

Sperm competition games played by dimorphic male beetles

L. W. Simmons*, J. L. Tomkins and J. Hunt

Department of Zoology, The University of Western Australia, Nedlands, WA 6907, Australia

Reproductive strategies often consist of two alternative tactics whereby males either compete for and guard females, or sneak copulations. By their nature, alternative tactics expose males to differing risks of sperm competition; sneaks will always be subject to sperm competition but guards will be subject to sperm competition with low probability, dependent on the number of sneaks. Recent game-theoretical models predict that males in the sneak role should have the greater gametic expenditure but that the disparity in expenditure should decrease with increasing numbers of sneaks. Male dung beetles in the genus *Onthophagus* can be separated into two morphs: major males have horns and guard females whereas minor males are hornless and sneak copulations. Here we compare testis size and ejaculate characteristics between these alternative morphs. We find that in *O. binodis* 30% of males are sneaks, and sneaks have larger testes, ejaculate volumes, and longer sperm than guards. In *O. taurus* 60% of males are sneaks and there are no differences in gametic traits. Our data thus provide empirical support for game-theoretical models of sperm competition.

Keywords: alternative mating tactics; dung beetles; male dimorphism; sperm competition

1. INTRODUCTION

Sperm competition occurs when the sperm of two or more males are present within the reproductive tract of a single female, so that there is competition among them for the fertilization of ova (Parker 1970). Sperm competition is widely recognized as a pervasive force in evolution (Smith 1984; Birkhead & Møller 1998). Recent game-theoretical analyses (for a review, see Parker 1998) have provided a theoretical framework within which to assess the evolutionary consequences of sperm competition for male gametic expenditure. Parker's sperm-competition games are based on the assumption that, because sperm are costly to produce (Dewsbury 1982; Olsson *et al.* 1997; Prowse & Partridge 1997), there should be a trade-off between expenditure on the ejaculate and expenditure on other reproductive activities. The best ejaculation strategy to adopt should depend critically on the strategies played by other males and the information currently available to the competitor. The evolutionarily stable strategy (ESS) should be resistant to invasion by any player that adopts a different strategy (Maynard Smith 1982).

Sperm-competition game theory predicts that, across species, male expenditure on the ejaculate should increase with sperm-competition risk (the probability that a female will mate with another male), a prediction supported by comparative studies of testis mass from a diverse array of taxa (reviewed in Parker *et al.* 1997). Within-species predictions are more complex, because the response to sperm-competition risk depends critically on whether males occupy 'roles' (cf. the timing and/or sequence of mating events). Only when roles are non-random should males in

the disfavoured role increase their expenditure on the ejaculate (Parker 1990a). One situation in which roles will be non-random occurs when males adopt alternative mating tactics (Gross 1996). Often, males who are unsuccessful in competition for mating opportunities exercise an alternative tactic of sneaking copulations with females when guarding males are occupied in disputes with other males. By the nature of their mating tactic, sneaking males are always subject to sperm competition. Guarding males, however, will be subject to sperm competition only with low probability, dependent on the relative frequency of sneaks and guards within the population. Parker's (1990b) sperm-competition game models for sneaks and guards predict that the male in the sneak role should have the greater ejaculate expenditure, but that the differential between sneak and guard should decline with increasing sperm-competition risk to the guarding males (see also Gage *et al.* 1995).

Male dung beetles in the genus *Onthophagus* often exhibit dimorphic male morphology: some males produce horns (major males) whereas others remain hornless (minor males), appearing morphologically similar to females (Emlen 1994, 1996; Hunt & Simmons 1997). Dimorphisms in body plan are associated with alternative mate-securing tactics (Cook 1990; Emlen 1997). Males and females arrive at fresh dung, where they feed and reproduce. Horned majors monopolize females by guarding the entrances to tunnels beneath the dung in which the male and his female provision brood masses. Hornless minors sneak into breeding tunnels and copulate with guarded females. A male's morphology appears to be largely determined by the amount of dung provided in the brood mass by its parents (Emlen 1994; Hunt & Simmons 1997) so that the alternative tactics

*Author for correspondence (lsimmons@cyllene.uwa.edu.au).

represent a conditional reproductive strategy (Gross 1996).

Here we compare the patterns of ejaculate expenditure by alternative morphs of two species of dung beetle, *O. taurus* and *O. binodis*. Sperm-competition games assume that the sperm from different males compete numerically, so that a male's fertilization success is dependent on the size of his ejaculate relative to that of other males. Thus, investment in sperm competition should be reflected in the mass of tissue devoted to sperm production, the sizes of ejaculates transferred to females, and possibly in the morphology of individual sperm (Parker 1993; Parker & Begon 1993).

2. METHODS

Beetles were attracted to traps baited with fresh dung at two sites in the south of Western Australia: *O. taurus* were collected from Margaret River and *O. binodis* from Narikup. The sexes were separated and held for one week with constant access to fresh dung; the pre-experimental feeding period was established to minimize potential differences between males in their recent mating history.

The pronotum width of males was determined as a linear measure of body size, and the length of the head horns (*O. taurus*) and pronotal horn (*O. binodis*) was measured. We used the models of Eberhard & Gutierrez (1991) to obtain an objective estimate of the critical body size (the switch point) that separates minor and major morphs (for a detailed outline of the use of these models and the meaning of coefficients given below, see also Tomkins & Simmons (1996) and Hunt & Simmons (1998a)). Both species showed nonlinearity in the relation between pronotum width and horn length (*O. taurus*: $\beta_2 = 26.69 \pm 3.32$, $t = 8.05$, 470 d.f., $p = 0.0001$; *O. binodis*: $\beta_2 = -4.48 \pm 1.42$, $t = 3.16$, 219 d.f., $p = 0.002$) (see figure 1). For *O. taurus*, the switch point explaining the greatest proportion of variance ($r^2 = 0.768$) occurred at a pronotum width of 5.10 mm; the dimorphism is characterized by a change in linear slope ($\beta_2 = 3.76 \pm 0.23$, $t = 16.67$, 470 d.f., $p = 0.0001$) and a discontinuous distribution of horn lengths ($\beta_3 = 0.505 \pm 0.076$, $t = 6.65$, 469 d.f., $p = 0.0001$). For *O. binodis*, the switch point explaining the greatest proportion of variance ($r^2 = 0.908$) occurred at a pronotum width of 5.77 mm; the dimorphism is characterized by a change in linear slope ($\beta_2 = 0.55 \pm 0.07$, $t = 7.45$, 219 d.f., $p = 0.0001$) and a continuous distribution of horn lengths ($\beta_3 = -0.03 \pm 0.04$, $t = 0.74$, 218 d.f., $p = 0.459$). Thus, all males smaller than the switch point were recognized as minor morphs and all males larger than the switch point as major morphs. The relative frequency of minors in the populations of *O. taurus* and *O. binodis* used in this study were 272:201 and 130:277, respectively ($\chi^2 = 57.62$, 1 d.f., $p = 0.0000$).

A sample of males were weighed to the nearest 0.01 mg. They were then dissected and their testes removed and weighed. We minimized variance in body mass that may arise owing to differences in food and/or water intake by first washing the beetles thoroughly and then holding them in a clean dry container for 48 h before weighing. The gut was devoid of dung at the time of dissection.

To obtain estimates of ejaculate volume, males and females were paired in artificial tunnels (6 cm in length and 1 cm in diameter) cast into plaster-of-Paris blocks. Tunnels were smeared with fresh dung before introducing a single male and female. The pair were left for 1.5 h before they were separated. The

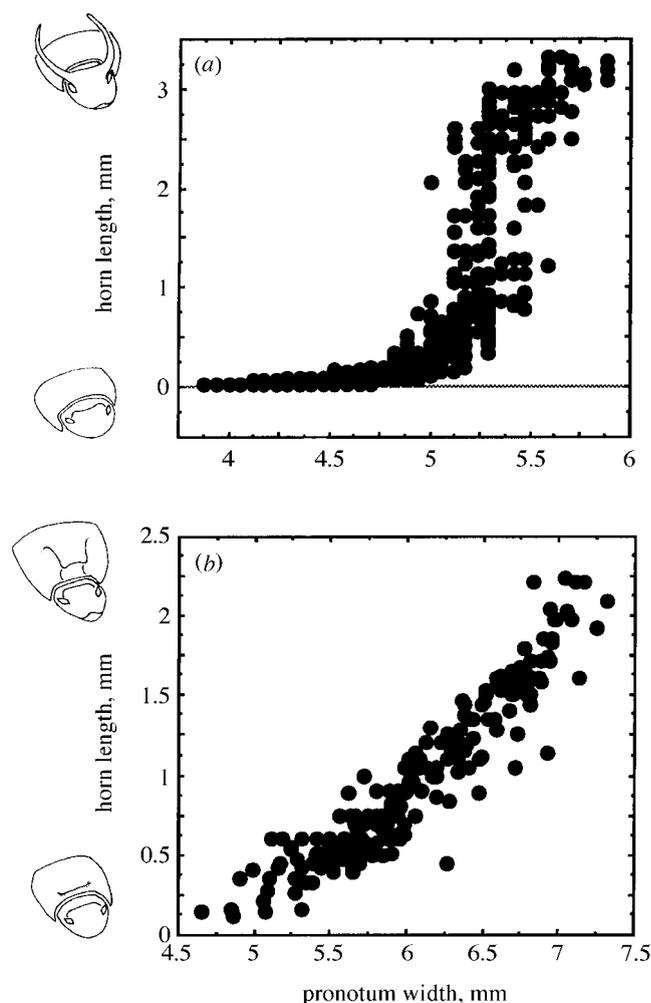


Figure 1. The distribution of horn length on pronotum width for (a) *O. taurus* and (b) *O. binodis*. Representative illustrations of major and minor males are shown at the extremes of the horn-length axes.

male was provided with a second female and left for a further 1.5 h. Females were dissected immediately and checked for the presence of an ejaculate in the bursa copulatrix. Sperm are transferred embedded in a spermatophore matrix from which they migrate to the females' spermatheca once liberated. We estimated ejaculate volume from linear measures of the height (h) and diameter (d) of the spermatophore. The spermatophore is ovoid in shape and we calculated its volume as $\frac{4}{3}\pi(d/2)^2(h/2)$. Although free sperm can be obtained from the spermatheca, the number of sperm stored may reflect female influences rather than male tactics. Sperm could not be counted accurately because they could not be evenly dispersed after removal from the spermatophore matrix. Thus, the estimate of ejaculate volume was the most reliable measure of male tactics available. We estimated the accuracy of our sperm-volume estimates by measuring the height and diameter of ten individual spermatophores, on five occasions. Each within-subject repeated measurement was separated by nine between-subject measurements. The repeatability of our measurements was high, with significantly greater variance between subjects than within subjects ($F_{9,40} = 277.75$, $p = 0.0001$) and a reliability estimate of 0.996.

After measurement, the spermatophore matrix was dissected from the bursa copulatrix and teased apart in 20 μ l of particle-free water on a clean dry microscope slide. The mixture was

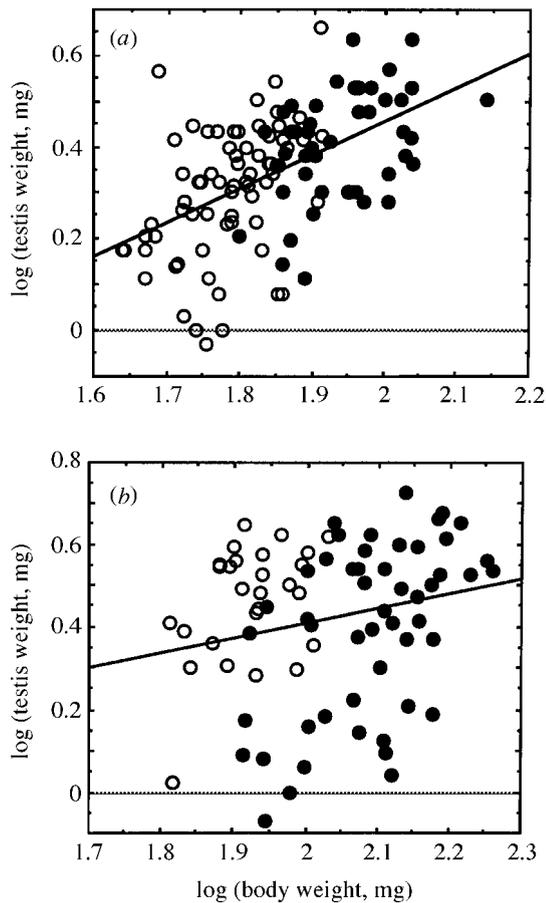


Figure 2. The allometric relation between testis mass and body mass for (a) *O. taurus* ($b=0.74 \pm 0.11$, $F_{1,111}=42.16$, $p=0.0001$) and (b) *O. binodis* ($b=0.36 \pm 0.19$, $F_{1,76}=3.59$, $p=0.062$). Minor morphs are represented by open symbols and major morphs by filled symbols.

smear across the slide and air-dried. The procedure provided enough free sperm to determine sperm length. We measured the length of eight sperm from a single ejaculate of each male, with the measurement explorer function of the Optimas Image Analysis package. Sperm were viewed at $\times 100$ under light field. Sperm were selected at random for measurement, subject to the condition that they showed no signs of damage. We assessed the accuracy of the image-analysis software by performing five repeated measurements of 20 individual sperm. The variance in length between sperm was significantly greater than the measurement error ($F_{19,80}=115.68$, $p<0.0001$; reliability estimate 0.991). The maximum difference between any two measurements of the same sperm was on average $1.5 \pm 0.1\%$ of mean sperm length.

Whenever data could not be normalized by transformation, appropriate non-parametric statistics were used. All means are presented ± 1 s.e.

3. RESULTS

(a) Testis mass

The allometry of testis mass differed between the species studied. For *O. taurus*, there was a negative allometric relation between testis mass and body mass (figure 2a); testis mass increased with body mass with an allometric slope of less than 1.0 ($b=0.737 \pm 0.114$, $t=2.307$,

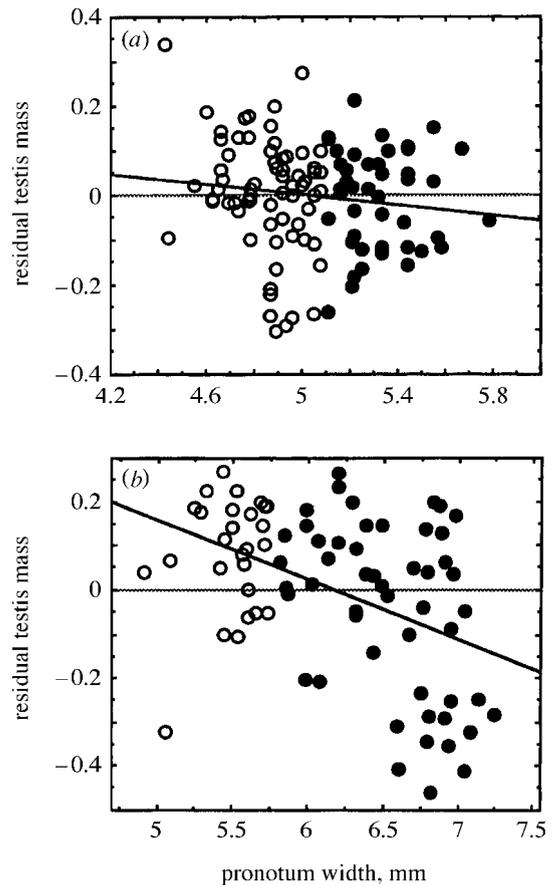


Figure 3. Values of residual testis mass taken from the allometric relation between testis mass and body mass in figure 2, plotted against male body size for (a) *O. taurus* ($r_s=-0.118$, $n=113$, $p=0.212$), and (b) *O. binodis* ($r_s=-0.412$, $n=78$, $p=0.0003$). Minor morphs are represented by open symbols and major morphs by filled symbols.

$p=0.023$). In contrast, there was no relation between testis mass and body mass in *O. binodis* (figure 2b). To control for allometry, we took the residual testis masses from the regressions shown in figure 2. There was no difference in mean residual testis mass between minor and major morphs of *O. taurus* (minors 0.01 ± 0.02 , majors -0.01 ± 0.02 , $t=0.481$, $p=0.632$) but minor male *O. binodis* had significantly higher residual testis mass than major males (minors 0.81 ± 0.03 , majors -0.04 ± 0.03 , $t=2.94$, 76 d.f., $p=0.004$; figure 3).

(b) Ejaculate volume

Although there was a general positive relation between body size and ejaculate volume in *O. taurus* (figure 4a), there was no variation attributable to male morph (mean log ejaculate volume: minors -1.31 ± 0.03 , majors -1.30 ± 0.02 , $t=0.24$, 63 d.f., $p=0.810$). A subset of the males in this experiment copulated with a second female. Repeated-measures ANOVA confirmed that there was no significant variance in ejaculate volume across males (between-subject $F_{17,18}=1.912$, $p=0.10$) although ejaculate volume declined with successive matings (within-subject $F_{1,17}=5.86$, $p=0.027$; mean log volume of first ejaculate -1.34 ± 0.03 , second ejaculate -1.50 ± 0.08).

In contrast, minor male *O. binodis* exhibited less variance in ejaculate volume ($F_{67,25}=2.49$, $p=0.007$) and

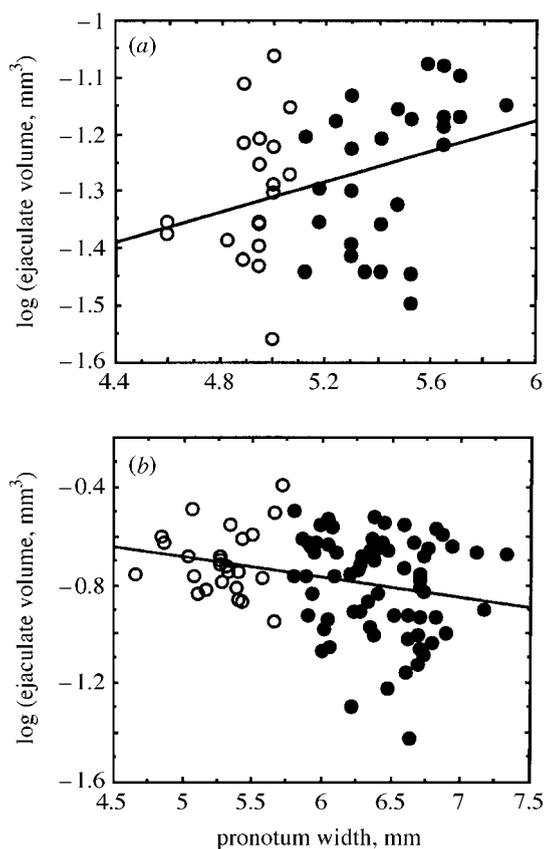


Figure 4. Volume of ejaculate transferred by males plotted against body size for (a) *O. taurus* ($r_s=0.314$, $n=46$, $p=0.035$), and (b) *O. binodis* ($r_s=-0.224$, $n=94$, $p=0.031$). Minor morphs are represented by open symbols and major morphs by filled symbols.

transferred larger ejaculates than major males (mean log ejaculate volume: minors -0.71 ± 0.03 , majors -0.80 ± 0.03 , unequal variance $t=2.738$, 71 d.f., $p=0.008$), generating a negative relation between body size and ejaculate volume (figure 4b). Again, a subset of males copulated with a second female. Repeated-measures ANOVA confirmed the presence of significant variance in ejaculate volume across males (between-subject $F_{36,37}=2.07$, $p=0.015$) and in this case ejaculate volumes were repeatable between matings (within-subject $F_{1,36}=1.03$, $p=0.316$).

(c) Sperm length

Sperm lengths were highly repeatable within male *O. taurus* (within-subject $F_{7,280}=1.52$, $p=0.162$; reliability estimate 0.828) and there was significant variation in sperm lengths between males ($F_{40,287}=5.83$, $p=0.0001$). Minor males were more variable in mean sperm length ($F_{18,21}=3.06$, $p=0.008$) but mean sperm lengths did not differ between morphs (minors 0.982 ± 0.005 mm, majors 0.978 ± 0.003 mm, separate variance estimate $t=0.58$, 29 d.f., $p=0.57$; figure 5a).

Sperm lengths were also highly repeatable within male *O. binodis* (within-subject $F_{7,439}=1.431$, $p=0.191$; reliability estimate 0.943) and there was significant variation in sperm lengths between males (between-subject $F_{54,385}=17.42$, $p=0.0001$). In this case minor morphs were less variable in their mean sperm length ($F_{22,31}=3.03$,

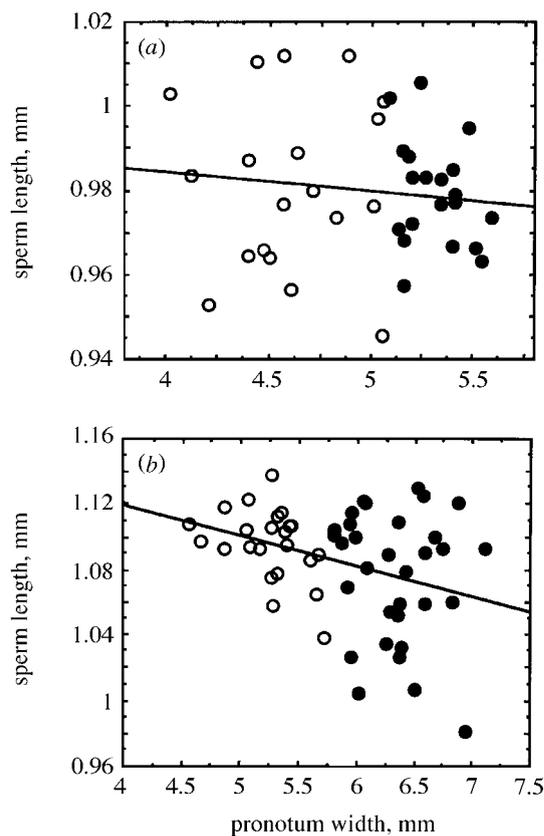


Figure 5. Male-specific mean sperm length plotted against body size for (a) *O. taurus* ($r_s=-0.116$, $n=41$, $p=0.46$), and (b) *O. binodis* ($r_s=-0.289$, $n=55$, $p=0.034$). Minor morphs represented by open symbols and major morphs by filled symbols.

$p=0.002$) and produced significantly longer sperm than did major morphs (minors 1.096 ± 0.005 mm, majors 1.076 ± 0.007 mm, separate variance $t=2.29$, 39 d.f., $p=0.027$); this result generated a negative relation between male size and mean sperm length (figure 5b).

4. DISCUSSION

Parker's game-theoretical models of sperm competition predict that males adopting a sneak tactic should invest more heavily in sperm production because they will always be subject to sperm competition (Parker 1990b). We found differences in the gametic tactics played by major and minor male morphs of *O. binodis* that are consistent with theoretical expectation: despite being smaller in body size, minor males had larger testes, transferred larger ejaculates and had longer sperm than did major males. However, we did not find differences in ejaculation tactics between the morphs of a second species, *O. taurus*.

In an extension of his original models, Parker presented some numerical results that illustrate how relative ejaculation tactics should vary with the frequency of sneaks in the population (Gage *et al.* 1995). Although presented in the context of alternative mating tactics adopted by externally fertilizing salmon, these extensions to the original models are applicable to any species in which sperm competition conforms to a raffle. As the frequency of

sneaks increases in the population, the risk of sperm competition for a guard will increase, so that there will be increased selection on guards to engage in sperm competition. Thus, Parker's numerical results showed that the disparity in expenditure between sneaks and guards should decrease with increasing frequency of sneaks. There was a significant difference in the relative frequencies of the male morphs in *O. taurus* and *O. binodis*: 57% of male *O. taurus* were minors compared with 31% of male *O. binodis*. Thus, risk of sperm competition for major males will be greater in *O. taurus*. Although we currently have data for only two species, the observed disparity in ejaculate expenditure between male morphs varies with sperm-competition risk in the predicted direction.

Intraspecific studies of variation in ejaculate expenditure represent the most rigorous tests of sperm-competition theory because, unlike comparative studies, they do not suffer from the problems of phylogenetic inertia and potentially confounding variables (Harvey & Pagel 1991). Currently, the only other intraspecific examinations of ejaculation strategies associated with alternative mating tactics come from studies of fish. Typically, comparisons have been made between alternative tactics and the gonosomatic index (GSI); sneaks have a higher GSI than do guards (reviewed in Taborsky 1994). We did not adopt this approach because such comparisons are themselves confounded by a lack of consideration of the allometric scaling of body parts (Huxley 1936). Sneaks are nearly always individuals of small body size who cannot compete with their larger conspecifics. It is sometimes the case that organ mass exhibits negative allometry (the slope of log organ mass on log body mass has an exponent less than 1.0; see Reiss 1989). Thus, *a priori* small individuals will be expected to have a larger GSI, irrespective of their mating tactic, when there is negative allometric scaling. It is therefore difficult to determine the extent to which sperm competition has influenced differences in testis size across tactics. Our analysis of onthophagines illustrates the problem. In *O. taurus* testis mass shows negative allometric scaling (figure 2a). If we had calculated the ratio of testis mass to body mass we would have concluded that minors had a greater expenditure in sperm competition, but our analysis of ejaculate characteristics clearly fails to support this conclusion. In contrast, examination of the plot of testis mass against body mass for *O. binodis* shows clearly the predicted response to selection via sperm competition: sneaks have an elevated testis mass so that the allometric slope of testis mass on body mass is shifted toward zero (figure 2b). Such changes in the allometric scaling of testis mass can provide an unbiased estimate of the influence of sperm competition on ejaculation tactics across species. In their comparative study of mammals, Stockley & Purvis (1993) found differences in testis allometry between continuous and seasonal breeders consistent with the notion that alternative ejaculation tactics occurred in species where large males are able to monopolize females and small males must sneak; the relation between testis mass and body mass was weak or absent in continuous breeders. Despite the problems inherent in calculations of GSI, some studies of fish have also shown differences in sperm motility between sneaks and guards (de Fraipont *et al.* 1993; Gage *et al.* 1995; Taborsky 1998) and thus provide

evidence for the theoretical expectation that sneaks should exhibit greater adaptation for sperm competition.

The adaptive significance of ejaculate volume in sperm competition is intuitively obvious: males transferring greater numbers of sperm are likely to father more offspring when sperm competition conforms to a lottery (Simmons 1987) or where sperm are involved in the active displacement of sperm stored from rival males (Simmons & Parker 1992). It is less obvious why selection should favour an increase in sperm length. Nevertheless, comparative studies have shown that sperm length increases with sperm-competition risk (Gage 1994; Briskie *et al.* 1997) and our data provide the first evidence that sperm-competition risk can increase sperm length within species. Parker's theoretical analyses suggest that the fitness gain of increasing sperm length will depend largely on the mechanism of sperm competition involved (Parker 1993; Parker & Begon 1993). In a comparative study of sperm length in birds, Briskie *et al.* (1997) found an evolutionary association between risk of sperm competition and the length of the female's sperm-storage tubules, which were in turn positively associated with sperm length. Similarly, sperm length is positively associated with spermathecal length in beetles of the genus *Bambaria* (Dybas & Dybas 1981). It may be that longer sperm are better able to enter the female's sperm-storage organs (Otronen *et al.* 1997) or that they are better able to resist displacement during copulations with rival males (Dybas & Dybas 1981; Sivinski 1984; Pitnick & Markow 1994; Briskie *et al.* 1997). Currently, the competitive significance of sperm morphometry is largely unknown (Simmons & Siva-Jothy 1998).

Darwin (1871) first noted the remarkable variability in morphology of male onthophagines. Research on this taxon has since revealed a suite of adaptive traits that characterize alternative reproductive tactics: discrete male morphs based on differences in morphology (Emlen 1994; Hunt & Simmons 1998a), competitive mate-searching behaviour (Emlen 1997), courtship (Cook 1990), and patterns of paternal care (Hunt & Simmons 1998b). To this list we now add differences in ejaculate expenditure and sperm morphometry that are consistent with recent game-theoretical models of sperm competition.

This work was funded by grants from NERC and ARC (L.W.S.) and the Royal Society (J.L.T.). We thank Kylie Gaull for assistance with dissections and Cows-R-Us for their continued cooperation.

REFERENCES

- Birkhead, T. R. & Møller, A. P. (eds) 1998 *Sperm competition and sexual selection*. London: Academic Press.
- Briskie, J. V., Montgomerie, R. & Birkhead, T. R. 1997 The evolution of sperm size in birds. *Evolution* **51**, 937–945.
- Cook, D. F. 1990 Differences in courtship, mating and postcopulatory behavior between male morphs of the dung beetle *Onthophagus binodis* Thunberg (Coleoptera: Scarabaeidae). *Anim. Behav.* **40**, 428–436.
- Darwin, C. R. 1871 *The descent of man and selection in relation to sex*. London: John Murray.
- de Fraipont, M., Fitzgerald, G. J. & Gurderley, H. 1993 Age related differences in reproductive tactics in the three-spined stickleback, *Gasterosteus aculeatus*. *Anim. Behav.* **46**, 961–968.

- Dewsbury, D. A. 1982 Ejaculate cost and male choice. *Am. Nat.* **119**, 601–610.
- Dybas, L. K. & Dybas, H. S. 1981 Coadaptation and taxonomic differentiation of sperm and spermathecae in featherwing beetles. *Evolution* **35**, 168–174.
- Eberhard, W. G. & Gutierrez, E. E. 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* **256**, 131–136.
- Emlen, D. J. 1996 Artificial selection on horn length-body size allometry in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Evolution* **50**, 1219–1230.
- Emlen, D. J. 1997 Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behav. Ecol. Sociobiol.* **41**, 335–342.
- Gage, M. J. G. 1994 Associations between body size, mating pattern, testis size and sperm lengths across butterflies. *Proc. R. Soc. Lond. B* **258**, 247–254.
- Gage, M. J. G., Stockley, P. & Parker, G. A. 1995 Effects of alternative male mating strategies on characteristics of sperm production in the Atlantic salmon (*Salmo salar*): theoretical and empirical investigations. *Phil. Trans. R. Soc. Lond. B* **350**, 391–399.
- Gross, M. R. 1996 Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* **11**, 92–98.
- Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford University Press.
- Hunt, J. & Simmons, L. W. 1997 Patterns of fluctuating asymmetry in beetle horns: an experimental examination of the honest signalling hypothesis. *Behav. Ecol. Sociobiol.* **41**, 109–114.
- Hunt, J. & Simmons, L. W. 1998a Patterns of fluctuating asymmetry in beetle horns: no evidence for reliable signalling. *Behav. Ecol.* **9**, 465–470.
- Hunt, J. & Simmons, L. W. 1998b Patterns of parental provisioning covary with male morphology in a horned beetle (*Onthophagus taurus*) (Coleoptera: Scarabaeidae). *Behav. Ecol. Sociobiol.* **42**, 447–451.
- Huxley, J. S. 1936 *Problems of relative growth*. London: Methuen.
- Maynard Smith, J. 1982 *Evolution and the theory of games*. Cambridge University Press.
- Olsson, M., Madson, T. & Shine, R. 1997 Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus*. *Proc. R. Soc. Lond. B* **264**, 455–459.
- Otronen, M., Reguera, P. & Ward, P. I. 1997 Sperm storage in the yellow dung fly *Scatophaga stercoraria*: identifying the sperm of competing males in separate female spermathecae. *Ethology* **103**, 844–854.
- Parker, G. A. 1970 Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* **45**, 525–567.
- Parker, G. A. 1990a Sperm competition games: raffles and roles. *Proc. R. Soc. Lond. B* **242**, 120–126.
- Parker, G. A. 1990b Sperm competition games: sneaks and extra-pair copulations. *Proc. R. Soc. Lond. B* **242**, 127–133.
- Parker, G. A. 1993 Sperm competition games: sperm size and sperm number under adult control. *Proc. R. Soc. Lond. B* **253**, 245–254.
- Parker, G. A. 1998 Sperm competition and the evolution of ejaculates: towards a theory base. In *Sperm competition and sexual selection* (ed. T. R. Birkhead & A. P. Møller), pp. 3–54. London: Academic Press.
- Parker, G. A. & Begon, M. 1993 Sperm competition games: sperm size and number under gametic control. *Proc. R. Soc. Lond. B* **253**, 255–262.
- Parker, G. A., Ball, M. A., Stockley, P. & Gage, M. J. G. 1997 Sperm competition games: a prospective analysis of risk assessment. *Proc. R. Soc. Lond. B* **264**, 1793–1802.
- Pitnick, S. & Markow, T. A. 1994 Male gametic strategies: sperm size, testes size, and the allocation of ejaculate among successive mates by the sperm-limited fly *Drosophila pachea* and its relatives. *Am. Nat.* **143**, 785–819.
- Prowse, N. & Partridge, L. 1997 The effects of reproduction on longevity and fertility in male *Drosophila melanogaster*. *J. Insect Physiol.* **43**, 501–511.
- Reiss, M. J. 1989 *The allometry of growth and reproduction*. Cambridge University Press.
- Simmons, L. W. 1987 Sperm competition as a mechanism of female choice in the field cricket, *Gryllus bimaculatus*. *Behav. Ecol. Sociobiol.* **21**, 197–202.
- Simmons, L. W. & Parker, G. A. 1992 Individual variation in sperm competition success of yellow dung flies, *Scatophaga stercoraria*. *Evolution* **46**, 366–375.
- Simmons, L. W. & Siva-Jothy, M. J. 1998 Sperm competition in insects: mechanisms and the potential for selection. In *Sperm competition and sexual selection* (ed. T. R. Birkhead & A. P. Møller), pp. 341–434. London: Academic Press.
- Sivinski, J. 1984 Sperm in competition. In *Sperm competition and the evolution of animal mating systems* (ed. R. L. Smith), pp. 86–115. London: Academic Press.
- Smith, R. L. (ed.) 1984 *Sperm competition and the evolution of animal mating systems*. London: Academic Press.
- Stockley, P. & Purvis, A. 1993 Sperm competition in mammals: a comparative study of male roles and relative investment in sperm production. *Funct. Ecol.* **7**, 560–570.
- Taborsky, M. 1994 Sneakers, satellites, and helpers: parasitic and co-operative behaviour in fish reproduction. *Adv. Study Behav.* **23**, 1–100.
- Taborsky, M. 1998 Sperm competition in fish: ‘bourgeois’ males and parasitic spawning. *Trends Ecol. Evol.* **13**, 222–227.
- Tomkins, J. L. & Simmons, L. W. 1996 Dimorphisms and fluctuating asymmetry in the forceps of male earwigs. *J. Evol. Biol.* **9**, 753–770.