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Research article

Treat 'em mean, keep 'em (sometimes) keen: evolution of female preferences for dominant and coercive males

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Abstract. How should females choose their mates if choice is not completely free, but at least partly dictated by outcomes of male–male competition, or sexual coercion? This question is of central importance when evaluating the relationship between sexually antagonistic 'chase-away' scenarios and models of more traditional female choice. Currently, there is a mismatch between theories: indirect benefits are seen to play a role in conventional mate choice, whereas they are not predicted to have an influence on the outcome if matings impose direct costs on females. This is at odds with the idea that resistance and preference are two sides of the same coin: either leads to a subset of males enjoying enhanced mating success. In the same way as choosy females benefit from mating with sexy males if this yields sexy sons, females could benefit from being manipulated or 'seduced', if the manipulative or seductive ability of males is heritable. Here I build a model where male dominance (or coerciveness) improves his mating success, and this relationship can be modified by female behaviour. This clarifies the definitions of resistance and preference: resisting females diminish the benefit a male gains from being dominant, while preferences enhance this pre-existing benefit enjoyed by dominant males. In keeping with earlier theory, females may evolve to resist costly mating attempts as a counterstrategy to male traits, particularly if male dominance is environmentally rather than genetically determined. Contrary to earlier results, however, indirect benefits are also predicted to influence female mating behaviour, and if sufficiently strong, they may produce female preferences for males that harm them.

Key words: dominance, indirect benefits, mathematical model, quantitative genetics, sexual coercion, sexual conflict

Introduction

The stereotype of a species with 'traditional' female choice depicts males that attempt to convince females of their quality as a mate, and females that are free to choose among the displaying males. Researchers interested in this scenario are fascinated by the benefits that the females might gain through their choosy behaviour. Recently, increasing attention has been paid to coercive cases, where males attempt to overcome female resistance to mate (for recent reviews, see Chapman et al., 2003; Pizzari and Snook, 2003). Examples include forceful mating (e.g., Clutton-Brock and Parker, 1995; McKinney and Evarts, 1998;

Markow, 2000; Bisazza *et al.*, 2001) and male pre-copulatory mate-guarding, which often takes the form of extended physical contact (Rowe, 1992; Jormlainen, 1998; Watson *et al.*, 1998; Arnqvist and Rowe, 2002). Various less obvious tactics exist too: males may damage female organs through physical action (Crudgington and Siva-Jothy, 2000; Stutt and Siva-Jothy, 2001; Reinhardt *et al.*, 2003) or cause chemical damage (Chapman *et al.*, 1995). The adaptive significance of such male traits is not always clear (Morrow *et al.*, 2003), but one possibility is an elevated level of paternity if females, when made to suffer costs during mating, lay eggs sooner or remate less often (Johnstone and Keller, 2000).

When mating is costly, females are expected to evolve 'resistance' to male mating attempts, rather than any form of preference (Holland and Rice, 1998). The fact that some males appear to be favoured over others is then seen simply as a reflection of their superior seductive or coercive ability which overcomes female resistance (Holland and Rice, 1998), rather than any adaptive behaviour from the female point of view. Multiple mating may still be optimal for the female if it is cheaper than resisting mating attempts ('convenience polyandry', Thornhill and Alcock, 1983; Rowe, 1992; Lee and Hays, 2004).

However, females have been shown to have a diverse array of responses to male coercion. Males often form dominance hierarchies, and the status of a male within this hierarchy has been found to correlate with his mating success in numerous species (e.g. feral fowl, Pizzari, 2003; elephant seals, Haley, 1994; fairy-wrens, Double and Cockburn, 2003). Is this simply due to the fact that a male who is dominant over other males can also more efficiently coerce females into mating, or do females actively seek to mate with dominant males? In experiments where females are free to choose, they sometimes show preferences for dominant males, but other times the opposite is found (reviewed in Qvarnström and Forsgren, 1998; Wong and Candolin, in press).

The cases where mating with dominant males offers females some form of direct benefit are relatively easy to explain (e.g. food and vigilance in feral fowl, Pizzari, 2003), as are those where subordinate males offer females better resources, such as superior parental care (e.g. sand gobies, Forsgren, 1997; Pacific blue-eyes, Wong, 2004). The diversity of possible (direct) benefits and costs could then explain why in some cases female behaviour appears to enhance, and in other cases to counteract, effects of male dominance on his mating success (Qvarnström and Forsgren, 1998; Moore and Moore, 1999; Ophir and Galef, 2003; Wong and Candolin, in press).

However, the matter is not that simple. The co-evolution of male dominance and female mating behaviour is relevant to a very deep question in the study of sexual selection: How widespread is sexual conflict, and how different are the various explanations of 'sexual chase-away' from more traditional female choice scenarios? Conflict as such is rife (Pizzari and Snook, 2003): it is almost

always less costly for members of one sex (usually males) to mate than for members of the other sex (Parker, 1979; Clutton-Brock and Parker, 1992; Partridge and Hurst, 1998; Kokko and Monaghan, 2001). Whether or not females have control over their mating rate, it is more in the male's interest to mate than in the female's – assuming, for simplicity, conventional sex roles (for a discussion of sex role reversals, see e.g. Cunningham and Birkhead, 1998; Berglund and Rosenqvist, 2003). This insight has led to the view that the evolution of 'resistance' is not necessarily a new and separate phenomenon from the more traditional ideas on female choice (e.g., Getty, 1999): maybe we are simply more prone to phrase a phenomenon as 'sexual conflict' when females clearly suffer strong direct costs when mating, even though the conflict itself is ubiquitous and is not qualitatively different in traditional choice models and in 'chase-away' scenarios (Kokko et al., 2003).

Yet, it is currently debated if this view can be supported (Cordero and Eberhard, 2003; Cameron et al., 2003; Chapman et al., 2003; Eberhard and Cordero, 2003). The enigmatic aspect is the following. Theoretical work on scenarios of traditional female choice has shown that indirect benefits can potentially explain the evolution of male sexual ornaments, and this view has found support in a large bulk of empirical literature (Møller and Alatalo, 1999; Jennions and Petrie, 2000; Jennions et al., 2001) – although some central predictions remain scarcely tested (Kokko et al., 2003). Evolution of female resistance, however, has not yet been subject to much theoretical or empirical study. The only major modelling work so far (Gavrilets et al., 2001) predicts that indirect effects will not have an influence on the coevolutionary equilibria of female and male traits at all.

In other words, when males can coerce females into mating, or otherwise directly influence their decisions (e.g. dominant males might make it difficult for females to join other males' harems), indirect benefits should not have any evolutionary effect. This is at odds with propositions that females should be able to use dominance-related traits as signals of male quality (Cox and Le Boeuf, 1977; Berglund et al., 1996; Candolin, 1999; Wong and Candolin, in press), as well as with the view that 'preference' and 'resistance' are two sides of the same coin (Getty, 1999; Kokko et al., 2002, 2003) and hence must be subject to similar evolutionary pressures. So, is female choice evolution under 'acute' sexual conflict – where coercive males impose direct mating costs – fundamentally different from 'traditional' female choice scenarios where the conflict is more gently expressed?

Here I will study this question by presenting a quantitative genetic model of male coerciveness and female mating behaviour. In the context of the current model, I use 'dominance' and 'coerciveness' synonymously, even though the many uses of dominance in the literature might include cases in which socially less dominant males spend more time in behaviours classified as active coercion. In

such cases, males could still conceivably be arranged according to their intrinsic ability to limit female's reproductive options to favour themselves as mates – and it is this ability that is meant by the dominance trait of the current study.

To study the co-evolutionary arms race between males and females, I also assume that the degree to which the male trait determines mating success can be modified by female behaviour (Wong and Candolin, in press). In extreme cases, females can completely overcome male coercion by actively favouring subordinate (less coercive) males, although they do so at a direct cost. Alternatively, females may actively reject subordinates, thus enhancing the effects of dominance further. I will show that females may evolve any behaviour in between these two extremes. A wide variety of evolutionary outcomes are possible, and in some of them, indirect benefits play a role in determining the course of evolution.

Methods

I consider the following two traits: a trait that determines male dominance, a, and a female behaviour trait b that can take either positive or negative values. Dominant males (high a) are able to fertilize more females, either through success in male–male competition that determines access to females, or by being directly more coercive than the average male. Male mating success is, however, determined by an interaction of dominance, a, and female behaviour, b. The variable b reflects either female preference or resistance, with the following interpretation: $b = 0$ describes passive females, who accept any male as a mate. They nevertheless tend to mate more with dominant males, because these by virtue of their dominance have better access to females. For example, dominant males may win harem ownership more often, or coerce females more strongly than less dominant males. Values of b that exceed zero describe females who mate more often with dominant males than the dominant males' own behaviour would dictate. In other words, these females show a preference for dominant males and actively reject subordinate ones (note that such a trait can, at the behavioural level, appear as resistance, and it has sometimes been described as females 'screening' males, e.g. Chapman *et al.*, 2003). Finally, values of $b < 0$ indicate that a female prefers to mate with subordinate, or non-coercive males; female behaviour thus (partly or completely) overrides the effects of male dominance.

I write male fitness as

$$w_{\mathrm{m}} = \exp(a[(1 + \overline{b}) - c_1]) \tag{1}$$

and female fitness as

$$w_{\mathrm{f}} = \exp(-c_2 b^2 - \overline{a} f(b) c_1) \tag{2}$$

These equations have the following interpretation (Fig. 1). Females bias the mating distribution either in the direction of subordinates at the expense of dominants ($b < 0$), or in the opposite direction ($b > 0$). The latter option gives subordinates even less paternity than they otherwise would have (Fig. 1a). c_1 is the direct cost of dominance: it is the reduction in female fecundity as a consequence of her mate being too dominant (coercive). If mating with dominant males has no direct costs, we set $c_1 = 0$, and if it is
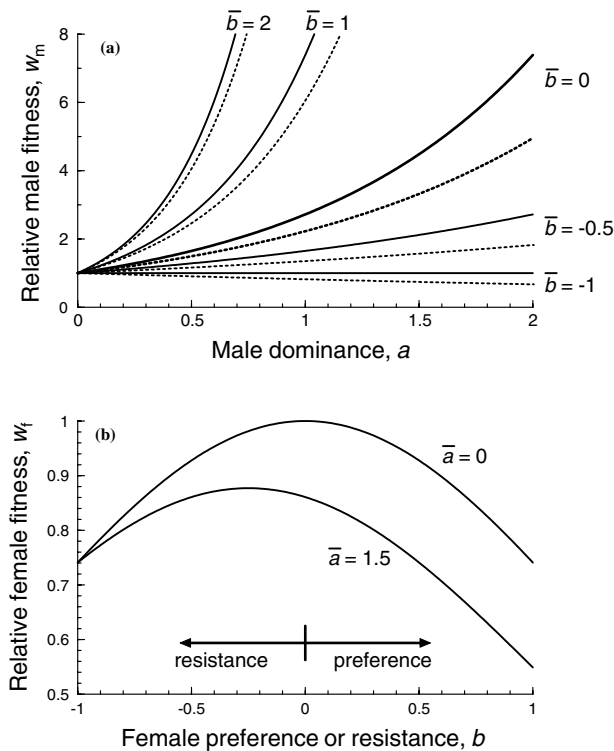

Figure 1. Assumptions of the model regarding male and female fitness. (a), Male fitness as a function of his dominance trait a, with different values of mean female behaviour $\bar{b}$. Dashed lines assume $c_1 = 0$ and thus indicate the mating success component of male fitness (ignoring the direct cost to the female). Solid lines assume $c_1 = 0.2$. If females are passive ($\bar{b} = 0$, bold lines), male mating success increases with his dominance status. This increase is enhanced if females prefer dominant males ($\bar{b} > 0$), and counteracted if females avoid them ($\bar{b} < 0$). Strong forms of female resistance $\bar{b} = -1$ can completely overcome the benefit that males gain from being dominant. (b), The direct fitness of females that resist ($b < 0$) or prefer ($b > 0$) coercive males, in two different environments: one in which males are not coercive $\bar{a} = 0$, and one in which they are strongly coercive $\bar{a} = 1.5$. Strong deviations from passively accepting the mating outcome dictated by male dominance, i.e. from $b = 0$, are costly and reduce female fitness. Where males are coercive, however, the direct fitness of the female is not maximized at $b = 0$, but at $b = -\frac{\bar{a}f'c_1}{2c_2}$ (here, -0.25). This is because a resisting female is able to avoid some of the costs c_1 imposed by male coercion. Example is calculated with $C_1 = 0.2$, $C_2 = 0.3$, $f(b) = (b+1)/2$.

directly beneficial (e.g. sexual harassment may be reduced when a dominant male is able to exclude other males from the area), we have $c_1 < 0$. Since a reduction in fecundity affects directly both female and male offspring production, this cost appears in both male and female equations.

The females' attempt to bias the mating distribution is likely to be more costly than passively accepting the outcome that males would prefer. Thus, females who deviate from being passive pay a direct cost c_2. This cost increases as b deviates from passive acceptance in either direction. Nevertheless, the maximum of direct fitness is not exactly at $b = 0$, because some resistance may bring about direct benefits in terms of avoiding direct costs of coercive matings (Fig. 1b).

In the female equation, the factor $\bar{a}\,f(b)$ describes the mean dominance trait value of males that the female mates with, if the population mean of male dominace is $\bar{a}$, and the female's own preference (or resistance) equals b. The function $f(b)$ must increase with b, and the only information we will need of it in further analyses is its derivative with respect to b, evaluated at the population mean $\bar{b}$; we denote this derivative by f'.

Males benefit from being dominant (high a) whenever $\bar{b} > -1$. This benefit is weak if females are partially able to resist mating attempt by too coercive males ($-1 < \bar{b} < 0$), and it is strong if $\bar{b} > 0$, i.e. when females discriminate against subordinate males.

It is worth noting that the parameter b allows a new interpretation of 'resistance' in models of sexual antagonistic co-evolution. It has been pointed out that 'resistance' can be interpreted as a preference for those males who are particularly good at manipulating females (Getty, 1999; Kokko *et al.*, 2003). Resisting females in other words reject disproportionately often those males that fail to meet some 'seductive' threshold. This would correspond to a positive value of b in the current model, and it effectively counts as a preference. But an alternative scenario is that females who resist are able to escape the direct costs imposed by coercive males. This implies that resisting females mate with particularly coercive males less often than expected if they did not resist; hence in this case more of her eggs are fertilized by less coercive (or seductive) males. This interpretation applies with $b < 0$ in the current model. Thus, Eqs. (1) and (2) clarify which kind of 'resistance' is meant in each case (either a *de facto* preference for dominant males, or not; Fig. 1).

We can now write the equations that specify the evolutionary trajectories of a and b. Male and female fitness, expressed as in w_M and in w_F, depend on their traits as

$$\frac{\partial \ln w_M}{\partial a} = 1 + \bar{b} - c_1 \qquad (3)$$

$$\frac{\partial \ln w_{\mathrm{F}}}{\partial b} = -2c_2 b - \bar{a}f'c_1 \tag{4}$$

To describe the evolution of the population mean for traits a and b we make the additional assumption that mean male dominance, $\bar{a}$, is subject to a downwards mutational pressure m.

This assumption can be justified in a similar manner to assuming a downwards pressure on complex male displays and male viability (Iwasa *et al.*, 1991; Pomiankowski *et al.*, 1991): being superior to other males is a difficult task, and random mutations are likely to diminish rather than enhance a male's ability to dominate other males, or females. We then get

$$\begin{pmatrix} \frac{d\bar{a}}{dt} \\ \frac{d\bar{b}}{dt} \end{pmatrix} = \frac{1}{2} \begin{pmatrix} G_{aa} & G_{ab} \\ G_{ba} & G_{bb} \end{pmatrix} \begin{pmatrix} \frac{\partial \ln w_{\mathrm{M}}}{\partial a} \\ \frac{\partial \ln w_{\mathrm{F}}}{\partial b} \end{pmatrix} - \begin{pmatrix} m \\ 0 \end{pmatrix} \tag{5}$$

The system has the equilibrium

$$\bar{a}^* = \frac{2}{c_1 f'} \left[m \frac{2c_2 G_{bb} - G_{ab}}{G_{ab}^2 - G_{aa}G_{bb}} + c_2(1 - c_1) \right] \tag{6}$$

$$\bar{b}^* = -(1 - c_1) - 2m \frac{G_{bb}}{G_{ab}^2 - G_{aa}G_{bb}} \tag{7}$$

The Jacobian matrix of (5) is

$$\mathbf{J} = \frac{1}{2} \begin{pmatrix} -c_1 f'G_{ab} & G_{aa} - 2c_2 G_{ab} \\ -c_1 f'G_{bb} & G_{ab} - 2c_2 G_{bb} \end{pmatrix} \tag{8}$$

The real parts of the eigenvalues of this matrix both equal $G_{ab}(1 - c_1 f')/4 - c_2 G_{bb}/2$. It follows that the equilibrium described by (6) and (7) is stable if, and only if,

$$G_{ab} < \frac{2c_2 G_{bb}}{1 - c_1 f'}. \tag{9}$$

Results

From Eqs. (6) and (7) it follows that if $G_{ab} = 0$, then $\bar{b}^* = -c_1 f'/(2c_2)\bar{a}^*$. This means that in the case of no positive covariance between the female preference/ resistance and the male trait, an equilibrium with male coercion ($\bar{a}^* > 0$) is always followed by female resistance ($\bar{b}^* < 0$), rather than a female preference for coercive males.

Unlike in earlier models (Gavrilets *et al.*, 2001), however, a genetic covariance between the male trait and female behaviour can alter the position of

equilibria. This is visible in the terms containing the mutational bias, m. From Eq. (7), it is easily seen that $\bar{b}^*$ increases with G_{ab}, if $m > 0$ and $G_{bb} > 0$. While this does not mean that a positive covariance between the male trait and female behaviour will automatically move $\bar{b}^*$ to a positive 'preference' region, such evolution can happen if the mutational bias is sufficiently strong. Examples of this effect are shown in Figure 2. With zero covariance, there is a stable equilibrium where males are coercive ($\bar{a}^* = 0.6$), and females resist ($\bar{b}^* < 0$; Fig. 2a). Increasing the covariance to $G_{ab} = 0.1$ produces again a stable equilibrium with male coercion, but now females are expected to evolve a slight preference for these harmful males ($\bar{b}^* = 0.04$; Fig. 2b). Increasing G_{ab} leads to further increases in both $\bar{a}^*$ and $\bar{b}^*$, until these equilibria become unstable: Figure 2c shows neutral stability with co-evolutionary cycles between
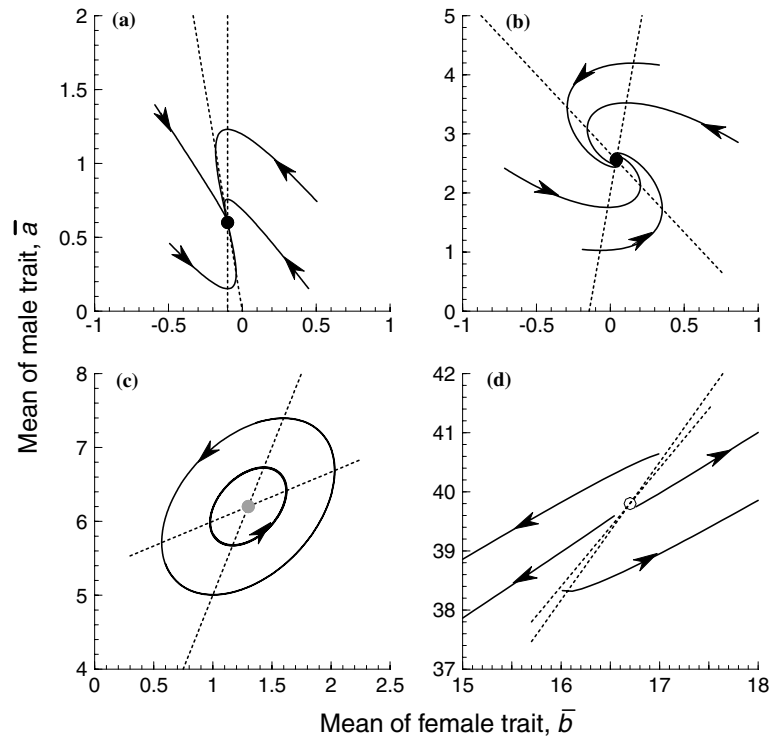

Figure 2. Evolutionary trajectories predicted by the model, for parameter values $c_1 = 0.2$, $c_2 = 0.3$, $f' = 0.5$, $m = 0.07$, $G_{aa} = 0.2$, $G_{bb} = 0.3$. Different panels depict the effect of different values for the genetic covariance: (a) $G_{ab} = 0$, (b) $G_{ab} = 0.1$, (c) $G_{ab} = 0.2$, (d) $G_{ab} = 0.24$. Dotted lines indicate zero isoclines where there is zero net selection pressure on either the male or the female trait. Solid lines with arrows show examples of evolutionary trajectories. Equilibria are indicated with filled, grey or open dots depending on their stability properties (stable, neutrally stable and unstable, respectively), and they occur at (a) $\bar{a}^* = 0.6$, $\bar{b}^* = -0.1$, (b) $\bar{a}^* = 2.56$, $\bar{b}^* = 0.04$, (c) $\bar{a}^* = 6.2$, $\bar{b}^* = 1.3$, *and* (d) $\bar{a}^* = 39.8$, $\bar{b}^* = 16.7$.

male and female traits, and Figure 2d exhibits runaway-like co-evolution between male and female traits, where either the preference or the resistance becomes ever stronger, depending on the initial starting point of the population.

Discussion

Should female prefer dominant males, be passive and simply accept the outcome of male–male competition, or to the contrary, actively counteract effects of male dominance? According to this model, the answer is 'it depends'. I have made the plausible assumption that the traits that determine male dominance are subject to a small biased mutational pressure. In other words, random changes in male genomes are more likely to deteriorate his competitiveness rather than improve it. Under such circumstances, the genetic covariance between the female behaviour and the male trait can influence the evolutionary trajectory. If the interaction between males and females does not lead to a genetic covariance between the two traits, e.g. because dominance is largely environmentally determined, females are always expected to evolve resistance to male coercion, in an attempt to minimize the direct costs suffered. A sufficiently strong covariance will, however, diminish the resistance, until it becomes a preference for the most coercive males. This is due to the indirect benefits of producing offspring who have high fertilization success.

The model's results thus solve the apparent conflict between models of sexual conflict in the strict and in the broad sense. In the former, mating *per se* is assumed to be costly to females (Gavrilets *et al.*, 2001). In the latter, more traditional choice scenarios, mating is not usually considered costly, but a female will suffer direct costs if she attempts to restrict the set of mating males to a subset of the original. These costs of choice (e.g. in the form of mate sampling) are usually considered of minor importance to the often drastic costs present in the 'strict sense' sexual conflict scenarios. Yet, the bottom line remains the same: if females can in the latter case evolve to a point in which they do not simply minimize direct costs (e.g., Iwasa *et al.*, 1991; Houle and Kondrashov, 2002), why not in the former? According to the current model's results, the answer is that indirect benefits can play a role in the case of coercive or harmful males too. Moreover, the solution is similar to the 'traditional' case of female choice: introducing a mechanism that maintains variation in the male trait allows the female preference to persist (Iwasa *et al.*, 1991; Pomiankowski, 1991; Kokko *et al.,* 2002).

The main prediction of the model, however, is a conceptual one. The model clearly distinguishes between preference and resistance, two concepts that have

been sometimes considered to have a somewhat overlapping meaning in cases where freedom of choice is compromised (Getty, 1999; Kokko *et al.*, 2003). The model offers the following definition: preferences reward males with traits that would have (in the absence of the preference) had neutral or enhancing effects on male mating success, while resistance to male traits means that these males gain fewer matings than in the absence of the female trait. Both are modelled using a single parameter b, thus preference and resistance evolution can be thought of two sides of the same coin.

To summarize, the current model allows for a wider variety of evolutionary trajectories than allowed for in Gavrilets *et al.* (2001), due to inclusion of a mutational pressure m, and possibly due to a wider range of possible female trait values, with both preference and resistance allowed. Avoiding direct costs is obviously of interest to females, but it can combine with quite cheap ways to favour some males: it is not necessarily more costly to resist matings in general (to help minimize direct costs) and give in once when a sufficiently 'sexy' male is encountered, than to resist in general and give in once but randomly. Male mating success often varies manifold more than female reproductive success. If male mating success has any heritable component (Wedell and Tregenza, 1999), the fitness of a female mating with a successful or an unsuccessful male can vary dramatically, and ignoring this fitness component can lead to erroneous evolutionary conclusions (Bernasconi and Keller, 2001; Pai and Yan, 2002).

There is an additional reason why male dominance may playa particularly important role in mate choice evolution. Models of conventional female choice often predict invasion barriers: something is needed to kick-start the co-evolutionary process of increasing female preference and male trait – if females do not prefer anything, male trait evolution is not favoured, and vice versa (Payne and Pagel, 2001; Kokko *et al.*, 2002). With male dominance, this problem disappears, if male dominance (at least partly) determines his mating success even if females passively accept the outcome of male-male competition. This means that dominant males are superior even in the absence of female preferences, and the incentive for female preference evolution is present from the start. The model presented in this paper does not include possible correlations with male or female viability. If more dominant males are also more viable, and these traits show any heritability, preferences for dominance could arise more easily in the current model.

The model here is based on adaptive reasoning: an equilibrium occurs when the male and the female trait no longer respond to selection. The possibility remains that evolution is not found at an equilibrium state. Firstly, many researchers argue that non-equilibrium dynamics can be important in evolution, particularly when there is ongoing conflict (Holland and Rice, 1998; Hall *et al.,* 2000). Secondly, even in the current model, limit cycles and runaways are sometimes predicted. It is important to notice, however, that the model also

easily produces equilibria where females adaptively resist male coercion. Females thus balance the costs and benefits, in a way that takes indirect benefits into account as well as direct ones. The fact that females suffer direct costs (Friberg and Arnqvist, 2003; Martin *et al.*, 2004) in such a setting therefore does not exclude the possibility that they have evolved an appropriate response to the conflict. In the examples derived here, such 'resisting' equilibria become more likely when the indirect benefit (the genetic covariation between the male and the female trait) diminishes.

Cases as diverse as female preferences counteracting male dominance in cockroaches (Moore *et al.*, 2001), females influencing outcomes of male coercion in mosquitofish (Bisazza *et al.,* 2001), female feral fowl ejecting sperm of subordinate males (Pizzari and Birkhead, 2000), and 'convenience polyandry' in marine turtles (Lee and Hays, 2004) can thus be potentially understood within the same framework. Nevertheless, the current model leaves many questions unanswered: how important indirect benefits turn out to be relative to direct ones in various cases of sexual conflict, how often females prefer or avoid dominant or coercive males, and how typical it is to find evolution near an equilibrium point – compared to rapid evolution along an evolutionary trajectory, or some non-equilibrium process due to stochasticity. The value of the current model, however, is to point out that 'sexual chase-away' scenarios should not ignore indirect benefits from the start, and that they should not be presented as a complete opposite to more traditional models of female choice.

Acknowledgements

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