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Patterns of parental provisioning covary with male morphology in a horned beetle (*Onthophagus taurus*) (Coleoptera: Scarabaeidae)

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Abstract Male dung beetles, *Onthophagus taurus*, are dimorphic for a secondary sexual trait, head horns. Horned males participate in the production of brood masses while hornless male do not. Here we examine the reproductive performance of females mated with males exhibiting alternative horn morphologies. We found that exposure to males may be costly for females in that it reduced the total number of brood masses produced. However, females paired with horned males produced significantly larger brood masses than females paired with hornless males or females producing broods alone. We discuss the possible selection pressures that may underlie horn evolution in this genus.

Key words *Onthophagus* · Paternal care · Male dimorphisms · Alternative strategies

Introduction

Strategies of parental care vary widely across animal taxa (Clutton-Brock 1991). In general, it will pay a parent to invest in parental care when the reproductive payoff from increased offspring fitness exceeds the costs associated with reduced access to additional mates (Maynard Smith 1977; Zeh and Smith 1985). Most often the evolutionarily stable strategy is for one parent to care and the other to desert (Maynard Smith 1977; Clutton-Brock 1991). Biparental care is rare but can be favoured if two parents can achieve twice the reproductive payoff of a single parent, or if the deserting parent has little chance of obtaining another mate (Maynard Smith 1977).

Biparental care in insects is rare, but it does occur in species where competition for a larval food source is intense and when parents must lay down provisions for or feed their young (Clutton-Brock 1991; Rasmussen 1994). In carrion-burying beetles, both parents have been shown to provision and guard the nest as well as regurgitate secretions to the larvae (Eggert and Muller 1997). In contrast, parental care in dung-burying beetles is generally restricted to brood mass construction (Halfpter and Edmonds 1982). In the majority of scarabaeid species, females are capable of successfully provisioning larvae when unaccompanied by males (Halfpter and Edmonds 1982). Yet numerous studies report extensive levels of cooperation between males and females; males assist in moving dung from the dung pad to the site of burial and oviposition (Sato and Imamori 1987; Edwards and Aschenborn 1988; Cook 1988; Otronen 1988; Rasmussen 1994; Moczek 1996). Thus, theory would predict that the reproductive benefits gained by males providing parental care should exceed the costs associated with lost reproductive opportunities.

Biparental care is common in dung beetles of the genus *Onthophagus*. During reproduction, members of this genus typically bury portions of dung removed from the dung pad (Halfpter and Edmonds 1982). A branched tunnelling system is excavated beneath the pad and dung is packed tightly into the blind ends of side tunnels. A single egg is deposited into an egg chamber and sealed; one egg and its associated dung provisions are referred to as a brood mass (Halfpter and Edmonds 1982).

Two possible avenues exist whereby male parental care may directly enhance reproductive success: (1) co-operation in moving dung may facilitate an increase in the number of brood masses (and hence offspring) produced, and/or (2) male provisioning may increase the amount of resources provided to each brood mass so that there is an increase in the quality of offspring produced. In *O. binodis* and *O. vacca*, the number of brood masses is increased by male assistance (Cook 1988; So-wig 1996). In addition, there is evidence to suggest that parental provisioning strategies may vary with parental

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size. In *O. gazella*, larger parents produce larger brood masses (Lee and Peng 1981). Moreover, the study of Cook (1988) on *O. binodis* suggests that it is the size of the male parent that determines variation in the number of brood masses produced.

Many onthophagines are characterised by dimorphisms in male body plan. Males have horns, either on the pronotum or head, which show a triphasic allometry with male body size (Emlen 1996; Hunt and Simmons 1997). Thus, there is discontinuous variation in horn size; large “major” males possess horns while small “minor” males do not. Cook (1990) only observed major males cooperating in brood provisioning which may explain why females paired with major males produced more brood masses than those paired with minor males, irrespective of male body size (Cook 1988).

We have examined the influence of male horn dimorphism on female reproductive performance in the horned beetle *O. taurus*. In common with many onthophagines (Emlen 1996), *O. taurus* exhibits dimorphisms in horn development (Hunt and Simmons 1997) and, in the absence of competitors, horned major males spend 57% of their time cooperating in brood provisioning compared with just 13% for hornless minor males (Moczek 1996). Here we compare the reproductive performance of females paired with major males with those paired with minor males. Since each brood mass represents a single offspring, the number of brood masses produced is a direct measure of female fecundity. Furthermore, larval development and final adult size depends critically on the quantity of dung provided in the brood mass (Lee and Peng 1981; Emlen 1994; Hunt and Simmons 1997) so that brood mass weight provides a reliable indicator of the quality of the offspring produced.

Materials and methods

Animals used in these experiments were the first generation bred from adults collected in the field near Narikup (34°45'S, 117°41'E), approximately 370 km south of Perth, Western Australia. After adult emergence animals were housed in single sexed groups and provided with fresh dung. Animals were allowed to feed for 2 weeks prior to experimentation.

To examine variation in brood provisioning across male morphs, we established four experimental treatments: (1) majors: six major males were paired with six females (8 replicates); (2) minors: six minor males were paired with six females (8 replicates); (3) mixed: three major and three minor males were paired with six females (7 replicates); and (4) Control: six previously mated females were allowed to produce brood masses unaccompanied by males (8 replicates). One replicate in the mixed treatment was excluded from analysis because two of the six females and three of the six males died during the course of the experiment. An even sex ratio was established to minimise competition.

Males were selected from the extremes of the horn size distribution (see Hunt and Simmons 1997). The mean (\pm SE) horn height of majors was 1.16 ± 0.09 mm and of minors 0.23 ± 0.02 mm. In all treatments, females were chosen at random from the female population so that female pronotum width did not significantly differ between treatments ($F = 0.374$, $df = 3, 26$, $P = 0.773$).

The 48 females to be used in the control treatment were selected at random one week prior to experiments and housed *en masse* with 20 randomly selected males (sex ratio 2.4 females to 1 male) in a container containing moist sand and fresh dung. This ensured that all females in the controls had been mated at least once and had an adequate supply of sperm to continue egg deposition through the course of the experiment. Experimental females were housed in a similar manner but without males.

The beetles of each replicate were placed into a $22.5 \times 22.5 \times 16$ cm container half filled with moistened sand (~ 30 – 40% moisture content) upon which 1 l of cow dung was placed. In order to standardise dung quality across the experiment, all dung samples to be used were fully homogenised before being allocated to containers. Each container was sealed with a single layer of fine nylon meshing and a single layer of black plastic. Both layers were secured with heavy duty elastic bands. Containers were housed in a constant temperature laboratory with a 20 °C (11 h) dark and 23 °C (13 h) light cycle. After 10 days, the sand in each of the containers was sifted using mechanical sieves (0.5-cm^2 grid mesh) which enabled brood masses to be collected. The number of broods from each of the treatment replicates were recorded and the weight of each individual brood mass was determined after removing any excess sand that had adhered to the surface. Partially completed brood masses were not included in the analyses.

All data were log-transformed to meet underlying statistical assumptions of parametric analyses (Zar 1984). Data were analysed by single factor ANOVAs and male treatment means were compared with the female controls using Dunnett's *t* as recommended by Day and Quinn (1989).

Results

The mean number of brood masses produced in each of the four treatments differed significantly ($F = 3.373$, $df = 3, 26$, $P = 0.033$) (Fig. 1). The mean number of brood masses produced in the control treatment was significantly greater than in all other treatments (Dunnett's *t*: majors, 2.242, $P < 0.05$; minors, 2.204, $P < 0.05$; mixed, 2.960, $P < 0.01$). Therefore the presence of males, regardless of their horn size, significantly reduced the number of brood masses produced.

The mean weight of brood masses produced in each of the treatments also differed significantly. To avoid pseudoreplication we first calculated a mean brood mass

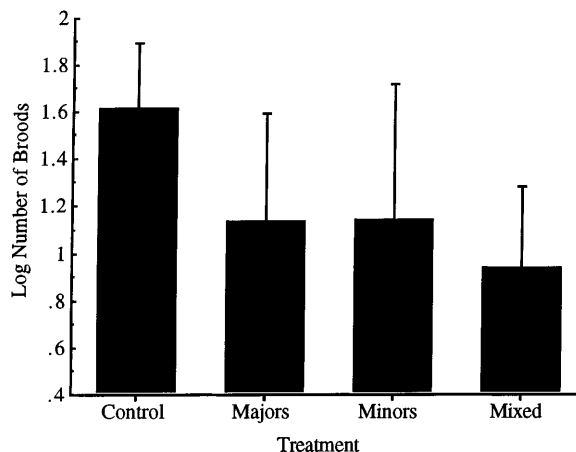


Fig. 1 The mean (\pm SD) Log number of brood masses produced by females in each treatment

weight for each replicate. The mean weights of brood masses produced differed significantly between treatments ($F = 6.094$, $df = 3, 26$, $P = 0.0028$) (Fig. 2). The mean weight of brood masses produced in both the major and mixed treatment was significantly greater than in the control (Dunnett's t : major, 2.994, $P < 0.01$; mixed, 2.946, $P < 0.01$). However, the mean brood mass weight in the minor treatment did not differ significantly from the control treatment (Dunnett's t , 0.103, $P > 0.50$). Therefore, the presence of major males significantly increased the mean weight of brood masses produced. This analysis does not take into account within-replicate variability. Therefore, we performed a repeated measures ANOVA using a subset of the data. We selected all replicates in which five or more brood masses were produced and used individual measures of the five brood masses as repeated measures for that replicate. For replicates containing more than five brood masses, we selected a random sample of five brood masses for the analysis. Our analysis showed that brood mass weight again differed significantly between treatments ($F = 6.292$, $df 3, 21$, $P = 0.003$) but that there was no significant within-replicate variance ($F = 0.202$, $df 4, 84$, $P = 0.934$) and no interaction between the treatment effects and within replicate variance ($F = 0.558$, $df 12, 84$, $P = 0.558$). Thus, the presence of major males resulted in a consistent increase in the weight of all brood masses produced.

Finally, the increased weight of brood masses and decreased number of brood masses produced in treatments containing majors did not appear to reflect a reproductive trade-off; there was no statistically significant relationship between brood mass weight and number within any treatment (control, $r = 0.445$, $df 6$; majors, $r = 0.005$, $df 6$; minors, $r = 0.588$, $df 6$; mixed, $r = 0.386$, $df 4$; all $P > 0.10$). Given the small sample sizes involved in these individual analyses it is difficult to reject the null hypotheses with confidence. We note that the correlations were of moderate size in three of the treatments. To strengthen our analysis we calculated Fisher's combined probability, which supported our

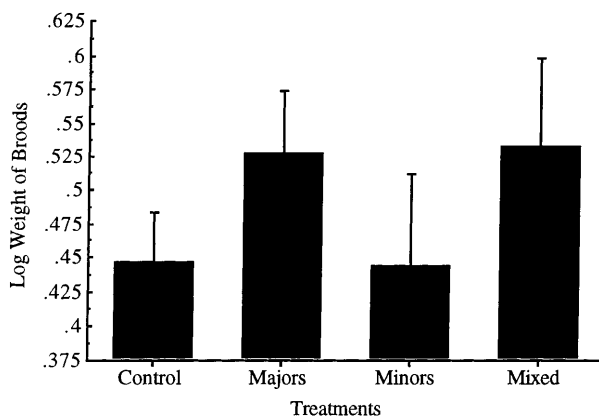


Fig. 2 The mean (\pm SD) Log weight of brood masses produced by females in each treatment

conclusion that there was no relation between the mean weight and number of brood masses produced ($\chi^2 = 8.397$, $df 8$, $P = 0.396$). Further, there was no significant relationship across treatments ($r = 0.024$, $df 28$, $P = 0.90$). It should also be noted that a reproductive trade-off predicts a negative association between brood mass size and number while our correlations were all positive.

Discussion

In the limited number of dung beetle species that have been examined, male assistance has been demonstrated to enhance reproductive success by increasing the number of brood masses produced, and hence female fecundity (Halffter and Lopez 1977; Cook 1988; Rasmussen 1994; Sowig 1996). In *O. binodis* and *O. vacca*, the mean number of brood masses produced by females paired with males was significantly greater than in unpaired females (Cook 1988; Sowig 1996). In *P. difformis* burrows provisioned with male assistance were supplied with dung at a faster rate than burrows provisioned by single females (Rasmussen 1994). In both instances the increase in brood mass numbers were not accompanied by increases in either brood mass weight (Cook 1988; Sowig 1996) or brood mass size (Rasmussen 1994).

In contrast, the data presented here for *O. taurus* show a reduction in the number of brood masses produced by females when placed with males of either morph. That is, the presence of males appeared to impose a direct reproductive cost on females in the total number of offspring produced. One possible explanation for the reduction in brood mass production could be the time out from provisioning required for mating activity. Costs to females of exposure to males have rarely been reported, although for *Drosophila melanogaster* a cost of mating for females is manifest as reduced longevity and lifetime egg production (Fowler and Partridge 1989; Chapman et al. 1995). However, it should be noted that control females were housed with males for a period of one week prior to experimentation. If mating activity increases reproductive output as it does in some species of insect (reviewed in Eberhard 1996), control females might be expected to have a higher initial rate of brood mass production which could account for the differences found. Females in treatments containing males had a greater total exposure to males over the duration of the experiment; control females had a total average exposure of 1 male per 2.5 females for 7 days, compared with experimental females who had an exposure of 1 male per female for 10 days. This difference in total exposure to males might be expected to oppose any initial mating effects on control females. Controlled breeding experiments will be necessary to confirm whether exposure to males decreases female fecundity in this species.

There is clear evidence that breeding with major males confers a reproductive advantage on females in terms of the weight of brood masses produced. Since the quantity of dung in a brood mass provides the nutritional basis for the developing larvae and ultimately determines adult body size, and thus fecundity in daughters and horn size and competitive ability in males (Lee and Peng 1981; Emlen 1994; Moczek 1996; Hunt and Simmons 1997; Emlen 1997), mating with major males is likely to produce both male and female offspring of higher reproductive value.

It could be argued that increased brood mass weight in the presence of majors is a manifestation of female choice; if females prefer major males because of some indirect benefit that can be transmitted to offspring, they may increase their investment in offspring that will be sired by preferred mates (Simmons 1987; Petrie and Williams 1993; Møller 1993). However, neither body size or male horn length appear to have any genetic variance (Emlen 1994; Moczek and Emlen in press) so that females are unlikely to gain indirect benefits for increased investment. Moreover, given that horned males are known to participate in brood mass provisioning in *O. taurus* (Moczek 1996) and *O. binodis* (Cook 1990), and that there is no apparent trade-off between brood mass number and size (see also Sato and Imamori 1987), it is more probable that the increased brood mass weight associated with major males reflects differences in the reproductive behaviours adopted by the male morphs. Direct evidence for alternate behaviours in this study comes from observations made during the collection of brood masses. While it was rare to encounter both a male and female within a partially constructed brood mass, in the 9 instances where this behaviour was observed, females were accompanied by major males. Likewise, in *O. binodis* horned males were observed twice as frequently in partially constructed brood masses as hornless males (Cook 1988).

Given that females breeding with major males have more dung with which to provision brood masses, the question arises as to why they should increase the amount of resources provided to each offspring, rather than the number of offspring produced. The answer is not a simple one, and is analogous to Parker and Simmons (1989) analysis of optimal egg size for nuptial feeding insects. In this instance, however, resources for larval development are laid down in the brood mass, rather than the egg. Females are likely to have an optimal brood mass dependent on the fitness gain per unit increase in dung provided, and the costs associated with foraging for dung. Intuitively, male assistance should decrease foraging costs and thus decrease the females optimal brood mass with the effect that total numbers of broods produced should be increased. However, Parker and Simmons (1989) showed that the influence of male provisioning would be dependent on the total amount of resources provided, and the stage in the females reproductive cycle at which they are provided. Male-contributed resources that are large or provided late in the

cycle will raise the brood mass above that which is optimal for the female, so that females should produce larger broods.

Our mixed treatment is closest to the environment experienced by beetles in the field, where females breed with both major and minor males present. Brood mass weight did not appear to differ between our major and mixed treatments. We would have expected to see greater variance in brood mass weight and perhaps a lower mean brood mass weight, given that only half of the females should have been breeding with majors while the remaining females should have been producing broods alone. This assumes however, that males are able to assist only one female at a time. Currently we have no data to support this assumption and it may be that under our experimental conditions males were capable of assisting more than one female. However, our data represent a baseline estimate of reproductive performance since sexual competition was minimised and dung provided ad libitum. Competition for dung and mates is intense in field populations where beetle densities can reach as high as 1000 adult beetles per dung pad (personal observations). Under such conditions it is unlikely that individual males could assist more than a single female and indeed, major males may engage more in female defence than brood provisioning (Moczek 1996).

Since the reproductive performance of female *O. taurus* appears to be enhanced by breeding with males possessing large horns, the potential exists for females to benefit from mating preferentially with horned males. Kirkpatrick (1985) incorporated cases where female fecundity depends on her choice of mate into a theoretical model of preference evolution, demonstrating how secondary sexual traits in males and female preferences for such traits can arise when females gain direct fitness benefits (see also Heywood 1989; Hoelzer 1989; Grafen 1990; Price et al. 1993). These theoretical models predict that the direct benefits to female fitness by mating with major males should result in females displaying a preference for males possessing ornamentation. Theoretically, horn dimorphism could have evolved, in part, as a signal of male parental investment. In this context, horned male *O. binodis* display their horns to females with upward jerks of the head and pronotum during courtship (Cook 1990). Nevertheless, selection via male competition is clearly important in the evolution of beetle horns (Eberhard 1977, 1979; Conner 1988). Emlen (1997) has recently shown that horned male *O. acuminatus* use their horns to block the entrance to tunnels in which their mate is constructing a brood mass. Males with longer horns are more successful in competitive interactions and hornless males sneak copulations by constructing side tunnels that bypass the female's guarding partner. The same appears true of *O. taurus* (Moczek 1996) and was suggested for *O. binodis* (Cook 1990). Thus, alternative reproductive strategies in onthophagines are characterised by differences in competitive and parental strategies, as well as morphology. Mate guarding behaviour might be expected in major

males given their high paternal investment, so that horns are likely to have been selected through mating competition, as a mechanism of paternity assurance. Once established in the population however, horns could become subject to further exaggeration via female choice for the immediate benefits of paternal investment that they signal. Kodric-Brown and Brown (1984) have proposed a theoretical model that shows how male traits can serve a dual function in the context of sexual selection. Berglund et al. (1996) show that the incidence of traits with dual functionality is quite prominent across a variety of animal taxa (77% of species examined), suggesting that the two selective processes may often become associated. Whether female onthophagines can use male horn dimorphisms as signals of parental investment warrants further study.

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