



# The role of ancestral phenotypic plasticity in evolutionary diversification: population density effects in horned beetles

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Plasticity's role in shaping phenotypic diversification continues to receive considerable attention. One especially debated issue concerns the significance of genetic accommodation in diversification, and the proposed role of ancestrally plastic responses in facilitating or biasing subsequent genetically canalized differentiation among taxa. Here, we investigated whether pre-existing plasticity in response to variation in population density present in the ancestral Mediterranean range of the bull-headed dung beetle *Onthophagus taurus* may have mediated previously documented rapid canalized divergences among descendent exotic populations that have been subject to dramatically different levels of competition for mates and resources in the field. We focused on two maternal behavioural traits, two life history traits and two morphological traits. We find that (1) Mediterranean *O. taurus* exhibited plasticity in response to adult densities for four of our six focal traits; (2) in two of those, plastic responses matched the direction of canalized divergences among natural populations; and (3) the presence and direction of plasticity appeared unrelated to trait type. More generally, our results provide partial support for the hypothesis that evolution by genetic accommodation could have contributed to the very early stages of population differentiation in a subset of traits in *O. taurus*.

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Phenotypic plasticity is well established as a mechanism enabling organisms to maintain high fitness in the face of fluctuating environments (Schlichting & Pigliucci, 1998). Furthermore, plasticity is increasingly being recognized as impacting the persistence of lineages by influencing populations' ability to colonize novel habitats or to resist extinction in the face of major environmental perturbations (Hendry, 2016; Yeh & Price, 2004). What is much less well understood, however, is plasticity's roles in more directly shaping phenotypic diversification and phenotypic innovation, in particular through the process of genetic accommodation (reviewed in Moczek et al., 2011; Pfennig et al., 2010; Wund, 2012). Genetic accommodation is defined most broadly as gene frequency change due to selection on the regulation of an environmentally induced response (West-Eberhard, 2003) and has received most attention because it proposes a mechanism whereby initially environmentally induced traits may become at least partly genetically canalized, or in other words, for phenotypic changes due to plastic responses to environmental conditions to precede corresponding genetic changes within populations. Such a

'plasticity-first' scenario may be possible, for instance, if plastic responses to environmental conditions make visible to selection previously cryptic genetic variation that was allowed to accumulate without resulting in selectable phenotypic variation (Ledón-Rettig, Pfennig, Chunco, & Dworkin, 2014; Paaby & Rockman, 2014).

The concept of genetic accommodation grew historically out of a broadening of the concept of 'genetic assimilation', now recognized as an extreme form of accommodation, whereby an initially environmentally determined phenotype becomes constitutively expressed. Initially focused on behavioural plasticity and learning (Baldwin, 1986, 1902), it has now grown to encompass all forms of plasticity, as well as all changes in the regulation of an environmentally induced response (Renn & Schumer, 2013; Waddington, 1953; West-Eberhard, 2003). Evidence in support of genetic accommodation initially derived primarily from environmental perturbation and artificial selection experiments in the laboratory, demonstrating that novel or stressful perturbations may elicit developmental responses that free up previously unexpressed genetic and phenotypic variation able to fuel rapid responses to artificial selection in the laboratory (*Drosophila*: Dworkin, 2005; Rutherford & Lindquist, 1998; Waddington, 1953; *Manduca sexta*: Suzuki & Nijhout, 2006; *Caenorhabditis*: Sikink, Reynolds, Ituarte, Cresko, & Phillips, 2014; *Arabidopsis*: Queitsch, Sangster, &

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Lindquist, 2002; fungi: Cowen & Lindquist, 2005; cyanobacteria: Walworth, Lee, Fu, Hutchins, & Webb, 2016). More recently, work on natural populations and species has also begun to accumulate evidence consistent with pre-existing plasticity as an initial mediator of subsequent genetic differentiation in the wild, including examples of morphological as well as behavioural plasticity: gut morphology and time of development in spadefoot toad tadpoles from diverse genera, including *Spea* and *Scaphiopus* (Gomez-Mestre & Buchholz, 2006; Ledón-Rettig, Pfennig, & Nascone-Yoder, 2008), trophic morphology, body form, size and behaviour in threespine sticklebacks, *Gasterosteus aculeatus* (Robinson, 2013; Shaw, Scotti, & Foster, 2007; Wund, Baker, Clancy, Golub, & Foster, 2008), melanization in *Daphnia melanica* (Scoville & Pfrender, 2010), reproductive physiology and behaviour in house finches, *Haemorrhous mexicanus* (Badyaev, 2009), and loss of eyes in cavefish, *Astyanax mexicanus* (Rohner, et al. 2013).

However, more studies remain necessary before the evolutionary significance of genetic accommodation can be fully assessed (Ehrenreich & Pfennig, 2016; Levis & Pfennig, 2016). For example, we need to learn more about the degree of phenotypic change that evolution by genetic accommodation may be capable of mediating, as well as potential biases it may exert toward certain trait types over others, possibly depending on their inherent sensitivity to the environment (Beldade, Mateus, & Keller, 2011; Foster, 2013; Foster, Wund, Graham et al., 2015; Ghalambor, McKay, Carroll, & Reznick, 2007). For instance, many types of behaviour exhibit extreme evolutionary lability (e.g. flight and flashing behaviour in fireflies: reviewed in Lewis & Cratsley, 2008; songs in birds and crickets: Desutter-Grandcolas & Robillard, 2003; Podos, Huber, Taft, 2004; Zuk, Rotenberry, & Simmons, 2001; nest building in social hymenoptera: Turner, 2002). Furthermore, behavioural plasticity has been documented extensively across a wide range of taxa (Foster & Endler, 1999), and shown to vary across populations of the same species (Foster, 1999; Foster & Endler, 1999). Yet, further comparative work is needed to assess whether behavioural traits are, as has been hypothesized (Allf, Durst, Pfennig, & McPeck, 2016; West-Eberhard, 1986, 2003), indeed more likely to undergo evolution by genetic accommodation compared to other traits that exhibit reduced lability and plasticity. Similarly, little is known about the speed with which initial, plasticity-mediated changes in phenotype expression may be accommodated into genetically canalized divergences, insights that may necessitate the study of the very early stages of population differentiation. Here we seek to contribute to a better understanding of both scope and speed of genetic accommodation by exploring the role of ancestral plasticity in mediating the early stages of rapid population differentiation in morphological, life history and maternal behavioural traits in recently established exotic populations of the bull-headed dung beetle *Onthophagus taurus*. We selected this species because it unites several features that make it a promising study organism to assess the role of phenotypic plasticity in the earliest stages of evolutionary diversification, most notably a diversity of ecologically relevant and experimentally accessible traits that are undergoing rapid diversification in recently established exotic populations (Beckers, Anderson, & Moczek, 2015; Moczek & Nijhout, 2003).

Adult *O. taurus* colonize dung pads of primarily cows and horses, establish tunnels underneath and provision dung in the form of brood balls at the blind end of each tunnel (Fincher & Woodruff, 1975; Halffter & Edmonds, 1982). Females oviposit a single egg in each brood ball, which then constitutes the entire food supply larvae have available to complete development to adult (Moczek & Emlen, 1999). Brood ball quantity and quality strongly affect offspring adult body size as well as sexual and male dimorphism: only male *O. taurus* develop a pair of long, curved horns on their

heads, and only if larval feeding conditions allow male larvae to metamorphose to an adult body size above a critical threshold value (Moczek & Emlen, 1999). Males smaller than this threshold size grow only rudimentary horns, whereas all females regardless of size develop a minor ridge instead. The resulting male horn polyphenism is paralleled by alternative reproductive tactics, where large horned males fight to gain access to females using horns as weapons, while small males rely on nonaggressive sneaking tactics to gain access to females (Moczek & Emlen, 2000). In the late 1960s *O. taurus* was introduced from its native range in the Mediterranean (Balthasar, 1963) to Western Australia to help control cow dung and dung-breeding flies (Tyndale-Biscoe, 1996), as well as into the eastern United States by accident (Fincher & Woodruff, 1975). Since introduction, both populations have diverged rapidly in diverse traits, attributed to substantial differences in local dung beetle densities and the resulting divergent intensities of mate and resource competition: *O. taurus* densities in the eastern United States rarely exceed a few individuals per dung pad, and competition from heterospecific species is essentially nonexistent (Moczek, 2003). As a consequence, competition among females for dung is minimal (most dung dries out above ground before being processed by adults), and male–male competition for females is moderate. In contrast, *O. taurus* densities in Western Australia reach into the hundreds to low thousands of individuals per dung pad, and densities from competing species can be similarly high (Moczek, 2003). As a consequence, competition among females within and across species for dung is severe (dung pads may be removed by beetle activity within hours) and intraspecific male–male competition for females is extreme. Earlier work posited that these extreme differences in competitive environments may have driven phenotypic divergences in a wide range of traits, including those in the following three categories. (1) Morphology: adults in Western Australia are consistently and significantly smaller than adults in the eastern United States. At the same time, the adult size threshold needed for horn induction has increased among males in Western Australia, but decreased in males in the eastern United States. Both divergences are maintained in common garden environments (Moczek & Nijhout, 2003; Moczek, Hunt, Emlen, & Simmons, 2002). (2) Maternal behavioural traits: females in Western Australia produce heavier brood balls, which are buried at a more shallow level compared to those in the eastern United States, and both divergences are again maintained in common garden environments (Beckers et al., 2015; Macagno, Moczek, & Pizzo, 2016). (3) Life history traits: females in Western Australia produce a much higher number of brood balls when given a breeding opportunity compared to their eastern United States counterparts and the resulting offspring exhibit significantly greater eclosion success. Of these life history divergences, only differences in brood ball number are retained in common garden conditions, whereas differences in eclosion success disappear in the F2 generation (Beckers et al., 2015). Interestingly, *O. taurus* from the ancestral range exhibit trait values intermediate to those described for Western Australia and the eastern United States (Macagno et al., 2016; Moczek, 2003; Moczek & Nijhout, 2003) for at least a subset of traits, suggesting that establishment of exotic populations was followed by rapid divergences in both exotic ranges, yet in opposite directions.

In this study, we sought to investigate whether pre-existing behavioural and/or morphological plasticity in response to adult densities present in the ancestral *O. taurus* population may have mediated these rapid divergences among descendent exotic populations. Specifically, we used a Mediterranean population obtained from Spain as a proxy for the ancestral population to quantify presence and direction of plastic responsiveness to high and low conspecific densities to answer the following three questions. (1)

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