

The behavioral ecology of threshold evolution in a polyphenic beetle

Armin P. Moczek

Department of Biology, Duke University, Durham, NC 27708, USA

Facultative expression of alternative male morphologies is thought to allow individual males to select the phenotype with the highest fitness gain given their competitive status relative to other males with which they compete for females. Choice of, or switching between, morphs commonly relies on developmental threshold responses. Evolutionary changes in developmental threshold responses are thought to provide an important avenue for phenotypic diversification and the evolution of morphological and behavioral novelties. However, the extent to which alternative male phenotypes and their underlying threshold responses actually evolve in natural populations is unclear. Likewise, the ecological factors that shape the evolution of threshold responses in natural populations are unexplored for most organisms, as are the consequences of such modifications for patterns of morphological diversity. I examined the ecological basis of rapid threshold evolution in exotic populations of the horn-polyphenic dung beetle *Onthophagus taurus*. Male *O. taurus* vary continuously in body size as a function of larval feeding conditions. Only males that exceed a critical threshold body size develop a pair of long horns on their heads, whereas males below this threshold remain hornless. Populations in two exotic ranges of this species, the eastern United States and western Australia, have diverged in the mean threshold body size, which has resulted in the evolution of highly divergent and novel horn length–body size allometries in these populations. Populations in a third and previously unstudied exotic range of *O. taurus* in eastern Australia exhibit threshold body sizes roughly intermediate between the eastern U.S. and western Australian populations. I tested three hypothesis to explain how differences in ecological and demographic factors can drive allometric divergences between populations, using data derived from comparative, standardized sampling of a large number of populations in each exotic range. Results suggest that differences in the intensity of both intra- and interspecific competition have contributed to the evolution of divergent thresholds in these populations. My results do not support the hypothesis that shifts in threshold body sizes to larger body sizes are a consequence of increases in the mean body size of competing males. I discuss my results in the context of *Onthophagus* mating systems and the evolutionary implications of threshold evolution. **Key words:** adaptive phenotypic plasticity, developmental threshold, exotic species, horned beetles, male–male competition, *Onthophagus*, polyphenism, resource competition, sex ratio evolution, status-dependent selection, threshold evolution. [*Behav Ecol* 14:841–854 (2003)]

Polyphenism can be defined as a single genotype's ability to express two or more discrete phenotypes in response to differences in external conditions, and represents an extreme yet common case of adaptive phenotypic plasticity (Nijhout, 1999). Facultative expression of alternative phenotypes is predicted to evolve when (1) a heterogeneous selection environment produces a reversal of fitness rankings of phenotypes across environments, (2) genotypes lack the ability to select only those environments suitable for their expression, and (3) some aspects of the environment send reliable signals to a developing individual as to the type of environment it is likely to encounter (Lively, 1986a,b; Moran, 1992). A particularly interesting case of polyphenic development involves the facultative expression of alternative reproductive morphologies within one sex, usually males (Crespi, 1988; Radwan, 1993; Moczek, 1998). Here, differences in the social environment experienced by different males are thought to be crucial for the origin and maintenance of alternative male phenotypes (Travis, 1994; West-Eberhard, 1989, 1992). Such differences may arise from differences in the competitive status of males, which in many taxa can be a direct consequence of the animal's own phenotype such as its body size (Dominey, 1984; Hazel and Smock, 1993; Hazel et al., 1990; Gross, 1996; Gross

and Repka, 1998). For example, relatively small or large males, by virtue of their different competitive status, often experience very different social conditions and hence selective environments. Such status-dependent selection may then result in the evolution of size-dependent expression of alternative reproductive morphs and behaviors, provided genotypes can predict their future competitive status during development based on some reliable environmental cue (Gross, 1996).

An important implication of this perspective is that a given male's competitive status is, by definition, a relative measure and a function of its own phenotype relative to the mean phenotype in the population within which it competes (Hazel and Smock, 1993). Consequently, as a population's mean phenotype changes, so does a given male's competitive status, even though his absolute phenotype may remain constant (Dominey, 1984; Hazel and Smock, 1993; Hazel et al., 1990; Gross, 1996; Gross and Repka, 1998). This view also allows for a better understanding of another important aspect of alternative reproductive phenotypes: the switch point, or threshold, that typically separates alternative morphs. As the competitive status of an individual changes, it is expected to switch phenotypes as the fitness gain associated with the original phenotype is outweighed by the fitness gain associated with the alternative phenotype (Figure 1a,b; point of equal fitness, *sensu* Dominey, 1984; Gross, 1996). If the relative fitness of a morph depends on its competitive status relative to other members of the population, this optimal switch point then, too, becomes a property of a population (Gross, 1996). Consequently, differences in ecological or demographic conditions may select for different optimal switch points or

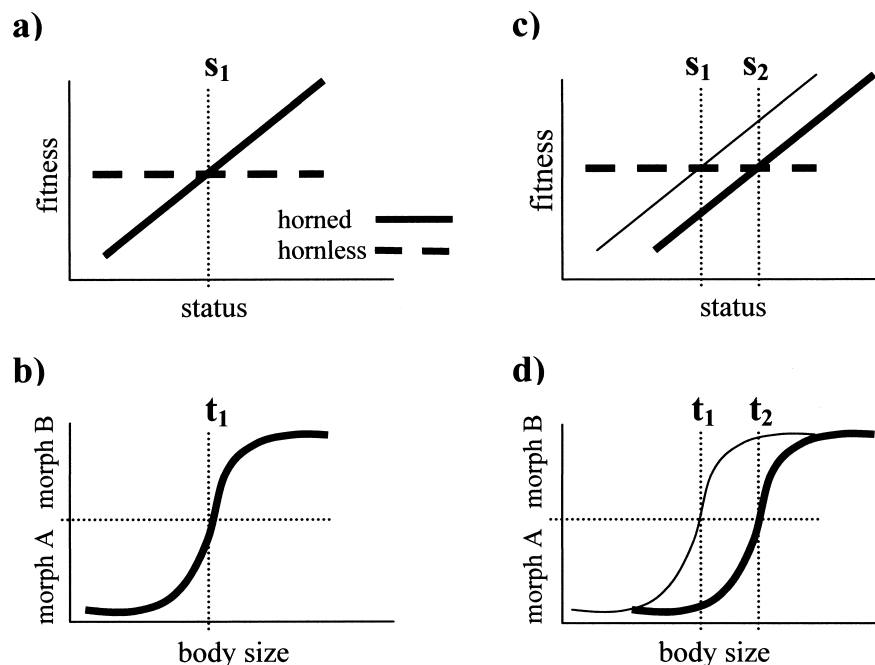
Address correspondence to A.P. Moczek, who is now at the Center for Insect Science, Department of Molecular and Cellular Biology, and Department of Ecology and Evolutionary Biology, University of Arizona, Tucson AZ 85721, USA. E-mail: arminmo@email.arizona.edu.

Received 22 June 2002; revised 20 January 2003; accepted 22 January 2003.

© 2003 International Society for Behavioral Ecology

Figure 1

Status-dependent selection and the evolution of developmental thresholds. (a) Status-dependent selection predicts that males should switch between alternative reproductive tactics as their competitive status exceeds s_1 , and the fitness gain associated with one tactic (e.g., sneaking) becomes outweighed by the fitness gain associated with the alternative tactic (e.g., fighting). (b) If alternative reproductive tactics are tightly linked to body size, s_1 should be manifest as a threshold body size, t_1 , that separates alternative male morphs in a population. (c) Changes in external conditions may alter the fitness functions associated with each morphology and associated behaviors, causing a change in the optimal switch point between morphs s_1 to s_2 . (d) Changes in the optimal switch point may subsequently result in a population-wide adjustment of the threshold body size t_1 to t_2 .



thresholds in different populations (e.g., Emlen, 1997; Moczek and Emlen, 1999). Given genetic variation for the threshold, this could then lead to evolutionary divergence among populations in the critical threshold separating alternative morphologies and associated behaviors (Figure 1c,d). However, despite considerable theoretical attention and important evolutionary implications, insights into how developmental thresholds evolve in natural populations remain scarce. Likewise, the ecological factors that shape the evolution of threshold responses in natural populations are unexplored for most polyphenic organisms, as are the consequences of such modifications for patterns of morphological and behavioral diversity.

I explored a case of rapid threshold evolution in the horn-polyphenic dung beetle *Onthophagus taurus*. Male *O. taurus* vary continuously in body size as a function of larval feeding conditions (Moczek, 1998). Only males that exceed a critical threshold body size develop a pair of long, curved horns on their heads, whereas males below this threshold remain hornless or develop only rudimentary horns (Figure 2; Moczek, 1998; Emlen and Nijhout, 1999). As a consequence of this threshold, natural populations are composed of two discrete horned and hornless male phenotypes separated by a clearly defined threshold body size (Figure 2; see also Paulian, 1935).

Male horn polyphenism in *O. taurus* plays an important role in male reproductive behavior as the two male morphs rely on strikingly different reproductive tactics to acquire matings (Moczek, 1999; Moczek and Emlen, 2000). Matings, resource provisioning for larvae, and oviposition take place exclusively in tunnels in and underneath dung pads, and gaining access to tunnels that contain females is therefore crucial for a male's reproductive success (Moczek and Emlen, 2000). Large, horned males guard tunnel entrances that contain females and rely on aggressive behaviors involving fights and the use of horns as weapons to deter rival males. Three factors have been shown to influence male fighting success. In pairwise

encounters larger males almost always win over smaller-sized competitors (Emlen, 1997). In fights between similar-sized males, the possession of long horns clearly increases a male's chances of winning a fight (Emlen, 1997; Moczek and Emlen, 2000). Finally, horned males are able to monopolize tunnel access when competing against a small number of smaller males but lose their monopoly as the number of competing males increases (Hunt and Simmons, 2002). Hornless males, on the other hand, rely on nonaggressive behaviors to secure breeding opportunities and sneak copulations. Earlier studies showed that the possession of horns appears detrimental to the performance of males that engage in sneaking behaviors (Moczek and Emlen, 2000). Combined, these findings support the hypothesis that both fighting and sneaking males benefit from their respective horned and hornless morphologies (Moczek and Emlen, 2000).

Onthophagus taurus originally exhibited a Mediterranean distribution (Balthasar, 1963). In the late 1960s *O. taurus* became introduced accidentally to the eastern United States (Fincher and Woodruff, 1975). Around the same time, *O. taurus* was introduced deliberately to eastern and western Australia to help control cow dung and dung-breeding flies (Bornemissza, 1976; Doube et al., 1991; Tyndale-Biscoe, 1990; Waterhouse, 1974). Although the exact origin of the eastern United States introduction is unknown, the beetle's introductions into eastern and western Australia are well documented. Both Australian introductions were derived from the same source populations collected originally in Spain, Greece, and Turkey (Australian Meat Research Council, 1982; Tyndale-Biscoe, 1990, 1996). Since introduction to eastern and western Australia, both Australian ranges have been largely, if not entirely, isolated from one another (Tyndale-Biscoe, 1996; Weir T, Feehan J, personal communication).

Recent work demonstrated that since introduction, populations in the eastern United States and western Australia have diverged in the critical threshold body size to a degree normally observed only between species (Moczek et al., 2002).

Threshold divergence is maintained in the field and laboratory over generations (Moczek et al., 2002) and reflects genetic modifications of the developmental machinery that produces alternative male morphs (Moczek and Nijhout, 2002a). Threshold divergence between eastern U.S. and western Australian populations resulted in the evolution of horn length–body size scaling relationships previously unrepresented in the native range of this species (Moczek and Nijhout, 2003). Here I document that populations in a third and previously unstudied exotic range of *O. taurus* in eastern Australia exhibit a threshold body size roughly intermediate to eastern U.S. and western Australian populations. I then examine the ecological and demographic mechanisms that may have driven allometric divergences between these three exotic ranges. Specifically, I tested the three hypotheses described below.

Intraspecific competition hypothesis

Differences in the degree of intraspecific competition may affect threshold body sizes in two ways. First, male *O. taurus* compete with each other in dung pads for access to females. A horned male's ability to gain and maintain access to females through fighting decreases with an increase in the number of males with which he has to compete (Hunt and Simmons, 2002). Under low-density conditions, male–male encounter frequencies in dung pads are likely to be low, and even medium-sized horned males may be able to deter rival males effectively enough to gain relatively higher fitness through fighting and the development of horns rather than through sneaking. Under such conditions, selection may favor a relatively low threshold body size. As the density of males per pad increases, however, the likelihood that a guarding male will be challenged by one or more intruders increases as well. Under high-density conditions, medium-sized males may no longer be able to maintain access to females through fights. Instead, such males may maximize fitness by remaining hornless and engaging in sneaking behaviors. Under such conditions, selection may favor a relatively high threshold body size.

Second, female *O. taurus* compete with each other for access to dung, which constitutes a patchy and ephemeral resource crucial for female reproduction (Hanski and Cambefort, 1991; Moczek, 1999; Otronen, 1988; Rasmussen, 1994). Female *O. taurus* use dung to provision food for their offspring in the form of brood balls. Brood balls are built inside tunnels and constitute the sole food source for developing larvae (Moczek, 1998). Without access to dung, female *O. taurus* are unable to reproduce. Under low-density conditions, most females will be able to secure enough dung to reproduce, resulting in a relatively even ratio of competing males to breeding females and relatively low levels of male–male competition. As the densities of competing females in a dung pad increases, females will eventually become resource limited, and a growing proportion of females will fail to secure enough dung to reproduce. Under such conditions, a relatively large number of males will compete for access to a relatively small number of breeding females. As a consequence, the overall intensity of male–male competition should increase. As before, increased levels of male–male competition should in turn limit the profitability of fighting behavior to only the largest males and favor a corresponding shift to a relatively high threshold body size. The intraspecific competition hypothesis therefore predicts a positive correlation between male threshold body sizes and population densities (Figure 3a–c).

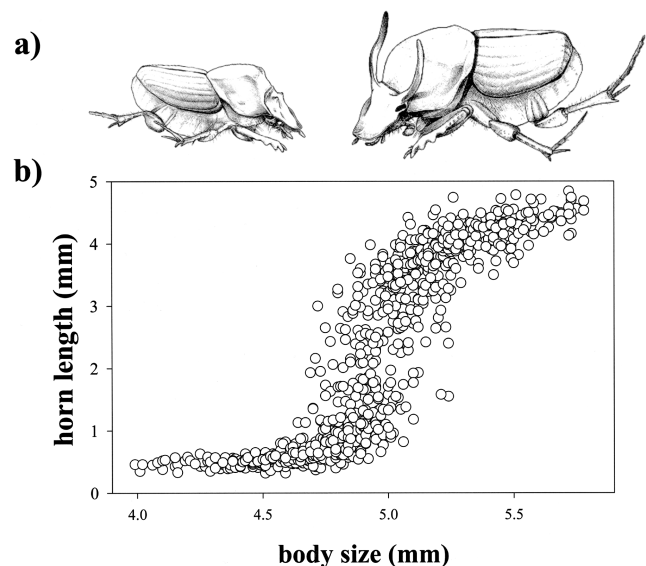


Figure 2

(a) Typical morphology of hornless and horned male *O. taurus* (drawings by Shane Richards). (b) Typical scaling relationship between horn length and body size of males *O. taurus* collected in Durham and Orange counties, North Carolina ($n = 821$). Data are taken from Moczek (2002).

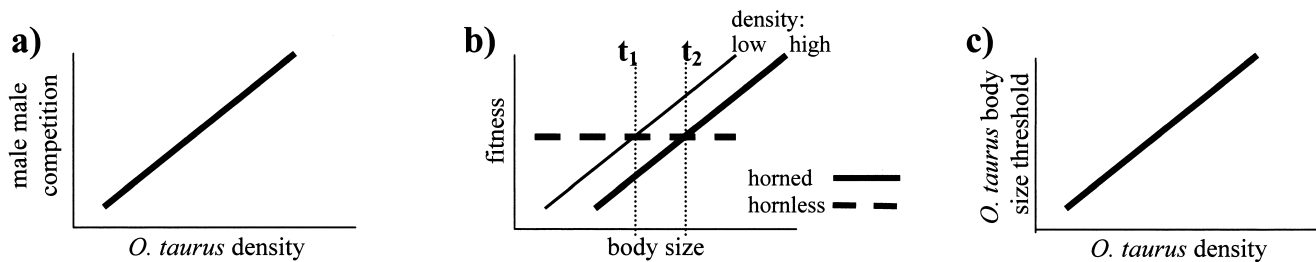
Interspecific competition hypothesis

In nature, *O. taurus* commonly competes with other species for access to dung pads (e.g., Giller and Doube, 1989; Ridsdill-Smith, 1993). Low levels of interspecific competition for dung should allow a relatively large portion of *O. taurus* females to secure enough dung to breed. In such a population, male *O. taurus* will compete for access to a relatively large number of breeding females, resulting in relatively low levels of male–male competition. As before, under such conditions selection is predicted to favor a relatively low threshold body size. As levels of interspecific competition increase, however, an increasing proportion of *O. taurus* females will be denied the opportunity to breed. Under such conditions males will compete for access to a relatively small number of breeding females, causing levels of male–male competition to increase (Figure 3d). As before, increased levels of male–male competition should in turn limit the profitability of fighting behavior to only the largest males and favor a shift of the threshold body size to relatively larger body sizes (Figure 3e). The interspecific competition hypothesis thus argues that increased competition from other species that compete for dung can intensify male–male competition indirectly by increasing the proportion of females that are unable to breed due to resource limitation. The interspecific competition hypothesis therefore predicts a positive correlation between male threshold body sizes and the densities of competing species (Figure 3f).

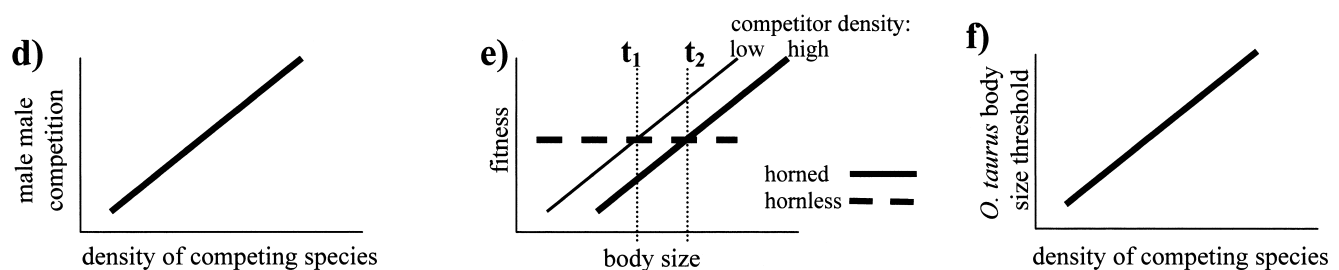
Differential body size hypothesis

In *O. taurus*, male fighting success is in part determined by male body size (Moczek and Emlen, 2000). A male's competitive status can therefore be considered a function of its own body size relative to the mean body size of males in the population within which he competes for mates. If the mean male body size in a population changes, so should the competitive status of a given male, even if his absolute body

I: intraspecific competition hypothesis



II) interspecific competition hypothesis



III) differential body size hypothesis

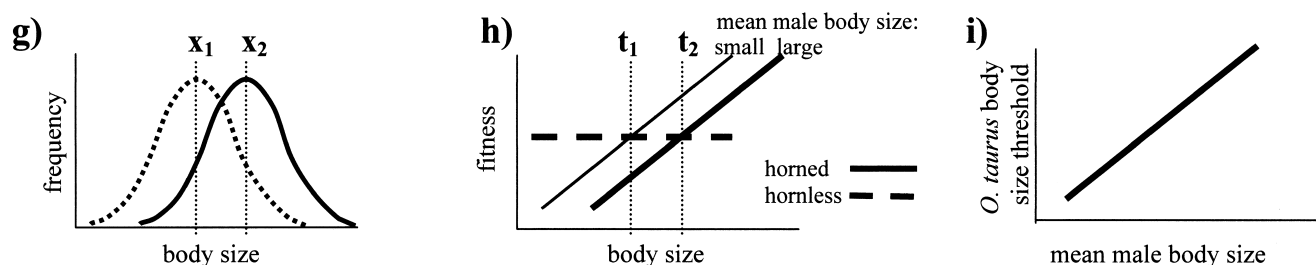


Figure 3

Ecological mechanisms of threshold evolution in onthophagine beetles. (I) Intraspecific competition hypothesis: (a) increasing local densities intensify male–male competition via increasing male encounter rates inside dung pads. Increased local densities also result in an increase in the relative proportion of females that fail to secure breeding opportunities due to resource limitation. This in turn causes the ratio of competing males to breeding females to become more male biased and causes levels of male–male competition to intensify. (b) As local densities increase and male–male competition intensifies, sneaking behavior becomes more profitable than fighting behavior over a wider range of male body sizes, selecting for a shift of the critical threshold body size, t_1 , to a larger body size, t_2 . (c) The intraspecific competition hypothesis therefore predicts a positive correlation between male threshold body sizes and *O. taurus* densities. (II) Interspecific competition hypothesis: (d) increasing competition from other species that compete for the same ephemeral resource crucial for reproduction (dung) indirectly intensifies male–male competition by increasing the proportion of females that are unable to breed due to resource limitation. This in turn causes males to compete for relatively fewer breeding females and causes levels of male–male competition to increase. Consequently, as interspecific competitor densities increase, male–male competition intensifies. (e) This in turn limits the profitability of fighting behavior to only but the largest males, causes sneaking behaviors to become more profitable over a wider range of body sizes, which selects for a shift of the critical threshold body size to larger body sizes. (f) The interspecific competition hypothesis therefore predicts a positive correlation between threshold body sizes of male *O. taurus* and the densities of competing dung beetle species. (III) Differential body size hypothesis: (g) changes in the mean body size of competing males (x_1 to x_2) alter the average body size of males with which a given male has to compete for access to females. If the competitive status of a male is determined by its own body size relative to that of other males in the same population, then changes in mean male body size should alter the competitive status of a given male, even if his own body size remains the same. (h) In a population with a relatively small mean male body size, males of an intermediate body size (on an absolute scale) may maximize their fitness through fighting and the development of horns, whereas in a population with a relatively large mean male body size, these same intermediate-sized males may fare better by remaining hornless and engaging in sneaking behaviors. Increases in the mean male body size in a population are therefore predicted to cause increases in the threshold body size that separates horned and hornless male morphs. (i) The differential body size hypothesis therefore predicts a positive correlation between male threshold body sizes and mean male body size in a population.

size remains the same. In a population with a relatively small mean male body size, males are therefore predicted to switch from the hornless to the horned morph at a relatively small threshold body size. Individuals in populations with relatively large mean male body size are instead predicted to delay the switch to a relatively larger body size (Figure 3g, h). The differential body size hypothesis therefore predicts a positive correlation between male threshold body sizes and mean male body size in a population (Figure 3i). This hypothesis was proposed earlier by Emlen (1996) to explain seasonal fluctuations in body size thresholds in *O. acuminatus*.

I used abundance data for *O. taurus* and competing dung beetle species collected from a large number of sites in three exotic and allometrically divergent ranges of *O. taurus* to test the predictions of the intra- and interspecific competition hypotheses. Estimates of populationwide mean male body sizes obtained from the same sites were used to test the predictions of the differential body size hypothesis.

METHODS

Sampling method

General

Recent studies indicate that male encounter rates and the intensity of male–male competition are directly proportional to the number of males present in a dung pad or experimental arena (Moczek, 1996; Hunt and Simmons, 2002). Furthermore, several studies have shown that dung removal rates increase with the number of conspecifics present in a given dung pad (Giller and Doube, 1989; Ridsdill-Smith et al., 1982) and that dung beetles, rather than other dung-associated insects, provide by far the greatest contribution to the removal of above-ground dung on Australian and eastern U.S. pastures (Bornemissza, 1970, 1976; Hanski and Cambefort, 1991; Ridsdill-Smith, 1993). Other dung beetles, rather than other dung-associated insects, are therefore most likely to exert significant interspecific competition for dung onto *O. taurus* populations (Hanski and Cambefort, 1991; Ridsdill-Smith, 1993). I therefore used the average densities of *O. taurus* and other dung beetle species in naturally occurring dung pads as an approximation of the degree of intra- and interspecific competition likely to be present in a given *O. taurus* population. The sampling method used in the present study (see below) was designed to accurately and reliably estimate the densities of *O. taurus* and co-occurring dung beetles in natural dung pads and proved very efficient in quantifying densities of dung beetles >1.5 mm in body size, including *O. taurus* and all of the exotic and native species known to contribute significantly to the removal of above-ground dung on eastern U.S. and Australian pastures (Bornemissza, 1976; Doube et al., 1991; Tyndale-Biscoe, 1990, 1996; Waterhouse, 1974). Beetles <1.5 mm in body size, such as small *Aphodius* species, could not be extracted reliably enough to allow for accurate density estimates and were therefore excluded from the analysis, as were dung flies and other dung-feeding and dung-associated insects. However, because these species are likely to exert comparatively little, if any, interspecific competition on *O. taurus*, their exclusion from the analysis is unlikely to affect the general conclusions of this study (Ridsdill-Smith, 1991).

Design and application

I collected beetles from naturally occurring cattle and horse dung pads. Once a dung pad of appropriate age (see below) was located, the entire pad or a portion thereof was quickly transferred into a heavy-duty plastic bag, weighed to the near-

est 10 g using a high-sensitivity Pesola™ spring scale, and then transferred into heavy-duty plastic containers. Containers were designed to separate beetles from dung and consisted of two round plastic containers (30 cm diam, 11.5 cm high), one stuck inside the other. The inner container had approximately 280 holes (9 mm diam) drilled into the bottom to allow beetles to follow their natural flight response and to escape into the space between the inner and outer container. This method proved sufficient to extract >95% of all dung beetles >1.5 mm in body size that inhabited a dung pad (Moczek, unpublished data). Beetles that accumulated in the space between containers were subsequently transferred into sample bottles, killed, and preserved in 70% ethanol. I checked the dung that remained in the inner container by hand for any leftover beetles, which, if present, were added to the sample. I sampled five to ten dung pads per site in this fashion. External conditions such as temperature, rainfall, and time of day commonly affect dung beetle activity. To standardize sampling conditions, I sampled sites only between 1200 and 1600 h on days with high temperatures exceeding at least 25°C and no rainfall during the preceding 24 h. Only dung pads were sampled whose texture and temperature indicated that they were produced in the morning of the collecting day and thus were able to attract potential dung beetles for several hours. In dung pads of this age, the majority of dung beetles has not yet begun to engage in tunneling behavior and can therefore be found above ground. Dry and old pads, and pads which were already largely buried due to dung beetle activity, were not used in this study. I used the same collecting containers and collecting protocol in each exotic range throughout the course of the entire project.

Sampling sites and dates

The active period of *Onthophagus taurus* in Australia ranges roughly from December to early May (Feehan J, Hunt J, personal communication), whereas U.S. populations are generally active from May to September (Moczek, unpublished data). Eastern Australian populations were sampled in February and March 2000, including 11 sites in New South Wales and Victoria covering a range of approximately 160,000 km². I sampled western Australian populations in March and April 2000, including 10 sites covering a range of approximately 20,000 km². Eastern U.S. populations were sampled in May, June, and July 2001. Ten sites in 5 states covering a range of approximately 300,000 km² were sampled. To quantify the magnitude of within-season fluctuations in beetle densities, I repeatedly sampled two sites in Durham County, North Carolina, from May to August 2000 and two sites near Canberra, eastern Australia from February to April 2000. Repeated sampling was conducted over 3–4 months in monthly intervals.

Data collection

Abundances

I sampled a total of 180 dung pads as described above. Samples were cleaned, sorted according to species, and counted. Several sites exhibited remarkably high densities of tunneling dung beetles, with the combined dung beetle mass accounting for up to 20% of pad weight. Consequently, I corrected all dung pad weights for beetle weight by weighing 100 randomly selected individuals of each of the common species, dividing this estimate by 100, and multiplying it with the actual number of individuals of each species found in a given sample. I calculated the weight of rare species using the average weight of common species of similar body sizes.

Beetle weights were then summed over all species found in a given sample and subtracted from the original dung pad weight to obtain net dung pad weights. Finally, abundances were standardized for 1 kg dung to correct for variation in net dung pad weights. I collected 54,381 dung beetles belonging to at least 15 different species during this study. Species identities were confirmed using specimens at the Australian National Insect Collection, CSIRO, Canberra. Of all beetles collected, 98.2% belonged to five highly abundant species: *O. taurus*, *O. binodis*, *Euoniticellus intermedius*, *E. pallipes* (all introduced), and *Onthophagus australis* (native). All five species are tunneling dung beetles of roughly similar body sizes that use the same resources (horse and cow dung) as food and for provisioning their offspring in subterranean tunnels in the form of brood balls. I used all samples collected at a given site to calculate mean densities of *O. taurus* and competing dung beetles for each site.

Morphometric measurements

I used morphometric measurements to quantify within and between-range variation in allometries and male body size and the extent to which allometric differences covary with local densities. Therefore, sites used to collect morphometric data were selected to maximize the geographic range of samples and to cover the full amount of variation in beetle densities present within each exotic range. Approximately half of all sites sampled in each exotic range were used to collect morphometric data. I measured beetles using a standard two-dimensional image analysis setup at the Duke University Morphometrics Laboratory (for details, see Moczek and Emlen, 1999). I used thorax width as an estimate for body size (Emlen, 1994; Moczek, 2002; Moczek and Emlen, 1999). Estimates of mean male body size for *O. taurus* at a given site were obtained by measuring thorax width of all male *O. taurus* collected from up to five dung pads sampled at a given site. I obtained estimates of the average scaling relationship between horn length and body size at a given site by measuring thorax width and horn length of 85 (± 12) males per site.

Sex ratios

I calculated absolute sex ratios for each site by sorting and counting all male and female *O. taurus* in a given sample. I used two to three samples per site for sites with high densities of *O. taurus*, and up to 10 samples for sites with low *O. taurus* densities, to calculate mean sex ratios for each site. Beetles were sexed based on the presence of horns (only large males develop clearly visible horns). Small individuals, which could be hornless males or small females, were sexed based on pygidium morphology using a WildTM dissecting scope (Balthasar, 1963).

Statistical analyses

I first analyzed allometric differences between samples globally using a residual analysis. A four-parameter nonlinear regression model of the form

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

was used to describe the average scaling relationship between horn length and body size of all males collected and measured in the context of this study combined (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 via Sigma PlotTM curve-fitting proce-

dures). I used c , or the inflection point of the sigmoid, as an estimate of the average threshold body size at which males switch from the hornless to the horned phenotype. Using Sigma Plot curve-fitting procedures, I obtained horn length = $0.465 + [4.1291(\text{body size}) \exp 35.4 / (5.193 \exp 35.4 + [\text{body size}] \exp 35.4)]$ as the equation with the best fit ($r^2 = .71$). I then used this equation to predict horn lengths for all possible body sizes. Individual males were then characterized by the degree to which their real horn length differed from the horn length predicted by this reference function (i.e., by their residual horn length). Populations that differed in their scaling relationship between horn length and body size could then be recognized by consistent differences in residual horn lengths (see also Moczek, 2002). Horn-length residuals were usually not normally distributed, and I therefore used nonparametric Kruskal-Wallis H tests for statistical analyses (Sachs, 1992; Sokal and Rohlf, 1995). Once significant differences in residual horn lengths were indicated, I repeated the curve-fitting procedure separately for each exotic range to obtain range and site-specific mean and standard error estimates for each regression parameter. I then used repeated Welch's t tests to examine the degree 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).

To compare *O. taurus* densities, densities of competing dung beetles, male body sizes, and sex ratios, I first calculated means for each sample site. To test for differences between exotic ranges, I then compared site means using nonparametric Kruskal-Wallis H tests. All significance levels reported below are adjusted for multiple comparisons using sequential Bonferroni corrections where this was necessary (Sachs, 1992; Sokal and Rohlf, 1995). Unless otherwise noted, all data are presented as means \pm SE.

RESULTS

Allometric variation and threshold location in eastern Australian populations

Eastern Australian male *O. taurus* exhibited significantly smaller horn length residuals than their eastern U.S. counterparts (i.e., expressed significantly shorter horns for a given body size) but exhibited significantly larger residual horn lengths compared to males collected in western Australia ($p < .01$ for each comparison; Figure 4). Comparing range-specific parameter estimates indicated that allometric differences between ranges could be attributed largely to differences in parameter c , or the average threshold body size at which males switched from the hornless to the horned phenotype ($p < .01$ for each comparison; Table 1, Figure 4). Eastern Australian individuals therefore exhibited a threshold body size intermediate to the highly divergent threshold body sizes present in eastern U.S. and Western Australian populations. Eastern, but not western Australian, males also expressed a significantly higher slope coefficient (parameter b) than males collected in the eastern United States ($p < .05$).

Intraspecific competition hypothesis

All three exotic ranges differed consistently and highly significantly in *O. taurus* densities. Eastern U.S. populations exhibited the lowest local densities, followed by intermediate densities in eastern Australian and highest densities in western Australian populations ($p < .01$ for each comparison; Figures 5a and 6a). Between-range differences in local *O. taurus* densities correlated with mean threshold body sizes, as predicted by the intraspecific competition hypothesis (Figures

3b, c and 7a). These results therefore support the notion that differences in local *O. taurus* densities could have driven allometric differentiation between exotic ranges. Results also indicated measurable, and in part significant, differences between sites within each exotic range. However, within-range differences did not correlate with significant differences in threshold body sizes, suggesting that density variation on a local level is insufficient to drive allometric divergences (Figures 5a and 7a).

Interspecific competition hypothesis

Densities of other dung beetle species with which *O. taurus* competes for dung also differed dramatically between exotic ranges of *O. taurus*. Eastern and western Australian populations exhibited competitor densities of up to three orders of magnitude higher than those present in eastern U.S. populations (Figure 5b and 6b). Competitor density differences between eastern U.S. and both Australian populations covaried with mean male threshold body sizes, as predicted by the interspecific competition hypothesis (Figure 7b). However, there were no significant differences in competitor densities between eastern and western Australian populations, even though male *O. taurus* in eastern Australia expressed significantly lower threshold body sizes than their western Australian counterparts ($p = .38$; Figure 7b). Differences in average threshold body sizes between eastern and western Australian populations can therefore not be attributed to differences in the degree of interspecific competition.

Differential body size hypothesis

Mean male body sizes also differed significantly between exotic ranges of *O. taurus* (Figure 7c). However, differences between exotic ranges were in a direction opposite to what was predicted by the differential body size hypothesis. Eastern U.S. males were significantly larger than their western or eastern Australian counterparts. Furthermore, western Australian males as a whole tended to be smaller, rather than larger than their eastern Australian counterparts, again contrary to what was predicted by the differential body size hypothesis ($p = .056$, Kruskal-Wallis H test, ns after corrections for multiple comparisons were applied; Figure 7c). Although these data indicate that differences in male body size may have played some role in the evolution of divergent threshold body sizes in exotic *O. taurus*, they clearly do not support the mechanism envisioned in the differential body size hypothesis as an explanation for allometric divergences between exotic ranges of this species.

Within-season fluctuations of beetle densities

To estimate whether short-term fluctuations in beetle densities during the active season of *O. taurus* could account for between-range differences in beetle densities, two eastern Australian and eastern U.S. sites were sampled repeatedly at monthly intervals. The results indicate measurable, and in part significant, temporal variation between samples of the same site (Figure 8). However, differences between sites within and between ranges remained largely unaffected. Both eastern Australian sites exhibited significantly higher densities of *O. taurus* and competing species compared to both eastern U.S. sites over the entire sample period ($p < .05$ for each comparison; Kruskal-Wallis H test including sequential Bonferroni correction for multiple comparisons). These data suggest that, although local population densities are likely to vary during *O. taurus*'s active season, this variation is unable to

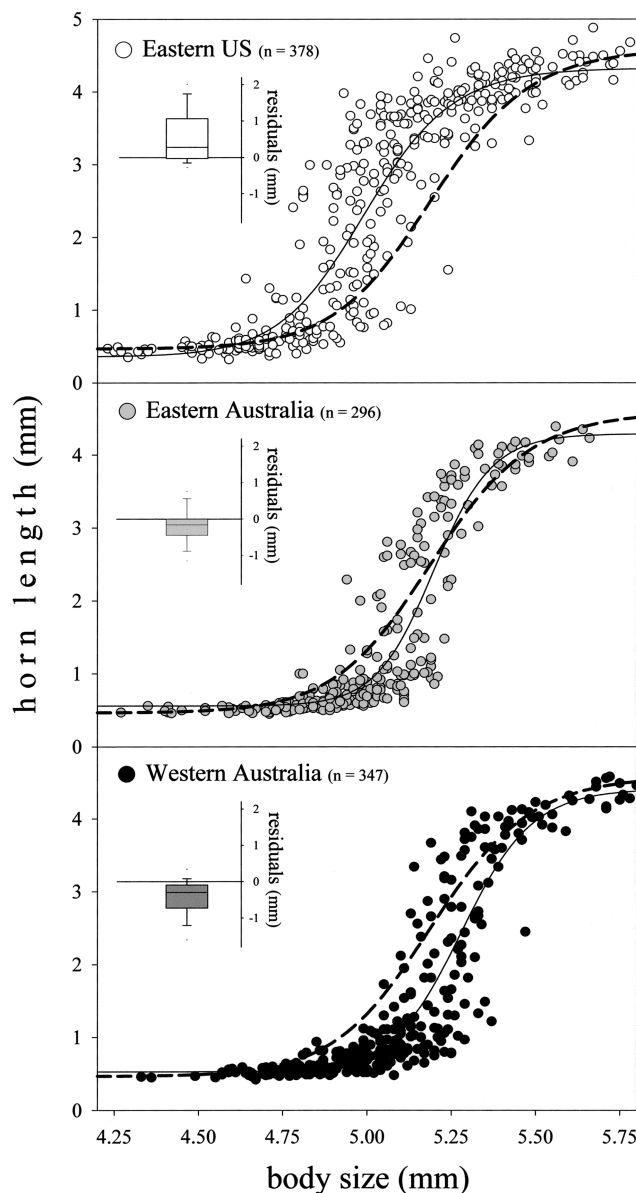


Figure 4

Scaling relationship between horn length and body size for three exotic ranges of *O. taurus*. Top panel: eastern United States, center panel: eastern Australia; bottom panel: western Australia. Dashed curve in all panels indicates a best-fit nonlinear regression for all three ranges combined. This regression was used to calculate residual horn lengths (shown in inserts). Solid curves indicate best-fit nonlinear regressions calculated separately for each exotic range (see Table 1 for regression parameters). Inserts: box plots of horn length residuals (with 90/10% confidence intervals) for each exotic range based on best-fit nonlinear regression for all three exotic ranges combined (dashed curve). All three exotic ranges differed significantly in residual horn length ($p < .01$; Kruskal-Wallis H test including sequential Bonferroni correction for multiple comparisons).

account for the large-scale, between-range differences in beetle densities detected in the present study.

Sex ratios

All three exotic ranges differed consistently and highly significantly in the average sex ratio found in local dung pads

Table 1
Male body size and allometric parameter values (means \pm SEs) for each exotic range of *O. taurus*

Range	Regression parameters				
	<i>a</i>	<i>b</i>	<i>c</i>	y_0	<i>n</i>
Eastern United States	3.97 \pm 0.159 ^a	38.62 \pm 3.561 ^a	4.995 \pm 0.012 ^a	0.356 \pm 0.099 ^a	378
Eastern Australia	3.73 \pm 0.156 ^a	60.5 \pm 5.577 ^b	5.199 \pm 0.01 ^b	0.56 \pm 0.05 ^a	296
Western Australia	3.887 \pm 0.145 ^a	50.79 \pm 4.179 ^{a,b}	5.283 \pm 0.01 ^c	0.528 \pm 0.048 ^a	347

a, range of horn lengths within a sample (amplitude); *b*, slope coefficient; *c*, body size at the point of inflection of the sigmoid, and y_0 , minimum horn length. Different superscript letters indicate significant differences between samples ($p < .05$; multiple Welch's *t* tests including sequential Bonferroni correction for multiple comparisons).

(Figure 9). Eastern U.S. populations exhibited female-biased sex ratios, followed by eastern Australian populations with roughly equal sex ratios, whereas western Australian populations exhibited male-biased sex ratios (Figure 9).

DISCUSSION

Male horn polyphenism has been observed in a variety of beetle families and appears to be widespread in the Scarabaeidae (Balthasar, 1963; Brown and Siegfried, 1983; Eberhard and Gutierrez, 1991; Halffter and Edmonds, 1982; Kawano, 1997; Matthews, 1972). It is interesting that closely related species often express similar horned and hornless male phenotypes, but often differ distinctly in the exact scaling relationship between horn length and body size and the exact location of the critical threshold body size that

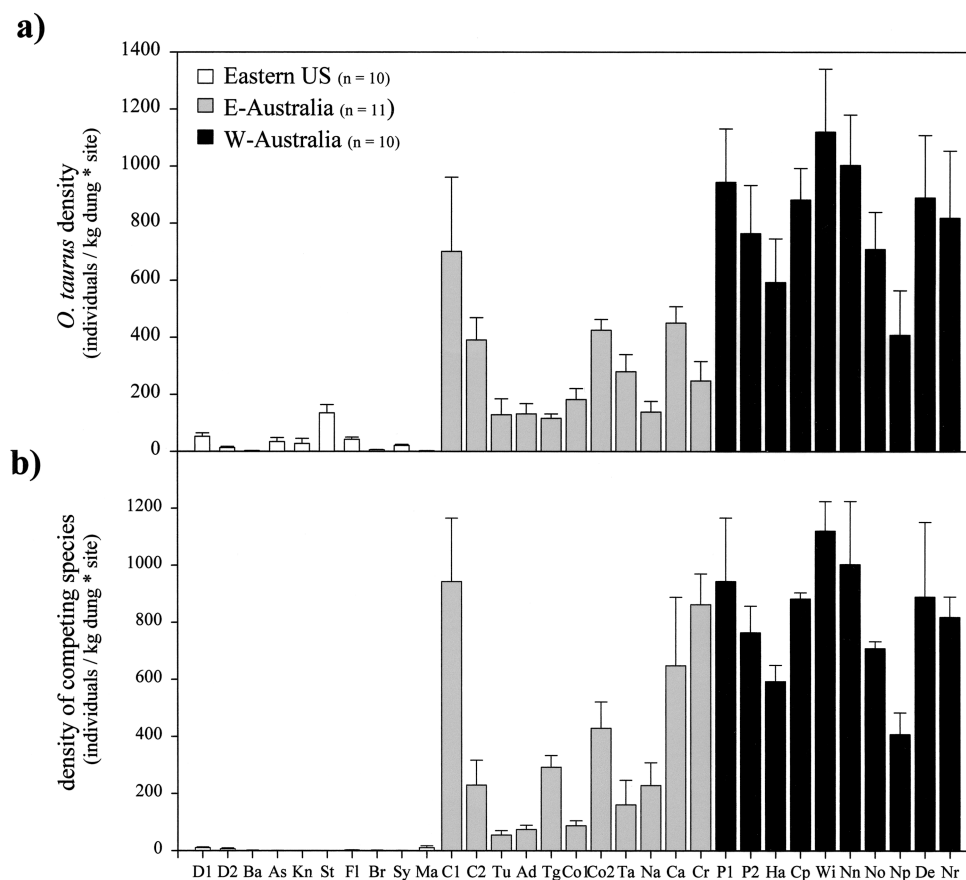
separates alternative male morphs (Emlen, 1996; Kawano, 1995a,b, 1997; Moczek and Nijhout, 2003). Several studies have therefore suggested that shifts in threshold body sizes have provided an important avenue for morphological diversification in these taxa (Moczek and Emlen, 1999; Emlen, 2000). However, the extent to which developmental thresholds actually evolve in natural populations and the ecological mechanisms that may drive threshold divergences in nature are poorly understood for most polyphenic organisms and have been a complete mystery for horn polyphenic beetles (Moczek and Nijhout, 2002a).

The behavioral ecology of horn polyphenisms

Earlier work showed that exotic populations of *O. taurus* in North Carolina and western Australia have diverged rapidly in

Figure 5

Densities of (a) *O. taurus* and (b) competing species in naturally occurring dung pads standardized for dung pad weight: Eastern United States (white bars), eastern Australia (gray bars), western Australia (black bars). Each bar represents one site within one of the three exotic ranges. Data are means \pm SE of 4–10 dung pads sampled for each site (Eastern US: D1, Durham I, NC; D2, Durham II, NC; BA, Bahama, NC; As, Asheville, NC; Kn, Knoxville, TN; St, Statesville, NC; Fl, Florence, SC; Br, Brunswick, GA; Sy, Sylvania, GA; Ma, Maxville, FL. Eastern Australia: C1, Canberra I, ACT; C2, Canberra II, ACT; Tu, Tublong, NSW; Ad, Adelong, NSW; Tg, Tumbalong, NSW; Co1, Cootamundra I, NSW; Co2, Cootamundra II, NSW; Ta, Tallangatta, VIC; Na, Nashdale, NSW; Ca, Cargo, NSW; Cr, Crowther, NSW. Western Australia: P1, Pinjarra I; P2, Pinjarra II; Ha, Harvey; Ca, Capel; Wi, Witchcliffe; Nn, Nannup; No, Northcliffe; Np, Nornalup; De, Denmark; Nr, Narrikup).



the critical threshold body size in less than 40 years since introduction to a new habitat (Moczek and Nijhout, 2003). The results of this study show that *O. taurus* populations in a third and previously unstudied exotic range in eastern Australia express threshold body sizes roughly intermediate to populations in the eastern U.S. and western Australia. Comparative sampling of dung beetle communities in all three exotic ranges furthermore revealed that per-dung pad densities of *O. taurus* differed consistently and highly significantly between all three exotic ranges in a direction, as predicted by the intraspecific competition hypothesis (Figure 3a–c). These results therefore support the notion that differences in the intensity of intraspecific competition for breeding opportunities could have driven allometric divergences between these exotic populations.

Per-dung pad densities of competitor species also differed highly significantly between Eastern U.S. and both Australian ranges. Differences between ranges were as predicted by the interspecific competition hypothesis (Figure 3d–f), suggesting that differences in the intensity of interspecific competition may have contributed to threshold divergences between populations in the eastern United States and Australia. However, the present study found no significant differences in competitor densities between eastern and western Australian populations, even though populations in both ranges expressed distinctly different threshold body sizes. This suggests that differences in threshold body sizes between both Australian ranges may have been driven solely by differential intraspecific competition. The differential body size hypothesis, in contrast, received no support because threshold body sizes did not correlate positively with mean male body sizes (Figure 3g–i). Instead, eastern U.S. males, which exhibited the smallest threshold body size and were predicted to exhibit the smallest mean male body size, were consistently and significantly larger than their Australian counterparts. Although these data suggest that population-wide differences in body size may play a role in the evolution of novel threshold responses that we do not yet understand, these data clearly do not support the mechanism envisioned in the differential body size hypothesis.

Results also indicated measurable, and in part significant, differences in *O. taurus* and competitor densities between sites within each exotic range (Figure 7a,b). However, within-range density differences did not covary with significant differences in threshold body sizes, suggesting that density variation on a local level is insufficient to drive threshold divergences. This may not be surprising as gene flow between sites within each range is likely to be considerable due to the generally high mobility and dispersal power of onthophagine beetles and the lack of efficient dispersal barriers (Barbero and Lopez-Guerrero, 1992; Hoebecke and Beucke, 1997; MacRae and Penn, 2001). At the same time, these results underscore the likely importance of geographic isolation as a crucial requirement in the initiation of allometric divergences.

Alternative interpretations

The above interpretations of the data presented here face two important challenges. First, the observed correlations among *O. taurus* densities, densities of competing species, and the average body size threshold in *O. taurus* populations could be coincidental and unrelated to the divergent allometries that have evolved in exotic ranges of *O. taurus*. Because individual sites within each exotic range are likely to exchange individuals, only the three range means can be considered truly independent sample points, which have a $1/6 = 0.167$ probability of exhibiting a certain ranking purely by chance. The present study is unable to rule out this possibility.

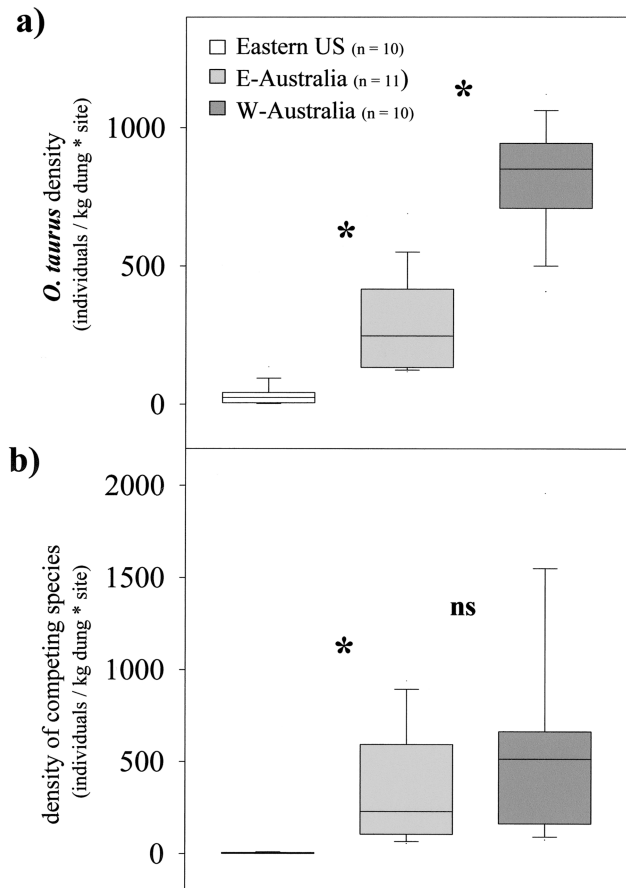


Figure 6
Range-wide average densities of (a) *O. taurus* and (b) competing species in naturally occurring dung pads in three exotic ranges of *O. taurus*. Data are standardized for dung pad weight. Boxes (with 90/10% confidence intervals) were calculated based on site means shown in Figure 5 (* $p < .01$; ns, not significant; Kruskal-Wallis H test including sequential Bonferroni correction for multiple comparisons).

However, at least two approaches should allow this issue to be addressed. Examination of additional exotic ranges of *O. taurus*, or native and exotic ranges of other horn polyphenic *Onthophagus* species, could provide additional, independent data points. Alternatively, quantification of fitness ratios of horned and hornless males of identical body sizes under a range of external conditions would allow for a more rigorous, experimental examination of the intra- and interspecific competition hypotheses. I am currently exploring both avenues to further shed light on the role of ecology and demography in shaping allometric variation.

The second major challenge to the results presented here arises from the common observation that insect population dynamics can be highly erratic and variable over a range of time scales (Andrewartha and Birch, 1954). As a consequence, local densities measured at a certain time point may not be indicative of densities present at other times. Densities of *O. taurus* and competing dung beetle species differed remarkably between Australian and U.S. pastures. These differences could theoretically be due to within- or between-season fluctuations in beetle densities and unrelated to the allometric divergences observed between exotic *O. taurus* populations. The present study showed, however, that at least for a single active season this appears not to be the case (Figure 8). Furthermore, density estimates presented here

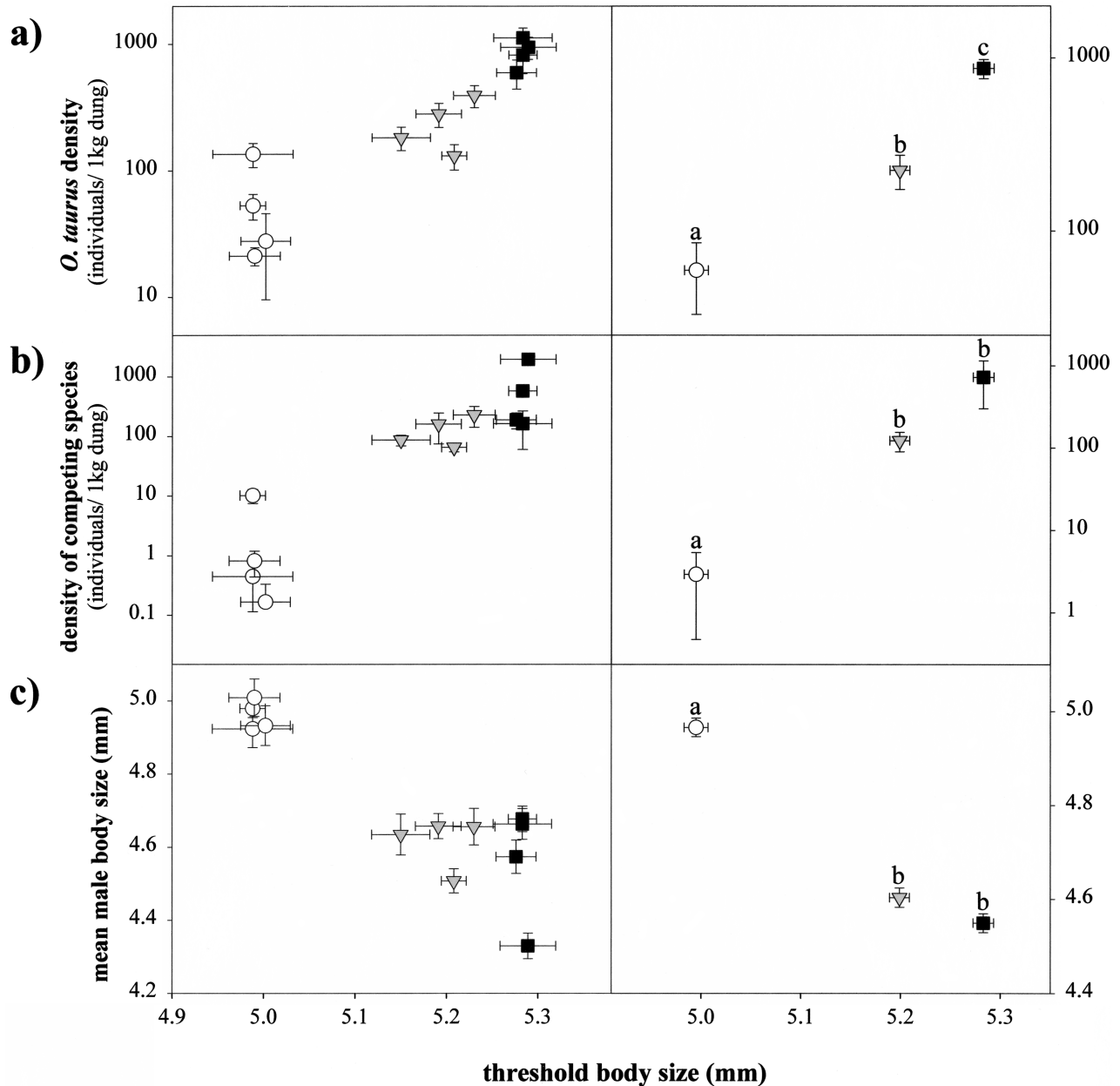


Figure 7

Relationship among threshold body size (x-axis) and (a) *O. taurus* density, (b) competitor density, and (c) mean male body size within and between exotic ranges. Left panels: sites within each exotic range. Right panels: means for each exotic range (open circles: eastern United States, shaded triangle: eastern Australia, solid squares: western Australia). All three exotic ranges expressed highly significantly different threshold body sizes (see Figure 3). Samples collected from different sites within each exotic range did not differ significantly in threshold body sizes, even though some sites differed considerably in densities or male body sizes. Different letters in the exponent denote significant differences in range-wide mean *O. taurus* densities, competitor densities, or mean male body sizes, respectively ($p < .01$; Kruskal-Wallis H test including sequential Bonferroni correction for multiple comparisons). Note that densities are plotted on a logarithmic scale.

matched those of earlier studies (United States: Moczek, 1996; western Australia: Dadour et al., 1999; Hunt et al., 1999; Ridsdill-Smith and Hall, 1984; Tyndale-Biscoe, 1990), suggesting that between-range differences in beetle densities presented here may be typical for each range and persist across seasons. If this is correct, the question remains why *O. taurus* and its competitors reach such high densities in Australia, but not in the eastern United States.

One possible explanation for these different geographic densities may lie in the fact that before the arrival of *O. taurus* in the eastern United States, cow dung was already used by

many native *Onthophagus* and other dung beetle species, which in turn provided an important resource for specialized dung beetle predators, parasitoids, and brood parasites (Davis, 1958; Hanski, 1991; Kohlmann, 1991). Specialized predators and parasites may therefore help limit current dung beetle populations on eastern U.S. pastures, including those of species such as *O. taurus* that originally had not been part of the native community. In Australia, however, cow dung is as exotic a resource as are the dung beetles that were released into the continent to help control it (Bornemissza, 1976). Although more than 200 *Onthophagus* species are native to

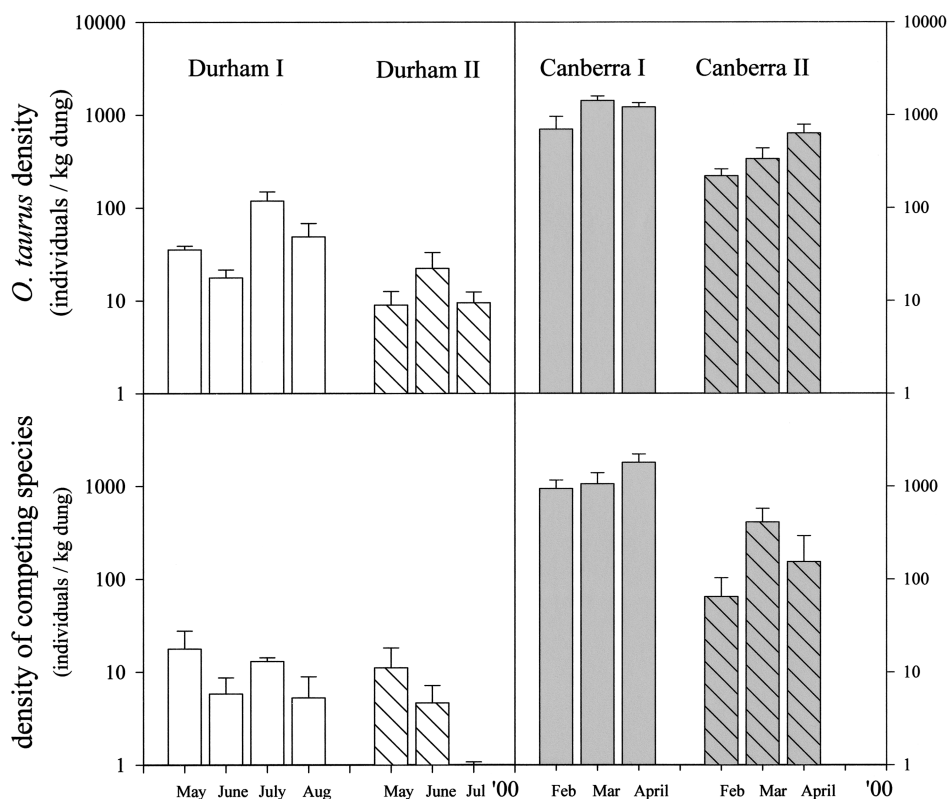


Figure 8
Within-season fluctuations in densities of *O. taurus* (top panels) and competing dung beetle species (bottom panels) at two sites in North Carolina (Durham I and II, eastern United States; left) and Canberra (Canberra I and II, eastern Australia; right). Each site was sampled in monthly intervals for 3–4 months. Each bar represents beetle densities (means \pm SE) measured during for a particular month based on 5–10 dung pads sampled for each site per month. Densities are standardized for dung pad weight. Although densities fluctuated at each site over the course of the season, the magnitude of differences between sites from different exotic ranges persisted throughout the sampling period. Note that densities are plotted on a logarithmic scale.

Australia (Matthews, 1972; Storey and Weir, 1988, 1990), most are specialized to feed and breed on marsupial dung and do not use cow dung as a resource (Matthews, 1972; Moczek, personal observation). As a consequence, exotic dung beetles released into Australia in the context of the dung control program are likely to have encountered an environment rich in resource but largely free of native competitors, predators, and parasites, which may have allowed *O. taurus* and other exotic dung beetles to expand their population densities to levels observed today.

Sex ratios

All three exotic ranges also differed significantly and consistently in the average sex ratio present in natural dung pads. Eastern U.S. populations exhibited female-biased sex ratios, followed by eastern Australian populations with roughly equal sex ratios, and western Australian populations with significantly male-biased sex ratios. Male bias therefore increased with the average density of *O. taurus* and the overall density of dung beetles that inhabited natural dung pads in each range. Sex ratio differences between strains may reflect range-specific differences in dung pad colonization behavior and dung pad persistence time of male and female *O. taurus* (Hunt et al., 1999), which may have evolved in response to differences in the temporal and spatial availability of dung and breeding females in different exotic ranges. Sex ratio differences between strains may also be a direct consequence of differences in brood ratios and parental sex allocation. If individuals collected from eastern U.S. populations are allowed to reproduce in the laboratory, F_1 larval sex ratios also exhibit a measureable female bias. Four independent replicate lines consisting of 25 pairs of beetles each yielded female-biased larval sex ratios (0.76 ± 0.074 ; $n = 4$; binomial probability $p = .0625$) similar to those measured for adults in

natural eastern U.S. dung pads (see Moczek and Nijhout, 2002b, for how to sex *Onthophagus* during the larval stage). This supports the hypothesis that female-biased sex ratios found in eastern U.S. dung pads may indeed be the product of differential sex allocation, rather than due to sex-specific differences in dung-pad colonization behavior.

Sex allocation in favor of one sex may evolve due to differences in the costs associated with producing male and female offspring or differences in the relative reproductive success of male and female offspring (Andersson, 1994; Bourke and Franks, 1995; Clutton-Brock, 1991). In the present case, intense competition for dung, as in western Australia, may indeed limit average female breeding success more than elevated male–male competition reduces average male reproductive success, and it may therefore be adaptive for parents to produce a male-biased brood ratio under conditions of high intra- and interspecific competition. How exactly densities of conspecifics and of other competing species affect the relative fitnesses of male and female *O. taurus* remains to be examined. Furthermore, whether eastern and western Australian populations also produce larval sex ratios that correspond to adult sex ratios measured in the field is unknown.

Evolutionary implications of threshold evolution

The results presented here suggest that differences in the degree of intra- and interspecific competition can drive rapid threshold divergences between geographically isolated populations. The degree of intra- and interspecific competition present at a given site is in turn likely to depend on a variety of factors, such as resource availability, predation pressure, or parasite density, which are likely to differ in intensity from one population to another (Giller and Doube, 1989; Ridsdill-Smith, 1991, 1993). As a consequence, geographically isolated

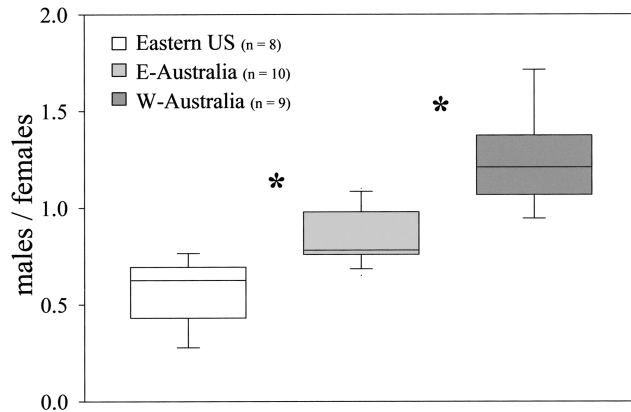


Figure 9

Absolute sex ratios (no. of males/no. of females) in the three exotic ranges of *O. taurus* (white: eastern United States; light gray: eastern Australia; dark gray: western Australia). Boxes (with 90/10% confidence intervals) are based on site-means derived from 8–10 sites within each exotic range (* $p < .01$; Kruskal-Wallis H test including sequential Bonferroni correction for multiple comparisons).

populations of onthophagine beetles are bound to differ in at least some of these factors, and therefore between-population divergences in threshold body sizes may be more widespread than currently appreciated.

Allometric diversification via changes in threshold body sizes may in turn have important consequences on several levels. For example, evolutionary changes in the developmental mechanisms that govern horn polyphenism have the potential to cause correlated changes in other developmental and life history events. Recent studies suggested that changes in threshold body sizes in exotic *O. taurus* populations have been mediated by changes in the degree and timing of sensitivity to juvenile hormone, which in turn has resulted in a correlated change in larval growth dynamics, the duration of larval development, and the timing of pupation, metamorphosis, and eclosion in both male and female larvae (Moczek and Nijhout, 2002a). Consequently, *O. taurus* populations that diverge in their horn polyphenism threshold beyond a certain degree may therefore also diverge in a variety of other developmental and physiological traits. A close genetic or developmental correlation between morph expression and other developmental and life-history events has also been implicated in earlier studies on wing-polyphenic crickets and hemipterans (Dingle and Winchell, 1997; Roff et al., 1997, 1999; Zera and Zhang, 1995).

The amount of developmental differentiation that accumulates between horn polyphenic populations may become important once populations reestablish contact and hybridize. Hybrids may express intermediate thresholds suboptimal for competition within either parental population. Furthermore, hybrids may have to contend with reduced developmental integration, as their ontogeny is now controlled by developmental mechanisms derived from two developmentally divergent parental strains. Consequently, hybrids may suffer reduced fitness, which may favor the spread of alleles that facilitate assortative mating among members of both parental populations. This, in turn, may lead to the subsequent evolution of reproductive isolation between these populations, an outcome also observed in recent theoretical models (Porter and Johnston, 2002). Although this scenario is entirely speculative, it provides a plausible and experimentally testable avenue for how divergent competitive regimes can cause geographically isolated populations to diverge in certain developmental and morphological properties, which in turn

may foster the evolution of reproductive isolation once these populations come into secondary contact. As a first step toward an empirical examination of this scenario, experiments are underway to quantify if and under what conditions hybrids derived from crosses between allometrically divergent populations suffer reduced fitness relative to parental populations. Should future results support the notion that threshold divergences evolve frequently in natural populations and that such divergences indeed provide a first step toward the evolution of reproductive isolation, this may help explain why the genus *Onthophagus*, despite several taxonomic revisions in the recent past, remains with more than 2000 species worldwide one of the most species rich genera in the animal kingdom (Balthasar, 1963; Matthews, 1972; Howden and Young, 1981; Storey and Weir, 1988, 1990; Villalba et al., 2002).

M. Beebe, H.F. Nijhout, L. Mojonner, M. Rausher, and A. Yang provided helpful advice on earlier versions of this manuscript. I am indebted to T. Weir for his continued support and advice during the course of this study and to J. Feehan for sharing his expert knowledge on Australian dung beetle populations. I also thank J. Hunt, J. Tomkins, and L. Simmons for many interesting discussion and their hospitality during my visits to Australia. I am grateful to D. Higdon and the Duke University Statistical Consulting Center for help with the statistical analyses, J. Mercer and the Duke Morphometrics Laboratory for access to equipment, and S. Richards for his outstanding drawings of *O. taurus* morphs. A. Camp and G. Daut helped with sorting and counting beetles. This work was carried out with support from the Department of Zoology and Biology, Duke University, a National Science Foundation Dissertation Improvement Grant IBN 9972567, a Sally Hughes-Schrader International Fellowship, a Duke University Grant for International Studies, a Robert R. Bryden/North Carolina Academy of Science Fellowship, a Sigma Xi Grant-in-Aid of Research, and a Kathryn Stern Dissertation Fellowship. Export of specimens from Australia was authorized under Commonwealth of Australia Wildlife Protection Permits 04/04684 and 04/08351 to the author. No import permit was required to import Australian dung beetles into the United States.

REFERENCES

- Andersson M, 1994. Sexual selection. Princeton, New Jersey: Princeton University Press.
- Andrewartha HG, Birch LC, 1954. The distribution and abundance of animals. Chicago, Illinois: University of Chicago Press.
- Australian Meat Research Committee, 1982. The biological control of dung in Australia. Australian Meat Research Committee workshop report 1982. Canberra: Australian Meat Research Committee.
- Balthasar V, 1963. Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalischen Region (Coleoptera: Lamellicornia). Band 2, Coprinae. Prag: Verlag der tschechoslowakischen Akademie der Wissenschaften.
- Barbero E, Lopez-Guerrero Y, 1992. Some considerations on the dispersal power of *Digionthophagus gazella* (Fabricius 1787) in the New World (Coleoptera Scarabaeidae Scarabaeinae). Trop Zool 5:115–120.
- Bornemissza GF, 1970. Insectary studies on the control of dung breeding flies by the activity of the dung beetle *Onthophagus gazella* F. (Coleoptera: Scarabaeinae). J Austr Entomol Soc 9:31–41.
- Bornemissza GF, 1976. The Australian dung beetle project, 1965–1975. Austr Meat Res Comm Rev 30:1–30.
- Bourke AFG, Franks NR, 1995. Social evolution in ants. Princeton, New Jersey: Princeton University Press.
- Brown L, Siegfried BD, 1983. Effects of male horn size on courtship activity in the forked fungus beetle, *Bolitotherus cornutus* (Coleoptera, Tenebrionidae). Ann Entomol Soc Am 76:253–255.
- Clutton-Brock TH, 1991. The evolution of parental care. Princeton, New Jersey: Princeton University Press.
- Crespi BJ, 1988. Adaptation, compromise and constraint: the development, morphometrics, and behavioral basis of a fighter-flier polymorphism in male *Hoplothrips karni* (Insecta: Thysanoptera). Behav Ecol Sociobiol 23:93–104.

- Dadour IR, Cook DF, Neesam C, 1999. Dispersal of dung containing Ivermectin in the field by *Onthophagus taurus* (Coleoptera: Scarabaeidae). *Bull Entomol Res* 89:119–123.
- Davis LV, 1958. The Scarabaeidae of Durham and Orange Counties, North Carolina. (MS thesis). Durham, North Carolina: Duke University.
- Dingle H, Winchell R, 1997. Juvenile hormone as a mediator of plasticity in insect life histories. *Arch Insect Biochem* 35:359–373.
- Dominey WJ, 1984. Alternative mating tactics and evolutionary stable strategies. *Am Zool* 24:385–396.
- Doube BM, Macqueen A, Ridsdill-Smith TJ, Weir T, 1991. Native and introduced dung beetles in Australia. In: *Dung beetle ecology* (Hanski I, Cambeftor Y, eds). Princeton, New Jersey: Princeton University Press; 255–278.
- Eberhard WG, Gutierrez EE, 1991. Male dimorphism in beetles and earwigs and the question of developmental constraints. *Evolution* 45:18–28.
- Emlen DJ, 1996. Artificial selection on horn length-body size allometry in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Evolution* 50:1219–30.
- Emlen DJ, 1997. Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behav Ecol Sociobio* 141:335–341.
- Emlen DJ, 2000. Integrating development with evolution: a case study with beetle horns. *Bioscience* 50:403–418.
- Emlen DJ, Nijhout HF, 1999. Hormonal control of male horn length dimorphism in the dung beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). *J Insect Physiol* 45:45–53.
- Fincher GT, Woodruff RE, 1975. A European dung beetle, *Onthophagus taurus* Schreber, new to the U.S. (Coleoptera: Scarabaeidae). *Coleopt Bull* 29:349–350.
- Giller PS, Doube BM, 1989. Experimental analysis of inter- and intraspecific competition in dung beetle communities. *J Anim Ecol* 58:129–144.
- Gross MR, 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol Evol* 11:92–98.
- Gross MR, Repka J, 1998. Stability with inheritance in the conditional strategy. *J Theor Biol* 192:445–453.
- Halffter G, Edmonds WG, 1982. The nesting behavior of dung beetles (Scarabaeidae). An ecological and evolutive approach. Mexico: Instituto de Ecología.
- Hanski I, 1991. North temperate dung beetles. In: *Dung beetle ecology* (Hanski I, Cambeftor Y, eds). Princeton, New Jersey: Princeton University Press; 75–96.
- Hanski I, Cambeftor Y, 1991. Competition in dung beetles. In: *Dung beetle ecology* (Hanski I, Cambeftor Y, eds). Princeton, New Jersey: Princeton University Press; 305–329.
- Hazel WN, Smock R, 1993. Modeling selection on conditional strategies in stochastic environments. In: *Adaptation in stochastic environments* (Yoshimura J, Clark CW, eds). Berlin: Springer Verlag; 147–154.
- Hazel WN, Smock R, Johnson MD, 1990. A polygenic model for the evolution and maintenance of conditional strategies. *Proc R Soc Lond B* 242:181–187.
- Hoebecke ER, Beucke K, 1997. Adventive *Onthophagus* (Coleoptera: Scarabaeidae) in North America: Geographic ranges, diagnoses, and new distributional records. *Entomol News* 108:345–362.
- Howden HF, Young OP, 1981. Panamanian Scarabaeinae: taxonomy, distribution, and habits (Coleoptera: Scarabaeidae). *Contrib Am Entomol Inst* 18:1–204.
- Hunt J, Kotiaho JS, Tomkins JL, 1999. Dung pad residence time covaries with male morphology in the dung beetle *Onthophagus taurus*. *Ecol Entomol* 24:174–180.
- Hunt J, Simmons LW, 2002. Confidence of paternity and paternal care: covariation revealed through experimental manipulation of a mating system in the beetle *Onthophagus taurus*. *J Evol Biol* 15: 784–795.
- Kawano K, 1995a. Habitat shift and phenotypic character displacement in sympatry of two closely related rhinoceros beetle species (Coleoptera: Scarabaeidae). *Ann Entomol Soc Am* 88:641–652.
- Kawano K, 1995b. Horn and wing allometry and male dimorphism in giant rhinoceros beetles (Coleoptera: Scarabaeidae) of tropical Asia and America. *Ann Entomol Soc Am* 88:92–99.
- Kawano K, 1997. Cost of evolving exaggerated mandibles in stag beetles (Coleoptera: Lucanidae). *Ann Entomol Soc Am* 90:453–461.
- Kohlmann B, 1991. Dung beetles in subtropical North America. In: *Dung beetle ecology* (Hanski I, Cambeftor Y, eds). Princeton, New Jersey: Princeton University Press; 116–132.
- Lively CM, 1986a. Competition, comparative life histories, and maintenance of shell dimorphism in a barnacle. *Ecology* 67:858–864.
- Lively CM, 1986b. Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. *Evolution* 40:232–42.
- MacRae TC, Penn SR, 2001. Additional records of adventive *Onthophagus* Latreille (Coleoptera: Scarabaeidae) in North America. *Coleopt Bull* 55:49–50.
- Matthews EG, 1972. A revision of the scarabaeinae dung beetles of Australia. I. Tribe Onthophagini. *Austr J Zool Suppl Ser* 9:1–330.
- Moczek AP, 1996. Male dimorphism in the scarab beetle *Onthophagus taurus* Schreber, 1759 (Scarabaeidae, Onthophagini): evolution and plasticity in a variable environment (MS thesis). Würzburg: Julius-Maximilians-University.
- Moczek AP, 1998. Horn polyphenism in the beetle *Onthophagus taurus*: larval diet quality and plasticity in parental investment determine adult body size and male horn morphology. *Behav Ecol* 9:636–641.
- Moczek AP, 1999. Facultative paternal investment in the polyphenic beetle *Onthophagus taurus*: the role of male morphology and social context. *Behav Ecol* 10:641–647.
- Moczek AP, 2002. Allometric plasticity in a polyphenic beetle. *Ecol Entomol* 27:58–67.
- Moczek AP, Emlen DJ, 1999. Proximate determination of male horn dimorphism in the beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). *J Evol Biol* 12:27–37.
- Moczek AP, Emlen DJ, 2000. Male horn dimorphism in the scarab beetle *Onthophagus taurus*: do alternative reproductive tactics favor alternative phenotypes? *Anim Behav* 59:459–466.
- Moczek AP, Hunt J, Emlen DJ, Simmons LW, 2002. Threshold evolution in exotic populations of a polyphenic beetle. *Evol Ecol Res* 4:587–601.
- Moczek AP, Nijhout HF, 2002a. Developmental mechanisms of threshold evolution in a polyphenic beetle. *Evol Dev* 4:252–264.
- Moczek AP, Nijhout HF, 2002b. A method for sexing final instar larvae of the genus *Onthophagus* Latreille (Coleoptera: Scarabaeidae). *Coleopt Bull* 56:279–284.
- Moczek AP, Nijhout HF, 2003. Rapid evolution of a polyphenic threshold. *Evol Dev* 5:259–268.
- Moran N, 1992. The evolutionary maintenance of alternative phenotypes. *Am Nat* 139:971–989.
- Nijhout HF, 1999. Control mechanisms of polyphenic development in insects. *Bioscience* 49:181–192.
- Otronen M, 1988. Intra- and intersexual interactions at breeding burrows in the horned beetle, *Coprophaneus ensifer*. *Anim Behav* 36:741–748.
- Paulian R, 1935. Le polymorphisme des mâles de coléoptères. In: *Exposés de biométrie et statistique biologique IV. Actualités scientifiques et industrielles* 255 (Tessier G, ed). Paris: Hermann and Cie; 1–33.
- Porter AH, Johnson NA, 2002. Speciation despite gene flow when developmental pathways diverge. *Evolution* 56:2103–2111.
- Radwan J, 1993. The adaptive significance of male polymorphism in the acarid mite *Caloglyphus berlesei*. *Behav Ecol Sociobiol* 33: 201–208.
- Rasmussen JL, 1994. The influence of horn and body size on the reproductive behavior of the horned rainbow scarab beetle *Phanaeus difformis* (Coleoptera: Scarabaeidae). *J Insect Behav* 7:67–82.
- Ridsdill-Smith TJ, 1991. Competition in dung-breeding insects. In: *Reproductive behaviour of insects*. (Baily WJ, Ridsdill-Smith J, eds). London: Chapman & Hall; 264–292.
- Ridsdill-Smith TJ, 1993. Asymmetric competition in cattle dung between two species of *Onthophagus* dung beetle and the bush fly, *Musca vetustissima*. *Ecol Entomol* 18:241–246.
- Ridsdill-Smith TJ, Hall GP, Craig GF, 1982. Effect of population density on reproduction and dung dispersal by the dung beetle *Onthophagus binodis* in the laboratory. *Entomol Exp Appl* 32:80–85.
- Ridsdill-Smith TJ, Hall GP, 1984. Beetles and mites attracted to fresh cattle dung in Southwestern Australian pastures. CSIRO Division of Entomology report no. 34. Canberra: CSIRO.

- Roff DE, Stirling G, Fairbairn DJ, 1997. The evolution of threshold traits: a quantitative genetic analysis of the physiological and life-history correlates of wing dimorphism in the sand cricket. *Evolution* 51:1910–1919.
- Roff DE, Tucker J, Stirling G, Fairbairn DJ, 1999. The evolution of threshold traits: effects of selection on fecundity and correlated response in wing dimorphism in the sand cricket. *J Evol Biol* 12:535–546.
- Sachs L, 1992. *Angewandte Statistik*. Berlin: Springer.
- Sokal RR, Rohlf FJ, 1995. *Biometry*. New York: Freeman.
- Storey RI, Weir TA, 1998. New localities and biological notes for the genus *Onthophagus* Latreille (Coleoptera: Scarabaeidae) in Australia. *Austr Entomol Mag* 15:17–24.
- Storey RI, Weir TA, 1990. New species of *Onthophagus* Latreille (Coleoptera: Scarabaeidae) from Australia. *Invert Taxon* 3:783–815.
- Travis J, 1994. Evaluating the adaptive role of morphological plasticity. In: *Ecological morphology* (Wainwright PC, Reilly SM, eds). Chicago, Illinois: University of Chicago Press; 99–122.
- Tyndale-Biscoe M, 1990. Common dung beetles in pastures of south-eastern Australia. Canberra: CSIRO.
- Tyndale-Biscoe M, 1996. Australia's introduced dung beetles: original releases and redistributions. CSIRO Division of Entomology technical report no. 62. Canberra: CSIRO.
- Villalba S, Lobo JM, Martín-Piera F, Zardoya R, 2002. Phylogenetic relationships of Iberian dung beetles (Coleoptera: Scarabaeinae): insights on the evolution of nesting behavior. *J Mol Evol* 55: 116–126.
- Waterhouse DF, 1974. The biological control of dung. *Sci Am* 230: 100–109.
- West-Eberhard MJ, 1989. Phenotypic plasticity and the origins of diversity. *Annu Rev Ecol Syst* 20:249–78.
- West-Eberhard MJ, 1992. Behavior and evolution. In: *Molds, molecules and metazoa: growing points in evolutionary biology* (Grant PR, Grant HS, eds.). Princeton, New Jersey: Princeton University Press; 57–75.
- Zera AJ, Zhang C, 1995. Evolutionary endocrinology of juvenile hormone esterase in *Gyllus assimilis*: direct and correlated responses to selection. *Genetics* 141:1125–1134.