

The evolution of male mate choice in insects: a synthesis of ideas and evidence

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ABSTRACT

Mate choice by males has been recognized at least since Darwin's time, but its phylogenetic distribution and effect on the evolution of female phenotypes remain poorly known. Moreover, the relative importance of factors thought to underlie the evolution of male mate choice (especially parental investment and mate quality variance) is still unresolved. Here I synthesize the empirical evidence and theory pertaining to the evolution of male mate choice and sex role reversal in insects, and examine the potential for male mating preferences to generate sexual selection on female phenotypes. Although male mate choice has received relatively little empirical study, the available evidence suggests that it is widespread among insects (and other animals). In addition to 'precopulatory' male mate choice, some insects exhibit 'cryptic' male mate choice, varying the amount of resources allocated to mating on the basis of female mate quality. As predicted by theory, the most commonly observed male mating preferences are those that tend to maximize a male's expected fertilization success from each mating. Such preferences tend to favour female phenotypes associated with high fecundity or reduced sperm competition intensity. Among insect species there is wide variation in mechanisms used by males to assess female mate quality, some of which (e.g. probing, antennating or repeatedly mounting the female) may be difficult to distinguish from copulatory courtship. According to theory, selection for male choosiness is an increasing function of mate quality variance and those reproductive costs that reduce, with each mating, the number of subsequent matings that a male can perform ('mating investment'). Conversely, choosiness is constrained by the costs of mate search and assessment, in combination with the accuracy of assessment of potential mates and of the distribution of mate qualities. Stronger selection for male choosiness may also be expected in systems where female fitness increases with each copulation than in systems where female fitness peaks at a small number of matings. This theoretical framework is consistent with most of the empirical evidence. Furthermore, a variety of observed male mating preferences have the potential to exert sexual selection on female phenotypes. However, because male insects typically choose females based on phenotypic indicators of fecundity such as body size, and these are usually amenable to direct visual or tactile assessment, male mate choice often tends to reinforce stronger vectors of fecundity or viability selection, and seldom results in the evolution of female display traits. Research on orthopterans has shown that complete sex role reversal (i.e. males choosy, females competitive) can occur when male parental investment limits female fecundity and reduces the potential rate of reproduction of males sufficiently to produce a female-biased operational sex ratio. By contrast, many systems exhibiting partial sex role reversal (i.e. males choosy and competitive) are not associated with elevated levels of male parental investment, reduced male reproductive rates, or reduced male bias in the operational sex ratio. Instead, large female mate quality variance resulting from factors such as strong last-male sperm precedence or large variance in female fecundity may select for both male choosiness and competitiveness in such systems. Thus, partial and complete sex role reversal do not merely represent different points along a continuum of increasing male parental investment, but may evolve *via* different evolutionary pathways.

Key words: Male mate choice, mutual mate choice, sexual selection, sex role theory, sex role reversal, mate quality, cryptic mate choice, constraints on mate choice, intra-sexual competition, display traits.

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I. INTRODUCTION

Darwin (1874) persuasively defined the roles of the sexes in courtship and parental care: typically, males compete for access to females and females select among males and provide for the offspring. Darwin's view of sex roles was reinforced by Bateman's (1948) influential study on *Drosophila melanogaster*. Bateman (1948) found that the number of progeny a male produced appeared to increase in proportion with the number of matings he achieved, whereas the number of offspring a female produced either increased more slowly or not at all with the number of matings she achieved. Nonetheless, some 'anomalous cases' were recognized by Darwin (1874), and many more examples of 'reversal' of the sex roles in courtship and parental care, including choosy or 'helpful' males and competitive or indiscriminate females, have since accumulated (Gwynne, 1991). How widespread are such 'anomalous cases', and how are they to be explained and situated within the theory of sex roles?

Trivers (1972) argued that males and females

should be equally choosy when both sexes contribute equally to offspring. When males contribute more than females to offspring, males should be the choosier sex and females the more competitive sex. These predictions have been supported by experimental work with crickets and katydids, demonstrating that 'complete sex role reversal' (i.e. male mate choice and female competition) can occur when the relative value of male investment in reproduction is high enough to limit female fecundity (Gwynne & Simmons, 1990; Gwynne, 1990, 1993; Simmons, 1993). However, 'partial sex role reversal' (i.e. male mate choice with female mate choice and/or male competition) is frequently observed in systems where males contribute little more than sperm to females. In such systems, male mate choice is thought to evolve in response to large variation in female quality (Gwynne, 1991). Unfortunately, partial sex role reversal has attracted relatively little research effort. Moreover, recent experimental work has challenged the importance of variation in female quality as a key factor in the evolution of sex roles (Kvarnemo & Simmons, 1998, 1999), potentially

leaving partial sex role reversal without an explanation. Consideration of such problematic systems may help to clarify accepted theory (Cunningham & Birkhead, 1998) and perhaps open the door to a more robust theory of sex roles.

Several insect species have provided convenient model systems for disentangling the causes of complete sex role reversal. However, insects as a group also provide a convenient model super-system for the analysis of a multi-species data set on male mate choice, because their incredible diversity is superimposed on a consistent basic body plan and physiology. My objectives were (i) to synthesize and clarify the theory pertaining to the evolution of male mate choice and sex role reversal, (ii) to chart the known distribution and characteristics of male mate choice in insects, (iii) to evaluate how well the theory is supported by the empirical evidence, and (iv) to examine the potential consequences of male mate choice in sexual selection on females and the evolution of female phenotypes. Although, by focusing on insects, I avoided a great deal of extraneous complexity in the theoretical analysis, I have also provided a brief comparative overview of male mate choice in other animal taxa.

II. FUNDAMENTAL MALE-FEMALE DIFFERENCES

In the great majority of sexually reproducing species (excepting those that exhibit parthenogenesis or haplodiploidy), every individual's fecundity depends on access to gametes of the opposite sex. When every offspring has a mother and a father, the mean reproductive success of males and females is always exactly equal, although the variance of reproductive success may differ between the sexes. However, the two sexes are characterized (and defined) by a fundamental difference in reproductive strategy: females produce a few large (costly) gametes designed to develop into offspring, and males produce many small (cheap) gametes designed to 'parasitise' the resources of females (Parker, Baker & Smith, 1972). As a result, in most species, a female's fecundity is more or less directly related to the number of gametes she produces, and it seems quite reasonable to estimate female fecundity by dissecting ovaries and counting eggs. By contrast, no one would set out to estimate male fecundity in any species by counting sperm in the testes. Instead, a male's fecundity usually depends on his ability to gain access to female gametes – his 'mating effort' (Low,

1978) and 'mating success' (Borgia, 1979; Arnold, 1994). One implication of this pattern is that females are unlikely to increase their fitness by shifting their effort from parental investment in gametes or young to competition for mates (see Fitzpatrick, Berglund & Rosenqvist, 1995), whereas males can usually adopt any strategy that increases their access to female gametes. As a result, female parental investment seems to exceed male parental investment in most species (Trivers, 1972).

Greater parental investment on the part of females in most species is thought to explain why males are usually subject to stronger sexual selection than females and compete for access to females (Trivers, 1972; Jennions & Petrie, 1997). It has also been argued that greater parental investment causes females to have a slower 'potential rate of reproduction' than males (Clutton-Brock & Vincent, 1991; Clutton-Brock & Parker, 1992), which in turn produces a male-biased operational sex ratio (OSR), defined as the ratio of sexually available males to sexually available females (Emlen & Oring, 1977). An excess of active males results in male competition for females. As part of the same pattern, males have often been thought to pursue every female with 'undiscriminating eagerness', and females to respond with 'discriminating passivity' to their advances (Bateman, 1948). In some species, however, males have adopted the female-like strategy of increased parental investment that, taken to the extreme, leads to complete reversal of the sex roles in courtship and mate choice (e.g. Gwynne, 1981, 1984*b*, *c*). Thus, male mate choice is usually expected in systems where males allocate valuable resources to parental investment (Simmons, 1992; Gwynne, 1993).

However, the elegant simplicity of this 'classic' sex role theory has not stood up well to the challenge of biological complexity. For example, both theory and data suggest that male mate choice (as well as competitiveness) may be expected, even in systems where males contribute little parental investment, when variation in female mate quality is sufficiently large (Parker, 1983; Gwynne, 1991). Thus, the relative importance of parental investment and variation in female quality as key factors underlying the evolution of male mate choice and sex role reversal remains in contention (Gwynne, 1991; Kvarnemo & Simmons, 1998, 1999). Moreover, even if OSR and relative potential rates of reproduction largely determine which is the more competitive sex (although see Vincent *et al.*, 1992), these factors do not account in any straightforward

way for observed differences in choosiness (Owens, Burke & Thompson, 1994; Amundsen, 2000).

III. THE EVOLUTION OF MALE MATE CHOICE: PREDICTIONS FROM SEX ROLE THEORY

(1) Mechanisms of male mate choice and definitions of terms

Like female mate choice, male mate choice in some form is probably a universal behavioural response in species where copulation occurs, in that males discriminate against heterospecific or immature females. Hence, I will use a narrower definition: male mate choice is differential male sexual response to different reproductively mature conspecific females. A 'reproductively mature' female is any female capable of copulating. Differential 'sexual response' may take the form of 'precopulatory' mate choice, or 'cryptic' mate choice, or a combination of the two. Precopulatory male mate choice might be exhibited as acceptance/rejection of particular females, or as variation in the intensity or frequency of courtship or copulation attempts delivered to females of varying mate quality, depending on how male mate choice is quantified, and whether or not females are also choosy. Precopulatory male mate choice may also be expressed as variation in the intensity of intra-sexual scramble or combat competition for females of varying mate quality: for example, males may reject low-quality females but compete for access to high-quality females. Thus, although male-male competition usually enables high-quality males to achieve high mating success (e.g. Alcock, 1996), male-male competition may also function to enhance the mean female quality experienced by high-quality males.

Cryptic male mate choice is defined here as variation in the amount of resources (e.g. the size of the ejaculate or nutritive 'nuptial gift', the duration of copulation or mate guarding, or the amount of parental investment) allocated to females of varying mate quality. This definition of cryptic male mate choice is consistent with previous uses of this term (Eberhard, 1996; Pitnick & Brown, 2000), and corresponds to cryptic female mate choice, defined as differential acceptance or use of sperm from mates of varying quality (Thornhill, 1983). Although, as defined above, cryptic male mate choice encompasses a class of male responses usually considered in the context of sperm competition, I will argue that

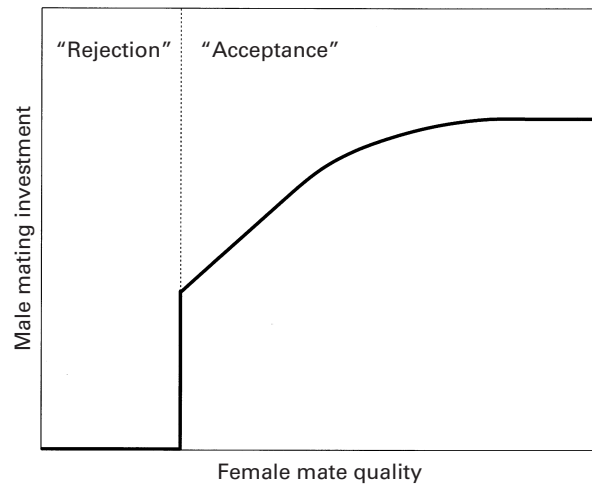


Fig. 1. A male 'mating investment curve' representing the pattern of allocation of a particular type of resource (e.g. sperm) for a particular female mate quality factor (e.g. body size) in a hypothetical system combining precopulatory male mate choice (i.e. the discontinuous 'acceptance' threshold represented by the broken line) and cryptic male mate choice (i.e. the continuous curve for female mate qualities exceeding the 'acceptance' threshold). In such a system, the discontinuous acceptance threshold may occur because ejaculates smaller than some critical size are unlikely to fertilize any eggs, whereas the 'maximum investment' plateau may occur because of finite testis size as well as diminishing returns on ejaculate expenditure (see text).

these are not mutually exclusive alternatives. However, the defining feature of cryptic male mate choice is variation in male response to different female phenotypes, rather than variation in male response to all females under different social conditions. For example, a system where males transfer more ejaculate to some females than to others involves cryptic male mate choice, but a system where males transfer more ejaculate to any female when the operational sex ratio is more male biased does not. Consideration of such phenomena as mate choice responses underscores the potential for variation in male investment to generate sexual selection on female phenotypes (see Section VI.5).

'Choosiness' was defined by Johnstone, Reynolds & Deutsch (1996) as the proportion of potential mates rejected. However, this definition does not take into account the potential importance of cryptic mate choice. A broader concept of mate choice, incorporating both precopulatory and cryptic mechanisms, requires a concept of choosiness reflecting the total pattern of variation in male investment across the range of female phenotypes (i.e. the male 'mating investment curve'). For a particular female

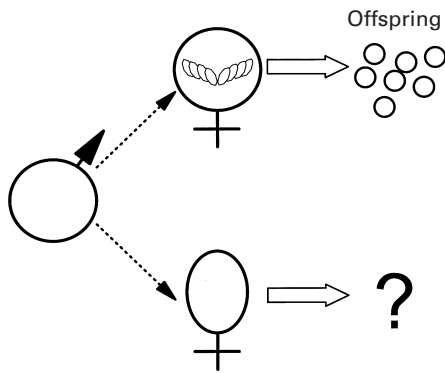


Fig. 2. Male mating preferences and female mate quality variance: in most systems, males are expected to choose females based on phenotypic indicators of fecundity such as 'fatness' (relative abdomen width) or body size (see text). In the example shown here, a male is expected to prefer a fat female to a thin one because the former is likely to carry (more) mature eggs and, hence, is less likely to re-mate and more likely to lay (more) eggs fertilized by the male.

trait and male preference, the mating investment curve may be a continuous function, or a discontinuous 'acceptance threshold' function (see Valone *et al.*, 1996), or (perhaps most likely) a combination of the two (Fig. 1). When cryptic male mate choice occurs, male mating investment curves are also likely to exhibit a 'maximum investment' plateau corresponding, for example, to maximum ejaculate size (e.g. Gage & Barnard, 1996, Fig. 2). Such a plateau may be expected not only because male testes and accessory glands have finite volumes, but also because increasing investment is likely to yield diminishing returns (see Parker & Simmons, 1994). The problem of characterizing and comparing mate choice strategies is, of course, further complicated by the observation that, in many species, mate choice may comprise several concurrent (probably interacting) preferences for several (seldom independent) traits (see Section VI.4; Johnstone, 1995). This diversity and complexity of mate choice strategies probably cannot be compressed meaningfully into a universal one-dimensional index of choosiness. Instead, it may be necessary to settle for a variety of operational definitions of choosiness tailored to particular systems, such as the proportion of potential mates rejected, or the proportion of potential mates allocated a quantity of resources below the maximum investment level, or the number of female traits assessed in mate choice. For the purposes of the discussion below, 'choosiness' can refer to any combination of these factors, depending on the

characteristics of the particular system under consideration.

(2) The basic model

A male's response to a particular female (to mate or not to mate? how much to invest in the mating?) should depend on the expected benefits and costs. Trivers (1972) identified relative parental investment as the fundamental determinant of the degrees of choosiness and intra-sexual competition favoured in males and females. However, Parker (1983) offered the first detailed model of mate choice for both sexes. Parker (1983) reasoned that choosiness in either sex is favoured by high variance in quality among individuals of the other sex ('mate quality'). If all potential mates are identical, there is no advantage to choosing among them, but if some potential mates are much better than others, choosiness can be highly advantageous. On the other hand, Parker (1983) argued, choosiness may be constrained by high costs of finding and assessing alternative mates, and high risk of 'mistakes' in mate assessment. In addition, Dewsbury (1982) pointed out that energetic costs associated with copulation itself (e.g. ejaculate costs), not just the costs of parental investment, should favour male choosiness. The effects of these factors on choosiness were also discussed by Petrie (1983).

Recently, these ideas have been elaborated into more complex models of 'mutual mate choice' (e.g. Owens & Thompson, 1994; Deutsch & Reynolds, 1995; Johnstone *et al.*, 1996; Johnstone, 1997). Although these models differ somewhat in their structure and predictions, they all incorporate in some way the three aforementioned factors: mate quality variance, mating investment, and constraints on choosiness. I will call this the 'basic model' of the evolution of male mate choice. Because each of these factors is very complex, I discuss each of them and some probable interactions among them in greater detail below. I then review the empirical evidence of male mate choice in insects with a view to evaluating the importance in nature of each factor in the model.

(3) Female mate quality variance

Mate quality variance represents the potential benefits of choosiness. For males in most 'promiscuous' systems (i.e. multiple mating with relatively brief male-female associations), the key factor in female mate quality is expected to be female

fecundity. Thus, in most cases, males are expected to assess female quality using phenotypic indicators of fecundity such as immediate reproductive condition (i.e. the number of mature eggs carried), or body size, which often predicts fecundity (Fig. 2). Female genetic quality is expected to be less important for males in most 'promiscuous' systems, and phenotypic indicators of genetic quality (i.e. 'revealing displays') are expected to be relatively rare in females (although exceptions certainly occur: see below). There are at least four reasons for these expectations. Firstly, in taxa where females produce large and highly variable numbers of eggs (i.e. most insects, other 'invertebrates' and fish), the number of offspring potentially gained by a male from a mating is likely to be more variable than the quality of those offspring. Hence, female traits associated with variation in offspring number (i.e. phenotypic indicators of fecundity) are likely to be more important, as factors of female mate quality assessed by choosy males, than female traits associated with variation in offspring quality (i.e. phenotypic indicators of 'good genes'). Secondly, because after the mating a male's sperm are rapidly displaced by other males' sperm, expelled or digested by the female, the female's genetic quality (which may predict her lifetime fecundity) will be relatively unimportant for the male. Thirdly, phenotypic correlates of female fecundity (e.g. body size or abdomen width) can usually be assessed directly by males through visual or tactile mechanisms, so that revealing displays would normally be redundant. Finally, as Fitzpatrick *et al.* (1995) pointed out, females are unlikely to invest in revealing displays because any resources spent on advertising would be subtracted from the pool of resources available for offspring production.

By contrast, when males are potentially able to mate with few different females, as in systems characterized by relatively long-term 'monogamous' male-female associations (e.g. see Eggert & Sakaluk, 1995), female genetic quality may have a large effect on male reproductive success and, correspondingly, have considerable importance in male mate choice. Two points need to be emphasized when considering such systems. Firstly, the key factor is the potential number of different mates that a male can have under the constraints imposed by a particular mating system (e.g. 'promiscuous' *versus* 'monogamous' mating), not a male's realized mating success in that system. Thus, in 'promiscuous' systems where most males have few mates because the distribution of male mating success is

highly skewed, the males with the fewest mates (i.e. the least successful males) are not expected to exhibit the most elaborate mating preferences. Indeed, the opposite is expected (Burley, 1977; Parker, 1983). Secondly, male mate choice on the basis of female 'good genes' is more likely to occur when the number of different mates that a male can potentially inseminate is low, not when female mating rate is low. If females mate only once but males can mate multiply (i.e. a combination of 'monandry' and 'polygyny'), a male's reproductive success may depend substantially on the genetic quality of his mates, but males are unlikely to be choosy because receptive females will normally be scarce (see Section IV). Long-term monogamous associations appear to occur in a relatively small number of insect species, but are more widespread in some other taxa, especially birds (Wittenberger & Tilson, 1980).

In addition, sperm competition is expected to contribute to female mate quality variance and favour male choosiness in some systems. For example, if first-male sperm precedence is high, males may be selected to reject recently mated females because of a low expected fecundity gain from such matings (Simmons *et al.*, 1994). The ability of males to exercise mate choice on the basis of female mating status would, of course, depend on males' ability to assess this factor, using evidence left by previous males (e.g. chemical traces or 'mating plugs'), or signals ('honest' or otherwise) emitted by the females themselves (see Section IV). But if last-male sperm precedence is high, as may be the case in most insects (Parker, 1970*a*), males may be selected to reject females likely to mate again before ovipositing (e.g. females with immature eggs). High last-male sperm precedence is also expected to select for mate-guarding strategies to prevent female re-mating before oviposition (Parker, 1974), an example of circumstances that may favour both choosiness and intra-sexual competition in males (for an example in females, see Owens *et al.*, 1994). Sperm competition may also favour cryptic male mate choice. If different female phenotypes are associated with varying intensities of sperm competition, males may be selected to adjust their ejaculate sizes accordingly (Parker, 1970*a*).

If males choose females on the basis of variable phenotypic characteristics such as reproductive condition (e.g. stage of egg development), male mate choice may usually be expected to exert little sexual selective pressure on females and produce little evolutionary response. This is because nearly all females are likely to exceed an average male's

acceptance threshold at the peak of their fertility cycle (i.e. when their eggs are mature). For example, if males evaluate female mate quality on the basis of female relative abdomen width ('fatness'), an indicator of the number of mature eggs carried (e.g. Otronen, 1984; Pitafi, Simpson & Day, 1995; Bonduriansky & Brooks, 1998*b*), male preference for fat females will generate little sexual selection on female phenotype because fatness fluctuates over the course of each female's reproductive cycle. Moreover, although genetic differences may cause some females to produce more eggs and be consistently fatter than others, the alleles underlying this variation will still be subject to much stronger fecundity selection than sexual selection in most systems. However, in systems where females receive important direct benefits such as food gifts, male mating preferences may generate sufficiently steep sexual selection gradients to cause the exaggeration or prolongation of phenotypic indicators of fecundity (e.g. Funk & Tallamy, 2000).

Sexual selection through male mate choice is also more likely to produce a substantial response when males choose on the basis of traits that do not vary over the reproductive life of an individual female (e.g. body size in insects). In such systems, some females may never exceed an average male's acceptance threshold, and thus experience reduced mating success or low male mate quality. Male mate choice in such systems is, thus, analogous to many examples of female mate choice based on male traits that do not vary over the course of adult life (body size, again, is a common example).

(4) Mating investment

High cost of resources (e.g. time or energy) invested in each mating is also thought to favour choosiness. However, it is necessary to distinguish two types of costs incurred by males. When males provide costly ejaculates or nuptial gifts to females, invest in lengthy courtship or copulation, or fight over particular females, each copulation reduces the number of future copulations that a male can potentially perform (e.g. see Partridge & Farquhar, 1981; Dewsbury, 1982; Rutowski, 1982, 1984; Partridge & Andrews, 1985; Sakaluk, 1985; Simmons, 1990; Hayashi, 1993; Cordts & Partridge, 1996; Clutton-Brock & Langley, 1997). Such costs, which may be called 'mating investment', are expected to favour male choosiness (Gwynne, 1991, 1993; Johnson & Burley, 1997) as well as adaptations that increase confidence of paternity (Gwynne, 1984*b*), because

selection should favour optimal allocation of limited resources. Mating investment can be defined as investment in each mating that occurs at the cost of the male's ability to invest in future matings. Thus, mating investment is directly analogous to Trivers' (1972) 'parental investment' (a parent's investment in an offspring at the cost of ability to invest in other offspring), but expanded to include all resources spent on a mating. Mating investment can also be related to other systems of categorizing male costs. Low (1978) subdivided total reproductive effort into 'parental effort' ('any expenditure of nutrient or effort or taking of risks in the production and raising of offspring or other kin') and 'mating effort' ('any expenditure of nutrient or effort or taking of risks to secure matings'). In Low's (1978) terms, then, mating investment is equivalent to the sum of parental effort and part of mating effort – that part which Gwynne (1984*b*) called 'nonpromiscuous' (i.e. yielding direct benefits to the female or offspring). In the terms of Johnson & Burley (1997), mating investment is equivalent to the sum of those parts of mating effort and parental effort that are 'focused' on a particular female.

On the other hand, investments that do not reduce, with each additional copulation, a male's capacity for subsequent copulations are not expected to favour male choosiness. Such investments represent 'diffuse' mating or parental effort that cannot be partitioned among particular mates (Johnson & Burley, 1997), including revealing displays that are not directed at particular females (e.g. pheromones, bright colours, ornaments), costs of male-male combat for control of resources such as territories or mate-searching sites (e.g. weapons, energy, risk of injury), or parental investments associated with reproduction in general, rather than with a particular batch of offspring (e.g. male adaptations for building a nest, or brooding eggs).

Thus, there is one key distinction between those male costs that are expected to select for male choosiness (mating investment) and those that are not (diffuse investment): selection for choosiness increases with costs that reduce, with each copulation, the number of subsequent copulations that a male can potentially perform. Note that even though diffuse investment may be as costly (or more costly) than mating investment, and these costs may limit male life-span, diffuse investment is not expected to select for male choosiness because, by definition, it contributes nothing to the costs of copulation. Thus, a hypothetical male that allocated all of its resources to diffuse investment (e.g. defending its territory on

a lek) and nothing at all to mating investment (i.e. it could mate infinitely fast and fertilize an entire clutch of eggs with an infinitely small ejaculate!) would maximize its fitness by mating with every female encountered, since copulations would be 'free'. Note that, for the same reason, variation among females in the expected number or quality of offspring (i.e. 'indirect' benefits of mate choice for males) is not sufficient to account for male choosiness: if mating investment costs are insignificant, males will benefit by mating with every female encountered. On the other hand, variation among females in factors that may affect the male itself, such as female parasite load (i.e. 'direct' benefits of mate choice for males), is sufficient to select for male choosiness because such variation also contributes to mating investment costs.

(5) Constraints on male mate choice

An individual can either always accept and invest maximally in the first potential mate it encounters – a strategy often called 'random mating', even though the results may not be truly random (see Wiley & Poston, 1996; Murphy, 1998) – or it can assess the potential mate's quality and, perhaps, reject it entirely or invest less than maximally in the mating. The choosy individual then faces the problem of finding and accurately assessing an alternative mate of higher quality in which to invest its resources. However, even if a mate of higher quality is subsequently encountered and correctly assessed, the choosy individual's strategy will have paid off only if the gain in mate quality more than compensates for the costs of finding and assessing the alternative mate.

Parker (1983) pointed out that the evolution of mate choice will be constrained by the costs of searching and assessment, as well as the accuracy of mate assessment mechanisms. Recent models of mate choice evolution have tended to focus on one particular type of cost: searching time (e.g. Sullivan, 1994; Deutsch & Reynolds, 1995; Johnstone *et al.*, 1996). Loss of time searching for an alternative mate may result in a reduced reproductive rate (Deutsch & Reynolds, 1995). Johnstone (1997) focused, instead, on the related cost of seasonal time constraints: a choosy individual faces the cost of potentially running out of time at the end of the breeding season and having to accept a low-quality mate. Although searching time and finite breeding season length are potentially important constraints on mate choice, several other types of constraints

may be equally important (Real, 1990). These include the risk of rejecting a potential mate of higher quality than those subsequently encountered (Parker, 1983; Real, 1990), energy expended on search or assessment (e.g. through struggle) of potential mates (e.g. Watson, Arnqvist & Stallmann, 1998), risk of predation (e.g. Crowley *et al.*, 1991; Rowe, 1994), risk of injury associated with assessment or rejection (e.g. Rowe, 1994; Bonduriansky & Brooks, 1998*a*) and, if assessment involves physical contact (see Section VI.3), risk of infection by parasites or pathogens (Daly, 1978; Watson, 1993). The relative importance of each type of cost is likely to vary among systems, depending on the ecology, breeding biology and physiology of the animals.

All else being equal, the risk of rejecting a high-quality mate will depend on the chooser's ability to assess accurately the quality of individual potential mates (see Section VI.6*c*), and may also depend on its ability to assess (or 'predict') the distribution of mate qualities in the population and in space (Dombrovsky & Perrin, 1994; Mazalov, Perrin & Dombrovsky, 1996). The costs of mate assessment (i.e. energy, time, risks incurred) are likely to depend primarily on the animal's morphology, physiology and behaviour (see Sections VI.3 and VI.6*c* for further discussion of these factors). Search costs (also a combination of time and energy spent and risks incurred) are expected to be inversely proportional to male life expectancy, female mating rate, density of fertile females (see Forsberg, 1987), or degree of 'clumping' of females in space or time. The density of fertile females that males experience depends on the operational sex ratio, which depends on the relative potential rates of reproduction of the two sexes (Clutton-Brock & Parker, 1992), as well as the simple sex ratio in the population (see Jiggins, Hurst & Majerus, 2000). The degree of 'clumping' of fertile females may depend on a variety of ecological and life-history parameters, such as breeding season length, degree of reproductive synchrony, distribution in space and time of food and oviposition resources, physical architecture of the habitat, phylogenetic inertia, and other factors.

Thus, the evolution of choosiness in a particular system may be constrained by a combination (or interaction) of the accuracy of assessment of individual potential mates, the accuracy of assessment of the demographic and spatial distribution of mate qualities, and the costs of search and assessment. For any given magnitude of search and assessment costs, the optimal degree of choosiness is likely to be lower

when accuracy of assessment is relatively poor, because choosy individuals will be less likely to benefit by discriminating against potential mates perceived to be of poor quality. A separate but related issue is what strategy of ‘adaptive search’ individuals can or should adopt, a question that has been the focus of numerous theoretical analyses (e.g. see Parker, 1978; Janetos, 1980; Real, 1990, 1991; Sandell & Liberg, 1992; Mazalov *et al.*, 1996; Wiegmann *et al.*, 1996) and some empirical research (e.g. see Moore & Moore, 1988; Reid & Stamps, 1997). Unfortunately, nearly all of the theoretical and empirical work done so far on these topics has focused on precopulatory mate choice by females. Future work should also address the distinct features and dynamics of male mate choice and cryptic mate choice.

The nature and magnitude of constraints on choosiness incurred by males probably depend to a considerable extent on the strategies and mechanisms employed. For example, when males engage in cryptic mate choice, the quantity of resources allocated to each mating is likely to be more tightly correlated with female mate quality, especially given the added opportunity for accurate mate assessment afforded by copulation itself (see Section VI.3), compared with systems where only precopulatory mate choice occurs. Hence, in cryptic mate choice systems, the risk of accidentally rejecting a high-quality mate may be lower, whereas the risk of parasite transmission may be higher. In some systems, males may also be able to reduce or circumvent some of the costs of choosiness by combining precopulatory and cryptic mate choice mechanisms. For example, males may engage in precopulatory assessment of female parasite load and reject parasitized females, but also assess the body size of non-parasitized females during copulation and allocate larger ejaculates to larger mates (see Sections III.1 and VI.4). Such systems present interesting optimization problems amenable to analytical modeling or simulation.

IV. MALE CHOOSINESS AND FEMALE MATING RATE

The theory outlined above suggests that selection for choosiness in males may be related to the way in which female fitness covaries with number of matings. Male fitness is nearly always an increasing function of the number of copulations achieved (e.g. Bateman, 1948; Royer & McNeil, 1993; Johnson &

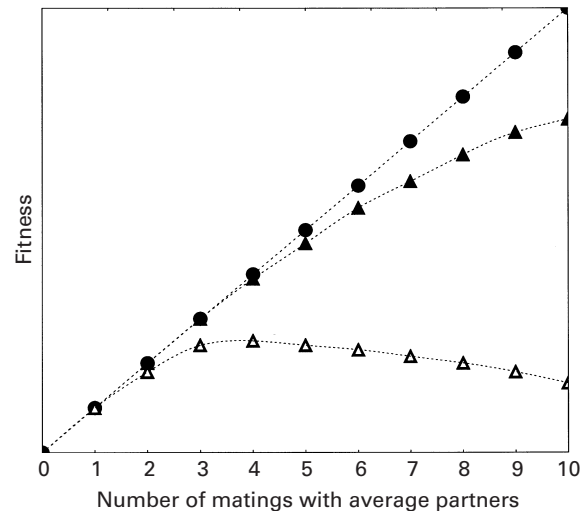


Fig. 3. Fitness as a function of number of matings for males (filled circles), and for females in two hypothetical types of system: in ‘Type 1’ systems (filled triangles), female fitness increases with each additional mating whereas, in ‘Type 2’ systems (open triangles), females maximize their fitness by mating only four times per reproductive cycle.

Table 1. *Expected associations of sex role parameters in systems where female fitness increases with each additional mating (‘Type 1’ systems), and systems where female fitness is maximized at a small number of matings (‘Type 2’ systems)*

	QV	MI	CC	Male Choosiness
Type 1 systems	High	High	Low	High
Type 2 systems	Low	Low?	High	Low

QV, variance in female mate quality; MI, male mating investment; CC, constraints on male choosiness.

Burley, 1997), but female fitness does not necessarily increase with each additional mating (e.g. Ridley, 1988; Arnold & Duvall, 1994; Ketterson *et al.*, 1997; Hayashi, 1998). Indeed, Bateman (1948) observed two distinctly different patterns among *Drosophila melanogaster* females. The basic relationships of fitness to number of copulations for males and females in species where both sexes mate multiply are represented in Fig. 3. Female fitness will increase initially with number of copulations whenever several copulations are required to fertilize all of the eggs. This seems to be the case in most insects (Ridley, 1988), and is probably true for most vertebrates with internal fertilization. Beyond the number of matings required to fertilize all the eggs, female fitness may either increase with additional

Table 2. *Some examples of mating investment and diffuse investment by males, and how these relate to cumulative and non-cumulative benefits of mating for females*

Male	Female	
	Cumulative benefits	Non-cumulative benefits
Mating investment	Nuptial gifts Access to food or habitation resources defended by ♂ Mate guarding that increases ♀ foraging efficiency	Mate guarding that does not increase ♀ foraging efficiency Focused revealing display Indirect ♀ mate choice of winners of focused combat
Diffuse investment	—	Diffuse revealing display Diffuse paternal investment Indirect ♀ mate choice of winners of diffuse combat

See text for explanation.

matings ('Type 1' system), or decrease with number of matings ('Type 2' system). The function relating female fitness to number of matings may also predict the mate quality variance, mating investment and constraints on choosiness experienced by males. Below, I argue that systems where female fitness increases with each additional mating may, in general, be associated with stronger selection for male choosiness than systems where female fitness peaks at a small number of matings (Table 1).

(1) Systems where female fitness increases with each copulation

When female fitness is an increasing function of number of copulations (or peaks at a large number of copulations), males are expected to experience relatively large female mate quality variance, costly mating investment, and low costs of search and assessment. Female fitness will be an increasing function of number of matings when females receive a certain type of direct benefit from males during copulation. This type of benefit might be called 'cumulative', because its effects on female fitness accumulate over multiple copulations. Some examples of cumulative benefits are nuptial gifts, access to food or habitation resources defended by males, and mate guarding that enables the female to forage with reduced risk of predation or harassment. Because every additional copulation increases a female's fitness, cumulative benefits may favour females that seek out copulations even when they are not fertile or gravid. For example, females of the butterfly *Pieris protodice* solicit copulations to obtain

fresh spermatophores from males (Rutowski, 1980), and some female birds may use deceptive signalling of fertility to prolong the duration of mate guarding by males, which reduces risk of predation or harassment (Lumpkin, 1981). From the male perspective, such female adaptations may be manifested as high variation in female mate quality, and males may then benefit by being choosy, rejecting solicitations from non-fertile females. Selection for male choosiness will be further intensified when cumulative benefits for females represent costly mating investment for males (Table 2).

Similarly, search and assessment costs are expected to be lower in systems where female fitness increases with each additional mating. If female mating rate is high, or if females solicit matings to obtain nuptial gifts (Gwynne, 1984*b*; Gwynne & Brown, 1994) or other cumulative benefits, males will experience a relatively high 'density' of receptive females and a relatively large proportion of females in the operational sex ratio. Clearly, males will experience the lowest costs of search and assessment in systems with complete sex role reversal, where females may fight for access to males (e.g. Gwynne & Simmons, 1990) or display in leks or swarms (e.g. Funk & Tallamy, 2000).

The ability of females to control the fate of sperm deposited in their reproductive tracts through cryptic mate choice (Thornhill, 1983) may also contribute to selection for male choosiness. Cryptic female mate choice may be favoured in systems where females copulate multiply to reduce costs of male harassment ('convenience polyandry') or can be forced to copulate by males. However, cryptic female mate choice may also be favoured in systems

where females receive cumulative benefits from males, because it would enable females to solicit benefits from every male, but use only sperm from males of high heritable quality to fertilize their eggs. A comparable female strategy occurs in the spider *Linyphia litigiosa*: females reduce losses of prey to male suitors by diverting males' activity into prolonged bouts of courtship and mating, while apparently controlling the fate of sperm they receive from these mates (Watson, 1993). If females evolve the capability of 'uncoupling mate and sire selection' (Watson, 1993) through cryptic mate choice, males may be expected to retaliate through antagonistic coevolution of choosiness, identifying and discriminating against females that are unlikely to use their sperm for fertilizations.

(2) Systems where female fitness peaks at a small number of matings

Conversely, systems where female fitness peaks at a small number of matings may be characterized by weaker selection for male choosiness. Female fitness is expected to peak at a small number of matings when females receive no cumulative benefits from copulations, or when the costs of copulation outweigh any benefits. Such costs may include ejaculate toxicity (Rice, 1996), risk of predation or injury (e.g. Rowe, 1994; Bonduriansky & Brooks, 1998*a*), energy spent carrying males (Watson *et al.*, 1998), loss of time available for foraging (Rutowski, 1984; Rowe, 1994), or infection by parasites or pathogens (Daly, 1978; Watson, 1993). Clearly, when females gain nothing but fertilization from copulations, they are not expected to solicit (or be receptive to) copulations when they are not fertile (Wiklund & Forsberg, 1985), except in the context of 'convenience polyandry' (Rowe, 1992). Similarly, non-cumulative benefits, whether direct (e.g. mate guarding that reduces harassment but does not facilitate female foraging, or low male parasite load) or indirect (e.g. male 'good genes'), are not expected to favour females seeking copulations when non-fertile. This is because, in such systems, copulation represents a net benefit for females (i.e. increases female fitness) only when they have eggs to be fertilized. Moreover, non-fertile females are expected to be non-receptive in such systems, to avoid the costs of unnecessary copulations. As a result, males may experience little variation in female mate quality, relatively low costs of mating investment (unless intense sperm competition selects for very large ejaculate expenditure), and very high search

costs. Thus, in systems where female fitness peaks at a small number of matings, males are likely to benefit by courting or pursuing every female they encounter.

V. THE EVIDENCE

(1) Sources and limitations

Table 3 summarizes the empirical evidence of male mate choice in insects. Besides the male mating preferences (where known), I included other data relating to the sex roles: mode of female-assessment employed by males, female mating preferences, intra-sexual competition, and operational sex ratio (OSR). The penultimate column is key to the assessment of how well the basic model stands up to the evidence. It contains, for each system, data on as many as possible of the three factors included in the model: mate quality variance, mating investment, and constraints on choosiness (although, because data on assessment accuracy are lacking, this factor reflects only the apparent costs of mate search and/or assessment). Mate choice data were obtained from published studies showing pre-copulatory or cryptic discrimination by males among females, including studies that inferred but did not establish that males were choosy (e.g. Smith, 1976, 1979), and a few studies that did not identify these patterns as male mate choice (e.g. Colwell & Shorey, 1977). Data on OSR were obtained from the same studies as the mate choice data. Other data were obtained from those or other studies on the same species.

The evidence compiled here is extremely heterogeneous and uneven in type and quality (hence, I did not attempt a quantitative meta-analysis). Nevertheless, I felt that it was important to include all these studies because so little is known of the phylogenetic distribution of male mate choice, or variation in sex roles among systems with partial sex role reversal.

The evidence also has a number of other limitations. A great deal of research effort has been focused on a few families and species, while most insect orders have received little or no study. For most species, male preferences have been assessed for only one female characteristic, whereas males may use several proximate criteria to evaluate female mate quality (e.g. see Rutowski, 1980, 1982; Wiernasz, 1995). Very few studies have tested for cryptic male mate choice, even though opportunities to vary mating duration (e.g. Otronen, 1984),

Table 3. *Taxa where male mate choice has been observed or inferred, female phenotype preferred by males, mode of female-assessment employed by males, male phenotype (if any) preferred by females, the nature of intrasexual competition, operational sex ratio (OSR) bias in the study population or experiment (if available), and factors that may select on male choosiness in the system*

Taxon	♂ Mating preference	Mode of ♀-assessment	♀ Mating preference	Intrasexual competition	OSR	Factors presumed to favour ♂ mate choice in this system (from ♂ perspective)	References
Coleoptera							
Brentidae							
<i>Brentis anchovago</i>	Large ♀; non-recently mated ♀	Chemical? tactile?	Large ♂?	♂-♂, ♀-♀ & ♂-♀ grappling	♂ = ♀	MI high: guarding of ♀ costly in time & energy QV high: large ♀ more fecund (mass varies by 10×) CC low: dense ♂-♀ aggregations; 40% of ♀♀ solitary	Johnson & Hubbell (1984)
Cerambycidae							
<i>Tetraopes tetraophthalmus</i>	Large ♀	Chemical?	None?	♂-♂ combat	♂ > ♀ to ♂ < ♀	MI high?: mating takes 'hours' QV high: large ♀ more fecund (mass varies by 4×) CC low?: dense ♂-♀ aggregations (0.055–0.46 m ⁻²)	Lawrence (1986); McLain & Boromisa (1987)
Coccinellidae							
<i>Harmonia axyridis</i>	♀ with developed ovaries	Chemical?	—	—	—	QV high?: [frequent encounters with ♀♀ lacking mature eggs?]	Osawa (1994)
Meloidae							
<i>Lytta magister</i>	Large ♀	Tactile (♂ mounts, antennates ♀)	Large ♂	♂-♂ interference	♂ = ♀	MI high: mating takes ~ 24 h; ♂ transfers large spermatophore QV high: large ♀ more fecund (volume varies by 10×) CC low: dense ♂-♀ aggregations (38 beetles/bush)	Snead & Alcock (1985); Brown (1990)
Scolytidae							
<i>Ips acuminatus</i>	Sexual ♀ > pseudogamous ♀	Tactile (♂ struggles with ♀)	—	♀♀ court ♂	—	MI high?: ♂ excavates, cleans, defends breeding tunnel (used by several ♀♀); clonal larvae (unrelated to ♂) compete with larvae sired by ♂ QV high: pseudogamous ♀ produces clones of herself CC low: ♀♀ solicit access to breeding tunnel	Løyning & Kirkendall (1996)
<i>I. pini</i>	?	—	—	♀♀ court ♂	—	MI high?: ♂ excavates, cleans, defends breeding tunnel (used by several ♀♀)	Reid & Roitberg (1994)
Tenebrionidae							
<i>Tribolium castaneum</i>	Virgin ♀; mature ♀; ♀ previously mated with another ♂	Tactile (♂ touches ♀ head, abdomen); chemical	?	♂ approaches ♀	—	MI high: ejaculate production is costly; no gain from re-mating with same ♀ QV high: sperm competition and last-♂ sperm precedence reduce fertilization success with mated ♀ or immature ♀ (likely to re-mate)	Lewis & Iannini (1995); Arnaud & Haubruge (1999)
Diptera							
Anthomyiidae							
<i>Delia antiqua</i>	10 day old ♀ > 2 day old ♀	Visual (♂ walks or flies near ♀); tactile (♂ touches ♀ with tarsi, proboscis)	—	♂-♂ interactions	—	QV high: 2 day old ♀♀ lack mature eggs	McDonald & Borden (1996)
Bibionidae							
<i>Plecia nearctica</i>	Large ♀	—	Heavy ♂?	♂-♂ interactions	♂ > ♀	MI high: mating takes 56 h (♂ lives 2–5 days) QV high?: large ♀ more fecund	Hieber & Cohen (1983)
Diopsidae							
<i>Cyrtodiopsis whitei</i>	Virgin ♀	—	♂ with long eye-stalks	♂-♂ combat & display	—	MI high: sperm may limit ♂ mating success QV high: temporary first-male sperm precedence CC low for high-quality ♂: ♀♀ aggregate near long-eyed ♂	Lorch <i>et al.</i> (1993); Burkhardt & de la Motte (1988)
Coelopidae							
<i>Coelopa frigida</i>	Large, fat ♀	Visual? Chemical?	♂ larger than ♀	—	—	MI high: ♂ transfers 1/4 of his body mass to ♀ QV high: large, fat ♀ more fecund CC low: dense ♂-♀ mating aggregations	Pitafi <i>et al.</i> (1990, 1995) but see Dunn <i>et al.</i> (1999)
Drosophilidae							
<i>Drosophila hibisci</i>	Young, virgin ♀	Chemical	—	—	—	MI high: mating plug production is costly QV high: mating with young, virgin ♀ involves less sperm competition	Polak <i>et al.</i> (1998)
<i>D. melanogaster</i>	Young, virgin ♀; sucrose-fed ♀ > protein-fed ♀	Chemical	?	♂-♂ combat & display competition	—	MI high?: ejaculate production is costly QV high: mating with young, virgin ♀ involves less sperm competition	Shorey & Bartell (1970); Cook (1975); Cook & Cook (1975); Dow & von Schilcher (1975); Siegel & Hall (1979); Partridge (1980)

<i>D. mojavensis</i>	Virgin or long-unmated ♀	Chemical?	—	—	MI high: ♂ transfers nutrients with ejaculate	Markow (1982, 1988)
<i>D. bogaca</i>	Cactus-fed ♀; ♀ from male's own population	Chemical	—	—	MI high: mating takes up to 14 h QV high?: ♀♀ raised on ancestral (cactus) medium are in better condition? QV high: [mating with young, virgin ♀ involves less sperm competition]	Wasserman <i>et al.</i> (1971); Wasserman & Zweig (1991) Noor (1997)
<i>D. psuedoboscara</i>	Virgin ♀	Chemical?	—	♂-♂ combat	—	—
Dryomyzidae						
<i>Dryomyza anilis</i>	Fat ♀	Tactile (♂ probes ♀ abdomen with hind legs)	?	♂-♂ combat	MI high?: mating takes 63 min & several ejaculates QV high: fat ♀ has more mature eggs (71% of arriving ♀♀ lack mature eggs)	Otronen (1984, 1990, 1994a, 1994b)
Empididae						
<i>Empis borealis</i>	Largest ♀ in swarm, young ♀, ♀ in large swarm	Visual (♂ flies through ♀ lek)	♂	♀ display & scramble?	MI high: ♂ captures prey 'gift' to offer to ♀ QV high?: large ♀ has more ovarioles (but all swarming ♀♀ non-gravid)	Svensson & Petersson (1987, 1988, 1992, 1994); Svensson <i>et al.</i> (1989, 1990)
<i>Ramphomyia longicauda</i>	Fat ♀	Visual (♂ flies through ♀ lek)	None	♀ display (abdomen inflation)	MI high: ♂ captures prey 'gift' to offer to ♀ QV high: fat ♀ has more developed eggs	Funk & Tallamy (2000)
<i>R. marginata</i>	?	Visual (♂ flies through ♀ lek)	None	♀♀ display wing size, colour	MI high: ♂ captures prey 'gift' to offer to ♀ QV high: ♀♀ vary in body size, stage of egg development	Svensson (1997)
Muscidae						
<i>Musca domestica</i>	[Small ♀; virgin ♀]	Tactile (♂ touches ♀ with forelegs)? chemical?	—	—	QV high?: [mating with virgin ♀ involves less sperm competition?]	Colwell & Shorey (1977)
Prophiliidae						
<i>Protophila litigata</i>	Fat ♀	Tactile (♂ taps ♀ abdomen with mid- and hind legs)	Large ♂	♂-♂ combat	MI high: mating (with mate guarding) takes 2-3 h; ejaculate partly ingested by ♀ QV high: fat ♀ has more mature eggs (82% of single ♀♀ lack mature eggs)	Bonduriansky & Brooks (1998a, 1998b, 1999)
Scatophagidae						
<i>Scatophaga stercoraria</i>	Gravid ♀ (pre-oviposition)	Chemical? tactile?	—	♂-♂ combat	MI high?: mating (with mate guarding) takes 65 min QV high?: frequent encounter with non-gravid ♀♀?	Parker (1970a, 1970b, 1970c, 1970d)
Hemiptera						
Gerridae						
<i>Gerris buenoi</i>	Large ♀ (♂ mates longer)	Tactile?	Large ♂?	♂-♂ competition	MI high?: ♂ guards ♀ QV high: large (long) ♀ more fecund CC low?: can occur in dense ♂-♀ aggregations	Rowe & Arqvist (1996); Arqvist <i>et al.</i> (1996); Fairbairn (1988)
<i>G. lacustris</i>	Long-winged, heavy ♀ > long-winged, light or short-winged ♀; large ♀ (♂ mates longer)	Tactile?	Large ♂?	♂-♂ competition	MI high?: ♂ guards ♀ QV high: large (heavy) long-winged ♀ has high fecundity and can fly (short-winged ♀ flightless); large (long) ♀ more fecund CC low?: can occur in dense ♂-♀ aggregations	Batorczak <i>et al.</i> (1994); Rowe & Arqvist (1996); Arqvist <i>et al.</i> (1996)
<i>G. lateralis</i>	Large ♀ (♂ mates longer)	Tactile?	Large ♂?	♂-♂ competition	MI high?: ♂ guards ♀ QV high: [large (long) ♀ more fecund?] CC low?: can occur in dense ♂-♀ aggregations	Rowe & Arqvist (1996); Arqvist <i>et al.</i> (1996)
Pentatomidae						
<i>Arosternum hilare</i>	Large ♀	Tactile (♂ 'head butts' & antennates ♀ abdomen)?	Large ♂	♂-♂ combat (rare) & pheromone	MI high: mating takes up to 14 days QV high?: large ♀ lays more eggs & more viable eggs CC low: OSR ♀-biased	Capone (1995)
Rhopalidae						
<i>Rhopalum lammatoloma</i>	? (♂ determines mating duration)	—	—	—	MI high: mating takes ~12 h (when OSR ♀-biased) to 30 h (when OSR ♂-biased)	Carroll & Corneli (1995)
Heteroptera						
Belostomatidae						
<i>Abdus herberti</i>	?	—	?	♂ displays or courts ♀	MI high: ♂ broods eggs for 1 month (costs: time, energy, reduced ability to forage, increased risk of predation) CC low: ♀♀ solicit matings; at low temperatures, ♀ max. reproductive rate > ♂ max. reproductive rate	Smith (1976, 1979); Kraus (1989)
<i>A. indentatus</i>						

Table 3. (cont.)

Taxon	♂ Mating preference	Mode of ♀-assessment	♀ Mating preference	Intrasexual competition	OSR	Factors presumed to favour ♂ mate choice in this system (from ♂ perspective)	References
Lygaeidae							
<i>Lygaeus equestris</i>	Gravid ♀	Tactile (♂ detects ♀ behaviours indicating readiness to oviposit?)	None?	—	—	MI high: mating can last 24 h or more QV high?: gravid ♀ less likely to remate (remating results in 90% sperm displacement)	Sillén-Tullberg (1981)
Hymenoptera							
Halictidae							
<i>Halictus confusus</i>	?	Chemical; visual?	—	♂-♂ scramble	—	QV high?: variation in ♀ fecundity (gynes <i>versus</i> workers)	Wcislo (1992)
<i>Lasioglossum figneresi</i>	Non-nestmate ♀	Chemical	—	—	—	QV high?: nestmate ♀♀ are less receptive? ♂♂ habituate to nestmate ♀♀?	Greenberg (1982)
<i>L. zephyrum</i>	> nestmate ♀	Chemical; visual?	—	♂-♂ scramble	♂ > ♀	QV high?: older ♀♀ are not receptive CC high?: OSR is 'heavily male-biased'	Wcislo (1992)
<i>Nomia triangulifera</i>	Young ♀	Chemical; visual?	—	—	—	—	—
Sphecidae							
<i>Bombix nostrata</i>	Virgin or mating ♀ > digging or foraging ♀	Chemical; tactile (♂ antennates ♀)	—	♂-♂ combat	—	QV high?: mating with virgin or mating ♀ may involve less sperm competition	Schöne & Tengö (1981)
Lepidoptera							
Geometridae							
<i>Operophora brumata</i>	Large ♀	Chemical	None?	♂-♂ interactions; ♀♀ release pheromone	♂ > ♀	MI high?: mating takes 'several hours' (♂ can mate up to seven times over lifetime) QV high: large ♀ more fecund (egg number varies by 10×) CC low?: ♀♀ produce sex pheromone to attract ♂♂	van Dongen <i>et al.</i> (1998)
Gelechiidae							
<i>Peciniophora gossypiella</i>	♀ producing 'natural' pheromone blend	Chemical	—	♀♀ release pheromone	—	CC low?: ♀♀ produce sex pheromone to attract ♂♂	Collins & Gardé (1989 <i>a</i> , 1989 <i>b</i> , 1989 <i>c</i>)
Noctuidae							
<i>Agrotis vegetum</i>	♀ from same population as ♂	Chemical	—	♀♀ release pheromone	—	QV high?: interpopulational hybrids less viable?	Löfstedt <i>et al.</i> (1986); Hansson <i>et al.</i> (1990)
Nymphalidae							
<i>Acraea anax</i>	Uninfected ♀	—	—	♀ scramble	♂ < ♀	MI high: mating takes a full day; male life-span is short QV high: ♀♀ infected with <i>Haemaphysalis</i> bacteria produce all-♀ broods; uninfected ♀♀ produce viable sons (20× more fit than daughters) CC low?: ♀♀ swarm	Jiggins <i>et al.</i> (2000); Rauderson <i>et al.</i> (2000)
Pieridae							
<i>Pieris protodice</i>	Large, young ♀; normally melanized ♀ > dark ♀	Visual (♂ flies past, inspects ♀); chemical?	—	♀-♀ interactions; ♂♂ search for ♀♀	—	MI high: ♂ transfers (unreplenishable?) nutrients to ♀ QV high: large ♀ more fecund (body size varies by 5×); young ♀ lives longer and is in better condition; 10-15% of ♀♀ are dark (thermoregulate poorly?) CC low?: ♀♀ with depleted nutrient supply solicit ♂♂	Rutowski (1980, 1982); Wiernasz (1995)
<i>P. occidentalis</i>	Normally melanized ♀ > dark ♀	Visual (♂ flies past, inspects ♀); chemical?	Darker ♂ > lighter ♂	♂♂ search for ♀♀	—	MI high: ♂ transfers (unreplenishable?) nutrients to ♀ QV high?: 10-15% of ♀♀ are dark (thermoregulate poorly?)	Wiernasz (1989, 1995)
<i>Colias philodice</i>	Large ♀	—	Large ♂?	♂-♂ scramble	—	MI high: ♂ transfers nutrients to ♀ QV high?: large ♀ more fecund	Marshall (1982)
<i>C. eurytheme</i>	Large ♀	Visual (♂ flies past, inspects ♀); chemical?	Large ♂?	♂-♂ scramble	—	MI high: ♂ transfers nutrients to ♀ (6% of ♂ body mass) QV high?: large ♀ more fecund	Marshall (1982); Rutowski <i>et al.</i> (1983)
<i>Anthracaris cardamines</i>	Virgin (young) ♀	Visual (♂ flies past, inspects ♀); chemical?	?	—	—	MI high: ejaculate costly QV high: old ♀ less fecund CC high?: most ♀♀ mate only once in lifetime	Wiklund & Forsberg (1985)
Psychidae							
<i>Obolitus kirbyi</i>	Large ♀	Chemical?	—	♀♀ release pheromone	♂ < ♀	MI high: mating takes 1 h (♂ lives 3 days; active 2 h day ⁻¹) QV high: large ♀ more fecund (large variation in body size) CC low: ♀♀ are fertile before ♂♂; compete for ♂♂	Rhainds <i>et al.</i> (1995)
Pyralidae							
<i>Ostrinia nubilalis</i>	♀ pheromone blend	Chemical	—	♀♀ release pheromone	—	QV high?: [interpopulational hybrids less viable?]	Löfstedt <i>et al.</i> (1989)
<i>Plodia interpunctella</i>	Heavy ♀	Chemical? tactile ('abdominal pressures')?	?	—	—	MI high: ♂ sperm supply is limited; ♂ transfers spermatophore QV high?: heavy ♀ has heavier ovary and lives longer	Gage (1998)

Mantodea							
Mantidae							
<i>Tenodera aridifolia</i>	Well-fed ♀	Visual (♂ observes ♀ response to courtship)	—	♂ and ♀ courtship	—	QV high: well-fed ♀ is less likely to eat her mate	Liske & Davis (1984); Jones (1997)
Neuroptera							
Corydalidae							
<i>Protohermes grandis</i>	[Virgin ♀]	—	—	—	—	MI high: ♂ transfers spermatophore (7–20% ♂ body mass); ♂ refractory period 2 days	Hayashi (1998)
Orthoptera							
Acrididae							
<i>Melanoplus sanguinipes</i>	Virgin ♀; ♀ with mature eggs	Chemical?	None?	♀♀ grapple for access to ♂♂	—	MI high?: [♂ transfers spermatophore]	Pickford & Gillott (1972)
Gryllidae							
<i>Acheta domesticus</i>	Large ♀ receives more sperm	—	—	—	—	QV high?: large ♀ more fecund?	Gage & Barnard (1996)
Tettigoniidae							
<i>Anabrus simplex</i>	Large ♀; ♂ is choosier in high density (HD) or poor diet treatment	Tactile (♂ assesses ♀ body size during antennation or mounting bouts)?	? (♀ is choosier in low-density (LD) or rich-diet treatment)	HD: ♀-♀ grappling; LD: ♂ calling	HD: ♂ < ♀ LD: ♂ > ♀	MI high: ♂ transfers spermatophore (up to 27% ♂ body mass); relative value of ♂ investment higher in HD or poor-diet conditions, limiting ♀ fecundity QV high?: large ♀ more fecund (more mature eggs) CC low at HD: 12 adults m ⁻² ; ♀♀ solicit ♂♂	Gwynne (1981, 1984c, 1993)
<i>Decticus verrucivorus</i>	Virgin ♀ receives heavier spermatophylax	Chemical?	—	—	—	MI high: ♂ transfers spermatophore (10% of ♂ body mass) QV high?: virgin ♀ will lay more eggs CC low: ♀♀ approach singing ♂♂	Wedell (1992); Wedell & Arak (1989)
<i>Kawanaphila nartee</i>	Heavy ♀; ♂ is choosier in food-limited (FL) or frequent ♀ encounter conditions	Tactile (♂ assesses ♀ mass during mounting bouts)?	? (♀ is choosier in non-food-limited (NL) conditions)	♀♀ grappled for access to ♂♂ in FL conditions	♂ < ♀	MI high: ♂ transfers spermatophore (~16% ♂ body mass); relative value of ♂ investment higher in FL conditions, limiting ♀ fecundity QV high: heavy ♀ more fecund CC low: ♀♀ solicit ♂♂, especially in FL conditions	Gwynne & Simmons (1990); Simmons & Bailey (1990); Simmons (1990); Shelly & Bailey (1992); Simmons & Kvarnemo (1997); Kvarnemo & Simmons (1999)
<i>Metaballus litus</i>	Food-limited site (FL): heavy ♀; non-food-limited site (NL): none?	Tactile (♂ antennates ♀ and probes her underside)?	None?	FL: ♀-♀ grappling NL: ♂ calling	—	MI high: ♂ transfers spermatophore (up to 1/4 of ♂ body mass); relative value of ♂ investment higher in FL, limiting ♀ fecundity QV high?: mated (heavy) ♀ had more mature eggs CC low in FL: mean time to attract ♀ < 4 min; CC higher in NL: mean time to attract ♀ > 30 min	Gwynne (1985)
<i>Requena verticalis</i>	Young or virgin ♀ preferred and receives larger nutrient 'gift'; ♂ is choosier in FL than in NL conditions	Chemical (♂ assesses ♀ age/mating status while 'running his genital claspers along the female's dorsum')?	? (♀ is choosier in NL than in FL conditions)	♀♀ grapple for access to ♂♂	FL: ♂ < ♀ NL: ♂ > ♀	MI high: ♂ transfers spermatophore (up to 40% of ♂ body mass); relative value of ♂ investment higher in FL conditions, limiting ♀ fecundity QV high: ♂ mating with non-virgin ♀ will be cuckolded because first ♂ has 100% sperm precedence CC low: ♀♀ solicit ♂♂ (in both FL and NL conditions)	Gwynne (1984a, 1988a, 1988b); Lynam <i>et al.</i> (1992); Schatral (1993); Simmons (1993); Simmons <i>et al.</i> (1993, 1994); Kvarnemo & Simmons (1998)
Phasmida							
Heteronemiidae							
<i>Diapheromera veliei</i>	Long (heavy) ♀	—	None?	♂-♂ combat	—	MI high: mating takes up to 136 h QV high: heavier ♀ carries more, larger eggs (♀ mass varies by 3.5×) CC low?: dense ♂-♀ aggregations (23 individuals/bush)	Seely <i>et al.</i> (1991)
Psocoptera							
Trogidae							
<i>Lepinotus patruelis</i>	Small, thin ♀	Tactile (♂ response to mounting attempts by ♀)?	None?	♂-♂ interference ♀-♀ grappling	♂ > ♀ to ♂ < ♀	MI high: ♂ transfers large spermatophore to ♀ QV high?: thin ♀ younger and more likely to be virgin (small ♀♀ produce as many eggs as large ♀♀) CC low: ♀♀ often outnumber and compete for ♂♂	Wearing-Wilde (1996)

Where required, '>' shows direction of mating preference, and '?' indicates mate choice with unknown preferences. Factors that may select on choosiness are classified as male mating investment [MI], variance in female mate quality [QV], or constraints on choosiness [CC]. Constraints on choosiness are considered to be 'low' when search or assessment costs appear to be low, and 'high' when the opposite appears to be true. Square brackets indicate an interpretation not given by the author of the study, and blank fields denote lack of information.

ejaculate volume (e.g. Gage, 1998), or nuptial gift size (e.g. Wedell, 1992) probably exist in many species. Moreover, few studies have tested for both male and female mate choice in the same system, even though mutual mate choice may be commonplace (e.g. Pitafi *et al.*, 1995; Johnstone *et al.*, 1996). Lastly, few studies have manipulated the key factors experimentally. Perhaps this review will help to highlight such deficiencies in knowledge and encourage empirical work to alleviate them.

(2) Phylogenetic patterns and distribution of male mate choice

Male mate choice has been observed or inferred in at least 58 species of insects, belonging to 37 families and 11 orders (Table 3). Although this represents a very small subset of all known insect species, the factors favouring male choosiness in these systems are also likely to operate in many other species, genera and orders where male mate choice has not been studied. Thus, further research is likely to reveal male mate choice in many more (perhaps most) insect species.

In Coleoptera (Table 3), male choosiness appears to be favoured by low search costs in some systems, where mating takes place in very dense male-female aggregations (e.g. *Brentis anchorago*, *Tetraopes tetraophthalmus*, *Lytta magister*). Male choosiness is also favoured in some systems by costly mating investment, involving large spermatophores or long copulation duration (e.g. *Brentis anchorago*, *Tetraopes tetraophthalmus*, *Lytta magister*, *Ips* species), and by high mate quality variance (e.g. *Brentis anchorago*, *Harmonia axyridis*, *Tribolium castaneum*). Thus, all three key factors in the basic model are important in this order.

Among the diverse mating systems observed in Diptera, several species (*Empis borealis*, *Ramphomyia* species) exhibit complete sex role reversal, apparently because male prey gifts limit female fecundity (Svensson & Petersson, 1987; Funk & Tallamy, 2000). In other species, male choosiness appears to be favoured by large mate quality variance, resulting from large variation in female fecundity or frequent encounter with females lacking mature eggs (e.g. *Delia antiqua*, *Plecia nearctica*, *Coelopa frigida*, *Drosophila hibisci*, *D. melanogaster*, *D. pseudoobscura*, *Dryomyza anilis*, *Musca domestica*, *Protophila litigata*, *Scatophaga stercoraria*), or by costly mating investment in copulation duration or ejaculate (e.g. *Drosophila mojavensis*, *D. pegasa*). In addition, because nuptial or ejaculate 'gifts' may often be quite cryptic in this

order (e.g. Markow, 1982; Steele, 1986; Bonduriansky & Brooks, 1998a), male mating investment may be higher than presently supposed in some Diptera. These factors suggest that male mate choice may be very widespread in Diptera.

Hemiptera and Heteroptera also comprise a variety of mating systems, including a family (Belostomatidae) where complete sex role reversals may be widespread because of high male mating investment in parental care (Kraus, 1989). In the water strider *Gerris lacustris*, the complex factors that may favour male preference for large females of the winged morph over (equally fecund) large females of the wingless morph (Batorczak, Jabłoński & Rowiński, 1994) suggest the need for further research. In many water striders, male choosiness may be favoured primarily by the mating investment costs of losing mate-searching opportunities while in copula. In the bugs *Acrosternum hilare* (Capone, 1995), *Jadera haematoloma* (Carroll & Corneli, 1995), and *Lygaeus equestris* (Sillén-Tullberg, 1981), male choosiness is clearly favoured by high mating investment in extremely long mating durations.

Within Lepidoptera, male choosiness may be very widespread among species with costly male mating investment in spermatophore nutrients (e.g. *Pieris* and *Colias* species, *Anthocharis cardamines*, *Plodia interpunctella*), or long copulation duration (e.g. *Operophtera brumata*, *Oiketicus kirbyi*). Moreover, pheromonal calling by female moths suggests a departure from the classic female role as recipient of male courtship (Darwin, 1874), and may represent an extra opportunity for male mate choice in this order. However, the apparently low mating rate of females in many species (Rutowski, 1984) suggests that male choosiness may be constrained by high search costs (see below). By contrast, in the butterfly *Acraea encedon*, male choosiness may have evolved in response to highly female-biased sex ratios resulting from widespread infection of females with the bacterium *Wolbachia* sp., which kills male embryos (Jiggins *et al.*, 2000).

In Orthoptera, immensely costly male mating investment in spermatophores is likely to favour male choosiness in many species, with or without complete sex role reversal. For example, male spermatophores represent 10% of male body mass in *Decticus verrucivorus* (Wedell & Arak, 1989), 16% of body mass in *Kawanaphila nartee* (Shelly & Bailey, 1992), 27% of body mass in *Anabrus simplex* (Gwynne, 1981), and up to 40% of body mass in *Requena verticalis* (Gwynne, 1984a). Male choosiness is also favoured by large variance in female mate

quality in many species, resulting from variation in number of eggs produced or laid (e.g. *Acheta domesticus*, *Anabrus simplex*, *Decticus verrucivorus*, *Metaballus litus*) or intense sperm competition associated with non-virgin females (*Requena verticalis*).

There is some evidence of male mate choice in five other insect orders, although much more work is needed on the nature and distribution of male choosiness in these groups. In the species-rich order Hymenoptera, the evidence for male mate choice is somewhat sketchy, and the factors favouring choosiness are not clear (see below). In Mantodea, variation in the likelihood of being eaten by females of varying nutritional states (Jones, 1997) represents extremely high female mate quality variance from the male perspective, suggesting that male choosiness may be widespread among species where sexual cannibalism occurs. Although little is presently known about mate choice in Neuroptera, Phasmida or Psocoptera, male choosiness may be widespread if males of many species produce costly spermatophores (as in *Protohermes grandis* and *Lepinotus patruelis*), or engage in prolonged mate guarding (as in *Diapheromera veliei*).

VI. DISCUSSION

(1) Does the evidence support the basic model?

Can the factors included in the basic model account for the observed examples of male mate choice in insects? Among the systems where male mate choice has been observed (Table 3, column 1), it was nearly always possible to 'explain' male choosiness in light of one or more of these factors (Table 3, column 7). In other words, as predicted by theory, systems where males are choosy tend to be characterized by some combination of relatively high male mating investment, large female mate quality variance, and low costs of mate search and/or assessment. Unfortunately, little is known about the accuracy of assessment of individual mates or of mate quality distributions in any system (see Section VI.3). Further evidence of the importance of these factors is provided by systems where males have been observed to adjust their level of choosiness facultatively. For example, greater male choosiness was associated with greater costs of male spermatophores (i.e. higher male mating investment) in food-stressed conditions (e.g. Gwynne, 1985, 1993; Kvarnemo &

Simmons, 1998), larger perceived variation in female body size (i.e. larger female mate quality variance) (Svensson & Petersson, 1992) and greater female encounter rate or a more female-biased operational sex ratio (i.e. lower search and assessment costs) perceived by males (Shelly & Bailey, 1992; Kvarnemo & Simmons, 1999). Thus, the basic model for the evolution of male mate choice is consistent with much of the empirical evidence.

However, not all the male mate choice systems and studies (Table 3) clearly support the model. The most difficult systems to reconcile with theory are some species of Lepidoptera. Because, in many butterfly species, females appear to mate very few times (Rutowski, 1984), males may experience high search costs. Yet male mate choice seems to be widespread. For example, males of *Anthocharis cardamines* are choosy, even though it appears that most females mate only once in their lifetimes (Wiklund & Forsberg, 1985). The model might be reconciled with these systems in three potential ways: (i) the costs of mating investment or the potential benefits of mate quality variance may be large enough to compensate for the high search costs in this group; (ii) the search costs experienced by male butterflies may be reduced by spatial or temporal 'clumping' of females (M. Cornish, personal communication); (iii) the mating rates of female butterflies may be underestimated by the usual method of quantifying this parameter – counting spermatophores inside females – because females may absorb spermatophores completely (Ehrlich & Ehrlich, 1978). In a number of other systems (e.g. Colwell & Shorey, 1977; Schöne & Tengö, 1981; Greenberg, 1982; Löfstedt *et al.*, 1986, 1989; Collins & Cardé, 1989*c*; Osawa, 1994; McDonald & Borden, 1996), much of the information required to test the model is not available, and further research is needed.

The model's structure is also challenged to some extent by the work of Kvarnemo & Simmons (1998, 1999). In a study using the bushcricket *Kawanaphila nartee*, Kvarnemo & Simmons (1999) detected an interaction between the effects of mate quality variance and operational sex ratio on male choosiness, but found no effect of mate quality variance by itself. However, their test of the direct effects of mate quality variance on male choosiness (experiment 2) may have been confounded by inter-treatment differences in female fecundity: a smaller proportion of males were expected to reject females in the low variance treatment, even though females in this treatment had less than half the number of

eggs, on average, as females in the high variance treatment. Thus, if the males had a 'built-in' tendency to discriminate against females of low fecundity, or were not able to assess and respond to the females' mean fecundity quickly enough, males may have been more likely to reject females in the low variance treatment simply because these females were less fecund. Similarly, in a study using the bushcricket *Requena verticalis*, Kvarnemo & Simmons (1998) detected no effect of perceived variance in female mate quality (age) on male choosiness. However, their experiment compared male responses to virgin females drawn from two groups, one in which female age ranged from 3 to 28 days (high variance treatment), and another where female age ranged from 11 to 18 days (low variance treatment). Males may have failed to detect a difference of this magnitude (Kvarnemo & Simmons, 1998), or simply responded to all virgin females as high-quality mates. Nonetheless, although they provide little evidence against the importance of female mate quality variance, the experiments of Kvarnemo & Simmons (1998, 1999) clearly suggest the need for further experimental investigation of possible interactions between factors associated with selection on male choosiness.

Is it possible to rank the factors in the basic model in order of importance? An inspection of Table 3 shows that, in most cases, male choosiness appeared to be associated with high male mating investment (e.g. costly spermatophores or long mating duration) and/or high female mate quality variance (e.g. large variation in fecundity or reproductive condition among females). Low costs of search and assessment (e.g. female mating aggregations, or courtship solicitation by females) appear to be associated with male choosiness in fewer systems. The high search costs apparently experienced by choosy male butterflies also suggest that this factor may be less important. However, the apparently greater importance of mating investment and mate quality variance may only reflect the greater ease with which these factors can be quantified. Moreover, experimental evidence suggests that search costs can have a direct effect on choosiness (Shelly & Bailey, 1992; Kvarnemo & Simmons, 1999). Thus, the relative importance of the three factors cannot be determined from the available evidence.

(2) Male choosiness and female mating rate

Does the evidence support the hypothesis that selection for male choosiness is stronger in systems

where female fitness increases with each additional mating than in systems where female fitness peaks at a small number of matings? This hypothesis may be tested in two ways: (i) by manipulating the effect of multiple copulation on female fitness and measuring the response in male choosiness; (ii) by performing a meta-analysis of the covariation of these two factors in many species. An experiment similar to that outlined above was performed with bushcrickets by Gwynne & Simmons (1990), who manipulated the effect of multiple copulation on female fitness by varying food abundance and measured the facultative response in male choosiness. Their finding that males were more choosy in 'low food' conditions appears to support the above hypothesis. However, the experiment of Gwynne & Simmons (1990) was designed to test a different hypothesis, and cannot be regarded as a convincing test of the above hypothesis for two reasons: (i) their experimental manipulation of food abundance probably affected both the costs of male spermatophylax production and the effect of mating rate on female fitness; (ii) they did not quantify the functions relating female fitness to mating rate in each treatment. An appropriate experimental test would involve manipulation of food abundance separately for each sex. It would also be interesting to test for an evolutionary response in male choosiness in populations maintained under conditions of abundant and limited food. As for inter-specific comparisons, the evidence suggests that females receive cumulative benefits that represent costly mating investment for males (e.g. nuptial gifts) in a substantial proportion of the systems where male mate choice has been observed (Table 3). Such systems occur in Diptera, Lepidoptera, Megaloptera, Orthoptera and Psocoptera, and perhaps in some of the other orders as well. However, it is not clear what specific combination(s) of factors selected for male choosiness in these systems. Moreover, male mate choice also occurs in some systems where female fitness probably peaks at a small number of matings (e.g. *Drosophila melanogaster*, *Gerris* species). Hence, the evidence reviewed here does not permit a test of the above hypothesis.

(3) Female-assessment mechanisms

The evidence suggests that a variety of mechanisms and behaviours are employed by males to assess female mate quality (Table 3). Because female-assessment mechanisms were deliberately investigated (or even mentioned) in few of the studies (with the exception of lepidopteran species: e.g. see Collins

& Cardé, 1989*a, b, c*; Rhainds, Gries & Rodriguez, 1995), the mechanisms were usually inferred from the nature of the male preference, or a description of male-female interactions. Males appear to use visual assessment (e.g. observing the female while hovering or walking nearby) in several species of Diptera (*Delia antiqua*, *Empis borealis*, *Ramphomyia* species), Lepidoptera (*Pieris* and *Colias* species, *Anthocharis cardamines*) and Mantodea (*Tenodera aridifolia*). Olfactory assessment (e.g. of pheromone blend) is employed by males in some species of nearly every order where male mate choice has been observed and, although poorly known in most systems, may be the most widespread form of mate assessment. Tactile assessment (e.g. probing, antennating, or mounting sequences, possibly involving acquisition of information through both mechanical and chemical means) appears to be important in Coleoptera (*Lytta magister*, *Tribolium castaneum*), Diptera (*Delia antiqua*, *Dryomyza anilis*, *Musca domestica*, *Protophila litigata*), Hemiptera (*Gerris lacustris*, *Acrosternum hilare*), Heteroptera (*Lygaeus equestris*), and Orthoptera (*Anabrus simplex*, *Metaballus litus*). It is quite likely that, in some species, combinations of visual, tactile and olfactory mechanisms are employed concurrently or sequentially by males to obtain information on different female traits. Almost nothing is known about the accuracy or reliability of mate-assessment mechanisms in any insect.

Interestingly, behaviours involved in visual assessment, such as flying or hovering near the female, may be easily misinterpreted as courtship sequences. Similarly, many behaviours associated with tactile assessment of female quality, such as probing, antennating or mounting bouts, may be mistaken for 'copulatory courtship'. Eberhard (1994) classified as copulatory courtship any behaviour that was repeated, not involved in maintaining contact with the female, and not associated with self-cleaning, repelling rival males, or transferring sperm. Explicitly included in the definition of copulatory courtship is 'drumming or rubbing with the legs or abdominal processes on the female's abdomen, thorax or wings' (Eberhard, 1991) or 'rhythmic movements causing portions of the male genitalia to rub or tap on the outside of the female' (Eberhard, 1994). But, clearly, there is an alternative explanation for such male movements prior to or during copulation: they may function in female-assessment. The difference between a male copulatory behaviour that functions as copulatory courtship associated with female mate choice, and one that functions in female-assessment associated with male mate choice, may be very

subtle. Indeed, there is no obvious reason why the same behavioural sequence could not serve both functions. Thus, because males may acquire information about female quality during copulation and discriminate by varying copulation duration or ejaculate size, only male behaviours performed after ejaculate transfer can be safely assumed to represent copulatory courtship.

(4) The nature and expression of male mating preferences

Male insects exhibit a variety of mating preferences, with substantial variation seen within orders and even within some families. The most common preferences are for (i) large females, (ii) heavy, fat or gravid females, (iii) virgin or young females (Table 3). As expected, these preferences tend to maximize a male's expected fertilization success from each mating. Large females are often preferred by males because body size tends to be a reliable proximate indicator of female fecundity. If larger females produce more eggs, a male's expected fertilization success will increase with female body size, as long as gains from greater fecundity are not balanced by losses from increased sperm competition (see Verrell, 1994). Heavy or fat females may often be preferred because they are likely to be gravid. For example, *Protophila litigata* males appear to use fatness rather than body size to evaluate female quality because fatness is a better predictor of the number of mature eggs a female is carrying (Bonduriansky & Brooks, 1998*b*). Similarly, virgin or young females are probably preferred because of increased fertilization success resulting from reduced sperm competition. Males preferred small or thin females in only two systems. In *Lepinotus patruelis*, male preference for thin females also appears to increase male fertilization success, since thin females are as fecund as fat ones, but more likely to be virgins (Wearing-Wilde, 1996). It is not clear why *Musca domestica* males apparently prefer small females (see Colwell & Shorey, 1977). Thus, the nature of male preferences in a particular system appears to depend on the relative effects of female body size, relative abdomen width and mating status (i.e. virgin/non-virgin, or time since last mating) on a male's expected fertilization success (although see Itzkowitz *et al.*, 1998).

Less common mating preferences include (i) females fed on particular substances, producing a particular pheromonal blend, or belonging to the male's own population, (ii) non-nestmate females,

and (iii) normally-melanized females (Table 3). Category (i) preferences all appear to favour females belonging to the male's own gene pool or population, and may be favoured because inter-populational hybrids are less viable. Such preferences may also be advantageous if females raised on particular media have better condition and, hence, greater fecundity than others (Wasserman & Zweig, 1991). Greenberg (1982) suggested a proximate explanation for discrimination against nestmate females in *Lasioglossum zephyrum*: habituation to nestmates makes males less eager to court nestmate females, and females less receptive to nestmate males. A possible ultimate explanation for this response is avoidance of inbreeding. Preference for normally-melanized females in *Pieris* butterflies may be advantageous because unusually dark females are less effective thermo-regulators and, hence, less fecund or viable (Wiernasz, 1995).

Among the most interesting are preferences for sexually reproducing females in the beetle *Ips acuminatus*, females uninfected with male-embryo-killing *Wolbachia* sp. bacteria in the butterfly *Acraea encedon*, and well-fed females in the mantis *Tenodera aridifolia*. Preference for sexual females in *Ips acuminatus* is probably advantageous because it reduces the amount of resources wasted on copulations that yield no fertilizations for the male, and because it increases the fitness of the male's offspring by reducing the number of clonal larvae with which they must compete (Løyning & Kirkendall, 1996). Offspring fitness may also select for male mate choice in *Acraea encedon*, although compelling evidence of male choosiness is still lacking. In this species, males may prefer females uninfected with *Wolbachia* sp. because only uninfected females produce male offspring. In heavily infected populations, where sex ratios are strongly female-biased, male offspring have much higher fitness than female offspring (Jiggins *et al.*, 2000; Randerson, Jiggins & Hurst, 2000). In *Tenodera aridifolia*, preference for well-fed females, which are less likely to cannibalize their mate (Jones, 1997), is particularly interesting because, in this case, female mate quality is largely determined not by the male's expected fertilization rate or offspring fitness from the mating, but by his probability of surviving to search for additional mates: in other words, his residual reproductive value (Williams, 1966). Thus, whereas the most commonly observed male preferences all appear to maximize expected fertilization rate, other observed preferences may increase offspring fitness or the male's own probability of survival (Table 4).

Male mating preferences are expressed either as precopulatory mate choice (i.e. reluctance to court or mount some potential mates), or as cryptic mate choice (i.e. variation in the amount of resources invested in copulation with females of varying mate quality), or a combination of the two. For example, dipteran males may discriminate against non-gravid females through precopulatory rejection (e.g. Wasserman & Zweig, 1991; Bonduriansky & Brooks, 1998*b*), or by varying the amount of time invested in copulation or mate guarding (e.g. Otronen, 1984), or both (e.g. Pitafi *et al.*, 1995; but see Dunn *et al.*, 1999). Cryptic male mate choice through variation in time investment also occurs in Hemiptera. For example, male water striders (*Gerris* species) tend to copulate for longer with large females than with small ones (Rowe & Arnqvist, 1996), probably because large females are more fecund (Fairbairn, 1988). Males also vary copulation duration in the bug *Jadera haematoloma* (Carroll & Corneli, 1995). Insect males are also known to exercise cryptic mate choice by varying the amounts of nutrients or ejaculate transferred to females of different mate qualities. For example, in the cricket *Acheta domesticus* and the moth *Plodia interpunctella*, males ejaculate more sperm into large females (Gage & Barnard, 1996; Gage, 1998) and, in the tettigoniid *Requena verticalis*, males appear to transfer larger amounts of spermatophylax material to virgin or young females (Simmons *et al.*, 1993). A particularly interesting example is provided by the spiny orbweaving spider *Micrathena gracilis*, where a male may inseminate only one side of a female's reproductive tract to reduce the risk of being eaten by her (Bukowski & Christenson, 2000).

However, patterns of variation in male mating investment may relate to male precopulatory responses and sexual selection on females in very complex and sometimes rather obscure ways. For example, males of *Drosophila hibisci* copulate longer with older females, against which they discriminate in precopulatory choice (Polak, Starmer & Barker, 1998), and males of *Decticus verrucivorus* copulate longer with non-virgin females, but transfer larger spermatophores to virgins (Wedell & Arak, 1989; Wedell, 1992). Courtship role-reversed male bush-crickets (*Kawanaphila nartee*) appear to favour large females in precopulatory mate choice (Gwynne & Simmons, 1990) but transfer larger ejaculates to small females (Simmons & Kvarnemo, 1997). Thus, males may optimize their mating investments through elaborate strategies involving different combinations of precopulatory and cryptic

Table 4. *Mating preferences observed in male insects, possible benefits of each preference to the males, and potential sexual selection vector generated on female phenotype by each type of preference*

Male mating preference	Possible benefit to male	Sexual selection on female phenotype
Large ♀	Increased fertilization success	For increased body size
Heavy, fat, gravid ♀	Increased fertilization success	None? For deceptive fertility signals?
Virgin, young ♀	Increased fertilization success	None? For deceptive virginity signals?
Particular ♀ pheromonal blend	Increased offspring fitness?	Stabilizing selection on pheromone blend
♀ belonging to same population as ♂	Increased offspring fitness?	Stabilizing selection on population-specific phenotypic signals
Normally-melanized ♀	Increased fertilization success? Increased offspring fitness?	Stabilizing selection on melanin level
Sexually-reproducing ♀	Increased offspring fitness; reduced waste of ♂ resources	None? For deceptive sexuality signals in clonal females?
♀ uninfected with male-killing <i>Wolbachia</i> sp.	Increased offspring fitness	For deceptive signals of uninfectedness?
Well-fed ♀	Increased reproductive value	None? For deceptive condition signals?
Small ♀	?	For decreased body size?
Thin ♀	Increased fertilization success	None? For deceptive virginity signals?
♀ fed particular substances	Increased fertilization success? Increased offspring fitness?	None?
Non-nestmate ♀	Increased offspring fitness?	None?

Preferences listed in approximate order of most to least commonly observed; see text for explanation.

responses. It would be very interesting to know what kinds of sexual selection vectors are generated by such complex male mate choice strategies. Unfortunately, cryptic male mate choice has so far received very little research attention.

(5) Male mating preferences and sexual selection on female phenotypes

Male mating preferences have the potential to exert sexual selection on females in many systems (Table 4). For example, one of the most commonly observed preferences, favouring large females (or females larger than the male), may generate sexual selection on female body size. Because adult insects do not grow, this male preference may result in consistent discrimination against small females, especially by high-quality males. Small females may then experience reduced reproductive success as a result of reduced fertilization rates, less frequent acquisition of cumulative benefits such as food gifts (e.g. Gwynne, 1984*a*, 1988*a*), or poor (male) mate quality (see Parker, 1983), relative to large females. A number of other male preferences, such as preference for particular female pheromone blends or levels of melanization, are also likely to generate sexual selection. Unfortunately, few attempts have been made to assess the strength of this sexual selection or

its effects on female phenotype (although see Gwynne, 1984*c*; McLain & Boromisa, 1987; Gwynne & Simmons, 1990). Indeed, male preference for certain female phenotypes, resulting in greater male attention or higher copulation rate for particular females, need not necessarily result in greater reproductive success for the preferred females, and may even have the opposite effect (see Byrne & Roberts, 1999).

By contrast, some male preferences are much less likely to exert sexual selection on females (Table 4). This is true of preferences for fat or virgin females, as well as (less common) preferences for females from the male's own population, females fed particular substances, non-nestmate females, or sexual females. Preference for heavy or well-fed females may exert sexual selection on aspects of female genetic quality, but the strength of such sexual selection may often be inconsequential relative to viability and fecundity selection and, thus, not likely to produce a noticeable response in most systems. However, response to sexual selection on behavioural or physiological traits that increase female attractiveness is evident in some systems where females receive cumulative benefits from males. For example, *Requena verticalis* females may disguise their mating status to avoid male discrimination against non-virgins (Simmons *et al.*, 1994), *Ramphomyia longicauda* females inflate their abdomens to increase their attractiveness to males

(Funk & Tallamy, 2000), and females may solicit copulations under some circumstances in *Pieris protodice* (Rutowski, 1980) and *Protopiophila litigata* (Bonduriansky & Brooks, 1998b).

Sex role theory and much of the empirical evidence suggest a fundamental difference between the sexes in the key determinants of mate quality, and resulting differences in the nature of male and female mating preferences and sexual selection vectors. For males, the most important element of mate quality tends to be female fecundity, which is usually the principle determinant of a male's fertilization success from the mating. Hence, the most common male mating preferences are for phenotypic indicators of fecundity, such as female body size or fatness (Table 4). These patterns are expected to have two consequences. Firstly, because the intensity of fecundity and viability selection acting on female body size and fatness (i.e. fecundity) will probably far exceed the intensity of sexual selection on these traits, male mating preferences will tend merely to reinforce those other, much stronger selection vectors. Secondly, because traits such as body size or fatness can be assessed directly by males (through visual or tactile mechanisms), sexual selection on females will not usually result in the evolution of female display traits that advertise quality, although exceptions to this rule certainly occur (e.g. Funk & Tallamy, 2000). By contrast, the key determinant of male quality for females in many systems may be genetic quality or overall condition, a combination of genetic and environmental factors (Rowe & Houle, 1996; Jennions & Petrie, 1997; although see Johnstone, 1995; Kirkpatrick, 1996; Kirkpatrick & Barton, 1997). Because male 'good genes' and condition cannot be assessed (i.e. seen or touched) directly by females, female preferences tend to select for the evolution of 'revealing displays' such as costly, condition-dependent ornaments (Rowe & Houle, 1996; Wilkinson & Taper, 1999), and sexual selection through female mate choice tends to oppose viability selection vectors acting on males.

(6) Evolution of the sex roles

(a) Complete sex role reversal

Although it has been the focus of much research interest, complete sex role reversal (i.e. males choosy, females competitive) occurs in a small minority of the systems where male mate choice has been observed (Table 3). These include several species of Diptera (in the genera *Empis* and *Ramphomyia*), a

number of species of Orthoptera and, possibly, species of Heteroptera (Belostomatidae, e.g. *Abedus* species). In some orthopterans, diet quality (i.e. resource limitation) has been shown to control the relative value of male parental investment (spermatophylax nutrients) and, thus, to determine the relative potential rates of reproduction of males and females (Gwynne & Simmons, 1990; Simmons & Bailey, 1990; Kvarnemo & Simmons, 1998). Hence, as predicted by Trivers (1972), relative parental investment affects the sex roles in courtship and mate choice in these systems (Simmons, 1992; Gwynne, 1993). However, even in rich-diet conditions where complete sex role reversal is not observed, males still tend to be choosy (e.g. Gwynne, 1993; Schatral, 1993). Thus, diet quality seems to control the switch from partial to complete sex role reversal in orthopterans.

An additional factor that can apparently result in complete sex role reversal is direct distortion of the adult sex ratio by male-killing cytoplasmic parasites. Sex-ratio-distorting parasites, usually transmitted only from mothers to offspring and lethal to male embryos, occur in a wide variety of animals (Hurst, 1991, 1993). Recent reports (Jiggins *et al.*, 2000; Randerson *et al.*, 2000; also see Section VI.4) suggest that such a parasite (the bacterium *Wolbachia* sp.) is responsible for the nearly complete elimination of males from some populations of the butterfly *Acraea encedon*. In such populations, females appear to display and compete for males in 'leks', and males are thought to discriminate against infected females (which do not produce male offspring). Although the behavioural evidence is still weak, this system suggests that complete sex role reversal can evolve as a result of direct sex ratio distortion, even when males contribute less than females to offspring and have a higher potential rate of reproduction.

(b) Partial sex role reversal

Partial sex role reversal (Gwynne, 1991) is characteristic of most systems where males are choosy. Such systems commonly exhibit both male and female mate choice (i.e. 'mutual mate choice'), as seen in some species of Coleoptera (*Brentis anchorago*, *Lytta magister*), Diptera (*Plecia nearctica*, *Coelopa frigida*, *Protopiophila litigata*), Hemiptera (*Acrosternum hilare*), Lepidoptera (*Pieris occidentalis*, *Colias philodice*, *C. eurytheme*) and Orthoptera (*Anabrus simplex*, *Requena verticalis*) (Table 3). Further research will probably reveal mutual mate choice in many other species, as predicted by several models (e.g. Parker, 1983;

Johnstone *et al.*, 1996). Even more commonly observed in partially sex-role-reversed systems is the co-occurrence in males of vigorous intra-sexual competition (e.g. scramble, combat or display) and mate choice. This occurs in species of Coleoptera (*Brentis anchorago*, *Tetraopes tetraophthalmus*, *Lytta magister*), Diptera (*Delia antiqua*, *Plecia nearctica*, *Drosophila* species, *Dryomyza anilis*, *Protopiophila litigata*, *Scatophaga stercoraria*), Hemiptera (*Gerris locustris*, *Acrosternum hilare*, *Abedus* species), Hymenoptera (*Lasioglossum figueresi*, *Nomia triangulifera*, *Bembix rostrata*), Lepidoptera (*Operophtera brumata*, *Pieris* and *Colias* species), Mantodea (*Tenodera aridifolia*), Orthoptera (e.g. *Anabrus simplex*, *Metaballus litus*), Phasmida (*Diapheromera veliei*) and Psocoptera (*Lepinotus patruelis*). Thus, male mate choice is most commonly observed in conjunction with male intra-sexual competition and/or female mate choice.

(c) *The evolution of sex role reversal*

Trivers (1972) argued that sex role reversal would occur when males and females contribute nearly equally to the production of offspring. In more recent parlance, it is said that relative levels of parental investment of males and females determine their relative potential rates of reproduction, relative representation in the operational sex ratio, and relative sexual selection gradients (Clutton-Brock & Vincent, 1991; Clutton-Brock & Parker, 1992). Thus, similar levels of parental investment are thought to cause sex role reversal (Simmons, 1992). This view has been supported by experimental work on completely sex-role-reversed orthopterans (see above), although work on sex-role-reversed pipefishes and seahorses (Vincent *et al.*, 1992) and butterflies infected with *Wolbachia* sp. (Jiggins *et al.*, 2000) suggests that other factors can also have important effects on the sex roles. However, in most partially sex-role-reversed species, sex ratios are even or male-biased, the relative value of male parental investment appears to be much lower than that of females, and their potential rates of reproduction appear to be much higher. For example, in *Protopiophila litigata*, an average male can potentially fertilize approximately 15 clutches over his lifetime (Bonduriansky & Brooks, 1998b), whereas an average female is unlikely to lay more than two clutches (R. Bonduriansky, unpublished data), and searching males outnumber single females at the mating site by approximately 10 to 1 (Bonduriansky & Brooks, 1999). Yet the males are still choosy

(Bonduriansky & Brooks, 1998b) because choosiness enables them to optimize the allocation of their reproductive resources. Similar systems occur in Coleoptera (e.g. *Brentis anchorago*, *Tetraopes tetraophthalmus*, *Harmonia axyridis*, *Tribolium castaneum*), Diptera (e.g. *Delia antiqua*, *Plecia nearctica*, *Cyrtodiopsis whitei*, *Drosophila* species, *Dryomyza anilis*, *Musca domestica*, *Scatophaga stercoraria*), Hemiptera (*Gerris* species), Mantodea (*Tenodera aridifolia*), Orthoptera (*Acheta domesticus*), and possibly Hymenoptera (e.g. *Lasioglossum* species, *Nomia triangulifera*, *Bembix rostrata*) and Lepidoptera (e.g. *Operophtera brumata*, *Pectinophora gossypiella*, *Agrotis segetum*, *Oiketicus kirbyi*, *Ostrinia nubilalis*). Thus, relative parental investment, potential rates of reproduction and operational sex ratios do not seem to account for the evolution of male choosiness in partially sex-role-reversed systems.

On the other hand, according to Parker (1983) and Gwynne (1991), large variance in female mate quality is expected to select for both choosiness and competitiveness in males, even in systems where males contribute little or no parental investment. For example, as noted above, a high degree of last-male sperm precedence will result in large differences in expected fertilization success with females bearing mature eggs (hence, ready to oviposit), and females bearing immature ovules (hence, likely to mate again before ovipositing). Thus, high last-male sperm precedence may result in large female mate quality variance, selecting for male discrimination against females with immature ovules. However, high last-male sperm precedence is also expected to select for intense agonistic competition to accomplish or prevent take-overs (Parker, 1974). In general, when variation in female mate quality is large, males may be selected to reject low-quality females and compete for access to high-quality females (Parker, 1983). Thus, large variance in female mate quality appears to explain the evolution of partial sex role reversal in many systems.

Hence, the empirical evidence reviewed here suggests that partial and complete sex role reversal do not generally represent different points along a continuum of increasing male parental investment and decreasing male reproductive rate. Changing ratios of parental investment and potential rates of reproduction represent one possible evolutionary pathway to choosiness. However, partial sex role reversal appears, in most cases, to have evolved primarily in response to large female mate quality variance. This diversity of evolutionary pathways to male choosiness is consistent with the three downstream factors included in the basic model – female

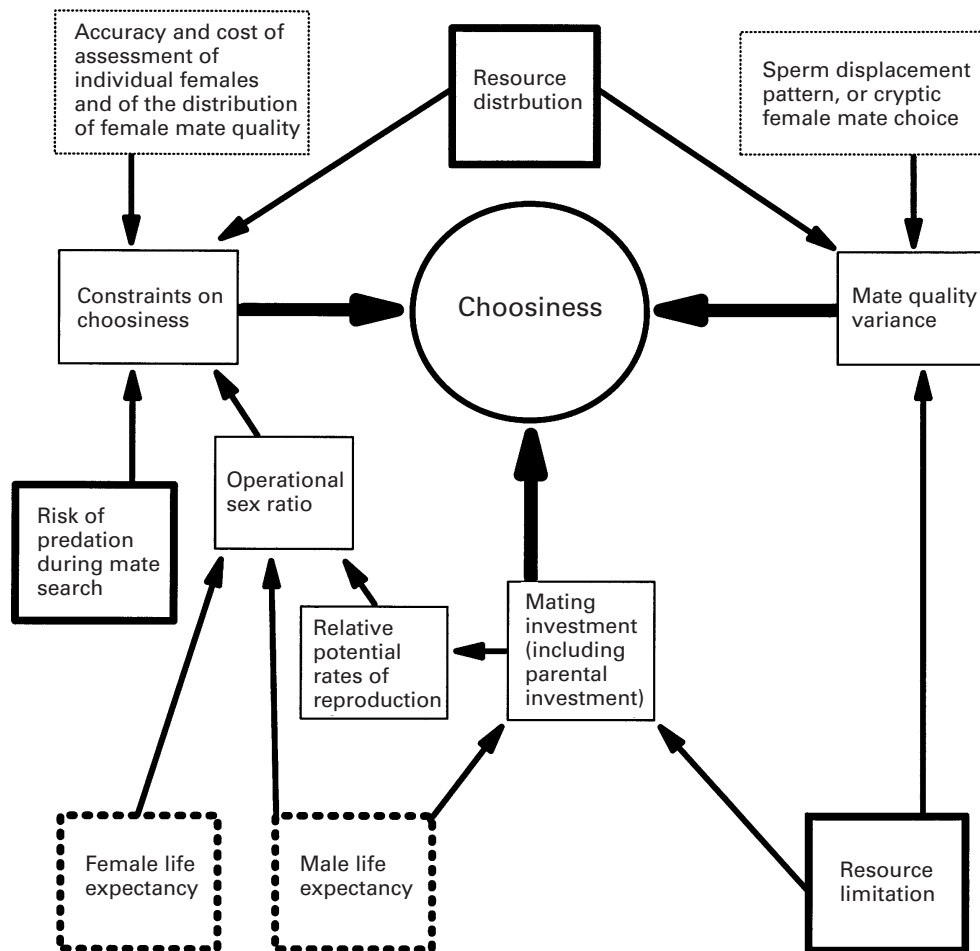


Fig. 4. Evolutionary pathways to male choosiness (see text for explanation). Thick solid boxes denote primarily environmental factors, thick dashed boxes denote life-history factors, thin dashed boxes represent primarily morphological or physiological factors, and thin solid boxes represent downstream factors associated with selection on choosiness.

mate quality variance, male mating investment, and constraints on choosiness (Fig. 4).

Furthermore, several upstream factors can be identified as key to the evolution of male choosiness (Fig. 4), although the complex interactions among them are likely to make prediction and explanation notoriously difficult. Two environmental factors, resource limitation and resource distribution, both temporal and spatial, are probably important in every system (Emlen & Oring, 1977; Gwynne, 1993). However, as the preceding discussion suggests, these factors do not predict choosiness in any straightforward way. For example, reduced 'clumping' of resources may increase male search costs (selecting for reduced choosiness), but also increase female mate quality variance (selecting for increased choosiness). Similarly, male and female life expectancy (a life-history trait) is likely to affect the cost of male mating investment and the operational sex ratio, although the net effect on male choosiness

is equally difficult to predict. For example, reduced life expectancy will increase costs of mating for males (selecting for increased choosiness), but also increase the search costs (selecting for reduced choosiness). In addition, several morphological/physiological factors, such as female-assessment mechanisms and patterns of sperm use or displacement, are likely to be important. The sensory mechanisms available to males (e.g. ability to detect female pheromones or chemical traces left by previous males, ability to inspect females visually from a distance, possession of tarsal chemoreceptors, etc.) may interact with key factors of female mate quality to facilitate or constrain the evolution of choosiness. For example, in systems where males locate females visually while in flight (e.g. some Lepidoptera and Diptera), males may be constrained to choose females based on traits that can be assessed visually from a distance, such as colour patterns (see Wiernasz, 1989, 1995), although these female traits may or may not reveal important

aspects of female mate quality. As well, the pattern of sperm displacement or the ability of females to exercise cryptic mate choice (i.e. to discriminate among ejaculates received from different males), may affect the variance in mate quality experienced by males. The study of mate choice evolution will have to confront such complexity to achieve a more robust theory of sex roles.

VII. COMPARATIVE CONSIDERATIONS: PARALLELS AND DIFFERENCES BETWEEN INSECTS AND OTHER ANIMALS

Male mate choice has been reported in a variety of taxa other than insects: the examples provided below represent a broad but incomplete survey of this literature. As noted above (see Section VI.4), cryptic male mate choice appears to occur in the spiny orbweaving spider *Micrathena gracilis* (Bukowski & Christenson, 2000). Considerable evidence of precopulatory male mate choice exists for crustaceans, including amphipods such as *Hyaella azteca* (Wen, 1993), *Corophium volutator* (Forbes *et al.*, 1996), *Gammarus lawrencianus* (Dunham, Alexander & Hurshman, 1986; Dunham & Hurshman, 1990) and *G. pulex* (Birkhead & Clarkson, 1980; Ward, 1984; Dick & Elwood, 1989), isopods such as *Thermosphaeroma thermophilum* (Shuster, 1981), *Idotea baltica* (Jormalainen, Merilata & Tuomi, 1994), and *Asellus aquaticus* (Manning, 1975; Thompson & Manning, 1981), and the parasitic copepod *Lernaocera branchialis* (Heuch & Schram, 1996). Evidence of male mate choice also exists for the acanthocephalan *Moniliformis moniliformis* (Lawlor *et al.*, 1990), the rotifer *Brachionis plicatilis* (Gómez & Serra, 1996), and the snail *Littorina littorea* (Erlandsson & Johannesson, 1994).

Among fishes, male mate choice has been reported in pipefishes such as *Syngnathus typhle* (Berglund, 1993, 1995; Sandvik, Rosenqvist & Berglund, 2000) and *Nerophis ophidion* (Rosenqvist, 1990), the damselfish *Stegastes leucosticus* (Itzkowitz *et al.*, 1998), the St. Peter's fish *Sarotherodon galilaeus* (Balshine-Earn, 1996), the Japanese medaka *Oryzias latipes* (Grant *et al.*, 1995), the sticklebacks *Gasterosteus aculeatus* (Rowland, 1982, 1989; Sargent, Gross & van den Berghe, 1986; Bakker & Rowland, 1995; Jenkins & Rowland, 1997) and *Culaea inconstans* (McLennan, 1995), the mollies *Poecilia latipinna* (Schlupp, Parzefall & Schartl, 1991; Schlupp & Ryan, 1997) and *Poeciliopsis lucida* (Keegan-Rogers, 1984), the convict cichlid *Cichlasoma nigrofasciatum* (Nuttall &

Keenleyside, 1993), the salmon *Oncorhynchus nerka* (Foote, 1988; Foote & Larkin, 1988) and *O. kisutch* (Sargent *et al.*, 1986), the redlip blenny *Ophioblennius atlanticus* (Côte & Hunte, 1989), and in the bluehead wrasse *Thalassoma bifasciatum* (van den Berghe & Warner, 1989). However, no male preference was detected in the orangethroat darter *Etheostoma spectabile* (Pyron, 1996). Among 'herptiles', male mate choice is known to occur in salamanders such as *Desmognathus fuscus* (Verrell, 1994) and *D. ochrophaeus* (Verrell, 1989), newts such as *Notophthalmus viridescens* (Verrell, 1982, 1985) and *Triturus vulgaris* (Verrell, 1986), possibly in frogs such as *Dendrobates auratus* (Wells, 1978), and in lizards such as *Platysaurus broadleyi* (Whiting & Bateman, 1999), *Lacerta agilis* (Olsson, 1993) and *Anolis sagrei* (Tokarz, 1992).

In birds, male mate choice has been reported in the bluethroat *Luscinia s. svecica* (Amundsen, Forsgren & Hansen, 1997; Hansen, Amundsen & Forsgren, 1999), the house sparrow *Passer domesticus* (Veiga, 1990), the house finch *Carpodacus mexicanus* (Hill, 1993), the zebra finch *Taeniopygia guttata* (Wynn & Price, 1993) the pinyon jay *Gymnorhinus cyanocephalus* (Johnson, 1988) and the phalarope *Phalaropus lobatus* (Whitfield, 1990). However, no male mate choice was detected in the pied flycatcher *Ficedula hypoleuca* (Dale & Slagsvold, 1994). Finally, in mammals, male mate choice has been reported in primates such as *Macaca* spp. (e.g. Herbert, 1968; Kuester & Paul, 1996; also see Keddy-Hector, 1992) and *Homo sapiens* (e.g. Wetsman & Marlowe, 1999), in ungulates such as *Ovus* sp. (e.g. Synnott, Fulkerson & Lindsay, 1981), in rodents such as the thirteen-lined ground squirrel *Spermophilus tridecemlineatus* (Schwagmeyer & Parker, 1990) and the mouse *Mus* sp. (Lenington, 1983; Yamazaki *et al.*, 1976; but see Eklund, Egid & Brown, 1991), and in the wolf *Canis lupus* (Rabb, 1967).

A comparison between insects and other taxa reveals a number of parallels in the nature of male mating preferences. Generally, in taxa where females produce relatively large and highly variable numbers of eggs (e.g. most 'invertebrates' and fish, some salamanders, newts and lizards), female body size predicts female fecundity (e.g. Ward, 1984; Verrell, 1989; Olsson, 1993; Wen, 1993; Lawlor *et al.*, 1990; Rosenqvist, 1990; Erlandsson & Johannesson, 1994; Grant *et al.*, 1995). Hence, as in insects, the most commonly observed male preference in these taxa is for large females (e.g. snails: Erlandsson & Johannesson, 1994; acanthocephalans: Lawlor *et al.*, 1990; crustaceans: Ward, 1984; Wen, 1993; fish: Rowland, 1982, 1989;

salamanders and newts: Verrell, 1982, 1985, 1989, 1994; lizards: Olsson, 1993). Conversely, in mammals and birds, where female fecundity is less variable and probably better predicted by other female traits (e.g. see Keddy-Hector, 1992; Kuester & Paul, 1996; Hansen *et al.*, 1999), males rarely exhibit preferences for large females (although see Wynn & Price, 1993). As in insects, males in a variety of taxa exhibit preferences for female traits (such as mating status or age) associated with reduced sperm competition (e.g. crustaceans: Heuch & Schram, 1996; mammals: Schwagmeyer & Parker, 1990; birds: Whitfield, 1990). Similarly, as in the beetle *Ips acuminatus* (Table 3), males discriminate against parthenogenetic or clonal females in other taxa where such females co-occur with sexual females (e.g. rotifers: Gómez & Serra, 1996; fish: Schlupp & Ryan, 1997; Keegan-Rogers, 1984). Preference for unfamiliar females, reported in anoles (Tokarz, 1992), may have evolved for similar reasons as preference for non-nestmate females in the bee *Lasioglossum zephyrum* (see Table 3 and Section VI.4). Thus, several types of male mating preferences observed in insects have also been reported in other animals. Moreover, two types of preference very commonly observed in insects (i.e. for large females and young or virgin females; see Section VI.4) also appear to be very widespread among other taxa.

However, some notable differences in male mating preferences are also apparent. For example, in many species of crustaceans, males exhibit strong preferences (expressed as differential probability of initiating precopulatory mate guarding) for females close to their pre-ovipositional moult (e.g. Manning, 1975; Birkhead & Clarkson, 1980; Shuster, 1981; Jormalainen *et al.*, 1994; Forbes *et al.*, 1996). This type of male mating behaviour and mate choice probably evolved because, in these species, females are able to copulate only during a brief interval after moulting (see Thompson & Manning, 1981; Yamamura, 1987). Thus, a female reproductive peculiarity of some crustaceans appears to have selected for a unique type of male mating preference in those species.

In a number of bird species, males choose females based on traits that are likely to reflect genetic quality as well as phenotypic condition (e.g. see Johnson, 1988; Hill, 1993; Wynn & Price, 1993; Amundsen *et al.*, 1997; Hansen *et al.*, 1999). For example, male bluethroats discriminate among females by both brightness of plumage and degree of symmetry (Amundsen *et al.*, 1997; Hansen *et al.*, 1999). By contrast, male preferences of this type

appear to be unusual in insects, although male mate choice based on female colouration occurs in some lepidopterans (see Table 3). Although the functions of female 'ornaments' in birds remain controversial (Amundsen, 2000), female genetic quality may be more important in male mate choice in birds because female birds are less variable in fecundity than female insects, and because long-term 'monogamous' associations are much more common in birds than in insects (see Section II.3). However, female phenotypic condition – reflected in female mass (e.g. Johnson, 1988; Wynn & Price, 1993), plumage brightness (e.g. Hill, 1993; Amundsen *et al.*, 1997) or symmetry (Hansen *et al.*, 1999) in birds, and in body size in insects (see Wilkinson & Taper, 1999) – appears to play an important role in male mate choice in both taxa.

Relatively strong evidence of male preferences for female genotypic traits associated with high offspring fitness exists in mice. For example, male mice may discriminate against females carrying certain major histocompatibility complex alleles, with the nature of the male preference apparently determined by the male's own genotype (Yamazaki *et al.*, 1976; but see Eklund *et al.*, 1991). Such choosy males may sire more disease-resistant offspring (Yamazaki *et al.*, 1976). Similarly, male mice discriminate against females carrying an allele that is lethal in homozygous offspring (Lenington, 1983). Male mate choice may be favoured in mice because of a combination of such indirect benefits and costly mating investment in ejaculates and mate guarding time (Lenington, 1983; also see Section III.4). A particularly interesting aspect of male mate choice in mice is that female mate quality is determined in part by an interaction with the male's own genotype. It is not clear how widespread such systems are, in comparison with systems where female mate quality is independent of the male.

Male mating preferences for socially dominant females, although not known in any insect, have been reported in some birds (e.g. Johnson, 1988) and in a number of mammals, including primates (e.g. Keddy-Hector, 1992), sheep (Synnott *et al.*, 1981) and wolves (e.g. Rabb, 1967). In primates, dominant (or 'high-ranking') females tend to produce more offspring (Keddy-Hector, 1992), or higher-ranking offspring (Kuester & Paul, 1996). Mating with a high-ranking female may also have a positive effect on the male's own social rank (Keddy-Hector, 1992). Evolution of this type of male mating preference, which involves individual recognition and long-term memory, is probably facilitated by highly developed

intelligence and associated with the complex social groups observed in many mammals.

Studies of male mate choice in fish have revealed a considerable scope for facultative modification of behaviour. For example, some male sailfin mollies are able to copy the mating preferences of other males (Schlupp & Ryan, 1997), whereas male pipefish reduce their level of choosiness in the presence of a predator (Berglund, 1993). Male sticklebacks become less choosy in response to negative reinforcement (Jenkins & Rowland, 1997) and can learn to ignore a female trait that is normally associated with receptivity but repeatedly fails to provide such information (Bakker & Rowland, 1995). Male sticklebacks of a different species increase their choosiness when they have eggs to guard and, hence, risk losing their brood (McLennan, 1995). Although some facultative responses have been reported in insects (see Section VI.1), it is not clear whether or not insects are capable of facultatively modifying their mate choice behaviour to the same extent as fish and (probably) other vertebrates.

VIII. SUMMARY AND CONCLUSIONS

I define male mate choice as differential male sexual response to different reproductively mature conspecific females. 'Precopulatory' male mate choice may be expressed as a discontinuous 'acceptance' threshold, or as variation in the frequency of courtship or copulation attempts or intensity of intra-sexual competition focused on females of varying mate quality. By contrast, 'cryptic' male mate choice represents differential allocation of copulatory or post-copulatory resources to females of varying mate quality.

According to theory, selection for male choosiness increases with variation in female quality from the male perspective ('mate quality variance'), and with the total costs of mating for males ('mating investment'). In most 'promiscuous' systems, the key determinant of female mate quality for males is expected to be fecundity, which determines a male's expected fertilization success from the mating. Female genetic quality may usually be less important, except in systems where males and females form long-term 'monogamous' associations. Variation in the intensity of sperm competition associated with different female phenotypes may also contribute to variation in female mate quality. Mating investment represents costs that reduce, with each

copulation, the number of subsequent copulations that a male can perform. When males experience costly mating investment, choosiness is expected to evolve as a strategy to optimize allocation of limited resources. Thus, even when males contribute little parental investment, other costs of mating investment can select for choosiness. On the other hand, choosiness is constrained by the costs of mate search and assessment (determined in part by the operational sex ratio), probably in combination with the accuracy of assessment of individual potential mates and of the demographic and spatial distribution of mate qualities.

Selection for male choosiness is expected to be strongest in systems where female fitness increases with each mating. This may occur when females receive direct benefits that accumulate with each mating ('cumulative benefits'). In such systems, males are expected to experience relatively large female mate quality variance and low search costs because females may solicit matings even when they are not fertile. Moreover, cumulative benefits for females, such as food gifts, may represent costly mating investment for males. Conversely, selection for male choosiness is expected to be weaker in systems where female fitness peaks at a small number of matings. In such systems, female mate quality variance is expected to be low, and search costs high, because females are likely to be unreceptive when not fertile. Male mating investment may usually be less costly as well, unless sperm competition selects for very large ejaculates.

Beyond a few species exhibiting complete sex role reversal, male mate choice has received relatively little attention in empirical and theoretical work. In spite of this, I found published evidence (or strong likelihood) of male mate choice in 58 insect species belonging to 37 families and 11 orders. Most of these studies are consistent with the theoretical framework outlined above. Some potential exceptions occur in species of Lepidoptera where males are choosy even though female mating rate appears to be very low, and search costs for males may be correspondingly high. Because the same factors that favour male mate choice in the systems reviewed here are also likely to operate in other species, families and orders, male mate choice is probably very common and widespread in insects. Male mate choice also appears to be widespread in other animals. Indeed, although based on the accumulated number of examples (e.g. see Jennions & Petrie, 1997) female mate choice may appear to be more common than male mate choice, this difference may reflect theory-based expectations

and the unequal research efforts devoted to these phenomena. Thus, it is not clear that the 'typical' sex roles defined by Darwin (1874) and Bateman (1948) are in fact characteristic of most species of insects (or other animals). In addition, the evidence compiled here certainly demonstrates the need to consider male mate choice as a potential confounding variable in studies of female mate choice.

Male insects assess female mate quality through visual, tactile or olfactory mechanisms. Some of the most commonly observed female-assessment behaviours, such as tapping, antennating or repeatedly mounting the female, may be easily mistaken for copulatory courtship. Thus, assessment of female mate quality represents an alternative hypothesis for the interpretation of male copulatory behaviours.

As predicted by theory, the male mating preferences most commonly observed in insects are for phenotypic indicators of fecundity (e.g. body size or abdomen width) or sperm competition intensity (e.g. insemination status or age). Other female traits assessed by choosy males in some insect species include female diet composition, nutritional status, colouration, pheromone blend, mode of reproduction (i.e. sexual *versus* clonal), and infection with the bacterium *Wolbachia* sp. In some species, males employ elaborate mate choice strategies involving both precopulatory and cryptic responses. Several observed types of male mating preferences may generate sexual selection on females. However, because the traits most commonly preferred by males (i.e. large female body size or relative abdomen width) are subject to strong fecundity and viability selection on females, and can be assessed directly by males through visual or tactile mechanisms, male mate choice tends to reinforce other (probably much stronger) selection vectors, and rarely selects for revealing displays in females. Two types of male preference commonly observed in insects (for large females and young or virgin females) are also widespread among other animals (although female body size may play a much smaller role in male mate choice in birds and mammals).

Experimental work on orthopterans has shown that complete sex role reversal (i.e. males choosy, females competitive) can occur when the costs of male parental investment are high enough to limit female reproductive success and reduce the potential rate of reproduction of males sufficiently to produce a female-biased operational sex ratio. However, male mate choice is much more commonly observed in systems exhibiting partial sex role reversal (i.e.

males choosy and competitive). In many partially sex-role-reversed systems, males contribute considerably less parental investment than females, have much higher potential rates of reproduction, and substantially outnumber females in the operational sex ratio. In such systems, male choosiness appears to have evolved in response to large female mate quality variance, which can select for both male choosiness and competitiveness, even in systems where males contribute little or no parental investment.

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