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## The optimal coyness game

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In many animal species, females will benefit if they can secure their mate's help in raising their young. It has been suggested that they can achieve this by being coy (i.e. reluctant to mate) when courted, because this gives them time to assess a prospective mate's helpfulness and hence allows them to reject non-helpful males. According to this view, coyness should (i) reflect a trade-off between information gain and time lost on the part of the female, and (ii) be subject to an evolutionary feedback between optimal female coyness and male helping behaviour. Previous theory has considered each of these aspects in isolation. By contrast, here we present a comprehensive game theory model of this situation, leading to qualitatively new insights. We predict that a high degree of coyness should be associated with a high encounter rate during mate search, with an intermediate rate of information gain during mate inspection and with an intermediate dependence of reproduction on male help. Strongly biased sex ratios, however, preclude coyness. Due to the mutual feedback between coyness and helpfulness in our model, alternatively stable evolutionary outcomes (with or without coyness) are possible under broad conditions. We also discuss alternative interpretations of coyness.

**Keywords:** 'battle of the sexes'; mate choice; courtship; sexual selection; parental care; game theory

Had we but world enough, and time,  
This coyness, Lady, were no crime.

Andrew Marvell  
To his coy mistress

### 1. INTRODUCTION

The interactions between males and females during courtship and parental care are fundamental topics in behavioural ecology. Trivers (1972) stressed the conflict between members of a mated pair over the extent to which each of them cares for the young. The success of the current breeding attempt increases with the total effort of both parents, but each parent may suffer a reduction in the success of future attempts as its own level of care increases. As a result, there is typically a conflict of interest between parents over the level of care, with each parent preferring the other to do the work (Trivers 1972; Dawkins 1976; Maynard Smith 1977; Houston *et al.* 2005; Kokko & Jennions 2008).

The above quotation from Marvell is typical of how coyness is discussed in the context of human behaviour. In this paper, we define coyness more broadly as a reluctance by one member of a pair to mate with a possible partner, a behaviour observed not only in females but also in males (e.g. Berglund & Rosenqvist 1993) and hermaphrodites (e.g. Michiels *et al.* 2003) of various species. Animals are

prepared to devote substantial amounts of time and energy to interacting with a potential partner before mating (Bastock 1967; Wickler 1980; Wachtmeister & Enquist 2000; Wachtmeister 2001). A possible reason for this is that the reluctance to mate gives individuals time to collect information about any direct and indirect benefits a prospective mate has to offer (Jennions & Petrie 1997; Candolin 2003). In this paper, we concentrate on a suggestion by Dawkins (1976), who, in the chapter called 'Battle of the sexes', discusses the conflict of interest between males and females, arguing that courtship gives females a chance to assess prospective mates' parental behaviour: 'There is bound to be variation in the population of males in their predisposition to be faithful husbands. If females could recognize such qualities in advance, they could benefit themselves by choosing males possessing them. One way for a female to do this is to play hard to get for a long time, to be coy'. (p. 161).

Dawkins proposed a game theory model to explore this view of coyness. In the game, there are two possible strategies for females (coy and fast) and two possible strategies for males (faithful and philanderer). Coy females refuse to mate with a male until he has completed an extended period of courtship, whereas fast females will mate with any male as soon as he is encountered. Philanderer males refuse to engage in a long period of courtship and if a female allows them to mate, they leave after mating, i.e. they do not care for the young. By contrast, faithful males are prepared to court a female and after mating they remain with the female and care for the young.

On the basis of the costs and benefits of care and the cost of courtship, Dawkins assigned pay-offs to each of the

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four possible combinations of female strategy and male strategy. For the pay-offs that Dawkins used, there is a frequency of fast females at which both the male strategies have the same pay-off and a frequency of faithful males at which both the female strategies have the same pay-off. This means that there is an equilibrium at which all the four strategies are present and it does not pay for any individual to change its strategy. Dawkins assumed that this equilibrium was an evolutionarily stable strategy (ESS). Schuster & Sigmund (1981) showed that this view is not correct; the equilibrium cannot meet one of the necessary stability conditions if pay-offs are fixed.

A general problem with the game proposed by Dawkins is that it does not capture a fundamental aspect of the interaction between the sexes. Dawkins assigns a fixed pay-off to (say) a male that depends on just his strategy and the strategy of the female that he interacts with. In reality, the pay-off consists of two components. One is the reproductive success from the current interaction; this depends on just the behaviour of the pair. The other is the future reproductive success; this will typically depend on both the behaviour of the pair and the behaviour of other members of the population (e.g. Webb *et al.* 1999; McNamara *et al.* 2000; Houston *et al.* 2005).

A model can be said to be consistent if it is possible to embed it within a broader model that includes more aspects of the whole system, including feedback between the components of the system (Houston & McNamara 2005). For the models of parental care that we are considering, consistency requires that the pay-offs are not arbitrary (as in the model of Dawkins) but are derived from a full account of the population (Fromhage *et al.* 2007; Seki *et al.* 2007; Kokko & Jennions 2008). This can be achieved by constructing an explicit account of future reproductive success. Mylius (1999) did this for the game that Dawkins proposed and gave a rigorous general analysis of the resulting dynamics of the male and female strategies.

We have a more specific concern with Dawkins's game: it does not capture the essence of Dawkins's idea that females can use courtship to assess potential mates. This is perhaps not surprising; when Dawkins was writing *The Selfish Gene*, information transfer and assessment in the context of animal behaviour was relatively unexplored. This aspect of courtship is explored by Wachtmeister & Enquist (1999). Their model considers the duration of coyness in terms of a trade-off between gaining information and wasting time. The female seeks to maximize her reproductive success from a single breeding attempt during a reproductive season. The success of an attempt decreases the later in the season it occurs. This means that an increase in the duration of courtship reduces reproductive success. The benefit of courtship is that it gives the female the chance to discover that a male is a philanderer; the longer the courtship, the higher the probability of detecting a philanderer. Given a particular proportion of philandering males, Wachtmeister & Enquist find the optimal level of female coyness, i.e. the duration of coyness that maximizes the female's reproductive success.

Wachtmeister & Enquist ignore the effect of the behaviour of the population on future encounters. This simplification means that they keep the probability that a female encounters a given type of male fixed over the season, and so reduces the problem from a game to an

optimization. In reality, the probability that a female encounters a given type of male is determined by the behaviour of the males and females. In this paper, we develop a game theory model that combines an explicit model of future behaviour (cf. Mylius 1999) with a model of optimal female coyness (cf. Wachtmeister & Enquist 1999).

## 2. THE MODEL

We consider a population in which each male adopts one of two mating strategies: helpful and non-helpful. If chosen as a mate by a female a helpful male joins the female in caring for the young. Care lasts unit time. After care, the pair split up and each seeks a new mate. If instead a female mates with a non-helpful male he deserts immediately after mating and provides no care for the young. Instead, he searches for a new mate. In this case, the female still cares for unit time before searching for a new mate. The reproductive success achieved by each parent in a reproductive bout is  $B_H$  if the male is helpful and  $B_N$  if the male is non-helpful. Here,  $0 < B_N < B_H$ .

During the search for a new mate a male encounters females at rate  $\lambda\rho_F$  where  $\lambda$  is a constant and  $\rho_F$  is the proportion of all females that are currently searching. During the search a female encounters males at rate  $\lambda s\rho_M$ , where  $\rho_M$  is the proportion of males that are currently searching and the sex ratio  $s$  is the ratio of numbers of males to females in the population as a whole. Whereas  $\lambda$  and  $s$  are input parameters of our model,  $\rho_F$  and  $\rho_M$  emerge from the behavioural rules adopted.

On encountering a male, a female inspects the male, accumulating information on male type over time. At any time during the inspection the female has the choice of deciding to mate with the male, rejecting the male and commencing search for another male, or continuing to take observations on the male. The choice of action at a given time will typically depend on the observations on the male type obtained so far. We refer to the relationship between the observations made and the choice of action as the strategy of inspection. The eventual outcome of using a particular strategy of inspection is characterized by two error probabilities and two mean inspection times:  $\alpha$ , probability the male is rejected given he is helpful (analogous to a type I error in statistics, where a true null hypothesis is wrongly rejected);  $\beta$ , probability the male is accepted given he is non-helpful (analogous to a type II error in statistics, where a false null hypothesis is wrongly accepted);  $\tau_H$ , mean time taken to inspect a male given he is helpful; and  $\tau_N$ , mean time taken to inspect a male given he is non-helpful.

In appendix 1 in the electronic supplementary material, we model the accumulation of observations on male type by assuming that there is a continuous stream of (conditionally) independent identically distributed observations. With this assumption, any optimal inspection strategy is necessarily in the form of a sequential probability ratio test (De Groot 1970). We assume normally distributed observations and characterize the information stream by the parameter  $\nu$  that gives a measure of the useful information per unit time from it; information is gained more quickly for higher values of  $\nu$ . Assuming the female employs the sequential probability ratio test it is then possible to express the mean inspection

times,  $\tau_H(\alpha, \beta; \nu)$  and  $\tau_N(\alpha, \beta; \nu)$ , as functions of the error probabilities  $\alpha$  and  $\beta$  and information rate  $\nu$ . Not surprisingly, for given  $\nu$  reduced error probabilities can only be achieved at the expense of increased inspection times, so that there is a trade-off between making the wrong decision and losing time.

We take the fitness of an individual to be the individual's long-term rate of reproductive success. We suppose that male type is genetically determined. Thus, if one type has higher fitness than another, the frequency of the fitter type in the population will increase. We seek the evolutionary endpoints when this frequency and the female inspection strategy are allowed to coevolve.

### (a) Balance equations and fitness

Consider a population in which the proportion of helpful males is  $p$ , the proportion of non-helpful males is  $1-p$ , and females in this population employ an inspection strategy with error probabilities  $\alpha$  and  $\beta$ , implying mean inspection times  $\tau_H$  and  $\tau_N$ . In this population, the mean time  $T(p)$  for a searching male to encounter a female is  $1/(\lambda\rho_F)$ . Thus, the proportion of time that a helpful male spends searching for a female is

$$\rho_H = \frac{1/(\lambda\rho_F)}{1/(\lambda\rho_F) + \tau_H + (1-\alpha)} \quad (2.1)$$

and the proportion of time that a non-helpful male spends searching is

$$\rho_N = \frac{1/(\lambda\rho_F)}{1/(\lambda\rho_F) + \tau_N} \quad (2.2)$$

For the helpful males (equation (2.1)), the denominator has three time components: the mean time to encounter a female; the mean time to be inspected by that female; and, in a proportion  $(1-\alpha)$  of cases (i.e. when the male is accepted), the time to care for the offspring ( $=1$ ). For non-helpful males, only the first two components are present in the denominator, since these males never care.

The overall proportion of males that are searching at any time is thus

$$\rho_M = p\rho_H + (1-p)\rho_N \quad (2.3)$$

and the probability that the male that a searching female encounters is helpful is

$$r = \frac{p\rho_H}{p\rho_H + (1-p)\rho_N} \quad (2.4)$$

The mean time taken for a searching female to encounter a male is  $1/(\lambda s\rho_M)$ ; with probability  $r$  he is helpful, in which case, on average, she spends time  $\tau_H$  assessing him and, with probability  $(1-\alpha)$ , accepts him and spends an additional one unit of time caring; otherwise (i.e. with probability  $1-r$ ) he is non-helpful, in which case on average she spends time  $\tau_N$  assessing him and, with probability  $\beta$ , accepts him and spends an additional one unit of time caring.

Thus, the proportion of time that a female spends searching is

$$\rho_F = \frac{1/(\lambda s\rho_M)}{1/(\lambda s\rho_M) + r[\tau_H + (1-\alpha)] + (1-r)[\tau_N + \beta]} \quad (2.5)$$

Equations (2.1)–(2.5) determine the five variables  $\rho_M$ ,  $\rho_H$ ,  $\rho_N$ ,  $\rho_F$  and  $r$ .

The fitness of the individuals in the population can be expressed as follows. A helpful male gains reproductive success at the rate

$$\gamma_H = \frac{(1-\alpha)B_H}{1/(\lambda\rho_F) + \tau_H + (1-\alpha)} \quad (2.6)$$

A non-helpful male gains reproductive success at the rate

$$\gamma_N = \frac{\beta B_N}{1/(\lambda\rho_F) + \tau_N} \quad (2.7)$$

A female gains reproductive success at the rate

$$\gamma_F = \frac{r(1-\alpha)B_H + (1-r)\beta B_N}{1/(\lambda s\rho_M) + r[\tau_H + (1-\alpha)] + (1-r)[\tau_N + \beta]} \quad (2.8)$$

### (b) Finding evolutionarily stable strategies

We consider first how female behaviour might evolve for given  $p$ . Consider a population in which there is a fixed proportion  $p$  of helpful males and where the resident female strategy is to employ a sequential probability ratio test with error probabilities  $\alpha$  and  $\beta$ . Equation (2.8), together with equations (2.1)–(2.5) and (A1.21)–(A1.22), then determines female fitness,  $\gamma_F$ , in terms of the parameters  $B_H$ ,  $B_N$ ,  $\lambda$ ,  $\nu$  and  $s$  and the variables  $p$ ,  $\alpha$  and  $\beta$ . Computations suggest that there is always a unique female strategy, characterized by a pair of  $\alpha$  and  $\beta$  values, that maximizes  $\gamma_F$  for given  $p$ . To find this strategy, we map the continuous variables  $\alpha$  and  $\beta$  onto a discrete grid, and then calculate  $\gamma_F$  for all combinations of  $\alpha$  and  $\beta$ . If the proportion of helpful males were held fixed at  $p$ , then the female strategy maximizing  $\gamma_F$  would have strictly higher fitness than any alternative strategy, and would thus be evolutionarily stable.

Now consider a population such that, for each given  $p$ , the females behave optimally for that  $p$ . Denote the gain rates of helpful and non-helpful males within this population by  $\gamma_H(p)$  and  $\gamma_N(p)$ , respectively. Let  $D(p) = \gamma_H(p) - \gamma_N(p)$  be the fitness advantage of helpful males over non-helpful males. Our computational procedure, by calculating  $D(p)$  for all possible values of  $p$ , seeks values  $p = p^*$  such that

- (i) if  $p^* = 1$  then  $D'(1) > 0$ ,
- (ii) if  $p^* = 0$  then  $D'(0) < 0$ , and
- (iii) if  $0 < p^* < 1$  then  $D(p^*) = 0$  and  $D'(p^*) < 0$ .

Here,  $D'$  is the first derivative of  $D$  with respect to  $p$ , and provides a measure of the change in the fitness advantage of helpful males with respect to the proportion of such males.

Each such  $p^*$  represents an ESS for males, meaning that any male type that is slightly more common than under  $p^*$  faces negative selection. Unstable equilibria, characterized by  $D(p) = 0$  and  $D'(p) > 0$ , are also possible. Here, the population tends to evolve away from  $p$  because any male type that becomes slightly more common than under  $p$  faces positive selection. A stable endpoint of male–female coevolution, where each sex behaves optimally given the behaviour of the other, is specified by a value of  $p^*$  and by the  $\alpha$  and  $\beta$  values that maximize  $\gamma_F$  given  $p = p^*$ .

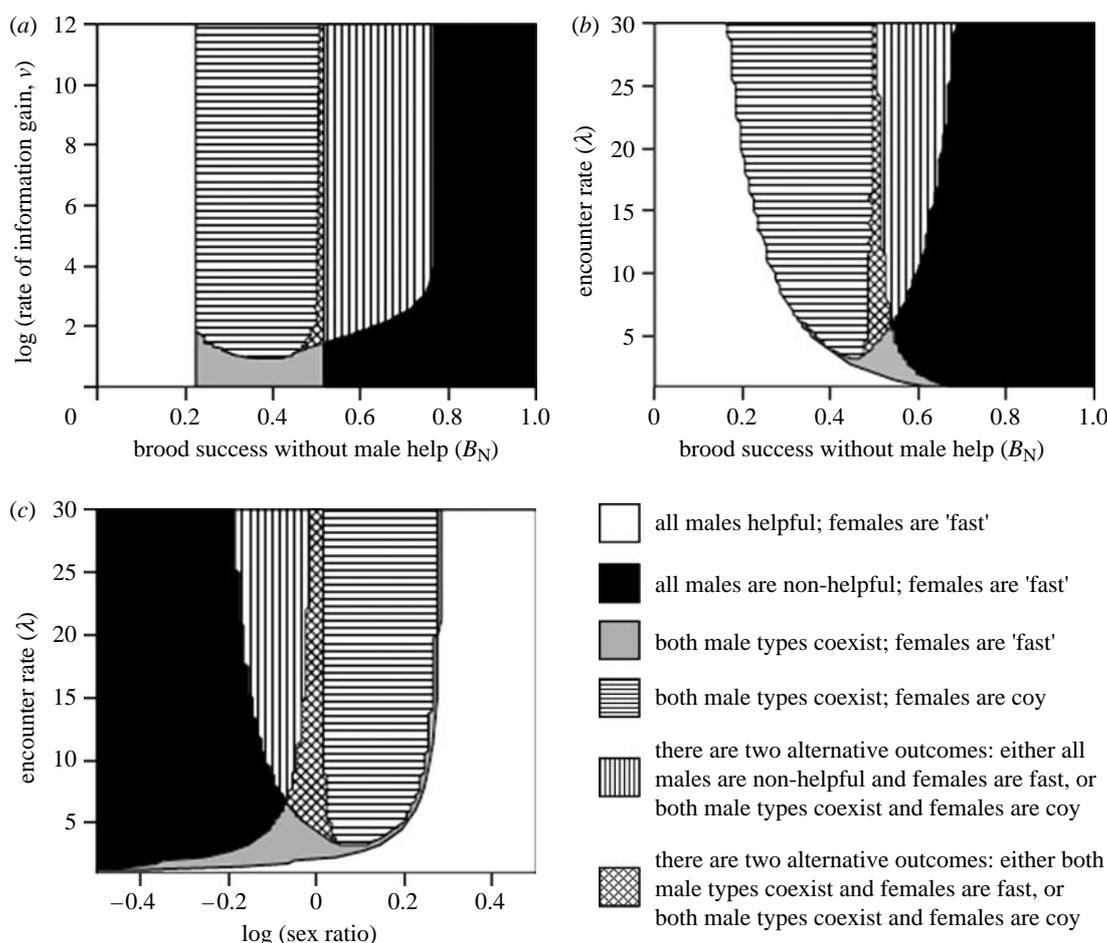


Figure 1. Location of the possible outcomes of the game in parameter space. Settings: brood success with male help  $B_H = 1$  throughout. (a) Sex ratio  $s = 1$ , encounter rate  $\lambda = 15$ ; (b)  $s = 1$ , rate of information gain  $\nu = 100$ ; and (c)  $B_N = 0.5$ ,  $\nu = 100$ .

### 3. RESULTS

Four qualitatively different outcomes, as characterized by the ESSs of each sex, emerge from our model. These outcomes are: (i) all males are helpful and all females are 'fast' (i.e. they immediately accept every encountered male); (ii) all males are non-helpful and all females are fast; (iii) both male types coexist and all females are fast; and (iv) both male types coexist and all females are coy (i.e. they engage in mate inspection and sometimes reject a male).

Each of these outcomes is uniquely stable for certain parameter combinations (figure 1). However, there are also parameter combinations where cases (ii) and (iv) are alternatively stable, meaning that depending on initial conditions, either alternative may become established and will then remain stable (figures 1 and 2*j,l*). Similarly, cases (iii) and (iv) are alternatively stable for certain parameter combinations (figures 1 and 2*i,k*). Under conditions where two alternatively stable equilibria exist, there is always also a third, unstable, equilibrium that delineates the stable equilibria's attraction zones (figure 2). If females cannot gain information about male type, then only outcomes (i)–(iii) are possible. This case is treated analytically in appendix 2 in the electronic supplementary material. The behaviour of the sexes depends on parameters as follows.

#### (a) Female behaviour

Females are coy in a region of parameter space that combines intermediate values of sex ratio ( $s$ ) and

reproductive success per bout of non-helpful males ( $B_N$ ), with sufficiently high values of encounter rate ( $\lambda$ ) and information rate ( $\nu$ ) (figure 1). However, at very high information rates, although coyness is maintained in the sense that females engage in mate inspection, the inspection times are so short that there is hardly any delay in mating (figure 3*d*). Mean inspection times, if non-zero, are always lower for helpful than non-helpful males (i.e.  $\tau_H < \tau_N$ ; figures 2*a–d* and 3*a–d*). Moreover, a helpful male's probability  $\alpha$  of being mistakenly rejected is much lower than an unhelpful male's probability  $\beta$  of being accepted (i.e.  $\alpha \ll \beta$ ; figures 2*e–h* and 3*e–h*).

#### (b) Male behaviour

The coexistence of both male types requires intermediate values of  $B_N$  and  $s$ , and is facilitated by high values of encounter rate  $\lambda$  (figure 1). This coexistence often concurs with coyness, but is maintained in the absence of coyness under low values of information rate  $\nu$  and encounter rate  $\lambda$  (figures 1 and 3*j,l*). In the parameter region where cases (ii) and (iv) are alternatively stable (figures 1 and 2*j,l*), the coexistence of male types is made possible specifically by the presence of coy females. In the parameter region where cases (iii) and (iv) are alternative stable outcomes (figures 1 and 2*i,k*), there is either a low but non-zero frequency  $p^*$  of helpful males, maintained in the absence of coyness, or a higher  $p^*$ , maintained in the presence of coyness.

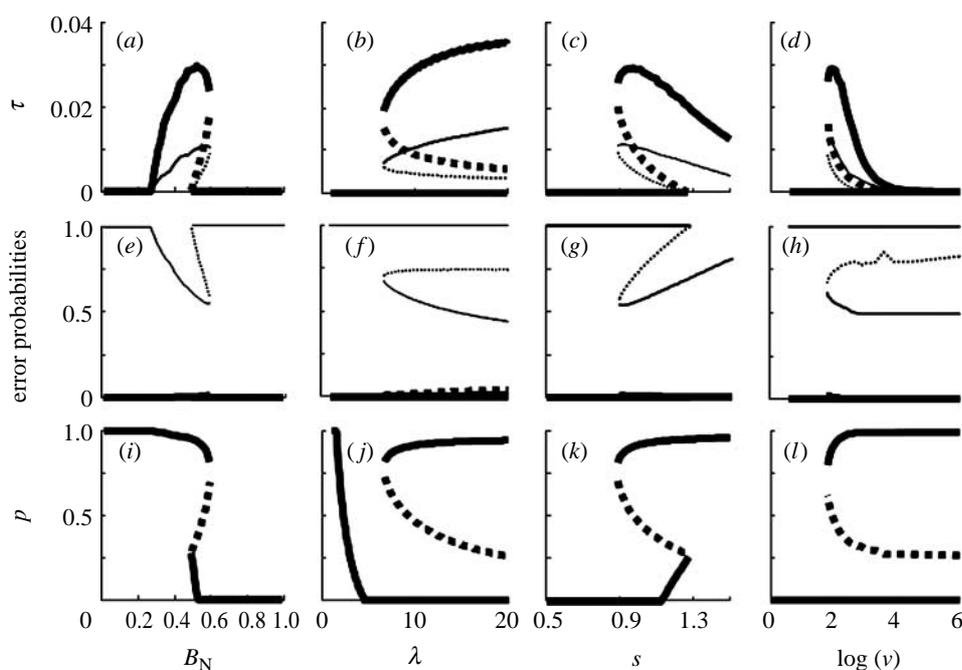


Figure 2. Effects of model parameters on inspection times, error probabilities and frequency of male types, in a region of parameter space where up to two alternative stable outcomes exist for the given parameter values. Bold curves pertain to helpful males, showing their (*a–d*) mean inspection time  $\tau_H$ , (*e–h*) probability  $\alpha$  of being rejected (hardly visible because of very low values) and (*i–l*) frequency  $p$ . Thin curves pertain to non-helpful males, showing their inspection time  $\tau_N$  and their probability  $\beta$  of being accepted by a female. The solid curves indicate stable equilibria and dashed curves indicate unstable equilibria. Default setting:  $B_H=1$ ;  $B_N=0.55$ ;  $\lambda=10$ ;  $s=1$ ;  $\nu=100$ .

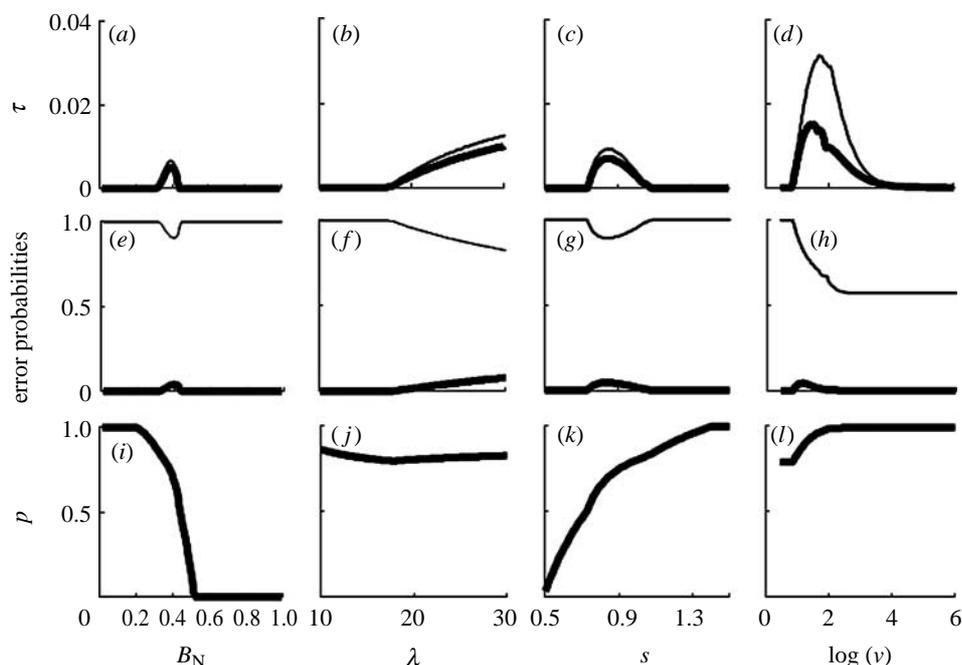


Figure 3. Effects of model parameters on inspection times, error probabilities and frequency of male types, in a region of parameter space where only one stable outcome exists for given parameter values. Bold curves pertain to helpful males, showing their (*a–d*) mean inspection time  $\tau_H$ , (*e–h*) probability  $\alpha$  of being rejected and (*i–l*) frequency  $p$ . Thin curves pertain to non-helpful males, showing their inspection time  $\tau_N$  (not visible in (*a*) because here  $\tau_H \approx \tau_N$ ) and their probability  $\beta$  of being accepted by a female. Default settings:  $B_H=1$ ;  $B_N=0.35$ ;  $\lambda=20$ ;  $s=1$ ;  $\nu=7.72$ .

#### 4. DISCUSSION

In many species, females will benefit if they can secure their mate's help in raising their young and aspects of either the male or his nest may provide a female with evidence about the parental care he will provide

(Ostlund-Nilsson 2000, 2001; Casagrande *et al.* 2006; Halupka & Borowiec 2006). We have modelled a situation where females can achieve this by collecting information about a prospective mate's helpfulness (e.g. Forsgren 1997). By simultaneously considering a trade-off between

the information gain and the time lost on the one hand (cf. [Wachtmeister & Enquist 1999](#)), and a coevolutionary feedback between male and female behaviour on the other hand (cf. [Mylius 1999](#)), our model provides a comprehensive account of this situation, leading to qualitatively new insights.

To gain an intuitive understanding of our results, it is helpful first to consider the simple case, where females cannot distinguish between male types (information rate  $\nu=0$ ). In this case females are not coy; our model then becomes analogous to that of [Yamamura & Tsuji \(1993\)](#), where males provide care for their offspring only if they can thus substantially improve offspring survival, and if the sex ratio is not too female-biased. The sex ratio is relevant here because a high number of males causes intense competition during mate search, thus reducing the rate at which searchers find females. For a male who has just mated, intense competition can therefore make immediate further searching less rewarding compared to the alternative option of caring for his young (see also [Kokko & Jennions 2008](#)). A similar argument can explain why in both Yamamura and Tsuji's model and in our model, there can be a stable mixture of helpful and non-helpful males in the absence of coyness ([figure 1](#)): because non-helpful males spend most of their time searching (rather than caring for offspring), search competition is more intense if more males are non-helpful. Hence, given that intense competition makes searching less rewarding, non-helpful males thrive better when rare. It is this negative feedback between frequency and success that stabilizes the mixture of male types. A quantitative analysis of this case is given in appendix 2 in the electronic supplementary material.

Turning to the case where females have the ability to distinguish between male types (information rate  $\nu>0$ ), we can see that the information gain, by allowing for the evolution of coyness, can make helpful and non-helpful males coexist under even broader conditions ([figure 1a](#)). The coexistence of different male types is a necessary precondition for the evolution of coyness, because mate inspection cannot yield information if all males are the same. Notably, however, coyness can itself be a precondition for the coexistence of male types: under conditions where other incentives for helping are weak, no males should be helpful unless they can thus increase their chances of being accepted by coy females. Thus, male helpfulness and female coyness can mutually depend on each other: though stable together, neither trait will evolve if the other is absent. Under such conditions (vertically striped area in [figure 1](#)), whether coyness is a viable strategy depends on the initial male and female strategy frequencies (see also [Mylius 1999](#)).

Let us now consider why the degree of coyness (i.e. the mating delay due to mate inspection) varies with parameter values as it does. Based on their optimization model of female coyness, [Wachtmeister & Enquist \(1999\)](#) concluded that the optimal degree of coyness should be high given (i) an intermediate rate of information gain, (ii) a high mate encounter rate, (iii) a high dependence of reproductive success on male help, and (iv) that most males are non-helpful. Of these four predictions, only the first two are supported by our model. First, both models agree that the rate of information gain must be intermediate for any non-trivial time investment in mate

inspection to be worthwhile ([figures 2d](#) and [3d](#)). This is because if this rate is very low, then information is gained at too slow a rate to make coyness viable; and if it is very high, a male's type is immediately evident, requiring no further inspection. Second, both models agree that a low mate encounter rate reduces coyness ([figures 2b](#) and [3b](#)), because females cannot afford to be choosy unless they have a good chance of encountering another male soon. From the perspective of our model, we can add that a low encounter rate further strengthens this effect by making mate search less rewarding when compared with helping: as helpful males become very common for this reason, females need not be coy to have a high chance of mating with a helpful male. However, in contrast to [Wachtmeister & Enquist's \(1999\)](#) result that a strong dependence of reproductive success on male help leads to high coyness, our model suggests that coyness requires an intermediate dependence of reproductive success on male help ([figures 2a](#) and [3a](#)). This is because given a strong beneficial effect of male help, males should provide help in any case, thus obliterating the females' need to be coy. Furthermore, whereas [Wachtmeister & Enquist](#) suggested that high coyness levels should coincide with non-helpful males being in the majority, our model suggests the opposite ([figures 2](#) and [3](#)). This is because if helpful males are few compared to the number of females, then, even given a high encounter rate, the reproduction of coy females is limited by a shortage of suitable mates. This limiting effect was not accounted for in [Wachtmeister & Enquist's \(1999\)](#) model, where the probability of encountering a helpful male was assumed to be constant, regardless of how many females were already paired with a helpful male.

Another interesting result of our model is that non-helpful males are on average inspected for longer than helpful males ([figures 2a–d](#) and [3a–d](#)). This is because quickly (but riskily) accepting a male who appears helpful at least saves time, whereas quickly rejecting a male who appears unhelpful incurs a twofold cost if the decision turns out to be wrong: not only does finding another male take time, but also this new male may actually be less helpful than the one rejected. To avoid this twofold cost, females require a higher level of certainty before rejecting a male as unhelpful.

Coyness, if effective in preventing non-helpful males from mating, can reduce the frequency of non-helpful males to near zero. This will in turn reduce the incentive for females to be coy, potentially leading to cyclical dynamics with the phases: high coyness  $\rightarrow$  high helpfulness  $\rightarrow$  low coyness  $\rightarrow$  low helpfulness  $\rightarrow$  high coyness, etc. Such cycles have been described in [Schuster & Sigmund's \(1981\)](#) analysis of [Dawkins's \(1976\)](#) original 'battle of the sexes' game and are also evident in the evolutionary trajectories approaching the ESS in [Mylius's \(1999\)](#) version of this game. Although in the present paper we have focused on equilibrium states rather than evolutionary dynamics, the above verbal argument suggests that such a tendency to cycle is inherent in our model too. However, to what degree this tendency can manifest itself will depend on additional assumptions, e.g. about the underlying genetics and life history. For example, a long lifespan and low recruitment rate may buffer oscillations, whereas the existence of a long time delay between birth and reproduction may increase

them (see Maynard Smith (1982) for a discussion of the destabilizing effect of time delays in games with oscillatory dynamics).

Here, we have considered a female's assessment of male helpfulness as a possible reason for coyness (i.e. prolonged courtship and delayed mating). However, female mate assessment in a more general sense may also concern other aspects of male quality, including species identity (Bastock 1967), genetic quality or genetic compatibility (Mays & Hill 2004). Female mate assessment (and hence coyness) may be beneficial whenever reproductive success depends on male type, regardless of the type of benefit involved. It is worth noting, however, that the nature of the feedback between male and female evolution is likely to depend strongly on such biological details.

Coyness may also serve functions other than mate assessment. For example, Dawkins (1976) suggested that a long courtship might reduce a male's probability of caring for offspring that are not his own by ensuring that the female has not recently mated with other males. Furthermore, as suggested by Maynard Smith (1977), females might be able to reduce the chances that a male deserts by imposing a delay between pairing and mating. If breeding is synchronous, this coyness makes it unlikely that a deserting male will find an unpaired female. This argument is based on a finite breeding season in which only one breeding attempt is possible. In a rate-based model, a female that reduced her coyness below the population level would increase her rate of reproduction. Finally, as suggested by Simão & Todd (2002), an extended courtship period may be beneficial because it gives individuals the chance, before committing themselves to mating, to tentatively hold on to a partner (thus reducing the risk of remaining unmated) while still looking for a higher-quality partner. We stress that these alternative explanations of coyness are not mutually exclusive. Rather, perhaps together with the need of the sexes to synchronize their reproductive physiology (Bastock 1967), they may contribute to varying degrees to the evolution of coyness in different species.

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