

No fecundity cost of female secondary sexual trait expression in the horned beetle *Onthophagus sagittarius*

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Abstract

Typically males bear the products of sexual selection in the form of ornaments and/or weapons used to compete for and attract females. Secondary sexual traits in females have been thought of as the product of correlated responses to sexual selection on males. However, there is increasing phylogenetic evidence that female secondary sexual traits can arise independently of selection on males, and may be subject to sexual selection. Theoretical models of the evolution of female ornamentation via male mate choice have assumed that females suffer a cost of ornament expression via reduced fecundity, and hence female ornaments are less likely to evolve than male ornaments. In the dung beetle *Onthophagus sagittarius*, there has been an independent evolutionary origin of horns in females that are qualitatively different from the horns produced by males. We use this system as a model to examine the costs of horn expression for females within a life-history context. We identified a longevity cost of reproduction for females that was independent of horn expression. Large females lived longer, and after controlling for lifespan, had a higher lifetime fecundity, and invested more heavily in maternal provisioning than did small females. We found no evidence of a cost to females of investment in horns. Rather, the rate of increase in fecundity and horn expression with body size were equal, so that absolute horn size provides an accurate indicator of body size and maternal quality. The effects we observe were independent of female contest competition and/or male mate choice, which were excluded in our experimental protocol. However, we speculate on the potential functional contributions female horns might make to female fitness.

Introduction

Typically, it is males that bear the products of sexual selection, in the form of sexual ornaments and/or weapons that are used to attract or compete for access to females (Darwin, 1871; Andersson, 1994). It is now generally accepted that males are subject to sexual selection because females have the greater investment in producing and rearing offspring, and therefore the lower potential reproductive rate (Clutton-Brock & Parker, 1992; Parker & Simmons, 1996). Thus, females represent a limiting resource over which males compete,

and females have the opportunity to choose among the abundant supply of competing males. However, it is the case that females often exhibit sexual ornamentation and/or weaponry, and understanding the adaptive significance of female secondary sexual traits is becoming the focus of increasing research effort (Kiltie, 1985; Roberts, 1996; Amundsen, 2000; Roulin *et al.*, 2001; Chenoweth *et al.*, 2006; LeBas, 2006; Servedio & Lande, 2006; Kraaijeveld *et al.*, 2007).

Traditionally, secondary sexual traits of females have been disregarded as artefacts of selection on male secondary sexual traits; because the sexes share most of their genome, females will inherit the genetic basis for secondary sexual trait expression so that a correlated response in females to selection on males should be expected (Lande, 1980). Thus, under the correlated selection hypothesis, female sexual ornaments have no

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adaptive function. Moreover, it has been argued that the costs of developing sexual traits should restrict the products of sexual selection to males; because females invest more heavily in offspring than do males, they should be less able to bear the costs associated with the development of sexual ornamentation, and females that produce exaggerated sexual traits should have reduced fecundity (Fitzpatrick *et al.*, 1995). The resulting sexually antagonistic selection (Rice, 1984; Arnqvist & Rowe, 2005) is expected to erode genetic covariance between male and female, leading to a reduction in trait expression in females to the extent that they can become 'vestigial' or 'rudimentary' versions of male traits (Lande, 1980), or reach their own phenotypic optima (Chenoweth *et al.*, 2008).

There is some evidence to support the view that extant cases of secondary sexual traits in females might be due to correlated responses to selection on males. Meta-analysis of the literature on mutual ornamentation supports the notion of a genetic correlation in sexual ornament expression between the sexes (Kraaijeveld *et al.*, 2007), and the evolutionary pattern of gains and losses in sexual ornaments seen across 240 species of dragon lizards suggests that ornament gains typically occur simultaneously in both sexes, with sexual dimorphism arising due to subsequent losses of ornaments in females (Ord & Stuart-Fox, 2006). Nevertheless, there are also many cases across the dragon lizard phylogeny in which female ornament expression appears to have arisen subsequent to a gain in ornament expression in males, and in general, evolutionary losses of male ornamentation seem more common than evolutionary losses of female ornamentation. Likewise, phylogenetic studies of phrynosomatid lizards (Wiens, 1999), New World blackbirds (Irwin, 1994) and South American tanagers (Burns, 1998) have all revealed that evolutionary gains of female ornamentation are common, and often independent of gains of male ornamentation. Importantly, recent work with fowl, *Gallus gallus*, has identified several quantitative trait loci (QTL) that are specific to female sexual ornaments (Wright *et al.*, 2008). Taken together with growing evidence for a role for female secondary sexual traits in female contest competition (Bernet *et al.*, 1998; Heinsohn *et al.*, 2005; Robinson & Kruuk, 2007) and male mate choice (Amundsen *et al.*, 1997; Amundsen & Forsgren, 2001; Chenoweth *et al.*, 2007; Kvarnemo *et al.*, 2007), it seems that sexual selection acting on females may be of far greater significance than evolutionary biologists had previously thought (Kraaijeveld *et al.*, 2007).

It has been argued that male preferences for female ornamentation are unlikely to evolve because females would face a trade-off between resources directed toward sexual ornamentation and resources directed toward fecundity. Thus, Fitzpatrick *et al.* (1995) argued that males choosing highly ornamented females would suffer a reduced fitness because of their mates lowered fecun-

dity. Formal analysis incorporating such a trade-off suggests that male preferences can evolve, although they should impose nondirectional or stabilizing selection for intermediate levels of female ornament expression (Chenoweth *et al.*, 2007). However, if the marginal fecundity costs of ornament expression are lower for females of high quality, even with a trade-off between ornaments and fecundity, high-quality females should have absolutely higher fecundity and greater ornament expression than low-quality females (Zahavi, 1975; Grafen, 1990). Indeed, a trade-off between fecundity and ornament expression may be an important mechanism by which female ornament expression remains honest.

Few studies on the relationship between female secondary sexual trait expression and fecundity are available. Some studies suggest that females can face a trade-off between fecundity and ornament expression (Wicker & Jallon, 1995; Nordeide *et al.*, 2006), whereas others suggest that the relationship between ornament expression and fitness might be positive (LeBas *et al.*, 2003; Kraaijeveld *et al.*, 2007; Doutrelant *et al.*, 2008). Here, we use a species of onthophagine beetle, in which females develop head and thoracic horns, to explore the relationship between horn expression and fecundity in females.

Beetles in the genus *Onthophagus* are dung breeding insects which arrive at fresh droppings shortly after they have been deposited. Females dig tunnels in the ground beneath the dung, and pack fragments of dung into the blind ends of these tunnels to form brood masses (Fabre, 1918). One brood mass provides all of the resources available for the growth and development to adulthood of a single offspring. Brood mass size is positively related to body size, horn expression and offspring fitness, making maternal investment an important component of reproductive success (Emlen, 1994; Hunt & Simmons, 2000). Sexual selection has been important in the evolution of onthophagine reproductive morphology and behaviour (Emlen *et al.*, 2005b; Pomfret & Knell, 2008). Males develop horns on the head and/or the thorax which they use in contests with other males for access to breeding tunnels (Emlen, 1997; Moczek & Emlen, 2000). These secondary sexual traits are subject to strong sexual selection, with larger horns being associated with greater male reproductive success (Hunt & Simmons, 2001). There is also evidence in this genus that male investment in the development of horns comes at a cost of investment in other aspects of reproduction; males appear to trade investment in horns used to acquire mating opportunities for investment in sperm production required to compete for fertilizations (Simmons & Emlen, 2006). Moreover, resource allocation trade-offs between horns and morphological structures, such as eyes, wings and genitalia, appear to occur throughout the developing body (Nijhout & Emlen, 1998; Emlen, 2001; Moczek & Nijhout, 2004). Thus,

the onthophagines represent a good model for exploring trade-offs between sexual trait expression and reproduction.

Among species of *Onthophagus*, the size, location, shape and number of horns vary greatly. A DNA sequence-based phylogeny of onthophagines has identified prolific evolutionary divergence of secondary sexual structures (Emlen *et al.*, 2005a, b). As with lizards (Wiens, 1999; Ord & Stuart-Fox, 2006) and birds (Irwin, 1994; Burns, 1998), evolutionary gains of secondary sexual traits in females are common; across just 48 species of *Onthophagus*, there have been 13 evolutionary gains of female horns, 10 of which are correlated with gains of horns in males, with female horns being similar in appearance to the horns found in their male conspecifics. However, there is also evidence for three gains in female horns that occurred independently of gains in male horns (Emlen *et al.*, 2005a, b). For one of these species, *Onthophagus sagittarius*, the female horns are qualitatively different from the horns found in males – in shape, size and location. *Onthophagus sagittarius* thus provides an ideal model system for addressing questions on the independent evolution of female secondary sexual traits. In the current study, we use a life-history approach to quantify the costs of reproduction for female *O. sagittarius* that vary in their expression of horns. We ask whether there is any evidence of a phenotypic trade-off between female investment in horns and fecundity.

Methods

Animals used in these experiments were the first generation offspring from beetles collected from fresh cattle droppings in the vicinity of Childers, Qld, Australia. Field-collected beetles were maintained in mixed sex cultures for 2 weeks. Females (200) were established in individual breeding chambers (PVC piping, 30 cm in length and 9 cm in diameter, three-quarters filled with moist sand and topped with 25 mL of fresh cow dung) and left to construct broods for 1 week. Breeding chambers were then sieved, and batches of *c.* 50 broods were buried in moist sand in 10-L plastic boxes. Broods were incubated under a constant temperature of 28 ± 2 °C and a 12 h : 12 h light : dark cycle. After 2 weeks, brood boxes were checked daily for emerging adults, which were housed in single sex cultures with constant access to fresh dung for 1 week prior to use in experiments.

We measured the width of the thorax and the length of the head and thoracic horns of 90 females, before placing each female into an individual breeding chamber. In the congeneric species *Onthophagus taurus*, female investment in reproduction depends on the availability of fresh dung; females provided with unlimited supplies of dung make more broods and suffer an elevated longevity cost of reproduction compared with females given limited access to dung (Hunt *et al.*, 2002). Thus, to manipulate experimentally the costs incurred by females from reproduc-

tion, females were allocated at random to one of two treatments; females were provided with either 25 or 50 mL of fresh dung. A single, randomly sampled male was placed with each female, and the pair left for 1 week to mate and produce broods. Brood chambers were sieved after 1 week, and both male and female recovered. Females were established alone in a fresh breeding chamber and males discarded. Broods were cleaned of any attached sand using a dissection probe, counted and weighed. Each female's breeding chamber was thus sieved once a week, broods counted and weighed, and surviving females placed into fresh breeding chambers. To ensure that females had enough sperm to remain reproductively active, on week 5 they were provided with a second randomly allocated male who was again discarded at the subsequent sieving. All females were monitored until death.

We calculated the average brood weight produced by each female as the total weight of broods produced during a female's lifespan divided by her total number of broods. Data were checked for normality of distribution and homoscedasticity of variances. Brood number was square root transformed to achieve normality for statistical analyses. Variation in brood number and weight were analysed with ANCOVAs, and female longevity with parametric survival analysis, using the procedures in JMP. All mean values are presented with ± 1 SE.

Results

There was a strong covariance between female body size and horn size (head horn: $r = 0.950$, d.f. = 89, $P < 0.001$; thoracic horn $r = 0.922$, d.f. = 89, $P < 0.001$), and between the sizes of head and thoracic horns ($r = 0.946$, d.f. = 89, $P < 0.001$) (Fig. 1). We used the length of the head horn as our measure of female horn expression in all analyses.

An ANCOVA with body size and dung availability entered as main effects explained a significant proportion of the variance in lifetime brood production (whole model: $F_{3,86} = 5.02$, $P = 0.003$). Thorax width was a significant predictor of lifetime fecundity, with large females producing more broods than small females ($F_{1,86} = 10.87$, $P = 0.001$). The effect of dung availability was not significant ($F_{1,86} = 1.91$, $P = 0.171$). Although not statistically significant ($F_{1,86} = 1.82$, $P = 0.181$), the probability associated with the interaction effect between dung availability and horn length was small enough that it could not be removed from the model (Hendrix *et al.*, 1982). There was a tendency for large females to be constrained in their brood production when dung availability was reduced (Fig. 2). Using absolute horn length in the model instead of thorax width returned qualitatively similar results (whole model: $F_{3,86} = 4.91$, $P = 0.003$). Because of the strong colinearity between body size and horn size, both variables could not be entered into a single model. We thus calculated residual

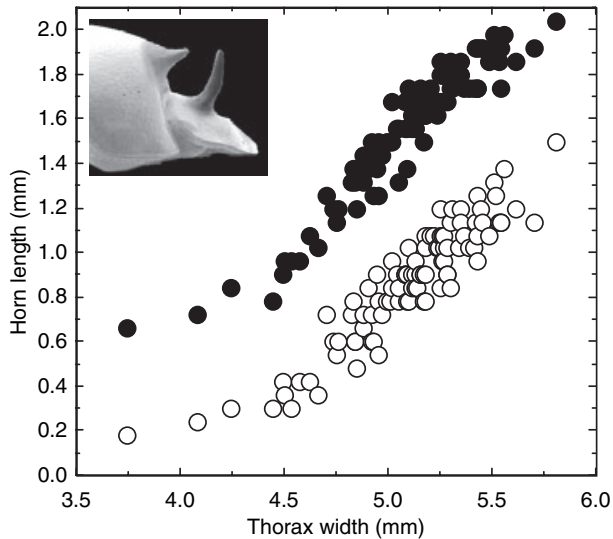


Fig. 1 Scaling relationship between body size (thorax width) and the length of the head (solid symbols) and thoracic (open symbols) horns in female *Onthophagus sagittarius*.

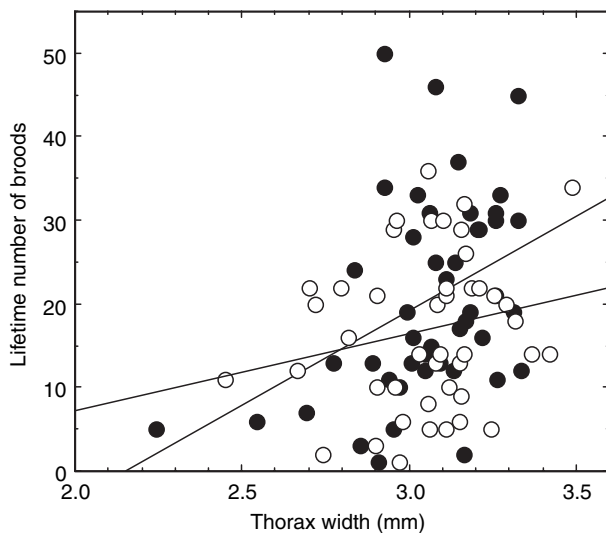


Fig. 2 The relationship between thorax width and lifetime number of broods produced by female *Onthophagus sagittarius* provided with 25 mL (open symbols) or 50 mL (closed symbols) of dung per week.

horn size from the relationship between body size and horn size, and residual fecundity from the relationship between lifetime brood production and body size, to see how relative horn length influenced relative fecundity. The model was not significant ($F_{3,86} = 1.39$, $P = 0.251$), indicating that individuals with relatively large horns for their body size were no less fecund than were individuals with relatively small horns.

Body size and dung availability also explained a significant proportion of the variance in the weight of

broods produced by females (whole model: $F_{3,86} = 8.27$, $P < 0.001$). Larger females produced heavier broods ($F_{1,87} = 16.71$, $P < 0.001$), and females produced heavier broods when provided with greater supplies of dung ($F_{1,87} = 7.12$, $P = 0.009$) (Fig. 3). The interaction between thorax width and dung availability was non-significant ($P > 0.3$), and was removed from the model. Again, entering absolute horn length rather than thorax width into the model yielded qualitatively similar results (whole model: $F_{3,86} = 8.30$, $P < 0.001$). Using residual brood weight and residual horn length in our analysis returned the same effect of diet availability ($F_{1,87} = 6.51$, $P = 0.012$) and no significant effect of residual horn length ($F_{1,87} = 0.37$, $P = 0.542$) on residual brood weight. The interaction term was nonsignificant and removed from the model ($P > 0.3$).

Survival analysis revealed a significant effect of dung availability ($\chi^2_1 = 7.95$, $P = 0.005$) and thorax width ($\chi^2_1 = 5.72$, $P = 0.017$) on female lifespan. The interaction between dung availability and thorax width was not significant ($\chi^2_1 = 0.76$, $P = 0.382$). Females provided with 50 mL of dung per week died earlier than females provided with 25 mL of dung per week (Fig. 4), and large females died earlier than small females (Fig. 5). Again using absolute horn length instead of thorax width yielded qualitatively similar results (dung availability: $\chi^2_1 = 8.40$, $P = 0.004$; horn length: $\chi^2_1 = 4.61$, $P = 0.032$). To estimate the effect of horn length on lifespan, independent of the covariation of both horn length and lifespan with body size, we calculated residual lifespan from a regression of body size on lifespan, and used this relative measure in an ANCOVA. Dung availability had a significant effect on relative lifespan ($F_{1,87} = 10.12$,

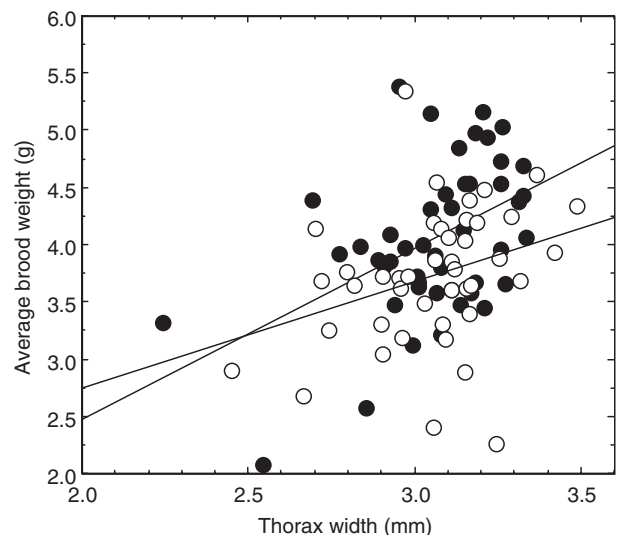


Fig. 3 The relationship between thorax width and the weight of broods produced by female *Onthophagus sagittarius* provided with 25 mL (open symbols) or 50 mL (closed symbols) of dung per week.

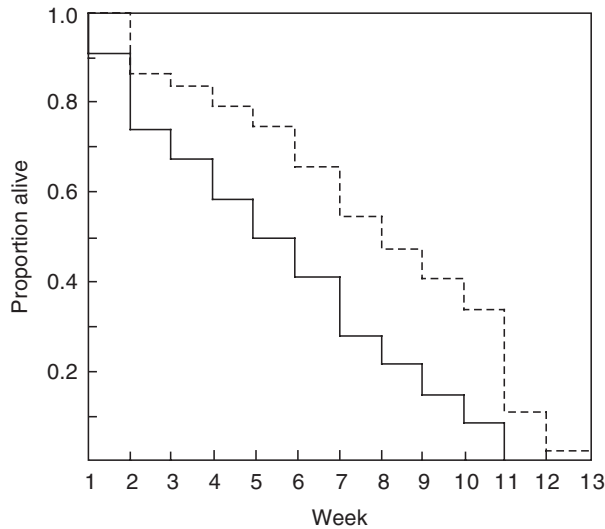


Fig. 4 Survival curves for female *Onthophagus sagittarius* provided with 25 mL (broken line) or 50 mL (solid line) of dung per week.

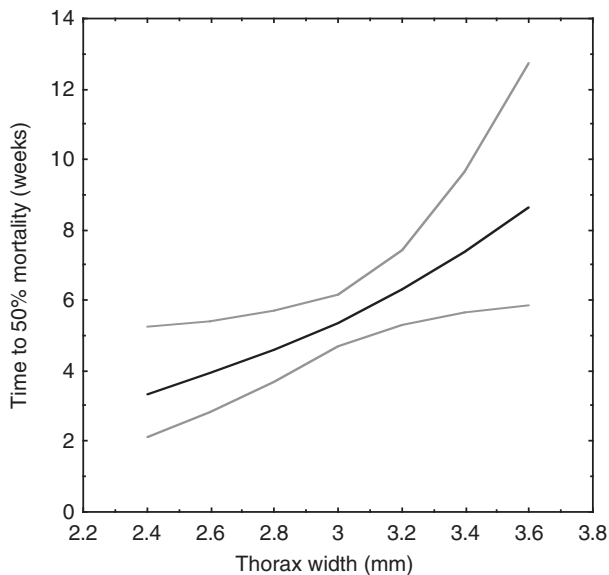


Fig. 5 The relationship between thorax width and the estimated time ($\pm 95\%$ confidence bands) to 50% female mortality.

$P = 0.002$), as shown previously in our survival analysis, but residual horn length did not ($F_{1,87} = 0.43$, $P = 0.513$). The interaction term was nonsignificant ($P > 0.3$) and removed from the model.

Finally, we explored the effects of dung availability and body size on lifetime fecundity independent of variation in female lifespan, by repeating our analysis of the data in Fig. 2 using lifespan as a covariate. After controlling for a significant effect of lifespan on the lifetime number of

broods females produced ($F_{1,85} = 99.06$, $P < 0.001$), there was a significant effect of dung availability ($F_{1,85} = 27.41$, $P < 0.001$) and thorax width ($F_{1,85} = 6.85$, $P = 0.011$). Moreover, the interaction between thorax width and dung availability noted in our previous analysis became significant ($F_{1,85} = 6.19$, $P = 0.015$); large females were constrained in their fecundity by low dung availability to a greater extent than small females, perhaps because of the greater amount of dung they provided to each brood (Fig. 3). All other interaction terms were nonsignificant ($P > 0.30$) and removed from the model. Qualitatively similar results were obtained when using absolute horn length instead of thorax width in the analysis, and reanalysis using relative measures of horn length, lifespan and fecundity that controlled for covariation of these variables with body size returned significant effects of relative lifespan ($F_{1,86} = 92.03$, $P < 0.001$) and dung availability ($F_{1,86} = 24.46$, $P < 0.001$), but no effect of relative horn length ($F_{1,86} = 0.37$, $P = 0.544$), and no interaction effects.

The analyses show that body size and absolute horn size predict lifetime female fecundity equally well. The allometric slopes of log body size on log brood numbers and log body size on log horn length did not differ significantly [b (95% CI): horn = 3.17 (2.95, 3.39); fecundity = 3.68 (1.43, 5.93)] indicating equal rates of increase in absolute horn expression and numbers of offspring with increasing female body size.

Discussion

Our data show that body size in *O. sagittarius* is a reliable predictor of maternal quality. Large females produced more offspring, invested more maternal care into each offspring, and had a greater lifespan than did small females. Furthermore, our data provide evidence of a longevity cost of reproduction for female *O. sagittarius*. The effects we observed were independent of male contributions to brood provisioning and/or contest competition over resources between females, both of which were eliminated in our experimental design. Absolute horn size was an accurate indicator of body size, and thus of maternal quality, and there was no evidence for a fecundity cost associated with the development of relatively long horns.

Longevity costs of reproduction are well documented, and can arise from mating (Chapman *et al.*, 1995; Blanckenhorn *et al.*, 2002), egg production (Partridge *et al.*, 1987) and maternal care (Visser & Lessells, 2001). Here, we found that females provided with a larger supply of dung produced a greater number of broods and provisioned each brood with more dung than females with smaller dung supplies. The increased reproductive investment of these females was associated with a reduced longevity. The longevity cost of reproduction we have observed in *O. sagittarius* most probably represents a cost of maternal provisioning. Previous studies

have shown that mating does not incur a longevity cost for female *O. binodis* (Kotiaho & Simmons, 2003), and paternal assistance during brood provisioning ameliorates the longevity cost of reproduction for female *O. taurus* (Hunt *et al.*, 2002). Although we found that large females had a greater lifespan than small females, the cost of reproduction was not dependent on body size. If it were, we would have expected significant interactions between dung availability and female size effects, which was not the case. Neither did we find an effect of relative horn length on female longevity. Thus, females that invest more in horn growth do not suffer a greater cost of reproduction.

Larger females had a higher lifetime fecundity, even after controlling for their longer lifespan, and they provided more dung per brood than did smaller females. Positive effects of female size on fecundity and brood provisioning appear widespread among studies of *Onthophagus* (e.g. Lee & Peng, 1981; Cook, 1988; Hunt & Simmons, 2000, 2002a; Hunt *et al.*, 2002). In their behavioural studies of *O. taurus*, Hunt & Simmons (2002a) found that larger females were more efficient at provisioning, requiring fewer trips to collect dung, even though they produced larger broods. The size of an adult offspring is largely dependent upon the size of the brood mass provided by its parents, and offspring size is in turn a phenotypic correlate of reproductive success of males (Emlen, 1997; Moczek & Emlen, 2000; Hunt & Simmons, 2001) as well as females. Thus, female size in *Onthophagus* seems generally to be a strong predictor of maternal fitness, due to maternal environmental and indirect genetic effects (Hunt & Simmons, 2002b).

The allometric slopes of fecundity and horn length suggest an equal rate of increase in offspring production and absolute horn expression with increasing female body size. Females that invested in relatively long or short horns for their body size did not differ in fecundity, or in the weight of broods they produced. These data indicate therefore that both body size and absolute horn length in *O. sagittarius* are accurate indicators of maternal quality. Positive correlations between sexual trait expression and fecundity have been found in other taxa in which females develop secondary sexual traits (Kraaijeveld *et al.*, 2007). For example, in the dance fly *Rhamphomyia tarsata*, females have an equal rate of increase in fecundity and in the length of pinnate scales with increasing body size (LeBas *et al.*, 2003), and in blue tits, *Cyanistes caeruleus*, female colouration is positively associated with aspects of female reproductive success (Doutrelant *et al.*, 2008). In fowl, *G. gallus*, QTL associated with female comb size are in significant linkage disequilibrium with QTL associated with female reproductive investment (Wright *et al.*, 2008).

These findings run counter to Fitzpatrick *et al.* (1995) who argued that fecundity costs of ornamentation should limit the expression of sexually selected traits in females. Our data suggest that there are no fecundity costs associ-

ated with sexual trait expression in *O. sagittarius*. Females allocate resources to horn growth during larval development (Emlen *et al.*, 2006), and resources to reproduction when adult. The separation of bouts of resource allocation between these life-history stages may provide an escape from allocation trade-offs that might otherwise limit the evolution of female ornamentation (Fitzpatrick *et al.*, 1995). Alternatively, phenotypic studies may be insufficient to reveal hidden costs of horn investment. For example, in *Onthophagus nigriventris*, ablation of the proliferating cells that would have given rise to male thoracic horns resulted in these males emerging with a larger body size. It could be that female *O. sagittarius* have the potential to grow larger if they did not allocate larval resources to horn growth, and thereby have the potential for even higher lifetime fecundity. If true, for horns to be maintained we should expect benefits associated with investment into horns to outweigh any costs associated with emerging as a smaller adult.

Horn length exhibited strong positive allometry, a pattern that is predicted to evolve only if the combined effect of sexual and viability selection on trait size and body size results in a greater relative advantage of increased trait size in larger individuals (Bonduriansky & Day, 2003). Secondary sexual traits are often characterized by positive allometry, a pattern that has been linked to honest signalling of competitive ability and/or mate quality (Alatalo *et al.*, 1988; Simmons & Tomkins, 1996; Bonduriansky & Day, 2003). The functional significance of female horns in *O. sagittarius* is currently unknown. It may be that horns act as weapons used in female contest competition over access to limited supplies of dung. Female *O. taurus*, for example, have been shown to steal brood made by conspecifics for their own offspring, with brood parasitism rates under laboratory conditions in the region of 12% (Moczek & Cochrane, 2006). Female *O. sagittarius* have also been observed stealing dung from adjacent tunnels, with horns being used in fights between rival females over these buried brood provisions (J. Marangelo, personal communication). Although the effects of horns in these encounters have yet to be investigated directly, these preliminary observations of behaviour suggest that if female *O. sagittarius* likewise steal dung from conspecifics, a female's investment in horns may contribute to her competitive success over access to partially built or completed brood masses, and her ability to defend against conspecific brood parasitism. The contribution of horn length to male competitive success is well documented in onthophagines, with horn length having a relatively greater contribution to male competitive ability than body size (Emlen, 1997; Moczek & Emlen, 2000).

Female horns might also be subject to selection via male mate choice. Female fecundity is often the focus of selection from male mate choice in insects (Bonduriansky, 2001), and the absolute size of horns of female *O. sagittarius* offer an accurate indication to males of female lifespan,

investment in maternal care and fecundity. Theory suggests that male mate choice can evolve when males target traits that indicate high fertility and viability (Servodio & Lande, 2006). Thus, male *O. sagittarius* have the potential to obtain fitness benefits from choosing females with long horns. At the same time, females could benefit from honestly signalling their quality by attracting males offering high levels of parental assistance. Paternal provisioning is widespread among onthophagines, and male care reduces the cost of reproduction for females while enhancing offspring fitness (Hunt & Simmons, 2000; Hunt *et al.*, 2002). Our data show that males could gain information on maternal quality from body size alone. Nevertheless, the positive allometry of horn expression means that small increments in female body size are associated with relatively large increments in horn length, so that horns may serve as amplifiers of body size cues to female quality (Hasson, 1990; Taylor *et al.*, 2000).

Finally, given that females do not appear to suffer a fecundity cost associated with horn expression, female horns might be free to evolve as a correlated response to selection on male horns. This seems unlikely to be the case in *O. sagittarius*, however, for two reasons. First, the origin of female horn expression represents an evolutionary event independent of the origin of horns in males (Emlen *et al.*, 2005a, b). Second, the horns of female *O. sagittarius* are qualitatively and quantitatively different structures from the horns of males (Emlen, 2001), making correlated evolution unlikely.

In conclusion, we found no evidence of a fecundity cost associated with female investment in secondary sexual traits. Rather, body size was positively correlated with both absolute horn length and maternal fitness. Both female contest competition and male mate choice were excluded in our experimental protocol, so that any fitness benefits associated with female investment in horns are likely to be additional to the body size effects reported here. Future studies will examine the role of female contest competition and male mate choice in determining female fitness, and thus the selection pressures operating on female sexual traits in this species.

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