

The evolution and significance of male mate choice

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The distinct reproductive roles of males and females, which for many years were characterised in terms of competitive males and choosy females, have remained a central focus of sexual selection since Darwin's time. Increasing evidence now shows that males can be choosy too, even in apparently unexpected situations, such as under polygyny or in the absence of male parental care. Here, we provide a synthesis of the theory on male mate choice and examine the factors that promote or constrain its evolution. We also discuss the evolutionary significance of male mate choice and the contrasts in male versus female mate choice. We conclude that mate choice by males is potentially widespread and has a distinct role in how mating systems evolve.

The evolution of male mate choice: males can be choosy too

Sexual selection can occur whenever there is non-random mating and/or fertilisation, and results from mate choice or intrasexual competition for mates [1]. The evolutionary significance of sexual selection is firmly established, but there has been a resurgence of interest over recent decades based upon: (i) the recognition of the evolutionary importance of sexual selection that occurs after mating [2,3]; (ii) the lability of sex roles and of mate choice; and (iii) the novel opportunities for selection arising from sexual conflict [4,5].

A dominant perspective has been one of indiscriminate males competing for the attention of choosy females [6,7]. Much research has therefore focused on describing the roles and importance of male–male competition and female mate choice in driving evolutionary change [1]. However, it has become increasingly clear that male and female sex roles can be dynamic and variable. ‘Reversed’ sex roles, with male mate choice and female–female competition, were first identified in species in which females compete for access to males that contribute paternal care [8]. However, male mate choice has also been observed in species in which males do not make a significant contribution to offspring care [9–11].

As in females, mate choice by males can occur either before or after mating. Examples of post-mating male mate choice are discussed in [Box 1](#). Pre-mating male preferences can be exerted by either rejecting or accepting courting females [12] or by choosing to court some females over others [13]. However, choice can also be exerted through increased intensity of courtship or increased male–male

aggression in competitions for preferred females [14,15]. This can make the relative contributions of male mate choice, female mate choice and male–male competition difficult to disentangle.

It was originally proposed that the sex that is most likely to exhibit mate choice could be determined by differences between males and females in parental investment [16]. However, it is now realised that male mate choice can evolve under a wider range of circumstances than predicted by parental investment alone (e.g. [17–20]). An appreciation for the wider significance of male mate choice and sexual selection in females [21–23] and a reappraisal of ‘sex roles’ [21] is now leading to renewed interest and novel research directions in the study of sexual selection.

In this review, we provide a synthesis of theory and discuss factors that promote the evolution of male mate choice. We also discuss the relative importance of male mate choice in evolution.

Synthesis of the theory for the evolution of male mate choice

Mate choice occurs when the effects of traits expressed in one sex lead to nonrandom matings, fertilisations or reproductive investment with specific individuals of the opposite sex [24,25]. Hence, mate choice comprises not only decisions about whether to mate, but also how many resources to allocate to each mate or mating. A key factor in the evolution of male mate choice is the relationship between the number of receptive females that are available to an individual male for mating (hereafter ‘mate availability’) and his capacity to mate with such females (‘capacity to mate’) ([Figure 1](#)). This is because males will inevitably reject available females if they lack the resources required to mate with them. It is for this reason that male mate choice is more likely to evolve when females are encountered simultaneously rather than sequentially [26]. The relationship between the availability of mates and the capacity of a male to mate with the females available to him was originally predicted from the level of parental investment (i.e. ‘any investment by the parent that increases the offspring's chance of surviving’ [16]) exhibited by males versus females [16]. This influences both the operational sex ratio (OSR, the ratio of sexually active males to females; [27]) and the potential reproductive rate (PRR) of each sex [28,29] (see *Parental investment, the OSR and PRR*). However, it is now clear that to predict the occurrence of mate choice accurately, mating effort (i.e. resources invested by a male resulting in an increased number of females available for mating) should also be

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Box 1. Post-copulatory male mate choice

An emerging field of study is post-copulatory male mate choice. Examples include the strategic allocation of ejaculates by males in response to a female trait or to the level of sperm competition [36] and the differential allocation of parental care [64]. Post-copulatory male mate choice could occur in response to assessment by males of traits such as fecundity [65,66], genetic compatibility [45], relatedness [67] or female mating status [40]. Post-copulatory male mate choice occurring through differential allocation of parental care has been largely overlooked as most research in this field has been heavily biased in favour of a female perspective [68]. One example comes from male rock sparrows, *Petronia petronia*, in which there is greater provision of nest defence by males that have mated with attractive females [69].

Post-copulatory male mate choice, although difficult to study, could be more common than pre-copulatory mate choice. This is because males might be able to assess female quality more accurately through physical contact that occurs once the male has been accepted by the female, rather than during the pre-mating stage. Physical contact might be necessary for males to assess female quality accurately, particularly when females are less likely to signal their status (Box 4). A wealth of theory describes the dynamics of post-copulatory competition (reviewed in [70]) and often focuses upon strategic sperm allocation in response to intrasexual competition between males. However, some studies also consider female quality variation (e.g. [71,72]). These models predict: (i) greater allocation of sperm to high quality females; and (ii) prudent sperm allocation as female quality increases in variance because future mates could be of higher quality [70–72]. Models that consider variation in female quality also find that the allocation of more sperm to high-quality females might not be an optimal strategy if sperm competition is intense [71]. One possible outcome is that low-quality males will avoid competition by becoming less choosy, leading to assortative mating for quality [71,73]. When the probability of future matings is low or unknown, then less discrimination will occur [70,71]. As models of strategic sperm allocation already incorporate key parameters of mate choice, such as the availability of mates, capacity to mate with multiple partners, female quality and male preference variation, it would be useful to integrate this theory base with models of pre-copulatory male mate choice. For example, it would be interesting to test whether the dynamics of mate choice expressed as differences in pre-copulatory male aggression follow equivalent dynamics to sperm competition.

considered. Increased mating effort can manifest in displays to attract females or traits that increase the success of a male during intrasexual competition. High investment in mating effort can therefore increase the number of females available for mating with each male, but can trade off with the capacity of the male to mate with all such females (see *Male investment in mating effort and mate choice*). A further key factor in the evolution of male mate choice is variation in female quality (see *Variation in female quality and the benefits of mate choice*). Finally, the evolution of male mate choice is more likely when there is variation in the strength and direction of individual male mating preferences see *Individual variation in male mate choice*). We discuss these factors and synthesise the supporting theory below (see also Figure 1).

Parental investment, the OSR and PRR

Sex differences in the evolution of mate choice were originally attributed to variation in parental investment between males and females [16], which is reflected in the OSR and PRR [27–29]. Parental investment is still acknowledged to be an important factor in the evolution of male mate choice [30] and experimental evidence has

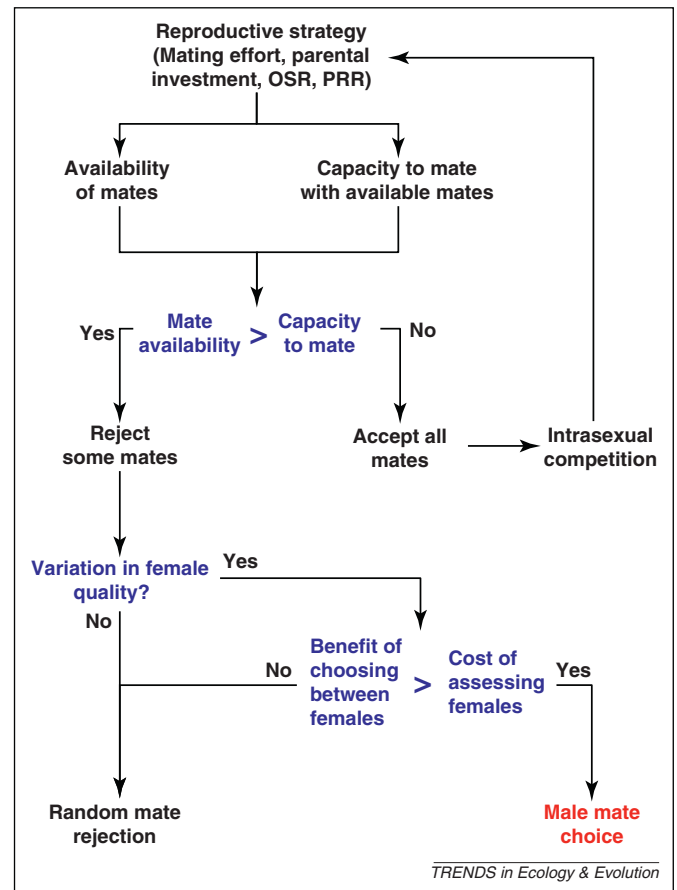


Figure 1. Selection for mate choice. Variation in reproductive strategies (i.e. investment in parental care and/or mating effort) will influence the availability of females to males and the capacity of males to mate with all the available females. If the number of females available does not exceed the capacity of males to mate with them, then selection will favour the acceptance of all mates. This will contribute to intrasexual competition for mates that, in turn, can select for a change in reproductive strategy, such as increased mating effort or parental care by males. Alternatively, if the number of females available exceeds the ability of males to mate with them, then selection will favour the rejection of some females. If a male rejects some females, there is variation in female quality and also a net benefit of choosing between females, then selection will favour male mate choice. In the absence of variation in female quality or a net benefit of choice, selection will favour random mate rejection. Abbreviations: OSR, operational sex ratio; PRR, potential reproductive rate.

demonstrated strong links between parental investment and the role of each sex during reproduction [31,32]. The sex providing more parental care is generally found to contribute more resources to each mating and to maximise reproductive fitness at a lower mating rate than the sex that exhibits lower parental care [7,16]. This is reflected in a reduced PRR for the sex providing more parental care for each reproductive bout, because the time spent caring, and in recovery following caring, makes individuals unavailable for mating [28,29]. Hence, the sex providing more parental care and with a lower PRR will then spend proportionally more time in a sexually unreceptive state and be underrepresented in the OSR [27].

If males invest less in parental care than females (resulting in a high PRR for males and a male-biased OSR) then the average number of females available as mates is likely to be low relative to the capacity of males to mate with those females that are available. In this situation, males are likely to be able to mate with all available females. There will therefore be no selection to reject any females, irrespective of

variation among them (Figure 1 [26,30]). If, by contrast, the situation is reversed and males invest more in parental care than do females (i.e. low PRR for males and a female-biased OSR), then the average number of females available as mates is likely to be high relative to the capacity of males to mate with them. Here, males are less likely to be able to mate with all available females. There will therefore be selection to reject some females and, if the benefit of mating with specific females exceeds the cost of assessing them, choice can evolve (Figure 1).

The finding that females often maximise reproductive fitness by providing greater parental care, with males gaining instead from greater investment in mating effort [16,33], is therefore consistent with the apparent prevalence of female mate choice in nature. Based on this reasoning, it was thought that the existence of mate choice in males and females could be predicted from levels of parental investment and biases in the OSR and PRR [16,27,29]. Indeed, these predictions are consistent with several empirical examples, as male mate choice can be observed in species in which males provide greater parental care, and mutual mate choice is also observed in species exhibiting biparental care [8,10,16,34]. However, as we explore below, the level of investment in mating effort is an additional key factor in the evolution of male mate choice. This is because investment into mating effort will influence both the ability of a male to attract females and his capacity to mate with them. To develop a full understanding of male mate choice, it is therefore important to understand the effect of these factors in addition to predictions based upon parental investment, OSR and PRR alone.

Male investment in mating effort and mate choice

As noted above, if a male makes a low investment into mating effort then he will probably retain the capacity to mate with many females. He will, however, have attracted, or competed for, fewer females. In this situation, a large proportion of the capacity of a male to mate with multiple females could therefore remain unused. Under these conditions, there will be strong selection for the male to alter his strategy of reproductive investment. One possible change that could be favoured would be to invest more in parental care if the probability of attracting other females is low [35]. Greater investment in parental care could then select for male mate choice (see *Parental investment, the OSR and PRR*). Alternatively, intrasexual competition between males for females could select for increased investment into mating effort. This could be investment in traits that increase the attractiveness of a male to females or that increase success in competition with other males. The consequence of investing more resources into mating effort is that the ability of the male to attract females is increased whereas his capacity to mate with those females is decreased (Figure 1), hence selecting for male mate choice. Therefore, male mate choice is more likely to evolve when a male investment in mating effort increases, just as it is when male investment in parental care is increased.

The potentially high costs of increased mating effort that occur under intrasexual competition for mates were recognised by Trivers to contribute to higher mortality rates among reproductively active males [16]. However,

the role of these costs in influencing the evolution of mate choice was not formally considered until much later [17]. This theory showed that the inclusion of a mortality cost of increased investment in mating effort under intrasexual competition would result in the adult sex ratio and, hence, in turn the OSR, becoming less male biased. Male mate choice is then more likely to be selected for among the surviving males [17]. A related example is that an increase in sperm competition can also select for greater investment in mating effort by males through the production of larger ejaculates or larger gametes (which could increase the success of a male in competition with other males). As a result, the capacity of males to mate with multiple females is reduced because of intrinsic limitations in the resources available to each male [36]. Likewise, if males that provide greater courtship to each female are more likely to mate, this increased mating effort reduces the capacity of males to court multiple females and, thus, male mate choice can be selected for [19,37].

To conclude, male mate choice can also evolve when there is greater investment of the resources of a male in mating effort, and this can be independent of investment into parental care. This could explain why male mate choice is found within polygynous species in which male investment in parental care is low [11]. For example, in *Drosophila melanogaster*, males provide no parental care and benefit from a high mating rate [7], yet there is evidence for male mate choice [38–40]. Significant contributors to the evolution of male mate choice in this species are likely to be high costs of ejaculate production or limits to courtship, which can reduce the capacity of a male to mate with multiple females [36,38]. Future work might also consider how different strategies of male mating effort might influence the evolution of male mate choice. Mating effort can range from traits involved in the competition for, or attraction of, many females to traits that are directed at individual females. The extent to which each type of strategy will attract available females and/or reduce the capacity of males to mate is expected to differ. Different types of mating effort might then be more likely to influence selection for male mate choice.

Variation in female quality and the benefits of mate choice

For male mate choice to evolve, there must be variation in the net benefit of mating with different females [18,41,42]. For example, significant variation in body size across females of many taxa is often positively associated with fecundity [11]. Males frequently prefer larger mates and, hence, gain fitness benefits [11,43,44]. Variation in the quality of females that are available as mates is a fundamental requirement for the evolution of male mate choice and the greater this variation, the larger the potential benefits of choice [41]. If the quality of all sexually available females is equal, or the cost of assessing mates exceeds the potential benefits of choice, then male mate choice should not evolve. There should then be random acceptance and rejection of females, or random allocation of reproductive effort between females, based solely upon the number of females with which a male has the capacity to mate (Figure 1).

As noted above, females often invest more into the production and care of offspring than do males. Interestingly, therefore, the potential direct benefits to males of mate choice can often exceed the equivalent direct benefits of mate choice in females [41,42]. However, irrespective of variation between potential mates, male mate choice is not expected to evolve if a low probability of future matings (i.e. low mate availability) means there are high opportunity costs of rejecting a current mate [41]. Hence, the sex with potentially more to gain from mate choice (males) can express choice less frequently [42]. For example, in a mating system with predictable and high male mating costs owing to sexual cannibalism, the evolution of male mate choice is nevertheless unlikely because potential mates are encountered sequentially and the likelihood of finding other mates is too low [26]. Thus, predictable variation in female quality is necessary but not sufficient to favour the evolution of male mate choice.

Individual variation in male mate choice

An important factor that could influence the evolution of male mate choice is that any male that prefers the same females as other males will face greater competition for mates [19]. Males with weak or alternative preferences would then be at an advantage, and the evolution of a shared male preference would not be selected. For this reason, male preferences might be more likely to evolve if there is individual variation in preferences or target traits preferred by different males. For example, the outcome if males prefer to mate with compatible females [45,46] is that no single female 'type' is favoured by all males. Therefore, an important factor in the evolution of male mate choice is the extent to which males vary in choosiness or prefer different female traits. In this respect, the OSR of the population is not informative because it does not account for variation in the availability of females to different males.

An important influence upon individual variation in male mate choice is the presence and strength of female choice. This is because the expression of choice by females will increase the variance in both male mating success and the number of females available to each male. This means that, for unattractive males, which might often be in the majority, the likelihood of mating will be reduced, leading to elevated intrasexual competition among males, which will limit the potential for male mate choice. However, for attractive males, the expression of female mate choice will increase the number of females available as mates, among whom mate choice should then be more likely to evolve. For example, large males of the two spotted goby, *Gobioculus flavescens*, in high condition are more successful at attracting mates, more successful in intrasexual competition and more likely to express a mate preference [47]. Post-copulatory male mate choice is also found in dominant, but not subordinate, male jungle fowl, *Gallus gallus* [48].

If female mate choice favours, or male competitive ability is highest in, good-condition males (e.g. [49]), male mate choice could evolve condition dependence. Male mate choice could also be more probable than female choice to evolve condition dependence (e.g. [50]) if the number of

females available as mates is more likely to covary with male condition. Positive correlations between individual male condition and the strength of male mate choice could then result in assortative mating with respect to condition. This is because a mating bias among high-condition males for high-condition females could lead to low-condition males and females mating with each other either by default, or as an adaptive mate choice strategy in low-condition males to avoid competition [20,51]. As an example, males of the orb-weaving spider, *Zygiella x-notata* will mate indiscriminately under low competition, yet under high competition there is size assortative mating [52]. Assortative mating with respect to condition is of broad ecological significance, and can increase genetic variance within a population because genes will tend to segregate according to their contribution to condition, which subsequently can increase the efficiency with which selection purges deleterious alleles [53].

In conclusion, it is important to realise that the expression of male choice and the traits in females that are the subject of choice can vary between males in a population in a manner that cannot be predicted by the OSR. This could make male choice hard to observe and thus appear to be rare. However, even though the average strength of male mate choice within a population could appear weak, the preferences of males with the highest mating success can nevertheless select strongly between females.

The evolutionary significance of male choice

Here, we consider the relative importance and, therefore, evolutionary significance of male mate choice in the wider context of the rate of adaptation to new environments [53,54] and creation of biodiversity through speciation [55]. There are likely to be widespread differences in the fitness benefits that maintain selection for either male or female mate choice (Box 2) and, consequently, sexual selection exerted by male mate choice upon female traits is predicted to differ (Box 3).

Based on the generally greater investment by females in parental care, we predict that, in most species, female mate choice will be expressed by most females. However, because of the often high costs of intrasexual competition, leading to increased male mating effort and increased variation in the expression of mate choice between males, male mate choice could also occur in many species, although in most it might only be expressed by a few males. Comparisons of the prevalence of male and female choice would therefore be useful and these should consider both inter- and intrasexual variation in the prevalence of choice. However, caution should be applied to ensure that experimental designs do not overestimate the opportunity for male mate choice, or indeed female mate choice, by ignoring the potentially significant barriers to it. For example, simultaneous presentation of mates to males could increase mate availability beyond that which males would normally encounter and thus encourage mate choice that would only rarely be expressed in a more natural setting [26].

Another way to assess the significance of male mate choice is by considering the sex-specific effects of choice on population fitness. The number of offspring produced in

Box 2. Contrasts in the benefits of mate choice between the sexes

Contrasts between male and female choice could arise because of fundamental differences in the way that benefits of choice maintain preferences in each sex. The benefits of mate choice can be direct or indirect. Direct benefits occur when the fitness of the choosing individual is increased because of choice, for example if choice favours more fecund mates or mates that provide greater parental care to offspring. Indirect ('genetic') benefits are gained by the choosing individual when choice enhances the genetic quality of their offspring, so that the offspring are more likely to reproduce (reviewed in [24]). Selection arising from direct benefits of choice will in general be stronger than selection arising from indirect benefits of choice [74].

Although the evolution of a common male preference for the same female trait can lead to greater intrasexual competition for mates, the costs arising can be overcome if the preferred female trait confers significant fitness benefits [19,75]. For this reason, male mate choice could be more likely than female mate choice to be based upon traits that indicate direct rather than indirect fitness benefits [19,37,75]. Importantly, females often vary considerably in traits such as fecundity, which can influence the magnitude of potential direct benefits of male mate choice [42]. Consistent with this, a growing

body of evidence shows there is male mate choice for female traits that indicate fecundity or reproductive status [1,11], and that sexual signals in females that could indicate indirect benefits seem relatively scarce (Box 4).

Although potential contrasts between male and female mate choice are beginning to be identified, the relative importance of the direct versus indirect benefits accrued by each sex is not yet clear [37]. That different fitness outcomes can occur can be seen in experimental contexts. For example, both male and female mate choice have been demonstrated in the fruit fly, *Drosophila melanogaster*. Female *D. melanogaster* mating with preferred males have significantly decreased lifespan and lifetime reproductive success [76,77]. Conversely, male mate choice is directed towards high-fecundity females [38]. A similar outcome is found in the sex role-reversed pipefish, *Syngnathus typhle*. Broods resulting from the expression of either male or female mate choice are superior at escaping predation, yet only broods resulting from female mate choice result in faster offspring development [78]. As males contribute significantly to parental care in this species, females will probably have greater opportunity to choose direct benefits that will contribute to offspring development.

each generation is generally determined by the limiting sex, most often females, which invest most into the production and care of offspring. Mate choice decisions made by males could therefore have significant potential to alter population fitness by influencing the contribution made to future generations by nonpreferred females [42]. For example, male mate choice could bias sperm limitation (e.g. [36,56]), decreasing it in chosen and increasing it in non-chosen females. However, in most cases, it is unlikely that male mate choice would cause females to remain unmated or sperm limited because of the high fitness benefits to males of mating with such females. Instead, male mate choice is more likely to influence population fitness when males provide significant benefits, for example greater parental care or nuptial gifts, to preferred females. The influence of male mate choice on population fitness could also be more subtle. For example, in oldfield mice *Peromyscus polionotus rhoadsi*, the number and size of litters is significantly higher when males are paired with preferred females, which results primarily from a male preference for compatible mates [46].

Male mate choice could decrease as well as increase population fitness. A combination of sexual conflict and male mate choice in *D. melanogaster* can lead to disproportionately more harm being caused to larger females that are preferred targets for male persistence [39]. This mating bias adversely impacts upon the fitness of the population and the rate of adaptive evolution. Such outcomes are likely to be a more widespread phenomenon among mating systems characterised by both sexually antagonistic coevolution and male mate choice [21]. Such conflict could select for female sexual signals that conceal the true fecundity of the female, although low-quality females could gain from developing signals attractive to high-quality males (e.g. [57]; Box 4). It would be interesting for future research to consider how sexually antagonistic traits in females might be used to manipulate mate choice in males.

A mixed picture is also emerging for the role of male mate choice in speciation. It has been suggested that sympatric speciation by sexual selection is more likely to occur under mutual mate choice than under female mate

Box 3. Male mate choice and sexual selection

Insight into the relative importance of male mate choice to sexual selection could be gleaned from investigation of the genetic architecture of preferred traits. Traits that are chosen on the basis of the indirect genetic benefits they confer must be heritable and might be expected to show relatively high heritability to maintain selection for a preference. By contrast, traits that are chosen on the basis of direct benefits are not necessarily heritable, for example they could be traits that all females adopt at different times, such as reproductive status (virgin, mated, recently mated, etc.) [11]. If male mate choice is more likely to favour traits that confer direct benefits (Box 2) and traits indicating direct benefits are not necessarily heritable, it follows that traits preferred by males will, on average, be subject to greater genetic variance than will traits preferred by females. The evolutionary response to sexual selection of preferred traits resulting from male mate choice could therefore be weaker than for female choice. However, traits that confer either direct or indirect benefits will also be subject to unpredictable environmental variation [79] and, therefore, further work is needed to test whether general predictions can be made regarding differences in the evolutionary response to selection arising from male or female

choice. Furthermore, traits such as fecundity might also be subject to strong natural selection, which could override, or conflict with, sexual selection owing to male choice [11].

Finally, because male mating success is typically skewed, with not all males gaining matings, the opportunity for sexual selection among males is generally high [80]. By contrast, as variation in female mating success is typically low, despite male mate choice, the opportunity for sexual selection among females will also be lower. The effects of sexual selection on females resulting from male choice will depend upon whether the fitness of preferred females is increased (e.g. [36,81]) or decreased (e.g. [82]) by greater male attention. Alternatively, female fitness could be relatively unaffected by male mate choice if the male preference is based on traits, such as reproductive maturity, that are expressed by all females (e.g. [11,83]).

There is undoubtedly much more to be understood about the strength of selection exerted by male mate choice upon preferred female traits. Further research investigating the sex-specific outcomes of male and female mate choice across a broader range of species would be very welcome.

Box 4. Sexual signals in females

Sexual selection through female choice has resulted in the evolution of exaggerated ornaments or behaviours in males [1]. However, such exaggeration appears less frequently in females. There are two main potential explanations. First, any investment in signalling traits by females would trade off with fecundity, reducing the direct benefits of male choice [11,19]. This argument was first proposed in relation to male sexual signals [84], yet might also be relevant to the evolution of female sexual signals, particularly if male mate choice is more dependent upon direct benefits. Second, if the OSR is male biased and males are able to mate multiply; it is less likely that females will not find a mate. Therefore, unless females gain direct benefits or potentially suffer greater costs [39] from signalling to attract additional mates, there might be little selection to invest in signals [85,86].

Despite the potential factors that could impede their evolution, female signalling traits have nevertheless been identified [10,22]. Male mate choice, however, is not the only factor that could select for sexual signalling in females. For example, it is increasingly clear that females can benefit from signalling to attract mates [56,81]. Signals

might also have a role during intrasexual competition between females [86] and some female signals can result from correlated responses to sexual selection for homologous traits in males [10,87]. However, at least some female signals can be attributed to selection arising from male choice, particularly in species with either 'reversed' sex roles or those that exhibit biparental care [10,87].

Female signalling could also be favoured by nonlinear male preference functions [88]. For example, if males prefer intermediate values of a female trait, this could lead to stabilising selection on that trait. The negative effects of investment in signalling upon fecundity could then be balanced against the benefits of signalling to attract additional mates. An example of this comes from *Drosophila serrata*, where the composition of the cuticular hydrocarbon profile is subject to stabilising selection in females, but directional selection in males [89,90]. Such nonlinear male preference functions could be widespread but easily overlooked. There is considerable opportunity to expand current theoretical understanding of the evolution of female signalling.

choice [58], for example in polymorphic cichlid fish [59]. Male mate choice has been demonstrated to contribute to reproductive isolation in some studies (e.g. [60,61]) but not others [62,63].

Concluding remarks

Theory and empirical data are increasingly showing the opportunity for selection for male mate choice across a wide range of species. We conclude that, in addition to variation in female quality, a key factor in the evolution of male mate choice is the availability of females relative to the capacity of an individual male to mate with those females. However, we note that male mate choice cannot be predicted solely from sex differences in parental care as reflected in biases in the OSR and PRRs. Instead, male investment in mating effort should also be considered, as this reflects the costs of mate attraction and intrasexual competition incurred by males. This newer understanding makes clear that there can be strong selection for male mate choice in situations where it would not previously have been predicted, such as in polygynous species and those that exhibit no male parental care. There are substantial opportunities for future research to understand important novel outcomes of sexual selection by adopting a more inclusive view of mate choice operating in both sexes and the likelihood of male mate choice across widely different mating systems. In particular, future work would benefit from greater comparison of the fitness benefits, costs of mate assessment and the strength of selection arising from male relative to female choice.

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