MATERNAL AND PATERNAL EFFECTS ON OFFSPRING PHENOTYPE IN THE DUNG BEETLE *ONTHOPHAGUS TAURUS*

J. HUNT[1] AND L. W. SIMMONS

Evolutionary Biology Research Group, Department of Zoology, University of Western Australia,
Nedlands, Western Australia 6907, Australia
[1]*E-mail: jhunt@cyllene.uwa.edu.au*

Abstract.—Parents often have important influences on the development of traits in their offspring. One mechanism by which parents are able to influence offspring phenotype is through the level of care they provide. In onthophagine dung beetles, parents typically provision their offspring by packing dung fragments into a brood mass. *Onthophagus taurus* males can be separated into two discrete morphs: Large, "major" males have head horns, whereas "minor" males are hornless. Here we show that a switch in parental provisioning strategies adopted by males coincides with the switch in male morphology. Male provisioning results in the production of heavier brood masses than females will produce alone. However, unlike females in which the level of provisioning increases with body size in a continuous manner, the level of provisioning provided by males represents an "all-or-none" tactic with all major males providing a fixed level of provisioning irrespective of their body size. Offspring size is determined largely by the quantity of dung provided to the developing larvae so that paternal and maternal provisioning affects the body size and horn size of offspring produced. The levels of provisioning by individual parents are significantly repeatable, suggesting paternal and maternal effects as candidate indirect genetic effects in the evolution of horn size in the genus *Onthophagus*.

Key words.—Alternative strategies, dung beetles, maternal effects, parental care, paternal effects.

The factors contributing to phenotypic variation in morphological and/or behavioral traits have traditionally been divided into variance that is genetic in origin and variance that is due to the environment. However, further subdivision reveals an additional set of factors that may significantly alter phenotypes (Falconer 1994). One factor that is currently the focus of theoretical attention is the effect that individuals in one generation may have on the phenotype expressed by individuals in subsequent generations, through the environment they provide (Cheverud and Moore 1994; Mousseau and Fox 1998). If the quality of this environment is variable and reflects genetic differences among individuals, then the environment will have a heritable component and may contribute to evolutionary change through indirect genetic effects (Wolf et al. 1998). Research involving indirect genetic effects has focussed predominantly on the effects of the environment provided by mothers to their offspring, called maternal effects (Cheverud and Moore 1994). However, the importance of indirect genetic effects applies equally to situations where the father provides the environment or even when the environment is provided by unrelated individuals (Wolf et al. 1998). Indirect genetic effects appear to be widespread in nature and have the potential to function as important driving forces in evolution (Moore et al. 1998; Wolf et al. 1998).

One mechanism by which parents are able to influence the phenotype of their offspring is through the level of care they provide (Cheverud and Moore 1994). In species exhibiting biparental care, the level of care provided to offspring will depend upon the provisioning competence of both parents (Clutton-Brock 1991). As such, both maternal and paternal effects have the ability to alter offspring phenotype. Biparental care appears common in dung beetles of the genus *Onthophagus* (Lee and Peng 1981; Cook 1988; Sowig 1996; Hunt and Simmons 1998a). During reproduction, members of this genus typically remove portions of dung and pack it into the blind end of tunnels excavated beneath the dung pad (Halffter and Edmonds 1982). A single egg is deposited into an egg chamber and sealed; one egg and its associated dung provision constitutes a brood mass (Halffter and Edmonds 1982).

Onthophagines typically exhibit dimorphisms in male body plan, in which large "major" males develop enlarged horns on the head and/or pronotum and small, "minor" males are hornless (Cook 1987; Emlen 1996; Hunt and Simmons 1998b). Male dimorphisms are associated with alternative behavioral tactics, with horned males fighting for access to females and hornless males sneaking copulations with females that are guarded by horned males (Emlen 1997). A male's morph is determined by a hormonal switch that controls his developmental pathway and is triggered by the amount of dung provided by his parents (Emlen and Nijhout 1999). As such, the alternative phenotypes are discrete and represent a conditional reproductive strategy (Gross 1996). Studies that have examined patterns of parental provisioning in onthophagines suggest that it is typically only the major males that provide assistance during brood construction (Cook 1988; Hunt and Simmons 1998a). In *O. taurus*, assistance by major males results in the production of significantly heavier brood masses (Hunt and Simmons 1998a). Because adult size is largely determined by the quantity of dung provided in the brood mass (Lee and Peng 1981; Emlen 1994; Hunt and Simmons, 1997), paternal assistance should increase the size of offspring produced. Thus, although horn size in onthophagines may not have a significant heritable basis (Emlen 1994; Moczek and Emlen 1999), father-son phenotypic resemblance may be generated through the level of paternal care provided.

Here, we quantified the level of provisioning provided to offspring when females construct brood masses alone or with the assistance of males and examine the relative influence of maternal and paternal effects on offspring phenotype. Furthermore, we examine the influence of parental phenotype on
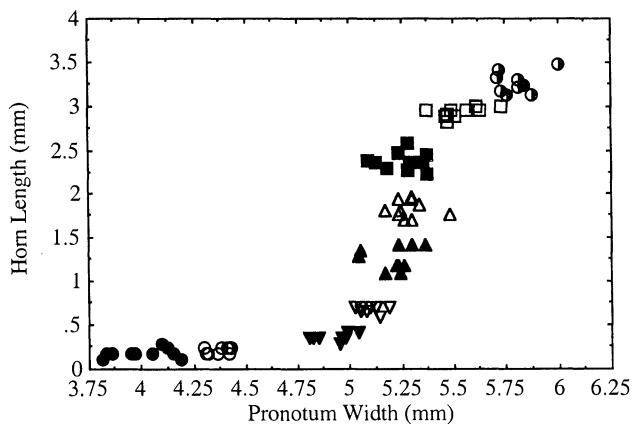
FIG. 1. The nine phenotypic categories located along the horn-pronotum sigmoid. The males in each category differed significantly in both horn length and pronotum width (males in each category are differentiated by the nine different symbols).

the level of provisioning and obtain an estimate of the repeatability of parental provisioning. We consider the possible significance of the observed parental effects for the evolution of horn dimorphisms in this genus.

METHODS

Onthophagus taurus were collected using pit traps from Margaret River in the south of Western Australia. The sexes were separated and maintained for two weeks in the laboratory with constant access to fresh cow dung to ensure all beetles were reproductively mature and in optimal condition. The pronotum widths of all experimental males and females were determined using digital calipers and male horn length determined using an eyepiece graticule with a binocular microscope.

Biparental Care

To examine variation in the level of paternal provisioning, we selected males based on their pronotum width and horn size so that we had nine male phenotypic categories along the horn-pronotum sigmoid (Fig. 1). Alternative male phenotypes can be distinguished statistically using the models of Eberhard and Gutiérrez (1991). Categories 1–3 were selected to the left of the switch point separating the male morphs (minor males) and categories 4–9 to the right of the switch point (major males; see Hunt and Simmons [1998b] and the results of this study for the statistical determination of the switch point). Ten males were selected for each of the male phenotype categories. Across our categories there was significant variation in both horn size ($F_{8,81}$ = 2086.22, P = 0.0001) and body size ($F_{8,81}$ = 353.12, P = 0.0001). To control for variation in provisioning by females, each male was paired with a female of average body size. There was no significant variation in female size across our nine male phenotype categories ($F_{8,81}$ = 0.73, P = 0.67; mean ($\pm$ SE) = 4.48 $\pm$ 0.021 mm). Each male-female pair was placed in an independent breeding chamber (PVC piping 25 cm in length and 6 cm in diameter), three-quarters filled with moist sand and one-quarter filled with homogenized cow dung, and

maintained for one week. Chambers were then sieved and brood masses removed. Chambers were reestablished for a second week of breeding in which we randomly selected half of the replicates in each treatment to have the male removed. At the end of the second week, breeding chambers were sieved and brood masses removed.

Excess sand was removed from brood masses using a dissecting probe and the brood masses dried to constant weight at 60°C; dry weights were taken to reduce variation in brood mass weight due to soil and dung moisture content. After drying, any remaining sand was brushed off with a toothbrush and all brood masses were counted and weighed to the nearest 0.01 mg.

Uniparental Care

To examine variation in female provisioning, we selected females based on their pronotum width so that we again had nine female phenotypic categories across the normal range of female body sizes. Ten females were assigned to each of the categories, which differed significantly in pronotum width ($F_{8,81}$ = 2187.74, P = 0.0001). Each female was placed in an independent breeding chamber and maintained for one week. Chambers were sieved and brood masses collected for drying, weighing, and counting as outlined above.

Influence of Brood Mass on Offspring Phenotype

A group of 30 females were established in individual breeding chambers supplied with the same homogenized cow dung used in the above experiments. Females were left to breed for one week. Chambers were sieved and the wet weights of brood masses determined after removing excess sand with a dissection needle. To allow us to calibrate wet weight to dry weight, we dried a subset of brood masses (n = 65) to constant weight and reweighed them as described above. The remaining brood masses were reburied in damp sand in individual boxes and left until beetles emerged. On emergence, measurements of pronotum width and horn length were made.

RESULTS

Biparental Care

There was a significant effect of male phenotype on the weight of brood masses produced during the first week of the experiment when all females provisioned with the assistance of males ($F_{8,68}$ = 6.15, P = 0.0001; Fig. 2a). The number of brood masses produced was not influenced by male phenotype ($F_{8,68}$ = 1.23, P = 0.29). The difference in brood mass weight arose because those produced in phenotype categories 4–9 (major males) were significantly heavier than those produced in categories 1–3 (minor males; Fig. 2a). Brood masses produced with minor males fell within the weight range expected for females provisioning alone, whereas those produced with major males were 48% larger than expected given the size of female used in the experiment. The relation between pronotum width and brood mass weights within major and minor morphs were not significant (majors, $F_{1,50}$ = 0.34, P = 0.56; minors, $F_{1,23}$ = 1.00, P = 0.33), indicating that the increased weight of broods was
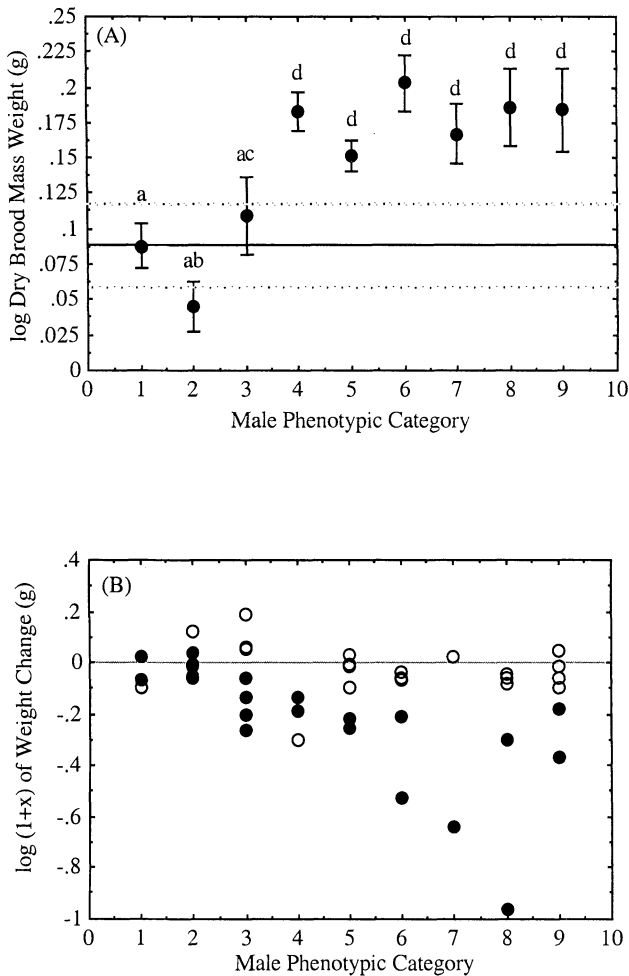
FIG. 2. (a) The mean dry weight of brood masses produced by male-female pairs in the first week of the biparental care experiment. Phenotypic categories with different letters are significantly different at $\alpha = 0.05$. The solid horizontal line represents the mean dry brood mass weight that would be produced if females were provisioning unassisted (estimated from the data in Fig. 3 with mean female size equal to 4.48 ± 0.021 mm). The broken horizontal lines represents the standard error about this mean. (b) The mean change in weight of brood masses produced during week 2, when females were either left with their males (open symbols) or when males were removed (solid symbols; see Fig. 1 for actual values of pronotum width and horn size in each category).

attributable to the dimorphism in male body plan, rather than continuous variation in male body size.

We also examined the influence of male provisioning by looking at the change in weight of brood masses produced in week two, after half of the females had had their partner removed. There was a significant effect of male phenotype ($F_{8,26} = 4.73$, $P = 0.0011$) and male removal ($F_{1,26} = 32.76$, $P = 0.0001$) on the change in brood mass weight across weeks 1 and 2, and a significant male phenotype-by-male removal interaction ($F_{8,26} = 4.20$, $P = 0.0025$). Females that had previously been paired with males in the major male categories had a reduction in brood mass weight after their partner had been removed, whereas those paired with males in the minor male categories produced brood masses of a similar size that they had produced when accompanied by their mate
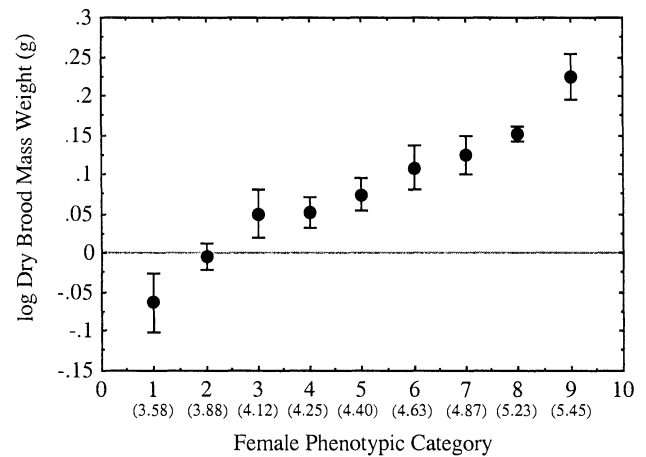

FIG. 3. The mean dry brood mass weight produced by unassisted females in each of the female size categories (the actual mean values for female pronotum width in each treatment are given in parentheses).

(Fig. 2b). Pairs allowed to remain together showed no change in brood mass weight. The change in the number of brood masses produced was not influenced by male phenotype ($F_{8,26} = 2.07$, $P = 0.08$) or male removal ($F_{1,26} = 0.004$, $P = 0.43$) and there was no significant interaction ($F_{8,26} = 1.05$, $P = 0.43$).

To obtain an estimate of the repeatability of brood mass weight when males were providing care, the weights of five randomly selected brood masses were taken from those produced during the first week of breeding. Repeatability was only examined for the six phenotypic categories (4–9) that exhibited paternal care (Fig. 2). A total of 53 pairs that produced five or more brood massess were avaialble for the analysis. Repeated-measures analysis of variance (ANOVA) was used to estimate the variance components of brood mass weights and the repeatability estimated according to Becker (1992). There was significantly greater variance in brood mass weight between pairs than within pairs ($F_{52,212} = 1.92$, $P = 0.0007$) with a repeatability of 0.155 ± 0.064.

Uniparental Care

Brood mass weight increased linearly with female size category ($F_{8,70} = 11.20$, $P = 0.0001$; Fig. 3). Brood mass number, however, was not influenced by female size ($F_{8,70} = 0.60$, $P = 0.77$). Brood mass weight was again significantly more variable between subjects than within subjects ($F_{70,284} = 8.74$, $P = 0.0001$) across 71 females that produced fiveeor more brood masses, but yielded a much higher estimate for repeatability than when males were assisting in brood mass production (0.607 ± 0.051).

Influence of Brood Mass on Offspring Phenotype

There was a significant effect of brood mass on the body size of emergent offspring ($F_{1,179} = 25.27$, $r^2 = 0.119$, $P < 0.0001$). However, biologically there must be an upper limit to offspring size, and an examination of the data in Figure 4 shows that the relationship deviates from linearity. Therefore, we fitted the data to the model:
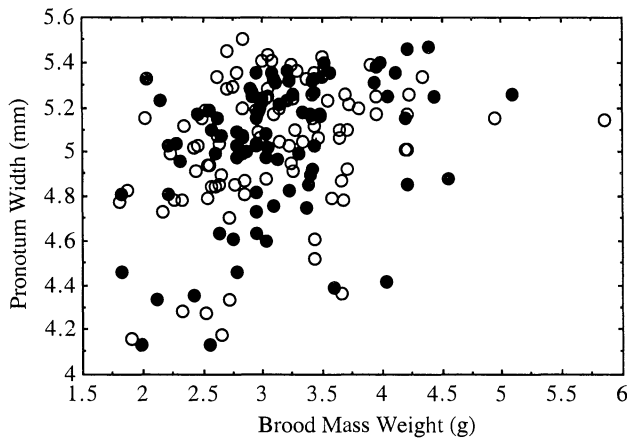
FIG. 4. The relationship between brood mass weight and the pronotum width of emerging male (open symbols) and female (closed symbols) offspring.

$$P(BM) = P_{max}[1 - e(-rBM)] \qquad (1)$$

where $P(BM)$ is the pronotum width reached at a given brood mass weight, P_{max} is the maximum pronotum width attainable, and r is the rate at which pronotum width rises to its maximum value. The model explained a greater proportion of the variance than the linear model ($r^2 = 0.166$) and yielded estimates of $P_{max} = 5.21 \pm 0.045$ and $r = 1.18 \pm 0.086$.

We estimated the critical body size (switch point) among offspring at which males switched from the minor hornless morph to the major morph using the models of Eberhard and Guitérriez (1991; for a detailed outline of the use of these models and meanings of the parameters in *O. taurus*, see also Hunt and Simmons 1998b). The relationship between pronotum width and horn length showed an identical nonlinearity to that illustrated for parental beetles in Figure 1 ($\beta_2 = 23.52 \pm 8.04$, $t = 6.438$, df = 98, $P = 0.0001$). The switch point explaining the greatest proportion of variance ($r^2 = 0.857$) occurred at a pronotum width of 5.00 mm. The dimorphism was characterised by a change in linear slope ($\beta_2 = 1.02 \pm 0.14$, $t = 7.13$, df = 98, $P = 0.0001$) and a discontinuous distribution of horn lengths ($\beta_3 = 2.32 \pm 0.49$, $t = 4.81$, df = 98, $P = 0.0001$) at the switch point. Thus, at a pronotum width ≥ 5.00 mm, males can be assigned to the major morph. Equation (1) shows that a brood mass weight of 2.72 g is required to produce an individual of this body size. Calibrating wet mass to dry mass using the equation dry mass = 0.343 wet mass + 0.19 ($r^2 = 0.57$, $F_{1,63} = 71.03$, $P = 0.0001$) yielded a corresponding dry weight of 1.12 g.

In Figure 5, we present a graphic representation of the relative influence of maternal and paternal effects on the phenotype of male offspring. When females breed alone, only females larger than average are capable of providing enough resources to produce major sons. However, with paternal assistance, females of all size classes are capable of producing majors. Moreover, given the size-dependent variation in maternal effects and the relation between pronotum width and horn length in Figure 1, larger females will produce major sons with longer horns.
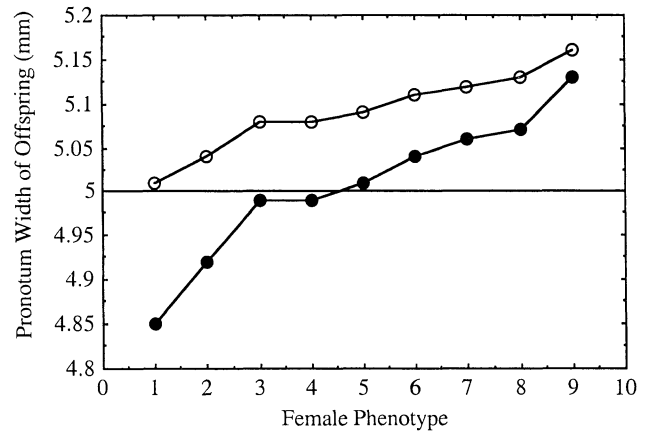

FIG. 5. Graphic representation of the relative influence of maternal effects (solid symbols) and combined maternal and paternal effects (open symbols) on the phenotype of male offspring. The brood mass weight expected for a female of given phenotype was taken from Figure 3 and converted to its wet-weight equivalent before calculating the expected offspring size from equation (1). Because the quantity of male care did not differ significantly in those categories exhibiting paternal care (see text), the mean combined brood mass increment across categories due to male provisioning (0.49 ± 0.06 g dry weight) was added to that expected from females in each phenotype category to estimate the combined paternal and maternal effect on offspring size. This estimate assumes that the level of investment provided by a major male does not alter with female size. The horizontal line represents the pronotum width at which males can be assigned to the major morph (see text).

DISCUSSION

Our finding that individual females breeding with major males produce heavier brood masses than those breeding with minor males or breeding alone is consistent with our previous study in which females were held in groups with either major or minor males (Hunt and Simmons 1998a). Paternal assistance also increases brood mass weight in *O. gazella* (Lee and Peng 1981), whereas in *O. binodis* and *O. vacca* male assistance leads to an increase in the number of brood masses produced (Cook 1988; Sowig 1996). In at least two of these species (*O. binodis* and *O. taurus*), paternal provisioning tactics are known to covary with male morphology, with only major males providing assistance (Cook 1988; Hunt and Simmons 1998a).

In all previous studies of alternative reproductive strategies in onthophagines, dichotomous experimental designs have been employed in which only males from the extremes of the horn-pronotum distribution are used. In contrast, we have measured variation in a dimorphic male behavior, paternal care, across the entire horn-pronotum distribution and provide the first empirical evidence that a switch in behavior coincides precisely with the switch in morphology. When male *O. taurus* reach a critical body size of 5 mm pronotum width, they invest in the production of horns and also switch parental provisioning tactics and assist females during brood mass construction. Thus, our behavioral observations support the notion that alternative male morphologies in onthophagines represent discrete life-history traits and that males with small, reduced or rudimentary horns are not intermediate phenotypes.

The level of care provided by major males did not increase continuously with their body size, but instead appeared to represent an "all-or-none" tactic, with all majors providing a fixed level of care. This is somewhat surprising given that the level of female care increased with female size. Numerous theoretical models have predicted that parents should show a single optimal level of investment (Smith and Fretwell 1974; Brockelman 1975; Charnov 1976), although empirical support for these models has not been forthcoming (Clutton-Brock 1991). Whether the level of paternal care shown by major male *O. taurus* reflects an optimal investment strategy warrants further study.

Our results also show that the presence of males had no impact on the number of brood masses produced. In our earlier study of this species we found that control females housed without males produced more brood masses, suggesting a cost of exposure to males (Hunt and Simmons 1998a). However, in that study the control females were housed with males for a period of one week prior to experimental breeding to ensure they were fertile. The greater number of brood masses produced most likely arose because of the effects of seminal products on female egg production, a phenomenon reported from other coleopteran species (Fox 1993a,b; Cruz and Martinez 1998; Savalli and Fox 1998) and insects in general (Eberhard 1996).

Brood mass explained only 17% of the variance in offspring size. Heritability studies suggest that body size exhibits very little additive genetic variance (Moczek and Emlen 1999). Although the quality of dung influences offspring size (Moczek 1998), this was standardized in our experiments. Our estimates of dry weight showed that, on average, brood masses were 58% water, but water content was highly variable (coefficient of variation 11.2%). Thus, the inaccuracy inherent in wet weights may account for the low proportion of variance in offspring weight explained.

Because the quantity of dung in the brood mass provides the nutrients for the developing larvae and ultimately determines adult body size (see also Lee and Peng 1981; Emlen 1994; Hunt and Simmons 1997), the additional dung provided by a major male increases the size of offspring produced. Body size in onthophagines is correlated with fecundity in females (J. Hunt, unpubl. data) and competitive ability in males (Emlen 1997) so that paternal assistance will increase the reproductive value of offspring produced. Moreover, females provisioning with the assistance of a major male are more likely to produce major sons with horns, and the length of those horns will depend on the size of the female and whether she is assisted by a major male, even though horn size appears to have no heritable basis (Emlen 1994; Moczek and Emlen 1999). The interaction between the level of care provided by both parents can thus promote phenotypic similarity with their offspring through the environment they provide.

Maternal and paternal effects are one class of indirect genetic effects that appear widespread in nature (Mousseau and Dingle 1991; Rossiter 1996; Wolf et al. 1998). In insects, indirect genetic effects have been shown to influence a large number of life-history traits, such as developmental period, wing development, and the onset of diapause (see review by Mousseau and Dingle 1991). However, if indirect genetic effects are to result in evolutionary change, the quality of the environment provided to offspring must exhibit some genetic variability (Wolf et al. 1998). Studies examining the genetics of paternal care are rare (Clutton-Brock 1991). To date, only one study has examined the genetics of paternal investment in an insect and this demonstrated significant heritability (Savalli and Fox 1998). In *O. taurus*, brood mass weight was repeatable when females provided uniparental care; most variation occured between females rather than within. Interestingly repeatability was lower, although still significant, under biparental care, suggesting that male provisioning contributes to an increase in the variance in the offspring's environment. Repeatability can arise from a number of factors including heritability of the trait measured (Becker 1992; see Boake 1989) so that male and female provisioning behaviors may exhibit some genetic variation. Quantitative genetic studies of male and female parental care will be required to fully elucidate the genetic basis of parental care.

Numerous quantitative genetic models have demonstrated that indirect genetic effects can have far reaching evolutionary consequences (Kirkpatrick and Lande 1989; Moore et al. 1997; Wolf et al. 1998). Theoretically, indirect genetic effects have been shown to accelerate the rate of evolutionary change (Moore et al. 1997; Wolf et al. 1998) and generate evolutionary time lags in the response to selection (Kirkpatrick and Lande, 1989; Wolf et al. 1998). However, the most important consequence of indirect genetic effects is that a lack of direct genetic variation in a trait subject to selection does not prevent evolution of that trait if there is genetic variation in the indirect genetic contribution (Moore et al. 1997). Thus, although horn size is typically not heritable in onthophagines (Emlen 1994; Moczek and Emlen 1999), horn size may still evolve through indirect effects in species with paternal care that influences brood mass weight. As such, indirect genetic effects may have widespread implications for the evolution of horn size dimorphisms in onthophagines and may account for the highly elaborate horn structures that characterize some of the species in this genus.

LITERATURE CITED

Becker, W. A. 1992. Manual of quantitative genetics. Academic Enterprises, Washington, DC.

Boake, C. R. B. 1989. Repeatability its role in evolutionary studies of mating behavior. Evol. Ecol. 3:173–182.

Brockelman, W. Y. 1975. Competition, the fitness of offspring, and optimal clutch size. Am. Nat. 109:677–699.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9:129–136.

Cheverud, J. M., and A. J. Moore. 1994. Quantitative genetics and the role of the environment provided by relatives in behavioural

evolution. Pp. 67–101 *in* C. Boake, eds. Quantitative genetic studies of behavioural evolution. Univ. of Chicago Press, Chicago.

Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton Univ. Press, Princeton, NJ.

Cook, D. 1987. Sexual selection in dung beetles. I. A multivariate study of the morphological variation in two species of *Onthophagus* (Scarabaeidae: Onthophagini). Aust. J. Zool. 35: 123–132.

———. 1988. Sexual selection in dung beetles. II. Female fecundity as an estimate of male reproductive success in relation to horn size, and alternative behavioural strategies in *Onthophagus binodis* Thunberg (Scarabaeidae: Onthophagini). Aust. J. Zool. 36: 521–532.

Cruz, M., and I. Martinez. 1998. Effect of male mesadene secretions on females of *Cantho cyanellus cyanellus* (Coleoptera: Scarabaeidae). Flor. Entomol. 81:23–30.

Eberhard, W. G. 1996. Female control: sexual selection by cryptic female choice. Princeton Univ. Press, Princeton, NJ.

Eberhard, W. G., and E. E. Gutierrez. 1991. Male dimorphisms in beetles and earwigs and the question of developmental constraints. Evolution. 45:18–28.

Emlen, D. J. 1994. Environmental control of horn length dimorphism in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). Proc. R. Soc. Lond. B Biol. Sci. 256:131–136.

———. 1996. Artificial selection on horn-body size allometry in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). Evolution 50:1219–1230.

———. 1997. Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). Behav. Ecol. Sociobiol. 41:335–341.

Emlen, D. J., and H. F. Nijhout. 1999. Hormonal control of male horn length dimorphism in the dung beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). J. Insect Physiol. 45:45–53.

Falconer, D. S. 1994. An introduction to quantitative genetics. Wiley, New York.

Fox, C. W. 1993a. The influence of maternal age and mating frequency on egg size and offspring performance in *Callosobruchus maculatus* (Coleoptera: Bruchidae). Oecologia 96:139–146.

———. 1993b. Multiple mating, lifetime fecundity and female mortality of the bruchid beetle, *Callosobruchus maculatus* (Coleoptera: Bruchidae). Funct. Ecol. 7:203–208.

Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends Ecol. Evol. 11:92–98.

Halffter, G., and W. G. Edmonds. 1982. The nesting behaviour of dung beetles (Scarabaeidae): an ecological and evolutionary approach. Instituto de Ecologia, México, Mexico City.

Hunt, J., and L. W. Simmons. 1997. Patterns of fluctuating asymmetry in beetle horns: an experimental examination of the honest signaling hypothesis. Behav. Ecol. Sociobiol. 41:109–115.

———. 1998a. Patterns of parental provisioning covary with male morphology in a horned beetle (*Onthophagus taurus*) (Coleoptera: Scarabaeidae). Behav. Ecol. Sociobiol. 42:447–451.

———. 1998b. Patterns of fluctuating asymmetry in beetle horns: no evidence for the reliable signaling. Behav. Ecol. 9:465–470.

Kirkpatrick, M., and R. Lande. 1989. The evolution of maternal characters. Evolution 43:485–503.

Lee, J. M., and Y. S. Peng. 1981. Influence of adult size of *Onthophagus gazella* on manure pat degradation, nest construction, and progeny size. Environ. Entomol. 10:626–630.

Moczek, A. P. 1998. Horn polyphenism in the beetle *Onthophagus taurus*: larval diet quality and plasticity in parental investment determine adult body size and male horn morphology. Behav. Ecol. 9:636–642.

Moczek, A. P., and D. J. Emlen. 1999. Proximate determination of male horn dimorphism in the beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). J. Evol. Biol. 12:27–37.

Moore, A. J., E. D. Brodie III, and J. B. Wolf. 1997. Interacting phenotypes and the evolutionary process. I. Direct and indirect genetic effects of social interactions. Evolution. 51:1352–1362.

Moore, A. J., J. B. Wolf, and E. D. Brodie III. 1998. The influence of direct and indirect genetic effects on the evolution of behavior: social and sexual selection meet maternal effects. Pp. 22–41 *in* T. A. Mousseau and C. W. Fox, eds. Maternal effects as adaptations. Oxford Univ. Press, Oxford, U.K.

Mousseau, T. A., and H. Dingle. 1991. Maternal effects in insect life histories. Annu. Rev. Entomol. 36:511–534.

Mousseau, T. A., and C. W. Fox. 1998. Maternal effects as Adaptations. Oxford Univ. Press, Oxford.

Rossiter, M. 1996. Incidence and consequences of inherited environmental effects. Annu. Rev. Ecol. Syst. 27:451–476.

Savalli, U. M., and C. W. Fox. 1998. Genetic variation in paternal investment in a seed beetle. Anim. Behav. 56:953–961.

Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. Am. Nat. 108:499–506.

Sowig, P. 1996. Duration and benefits of biparental brood care in the dung beetle *Onthophagus vacca* (Coleoptera: Scarabaeidae). Ecol. Entomol. 21:313–321.

Wolf, J. B., E. D. Brodie III, J. M. Cheverud, A. J. Moore, and M. J. Wade. 1998. Evolutionary consequences of indirect genetic effects. Trends Ecol. Evol. 13:64–69.

Corresponding Editor: D. Wheeler