The genetic basis of traits regulating sperm competition and polyandry: can selection favour the evolution of good- and sexy-sperm?

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Abstract

The good-sperm and sexy-sperm (GS-SS) hypotheses predict that female multiple mating (polyandry) can fuel sexual selection for heritable male traits that promote success in sperm competition. A major prediction generated by these models, therefore, is that polyandry will benefit females indirectly via their sons' enhanced fertilization success. Furthermore, like classic 'good genes' and 'sexy son' models for the evolution of female preferences, GS-SS processes predict a genetic correlation between genes for female mating frequency (analogous to the female preference) and those for traits influencing fertilization success (the sexually selected traits). We examine the premise for these predictions by exploring the genetic basis of traits thought to influence fertilization success and female mating frequency. We also highlight recent debates that stress the possible genetic constraints to evolution of traits influencing fertilization success via GS-SS processes, including sex-linked inheritance, nonadditive effects, interacting parental genotypes, and trade-offs between integrated ejaculate components. Despite these possible constraints, the available data suggest that male traits involved in sperm competition typically exhibit substantial additive genetic variance and rapid evolutionary responses to selection. Nevertheless, the limited data on the genetic variation in female mating frequency implicate strong genetic maternal effects, including X-linkage, which is inconsistent with GS-SS processes. Although the relative paucity of studies on the genetic basis of polyandry does not allow us to draw firm conclusions about the evolutionary origins of this trait, the emerging pattern of sex linkage in genes for polyandry is more consistent with an evolutionary history of antagonistic selection over mating frequency. We advocate further development of GS-SS theory to take account of the complex evolutionary dynamics imposed by sexual conflict over mating frequency.

General introduction

Polyandry, where females mate with two or more males within a single reproductive episode, is taxonomically widespread (Jennions & Petrie 2000; Simmons 2005) and has important evolutionary implications because of its potential to generate postmating sexual selection for traits that influence fertilization success (Birkhead & Pizzari 2002). Polyandry can fuel sexual selection via sperm competition, where ejaculates from different males compete to fertilize a female's eggs (Parker 1970), cryptic female choice, where females mediate the outcome of this competition (Eberhard 1996; Thornhill 1983), and sexual conflict, where differences in male and female interests over fertilization events generates antagonistic coevolution (Arnqvist & Rowe 2005; Parker 1979). While numerous studies focus on the potential (genetic) benefits derived by polyandrous females, especially in mating systems where there are no obvious material benefits to be gained from additional matings (see reviews by Jennions & Petrie 2000; Simmons 2005), a number of theoretical papers highlight the potential for polyandry to fuel sexual selection for male fertilizing efficiency (Curtsinger 1991; Keller & Reeve 1995; Yasui 1997). These models reduce to a simple argument: polyandry is expected to fuel selection for male traits that are favoured by sperm competition and/or cryptic female choice. By encouraging sperm competition or exercising cryptic choice, females are therefore expected to produce sons that are successful sperm competitors, or exhibit traits that induce females to differentially use their sperm.

According to the sexy-sperm argument, polyandry is a form of mate choice, in the sense that this behaviour facilitates sperm competition or cryptic female choice which act as filtering mechanisms for males better equipped to gain fertilizations (Curtsinger 1991; Harvey & May 1989; Keller & Reeve 1995; Sivinski 1984). This process will

therefore favour the evolution of any adaptation that influences fertilization success, assuming the indirect benefits of producing sons with enhanced fertilization success outweigh the direct costs of mating multiply. The theoretical basis for this model is therefore similar to that proposed in classic ‘Fisherian’ models for the evolution of (pre) mating female preferences. The main requirements are that traits influencing fertilization success exhibit additive genetic variance due to sires and are genetically correlated (due to positive linkage disequilibrium) with genes for polyandry. One other obvious requirement is that the genetic architecture of the species allows father-to-son heritability of traits that regulate fertilization success. Predictions under the good-sperm model are identical to the sexy-sperm hypothesis with the additional requirement that traits regulating sperm competition will be genetically correlated with heritable variation in viability (Yasui 1997). As such, the good sperm process will benefit polyandrous females both via the enhanced competitive abilities of her male offspring and through the increased viability of both sons and daughters.

Aims and scope of this review

Our aim in this review is to assess the genetic processes by which postmating sexual selection favours adaptations in traits that function during sperm competition. We begin by focussing on traits that can influence competitive fertilization success, including sperm phenotype, testes size and genital morphology. We then review the available studies that examine the genetic basis of these traits and ask whether their genetic architectures are conducive to evolution via good-sperm and sexy-sperm (hereafter referred to as GS-SS) processes. During this process we consider possible genetic constraints on the evolvability of traits that are thought to influence fertilization success. We then briefly review the evidence that phenotypes associated

with fertilization success can exhibit sufficient additive genetic variance for selection via GS-SS processes. Finally, we consider often overlooked but crucial aspects of the GS-SS models: that there is underlying additive genetic variance for female remating behaviour, and that genes for polyandry are genetically correlated with those that influence male fertilization success. We therefore ask whether polyandry can respond to sexual selection according to the predictions generated by the GS-SS models.

Male traits subject to postmating sexual selection

In common with traits subject to intense sexual selection, sperm phenotype, sperm production, and genital morphology can exhibit patterns of rapid evolutionary divergence, and exhibit considerable intraspecific variability in form (Arnaud et al. 2001; Baer et al. 2003; Hosken & Stockley 2004; Joly et al. 2004; Malo et al. 2006; Merilä & Sheldon 1999b; Minoretti & Baur 2006; Morrow & Gage 2001b; Schulte-Hostedde & Millar 2004; Simmons et al. 2003; Ward 1998). Although many authors have attributed this diversity to postmating sexual selection, relatively few studies have explored its adaptive basis in the context of sperm competition. In this section we briefly review the available studies that relate variability in sperm phenotype, sperm production and genital morphology to male reproductive fitness, before considering their potential to respond to sexual selection via GS-SS processes.

Sperm phenotype

Recent studies reveal that both sperm quality (e.g. viability, longevity, motility etc.) and sperm size (aflagellate head size and flagellated sperm length) influence competitive fertilization success (see review by Snook 2005). Among insects, for example, sperm viability (estimated as the proportion of live sperm in an ejaculate)

covaries positively with the intensity of sperm competition (Hunter & Birkhead 2002) and has recently been shown to influence relative paternity in the cricket *Teleogryllus oceanicus* (García-González & Simmons 2005). Further indirect evidence that sperm viability plays a role in mediating sperm competition comes from guppies (*Poecilia reticulata*). Locatello *et al.* (2006) reported that male guppies with relatively high levels of orange pigmentation had higher proportions of viable sperm in their ejaculates (in addition to producing faster swimming sperm; see also Pitcher *et al.* 2007). This link between sperm viability and male sexual ornamentation in guppies may explain why paternity is biased towards highly ornamented males when the number of sperm from competing males is held constant (Evans *et al.* 2003). Other measures of sperm quality, including sperm mobility (ability to penetrate an inert medium), have been implicated in mediating paternity success in chickens (Birkhead *et al.* 1999), while sperm swimming speeds (Gage *et al.* 2004) and the percentage of motile sperm (Linhart *et al.* 2005) are known to regulate competitive fertilization success in externally fertilizing fishes. Among rodents, sperm competition intensity covaries positively with the ability of sperm to become capacitated and undergo the acrosome reaction, both of which are important prerequisites to fertilization (Gomendio *et al.* 2006).

Sperm morphology can also be an important broker of fertilization success. For example, evidence that intraspecific variation in sperm size is associated with male fertilization success is accumulating, although studies relating this trait with either sperm competitiveness (within species) or the risk or intensity of sperm competition (among species) have produced mixed results. For example, Radwan (1996) found that in the bulb mite, *Rhizoglyphus robini*, males producing larger sperm cells (estimated from the area of flagellate cells) sired a higher proportion of offspring

than their rivals producing smaller sperm. Likewise, sperm cell size was positively correlated with paternity success in a nematode (*Caenorhabditis elegans*) (LaMunyon & Ward 1998) and flagellate sperm length in the fruitfly *Drosophila melanogaster* (Miller & Pitnick 2002), although in the fruitfly example female tract morphology and sperm length interact to influence male reproductive success (see Miller & Pitnick 2002; Pattarini et al. 2006). Similarly, the length of nonfertile oligopyrene sperm was positively correlated with paternity success in a freshwater snail (*Viviparus ater*) (Oppliger et al. 2003). Further evidence that selection for increased sperm length is attributable to the level of sperm competition comes from comparative studies spanning a diverse range of taxonomic groups (Baer et al. 2003; Balshine et al. 2001; Byrne et al. 2003; Gage 1994; Gomendio & Roldan 1991; Johnson & Briskie 1999; Morrow & Gage 2000), although these studies differ in the way that levels of sperm competition were assessed, and the way in which phylogenetic similarities among species were controlled. The conclusion that selection imposed by sperm competition favours increased sperm length therefore needs to be interpreted cautiously.

Indeed, the role of sperm size in mediating paternity success is not universal, nor does all of the evidence point to selection for increased sperm size in promoting fertilization success. Several studies have reported no evidence for a role of sperm length in mediating competitive fertilization success (Gage et al. 2004; Morrow & Gage 2001c; Simmons et al. 2003), and some interspecific studies of mammals (Anderson & Dixson 2002; Gage & Freckleton 2003; Harcourt 1991; Hosken 1997) and birds (Briskie & Montgomerie 1992) have failed to uncover a link between the level of sperm competition and species-specific sperm length. Other studies have reported that males with shorter sperm have an advantage in sperm competition, which would be expected if sperm size were traded-off against the number of sperm

produced (Parker 1982). Thus, while Stockley *et al.*'s (1997) comparative study of fishes yielded a negative relationship between relative sperm length and the intensity of sperm competition, but a positive relationship for relative gonad size and the intensity of sperm competition, Gage and Morrow's (2003) intraspecific study of the cricket *Gryllus bimaculatus* showed that males producing both relatively small and numerous sperm were more successful during sperm competition. Similarly, in an experiment involving males pre-screened for sperm length, García-González and Simmons (2007) have recently shown that in the dung beetle *Onthophagus taurus*, paternity is biased towards males with the shortest sperm. However, in this system a trade-off between sperm size and sperm number seems unlikely because sperm production (testes size and ejaculate size) is not negatively associated with sperm length (Simmons & Kotiaho 2002). Interestingly, the advantage in sperm competition enjoyed by short-sperm males reported by García-González and Simmons (2007) in *O. taurus* was contingent on the shape and size of the female's spermatheca (see also Miller & Pitnick 2002; Pattarini et al. 2006). This finding suggests that cryptic female preferences (facilitated by variation in female reproductive tract morphology) will favour males with different sperm characteristics in the same way that pre-mating female preferences favour males with elaborated ornaments. Finally, returning to interspecific analyses, Morrow's (2004) review of the occurrence of aflagellate sperm suggests that the evolutionary loss of sperm flagella may be associated with the evolutionary loss of the selective pressure of sperm competition, and comparative analysis across murine rodents suggests that sperm competition has been important in the evolution of the sperm head, and in particular the shape of the apical hook (Immler et al. 2007). Thus, although the available evidence does not allow us to draw general conclusions regarding the direction of selection acting on sperm length, it

does seem clear that sperm competition imposes a significant selection pressure on sperm structure and function.

Sperm production

Traits that influence ejaculate production (and therefore potentially ejaculate size, sperm quantity, and sperm quality) have also been shown to exhibit considerable intraspecific variation (mammals: Gomendio et al. 1998; Schulte-Hostedde & Millar 2004; Schulte-Hostedde et al. 2003; Stockley et al. 1994) (birds: Merilä & Sheldon 1999b) (fish: Neff et al. 2003) (insects: Blanckenhorn et al. 2004; Gage 1995; Hosken et al. 2003a; Simmons et al. 1999) (frogs: Hettyey & Roberts 2006), although only a handful of studies have investigated the adaptive basis of this variability with respect to competitive fertilization success. In this regard, studies of wild mammals have been instructive. Using microsatellite markers, Holleley et al.(2006) found that 96% of free living female *Antechinus stuartii* produced litters with mixed paternity, and that paternity success was strongly related to both body size and testes size. Likewise, in a natural population of Soay sheep (*Ovis aries*), residual testes size (corrected for body size) was positively associated with male reproductive success during the breeding season (Preston et al. 2003). Similar results were subsequently presented for natural populations of the yellow-pine chipmunk *Tamias amoenus*, where males with relatively large testes had higher annual reproductive success and were in better condition (size corrected body mass) than males with smaller testes (Schulte-Hostedde & Millar 2004). The fact that traits contributing to ejaculate production, such as testis size and/or male reproductive accessory gland sizes, are subject to the selective pressures of sperm competition is borne out by interspecific comparative

analyses across many different taxa (e.g. Gage 1994; Harcourt et al. 1995; Hosken 1997; Pitcher et al. 2005; Ramm et al. 2005).

Genital morphology

There is enormous intra- and interspecific diversity in the size and shape of male genitalia in animals with internal fertilization (for a review of this topic see Hosken & Stockley 2004). Male genitalia can be subject to premating sexual selection, where their structure influences a male's ability to engage a female in copula (e.g. Fairbairn et al. 2003; Langerhans et al. 2005; Preziosi & Fairbairn 2000). However, interspecific studies of insects also support the notion that postcopulatory sexual selection is associated with increased complexity in male genital morphology (Arnqvist 1998). Nevertheless, only a handful of studies have specifically examined the adaptive significance of this variation for male fertilization success. This paucity of information on the role of genital complexity in determining fertilizations success has been partly redressed by recent studies on insects that have related differences in genital shape between competing males to relative paternity success. Among these, the earliest studies to reveal an explicit link between male genital morphology and competitive fertilization success (inferred from paternity outcomes) focused on two species of water strider from the genus *Gerris* (Arnqvist & Danielsson 1999; Danielsson & Askenmo 1999). Subsequent studies on the dung beetle *O. taurus* (House & Simmons 2005b) and the oriental beetle *Anomala orientalis* (Wenninger & Averill 2006) have similarly revealed a link between variation in male genital morphology and paternity success.

Are there genetic constraints on the evolvability of sperm competition traits?

A major assumption of models that invoke indirect benefits to polyandrous females is that sons can inherit from their fathers the traits which promote fertilization success.

At least three factors may complicate this assumption. First, genes that regulate sperm performance may not exhibit a genetic architecture that allows father-to-son heritability. Maternal genetic effects (e.g. sex-linkage) and cytoplasmic genes (e.g. mitochondrial DNA) have been suggested to be important in this regard. Second, the nonadditive and/or non-transitive nature of genes involved in sperm competition may prevent directional selection for improved fertilizing efficiency over successive generations. Third, negative genetic associations (trade-offs) among different ejaculate components may constrain the direction of evolutionary responses to selection.

Maternal and cytoplasmic genetic effects

Good- and sexy-sperm processes rely on father-to-son transmission of genes that code for traits influencing fertilization success. Variance in fertilization success must therefore be attributable to genes inherited from males. A number of recent commentaries have questioned this central premise by asking whether ejaculate traits that function during sperm competition can exhibit a genetic architecture conducive to GS-SS processes (see reviews by Gemmell et al. 2004; Pizzari & Birkhead 2002; Zeh 2004; Zeh & Zeh 2005). These focus on the possible influences of maternal and cytoplasmic genes on sperm structure and function, and emphasise how these processes will constrain the evolution of sperm traits via GS-SS processes.

Two insect studies have reported patterns of inheritance in sperm length consistent with maternal genetic effects due to sex-linkage to the X-chromosome (although neither study could rule out a role for mitochondrial genes in regulating sperm length – see below). In an artificial selection experiment, Morrow and Gage (2001a) reported that selection for increased or decreased sperm length in the cricket *Gryllus bimaculatus* was only successful when the maternal line was incorporated into their selection lines. Ward's (2000) study of sperm length in yellow dung flies, *Scathophaga stercoraria*, revealed non-additive (epistatic) interactions between the X-chromosome and the autosomes, suggesting that both sex-linkage and autosomal effects influence variation in this trait. However, the relevance of this finding for sperm competition is unclear, especially since in dung flies sperm length does not respond to selection imposed by sperm competition (Hosken et al. 2001).

Cytoplasmic (mitochondrial) genetic effects on sperm function (and thus potentially on sperm competitiveness) may similarly constrain the evolution of sperm traits via GS-SS processes (Gemmell et al. 2004; Pizzari & Birkhead 2002; Zeh 2004; Zeh & Zeh 2005). Because mitochondrial DNA (mtDNA) is maternally inherited in most anisogamous species, sperm competitive traits that are determined by mtDNA cannot respond to selection operating on males. Consequently, as in the case of genetic maternal effects (e.g. Birkhead et al. 2005), the adaptive evolution of sperm traits may be constrained by a genetic architecture that does not allow a genetic response through males to postmating selection. The mitochondria are known to play a role in regulating sperm mobility in chickens (Froman & Kirby 2005), and both sperm motility (Moore & Reijo-Pera 2000) and fertility in mammals (Gallon et al. 2006; Nakada et al. 2006). Recently, Dowling *et al.* (2006) reported sizable cytoplasmic (mtDNA) effects on sperm viability in the seed beetle *Callosobruchus*

maculatus, but interestingly no effect of these genes on sperm length, which was influenced by nuclear genes. If sperm viability (rather than sperm length) influences sperm competitiveness in *C. maculatus* (e.g. García-González & Simmons 2005), this finding may indicate that the genetic architecture of sperm viability reduces the potential strength of GS-SS processes acting on this particular trait. Nevertheless, other traits that contribute to fertilization success in this species, such as ejaculate size (Eady 1995), may still be subject to GS-SS processes.

Some of the strongest evidence that maternal genes contribute to fertilization success during sperm competition comes from the domestic fowl *G. gallus domesticus*. In this species, sperm mobility – a trait known to influence fertilization success during controlled artificial fertilization assays (Birkhead et al. 1999) – is under the control of both autosomal genes and maternally-derived genes (Froman et al. 2002), almost certainly mtDNA. The role of mtDNA in regulating sperm performance in domestic fowl was confirmed by Froman and Kirby (2005), who found that sperm mobility depended on sperm oxygen consumption (which is under the control of mitochondria), and that immobile sperm were characterised by aberrant mitochondria. Crucially, Froman and Kirby (2005) showed that mitochondrial function diverged significantly between lines selected for high- and low-mobility sperm, confirming that additive genetic variance (due to maternal genes) in male fertilizing efficacy is sufficient to promote a genetic response to selection (see also Froman et al. 2002). Taken together, these studies on domestic fowl suggest that selection on male fertilization efficiency under GS-SS processes will be confined to that proportion of the genetic variance in sperm mobility that is attributable to autosomal genes. Maternal transmission of genes influencing sperm competitiveness has been offered as one explanation why such high variability in sperm performance

can be maintained in populations despite the expectation of persistent directional selection acting on males for improved fertilization success (Gemmell et al. 2004). However, in domestic fowl autosomal genes contribute twice as much heritable variation (proportion of phenotypic variation due to paternal genes =0.30) in sperm mobility as maternal genetic effects (proportion due to maternal genes =0.15) (Froman et al. 2002).

Nonadditive genetic effects

Models of postmating sexual selection that invoke indirect genetic benefits to females via GS-SS processes necessarily assume that fertilization success itself has an additive genetic basis. Yet only a handful of studies have specifically explored the genetic basis of fertilization success. Among these, studies on *Drosophila melanogaster* suggest that genetic variance for sperm precedence (non-random fertilization success) is mainly non-additive (Hughes 1997; but see below) or depends on interacting parental genotypes (Clark 2002; Clark & Begun 1998; Clark et al. 1999). For example, early studies on this system revealed that genetic variance for sperm precedence, including P_1 (offensive sperm competitive ability) and P_2 (defensive ability), exists among lines of inbred male genotypes (Clark et al. 1995; Hughes 1997). Nevertheless, when outbred genomes were studied, Hughes (1997) found that the influence of male genotype on sperm precedence was due exclusively to dominance rather than additive genetic variance.

While Hughes (1997) studied genetic variance in *D. melanogaster* in a single chromosome (III), Friberg et al. (2005) have recently employed hemiclonal analysis to investigate genetic variance in sperm precedence (P_1 and P_2) across most of the genome. Hemiclonal analysis allows the estimation of the standing (additive) genetic

variance by controlling dominance and maternal effects; each hemiclone is the product of multiple maternal genetic backgrounds crossed with cloned copies of the same male (haploid) genome. Hence, variation among hemiclones must be due to additive genetic effects. Using this technique, Friberg et al. (2005) reported low but statistically significant additive genetic variation in both P_1 and P_2 in their (locally adapted) base population, confirming that these traits were available for selection, albeit with low levels of additive genetic variance.

Work on *D. melanogaster* by Clark and co-workers (Clark & Begun 1998; Clark et al. 1999) has also revealed that male success in sperm competition depends on female genotype, which was held constant in Hughes's (1997) experiments. For example, pairwise tests among six isogenic lines of *D. melanogaster* confirmed that there were genotype-specific interactions in sperm competitiveness (Clark et al. 1999). Similar non-transitive effects in sperm competition have been reported in the seed beetle *C. maculatus* (Wilson et al. 1997) and domestic fowl (Birkhead et al. 2004), and have been implicated in studies of polyandry in marine broadcast spawners (Evans & Marshall 2005; Marshall & Evans 2005).

Despite the nonadditive and non-transitive effects on sperm competition in *D. melanogaster*, Fiumera et al. (2005) have recently identified significant associations between male genes coding for reproductive proteins and both offensive and defensive components of sperm competitive ability (see also Clark et al. 1995). Their study, which focused on fly lines derived from a wild population, demonstrates how natural polymorphisms in male reproductive genes can influence male fitness. Fiumera et al.'s (2005) analysis also revealed evidence that antagonistic pleiotropy operates on a gene affecting P_2 and female refractoriness; males that attained high P_2 scores consequently suffered a fitness cost in terms of their mates' reduced latency to

remate. This potential genetic constraint to directional selection, coupled with genotype-specific interactions in sperm competitiveness, may contribute towards the maintenance of genetic variance in sperm competition phenotypes and explain the occurrence of nonadditive genetic variance for these traits documented by Hughes (1997).

Trade-offs between functional components of the ejaculate

Negative associations (trade-offs) among different ejaculate components may also prevent the evolution of individual features of the ejaculate toward phenotypic values that would confer higher fitness (Moore et al. 2004). Although many sperm competition studies focus on single traits (e.g. sperm length or sperm number), a typical ejaculate comprises multiple traits that function as an integrated unit during fertilization. Negative genetic correlations between these different components may therefore constrain directional sexual selection on any single trait. Moore et al. (2004) have recently explored this idea by partitioning variance in ejaculate and sperm production characters (sperm number, testes mass, sperm ampulla mass, spermatophore mass, and sperm viability) in the cockroach *Nauphoeta cinerea*. Despite reporting significant additive genetic variation attributable for all ejaculate traits except sperm viability, Moore *et al.*'s (2004) analysis revealed significant negative genetic correlations between testes mass and sperm viability, and between sperm number and spermatophore mass, sperm viability, and testes mass. These results therefore suggest that increased sperm production can be constrained by declines in sperm quality, although it is unclear how such trade-offs impact on postcopulatory sexual selection in *N. cinerea*, since the potential for sperm competition is relatively low in this system (Moore et al. 2001). Indeed, in *N. cinerea*

the physical presence of the spermatophore suppresses female remating, and therefore these genetic ‘constraints’ may actually reflect a trade-off between investment in traits that function in the avoidance in sperm competition (e.g. spermatophore size) versus those that influence sperm competitiveness (e.g. sperm numbers and viability) (see Moore et al. 2004). Unfortunately, few quantitative genetic studies have examined multiple ejaculate traits in polyandrous species (but see also Simmons & Kotiaho 2002), although results from artificial selection experiments suggest that selection on one sperm trait generally results in positive correlated responses in fertility-related traits (reviewed by Simmons & Moore 2007).

Fertilization success as an intrinsic male ‘trait’

As emphasised by Simmons and Moore (2007), fertilization success can hardly be regarded as a ‘male trait’ because its phenotype (P_1 or P_2) can be influenced by interactions between parental genotypes (Birkhead et al. 2004; Clark & Begun 1998; Clark et al. 1999; Wilson et al. 1997). Nevertheless, there is increasing evidence to suggest that traits involved in regulating fertilization success can be explained (at least in part) by intrinsic differences among males. This evidence stems from several sources, including (1) quantitative genetic studies that reveal additive genetic variance in traits regulating fertilization success, (2) the responses of these traits to artificial selection, (3) studies that investigate additive genetic variance due to sires and repeatability of fertilization success, and (4) studies revealing condition-dependent nature of traits that contribute to fertilization success.

Additive genetic variance in traits regulating fertilization success

A recent prospective analysis of the available data on the quantitative genetics of sperm phenotypes and sperm production traits such as testis size suggests that an overwhelming array of these traits exhibit substantial additive genetic variation due to autosomal genes, and in some cases Y-linked genes, thus potentially making them available to selection via GS-SS processes (Simmons & Moore 2007). Even where maternal influences on sperm traits have been identified (e.g. Birkhead et al. 2005; Froman et al. 2002; Ward 2000), they are typically smaller in magnitude than additive effects. Additionally, Simmons and Moore's (2007) analysis revealed that traits most closely associated with fitness, such as sperm performance (sperm motility and viability) and reproductive success (competitive fertilization success, conception rate), exhibited the lowest (narrow sense) heritabilities. This pattern of low heritability is typical of fitness traits (Gustafsson 1986) because heritabilities (h^2) are estimated as the ratio of additive genetic variance (V_A) to total phenotypic variation (V_P), which comprises both additive and non-additive (dominance, epistasis, interaction variance) sources of variance, as well as a (typically) large environmental component. The high residual variance in many life-history traits is therefore likely to contribute towards the low h^2 ratios often reported for traits influencing male reproductive fitness (Merilä & Sheldon 1999a; 2000).

Moore *et al.* (2004) reported that in the cockroach *Nauphoeta cinerea*, genetic variance in spermatophore mass, ampulla mass, testes mass and sperm counts was significantly associated with sire effects, although as highlighted above negative genetic correlations between sperm viability and these sperm production traits may constrain their evolution. Simmons and Kotiaho (2002) similarly reported that in the dung beetle *Onthophagus taurus*, sire effects explained significant variance in traits involved in sperm production (testis weight and ejaculate volume). In both species,

additive genetic effects on testis size were high, making sperm production a potential candidate trait for selection imposed through sperm competition in these systems (Moore et al. 2004; Simmons & Kotiaho 2002).

Although male genital morphology has long been argued to be subject to postcopulatory sexual selection through its effects on fertilization success, quantitative genetic studies of male genital traits that contribute to fertilization success are limited to just two species. In the water strider, *G. incognitus* (Arnqvist & Thornhill 1998), and the dung beetle *O. taurus* (House & Simmons 2005a), average narrow-sense heritabilities of genital traits were 0.47 (16 genital traits) and 0.08 (23 genital traits), respectively. Although the heritability of individual genital traits seems low in *O. taurus*, these traits constitute a functionally and genetically integrated unit (see also Werner & Simmons 2007) so that low levels of additive genetic variation in individual traits may provide sufficient variation in multivariate trait space upon which selection can operate (House & Simmons 2005a). Hybridization studies involving two species of fruit fly, *D. simulans* and *D. mauritiana* suggest that additive genetic variation accounts for 11% of the variation in male genital morphology, and the genetic architecture in these species suggests a history of strong directional selection (Zeng et al. 2000).

Responses to selection

Direct evidence that sperm competition selects for larger testes comes from artificial selection experiments in insects. Hosken *et al.* (2001) maintained selected lines of yellow dung flies (*Scathophaga stercoraria*) with different levels of sperm competition (polyandry vs. enforced monandry). They reported significant divergence in testis size and competitive fertilization success over ten generations; males selected

under polyandry evolved larger testes and subsequently out-performed monandrous males during controlled sperm competition experiments. The lack of divergence in sperm length, coupled with the results from sperm competition experiments, indicates that larger testes (rather than longer sperm) are advantageous during sperm competition in this species. Similarly, Pitnick et al. (2001) found that experimentally imposing monogamy on populations of the fruitfly *Drosophila melanogaster* resulted in an evolutionary reduction in testes size and sperm production, but no consistent response in sperm length. Although not designed to investigate selection on testis size imposed by sperm competition, Pitnick and Millar's (2000) study of *D. hydei* found a direct response to bidirectional selection for low and high testes length. In addition to revealing correlated responses to their selection regime on body size, development time and adult maturation time, their analysis also revealed a positive correlated response on sperm length, confirming that to some extent these traits share a common genetic basis (Pitnick & Miller 2000).

Heritability and repeatability of competitive fertilization success

Radwan (1998) reported a significant association between father and son competitive fertilization success, with a narrow sense heritability of 0.28 ± 0.16 (mean $\pm$ s.e.). In the same study, repeatability estimates confirmed that males differed consistently in their competitive fertilization success (Radwan 1998). Subsequent work on this system confirmed that competitive fertilization success did indeed respond to bidirectional artificial selection (Konior et al. 2005) and that a male's genotype predicts the outcome of sperm competition (Konior et al. 2006).

Studies that partition variance in competitive fertilization success following sequential (and replicated) matings between a pair of males and two or more females

provide additional evidence that this trait can be due to the intrinsic competitive properties of particular males (Arnqvist & Danielsson 1999; House & Simmons 2005b; Lewis & Austad 1990; Radwan 1998; Wilson et al. 1997). For example, in their study of red flour beetles (*Tribolium castaneum*), Lewis and Austad (1990) analysed variance in P_2 and found that almost 18% of the total variance in relative paternity was attributable to male-pair identity. However, their analysis also uncovered a significant interaction between female and second-male genotypes (explaining 9.6% of the variance in paternity). Arnqvist and Danielsson (1999) similarly analysed sources of variation in competitive fertilization success in the water strider *Gerris lateralis*, reporting significant repeatability across different females. Studies using repeatability analyses (e.g. see Lessells & Boag 1987) to partition variance in competitive fertilization success have also provided evidence that intrinsic male effects can be important sources of variance in the outcome of sperm competition. For example, in their study of the dung beetle *O. taurus*, House and Simmons (2005b) showed that male effects have consistent and repeatable influences on paternity, irrespective of the genetic background in which sperm compete for fertilization (c.f. Wilson et al. 1997). Similarly, recent work on the guppy *P. reticulata* confirms that relative paternity is consistently biased towards particular males when artificial insemination is used to mate pairs of males (simultaneously) to different unrelated females (J. P. Evans, unpublished data). It should be remembered, however, that repeatability of traits can reflect environmentally induced differences between males in their ability to gain fertilizations, rather than genetic differences.

Condition-dependence in sperm competition traits

If traits mediating the outcome of sperm competition are costly and depend on male condition, the numerous loci that influence condition will also create substantial additive genetic variance in traits regulating competitive fertilization success. This process of ‘genetic capture’ is thought to contribute towards the maintenance of genetic variation in overt sexually selected traits in the face of variance-depleting directional selection (Rowe & Houle 1996; see also Tomkins et al. 2004). Condition dependence may likewise explain the extreme intraspecific phenotypic variability in sperm phenotypes, sperm production, and genital morphology, as well as the high coefficients of additive genetic variance for these traits (see above). To the extent that condition has an additive genetic basis, this mechanism also provides an avenue by which sperm competition can facilitate post-mating selection for paternal good genes (Yasui 1997). Nevertheless, only a handful of studies have tested whether traits involved in sperm competition depend on male condition, and to our knowledge only two studies have explored this subject in a quantitative genetic framework (Arnqvist & Thornhill 1998; Simmons & Kotiaho 2002).

Evidence that variance in sperm production depends on male condition comes mainly from phenotypic correlations linking relative testes mass to body condition (typically size adjusted body mass). For example, testes size is positively associated with residual body mass in several small mammals (Schulte-Hostedde & Millar 2004; Schulte-Hostedde et al. 2005), and the Hawaiian fruitfly *Drosophila grimshawi* (Droney 1998). Indirect evidence that sperm competition traits reflect male condition also comes from correlative studies linking ejaculate size, sperm quality and testes mass to the expression of costly male ornaments. For example, in the Trinidadian guppy *Poecilia reticulata*, orange ornamentation in males is positively correlated with sperm quality (Locatello et al. 2006; Pitcher et al. 2007) and differences between rival

males in orange area predicts the outcome of sperm competition (Evans et al. 2003). Because male guppies must obtain carotenoids from dietary sources, the link between sexual coloration and competitive fertilization success in this species is consistent with the possibility that male foraging ability (and therefore condition) determines competitiveness (see also Droney 1998). Similarly, in the red deer *Cervus elaphus*, the size and complexity of male antlers is associated with relative testes mass and sperm velocity (Malo et al. 2005). However, the influence of male body condition on primary sex traits is not universal and no evidence for condition dependence was found for ejaculate traits in the northern watersnake *Nerodia sipedon* (Schulte-Hostedde & Montgomerie 2006) and the fish *Lepomis macrochirus* (Casselman & Montgomerie 2004), or on ejaculate size in the grasshopper *Chorthippus parallelus* (Reinhardt 2001).

Other studies have implicated male condition in regulating both mating success and paternity success. For example, in the Atlantic cod *Gadus morhua*, two experiments suggested that body condition (calculated as weight divided by length cubed) influenced progeny success (the proportion of offspring sired) when relative sperm density from rival males was regulated using *in vitro* fertilization (Rakitin et al. 1999). In the scorpionfly *Panorpa cognata*, males with high residual body mass are able to provide females with larger nuptial gifts and can therefore copulate for longer (Engqvist & Sauer 2001) and inseminate higher numbers of sperm (Engqvist & Sauer 2003). In the wren *Troglodytes troglodytes*, testes mass is an increasing function of body mass and males with larger testes commence breeding sooner than their smaller and less well-endowed counterparts (Evans & Goldsmith 2000). To the extent that body mass reflects male condition in these species, these findings suggest that the

onset of gonad and breeding readiness (or reproductive success) are condition-dependent traits.

Some of the most convincing evidence for the condition-dependent expression of traits that regulate sperm competition comes from the positive (genetic) association between male condition and sperm phenotype in the dung beetle *O. taurus*. Simmons and Kotiaho (2002) reported patterns of genetic variation that implicated Y-linked inheritance for sperm length (see above). Their analysis also revealed that male condition (residuals from regression of soma weight on body size) exhibited significant additive genetic variance and was strongly negatively correlated with sperm length ($r_g = -0.897 \pm 0.255$ s.e.). Subsequent research on this species revealed that the production of shorter sperm was associated with enhanced paternity success following experimental sperm competition trials involving males producing long and short sperm (García-González & Simmons 2007). This short-sperm advantage, coupled with the previously reported patterns of genetic (co)variances for male condition and sperm length, provides a clear avenue by which polyandrous females may secure genetic benefits for their offspring. Although Arnqvist & Thornhill's (1998) quantitative genetic study of genital morphology in the water strider *G. incognitus* found the phenotypic expression of genital traits depended on food stress during development, and thus were condition dependent, different genotypes did not differ in their ability to cope with food stress, showing that variation in genital morphology was not a reliable indicator of this aspect of male genetic quality.

Heritability of polyandry

Female remating behaviour and mating frequency can exhibit substantial intraspecific variability (Miyatake & Matsumura 2004) and a number of studies have identified a

genetic basis to this variation (Gromko & Newport 1988; Harano & Miyatake 2005; Kraus et al. 2005; Pyle & Gromko 1979; Shuker et al. 2007; Solymar & Wade 1990; Wedell 2001). There is also increasing evidence for rapid and divergent responses to artificial selection for female mating speeds, and correlated responses for female mating frequency. Despite this progress, however, there is currently no evidence that female mating frequency is genetically correlated with male competitive fertilization success, which is a central requirement of both the good sperm and sexy sperm models (Keller & Reeve 1995; Yasui 1997). Indeed, the only test for such a correlation failed to uncover a significant association between polyandry (female mating frequency) and competitive fertilization success in the field cricket *Teleogryllus oceanicus* (Simmons 2003).

Genetic basis of polyandry

There are just a handful of studies that have examined quantitative genetic variation in polyandry, and all come from studies of insects (Table 1). Broad sense estimates suggest that heritability may be quite high. However, studies of crickets and wasps that have used methods which allow the partitioning of genetic variance between sires and dams suggest that the levels of additive genetic variance may be rather low in contrast with the very strong dam effects (Shuker et al. 2007; Simmons 2003). Dam effects include maternal genetic, environmental, dominance and epistatic effects (Lynch & Walsh 1998) all of which are unavailable for GS-SS processes (see Crnokrak & Roff 1995; Roff & Emerson 2006 for discussion of how traits with high dominance variance relate to fitness).

Harano and Miyatake (2005) used reciprocal crosses between strains of bean beetle, *Callosobruchus chinensis*, previously shown to exhibit different remating

frequencies (Miyatake & Matsumura 2004). This approach identifies nonadditive gene action because such effects cause departures of the phenotypes of F_1 offspring from mid-parental values, which were evident in Harano and Miyatake's (2005) crosses. This approach implicated dominance variance as a major contributor to female mating frequency. By contrast, Torres-Vila et al.'s (2001) study of the moth *Spodoptera exigua* involving back-crosses from divergent selection lines for polyandry revealed no difference between F_1 progeny and mid-parental values. Instead, they concluded that female mating frequency was a polygenic, autosomal heritable trait with substantial additive genetic variance available for selection. Indeed, Torres-Vila et al. (2001) were successful in artificially selecting for high and low female mating frequencies in this species, and subsequently in the moth *Lobesia botrana* (Torres-Vila et al. 2002).

Response to selection

Several studies report evolutionary responses to selection on female remating speed, which can be associated with mating frequency (e.g. Wedell 2001). For example, in an unreplicated selection experiment, Pyle and Gromko (1979) subjected *D. melanogaster* females to repeated matings, selecting for the fastest female remating speeds over 20 generations (see also Sgro et al. 1998; Singh & Singh 2001). Over the course of their experiment they compared time to remating by females (and males) with flies from an unselected control line and reported a rapid decrease in remating time in both sexes. Unfortunately, their study confounded male and female responses to the selection regime and they were therefore unable to determine the genetic basis of female remating speeds. Nevertheless, results from F_1 hybrids from reciprocal crosses between selected and control lines suggested that genes on the X chromosome

influenced female remating speed. A subsequent selection experiment (Gromko & Newport 1988) based on the behaviour of just one sex was also consistent with sex-linkage (see also Sgro et al. 1998).

Studies on *Drosophila* have also revealed correlated responses to selection on remating speed, including remating frequency (i.e. propensity to mate polyandrously). For example, Sgro et al. (1998) reported a direct response to selection on mating speed by females and a correlated response on mating frequency in lines selected for faster mating times, confirming that remating speed is both heritable and pleiotropically associated with frequent mating. Similar correlated responses on mating propensity (total number of matings) were observed by Singh and Singh (2001).

Good sperm and sexy sperm processes rely on females mating in such a way as to promote the temporal and spatial overlap of sperm from multiple males, so that it is genetic variation in the tendency for females to promote the overlap of ejaculates that is relevant for GS-SS processes. Some of the studies reviewed above focus on variables such as female mating speed or remating rates, which may or may not correlate the degree of polyandry, and importantly need not generate the overlap of sperm from different males required by GS-SS processes. For example, females may mate multiply through their lifetime but there may be no overlap of ejaculates if they do so between, rather than within reproductive episodes, or remate following depletion of sperm reserves. Thus, the evidence for genetic variation in the type of polyandry required for GS-SS processes is extremely limited.

Conclusions and future directions

Since their inception more than a decade ago, the good-sperm and sexy-sperm models have gained limited explicit experimental support, other than correlative studies linking paternity biases to offspring performance or viability (e.g. Fisher et al. 2006; Hosken et al. 2003b), or studies that compare the reproductive fitness of offspring between polyandrous and monandrous broods (Bernasconi & Keller 2001; Pai & Yan 2002). Importantly, relatively few studies have focused on the genetic basis of traits that regulate competitive fertilization success or female remating behaviour, despite the fact that both models make explicit and testable predictions in this regard. One obvious prediction generated by these models is that competitive fertilization success will exhibit additive genetic variance due to sires.

Our review highlights the recent and ongoing debates surrounding the evolvability of traits involved in regulating sperm competition, and in particular the possibility that these may be constrained by sex-linked genes, nonadditive gene action, male-female interactions and trade-offs between functionally integrated ejaculate components. Despite these possible genetic constraints, however, quantitative genetic studies continue to report that traits likely to be subject to selection imposed by sperm competition (and in some cases competitive fertilization success) often exhibit substantial additive genetic variance attributable to sires (Simmons & Moore 2007). Heritability and repeatability studies of sperm precedence (e.g. Radwan 1998) and those revealing the condition-dependent nature of sperm performance traits (Simmons & Kotiaho 2002) further support the notion that fertilization success can be attributed to the intrinsic (genetic) quality of males. Nevertheless, several studies provide important exceptions to this trend. For example, laboratory studies on *Drosophila melanogaster* indicate that the level of additive genetic variance for sperm precedence is low or zero (Friberg et al. 2005; Hughes 1997) and that P_1 and P_2 depend on

interacting parental genotypes (Clark 2002; Clark & Begun 1998; Clark et al. 1999) or morphologies (Miller & Pitnick 2002; Pattarini et al. 2006).

Meanwhile, research on the feral fowl *Gallus gallus domesticus* suggests that maternally derived cytoplasmic genes (mtDNA) can have consequences for male fertilization success independent of nuclear genes (Froman & Kirby 2005; Froman et al. 2002). There is clearly a need for further studies of this kind to examine these processes more generally, and to determine how maternally derived components of variation in fertilization success influence responses to the type of selection expected via GS-SS processes.

The paucity of studies investigating the genetic basis of female remating behaviour in the context of testing predictions generated by the GS-SS models is unfortunate. While our review highlights several studies that uncover a strong genetic basis to polyandry, there is currently no evidence that selection for increased mating frequency results in the predicted correlated genetic responses on male traits that influence fertilization success. Yet indirect selection arising from the linkage disequilibrium between genes for female mating frequency and those that regulate sperm competitiveness is a basic requirement of the GS-SS models for the evolution of polyandry (Curtisinger 1991; Yasui 1997). The only attempt to test for a genetic correlation between paternity and female mating frequency suggests that this basic requirement is absent (Simmons 2003).

Good sperm and sexy sperm models focus on the indirect benefits that may accrue to females from multiple mating. However, it is becoming increasingly clear that females in many species suffer direct fitness costs associated with multiple mating, and many adaptations in males to sperm competition involve manipulations of female reproductive biology that reduce female fitness (Arnqvist & Rowe 2005; Chapman et

al. 1995; Rice 1996). Theoretical models of precopulatory mechanisms show that costly female preferences can be maintained (Iwasa et al. 1991; Pomiankowski et al. 1991), and it is possible that indirect genetic benefits could be large enough to offset the costs incurred by polyandrous females (Eberhard & Cordero 2003) (but see Cameron et al. 2003). However, female remating behaviour can be subject to intense antagonistic selection, the strength of which could undermine the potential for positive coevolution between male competitive fertilization success and polyandry required by the GS-SS processes (Pizzari & Birkhead 2002). For example, in their recent study of *Drosophila melanogaster*, Pischedda and Chippindale (2006) show how intralocus sexual conflict diminishes the indirect genetic benefits of sexual selection. They used hemiclinal analysis to show how genes that promote male fitness (proportion of offspring sired) reduce female fitness (fecundity) so that daughters sired by high-fitness males have the lowest fitness. Likewise in bulb mites *R. robini*, males homozygous for the slow allele *Pgdh* have superior competitive fertilization success, but their mates have lower fecundity (Konior et al. 2006).

Antagonistic selection can generate complex evolutionary dynamics. Theory suggests that, in general, alleles involved in reproduction should become linked to the X-chromosome when there is antagonistic coevolution between males and females (Gibson et al. 2002; Rice 1984; Rice & Holland 1997). The limited data on the patterns of genetic variation in female mating frequency (Table 1) suggest strong maternal effects on this trait, and in some cases X-linkage has been implicated (Gromko & Newport 1988; Sgro et al. 1998; Simmons 2003), a pattern that is consistent with a history of antagonistic selection over female mating frequency and inconsistent with GS-SS theory. Interestingly, of the three studies that suggest high levels of additive genetic variance in polyandry, one comes from a study of honey

bees where the haplodiploid sex determination system precludes father-to-son transmission of genes required for GS-SS processes, and two come from studies of lepidoptera where the sex determination system is ZZ/ZW. Species with male homogametic sex determination systems may be more conducive to GS-SS evolutionary dynamics because males pass their X chromosomes (or in the case of lepidoptera Z chromosomes) to their sons, increasing the heritability of X-linked traits and the potential for indirect genetic benefits of sexual selection (Reeve & Pfennig 2003; Rice & Chippindale 2001). Lepidoptera may thereby provide good systems with which to pursue evidence for GS-SS processes. Clearly studies aimed at elucidating the genetic architecture of competitive fertilization success, polyandry, and their genetic covariance are required if we are to make progress in testing GS-SS processes.

Finally, GS-SS models have been used exclusively to explain the evolution of mating frequency as a mechanism of post-mating female preference (Curtisinger 1991; Yasui 1997). Although antagonistic selection and sex linkage can inhibit the predicted positive covariance between this mechanism of 'preference' and male traits, GS-SS processes may still operate via alternative preference mechanisms. For example, the effect of sperm length on a male's competitive fertilization success is dependent on the female's reproductive tract morphology in both fruit flies (Miller & Pitnick 2002; Pattarini et al. 2006) and dung beetles (García-González & Simmons 2007). These studies illustrate that the correlated evolution of female mating frequency and male traits, explicit to current GS-SS models, may be unnecessary. Instead, we might expect to see covariation between female and sperm morphologies, even where sexual conflict opposes directional selection on female mating frequency. Indeed, selection for increased seminal receptacle length in female *D. melanogaster* generates a

correlated response in sperm length, a result expected if these traits are in linkage disequilibrium (Miller & Pitnick 2002). Further development of GS-SS theory might focus on mechanisms of female preference other than polyandry, while accounting for the co-evolutionary dynamics imposed by sexual conflict.

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References

- Anderson, M. J. & Dixon, A. F. 2002 Motility and the midpiece in primates. *Nature* **416**, 496.
- Arnaud, L., Haubruge, E. & Gage, M. J. G. 2001 Sperm size and number variation in the red flour beetle. *Zoological Journal of the Linnean Society* **133**, 369-375.
- Arnqvist, G. 1998 Comparative evidence for the evolution of genitalia by sexual selection. *Nature* **393**, 784-786.
- Arnqvist, G. & Danielsson, I. 1999 Copulatory behavior, genital morphology, and male fertilization success in water striders. *Evolution* **53**, 147-156.
- Arnqvist, G. & Rowe, L. 2005 *Sexual Conflict*. New Jersey: Princeton University Press.
- Arnqvist, G. & Thornhill, R. 1998 Evolution of animal genitalia: patterns of phenotypic and genotypic variation and condition dependence of genital and non-genital morphology in water strider (Heteroptera: Gerridae: Insecta). *Genetical Research* **71**, 193-212.
- Baer, B., Schmid-Hempel, P., Hoeg, J. T. & Boomsma, J. J. 2003 Sperm length, sperm storage and mating system characteristics in bumblebees. *Insectes Sociaux* **50**, 101-108.
- Balshine, S., Leach, B. J., Neat, F., Werner, N. Y. & Montgomerie, R. 2001 Sperm size of African cichlids in relation to sperm competition. *Behavioral Ecology* **12**, 726-731.
- Bernasconi, G. & Keller, L. 2001 Female polyandry affects their sons' reproductive success in the red flour beetle *Tribolium castaneum*. *Journal of Evolutionary Biology* **14**, 186-193.
- Birkhead, T. R., Chaline, N., Biggins, J. D., Burke, T. & Pizzari, T. 2004 Nontransitivity of paternity in a bird. *Evolution* **58**, 416-420.
- Birkhead, T. R., Martínez, J. G., Burke, T. & Froman, D. P. 1999 Sperm mobility determines the outcome of sperm competition in the domestic fowl. *Proceedings of the Royal Society London B* **266**, 1759-1764.
- Birkhead, T. R., Pellatt, E. J., Brekke, P., Yeates, R. & Castillo-Juarez, H. 2005 Genetic effects on sperm design in the zebra finch. *Nature* **434**, 383-387.
- Birkhead, T. R. & Pizzari, T. 2002 Postcopulatory sexual selection. *Nature Reviews Genetics* **3**, 262-273.
- Blanckenhorn, W. U., Hellriegel, B., Hosken, D. J., Jann, P., Altwegg, R. & Ward, P. I. 2004 Does testis size track expected mating success in yellow dung flies? *Functional Ecology* **18**, 414-418.
- Briskie, J. V. & Montgomerie, R. 1992 Sperm size and sperm competition in birds. *Proceedings of the Royal Society London B* **247**, 89-95.
- Byrne, P. G., Simmons, L. W. & Roberts, J. D. 2003 Sperm competition and the evolution of gamete morphology in frogs. *Proceedings of the Royal Society London B* **270**, 2079-2086.
- Cameron, E., Day, T. & Rowe, L. 2003 Sexual conflict and indirect benefits. *Journal of Evolutionary Biology* **16**, 1055-1060.
- Casselman, S. J. & Montgomerie, R. 2004 Sperm traits in relation to male quality in colonial spawning bluegill. *Journal of Fish Biology* **64**, 1700-1711.

- Chapman, T., Liddle, L. F., Kalb, J. M., Wolfner, M. F. & Partridge, L. 1995 Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature* **373**: 241-244.
- Clark, A. G. 2002 Sperm competition and the maintenance of polymorphism. *Heredity* **88**, 148-153.
- Clark, A. G., Aguade, M., Prout, T., Harshman, L. G. & Langley, C. H. 1995 Variation in sperm displacement and its association with accessory-gland protein loci in *Drosophila melanogaster*. *Genetics* **139**, 189-201.
- Clark, A. G. & Begun, D. J. 1998 Female genotypes affect sperm displacement in *Drosophila*. *Genetics* **149**, 1487-1493.
- Clark, A. G., Begun, D. J. & Prout, T. 1999 Female x male interactions in *Drosophila* sperm competition. *Science* **283**, 217-220.
- Crnokrak, P. & Roff, D. A. 1995 Dominance variance - associations with selection and fitness. *Heredity* **75**, 530-540.
- Curtsinger, J. W. 1991 Sperm competition and the evolution of multiple mating. *The American Naturalist* **138**, 93-102.
- Danielsson, I. & Askenmo, C. 1999 Male genital traits and mating interval affect male fertilization success in the water strider *Gerris lacustris*. *Behavioral Ecology and Sociobiology* **46**, 149-156.
- Dowling, D. K., Nowostawski, A. L. & Arnqvist, G. 2006 Effects of cytoplasmic genes on sperm viability and sperm morphology in a seed beetle: implications for sperm competition theory? *Journal of Evolutionary Biology* **20**, 358-368.
- Droney, D. C. 1998 The influence of the nutritional content of the adult male diet on testis mass, body condition and courtship vigour in a Hawaiian *Drosophila*. *Functional Ecology* **12**, 920-928.
- Eady, P. E. 1995 Why do male *Callosobruchus maculatus* beetles inseminate so many sperm? *Behavioral Ecology and Sociobiology* **36**, 25-32.
- Eberhard, W. G. 1996 *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton: Princeton University Press.
- Eberhard, W. G. & Cordero, C. 2003 Sexual conflict and female choice. *Trends in Ecology and Evolution* **18**, 438-439.
- Engqvist, L. & Sauer, K. P. 2001 Strategic male mating effort and cryptic male choice in a scorpionfly. *Proceedings of the Royal Society London B* **268**, 729-735.
- Engqvist, L. & Sauer, K. P. 2003 Determinants of sperm transfer in the scorpionfly *Panorpa cognata*: male variation, female condition and copulation duration. *Journal of Evolutionary Biology* **16**, 1196-1204.
- Evans, J. P. & Marshall, D. J. 2005 Male-by-female interactions influence fertilization success and mediate the benefits of polyandry in the sea urchin *Heliocidaris erythrogramma*. *Evolution* **59**, 106-112.
- Evans, J. P., Zane, L., Francescato, S. & Pilastro, A. 2003 Directional postcopulatory sexual selection revealed by artificial insemination. *Nature* **421**, 360-363.
- Evans, M. R. & Goldsmith, A. R. 2000 Male wrens with large testes breed early. *Animal Behaviour* **60**, 101-105.
- Fairbairn, D. J., Vermette, R., Kapoor, N. N. & Zahiri, N. 2003 Functional morphology of sexually selected genitalia in the water strider *Aquarius remigis*. *Canadian Journal of Zoology* **81**, 400-413.
- Fisher, D. O., Double, M. C., Blomberg, S. P., Jennions, M. D. & Cockburn, A. 2006 Post-mating sexual selection increases lifetime fitness of polyandrous females in the wild. *Nature* **444**, 89-92.

- Fiumera, A. C., Dumont, B. L. & Clark, A. G. 2005 Sperm competitive ability in *Drosophila melanogaster* associated with variation in male reproductive proteins. *Genetics* **169**, 243-257.
- Friberg, U., Lew, T. A., Byrne, P. G. & Rice, W. R. 2005 Assessing the potential for an ongoing arms race within and between the sexes: selection and heritable variation. *Evolution* **59**, 1540-1551.
- Froman, D. P. & Kirby, J. D. 2005 Sperm mobility: Phenotype in roosters (*Gallus domesticus*) determined by mitochondrial function. *Biology of Reproduction* **72**, 562-567.
- Froman, D. P., Pizzari, T., Feltmann, A. J., Castillo-Juarez, H. & Birkhead, T. R. 2002 Sperm mobility: mechanisms of fertilizing efficiency, genetic variation and phenotypic relationship with male status in the domestic fowl, *Gallus gallus domesticus*. *Proceedings of the Royal Society London B* **269**, 607-612.
- Gage, M. J. G. 1994 Associations between body size, mating pattern, testis size and sperm lengths across butterflies. *Proceedings of the Royal Society London B* **258**, 247-254.
- Gage, M. J. G. 1995 Continuous variation in reproductive strategy as an adaptive response to population density in the moth *Plodia interpunctella*. *Proceedings of the Royal Society London B* **261**, 25-30.
- Gage, M. J. G. & Freckleton, R. P. 2003 Relative testis size and sperm morphometry across mammals: no evidence for an association between sperm competition and sperm length. *Proceedings of the Royal Society London B* **270**, 625-632.
- Gage, M. J. G., Macfarlane, C. P., Yeates, S., Ward, R. G., Searle, J. B. & Parker, G. A. 2004 Spermatozoal traits and sperm competition in Atlantic salmon: relative velocity is the primary determinant of fertilization success. *Current Biology* **14**, 44-47.
- Gage, M. J. G. & Morrow, E. H. 2003 Experimental evidence for the evolution of numerous, tiny sperm via sperm competition. *Current Biology* **13**, 754-757.
- Gallon, F., Marchetti, C., Jouy, N. & Marchetti, P. 2006 The functionality of mitochondria differentiates human spermatozoa with high and low fertilizing capability. *Fertility and Sterility* **86**, 1526-1530.
- García-González, F. & Simmons, L. W. 2005 Sperm viability matters in insect sperm competition. *Current Biology* **15**, 271-275.
- García-González, F. & Simmons, L. W. 2007 Shorter sperm confer higher competitive fertilization success. *Evolution* **61**, 816-824.
- Gemmell, N. J., Metcalf, V. J. & Allendorf, F. W. 2004 Mother's curse: the effect of mtDNA on individual fitness and population viability. *Trends In Ecology & Evolution* **19**, 238-244.
- Gibson, J. R., Chippindale, A. K. & Rice, W. R. 2002 The X chromosome is a hot spot for sexually antagonistic fitness variation. *Proceedings of the Royal Society London B* **269**, 499-505.
- Gomendio, M., Coello-Martin, J., Crespo, C., Magaña, C. & Roldan, E. R. S. 2006 Sperm competition enhances functional capacity of mammalian spermatozoa. *Proceedings of the National Academy of Sciences USA* **203**, 15113-15117.
- Gomendio, M., Harcourt, A. H. & Roldan, E. R. S. 1998 Sperm Competition in Mammals. In *Sperm Competition and Sexual Selection*. (ed. T. R. Birkhead & A. P. Møller), pp. 667-751. San Diego: Academic Press.
- Gomendio, M. & Roldan, E. R. S. 1991 Sperm competition influences sperm size in mammals. *Proceedings of the Royal Society London B* **243**, 181-185.

- Gromko, M. H. & Newport, M. E. A. 1988 Genetic basis for remating in *Drosophila melanogaster*. II. Response to selection based on the behavior of one sex. *Behavior Genetics* **18**, 621-632.
- Gustafsson, L. 1986 Lifetime reproductive success and heritability: empirical support for Fisher's fundamental theorem. *American Naturalist* **128**, 761-764.
- Harano, T. & Miyatake, T. 2005 Heritable variation in polyandry in *Callosobruchus chinensis*. *Animal Behaviour* **70**, 299-304.
- Harcourt, A. H. 1991 Sperm competition and the evolution of nonfertilizing sperm in mammals. *Evolution* **45**, 314-328.
- Harcourt, A. H., Purvis, A. & Liles, L. 1995 Sperm competition: Mating system, not breeding season, affects testes size of primates. *Functional Ecology* **9**, 468-476.
- Harvey, P. H. & May, R. M. 1989 Out for the sperm count. *Nature* **337**, 508-509.
- Hettyey, A. & Roberts, J. D. 2006 Sperm traits of the quacking frog, *Crinia georgiana*: intra- and interpopulation variation in a species with a high risk of sperm competition. *Behavioral Ecology and Sociobiology* **59**, 389-396.
- Holleley, C. E., Dickman, C. R., Crowther, M. S. & Oldroyd, B. P. 2006 Size breeds success: multiple paternity, multivariate selection and male semelparity in a small marsupial, *Antechinus stuartii*. *Molecular Ecology* **15**, 3439-3448.
- Hosken, D. J. 1997 Sperm competition in bats. *Proceedings of the Royal Society London B* **264**, 385-392.
- Hosken, D. J., Garner, T. W. J. & Blanckenhorn, W. U. 2003a Asymmetry, testis and sperm size in yellow dung flies. *Functional Ecology* **17**, 231-236.
- Hosken, D. J., Garner, T. W. J., Tregenza, T., Wedell, N. & Ward, P. I. 2003b Superior sperm competitors sire higher-quality young. *Proceedings of the Royal Society London B* **270**, 1933-1938.
- Hosken, D. J., Garner, T. W. J. & Ward, P. I. 2001 Sexual conflict selects for male and female reproductive characters. *Current Biology* **11**, 489-493.
- Hosken, D. J. & Stockley, P. 2004 Sexual selection and genital evolution. *Trends in Ecology and Evolution* **19**, 87-93.
- House, C. M. & Simmons, L. W. 2005a The evolution of male genitalia: patterns of genetic variation and covariation in the genital sclerites of the dung beetle *Onthophagus taurus*. *Journal of Evolutionary Biology* **18**, 1281-1292.
- House, C. M. & Simmons, L. W. 2005b Relative influence of male and female genital morphology on paternity in the dung beetle *Onthophagus taurus*. *Behavioral Ecology* **16**, 889-897.
- Hughes, K. A. 1997 Quantitative genetics of sperm precedence in *Drosophila melanogaster*. *Genetics* **145**, 139-151.
- Hunter, F. M. & Birkhead, T. R. 2002 Sperm viability and sperm competition in insects. *Current Biology* **12**, 121-123.
- Immler, S., Moore, H. D. M., Breed, W. G. & Birkhead, T. R. 2007 By hook or by crook? Morphometry, competition and cooperation in roden sperm. *Plos One* **1**, e170.
- Iwasa, Y., Pomiankowski, A. & Nee, S. 1991 The evolution of costly mate preferences II. The "handicap" principle. *Evolution* **45**, 1431-1442.
- Jennions, M. D. & Petrie, M. 2000 Why do females mate multiply? a review of the genetic benefits. *Biological Review* **75**, 21-64.
- Johnson, D. D. P. & Briskie, J. V. 1999 Sperm competition and sperm length in shorebirds. *Condor* **101**, 848-854.

- Joly, D., Korol, A. & Nevo, E. 2004 Sperm size evolution in *Drosophila*: inter- and intraspecific analysis. *Genetica* **120**, 233-244.
- Keller, L. & Reeve, H. K. 1995 Why do females mate with multiple males? The sexually selected sperm hypothesis. *Advances in the Study of Animal Behavior* **24**, 291-315.
- Konior, M., Keller, L. & Radwan, J. 2005 Effect of inbreeding and heritability of sperm competition success in the bulb mite *Rhizoglyphus robini*. *Heredity* **94**, 577-581.
- Konior, M., Radwan, J., Kolodziejczyk, M. & Keller, L. 2006 Strong association between a single gene and fertilization efficiency of males and fecundity of their mates in the bulb mite. *Proceedings of the Royal Society London B* **273**, 309-314.
- Kraus, F. B., Neumann, P. & Moritz, R. F. A. 2005 Genetic variance of mating frequency in the honeybee (*Apis mellifera* L.). *Insectes Sociaux* **52**, 1-5.
- LaMunyon, C. W. & Ward, S. 1998 Larger sperm outcompete smaller sperm in the nematode *Caenorhabditis elegans*. *Proceedings of the Royal Society London B* **265**, 1997-2002.
- Langerhans, R. B., Layman, C. A. & DeWitt, T. J. 2005 Male genital size reflects a tradeoff between attracting mates and avoiding predators in two live-bearing fish species. *Proceedings of the National Academy of Sciences USA* **102**, 7618-7623.
- Lessells, C. M. & Boag, P. T. 1987 Unrepeatable repeatabilities: a common mistake. *Auk* **104**, 116-121.
- Lewis, S. M. & Austad, S. N. 1990 Sources of intraspecific variation in sperm precedence in red flour beetles. *The American Naturalist* **135**, 351-359.
- Linhart, O., Rodina, M., Gela, D., Kocour, M. & Vandeputte, M. 2005 Spermatozoal competition in common carp (*Cyprinus carpio*): what is the primary determinant of competition success? *Reproduction* **130**, 705-711.
- Locatello, L., Rasotto, M. B., Evans, J. P. & Pilastro, A. 2006 Colourful male guppies produce faster and more viable sperm. *Journal of Evolutionary Biology* **19**, 1595-1602.
- Lynch, M. & Walsh, B. 1998 *Genetics and Analysis of Quantitative Traits*. Sunderland: Sinauer Associates, Inc.
- Malo, A. F., Gomendio, M., Garde, J., Lang-Lenton, B., Soler, A. J. & Roldan, E. R. S. 2006 Sperm design and sperm function. *Biology Letters* **2**, 246-249.
- Malo, A. F., Roldan, E. R. S., Garde, J., Soler, A. J. & Gomendio, M. 2005 Antlers honestly advertise sperm production and quality. *Proceedings of the Royal Society London B* **272**, 149-157.
- Marshall, D. J. & Evans, J. P. 2005 The benefits of polyandry in the free-spawning polychaete *Galeolaria caespitosa*. *Journal of Evolutionary Biology* **18**, 735-741.
- Merilä, J. & Sheldon, B. C. 1999a Genetic architecture of fitness and nonfitness traits: empirical patterns and development of ideas. *Heredity* **83**, 103-109.
- Merilä, J. & Sheldon, B. C. 1999b Testis size variation in the greenfinch *Carduelis chloris*: relevance for some recent models of sexual selection. *Behavioural Ecology and Sociobiology* **45**, 115-123.
- Merilä, J. & Sheldon, B. C. 2000 Lifetime reproductive success and heritability in nature. *American Naturalist* **155**, 301-310.
- Miller, G. T. & Pitnick, S. 2002 Sperm-female coevolution in *Drosophila*. *Science* **298**, 1230-1233.

- Minoretti, N. & Baur, B. 2006 Among- and within-population variation in sperm quality in the simultaneously hermaphroditic land snail *Arianta arbustorum*. *Behavioral Ecology and Sociobiology* **60**, 270-280.
- Miyatake, T. & Matsumura, F. 2004 Intra-specific variation in female remating in *Callosobruchus chinensis* and *C. maculatus*. *Journal of Insect Physiology* **50**, 403-408.
- Moore, A. J., Gowaty, P. A., Wallin, W. G. & Moore, P. J. 2001 Sexual conflict and the evolution of female mate choice and male social dominance. *Proceedings of the Royal Society London B* **268**, 517-523.
- Moore, F. L. & Reijo-Pera, R. A. 2000 Male sperm motility dictated by mother's mtDNA. *American Journal of Human Genetics* **67**, 543-548.
- Moore, P. J., Harris, W. E., Montrose, V. T., Levin, D. & Moore, A. J. 2004 Constraints on evolution and postcopulatory sexual selection: trade-offs among ejaculate characteristics. *Evolution* **58**, 1773-1780.
- Morrow, E. H. & Gage, M. J. G. 2000 The evolution of sperm length in moths. *Proceedings of the Royal Society London B* **267**, 307-313.
- Morrow, E. H. & Gage, M. J. G. 2001a Artificial selection and heritability of sperm length in *Gryllus bimaculatus*. *Heredity* **87**, 356-362.
- Morrow, E. H. & Gage, M. J. G. 2001b Consistent significant variation between individual males in spermatozoal morphology. *Journal of Zoology* **254**, 147-153.
- Morrow, E. H. & Gage, M. J. G. 2001c Sperm competition experiments between lines of crickets producing different sperm lengths. *Proceedings of the Royal Society London B* **268**, 2281-2286.
- Nakada, K., Sato, A., Yoshida, K., Morita, T., Tanaka, H., Inoue, S. I., Yonekawa, H. & Hayashi, J. I. 2006 Mitochondria-related male infertility. *Proceedings of the National Academy of Sciences USA* **103**, 15148-15153.
- Neff, B. D., Fu, P. & Gross, M. R. 2003 Sperm investment and alternative mating tactics in bluegill sunfish (*Lepomis macrochirus*). *Behavioral Ecology* **14**, 634-641.
- Oppliger, A., Naciri-Graven, Y., Ribi, G. & Hosken, D. J. 2003 Sperm length influences fertilization success during sperm competition in the snail *Viviparus ater*. *Molecular Ecology* **12**, 485-492.
- Pai, A. T. & Yan, G. Y. 2002 Polyandry produces sexy sons at the cost of daughters in red flour beetles. *Proceedings of the Royal Society London B* **269**, 361-368.
- Parker, G. A. 1970 Sperm competition and its evolutionary consequences in the insects. *Biological Review* **45**, 525-567.
- Parker, G. A. 1979 Sexual selection and sexual conflict. In *Sexual Selection and Reproductive Competition in Insects*. (ed. M. S. Blum & N. A. Blum), pp. 123-166. New York: Academic Press.
- Parker, G. A. 1982 Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. *Journal of Theoretical Biology* **96**, 281-294.
- Pattarini, J. A., Starmer, W. T., Bjork, A. & Pitnick, S. 2006 Mechanisms underlying the sperm quality advantage in *Drosophila melanogaster*. *Evolution* **60**, 2064-2080.
- Pischedda, A. & Chippindale, A. K. 2006 Intralocus sexual conflict diminishes the benefits of sexual selection. *Plos Biology* **4**, 2099-2103.
- Pitcher, T. E., Dunn, P. O. & Whittingham, L. A. 2005 Sperm competition and the evolution of testes size in birds. *Journal of Evolutionary Biology* **18**, 557-567.

- Pitcher, T. E., Rodd, F. H. & Rowe, L. 2007 Sexual colouration and sperm traits in guppies. *Journal of Fish Biology* **70**, 165-177.
- Pitnick, S. & Miller, G. T. 2000 Correlated response in reproductive and life history traits to selection on testis length in *Drosophila hydei*. *Heredity* **84**, 416-426.
- Pizzari, T. & Birkhead, T. R. 2002 The sexually-selected sperm hypothesis: sex-biased inheritance and sexual antagonism. *Biological Reviews* **77**, 183-209.
- Pomiankowski, A., Iwasa, Y. & Nee, S. 1991 The evolution of costly mate preferences I. Fisher and biased mutation. *Evolution* **45**, 1422-1430.
- Preston, B. T., Stevenson, I. R., Pemberton, J. M., Coltman, D. W. & Wilson, K. 2003 Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. *Proceedings of the Royal Society London B* **270**, 633-640.
- Preziosi, R. F. & Fairbairn, D. J. 2000 Lifetime selection on adult body size and components of body size in a waterstrider: opposing selection and maintenance of sexual size dimorphism. *Evolution* **54**, 558-566.
- Pyle, D. W. & Gromko, M. H. 1979 Genetic basis for repeated mating in *Drosophila melanogaster*. *American Naturalist* **117**, 133-146.
- Radwan, J. 1996 Intraspecific variation in sperm competition success in the bulb mite: a role for sperm size. *Proceedings of the Royal Society London B* **263**, 855-859.
- Radwan, J. 1998 Heritability of sperm competition success in the bulb mite, *Rhizoglyphus robini*. *Journal of Evolutionary Biology* **11**, 321-327.
- Rakitin, A., Ferguson, M. M. & Trippel, E. A. 1999 Sperm competition and fertilization success in Atlantic cod (*Gadus morhua*): effect of sire size and condition factor on gamete quality. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 2315-2323.
- Ramm, S. A., Parker, G. A. & Stockley, P. 2005 Sperm competition and the evolution of male reproductive anatomy in rodents. *Proceedings of the Royal Society London B* **272**, 949-955.
- Reeve, H. K. & Pfennig, D. W. 2003 Genetic biases for showy males: are some genetic systems especially conducive to sexual selection? *Proceedings of the National Academy of Sciences USA* **100**, 1089-1094.
- Reinhardt, K. 2001 Determinants of ejaculate size in a grasshopper (*Chorthippus parallelus*). *Behavioral Ecology and Sociobiology* **50**, 503-510.
- Rice, W. R. 1984 Sex chromosomes and the evolution of sexual dimorphism. *Evolution* **38**, 735-742.
- Rice, W. R. 1996 Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature* **381**, 232-234.
- Rice, W. R. & Chippindale, A. K. 2001 Intersexual ontogenetic conflict. *Journal of Evolutionary Biology* **14**, 685-693.
- Rice, W. R. & Holland, B. 1997 The enemies within: intergenomic conflict, interlocus contest evolution (ICE), and the intraspecific Red Queen. *Behavioral Ecology and Sociobiology* **41**, 1-10.
- Roff, D. A. & Emerson, K. 2006 Epistasis and dominance: evidence for differential effects in life-history versus morphological traits. *Evolution* **60**, 1981-1990.
- Rowe, L. & Houle, D. 1996 The lek paradox and the capture of genetic variance by condition dependent traits. *Proceedings of the Royal Society London B* **263**, 1415-1421.
- Schulte-Hostedde, A. I. & Millar, J. S. 2004 Intraspecific variation of testis size and sperm length in the yellow-pine chipmunk (*Tamias amoenus*): implications for

- sperm competition and reproductive success. *Behavioral Ecology and Sociobiology* **55**, 272-277.
- Schulte-Hostedde, A. I., Millar, J. S. & Hickling, G. J. 2003 Intraspecific variation in testis size of small mammals: implications for muscle mass. *Canadian Journal of Zoology* **81**, 591-595.
- Schulte-Hostedde, A. I., Millar, J. S. & Hickling, G. J. 2005 Condition dependence of testis size in small mammals. *Evolutionary Ecology Research* **7**, 143-149.
- Schulte-Hostedde, A. I. & Montgomerie, R. 2006 Intraspecific variation in ejaculate traits of the northern watersnake (*Nerodia sipedon*). *Journal of Zoology* **270**, 147-152.
- Sgro, C. M., Chapman, T. & Partridge, L. 1998 Sex-specific selection on time to remate in *Drosophila melanogaster*. *Animal Behaviour* **56**, 1267-1278.
- Shuker, D. M., Phillimore, A. J., Burton-Chellew, M. N., Hodge, S. E. & West, S. A. 2007 The quantitative genetic basis of polyandry in the parasitoid wasp, *Nasonia vitripennis*. *Heredity* **98**, 69-73.
- Simmons, L. W. 2003 The evolution of polyandry: patterns of genotypic variation in female mating frequency, male fertilization success and a test of the sexy-sperm hypothesis. *Journal of Evolutionary Biology* **16**, 624-634.
- Simmons, L. W. 2005 The evolution of polyandry: sperm competition, sperm selection and offspring viability. *Annual Review of Ecology, Evolution and Systematics* **36**, 125-146.
- Simmons, L. W. & Kotiaho, J. S. 2002 Evolution of ejaculates: patterns of phenotypic and genotypic variation and condition dependence in sperm competition traits. *Evolution* **56**, 1622-1631.
- Simmons, L. W. & Moore, A. J. 2007 Evolutionary Quantitative Genetics of Sperm. In *Sperm Evolution*, vol. In press. (ed. T. R. Birkhead, D. J. Hosken & S. Pitnick).
- Simmons, L. W., Tomkins, J. L. & Hunt, J. 1999 Sperm competition games played by dimorphic male beetles. *Proceedings of the Royal Society London B* **266**, 145-150.
- Simmons, L. W., Wernham, J., Garcia-Gonzalez, F. & Kamien, D. 2003 Variation in paternity in the field cricket *Teleogryllus oceanicus*: no detectable influence of sperm numbers or sperm length. *Behavioral Ecology* **14**, 539-545.
- Singh, S. R. & Singh, B. N. 2001 Female remating in *Drosophila ananassae*: bidirectional selection for remating speed. *Behavior Genetics* **31**, 361-370.
- Sivinski, J. 1984 Sperm in competition. IN: *Smith, R.L. (Ed.) Sperm competition and the evolution of animal mating systems*.
- Snook, R. R. 2005 Sperm in competition: not playing by the numbers. *Trends in Ecology and Evolution* **20**, 46-53.
- Solymar, B. D. & Wade, W. H. 1990 Heritable variation for female mating frequency in field crickets, *Gryllus integer*. *Behavioral Ecology and Sociobiology* **26**, 73-76.
- Stockley, P., Gage, M. J. G., Parker, G. A. & Møller, A. P. 1997 Sperm competition in fishes: the evolution of testis size and ejaculate characteristics. *The American Naturalist* **149**, 933-954.
- Stockley, P., Searle, J. B., Macdonald, D. W. & Jones, C. S. 1994 Alternative reproductive tactics in male common shrews - relationships between mate searching behavior, sperm production, and reproductive success as revealed by DNA fingerprinting. *Behavioral Ecology and Sociobiology* **34**, 71-78.

- Thornhill, R. 1983 Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *The American Naturalist* **122**, 765-788.
- Tomkins, J. L., Radwan, J., Kotiaho, J. S. & Tregenza, T. 2004 Genic capture and resolving the lek paradox. *Trends in Ecology and Evolution* **19**, 323-328.
- Torres-Vila, L. M., Gragera, J., Rodriguez-Molina, M. C. & Stockel, J. 2002 Heritable variation for female remating in *Lobesia botrana*, a usually monandrous moth. *Animal Behaviour* **64**, 899-907.
- Torres-Vila, L. M., Rodriguez-Molina, M. C., Gragera, J. & Bielza-Lino, P. 2001 Polyandry in Lepidoptera: a heritable trait in *Spodoptera exigua* Hubner. *Heredity* **86**, 177-183.
- Ward, P. I. 1998 Intraspecific variation in sperm size characters. *Heredity* **80**, 655-659.
- Ward, P. I. 2000 Sperm length is heritable and sex-linked in the yellow dung fly (*Scathophaga stercoraria*). *Journal of Zoology* **251**, 349-353.
- Wedell, N. 2001 Female remating in butterflies: interaction between female genotype and nonfertile sperm. *Journal of Evolutionary Biology* **14**, 746-754.
- Wenninger, E. J. & Averill, A. L. 2006 Influence of body and genital morphology on relative male fertilization success in oriental beetle. *Behavioral Ecology* **17**, 656-663.
- Werner, M. & Simmons, L. W. 2007 The evolution of male genitalia: functional integration of genital sclerites in the dung beetle *Onthophagus taurus*. *Biological Journal of the Linnean Society* **In press**.
- Wilson, N., Tubman, S. C., Eady, P. E. & Robertson, G. W. 1997 Female genotype affects male success in sperm competition. *Proceedings of the Royal Society London B* **264**, 1491-1495.
- Yasui, Y. 1997 A "good-sperm" model can explain the evolution of costly multiple mating by females. *American Naturalist* **149**, 573-584.
- Zeh, J. A. 2004 Sexy sons: a dead end for cytoplasmic genes. *Proceedings of the Royal Society London B* **271**, S306-S309.
- Zeh, J. A. & Zeh, D. W. 2005 Maternal inheritance, sexual conflict and the maladapted male. *Trends in Genetics* **21**, 281-286.
- Zeng, Z. B., Liu, J. J., Stam, L. F., Kao, C. H., Mercer, J. M. & Laurie, C. C. 2000 Genetic architecture of a morphological shape difference between two *Drosophila* species. *Genetics* **154**, 299-310.

Table 1. Estimates of heritability in the degree of polyandry

Species	Trait	$h^2 \pm \text{SE}$	component	method	reference
Lepidoptera					
<i>Lobesia botrana</i>	remating	0.40±0.12	broad	fullsib	Torres-Vila et al. 2002
	remating	0.53	realised	selection	
<i>Pieris napi</i>	mating frequency	0.63±0.31	broad	fullsib	Wedell 2002
	remating interval	0.85±0.19	broad	fullsib	Wedell 2001
<i>Spodoptera exigua</i>	mating frequency	0.51±0.10	realised	selection	Torres-Vila et al. 2001
Orthoptera					
<i>Gryllus integer</i>	mating frequency	0.69±0.29	dam	parent-offspring	Solymar & Cade 1990
<i>Teleogryllus oceanicus</i>	mating frequency	0.00	sire	halfsib	Simmons 2003
		0.55±0.22	dam	halfsib	
Hymenoptera					
<i>Apis mellifera</i>	mating frequency	0.45±0.14	line	halfsib	Kraus et al. 2005
	paternity frequency	0.26±0.10	line		
<i>Nasonia vitripennis</i>	remating in 1min	0.11±0.06	sire	halfsib	Shuker et al. 2007
		0.55±0.17	dam		
	remating in 10 mins	0.07±0.05 0.82±0.21	sire dam	halfsib	