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Costly but worthless gifts facilitate courtship

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What are the characteristics of a good courtship gift? We address this question by modelling courtship as a sequential game. This is structured as follows: the male offers a gift to a female; after observing the gift, the female decides whether or not to accept it; she then chooses whether or not to mate with the male. In one version of the game, based on human courtship, the female is uncertain about whether the male intends to stay or desert after mating. In a second version, there is no paternal care but the female is uncertain about the male's quality. The two versions of the game are shown to be mathematically equivalent. We find robust equilibrium solutions in which mating is predominantly facilitated by an 'extravagant' gift which is costly to the male but intrinsically worthless to the female. By being costly to the male, the gift acts as a credible signal of his intentions or quality. At the same time, its lack of intrinsic value to the female serves to deter a 'gold-digger', who has no intention of mating with the male, from accepting the gift. In this way, an economically inefficient gift enables mutually suitable partners to be matched.

Keywords: gift; courtship; signalling; paternal care; sexual selection

1. INTRODUCTION

Gift-giving is a feature of human courtship (Miller 2000), and mating systems in a number of arthropod species involve nuptial gifts (Schneider & Lubin 1998; Vahed 1998). The role of gifts in essentially symmetric interactions has been modelled by economists (Camerer 1988; Carmichael & MacLeod 1997). Reproduction, however, is asymmetric; in the vast majority of species, females invest more resources in the offspring than do males (Trivers 1972). Here we ask: given this asymmetry, what is the function of a courtship gift, and what are the characteristics of a 'good' gift?

In human reproduction, the male may stay to help rear the offspring, or else desert after mating. One attempt to understand this (Dawkins 1976) involves a game with two possible female strategies and two possible male strategies. Females are either willing to mate immediately ('fast') or require a delay before mating ('coy'), while males are either willing to accept a delay and to care for the young ('faithful') or unwilling to do either ('philanderer'). This results in a population equilibrium containing a mixture of each type for each sex. It has been pointed out, however (Carmichael & MacLeod 1997), that this solution is based on artificially excluding a male strategy of wait-before-mating-but-then-desert. A satisfactory model of courtship requires an account of *why* in some cases males choose to stay and help care for the young and in others choose to desert, when the choice is made *after* mating has taken place. Human courtship is characterized by males offering gifts which are costly to them but of low intrinsic benefit to the recipient (Miller 2000). Could this type of gift have a function related to the question of whether a male will stay or desert, encompassing the uncertainties and risks faced by each player in the mating game?

While the possibility of desertion by the male may be relevant to mate choice in human females, females are also frequently choosy in mating systems with no paternal care. The precise reasons for such choosiness are an open problem (Cronin 1991; Kirkpatrick & Ryan 1991). It has been postulated that variation in costly male traits which influence female choice may reflect variation in some underlying measure of quality (Zahavi 1975; Grafen 1990*a*; Norris 1993; Welch *et al.* 1998), such as the ability to resist parasites (Hamilton 1980).

A number of arthropod mating systems involve males giving nuptial gifts to females. While such gifts are of nutritional value in some species (e.g. Karlsson 1998), this may not be the case for all species (Wedell 1993; Vahed 1998; Stalhandske 2001). This leads to the possibility that, in some mating systems involving nuptial gifts, the primary purpose of the gift may be to convey information about the male rather than provide nourishment to the female (Cumming 1994; Will & Sakaluk 1994; LeBas *et al.* 2004).

In this paper, we model courtship as a sequential game between the sexes in which there is gift giving along with uncertainty and possible conflicts of interest. We consider two mating systems, one with facultative paternal care and the other with sexual selection and no paternal care.

2. MODEL 1: FACULTATIVE PATERNAL CARE

A mating season may potentially involve a series of courtship encounters for a given animal. Here we consider the fitness consequences of a single encounter involving a male player and a female player. Each makes an assessment of whether the other is *attractive* or *unattractive*. Attractiveness is a noisy indicator of quality. Each player, however, does not know if he or she is attractive to the other. This captures the idea that a player has *some uncertainty* about his or her own attractiveness to a given potential mate, and bears some relationship to the 'random roles' model of preferences suggested by Ball & Parker (2003). We assume that there is a probability $P_{\rm f}$ that the

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female will be rated as attractive by the male, and a probability $(1-P_f)$ that she will be rated unattractive. Similarly, there is a probability P_m that the male will be rated as attractive by the female and a probability $(1-P_m)$ that he will be rated unattractive. The proportions P_m and P_f are assumed to be 'known' to all players, and to act as prior probabilities with respect to attractiveness. This knowledge may be hard-wired by natural selection or learnt during the juvenile phase.

Payoffs represent each player's change in fitness as a result of the mating encounter, so that a payoff of zero is equivalent in fitness terms to the players not having encountered each other. We assume that a male's expected payoff from mating with any female is positive. But it is greater if he finds her attractive, and in this case it is worth his while to stay and help after mating: this gives him a payoff of M_{AH}. Conversely, if he finds her unattractive, his post-mating payoff is maximized by deserting, giving him a payoff of M_{UD}.

A female gets a positive post-mating payoff F_{AH}, if she finds the male attractive and he stays. She gets a negative payoff F_{AD}, if the male is attractive but deserts. Her payoff is also negative if she mates with an unattractive male who helps: she would be better off not mating with such a male, on the prospect of a future encounter with an attractive male who will help. The worst possible payoff (i.e. most negative) for the female is to mate with an unattractive male who deserts.

Assuming that each player seeks to maximize his or her own payoff, and that players cannot commit to sub-optimal future actions, we deduce that:

(i) the female will not mate with an unattractive male;
(ii) the male will always desert an unattractive female;
(iii) hence, a positive payoff to both players will occur only if each finds the other attractive.

We further assume that the female's expected payoff if she mates with a random attractive male with no additional information as to whether he will stay or desert is negative, i.e.

$$P_f F_{AH} + (1 - P_f) F_{AD} < 0. \quad (2.1)$$

It follows that in the absence of specific information about whether or not the male finds her attractive, mating will not take place.

We now allow for gift giving, modelling courtship as a series of moves (figure 1).

(i) First, the male decides what type of gift to offer: cheap, valuable or extravagant:
  (a) a *cheap* gift costs the male nothing and is worth nothing to the female;
  (b) a *valuable* gift costs the male X and carries a benefit X to the female if she accepts it;
  (c) an *extravagant* gift also costs the male X, but is intrinsically worthless to the female.
  The male does not pay any gift cost if the gift is not accepted.
(ii) The female observes the gift, but her observation is subject to error. We assume a probability $(1-\eta)$ that she observes the offered gift correctly, and a probability $\eta/2$ that she observes it as each of the possible incorrect types.

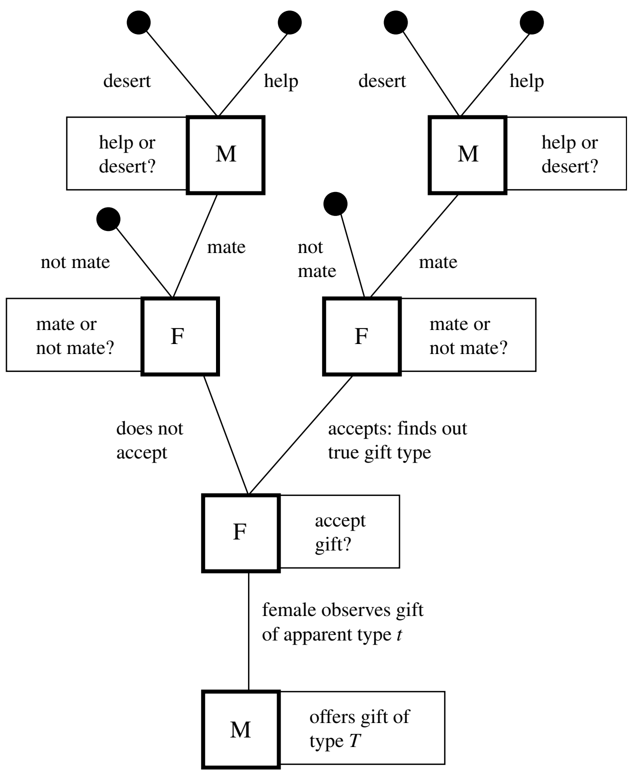

Figure 1. Game tree for model 1 (facultative paternal care).

(iii) The female decides whether or not to accept the gift. Acceptance removes the uncertainty regarding the gift type, but imposes a small cost ε on her. She also gets the benefit X if the gift turns out to be valuable. If she accepts, the male pays the cost X if the gift is either valuable or extravagant.
(iv) The female then decides whether to mate. She is at liberty to decide not to mate after accepting the gift. Equally she has the option of mating even if she has not accepted the gift.
(v) Finally, if mating occurs the male then decides whether to stay or desert.

The male's strategy is specified by what gift to offer, depending on whether the female is attractive or unattractive. His other actions follow directly from his payoffs: he will mate if given the opportunity; after mating, he will stay if the female is attractive and desert otherwise.

The female's strategy is straightforward if the male is unattractive: she must decide whether to accept the gift according to the probability, based on its appearance, that it is valuable. The game then ends, as she will not mate with an unattractive male.

If the male is attractive, she must choose:

(i) whether to accept the gift according to its apparent type;
(ii) if she has accepted it, whether to mate, depending on the now known gift type;
(iii) if she has not accepted the gift, whether to mate according to the apparent gift type.

The female's judgment of the probabilities of the true gift type, according to the apparent gift type, depends on a Bayesian calculation (Appendix A). The starting point for

Table 1. Parameters.

symbol	meaning	value
P_f	probability of female being found attractive by male	0.25
P_m	probability of male being found attractive by female	0.25
M_{AH}	payoff to male for mating with attractive female	20
M_{UD}	payoff to male for mating with unattractive female	5
F_{AH}	payoff to female for mating with attractive male who stays	10
F_{AD}	payoff to female for mating with attractive male who deserts	-40
η	probability that a gift is wrongly observed	0.2
ε	cost to female for accepting a gift	1
X	cost to male of valuable or extravagant gift, and value to female of valuable gift	10

a solution of the game is a Nash equilibrium, such that each player's strategy is an optimal response to that of the other player. Stability considerations must then be taken into account.

We develop the analysis of the model by first considering the outcome under a specific set of parameters. This is followed by a more general analysis. A full specification of the equilibria we consider is given in Electronic Appendix A, with supporting mathematical derivations provided in Electronic Appendix B.

3. NUMERICAL EXAMPLE

Suppose that probabilities and payoffs are as in table 1. Is there an equilibrium solution in which mating occurs?

(a) *Solution attempt 1*

First attempt the following solution: *male always offers a cheap gift to an unattractive female and a valuable gift to an attractive female.*

For the female, using the Bayesian methods outlined in Appendix A, the probabilities for the true gift type as a function of the apparent gift type are given in table 2.

Table 2. Probabilities for the true gift type to be cheap (first row) or valuable (second row) as a function of the apparent gift type, for solution attempt 1.

	gift looks cheap	gift looks valuable	gift looks extravagant
gift is cheap	0.96	0.27	0.75
gift is valuable	0.04	0.73	0.25

The female's best response to the male is:

(i) *if the gift looks cheap*: she should not accept the gift and not mate;

(ii) *if the gift looks valuable or extravagant and the male is attractive*: she should accept and then mate if it turns out to be valuable;

(iii) *if the gift looks valuable or extravagant and the male is unattractive*: she should accept the gift on the prospect that it will turn out to be valuable, but not mate with the male.

This gives the male a *negative* expected payoff against an attractive female. His prospect of a positive payoff if mating occurs is outweighed by his expected loss arising from the possibility of the gift being accepted by a female with no intention of mating with him.

This solution attempt is not a Nash equilibrium as the male would do better by offering a cheap gift to an attractive female, resulting in a payoff of zero.

(b) *Solution attempt 2*

Now attempt a different solution: *male always offers a cheap gift to an unattractive female and an extravagant gift to an attractive female.*

Table 3. Probabilities for the true gift type to be cheap (first row) or extravagant (second row) as a function of the apparent gift type, for solution attempt 2.

	gift looks cheap	gift looks valuable	gift looks extravagant
gift is cheap	0.96	0.75	0.27
gift is extravagant	0.04	0.25	0.73

For the female, using the Bayesian methods outlined in Appendix A, the probabilities for the true gift type as a function of the apparent gift type are now given in table 3.

The female's best response to the male is now:

(i) *if the gift looks cheap*: she should not accept the gift and not mate;

(ii) *if the gift looks extravagant or valuable and the male is attractive*: she should accept and then mate if it turns out to be extravagant;

(iii) *if the gift looks extravagant or valuable and the male is unattractive*: she should not accept and not mate. As valuable gifts are never offered, the gift will have no intrinsic value to her.

The male now does not pay the cost of the gift being accepted unless the female intends to mate with him. His payoff from an attractive female who accepts his gift is positive because the benefit from mating is greater than the cost of an extravagant gift.

If the male finds the female unattractive, it is not worthwhile for him to offer an extravagant gift as the cost is greater than the value of mating.

Could the female mate with an attractive male on the *appearance* of an extravagant gift, and avoid the acceptance cost ε? Because her observation is imperfect, there is a small chance that the gift will actually be cheap rather than extravagant, with the male intending to desert. For the parameter values given in table 1, it is better for her to pay ε and make certain of the gift type rather than take this risk.

This is therefore a Nash equilibrium. Now consider invasion and drift. Valuable gifts are never offered in this equilibrium; what a female will do if she accepts a gift that turns out to be valuable is unspecified. Suppose this unspecified behaviour drifts to a point where females will always treat a valuable gift as if it were extravagant. A male will then get the same payoff from offering either an extravagant or a valuable gift to an attractive female. Male behaviour can then drift in the direction of sometimes offering valuable rather than extravagant gifts to attractive females. But this can only go so far. If the proportion of valuable gifts offered exceeds a certain threshold, females should start accepting valuable-looking gifts from unattractive males; selection will then push males back in the direction of offering extravagant rather than valuable gifts to attractive females. The threshold occurs when a female's posterior belief that a valuable-looking gift will in reality be valuable is equal to ε/X. For the parameter values in table 1, this occurs when 94.5% of gifts to attractive females are extravagant and 5.5% valuable. (A derivation of this result is given in Electronic Appendix C.) Thus, extravagant gifts will predominate over valuable gifts.

4. GENERAL ANALYSIS

The calculation above has considered a specific set of parameter values. How does the model behave more generally, when parameters are allowed to vary?

We restrict detailed consideration to equilibria in which males offer only cheap gifts to unattractive females, and costly gifts (valuable, extravagant or a mixture of the two) to attractive females. We find five Nash equilibria of this type. The equilibrium play for each of these equilibia is as follows

(a) *Equilibrium without valuable gifts*

There is one equilibrium with mating in which valuable gifts are never offered by males.

- *Equilibrium 1*

  (i) Males offer only extravagant gifts to attractive females, and only cheap gifts to unattractive females.
  (ii) A female will accept a gift only if she perceives it to be extravagant and the male is attractive. She will mate only if the gift turns out actually to be extravagant.
  (iii) Otherwise, mating does not take place.

(b) *Equilibria without extravagant gifts*

There are two equilibria in which extravagant gifts are never offered by males.

- *Equilibrium 2*

  (i) Males offer only valuable gifts to attractive females, and only cheap gifts to unattractive females
  (ii) A female will accept a gift only if it is observed to be valuable and the male is attractive. She will mate only if the gift turns out actually to be valuable.
  (iii) Otherwise, mating does not take place.

- *Equilibrium 3*

  (i) Males offer only valuable gifts to attractive females and only cheap gifts to unattractive females.
  (ii) A female will not accept a gift from, nor mate with, any male whose gift appears to be cheap or extravagant.
  (iii) A female will accept a gift which is observed to be valuable from *any* male (whether attractive or unattractive). She will mate if the male is attractive and the gift actually is valuable.

This is the only equilibrium of the five in which females accept gifts from unattractive males.

(c) *Equilibria with both valuable and extravagant gifts*

For the final two equilibria, either valuable or extravagant gifts are offered to attractive females; the general equilibrium solution involves a mixture of valuable and extravagant gifts at the population level. We represent such a mixture using the variable ρ to denote the proportion of costly gifts offered to females that are valuable, with a proportion $(1-\rho)$ being extravagant.

- *Equilibrium 4*

  (i) Males offer valuable gifts with probability ρ and extravagant gifts with probability $(1-\rho)$ to attractive females, but only cheap gifts to unattractive females.
  (ii) A female will accept a gift which is observed to be valuable or extravagant if the male is attractive. Otherwise the gift is rejected and mating will not take place.
  (iii) A female will mate only with an attractive male whose accepted gift is actually valuable or extravagant.

This is the equilibrium which holds for the parameter values given in table 1 and assumed for the numerical example of §3 (i.e. solution attempt 2).

- *Equilibrium 5*

  (i) Males offer valuable gifts with probability ρ and extravagant gifts with probability $(1-\rho)$ to attractive females, but only cheap gifts to unattractive females.
  (ii) A female will accept any gift from an attractive male. If the male is unattractive she will reject all gifts.
  (iii) A female will mate only with an attractive male whose accepted gift is actually valuable or extravagant.

(d) *Stability and sensitivity*

Figure 2 shows the five equilibria, for ρ plotted against P_f, for two different values of the uncertainty parameter η. The costly gift type or mixture is plotted against P_f. We are concerned only with circumstances where condition (2.1) applies, i.e. no mating could take place without gift-giving, giving a range for P_f of 0–0.8 for the parameter values

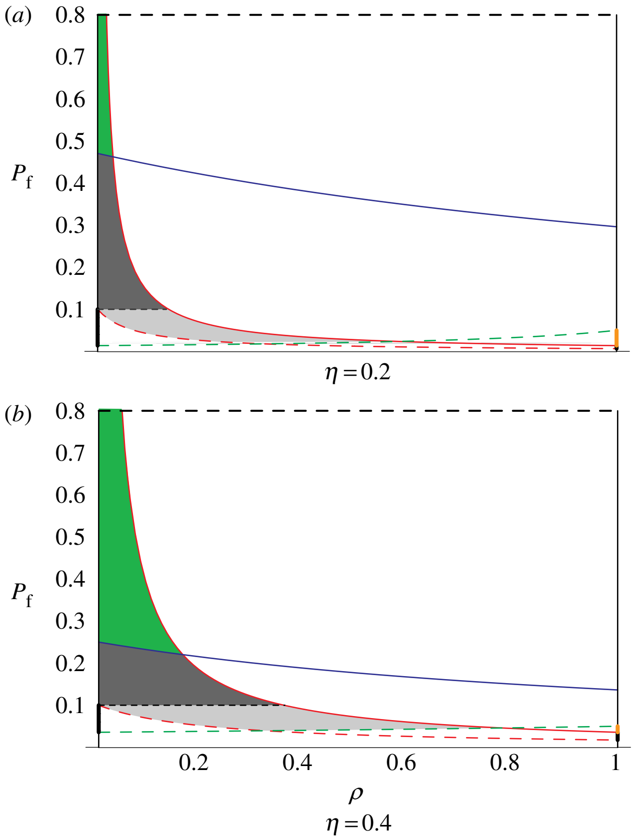

Figure 2. The five equilibria of the game, plotted on the (ρ, P_f)-plane, for two values of the misperception probability η: (*a*) $\eta = 0.2$; (*b*) $\eta = 0.4$. The other parameter values are: $F_{AH} = 10$, $F_{AD} = -40$, $X = 10$, $\varepsilon = 1$. The heavy black line on the $\rho = 0$ axis is the equilibrium 1 range, and the corresponding region on the $\rho = 1$ axis is the equilibrium 2 range. Equilibrium 3 is the orange range on the $\rho = 1$ axis. The grey shaded areas are the equilibrium 4 regions, and the green shaded area is the equilibrium 5 region. These regions all have a stable upper bound for ρ (solid red curve), but the light grey shaded area has an unstable lower bound, marked by the dashed red curve, below and to the left of which a female should not accept a valuable-looking gift from an attractive male. Below the dashed green curve, a female should not accept an extravagant-looking gift from an attractive male. The solid blue curve is the boundary delimiting whether a female should or should not accept a cheap-looking gift from an attractive male. The equilibrium 4 region is below this curve; the equilibrium 5 region is above this curve.

used. Plots for two further values of η are shown in Electronic Appendix A.

Equilibria 1, 2 and 3 are all evolutionarily stable strategy (ESS) solutions (Maynard Smith & Price 1973), and thus resistant to invasion by low frequency mutant strategies. (See electronic appendix for a fuller discussion of evolutionary stability considerations.) They hold for relatively low P_f, for which most gifts offered are cheap, and it is only worthwhile for a female to accept a gift if it appears to be of the 'correct' costly type. Equilibria 1 and 2 differ insofar as the correct type is extravagant for equilibrium 1, but valuable for equilibrium 2. For equilibrium 3, unlike equilibrium 2, males pay the cost of 'gold-diggers', i.e. females who accept their valuable gifts with no intention of mating. Equilibrium 3 holds only if parameter values representing male costs and payoffs are such that males can afford this cost. For both equilibria 2 and 3, males always offer valuable gifts to attractive females and cheap gifts to unattractive females; in this situation a higher prior probability P_f that a male will find a female attractive gives rise to a higher posterior probability that a gift which looks valuable will turn out to be valuable. It is for this reason that equilibrium 3 holds for higher values of P_f than equilibrium 2.

The game considered here is an asymmetric contest, i.e. players have distinct roles. In such a game, an ESS cannot involve a mixed strategy (Selten 1980); restricting analysis to formal ESS outcomes may mean disregarding solutions that can be considered to be effectively stable under reasonable dynamic assumptions (Hofbauer & Sigmund 1998). Instead, the stability of solutions involving mixed strategies must be assessed on a case-by-case basis.

Both equilibrium 4 and equilibrium 5 involve mixed strategies, and hence neither is a formal ESS. They differ only in that cheap-looking gifts from attractive males are rejected in equilibrium 4 but accepted in equilibrium 5. To determine stability, the dynamics of drift and selection pressure must be considered. For fixed P_f there is a range of values of ρ for which equilibria of type 4 or 5 are Nash equilibria of the game. If the value of ρ drifts above the upper ρ boundary (the solid red boundary in figure 2), it becomes optimal for females to accept valuable-looking gifts from unattractive males; this in turn causes selection to push the male population back below the boundary. Thus this upper boundary for ρ is an attracting boundary. For values of P_f toward the bottom of the range for which equilibrium 4 applies, there is also a non-zero lower boundary for ρ (figure 2; dashed red line). This, however, behaves very differently from the upper boundary. If the value of ρ drifts below this boundary, females should stop accepting valuable-looking gifts from attractive males, hence there will be selection for ρ to decline further, until equilibrium 1 is reached. Equilibrium 4 is, therefore, effectively unstable for values of P_f for which this lower boundary (a repelling boundary) exists.

Figure 2 indicates that for a wide range of values of P_f, a significant or dominant proportion of costly gifts offered to attractive females are extravagant. (We do not consider variation in P_m in the same way as variation in P_f because equilibrium 3 has only limited sensitivity to variation in P_m, and the other four equilibria hold for all P_m in the range $0 < P_m < 1$. P_f is, therefore, the more important parameter for sensitivity purposes.)

5. MODEL 2: SEXUAL SELECTION WITH NO PATERNAL CARE

We now consider a mating system involving no paternal care, but with choosy females and nuptial gifts. We assume that males are in either 'good' or 'poor' condition. Condition is correlated with male quality, so that a female gets a positive expected payoff from mating only if the male is in good condition. If condition affects the ease with which a male can procure different types of gift, then a gift may function as an indicator of condition.

A female is in either a sexually receptive or non-receptive physiological state. A receptive female is willing to mate with a male who is in good condition. By 'mate with' we mean here accept his gametes *with the purpose of using them for fertilization*. A non-receptive female will not mate, i.e. not accept gametes for fertilization purposes, but

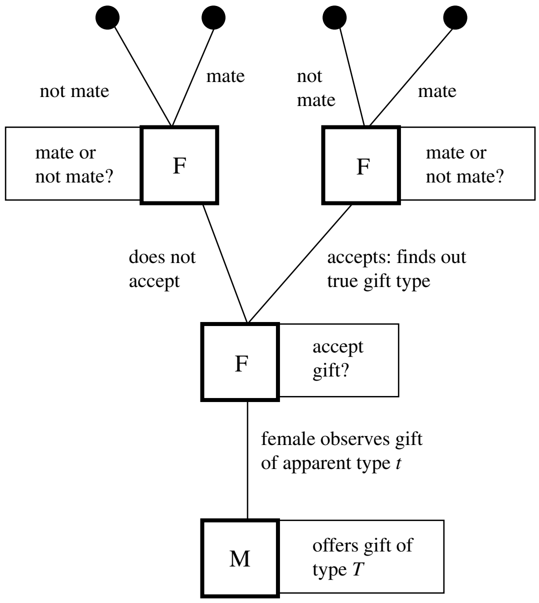

Figure 3. Game tree for model 2 (no paternal care, variable male condition).

may nevertheless be willing to accept gifts which have intrinsic value.

As before, a male is able to offer a cheap, valuable or extravagant gift; the female observes the gift imperfectly and must pay a small cost to accept it. The game, illustrated in figure 3, has the same structure as the facultative paternal care game of model 1, but there is no post-mating move in which males choose whether or not to help. It can be shown that the two games are mathematically equivalent (this equivalence is summarized in table 4 and explained in more detail in Electronic Appendix D), and can therefore be treated as the same for the purpose of analysis. So model 2 also readily yields solutions in which extravagant gifts dominate over valuable gifts as facilitators of mating. In such solutions, the gift acts as an honest indicator of the male's condition: males in good condition should offer mostly extravagant gifts, whereas those in poor condition should offer only cheap gifts as the fitness cost to them of procuring any other gift is too high. At the same time, the dominance of extravagant over valuable gifts as an indicator of good male condition deters non-receptive females from acting as gold-diggers.

Table 4. Equivalence of the two models.

model 1	model 2
female wants to mate if (i) male is attractive to her and (ii) he will stay after mating.	female wants to mate if (i) she is in a sexually receptive state and (ii) male is in good condition.
female is uncertain about whether male finds her attractive, and hence whether he will stay or desert after mating.	female is uncertain about male's condition.
male is always willing to mate, but the value to him of mating, relative to the cost of a valuable or extravagant gift, is greater if he finds the female attractive.	the cost to the male of a valuable or extravagant gift is prohibitive if he is in poor condition. Hence the value to him of mating, relative to the cost of such a gift, is greater if he is in good condition.
male is uncertain about whether female finds him attractive, and hence whether she will mate with him.	male is uncertain about female's sexual receptivity status, and hence whether she will mate with him.

For costly gifts to evolve as courtship signals requires variability among males in some attribute which has an important bearing on female fitness if mating occurs. Females must have imperfect information about this attribute from general cues such as the male's appearance, sound or scent. A courtship gift will then provide a female with useful information about the male if the type of courtship gift a male is able or willing to procure is correlated to the relevant attribute. This follows the principle that more should be spent on advertising by agents for whom the benefits of advertising, in comparison to the costs, are greater (Parker 1982; Grafen 1990*b*).

If the gift is valuable to a female, the male faces the risk of having the gift accepted by a gold-digging female who will not ultimately have his progeny. A costly but worthless gift may be better if a male would be better off for such a female to decline his gift. In the main text, we have assumed that males pay no cost if a gift is not accepted. For human courtship, this would correspond to a gift offer of, for example, an expensive outing. In Electronic Appendix A, we show that the same qualitative pattern of equilibria holds if the male forfeits some but not all of the cost of a gift when a female does not accept it.

In nuptial gift-giving arthropods, the transfer of the gift generally occurs simultaneously with sperm transfer. This may suggest a simple exchange, by which a male offers nutrients in return for reproductive access. But insofar as the female may be able to use sperm from different males non-randomly (Gwynne 1988; Ball & Parker 2003; Hockham *et al.* 2004), the male faces the potential risk of a female accepting valuable resources from him without giving him significant paternity of her offspring. This does not preclude the possibility of evolutionary equilibria in which a male is not able to avoid this risk—our analysis includes such an equilibrium in the form of equilibrium 3—and valuable gifts including nutritious spermatophylaxes may dominate in some species (Simmons 1990; Gwynne 1988). There is,

6. DISCUSSION

This study has modelled courtship as a sequential game. Two versions of the game, with rather different biological assumptions, have been presented. In model 1, motivated by human courtship, there is facultative paternal care and each player is uncertain about his or her own attractiveness to a potential partner. In model 2, based on systems with no paternal care, the male knows his own condition but not the female's receptivity, while the female knows her own receptivity but not the male's condition. To simplify the analysis, attractiveness (model 1), and male condition and female receptivity (model 2) are represented as binary variables. Despite the different biological assumptions, the two models have the same underlying mathematical structure, and therefore the same equilibrium solutions. We find an important role for extravagant gifts, i.e. gifts that are costly to the male but worthless to the female.

however, support for the idea that a rejected (and therefore retained) gift is worth something to the male from the hanging fly *Bittacus appicalis*, where the male tries to retrieve the gift after copulation, and may use it for his next mating attempt (Thornhill 1976). Similarly, in an experimental manipulation of the empidid dance fly *Rhamphomyia sulcata*, males sometimes reuse inedible token gifts (LeBas & Hockham 2005). This benefit from a retained gift suggests a possible role for costly but worthless gifts in order to deter a female who does not intend to use a male's gametes for fertilization from accepting his gift. In some species nuptial gifts are not of high value to females (Stalhandske 2001), while in other species males are polymorphic in gift types with edible and inedible gifts coexisting (Vahed 1998). The finding by LeBas & Hockham (2005) that *R. sulcata* females will sometimes mate after being presented with unfamiliar and worthless tokens suggests that the nuptial gift type can change over a short time-scale.

In conclusion, this study points to the possibility that, while an effective courtship gift should be costly to the male, in certain circumstances there may a positive reason for the gift to be worthless to the female.

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APPENDIX A

The male offers a gift of one of three types: *cheap*, *valuable* or *extravagant*. The overall probabilities with which each type is offered are π_C, π_V and π_E, respectively. The probability that an offered gift of type T is observed as a gift of type t is denoted as r_T^t. This is equal to $(1-\eta)$ for a correct observation, and $\eta/2$ for either of the possible wrong observations. For example, the probability that a cheap gift will appear to be cheap is $r_C^C = (1-\eta)$, and the probability that a valuable gift will appear to be extravagant is $r_V^E = \eta/2$.

The probability p_T^t that the true gift type is T when the observed gift type is t is

$$p_T^t = \text{(joint probability that } T \text{ is offered and } t \text{ is observed)/} \\ \text{(probability that } t \text{ is observed).}$$

For example, the probability that a gift which appears to be cheap is in reality cheap is

$$p_C^C = \frac{r_C^C \pi_C}{r_C^C \pi_C + r_V^C \pi_V + r_E^C \pi_E} = \frac{(1-\eta)\pi_C}{(1-\eta)\pi_C + \frac{1}{2}\eta\pi_V + \frac{1}{2}\eta\pi_E},$$

and the probability that a gift which appears to be extravagant is in reality valuable is

$$p_V^E = \frac{r_V^E \pi_V}{r_E^E \pi_E + r_V^E \pi_V + r_C^E \pi_C} = \frac{\frac{1}{2}\eta\pi_V}{(1-\eta)\pi_E + \frac{1}{2}\eta\pi_V + \frac{1}{2}\eta\pi_C}.$$

These expressions can be construed as the female's posterior (Bayesian) *beliefs* about the true gift type. We assume that natural selection or social learning will lead to the optimal decision rule in equilibrium, without the female needing to evaluate these expressions consciously.

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