

Why do females mate multiply? A review of the genetic benefits

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ABSTRACT

The aim of this review is to consider the potential benefits that females may gain from mating more than once in a single reproductive cycle. The relationship between non-genetic and genetic benefits is briefly explored. We suggest that multiple mating for purely non-genetic benefits is unlikely as it invariably leads to the possibility of genetic benefits as well. We begin by briefly reviewing the main models for genetic benefits to mate choice, and the supporting evidence that choice can increase offspring performance and the sexual attractiveness of sons. We then explain how multiple mating can elevate offspring fitness by increasing the number of potential sires that compete, when this occurs in conjunction with mechanisms of paternity biasing that function *in copula* or post-copulation. We begin by identifying cases where females use pre-copulatory cues to identify mates prior to remating. In the simplest case, females remate because they identify a superior mate and ‘trade up’ genetically. The main evidence for this process comes from extra-pair copulation in birds. Second, we note other cases where pre-copulatory cues may be less reliable and females mate with several males to promote post-copulatory mechanisms that bias paternity. Although a distinction is drawn between sperm competition and cryptic female choice, we point out that the genetic benefits to polyandry in terms of producing more viable or sexually attractive offspring do not depend on the exact mechanism that leads to biased paternity. Post-copulatory mechanisms of paternity biasing may: (1) reduce genetic incompatibility between male and female genetic contributions to offspring; (2) increase offspring viability if there is a positive correlation between traits favoured post-copulation and those that improve performance under natural selection; (3) increase the ability of sons to gain paternity when they mate with polyandrous females. A third possibility is that genetic diversity among offspring is directly favoured. This can be due to bet-hedging (due to mate assessment errors or temporal fluctuations in the environment), beneficial interactions between less related siblings or the opportunity to preferentially fertilise eggs with sperm of a specific genotype drawn from a range of stored sperm depending on prevailing environmental conditions. We use case studies from the social insects to provide some concrete examples of the role of genetic diversity among progeny in elevating fitness. We conclude that post-copulatory mechanisms provide a more reliable way of selecting a genetically compatible mate than pre-copulatory mate choice. Some of the best evidence for cryptic female choice by sperm selection is due to selection of more compatible sperm. Two future areas of research seem likely to be profitable. First, more experimental evidence is needed demonstrating that multiple mating increases offspring fitness *via* genetic gains. Second, the role of multiple mating in promoting assortative fertilization and increasing reproductive isolation between populations may help us to understand sympatric speciation.

Key words: cryptic female choice, Fisherian runaway, genetic diversity, genetic incompatibility, genetic benefits, good genes, mate choice, multiple mating, polyandry, sexual selection, sperm competition.

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I. INTRODUCTION

(1) Are there genetic benefits to being fertilized by certain males? A brief history

The increased use of molecular techniques reveals moderate to high levels of multiple paternity in a wide range of animal groups (taxonomic reviews in Birkhead & Møller, 1998). Careful behavioural observations and knowledge of natural history reveal that mixed paternity is often due to active female solicitation of copulations from several males, rather than forced copulation or sneaky fertilization by satellite males (e.g. Kempenaers, Verheyren & Dhondt, 1997; Currie *et al.*, 1998; Stutchbury, 1998). The possible benefits of multiple mating by females have long been debated, especially when there are no apparent fecundity-enhancing, ‘material’ benefits generating natural selection for polyandry (Andersson, 1994). Hereafter, we use ‘polyandry’ to denote cases where females mate with two or more males over a single reproductive cycle (Thornhill & Alcock, 1983). In the absence of direct material benefits, only indirect, genetic advantages can offset the costs associated with polyandry. That is, certain genes or genetic combinations raise the mean offspring fitness of polyandrous females above the average value obtained after a single mating. The exact nature of these genetic benefits remains controversial, although most of the debate has been framed in terms of the evolution of costly female mating preferences, rather than polyandry as such (Yasui, 1997).

Female mate choice can potentially benefit offspring due to the inheritance of ‘good genes’. These genes may enhance the viability of offspring and/or increase sexual attractiveness (Fisherian traits) (reviews: Andersson, 1994; Johnstone, 1995). For years these claims were substantially weakened by the prevailing orthodoxy that the heritability of fitness-enhancing traits is rapidly eroded in the face of the directional selection imposed by female choice for elaborate male traits. This is central to the so-called ‘lek paradox’: why choose males solely for genetic benefits when these benefits are so small? (Williams, 1992). Then, in the early to mid-1990s, new theoretical models for the maintenance of additive genetic variability (V_A) in sexual traits began to proliferate (e.g. Iwasa, Pomiankowski & Nee, 1991; Pomiankowski, Iwasa & Nee, 1991; Rowe & Houle, 1996). In a related area of research, Houle (1992) noted that life-history traits (subject to directional selection and major determinants of

fitness) may have low heritability because they have high environmental variance (V_E) (Price & Schluter, 1991), not because they are lacking in additive genetic variance. Narrow-sense heritability (h^2) is equal to the ratio of V_A to V_P , where V_P is the total phenotypic variation in the trait, a large part of which may be due to environmental variation. [The other factors that contribute to V_P are V_A , non-additive genetic variation such as dominance and interaction variation, linkage disequilibrium due to non-random mating, and covariance between genotypes and environments and genotype by environment interactions (Falconer, 1989). The portion of V_P not due to V_A is sometimes called the residual variation, V_R]. The response to selection is positively related to V_A rather than h^2 , and standardizing this response by the mean trait value shows that the coefficient of variation in V_A (CV_A) is a key variable when considering the ‘evolvability’ of a trait (Houle, 1992). The previous emphasis on the heritability of sexual traits was therefore misleading. Houle (1992) went on to show that life-history traits, despite low heritability, tend to have higher additive genetic variance than ordinary morphological traits. Life-history traits are the outcome of the interaction of many different processes and thus result from selection acting on numerous traits. A large number of loci are therefore likely to contribute to their expression. Evidence in support of this claim comes from studies showing that mutations tend to have simultaneous effects on several life-history traits (Houle *et al.*, 1994), and that life-history traits have relatively high mutational variance (Houle, Morikawa & Lynch, 1996). A greater number of loci increases the ‘mutational target size’ of a trait which helps to maintain additive genetic variation. A slight confounding factor is that target size and the timing of expression of traits are correlated. Traits that are expressed later (i.e. ornaments in adults) may inherit variation from other traits expressed earlier in life history if these traits influence the target trait’s expression (i.e. traits that effect condition) (Houle, 1998a).

Sexually selected traits bear many similarities to life-history traits (Rowe & Houle, 1996; Höglund & Sheldon, 1998). They may also have low heritability because of high environmental variance related to condition-dependent expression. More importantly, if sexually selected traits are condition-dependent, as often appears to be the case (e.g. Jennions & Backwell, 1998), then the many loci that create V_A in condition will also create V_A in sexual traits. Rowe & Houle (1996) have described this as ‘genetic cap-

ture' of variation in condition by sexual traits. The accumulating evidence that there is high additive genetic variation in life-history traits, and by implication in condition, therefore supports the argument that sexual traits should also demonstrate high additive genetic variance. Indeed, an influential empirical review by Pomiankowski & Møller (1995) showed that CV_A for preferred male sexual traits is larger than that for ordinary morphological traits, although the coefficient of variation for residual variation did not differ between trait types. They explained the high level of CV_A as a consequence of non-linear directional selection on sexual traits. When fitness increases in a greater than linear fashion with trait size there is selection for modifier genes that affect the expression of other genes and increase the phenotypic variance in the trait (Lande, 1980).

The contrast between the model for the maintenance of additive genetic variance in sexually selected traits proposed by Pomiankowski & Møller (1995) and that of Rowe & Houle (1996) is currently generating some debate in sexual selection circles. One explanation for this controversy is that the generality of Pomiankowski & Møller's (1995) model is questionable. First, most sexually selected traits are probably under stabilizing rather than directional selection. Experimental manipulations suggest a trade-off between the mating success gains and survival costs of sexual traits (Rowe & Houle, 1996). Second, even prior to reaching equilibrium, it is unclear whether directional selection on sexual traits is greater than linear (Brookfield, 1996). This is an empirical issue that needs to be resolved. Third, modifier gene theory raises the question: what prevents fixation of fitness-enhancing alleles at modifier loci? Another explanation for the debate is that scientists cherish the idea of a simple dichotomy between competing models. However, as Houle himself has carefully pointed out, these are only two of many possible models (Houle, 1998*a, b*). In fact, Rowe & Houle's (1996) model only raises the inevitable question as to how V_A in condition is maintained. In general, the exact mechanisms that maintain additive genetic variance for most traits (including condition) remain unknown. They include: mutation-drift balance, mutation-selection balance, coadapted gene complexes, counteracting effects of gene flow and fluctuating or cyclic selection. There are other candidates that are more specifically tailored to the maintenance of V_A in traits closely linked to viability or fitness. For example, genotype by environment interactions may be important

because the direction of the correlation between male sexual signals and offspring viability may vary across environments (e.g. Jia & Greenfield, 1997; Sheldon, 1999).

The most cited example of temporal fluctuations in the selective environment that will select for rarer genotypes (rather than simply introduce noise) and thereby maintain genetic diversity comes from parasite-host cycles. In theory, these lead to continual selection on hosts for new genetic combinations for resistance to evolving parasites and diseases (Dybdhal & Lively, 1998). Recurrent biased deleterious mutation may also be a factor as mutations are, on average, likely to decrease rather than increase viability (Pomiankowski *et al.*, 1991). A full review of the maintenance of additive genetic variance in viability is not attempted here, and the interested reader is referred to Burt (1995), Roff (1997) and Houle (1998*b*).

For us, the main point is that there is growing acceptance of, and evidence for, explanations for polyandry that rely on inter-male variation in 'good genes'. Mean estimates of the heritability of male secondary sexual characters increased rapidly between 1988 and the present (Alatalo, Mappes & Elgar, 1997), although the correlation between male trait size and offspring viability decreased between 1985 and 1999 (Møller & Alatalo, 1999). The finding that male secondary sexual traits can predict offspring viability in individual studies (e.g. Petrie, 1994; Welch, Semlitsch & Gerhardt, 1998) has, in our opinion, led to viability gene models eclipsing the role of Fisherian runaway as an explanation for polyandry, at least in birds (Petrie & Kempenaers, 1998). Evidence for a positive genetic correlation between male sexual traits and female mating preferences has lent some credence to Fisherian models, but viability gene models also predict this outcome (review: Jennions & Petrie, 1997). Ultimately, it will prove necessary to determine empirically the relative importance of direct benefits, Fisherian and viability gene effects on offspring performance (e.g. Jones, Quinnell & Balmford, 1998). Recently, Wedell & Tregenza (1999) showed that male field crickets *Gryllus bimaculatus* with higher mating success sire sons that obtain significantly more copulations than the sons of less successful males. This directly demonstrates that sexual 'attractiveness' is heritable, rather than simply showing that a trait correlated with mating success is heritable. However, the extent to which the benefit of increased attractiveness and hence greater mating success is balanced by naturally selected costs

remains to be seen. For example, the sons of successful fathers had a significantly longer development time.

Finally, studies in related fields, most notably concerning the evolution of immune-defence, the major histocompatibility complex (MHC) and intra-genomic conflict, suggest new benefits to mate choice. In particular, ensuring genetic compatibility (Zeh & Zeh, 1996) and maintaining heterozygosity may be sources of selection on mate choice, equal in importance to those for universal 'good genes', if genetic variation among females creates inconsistency among males in their ability to sire viable offspring (Brown, 1997; Jennions, 1997). In an influential review, Zeh & Zeh (1996) recently promoted the importance of genetic incompatibility. In addition to inbreeding avoidance, they specifically noted that intra-genomic conflict is a source of incompatibility that can potentially reduce female reproductive success. They therefore suggested that polyandry has evolved because it creates greater opportunities for post-copulatory female choice (including differential abortions against incompatible sperm or less viable embryos (Zeh & Zeh, 1997). Genetic incompatibility can be said to occur when certain gamete combinations reduce fitness either due to within-loci effects that are additive (e.g. double recessive lethals) or non-additive (e.g. negative heterosis) or epistatic interactions between loci. Clearly this is an exceptionally broad definition because some genetic combinations are always favoured over others. Genetic incompatibility can therefore be said to be inevitable. To make the term meaningful, we need to focus on its importance to female choice decisions. This will depend on both the strength of selection against certain genotypes, the likelihood that these genotypes will be produced if eggs are fertilized at random and the cost to or ability of females to discriminate. For example, if a recessive lethal is rare it is unlikely to generate much selection for a mating or fertilization preference to avoid males or gametes carrying the allele. Conversely, mating preferences to avoid kin may arise even if inbreeding only has moderately negative effects on fitness, but is likely to occur due to the population structure.

(2) What are the possible genetic benefits of polyandry?

Polyandry is likely to arise when initial constraints prevent females from mating with the genetically most preferred partner. Multiple mating is not itself

selected for, but females 'trade up' and perform additional matings if they subsequently encounter males that are potentially superior genetic sources. Most examples of 'trading up' come from birds, where females pair with a social male for the direct benefits of parental care and access to a nesting site, but perform extra-pair copulations to obtain 'good genes' for their offspring (Møller, 1992, 1997). Females use pre-copulatory mate choice to select subsequent mates.

There may also be selection for multiple mating itself. Pre-copulatory mechanisms that allow females to identify their ideal mates may not exist, either because males can not reliably signal, or females can not readily detect this information. Instead, by mating polyandrously, females may use post-copulatory or *in copula* mechanisms to ensure preferential fertilization by sperm that increase genetic benefits to offspring. Trading up and post-copulatory choice both increase the bias in fertilization towards genetically superior sperm. If females control paternity there should thus be a strong bias in paternity within a clutch or litter towards the most preferred male.

Finally, polyandry may be selected for because it increases genetic diversity among progeny which itself raises offspring fitness; or because females bet-hedge in the absence of reliable pre-copulatory mate choice cues as to which male is genetically their best partner. Comparative studies of mating in ants suggest selection for genetic variability in the colony workforce. Multiply mated queens are common in species where colonies only have a single queen and singly mated queens are common in colonies founded by several queens (Keller & Reeve, 1994; Keller, 1995). Direct experimental studies show that greater genetic variability in a colony decreases parasite loads (Liersch & Schmid-Hempel, 1998; Baer & Schmid-Hempel, 1999), and this provides one proximate explanation for an advantage to greater genetic diversity. More generally, in several species the number of males gaining paternity in a brood exceeds that which can reasonably be accountable for on the basis of females improving on earlier matings or remating to select the best male's sperm (e.g. Kellog *et al.*, 1995).

(3) What is the relationship between genetic benefits, sperm competition and cryptic female choice?

Most explanations for polyandry that are based on genetic benefits require females to exert at least

partial control of paternity. For example, females can not 'trade up' if the first male to mate can guarantee his paternity, or if a female's social mate can fully restore paternity following extra-pair copulation. Nor can they increase genetic diversity if the last male to mate sires most of the offspring. There is, however, greater selection on males to ensure paternity than there is on females to manipulate paternity (Parker, 1984; Knowlton & Greenwell, 1984). As such we might predict that mechanisms of male-mediated sperm competition can fully explain patterns of paternity. Instead, there is increasing evidence from comparative and single-species studies that females play a direct role in determining paternity and are not passive recipients of sperm (e.g. Møller & Briskie, 1995; Bishop, 1996; Price, 1997; Wilson *et al.*, 1997; Clark, Begun & Prout, 1999).

When cryptic female choice occurs male paternity can not be predicted by the traditional method of counting the number of copulations a male performs (Thornhill, 1983). This occurs because female-controlled processes or structures selectively favour paternity by males with a particular trait over that of other males that lack the trait when females have copulated with both types (Eberhard, 1996: p. 7). The role the female plays in 'setting the rules' that influence paternity is therefore considered to be a passive form of choice. This resonates with the recent view that female traits which lead to non-random mating biased towards males that possess certain traits without direct discrimination between males generates a form of indirect mate choice (Wiley & Poston, 1996; Wiley, 1997; Murphy, 1998). Other definitions of cryptic choice are more restrictive. Some argue that cryptic female choice should only be invoked if it accounts for residual variation once the effects of mechanisms of male-mediated sperm competition (such as sperm displacement or flushing and the relative numerical input of sperm) are accounted for (Simmons *et al.*, 1996). The role that standard female processes or morphology play in determining the form of sperm competition is taken as given and not regarded as part of cryptic female choice (Telford & Jennions, 1998). Birkhead & Møller (1998: chapter 17) suggest that a key criterion for cryptic female choice of sperm is that there is variation in last-male paternity, some of which is attributable to females so that variation can be partitioned among males and females. Birkhead & Møller (1998) are correct when they note that cryptic choice occurs if variation among females explains a significant amount of variation in pa-

ternity – but we would argue that this is not a necessary criterion for demonstrating cryptic choice. For example, females may have almost unanimous preferences (i.e. the same paternity-biasing morphology or responses to a given multiple mating scenario) as sometimes occur with pre-copulatory female choice. No one would dismiss the existence of pre-copulatory female choice simply because all the females tested preferred the longest tailed males. The same logic should hold for post-copulatory choice. Moreover, if female preferences based on genetic compatibility are uncommon we actually expect females to show similar preferences for those males that are most successful in sperm competition.

Eberhard (1998) argued that sperm competition almost never occurs without females influencing the outcome, if only because her morphology determines how much sperm is stored and the degree of access males have to sperm stores. (It is encouraging that more realistic models to explain variation in paternity that take into account female effects are now being developed, even though these may yield similar predictions to earlier models based purely on male sperm input, e.g. Simmons, Parker & Stockley, 1999). Eberhard (1998) therefore implies that sperm competition *sensu stricto* is unlikely to occur and that cryptic female choice will always be a factor. Unfortunately, there has been a tendency to equate cryptic female choice with a single mechanism of choice, namely post-copulatory, pre-fertilization selection of sperm so-called sperm selection (Birkhead, 1998). In fact, there are at least 19 other plausible mechanisms of cryptic female choice, several of which are fairly well supported by empirical evidence (Eberhard, 1996). Some of the mechanisms that bias paternity such as differential abortion or changes in the rate of oviposition are actually completely independent of sperm competition as traditionally defined (Simmons & Siva-Jothy, 1998: p. 432). It is therefore perfectly reasonable to say that cryptic female choice and sperm competition can be clearly distinguished in some cases. In truth, however, it may be particularly difficult to distinguish between female choice and sperm competition when addressing many aspects of insemination, displacement and storage of sperm (Simmons *et al.*, 1996). This is similarly true for pre-copulatory mate choice and male–male competition when a wider view is taken (Wiley & Poston, 1996). For example, if two males fight over a female it is ultimately the female indirect choice behaviour 'accept the winner' which determines who mates. This is not to discount the importance of male–male

competition (males still have to win fights), but it does highlight the role the female plays in translating male competitive success into actual mating or fertilization success.

Simmons & Siva-Jothy (1998) and Eberhard (1998) both pointed out that observed fertilization patterns reflect the resolution of conflict between the sexes and the partial control by both sexes of many processes. They differ mainly in the extent to which they think that females can exert an influence. 'Cryptic female choice' and 'sperm competition' are therefore intimately related processes. So what terms should we use to describe processes that influence paternity? In this review, we use the phrase 'post-copulatory paternity biasing' to refer to the range of processes whereby male and female sexual traits influence fertilization patterns and subsequent investment in offspring (for brevity we will not repeatedly write '*in copula* or post-copulatory', even though, in most cases, the former is also possible, see Eberhard, 1996). This term therefore includes sperm competition *sensu stricto*, female-mediated sperm competition, pure cryptic female choice, sperm selection, differential investment in offspring and differential abortion. Post-copulatory paternity biasing, if attributable to specific, heritable male traits, creates the potential for the female to gain genetic benefits because these traits increase the fertilization success of their sons. We also note that cryptic female choice may sometimes select for more equitable genetic contribution from several males regardless of their phenotype (Boomsma, 1996). This might occur when females mate polyandrously to ensure genetic diversity of their progeny. This type of cryptic choice should counter male-mediated sperm competition which otherwise leads to biased fertilization by males that are superior at sperm competition.

Rarely emphasized genetic benefits are essential for the selection and evolution of female mechanisms of post-copulatory paternity biasing. Females will not benefit from biasing paternity unless some sperm produce fitter progeny than others. In the absence of genetic variation for fitness-enhancing traits, females will be indifferent to which male fertilises their eggs and non-heritable traits influencing male-male competition should fully control paternity. Male-female conflict will only arise when male attempts to control paternity impose naturally selected costs on females (e.g. Chapman *et al.*, 1995; Rice, 1996). Ironically, because females will be selected to reduce these costs, the resultant changes in female behaviour or morphology may drive selection on novel male traits that increase paternity. This process is likely to generate

additive genetic variation among males (because more loci have an effect on fitness) and thereby restore the conditions selecting for cryptic female choice, possibly leading to antagonist co-evolution between the sexes (Holland & Rice, 1998). It therefore seems almost inevitable that there will always be the potential for females to gain genetic benefits from post-copulatory paternity biasing (Eberhard, 1996).

(4) What is the relationship between genetic and non-genetic benefits to polyandry?

Of course, females frequently obtain material, fecundity-enhancing benefits from multiple mating. We will not review these as they are well known (Reynolds, 1996). They include: increased parental care because more males have a stake in brood paternity (Nakamura, 1998), greater access to breeding resources (e.g. from mate switching: Birkhead & Møller, 1992), direct protection from male harassment ('convenience polyandry') (Rowe *et al.*, 1994; Stone, 1995; Watson, Arnqvist & Stallmann, 1998), anti-aphrodisiacs that temporarily repel other males (Kukuk, 1985; but for an opposing view see Bubis *et al.*, 1998), male transfer of nutrients or nuptial food gifts that increase female fecundity (Wedell, 1997; McLain, 1998), substances that promote egg maturation and oviposition (Cordero, 1995), avoidance of male punishment (Clutton-Brock & Parker, 1995), decreasing the risk of infanticide (Smuts & Smuts, 1993), formation of social coalitions (Smuts, 1985), preventing other females from mating (Petrie *et al.*, 1992), stimulation of ovulation or increased likelihood of pregnancy (Hoogland, 1998), ensuring fertilization because (a) some males are sterile (Sheldon, 1994; but see Olsson & Shine, 1997) or (b) males invest less sperm than each female requires because they partition their ejaculate among females (Pitnick & Markow, 1994) or (c) there is a reduction of sperm in storage organs due to passive loss (Barnett, Telford & Tibbles, 1995) or sperm mortality (Yamagishi, Ito & Tsubaki, 1992). Ensuring a supply of active sperm is viewed as a direct, not genetic, benefit of polyandry because the absence of sperm reduces fecundity.

Although few studies have rigorously quantified the costs, both mate-searching and the act of mating appear to be costly activities that increase energetic costs or predation risks and are therefore best minimized by females (e.g. Koga *et al.*, 1998; Watson *et al.*, 1998; Holland & Rice, 1999; Section V). The fact that polyandry regularly occurs and is wide-

spread across many taxa is therefore something of a conundrum. One obvious solution to this mystery is that females gain direct material benefit from multiple mating by obtaining resources from more than one male. However, given the potential cost to males of a reduction in paternity it is necessary to explain why natural selection has not favoured those males who succeed in preventing their females from remating by providing them with all the sperm and nutrients needed for their joint reproduction. One reason why males do not invest this much reproductive effort into a single female is when they have the potential to gain a disproportionate share of the available matings. For males there could then be a trade-off between investing in current and future reproductive events (Parker, 1990*a, b*). There is some evidence for such a trade-off in blue headed wrasse *Thalassoma bifasciatum* (Warner *et al.*, 1995) where dominant males that gain a higher number of matings also have lower fertilisation success per mating. Although the potential for further matings might explain why males provide any one female with less resources than she needs, it does not explain why females might mate with a male who provides less resources than they need for reproduction. In blue-headed wrasse, females appear to accept the reduction in fertilization success from dominant males in order to have at least some of their eggs fertilized by the best male.

It is generally true that for a mating strategy to be maintained over evolutionary time it must be evolutionarily stable for both sexes. Females will only be prepared to accept the cost of reduced investment by a particular male if the genetic benefits gained from mating with him outweigh the costs in terms of lowered fecundity (Petrie & Lipsitch, 1994). Thus, if a female is required to remate for material benefits, the genetic benefits from earlier matings must potentially partially offset the costs of remating. Thus, whilst it may appear that females re-mate only for non-genetic benefits because further matings are necessary to ensure her entire reproductive effort, it is clear that genetic differences between males could ultimately be the factor that promoted multiple mating by females in the first instance.

Just because there are readily identifiable material benefits to mating multiply in some cases this does not mean that females are not simultaneously gaining genetic benefits. Females often gain several material benefits from mate choice (e.g. parental care, a nest site and protection from harassment), and there is likewise no reason to suppose that material and genetic benefits can not occur sim-

ultaneously. Mechanisms that select for material and genetic benefits need not show fitness trade-offs (Eberhard, 1996). If females have some control over paternity they may evolve both types of mechanism, especially if the costs of cryptic female choice are small. Once polyandry occurs any variation among males creates the opportunity for post-copulatory paternity biasing. If any of this male variation is heritable then females will gain genetic benefits from polyandry because sons from polyandrous females are better at biasing paternity than the sons of monandrous females whose fathers have not competed in the arena of the female's reproductive tract.

The importance of genetic benefits has been downplayed because of the claim that polyandry is primarily a mechanism to increase fecundity (Ridley, 1988, 1990). It is worth noting that the data showing that animals, especially insects, remate to replenish depleted sperm supplies may be less clear-cut than sometimes thought. The higher fecundity rate (which is fertility \times number of eggs) of polyandrous than monandrous females reported by Ridley (1988) could, for example, be due to the greater likelihood that the latter were inseminated by males with low quality or genetically incompatible sperm. Lower egg hatching rates of monandrous females may be due to sperm depletion or genetic incompatibility (e.g. Tregenza & Wedell, 1998). Conversely, it is also possible to misclassify subtle but material benefits as genetic benefits (Weigensberg, Carrière & Roff, 1998; Savalli & Fox, 1998). This is often a problem when maternal effects are adaptive and mimic patterns expected when offspring inherit 'good genes' (Mousseau & Fox, 1998). Sometimes it is the absence of evidence, rather than the reverse, which leads to the claim that females remate for genetic benefits. When no material benefits can be found, genetic benefits are assumed by default. This is most often the case when males appear to provide only ejaculate to females and do not participate in parental care or provide nuptial or courtship food gifts. This assumption can be erroneous, however, as direct benefits are sometimes very subtle. For example, in the stink bug *Nezara viridula* studies of female choice suggest that the attractiveness of sons is due to non-genetic paternal contributions rather than genetic contributions (McLain, 1998). The sons of females not allowed to choose a mate were equally attractive when the father was a previously accepted (NA) *versus* a previously rejected male (NR). However, they were less attractive than the sons of females allowed to choose between inexperienced males

(CI). Sons from NA and CI matings shared the same fathers and the difference is therefore unrelated to male genetic contribution.

II. IMPROVING ON PREVIOUS MATES BY PRE-COPULATORY CHOICE

Multiple mating may be a consequence of initially mating with a genetically inferior partner. This is most likely to occur when: (a) there are costs to locating, assessing or acquiring males; (b) the reproductive season is limited; (c) offspring produced later are of lower quality due to environmental effects; (d) early mating confers direct benefits to females; (e) refusal to accept a mating is costly, as it may lead to forced copulation. Early matings may therefore occur to guarantee a sperm supply, to ensure timely access to material benefits or to avoid the costs of mate refusal. The costs of locating and obtaining the ideal mate could be environmentally imposed, and apply uniformly to all females; or vary between females depending on their ability to withstand environmental and social costs (Jennions & Petrie, 1997). If costs vary then females in better condition are less likely to mate multiply because they are more likely initially to acquire a high quality mate. In pair-bonded species, a female may not be attractive or competitive enough to pair with their ideal partner if male mate choice or female–female competition determine pairing patterns (Møller, 1992; Petrie & Hunter, 1993). Lower quality females may therefore be forced to seek additional matings even though they pay higher costs. The potential for natural variation in female quality to obscure the causal relationship between levels of polyandry and offspring quality should therefore caution us against inferring the benefits of polyandry from correlational studies.

Socially monogamous species are most likely to provide evidence of remating for ‘genetic improvements’. To date, almost all the available examples come from extra-pair paternity in birds with biparental care. In the majority of birds, successful reproduction requires biparental care and female–female competition tends to limit male polygamy (Sandell & Smith, 1996; Sandell, 1998). Many females must therefore pair socially with genetically inferior males. This should select for extra-pair copulations (EPCs) with males more attractive than their social partner. Indeed, numerous field studies of birds show that females are more likely to perform an EPC or switch mates to more attractive or

dominant males (e.g. Bollinger & Gavin, 1991; Houtman, 1992; Graves, Ortega-Ruano & Slater, 1993; Møller, 1994*b*; Mulder *et al.*, 1994; Sundberg & Dixon, 1996; Hasselquist, Bensch & von Schantz, 1996; Kempnaers *et al.*, 1997; Saino *et al.*, 1997; Otter *et al.*, 1998; Johnsen *et al.*, 1998; Sheldon & Ellegren, 1999; but see Hill *et al.*, 1994; Rätti *et al.*, 1995; Strohbach *et al.*, 1998). There is similar evidence from at least one mammal. Some socially monogamous Allied rock wallaby (*Petrogale assimilis*) females engage in extra-pair copulations. The available evidence suggested that genetic benefits may be responsible for some females mating polyandrously (Spencer, Horsup & Marsh, 1998). Additional data on the prevalence of EPCs and attempts to relate this to male quality in other socially monogamous taxa with biparental care would be illuminating. For recent mammalian and reptilian examples see Goossens *et al.* (1998), Topping & Milla (1998), and Bull, Cooper & Baghurst (1998).

Constraints imposed by long-term pair formation and biparental care are not essential requirements for remating for genetic benefits. For example, in smooth newts (*Triturus vulgaris vulgaris*) 79% of singly mated females accepted a spermatheca from a second male with a larger dorsal crest than their original mate, but 0% accepted when the second male’s dorsal crest was smaller than that of the first male (Gabor & Halliday, 1997). Crest size is a condition-dependent character (Green, 1991) suggesting that females accepted an additional spermatheca for genetic benefits. Unfortunately, there is frequently a problem in detecting ‘genetic trading up’ in species without stable pair-bonds because remating also confers material benefits. For example, many insects remate sooner when a previous male transfers fewer nutrients or less sperm (Bissoondath & Wiklund, 1997; Sakaluk, 1997; Wedell & Cook, 1998). If there is a positive correlation between a presumed index of male genetic quality and the material benefits provided (males with good ‘viability genes’ are usually in better condition), it may be difficult to determine whether females remate for genetic or material benefits. The observed mating pattern is one of females initially mated to phenotypically inferior males being more likely to remate. In such cases, parsimony is usually invoked and the explanation is framed solely in terms of material benefits. Unfortunately, evolution need not be parsimonious. It is thus essential to test whether males that provide larger gifts or transfer more sperm also raise offspring fitness *via* their genetic contribution.

(1) Viability and attractiveness genes: model definitions, pitfalls and evidence

Some fathers may be better than others because they possess genes that increase the viability of sons and daughters and/or the mating or fertilization success of sons. Consequently, numerous theoretical models have been developed which show that female choice can evolve *via* indirect selection for genetic gains that increase offspring fitness, even if there are naturally selected costs that directly decrease choosy female's lifetime fecundity (reviews: Andersson, 1994; Møller, 1994*b*; Johnstone, 1995). There are four main models, but several processes may operate simultaneously.

(A) *Fisherian run-away models*: an initial female preference for a male trait reaches a threshold frequency in the population that selects for more ornamented males. Females that mate with more ornamented males produce more attractive sons who also carry the genes for the mating preference for more ornamented males. A genetic correlation is therefore established between genes for the female mating preference and the preferred male trait because non-random mating creates linkage disequilibrium (e.g. Pomiankowski *et al.*, 1991). This genetic correlation will lead to a positive feedback whereby sexual selection on male attractiveness indirectly selects for the female preference genes because they are more likely to be carried by attractive males. Male traits need not be indices of general viability and are often described as 'arbitrary' traits. Balmford & Read (1991) have, however, pointed out that a trait that evolved *via* Fisherian runaway may ultimately evolve condition-dependence. If this leads to the trait signalling viability (see below), the potential for conflict between historical *versus* current functional explanations for traits arises. Female preferences and male traits must both be heritable. Female choice increases their sons' attractiveness.

(B) *Viability indicator models*: some females prefer males with traits that are honest indicators of heritable viability. Female choosiness therefore increases because of indirect selection due to greater offspring viability (Pomiankowski & Iwasa, 1998). Coevolution of the female mating preference and preferred male trait then occurs (e.g. Iwasa *et al.*, 1991). A major assumption of this model is that males can honestly signal their genetic viability (Johnstone, 1995). Female choice increases their sons' and daughters' viability as well as their sons' attractiveness.

(C) *Sensory exploitation models*: a pre-existing, static female sensory bias selects for male traits that increase sexual attractiveness (West-Eberhard, 1984; Ryan, 1990, 1998). The female mating preference evolves as a pleiotropic effect of natural selection on the female sensory system (e.g. Christy, 1995). The female mating preference does not evolve in response to changes in the male trait and a genetic correlation is therefore not established. Endler & Basolo (1998) argue that sensory drive models, of which sensory exploitation is only one example, allow for genetic correlations. Historically this view has not been widely held, however, at least with respect to sensory exploitation which has emphasised preference stasis. It is also unclear which sensory drive models should be considered genuine alternatives to the other three models we describe here. Endler & Basolo (1998) suggest that none are 'realistic' alternatives, but others have presented them as such (e.g. Shaw, 1995). The male trait need not indicate viability. Female choice increases their sons' attractiveness if preferred male traits are heritable.

(D) *The antagonistic seduction model*: a pre-existing female sensory bias selects for a male trait that enhances attractiveness or male competitiveness, but also leads to females mating sub-optimally (e.g. too soon, too often, at a less-than-ideal place or time). This creates counter-selection for female resistance (reduced preference) for the trait. Continuing cycles of male trait elaboration to overcome female resistance and higher mating thresholds in females results in antagonistic coevolution (Holland & Rice, 1998). This model therefore predicts coevolution between the sexes, but the direction is opposite to that in Fisherian and viability gene models, because females with a greater preference for the male trait produce less attractive sons. This model can only be tested using information on the historical sequence of events. Recent discussion of this model can be found in Getty (1999), Rosenthal & Servendio (1999) and Rice & Holland (1999). The main question seems to be whether 'resistance' can be defined in such a way that it is distinct from a preference. Female resistance to seductive male signals increases their sons' attractiveness.

A common prediction if a trait has evolved by Fisherian, viability indicator or antagonistic seduction models is the existence of a genetic correlation between female mating preference and genes for preferred male traits (e.g. Iwasa *et al.*, 1991). There is supporting evidence for a genetic correlation between female mating preference and preferred male trait genes in guppies, seaweed flies,

stickleback and stalk-eyed flies (review: Jennions & Petrie, 1997). It is argued that the strength of indirect selection *via* genetic benefits is likely to be very weak compared to direct selection on female preferences to maximise fecundity (Burt, 1995; Kirkpatrick, 1996; Kirkpatrick & Barton, 1997), but only empirical data can resolve this debate.

As noted previously, the heritability of secondary sexual characters, like that of life-history traits, may generally be low because of high environmental variance due to condition-dependent expression (Price & Schluter, 1991; Rowe & Houle, 1996). This strong environmental effect is sometimes described as 'swamping' the ability of females to distinguish males on the basis of genotype (Cordero, 1998). In fact, if there is positive covariance between genotype and environment (i.e. males with better genes gain access to more resources), it may be easier for females to identify genetically superior males. In the last decade, estimates of the heritability of secondary sexual traits have increased significantly. The reasons for this trend remain unclear and may be related to superior experimental design, choice of study animal or publication bias (Alatalo *et al.*, 1997; Tregenza & Wedell, 1997). More important than heritability, however, is the coefficient of variation for additive genetic variation (Houle, 1992). Recent breeding studies and artificial selection experiments provide evidence that male secondary sexual traits subject to female choice have higher levels of additive genetic variance than naturally selected traits (review: Pomiankowski & Møller, 1995). The estimated level of variance may be inflated, however, because several of these studies do not adequately control for common environmental effects between parents and offspring, or maternal effects. If the degree of variance estimated is correct though, Rowe & Houle (1996) estimate that there is the potential for a 1% change per generation in response to linear directional selection.

One problem for viability gene models is whether male sexual traits can reliably signal underlying genetic viability to females. By definition, these traits must be handicaps that act as honest indicators (Johnstone, 1995). Despite nearly two decades of research, experimental evidence that traits have the properties of handicaps is almost completely lacking. The main problem is that experimental manipulation of investment in traits is required, but it is technically difficult to adjust trait size in a biologically meaningful manner – especially when there are correlated changes in other body parts, physiology, hormone levels and so on. Instead, the

main focus has been to test whether male ornamentation or display is correlated with offspring viability, survivorship or a close correlate thereof. In the last five years, positive evidence has started to accumulate for fairly strong relationships in some species (e.g. Norris, 1993; Petrie, 1994; Moore, 1994; Møller, 1994*b*; Hasselquist *et al.*, 1996; Sheldon *et al.*, 1997*a*; Welch *et al.*, 1998; Hoikkala, Aspi & Suvanto, 1998). In other species, there is either the absence of, or even a weakly negative correlation, between male secondary sexual traits and offspring viability (e.g. Simmons, 1987; Semlitsch, 1994; Nicoletto, 1995; Parri, Alatalo & Mappes, 1997). A recent meta-analysis of the available studies suggests that there is a small but significant positive relationship ($r = 0.10$) between the expression of male secondary sexual traits and offspring survivorship due to inheritance of 'viability genes' (Møller & Alatalo, 1999). None of these studies control for differences in coefficients of relatedness between parents. Some of these studies do not fully control for confounding variables such as maternal quality or parental investment, subtle forms of male–male competition and environmental factors that may also generate a positive relationship. Depending on the species, however, more attractive males may invest disproportionately more or less in parental care (Møller & Thornhill, 1998*b*). The overall positive relationship between male attractiveness and offspring survival is therefore unlikely to be attributable solely to variation in male parental investment.

Another explanation for the positive relationship between male attractiveness and offspring survival is that females mated to more attractive males invest disproportionately more in their offspring. Møller & Thornhill (1998*b*) have suggested that artificial insemination will be required to control for possible variation in maternal effects due to female assessment of male attractiveness. Even then, post-copulatory signalling may indicate male quality and result in differential investment in offspring by females. Greater investment by females in the offspring of certain males may then be considered a phenotypic effect of the offspring bearing genes from more attractive males (Sheldon, 1999).

A potential difficulty when testing viability models is that sons may inherit good viability genes, but still have lower survivorship than males with worse viability genes. This occurs if the benefits of increased investment in attractiveness (which is only possible for males in good condition) outweigh any reduction in survivorship (Grafen, 1990). One solution is only

to examine survivorship prior to investment in sexual traits although it may be impossible to determine when such investment begins during ontogeny. Another solution is to look only at the survivorship of daughters (Yasui, 1998). Finally, there has been a tendency to examine only offspring fitness at the juvenile stage (Promislow, Smith & Pearse, 1998, provide a notable exception). Ideally, one would like to determine the lifespan, mating success and total reproductive output of offspring. Given that the effects of selection decline with increasing age however, it seems unlikely that antagonistic selection can overcome the observed benefits of greater survival during juvenile stages. Moreover, a recent meta-analysis suggests that more attractive males (those with larger sexual ornaments) rarely invest so much in a sexual trait as to decrease their adult survivorship (M. D. Jennions, A. P. Møller & M. Petrie, unpublished study). Evidence for a negative trade-off between juvenile and adult survival is therefore lacking.

(2) What is the evidence that females improve on previous mates for 'viability' or 'attractiveness' genes?

Invertebrates may provide examples of genetic trading up, but the confounding effect of material benefits (hidden or obvious) may make it difficult to assess the possible role of genetic benefits without carrying out heritability studies (e.g. Weigensberg *et al.*, 1998). Thus, with a few exceptions (e.g. Gabor & Halliday, 1997; Spencer *et al.*, 1998), all the available data come from studies of extra-pair copulations (EPCs) in birds. EPCs do not generally appear to provide direct benefits to females (but see Gray, 1997*a, b*). They may even lower female fecundity (Weatherhead *et al.*, 1994), especially if males decrease parental care when they have a smaller share of paternity (e.g. Dixon *et al.*, 1994; Sheldon & Ellegren, 1998). Several lines of evidence suggest EPCs in birds are for genetic benefits.

(1) A meta-analysis of paternity in birds indicates that males with more elaborate secondary sexual traits have higher paternity in their own nests, presumably because their mates are less likely to engage in EPC (Møller & Ninni, 1998). Given the general finding that males with high own-nest paternity are more likely to be sought out for EPC, this also suggests that males with more elaborate secondary sexual traits engage in more EPCs. Male survival prospects were also positively associated with paternity in own nest. Many individual studies

have shown that extra-pair mates are significantly older, more dominant or more attractive than social mates. Although some studies do not report this effect (e.g. Perreault, Lemon & Kuhnlein, 1997; Strohbach *et al.*, 1998), it is notable that few show a significant reverse trend (e.g. Lifjeld *et al.*, 1997). Multiple mating *via* EPC is therefore likely to increase offspring attractiveness.

(2) In some species, attractive males invest more in parental care than unattractive males and there is a direct benefit to pairing with an attractive male. In contrast, in other species more attractive males invest less in parental care. Females must then compensate and invest relatively more in parental care when paired to an attractive male. Møller & Thornhill (1998*b*) found that the latter species have higher levels of extra-pair paternity (EPP) than the former. Thus, the species in which females sacrifice male parental care to mate with more attractive males appear to be the ones in which there is more EPC (which is the main source of EPP). This is consistent with the claim that females in these species gain genetic benefits from mating with more attractive males to compensate for the loss in direct fitness benefits due to reduced male care.

(3) Comparative studies of birds indicate that extra-pair paternity is higher in species or populations with greater genetic variability (Petrie, Doums & Møller, 1998). All else being equal, EPP should decrease rather than increase genetic variability as it increases the variance in male reproductive success compared to that based on counts of nestlings (Møller & Ninni, 1998; but see Perreault *et al.*, 1997, for a counter-example). This increase in variance is due to non-random mating with respect to male phenotype because males with larger sexual traits are less likely to be cuckolded (Møller & Ninni, 1998) and more likely to seek EPC (Stutchbury, 1998). The effective breeding population size is therefore reduced as fewer males contribute genetically to the next generation (Petrie & Kempnaers, 1998), although the reduction in effective population size may be fairly small (Waite & Parker, 1997). One explanation for the positive relationship between EPP and genetic variation is that there is greater variation in potential genetic benefits to EPC when males differ widely in genetic composition (Petrie & Lipsitch, 1994). The value of individual studies relating levels of EPP or EPC to differences in genetic variation between two populations will depend on the rapidity with which female EPC rates evolve in response to changes in genetic variation. Additionally, if the evolutionary relationship is

mediated by the level of phenotypic variation among males (females are less likely to remate the lower the variation among males) then, in some cases, high levels of EPC may occur even when there is little genetic variation. High levels of phenotypic variation may be due to strong environmental effects.

(4) Comparative studies show that EPP in birds is positively correlated with plumage brightness. More sexually dichromatic species show higher levels of EPP (Møller & Birkhead, 1994). Owens & Hartley (1998) recently extended this analysis and showed that, in particular, structural colour dichromatism is associated with EPP. This provides corroborating evidence that females direct EPC towards more highly ornamented males and that over evolutionary time this has selected for an increase in male ornamentation to attract females for EPC. This finding could also be due to direct benefits of EPC with more ornamented males such as fertility insurance (Sheldon, 1994). However, most studies that have looked have failed to find fertility benefits (e.g. Kempenaers *et al.*, 1996; Olsson & Shine, 1997), while genetic benefits have now been shown for several species (review: Petrie & Kempenaers, 1998).

(5) In blue tits (*Parus caeruleus*) and pied flycatchers (*Ficedula albicollis*) offspring production is male-biased when females pair with males that are sexually more attractive (Svensson & Nilsson, 1996; Ellegren, Gustafsson & Sheldon, 1996). There is abundant evidence from insects, especially parasitoids, that parents bias sex allocation towards the sex with the greatest potential fitness benefits (Charnov, 1982; Godfray, 1994). The bird examples therefore suggest that attractiveness is heritable and EPC leads to the production of sons of above-average attractiveness. In pied flycatchers, the preferred sexual character of forehead patch size is heritable (Sheldon *et al.*, 1997a), comparable information does not exist for blue tits. There is no evidence that females bias the primary sex ratio of offspring from extra-pair males towards sons (Westneat, Clark & Rambo, 1995; Sheldon & Ellegren, 1996), but this would require a highly specialised mechanism for the control of offspring sex.

(6) There is a positive correlation between sexual dichromatism and spleen size. As already noted, EPP in birds is also positively correlated with sexual dichromatism. Møller (1997) found that spleen size and sexual dichromatism are independent predictors of levels of EPP in birds. Spleen size is an index of the efficiency of the immune system because larger spleens produce a greater immune response. Thus, females in species exposed to high levels of parasitism

and disease seem to be more likely to engage in EPC. This suggests that EPC may be more strongly sought when there are larger gains to be made from obtaining viability genes that increase offspring resistance to parasites and other infections. The use of data on spleen size or the bursa of Fabricius is an improvement over earlier studies that used counts of parasites as an index of the immune challenge faced by a species. Parasite counts are likely to be poor estimates of abundance and there are logistic constraints on the number of parasitic taxa that can feasibly be examined. It is possible that the positive correlation between sexual dichromatism and spleen size is due to stronger sexual selection causing greater exposure to parasites and thereby selection for larger spleen size. However, the independent predictive power of sexual dichromatism and spleen size to explain variation in EPP suggests that greater spleen size may not be a simple correlate of stronger sexual selection.

In sum, field studies of birds show that females generally remate with more attractive males. Interestingly, birds seem to provide higher estimates of the genetic contribution of males to offspring performance than do studies of other taxa (Alatalo *et al.*, 1998). As such, the fact that almost all evidence for 'trading up' comes from birds should caution us about extrapolating to other taxa. There is a clear need for more data on patterns of extra-pair mating in other taxa, or of remating in non-pair-bonded species.

(3) Genetic compatibility: an alternative basis for improving offspring fitness

In the preceding sections, we made reference to general 'good genes' that increase offspring attractiveness or viability. This assumes that all females in a population benefit from mating with certain males. This is almost certainly wrong. There is every reason to believe that the ideal genetic partner varies among females. In particular, as Zeh & Zeh (1996) first noted in a recent review, genetic antagonism and intra-genomic conflict are taxonomically widespread and sometimes persistent sources of genetic incompatibility between potential mates. They therefore suggested that this may select for female mate choice on the basis of male and female genotypes, rather than an unvarying female preference for the same 'good genes'. Male-female pairings yield offspring that are either more or less genetically compatible and this can have major effects on offspring fitness.

(a) *Genetic relatedness between mates*

Variation in the genetic suitability of mates is most simply illustrated by the phenomenon of inbreeding depression. Inbreeding may lower offspring viability because it: (a) reduces overall heterozygosity that is itself advantageous, (b) increases the phenotypic expression of deleterious recessive alleles, or (c) leads to negative epistatic interactions between homozygous loci (Thornhill, 1994; Olsson, Gullberg & Tegelström, 1996*b*; Brown, 1997). There are few data on the effects of inbreeding in the field and these are confined to a limited number of taxa (mainly plants, birds and mammals). Recently though, evidence that inbreeding results in abortion, stillborn or otherwise inviable offspring in wild animals has started to accumulate (Stockley *et al.*, 1993; Bensch, Hasselquist & von Schantz, 1994; Keller *et al.*, 1994; Jiminez *et al.*, 1994; Olsson *et al.*, 1996*b*; Kempnaers *et al.*, 1996). There are even recent field data that inbreeding may increase the risk of population extinction (Saccheri *et al.*, 1998). There is also a positive relationship between heterozygosity and developmental stability, as measured by fluctuating asymmetry (Møller & Swaddle, 1997). This provides further evidence that inbreeding reduces offspring fitness, because greater symmetry is generally correlated with higher mating success (Møller & Thornhill, 1998*a*; Thornhill & Møller, 1998) (for a very different view see Houle, 1998*b*). Outbreeding depression may also occur, but this is less often studied in animals (Rätti *et al.*, 1995). The main point is that relatedness between potential mates may be as important as inheritance of genes for greater attractiveness or viability in determining offspring fitness and female mating behaviour.

(b) *Intra-genomic conflict and self-promoting elements*

On-going research on selfish genetic elements continues to reveal nuclear genes and cellular endosymbionts that affect sperm production, offspring sex ratios and viability. In most cases, the effects on offspring vary depending on parental genotype or the presence of cellular endosymbionts. The ability of females to identify male genotype or the presence of cellular endosymbionts would allow them to avoid mating with incompatible males. Here, we briefly list the main factors responsible for genetic incompatibility between mates. For more detailed reviews we recommend Hurst, Atlan & Bengtsson (1996; especially Figs 1–5), Zeh & Zeh (1996) and Partridge & Hurst (1998).

(i) *Segregation distorters*

Pre-zygotic segregation distorters act to increase their proportional representation in gametes. They do this either by inhibiting or killing gametes-carrying allelic alternatives (inhibitor distorters), or by manipulating meiosis so that they are over-represented (over-replicating distorters). In some cases, the locus in question is on a sex chromosome in which case the driving allele becomes a sex ratio distorter. These distorters are taxonomically widely distributed from fungi and plants to insects and mammals. Examples include the meiotic drive alleles at the SD locus on chromosome 2 of *Drosophila* spp., the *t*-complex on chromosome 17 in house mice and sex distorters in *Drosophila quinaria* (Jaenike, 1996). The main costs of these distorters are a reduction in sperm production by heterozygous males that decreases their fitness, especially if females are polyandrous (Haig & Bergstrom, 1995), and sterility, reduced viability or death for homozygotes of both sexes. Nuclear genetic suppressors of distorters are known to occur (Hurst *et al.*, 1996). Females, especially when they are heterozygous, should therefore be selected to choose males without the drive allele, and males with suppressors. The notion that females can identify male genotype for distorters and suppressors may seem fanciful, but there are at least two known examples. In the stalk-eyed fly (*Cyrtodiopsis dalmanni*), male eye span is an indicator of the presence of a suppressor of sex ratio distortion. Females that mate with males with wider eye spans have higher fitness because they produce more sons in a population with a female-biased sex ratio due to an X-linked meiotic drive allele (Wilkinson, Presgraves & Crymes, 1998). Females can therefore detect the suppressor allele. In house mice, females heterozygous at the *t*-locus preferentially mate with homozygous wild-type males thereby avoiding the production of inviable *t/t* offspring (Lenington, 1991; Silver, 1993). Females therefore possess the ability to detect the drive allele in males.

(ii) *Maternal-effect lethals*

These alleles function as post-zygotic distorters. They act to kill zygotes that lack the drive allele. Two examples are *Medea* in mealworm beetles and *Scat* in mice (Thomson & Beeman, 1999; Peters *et al.*, 1990; Hurst 1993*b*). The allele does not kill progeny when it is inherited from the father. However, when heterozygous females mate with wild-type males, progeny homozygous for the wild-type allele are killed. There are no known modifiers or suppressors.

There should therefore be selection for heterozygous females to mate with males (ideally homozygotes) that possess the lethal allele.

(iii) Genomic imprinting

Sperm competition and selection show that sexual selection continues after copulation. Sexual selection also continues post-fertilization if females invest more heavily in some offspring than others depending on the males attractiveness or 'persuasiveness' (Møller & Thornhill, 1998*b*) or differentially abort offspring (Eberhard, 1996). This raises the possibility of male–female conflict over investment in offspring. Queller (1994) noted the general similarity between parent–offspring and male–female conflict. More importantly, he pointed out that in some instances parent–offspring conflict may directly reflect inter-sexual conflict. For example, genomic imprinting leads to differential expression of genes depending on which parent they are inherited from (Reik & Surani, 1997). Paternally inherited genes may be expressed to enhance offspring growth at the mother's expense, while maternally inherited genes may be expressed to counter the effect of the paternally inherited gene (Moore & Haig, 1991; Burt & Trivers, 1998). For example, in house mice only the paternal copy of the *Igf2* gene is expressed. This transcribes the insulin-like growth factor IGF-II that increases nutrient transfer to offspring. In contrast, only the maternal copy of the *Igf2r* gene is expressed. The transcription product of this gene assists in the degradation of IGF-II (Haig & Graham, 1991). If there is genetic variation in the extent to which paternally derived genes promote nutrient transfer and maternally derived genes retard transfer then genetic incompatibility will occur whenever the two sets of genes differ excessively in their relative strength. The variability in factor production seems to be due to modifier loci rather than allelic variation among the imprinted genes themselves (Zeh & Zeh, 1996). There should thus be selection for females to mate with males whose imprinted genes do not promote excess or inadequate nutrient transfer to offspring relative to that of their own imprinted genes. Interestingly, some recent models suggest that multiple paternity (hence multiple mating) is a prerequisite for imprinting (references in Spencer, Clark & Feldman, 1999).

(iv) Cellular endosymbionts

These bacteria, protists and viruses are usually sex ratio distorters because they can only be transmitted

through females (they are not carried by sperm). They therefore act to increase the number of host females. This is achieved either by killing male embryos, so that maternal resources are reallocated to daughters, or by feminizing male embryos. The former process is clearly more detrimental to parental fitness. Even in the latter case, as the population sex ratio becomes more female biased there is selection on parents (i.e. nuclear genes) to restore the sex ratio to 1:1 (Charnov, 1982; Godfray, 1994). In crustaceans, nuclear suppressor genes of cytoplasmic feminizers exist. There is also some evidence for nuclear genes in both sexes that reduce the expression of male-killing endosymbionts in *Drosophilla* spp., but their effects are weak (Williamson & Poulson, 1979). In both cases, females should be selected to mate with males possessing nuclear genes that reduce endosymbiont effects. There are also male-transmitted factors that masculinize offspring (for a general review of endosymbionts see Hurst, 1993). Generally, there should be selection for female mate choice for uninfected males when females are themselves uninfected and for males with suppressors when females become infected.

Finally, the maternally inherited bacteria *Wolbachia*, although they do not cause sex ratio distortion, are responsible for cytoplasmic incompatibility. Mating between uninfected females and infected males produces inviable embryos. All other matings proceed normally. There are no known nuclear modifiers, possibly because the rate at which it spreads is so rapid. The only advantage of mate choice comes from uninfected females avoiding matings with infected males. In mealworm beetles (*Tribolium confusum*), however, females do not appear to discriminate against infected males (Wade & Chang, 1995).

(v) Transposable elements

These genetic elements ('transposons' like *P*, *hobo* and *mariner* in *Drosophila* spp.) either duplicate themselves or use the host's genetic system to make copies and then insert themselves into the genome (e.g. Maruyama & Hartl, 1991; Boussy & Daniels, 1991). If they insert into functional genes this may have disruptive, mutagenic effects (Hurst, Hurst & Johnstone, 1992). Replication within somatic tissue does not lead to increased representation in future generations though, and this is probably why most duplication occurs in the germline. As such, it may benefit the organism to remove this 'junk DNA'. This excision mainly occurs in somatic cells. Because

transposons can decrease organism fitness there is selection for factors that reduce their rate of duplication. Evidence for these ameliorating factors comes from hybrid crosses between strains with and without transposons. In reciprocal crosses, females from the strain lacking transposons (and by implication suppressors) produce offspring of lower viability when mated to males from the strain with transposons. The suppression of transposons appears to be due to both nuclear genes and cytoplasmic elements (Zeh & Zeh, 1996). As such, there should be selection on females either to avoid males with high levels of transposons and/or to mate with males with nuclear or cytoplasmic suppressors.

(vi) *Sex-determining nuclear genes*

Complementary sex determination (CSD) occurs in many haplodiploid hymenopterans and leads to the production of sterile, diploid males. The system is complementary because it is the combination action of two alleles that determines gender. There are no sex alleles as such. In the simplest case, there is a single CSD locus and diploid homozygotes develop as sterile males. In more complex cases, there is multilocus CSD and homozygosity at any of several loci leads to diploids developing as sterile males (review: Cook & Crozier, 1995). In general, there should thus be selection on females to avoid matings that might result in sterile diploids.

(c) *Heterosis*

The seaweed fly (*Coelopa frigida*) has an inversion on chromosome I that is responsible for most of the additive genetic variation in male body size: $\alpha\alpha$ are large, $\beta\beta$ are small and $\alpha\beta$ are intermediate in size (Day *et al.*, 1996). There is strong heterosis and homozygous females that mate with homozygous males of the opposite inversion type maximise offspring viability. There is, however, also close genetic linkage between female mating preference genes and male size genes which both occur on the inversion (preventing recombination) making Fisherian runaway more likely. At locations where there is a high tidal range population crashes occur more often. These crashes reduce the strength of the genetic correlation between female preference and male trait (Nichols & Butlin, 1989) and make indirect Fisherian benefits to female choice less likely. As such, female choice for large males for Fisherian gains should be less likely in populations with high tidal ranges. Consistent with this, in

populations with high tidal ranges, $\beta\beta$ females prefer larger males (i.e. $\alpha\alpha$ males), but $\alpha\alpha$ females are more likely to mate with intermediate or smaller males. This disassortative mating increases the likelihood of producing fitter $\alpha\beta$ offspring. At sites with lower tidal ranges, however, all female genotypes prefer to mate with larger males. This reduces the likelihood that $\alpha\alpha$ females will produce heterozygotic progeny, but they are more likely to produce larger, more attractive $\alpha\alpha$ sons. The indirect, genetic benefits of mate choice therefore vary among populations (review: Gilburn, Crean & Day, 1996). Even though the measured genetic benefits of female choice were very small, this example illustrates that mate choice for heterozygosity can occur when there is a phenotypic cue of genotype.

(d) *Genetic antagonism*

If female *Drosophila melanogaster* are prevented from co-evolving with males then, within 32 generations, there is a reduction in female survival which is related to an elevated rate of remating and higher mortality per insemination (Rice, 1996). Females did not gain fecundity benefits to compensate for reduced lifespan. Moreover, in an artificial-selection experiment, Holland & Rice (1999) showed that enforced monogamy (which removes any conflict between male and female reproductive interests) increased female longevity and reproductive output relative to that of lineages where females were placed with three competing males. This demonstrates that male traits have negative effects on females, to the extent that they reduced the population's total reproductive output. In an earlier study, Rice (1992) showed the reverse effect by forcing a segment of the genome to be transmitted only from mothers to daughters. Over 29 generations of artificial selection, this segment had increasingly detrimental effects on male fitness. In a similar vein, Rice (1998) created a 'virtual Y chromosome' from 99% of the haploid genome. After 40 or so generations of Y-chromosome-like segregation (i.e. male-limited segregation), this portion of the genome accumulated genes that increased male fitness at a cost to female fertility and survivorship (when compared to females mating with control-line males). This demonstrates that genes selected for when they are expressed in males may evolve even though they are selected against by females. One likely cause of the increased female mortality is the effect of more virulent male seminal substances that increased male paternity at the expense of reducing female lifespan (Chapman *et al.*,

1995; but for a criticism of this study see Eberhard, 1998, p. 106). In general, there appears to be continuous co-evolution because of sexual antagonism between alleles at different (sex-limited) loci and selection for traits that increase male and female fitness, respectively (Holland & Rice, 1998; Parker & Partridge, 1998). Any gene that increases male fitness, even at a cost to female fitness, will be selected for in males and against in females and *vice versa*. Because a continual 'arms race' or 'internal Red Queen' situation arises (Rice & Holland, 1997), this may maintain high levels of genetic variation and as such females may benefit by choosing males with more compatible genes.

(e) *The immune system*

The major histocompatibility complex (MHC) is a set of polymorphic genes coding for glycoproteins in the T-cell-mediated immune system (Potts & Wakeland, 1993). Specific MHC haplotypes may confer greater resistance to certain diseases (review: von Schantz *et al.*, 1996), and MHC heterozygosity may increase fitness by conferring greater resistance to a broader range of diseases (although not necessarily to specific single diseases). Female mating preferences for specific MHC haplotypes have been found in rodents, humans and birds, but not sheep. These are apparently based on odour perception (review: Rüllicke *et al.*, 1998) or sexual trait size (von Schantz *et al.*, 1996). Female preferences for dissassortative mating that increases MHC heterozygosity have also been reported in mice (e.g. Potts, Manning & Wakeland, 1991) and North American Hutterite communities (Ober *et al.*, 1997). Therefore, female mating preferences for MHC haplotypes may be influenced by both the female's genotype and that of her potential mates. Recently, there has been mounting evidence that familial imprinting (rather than self-assessment) may be the proximate mechanism by which females acquire MHC mating preferences (references in Owens, Rowe & Thomas, 1999). It is worth noting though that this 'non-genetic' proximate mechanism does not invalidate the claim that female preferences will generally reflect their own genotype. Indeed, it is only when experimental, but unnatural, situations such as cross-fostering are employed that the non-genetic basis of these preferences is detected. There are, however, more profound implications with regards to the ways in which preferences will evolve (Owens *et al.*, 1999). Recent detailed reviews of the MHC can be found in Apanius *et al.* (1997) and Penn & Potts (1999).

(4) What evidence is there that females remate to improve genetic compatibility?

Parker (1992, p. 395) stated: 'to expect selection to produce mate choices which take account of the combined result of a female's genotype and that of her suitor is indeed to have faith'. This is an overly pessimistic view. Females can obtain pre-copulatory clues as to a male's genetic compatibility. Female mice and stalk-eyed flies discriminate against males with loci that effect pre-zygotic segregation (Silver, 1993; Lenington, Coopersmith & Erhart, 1994; Wilkinson *et al.*, 1998). Female rats, mice and humans preferentially choose males with different MHC haplotypes to their own (Potts *et al.*, 1991; Brown, Roser & Singh, 1989; Wedekind & Furi, 1997). Female seaweed flies choose males that differ at a chromosomal inversion increasing the likelihood of heterosis (Gilburn *et al.*, 1996), and females in many taxa exhibit kin recognition and may preferentially mate with less closely related individuals (Thornhill, 1994). The possibility therefore exists that females can identify genetically more compatible males and improve on previous matings. To our knowledge, however, there has been no direct examination of female remating behaviour for greater genetic compatibility in species where appropriate pre-copulatory choice has been reported. For example, if a female mouse is initially mated with a homologous haplotype MHC male, is she more likely to remate when subsequently offered a male with a different haplotype than is a female whose first mate had haplotype different to her own? This is a straightforward experiment.

At present there is little evidence for female pre-copulatory choice to avoid self-promoting elements or genes associated with sexual antagonism. One explanation is that males gain little (or even lose) by advertising their genetic identity to females. In general, because males only make a small parental investment and are usually not sperm limited, they still benefit from mating, even if the offspring are of low fitness (Parker & Partridge, 1998). Post-copulatory mechanisms of female choice may be more successful at detecting genetic compatibility though because males can not disguise their identity as easily (Zeh & Zeh, 1997).

Studies of inbreeding avoidance provide the strongest evidence that females remate to improve genetic compatibility in offspring. In some species, constraints on dispersal lead to females being socially paired with close relatives. As such, extra-pair or extra-group mating may reduce the risk of in-

breeding depression. For example, in group-living, cooperatively breeding Simien wolves (*Canis ethiopia*) the breeding female mates with both the resident alpha male and neighbouring males. Dispersal is rare and within-pack matings are likely to be between close kin (Sillero-Zubiri, Gottelli & Macdonald, 1996). Females, however, pursue extra-group matings with both dominant and subordinate males, suggesting that these matings are not simply to obtain sperm from genetically superior males. Similar extra-group matings have been reported in other mammals (e.g. Sauter, 1991).

In cooperatively breeding splendid fairy wrens (*Malurus splendens*), the breeding pair are often closely related. Males actively seek extra-pair copulations on neighbours' territories and resident females willingly copulate (Rowley & Russell, 1990). The high level of extra-pair paternity in this species (65%) may therefore be due to inbreeding avoidance (Brooker *et al.*, 1990). However, a study of the close congeneric superb fairy wren (*Malurus cyaneus*) suggests that females perform EPC to obtain 'good genes' as 4% of males (all from a single lineage) fathered 47% of extra-pair young (Mulder *et al.*, 1994). The presence of helpers may allow higher rates of EPC because they can compensate for any reduction in care by the dominant male following female EPC. Indeed, EPP increases with the number of helpers (Mulder *et al.*, 1994). To determine whether high rates of EPC are due to dominant pair relatedness or the presence of helpers, a comparison could be made of the level of EPP in cooperative breeders with similar ecologies but differences in the average coefficient of relatedness within the dominant, breeding pair.

Finally, hatching failure of bird eggs may be due to inbreeding depression or other forms of genetic incompatibility rather than male sterility. Failure to hatch is not always a consequence of a lack of sperm, as revealed by the presence of sperm on the outer perivitelline layer of unhatched eggs (Birkhead, Veiga & Fletcher, 1995). In house sparrows (*Passer domesticus*), there was greater EPP in nests with unhatched eggs (Wetton & Parkin, 1991). In redwinged blackbirds (*Agelaius phoeniceus*), females that performed EPCs hatched a greater proportion of eggs than those who did not (Gray, 1997a). Similarly, in aquatic warblers *Acrocephalus paludicola*, nests with multiple paternity have higher hatching success (Dyrce, A., personal communication). One – admittedly of several – explanation is that females paired to genetically similar males are more likely to perform EPCs and that genetic incompatibility is

responsible for hatching failure. Verbal arguments for and against this view have been constructed (e.g. Gray, 1997a), but clearer *a priori* tests or predictions are needed. A more intriguing example comes from greater reed warblers (*Acrocephalus arundinaceus*) where hatching success correlated negatively with the degree of genetic similarity of the breeding pair (Bensch *et al.*, 1994). This species has very low levels of EPP (< 4%) so male genotype is a good indicator of offspring genotype. Knowledge of the breeding history of the study population revealed that high pair similarity was not indicative of close inbreeding. This study suggests that genetic similarity, independent of inbreeding effects, may lead to non-viable offspring production. In blue tits (*Parus caeruleus*) the proportion of unhatched eggs was repeatable across breeding pairs but not across individuals of either sex. Thus, hatching failure is unlikely to be due to male or female sterility. Pedigree analysis showed that more closely related breeding pairs have a lower egg hatching rate (Kempenaers *et al.*, 1996). This appears to be due to inbreeding depression but there is no relationship between EPP and pair relatedness. In pied flycatchers *Ficedula hypoleuca*, the reverse trend occurs and breeding pairs with low genetic similarity show greater levels of EPP suggesting that females may perform EPCs to avoid excessive outbreeding (Rätti *et al.*, 1995).

III. USING POST-COPULATORY CHOICE TO BIAS PATERNITY TOWARDS THE BEST MALE

In the preceding section, we argued that females remate because they subsequently encounter a male perceived to be a genetically superior partner. Although it may seem recent, the notion that females can select sperm from different males after multiple mating was raised over 30 years ago by workers like Bedford (1965) and Cohen (1969) (mini-review: Olsson *et al.*, 1999). More generally, it is possible that females choose which males will fertilise their eggs using a range of post-copulatory paternity-biasing processes like cryptic female choice and sperm competition (e.g. Semple, 1998) or that paternity biasing is *via* selective abortion. Genetic benefits from post-copulatory biasing could be the main factor that initially selects for polyandry. Alternatively, polyandry may first evolve for material benefits (Ridley, 1988). Once females mate multiply, however, this creates a climate in which females can gain genetic benefits at little cost. Thus, while some

theoretical models try to determine whether genetic benefits alone can maintain polyandry, in many instances this need not be the key question. Instead, polyandry can be taken as given, and the consequences for cryptic choice or sperm competition then explored (Eberhard, 1996). The question becomes: are the costs to females of a given post-copulatory paternity-biasing mechanism less than the genetic benefits conferred? We distinguish between genetic benefits that arise solely due to polyandrous females producing sons that sire more offspring per mating (see Sections III. 1 and III. 2) and benefits due to the production of more viable offspring (Sections III.3 and III.4).

(1) How does polyandry bias paternity towards males with genes that increase sons' post-copulatory reproductive success?

Several models discuss the effect of polyandry on male reproductive traits that affect post-copulatory success (Curtisinger, 1991; Keller & Reeve, 1995; Haig & Bergstrom, 1995; Eberhard, 1985, 1996). They all reduce to a very simple argument: when females are polyandrous there is selection for male traits favoured by cryptic female choice, or traits that increase competitiveness during sperm competition. If these traits are heritable then polyandrous females, by encouraging sperm competition and exercising cryptic female choice, will produce sons that are also more successful at fertilizing females or inducing differential investment in offspring. Females that mate singly can not choose among males for traits that function post-copulation, and are thus less likely to produce competitive sons. Male traits that potentially increase fertilization success include genitalic morphology (for the first clear empirical example see Arnqvist & Danielsson, 1999), sperm size and morphology (Parker, 1993; Parker & Begon, 1993; LaMunyon & Ward, 1998), the number of sperm per ejaculate (Parker, 1990*a*, *b*), ejaculate size (Simmons & Siva-Jothy, 1998), copulatory plugs, copulatory and post-copulatory courtship behaviour (Eberhard, 1994), seminal substances (Eberhard & Cordero, 1995; Eberhard, 1996), anti-aphrodisiacs and nutrients transferred (Pitnick, Spicer & Markow, 1997) and courtship gifts (Sakaluk, 1997; Calos & Sakaluk, 1998). Broadly speaking, these traits either increase the likelihood a female will accept and store sperm, increase a male's ability to displace or reposition previously stored sperm, reduce the likelihood of the female remating, increase fertilization rates before

the female remates, reduce sperm loss when females remate or increase maternal investment.

(a) Fisherian runaway

Genes for greater levels of polyandry could increase due to indirect selection arising from linkage disequilibrium with genes for male traits that function post-copulation to bias paternity (Keller & Reeve, 1995). The tendency for females with genes for polyandry to fertilise eggs with sperm from males that are more successful at fertilizing polyandrous females creates a genetic correlation. This correlation is identical to that between mating preference and male signal genes in Fisherian models of pre-copulatory mate choice. If an initial threshold frequency of polyandry is exceeded, in this case for multiple mating rather than mating preference genes, runaway occurs. Direct benefits to polyandry for some females could initially select for an increase in the frequency of genes for polyandry. There is no requirement that selected male traits signal offspring viability. The processes may either be halted by the costs of additional matings for females, diminishing genetic benefits from mating with an increasing number of males or loss of genetic variability among males.

Curtisinger (1991) produced a simple two-locus, four-allele genetic model of 'sexy sperm' evolution (one loci for polyandry and one for the male trait). He concluded that Fisherian mechanisms can not sustain multiple mating because the costs of polyandry are no longer compensated for once the advantageous male trait approaches a selective equilibrium. If the equilibrium is near fixation of the superior male allele, single-mated females also mate with competitively superior males but do not pay the costs of multiple mating. If the male selective equilibrium is below fixation, the linkage disequilibrium decays and levels of multiple mating either drift or rapidly decrease if mating is costly. There are, however, several factors that could maintain genetic variation in male traits that bias paternity. These include: (i) biased mutation that reduces sperm competitiveness or post-copulatory male attractiveness (Pomiankowski *et al.*, 1991); (ii) non-transitive relationships between the competitiveness of different sperm types (e.g. B sperm out-compete C sperm, C outcompete D, and D outcompete B) (Prout & Bundgaard, 1977; Keller & Reeve, 1995); (iii) condition-dependent expression of sperm competitiveness, for example, in terms of the number of sperm produced (Parker, 1990*b*) or

the size of courtship gifts that increase paternity (Sakaluk & Eggert, 1996; Wedell, 1997). Genes that affect male condition are rarely likely to go to fixation (Rowe & Houle, 1996); (iv) gene flow between populations where females select for different male traits; (v) the wide diversity of mechanisms by which males can increase their share of paternity (Eberhard, 1996). If there are energetic trade-offs between sexually selected traits (Basolo, 1998), shifts from investment on one trait to another will occur as variability decreases in the main trait currently under indirect selection; (vi) negative pleiotropic effects on other traits (Prout & Clark, 1996).

(b) *Antagonistic seduction or sensory exploitation*

Sensory biases in females that subsequently lead to cryptic female choice may derive initially from traits under natural selection (Eberhard, 1996, p. 45–50). First, even in monandrous species, there is probably natural selection for females to respond to male signals that indicate successful copulation and insemination. In many parthenogenetic species, sperm is still required to trigger development even when it is not incorporated into the genome (Schlupp, Marler & Ryan, 1994), or females still require the stimulus of copulation to induce oviposition (Crews, 1989). These examples suggest that male-derived signals are important and conservative features of female reproductive biology. Second, the potential for intra-ejaculate competition between sperm is unavoidable (Haig & Bergstrom, 1995). Even monandrous females may benefit from mechanisms that prevent defective sperm fertilising eggs. There may also be natural selection on females to reduce the risk of polyspermy by decreasing the number of sperm that reach the egg. Third, intersexual conflict may select for male traits, notably chemical stimuli, that increase investment in offspring or egg production more than is optimal for the female. This leads to natural selection for females to resist these signals. In general then, natural selection sets the stage for cryptic female choice.

Sensory exploitation occurs when males exploit a static, pre-existing female sensory bias to increase their mating/fertilization success. By some definitions though the female preference does not evolve in response to changes in the male trait (Ryan, 1998) (but see Endler & Basolo, 1998). For this reason, sensory exploitation is unlikely to provide a general evolutionary model to explain cryptic female choice. Male traits that are selected due to polyandry are likely to evolve in directions that increase direct costs

to females due to the almost inevitable occurrence of male-female conflict (Stockley, 1997*b*). This conflict must arise because each male benefits most when only his sperm is used, while females bias paternity in ways that disfavour some males. Male-imposed costs therefore select for modification of female preferences. As such, the recent model of ‘antagonistic seduction’ seems a more appropriate description of the evolutionary process (Holland & Rice, 1998). Endless cycles of selection on males to seduce females into preferentially using their sperm and females evolving greater resistance to these signals may occur. Given polyandry, females with greater resistance are likely to bias paternity towards males that produce more seductive signals.

Under some circumstances, female traits that lead to post-copulatory paternity biasing could remain static and sensory exploitation can then be said to occur (Ryan, 1990). One possibility is that the net benefit of a fixed sensory bias outweighs any costs that arise from its role in biasing paternity. Christy (1995) has provided a proximate account of sensory exploitation arguing that ‘sensory traps’ occur when a male trait directly mimics a stimulus that the female has been naturally selected to respond to. For example, copulatory movements by the male genitalia in a bushcricket may mimic oviposition and the passage of eggs down the reproductive tract and thereby stimulate females to release sperm from previous mates (von Helversen & von Helversen, 1991). Females will not evolve the ability to discriminate against a male signal if the cost of failing to respond to the mimicked signal outweighs the benefit of reduced responsiveness to the mimicking male signal. The same constraint of high costs to false rejection is important in a range of biological systems, from the detection of cuckoo eggs by hosts to Batesian mimics of unpalatable prey items. Eberhard (1996, p. 69) notes, however, that signals informing the female she has been mated are unusual because the signal ‘you have mated’ is actually ‘true’ whereas in many other signalling systems the signal is a lie (e.g. the egg is that of a brood parasite). As long as male signals do not impose undue costs on females, female paternity-biasing traits may remain static.

(2) Is there evidence that polyandry biases paternity towards ‘sexier’ males?

The most direct evidence is a demonstration that the sons of polyandrous females achieve greater post-mating reproductive success than that of the sons of

monandrous females. Experiments in which females are assigned variable numbers of mates are required. To our knowledge no such data exists for animals. This is a quite remarkable oversight given how much has been written about this potential benefit to polyandry. Indeed, studies in which the number of matings (intensity of sperm competition) is experimentally controlled are very few. Even in plants there are few studies. Tests in *Raphanus raphanistrum* showed that a greater intensity of pollen competition (broadly equivalent to degree of polyandry in animals) did not result in offspring whose pollen had greater success at siring seeds (Delph & Havens, 1998, p. 163).

To test whether polyandry selects for post-copulatory male traits that bias paternity one could also compare the fertilization success of males from lineages in which females are allowed to mate only singly or multiply. After several generations, males from single-mating female lineages should be less competitive than males from multiple-mating female lineages. There is some indirect evidence for this being the case in *D. melanogaster* (Holland & Rice, 1999). Rice (1996) showed that substantial heritable variation exists for traits that increase fertilization success when females mate multiply. Evidence of a positive genetic correlation between sperm competitiveness and the female tendency to mate multiply would also provide support for co-evolutionary Fisherian models (for experimental designs see Bakker & Pomiankowski, 1995). Given the absence of direct tests the available evidence is currently limited to studies examining key assumptions of the various models. The first line of evidence is to show that fertilisation success is heritable. This is difficult. The second, weaker line of evidence is to identify traits that seem to determine paternity and show that they are heritable.

(a) *Evidence that fertilisation success is heritable*

There is some evidence for heritable genetic variation in sperm and ejaculate features that influence paternity. In *D. melanogaster*, double-mating experiments using spermless second males show that main cell products reduce the number of first male sperm (Harshman & Prout, 1994). Seminal fluid contains accessory gland substances that destroy previous males' sperm (review: Chen, 1996). Clark *et al.* (1995) demonstrated genetic polymorphism in genes giving males high paternity when they mate first. Four out of seven accessory gland protein loci examined influenced the ability to resist sperm

displacement, but not the ability to displace sperm. Hughes (1997), however, found little additive genetic variation in sperm number in *D. melanogaster* and the number of sperm inseminated is arguably the major source of variation in post-copulatory paternity biasing in insects (Simmons & Siva-Jothy, 1998). In general, artificial insemination studies using males from different genetic strains also show variation in fertilization ability (Dziuk, 1996). Finally, a somewhat unusual result is that male beetles infected with *Wolbachia* have greater fertilization success than uninfected males even though this reduces offspring production by uninfected females (Wade & Chang, 1995).

Few studies have looked directly at the heritability of the ability to bias paternity. In the bulb mite *Rhizoglyphus robini*, focal males were mated to each of the three females with full sperm stores. The males' paternity was significantly repeatable. Some males were consistently better than others at gaining paternity. There was also a significant correlation between the mean paternity of fathers and sons, giving a narrow-sense heritability (h^2) of 0.28 which was significant with a one-tailed test (Radwan, 1998). Radwan (1996) found that paternity was not related to copulation duration, male size or sperm number, but did increase with greater sperm size. A future study determining whether sperm size is heritable would therefore be illuminating. In Radwan's (1998) study, paternity was based on the proportion of eggs hatching as non-focal males were irradiated. The estimate of paternity is therefore likely to be accurate. In studies where paternity is based on counts of adult progeny, however, there is a real danger that heritable variation in pre-adult mortality will be mistaken for variation in traits influencing paternity (e.g. Gilchrist & Partridge, 1997). Workers estimating heritability of fertilization success should therefore try to estimate paternity as soon as possible after birth. Even in plants, there is little data on heritability. Only two studies – of maize and courgette – have shown that there is heritable variation in pollen tube growth rate, which is a major determinant of fertilisation success (Delph & Havens, 1998, p. 163). Even so, the available evidence, although scant, suggests that the necessary additive genetic variation will exist for females to produce sons with 'sexy sperm'.

(b) *Evidence that specific post-copulatory male traits bias paternity*

There is abundant evidence that an increase in the

number of sperm inseminated increases paternity (review: Simmons & Siva-Jothy, 1998). Presence/absence studies also show that main cell products in semen increase paternity (Harshman & Prout, 1994). In fact, biased paternity is known to correlate positively with dozens of traits including the timing of copulation, copulation duration, copulatory courtship behaviour (Otronen, 1997), genitalic structure (Arnqvist & Danielsson, 1999), spermatophore size (Wedell & Cook, 1998), male body size (LaMunyon & Eisner, 1994), sperm size (Radwan, 1996; LaMunyon & Ward, 1998) and the production of seminal chemicals (Eberhard & Cordero, 1995). Given the diversity of mechanisms whereby females can bias paternity, and the limited number of male traits measured, many studies will fail to identify male traits that correlate with paternity (still less those causally responsible). The easiest traits to identify are probably those that are primarily selected due to male–male competition like sperm number.

Assuming that traits correlated with biased paternity are causally responsible for the bias, is there evidence that they are heritable? Given the focus on male genitalia either as ‘internal courtship devices’ or as tools to displace or reposition sperm it is surprising that there are no studies on the heritability or underlying additive genetic variability in genitalic traits (Arnqvist, 1997). However, there is additive genetic variation in male genitalic traits in the waterstrider *Gerris incognitus* (unpublished data cited in Arnqvist, Thornhill & Rowe, 1997). Easily measured traits like number of sperm per ejaculate and courtship gift size that are most likely to have a causal role (rather than, say, body size) are probably the most obvious traits in which to calculate the amount of additive genetic variation. To our knowledge, there are few such studies. Most of the evidence is confined to data showing differences in fertilisation success between different genetic strains (references in Radwan, 1998).

(3) Can post-copulatory mechanisms allow females to bias paternity towards sires who improve offspring viability?

In the absence of pre-copulatory cues, can females use post-copulatory mechanisms as a ‘filter’ to select males with good ‘viability genes’ (Olsson & Madsen, 1995)? Yasui (1997) has formally modeled the evolution of cryptic female choice for increased offspring viability. Polyandrous females should gain more attractive sons, and daughters and sons with

greater viability than monandrous females because they have greater scope for choice. As with viability indicator models for pre-copulatory mating signals, as long as there is heritable variation in viability, female traits that bias paternity (such as polyandry) can persist, even if there are direct costs (e.g. Iwasa *et al.*, 1991). As always, whether indirect selection on polyandry from genetic benefits is sufficient to outweigh direct selection as a result of the cost of remating to females is an open empirical question which will depend on the amount of additive genetic variation among males (Kirkpatrick, 1996; Kirkpatrick & Barton, 1997).

What is the likelihood that post-copulatory male traits that bias paternity are correlated with heritable viability? Eberhard (1996) has argued that this correlation is unlikely because most traits selected for by cryptic female choice appear to be low-cost, arbitrary traits and therefore unlikely to be condition-dependent (Grafen, 1990). This may be true for traits subject to pure cryptic female choice, but ‘competitive’ traits that are involved in sperm competition are more likely to be costly. In particular, if the marginal costs of increased sperm production depend on male quality, males with good ‘viability genes’ may transfer more sperm thereby increasing their share of paternity *via* numerical superiority during raffle-like sperm competition (Parker, 1990*b*, 1992). Nutritional gifts that prolong sperm transfer are also likely to be condition-dependent traits (Sakaluk & Eggert, 1996). Cordero (1995) also noted that those chemical signals that increase female-mediated paternity biasing may be expensive to synthesize or accumulate. Alternatively, deleterious mutations, especially those that affect mitochondrial functioning, may affect both sperm and diploid phenotype (Parker, 1992).

Another important new idea, which seems to have received little attention, invokes immunosuppression. Sperm are recognized as non-self in the male’s reproductive tract and are subject to immunological attack. Males that can afford to suppress their immune system are therefore more likely to produce higher quality ejaculate (i.e. more sperm). Males that have greater parasite resistance are more likely to be able to elevate levels of immunosuppressive hormones like testosterone and other androgens. Ejaculate quality may therefore be an index of parasite resistance that could increase offspring viability. Yan & Stevens (1995) found that parasitic infection decreased second-male paternity (P_2) in *Tribolium* beetles. In addition, parasitised males may produce fewer sperm because androgens stimulate

spermatogenesis while parasite infection leads to a reduction in circulating levels of androgens (for details see Hillgarth, Ramenofsky & Wingfield, 1997; Folstad & Skarstein, 1997). 'By initiating sperm competition, females can increase their chances of fertilizing their eggs with sperm from parasite-resistant males... (moreover) females may also ensure that any cheaters, males that develop attractive ornaments without undergoing immunosuppression, have reduced chances of fertilizing eggs' (Folstad & Skarstein, 1997, p. 111).

(4) Is there evidence that post-copulatory paternity biasing increases offspring viability?

The main line of evidence to demonstrate that polyandry increases offspring viability is from experimentally controlling the number of matings per female and then comparing offspring viability between polyandrous and monandrous females. In the European adder *Vipera berus*, there is a negative correlation between the number of mates and the proportion of stillborn offspring (Madsen *et al.*, 1992). In the European sand lizard *Lacerta agilis*, the number of mating partners is correlated with the proportion of offspring surviving to one year of age (Olsson *et al.*, 1994b). These results, however, appear to reflect post-copulatory inbreeding avoidance rather than choice of sperm with general good 'viability genes' (see Section III.6). Both studies are also correlational. Watson (1998) experimentally controlled the level of multiple mating in the spider *Neriene litigiosa* and found that polyandrous females' offspring had higher growth rates and were larger. This suggests higher viability, but these offspring actually had lower survival rates (Schneider & Elgar, 1998). However, sons with high-quality viability genes may invest disproportionately in costly sexually selected traits, reducing their survivorship (Grafen, 1990). Unfortunately, separate data on daughter survivorship were not presented. If viability genes are inherited, daughters should show higher survivorship. Zeh (1997) found an increase in offspring production with experimental variation in number of mates in a pseudoscorpion (*Cordylochernes scorpioides*), but this appears to be due to avoidance of genetic incompatibility rather than biasing paternity towards males with good viability genes (see Section III.6). A similar finding to that of Zeh (1997) has recently been reported for the field cricket *Gryllus bimaculatus* (Tregenza & Wedell, 1998). In the waterstrider *Gerris odontogaster*, there was no dif-

ference in size or survivorship between the offspring of experimentally controlled single-mated and multiple-mated females (Arnqvist, 1989). Non-experimental studies of multiple mating in mammals showed no effect of the number of matings in three studies (Schwagmeyer, 1986; Hoogland, 1995; Murie, 1996), negative effects in two studies (Dewsbury, 1982; Wynne-Edwards & Lisk, 1984) and a positive effect in one study (Hoogland, 1998). Stockley & Simmons (1998) found no difference in the survival rate, time to development, size or fluctuating asymmetry of offspring between female dungflies (*Scatophaga stercoraria*) that remated and those that did not. However, females that did not remate produced a male-biased clutch.

Another line of evidence is if secondary sexual traits, or general phenotypic cues that are likely to be condition-dependent indicators of viability, are positively correlated with traits that could function in post-copulatory paternity biasing. For example, when song rate or ornament size correlates with sperm production. Ejaculate size is correlated with male display rate in the Trinidadian guppy, *Poecilia reticulata* (Matthews, Evans & Magurran, 1997). Assuming courtship display is an index of male viability, this supports the claim that multiple mating and paternity bias due to numerical sperm advantage will yield more viable offspring. Sheldon (1994) also cites several studies that indicate a positive correlation between ejaculate size and costly male traits such as display rate, central position on leks and male dominance. In barn swallows, *Hirundo rustica*, and house sparrows *Passer domesticus* there is a positive correlation between secondary sexual trait size and total testes mass, which should lead to increased ejaculate size (Møller, 1994a). However, in sedge warblers *Acrocephalus schoenobaenus* there was no correlation between song repertoire size, testes asymmetry and sperm length, number and abnormality (Birkhead *et al.*, 1997). A number of other studies have also failed to show a relationship between costly traits and ejaculate quality (references in Birkhead *et al.*, 1997), but low statistical power needs to be taken into consideration when considering negative results. It is also important to show that male traits that bias paternity are measurably repeatable among males (Birkhead & Fletcher, 1995).

Fluctuating asymmetry has recently been promoted as an index of male quality (Møller & Swaddle, 1997). It is claimed that greater symmetry is a measure of higher developmental stability, which is the product of a well-adapted genome. As

such, more symmetric males should have greater fertilization success and produce more viable offspring. Supporting this claim, males with more symmetric wings had higher fertilisation success in the fly *Dryomyza anilis* (Otronen, 1998). To date, this is the only study looking at the relationship between post-copulatory sexual selection and male symmetry. The claim that symmetry reflects heritable genetic variation must be assessed in each case though, because much of the variation in symmetry may be due to environmental effects (for a detailed study of genitalia see Arnqvist *et al.*, 1997) or non-heritable variation in heterozygosity.

(5) What mechanisms could allow females to bias paternity towards genetically more compatible males?

Although genetic compatibility can sometimes be detected by pre-copulatory mate choice, in many cases this might be difficult. To identify genetically suitable mates, and perhaps even distinguish between sperm within and between ejaculates requires very precise mechanisms because the genetic differences may be as small as the presence or absence of a single allele. Zeh & Zeh (1997) therefore point out that genetic compatibility is probably more easily detected post-copulation *via* signals on sperm, or sperm-soma or egg-sperm interactions. If true, polyandry has evolved as a mechanism for female choice because it increases the number of sperm genotypes amongst which the female can bias paternity. There are at least four general mechanisms of paternity-biasing mechanisms for genetic compatibility.

First, females may be able to detect sperm genotype *via* female soma-sperm interactions (Vacquier, 1998). Cell-surface proteins on sperm act as antigens that are attacked in the female reproductive tract by anti-sperm leucocytes and antibodies (Birkhead, Møller & Sutherland, 1993). In some cases, these proteins reflect diploid genotype in which case they will only permit inter-ejaculate recognition. In plants, haploid expression of genes in pollen is commonplace. It is generally argued that sperm phenotype is determined by diploid gene expression (see Delph & Havens, 1998, p. 152), but there are some genes in animals known to be haploid expressed in sperm (e.g. Nayernia *et al.*, 1996). Interestingly, driver alleles and the like (which create incompatibility) are the kinds of genes that are expressed as haploids. However, selection acts against haploid expression because it increases competition within

an ejaculate (Haig & Bergstrom, 1995). This is less of a problem in many plants where pollen is widely dispersed and there is less likelihood of pollen from the same parent competing against each other. Regardless, sperm surface proteins may provide cues for sperm recognition and sperm-soma interactions may allow females selectively to eliminate sperm before they reach the fertilization site (e.g. Bishop, Jones & Noble, 1996). Alternatively, the same recognition processes could be used to bias sperm uptake and storage into different long-term storage sites (Otronen, Reguera & Ward, 1997), and/or to bias use of stored sperm (Ward, 1998). Female soma-sperm interactions may affect the relative competitiveness of sperm types and the likelihood that they will end up at the site of fertilization. The main message is that surface chemicals provide cues to sperm genotype (Vacquier, 1998). A fuller review of potential chemical mechanisms of sperm recognition can be found in Zeh & Zeh (1997).

Second, there is circumstantial evidence that eggs can directly select sperm based on sperm haplotype (e.g. Rülcke *et al.*, 1998). Several sperm may penetrate the egg (polyspermy) and the egg may then choose with which sperm to fuse (review: Eberhard, 1996, p. 187).

Third, promoting sperm competition may decrease the fertilization success of males with meiotic-drive genes (Haig & Bergstrom, 1995). If the presence of a driver gene decreases the number of functional sperm in an ejaculate, then polyandry decreases the likelihood that a sperm with a driver allele will fertilise an egg. The advantage the driver allele gains during intra-ejaculate competition is reduced by greater inter-ejaculate competition. Genes for polyandry can be thought of as modifiers of meiotic drive.

Fourth, paternity biasing may continue post-fertilization if females preferentially invest in some males' offspring (review: Møller & Thornhill, 1998*b*). One option is to selectively abort defective zygotes. This option is only open to species with viviparity (Zeh & Zeh, 1997). Once fertilization has occurred, females may be able to recognize genetically defective zygotes and preferentially allocate nutrients to more viable zygotes. This can occur in both viviparous and oviparous species where there is some form of maternal care. In species where egg size or nutrient content affect offspring fitness, females could even vary egg size prior to fertilization if there are reliable ways to estimate the genetic compatibility of stored sperm and mechanisms of paternity biasing exist.

(6) Is there evidence that polyandry allows post-copulation selection of genetically compatible male sperm?

Although some of the mechanisms we have described for detecting genetically compatible sperm sound like science fiction, several recent studies provide evidence that post-copulatory paternity biasing for greater genetic compatibility does occur. If one takes into account how recent is the interest in genetic compatibility *versus* universal good gene explanations for polyandry then the proportion of studies that show genetic incompatibility rather than good gene effects being important is sobering. First, numerous studies involving reciprocal hybrid double-matings show that, irrespective of mating order, conspecific sperm are more likely to gain paternity than heterospecific sperm (e.g. Howard *et al.*, 1998). Similar findings have also been reported for intra-specific hybrid matings between different strains or geographic races (e.g. Wade *et al.*, 1994; Wade, Chang & McNaughton, 1995; review: Markow, 1997). Interactions between male and female (or egg and sperm) of widely differing genotypes appear to decrease the likelihood of producing lower viability hybrids. Unfortunately, the proximate mechanisms responsible for this biased paternity are generally unknown. Price (1997) has, however, shown that the normal pattern of high P_2 (the proportion of offspring sired by the second of two males) in *Drosophila melanogaster* is eliminated when a female mates with two heterospecifics. This confirms that male-female interactions, as opposed to wholly male-mediated sperm competition and fixed constraints on female sperm storage are responsible for the usual pattern of last-male sperm precedence following double matings. In an enormous study, Clark, Begun & Prout (1999) carried out pairwise matings between six isogenic lines of *Drosophila melanogaster*. They found that both the ranking of the ability of males from different isogenic lines to maintain paternity when they mated first, and to gain paternity when they mated second, varied depending on the genotype (line) of the females with which they mated. Genetically based male-female interactions seem to be an important source of variation in paternity in *Drosophila melanogaster*.

Second, Bishop (1996) reported phagocytosis of sperm before it reached the site of fertilization in the compound ascidian *Diplosoma listerianum*. Female soma-sperm interactions lead to the preferential destruction of genetically more similar sperm (Bishop *et al.*, 1996). This may occur because there is general

selection to avoid self-fertilization and sperm from genetically similar clones share more self-recognition markers with the female somatic tissue; although it is unknown whether the eliminated genetic combinations would lead to less-viable offspring. This kind of female soma-male gamete interaction has been well studied in the self-incompatibility system of plants whereby stigma-pollen interactions influence pollen tube growth. Although there is evidence that some pollen are competitively superior across a range of maternal genotypes (Snow & Spira, 1991), this is not always the case (e.g. Cruzan, 1990). Similarly, in animals, some sperm are consistently superior fertilisers (Dziuk, 1996), but less is known about variation in fertilisation success due to genetic differences among females.

Third, there is evidence that sperm of related males are less likely to fertilise eggs. In the European lizard *Lacerta agilis*, physical deformities result when closely related lizards breed (Olsson *et al.*, 1996*b*). These deformities are less common when females mate multiply (Olsson *et al.*, 1994*a,b*). DNA fingerprinting shows that the more closely related a male is to a female (relative to the other males with whom she mates), the smaller the proportion of the brood sired (Olsson *et al.*, 1996*a*; Olsson, Madsen & Shine, 1997). Post-copulatory paternity biasing therefore leads to male fertilization success being dependent on his genetic similarity to the female. The proximate mechanism responsible for this result is currently unknown. Similarly, in one Swedish population of European adders (*Vipera berus*) the number of mates is negatively correlated with the proportion of offspring that are stillborn (Madsen *et al.*, 1992). Although this may be due to cryptic female choice for universal 'good genes' for viability, the small size of the study population and the extreme nature of stillbirth is more suggestive of inbreeding depression. This result is unlikely to apply in a larger Alpine population where multiple mating is rare (Luiselli, 1993). In a controlled experiment where females from the Alpine population either mated once or multiply (3–8 times), there was no difference in the proportion of stillborn offspring between the two groups (Capula & Luiselli, 1994). In shrews (*Sorex araneus*), there was also no evidence that polyandry led to biased fertilization towards more distantly related males, despite the fact that mating with close relatives is both common and deleterious (Stockley, 1997*a*). However, sample sizes were small and statistical power is therefore low, and we should be cautious about accepting the null hypothesis of no difference.

Fourth, polyandry occurs due to active female choice in the Neotropical pseudoscorpion, *Cordyloderma scorpioides* and there are no apparent direct benefits to repeat mating with the same male (Zeh, Newcomer & Zeh, 1998). Zeh (1997) compared offspring production by naturally mated females and females mated to either 2–3 males or a single male in the laboratory. There was no difference in the number of hatchlings from field-mated females and females that mated multiply in the laboratory, but there were significantly fewer hatchlings from single-mated laboratory females. The main cause of this difference in output was complete brood failure; but even when failed broods were excluded, single-mated females still produced fewer offspring. This does not appear to be due to cryptic choice of universal ‘viability genes’. When males were mated to two females, females mated to the same male did not have similar reproductive success. Brood failure by both females was rare. The most plausible source of brood failure is genetic incompatibility, which suggests there are post-copulatory paternity-biasing mechanisms for genetically more compatible males (Zeh, 1997; Jennions, 1997).

Fifth, Trengenza & Wedell (1998) assigned one, two or four males to female field crickets (*Gryllus bimaculatus*) and then allowed each female to mate a total of four times. The total number of matings per female was therefore the same while the number of mates varied. Egg hatching success increased with the number of mates. A separate comparison of females mated to one male twice or one male four times revealed no differences in hatching success, which suggests that the number of matings is not correlated with material gains and that the main result is not due to non-genetic benefits. There was no significant repeatability in egg hatching success among males when they were mated to several different females. Variation in hatching success therefore can not be due solely to differences in intrinsic quality among males. It appears that post-copulatory mechanisms lead to differential fertilization by sperm that produce more viable offspring reducing hatching failure. As with Zeh (1997) this suggests that avoiding genetic incompatibility may drive polyandry.

Sixth, Wilson *et al.* (1997) carried out double-mating experiments on bruchid beetles *Callosobruchus maculatus* to estimate second-male paternity (P_2). The same pair of males were mated to a set of three females with male mating order held constant. For each male pair the three females were either unrelated or full sisters. P_2 was only marginally

repeatable among male pairs mated to sets of unrelated females, but repeatability was highly significant when the females were full sisters. Reducing the genetic variability among females therefore increased the repeatability of sperm precedence. This could arise if some female genotypes consistently generate higher P_2 values than others. However, repeatability of P_2 was not significant among sets of full sisters mated to different pairs of males. This suggests there is an interaction between male and female genotypes that influences P_2 . To test this Wilson *et al.* (1997) created groups within which the females in each set were full sisters and the paired males in the group always had the same genetic relationships with each other. So, for example, in group 1 there were four male pairs where the first male was always genotype A and the second genotype B, and all females were from family C. Again, P_2 was repeatable with greater variation among than within groups. The best explanation for the combined results is that interactions dependent on male-female genotype determine male fertilization success (review: Telford & Jennions, 1998). However, it is unclear if this process leads to preferential fertilization by genetically more compatible sperm. Indeed, the method of estimating male fertilization success assumed there was no biased offspring mortality, an assumption known to be erroneous in certain species (e.g. Gilchrist & Partridge, 1997).

Finally, *in vitro* fertilization experiments with mice suggest that non-random fertilization with respect to MHC haplotype occurs due to selection of sperm by eggs (Wedekind *et al.*, 1996). Furthermore, this process seems to depend on whether the mice are infected with a hepatitis virus. When mice are infected, more MHC-heterozygotes are produced than expected by chance. When mice are uninfected, more MHC-homozygotes than expected are produced (Rülicke *et al.*, 1998).

IV. GENETIC BET-HEDGING, GENETIC DIVERSITY AND MULTIPLE PATERNITY

In Sections II and III there was always a ‘best male’ that females could identify based on pre-copulatory or post-copulatory cues. Sometimes females can not identify the best male and under these circumstances selection may favour females that mate multiply in order to hedge their bets. In some cases, more males gain paternity than can reasonably be accountable for on the basis of females improving on earlier

matings. For example, multiple paternity by up to six males per brood seems to be widespread in Lake Malawi cichlids (Kellog *et al.*, 1995, 1998; Parker & Kornfeld, 1996). This is due to active female choice of multiple mates because females mate on leks, a single male sheds enough sperm to fertilise fully a clutch, fertilization is external and sneaky matings have not been observed. Moreover, mating is costly as it attracts predators and the risk of losing some offspring to predators is higher while mate searching (Konings, 1995). These data therefore suggest that a fitness advantage to multiple paternity can offset the costs of increased risk of female mortality and the production of fewer offspring. High levels of mixed paternity have also been reported for tree swallows, *Tachycineta bicolor* (Lifjeld *et al.*, 1993), aquatic warblers, *Acrocephalus paludicola* (Schulze-Hagen *et al.*, 1993), several fish with internal fertilization (e.g. Travis, Trexler & Mulvey, 1990), gastropod molluscs (review: Baur, 1998) and insects (e.g. Zeh, Zeh & Bermingham, 1997). As molecular techniques improve resolution, estimates of sperm diversity are likely to increase still further (e.g. Harshman & Clark, 1998). A second reason for polyandry is that a genetically diverse set of offspring may do better because of positive interactions between siblings. A third reason is that a genetically diverse supply of sperm could potentially be used to optimise offspring genotype in a heterogeneous environment. We illustrate some of these mechanisms using well-studied examples from social insects.

(1) Is genetic bet-hedging important?

The term 'bet-hedging' is used in many ways in biology (review: Seger & Brockmann, 1987). One widely accepted definition is that it is a strategy whereby variance in individual fitness is reduced at some cost to expected mean fitness. Simply put, there is a long-term evolutionary advantage to a strategy in which the risk of failure is reduced (e.g. variance in fitness is lower) even though there is some sacrifice in terms of immediate average fitness (Gillespie, 1974, 1977).

There are two ways in which polyandry could be favoured by bet-hedging. First, females may only be able to distinguish broad categories of males due to perceptual errors in assessment; or there may only be a few discrete levels of signalling by males, despite continuous variation in male quality (Johnstone, 1994). Second, there may be temporal fluctuations in the environment that lead to variable selection on fitness-enhancing traits under natural selection (e.g.

Jia & Greenfield, 1997). As such, females can not identify the male with the best viability genes for the future. In both cases, females can reduce the variance in mate quality by mating with several males whom they perceive to be broadly genetically suitable as mates (so-called 'genetic bet-hedging'; Watson, 1991). Another advantage is a form of diversified bet-hedging akin to not putting all your eggs in one basket (Kaplan & Cooper, 1984). Polyandrous females that produce a genetically diverse range of offspring increase the likelihood that at least some of them will possess viability genes that enable them to survive and breed in the next generation (Yasui, 1998).

Unfortunately, the benefits of the variance reduction due to genetic bet-hedging may have been overestimated. In a large population, the advantage is vanishingly small. Yasui (1998) provides a concise review of why this is so, and provides a simple example. Imagine good and bad males (within the set of males females consider as potential mates) exist in the proportions p and $1-p$ and that females either mate polyandrously (at a high level) or monandrously. In a large population, a fixed proportion p of polyandrous females' offspring is from bad males, while the same proportion p of monandrous females mate with bad males. Thus, the proportion of offspring sired by good and bad males is equal for the two female mating types and both mating strategies have the same mean arithmetic fitness. It is only when the population is small that the ratio of $p:-p$ matings by monandrous females deviates from $p:1-p$. If there are only a few monandrous females then the likelihood that they can be divided into this exact ratio is low. As the number of females increases, however, the 'sampling error' decreases and the ratio moves even closer to $p:1-p$. The between-generation variance in fitness decreases as a hyperbolic function of population size (Yasui, 1998, Fig. 1). Computer simulations show that, in the absence of a cost to polyandry, polyandry has a higher fixation probability than monandry, independent of population size. However, with a 1% decrease in arithmetic mean fitness per generation, the advantages of polyandry decrease with increasing population size and it does not persist when populations are even moderately large (400 individuals) (Yasui, 1998). Unless polyandry is almost cost-free it is unlikely that genetic bet-hedging is solely responsible for its maintenance.

Several authors have argued that genetic bet-hedging can explain polyandry, especially when females appear to mate indiscriminately or with

males 'inferior' to their initial choice (Kellog *et al.*, 1995, 1998; Parker & Kornfield, 1996; Watson, 1991, 1998; Stockley *et al.*, 1993). For example, Watson (1991) suggested that a second mating by female doily spiders (*Linyphia litigosa*) represents genuine bet-hedging. Females first mate with males who have had to fight, on average twice, for access to a female. This therefore provides an initial 'filter' selecting for vigorous males. In contrast, only 58% of second males fight before mating. They must therefore be assessed primarily on the basis of courtship behaviour. Female choice seems to be for the same traits that increase male fighting success. Unless females have very accurate ways of assessing male vigour it therefore seems likely that, on average, the female's second mate will be of lower quality than the first. If true, females suffer a reduction in expected fitness by remating, although this is somewhat reduced by first-male sperm precedence. However, because there is a risk, albeit small, that the first male was of low quality there is a reduction in the variance in offspring quality. Similarly, Stockley *et al.* (1993) argue that female European shrews mate multiply to reduce the risk that all their offspring are sired by a close relative. Given there is no apparent sperm selection against related males (Stockley, 1997a) the proportion of inferior, inbred offspring produced by polyandrous females will be equal to the proportion of monandrous females mating with relatives. The only benefit of polyandry is therefore a reduction in the variance in the proportion of inbred offspring per generation. Given the arguments of Yasui (1998) regarding population size effects, bet-hedging is unlikely to explain polyandry in either doily spiders or European shrews.

What evidence is there for bet-hedging? The claim that bet-hedging occurs has been tested by asking whether polyandry increases female reproductive success or offspring fitness (Watson, 1998; Schneider & Elgar, 1998). In fact, by definition, bet-hedging polyandry should reduce mean expected fitness of polyandrous females relative to monandrous females! The key prediction of bet-hedging is that there will be a reduction in the between-generation variance in fitness and an increase in geometric mean fitness of polyandrous females relative to that of monandrous females. To our knowledge there are no data comparing the geometric fitness of polyandrous *versus* monandrous females, nor the more easily obtained evidence that polyandry reduces the variance in fitness among individuals within a generation.

(2) Genetic diversity and sibling interactions

Offspring of a half-sib family are twice as diverse as offspring from a full-sib family (Yasui, 1998). There are two other ways in which greater genetic diversity within a brood may raise offspring fitness: full-sib competition and half-sib cooperation. Full-sib competition occurs when full-sibs compete with each other more intensively than half-sibs. This is only important if there are limiting resources distributed such that those required by different genotypes co-occur and can be partitioned to reduce competition. Half-sib cooperation occurs when individuals that vary genotypically interact in a cooperative manner. The most generally applicable possibility is that disease intensity and/or transfer is reduced if different genotypes have different susceptibilities to disease so that half-sib progeny are less likely to infect one another.

The best evidence supporting the notion of full-sib competition comes from a cross-species study showing that the number of matings per female is higher in parasitoid hymenoptera which lay several eggs per host (gregarious) than those laying a single egg per host (solitary) (Ridley, 1993). Polyandry by gregarious species may reduce full-sib competition, while females that lay solitary eggs can not gain this advantage. One mechanistic explanation for reduced competition is that inferior genotypes are more rapidly eliminated reducing subsequent competition. A problem, however, is that multiple mating reduces relatedness between offspring and may actually increase sibling competition due to smaller inclusive fitness gains and greater sibling rivalry (Hardy, 1994). Evidence that clutches of polyandrous females show greater levels of earlier brood reduction is therefore needed. An alternative explanation for polyandry by gregarious parasitoids is that they gain greater direct benefits than solitary species from ensuring a sufficient sperm supply. The optimal sex ratio is usually female-biased for gregarious broods, therefore mothers need more sperm to fertilise eggs than do solitary brood parasitoids, where the cost of producing only males from unfertilised eggs is far smaller (Godfray, 1994).

(3) Do females preferentially use sperm, or invest in offspring, of different genotypes depending on environmental context?

While spatial variation can not select for bet-hedging, it can maintain a stable genetic polymorphism (review: Seger & Brockmann, 1987). If

females can identify the conditions under which their offspring will develop, and they possess sperm from several males, they may be able to preferentially use sperm from the male with the most suitable genotype for the prevailing conditions. At present, this is a possible benefit of polyandry which has very little supporting evidence. In species with genetic sex determination, cases of very strong deviation from a primary sex ratio of unity are known and can be related to the relative benefits of producing sons and daughters (review: Sheldon, 1998). For example, in the cooperatively breeding Seychelle's warbler (*Acrocephalus sechellensis*) the sex of their single-egg clutch depends on the quality of the territory and the number of helpers (Komdeur, 1996). Gunnarsson & Andersson (1996) also showed that the primary sex ratio of broods depended on the posture the mother assumed on the web in a sheet web spider (dorsal or ventral side up). Females are the heterogametic sex in spiders and birds though, so these results can not reflect sperm selection. The proximate mechanisms biasing the sex ratio remain unknown. In mammals, however, males are the heterogametic sex and seemingly adaptive biasing of the primary sex ratio has been reported (Clutton-Brock, 1991). It is therefore possible that females can preferentially select sperm with X or Y chromosomes, although selective abortion may be more common. While unrelated to polyandry, sperm selection of sex chromosomes in relation to environmental factors could provide an example of genotype-by-environment sperm selection.

Ward (1998) has argued that dungflies *S. stercoraria* fertilize eggs with sperm carrying different genotypes at the locus for the enzyme phosphoglucosmutase (PGM) depending on whether the oviposition site is sunny or shady. This finding was, however, only reported in one of four experiments. It is therefore unclear whether females do consistently bias sperm usage in response to environmental conditions. There was an effect of PGM genotype on larval growth, but this was not clearly related to the non-random use of sperm observed in the earlier experiments. Given the potential importance of the process, this system merits further investigation. It needs to be clearly shown that females bias the use of sperm towards genotypes that elevate offspring fitness under the prevailing conditions compared to available alternative genotypes. At present the data are inconclusive.

If females can select sperm based on sperm genotype, as the data on post-copulatory selection against genetic incompatibility suggest, then females

should evolve traits that facilitate fertilization by sperm with genotypes appropriate to the prevailing conditions. For example, multiple sperm storage organs provide greater opportunities for females to engage in sperm selection (review and model: Hellriegel & Ward, 1998). Diptera often have a singlet spermatheca and a paired doublet which are long-term sperm stores. Otronen *et al.* (1997) showed that the distribution of sperm among spermatheca in the dungfly *S. stercoraria* varies depending on male size (see also Ward, 1993). There is a complex interaction between the relative size of males and sperm length that determines the proportion of sperm stored in the singlet spermatheca. The consequences of these storage patterns on sperm use and offspring fitness remain unclear. In the fly *Dryomyza anilis*, sperm storage also varies in relation to male behaviour. Males tap the female's abdomen with their genital claspers which increases the amount of sperm stored in the singlet spermatheca. Multiple mating leads to an increase in the number of sperm in the doublet spermathecae but not in the singlet. Sperm used for fertilization come primarily from the latter storage site (Otronen, 1997). These data therefore suggest that females can control the location in which sperm is stored. Again, whether this leads to differential usage of sperm depending on context and any subsequent effect on offspring fitness is unknown. Finally, in a damselfly, *Calopteryx splendens*, the genetic diversity of sperm stored in the paired spermathecae is greater than that in the bursa copulatrix. When females avoid remating before ovipositing they use sperm from the spermathecae, when they remate they use sperm from the bursa copulatrix (Siva-Jothy & Hooper, 1996).

(4) Genetic diversity in social insects

Genetic variability appears to be selected for in eusocial hymenoptera (monogamy in eusocial termites is an interesting contrast). Ant species with monogamous queens tend to have colonies founded by several queens, while polyandrous queens tend to form single-foundress colonies (Keller & Reeve, 1994; for an opposing interpretation of the evidence see Boomsma & Ratnieks, 1996). Greater genetic diversity among the workforce may increase colony output and thereby provide a direct fecundity benefit to queens as well as increasing the fitness of sterile worker offspring *via* inclusive fitness gains. Multiple mating by queens is common in eusocial insects. Honeybees *Apis mellifera* mate 10–20 times, and ant queens may mate several times (review: Keller &

Reeve, 1994). The extent to which this translates into multiple paternity is less clear (Boomsma & Ratnieks, 1996). Although the genetic consequences of multiple mating are theoretically stimulating, the possibility that queens mainly remate to increase sperm stores should not be ignored (Fjerdingstad & Boomsma, 1998).

There are at least four major hypotheses for why increased genetic diversity is favoured in eusocial insects (review: Page, 1986). A common assumption of each explanation is that polyandry leads to simultaneous, mixed paternity among progeny. There is some evidence that multiply mated females show mixed paternity and that the proportion of offspring sired per male remains fairly constant over time (Keller, Sundström & Chapuisat, 1997). There is, however, sometimes counter-selection on males to ensure complete paternity, or sequential single-sire paternity (Boomsma, 1996). Under these circumstances, genetic diversity in any given sample of progeny may be lower than that expected based on the number of males that mated.

(a) *More efficient division of labour*

In honeybees and ants, different patriline (workers sired by different males) tend to specialise on different colony tasks (reviews: Robinson, 1992; Page, Robinson & Nasr, 1995), which may result in improved efficiency and greater reproductive output. This is a form of half-sib cooperation. Supporting this, multiple mating and increased genetic diversity seem to increase reproductive output in honeybees (references in Bourke & Franks, 1995, p. 383). Conversely, if there are genetic cues allowing workers to discriminate against other patrilines (e.g. Sundström, 1994), inter-patriline competition due to biased rearing of full-sisters could reduce colony efficiency.

(b) *Reduced variance in diploid male production*

Complementary sex determination (CSD) occurs in many haplodiploid hymenopterans and causes the production of sterile, diploid males (SDMs). SDMs are produced when offspring are homozygous at any CSD locus. The probability of a matched mating in which a male shares a sex locus allele with the queen is $2/k$, where k = the number of alleles at the sex loci and there is random mating. With random mating the mean production of SDMs in the population is $1/k$. As the number of mates increases, a female is less likely to receive only sperm that is matched or unmatched. Polyandry therefore reduces the vari-

ance in the proportion of SDM offspring (review: Cook & Crozier, 1995). For example, when $k = 10$ then 10% of diploids will be sterile males and 80% of single matings yield 0% SDMs and the remaining 20% of matched matings yield 50% SDMs. With greater levels of polyandry, however, the modal proportion of SDMs stays at 10% ($1/k$) but the frequency distribution of the percentage (SDMs per brood) becomes increasingly tightly clustered around this value.

There are two main costs to SDM production. First, since workers are females, SDM production reduces the effective workforce, which can reduce colony growth rate and lower investment in reproductive output. Second, SDM production decreases the total number of fertile reproductives a colony raises. If there is a non-linear relationship between the proportion of offspring that are SDM and queen fitness (i.e. colony reproductive output) polyandry may be favoured. For example, a low level of production of SDMs may have little effect on colony success. This is most easily visualised as a threshold for the proportion of offspring that are SDM which, when exceeded, causes colonies to collapse. If the mean proportion of offspring that are likely to be SDM ($= 1/k$) is below the threshold, the reduction in variance from multiple mating results in fewer colonies collapsing compared to that following single mating. Conversely, if the mean lies well above the threshold, single mating may be selected for because there is a small chance that at least sometimes this will lead to low SDM production and colony survival (see Schmid-Hempel, 1994 for an analogous model).

(c) *Reduced susceptibility of colonies to parasites*

Sherman, Seeley & Reeve (1988) suggested that queen polyandry, by raising within-colony genetic variability, may reduce the proportion of workers that fall victim to parasites or pathogens. There is good evidence that genotypes vary in their susceptibilities to different diseases (review: Schmid-Hempel, 1998). The model of Sherman *et al.* (1988) based on the reasonable premise that the more genotypes there are in a colony, the smaller the proportion of workers that are susceptible to infection and die. When the function relating queen fitness to colony size is non-linear and has a threshold below which colonies are non-viable, a reduction in the variance in expected colony size will select for polyandry if fewer colonies then fall below threshold size. This benefit is incurred even if the mean level

of infection is identical for both monandrous and polyandrous queen colonies. Another possible benefit of genetic variability is that the rate of transmission of parasites is higher between more closely related individuals (Schmid-Hempel, 1994). If so, the mean levels of infection will be lower in colonies with greater genetic variance. This prediction was not supported in a comparison of multiply mated honeybees (Woyciechowski *et al.*, 1994 cited in Bourke & Franks, 1995). Liersch & Schmid-Hempel (1998) manipulated colony genetic diversity of the bumble bee *Bombus terrestris* via brood-replacement experiments. Genetically more diverse colonies had a lower parasite load in terms of the intensity, prevalence and species richness of parasites. The transmission of a parasite in the laboratory was also lower in genetically more diverse colonies of *B. terrestris* (Shykoff & Schmid-Hempel, 1991). More recently, in a direct experimental test of the value of polyandry, Baer & Schmid-Hempel (1999) artificially inseminated queens with sperm of either high or low genetic diversity. These treatments mimic low or high levels of polyandry, while controlling for factors that might correlate with natural variation in the number of mates. The high-diversity colonies had significantly lower levels of parasitism (load and intensity) and, on average, produced more males (but not queens) and had higher overall sexual productivity.

Schmid-Hempel (1994) formally modelled the benefits of multiple mating *via* non-linear effects on colony size. Polyandry is most advantageous when the costs of mating (which include any reduction in colony efficiency due to decreased worker relatedness and elevated within-colony conflict) are small relative to the intensity of parasitism. It is also more strongly favoured when the function relating queen fitness to colony size at reproduction shows diminishing returns with increasing colony size ('concave' relationship). If queen fitness increases exponentially with colony size, this selects against polyandry as increased variance increases the likelihood that some highly productive large colonies will be produced that 'overcompensate' for the very low productivity of smaller colonies.

(d) Sex allocation and worker-queen conflict

The population sex ratio is stable when the fitness gains per unit cost of investment for each sex are equal, otherwise there should be greater investment in the sex which provides larger net fitness gains (Fisher, 1930). All else being equal, frequency-

dependent selection maintains the sex ratio at 1:1, because the rarer sex enjoys a mating advantage. Fitness gains per sex must, however, be scaled by the coefficient of relatedness of each sex to the investor (parent, worker or helper). With random mating and equal production costs the stable sex ratio is therefore proportional to the asymmetry in relatedness of each sex to the investor. In haplodiploid social insects with monogamous queens, workers have a 'life-for-life' relatedness to their sisters of 0.75 and to brothers of 0.25. The stable sex ratio for workers is therefore 3:1 (0.75/0.25). This is known as the relatedness asymmetry (RA). Queens are equally related to their sons and daughters (0.5) and maximise inclusive fitness with a 1:1 sex ratio (for confounding factors see Queller, 1993). There is thus queen-worker conflict over the optimal sex ratio. In many social insects, sex allocation appears to be worker controlled because it is female biased and approximates to the workers' relatedness asymmetry (Trivers & Hare, 1976; Sundström, 1994).

Queens may benefit from polyandry because it reduces the difference between worker and queen RA and lessens conflict over sex allocation (Starr, 1984; Moritz, 1985). Worker RA drops rapidly when queens mate multiply ($RA = 1 + 2/z : 1$, where z = number of matings, assuming equal male paternity). Workers of polyandrous queens should invest more equally in the sexes than monogamous queens' workers because of the lower RA. It is important to note that this reduction in conflict can only occur if workers facultatively adjust sex allocation. Moreover, this worker ability must be a pre-existing ability. There is therefore the implicit assumption that there is already be a level of polyandry in the population. If not there is no initial benefit from polyandry to queens with respect to reducing sex allocation conflict by split sex ratios (Ratnieks & Reeve, 1992).

In a population with worker control and predominantly monogamous queens, the population sex ratio is female biased. A queen would therefore actually benefit most by producing only males, rather than a 1:1 ratio, because males have higher mating success than females. From the queen's perspective, the advantage of male-biased production continues until the population sex ratio is 1:1. The situation is even more complex, however, because differences in the relatedness asymmetry of workers (for example, due to variable numbers of matings by queens or replacement of the queen) create so-called 'split sex ratios' when there is worker control. Workers increase their fitness by

raising only or mainly females when the RA is higher (e.g. singly mated queens) and only or mainly males when the RA is smaller (Boomsma & Grafen, 1991; review: Bourke & Franks, 1995). The best empirical support for split sex ratios comes from work on the ant *Formica truncorum*. Colonies with queens that mated two or three times produced male-biased broods, while colonies with single-mated queens produced female-biased broods (Sundström, 1994; Sundström, Chapuisat & Keller, 1996).

Split sex ratios potentially benefit queens because they can gain fitness when their workers produce mainly males (although they lose more when workers produce mainly females). Sundström & Ratnieks (1998) present data from *F. truncorum* that colonies with doubly mated queens have a 37% fitness advantage over singly mated queen colonies. Queller (1993) argued that split sex ratios favour a period of continual increase in queen mating frequency. As the frequency of queens that mate multiply increases, more colonies produce a male-biased sex ratio and the population sex ratio ends up being more male-biased than the workers' optimum (i.e. worker RA). Split sex ratios evolve because workers who invest in male-biased broods when their RA is below some threshold pass on more genes than those lacking such a threshold (and *vice-versa* for female-biased production). The problem, however, is that the threshold depends on the population frequency of queen multiple mating. When the threshold changes rapidly due to selection on queen mating frequency, the old worker threshold is sub-optimal because they incorrectly assume their queen has an above-average mating frequency and produce males when they should be producing females. There is therefore selection on workers to adjust their threshold so that greater levels of queen polyandry are required before male-biased brood production occurs. In turn, this selects for queens that perform more matings. Queller (1993) therefore suggests that polyandry does not occur because it reduces worker-queen conflict over the sex ratio. Rather it is an evolutionary arms race, which eventually ends in extreme polyandry and a reduction in queen-worker conflict. This verbal model predicts very high numbers of matings until additional matings becomes prohibitively costly (see also Moritz, 1985).

Formal quantitative models confirm that facultative sex allocation by workers favours an increase in queen mating frequency from a state of monogamy (Ratnieks & Boomsma, 1995). However, the benefits to queens from increased mating frequency diminish rapidly as the proportion of double-mated queens in

the population increases (cf. Queller, 1993). As more colonies produce male-biased broods, the benefit attributable to greater male than female mating success diminishes as the population sex ratio becomes less female biased. This may act as a possible brake on the process. The benefits of double mating over single mating vary from a threefold advantage to no advantage. In the latter case, a mixed mating strategy could evolve. Triple mating is even less likely to evolve than double mating. This modelling exercise is important, because it shows that double mating can be favoured and indicates which variables are likely to reduce the advantages of polyandry. It also suggests that only moderate levels of polyandry will occur. A critical model parameter was the cost of remating, which selected against further mating as the marginal inclusive fitness gains from remating diminished.

A missing factor in the above discussion is the role of fathers. In haplodiploids, there is always selection on males to ensure that females produce daughters, as sons come from unfertilised eggs. In general, males appear to be unsuccessful because females control the act of fertilization (Brockmann & Grafen, 1989; Hawkes, 1992; Ratnieks & Keller, 1998). Boomsma (1996) noted, however, that there are several ways in which males could take advantage of split sex ratios to regain some control over daughter production by 'enlisting' workers' cooperation. Males benefit when workers produce female-biased broods. They should therefore ensure that workers assess RA as being above the RA threshold (e.g. that the female is singly mated). The predictions are therefore: (a) if males are sperm limited they should only mate with virgins; (b) if workers assess RA based on relatedness to fellow workers (perhaps *via* genetically based pheromonal cues), sperm clumping should occur so that, for a period at least, workers assess females as singly mated (Starr, 1984); (c) paternity should be unevenly shared so that RA is high. This could be achieved *via* strong first- or last-male sperm precedence but females benefit from lowering RA so they should make sperm removal difficult and maximise mixing of sperm. As such, second males may be in the unusual position of being selected to inseminate only a tiny amount of sperm. The conditions for invasion of second males that inseminate small amounts of sperm were reviewed by Boomsma (1996). An empirical demonstration of greatly reduced sperm input by second males, because it runs counter to the general pattern in animals (reviews in Birkhead & Møller, 1998), would provide strong evidence that RA and queen-worker conflict

are driving factors in the evolution of polyandry in social insects. There is some recent evidence of a negative association between the frequency of doubly mated queens and the degree of paternity skew in *Formica* ants which is consistent with Boomsma's argument (Boomsma & Sundström, 1998).

V. COSTS AND CONSTRAINTS ON MULTIPLE MATING

There may be increased predation risks associated with searching for and mating with males, either because females have to search in risky areas (Koga *et al.*, 1998) or because during mating vigilance and mobility are reduced. Seeking out additional mates, and the act of mating, may incur energetic or time costs. The act of mating may carry a risk of injury, or even mortality, from the male whom the female is attempting to mate. In the era of AIDS awareness, the potential dangers of acquiring a sexually transmitted disease while copulating are only too apparent. Given that there are readily identifiable costs to mating it is surprising that polyandry can initially invade a population. Moreover, once multiple mating has initially evolved there are several reasons to suspect further and increasing costs which make the subsequent maintenance of multiple mating within a population even less likely. If there is an increase in the frequency of mated pairs within a population as a result of females mating more than once, then this could have consequences for the subsequent behaviour of both parasites and prey. For example, an increase in the frequency of mated pairs in a population could select for sexual methods of transmission of disease organisms, as well as increase horizontal transfer which is sometimes associated with greater parasite virulence (e.g. Herre, 1993). It could also affect the pay-off to predators of searching for and specialising in preying upon mating individuals. Moreover, an increase in the likelihood that a female will mate with a subsequent individual will select for male behaviours or traits that act to prevent a female from remating and females will therefore have to incur further costs in order to overcome these male-imposed constraints (Rice, 1996). Stockley (1997*b*) reviews the range of male-imposed costs that have evolved to prevent remating. These costs are not necessarily trivial. One example are substances contained within the seminal fluid of male *Drosophila melanogaster* that reduce female receptivity to further matings; increasing exposure to these seminal products also leads to an

increase in the death rate of females (Chapman *et al.*, 1995; but see Eberhard, 1998). In *Melipona* bees, queens that produce sterile, diploid males are executed by the workers (Cook & Crozier, 1995). Queens should thus mate singly to minimise the risk of diploid male production and summary execution. In some mammals, there is evidence that copulating with more than one male may inhibit pregnancy, for example in Djungarian hamsters, *Phodopus sungorus campbelli* (Wynne-Edwards & Lisk, 1984). Any adaptations that overcome these male-imposed costs create an environment that selects for further adaptations in males to prevent remating or maintain paternity if females remate.

The fact that multiple mating persists in spite of several selection pressures continually acting against it, and the fact that it acts to promote additional male-imposed costs does suggest that it is unlikely to be sufficient to argue that polyandry tends to occur when costs to mating are low. Benefits have to be considered.

VI. CONCLUSIONS AND FUTURE DIRECTIONS

Several general points and suggestions for future areas of research emerge from this review.

(1) There has been heated debate as to whether non-random fertilization is due to cryptic female choice or sperm competition. From the female's perspective, however, the genetic benefits of multiple mating due to improvement of their sons' fertilization success do not depend on the exact mechanism of paternity biasing. Sperm selection by females, sperm competition *sensu stricto*, differential investment in offspring and differential abortion will all lead to polyandrous females producing sons with traits that make them more successful than the sons of monandrous females when they mate with polyandrous females. For this reason, when the extent of female or male control of a process is unclear we have simply used the neutral term 'post-copulatory paternity-biasing' mechanisms (strictly speaking, we should also include mechanisms that function *in copula* such as copulatory courtship).

(2) Even if the focus is on proximate mechanisms, there is a need to think of post-copulatory paternity biasing in a probabilistic way. A tight focus on active female selection of sperm (e.g. Birkhead, 1998), for example, implies that females can only increase their fitness if they strongly bias paternity to the single, best male. However, even a slight tendency for biased paternity will result in selection on those male

traits that influence this process. For example, it is the variation in the ability of males to gain paternity in the same context, such as mating second, rather than the difference in paternity between the first and second mate of an individual female that we should be investigating (e.g. Simmons *et al.*, 1996). It is also worth noting that traits that explain the general pattern of P_2 (such as relative sperm input) may differ from the traits that explain the residual variation in P_2 (such as genital morphology or copulatory courtship behaviour). The huge amount of residual variation in paternity left unexplained by conventional models based on sperm number and fixed mechanisms of sperm flushing or displacement suggests this is a worthwhile task (Cook, Harvey & Parker, 1997). It is also clear that some models have been successful in predicting paternity even though they conflict with the actual processes going on inside the female (e.g. Simmons *et al.*, 1999). To determine sources of residual variation it will help to try to identify those traits that are most likely to be causally responsible for variation in paternity (methods: Arnqvist *et al.*, 1997; Briskie, Montgomerie & Birkhead, 1997; example: Arnqvist & Danielsson, 1999).

(3) Despite the fact that the potential genetic benefits to females of multiple mating have previously been pointed out, relatively few studies have tried to test for them empirically or to distinguish between the various potential advantages. For example, no study has looked to see whether the sons of polyandrous females do achieve higher fertilisation success than the sons of monandrous females. Far more comparisons of the offspring performance of females experimentally assigned different numbers of mates are needed (e.g. Zeh, 1997; Tregenza & Wedell, 1998).

(4) Pre- and post-copulatory mechanisms to discriminate among males could potentially achieve the same genetic benefits. For example, both could select for improved offspring viability *via* good genes. However, it is interesting to ask why post-copulatory mechanisms evolve given that, when using such mechanisms, females incur the additional costs of mating more than once. One answer may be that post-copulatory mechanisms provide a more reliable way of selecting a genetically compatible mate (Zeh & Zeh, 1997).

(5) There is a lack of appreciation that females could be using post-copulatory mechanisms to simultaneously gain several types of genetic benefits. For example, there is no reason to exclude the possibility that females use post-copulatory mech-

anisms to detect genetically superior as well as genetically more compatible males. Therefore, to show a post-copulatory paternity bias towards genetically superior males, it is important to control for any effects of variation in genetic compatibility. Specifically, coefficients of relatedness could mask the effect of post-copulatory paternity biasing to improve offspring performance or attractiveness. The recent study by Wilson *et al.* (1997) provides a fine example of the possible effect of variation in female genetic constitution in patterns of paternity.

(6) Additive genetic variation among males is a prerequisite for the evolution of any mechanism by which females choose males for genetic benefits based on viability or attractiveness 'good genes' (Petrie *et al.*, 1998). It is currently unclear whether proposed mechanisms for the maintenance of additive genetic variation in preferred male traits that function pre-copulation can also account for the variation in traits that function post-copulation. For example, condition dependence is seen as a major factor in the former (Rowe & Houle, 1996), while inter-sexual conflict and endless 'arms races' may be invoked for the latter (Holland & Rice, 1998). The implications of these different mechanisms need to be explored more fully. The relative importance of non-additive sources of genetic variation to the maintenance of genetic incompatibility should also be clarified.

(7) Post-copulatory paternity-biasing mechanisms seem to provide a more precise genotype matching between males and females than error-prone, pre-copulatory mate choice. Polyandry could therefore result in more rapid restriction in gene flow and eventual reproductive isolation of a part of a population. It can generate stronger assortative mating with respect to genotypes than mate choice by monogamous females. The evolutionary implications of assortative fertilization resemble those for assortative mating (Markow, 1997). As such, the role of multiple mating in promoting speciation needs to be considered more carefully (review: Howard *et al.*, 1998). For example, we suggest that clades where females mate multiply should be more speciose than clades with monandrous females.

(8) The benefits of pre-copulatory choice may differ from those of post-copulatory choice. Females may use pre-copulatory choice to identify and mate with a number of high-quality males and then use post-copulatory mechanisms to identify a male that is genetically compatible. Under these circumstances high-quality males need not be better at fertilising and there need not be a positive relationship between

males' pre- and post-copulatory reproductive success. Whether there are positive correlations within individuals for traits that function pre- and post-copulation may depend on the reasons for polyandry. Positive correlation may occur when remating is a mechanism to trade-up genetically, as with EPC in birds, but negative correlation or the absence of any relationship seems more likely when, for example, pre-copulatory mate choice for quality is combined with polyandry for genetic diversity.

(9) Comparative analyses often use pre-copulatory secondary sexual signals like plumage dimorphism as measures of the degree of sexual selection. This may be misleading as sexual selection could result solely from post-copulatory paternity-biasing mechanisms. This may lead to less readily identifiable evidence of variation in the intensity of sexual selection. For example, there is enormous variation in the complexity of male genitalia which seems to be due to post-copulatory sexual selection (see Arnqvist, 1998) but this has no known relationship with sexual size or colour dimorphism. The bottom line is that measures of the intensity of sexual selection should be based on variation in paternity not mating success (see Møller & Ninni, 1998) or simplistic measures of sexual size dimorphism. Sexual selection does not end with copulation.

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