

Facultative paternal investment in the polyphenic beetle *Onthophagus taurus*: the role of male morphology and social context

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Members of a population often differ significantly in their parental investment. Such variation is generally believed to have important consequences for mating system evolution and has been suggested to play an important role in the evolution of some secondary sexual traits and displays. Recent studies suggest that individuals are able to adjust the intensity and kind of parental investment they provide according to the breeding conditions they encounter. As a consequence, between-individual variation in parental investment may depend more on external conditions than previously thought for these taxa. This may have important implications for current perspectives on the role of differential parental investment in the evolution and maintenance of certain mating systems and sexual selection regimes. Here I quantify patterns of variation in paternal investment as a function of social conditions in a species of beetle that is dimorphic for male horn morphology. I demonstrate that under certain conditions (namely, the absence of other males), paternal assistance covaries with male morphology, with horned males investing substantially more time in assisting females than hornless males. I also show that the magnitude of differences in paternal investment between male morphs varies in response to external conditions. In the presence of other males, paternal assistance was negligible for both male morphs, who instead invested substantially and equally in mate-securing behaviors. I use my findings to discuss the significance of variation in paternal assistance for onthophagine mating systems and evaluate ideas proposed to explain the evolution of alternative morphologies in the genus *Onthophagus*. *Key words*: beetles, facultative parental investment, honest indicators, phenotypic plasticity, polyphenism, sexual selection, *Onthophagus*. [*Behav Ecol* 10:641–647 (1999)]

Members of the same population often differ significantly in the kind and intensity of parental investment they provide for their offspring (Clutton-Brock, 1991). Such variation has important implications for the evolution and maintenance of animal mating systems (Choe and Crespi, 1997a; Thornhill and Alcock, 1983) and for the intensity and direction of sexual selection in populations (Andersson, 1994; Choe and Crespi, 1997b). Furthermore, certain secondary sexual traits and displays have been suggested to have evolved in part because they reliably reflect a parent's investment potential (Andersson, 1994; Hunt and Simmons, 1997, 1998; Knapp and Kovach, 1991; Nisbet, 1973; Sundberg and Larsson, 1994). It has become clear in recent years, however, that the parental investment provided by an individual needs to be recognized as a trait that can itself be variable (Bartlett, 1987; Dijkstra, 1986; Moczek, 1996, 1998; Scott, 1998a,b; Trumbo, 1990). Flexible parental investment has been suggested to provide a mechanism by which a parent can adjust the intensity and kind of parental investment it provides according to the breeding conditions it encounters, thereby maximizing its reproductive success under heterogeneous social and ecological conditions (Moczek, 1998; Scott, 1998a,b). As a consequence, external conditions may play an important role in determining the parental investment an individual will provide, as well as whether individuals will differ in their parental investment. Therefore, correct interpretation of the significance of differential parental investment for the sexual selection regime and the evolution and maintenance of mating systems requires a thorough understanding of how different

ecological and social conditions influence individual parental investment, as well as knowledge of the relative frequencies of these conditions in natural populations. Here I quantify patterns of variation in paternal investment as a function of social conditions in a species of horned beetle (*Onthophagus taurus*) characterized by a spectacular morphological and behavioral polyphenism in males (Moczek, 1998; Moczek and Emlen, 1999).

Like many onthophagine species, male *O. taurus* express two discrete morphologies. Males larger than a critical body size develop a pair of disproportionately long horns on their heads, whereas males smaller than this critical threshold develop only rudimentary horns, which results in the co-occurrence of two discrete male morphs within populations (Hunt and Simmons, 1997; Moczek, 1996, 1998). Previous studies have demonstrated that larval feeding conditions are the primary determinants of adult body size and, by means of a threshold response, the presence or absence of horns in males (Moczek, 1996, 1998; Moczek and Emlen, 1999). Earlier work showed that male horn dimorphism plays an important role in male–male competition over mates. Horned males rely exclusively on aggressive fighting behaviors to gain and maintain access to females, whereas hornless males engage in nonaggressive sneaking behaviors when confronted with physically superior males (Moczek, 1996).

Like many coprophagous beetles, *O. taurus* adults provision dung for their offspring in tunnels excavated underneath dung pads (Halffter and Edmonds, 1982). Dung fragments are transported to the blind end of these tunnels and formed into compact brood balls. At the top end of each brood ball an egg chamber is formed, provided with a single egg, and sealed with an excrement cap. No further care is given to the offspring, and each brood ball constitutes the total quantity of food available to a single larva (Goidanich and Malan, 1962, 1964; Moczek, 1996). Competition for both dung and

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Received 12 January 1999; accepted 18 April 1999.

matings is likely to be severe in field populations, as *O. taurus* densities in single dung pads often exceed 100 individuals and dung pads are patchy and short-lived resources (Moczek, 1996, unpublished data; see also Emlen, 1994; Halffter and Edmonds, 1982; Hanski and Cambefort, 1991).

Several studies have indicated that males and females cooperate in the process of brood ball production (Emlen, 1994; Hunt and Simmons, 1998; Moczek, 1996) and that male assistance can increase the number of brood balls a female can produce (Cook, 1988; Rasmussen, 1994; Sowig, 1996b). Alternatively, male assistance may result in an increase of the average size of brood balls produced by a female (Cook, 1988; Hunt and Simmons, 1998). Brood ball size is an important determinant of larval development, adult body size, and male horn phenotype (Hunt and Simmons, 1997; Moczek, 1998; Moczek and Emlen, 1999). Although the fitness consequences of increased brood ball weight are not fully understood, recent studies argued that an increase in average brood ball size due to male assistance improves female fitness via the production of offspring of higher reproductive value (Hunt and Simmons, 1997, 1998). If males differ in their potential to assist females, this should favor female preferences for males with high investment potential, provided signals exist that reliably indicate a male's ability to assist a female. Using breeding experiments, Hunt and Simmons (1998) found, contrary to expectations, that female *O. taurus* paired with either horned or hornless males produced fewer brood balls compared to females breeding alone. However, they also observed that females paired with horned males produced brood balls that were significantly heavier than brood balls produced by females paired with hornless males or females alone. They concluded that breeding with horned males confers a reproductive advantage to females and raised the possibility that horn evolution may in part have been driven by female choice for the benefits of paternal investment that horns signal (Hunt and Simmons, 1998).

Variable degrees of competition for resources and mates are important aspects of onthophagine mating systems (Emlen, 1994, 1997; Moczek, 1996; Moczek and Emlen, 1999), and onthophagine beetles show a remarkable degree of adaptive plasticity in both male and female breeding behavior (Moczek, 1996, 1998; Sowig, 1996a). I explored paternal investment of horned and hornless *O. taurus* as a function of the social conditions encountered by the investing individual. Using direct observations of male underground behavior, I estimated paternal investment of both morphs in the absence and in the presence of potential competitors. I used the proportion of time invested in cooperative versus mate-securing behaviors as an estimate of paternal assistance. I use my findings to discuss the significance of variation in paternal assistance for onthophagine mating systems and refine recent ideas proposed to explain the evolution of alternative morphologies in the genus *Onthophagus*.

MATERIALS AND METHODS

Onthophagus taurus is a common dung beetle in open pasture land in North Carolina. *O. taurus* became introduced to the United States by accident, probably in the late 1960s, and was first recorded in Santa Rosa County, Florida, in 1971 (Fincher and Woodruff, 1975). *O. taurus* has continuously extended its range since then and now represents the dominant onthophagine species in open pasture land in North Carolina (Moczek, 1996, 1998). Beetles used in these experiments were collected as adults from a pasture near Durham, North Carolina, and maintained on cow manure in the laboratory (for details on *O. taurus*'s natural history, see Moczek, 1996, 1998, Moczek and Emlen, 1999).

Underground observations

To observe underground behavior, I constructed ant farms consisting of 25 × 35 cm glass panes separated by a 4-mm wide U-frame made of plywood. Horizontal Plexiglas™ panes were constructed to fit over these farms to allow beetles to walk freely on this surface once they chose to leave the farm. Ant farms were filled three-quarters full with a sand/soil mixture, and the remaining space was filled with dung. Additional dung was provided on the Plexiglas surface. Because tunneling behavior naturally occurs in darkness, I conducted all behavioral observations in a darkroom using only red filtered light. In all experiments beetles tunneled readily into the space provided by the ant farm, engaged in courtship and mating, and produced brood balls and oviposited, suggesting that the farms used in this study effectively imitated natural conditions of *O. taurus* (design followed suggestions in Emlen, 1993, 1997).

Classification of male behavior

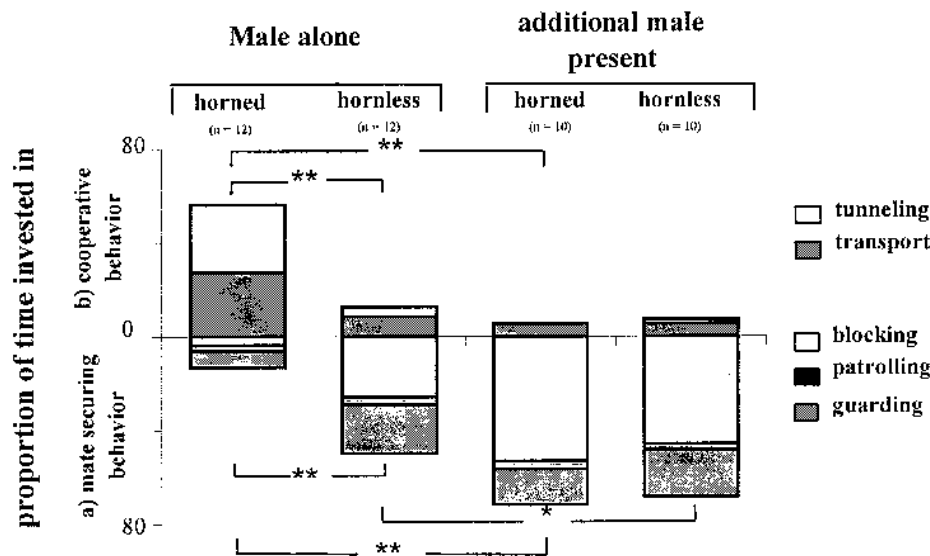
Qualitative behavioral observations were used to define types of behavior displayed by male *O. taurus*. Males engaged in seven clearly recognizable types of behavior during the process of tunneling and brood ball production: (1) tunneling: removal of soil with front legs, pushing of soil tunnel upward using either abdomen or prothorax; (2) acquisition and transport of dung: removal of dung fragments from the pad with dung fragments either held by front legs and pulled, pushed using the prothorax, or dropped through steep parts of the tunnel; (3) tunnel blocking: male remains motionless inside the tunnel close to, and facing, the tunnel entrance; usually displayed while female is below the male and after contact with other males; (4) patrolling: male runs quickly down the tunnel, remains inside the brood ball for a few seconds, and proceeds quickly back to the tunnel entrance, both times without carrying dung or soil with him; (5) guarding the female: male stays in close proximity to the female's head or abdomen (<1 cm) and initiates frequent body contact with his front legs and antennae but does not assist the female; (6) mating: time spent in copula; (7) eating: dung fragments are held in front of the head while mouth parts move frequently. Male behavior was scored as not classified if it did not fit any of the above definitions or if only certain aspects of a behavior category were displayed. For example, males in close proximity to a female but without displaying frequent body contact were not scored as guarding the female (for detailed description of each type of behavior, see Moczek, 1996).

I quantified the behavior of horned and hornless male *O. taurus* after exposing them to two experimentally controlled situations: both morphs were given access to a female either alone (noncompetitive situation) or in the presence of a second male (competitive situation).

Quantification of male behavior

Non-competitive situation

I placed a randomly selected, field-caught female in an ant farm and provided her with dung. Tunnel digging usually occurred within 2 h, then either a horned or hornless male was added. I allowed the pair to adjust to the situation for an additional 2 h and then observed them for a minimum of three 30-min periods distributed over the course of the next 24 h. All behavior displayed by both male and female were recorded in 30-s intervals using instantaneous scan sampling (Martin and Bateson, 1993). I used the total number of intervals during which a male was scored as displaying a particular type of behavior to calculate the proportion of time (rel-

**Figure 1**

Proportion of time allocated by horned and hornless male *O. taurus* to (a) mate securing (blocking, patrolling, and guarding, shown below x-axis) and (b) cooperative behaviors (tunneling and dung transport, shown above x-axis) under two situations: (1) in the absence of additional males (male alone), and (2) in the presence of a potential competitor (additional male present). Different shading represents different types of behavior. The proportions of time allocated to either cooperative or mate-securing behavior were compared using nonparametric Mann-Whitney *U* tests including sequential Bonferroni corrections for multiple comparisons (** $p < .01$, * $p < .05$).

ative to the total time observed) that a male invested in this particular behavior. I conducted this experiment for a total of 12 males of each morph. All individuals were only used once.

Competitive situation

Ant farms were set up as described above. After introducing either a horned or hornless male and a subsequent accommodation period of 2 h, I added a second male. Contact between males was ensured by placing the second male head first in the tunnel occupied by the first male. In all cases beetles ran down the tunnel and encountered the previously introduced male, which always resulted in fights between males until one of them was defeated. I then recorded the behaviors of the dominant male and the female for at least three 30-min periods as described above. Behavior of the defeated male was recorded qualitatively.

Previous work demonstrated that hornless males are unable to win fights and cannot maintain residency inside a tunnel in competition with a horned (and therefore physically larger) male (Moczek and Emlen, 1999). Therefore, I was not able to randomly select the second male added to a farm for those experimental trials involving hornless males as focal males. Because one aim of this experiment was to quantify patterns of horned and hornless males' assistance to a female in the presence of potential competitors, I had to ascertain that, in spite of the presence of a second male, a hornless male remained resident inside a tunnel and thus maintained at least the option to assist the female. The only way to achieve this was by using only hornless males as opponents if the focal male was himself hornless. For trials involving horned males as focal males, competing males were selected randomly. I conducted this experiment for 10 males of each morph. Individuals were only used once.

Duration of copulation

O. taurus courtship behavior consists of the male drumming his forelegs over the back and sides of the female until the female moves into a position appropriate for intromission (see also Emlen, 1994; Moczek, 1996). Drumming stops immediately with intromission. Copulation is terminated by the female either by running down the tunnel and dragging the male behind her for a short distance, or by using her hind legs to slip off the male. Hence, copulation duration is clearly

definable. I observed more than 120 matings and measured copulation durations of 83 males including both male morphs in noncompetitive as well as competitive situations. Durations were measured to the nearest second using a stop watch. In nine cases I measured two copulation durations of the same individual male (mean variation between measurements: 22 s). In these instances I used the individuals' mean copulation duration for analysis.

Statistical analysis

Males assisted females in the process of brood ball production via tunneling and the acquisition and transport of dung fragments down the tunnel. I calculated the proportion of time (i.e., relative to the total time observed) that a male invested in these particular behaviors and used the combined proportion as an estimate of a male's investment in cooperative behavior. Analogously, I calculated the proportion of time invested in blocking, patrolling, and guarding and used the combined proportion as an estimate of a male's investment in mate-securing behavior. The time spent eating was generally brief in all trials and was excluded from the analysis. Mating durations were analyzed separately (see below). I compared male investment in cooperative versus mate-securing behavior as a function of male morphology (horned versus hornless) and the behavioral context (competitive versus noncompetitive situations) using nonparametric Mann-Whitney *U* tests (Sachs, 1992). I used *t* tests to compare copulation durations of horned and hornless males in both behavioral contexts. All significance levels reported below, including both parametric and nonparametric tests, were corrected for multiple comparisons using sequential Bonferroni corrections where necessary (Sachs, 1992; Sokal and Rohlf, 1995).

RESULTS

Male investment in the absence of competitors

Horned and hornless *O. taurus* differed substantially in the amount of time spent assisting females (Figure 1; unless otherwise noted all data are shown as means with standard deviations in parentheses). Horned males were observed either excavating or transporting dung for 56% (20.4) of the time observed, whereas hornless males were only observed to invest

12% (5.8) of the time observed in these behaviors ($n = 12$ each, $p < .01$). Instead, hornless males spent considerably more time blocking the tunnel entrance, patrolling, and guarding the female than did horned males [horned males: 13% (11.5), $n = 12$; hornless males: 50 (19.8), $n = 12$, $p < .01$].

Male investment in the presence of competitors

Horned and hornless males did not differ in their allocation of time to particular behaviors when an additional male was present (Figure 1). Both morphs invested an almost equal proportion of time in mate-securing behaviors [horned males: 72% (21), $n = 10$; hornless males: 69% (18), $n = 10$, $p > .5$], and relatively little in cooperative behaviors [horned males: 5% (4.8), $n = 10$; hornless males: 7% (7.5), $n = 10$, $p > .3$].

Comparing time allocation across both social situations (presence versus absence of additional male) indicated that both male morphs invested significantly more time in mate-securing behaviors when an additional male was present [horned males: no additional male: 13% (11.5), $n = 12$ versus additional male present: 72% (21), $n = 10$, $p < .01$; hornless males: no additional male: 50% (19.8), $n = 12$ versus additional male present: 69% (18), $n = 10$, $p < .05$; Figure 1]. In horned males, increased investment in these behaviors was clearly at the expense of cooperation with the female [time spent cooperating in the absence of other males: 56% (20.4), $n = 12$; in the presence of other males: 5% (4.8), $n = 10$; $p < .01$]. Hornless males appeared to respond in a similar, albeit much less dramatic, fashion to the presence of potential competitors [time spent cooperating in the absence of other males: 12% (5.8), $n = 12$; in the presence of other males: 7% (7.5), $n = 10$, $p < .05$ before Bonferroni correction, not significant after Bonferroni correction]. The time spent eating did not differ as a function of male morphology or behavioral context (not shown).

Duration of copulation

Horned males copulated significantly longer than hornless males, both in the presence and absence of additional males [no additional male: horned males 146 s (26), $n = 24$, hornless males 104 s (18), $n = 23$, $p < .01$; additional male present: horned males 104 s (22), $n = 18$, hornless males 82 s (21), $n = 18$, $p < .01$; Figure 2]. Although the difference between morphs was significant both in the presence and absence of additional males, both male morphs exhibited significantly shorter copulation durations when an additional male was present ($p < .01$ for each comparison; Figure 2).

DISCUSSION

Paternal investment in dung beetles has long been recognized, although its implications continue to be debated (e.g., Cook, 1988; Goidanich and Malan, 1964; Halfpiter and Edwards, 1982; Hunt and Simmons, 1998; Rasmussen, 1994). In this study I demonstrated that, under certain conditions, assistance by male *O. taurus* covaries with male morphology (see also Cook, 1988; Emlen, 1994, 1997; Hunt and Simmons, 1998; but see Rasmussen, 1994). Horned males invested considerably in tunnel excavation and transport of dung into tunnels, whereas hornless males exhibited comparatively little investment in these behaviors and instead engaged in mate-securing behaviors. However, differential paternal assistance depended on the absence of potential competitors. Paternal investment in cooperative behaviors was negligible for both male morphs when competitors were present, and instead both morphs allocated most of their time to mate-securing

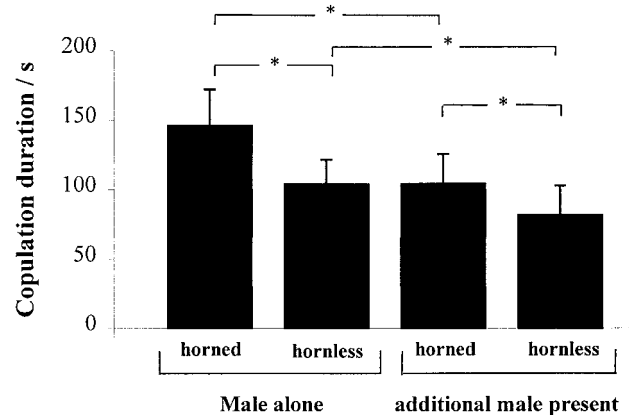


Figure 2

Copulation durations of horned and hornless male *O. taurus* (1) in the absence of additional males (male alone), and (2) in the presence of a potential competitor (additional male present). Error bars represent 1 SD. Copulation durations were compared using t tests including sequential Bonferroni corrections for multiple comparisons ($*p < .01$).

behaviors. Most previous studies on paternal assistance in dimorphic scarab species examined male cooperation without varying the social conditions (e.g., Cook, 1988; Hunt and Simmons, 1998; Rasmussen, 1994; but see Emlen, 1994). Thus, whether facultative paternal assistance is restricted to *O. taurus* or a more general component of dung beetle mating systems remains to be shown. Interestingly, Emlen's (1994) study on the congener *O. acuminatus* entailed examination of male assistance in the presence and absence of other males but did not find any indication that males adjust their behavior accordingly.

Evolution of facultative paternal assistance in dung beetles

Competition for breeding opportunities in the field is intense in many dung beetle communities, as dung pads are patchy and often short-lived resources (Halfpiter and Edmonds, 1982; Hanski and Cambefort, 1991). In North Carolina *O. taurus* densities in single dung pads typically exceed 100 individuals, and dung pads often dry out (and hence can no longer be used for brood ball production) in less than 24 h (Moczek, 1996, personal observation). Assisting a female in using such an ephemeral resource appears adaptive because it may allow a female to produce a greater number and size of brood balls within a given amount of time and hence would allow the male to sire a greater number of offspring (e.g., Cook, 1988; Rasmussen, 1994).

Earlier work suggested that, besides competition for dung, intense male–male competition for females may also be an important determinant of male fitness and that males have evolved alternative reproductive tactics to access females (Moczek, 1996; Moczek and Emlen, 1999). Horned males rely exclusively on aggressive fighting behaviors to gain and maintain access to females in breeding tunnels, whereas hornless males engage in nonaggressive sneaking behaviors when confronted with physically superior males (Moczek, 1996; Moczek and Emlen, 1999). These studies also indicated that tunnel possession is crucial for gaining mating opportunities, as matings almost exclusively occur inside tunnels, and the male in possession of a tunnel is likely to be the last male mating before oviposition (Moczek, 1996; Moczek and Emlen, 1999). Studies on the alternative reproductive tactics of *O. taurus* (Moczek, 1996) and *O. acuminatus* (Emlen, 1994, 1997) revealed that males who leave tunnel entrances to assist in dung acquisition

or to dispose of excavated material are particularly vulnerable to sneaking by other males, who can temporarily gain access to the female and mate with her, or to losing tunnel ownership altogether. Therefore, although paternal assistance is likely to increase male reproductive success via increasing the number and weight of brood balls a pair can produce, it entails the cost of putting tunnel possession, and thus current and future mating opportunities, at risk. It therefore would appear adaptive for resident males to reduce cooperative behaviors in the presence of other males and instead to allocate more time to mate securing behaviors such as guarding.

The present study suggests that both horned and hornless male *O. taurus* are indeed able to recognize the presence or absence of other males and respond by adjusting their investment into cooperative versus mate-securing behaviors accordingly. Such condition-dependent paternal assistance may represent a mechanism by which males maximize fitness in a social environment composed of variable degrees of male–male competition for females. Facultative parental investment may be particularly likely to evolve if a patchy and ephemeral resource environment favors cooperation, while at the same time intraspecific mating competition selects for behaviors that secure mates and breeding opportunities (see also Scott, 1998a,b; Trumbo, 1991; Trumbo and Fernandez, 1995). Such ecological and social conditions are not uncommon (e.g., Choe and Crespi, 1997a,b), and condition-dependent parental investment may be more widespread than currently recognized.

The evolution of alternative paternal investment

Several studies on paternal assistance in dimorphic scarab species found evidence that horned (major) males invest considerably more time in assisting females than hornless (minor) males (Cook, 1988; Hunt and Simmons, 1998; Emlen, 1994; but see Rasmussen, 1992, 1994). Although cooperation in horned males appears adaptive as it is likely to increase a pair's efficiency to use an ephemeral resource, the lack of assistance by hornless males appears maladaptive at first sight. However, not assisting a female may in fact increase a hornless male's fitness if this permits him to locate and mate with other females. Although this behavior would entail the risk that other males may displace his sperm in abandoned females, this risk may be outweighed by opportunities to inseminate additional females, provided such additional mating opportunities are indeed available (Parker, 1970, 1974; see below). Why then do horned males generally stay, assist females, and defend tunnel entrances? Earlier work suggests that the possession of horns, albeit beneficial in direct combat, reduces male maneuverability inside breeding tunnels (Emlen, 1994; 1997; Moczek, 1996). For example, horns scrape against tunnel walls as beetles run below ground and impede a horned male's ability to turn around inside tunnels (Moczek, 1996). In contrast, hornless males appear well equipped to move quickly inside tunnels and to acquire mating opportunities even in the presence of guarding males (Emlen, 1997; Moczek, 1996). Earlier work conducted on *O. taurus* males of similar body size with different horn lengths demonstrated that short-horned males moved significantly faster through standardized tunnels than their long horned counterparts (Moczek, 1996). As a consequence, it may be more difficult for horned males to effectively access multiple females in dung pads, and staying with a female, assisting her, and defending a once acquired residency inside a tunnel may present the tactic with the highest fitness gain for horned males.

Whether hornless males can indeed maximize their fitness by locating and mating with multiple females while minimizing their investment into cooperative behaviors would criti-

cally depend on the availability of additional females (see also Carroll, 1991, 1993; Carroll and Corneli, 1995; Parker, 1970, 1974; Shivashankar and Pearson, 1994). As a single dung pad may contain more than 100 *O. taurus* individuals, the probability that a male will succeed in locating multiple females in the same pad appears high. In contrast, in species with low population densities, hornless males may not always have the option to locate additional females. In this case, hornless males might be predicted to maximize their fitness by behaving like horned males (i.e., to stay with a female and to cooperate in the process of brood ball production).

It is worth noting that correlations between a male's assistance potential and horn morphology have so far been documented in three species that all exhibit extremely high field densities of several hundred individuals per single dung pad (*O. binodis*: Cook, 1988; Ridsdill-Smith and Hall, 1984; Ridsdill-Smith et al. 1982; *O. taurus*: Dadour et al., 1999; Hunt and Simmons, 1998; Hunt et al. 1999; Moczek, 1996; this study; *O. acuminatus*: Emlen, 1994; 1997; Howden and Young, 1981). The only study in which both horned and hornless males did not differ in their investment in cooperative behaviors was conducted on the horned rainbow scarab *Phanaeus difformis* (Rasmussen, 1994). In this species natural dung pads typically attract 5–10 beetles (Rasmussen, 1992), resulting in densities 1–2 orders of magnitude lower than in any of the 3 onthophagine species (see also Blume and Aga, 1976; Fincher et al., 1986). I expect that further integration of population structure and demography into studies on alternative and facultative paternal assistance will provide interesting insights into how social and ecological environments shape individual behavior in dung breeding beetles.

Implications of facultative paternal care: male morphology as a reliable signal

A number of studies have demonstrated that the presence of males correlates either with an increase in the number of brood balls produced (Cook, 1988; Rasmussen, 1994; Sowig, 1996b) or an increase in average brood ball weight (Hunt and Simmons, 1998) and may therefore increase parent fitness. Several studies have also investigated paternal investment in dung beetles that are dimorphic for male shape (Cook, 1988; Emlen, 1994, 1997; Hunt and Simmons, 1998). Cook (1988) found that *O. binodis* females paired with horned males produced a greater number of brood balls than females paired with hornless males or single females. In contrast, Hunt and Simmons (1998) found that *O. taurus* females paired with males of either morph produced significantly fewer brood balls than single females and suggested that the time paired females spent mating instead of building brood balls accounted for this observation. However, they also observed that females paired with horned males produced significantly heavier brood balls than any other treatment group. Although the fitness consequences of the production of heavier brood balls remain to be quantified, both Cook and Hunt and Simmons interpreted their findings as a reflection of higher levels of assistance in horned males and suggested that the possession of horns may serve as an indicator of a males' cooperation potential (Cook, 1990; Hunt and Simmons, 1998). Consequently, Hunt and Simmons (1997, 1998) suggested that horn evolution may in part be driven by female choice for the benefits of paternal investment that horns signal.

The present study may help to refine this notion. Both Cook (1988) and Hunt and Simmons (1998) used the number and weight of brood balls produced by multiple males and females in single-breeding containers as an indirect estimate of relative paternal investment (Cook—three treatments: two horned males per female, two hornless males per female, and

single females; Hunt and Simmons—four treatments: six horned males + six females, six hornless males + six females, three horned + three hornless males + six females, and six females without males). Here I demonstrated that males respond to the presence of other males by engaging in mate-securing behaviors at the expense of cooperation. In many observations the resident male had to interact only once with the second male introduced to an ant farm to terminate cooperative behavior for the entire observation period. Furthermore, pilot observations revealed that both male morphs try to mate with as many females as are tunneling in a container or ant farm, abandoning the female they originally assisted and interfering with brood ball production of neighboring pairs (Moczek 1996, unpublished data). Comparing the breeding success of unpaired females with the breeding success of multiple males and females in single-breeding containers may therefore not be a meaningful estimate of relative male assistance potential, as it confounds possible contributions of individual male behavior and male–male interactions to breeding success. Male interference with brood ball production of neighboring pairs may also explain why Hunt and Simmons (1998) found that single females produced a larger number of brood balls than females paired with males of either morph, a result that was not found using single pairs and single females (Moczek and Scott, unpublished data).

The hypothesis that male horn morphology may serve as an indicator of paternal quality nonetheless remains interesting. The present study shows that in the absence of other males, horned males allocate a substantially larger amount of time to cooperative behaviors than hornless males. Under these conditions horn expression may indeed have the potential to reliably signal a males' assistance potential, and females may be expected to express a corresponding preference under such circumstances. So far, however, there is no evidence that females discriminate among morphs. In all experiments and behavioral observations females appeared to mate readily with both male morphs (see also Moczek and Emlen, 1999). However, early termination of copulations may provide a mechanism by which females exert cryptic choice (Eberhard, 1996). The differences in copulation durations between male *O. taurus* morphs are consistent with this view (Figure 2). Horned males copulated significantly longer than hornless males. This difference persisted in the presence of other males, although, interestingly, both morphs exhibited reduced copulation durations under these conditions.

Alternatively, differences in copulation duration may simply be a reflection of variation in copulatory properties of both morphs and therefore may indicate sperm competition between males rather than discrimination by females (Simmons et al., 1999). In a recent study, Simmons et al. (1999) found that in *O. binodis*, large, horned males develop relatively smaller testes and produce relatively smaller ejaculate volumes than hornless males. This suggests that large, horned males may simply require more time to release the same amount of sperm, which may explain differences in copulation durations between morphs observed in the present study. However, Simmons et al. (1999) did not find a corresponding correlation between male morphology, testes size, and ejaculate volume for *O. taurus*, which suggests that additional factors may be important in determining copulation durations in this species.

Although the possible signaling function of horns in horn dimorphic species remains an intriguing possibility, it is important to note that, at least in *O. taurus*, any correlation between male horn expression and the extent of paternal assistance disappears in the presence of additional males (see Figure 1). In *O. taurus* and many other horn dimorphic dung beetles, competition for both dung resources and mates is severe in field populations (see above). Assisting a female in

the absence of competing males may therefore not be an option for most males most of the time, regardless of male morphology. Although there is substantial evidence that supports the view that horns and horn dimorphisms have evolved and are maintained in the context of male–male competition, any association between horn possession and signaling of paternal quality remains to be demonstrated (e.g., Eberhard, 1978, 1979, 1981, 1982, 1987; Emlen, 1997; Moczek, 1996; Moczek and Emlen, 1999; Otronen, 1988; Palmer, 1978; Rasmussen, 1994; Siva-Jothy 1987).

This paper benefited from the constructive comments and suggestions by two anonymous reviewers. M. Beebe, L. Mojonier, C.P. Klingenberg, and H.F. Nijhout provided helpful comments on previous versions of the manuscript. I also thank L.W. Simmons, J.L. Tomkins, and J. Hunt for helpful discussions and for making their unpublished results available to me. I am grateful to K. Fiedler, D. Emlen, P. Klopfer, and B. Hölldobler for valuable advice and support during the course of this study. P. and M. Klopfer kindly allowed me to collect beetles on their pastures. This work was carried out while I was funded by a scholarship by the German Academic Exchange Service (DAAD).

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