Review Paper

The evolution of mate choice and mating biases

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We review the current status of three well-established models (direct benefits, indirect benefits and sensory drive) and one newcomer (antagonistic chase-away) of the evolution of mate choice and the biases that are expressed during choice. We highlight the differences and commonalities in the underlying genetics and evolutionary dynamics of these models. We then argue that progress in understanding the evolution of mate choice is currently hampered by spurious distinctions among models and a misguided tendency to test the processes underlying each model as mutually exclusive alternatives. Finally, we suggest potentially fruitful directions for future theoretical and empirical research.

Keywords: mating preference; sexual conflict; direct and indirect benefits; Fisher process; good genes; sensory drive

1. INTRODUCTION

Mate choice is an important evolutionary process that imposes sexual selection on the other sex and accounts for spectacular ornaments that would otherwise remain unexplained by natural selection (Darwin 1871; Andersson 1994). How and why mate choice evolves has been vigorously debated for much of the history of evolutionary biology, and particularly so in the past 25 years (Kirkpatrick & Ryan 1991; Andersson 1994). Recently, the importance of mating biases other than conventional 'choice' has been recognized. First, females may resist mating *per se*, and copulate only with males that overcome female reluctance to mate (Holland & Rice 1998; Gavrilets *et al.* 2001). Second, female choice may be cryptic, occurring during or after mating, thereby generating a fertilization bias that favours certain males (Eberhard 1996; Tallamy *et al.* 2002). While most of this review draws on examples of pre-copulatory choice, most of the issues raised apply equally to the evolution of female fertilization biases.

We begin with a few notes on terminology. Preference and resistance are both terms for female *mating biases* that, when expressed, generate higher mating success for a subset of males. By definition, mate choice is the process leading to the tendency of members of one sex to mate non-randomly with respect to one or more varying traits in members of the other sex (Heisler *et al.* 1987). In this broad sense, mating biases that generate 'choice' require neither active sampling nor discrimination between potential mates, and may even involve passive acceptance of the first conspecific encountered (Parker 1983; Wiley & Poston 1996). Mating biases are detectable only when expressed, so we refer interchangeably to the evolution of mate choice, mating biases and mating preferences.

Recently, some authors have distinguished between female 'preference for' and female 'resistance to' male displays (e.g. Alexander *et al.* 1997; Holland & Rice 1998). Gavrilets *et al.* (2001) suggest that 'preference' applies only to cases where there is no direct selection on a mating bias. This is, however, inconsistent with conventional usage. Direct fecundity costs incurred by females that are too discriminating have long been a component of theoretical models of choice evolution (e.g. Pomiankowski 1988; Iwasa *et al.* 1991). 'Resistance' or 'reluctance' is favoured, however, if females suffer direct fitness costs from mating too frequently (e.g. Parker 1979; Thornhill 1980; Blanckenhorn *et al.* 2002). Both types of cost impose direct selection on mating biases. Such selection, together with direct and indirect selection due to the benefits conferred by males, results in female discrimination between males, which in turn generates non-random variation in male mating success. While the terms 'preference' and 'resistance' may be used following the conventions of the current literature, they are logically interchangeable, as both refer to the effort that females make to 'screen' potential mates. To emphasize this we use 'mating bias' to cover both terms.

As a final terminological note, we use 'sexy sons' in the wide sense to refer to any situation where females gain fitness benefits through attractive, or seductive, male offspring. This term has also been used to describe a specific hypothesis where the production of attractive sons is at the cost of lower fecundity (Weatherhead & Robertson 1979). While it is important to examine the costs of preferences

Proc. R. Soc. Lond. B (2003) **270**, 653–664
DOI 10.1098/rspb.2002.2235

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to understand the mating system, it appears more natural to be allowed to speak about sexy-son benefits whenever such benefits exist, regardless of the costs that choice might incur.

(a) *Direct and indirect selection on mating preferences*

The two ways that natural selection can effect change in any trait, female mating biases included, are direct and indirect selection. Direct selection occurs when the trait itself confers an increase in fitness. A female's mating biases are favoured by direct selection if they increase her own lifetime reproductive output. Direct selection favours mating biases (in the sense of 'preferences') toward males that are more fertile, provide superior resources, offer more parental care or otherwise reduce the female's current reproductive costs (Heywood 1989). Recent research on sexual conflict (differences between male and female interests) indicates that female mating biases (in the sense of 'resistance') can also be favoured by direct selection because excess mating reduces female longevity (for a review see Arnqvist & Nilsson (2000)) and males vary in the survival costs they impose on females (Pitnick & García-González 2002). Additionally, costs associated with the possession and/or expression of a mating bias (e.g. energetic costs of sampling or refusing to mate and lost breeding opportunities caused by rejecting potential mates) will, in the absence of the aforementioned benefits, lead to direct selection against mating biases (Bulmer 1989), or select for context-dependent modification (e.g. Rowe *et al.* 1994; Qvarnström *et al.* 2000).

Indirect selection occurs when there is direct selection on a trait that is genetically correlated with the focal trait. For example, in guppies (*Poecilia reticulata*) there are negative and positive genetic correlations among traits such as tail size and brightness of orange spots associated with male attractiveness. Although direct selection favours exaggeration of all traits, the indirect selection that results from the pattern of covariation among traits (half the genetic correlations between traits are negative) appears to prevent substantial evolutionary change in each (Brooks & Endler 2001). In general terms, indirect selection on a focal trait when a genetically correlated trait is under direct selection is a function of the strength of direct selection, the magnitude and direction of the genetic correlation between the two traits and the ability to inherit the directly selected trait.

Female mating biases may evolve by indirect selection when natural selection directly favours a correlated trait such as fecundity, longevity or male attractiveness. Genetic correlations between female mating biases, attractiveness and other fitness components are thus an important and measurable element of indirect selection on mate choice. Genetic correlations may result from a common genetic basis (pleiotropy), physical linkage or a statistical association between alleles underlying choice and those underlying other fitness components (linkage disequilibrium). An example of pleiotropy occurs in fiddler crabs, where the genes that cause female crabs to orientate towards vertical structures as a fitness-enhancing anti-predator response, also generate a mating bias for males that construct mud pillars by their burrows (Christy *et al.* 2002). Associations between alleles for mating biases and those for fitness components arise in the offspring of females who express a bias and thus mate with males that signal their genetic 'quality' (Fisher 1930; Lande 1981). While physical linkage may influence linkage disequilibrium (e.g. Gilburn & Day 1996, 1999), it is not necessary for the disequilibrium to arise. Linkage disequilibrium without physical linkage is sometimes referred to as gametic-phase disequilibrium. Examples of genetic correlations between mating biases and preferred male traits caused by linkage disequilibrium have been reported in sticklebacks (Bakker 1993), *Drosophila* (Blows 1999), guppies (Houde 1994; Brooks & Couldridge 1999), the cricket *Gryllus integer* (Gray & Cade 1999) and the moth *Utetheisa ornatrix* (Iyengar *et al.* 2002).

We review the four main models of mate-choice evolution paying particular attention to their underlying evolutionary genetics. These models are: direct benefits, indirect benefits, sensory drive and sexually antagonistic coevolution ('chase-away').

(b) *Direct benefits*

The historically least controversial models of mating-bias evolution cite direct ('material') benefits to mate choice (e.g. Heywood 1989; Hoelzer 1989; Kirkpatrick 1996; Iwasa & Pomiankowski 1999). These models are non-controversial for two reasons. First, they are conceptually simple as they invoke only direct selection. Females that exhibit a mating bias either obtain a direct fecundity benefit or ameliorate a cost, and this alone favours the bias. Second, for females to benefit from mate choice there must be detectable differences among males in the benefits they offer or the costs they impose (e.g. Pitnick & García-González 2002). The maintenance of variation among males in the direct benefits they provide is more easily understood than the maintenance of detectable variation in genetic quality (indirect benefits; see § 1c). Stochastic environmental variation alone can readily generate differences in the direct benefits that individual males offer females. For example, unpredictable variation in food availability may result in some males being in better condition to assist in rearing offspring than others.

(c) *Indirect benefits*

Although choice for direct benefits conferred by males is common, research on mate choice has concentrated heavily on species where direct benefits appear to be absent. In these cases less straightforward models are required to explain mate choice. Chief among these explanations is the indirect-benefit model, which descends directly from a verbal argument published by R. A. Fisher (1930). Fitter males, and the females who preferentially mate with them, will have offspring that inherit the genes for both fitness and the mating preference. The resulting linkage disequilibrium between preference genes and male fitness favours the spread and elaboration of the preference by indirect selection. Fisher's insight, that the increased importance of attractiveness as a component of male fitness can then drive the exaggeration of a male trait that signals fitness beyond its otherwise naturally selected optimum, has come to be known as the 'Fisherian runaway' process. It is this component of Fisher's model that first attracted the attention of theorists. Notably, in 1981,

Lande formally demonstrated that a positive genetic correlation between mate choice and an attractive signal is an inevitable consequence of mate choice if there is additive genetic variation in both choosiness and the signal.

As Fisher's model became synonymous with the runaway process, biologists rediscovered the importance of the first component of Fisher's model: that females should prefer more vigorous and long-lived males, and that attractiveness might therefore indicate viability (Zahavi 1975; Jennions *et al.* 2001). This precipitated the polarization of Fisher's runaway process from the so-called 'good-genes' hypothesis. A dichotomy arose between Fisherian runaway, thought to be driven solely by the benefits of mating with 'arbitrarily' attractive males to produce sexy sons, and the 'good-genes' process, in which evolution of mate choice occurs because attractive males have higher breeding values for longevity and fecundity. In an influential review, Kirkpatrick & Ryan (1991) pointed out that because preferences necessarily become correlated with male traits when both have a heritable genetic basis, runaways ('sexy son' benefits) should be regarded as an integral component of any realistic indirect-benefit model. Nevertheless, the dichotomous view is still reflected in papers attempting to distinguish between preferences for 'arbitrary' traits and preferences for traits that indicate some component of offspring viability. For example, it has been suggested that when female choice is based on a single male trait this trait is less likely to be 'arbitrary' than when female choice is for several traits (Møller & Pomiankowski 1993).

Recently, Eshel *et al.* (2000) and Kokko *et al.* (2002) have emphasized the point that attractive male signals always function as indicators of whatever other fitness components they are genetically correlated with. Fisher's (1930) original model hinged on the fact that indirect selection on mating biases results from a genetic correlation between the bias and total offspring fitness, which includes any 'sexy son' benefit present as a result of the inheritance of the attractive signal. Genes that are 'good' in that they enable sons to achieve high mating success are conceptually no different from genes that primarily enhance offspring survival. The key questions that remain are how these genes influence the life-history trade-off between survival and reproductive investment for sons and daughters (Kokko 1997, 2001; Höglund & Sheldon 1998; Badyaev & Qvarnström 2002), whether they have similar or opposing effects on the fitnesses of sons and daughters (Chippindale *et al.* 2001) and how sufficient variation in male signals of fitness can be maintained despite the depleting action of directional selection (Hamilton & Zuk 1982; Rowe & Houle 1996; Kotiaho *et al.* 2001). The strength and direction of genetic correlations will influence the ease with which preferences initially evolve. If a male trait is initially negatively correlated with viability, a preference somehow has to cross an invasion barrier, where it is selected against before it can spread further (Payne & Pagel 2000). As there is no critical distinction between the erstwhile 'Fisherian runaway' and 'good-genes' processes, we suggest that the use of 'the Fisher-Zahavi model' by Eshel *et al.* (2000) be adopted to describe the process of mating-bias evolution by indirect benefits.

(d) *Sensory drive*

Selection operating directly on the psychosensory system in contexts other than mate choice may either maintain or drive changes in mating biases. Mate choice may thus evolve 'exaptively' to some extent by a process known variously as sensory drive, sensory exploitation, pre-existing bias or sensory traps (Endler & Basolo 1998). For example, across some populations of guppies the strength of attraction to orange objects in a non-mating context explains 94% of the inter-population variation in female mating preferences for orange male ornaments (Rodd *et al.* 2002). Thus, female sensitivity to orange-coloured food items may be at least as important to the evolution of female mating preferences for males with large orange spots as any direct and indirect benefits that more-orange males deliver to their mates.

Sensory drive may do more than offer a quirky exaptive alternative for how mate choice and mating biases evolve. It may provide the initial 'nudge' often required to initiate choice–display coevolution (Arak & Enquist 1995; Payne & Pagel 2000). If males are not advertising, females are unable to choose; and it does not pay males to advertise unless females are choosing. Something needs to happen to make females choose and thereby make it worthwhile for males to display. The magnitude of this 'something' is described by the barriers to invasion of mating biases in game-theory models such as Kokko *et al.* (2002). The 'nudge' may be provided when females incidentally respond to a male trait that is correlated with heritable fitness. Alternatively, even very subtle mating biases that arise as a result of selection on the sensory system in another context may make it worthwhile for males to advertise, thereby starting coevolutionary cycles of sexual selection on male display and runaway indirect selection on female choice (Payne & Pagel 2000).

All sensory systems have biases, and mating biases are therefore inevitable (Kirkpatrick & Ryan 1991; Arak & Enquist 1995). Even when a male trait has evolved to 'exploit' a pre-existing sensory bias, indirect selection on the female preference may occur owing to the benefits accruing from the production of more-attractive sons. Such a signal may potentially then become secondarily genetically correlated with other fitness-enhancing traits. In fiddler crabs, for example, mud pillars built by males near their burrows appear to increase male mating success because they invoke a female anti-predator response (Christy *et al.* 2002). The ability to build mud structures is, however, condition dependent, suggesting that choosy females will receive additional indirect benefits if condition is heritable (Backwell *et al.* 1995).

(e) *Sexually antagonistic coevolution*

Evidence for sexually antagonistic genes, which benefit one sex but harm the other, has accumulated rapidly in recent years (Rice 1992, 1996; Holland & Rice 1999; Chippindale *et al.* 2001). Sexual antagonism can influence a choosy female's fitness in two important ways. First, the optimal expression of a trait may differ between the sexes. For example, humans show greater sexual dimorphism in hip width than other primates. This may have arisen because there is strong selection on females for wider hips, to reduce mortality during childbirth, while wider hips reduce male fitness because they decrease running

efficiency (Rice & Chippindale 2001). When optima differ between the sexes, sex-limited expression of traits is expected to evolve, but such evolution can be slow (Lande 1980; Rhen 2000). Therefore, females may often have to trade off good performance in sons with poor performance in daughters, an *indirect* cost of sexual antagonism. In *Drosophila*, for example, adult performance is negatively genetically correlated, but juvenile performance is positively genetically correlated, between males and females (Chippindale *et al.* 2001). There is thus no net genetic correlation between male and female fitnesses. Thus, a female choosing to mate with a 'good' male will, on average, produce average daughters (Chippindale *et al.* 2001).

Second, whenever mating partners are not strictly monogamous, a male benefits from enhancing his paternity or the current reproductive rate of his mate, even at the expense of lowering her lifetime reproductive output. Examples of such *direct* costs of sexually antagonistic evolution include toxic seminal products in *Drosophila* that shorten female lifespan (Chapman *et al.* 1995; Civetta & Clark 2000), physical genital damage in bean weevils (Crudgington & Siva-Jothy 2000) energetic and predation costs of mating and sexual harassment in dung flies (Mühlhäuser & Blankenhorn 2002) and mortality resulting from male harassment in feral sheep (Reale *et al.* 1996).

Holland & Rice (1998) provided a conceptual synthesis of such findings by presenting the 'chase-away' model as an alternative framework for understanding the evolution of mating biases. According to this hypothesis, accepting superfluous matings is a fundamentally maladaptive response to antagonistic 'seduction' by males. Evolution is expected to strengthen female resistance to male traits, while a coevolutionary response in males continually leads to the development of new 'seductive' traits to overcome female resistance.

It has been argued that the chase-away model does not differ from direct-benefits models for the evolution of female choice, in which females benefit from accepting or rejecting a subset of males that differ in the benefits they offer or the costs they impose (Rosenthal & Servedio 1999; Getty 1999; Rice & Holland 1999). The effort males make to induce females to mate is the 'why' behind male ornament evolution. It follows that resistance to males that provide weak stimuli is conceptually no different from a preference for males with strong stimuli.

Cordero & Eberhard (2003) have recently elaborated on Parker's original point (Parker 1979) that if male ability to manipulate females is heritable, there will be indirect benefits to females that prefer more-manipulative males (see Kirkpatrick & Ryan 1991; Keller & Reeve 1995; Rowe & Houle 1996; Andrés & Morrow 2003). As with direct benefits and sensory drive, the ubiquity and inevitability of indirect selection is a crucial factor generally overlooked in discussions of the evolution of female resistance. We believe that the field has become unnecessarily divided. Those studying sexual antagonism have focused on direct costs only, while those interested in the genetic benefits of female choice have tended to ignore the fact that mating *per se* may be costly to females. Indicative of such thinking, Gavrilets *et al.* (2001) noted: 'female mate choice may result from females evolving to avoid direct costs [...] rather than to gain some indirect benefits' (p.

531). However, because indirect benefits arise automatically when male traits are heritable, direct and indirect benefits must be taken into account equally in both sexually antagonistic coevolution and conventional female-choice scenarios. In § 2d we sketch a model that addresses both types of cost.

2. THEORETICAL AND EMPIRICAL CHALLENGES

To maximize the potential usefulness of this review to workers in the field we conclude by identifying and briefly discussing what are, in our opinion, some important outstanding issues and potential avenues for future research.

(a) *Female choice for indirect benefits*

A vast amount of modelling effort and empirical work has explored indirect selection within the 'Fisher versus good-genes' paradigm. Although it has been conceptually useful to model one process in the artificially induced absence of the other (see Grafen (1990) for a classic example), we believe that a more inclusive understanding of indirect selection on mate choice is now required. We have already stressed that indirect selection favours mate choice when females choose males with high breeding values for total fitness, irrespective of the relative contributions of viability, attractiveness, fecundity and other fitness components. We believe that this challenges the widespread view that certain male sexual displays are functionally designed to signal specific components of male viability (e.g. immunocompetence or developmental stability). Given the range of fitness components, or indicators thereof, routinely examined by researchers (e.g. dominance, immunocompetence, survivorship, parasite load, swimming speed, body size, etc.), it is no surprise that some fitness components are positively correlated with the expression of specific sexual traits. It is inappropriate for researchers to argue *post hoc* that a trait is designed to signal the specific component of fitness that they happen to have measured. Studies that delve into the mechanistic, physiological or ecological bases of trade-offs are required before we can assess how narrowly signals indicate specific fitness components. In principle, we would expect signals of specific fitness components only if a specific resource were used for these components, so that the allocation does not interact with other aspects of condition.

Despite the large amount of empirical work on indirect benefits of mate choice, an astonishing fact remains: the fundamental prediction that mating preferences increase net offspring fitness in species where direct benefits to mate choice can be excluded has not been empirically tested. We have data showing that mating with an attractive male increases specific components of offspring fitness (e.g. Norris 1993; Petrie 1994; Sheldon *et al.* 1997; Welch *et al.* 1998; Møller & Alatalo 1999; Wedell & Tregenza 1999; Brooks 2000; Hine *et al.* 2002), and that in some cases this comes at the expense of other fitness components (Wedell & Tregenza 1999; Brooks 2000; Hine *et al.* 2002), but after two decades of work there is still no study showing that mean offspring fitness is elevated.

Genetic representation in distant future generations is the key parameter, so a reasonable goal is to compare the number of grandchildren produced by females assigned

attractive and unattractive males (or allowed to choose a mate or assigned one at random). Boake (1985) and Reynolds & Gross (1992) did just this, but their experimental designs excluded the key variable of differences in sons' mating success. Clearly, it is a substantial challenge to calculate the production of grandchildren, but now that molecular techniques to assign ancestry are widely available and more affordable it should be possible to do so.

Although the work we have reviewed thus far should extinguish any vestiges of a 'Fisher versus good-genes controversy', a unified Fisher–Zahavi indirect-benefits model should not stifle interest in studying mate-choice evolution. By analogy, life-history studies provide a unifying theory of the full diversity of reproductive schedules, based on a few simple trade-offs. In the same way that it is fruitful to ask why mammals and birds tend to be iteroparous when a general life-history model predicts iteroparity or semelparity from the same set of trade-offs, it is worthwhile asking why small positive correlations between attractiveness and viability appear to be the norm (Møller & Alatalo 1999; Jennions *et al.* 2001) when a general model of sexual selection can generate preferences for traits that either reduce or enhance offspring viability.

(b) *The paradox of the lek*

If females are to derive an indirect benefit from a mating bias, there must be detectable variation among males in signals that indicate fitness. How such variation arises and persists when we expect favoured alleles to be rapidly fixed by the parallel action of natural selection and sexual selection is the 'paradox of the lek' (Borgia 1979; Taylor & Williams 1982). The maintenance of additive genetic variation in fitness is a more general paradox and a source of much angst in genetics (Barton & Turelli 1989). Fortunately, the question of why there is additive genetic variation in fitness, and in male attractiveness, is peripheral to the question of how females derive indirect benefits from mating biases. It is an empirical fact that such variation exists (Burt 1995; Bakker 1999).

Theory demonstrates that mate choice evolves in similar ways, irrespective of how variations in male fitness and attractiveness arise. Models that assume that male attractiveness itself mutates (e.g. Pomiankowski *et al.* 1991; 'constrained display' model of Kokko *et al.* (2002)) allow for the evolution of costly mate choice equally as well as models where attractiveness is condition dependent, and condition is heritable and subject to mutation (e.g. Iwasa *et al.* 1991; Houle & Kondrashov 2002; 'evolvable display' model of Kokko *et al.* (2002)). The ease with which mating biases become established, however, depends on how much males vary in fitness, and the genetic architecture will dictate how easily variation is expressed and maintained. Thus, a fuller understanding of the processes maintaining additive genetic variation remains an important priority for the field. This is a dynamic and fast-evolving research area that merits its own review. However, recent proposals suggest that condition dependence (Rowe & Houle 1996; Wilkinson & Taper 1999), genotype-by-environment interaction (Lesna & Sabelis 1999; Kotiaho *et al.* 2001) and sexually antagonistic effects (Chippindale *et al.* 2001) may show particular promise as general explanations.

The recent focus on condition dependence of male displays is particularly welcome. Single male signals and minor fitness components may be under the influence of relatively few loci. The large number of loci influencing overall condition may, by contrast, provide a large mutational target and thus harbour additive genetic variation more easily (Rowe & Houle 1996).

Condition dependence complements an emerging understanding that male sexual signals are expressed as a product of genotype-by-environment interaction. Male attractiveness is not absolute but depends on genotypic quality in a particular environmental context. Consequently, the direction and strength of sexual selection may vary between environments and fluctuate over time, slowing or even preventing the loss of genetic variation caused by selection.

Understanding genetic architecture also provides interesting possibilities for solving the lek paradox. For example, heterosis in conjunction with genotype-by-environment interactions (hybrids are fitter in only some circumstances) and context-dependent female choice in soil mites provides a novel, but perhaps widespread, explanation for the maintenance of female choice for genetic benefits (Lesna & Sabelis 1999). Another example is provided by genetic hitch-hiking of deleterious genes with attractiveness genes on the Y sex chromosome of guppies (Brooks 2000). Viability-reducing mutations can accumulate rapidly if they are partly 'protected' by physical linkage with attractiveness genes.

(c) *The genetics of male attractiveness and female mate choice*

We still know remarkably little about the genetic basis of mate choice (Bakker 1999). This is especially relevant to indirect selection that requires genetic correlations between mating biases, preferred male signals and overall fitness. Substantial opportunities exist for empiricists willing to study the quantitative genetics of mating biases. For example, we know almost nothing about the relative contribution of sex-linked and autosomal genes to female mate choice, despite the fact that sex linkage may considerably favour the accumulation of genes underlying mate choice rapid accumulation—especially in species with ZZ/ZW sex determination (Iyengar *et al.* 2002).

We also know very little about the process by which genetic covariation between mate choice and fitness evolves within populations. There is only a single experimental demonstration of the build-up of a genetic correlation between female preference and male display (Blows 1999), a handful of estimates of genetic correlations between female choice and male signal (Bakker 1993; Gray & Cade 1999; Iyengar *et al.* 2002), and a few artificial selection experiments that have formally shown that sexual selection on male signals results in preference evolution as a result of genetic correlations (e.g. Houde 1994; Wilkinson & Reillo 1994; Brooks & Couldridge 1999). More glaringly, there is only a single study that shows a significant positive genetic correlation between female preference and a measure of offspring performance (Hine *et al.* 2002). Interestingly, this study also revealed that male attractiveness is negatively genetically correlated with productivity (a measure incorporating fecundity and offspring survival), and suggested that female choice is under

stabilizing selection. Important insights into the process of mate-choice evolution will reward those who invest time and effort in careful studies of the quantitative genetics of female choice, male attractiveness and offspring fitness.

When estimating the heritability of male signals and genetic correlations with female mating biases there are a few simple messages from recent theory and experiments. First, allocation of resources to attractiveness may vary with male age (Kokko 1997, 1998*a*). One prediction is therefore that the genetic basis of variation in attractiveness can change as a cohort ages, so attractiveness at one age may be weakly or even negatively genetically correlated with attractiveness at another (Hansen & Price 1995; Brooks & Kemp 2001). It follows that sexual traits must be measured at comparable life stages to obtain sensible estimates of heritability. For example, if sons of high-quality males invest less in attractiveness when young than do low-quality males' sons (e.g. Candolin 2000), the estimate of heritability or, for that matter, the genetic correlation between choosiness and attractiveness will change depending on the age at which offspring attractiveness is measured. More importantly, estimating genetic correlations between measures of attractiveness at different ages will allow an assessment of the usefulness of instantaneous 'snapshots' of male attractiveness relative to lifetime measures of attractiveness. Such snapshots are useful only if attractivenesses at different ages are positively genetically correlated.

Second, additive genetic variance in fitness is often measured using lifetime reproductive success (e.g. number of offspring or, when partially taking offspring value into account, the number of fledglings or yearlings produced) (e.g. Kruuk *et al.* 2000; Merilä & Sheldon 2000). Unfortunately, this is an inadequate measure because it fails to take into consideration offspring breeding value (Brommer *et al.* 2002). For example, if multiple mating reduces female fecundity, this does not mean that it is selected against if sons of multiply mated females have greater fitness than those of singly mated females (e.g. Bernasconi & Keller 2001). This is not reflected in studies measuring lifetime reproductive success, even when the measure of reproductive success is 'number of offspring reaching maturity'. Specifically, producing 'sexy sons' (or 'choosy daughters') can increase the genetic contribution to future generations and outweigh any immediate decline in offspring production. In short, the counter-intuitive possibility exists that females with lower than average lifetime reproductive success may actually be fitter.

(d) Costs of mate choice: costs of mating

The costs of searching for and discriminating among males (costs of being choosy) and the costs of mating too often (costs of not being choosy enough) are issues of significant importance in the evolution of choice. This is particularly true in the context of the antagonistic chase-away models of choice evolution. There are considerable challenges ahead in measuring these costs and their evolutionary consequences. We briefly review these challenges and try to reconcile these two very different types of cost within a single framework.

If female choice is cost free, even minuscule benefits will select for it and the evolution of exaggerated male sexual signals follows (Lande 1981). It has taken much longer

to build a theory of mate choice when choice is costly (e.g. Iwasa *et al.* 1991; Pomiankowski *et al.* 1991; Houle & Kondrashov 2002). It is difficult to conceive that females could exhibit a mating bias, especially if it involves mate sampling, without suffering some costs in terms of lower fecundity or longevity (Pomiankowski 1988). At equilibrium, however, expression of these costs can be exceedingly small (Kokko *et al.* 2002), which may be one reason why the costs of mate choice are notoriously difficult to demonstrate, let alone quantify.

Measuring the costs of choice is an important empirical gap that presents an opportunity for the creative empiricist. In the models of Kokko *et al.* (2002), the net benefit of being choosy, and thus the equilibrium level of choosiness, is determined by the rate at which the costs of choice increase with increasing effort of choice. The net cost of choosiness therefore determines the trade-offs between male attractiveness and other fitness components, and the equilibrium point along the 'sexual selection continuum'. Varying the costs of being choosy presents an excellent opportunity to test how mate choice evolves and how males resolve the trade-off between current signalling and residual reproductive value. Small changes in the costs of exercising a mating bias can alter female mate-choice decisions (e.g. Milinski & Bakker 1992). This suggests that even moderate heritability of male signals creates possibilities to set up laboratory environments where only minor environmental modifications may result in differences in male trait expression within a few generations.

The costs of mating are a key parameter of the sexually antagonistic or chase-away model with its emphasis on sexual conflict (Holland & Rice 1998). Indiscriminate mating by females can incur direct costs, which can be avoided or reduced by increased choosiness. This has rarely been considered in conventional models of female preference evolution. Under sexual conflict with direct costs, female reproductive success is a hump-shaped function of her mating rate (Gavrilets *et al.* 2001). Therefore, the direct cost—roughly the inverse of the female's fecundity—is a U-shaped function of the effort that females expend screening males. Low screening effort leads to maladaptively frequent mating, whereas too high an effort leads to infertility, or is, by itself, costly (for example, Holland & Rice (1998) discuss a hypothetical case where strong resistance to a male colour patch leads to viability costs resulting from negative pleiotropic effects on foraging efficiency). However, many female choice models simply assume costs are either absent or increase with female choosiness.

In figure 1, we have modified the model of Kokko *et al.* (2002) to include the costs of sexual antagonism. These costs can be direct (parameter d; absence of cost $d = 0$ indicated by asterisks) and/or indirect (figure 1*a*, no indirect costs of mating with attractive or 'seductive' males; figure 1*b*, indirect antagonistic viability cost to male or female offspring; figure 1*c*, indirect antagonistic viability cost to both male and female offspring). The parameter d modifies the female fecundity function from that of Kokko *et al.* (2002) by introducing a direct cost of mating too indiscriminately. When $d = 1$, indiscriminately mating females have zero reproductive success, while at $d = 0$, the cost disappears, resulting in the constrained dis-
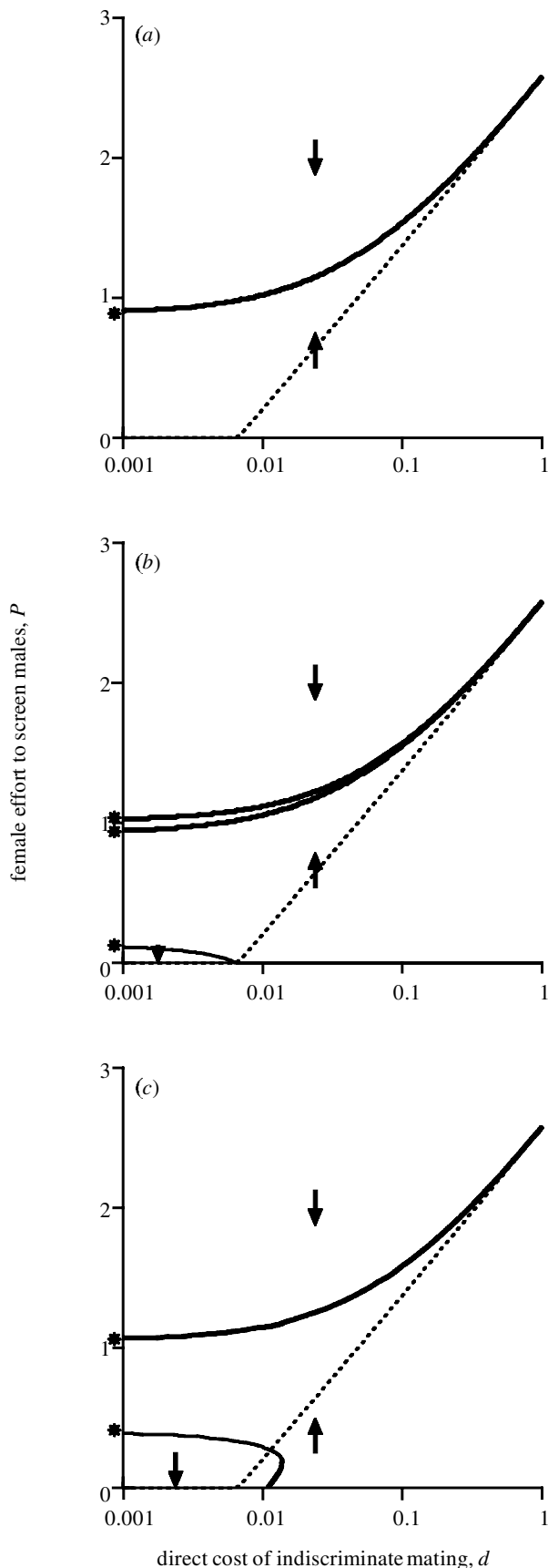
Figure 1. Predictions for female preference P (solid lines), i.e. the evolutionarily stable effort with which females screen males, in the constrained display model of Kokko *et al.* (2002), with male trait values $T_1 = 1$ and $T_2 = 0$, mutation rates between male types $m_1 = 0.05$ and $m_2 = 0.01$, and costliness of choice $E = 0.2$ (see Kokko *et al.* (2002) for details of the model). Additionally, we modify the female fecundity function of Kokko *et al.* (2002) to become $F(P) = (1 - d\exp(-P))(1 - (1 + \exp(-(P - E^{-1}))))^{-1}$, where d measures the cost of mating indiscriminately; $d = 0$ characterizes the conventional female choice scenario of Kokko *et al.* (2002), and increasing d corresponds to stronger sexual conflict over mating. Also, we allow the trait to influence daughters' viability (mortalities μ_{F1}, μ_{F2}) as well as sons' (μ_{M1}, μ_{M2}). The dotted lines indicate the value of P that minimizes the direct cost of mating. (*a*) T, the male trait that specifies 'attractiveness or manipulative ability' of the male, correlates positively with survival of male and female offspring: $\mu_{F1} = \mu_{M1} = 0.9$, $\mu_{F2} = \mu_{M2} = 1$. (*b*) Upper solid curve: T correlates positively with male but negatively with female offspring survival: $\mu_{F2} = \mu_{M1} = 0.9$, $\mu_{F1} = \mu_{M2} = 1$. Lower solid curve: T correlates positively with female but negatively with male offspring survival: $\mu_{F1} = \mu_{M2} = 0.9$, $\mu_{F2} = \mu_{M1} = 1$. (*c*) T correlates negatively with offspring survival in both sexes: $\mu_{F2} = \mu_{M2} = 0.9$, $\mu_{F1} = \mu_{M1} = 1$. Thin lines indicate invasion barriers, and arrows indicate the direction in which the preference (or resistance) evolves. The solutions for $d = 0$ (outside the logarithmic axis) are indicated by asterisks. In (*c*) there is a region with two equilibria, and initial preferences determine which one will be reached.

($d = 0$) and is gradually replaced by stronger female preferences for attractive males ($T = 1$) or, equivalently, more pronounced resistance against less attractive males ($T = 0$), as d increases (figure 1).

Two points merit attention. First, the direct cost of indiscriminate mating can remove invasion barriers that otherwise have to be crossed before female choice evolves. The invasion barrier is the intensity of female preference that must exist for male signals to evolve and female preferences to persist. This invasion barrier is wider if attractive males sire offspring of poor viability (figure 1*c*), and absent if the trait covaries positively with survival (figure 1*a*). Thus, sexual conflict can be a powerful force initiating female preference evolution if such a preference is initially absent.

Second, at equilibrium, females always show stronger preferences than would be predicted if they simply minimized the direct costs of mating (compare solid with dotted lines in figure 1). This is because this model automatically takes into account the 'sexy son' benefit of passing on genes for high mating success of males (Cordero & Eberhard 2003; figure 1), hitherto largely ignored in models of sexually antagonistic coevolution (although Gavrilets *et al.* (2001) mention this possibility in their appendix).

The theory of sexually antagonistic coevolution harbours two additional assumptions that differ from conventional female choice. First, in the antagonistic scenario, females in the ancestral state are assumed to respond initially to a male trait and then evolve to be less responsive. The opposite is true in the conventional female

play model of conventional female choice in Kokko *et al.* (2002).

Clearly, we predict a 'continuum' where conventional female choice occurs when there is no sexual conflict

choice model. One simple interpretation is that the equilibria of figure 1 can be approached from either below or above the line. The equilibria reached are the same, except for a curious case with multiple equilibria (figure 1c with d slightly exceeding 0.01) that warrants further study. Second, antagonistic scenarios assume a continuous supply of novel mutations that allow males to overcome the current level of female resistance. New mutations are then needed for females to 'catch up'. So far, modelling has not explicitly dealt with this assumption, although the framework of Gavrilets et al. (2001) can be interpreted in this way if open-ended evolution along a single axis is taken to mean the continuous supply of new mutations.

(e) *Equilibria or runaways?*

In quantitative genetic models of mating biases, two main results commonly appear. Coevolution of preferences and male traits can stop at equilibrium (or, in models of cost-free female choice, a line of alternative equilibria), or such equilibrium can be unstable, in which case models predict open-ended evolution away from the equilibrium. Some authors (Hall et al. 2000) explicitly focus on deriving conditions for open-ended runaways, and place less emphasis on finding the position of an evolutionary equilibrium.

The biological merits of equilibrium versus 'open-ended' evolution models need to be assessed. In our view, an open-ended runaway might be a dissatisfying theoretical construction. Whenever it occurs, authors are quick to note that further exaggeration of the trait will eventually grind to a halt as a result of natural selection or depletion of genetic variation (Lande 1981). The interpretation of this assertion is problematic because the model does not track what happens at this stage of evolution. Being vague about the endpoints of open-ended runaways is not a trivial concern. Models that are explicit about long-term trait exaggeration can even predict population extinction (Houle & Kondrashov 2002). By contrast, stable equilibria indicate evolutionary endpoints that persist over time and thereby characterize outcomes likely to be seen in nature. Contrasting with Hall et al. (2000), we encourage the study of locations of stable equilibria. Whether these occur where female mating biases simply minimize direct costs to females, or whether coevolution can shift the equilibrium to a point where females expend additional effort to gain indirect benefits, is a key question in the study of mate choice. Where equilibria turn out to be unstable, we strongly recommend incorporating assumptions that allow tracking of the eventual endpoint of evolution (or identify stable limit cycles; Iwasa & Pomiankowski 1995; Houle & Kondrashov 2002). Replacing the abstract fitness formulations of some quantitative genetics models with costs that have an explicit biological interpretation (e.g. female fecundity declines and eventually approaches zero as her mate-choice effort increases; Kokko et al. 2002), appears to replace open-ended runaways with more easily interpretable stable equilibria (figure 1). On the empirical front, the approach by Hine et al. (2002) allows the examination of whether female preferences are under stabilizing selection. We thus recommend both empirical and theoretical work on this issue.

(f) *The relative importance of direct and indirect selection in mating-bias evolution*

Another subject ripe for testing is the assertion that indirect selection on mate choice is a weak evolutionary force relative to direct selection (Kirkpatrick 1996; Kirkpatrick & Barton 1997; but see Houle & Kondrashov 2002). Such statements of relative strength should not, however, be taken to imply that one process (in this case indirect selection) is of little evolutionary importance. This would be true only if direct and indirect selection were usually opposed but, as we have repeatedly pointed out, direct selection may lead to indirect benefits if the offspring of chosen males inherit the ability to deliver direct benefits (e.g. heritable body size and seminal nutrient/chemical defence contributions made by males of the moth *Utetheisa ornatrix*; Iyengar & Eisner 1999; Iyengar et al. 2002). Thus indirect selection may enhance, and certainly accelerate, the evolution of mate choice for direct benefits. Even when direct and indirect benefits are apparently opposed, indirect selection may be stronger than direct selection. For example, in several bird species females clearly prefer males offering reduced direct benefits (less parental care) (for a review see Møller & Jennions (2001)). There is no evidence that other direct benefits compensate for this reduced parental care. The relative strength and the relative evolutionary importance of direct and indirect benefits of mate choice present an open opportunity for original empirical contributions.

Most of what we know about indirect benefits comes from species lacking obvious direct benefits to mate choice. Studying indirect benefits in lek-breeding species makes for simpler interpretation, but indirect benefits are expected to be important at some time in the evolution of all mating biases (Kirkpatrick & Ryan 1991; Cordero & Eberhard 2003). Few studies have attempted to investigate direct and indirect benefits and their possible interactions simultaneously (for notable exceptions, see Jones et al. 1998; Gilburn & Day 1999; Iyengar & Eisner 1999). The fact that males can potentially vary more in direct than in indirect benefits does not mean that signals of direct benefits are more reliable or more exaggerated (Kokko 1998b).

Although direct benefits favour the evolution of mating biases for males that increase female reproductive success, and males may vary widely in the benefits they can provide, exaggeration of signals of direct benefits may be modest. The marginal gains from increased investment in signals soon diminish if there is an upper limit to male mating success. For example, with obligate male parental care polygyny is constrained and most variation in male reproductive success is the result of differences in female fecundity or quality (Kokko 1998b; Morley & Balshine 2002). If male mating opportunities increase, this will often erode honest signalling of care (Kokko 1998b, 1999) as the benefits of mate desertion outweigh those of continuing to provide care. Modellers must therefore consider how mating rate influences the direct benefits males provide. Another question is whether the evolution of exaggerated male signals reduces the direct benefits being advertised (Price et al. 1993; Fitzpatrick et al. 1995). Surprisingly few studies have adequately examined the relationship between male attractiveness and direct benefits. This is challenging because assortative mating, genetic

effects and differential allocation of resources by females obscure the direct benefits males offer.

(g) *The interaction between sexual and natural selection*

If females choose to mate with males bearing high breeding values for fitness (as in the Fisher–Zahavi model), then sexual selection is likely to be a major contributor to adaptive evolutionary change. Recent theoretical studies have shown that sexual selection can accelerate the spread of beneficial mutations (Proulx 1999; Whitlock 2000) and contribute to the shedding of genetic load (Agrawal 2001; Siller 2001). Moreover, Blows (2002) has demonstrated that, in *Drosophila,* cuticular hydrocarbons evolve significantly faster when natural selection and sexual selection are both allowed to act than when either process occurs alone.

Darwin (1871) originally proposed sexual selection (and its agents: female choice and male–male competition) to explain the evolution of seemingly maladaptive male displays and weapons. The time has come, however, for us to consider seriously the more general role of sexual selection in adaptive evolution. This may lead to interesting insights about population-level and species-level phenomena including the maintenance of sex (Agrawal 2001; Siller 2001) and species-specific mortality rates (Moore & Wilson 2002), which may affect the likelihood of extinction (see the review by Kokko & Brooks (2003)).

(h) *Post-copulatory female resistance?*

In the sexual-antagonism model female 'resistance' evolves because it reduces the naturally selected cost of mating. It therefore functions prior to copulation. However, pre-copulatory female resistance, rather than failing to prevent mating, can change the identity of the male mating. This is better described as a cryptic mating preference (e.g. female primates incite competition among males by giving copulatory calls; Semple 1998). In some cases, such as females trying to evade males, it is unclear whether this behaviour reduces mating costs, or increases indirect benefits by selecting for persistent males. This simply reiterates the point that female 'resistance' may confer both direct and indirect benefits.

The concept of female 'resistance' has also been used in the post-copulatory context of increasing the difficulty of fertilization (Birkhead *et al.* 1993). This is also better described as a cryptic preference because the process serves only to bias fertilization towards a subset of males, and the only benefits of biasing paternity are indirect genetic ones. As with any mating preference driven by indirect benefits, this process can generate a positive-feedback loop leading to increased post-copulatory selectivity until halted by natural selection. Strictly speaking, there could be direct selection on female post-copulatory resistance if it reduces polyspermy that lowers fertilization success (Eberhard 1996).

3. SUMMARY

In conclusion, we believe that mate-choice research has continually generated false dichotomies: Fisherian versus 'good-genes'; 'resistance' versus 'preference'; direct versus indirect benefits models. In practice, even mating biases

that evolve because preferred males provide greater direct benefits, or because a naturally selected sensory bias has a pleiotropic effect on mate choice, end up producing indirect benefits because males almost always vary in their ability to produce attractive signals. Indirect benefits arise because choosy females acquire genes for their offspring that increase net fitness through any possible mixture of increased mating success, fecundity and survival in sons and/or daughters. The key goals for the future are therefore to document the magnitude of key parameters (e.g. genetic correlations, intensity of selection on mating biases, additive genetic variation in mating biases, preferred male traits and net fitness) and to find general patterns to see whether there are repeatable differences in these across taxa or ecological contexts.

REFERENCES

Agrawal, A. F. 2001 Sexual selection and the maintenance of sexual reproduction. *Nature* **411,** 692–695.

Alexander, R. D., Marshall, D. C. & Cooley, J. R. 1997 Evolutionary perspectives on insect mating. In *Mating systems in insects and arachnids* (ed. J. C. Choe & B. J. Crespi), pp. 4–31. Cambridge University Press.

Andersson, M. 1994 *Sexual selection*. Princeton University Press.

Andrés, J. A. & Morrow, E. H. 2003 The origin of interlocus sexual conflict: is sex-linkage important? *J. Evol. Biol.* (In the press.)

Arak, A. & Enquist, M. 1995 Conflict, receiver bias and the evolution of signal form. *Phil. Trans. R. Soc. Lond.* B **349,** 337–344.

Arnqvist, G. & Nilsson, T. 2000 The evolution of polyandry: multiple mating and female fitness in insects. *Anim. Behav.* **60,** 145–164.

Backwell, P. R. Y., Jennions, M. D., Christy, J. H. & Shuber, U. 1995 Pillar building in the fiddler crab *Uca beebei*: evidence for a condition-dependent ornament. *Behav. Ecol. Sociobiol.* **36,** 185–192.

Badyaev, A. V. & Qvarnström, A. 2002 Putting sexual traits into the context of an organism: a life-history perspective in studies of sexual selection. *Auk* **119,** 301–310.

Bakker, T. C. M. 1993 Positive genetic correlation between female preference and preferred male ornament in sticklebacks. *Nature* **363,** 255–257.

Bakker, T. C. M. 1999 The study of intersexual selection using quantitative genetics. *Behaviour* **136,** 1237–1266.

Barton, N. H. & Turelli, M. 1989 Evolutionary quantitative genetics: how little do we know? *A. Rev. Genet.* **23,** 337–370.

Bernasconi, G. & Keller, L. 2001 Female polyandry affects their sons' reproductive success in the red flour beetle *Tribolium castaneum*. *J. Evol. Biol.* **14,** 186–193.

Birkhead, T. R., Møller, A. P. & Sutherland, W. J. 1993 Why do females make it so difficult for males to fertilize their eggs? *J. Theor. Biol.* **161,** 51–60.

Blanckenhorn, W. U., Hosken, D. J., Martin, O. Y., Reim, C., Teuschl, Y. & Ward, P. I. 2002 The costs of copulating in the dung fly *Sepsis cynipsea*. *Behav. Ecol.* **13,** 353–358.

Blows, M. W. 1999 Evolution of the genetic covariance between male and female components of mate recognition: an experimental test. *Proc. R. Soc. Lond.* B **266**, 2169–2174. (DOI 10.1098/rspb.1999.0904.)

Blows, M. W. 2002 Interaction between natural and sexual selection during the evolution of mate recognition. *Proc. R. Soc. Lond.* B **269**, 1113–1118. (DOI 10.1098/rspb.2002. 2002.)

Boake, C. B. 1985 Genetic consequences of mate choice: a quantitative genetic method for testing sexual selection theory. *Science* **227**, 1061–1063.

Borgia, G. 1979 Sexual selection and the evolution of mating systems. In *Sexual selection and reproductive competition in insects* (ed. M. S. Blum & N. A. Blum), pp. 19–80. New York: Academic Press.

Brommer, J. E., Merilä, J. & Kokko, H. 2002 Reproductive timing and individual fitness. *Ecol. Lett.* **5**, 802–810.

Brooks, R. 2000 Negative genetic correlation between male sexual attractiveness and survival. *Nature* **406**, 67–70.

Brooks, R. & Couldridge, V. 1999 Multiple sexual ornaments coevolve with multiple mating preferences. *Am. Nat.* **154**, 37–45.

Brooks, R. & Endler, J. A. 2001 Direct and indirect selection and quantitative genetics of male traits in guppies (*Poecilia reticulata*). *Evolution* **55**, 1002–1015.

Brooks, R. & Kemp, D. J. 2001 Can older males deliver the good genes? *Trends Ecol. Evol.* **16**, 308–313.

Bulmer, M. G. 1989 Structural instability of models of sexual selection. *Theor. Popul. Biol.* **35**, 195–206.

Burt, A. 1995 Perspective: the evolution of fitness. *Evolution* **49**, 1–8.

Candolin, U. 2000 Changes in expression and honesty of sexual signalling over the reproductive lifetime of sticklebacks. *Proc. R. Soc. Lond.* B **267**, 2425–2430. (DOI 10.1098/rspb. 2000.1301.)

Chapman, T., Liddle, L. F., Kalb, J. M., Wolfner, M. F. & Partridge, L. 1995 Cost of mating in *Drosophila melanogaster* females is mediated by male accessory-gland products. *Nature* **373**, 241–244.

Chippindale, A. K., Gibson, J. R. & Rice, W. R. 2001 Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in *Drosophila*. *Proc. Natl Acad. Sci. USA* **98**, 1671–1675.

Christy, J. H., Backwell, P. R. Y., Goshima, S. & Kreuter, T. 2002 Sexual selection for structure building by courting male fiddler crabs: an experimental study of behavioral mechanisms. *Behav. Ecol.* **13**, 366–374.

Civetta, A. & Clark, A. G. 2000 Correlated effects of sperm competition and post-mating female mortality. *Proc. Natl Acad. Sci. USA* **97**, 13 162–13 165.

Cordero, C. & Eberhard, W. G. 2003 Female choice of sexually antagonistic male adaptations: a critical review of some current research. *J. Evol. Biol.* **16**, 1–6.

Crudgington, H. S. & Siva-Jothy, M. T. 2000 Genital damage, kicking and early death: the battle of the sexes takes a sinister turn in the bean weevil. *Nature* **407**, 855–856.

Darwin, C. 1871 *The descent of man and selection in relation to sex*. London: Murray.

Eberhard, W. 1996 *Female control: sexual selection by cryptic female choice*. Princeton University Press.

Endler, J. A. & Basolo, A. 1998 Sensory ecology, receiver biases and sexual selection. *Trends Ecol. Evol.* **13**, 415–420.

Eshel, I., Volovik, I. & Sansone, E. 2000 On Fisher–Zahavi's handicapped sexy son. *Evol. Ecol. Res.* **2**, 509–523.

Fisher, R. A. 1930 *The genetical theory of natural selection*. Oxford: Clarendon Press.

Fitzpatrick, S., Berglund, A. & Rosenqvist, G. 1995 Ornaments or offspring: costs to reproductive success restrict sexual selection processes. *Biol. J. Linn. Soc.* **55**, 251–260.

Gavrilets, S., Arnqvist, G. & Friberg, U. 2001 The evolution of female mate choice by sexual conflict. *Proc. R. Soc. Lond.* B **268**, 531–539. (DOI 10.1098/rspb.2000.1382.)

Getty, T. 1999 Chase-away sexual selection as noisy reliable signaling. *Evolution* **53**, 299–302.

Gilburn, A. S. & Day, T. H. 1996 The evolution of female choice when the preference and the preferred trait are linked to the same inversion system. *Heredity* **76**, 19–27.

Gilburn, A. S. & Day, T. H. 1999 Female mating behaviour, sexual selection and chromosome I inversion karyotype in the seaweed fly, *Coelopa frigida*. *Heredity* **82**, 276–281.

Grafen, A. 1990 Biological signals as handicaps. *J. Theor. Biol.* **144**, 517–546.

Gray, D. A. & Cade, W. H. 1999 Quantitative genetics of sexual selection in the field cricket, *Gryllus integer*. *Evolution* **53**, 848–854.

Hall, D. W., Kirkpatrick, M. & West, B. 2000 Runaway sexual selection when female preferences are directly selected. *Evolution* **54**, 1862–1869.

Hamilton, W. D. & Zuk, M. 1982 Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387.

Hansen, T. F. & Price, D. K. 1995 Good genes and old age: do old mates provide superior genes? *J. Evol. Biol.* **8**, 759–778.

Heisler, I. L. (and 11 others) 1987 The evolution of mating preferences and sexually selected traits: group report. In *Sexual selection: testing the alternatives* (ed. J. W. Bradbury & M. B. Andersson), pp. 96–118. Chichester: Wiley.

Heywood, J. S. 1989 Sexual selection by the handicap mechanism. *Evolution* **43**, 1387–1397.

Hine, E., Lachish, S., Higgie, M. & Blows, M. W. 2002 Positive genetic correlation between female preference and offspring fitness. *Proc. R. Soc. Lond.* B **269**, 2215–2219. (DOI: 10.1098/rspb.2002.2149.)

Hoelzer, G. A. 1989 The good parent process of sexual selection. *Anim. Behav.* **38**, 1067–1078.

Höglund, J. & Sheldon, B. C. 1998 The cost of reproduction and sexual selection. *Oikos* **83**, 478–483.

Holland, B. & Rice, W. R. 1998 Chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* **52**, 1–7.

Holland, B. & Rice, W. R. 1999 Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc. Natl Acad. Sci. USA* **96**, 5083–5088.

Houde, A. E. 1994 Effect of artificial selection on male colour patterns on mating preference of female guppies. *Proc. R. Soc. Lond.* B **256**, 125–130.

Houle, D. & Kondrashov, A. S. 2002 Coevolution of costly mate choice and condition-dependent display of good genes. *Proc. R. Soc. Lond.* B **269**, 97–104. (DOI 10.1098/rspb.2001. 1823.)

Iwasa, Y. & Pomiankowski, A. 1995 A continual change in mate preferences. *Nature* **377**, 420–422.

Iwasa, Y. & Pomiankowski, A. 1999 A good parent and good genes models of handicap evolution. *J. Theor. Biol.* **200**, 97–109.

Iwasa, Y., Pomiankowski, A. & Nee, S. 1991 The evolution of costly mate preferences. II. The handicap principle. *Evolution* **45**, 1431–1442.

Iyengar, V. K. & Eisner, T. 1999 Heritability of body mass, a sexually selected trait, in an arctiid moth (*Utetheisa ornatrix*). *Proc. Natl Acad. Sci. USA* **96**, 9169–9171.

Iyengar, V. K., Reeve, H. K. & Eisner, T. 2002 Paternal inheritance of a female moth's mating preference: consequences for sexual selection. *Nature* **419**, 830–832.

Jennions, M. D., Møller, A. P. & Petrie, M. 2001 Sexually selected traits and adult survival: a meta-analysis. *Q. Rev. Biol.* **76**, 3–36.

Jones, T. M., Quinnell, R. J. & Balmford, A. 1998 Fisherian flies: benefits of female choice in a lekking sandfly. *Proc. R. Soc. Lond.* B **265**, 1651–1657. (DOI 10.1098/rspb.1998.0484.)

Keller, L. & Reeve, H. K. 1995 Why do females mate with multiple males? The sexually selected sperm hypothesis. *Adv. Study Behav.* **24**, 291–315.

Kirkpatrick, M. 1996 Good genes and direct selection in the evolution of mating preferences. *Evolution* **50**, 2125–2140.

Kirkpatrick, M. & Barton, N. H. 1997 The strength of indirect selection on female mating preferences. *Proc. Natl Acad. Sci. USA* **94**, 1282–1286.

Kirkpatrick, M. & Ryan, M. J. 1991 The evolution of mating preferences and the paradox of the lek. *Nature* **350**, 33–38.

Kokko, H. 1997 Evolutionarily stable strategies of age-dependent sexual advertisement. *Behav. Ecol. Sociobiol.* **41**, 99–107.

Kokko, H. 1998a Good genes, old age and life-history trade-offs. *Evol. Ecol.* **12**, 739–750.

Kokko, H. 1998b Should advertising parental care be honest? *Proc. R. Soc. Lond.* B **265**, 1871–1878. (DOI 10.1098/rspb.1998.0515.)

Kokko, H. 1999 Cuckoldry and the stability of biparental care. *Ecol. Lett.* **2**, 247–255.

Kokko, H. 2001 Fisherian and 'good genes' benefits of mate choice: how (not) to distinguish between them. *Ecol. Lett.* **4**, 322–326.

Kokko, H. & Brooks, R. 2003 Sexy to die for? Sexual selection and the risk of extinction. *Ann. Zool. Fennici* (In the press.)

Kokko, H., Brooks, R., McNamara, J. M. & Houston, A. I. 2002 The sexual selection continuum. *Proc. R. Soc. Lond.* B **269**, 1331–1340. (DOI 10.1098/rspb.2002.2020.)

Kotiaho, J. S., Simmons, L. W. & Tomkins, J. L. 2001 Towards a resolution of the lek paradox. *Nature* **410**, 684–686.

Kruuk, L. E. B., Clutton-Brock, T. H., Slate, J., Pemberton, J. M., Brotherstone, S. & Guinness, F. E. 2000 Heritability of fitness in a wild mammal population. *Proc. Natl Acad. Sci. USA* **97**, 698–703.

Lande, R. 1980 Sexual dimorphism, sexual selection and adaptation in polygenic characters. *Evolution* **34**, 292–305.

Lande, R. 1981 Models of speciation by sexual selection on polygenic traits. *Proc. Natl Acad. Sci. USA* **78**, 3721–3725.

Lesna, I. & Sabelis, M. W. 1999 Diet-dependent female choice for males with 'good genes' in a soil predatory mite. *Nature* **401**, 581–584.

Merilä, J. & Sheldon, B. C. 2000 Lifetime reproductive success and heritability in nature. *Am. Nat.* **155**, 301–310.

Milinski, M. & Bakker, T. C. M. 1992 Costs influence sequential mate choice in stickleback *Gasterosteus aculeatus*. *Proc. R. Soc. Lond.* B **250**, 229–233.

Møller, A. P. & Alatalo, R. V. 1999 Good-genes effects in sexual selection. *Proc. R. Soc. Lond.* B **266**, 85–91. (DOI 10.1098/rspb.1999.0607.)

Møller, A. P. & Jennions, M. D. 2001 How important are direct fitness benefits of sexual selection? *Naturwissenschaften* **88**, 401–415.

Møller, A. P. & Pomiankowski, A. 1993 Why have birds got multiple sexual ornaments? *Behav. Ecol. Sociobiol.* **32**, 167–176.

Moore, S. L. & Wilson, K. 2002 Parasites as a viability cost of sexual selection in natural populations of mammals. *Science* **297**, 2015–2018.

Morley, J. I. & Balshine, S. 2002 Faithful fish: territory and mate defence favour monogamy in an African cichlid fish. *Behav. Ecol. Sociobiol.* **52**, 326–331.

Mühlhäuser, C. & Blankenhorn, W. U. 2002 The costs of avoiding matings in the dung fly *Sepsis cynipsea*. *Behav. Ecol.* **13**, 359–365.

Norris, K. J. 1993 Heritable variation in a plumage indicator of viability in male great tits *Parus major*. *Nature* **362**, 537–539.

Parker, G. A. 1979 Sexual selection and sexual conflict. In *Sexual selection and reproductive competition in insects* (ed. M. S. Blum & N. A. Blum), pp. 123–166. New York: Academic Press.

Parker, G. A. 1983 Mate quality and mating decisions. In *Mate choice* (ed. P. Bateson), pp. 141–166. Cambridge University Press.

Payne, R. J. H. & Pagel, M. 2000 Inferring the origins of state-dependent courtship traits. *Am. Nat.* **157**, 42–50.

Petrie, M. 1994 Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* **371**, 598–599.

Pitnick, S. & García-González, F. 2002 Harm to females increases with male body size in *Drosophila melanogaster*. *Proc. R. Soc. Lond.* B **269**, 1821–1828. (DOI 10.1098/rspb.2002.2090.)

Pomiankowski, A. 1988 The evolution of female mating preferences for male genetic quality. *Oxf. Surv. Evol. Biol.* **5**, 136–184.

Pomiankowski, A., Iwasa, Y. & Nee, S. 1991 The evolution of costly mate preferences. I. Fisher and biased mutation. *Evolution* **45**, 1422–1430.

Price, T. D., Schluter, D. & Heckman, N. E. 1993 Sexual selection when the female benefits directly. *Biol. J. Linn. Soc.* **48**, 187–211.

Proulx, S. 1999 Mating systems and the evolution of niche breadth. *Am. Nat.* **154**, 89–98.

Qvarnström, A., Pärt, T. & Sheldon, B. C. 2000 Adaptive plasticity in mate preference linked to differences in reproductive effort. *Nature* **405**, 344–347.

Reale, D., Bousses, P. & Chapuis, J. L. 1996 Female-biased mortality induced by male sexual harassment in a feral sheep population. *Can. J. Zool.* **74**, 1812–1818.

Reynolds, J. D. & Gross, M. R. 1992 Female mate preference enhances offspring growth and reproduction in a fish, *Poecilia reticulata*. *Proc. R. Soc. Lond.* B **250**, 57–62.

Rhen, T. 2000 Sex-limited mutations and the evolution of sexual dimorphism. *Evolution* **54**, 37–43.

Rice, W. R. 1992 Sexually antagonistic genes: experimental evidence. *Science* **256**, 1436–1439.

Rice, W. R. 1996 Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature* **381**, 232–234.

Rice, W. R. & Chippindale, A. K. 2001 Intersexual ontogenetic conflict. *J. Evol. Biol.* **14**, 685–693.

Rice, W. R. & Holland, B. 1999 Reply to comments on the chase-away model of sexual selection. *Evolution* **53**, 302–306.

Rodd, F. H., Hughes, K. A., Grether, G. F. & Baril, C. T. 2002 A possible non-sexual origin of a mate preference: are male guppies mimicking fruit? *Proc. R. Soc. Lond.* B **269**, 475–481. (DOI 10.1098/rspb.2001.1891.)

Rosenthal, G. G. & Servedio, M. R. 1999 Chase-away sexual selection: resistance to 'resistance'. *Evolution* **53**, 296–299.

Rowe, L. & Houle, D. 1996 The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. Lond.* B **263**, 1415–1421.

Rowe, L., Arnqvist, G., Sih, A. & Krupa, J. 1994 Sexual conflict and the evolutionary ecology of mating patterns—water striders as a model system. *Trends Ecol. Evol.* **9**, 289–293.

Semple, S. 1998 The function of Barbary macaque copulation calls. *Proc. R. Soc. Lond.* B **265**, 287–291. (DOI 10.1098/rspb.1998.0294.)

Sheldon, B. C., Merilä, J., Qvarnström, A., Gustafsson, L. & Ellegren, H. 1997 Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. *Proc. R. Soc. Lond.* B **264**, 297–302. (DOI 10.1098/rspb.1997.0042.)

Siller, S. 2001 Sexual selection and the maintenance of sex. *Nature* **411**, 689–692.

Tallamy, D. W., Powell, B. E. & McClafferty, J. A. 2002 Male traits under cryptic female choice in the spotted cucumber beetle (Coleoptera: Chrysomelidae). *Behav. Ecol.* **13**, 511–518.

Taylor, P. D. & Williams, G. C. 1982 The lek paradox is not resolved. *Theor. Popul. Biol.* **22**, 392–409.

Thornhill, R. 1980 Rape in *Panorpa* scorpionflies and a general rape hypothesis. *Anim. Behav.* **28**, 52–59.

Weatherhead, P. J. & Robertson, R. J. 1979 Offspring quality and the polygyny threshold: 'the sexy son hypothesis'. *Am. Nat.* **113**, 201–208.

Wedell, N. & Tregenza, T. 1999 Successful fathers sire successful sons. *Evolution* **53**, 620–625.

Welch, A. M., Semlitsch, R. D. & Gerhardt, H. C. 1998 Call duration as an indicator of genetic quality in male gray tree frog. *Science* **280**, 1928–1930.

Whitlock, M. C. 2000 Fixation of new alleles and the extinction of small populations: drift load, beneficial alleles, and sexual selection. *Evolution* **54**, 1855–1861.

Wiley, R. H. & Poston, J. 1996 Perspective: indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution* **50**, 1371–1381.

Wilkinson, G. S. & Reillo, P. R. 1994 Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. *Proc. R. Soc. Lond.* B **255**, 1–6.

Wilkinson, G. S. & Taper, M. 1999 Evolution of genetic variation for condition-dependent traits in stalk-eyed flies. *Proc. R. Soc. Lond.* B **266**, 1685–1690. (DOI 10.1098/rspb.1999.0832.)

Zahavi, A. 1975 Mate selection: a selection for a handicap. *J. Theor. Biol.* **53**, 205–214.