



Male horn dimorphism in the scarab beetle, *Onthophagus taurus*: do alternative reproductive tactics favour alternative phenotypes?

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In a variety of organisms morphological variation is discrete rather than continuous. Discrete variation within a sex has attracted particular interest as it is thought to reflect the existence of alternative adaptations to a heterogeneous selection environment. The beetle *Onthophagus taurus* shows a dimorphism for male horns: males that exceed a critical body size develop a pair of long, curved horns on their heads, while smaller males remain hornless. In this study we report on the alternative reproductive tactics used by males with these two morphologies, and present experimental and behavioural data suggesting that these alternative tactics selectively favour discretely different male phenotypes. Horned males aggressively defended tunnel entrances containing breeding females. Fights involved the use of horns, and males with longer horns were more likely to win fights. In contrast, hornless males employed nonaggressive sneaking behaviours when faced with competitively superior males. Sneaking behaviours appeared to require high degrees of manoeuvrability inside tunnels to access and mate with females despite the presence of a guarding male. Comparisons of running performances of males with identical body sizes but different horn lengths suggest that the possession of horns reduces male agility inside tunnels. Thus, horn possession confers a clear advantage to males using fighting behaviours to access females, whereas hornlessness may be favoured in males that rely primarily on sneaking behaviours. Combined, the two alternative reproductive tactics used by male *O. taurus* appear to favour opposite horn phenotypes, which may explain the paucity of intermediate morphologies in natural populations of *O. taurus*.

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Males in many species vary greatly in the expression of secondary sexual traits (Andersson 1994). In some species, variation in the expression of such traits is discontinuous, resulting in the co-occurrence of two or more discrete phenotypes within one sex (Gross 1996). The discrete expression of secondary sexual traits has attracted particular attention, as it is thought to reflect alternative adaptations to heterogeneous social conditions (e.g. West-Eberhard 1989; Travis 1994). Social conditions permitting the coexistence of more than one phenotype may arise from differential competitive abilities of competing individuals and the adoption of alternative reproductive behaviours (Gross 1996). However, few studies have explored whether differences in competitive status shape patterns of behavioural and morphological variation in natural populations (Gross 1996).

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Males in many beetle species express secondary sexual characters such as horn-like outgrowths of their thorax and head, disproportionately enlarged mandibles or elongated front legs. In some species expression of these characters is discontinuous (e.g. Darwin 1871; Wallace 1878; Huxley 1932; Paulian 1935; Arrow 1951), and males can be grouped into majors (large males with fully developed characters) and minors (smaller males with only rudimentarily developed characters), which can often be separated by a critical body size (e.g. Siva-Jothy 1987; Eberhard & Gutierrez 1991; Emlen 1994a; Kawano 1995; Moczek & Emlen 1999). Because body size has been identified as an important determinant of male competitiveness in aggressive encounters, the size-dependent expression of either a horned or hornless morphology has been suggested to reflect the existence of alternative reproductive tactics favouring alternative male horn morphologies (Eberhard 1979, 1987; Brown & Siegfried 1983; Cook 1990; Hazel et al. 1990; Rasmussen 1994; Emlen 1997).

Studies of the reproductive behaviour of horn dimorphic beetle species have found that males possessing

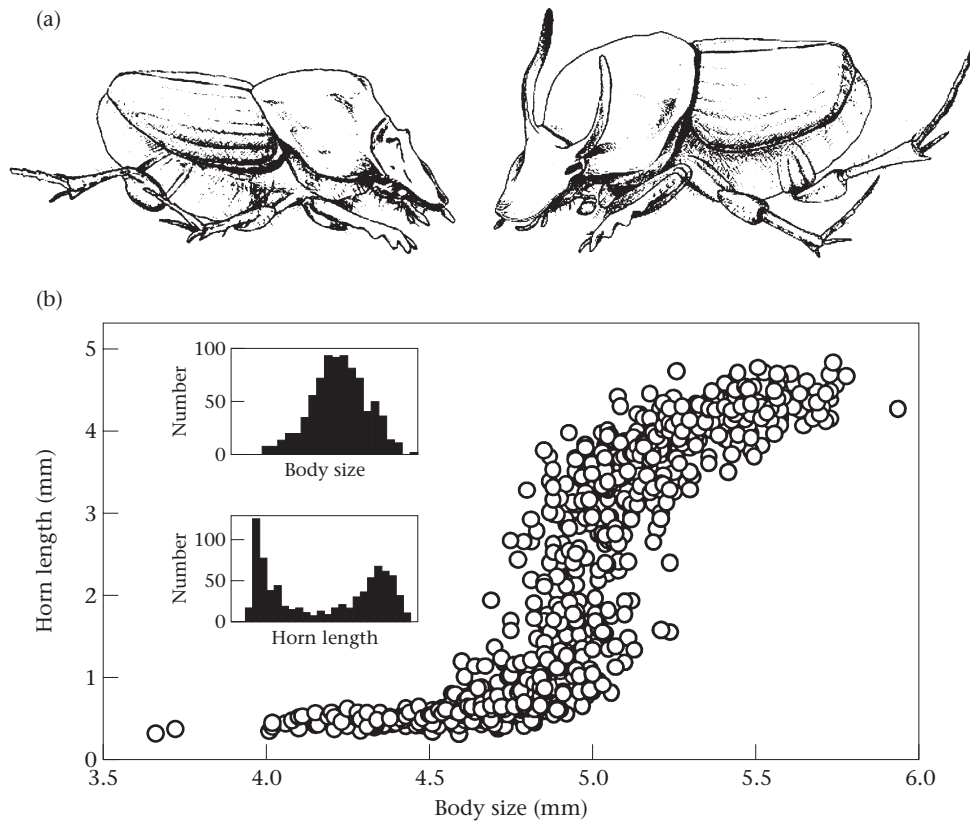


Figure 1. (a) Typical hornless and horned morphology of male *O. taurus* (drawings by Shane Richards). (b) Scaling relationship between horn length and body size (thorax width) for 810 male *O. taurus* collected from pastures in Durham County, North Carolina. Inserts illustrate frequency distributions of body sizes and horn lengths, respectively.

horns use them as weapons in combat with conspecific males over access to females, suggesting that a horned phenotype is favoured in direct male–male competition (Beebe 1944, 1947; Eberhard 1978, 1979, 1981, 1982, 1987; Palmer 1978; Siva-Jothy 1987; Otronen 1988; Rasmussen 1994; Emlen 1997; Moczek & Emlen 1999). Hornless males, however, have been found to generally avoid physical contact with other males, suggesting that hornless males rely on an alternative reproductive tactic to gain access to females (Siva-Jothy 1987; Emlen 1997). However, it remains unclear whether the lack of horns might be advantageous for the reproductive behaviour displayed by hornless males, or whether selective forces outside the realm of reproductive behaviour need to be invoked in order to explain discontinuous variation in male horn morphology.

Males in the common dung beetle *Onthophagus taurus* exhibit a striking male horn dimorphism (Fig. 1). Male *O. taurus* larger than a critical body size develop a pair of disproportionately long horns on their heads ('horned' males), while smaller males develop only rudimentary horns or no horns at all ('hornless' males), resulting in the co-occurrence of two discrete male morphs within populations (Fig. 1; see also Paulian 1935; Moczek 1996, 1998; Hunt & Simmons 1997; Emlen & Nijhout 1999; Moczek & Emlen 1999). *Onthophagus taurus* adults colonize dung pads of primarily cattle and horse, and provision dung fragments for their offspring in

subterranean tunnels dug directly underneath dung pads (for information on the natural history of *O. taurus* see Fabre 1899; Goidanich & Malan 1962, 1964; Halffter & Edmonds 1982; Moczek 1996, 1998, in press; Hunt et al. 1999; Moczek & Emlen 1999). Competition between males for access to breeding tunnels and females in and underneath dung pads is generally intense and males engage in aggressive fighting behaviour as well as non-aggressive sneaking behaviour to acquire mating opportunities (see below). Here we document the repertoires of reproductive behaviours of horned and hornless male *O. taurus*. We then present the results of several experiments that explore how the presence or absence of horns affects the performance of males engaging in fighting and sneaking behaviours. In particular, we investigate whether (1) the possession of horns improves a male's ability to succeed in aggressive encounters with other males, and (2) whether hornlessness increases male manoeuvrability inside tunnels. We discuss the role of male mating behaviour in the evolution of horns and horn dimorphisms.

METHODS

Underground Observations

To observe underground behaviour, we constructed observation nests (similar to ant farms) consisting of two

parallel glass panes, 25 × 35 cm, separated with a 4-mm U-frame made of plywood. Horizontal panes of Plexiglas were constructed to fit over these observation nests allowing beetles to walk freely on this surface once they had left the nest. Because tunnelling behaviour naturally occurs in darkness, all behavioural observations were conducted in a dark room using only red-filtered light. Observation nests were three-quarters filled with sand-soil mixture, with the remaining space being filled with dung. In all experiments beetles tunneled readily into the space provided by the observation nest, engaged in courtship behaviour, mating, brood-ball production and oviposition, suggesting that observation nests adequately imitated natural conditions (see also Emlén 1994b). All individuals used in this study were collected as adults from pastures in Durham County, North Carolina.

Observation of Male Reproductive Behaviour

To characterize the reproductive behaviour of horned and hornless males, we observed pairs of males as they competed for access to a single female. For each competition between males, we randomly selected a female and placed her in an observation chamber provided with dung. After the female had dug a tunnel (usually within 2 h), we added the first male. We allowed the pair to adjust to the observation chamber for at least 2 h, then placed a second male into the main tunnel. Because newly introduced males always immediately ran down the tunnel, they quickly encountered the previously introduced male, which usually resulted in immediate fights between males (see below). We observed the beetles continuously for at least 60 min following the introduction of the second male and then conducted scan samples over the next 2–4 days. A competition between two males was considered to be over once one of the males became dormant or attempted to leave the arena. All individuals used for this experiment were field collected and used only once. We observed a total of 67 competitions, including 19 competitions between horned males, 17 competitions between hornless males, and 31 competitions between horned and hornless males.

Male Fighting Performance as a Function of Horn Length

To quantify the effect of variation in male horn length on fighting performance, we staged an additional 27 contests between males. This time, contests were between males of equal body size but different horn lengths. To quantify the importance of horn length per se on fighting success, we had to exclude possible effects of body size by keeping body size between contestants constant. Thorax width has been shown to be a sufficient predictor of overall body size in *O. acuminatus* (Emlén 1994a, 1997), thus for this study, we considered body sizes of male *O. taurus* to be equal if their thorax widths were the same ($\pm 0.01 \text{ mm} \leq 0.2\%$ of total thorax width). All individuals were measured by one of us (A.P.M.) using a standard two-dimensional image analysis system in the

Duke Morphometrics Laboratory, Duke University (for details see Moczek 1998; Moczek & Emlén 1999). We used the observation nests as described above to stage contests. We observed the beetles continuously for at least 60 min and then conducted scan samples for at least 24 h. In all fights the winner was determined as the male that remained in the tunnel with the female after 24 h. We alternated the order of introduction of individual males to the observation nest to exclude potential positional advantages. If males were thought to be difficult to distinguish, we marked one of them 1 h prior to the experiment using typewriter correction fluid. Marks consisted of small dots on both elytra. The marked individual was selected randomly and individuals were only used once.

Male Agility as a Function of Horn Length

Initial observations suggested that small, hornless males rely on their agility inside tunnels in order to gain access to females despite the presence of a large, horned male (see below). The manoeuvrability of horned males, in contrast, appeared impeded inside tunnels. Unlike hornless males, horned males scraped their horns along tunnel walls and appeared to experience difficulties in turning around inside tunnels when attempting to evict intruders. To explore whether differential agility of horned and hornless males was indeed attributable to the presence/absence of horns, rather than simply a function of body size, we quantified male running performance in artificial tunnels comparing males with identical body sizes but pronounced differences in the length of horns.

We constructed artificial tunnels using observation nests similar to those used for behavioural observations (see also Moczek 1996). Diameters of artificial tunnels ranged from 6 to 7 mm, similar to those produced by beetles during behavioural observations and those found underneath dung pads in the wild (A. P. Moczek, unpublished data). We painted two marks approximately 26 cm apart on the outside of one glass pane using typewriter correction fluid. All beetles immediately ran through the tunnel when released. We videotaped the beetles while running between the white marks, and later measured the time required to run along the marked distance to the nearest 0.1 s by examination of the videotapes. We selected 30 pairs, each pair consisting of two males of equal body size ($\pm 0.01 \text{ mm} \leq 0.2\%$), but a natural minimum difference in horn length of 0.5 mm ($\geq 15\%$ of total horn length). Each male in each pair was videotaped while running through the same artificial tunnel. Order of runners within a pair was randomized by the flip of a coin. If short-horned males achieve consistently higher running performances than their long-horned but otherwise equally sized counterparts, this would support the hypothesis that horns represent a mobility handicap to males inside tunnels.

During these experiments it was not feasible to quantify whether artificial tunnels remained constant in their quality. We therefore restricted our design and analysis to pairwise comparisons of consecutive runs executed immediately one after another. We analysed



Figure 2. Typical fighting position of horned male *O. taurus*. Only one horn is shown (drawing by Shane Richards).

performance by scoring males on the basis of whether or not they showed detectable differences in running time using Wilcoxon signed-rank tests (Sachs 1992). Because running performances were quantified to the nearest 0.1 s, differences of less than or equal to 0.2 s between runs were scored as 0.

RESULTS

Male Reproductive Behaviour

Competition between horned males

We observed a total of 19 competitions between horned males. In all 19 cases interactions between males were aggressive and involved head-to-head combat. After initial contact between contestants, both the defending resident and the intruding male assumed a typical fighting position with the head and the thorax held low, the abdomen held high, and the legs braced against the tunnel walls (Fig. 2). This lowering of the head resulted in head horns pointing towards the opponent. Horns in *O. taurus* consist of two long, bow-shaped structures (Fig. 1), and males engaged in head-to-head contact tightly embraced the thorax of their opponent with their horns (19/19 competitions, Fig. 2). At this stage both males vigorously pushed each other while performing frequent and rapid upward jerks with their heads (19/19 competitions). Clicking sounds could be heard clearly through the glass panes as the head and horns of both males came into contact during head-to-head combat. Fights continued in this fashion until one male was able to dislodge his opponent sufficiently from the substrate. Once this was achieved, subsequent forward pushes and upward jerks allowed the stronger male either to drive his opponent out of the tunnel (if the stronger male started out lower in the tunnel) or to push his opponent further into the tunnel until the tunnel diameter permitted the stronger male to climb around his opponent and then force the opponent out of the tunnel. In all cases, fights ended when one male left the tunnel. Seventeen of the 19 defeated males (males that were successfully expelled from a tunnel) attempted to leave the arena (17/19 males) and did not attempt to enter the tunnel again. The remaining two males stayed nearby but also did not attempt to re-enter the tunnel. Fights were never observed outside tunnels.

Competition between hornless males

We observed 17 competitions between hornless males. In all cases hornless males initially interacted in a manner similar to fights between horned males. Hornless males took similar fighting positions and employed vigorous head-to-head pushes with frequent upward jerks to expel their competitor from the tunnel (17/17 competitions). However, in contrast to horned males, defeated hornless males rarely attempted to leave the experimental arena (3/17 competitions) but instead remained close to the tunnel entrance repeatedly attempting to re-enter the tunnel (12/17 competitions). The behaviour employed by defeated hornless males in these situations was qualitatively similar to what we observed in competitions between hornless and horned males and is described in detail below.

Competition between horned and hornless males

We observed 31 competitions between horned and hornless males including 15 competitions with hornless males as initial residents. Horned males did not display any differences in their behaviour when competing with a hornless as compared to a horned male. In all 31 cases, horned males employed the aggressive fighting behaviour described above. Whether a horned male was invading or defending a tunnel did not have any noticeable effects on its behaviour.

The behaviour employed by a hornless male when competing against a horned male was more complex. In 15 out of 31 competitions, a hornless male was allowed to establish residency inside a tunnel containing a female before a horned male was added. In all 15 cases, the hornless male employed the kind of head-to-head fighting behaviour described above, but in no instance was the hornless male able to maintain residency and instead was expelled by its horned competitor. Once defeated, these hornless males were behaviourally indistinguishable from the remaining 16 hornless males that were added after a horned male had already established residency inside a tunnel ($N=16$). To describe the behaviour of hornless males we will therefore consider both of these groups together ($N=31$).

After being defeated, hornless males remained close to the tunnel entrance, either in the dung, in a small gap between dung and soil, or covered with soil next to the tunnel entrance (30/31 males). No hornless males were observed to leave the arena. Over the next several hours hornless males repeatedly entered main tunnels and tried to pass the resident male. Encounters with the resident male resulted in very brief aggressive interactions and the hornless males' immediate withdrawal from the tunnel (28/31 competitions). However, hornless males managed to mate with females in the presence of a horned male in the following situations.

(1) Attempts to pass a horned male in the main tunnel were observed to be successful in two cases. In both cases the hornless male proceeded quickly down the tunnel and mated with the female. In the meantime, the horned resident male left the tunnel, turned around above ground and then proceeded down the tunnel. In both

instances the horned male remained close to the copulating hornless male but did not interfere with the mating. After copulations ended, the hornless male was evicted from the tunnel, followed by a mating between the female and the horned male in both instances.

(2) Female *O. taurus* left main tunnels on a regular basis (several times per hour) to gather pieces of dung from the pad. Horned resident males sometimes assisted females in gathering and transporting dung from the pad into the tunnel even in the presence of other males (see Moczek, *in press*) and, as a consequence, left tunnel entrances temporarily unguarded. Hornless males that remained in the proximity of the tunnel entrance regularly used these situations to gain access to the female and to mate with her either in tunnels in the dung above the soil surface (4/31 competitions) or in the main tunnel in the absence of a resident male (23/31 competitions; two males employed both behaviours). Hornless males left main tunnels quickly after copulations. Matings between females and hornless males in the dung did not result in direct physical contact between males. No obvious response by the resident male was detected after the return of the female. If a mating between the female and the hornless male occurred below ground in the main tunnel, the hornless male was often encountered by the returning resident on the way out of the tunnel (20/23 matings), which resulted in short yet intense fights and the expulsion of the hornless intruder. Successful defeat and eviction of the intruder was followed by a mating between the female and the horned male in all instances where the returning resident male had physical contact with the intruder.

(3) The continuous excavation of new tunnels and the process of brood-ball production led to the establishment of a complex system of tunnels in most experimental trials. Both dung and soil contained a multitude of interconnected tunnels. Hornless males were observed to move around frequently using below-ground tunnel interceptions, which often permitted them access to the main tunnel that contained the female. In 28 of the 31 experimental trials the main tunnel was intercepted by accessory tunnels, and in all of these 28 trials hornless males used these accessory tunnels to enter the main tunnel. In the remaining three experimental trials, no tunnels were present that could have been used. In all cases in which hornless males accessed the main tunnel in this fashion, however, they were encountered by the resident male and expelled.

Male Fighting Performance as a Function of Horn Length

Twenty-seven contests were staged between males of equal body size but varying differences in horn length in order to identify the significance of horns for fights between males (Fig. 2). In 22 out of 27 competitions the male with longer horns remained in possession of the tunnel and maintained access to the female (Wilcoxon signed-rank test: $Z = -2.43$, $N=27$, two-tailed, $P=0.015$; Fig. 2). Also, the proportion of fights won by males with longer horns increased significantly with increasing

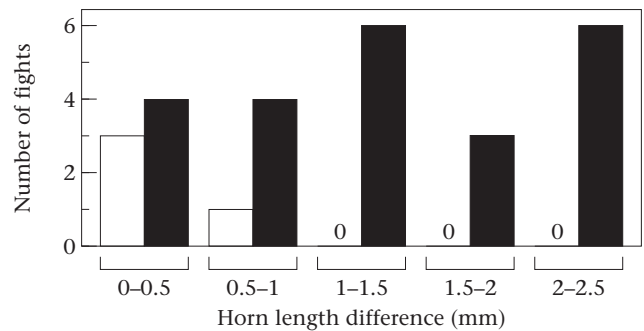


Figure 3. Male fighting success as a function of male horn length. Results are from 27 contests between males of equal body size and variable horn length. ■: Fights won by male with longer horns; □: fights won by male with shorter horns.

disparity in horn length between otherwise equally sized contestants (calculated over the five horn length difference classes depicted in Fig. 2; Spearman rank correlation: $r_s=0.894$, $N=5$, $P=0.02$).

Male Agility as a Function of Horn Length

Beetles required, on average \pm SE, 6.82 ± 0.42 s ($N=60$) to run through the approximately 26-cm tunnel distance. Small-horned males required significantly less time to run the same distance than their longer-horned but otherwise equally sized counterparts (Wilcoxon signed-rank test: $Z = -3.1$, $N=30$, two-tailed, $P<0.01$; mean \pm SE difference between runs = 1.1 ± 0.35 s, $N=30$; Fig. 3). In 20 of 30 pairwise comparisons, the male with relatively smaller horns moved faster through the tunnel. In three cases the longer-horned male was faster, and in seven pairwise comparisons, no measurable difference was detected (Fig. 3). The proportion of pairwise comparisons in which the short-horned male outperformed his long-horned counterpart tended to increase with increasing disparity in horn length between otherwise equally sized contestants (Kendall's tau: $N=3$, $P=0.059$; Fig. 3).

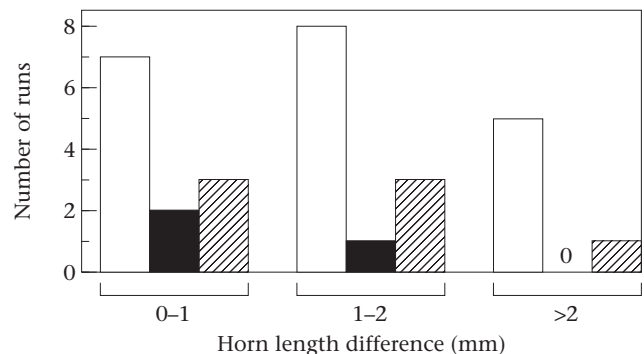


Figure 4. Male running performance as a function of male horn length. Results are from 30 pairwise comparisons between males of equal body size and variable horn length. □: Short-horned male outperformed long-horned male; ■: long-horned male outperformed short-horned male; ▨: no difference in performance between morphs.

DISCUSSION

Mating Tactics of Horned and Hornless Males

The functional significance of beetle horns has received considerable attention. Horns have been interpreted as protection devices against predators (Wallace 1878), as digging implements (Lameere 1904; Doane 1913), and as functionless and incidental by-products of selection for larger body size (Arrow 1951). However, most studies investigating the reproductive behaviour of horned beetles have demonstrated that horns serve as weapons in intermale contests (Eberhard 1978, 1979, 1981, 1982, 1987; Palmer 1978; Siva-Jothy 1987; Otronen 1988; Emlen 1994b, 1997; Rasmussen 1994; Moczek 1996), although some recent studies suggest that horns may also serve as display ornaments that indicate male quality to choosy females (Cook 1990; Hunt & Simmons 1997, 1998). Here we demonstrate that horns in *O. taurus* are used in fights between males over possession of tunnels containing breeding females. Horned males always fought to expel rival males from tunnels, independent of their opponent's morphology, or whether they invaded or defended a tunnel. Horned males that lost did not adopt alternative tactics but left the experimental arenas.

Hornless males also fought aggressively for access to breeding tunnels using similar head-to-head combat. Hornless males regularly expelled other hornless males from tunnels using this type of behaviour, demonstrating that the possession of horns is not a prerequisite for the successful adoption of fighting behaviour. However, no hornless male was ever observed to defend a tunnel successfully against a horned male using this type of behaviour, and hornless males were defeated by horned intruders in each instance. In contrast to horned males, evicted hornless males did not attempt to leave the arena, but instead adopted a set of alternative behaviours. These behaviours were nonaggressive and entailed manoeuvring in and out of tunnels quickly, sliding by guarding males and exploiting tunnel intersections in both the dung and soil to circumvent competitively superior males.

Female *O. taurus* appear to accept courting males and engaged in matings regardless of male horn morphology (Moczek 1996). Mating durations, however, did differ among morphs with horned males remaining in copula significantly longer than hornless males (Moczek, *in press*). In the present study it was not feasible to correlate mating frequencies with actual fertilization success of males. More direct fitness measurements are needed to quantify the success rate of horned and hornless males' reproductive behaviour.

Matings were predominantly observed to occur inside the main tunnel (88/92 copulations observed). Consequently, access to breeding tunnels, whether achieved by means of fighting or sneaking behaviour, is likely to be crucial to male reproductive success. Because both fighting and sneaking tactics observed in this study enabled males to access tunnels and gain mating opportunities, they may reflect discrete, alternative solutions to the problem of encountering females in a

mating system characterized by high levels of male-male competition, and by the limitation of mating opportunities to a spatially restricted and therefore defensible locality.

Alternative Mating Tactics and the Evolution of Male Horn Dimorphism

Male *O. taurus* express two alternative male morphologies in response to larval nutrition, which results in a bimodal distribution of horn lengths in natural populations (Fig. 1). Here we show that horned and hornless males differ in the behavioural tactics they employ to obtain mating opportunities. Alternative reproductive tactics may favour the evolution of male dimorphisms if the morphology performing best at one tactic differs from the morphology performing best at the other tactic (Eberhard 1979, 1987; Brown & Siegfried 1982; Lively 1986; Hazel et al. 1990; Emlen 1994b, 1997; Gross 1996; Moczek & Emlen 1999). Our results suggest that the possession of horns is indeed advantageous for males that engage in fighting behaviour. While studies of several species have now established the importance of horns for aggressive encounters, little was known regarding the extent to which hornlessness may also represent an adaptation to a particular competitive niche (Eberhard 1978, 1979, 1981, 1982, 1987; Palmer 1978; Siva-Jothy 1987; Otronen 1988; Emlen 1994b, 1997; Rasmussen 1994). Earlier studies suggested that hornless males may disperse more efficiently, emerge earlier in the season (Eberhard 1979, 1982), engage in sneaking behaviour around and inside tunnels (Rasmussen 1994; Emlen 1997), or at least avoid potentially damaging fights (Siva-Jothy 1987). However, these studies did not identify whether the lack of horns actually benefits the male adopting the respective alternative behaviour directly, or whether other selective forces outside the context of sexual selection are responsible for the evolution of hornlessness in these males (e.g. costs associated with the development of horns). At least two studies support the latter view: horn expression correlates with extended larval development and increased larval mortality (Hunt & Simmons 1997), and horn production may limit the allocation of resources to other morphological traits during development (Nijhout & Emlen 1998). However, while hornless males may indeed benefit from avoiding such costs by not developing horns, it remains questionable whether these costs alone suffice to explain the lack of intermediate morphologies in natural populations of *O. taurus*.

Here we explored whether hornlessness may be directly advantageous for the particular competitive situation encountered by small male *O. taurus*. Because sneaking males depend on being able to manoeuvre rapidly inside tunnels, we reasoned that structures that slow beetles down (e.g. horns that scrape against tunnel walls) would be detrimental to the reproductive success of sneaking males. We found in our experiment that long-horned males moved consistently slower through artificial tunnels than their short-horned but otherwise same-sized contestants. However, two problems with our experiment

deserve mention. First, all the males used in this experiment had horns, and presumably would employ fighting behaviour (rather than sneaking) to access females. This was unavoidable as sneaking males are never horned in natural populations. Consequently, we have to make the assumption that the possession of horns would be a similar hindrance to small, hornless males as for the horned males used in our experiment. Second, we used male mobility inside tunnels as an estimate of male performance. The actual importance of mobility for the reproductive success of males cannot be quantified with our data and hence warrants further study. Despite these caveats, however, our results indicate that horns impede male manoeuvrability inside tunnels, and raise the possibility that horn possession may detract from the reproductive success of males that use sneaking behaviours.

Our findings that (1) long horns are advantageous for males engaging in fights with other males, and (2) the lack of horns is potentially advantageous to the performance of sneaking behaviour, enable us to propose a selective context for the evolution of male horns, and in particular for the evolution of a body size-dependent dimorphism in the length of male horns. We suggest that the occurrence of two discrete male morphologies in *O. taurus* reflects a history of heterogeneous selection, with two discrete alternative reproductive behaviours (fighting and sneaking) each favouring opposite phenotypes with respect to male horn morphology. In this scenario, males with intermediate horn lengths may perform both reproductive tactics relatively poorly. Intermediate phenotypes are likely to retain some of the mobility handicap associated with the possession of horns (assuming that reduced mobility indeed results in reduced sneaking performance; see above) and should therefore be suboptimal sneakers, yet by producing only intermediate horn lengths these same males are likely to be inferior competitors in fights with males possessing fully developed horns. In such a selection environment, genotypes that express intermediate morphologies would be selected against, eventually favouring genotypes capable of facultatively switching between either minimal or complete horn expression during development.

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