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LETTER

Can non-directional male mating preferences facilitate honest female ornamentation?

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Abstract

Recent studies have demonstrated male mate choice for female ornaments in species without sex-role reversal. Despite these empirical findings, little is known about the adaptive dynamics of female signalling, in particular the evolution of male mating preferences. The evolution of traits that signal mate quality is more complex in females than in males because females usually provide the bulk of resources for the developing offspring. Here, we investigate the evolution of male mating preferences using a mathematical model which: (i) specifically accounts for the fact that females must trade-off resources invested in ornaments with reproduction; and (ii) allows male mating preferences to evolve a non-directional shape. The optimal adaptive strategy for males is to develop stabilizing mating preferences for female display traits to avoid females that either invests too many or too few resources in ornamentation. However, the evolutionary stability of this prediction is dependent upon the level of error made by females when allocating resources to either signal or fecundity.

Keywords

Female ornamentation, male mate choice, mating preferences, sexual selection.

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INTRODUCTION

Most studies of mating preferences and the sexual selection that they generate have focused on female mating preferences, perhaps owing to their ubiquity in nature (Andersson 1994) and the long-standing theoretical expectation that mating preferences are adaptive in females when they invest more heavily in reproduction than males (Trivers 1972). Subsequent theoretical work has suggested that the link between investment and choice is a feedback loop rather than a straightforward causative connection (Queller 1997; Kokko & Johnstone 2002; Wade & Shuster 2002; Kokko & Jennions 2003). Comparatively less attention has been given to the study of male mating preferences. However, there are a growing number of empirical studies demonstrating male mating preferences in species with conventional sex roles (birds: Jones & Hunter 1993; Amundsen 2000; fishes: Amundsen & Forsgren 2001, insects: see Bonduriansky 2001 for a review). Studies of male mate choice are thus interesting: if male mate choice is generally difficult to achieve (Kokko & Johnstone 2002), examples of such choice will shed light on the borderline conditions for the evolution of mate choice in general.

Theoretically, the evolution of male mating preferences for direct benefits is favoured whenever female mate quality variance is high, the cost of searching for a mate is low or male parental investment is high (Burley 1977; Parker 1983; Owens & Thompson 1994; Johnstone *et al.* 1996; Kokko & Monaghan 2001). However, even in circumstances where males can receive direct benefits from mate choice because of substantial variance in female quality, male preferences are unlikely to evolve without a cost associated with male mating (Bonduriansky 2001; Kokko & Monaghan 2001). That is, if a male can mate without any cost at all, he should never reject a female even if she provides very low fecundity benefits, because mating with this female does not form a trade-off with fitness acquired in future matings. Examples of such mating costs include opportunity costs of mating with one female over another of potentially higher quality (Kokko & Monaghan 2001) or the physiological cost of sperm production which may limit the number of females that a male can successfully inseminate over a set period of time (Reinhold *et al.* 2002).

When choosing female mating partners, males are faced with the problem of how to assess a female's quality. Studies report that for species in which fecundity variance is high, such as insects and fishes, male mating preferences are often for female traits that are highly correlated with fecundity such as body mass or body size (Itzkowitz *et al.* 1998; Bonduriansky 2001), suggesting a preference for the direct benefit of increased fecundity. However, in some species males may be unable to assess female fecundity via a direct assessment of mass or size, for example, if female body size does not scale predictably with fecundity or when courtship occurs during flight as is the case for some insects (LeBas *et al.* 2003). In such cases the evolution of female 'ornamentation' or signal traits may be expected (e.g. Hill 1993; Hunt *et al.* 1999; Amundsen & Forsgren 2001; Domb & Pagel 2001; Velando *et al.* 2001; LeBas *et al.* 2003). The evolution of traits that signal mate quality is more complex in females than in males, because females provide the bulk of resources for the developing offspring. To ensure honest signalling, the ornament should be costly, but males should not prefer females that suffer such a high cost of signalling that their fecundity is greatly reduced (Fitzpatrick *et al.* 1995; see also Kokko 1998). Consequently, sexual selection for the evolution of female ornaments may be fundamentally self-limiting (Fitzpatrick *et al.* 1995).

However, it has been shown theoretically – albeit within a different context (female choice for direct benefits provided by males) – that when direct benefits are being sought, if there is sufficient quality variation in one sex, a costly trait can function as a simultaneous cue for both direct and indirect benefits, despite an intrinsic trade-off between the trait and the direct benefit obtained (Price *et al.* 1993; Kokko 1998). This suggests that male preferences for female traits that signal direct benefits can be adaptive.

Further developing the ideas of Fitzpatrick *et al.* (1995), a means by which female ornamentation may persist but essentially remain self-limited is via the evolution of male mating preferences that exert stabilizing sexual selection on female ornaments. The logic is relatively straightforward: if males seek direct fecundity benefits when they choose female mating partners, they may avoid females that invest too heavily in signals at the expense of fecundity. Alternatively, if females do not invest sufficient resources in signals, males will not be able to assess their potential fecundity. Thus under this scenario male mating preferences should be convex and generate stabilizing sexual selection on the female indicator traits.

In this paper, we explore theoretically the evolution of male mating preferences for direct benefits under the particularly unique constraint placed on females – that honest signals must be traded off with quality (which equals fecundity). We use a mathematical model to ask whether it is possible for males to receive direct fecundity benefits by exercising stabilizing mating preferences for female ornaments that signal quality. Earlier models have not considered whether non-directional rather than directional preferences could form a solution to this problem.

THE MODEL

We developed a model to quantitatively explore how male mating preferences will evolve when female signalling trades off with female quality. In this initial treatment we limit our attention to cases in which males seek direct benefits to match closely the verbal argument posited by (Fitzpatrick *et al.* 1995) and for two additional reasons. First, theory suggests that, in the case of female choice for male traits, indirect selection on mating preferences is likely to be weak when compared with the strength of direct selection (Kirkpatrick & Barton 1997). Second, in the situation of male choice for female signal traits, this result appears to be particularly important. Empirical evidence suggests that in the majority of cases males favour mating with more fecund females (Andersson 1994; Fitzpatrick *et al.* 1995; Bonduriansky 2001) implying a direct benefit to males. Because phenotypic variance in female fecundity is often extreme (e.g. invertebrates and fish), this variation is likely to far exceed any fitness benefit because of the genetic quality of those offspring (Bonduriansky 2001).

We assume that both females and males must obey certain constraints. For computational simplicity, we assume that female quality is normally distributed (mean μ, variance σ_q^2) but truncated such that qualities range between 0 and 1. We denote this frequency distribution by $f(q)$. A female of quality q can choose a signalling effort e, which produces a distribution of signals drawn from a normal distribution with mean e and environmental variance (error) σ_S^2. We assume a truncated distribution for the signal too, such that signals exceeding 1 or falling below 0 are excluded.

Females can detect their own quality and choose the signalling level accordingly, but this signalling decision is also affected by random environmental variation. Thus, a female that 'intends' to produce a signal of strength 0.4 will actually produce a signal drawn from a distribution that centres around 0.4. On the contrary, males can evolve to have either directional or stabilizing preferences, but due to sensory constraints they must have roughly similar preferences for females with similar signals. Male preference is therefore modelled as $\exp(as + bs^2)$, where a and b are parameters that specify female behaviour, and s ($0 \leq s \leq 1$) is the female signal. Negative values of b allow stabilizing selection to occur (to be exact, selection is stabilizing when $-a/b$ falls between 0 and 1). The larger the absolute values of a and b, the steeper the possible changes in preferences with changes in the signal. In our example, we assume $-10 \le a \le 10$ and $-10 \le b \le 10$, but results were qualitatively similar with other values.

If a male uses preferences specified by a and b, a female with quality q has fitness:

$$\int_0^1 F(q-s)\mathrm{e}^{as+bs^2}P(s,e)\mathrm{d}s, \tag{1}$$

where $F(q - s)$ is her fecundity, e^{as+bs^2} is the benefit she draws from being more readily accepted as a mate, and $p(s,e)$ is the distribution of signals s that she produces when her signalling effort equals e. Note that she has positive fitness $F(q)$ even if she does not signal, $s = 0$; thus mating effort for the females has the effect of enhancing fitness (e.g. through reducing the time required to find a mate) but it is not a necessary requirement for mating. Fecundity is defined as:

$$F(x) = \begin{cases} 0 & \text{if } x<0 \\ x^{\alpha} & \text{if } x>0 \end{cases} \tag{2}$$

where $x = q - s$. Thus, fecundity increases with female quality, decreases with her signalling effort, and shows diminishing returns if $\alpha < 1$.

For each quality q of females we obtained the best e that maximizes female fitness, $e^*(q)$. When females use $e^*(q)$, we can calculate the frequency of females $P(s)$ that signal at a level s,

$$P(s) = \int_0^1 f(q)p(s, e*(q))\mathrm{d}q \tag{3}$$

as well as the expected fecundity of those females,

$$E(s) = \frac{\int_0^1 f(q)p(s, e*(q))F(q-s)\mathrm{d}q}{P(s)}. \tag{4}$$

The task of a male is now to choose the best values a and b that maximize the number of his offspring,

$$\frac{\int_0^1 E(s)P(s)\mathrm{e}^{as+bs^2}\mathrm{d}s}{\int_0^1 P(s)\mathrm{e}^{as+bs^2}\mathrm{d}s}. \tag{5}$$

In practice, the stable preference functions used by males are solved iteratively, as in Houston & McNamara (1999, p. 188): $a(t + 1) = (1 - \lambda)\, a(t) + \lambda a^*(e)$, where a^* is the best response to female signalling effort, and λ is a parameter that specifies how quickly evolution proceeds towards the best response. It is worth noting that evolution only proceeds towards an equilibrium if it is convergence stable, not only evolutionarily stable (e.g. Houston & McNamara 1999, pp. 167–170). During our iterative process males are only allowed to respond to females' current signalling effort in a gradual way: the whole population shifts towards parameter values that are currently selected for, but does not reach these values instantly. While this does not constitute a formal proof of convergence stability, in a model like ours that is only numerically tractable, the process very strongly resembles the criterion of allelic substitutions towards an equilibrium that defines convergence stability (see also Houston & McNamara 1999, p. 167).

RESULTS

Figure 1 shows the shape of the stable male preference function, the evolution of a and b over time, as well as the distribution of signalling females and the relationships between net fecundity and female signal, and between signalling effort and female quality. Males evolve to exert stabilizing selection on the female signal. Higher quality females show the largest signalling effort, but the relationship between observed fecundity and the female signal is

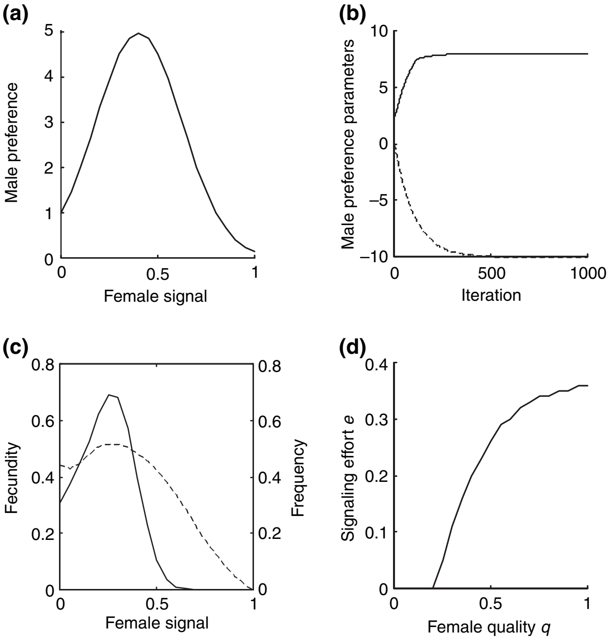

Figure 1 Evolutionary dynamics of male preferences and female signalling effort when female signalling trades off with female quality. (a) The equilibrium mate preference function of males in the evolutionary model. (b) Evolutionary trajectories for mate preference function parameters a (solid line) and b (dashed line). When stabilizing selection evolves, it typically evolves to the maximum degree (i.e. smallest b) allowed by cognitive constraints of males; here, we set this limit at b greater than or equal to − 10. Lower negative values would have produced a more sharply peaked distribution in (a). (c) The frequency of females who signal at a particular strength (solid line), and the mean fecundity of a female who signals at a particular strength (dashed line). (d) Higher quality females give on average stronger signals. Parameters used: $\mu = 0.5$, $\sigma_q^2 = 0.0001$, $\sigma_S^2 = 0.0025$, $\alpha = 0.5$.

hump shaped. This is because the strongest signals are found in females who 'erroneously' (perhaps as a consequence of environmental variance) signal too strongly for their quality, and are penalized with lower fecundity. Therefore, males evolve stabilizing preferences for females that signal at an intermediate level. This result does not require particularly high variance around the optimal female signal; the environmental variance (error) we have used is $\sigma^2 = 0.0001$. Some environmental variance is essential for producing this outcome, otherwise, we could not explain why some females evolve to signal in a way that makes them less attractive to males while also reducing their fecundity.

It is noteworthy that for much of the signal range male choice can be directional: in the example of Fig. 1, the female quality distribution centres around the value 0.5, where signalling effort is in the range of 0.2–0.3 (Fig. 1d). Therefore, average females lie in the region where male preferences favour more strongly signalling females (e.g. 0.3 over 0.2, Fig. 1a). Also, average female effort $e^*(q)$ evolves to be below the value that males prefer most. This means that for most females, increasing effort is selected for in terms of sexual selection, but balanced by natural selection penalizing their fecundity (most females show smaller signals than males prefer, Fig. 1c).

Male choice tends to break down and evolves towards no preference or indeed a preference for non-signalling females, if female signalling errors are so large that signalling becomes an unreliable cue of female quality, if females do not vary enough in their quality or if the initial values of *a* and *b* do not yield a large enough preference for female signal evolution (Fig. 2). This is not surprising, as it is a qualitatively similar argument as the invasion barrier present in conventional models of coevolving signals and preferences (Payne & Pagel 2001; Kokko *et al.* 2002). However, it is interesting that male preferences can evolve to become stabilizing from either a directional or a stabilizing starting point (Fig. 2).

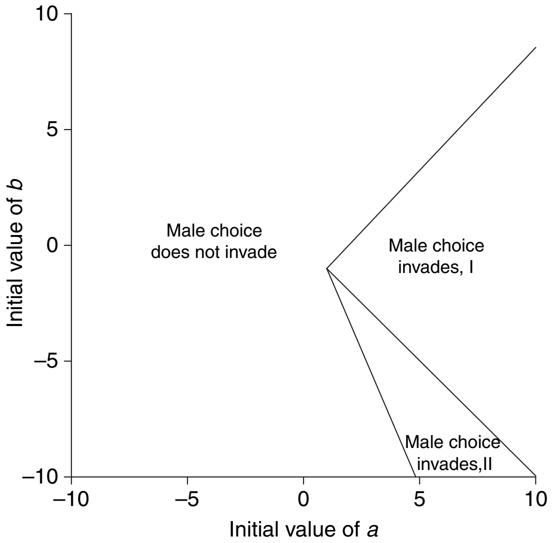

Figure 2 The evolutionary endpoint depends on the starting conditions, i.e. the initial values of *a* and *b* that determine male preferences in an ancestral population. In the absence of the male preference ($a < 0$), females will not evolve to signal, and in the absence of female signals the evolution of male preferences does not proceed. However, the threshold value required for the initial value of *a* also depends on the initial value of *b*. In the region 'male choice invades I', the initial values of *a* and *b* imply directional selection on the female trait across all female signal efforts. In region II, the initial value of *b* implies stabilizing selection. In both cases, the same equilibrium is reached (depicted in Fig. 1), where male preferences evolve to be stabilizing. Parameter values as in Fig. 1.

DISCUSSION

It has been suggested that, owing to a high cost and corresponding diversion of resources from reproduction, intersexual selection for the evolution of excessively ornamented females is likely to be self-limited as a consequence of male mating behaviour (Fitzpatrick *et al.* 1995). We developed a mathematical model to assess if it was possible for this self-limitation to take the form of male mating preferences that exert stabilizing sexual selection on the female display trait. The results suggest that stabilizing male mating preferences are possible, and that at equilibrium, males can draw true fitness benefits from expressing such a preference. Further, females do maintain a degree of ornamentation when preferences are stabilizing.

However, it is theoretically puzzling how a male stabilizing preference may persist. Heavily ornamented females suffer a double cost, low attractiveness and, in addition, their fecundity is greatly reduced owing to a large investment in ornamentation. Earlier models that assume optimal decisions therefore predict that preferences for traits signalling direct benefits should be directional, rather than stabilizing (Kokko 1998). From the current modelling results, it appears that the necessary addition to produce stabilizing male mating preferences is a level of error that females make when allocating resources to signal and fecundity. The error should be sufficient to make males avoid too ornamented females, but not so large that the signal fails to accurately reflect quality. In the latter situation the system evolves towards non-signalling females.

Our study highlights how 'errors' in allocation between traits can have a qualitatively important influence on mate choice. Note that the error we refer to is not exclusively decision-making error, rather it encompasses stochastic environmental variation such as environmental variations during development as well that may cause a female to signal at a level that deviates from her true quality. If there is a possibility that some individuals signal 'too strongly' and therefore lie at a suboptimal point along a trade-off curve, we expect this to curb the evolution of preferences in the opposite sex. Erroneous, suboptimal behaviour is a biologically realistic assumption: it is unreasonable to assume all individuals to be perfectly optimized (McNamara *et al.* 1997). Including such variability in behaviour has been shown to lead to qualitative differences in evolutionary outcomes, e.g. in the context of fighting behaviour (McNamara *et al.* 1997; Morrell & Kokko 2003), and the formation of cooperative breeding groups (Kokko 2003). Our study adds the evolution of mate preferences to this list. An interesting question for further study is whether perception errors by males could contribute to the signalling system in a similar way as the errors made by females that we focused on in the current model. As perception errors tend to shift the mating system towards random mating, the range of parameter values where females signal could be to some extent reduced.

Although many reports of male mating preferences suggest that males favour larger female ornaments, some recent empirical results suggest the existence of stabilizing male mating preferences for female ornaments. Generally, empirical estimates of nonlinear sexual selection on female signal traits are scarce (but see LeBas *et al.* 2003). In the fruit fly, *Drosophila serrata*, both females and males choose mates on the basis of their cuticular hydrocarbons (CHCs) (Chenoweth & Blows 2003). When the form of sexual selection generated by mutual mate choice was compared between the sexes, as expected, female choice generated directional sexual selection for the evolution of extreme CHC blends. However, in sharp contrast male choice generated convex nonlinear sexual selection that resembled stabilizing selection on female CHCs (Chenoweth & Blows 2005).

Manipulative evidence for a trade-off between female ornamentation and fecundity exists for *Drosophila melanogaster*. Gene knockout techniques have demonstrated that pheromonal CHCs, which are important targets of male mate choice, display a direct resource allocation trade-off with egg production (Wicker & Jallon 1995). Furthermore, the ovaries and the cuticle appear to be competing targets for the deposition of internal hydrocarbons from the same resource pool in many insects (Schal *et al.* 1994). Clearly, more empirical work will be needed to gain a better understanding of both the strength and form of sexual selection acting on female ornaments via male mate choice and also the nature of resource allocation trade-offs between female ornaments and fecundity.

The rarity attributed to male mate choice for female ornamentation (Bonduriansky 2001), may have been overstated partly for methodological reasons. Experiments and analyses designed to find directional preferences may not detect nonlinear mating preferences. For example, commonly used fixed-stimulus mate choice experimental designs cannot detect nonlinear mating preferences (Wagner 1998). Moreover, if preferences are predominantly nonlinear, this experimental design will lead to the conclusion of no male mate choice.

Our model is based on direct benefits only. Naturally, any kind of mating biases for direct benefits always leads to the possibility of indirect benefits (Jennions & Petrie 2000; Kokko *et al.* 2003). Given the typically large environmentally determined component of phenotypic variance in female fecundity, we consider it unlikely that indirect benefits play a large role in male mate choice evolution (Bonduriansky 2001). However, where they do, the likely effect is a shift of the preference towards more uniform preferences for strongly signalling (i.e. high quality, Fig. 1d) females. Outlining the conditions under which such benefits could be important in male mate choice is clearly beyond the scope of the current paper, but it remains an interesting question that future theoretical work should address.

In conclusion, our results suggest that non-directional (stabilizing) mating preferences for female ornaments can be an adaptive strategy for males and that females do maintain a degree of ornamentation under such conditions. This result is consistent with the idea that male interest in female reproduction limits the resources expended by females on sexual ornaments. Future theoretical and empirical studies of male mating preferences and the sexual selection that they generate on females are needed to further our understanding of the evolution of female ornamentation.

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