

Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling

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Biases in the operational sex ratio (OSR) are seen as the fundamental reason behind differential competition for mates in the two sexes, and as a strong determinant behind differences in choosiness. This view has been challenged by Kokko and Monaghan, who argue that sex-specific parental investment, mortalities, mate-encounter rates and quality variation determine the mating system in a way that is not reducible to the OSR. We develop a game-theoretic model of choosiness, signalling and parental care, to examine (i) whether the results of Kokko and Monaghan remain robust when its simplifying assumptions are relaxed, (ii) how parental care coevolves with mating strategies and the OSR and (iii) why mutual mate choice is observed relatively rarely even when both sexes vary in quality. We find qualitative agreement with the simpler approach: parental investment is the primary determinant of sex roles instead of the OSR, and factors promoting choosiness are high species-specific mate-encounter rate, high sex-specific mate-encounter rate, high cost of breeding (parental investment), low cost of mate searching and highly variable quality of the opposite sex. The coevolution of parental care and mating strategies hinders mutual mate choice if one parent can compensate for reduced care by the other, but promotes it if offspring survival depends greatly on biparental care. We argue that the relative rarity of mutual mate choice is not due to biases in the OSR. Instead, we describe processes by which sexual strategies tend to diverge. This divergence is prevented, and mutual mate choice maintained, if synergistic benefits of biparental care render parental investment both high and not too different in the two sexes.

Keywords: mutual mate choice; operational sex ratio; parental investment; sexual advertisement

1. INTRODUCTION

The OSR is defined as the ratio of the numbers of sexually receptive males and females (Emlen & Oring 1977). This ratio becomes biased towards one sex if the sexes share parenting duties unequally, which leads to intense competition for mates in the less caring sex (Trivers 1972). The other, limiting sex can then afford to be choosy. The OSR is primarily determined by the PRRs of the two sexes, but is also influenced by mortality rates in the two sexes (Clutton-Brock & Parker 1992; Parker & Simmons 1996) and on qualifications—such as owning a suitable nest site—that individuals have to meet before they can mate (Ahnesjö *et al.* 2001). It is currently recognized that other factors such as quality variation also influence the evolution of choosiness (Parker 1983; Owens & Thompson 1994; Johnstone *et al.* 1996). Yet, sex roles—i.e. competitiveness for matings—are assumed to depend solely on the OSR (including, naturally, any factors that alter the OSR bias; for example, Kvarnemo & Ahnesjö (1996); Parker & Simmons (1996); Eens & Pinxten (2000)).

Recently, Kokko & Monaghan (2001) combined the effects of PRRs, sex-specific mortalities and mate-encounter rates to a single model of competition and choosiness in the two sexes. They showed that the effect of mortality on mate competition and choosiness depends on whether it occurs as a cost of breeding or mate searching, or as a result of non-breeding activities (e.g. juvenile growth). Therefore, it is not sufficient to calculate the effect of mortality on OSR in order to predict sex roles (relative strength of competition for mates in the two sexes (Vincent *et al.* 1992)) or choosiness. As a result, Kokko & Monaghan (2001) advocated the use of the cost of breeding as a more direct and fundamental determinant of the direction of sexual selection than the OSR.

In this paper, our aim is threefold as follows.

- (i) We expand on the rather simplified model of Kokko & Monaghan (2001), to determine whether its result remains robust when individual quality is modelled explicitly. Kokko & Monaghan (2001) assumed a fixed difference in mortalities and parental care in the two sexes, and modelled individual quality only implicitly. In our approach, mating rates and choosiness are allowed to depend on individual quality, quality is revealed through signalling, signalling and parental investment carry a mortality cost,

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and the division of parental duties among the two sexes is not determined *a priori*. These factors prevent us from obtaining analytical results as in Kokko & Monaghan (2001), but they add realism to modelling mating strategies.

- (ii) We consider the coevolution of parental investment, the mating system, and the OSR. Since the seminal paper of Trivers (1972), differences in parental investment are seen as the causal basis for the evolution of choosiness and competition, and competition for matings when the other sex is choosy is then viewed as the causation behind ornamentation and signalling of quality (Andersson 1994). However, if parental care can coevolve with the mating system, evolving costs can feed back into mating strategies (McNamara *et al.* 2000) and hence influence choosiness and signalling. For example, Fitzpatrick *et al.* (1995) have argued that the expression of signals should remain limited in species with biparental care, due to fecundity costs of signals in such settings, but this idea has not been formalized. Instead of examining the effect of one parameter and assuming that others are fixed, we derive population characteristics, such as the OSR or the sex-specific cost of breeding or signalling, from strategies that maximize lifetime fitness.
- (iii) We ask why mutual mate choice is relatively rare. The 'classical scenario' of sexual selection considers a species in which one sex is choosy and the other invests in mate acquisition. The true spectrum of sexual selection is much broader than this (Cunningham & Birkhead 1998). Some species show ornamentation and choosiness in both sexes (e.g. Johnson 1988*a,b*; Jones & Hunter 1993; Langmore *et al.* 1996; Kraak & Bakker 1998), and theory predicts that mutual choosiness can be adaptive when both sexes vary in quality (Parker 1983; Johnstone *et al.* 1996; Bergstrom & Real 2000). Especially in monogamous mating systems, access to high-quality mates may limit reproductive success in both sexes. Parental care provided by a (socially) monogamous pair may thus promote mutual choice, especially as it is well established that condition-dependent signals can advertise direct benefits (Hoelzer 1989; Kokko 1998; Iwasa & Pomiankowski 1999) in addition to indirect ones.

In a very large number of species with biparental care, sexual strategies are clearly divergent: one sex is competitive and develops elaborate signals or ornaments, the other sex is choosy (Andersson 1994). Why should mutual choice be so rare, given that quality presumably varies in both sexes? Johnstone *et al.* (1996) show that choice is more costly for the limited sex (the sex towards which the OSR is biased), and this is predicted to have a stronger effect on choosiness than quality variation of the two sexes. However, Johnstone *et al.* (1996) did not explicitly predict how large OSR biases mutual choice will tolerate, nor did they consider signal evolution under mutual choice. Also, Kokko & Monaghan (2001) show that the role of OSR as a determinant of competition and choice may have been overestimated, and the relationship between OSR and choosiness is in any case less straight-

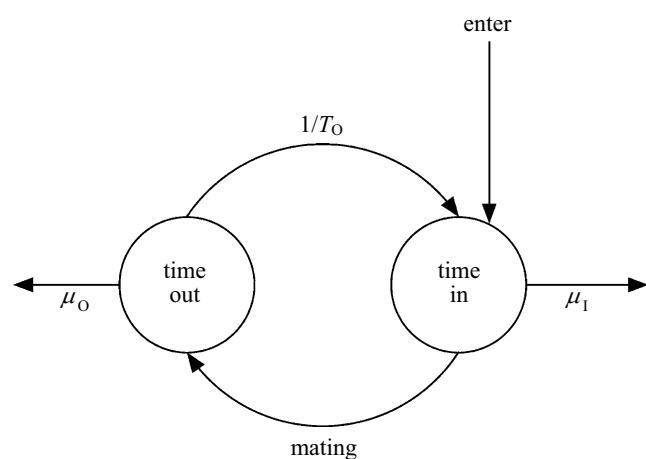


Figure 1. The dynamics of mating and death. Individuals are in either a 'time in' (searching for mates) or a 'time out' (processing the previous mating) state. The initial state of virgins entering the mating pool is 'time in'. Individuals may die in either state, and the mortality rates are state-dependent: μ_I and μ_O . In the full signalling model, the mortalities also depend on signalling effort (equation (2.3)). The rate of mating is M in the simple invasion model, and $\int_q m(q') dq'$ in the full signalling model. An individual in the 'time out' state finishes breeding and rejoins the mating pool at a rate $1/T_O$, where T_O is the time out. T_O is fixed in the simple invasion model, but comprises a fixed minimum time and an evolving parenting time in the full signalling model.

forward than that between OSR and competition (Owens & Thompson 1994; Kvarnemo & Ahnesjö 1996; Kokko & Monaghan 2001). Here, we ask whether mutual mate choice is rare because OSR biases often become too large to sustain mutual choice, or whether other factors are to blame.

2. THE MODEL

We consider a temporally stable population, where breeding occurs continuously. We denote the sex ratio among newly matured individuals by α , and the OSR by β (both measured as males : females). Mature individuals can at any time be in two different states: 'time in', when individuals search for mates (denoted I), and 'time out' (denoted O), when the individual is processing the last mating (figure 1). We describe the life cycle from the viewpoint of females, with primed (') symbols denoting the corresponding variable for males. Each equation can be replicated for the other sex by switching the primed and non-primed variables. Two variables, M and β , are exceptions. M denotes the species-specific mate-encounter rate in a population with 1 : 1 OSR. M is equal for both sexes as it describes the baseline mate-encounter rate in a species—e.g. high for colonial birds, low for some snails (Ribi & Arter 1986) and turtles (Mosimann 1958)—whereas β captures the sex difference in the encounter rate. Thus, β in female equations has to be replaced by $1/\beta$ in male equations, and M remains the same for both sexes.

(a) *The simple invasion model*

We first review the basic life-history model of competition and choosiness (Kokko & Monaghan 2001), where

parental care is fixed, and breeding activities form the sex-specific 'time out' T_O . Mortality during time out equals μ_O , and during time in, μ_I . The definitions of the species-specific mate-encounter rate M and OSR β imply that females encounter males at a rate $M\sqrt{\beta}$, and males encounter females at a rate $M/\sqrt{\beta}$. These values correctly produce a ratio of β for the mating rates of females and males.

An individual can either be non-choosy, in which case the mate-encounter rate equals the mating rate, or reject some potential mates. Rejecting low-quality mates improves expected mate quality at the expense of a reduction in the mating rate. This trade-off depends on the quality distribution of the opposite sex, and is described by two parameters p' and q' . Accepting a fraction p' of mates improves the quality of mates by a factor $q' > 1$, but reduces the mating rate to a fraction p' of the original ($p' < 1$). If mate quality is highly variable, a significant increase in quality (high q') can be achieved whilst still maintaining a relatively high mating rate (high p') (as in Owens & Thompson 1994).

The conditions under which choosiness invades a non-choosy male or female population are derived in Kokko & Monaghan (2001), and we present their central results here. Choosiness will invade the female population under the condition

$$CM\sqrt{\beta} > \mu_I \frac{1 - p'q'}{p'(1 - q')}, \quad (2.1a)$$

where

$$C = \frac{\mu_O T_O}{1 + \mu_O T_O}. \quad (2.1b)$$

Here, C is a measure of the cost of breeding. It corresponds to the definition of Trivers (1972) of parenting investment as the reduction of ability to invest to future offspring: C equals the probability that the current breeding attempt is the last one for an individual, and it increases both with time out, T_O , and with breeding-induced mortality, μ_O . For males, the condition for the invasion of choosiness becomes

$$C' \frac{M}{\sqrt{\beta}} > \mu_I' \frac{1 - pq}{p(1 - q)}. \quad (2.2)$$

The model also predicts the strength of competition for mates; males are more competitive than females if the OSR β is sufficiently biased:

$$\beta > \frac{\mu_I C'}{\mu_I' C}. \quad (2.3)$$

The OSR itself, β , is determined by solving (Kokko & Monaghan 2001)

$$\beta = \alpha \frac{\mu_I + CM\sqrt{\beta}}{\mu_I' + C'M/\sqrt{\beta}}. \quad (2.4)$$

This simple model makes several predictions. Choosiness can invade both sexes, if breeding is costly for both sexes, if the mate-encounter rate M is high, if the quality of both sexes varies significantly (pq and $p'q'$ are both high), and if mortality during mate searching, μ_I , is not too high. Where the OSR falls within the permitted range,

mutual choice has the potential to invade (figure 2). Mutual choice will be most likely when breeding imposes high mortality cost on both sexes, allowing for only a few breeding attempts in a lifetime. A high species-specific mate-encounter rate, M , similarly enhances mutual choice (figure 3).

However, several consequences of mutual choice are not fully captured in this simple model. When one sex (e.g. female) becomes choosy and reduces its mating rate from M to $p'M$, the average mating rate is diminished by the same factor for the opposite sex. Since reductions in M select against choice (figure 3), the opposite sex will tend to become less choosy. Sexual strategies are therefore prone to diverge between the sexes. However, if females are consistent in their choices, some males are chosen more often than others, and the reduction in mating rate then does not apply to all males equally. The better-off individuals enjoying a higher mating rate have more potential to fulfil the invasion criterion equations ((2.1) and (2.2)) and remain choosy.

Another tendency for sexual strategies to diverge is found when the limited sex seeks to improve its access to mates by investing in mate acquisition. Such investment often incurs mortality costs either in adults or in juveniles (Promislow 1992; Promislow *et al.* 1992; Owens & Bennett 1994), which, in turn, have two opposing effects on mutual choosiness. High mortality in the limited sex will reduce the bias in the sex ratio (equation (2.4)), which will favour mutual choice. On the other hand, high mortality during 'time in' also selects directly against choosiness (equation (2.1)).

It is because of these complications that a fully developed model of mutual mate choice must consider quality-dependent mating rates, allow choice strategies to depend on quality, and make mortality during 'time out' dependent on mate acquisition effort. We now turn to developing such a model, where individuals can simultaneously be choosy and compete to be accepted as mates through signalling.

(b) The quality-dependent signalling model

In the detailed model, individuals vary in their quality, q . Quality has a dual meaning: individuals of high quality suffer less mortality (especially when signalling), and are also more desirable as mates. The details of these relationships are described in sections 'breeding' and 'signalling and mortality' below. The qualities of newly maturing individuals follow the frequency distribution $f(q)$, and we use distributions that have $q = 1$ as the mean quality. The density of individuals of quality q in the mating pool ('time in' state) is $n(q)$. Appendix A derives the relationship between $f(q)$ and $n(q)$.

(i) Signalling and mortality

An individual of quality q chooses a signalling level $s(q)$. This will affect its acceptability as a mate (see § 2b(ii)) but also increases mortality. Mortality during 'time out' may differ from the mortality during 'time in', and we denote these by μ_O and μ_I , respectively. Signals are assumed to be differentially costly so that lower quality individuals experience a stronger increase in mortality with increasing signalling effort as follows:

$$\mu_I(s, q) = \mu_{I0}(q - s)^{-1}, \quad (2.5a)$$

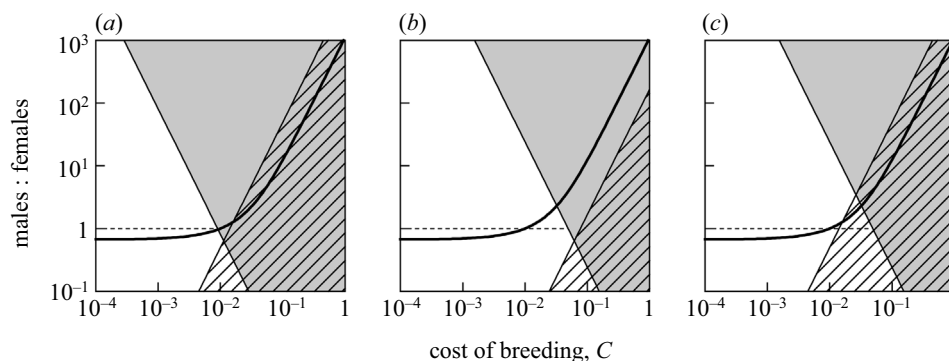


Figure 2. Mutual choice in the simple invasion model. Areas indicate the range of values of OSR, β , for which male or female choosiness would invade the population. The actual OSR predicted by the mating dynamics is given by a solid line, and solutions are to be read along this curve. All examples have almost equal time out for males and females, so that cost of breeding equals C for females, and $0.95C$ for males (both have breeding mortality $\mu_o = \mu'_o = 1$). Males, however, survive less well during time in: $\mu_1 = 1, \mu'_1 = 1.5$. (a) Both sexes gain 10% improvement in mate quality by rejecting half of the matings ($p = p' = 0.5, q = q' = 1.1$). Mutual mate choice is observed if the cost of breeding is high; at intermediate cost, only females are choosy, and at low cost, neither sex is choosy. (b) Improvement in mate quality is only 2% ($q = q' = 1.02$). Regions of choice shift to the right, and mutual choice does not invade the male population at any value of breeding cost. Females become choosy at high C values, mainly as a direct response to increasing breeding cost (region of female choice widens as C increases), and to a lesser degree because the OSR turns male-biased as C increases (OSR curve meets female-choice region sooner as it turns upwards). (c) Female quality varies more than male quality: $q = 1.1, q' = 1.02$. Male region of choice shifts back towards the left, and mutual mate choice occurs when breeding is very costly (high C). At intermediate C , only males are choosy, despite a male-biased OSR. Shaded area, female choice; white hatched area, male choice; shaded hatched area, mutual choice; white area, no choice.

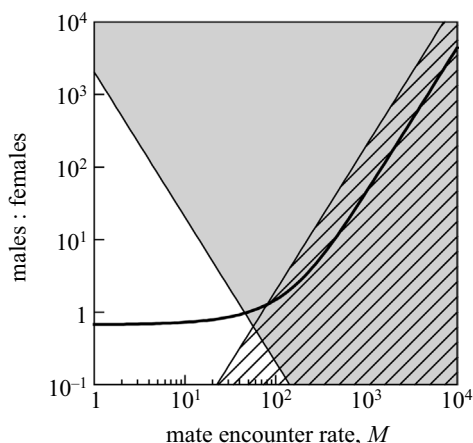


Figure 3. Mutual choice in the simple invasion model as a function of mate-encounter rate, M . Parameters as in figure 2a with $C = 0.2$, but with M varying between 1 (i.e. an individual of average lifespan in a 1 : 1 sex ratio meets only one opposite-sex member during its life) and 10 000 (the individual can compare an average of 10 000 mates before dying, if it never breeds). Mutual choice sets in at $M > 83$. Key as in figure 2.

$$\mu_o(s, q) = \mu_{o0}(q - \gamma s)^{-1}. \tag{2.5b}$$

The parameters μ_{o0} and μ_{10} specify population-wide mortality rates, and hence scale the longevity of individuals. We use $\mu_{10} = 1$ unless otherwise indicated. This value gives a lifespan of 1 time-unit for an average-quality individual ($q = 1$) who does not signal and never breeds. The parameter γ scales the costliness of the signal during the breeding season. With $\gamma > 1$, a signal is especially costly to bear during breeding. A morphological ornament that

hinders feeding of offspring, or bright plumage that increases the risk of predation during incubation, would have $\gamma > 1$. With $\gamma = 0$, the signal does not affect mortality during breeding (time out). This is an appropriate description for signals that can be removed once breeding starts, and that lack long-term physiological costs. For example, a behavioural display that has increased predation risk as its main cost would fall into this category. The mortalities in equation (2.3) approach infinity when $(q - s)$ or $(q - \gamma s)$ approach zero, and therefore the signal of an individual of quality q has a maximum q if $\gamma < 1$, and q/γ if $\gamma > 1$.

(ii) *Choosiness and mating*

The choosiness of an individual, $c(q)$, describes the threshold of acceptability for signals s' of the other sex. The probability that an individual of choosiness c accepts a mate whose signal equals s' is given by a function $p(s', c)$

$$p(s', c) = [1 + e^{-k(s'-c)}]^{-1}. \tag{2.6}$$

In this function, individuals of the opposite sex become acceptable as their signalling level exceeds c , but due to errors in decision making (Johnstone 1994; McNamara *et al.* 1997) weaker signals are sometimes accepted and stronger ones rejected. Thus, $c(q)$ specifies the signal level that leads to 50% probability of acceptance by individual of quality q . The level of error is scaled by the parameter k ; we use $k = 10$ in our examples. $c(q)$ can take negative values, since $c(q) = 0$ produces 50% acceptance for non-signallers, and smaller values of $c(q)$ are required to describe completely indiscriminate mating. In practice, we set $c(q) = -2$ as the lowest possible choosiness value, which is sufficiently low to describe a completely non-choosy strategy (acceptance of non-signallers $p(0, -2) > 0.999\ 999$).

Every individual starts its adult life in 'time in', and

returns to this state every time it finishes the ‘time out’ (figure 1). ‘Time in’ individuals search for mates. They meet potential mates of quality q' at a rate $Mn'(q')$. This rate is proportional to the density $n'(q')$ of opposite-sex non-breeders of quality q' . The mate-encounter rate M specifies the number of mates that an average-quality individual can inspect during its lifetime, if it spends all its time searching for mates (and neither breeding nor signalling) in a population where the OSR equals unity. We use $M = 1000$ in our examples, which is sufficient to produce mutual choice in the simple invasion model, provided that breeding is costly (figure 2). Non-breeders (‘time in’ individuals) become breeders and enter the ‘time out’ stage when they meet an acceptable mate who is also willing to accept them; the rate at which they do so is $m(q)$.

(iii) *Breeding and parental care*

A breeder rejoins the pool of non-breeders after an exponentially distributed time out t . Time out has the expectation T_O (thus producing a rate $1/T_O$ for rejoining, figure 1).

There is no *a priori* reason why females should care more than males, and a difference in parental investment could easily override any difference in gametic investment. Therefore, we specify that the investment T_O consists of a minimum time investment T_{\min} and a parenting time T_P : $T_O = T_{\min} + T_P$. The minimum time investment T_{\min} cannot be changed by an individual. It is typically based on physiological constraints such as time needed for replenishing egg or sperm supplies, although it can also include parenting duties where there are evolutionary constraints that render one sex the care provider. $1/T_{\min}$ specifies the maximum rate at which an individual could breed if it spent a negligible time searching for mates, and had its mate perform all the parenting duties which can be toggled from one to another sex. This rate is sex-dependent, T_{\min} being typically much smaller (and the maximum reproductive rate $1/T_{\min}$ correspondingly higher) for males than females.

Parenting investment T_P is additional time that the parent opts to spend caring for the offspring and is during this time not able to mate and breed again. We allow T_P to be sex specific but do not assume any *a priori* sex asymmetry in T_P . Instead, T_P evolves freely for either sex. For the sake of simplicity, we exclude quality-dependent variation in T_P , which would require us to model differential allocation strategies (Burley 1986; Sheldon 2000).

The fitness gain from a single breeding attempt is given by

$$F(q, q') = qq'R(T_P, T'_P). \quad (2.7)$$

Equation (2.7) takes into account the intrinsic benefits of mating with a high-quality mate, q' , as well as the need to provide parental care to produce surviving offspring, R . The multiplicative form of fitness means that, say, a 5% increase in the male’s quality will improve the female’s fitness gain by 5% regardless of the female’s own quality. For the relationship between parental care and the number of survived offspring R , we examine three different scenarios as follows.

(i) No care:

$$R(T_P, T'_P) = 1. \quad (2.8a)$$

(ii) Additive care:

$$R(T_P, T'_P) = \sqrt{T_P + T'_P}. \quad (2.8b)$$

(iii) Synergistic care:

$$R(T_P, T'_P) = \sqrt{0.001 T_P + 0.001 T'_P + T_P T'_P}. \quad (2.8c)$$

In the case of no care (i), parental care is not needed and does not improve offspring survival. This option serves as a comparison to the simple analytical model that ignores parental care as a decision; sex differences in ‘time out’ do not evolve but are fixed (T_{\min} and T'_{\min}). Options (ii) and (iii) describe cases where parental effort increases the survival of offspring with diminishing returns. In the additive care scenario (ii), offspring survival depends on the sum of care by both parents. In synergistic care (iii), two parents caring together can produce more offspring than a lone parent, even if the lone parent attempts to compensate for the absence of the other parent (e.g. $T_P = T'_P = 0.01$ produces 12 times as many offspring as $T_P = 0.02$, $T'_P = 0$). This option is relevant if raising offspring requires several simultaneous tasks, which cannot be efficiently performed by a lone parent (Motro 1994). As an example, parent birds with altricial young need to forage outside the nest, but nestlings may simultaneously need protection and warming.

(iv) *Solving the model: ESSs*

Appendix A describes the numerical procedure to derive the OSR and individual fitness. The sex-specific mating rates and ‘time in’ population densities $m(q')$, $m'(q)$, $n(q)$ and $n'(q')$ depend on each other in a way (equations (A 1) and (A 10)) that precludes maximizing fitness (equation (A 9)) analytically. Instead, we solved the ESS iteratively for both sexes. We started with randomly chosen values of T_P , T'_P , $s(q)$, $s'(q')$, $c(q)$ and $c'(q')$. At each iteration, we sought the best response of an individual of quality q for these variables (one variable at a time), assuming a population that uses previous strategy values. Since we exclude quality-dependent parental investment, the best response for parental investment, T_P , is the one that maximizes fitness under the distribution $n(q)$ of qualities, $\int W(q)n(q) dq$. To aid convergence, the new strategy was formed as a weighted average of the strategies of the previous iteration. Exemplified for T_P this gives

$$T_{P,\text{new}} = \lambda T_{P,\text{best response}} + (1 - \lambda)T_{P,\text{old}}.$$

In practice, we let λ have the value 0.5 for the first 10 iterations, from where it was gradually reduced to $\lambda = 0.05$, if convergence had not happened by then. We stopped the iteration once none of the best responses of T_P , T'_P , $s(q)$, $s'(q')$, $c(q)$ and $c'(q')$ differed from the current values by more than 0.001.

(c) Results from the signalling model

We first compare the predictions of the simple invasion model and the full quality-dependent model in the setting of figure 2*a*. Here, the simple invasion model (figure 2*a*) predicts that increasing cost of breeding leads to female choice once cost of breeding exceeds $C = 0.0092$, and to mutual choice at $C = 0.016$ or higher. Increasing the cost of breeding makes the OSR more male biased, since females spend more of their time in risky breeding activities.

The full signalling model produces the same sequence of solutions: as the cost of breeding C increases, males are the first to start signalling, at which point females become choosy. When C increases further, mutual choice appears, where both sexes signal and reject some matings (figure 4). However, the exact values of C at which these switches occur depend on the type of parental care provided. In figure 4*a*, no care is provided, and regions of choosiness occur only at much higher breeding costs C than in the simple invasion model. This demonstrates the divergence of sexual strategies: once choosiness spreads in the (female) population, mating rates become reduced, which selects against choosiness in the opposite (male) sex. Also, when signalling individuals suffer from higher mortality, they become less choosy, which further pushes the mutual threshold towards higher breeding cost C . The interaction of signalling and mortality also keeps biases in the OSR within bounds (figure 4*a*): once males evolve to become competitive (i.e. usually at high OSR values), their mortality increases, which reduces the OSR bias. As the breeding cost of males with the short time out is lower than that of females, males may remain the competitive sex even if mortality associated with male competition causes the OSR to become female biased (figure 4*a*, with C between 0.01 and 0.5). Such solutions can also be produced by the simple invasion model (e.g. figure 2*c*). Our results are qualitatively similar to those of Kokko & Monaghan (2001): the mortality cost of breeding is a more fundamental variable than the OSR in determining sexual competition and choosiness.

A requirement to provide parental care for offspring does not necessarily improve prospects for mutual mate choice. Figure 4*c* describes mutual signalling in the 'additive care' setting. Male signalling occurs now at a wider range of breeding cost C , but mutual choice and signalling evolve only if breeding is extremely costly (almost suicidal). Females with the longer minimum time out evolve to provide all the care, and this causes mate acquisition strategies to diverge between the two sexes. By contrast, synergistic benefits of care lead to more equal care provisioning by the two parents. This kind of care improves the prospects for mutual signalling and choice (onset of mutual choice occurs at a lower breeding cost C , figure 4*d*). It should also be noted that the more choosy sex can be more competitive as well (as indicated by stronger signals in females, figure 4*d* (Johnstone *et al.* 1996)).

For the sake of comparison, the results in figure 4 are derived assuming parameters equal to that of the invasion model (figure 2*a*). This includes an *a priori* assumption of higher male than female mortality ($\mu_{10}^m > \mu_{10}^f$). Since one of our goals is to investigate sex differences in choosiness while avoiding making any other sex-specific assumptions

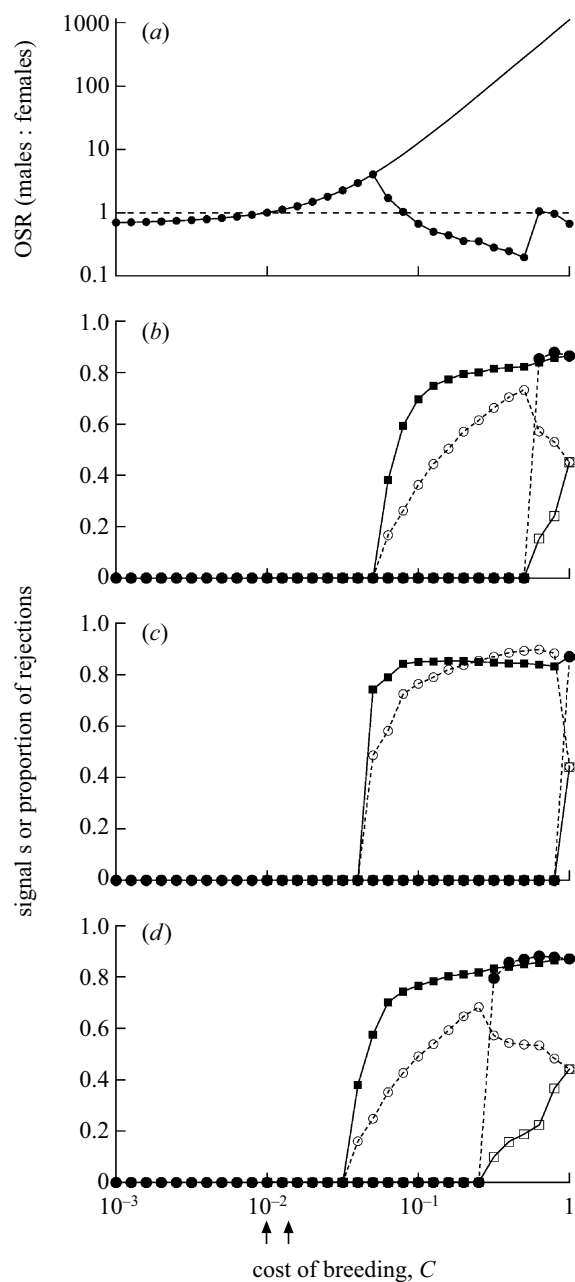


Figure 4. Solutions of the full signalling model with increasing cost of breeding, when minimum time out is smaller, but 'time in' mortality is greater for males. Parameters are as in figure 2*a*, with T_O replaced by T_{min} . There are two quality classes, $q = 0.9$ and $q = 1.1$, each sex comprising 50% of individuals of either quality at maturation (which corresponds to a 10% improvement in mate quality for choosy individuals as in figure 2*a*). (a) OSR in the 'no care' setting, compared to the invasion-model solution; deviations occur once signals evolve (see (b)), affecting mortality rates of the sexes. Solid curve, invasion model; circles, full signalling model with no care. (b–d) Signals of males and females (averaged over qualities), and choosiness (measured as the proportion of mates rejected) of males and females, in the different parental care scenarios as indicated. Arrows indicate the onset of choosiness (female, then mutual) in the invasion model; the full signalling model requires higher cost C before choosiness sets in. (b) No care, (c) additive care and (d) synergistic care. Black squares, male signal; black circles, female signal; white squares, male choosiness; white circles, female choosiness.

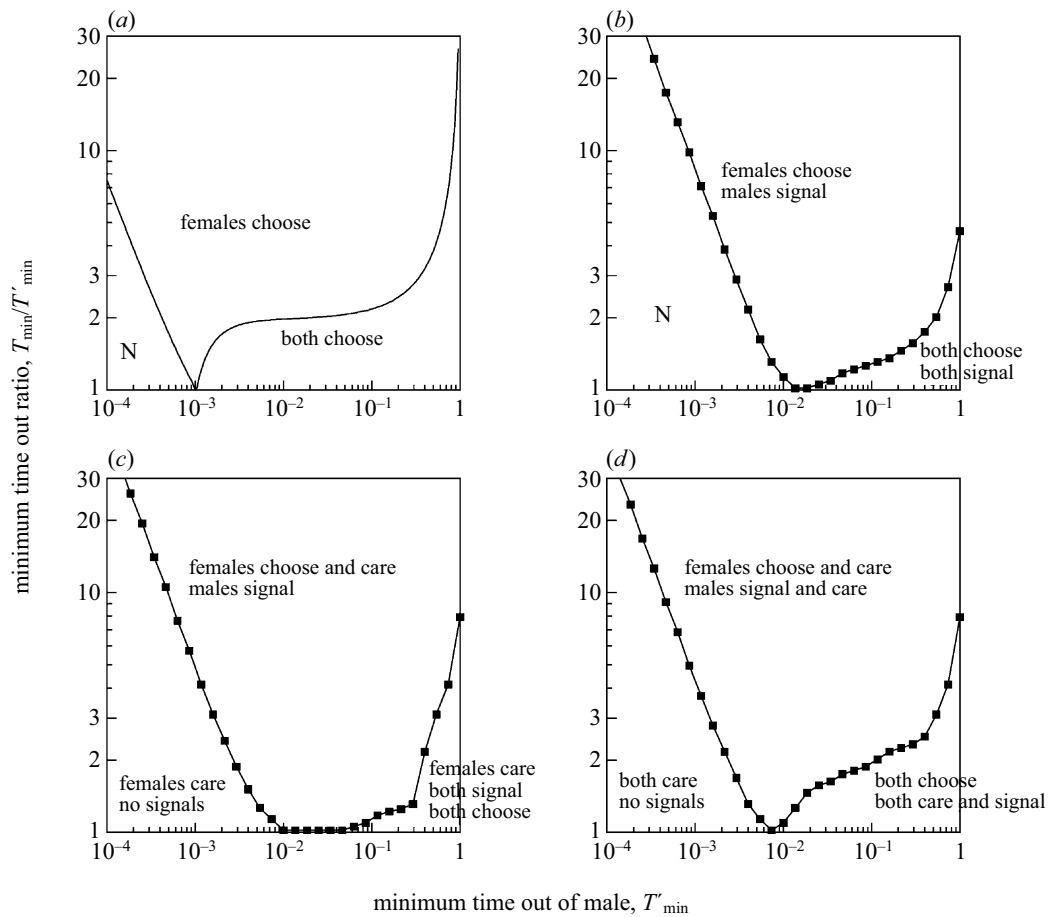


Figure 5. Choosiness, care and signalling in (a), the invasion model, (b–d), the full signalling model, when sexes differ only in their minimum time out T_{\min} ($=T_O$ for the invasion model). Female time out is T_{\min} is higher than the male time out T'_{\min} , by a factor indicated on the y-axis (extending the y-axis downwards would produce mirror image solutions). If times out are small (implying low cost of breeding), neither sex is choosy; if times out are large and not too dissimilar, both sexes are choosy. Large differences in times out lead to female choice without male choice. Parameters used: quality q takes six discrete values between 0.5 and 1.5, with frequencies derived from the normal probability density function (mean 1, s.d. 0.07). The corresponding parameters in the simple invasion model are $p = 0.948$, $q = 1.027$ (maximizing $(1 - pq)/(p(1 - q))$ under the given distribution). All basic mortality rates (before signalling) equal unity, and signal cost during breeding $\gamma = 0$.

than differential minimum time investment in breeding, we now consider solutions with varying minimum times out of the two sexes, but with no other asymmetries. Figure 5 depicts solutions with the less investing sex on the x-axis and the more investing sex on the y-axis. For convenience, these are termed males and females, but solutions remain unchanged if their roles are swapped. According to the analytical invasion model, mutual choice requires a large time out (leading to high breeding cost, equation (2.1b)) in both sexes. Also, the difference in the time out between the two sexes should not be too large; otherwise only one sex is choosy (figure 5a). If times out are small for both sexes, neither sex should be choosy (marked with 'N' in figure 5a).

In the full signalling model, mutual choice occurs at a narrower parameter range than in the invasion model (figure 5b–d). Again, this is because signalling-induced mortality and choice-induced reductions in mating rate select against choosiness. However, the results from the full signalling model are qualitatively very similar to the invasion model: mutual choice requires that the time out is both long and of roughly similar length in both sexes.

The longer the times out, the bigger differences in time out between sexes can still lead to mutual choice. The best prospects for mutual choice again occur with synergistic benefits of care (figure 5d). Even there, however, too large differences in time out will lead to a setting where both sexes care, but only one sex remains selective and the other signals.

Even though we are not assuming any differences between the sexes apart from the minimum time out in figure 5, mortalities and parental investment evolve to be sex specific. Therefore, the OSR is no longer simply determined by the time out ratio, but instead shows a complicated relationship to the strategies of the two sexes (figure 6 shows the OSR for synergistic parental care). If the times out of sexes are similar and large, so that neither sex has many breeding attempts per lifetime, mutual choice can occur even at relatively highly biased OSRs (greater than 3.5; figure 6). But highly biased OSRs may also occur in situations where breeding is cheap for both sexes, and no choice evolves (left of the 'females choose' line in figure 6). Finally, as in figure 4, intense signalling may impose such a heavy mortality cost on the signalling

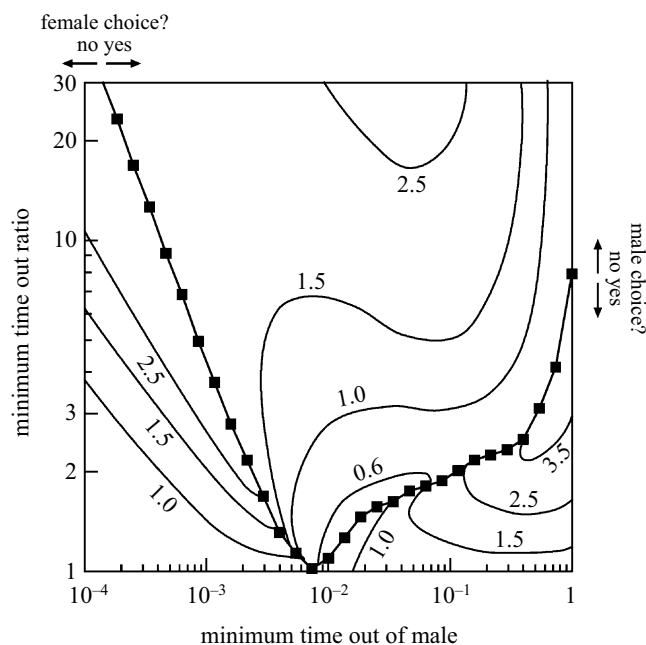


Figure 6. Contour lines for the OSR in the setting of figure 5*d*. The solid curve with squares indicates qualitative changes in male or female strategies, and the OSR changes abruptly at such boundaries. Highly biased OSR does not necessarily associate with single-sex choosiness, nor does a female-biased sex ratio (even OSR < 0.6 males : females) prevent females, rather than males, from being choosy, when females have a longer time out. The low OSR is produced by high male signalling effort, which kills off males at a high rate.

sex, that they become the minority in the mating pool—yet they remain the competitive sex as they suffer lower costs through each breeding attempt (OSR reaches values less than 0.6 males : females in the region where only females are choosy, figure 6).

We have derived the results so far assuming that $\gamma = 0$, i.e. that signalling does not affect mortality during breeding itself. Fitzpatrick *et al.* (1995) argued that if signals have fecundity costs in addition to viability costs, the trade-off between offspring production and ornamentation should limit the evolution of exaggerated ornaments. Our results support this prediction: if signals are retained into the breeding season, during which they continue to be costly, the prospects for mutual choice and signalling are meagre. Just half of the ‘time in’ cost ($\gamma = 0.5$) is sufficient to remove signals from both sexes in all different scenarios of parental care, if sexes have symmetric roles (in the example of figure 7; other parameters yielded similar results). However, mutual signalling tolerates costs that are incurred during the breeding season to some extent (figure 7); signals based on the handicap principle can be selected for and favoured by the opposite sex, even if this means a reduction in the parenting abilities of the signalling sex (see also Kokko 1998). If only one sex signals, the cost during the breeding season hardly affects the signal, even if both sexes provide some care. If the signalling sex does not provide care, the ‘time out’ is too short to influence the total cost of the signal to any appreciable degree. If the signaller does provide care, it will more probably compensate for increased signal cost by reducing

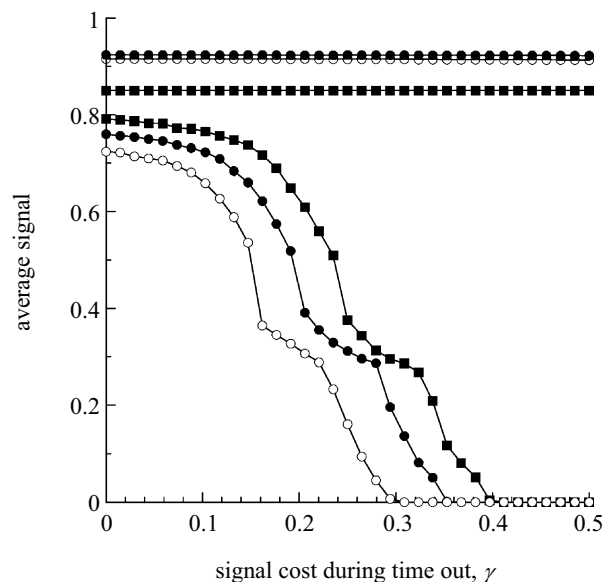


Figure 7. Average mutual signals (lower three curves) and male-only signals (upper three curves), as a function of signal cost during time out, γ . Minimum time out is relatively high for both sexes in the lower three curves ($T_{\min} = T'_{\min} = 0.05$), but much lower for males in the upper three curves ($T_{\min} = 0.05, T'_{\min} = 0.001$). Mutual signals only persist if they are not very costly during breeding. Signals in the sex with the shorter minimum time out can persist even if they are costly during breeding; if this sex also provides care, the response to an increasing signal cost is a reduction in parental care rather than in signalling effort. White circles, no care; black circles, additive care; black squares, synergistic care.

its parenting effort, not by removing the signal (in the example of figure 7, males who provide ‘synergistic care’ reduce their care time from $T'_p = 0.03$ to $T'_p = 0.017$ when γ increases from 0 to 0.5).

3. DISCUSSION

Our model shows that the results of Kokko & Monaghan (2001) are robust: contrary to prevailing theory (Kvarnemo & Ahnesjö 1996; Parker & Simmons 1996), the OSR is not the most fundamental determinant of competition for matings and choosiness in the two sexes. Triversian parental investment (Trivers 1972)—which in our life history setting equals the mortality cost of breeding—has a strong impact on choosiness and competition, which is not fully captured by its effect on the OSR. Males do not always invest more in competitive traits (signalling) than females when they are the more common sex in the mating pool. This is because both sexual strategies and the OSR are influenced by sex ratio at maturation and by the sex-specific mortalities during breeding and non-breeding (mate searching) activities. Consider a case where, at equilibrium, sex roles are not reversed: females care more than males but males signal more strongly, and males experience increased mortality because of costly signalling (Promislow 1992; Promislow *et al.* 1992; Owens & Bennett 1994). While caring tends to make the OSR male-biased, signalling-induced mortality pushes it back towards a female bias. The exact balance will depend on

details of the life history, but overall there is no guarantee that the OSR is always biased towards the more competitive (more strongly signalling) sex.

However, all other factors being equal, biasing the OSR makes the limiting sex more choosy (equations (2.1) and (2.2)) and the limited sex more competitive (Kokko & Monaghan 2001). Empirical work within species with flexible sex roles (reviewed in Kvarnemo & Ahnesjö 1996), as well as interspecific analyses (Clutton-Brock & Vincent 1991), generally agree with theory purely based on OSR. Yet, no studies have set out to test explicitly if the switch in sex roles occurs at OSR = 1, or at some other value, as our model would suggest. It is certainly not easy to measure the OSR and parental investment in the field without resorting to 'proxies' such as PRRs (Kvarnemo & Ahnesjö 1996), yet this task seems necessary to test the life-history model of sexual competition and choosiness. In species where adults do not change their breeding performance much as they age, and breeding is costly in terms of parental survival, the cost of breeding may be relatively easy to measure: it equals the probability of dying as a consequence of the current breeding attempt.

We have replaced the very general and abstract formulation of competition for mates of the approach of Kokko & Monaghan (2001) by a detailed model of quality-dependent signalling and choice. This approach has the advantage of added realism, but it inevitably means that we have obtained results for particular cases and assumptions only. Also, unlike Kokko & Monaghan (2001), we exclude competition that does not rely on choice in the opposite sex. The qualitative similarity of the results of our model and that of Kokko & Monaghan (2001) is encouraging: factors promoting choosiness are high species-specific mate-encounter rate, high sex-specific mate-encounter rate (OSR biased towards the opposite sex), high cost of breeding (allowing only few breeding attempts in a lifetime), low costs of mate searching, and highly variable quality of the opposite sex. Of these, the sex-specific mate-encounter rate is the only factor that is automatically high for one sex if it is low for the other. Other variables can promote or exclude choosiness in both sexes simultaneously. Empirical support for these predictions already exists (sex-specific encounter rate and cost of breeding (Simmons 1992; Berglund 1994; Balshine-Earn 1996; Bonduriansky & Brooks 1998; Kvarnemo & Simmons 1998; Engqvist & Sauer 2001); costs of mate searching (Magnhagen 1990, 1991; Forsgren 1992; Forsgren & Magnhagen 1993; Berglund 1993); variation in mate quality (Kvarnemo & Simmons 1999; Kvarnemo & Forsgren 2000)), but it remains to be investigated if our modelling can explain why specific factors are more important in certain species than others (e.g. Balshine-Earn 1996; Kvarnemo & Simmons 1999; Kvarnemo & Forsgren 2000).

Although our results generally support the results of the simple invasion model (Kokko & Monaghan 2001), we find that the coevolution of parental care and mating strategies will cause differences in the quantitative values at which switches in strategies occur. The most significant difference between the model of Kokko & Monaghan (2001) and our results is found in the evolution of mutual mate choice. Evolving choosiness in one sex will reduce the mating rate of the opposite sex, which is selected to

become less choosy and more competitive as a result. This tendency of sexual strategies to diverge hinders the evolution of mutual choice. Whether mutual choice can be maintained depends on the needs of offspring. Mutual choice is unlikely in species with no parental care. If care is necessary and either parent can provide it, the likely outcome is that only one sex—the one with the longer physiological 'minimum time out'—will provide prolonged care (see also Queller (1997); although factors such as sequential monogamy may provide reasons for exceptions (S. Balshine, personal communication)). This amplifies the difference in total time out between the sexes, making mutual choice again less, not more, likely. Instead, mutual choice will be favoured if synergistic benefits of biparental care greatly improve offspring survival (Lack 1968; Larsen 1991; Motro 1994). In this case, the 'times out' of both sexes will be substantial. If the parental investments of both sexes are large and also not too different from each other, the conditions for stable mutual mate choice are satisfied. We therefore predict that mutual choice should mostly occur when biparental care is essential for the survival of offspring.

Why is mutual choice apparently the exception rather than the rule in nature? One possibility is that mutual choice is more common than thought. For example, zebra finches (*Taeniopygia guttata*) are sexually dimorphic, but males prefer highly fecund females (Monaghan *et al.* 1996). Our model indeed predicts that mutual choice can evolve when the encounter rate of potential mates is high—which is true for the zebra finch that lives in large colonies. Nevertheless, female zebra finches lack any conspicuous mate acquisition effort, and it is unknown how male finches assess female fecundity. It is also worth keeping in mind that male choice may be cryptic (Engqvist & Sauer 2001), meaning that males spend less mating effort on low-quality females.

The above two processes of divergence (divergence in mating rates once choosiness spreads, and possible divergence in 'time out' under evolving parental care) may explain why conditions for mutual choice are not too often fulfilled. Even under biparental care, our model produces clear sex roles (signalling and competition in one sex only) instead of mutual choice and signalling in both sexes, if parental investment differs considerably between sexes. Apart from the processes considered in our model, sex differences such as EPFs can cause divergence in sexual strategies. Extra-pair paternity enables a male to fertilize the eggs of several females, while he may still provide care for just one clutch (Birkhead & Møller 1998). Such a scenario is not explicitly considered in our model, which allows individuals to refrain from parental investment but assumes that they invest equally in each brood. Kokko (1999) derived a model of the coevolution of parental care and extra-pair paternity, and predicted that males should invest more in mate acquisition at the expense of paternal care, and females compensate by providing more care, as EPF frequencies increase. Depending on how accurately males can assess their paternity, this may lead to either a mating system with a stable fraction of extra-pair young and active mate acquisition in one sex only, or to a complete breakdown of biparental care and evolution towards polygyny—both examples of diverging sex roles.

We argue that such divergence mechanisms explain the

rarity of mutual mate choice better than biases in the OSR. Our model shows that mutual choice can, as such, tolerate strong biases in the OSR, as long as both sexes vary in quality, mortality during mate-searching is not too high, and each breeding attempt is costly for the individual and this cost does not differ greatly between the sexes. By contrast, if breeding imposes little mortality cost on either males or females, neither sex should be choosy, regardless of OSRs. Thus, our model shows that all three scenarios of no choosiness, choosiness in one sex only, and mutual choice, can exhibit highly biased OSRs. An empiricist testing our theory should attempt to measure both the difference in parental investment between the sexes and the OSR, to find out which influences the mating system more strongly.

Given that mutual choice should be relatively rare, the question remains whether sexually monomorphic signals are indeed signs of adaptive mutual choice, or a by-product of genetic constraints on sex-limited trait expression (Lande 1980). Genetic constraints can take considerable time to break down (Rhen 2000), which could allow ‘maladaptive’ signalling to persist in populations. This question appears to require empirical studies. If signalling is adaptive in one sex only, we expect the limited sex not to be choosy, and fitness to be negatively related to the expression of the ornament in the limiting sex (assuming that the ornament is costly to bear). Alternatively, a preference for a trait, rather than the trait itself, may be selected for in one sex, and evolve as a correlated character in the other (Hill 1993). Birds—a particularly well-studied taxa in which biparental care is the norm—provide evidence for frequent evolutionary changes from dimorphism to monomorphism (Irwin 1994; Burns 1998), which suggests that showiness can be selected for in both sexes independently of each other (Amundsen 2000). Regarding the interpretation of monomorphic and dimorphic signalling, an interesting feature of our model is that it often produces signals of roughly the same magnitude even if sexes differ considerably in their choosiness (in the proportion of mates rejected), assuming that conditions for mutual choice are otherwise met. While this does not reject alternative explanations, the result means that it is not necessary to evoke genetic constraints to explain monomorphic signalling, when the intensity of competition appears to differ between the sexes.

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APPENDIX A: SOLVING THE MODEL: FITNESS AND THE OSR

The rate $m(q, q')$ with which a focal individual of quality q mates with a partner of quality q' is

$$m(q, q') = Mn'(q')p[s'(q'), c(q)] p[s(q), c'(q')]. \tag{A 1}$$

The overall rate at which the individual mates is the sum of rates over the qualities of the opposite sex, $\int_{q'} m(q, q') dq'$ (figure 1).

An individual that is born at time $t_0 = 0$ gains fitness every time it finishes breeding (time out). The probability that it does so at time t is $P_1(q, t)T_0^{-1}$, where $P_1(q, t)$ denotes the probability that the individual is in the ‘time out’ state at time t , and T_0^{-1} indicates the rate of finishing breeding when in this state (figure 1). Total lifetime fitness equals

$$W(q) = \int_{t=0}^{\infty} P_0(q, t) T_0^{-1} G(q) dt, \tag{A 2}$$

where $G(q)$ describes the expected fitness gain from a single brood. $G(q)$ is the expected value of $F(q, q')$, taking into account probabilities of mating with different qualities q' as follows:

$$G(q) = \frac{\int_{q'} m(q, q') F(q, q') dq'}{\int_{q'} m(q, q') dq'}. \tag{A 3}$$

Here, $m(q, q')$ is given by equation (A 1), and $F(q, q')$ by equation (2.7).

We now need to solve the probability $P_0(q, t)$ that an individual of quality q , born at $t_0 = 0$, is alive and in ‘time out’ state at time t , and the probability $P_1(q, t)$ that it is alive and in ‘time in’ state at this time. The dynamical system (figure 1) is described by the set of differential equations

$$\begin{cases} \frac{dP_0(q, t)}{dt} = P_0(q, t)(-\mu_0 - T_0^{-1}) + P_1(q, t) \int_{q'} m(q, q') dq' \\ \frac{dP_1(q, t)}{dt} = P_0(q, t)T_0^{-1} + P_1(q, t)(-\mu_1 - \int_{q'} m(q, q') dq') \\ P_0(q, 0) = 0 \\ P_1(q, 0) = 1 \end{cases} \tag{A 4}$$

The solution of equation set (A 4) is

$$P_0(q, t) = A^{-1}a_{12} \exp\left[\left(a_{11} + a_{22} - A\right)\frac{t}{2}\right] [\exp(At) - 1], \tag{A 5}$$

$$P_1(q, t) = (2A)^{-1}(a_{11} + a_{22} + A) \exp\left[\left(a_{11} + a_{22} - A\right)\frac{t}{2}\right] + (-a_{11} + a_{22} + A) \exp\left[\left(a_{11} + a_{22} + A\right)\frac{t}{2}\right]. \tag{A 6}$$

Here, we use the shorthand notations

$$\begin{aligned} a_{11} &= -\mu_0 - T_0^{-1}, \\ a_{12} &= \int_{q'} m(q, q') dq, \quad a_{21} = T_0^{-1}, \\ a_{22} &= -\mu_1 - \int_{q'} m(q, q') dq', \end{aligned} \tag{A 7}$$

$$\text{and } A = \sqrt{a_{11}^2 + 4a_{12}a_{21} - 2a_{11}a_{22} + a_{22}^2}.$$

Integrating equation (A 5) yields

$$\int_{t=0}^{\infty} P_0(q, t) dt = \frac{a_{12}}{a_{11}a_{22} - a_{12}a_{21}}. \tag{A 8}$$

Substituting equations (A 3) and (A 8) into (A 2) and simplifying yields female lifetime fitness as follows:

$$W(q) = \frac{\int_{q'} m(q, q') F(q, q') dq'}{T_O \left(\mu_O \mu_I + \mu_I T_O^{-1} + \mu_O \int_{q'} m(q, q') dq' \right)} \quad (\text{A } 9)$$

Note that the values of μ_I , μ_O , $m(q')$, $F(q')$ and T_O depend on the strategic choices $s(q)$, $c(q)$ and T_P of females and males, as indicated by equations (2.5) and (2.7).

Breeding is assumed to be continuous, so that there is a continuous quality-dependent influx $f(q)$ of newly matured individuals into the population. When each individual's life is governed by equation (A 4), the relative density of 'time in' females of quality q is proportional to the probability $P_1(t)$ that it is alive and in 'time in' at any time of its potential lifespan, i.e. integrated over all possible ages t :

$$\begin{aligned} n(q) &= Df(q) \int_{t=0}^{\infty} P_1(t) dt = Df(q) \frac{a_{11}}{a_{12}a_{21} - a_{11}a_{22}} \\ &= Df(q) \frac{\mu_O + T_O^{-1}}{\mu_O \mu_I + \mu_I T_O^{-1} + \mu_O \int_{q'} m(q') dq'} \end{aligned} \quad (\text{A } 10)$$

Here, D is a factor that scales population density. We choose D such that $\int_q n(q) dq + \int_{q'} n'(q') dq' = 2$, which produces a density of unity for each sex if the OSR is even. The OSR β , expressed as males : females in the non-breeding population, then equals

$$\beta = \alpha \frac{\int_{q'} n'(q') dq'}{\int_q n(q) dq} \quad (\text{A } 11)$$

We use $\alpha = 1$ in all our examples.

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