for  $y$  intercepts,  $p > .1$  for slope; Table 1, Figure 1a). Horse dung appeared to be a higher quality food, with almost twice the amount of cow dung required to yield the development of the body size obtained with a given amount of horse dung.

The results also confirmed the existence of a critical food

**Table 1**  
ANCOVA for the effects of larval food quantity (brood ball mass) and quality (horse dung versus cow manure) on adult body size for both sexes combined

Source of variation	df	SS	F
Brood ball mass ( <i>BB</i> )	1	4.74	29.27**
Resource ( <i>R</i> )	1	2.75	16.98**
<i>BB</i> × <i>R</i>	1	0.36	2.20
Total	85	22.49	
Error	82	13.27	

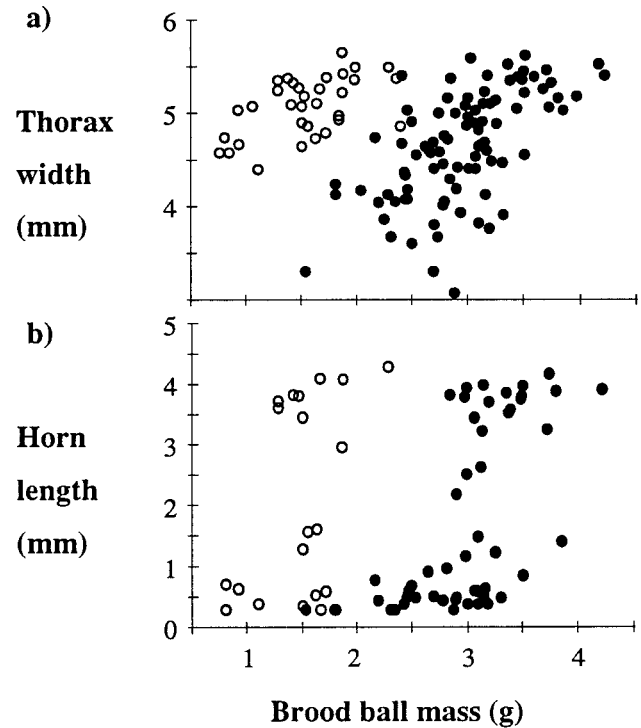
Sums of squares (SS) are type III. See text for further explanation.

\*\*  $p < .0001$ .

quantity threshold, separating the development of horned and hornless male phenotypes on both resources (Figure 1b). Males confined to a food amount below a critical quantity failed to produce horns, but went from minimal to complete horn expression abruptly once food amounts larger than this critical quantity were available to larvae. As a consequence, variation in the horn length–brood ball weight relationship was pronounced only around the threshold quantity (see also Moczek and Emlen, in press). While this was true for both resources, the exact location of the threshold differed dramatically between the two resources (Mann-Whitney  $U$  test on horn length/brood ball weight ratios:  $z = 3.38$ ,  $p < .0001$ , Figure 1b). Although roughly 1.5 g horse dung sufficed for the development of horned males, about 2.5–3.0 g of cow dung were necessary to yield the same result (Figure 1b). Again, this suggests that compensating for the apparently low quality of cow dung relative to horse dung requires more than a 50 % increase in brood ball mass.

#### Parental provisioning as a function of resource quality

Although each resource was offered ad libitum during the experiment described above, brood balls produced on horse dung by parent beetles rarely exceeded 2 g (Figure 1a,b), an amount that appears sufficient for the development of large adults ( $>5$  mm; Figure 1a). The same quantity of cow dung supported the development of only small individuals ( $<3.5$  mm; Figure 1a), and parent beetles only infrequently produced such brood balls. Instead, when using cow dung, parent beetles provisioned their offspring with 3 g of dung or more on a regular basis, a brood ball weight never observed to be produced on horse dung. These observations suggested that *O. taurus* adults adjust the amount of food provisioned for offspring according to the quality of the resource available. To test this hypothesis I offered both resources successively to 12 pairs of beetles and weighed brood masses produced by parents on each resource. Pairs provisioned consistently larger quantities of food for their offspring when given cow dung as compared to horse dung (mean fresh weight : horse dung = 2.09 g, SD = 0.32 g; cow dung: 3.08 g, SD = 0.37 g; Wilcoxon matched-pairs signed-rank test:  $p < .001$ ;  $n = 12$ ; Figure 2). Brood ball dry weight showed statistically significant differences in the same direction and of similar magnitude, suggesting that differences in water content alone do not explain brood ball weight variation between resources (dry weight horse dung: 0.85 g, SD = 0.12 g; cow dung: 1.29 g, SD = 0.21 g; Wilcoxon matched-pairs signed-rank test:  $p < .001$ ;  $n = 12$ ; Figure 2). These results support the hypothesis that adult *O. taurus* are able to identify resource quality and to adjust the quantity of food provisioned for their offspring accordingly.



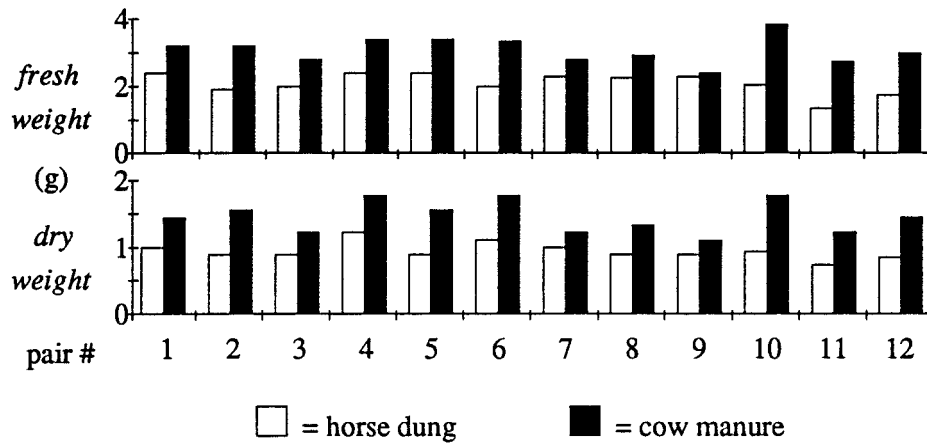
**Figure 1**  
Effects of quantity and quality of larval diet on adult development. (a) Adult body size increases linearly with diet quantity on both horse (open circles) and cow dung (filled circles). In comparing relationships between body size and brood ball mass in cow versus horse dung, highly significant differences were found in  $y$  intercepts (ANCOVA,  $p < .0001$ ; Table 1), but not in slope ( $p = .14$ ; Table 1). (b) Horn development in males increases discontinuously with increasing food amounts of either quality with a substantially higher threshold for the amount of cow dung (filled circles) required to initiate horn expression.

#### DISCUSSION

##### Environmental determination of adult morphology in *O. taurus*

Several studies have investigated the determination of adult body size and size-dependent expression of horns in males in the genus *Onthophagus* (Emlen, 1994, 1997; Hunt and Simmons, 1997; Moczek, 1996; Moczek and Emlen, in press). Estimates of heritability of body size and horn length by Emlen (1994, on *O. acuminatus*) and Moczek and Emlen (in press, on *O. taurus*) suggested little or no genetic variation for these traits in natural populations. Instead, Moczek and Emlen (in press) demonstrated that natural variation in brood ball mass represents the primary determinant of adult body size, and, by means of a threshold response, the presence or absence of horns. Here I demonstrate the importance of a second environmental variable, food quality, for the determination of adult morphology. Although both horse and cow dung are readily utilized by natural populations, these resources differed substantially in how they affected adult body size and male morph determination. Horse dung was shown to be a higher quality resource for developing larvae, with relatively small amounts being sufficient to support the development of adult body sizes  $> 5$  mm. Cow dung, in contrast, required a roughly 50–75% increase in brood ball mass to yield comparable adult body sizes. Both resources supported the development of the horned male morph, but the threshold quantity required to initiate horn growth differed substantially be-



**Figure 2**

Amount of food provisioned by parent beetles (brood ball mass) as a function of food quality. Shown are mean brood ball masses (upper row: fresh weight; bottom row: dry weight) produced by 12 *O. taurus* pairs to which both resources were offered successively, with reversed order of treatment in 6 pairs. Pairs provisioned significantly more food for offspring on the low-quality resource, cow dung (Wilcoxon matched-pairs signed-rank test:  $p < .001$ ,  $n = 12$ , for fresh and dry weight, respectively).

tween resources. The minimum cow dung brood ball mass needed for the production of a horned morph (2.78 g; Figure 1b) was more than twice the minimum horse dung mass needed for horn production (1.28 g; Figure 1b). Although these results confirm earlier findings that adult body size and male horn morphology is largely under environmental control and is determined in part by differences in the quantity of food available to larvae, the present study suggests that natural variation in larval food quality may present an equally important determinant of adult morphology in *O. taurus*.

### Resource-dependent parental investment

Numerous studies have examined how variation in ecological and social conditions may have led to the evolution of different patterns of parental care in different taxa (e.g., Choe and Crespi, 1997; Clutton-Brock, 1991). Also, patterns of variation in the intensity and kind of parental care provided by different members of a population have been studied for many species, and between-individual variation in parental investment has been found to have fundamental implications for the evolution and maintenance of animal mating systems and the intensity and direction of sexual selection (e.g., Andersson, 1994; Thornhill and Alcock, 1983). However, it has only been recently that individual parental investment has been recognized as a trait that itself can be plastic and that individuals within a population can flexibly and adaptively adjust the intensity and kind of parental investment they provide in response to environmental conditions, thereby maximizing their fitness in socially and ecologically heterogeneous environments (e.g., Bartlett, 1987; Dijkstra, 1986; James and Whitford, 1994; Marinelli and Messier, 1995; Scott, 1998a,b; Trumbo, 1990; Trumbo and Fernandez, 1995).

Burying beetles (genus *Nicrophorus*) represent one of the few taxa for which the ecological factors relevant to the evolution of parental care have been studied in detail, and we are beginning to appreciate individual behavioral plasticity in parental investment as a trait that confers a selective advantage under heterogeneous environmental conditions (reviewed in Scott, 1998a). Burying beetles colonize vertebrate carcasses and prepare them for consumption by their young. The ecological (carcass availability, size, quality) and social conditions (e.g., competition among adults for carcasses) of breeding opportunities encountered by adult burying beetles are not only highly variable in nature, but are also important determinants of larval survival and, therefore, parent fitness (Scott, 1998a). Several studies have indicated that burying beetles have evolved the ability to approximate breeding conditions and to adjust patterns of parental care accordingly. For

example, adult beetles facultatively adjust their brood sizes based on carcass quality and size, including infanticide of excess young (Bartlett, 1987; Trumbo, 1990; Trumbo and Fernandez, 1995), and alter the duration of parental care in response to population density (Scott, 1998b).

In onthophagine dung beetles such as *O. taurus*, adults also encounter highly variable breeding conditions. Adults naturally colonize both horse and cow dung pads for reproduction, and the results presented here strongly indicate that resource quality used for larval provisioning is likely to be an important determinant of parent fitness via determining adult body size and male horn morphology of offspring. However, despite the dramatic effects of resource quality on offspring morphology detected in this study, corresponding differences in average adult body sizes and morph ratios were not found between field populations restricted to either horse or cow dung (Moczek, 1996, in preparation). Instead, close inspection of parental provisioning behavior showed that parent beetles consistently and predictably provisioned larger food quantities for their offspring when food quality was low (cow dung) and provisioned smaller quantities when food quality was high (horse dung). On average, cow dung brood balls produced by the 12 pairs in this study were 51% (SD = 28.5; dry weight: 54%, SD = 23.2;  $n = 12$ ) heavier than horse dung brood balls produced by the same pair. A roughly 50% increase in brood ball mass was shown (see Figure 1a,b) to be the minimum increase in brood ball mass necessary to compensate for the apparently low quality of cow dung. This suggests that adult beetles are able to measure resource quality as they provision food for their offspring and to adjust food amounts accordingly.

In nature, *O. taurus* not only encounter dung resources of varying quality, but dung pads are generally patchy and, most importantly, short-lived resources (e.g., Hanski and Camberfort, 1991; Moczek 1996). For adults that provision food for their offspring, this may entail a trade-off between the total number of offspring for which food can potentially be provisioned and the average food amount available to individual offspring. Adjusting the amount of food provisioned according to food quality may therefore maximize parent fitness by optimizing the allocation of parental investment into offspring in an ephemeral resource environment composed of unpredictable variation in resource qualities. The exact mechanism by which adult *O. taurus* measure resource quality remains to be investigated.

An important implication of these findings is that in species exhibiting plastic parental care under heterogeneous environmental conditions, superficially similar offspring phenotypes can be the outcome of very different parental investments. As

a consequence, correct interpretation of the mechanisms generating morphological and behavioral variation in natural populations (or the lack thereof) requires a thorough understanding of how parental investment mediates between variation in ecological conditions and the environment experienced by developing offspring.

#### Environmental heterogeneity and morphological diversity in the genus *Onthophagus*

The origin and maintenance of discrete morphological variants within sexes has attracted considerable theoretical attention (Andersson, 1994; Andersson and Iwasa 1996; Dominey, 1984; Gross, 1996; Moran, 1992; West-Eberhard, 1989, 1992). Alternative phenotypes have generally been construed as reflecting discrete sets of adaptations to heterogeneous ecological or social conditions, precluding the evolution of a single, optimal phenotype (Gross, 1996). Results from a companion study suggest that alternative male morphologies in *O. taurus* reflect discrete adaptations to different competitive niches in male–male competition over mating opportunities (Moczek and Emlen, in press). Large, horned males rely exclusively on aggressive behaviors and monopolize females by invading and defending tunnels underneath dung pads, while small, hornless males engage in a complex set of sneaking behaviors when confronted with physically superior males. Body size and the length of horns have been identified as major determinants of male competitiveness, and contests between selected individuals strongly indicated that both horn possession in horned, fighting males and the lack of horns in hornless, sneaking males are adaptive in the context of the respective reproductive tactics used by the two morphs (Moczek and Emlen, in press). The critical threshold body size separating horned from hornless morphologies is of particular interest because following current theory it is assumed to reflect the location of an “equal-fitness point” between tactics (Gross, 1996). Equal-fitness points are considered to mark the optimal switch point between alternative tactics, and in cases where success of tactic is tightly linked to body size, this is expected to result in an optimal body size separating alternative reproductive tactics and morphologies (Gross, 1996; Radwan, 1993). Applying this theory to *O. taurus*, Moczek and Emlen (in press) argued that males larger than a critical body size threshold maximize their fitness by expressing horns and fighting for access to females, whereas males smaller than this threshold maximize their fitness by not expressing horns and instead engaging in nonaggressive sneaking behaviors.

The exact location of the optimal switch point between alternative tactics is considered to be determined in part by the ecological and demographic conditions present in a particular population and the extent to which relative fitnesses of alternative phenotypes are affected by their frequencies in a given population (frequency-dependent selection; Gross, 1996; Radwan, 1993). In populations of horn-dimorphic onthophagine beetles, the body-size range of competing males as well as morph frequencies and overall population densities are likely to be important aspects of the selective regime determining the optimal switch-point between horned and hornless male phenotypes (Emlen, 1997; Gross, 1996). Theoretically, altering these conditions for a population should therefore change the exact location of a switch-point, and with it different optimal body-size thresholds may be selected for (Emlen, 1997; Gross, 1996; Radwan, 1993). For example, if ecological conditions such as increased food availability or quality cause population-wide body-size ranges to shift to larger mean body sizes, this may favor new critical threshold values (Emlen, 1997; Moczek and Emlen, in press). Given genetic variation, this could lead to evolutionary divergence among populations

in the critical threshold separating alternative morphologies (Emlen, 1996).

Here I illustrate that natural variation in ecological conditions—quantity and quality of larval diet—profoundly affect two major determinants of male–male competition in *O. taurus*: body size and the length of horns. Although the present study indicates that resource-dependent parental investment may compensate for variation in resource quality, it remains to be shown to what extent this mechanism suffices in natural populations. Several natural populations of *O. taurus* have recently been shown to vary dramatically in the location of the threshold body size, resulting in substantial variation in morph ratios between populations (Moczek, in preparation). It is worth noting that, despite the widespread occurrence of horn polyphenism in the genus *Onthophagus*, closely related species often differ relatively little in the specific morphology of the horned phenotype (Moczek, unpublished data). However, species can differ considerably in the body-size ranges present in particular populations and in the critical body sizes separating alternate male morphs (Emlen, 1996; Moczek, unpublished data). I expect that integrating patterns of variation in the ecological and demographic conditions of polyphenic populations into further study of the genetic and developmental control of horn polyphenism is likely to aid our understanding of the origins of morphological diversity in the genus *Onthophagus*.

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