



REVIEW

Sex roles and sexual selection

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ABSTRACT

Sexual selection has been portrayed as acting predominantly on males who compete with each other over copulatory access to females; selection was considered to be driven by females choosing between males at the pre- or postcopulatory level. However, a broader view of sexual selection is now emerging. Examining male discrimination between females and female–female competition has been beneficial in identifying factors influencing the direction and strength of sexual selection. Furthermore, consideration of processes such as sexual coercion or genetic incompatibility, which indirectly influence an individual's set of copulation partners, gamete set or their offspring success, has helped to clarify the ways in which sexual selection may operate. Moreover, there is increasing evidence that not all copulations translate directly to paternity and that paternity does not necessarily translate into successful offspring. Postcopulatory and postfertilization mechanisms that influence not only paternity share but offspring recruitment now require further consideration. The benefits to each sex of copulating with particular partners or with more than one partner remains an area of debate. More carefully designed studies which eliminate alternative possibilities or quantify the relative importance of different selective pressures will also benefit from considering that not all copulations function solely to inseminate or receive sperm. It is also now clear that not all individuals of one sex follow the same strategy. Examining the variation between individuals in reproductive behaviour, fertilization success and offspring success will be important in establishing the selective pressures and mechanisms underlying the operation of sexual selection.

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The relative importance of male and female roles in sexual selection has been controversial from the outset, from the neglect of any female perspective at the start of the century, to the championing of female control of reproduction in both the scientific and popular literature in the 1990s. While the relative contribution of factors internal and external to science responsible for these changes has itself been a controversial topic (Cronin 1991; Cunningham & Birkhead 1997; Gowaty 1997), most will agree that the aim in studying sexual selection is to gain an objective view of the relative importance of both sexes in driving sexual selection. Recent develop-

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ments have led to a continued expansion of the framework in which we study sexual selection and there is therefore a constant need to reassess our generalizations, including the relative role of the sexes in influencing the outcome of reproduction. Our aim in this review is to highlight the benefits to be gained from looking beyond the traditional roles of the sexes we have come to expect.

We briefly outline how biologists have viewed the operation of sexual selection and the way in which the relative roles of the sexes have been considered. We then discuss some mechanisms of sexual selection and how they act on the different sexes at precopulation, postcopulation and postfertilization stages. Finally, we consider the selective advantages driving sexual selection, taking into account the possibility that not all members of one sex adopt the same strategy.

SEX ROLES AND SEXUAL SELECTION

In evolutionary terms, the success of individuals depends not only on their ability to survive, but also on the ability to reproduce successfully and produce more successful offspring than their counterparts. This can lead to competition between individuals over reproductive opportunities; individuals that are successful in this competition will produce more descendants that are successfully recruited into future breeding populations. This differential reproductive success can give rise to sexual selection: selection for behavioural, morphological or physiological characteristics that increase reproductive success (Darwin 1859, 1871).

While there are many stages of reproduction at which sexual selection can act, the emphasis has traditionally focused on two mechanisms that were originally proposed by Darwin: sexual competition over access to mates (usually between males) and mate choice (usually by females). The theoretical framework for the different roles of the sexes was laid down by Bateman (1948). He established that the relative strength of sexual selection in males and females is determined by the relationship between mating success (number of copulation partners) and reproductive success (offspring production). Bateman found in his studies of *Drosophila melanogaster* that multiple copulations led to a greater increase in the number of offspring produced in males than in females. Hence, he concluded that there is a greater advantage for males in copulating with several partners than there is for females, leading to stronger competition between males over mates and stronger selection on males than on females. However, Bateman also showed that sexual selection in females may be strong because multiple mating by females also influenced their reproductive success. Bateman's experiments were divided into two groups, one set in which the flies had an adequate food supply and another in which the food supply was inadvertently sub-optimal. In the experiments where food was abundant, males gained additional reproductive success from copulating with more than one female but females gained little from multiple copulations. However, in the experiments where food was limited, females did gain from copulating with more than one male (see also Arnold & Duvall 1994). Bateman believed this was because males in poor food conditions produced fewer sperm and females needed to recopulate to replenish their sperm supply sooner than those in the abundant food condition. Furthermore, *D. melanogaster* is a species in which, under optimal conditions, females have enough sperm to maintain optimal fertility of eggs for approximately 4 days. After this, because sperm utilization is inefficient, females start to lay infertile eggs and begin to copulate again (Gromko et al. 1984). Bateman's experiments ran for only 3–4 days and so the benefit of remating under optimal conditions might also have been underestimated. In other species of *Drosophila*, females store fewer sperm than *D. melanogaster* and have to copulate more frequently to maintain high egg fertility (Pitnick & Markow 1994).

The roles of the different sexes in sexual selection were later expanded by Trivers's (1972) parental investment

theory. When one sex invests less in reproduction than the other and is able to reproduce at a faster rate, members of the sex investing least will compete amongst themselves over access to those investing most. An empirical measure of this is the operational sex ratio (OSR); the ratio of fertilizable females available to sexually active males (Emlen & Oring 1977). As males are generally considered to invest less in reproduction than females, at both the gamete and offspring stage, the OSR is considered to be biased towards males; it is therefore expected that males will compete over females and that sexual selection will be stronger on males than females. This has been difficult to test empirically, however, and it has been suggested that an alternative and more tractable approach is to consider the potential reproductive rates of males and females to determine the direction of mating competition (Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992; Parker & Simmons 1996; Simmons & Parker 1996). This is the maximum number of offspring that parents can produce per unit time (averaged across all individuals in a population).

The way in which sexual selection will operate on males and females is influenced by the relationship between the number of copulation partners and reproductive success. The potential for sexual selection is dependent on the variance in the reproductive success of males and females (Arnold & Duvall 1994). This has previously been assumed to be low, and hence sexual selection is considered to be weak, in monogamous species. However, the realization that the underlying genetic mating system may be quite different from the apparent social mating system has shown that the opportunity for sexual selection in both sexes may be higher than previously thought (Fig. 1).

An empirical test of the way in which the number of copulation partners may influence the potential for sexual selection has been conducted in the socially monogamous dark-eyed junco, *Junco hyemalis* (Ketterson et al. 1998). Although socially monogamous, both males and females participate in copulations with individuals other than their social partner. The impact of extrapair fertilizations on the variance in reproductive success for male and female juncos was calculated by measuring: (1) the number of copulation partners; (2) the apparent reproductive success (the number of young produced in the nests of social mates); and (3) the genetic reproductive success (true number of offspring produced as revealed by molecular analysis). Among males, the variance in genetic reproductive success was higher than the apparent variance in reproductive success, indicating that extrapair copulations increased variance in reproductive success and hence the potential for sexual selection in males. The same was also true for females, with reproductive success increasing with the number of copulation partners. However, the reason for this increased female success was unclear and may have resulted from extrapair males targeting particularly fecund females. Moreover, the difference in variances in reproductive success between males and females was less for genetic reproductive success than for apparent reproductive success, suggesting a smaller difference in the intensity of sexual

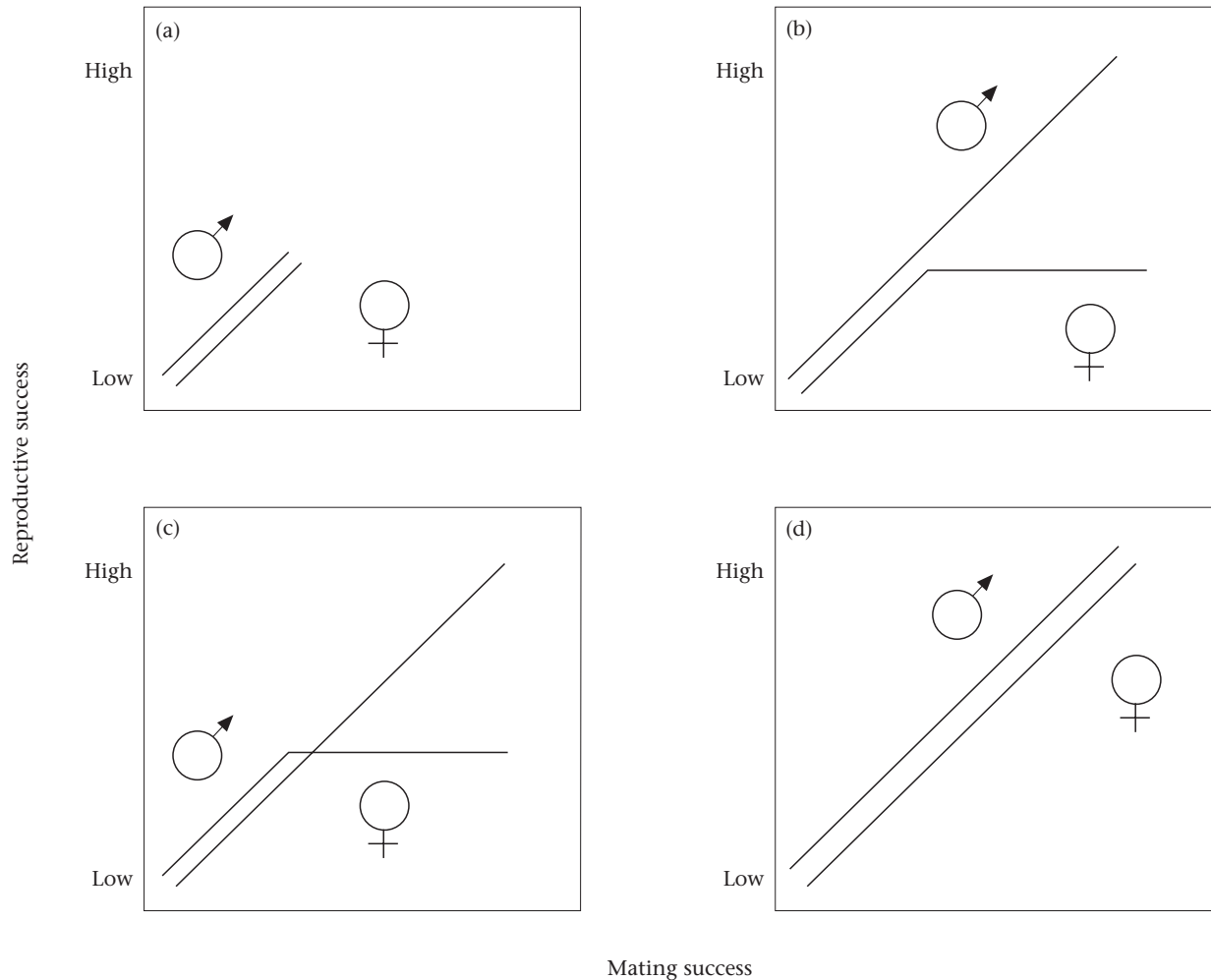


Figure 1. Implications for the relative intensity of sexual selection on the sexes and the expected relationships between the number of mates (mating success) and the number of offspring (reproductive success) of males and females where (a) there is true genetic monogamy, (b) male, but not female reproductive success increases with multiple copulation partners, (c) female, but not male reproductive success increases with multiple copulation partners and (d) both male and female reproductive success increase with multiple copulation partners (modified from Arnold & Duvall 1994 and Ketterson et al. 1998).

selection acting on the two sexes than previously thought. With molecular data now available for populations of many different species, this type of approach could potentially offer considerable insight into the relative importance of the sexes in sexual selection. However, in future it will also be important to consider differences in offspring success and this approach could provide further important information by looking at offspring recruitment to breeding populations rather than the number of offspring produced.

MECHANISMS OF SEXUAL SELECTION

The two most familiar mechanisms through which sexual selection may act are competition over copulation partners and mate choice. However, it is useful to consider other mechanisms of sexual selection that are not immediately obvious within this framework. For example, Wiley & Poston (1996) distinguished between direct and indirect mate choice. They considered direct mate choice

to require discrimination between individuals of the opposite sex and indirect mate choice to involve all other behaviour, morphology or physiology that restricts an individual's set of potential copulation partners, for example, sexual coercion, aggregation and preference for particular mating locations. Indirect choice may then result in assortative mating leading to sexual selection. Although these indirect mechanisms may be considered as forms of mate competition and choice, differentiating between these behaviour patterns may help to identify the different processes that generate nonrandom choice of copulatory partner (Andersson 1994; Wiley & Poston 1996). This differentiation does not form two discrete categories of sexual selection but can serve to offer a clearer framework to think about different ways in which sexual selection may act. The distinction between direct and indirect processes also highlights areas requiring further clarification as exhibited by the recent debate over cryptic female choice and sperm competition where the relative importance of male and female direct and

indirect effects governing sperm utilization remain to be elucidated (see Postcopulatory, Prefertilization Choice below).

A further complication in predicting the strength of sexual selection in each sex has been that it can be difficult to assess the relative importance of the roles of the sexes at pre- and postcopulatory stages of sexual selection. Postcopulatory processes are difficult to observe directly and distinguishing between male and female postcopulatory effects is particularly problematic. For example, to be certain of the existence of differential sperm utilization by females it is necessary to control for sperm competition effects (Simmons et al. 1996; Birkhead 1998b). Many aspects of postfertilization choice through differential investment or abortion remain to be examined yet have the potential to play a large role in sexual selection as the last stage at which either sex can influence the outcome of reproduction.

Here we consider some ways in which sexual selection may act in direct and indirect ways during the (1) precopulatory, (2) postcopulatory but prefertilization and (3) postfertilization stages of reproduction.

Precopulatory Choice

The main focus of the precopulatory phase of sexual selection has been on female choice. While the traditional view of the sex roles has been that males compete over access to females and that females may choose between them, female–female competition and male choice can also play an important role. Here we highlight some studies that demonstrate the benefits of considering the sexes outside their traditional roles.

Competition between females over access to males will tend to occur when males limit their reproduction. In some of the Australian katydid (Tettigonidae), sperm are transferred in nutritious spermatophores. Changes in food availability show how the relative investment of males and females can influence the strength of sexual competition and choice in the two sexes. When food is in short supply, females fight over males as their spermatophores become a scarce resource. In experimental studies, not only did females fight at a higher frequency when food was scarce, but males were more discriminating, preferring to copulate with large, fecund females (Gwynne & Simmons 1990).

There is increasing evidence that female–female competition plays a role in shaping mating systems (Slagsvold & Lifjeld 1994). The European starling, *Sturnus vulgaris*, is facultatively polygynous and individuals may breed either as a pair, or as a trio of one male and two females. Although beneficial for males, polygyny can be costly to females as polygynous males provide less care per nest than monogamous males. Female–female aggression appears to influence which mating pattern males adopt. Females that remained monogamous when there was the opportunity for the male to attract a secondary female were significantly more aggressive towards simulated female intrusions than females that became part of a polygynous trio. Female aggression was subsequently

shown to be the only predictor of male mating status (Sandell & Smith 1996, 1997). In the polygynandrous dunnock, *Prunella modularis*, female song also appears to function in intrasexual selection to deter rival females, possibly to ensure male parental investment (Langmore et al. 1996; Langmore & Davies 1997). In a study of a closely related species, the alpine accentor, *P. collaris*, female song was found to attract potential partners; however, in another population of alpine accentors, where the population sex ratio was more male-biased and female–female competition likely to be low, female song was uncommon (Heer 1994, 1996, cited in Langmore & Davies 1997).

With the conventional interpretation of sexual selection being that males compete for females and females choose between them, females are commonly thought to prefer the most dominant male. However, the outcome of male–male competition does not always predict male reproductive success. In the sand goby, *Pomatoschistus minutus*, females prefer nondominant males that are good fathers (Forsgren 1997). In pintail ducks, *Anas acuta*, male dominance appears to be a result of pairing success rather than the cause (Sorenson & Derrickson 1994): females do not choose to pair with the most dominant male but male rank is subsequently influenced by pairing success, with preferred males later becoming dominant.

Mate choice has generally been taken to mean female choice. However, this was not inherent in Darwin's theory. Although he considered mainly female choice of ornamented males, Darwin recognized that males may also differentiate between females (Cronin 1991). Male and female crested auklets, *Aethia cristatella*, for example, both possess small, feathered crests which are displayed during courtship displays. When model auklets with crests were placed among the colony, both sexes preferentially directed sexual displays towards models with the largest crests, suggesting the occurrence of mutual mate choice (Jones & Hunter 1993).

Male choice may be expected to occur where male investment is high, when males are limited in the extent to which they can allocate resources or where choice has a large implication for male success. Males may be limited in the number of ejaculates or sperm they can deliver, for example, and may allocate their sperm carefully (Dewsbury 1982). For example, in the mormon cricket, *Anabrus simplex*, females mount males to copulate but males reject females in the majority of mountings before spermatophore transfer. Accepted females are significantly heavier and more fecund than rejected females. Male mate choice for fecund females has also been demonstrated in birds. Male zebra finches, *Taeniopygia guttata*, selectively pair with females independently of their age, experience, body size and body weight, but that had been fed a high-quality diet over those fed a poor-quality diet and who could therefore lay larger eggs (Monaghan et al. 1996).

Mutual mate choice has the potential to generate constraints on an individual's optimal choice as each individual is limited to choosing a subset of the population that will accept them as a copulation partner (Johnstone et al. 1996; Johnstone 1997). Therefore, experimental studies

of female choice should consider the possible effects of male preference on female decisions.

Other mechanisms have been considered as indirect forms of mate competition and choice. Any behaviour that restricts an individual's set of potential copulation partners (reviewed in [Wiley & Poston 1996](#)) can potentially result in sexual selection. Sexual coercion, for example, in which individuals harass or force another individual to copulate, may bias an individual's set of copulation partners to individuals that are good at forcing copulations and hence may be classed as a mechanism of indirect choice ([Wiley & Poston 1996](#)). However, in many cases, the differentiation between direct and indirect mechanisms may not yet be clear and can therefore highlight areas where the underlying mechanisms and the direction of sexual selection require further clarification. For example, female responses to sexual coercion have seldom been addressed because it is difficult to establish the underlying function of resistance behaviour ([McKinney et al. 1983](#); [Evarts 1990](#); [Westneat et al. 1990](#)). Resistance behaviour may not always be an attempt to avoid copulation but may be a mechanism to facilitate female choice directly ([Westneat et al. 1990](#)). Resistance may generate precopulatory mate choice, whereby females test or assess males before choosing from which male to accept a copulation. Resistance behaviour may also attract and promote competition between males so that resisting females are eventually inseminated by the male of highest heritable genetic quality. If female resistance functions as a mechanism for precopulatory female choice, the predicted outcome of resisted copulations would be that females copulate with preferred males and that these females have a higher reproductive fitness. A further possibility is that resistance may function to promote postcopulatory mate choice; by resisting copulation until several males are present, females could then copulate with the males in quick succession to encourage sperm competition or selection within the female's reproductive tract. If female resistance functions as a mechanism to promote postcopulatory choice, resisted copulations would be predicted to attract the attention of several copulatory partners and females that copulate with several males should have a higher reproductive success than those that copulate with fewer males. However, it is also important to be aware that a female's mating decision may not be based on any inherent value of the male attempting copulation. Resistance and copulation both have their associated costs; factors independent of male quality, such as an individual's immediate energetic requirements, may dictate when it pays a male or female to resist or accept copulation attempts ([Watson et al. 1998](#)). Considering the underlying mechanisms driving this type of behaviour may elucidate the function of the observed pattern of behaviour. In many cases of apparent sexual coercion, these possibilities have yet to be established.

Other types of indirect effects on traits, not directly involved in sexual selection, must also be considered. For example, sexual selection for a long tail may also select for long wings, not because long wings are attractive but because they are required to compensate for the cost of

carrying a large tail ([Balmford et al. 1994](#)). Indirect effects are often difficult to establish and disentangle from the effects of direct choice (see [Partridge 1994](#)). None the less, it is crucial that we find ways to separate the effects if we are to clarify the relative importance of different mechanisms of sexual selection and hence its strength and direction.

Postcopulatory, Prefertilization Choice

Sexual selection can continue after insemination through sperm competition ([Parker 1970](#)); when a female is inseminated by more than one male, their sperm will compete inside the female's reproductive tract to fertilize her ova. In addition, females may have the potential to choose between the sperm of different males ([Thornhill 1983](#); [Eberhard 1996](#)). Most studies of sperm competition have concentrated on precopulatory behavioural mechanisms that influence subsequent sperm competition; the pattern of copulation behaviour an individual pursues will determine which individuals will be contestants in the ensuing sperm competition. It has often been assumed that the proportion of copulations achieved by an individual male will then translate directly into the proportion of offspring he sires. However, patterns of sperm utilization after multiple copulation are extremely variable, both between species (see [Walker 1980](#)) and between individuals within a species ([Lewis & Austad 1990](#)). For example, in some spiders, the first male to copulate with a female generally fathers the majority of her offspring ([Austad 1984](#)). In most species of bird and some insects, however, the last male to copulate gains the greatest share of paternity. The basic mechanisms underlying this last-male sperm precedence have been examined in several species (reviewed in [Birkhead & Parker 1997](#)). Basic models exploring sperm utilization appear consistent with average levels of sperm precedence. However, in empirical tests of these models, there is always considerable variation in paternity patterns between individuals (e.g. [Cook et al. 1997](#); [Birkhead & Biggins 1998](#)). Within a species, some males appear consistently to father more offspring than others (e.g. [Dziuk 1996](#)). In many insects, for example, larger males father more offspring than smaller males, even when they achieve the same number of copulations ([Simmons & Siva-Jothy 1998](#)). It is now this variation that requires explanation to establish whether either of the sexes may be biasing sperm utilization in any way to their own advantage.

Much debate surrounds the question of whether females can influence paternity through cryptic female choice ([Eberhard 1996](#)), by selecting between the sperm of different males in their reproductive tract to fertilize their eggs. In some cases, animals appear to use sperm selectively on the basis of genotype. In the hermaphroditic, colonial ascidian, *Diplosoma listerianum*, individuals release sperm into the surrounding water and potential partners within the colony collect this sperm in their oviducts. If a clone takes up its own sperm, a block prevents fertilization ([Bishop 1996a](#); [Bishop et al. 1996](#)). In the sand lizard, *Lacerta agilis*, when a female copulates

with two males, the most genetically similar male fathers fewer offspring (Olsson et al. 1996) and in the cowpea weevil, *Callosobruchus maculatus*, the paternity share of males is more highly repeatable between sisters than between unrelated females (Wilson et al. 1997) suggesting a genetic component to sperm utilization. However, similar studies in birds (Cunningham 1997) and mammals (Stockley 1997) have found no evidence for such an effect.

Whether this type of sperm utilization gives rise to sexual selection, however, is not clear. It is important to distinguish between compatibility effects (Zeh & Zeh 1996, 1997) and utilization of sperm from preferred males for viability or attractiveness genes. Females of some species may have the ability to reject like-sperm to prevent inbreeding, as occurs in many plants (Willson & Burley 1983; Delph & Havens 1998). Although this may be beneficial to offspring viability, this type of choice does not favour any particular phenotypic trait and does not usually lead to sexual selection (Waser et al. 1987). Moreover, mechanisms to select compatible genotypes could potentially conflict with the optimal choice of partner if genetic benefits are important; males with preferred traits, which their offspring could inherit, may not be the most genetically compatible for an individual female. Alternatively, genetically incompatible males may be those providing superior direct benefits.

Distinguishing between direct and indirect mechanisms of postcopulatory choice is also extremely difficult. To demonstrate that direct choice between sperm types is occurring, it is important to control for all male effects. For example, when female yellow dungflies, *Scatophaga stercoraria*, copulated for a fixed amount of time with two males, the larger male fertilized more eggs. This was because females stored more sperm from large males. This effect was initially attributed to active selection of sperm by females from large males (Ward 1993). However, Simmons et al. (1996) showed that the findings could equally be explained by larger males having a higher rate of sperm transfer and displacement. When Simmons et al. (1996) controlled for such effects, they found no difference in levels of paternity between large and small males.

Care is needed to distinguish between direct and indirect mechanisms in order to establish the relative importance of the sex roles in determining paternity. The way copulation patterns translate into paternity can have important implications for the optimal behavioural strategies of animals. Hence, an understanding of the mechanisms determining patterns of paternity is essential.

Postfertilization Choice

Postfertilization direct or indirect mate choice may occur through individuals biasing their reproductive effort towards zygotes, embryos or young of preferred partners. This may operate through differential abortion or mortality, differential investment in offspring of different individuals or the differential production of, or investment in, male and female offspring.

There is some evidence for differential abortion. The best known example is the socially induced 'Bruce effect' in which pregnant rodents abort embryos after exposure to unfamiliar males or their urine (Bruce 1959). Abortion may have some adaptive function under these circumstances; males gain because females become receptive sooner and females may gain by not wasting further reproductive effort if their offspring are likely to be killed by the strange male. In mice, females may abort up to one-third of all fertilized eggs without affecting litter size (Hull 1964). Huck (1982) found that the urine of dominant males was more effective in causing abortion than that of subordinate males, suggesting a potential benefit for females may be that they are subsequently inseminated by a more dominant male. In other cases, abortion may occur as a result of genetic incompatibility (Wedekind et al. 1995).

A less extreme strategy is differential investment. Differential investment, through direct or indirect processes, can operate on at least four levels. Individuals may (1) commence breeding earlier; (2) increase the number of eggs laid or young produced; (3) increase their investment in each egg or young; or (4) invest parental care differentially between young after hatching or birth. For example, in some species, females lay more eggs (Norris 1993; Petrie & Williams 1993; Petrie 1994), or larger, heavier eggs (Cunningham 1997) and feed chicks at a higher rate (Burley 1988; de Lope & Møller 1993) when paired to more attractive males than when paired to unattractive males. Increased investment is assumed to have a cost in terms of either reduced resources for future reproduction or female survival (Trivers 1972). Attractive partners, may then be able to invest less in reproduction and unattractive individuals may be able to gain partners by offering a higher level of investment than more attractive males (Burley 1988). In barn swallows, *Hirundo rustica*, de Lope & Møller (1993) increased and decreased male attractiveness by extending and shortening tail length, respectively. Females invested more in reproduction when paired to males with lengthened tails. This study, however, does not show whether females are altering their investment according to perceived male attractiveness; if attractive males are handicapped by the lengthened tails, females may have to alter their investment to compensate for reduced provisioning (Witte 1995).

While differential investment in offspring provisioning is relatively easy to observe, the mechanisms underlying differential zygote provisioning in the absence of any direct male benefits remains unclear. Hormonal mechanisms for parental favouritism in birds have recently been addressed and have the potential to play an important role (Schwabl et al. 1997). By depositing different amounts of testosterone in different eggs in a clutch, females may influence the competitive ability of different offspring within a brood (Schwabl 1993); if the clutch is of mixed paternity, females may have the potential to favour particular offspring. The mechanisms determining egg investment, and the flexibility of these mechanisms, require further investigation.

Differential investment may also occur through indirect mechanisms. While mate choice decisions by females

may not directly depend on resources held by preferred males, mate preference may correlate with, or subsequently influence, the quality of resources available to a female. In the comma butterfly, *Polygonia c-album*, preferred males produced large spermatophores because they had access to superior food resources; females that had copulated with these males had a higher somatic and reproductive investment resulting in higher female fitness (Weddell 1996).

Whether the mechanism is direct or indirect, it is particularly important to establish whether females invest differentially in offspring of different males, in order to establish the relative importance of maternal and paternal effects on offspring success. For example in the mallard, *Anas platyrhynchos*, the same group of females produced heavier, although not skeletally bigger, chicks when experimentally assigned to attractive males than when assigned to unattractive males. This effect suggests that attractive males produce better quality offspring, but in fact, this effect was due to the same females laying larger eggs when paired to attractive males than when they were assigned to less attractive males. Once differences in egg investment had been controlled for, there was no effect of paternal attractiveness on offspring condition. The precise mechanism remains unclear; but when females were paired to attractive males, they may have gained direct benefits in the form of reduced harassment and have been able to invest more in reproductive attempts (Cunningham 1997).

In summary, to establish the relative contribution of male and female reproductive effort and hence the intensity of sexual selection, it is necessary to consider male and female precopulatory, postcopulatory but prefertilization and postfertilization effects as a whole. Since choice may continue to act through differential investment after hatching or birth, the best measure of reproductive success may be offspring recruitment rather than offspring production in order to consider how sexual selection may be acting.

FUNCTIONAL ASPECTS OF SEXUAL SELECTION

Darwin's theory of sexual selection questioned how male traits could evolve by female preference. However, he provided no satisfactory solution to the question of why mate choice occurs. While males are assumed to seek as many copulations as possible in order to produce more offspring, the benefits of female choice have been more difficult to establish. The observation that females appear to seek copulations in the apparent absence of direct benefits, on leks and through extrapair copulations, has led to the assumption that females may be seeking heritable genetic quality for their offspring. The importance of such benefits has been controversial and, in part, this might have been responsible for the lack of examination of the relative strength of sexual selection operating on each sex.

We have three objectives in this section: (1) to consider the importance of examining all the potential functions of mate choice, including those not generally considered within the framework of explanations for multiple

mating; (2) to show that the traditional assumptions that males gain more offspring by having more copulation partners and that competition is always strongest on males need readdressing; (3) to show that not all offspring will breed with the same success and that it is important to consider that not all members of one sex may be seeking the same immediate benefits or seeking benefits in the same way.

The Relative Importance of Different Functions

The potential benefits of copulating with more than one partner or with preferred partners are generally classed in two groups: (1) females may gain directly from resources offered by the male or by avoiding males more costly to copulate with (for example males with a high level of disease or reduced fertility) and/or (2) females may gain indirectly by gaining advantages for their offspring either because male attractiveness is heritable, or because attractive males are of high heritable viability. These effects are not mutually exclusive and evidence for one does not constitute evidence against the other. However, it is important to consider the relative importance of both possibilities in studies examining the benefits of mate choice (1) so that effects are not attributed to one when they may be partly accounted for by the other and (2) because it is important to consider the relative importance of different effects if more than one plays a role, for example, direct effects are likely to outweigh any indirect effects that may be present (Price et al. 1993; Kirkpatrick & Barton 1997).

Few studies have looked at the relative importance of the various direct and indirect benefits of multiple mating and many have tended to consider one benefit in isolation without totally excluding the effects of others. One exception is a study of the lekking sandfly, *Lutzomyia longipalpis* (Jones et al. 1998). When females were assigned to preferred and less preferred males, no clear effects of paternity were found on female fecundity or survival, or the viability of their offspring. However, preferred males fathered preferred offspring suggesting that indirect benefits that influence offspring attractiveness but not viability may be important.

Furthermore, it is important to consider the overall net benefit once the costs of reproduction are taken into account. Copulation itself can be costly for females (Chapman et al. 1993; Rice 1996) and direct costs of copulation may influence not only female survival but fecundity as well. For example, sexually transmitted pathogens, although often cited as a potential cost (Sheldon 1994), have received little empirical attention but many have sublethal effects that can have a greater detrimental effect on females than on males (Wobeser 1981) and can reduce female fertility and egg production (Stipkovits et al. 1986; Marius-Jestin et al. 1987). The costs associated with sexual selection are perhaps one of the most important areas now requiring empirical investigation.

In many cases, females may benefit from copulations with more than one partner by gaining direct benefits, for example, increased fertility or fecundity (e.g. many

insects: Ridley 1988; prairie dogs, *Cynomys gunnisoni*: Hoogland 1998), increased parental care (dunnock: Davies et al. 1996) or increased longevity (Burpee & Sakaluk 1993; Weddell 1996). However, there are many cases of multiple mating where no direct benefits are immediately apparent, such as when socially monogamous birds seek extrapair copulations (Birkhead & Møller 1992). This has led to the assumption that indirect benefits must be important in these situations (Møller 1998). While in some species, indirect effects do indeed appear to be important (e.g. Petrie 1994; Welch et al. 1998), studies of other species have not found similar effects (e.g. Whittier & Kaneshiro 1995). While we need to establish whether indirect effects are important, the abandonment of the importance of direct benefits might have been premature. Several recent studies have suggested that females of socially monogamous species may obtain direct benefits from having multiple copulation partners. These benefits include access to extra feeding resources, additional antipredator nest defence and possible fertility benefits (Gray 1997a, b). One observation that is commonly used to support the indirect benefits hypothesis is that females seek extrapair copulations with more attractive and more dominant males (Birkhead 1998a; Møller 1998). We propose that in some cases, this may be because relatively attractive, dominant males may be more available for extrapair copulations simply because they have larger sperm reserves, spend more time patrolling territory boundaries, or are less likely to be excluded from the territories of less dominant males. While good genes effects may indeed be important, these alternatives need to be excluded before drawing conclusions that females seek extrapair copulations with these males to gain good genes.

Some Traditional Assumptions Need Readdressing

Our assumptions about the roles of the sexes may not always be correct. It is generally assumed within the framework of sexual selection that all copulations function to inseminate sperm and gain fertilizations. Males are assumed to copulate with as many females as possible in order to produce many offspring. However, this may not always be the case. In several duck species, for example, pairs copulate outside the breeding season when testes are regressed and no sperm can be transferred. A recent study of oystercatchers, *Haematopus ostralegus*, has provided further evidence that not all copulations function to inseminate sperm since some copulations occurred between bonded females. Homosexual copulations have previously been considered abnormal because they do not fit within the framework of sperm competition, but in this case copulations may function in a social capacity in the maintenance of pair bonds (Heg & van Treuren 1998). This paper also brings into question another assumption that underlies the interpretation of reproductive behaviour: males did not derive greater reproductive benefits from having more copulation partners.

Other factors may also influence an individual's decision making in relation to mate choice. For example, the

most competitive sperm may not always come from males of the highest quality. For example, in *Tribolium confusum*, males infected with the intracellular parasite *Wolbachia pipientis* appear to be more successful than uninfected males during sperm competition (Wade & Chang 1995). The parasite's own fitness is enhanced, but at the expense of female reproductive success.

Not All Individuals of One Sex Adopt the Same Strategy

Although the role of the sexes and the strength of sexual selection is determined by the degree of investment by the two sexes, not all members of one sex behave in the same way. Alternative tactics within the sexes may arise from different ways of achieving the same success or because not all individuals can successfully follow the best tactic. The payoffs of any particular strategy may then vary between individuals in a population, for example between individuals of different quality (Wagner et al. 1996). The underlying mechanisms could be: (1) the polymorphism is purely genetic and the population consists of a mixture of genotypes; (2) individuals are phenotypically flexible but play different evolutionarily stable strategies (Parker 1984); or (3) individuals of different condition may be constrained by varying amounts in the tactics they can play and in the fitness benefits they can gain.

An example where males appear to use alternative, genetically determined tactics with equal success is the marine isopod *Paracerceis sculpata*. Three morphs exist: alpha, beta and gamma males. Alpha males defend groups of females in intertidal areas in the shelter of sponges; beta males resemble females and can gain access to females without being excluded by the alpha male; and gamma males are extremely small and are able to sneak into defended areas to gain access to females, unnoticed by the alpha male. Over a 2-year period, reproductive success was roughly equal between the three morphs (Shuster & Wade 1991; Shuster & Sassaman 1997).

On the other hand, alternative strategies may be conditional, where the role an individual subsequently plays is dependent on body condition at a critical threshold. In the horseshoe crab, *Limulus polyphemus*, for example, young males that are generally in better condition pair with females, while older males generally in poorer condition typically adopt a satellite strategy to fertilize eggs. Pair males fertilize approximately 60% of the eggs and satellite males approximately 40% (Brockman et al. 1994).

It is likely, however, that a more common scenario is that success is unevenly distributed among individuals within each sex, depending on body condition, and that some individuals are more constrained than others in achieving the same success. Different tactics may therefore arise from individuals making the best of their situation within these constraints. In goldeneye ducks, *Bucephala islandica*, for example, some females parasitize other females by laying eggs in their nests. Parasites are the oldest females who are in better condition and can afford both to have their own nest and produce extra eggs

to lay in other nests. Other females appear incapable of investing the same energy in egg production (Eadie & Fryxell 1992).

The role of experience and learning may be important in influencing sexual selection. Most mechanisms of sexual selection assume mate choice to be genetically determined. As a result, the role of learning in mate choice is often neglected. Cues during development have been shown to be important in shaping mate choice in a number of species (Immelman 1972; West & King 1988). However, learning and experience may also modify mate choice throughout an individual's lifetime. Male fruit flies, *D. melanogaster*, will persistently court virgin females for several hours. However, the frequency with which they court nonvirgin females declines over time; males may learn to associate chemical signals with female non-receptivity. The effect of learning may be to increase the variability in mate choice, to an extent dependent upon the proportion of experienced and inexperienced individuals. As age is likely to be a factor in this, the potential for sexual selection may vary between populations differing in their population structure. Several studies have shown that individuals may modify their mate choice in response to predation. For example, female guppies, *Poecilia reticulata*, that initially showed a strong preference for the brighter of two males reversed their mate choice after exposure to a predator and subsequently preferred dull males that were less conspicuous (Gong & Gibson 1996). Hence, external cues may modify the direction in which sexual selection could act within an individual's lifetime.

Conclusion

In this review we have attempted to reaffirm the importance of considering the influence of different mechanisms of sexual selection acting throughout the whole reproductive cycle. This includes postcopulatory and postfertilization stages of reproduction and parental behaviour which may influence patterns of offspring recruitment into breeding populations. There are advantages to be gained from looking beyond the roles traditionally attributed to the sexes, and at the variability between individuals in reproductive behaviour and success, in establishing the mechanisms that determine the operation of sexual selection.

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