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Quantitative genetic correlation between trait and preference supports a sexually selected sperm process

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Sperm show patterns of rapid and divergent evolution that are characteristic of sexual selection. Sperm competition has been proposed as an important selective agent in the evolution of sperm morphology. However, several comparative analyses have revealed evolutionary associations between sperm length and female reproductive tract morphology that suggest patterns of male–female coevolution. In the dung beetle *Onthophagus taurus*, males with short sperm have a fertilization advantage that depends on the size of the female's sperm storage organ, the spermatheca; large spermathecae select for short sperm. Sperm length is heritable and is genetically correlated with male condition. Here we report significant additive genetic variation and heritability for spermatheca size and genetic covariance between spermatheca size and sperm length predicted by both the “good-sperm” and “sexy-sperm” models of postcopulatory female preference. Our data thus provide quantitative genetic support for the role of a sexually selected sperm process in the evolutionary divergence of sperm morphology, in much the same manner as precopulatory female preferences drive the evolutionary divergence of male secondary sexual traits.

male–female coevolution | postcopulatory female choice | sperm length

Female mating preferences are widely recognized as being responsible for the rapid and divergent evolution of male secondary sexual traits (1). Indicator or good gene models envisage genetic coupling between male sexual trait expression and offspring fitness, so that females with a preference for male traits produce offspring of greater viability (2). Once a preference becomes established, females choosing males with elaborate secondary sexual traits will produce sons that carry alleles for the trait and daughters that carry alleles for the preference, generating genetic coupling that will drive self-reinforcing coevolution of both trait and preference because of the mating advantage to males with the trait. Thus, the original viability benefits associated with the preference can be undermined by a runaway Fisherian sexy sons process (2). Analogous models have been proposed for postcopulatory female preferences (3). “Good-sperm” models predict positive genetic associations between a male's sperm competitiveness and the general viability of his offspring (4), whereas “sexy-sperm” models predict that multiply mating females produce sons successful in sperm competition and daughters that incite sperm competition through multiple mating (5, 6). As with precopulatory processes, postcopulatory models predict that the trait in males that determines fertilization success will become genetically coupled with the mechanism by which females bias sperm use toward preferred males (7).

Although spermatozoa are well known for their rapid and divergent morphological variation (8, 9), little is known of the selective processes that drive sperm evolution. Patterns of divergent evolution are characteristic of strong sexual selection, and researchers have suggested that postcopulatory sexual se-

lection via sperm competition may be responsible for evolutionary divergence in sperm morphology (10, 11). Thus, among frogs (12), birds (13), and butterflies (14) there are evolutionary associations between the strength of selection acting via sperm competition and sperm length. These patterns, however, are by no means consistent. In fish both positive (15) and negative (16) evolutionary associations have been found, whereas in mammals no evolutionary associations have been found (17). In birds the association between sperm competition and sperm length appears to be indirect, via an effect of sperm competition on the length of sperm storage tubules in the female reproductive tract and evolutionary covariation between sperm storage tubule and sperm lengths (18).

Associations between sperm lengths and the lengths of female reproductive ducts and/or sperm storage organs are well documented in the insects (19–23). These patterns of correlated evolution implicate selection processes imposed by females during the evolution of sperm morphology. Using populations of *Drosophila melanogaster* artificially selected for long or short sperm, Miller and Pitnick (24) showed that males with long sperm had a fertilization advantage over males with short sperm when both were mated to females artificially selected to have long seminal receptacles. The heads of long sperm lie closer to the exit of the seminal receptacle, giving them precedence over short sperm at the time of fertilization (25). Miller and Pitnick (24) also showed that artificial selection for increased seminal receptacle length in females resulted in a correlated response in sperm length, suggesting that seminal receptacle length imposed directional selection on sperm length. Although the selective pressures driving female seminal receptacle evolution are unknown, the data for *D. melanogaster* implicate a sexually selected sperm process in the evolution of sperm gigantism in this group of flies (24).

Here we provide a critical test of the key prediction underlying both good-sperm (4) and sexy-sperm (5) models of postcopulatory sexual selection, that there is a genetic correlation between a sperm trait that contributes to male fertilizations success and the mechanism used by females to select sperm. Previously, we documented patterns of quantitative genetic variation in sperm competition traits in the dung beetle *Onthophagus taurus*. We found significant levels of additive genetic variation in sperm length and the high heritability for this trait that is necessary for a sexually selected sperm process. Moreover, we found significant additive genetic variation in male condition (26) and strong genetic covariance between male condition and sperm length;

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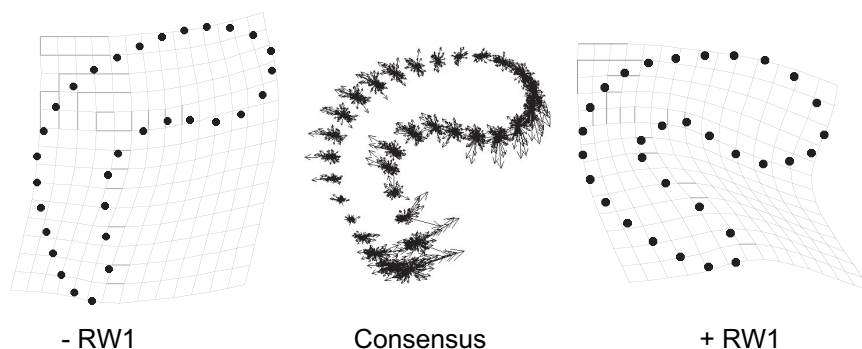


Fig. 2. The consensus shape (Center) from geometric morphometric analysis is shown with partial warps shown as vectors with their origin at the consensus position of each landmark. Thin-plate splines show variation in shape along the first relative warp, with extreme negative scores shown in Left and extreme positive scores shown in Right.

Spermatheca shape has also been shown to influence paternity in *O. taurus*, but independent of sperm length (28). As such we would not expect to find genetic covariance between spermatheca shape and sperm length, an expectation borne out by our quantitative genetic analysis. Previously, sperm competition has been argued to favor increasingly numerous and small sperm and to drive the evolution of anisogamy (32, 33). Our data suggest an additional role for females in the evolutionary reduction in male gamete size, at least in *Onthophagus*.

Before our study, the only other quantitative genetic evidence in favor of a sexually selected sperm process came from studies of *Drosophila*. In contrast to our findings, female *D. melanogaster* with longer seminal receptacles favor males producing longer sperm so that selection drives the evolutionary exaggeration of sperm length (24, 25). Genetic covariances between female morphologies that bias paternity toward males with particular sperm characteristics are likely to underlie the increasing number of comparative analyses that are revealing evolutionary associations between sperm morphology and female reproductive tract morphology (19–23, 34). The contrasting findings for *Onthophagus* and *Drosophila* illustrate how postcopulatory female preferences can generate divergent patterns of evolution across taxa and contribution to the rapid and divergent variation that is characteristic of sperm morphology.

Previously, we found male condition in *O. taurus* to be heritable and genetically correlated with sperm length; males of high condition produce shorter sperm, suggesting that short sperm may be costly to produce (27). Thus, the costs of producing shorter sperm may counter the continued reduction in sperm length imposed by postcopulatory female preferences. Moreover, the condition-dependent nature of sperm length in this species means that females could gain indirect benefits from their selection of short sperm via an indicator process if short-spermed males sire offspring of higher viability. Such a relationship is implicit in the genetic covariances between male condition and both courtship rate and sperm length, traits that contribute to male attractiveness in precopulatory female choice (26) and paternity in postcopulatory choice (28), respectively. In other species, phenotypic studies have revealed correlations between a male's success in sperm competition and life history characteristics of offspring, such as development speed in dung flies (35), fecundity in bulb mites (36), and viability in *Antechinus* (37), that are consistent with an indicator process. However, differential maternal allocation by females after copulations with males found attractive during precopulatory mate choice (38) offers a viable alternative explanation for some of these findings (39). Quantitative genetic approaches such as ours offer greater power for testing models of preference evolution (40), and, if females of these species are exercising postcopulatory preferences, then we expect to see genetic covariance between competitive fertilization success, measures of offspring performance, and the behavior and/or morphology of females that biases paternity (7).

In conclusion, spermatozoa are the most morphologically diverse cells in nature, offering a reliable toolkit for the construction of animal phylogenies (8, 9). It has long been argued that sperm competition plays an important role in the evolution of sperm form and function (10, 11). Our quantitative genetic data provide support for a role of postcopulatory female preferences in driving evolutionary divergence in sperm morphology, in much the same way as precopulatory preferences drive the evolutionary divergence of male secondary sexual traits.

Methods

Breeding Design. We used a standard half-sibling breeding design (41). Beetles were collected from fresh cattle dung from a field in Margaret River, Western Australia. Beetles were maintained in mixed-sex cultures for 1 week before females were established in individual breeding chambers (PVC pipe, 25 cm in length, 6 cm in diameter, three-quarters filled with damp sand topped with 200 ml of cow dung). Chambers were left at 28°C for 1 week and sieved, and brood masses were buried en masse in 6-liter boxes containing moist sand. When adult beetles emerged, females

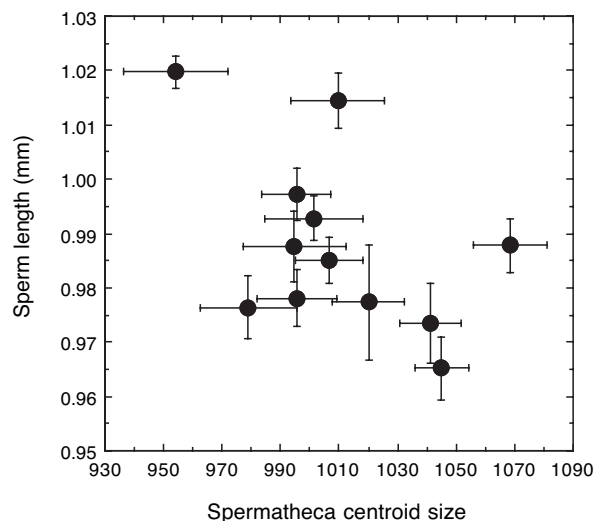


Fig. 3. Plot of the sire family mean (\pm SE) sperm lengths against sire family mean (\pm SE) spermatheca centroid size. The data show a genetic correlation across the sexes for these sperm and sperm storage traits.

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