A general time-in, time-out model for the evolution of nuptial gift-giving

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Nuptial gift-giving occurs in several taxonomic groups including insects, snails, birds, squid, arachnids and humans. Although this trait has evolved many times independently, no general framework has been developed to predict the conditions necessary for nuptial gift-giving to evolve. We use a time-in time-out model to derive analytical results describing the requirements necessary for selection to favour nuptial gift-giving. Specifically, selection will favour nuptial gift-giving if the fitness increase caused by gift-giving exceeds the product of expected gift search time and encounter rate of the opposite sex. Selection will favour choosiness in the opposite sex if the value of a nuptial gift exceeds the inverse of offspring processing time multiplied by the rate at which mates with nuptial gifts are encountered. Importantly, selection can differ between the sexes, potentially causing sexual conflict. We test these results using an individual-based model applied to a system of nuptial gift-giving spiders, *Pisaura mirabilis*, by estimating parameter values using experimental data from several studies. Our results provide a general framework for understanding when the evolution of nuptial gift-giving can occur, and also provide novel insight into the evolution of worthless nuptial gifts, which occur in multiple taxonomic groups with implications for understanding parental investment.

Introduction

Nuptial gift-giving occurs when the choosy sex (usually the female) receives gifts from the opposite sex (usually the male) during courtship. It is a widespread phenomenon, occurring within several diverse taxonomic groups such as insects, snails, birds, squid, arachnids and humans[1–3]. Despite the ubiquity of this behaviour, little effort has been made to conceptualise the evolution of nuptial gift-giving within a general modelling framework[1,4]. Recent models describing the evolution of nuptial gift-giving have focused on co-evolution between male nuptial gift-giving and female propensity to remate, and the evolutionarily stable nuptial gift sizes[4,5], but a general framework describing the conditions necessary for nuptial gift-giving to be initially favoured by selection is needed to understand when gift-giving should evolve.

Nuptial gift-giving may allow males to increase fitness by acquiring additional mates, indirect benefits (by increasing the fitness of offspring), prolonged copulations, and success in sperm competition[1,6,7]. However, this potential fitness increase comes at the expense of producing a nuptial gift, which may be costly in terms of time and resources. Females may increase their fitness by receiving nutritionally valuable nuptial gifts, but expressing a preference for males with gifts might result in a mating opportunity cost if available males without gifts are rejected.

Much work has sought to explain how gift-giving tactics are maintained, with explanations including condition-dependent strategies, gift-giving as a way to decrease female aggression during copulation, or gifts as sensory traps[8–11]. An example of such a system is the nuptial gift-giving nursery-web spider *Pisaura mirabilis* where males may court females with or without nuptial gifts[12]. Here, males may provide females with costly nuptial gifts in the form of captured arthropod prey, and females may exhibit preference for males with a nuptial gift by rejecting males without a nuptial gift[6].

We develop a general framework for investigating the evolution of nuptial gift-giving and choosiness using a time-in, time-out modelling approach and an individual-based model[13]. Specifically, we derive conditions under which selection will favour male search for nuptial gifts and female rejection of gift-less males. We show that selection for searching and choosiness depend on whether a threshold fitness value of the nuptial gift is exceeded. Our model demonstrates the importance of nuptial gift cost, sex ratio, and mate encounter rate in determining the threshold above which selection will favour the evolution of nuptial gift-giving. Importantly, we show that the threshold value differs for males and females. We test predictions of our analytical model by formulating an individual-based model to simulate the *P. mirabilis* system, allowing us to calculate estimates of key parameters from empirical data. Our results provide a general framework for understanding why nuptial gift-giving evolves in some systems and not in others, and it provides insight into the evolution of worthless and deceitful nuptial gifts, which occur in several different taxonomic groups[7,14].

Results

Analytical model

We use a time-in and time-out model[13,15,16] in which choosy (female) and non-choosy (male) individuals spend some period of time within the mating pool searching for a mate (time-in) followed by a period outside the mating pool (time-out). During time-out, females spend some duration of time (T_f) gestating or rearing (hereafter 'processing') λ offspring. Since females enter time-out after mating, this assumption is equivalent to assuming a system with sequential polyandry. For simplicity, we assume male time to replenish sperm is negligible, but males can spend some duration of time (T_m) out of the mating pool searching for nuptial gifts.

Criteria for male search and female choosiness

The probability that a male succeeds in securing a nuptial gift (G) is defined by,

$$G = 1 - e^{-\frac{1}{\alpha}T_m}. \tag{1}$$

In Eq. 1, α defines the expected search time before encountering a nuptial gift. During time-in, females and males encounter each other at a rate of M, and we define the sex ratio β as the ratio of males to females in the mating pool[15,16]. Hence, females in the mating pool will encounter males at a rate of $M\sqrt{\beta}$, and males will encounter females at a rate of $M/\sqrt{\beta}$[15,16]. We assume that when males provide a nuptial gift during a reproductive bout, they increase the fitness of each offspring by an increment of γ. We can show (see Methods) that the threshold value of γ (γ_m) necessary for males to increase their fitness by investing time searching for a nuptial gift (time that could otherwise be time invested searching for a mate) is,

$$\gamma_m > \alpha\frac{M}{\sqrt{\beta}}. \tag{2}$$

Verbally, Eq. 2 shows that the increase in offspring fitness from a nuptial gift must exceed the product of expected search time and female encounter rate. Under such conditions, we predict selection to favour the evolution of nuptial gift-giving.

We can similarly predict the conditions for which there is selection for female choosiness. If γ is sufficiently high, then females increase their fitness by rejecting males without gifts and mating only with males that

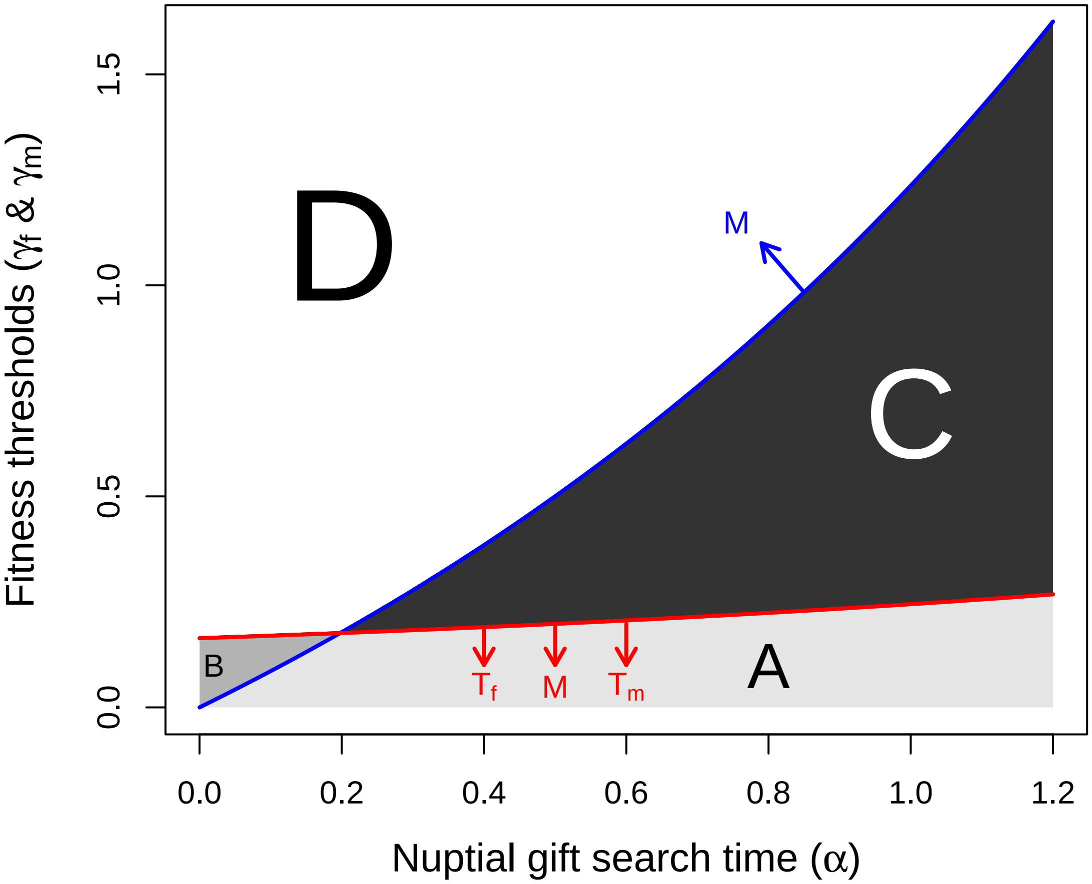

Figure 1: Fitness thresholds above which males increase their fitness by searching for nuptial gifts (blue line; Eq. 2) and females increase their fitness by rejecting males that do not offer gifts (red line; Eq. 3). Parameter space includes areas in which males do not search for nuptial gifts and females are not choosy (A), males search but females are not choosy (B), females would be choosy but males do not search (C), and males search and females are choosy (D). Arrows indicate the effect of increasing interaction rate (M), female time-out (T_f), and male search time (T_m).

provide nuptial gifts. To illustrate, we assume that all males in a population search for a duration of T_m, in which case the threshold fitness increment for females (γ_f) is,

$$\gamma_f > \frac{1}{T_f M \sqrt{\beta}\left(1 - e^{-\frac{1}{\alpha}T_m}\right)}. \tag{3}$$

Verbally, Eq. 3 shows that γ must exceed the inverse of the product of female processing time and the rate at which males with gifts are encountered. Figure 1 shows how γ_m and γ_f change with increasing α given $M = 1$ and $T_f = 2$. For γ_f, we assume that males search for the expected time required to obtain a nuptial gift ($T_m = \alpha$). Note that β has a closed form solution and can be redefined in terms of M, T_f, and T_m (see Methods).

The analytical framework predicts 4 zones, which are delineated by Eq. 2 and Eq. 3 and describe the initial threshold for favouring search of nuptial gifts in males and preference for nuptial gifts in females (Figure 1). Consequently, the modelling framework gives a description of the conditions under which nuptial gift-giving is expected to occur (Figure 1, Zone D) and the conditions under which only selection for male searching (Figure 1, Zone B) or female choosiness (Figure 1, Zone C) are predicted. These results therefore highlight the potential for sexual conflict over nuptial gift-giving.

Evolution of male search and female choosiness

We use an individual-based model (IBM) to simulate the evolution of nuptial gift-giving and female choosiness from an ancestral condition in which neither exists. The IBM was written to satisfy the assumptions of our analytical time-in and time-out model as much as practical. We modelled a spatially-implicit, finite population of females and males. At each time step, some individuals enter or remain within the mating pool (time-in), where they potentially interact and mate. After mating, males and females may leave the mating pool to search for nuptial gifts and to produce offspring, respectively (time-out). Mortality occurs with a fixed probability in each time step, then a ceiling regulation is applied to limit population growth (see Methods).

The rates at which males encounter females M_m and females encounter males with nuptial gifts $M_{f,G}$ are calculated directly from the IBM, so the male threshold for increasing fitness by searching is,

$$\gamma_{m,IBM} > \alpha M_m. \tag{4}$$

Similarly, female threshold for increasing fitness by choosiness is,

$$\gamma_{f,IBM} > \frac{1}{T_m M_{f,G}}. \tag{5}$$

The male thresholds $\gamma_{m,IBM}$ given by Eq. 4 accurately predict the evolution of searching in the IBM across α values, and the female threshold $\gamma_{f,IBM}$ (Eq. 5) accurately predicts the evolution of female choice (Figure 2). In other words, IBM simulations demonstrate that nuptial gift search in males, and choosiness in females, will evolve from an ancestral state of no searching and no choosiness in the same regions of parameter space (Figure 2) predicted by the analytical model (Figure 1).

By estimating γ using data from a system wherein choosiness among females, and nuptial gift search among males, occur, we ran IBM simulations with a realistic value of γ (Figure 3). We found that our IBM predicts both the evolution of choosiness and nuptial gift searching observed in the *P. mirabilis* system.

Discussion

Nuptial gift-giving has arisen several times independently throughout the animal kingdom[2], so understanding how selection favours nuptial gift giving and choosiness is important for a broad range of mating systems. We provide a general framework that defines the necessary conditions for selection to favour the evolution

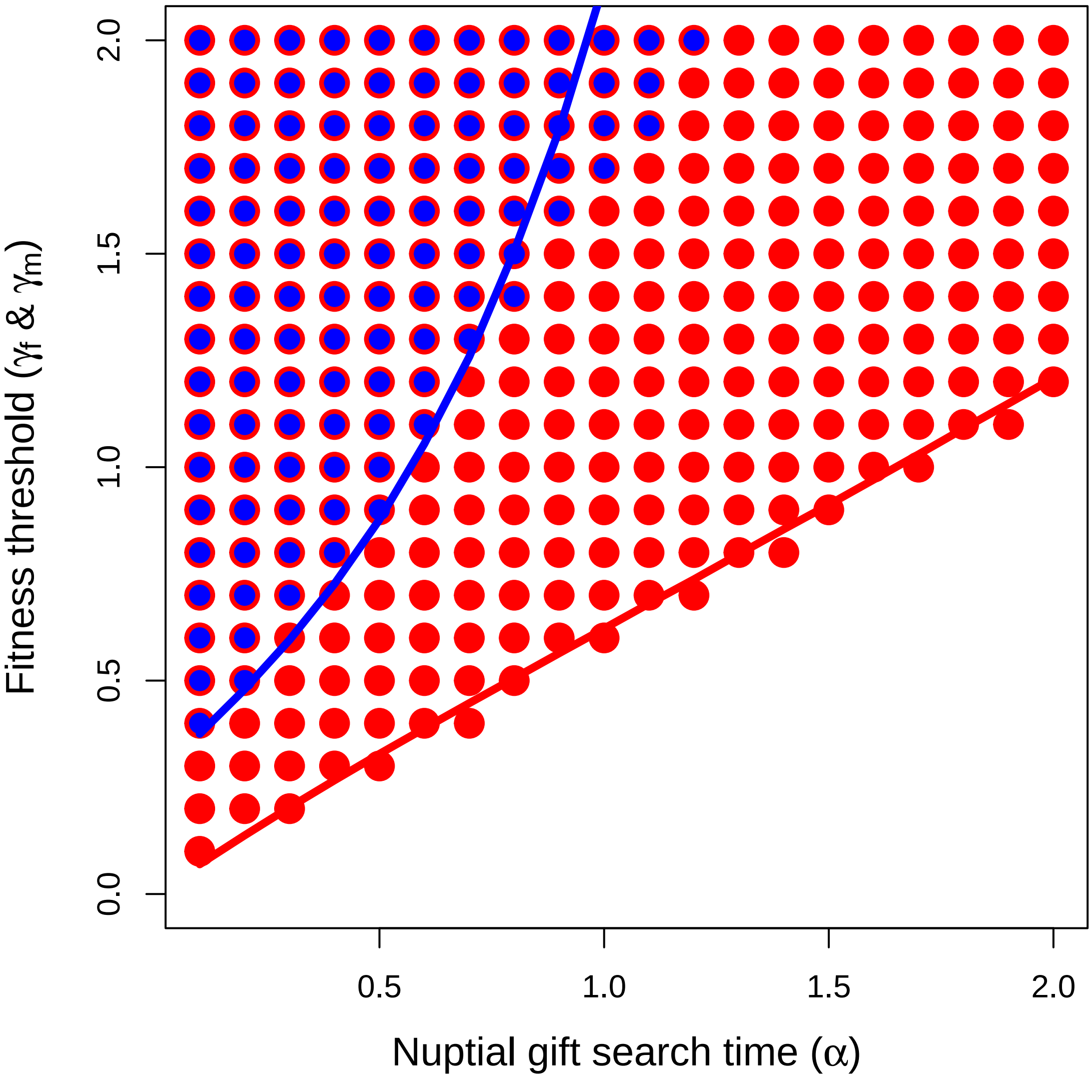

Figure 2: The joint evolution of male search and female choosiness as a function of nuptial gift search time. Points show where the lower 95% confidence interval of female choosiness (blue) and male search (red) exceeds zero, indicating evolution of choosiness or nuptial gift search. Each point includes data from 1600 replicate simulations with identical starting conditions. Red and blue lines show thresholds above which an mathematical modelling predicts that females should be choosy and males should search, respectively (in agreement with Figure 1).

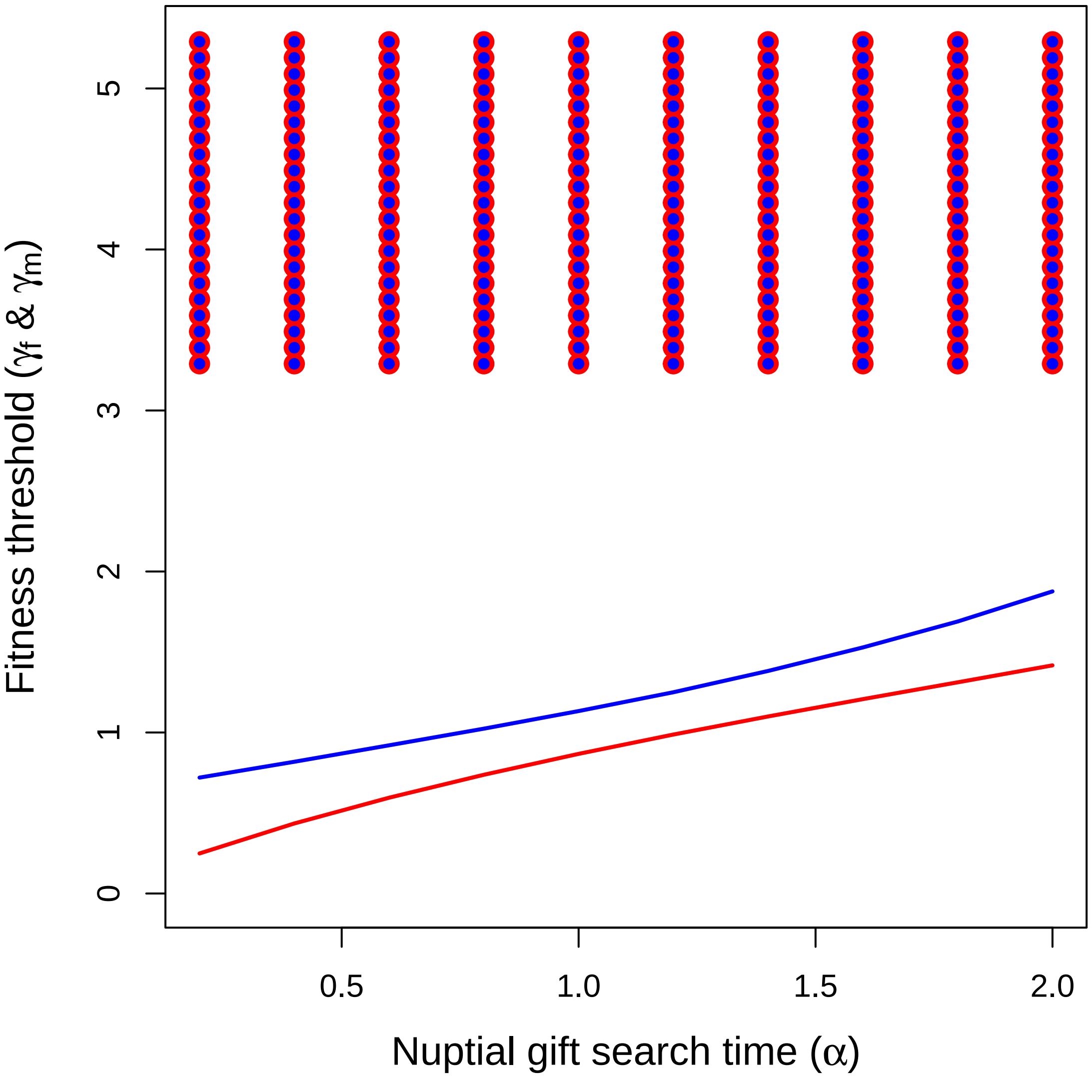

Figure 3: The joint evolution of male search and female choosiness using a nuptial gift fitness increment (γ) that was estimated from experimental data[17] along with replicates using upper and lower bound values of experimentally estimated γ. The remaining parameter values for these simulations were identical to those applied in Figure 2. Points show where the 95% confidence interval exceeds 0 for female choosiness (blue) and male search (red). Each point includes data from 1600 replicate simulations with identical starting conditions. The red line shows the threshold above which females should be choosy and the blue line shows the threshold above which males should search.

of nuptial gift-giving. We show that males should give nuptial gifts if the value of a nuptial gift exceeds a threshold dependent on the encounter rate between males and females and the cost or time necessary to find or produce a nuptial gift (see Eq. 2). This result makes intuitive sense because if males rarely encounter females, time searching for a gift is a minor cost relative to mate search time. If males encounter many females, it is not worth seeking nuptial gifts unless gifts are very valuable since the male will meet many prospective mates, and nuptial gift search time might come at a cost of decreased mating opportunities. In practice, male biased sex ratios will not necessarily favour male search for nuptial gifts if the female encounter rate is very high, so the key variable is how often males and females encounter each other. If the search time or cost of finding a nuptial gift is high, nuptial gifts must be very valuable before search is favoured by selection.

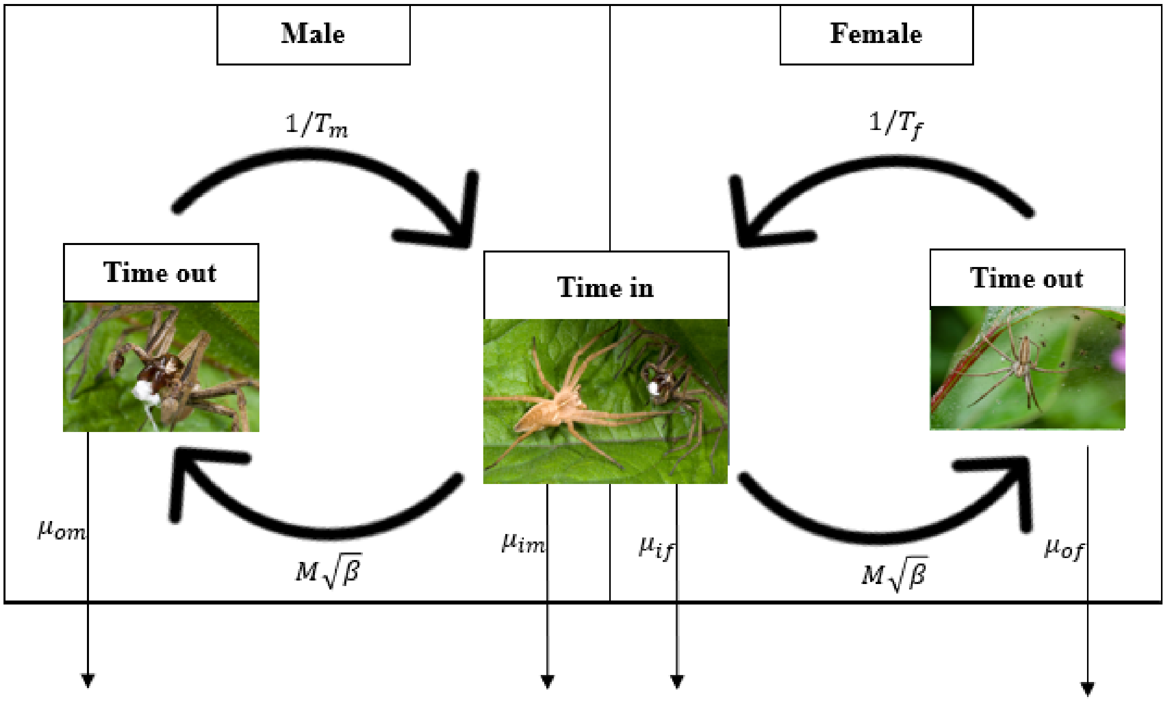

Figure 4: Conceptual figure inspired by Kokko and Ots[16] illustrating how the modelling framework maps onto an example of a system wherein nuptial gifts are used, here *Pisaura mirabilis*. Males have a probability of obtaining a nuptial gift while in time-out, which will affect their probability of mating while in time-in. They return to the mating pool (time-in) at a rate determined by the time spent searching for a nuptial gifts (T_m) and leave the mating pool (i.e. enter time-out) following the female encounter rate which is dependent on the sex ratio ($M\sqrt{\beta}$). The choosy sex (females) enter the mating pool at a rate depending in the time spent processing offspring (T_f) and leave the mating pool (i.e. enter time-out) following the male encounter rate, which is dependent on the sex ratio. Males and females undergo sex-specific mortality μ during time-in and time-out. Image left to right: (1) male *P. mirabilis*. (2) male *P. mirabilis* presenting nuptial gift (white) to female. (3) Female *P. mirabilis* protecting offspring. Photos: Alamy.

Importantly, we show that the threshold nuptial gift value at which females are favoured to express choosiness for nuptial gifts is rarely equivalent to the threshold value at which males are favoured to search for nuptial gifts, potentially leading to sexual conflict[18,19]. Sizable areas of parameter space exist for which only males (Figure 1, Zone B) or only females (Figure 1, Zone C) obtain a fitness benefit from male nuptial gift searching. Nuptial gift-giving and choosiness for nuptial gifts will only evolve when both thresholds are exceeded. That is, when females gain from discriminating for nuptial gifts and males gain from searching for them (Figure 1, Zone D). In many systems, ecological variables such as search time required to find a nuptial gift will likely depend on prey abundance, which can vary substantially with time in some species with nuptial gift-giving[10]. Since several ecological variables likely affect the value of these thresholds, our results can be seen as providing some formalised description of why nuptial gift-giving only occurs in some but not all systems.

When modelling nuptial gift evolution, the challenge is to construct a modelling framework that captures the frequency-dependent selection between male nuptial gift-giving and female preference for nuptial gifts, and we do this using a time-in, time-out model. Recent studies have modelled some frequency-dependent aspect of nuptial gift giving using evolutionary game theory[20,21]. Two such studies formulated a quantitative genetics model to study evolutionarily stable nuptial gifts sizes in populations where the female propensity to remate was evolving[4,5]. The results obtained in these studies complement our results by giving equilibrium solutions to the evolutionary stable nuptial gift size, whereas we determine the general conditions under which nuptial gift-giving will evolve as given by the inequalities we derive.

Other modelling frameworks have made general predictions about sexually selected traits, and these predictions are not mutually exclusive to those made by our model. For example, the good genes hypothesis predicts that costly traits such as nuptial gift-giving can be favoured since males enduring the cost of a nuptial gift signals to females that their genes confer high fitness precisely because they can afford this cost[22,23,but see 24]. In other words, costly sexually selected traits are favoured because they are indicators of overall genetic quality[25]. Because of this, nuptial gift-giving could be a case of condition-dependence where engaging in nuptial gift-giving is only favourable for male in good condition (e.g., males capable of successful search[10,20,26]). In general, our model demonstrates how nuptial gift-giving initially evolves before other mechanisms, such as good gene effects, become relevant.

A nuptial gift can also constitute a dishonest signal of good body condition since worthless, deceptive nuptial gifts have evolved in several systems[7,14]. This is also the case in *P. mirabilis* where males will wrap plant parts or an empty exoskeleton in silk, as opposed to an arthropod prey, and use this as a nuptial gift[7,27]. In such systems, worthless nuptial gifts have been shown to reduce the likelihood that a male is rejected by a female compared to the case where no nuptial gift is given. However, males offering worthless nuptial gifts may be at a slight disadvantage in sperm competition since worthless gifts result in a shorter copulation duration and hence less sperm transfer[6,7]. Worthless gifts should not result in any paternal care benefits to the male since the offspring he may sire will not gain nutrition from a worthless nuptial gift. Given our modelling framework, worthless nuptial gifts may be expected to evolve in cases where females are discriminating in favour of nuptial gifts, but the cost of search time for a true nuptial gift is very high.

While the main drivers of male nuptial gift-giving are thought to be increased success in sperm competition and indirect fitness benefits, nuptial gifts might also function to modulate female aggression and prevent sexual cannibalism[28]. In some systems, such as *P. mirabilis*, males have been shown to reduce the risk of being cannibalised by the female after mating when offering a nuptial gift, such that the nuptial gift may result in a “shield effect”, protecting the male[11].

The simulations parameterised with an experimentally estimated value of γ showed evolution of nuptial gift searching in males and preference for nuptial gifts in females. The model thus predicts that *P. mirabilis* living under conditions with the estimated fitness value of nuptial gifts should exhibit both search for nuptial gifts and preference for males with nuptial gifts, and this is what is observed in empirical populations. Parameterising γ with data from experimental studies may only yield a rough approximation of the true γ. This is because the estimated value of γ is based on data from current populations (rather than ancestral populations, which are being simulated), and because the literature is inconclusive as to how much (if any) effect nuptial gifts have on female fitness[29]. Despite this, it is encouraging that our modelling framework predicts both search for nuptial gifts and preference for males with nuptial gifts, which is in agreement with observation.

Overall, we found that a simple and elegant relationship between nuptial gift search time and mate encounter rate yields a threshold that determines whether selection will favour males who search for nuptial gifts. Similarly, we found that the threshold determining whether females will be favoured to reject males without nuptial gifts is also dependent on these variables, along with offspring processing time. Together, these thresholds describe the conditions under which nuptial gift-giving is expected to evolve. The applications of these thresholds are numerous. They can be used as a starting point for more complex or more system-specific models of nuptial gift-giving evolution. They can also provide novel insight into how populations can evolve to use worthless or token nuptial gifts. Since time spent during time-in relates to investment in mating and time spent during time-out relates to investment in nuptial gift search and parental investment, the thresholds may be used to gain novel insight into how parental investment relates to sexual conflict.

Methods

Model

Here we first present more detail for the derivation of fitness threshold values γ_m and γ_f. We then present full details for IBM simulations. Code for simulations is available on GitHub (see "Simulations").

Derivation of fitness thresholds

We use a time-in and time-out model in which females and males spend some time searching for a mate (time-in) followed by a period of cool down outside the mating pool (time-out).

After mating, females must spend some time processing offspring (T_f). Male time to replenish sperm is assumed to be negligible, but males can spend time out of the mating pool to search for a nuptial gift. When males return from time-out, they encounter females with some probability that is a function of the encounter rate between opposite sex conspecifics (M) and the sex ratio (β; males:females). Mortality occurs for females and males in ($\mu_{i,f}$, $\mu_{i,m}$) and out ($\mu_{o,f}$, $\mu_{o,m}$) of the mating pool. Following Kokko et al.[16], we assume $m_{i,f} = m_{o,f} = 1$ and $m_{i,m} = m_{o,m} = 1$. First, we describe the fitness consequences of male search time for a nuptial gifts. We then describe the fitness consequences of female choice to accept or reject males based on their provision of a nuptial gift.

Male fitness

During time-out, males search for a nuptial gift for a period of T_m. Initially, we assume that males must spend the full T_m in the time-out phase, even if they succeed in finding a nuptial gift. The probability that a male obtains a nuptial gift during this time is modelled in Eq. 1 (see Results),

$$G = 1 - e^{-\frac{1}{\alpha}T_m}.$$

In Eq. 1, α is the amount of time expected to pass before a male encounters a nuptial gift. We assume that a male will only enter the mating pool with no gift if they are unsuccessful in obtaining a gift, so the probability that a male obtains no gift after T_m is modelled as,

$$L = e^{-\frac{1}{\alpha_1}T_m}.$$

For simplicity, we assume that the fitness increments to offspring associated with receiving a nuptial gift versus no nuptial gift are $1 + \gamma$ and 1, respectively. The rate at which males increase their fitness can then be defined as the expected fitness increment from their nuptial gift search divided by T_m plus the time spent in the mating pool waiting to encounter a mate,

$$W_m = \lambda \frac{G(1+\gamma) + L}{T_m + \frac{\sqrt{\beta}}{M}}.$$

Our objective now is to determine the conditions under which a focal male increases its fitness by searching for a nuptial gift ($T_m > 0$) in a population of resident males that do not search ($T_m = 0$). Females are assumed to exhibit no choice in males with versus without nuptial gifts. Under such conditions, male fitness cannot be affected by female choice, so selection to increase $T_m > 0$ must be based solely on α, β, M, and γ.

To determine under what conditions male inclusive fitness increases with nuptial gift search time, we can differentiate W_m with respect to T_m,

$$\frac{\partial W_m}{\partial T_m} = \lambda \frac{\frac{\gamma\left(M^2 + \frac{T_m M^2 + M\sqrt{\beta}}{\alpha}\right)}{e^{\frac{1}{\alpha}T_m}} - M^2\left(1+\gamma\right)}{\left(T_m M + \sqrt{\beta}\right)^2}.$$

Because $T_m = 0$, the above simplifies,

$$\frac{\partial W_m}{\partial T_m} = \lambda \frac{\gamma M}{\alpha\sqrt{\beta}} - \lambda \frac{M^2}{\beta}.$$

Note that if $M = 0$ or $\lambda = 0$, then, trivially, no change in fitness occurs (since females and males cannot mate or do not produce offspring). Fitness is increased by searching for nuptial gifts when γ is high, scaled by the expect search time needed to find a nuptial gift. A second term on the right-hand side is subtracted, which reflects a loss in fitness proportional to the encounter rate of potential mates in the mating pool. The conditions under which male inclusive fitness increases by searching for a nuptial gift are found by setting $\partial W_m / \partial T_m = 0$ and solving for γ to get Eq. 2.

We can calculate the same threshold with a slightly different set of assumptions. Instead of spending a fixed amount of time in time-out phase, males might instead select one of two strategies; either search or do not search for a nuptial gift. Males with the former strategy continue to search until a nuptial gift is found, while males that do not search will immediately re-enter the mating pool. In this case, time searching for a nuptial gift will come at the cost of mating opportunities, but might increase the fitness of offspring. We therefore need to model the expected length of time $E[T_m]$ spent outside of the mating pool for males that search for nuptial gifts, which is simply α. Note that we can integrate search time t over the rate at which nuptial gifts are encountered ($\exp(-1/\alpha)$) to show $E[T_m] = \alpha$,

$$E[T_m] = \int_0^{\infty} e^{-\frac{1}{\alpha}t} dt = \alpha.$$

The rate at which a focal male that searches for a nuptial gift increases his fitness is therefore the fitness of offspring $(1+\gamma)$ divided by expected time spent searching for a nuptial gift (α) plus time spent in the mating pool $(\sqrt{\beta}/M)$,

$$W_{m,G} = \frac{1+\gamma}{\alpha + \left(\frac{\sqrt{\beta}}{M}\right)}.$$

In contrast, a male that does not search for a nuptial gift has offspring with lower fitness, but spends less time outside of the mating pool,

$$W_{m,L} = \frac{1}{\left(\frac{\sqrt{\beta}}{M}\right)} = \frac{M}{\sqrt{\beta}}.$$

We can then determine the conditions for which $W_{m,G} > W_{m,L}$, isolating γ to find how large of a fitness benefit must be provided by the nuptial gift to make the search cost worthwhile, which again simplifies to Eq. 2. Hence, the thresholds are consistent under different assumptions concerning male searching strategy. Selection will cause males to search for nuptial gifts if the fitness increase to offspring exceeds the product of search time and female encounter rate.

Female fitness

During time-out, females process offspring over a duration of T_f (we assume that $T_f > \alpha$, else females are not the choosy sex). When females re-enter the mating pool, they encounter males at a rate of $M\sqrt{\beta}$. If a female encounters a male with a nuptial gift, we assume that she will mate with him. But if a female encounters a male with no nuptial gift, then she might accept or reject the male. If she rejects the male, then she will remain in the mating pool. The rate at which a female encounters a male with a nuptial gift is,

$$M_{f,G} = M\sqrt{\beta}\left(1 - e^{-\frac{1}{\alpha}T_m}\right).$$

We can similarly model the rate at which a female encounters a gift-less male,

$$M_{f,L} = M\sqrt{\beta}\left(e^{-\frac{1}{\alpha}T_m}\right).$$

Note that we can recover the rate at which a female encounters any male,

$$M_{f,L} = M\sqrt{\beta}\left(1 - e^{-\frac{1}{\alpha}T_m}\right) + M\sqrt{\beta}\left(e^{-\frac{1}{\alpha}T_m}\right) = M\sqrt{\beta}.$$

Note that if $M_{f,G}$ is sufficiently high and $M_{f,L}$ is sufficiently low, then finding a male with a gift will be easier than finding a male without one. Also, the expected time spent in the mating pool before a focal female encounters a male with a gift will be $1/M_{f,G}$, while the expected time spent in the mating pool before a focal female encounters any male will be $1/(M_{f,G} + M_{f,L})$. Finally note that the rates at which a female encounters males with and without a gift, $M_{f,G}$ and $M_{f,L}$, are different from the probabilities that a male encounter has or does not have a gift. The rate of encounter is no longer relevant in this case because we are assuming that an encounter has occurred. Hence, the probability of an encountered male having a gift is simply,

$$g = \frac{1 - e^{-\frac{1}{\alpha}T_m}}{\left(1 - e^{-\frac{1}{\alpha}T_m}\right) + e^{-\frac{1}{\alpha}T_m}} = 1 - e^{-\frac{1}{\alpha}T_m}.$$

Similarly, the probability of an encountered male not having a gift is simply,

$$l = e^{-\frac{1}{\alpha}T_m}.$$

The rate at which a female increases her fitness by being choosy and mating only when she encounters a male with a gift is,

$$W_{f,g} = \frac{1+\gamma}{T_F + \frac{1}{M_{f,G}}}. \tag{6}$$

The top of the right-hand side of Eq. 6 gives the fitness increase, and the bottom gives the total time it takes to obtain this fitness. The $M_{f,G}$ is inverted because it represents the expected time to encountering a male with a gift. We can expand Eq. 6,

$$W_{f,g} = \lambda\frac{1+\gamma}{T_F + \frac{1}{M\sqrt{\beta}\left(1 - e^{-\frac{1}{\alpha}T_m}\right)}}.$$

If the focal female is not choosy and accepts the first male that she encounters, then the rate at which she increases her fitness is,

$$W_{f,l} = \lambda \frac{(1+\gamma)\left(1-e^{-\frac{1}{\alpha}T_m}\right)+e^{-\frac{1}{\alpha}T_m}}{T_F+\frac{1}{M\sqrt{\beta}}}.$$

We then evaluate the conditions under which $W_{f,g} > W_{f,l}$. We isolate γ to determine how much offspring fitness must be increase to make choosiness beneficial (γ_f),

$$\gamma_f > \frac{e^{\frac{1}{\alpha}T_M}}{T_F M\sqrt{\beta}\left(e^{\frac{1}{\alpha}T_M}-1\right)}.$$

The above reduces to Eq. 7 below,

$$\gamma_f > \frac{1}{T_F M\sqrt{\beta}\left(1-e^{-\frac{1}{\alpha}T_M}\right)}. \tag{7}$$

Note that that the expression $M\sqrt{\beta}\left(1-e^{-\frac{1}{\alpha}T_M}\right)$ defines the rate at which a female in the mating pool encounters males with nuptial gifts. Hence, female choosiness is ultimately determined by time spent out of the mating pool to process offspring (T_f) and the rate at which a female in the mating pool encounters males with nuptial gifts.

Operational sex ratio

We assume that the sex ratio at maturation is unity (i.e., equal number of males and females upon maturation). Under this condition, Kokko and Monaghan[15] show that the operational sex ratio depends on the probability of finding an individual in 'time in',

$$\beta = \frac{\int_{t=0}^{\infty} P_{IM}(t)dt}{\int_{t=0}^{\infty} P_{IF}(t)dt}. \tag{8}$$

In Eq. 8, $P_{IM}(t)$ and $P_{IF}(t)$ are the probabilities of finding a male and female in 'time in', respectively. Kokko and Monaghan[15] find these probabilities in terms of the cost of mating. For our purpose, we can obtain the probability of finding a male in 'time in' as the time spent in the mating pool waiting to encounter females ($\sqrt{\beta}/M$) divided by total time in and out,

$$P_{IM}(t) = \frac{\left(\frac{\sqrt{\beta}}{M}\right)}{T_m+\left(\frac{\sqrt{\beta}}{M}\right)}.$$

We define $P_{IF}(t)$ similarly,

$$P_{IF}(t) = \frac{\left(\frac{1}{M\sqrt{\beta}}\right)}{T_f+\left(\frac{1}{M\sqrt{\beta}}\right)}.$$

We therefore can define β as below,

$$\beta = \frac{\left(\frac{\left(\frac{\sqrt{\beta}}{M}\right)}{T_m + \left(\frac{\sqrt{\beta}}{M}\right)}\right)}{\left(\frac{\left(\frac{1}{M\sqrt{\beta}}\right)}{T_f + \left(\frac{1}{M\sqrt{\beta}}\right)}\right)}.$$

This can be simplified,

$$\beta = \frac{\beta T_f M + \sqrt{\beta}}{T_m M + \sqrt{\beta}}.$$

A closed form solution for the above equation can be found,

$$\beta = \frac{1}{2}\left(\left(M\left(T_f - T_m\right)\right)^2 \pm \left(\left(M\left(T_f - T_m\right)\right)^4 + 4\left(M\left(T_f - T_m\right)\right)^2 \right)^{\frac{1}{2}} \right) + 1. \tag{9}$$

We can use Eq. 9 to define β in terms of M, T_f, and T_m. Note that there are two solutions to β, but when $T_m > T_f$, then $\beta > 1$, and when $T_m < T_f$, then $\beta < 1$ (if $T_m = T_f$, then $\beta = 1$).

Individual-based model

Here we describe the details of initialisation, time-in (mating), time-out (reproduction and nuptial gift search), and mortality. We then summarise the simulations run and data collected.

Initialisation

Before the first time step, a population of $N = 1000$ individuals is initialised. Individuals are assigned unique IDs, and each is assigned to be female with a probability of 0.5, else male. Each individual i is initialised with a starting value of female offspring processing time (T_f^i), rejection rate for females (R^i), and male search time (T_m^i). For all simulations, initialised values are set to $T_f^i = 2$, $R^i = 0$, and $T_m^i = 0$. All individuals are initalised outside of the mating pool in the first time step $t = 1$. The first time step then proceeds with females immediately entering the mating pool and males either entering the mating pool or searching for nuptial gifts.

Time-in

At the start of each time step, females and males in the mating pool remain in it. Females will enter the mating pool after processing offspring, and males will enter it after searching for nuptial gifts (see 'Time-out' below). A fixed number of $\Psi = N\psi$ interactions between individuals occur in a single time step, where N is population size and ψ is a scaling parameter. For each interaction, two individuals are randomly sampled, each with equal probability. If both sampled individuals are within the mating pool and of different sexes, then a mating encounter occurs. If the male does not have a nuptial gift, then the female will reject him with a probability of R^i; if rejection occurs, then both individuals stay in the mating pool. If rejection does not occur, or the male has a nuptial gift in the mating encounter, then the individuals mate. Females leave the mating pool and enter time-out to process offspring, and males leave and enter time-out to potentially search for new nuptial gifts (note that females and males might re-enter the mating pool immediately within the same time step given sufficiently low search time; see Time-out below).

Time-out

During time out, a focal female i will produce $\lambda_i \sim Poisson(\lambda)$ offspring if no nuptial gift was provided or $\lambda_i \sim Poisson(\lambda + \gamma)$ if a gift was provided. Females remain outside of the mating pool to process offspring for

$T_{i,f}$ time steps, where $T_{i,f}$ is sampled randomly for each individual from a Poisson distribution with a rate parameter of T_f, $T_{i,f} \sim Poisson(T_f)$. Offspring are added to the population immediately, with R_i and $T_{i,m}$ values that are the average of each parent plus some normally distributed error μ_R and μ_{T_m}. For example,

$$T_{m,offspring} \sim \mathcal{N}\left(\frac{T_{m,mother} + T_{m,father}}{2}, \mu_{T_m}\right).$$

The variation generated by μ values simulates mutation upon which selection for traits can act. In all simulations, $\mu = 0$ if a trait is fixed and $\mu = 0.01$ if the trait evolves. Offspring sex is randomly assigned with equal probability as female or male. Female offspring are immediately placed in the mating pool, and male offspring are out of the mating pool to search for nuptial gifts. After a female has spent $T_{i,f}$ time steps outside the mating pool, she will re-enter it.

A focal male i outside the mating pool will enter it if they have searched for a fixed number of $T_{i,m}$ time steps, which is also sampled randomly from a Poisson distribution, $T_{i,m} \sim Poisson(T_m)$. If $T_{i,m} = 0$, then the male immediately returns to the mating pool (in the same time step). If $T_{i,m} > 0$, then the male must wait outside the mating pool for $T_{i,m}$ time steps, but will enter the mating pool with a nuptial gift with a probability,

$$G_i = 1 - e^{-\frac{1}{\alpha}T_{i,m}}.$$

Males must always spend $T_{i,m}$ time steps outside of the mating pool regardless of whether or not they are successful in obtaining a nuptial gift.

Mortality

At the end of time step, mortality occurs first with a fixed probability m for all adults in the population, then with a probability caused by carrying capacity K applied to all individuals (adults and offspring). Mortality occurs in each time step with a fixed probability of $m^i = 1 - \exp(-0.01)$ regardless of the sex of the individual or its position in or out of the mating pool. If after this fixed mortality is applied, the total population size $N > K$, then individuals are removed at random with equal probability until $N = K$. Following adult mortality, a new time step begins with newly added offspring becoming adults.

Simulations

We ran simulations in which male search time and female choosiness evolved from an ancestral state of no searching and no choosiness. In all simulations, N was initialised at 1000 and $K = 1000$. Simulations ran for $t_{max} = 40000$ time steps. We set $T_f = 2$, $\psi = 3$, and $\lambda = 1$ for all simulations, and we simulated across a range of $\alpha = \{0.1, 0.2, ..., 1.9, 2.0\}$ and $\gamma = \{0, 0.1, ..., 1.9, 2.0\}$ parameter values for 1600 replicates. Summary statistics for mean trait values, population size, sex ratios, proportion of females and males in and out of the mating pool, and mean number of encounters per female and male within the mating pool were all calculated in the last time step. The C code used for simulating these IBMs also allows for the reporting of statistics in each time step. Additionally, it can simulate explicit space and individual movement through the landscape A neutral evolving trait was also modelled to ensure that the code functioned as intended, and processes were compartmentalised into individual functions to facilitate code testing. All code is publicly available on GitHub (https://github.com/bradduthie/Pisaura).

A set of simulations with a value of γ calculated from empirical data was also conducted. Here, γ was parameterised using data on egg production as a function of eating nuptial gifts (see below). Additional simulation sets with lower and upper bounds of the estimated γ were subsequently run. In the simulation sets with experimentally derived parameter values, all other parameters were identical to previous simulation batches.

We can produce an estimate of the fitness increment obtained by females when receiving a gift ($\hat{\gamma}$) by using data on female *P. mirabilis* egg production and hatching success under diferent feeding regimes from Tuni et al.[17]. Tuni et al.[17] found differences in egg production and hatching success in female *P. mirabilis* under different feeding regimes. Assuming these differences in feeding regimes correspond to eating versus not eating nuptial gifts, the mean number of offspring produced by a female who eats nuptial gifts can be calculated (Table 1).

Table 1: Estimates showing mean number of offspring produced by female *Pisaura mirabilis* that ate nuptial gifts and females who did not. Means were calculated with raw data from Tuni et al.[17] and results are shown ± SE.

	Received nuptial gifts	Received no nuptial gift
Expected number of hatched eggs	25.74 ± 0.96	6.00 ± 2.1

Under these assumptions, the relative gain in fitness from receiving nuptial gifts for a female is,

$$\hat{\delta_f} = \frac{25.74}{6.00} = 4.29.$$

Since the baseline fitness is 1, the increase in fitness resulting from a nuptial gift then becomes,

$$\hat{\gamma} = \hat{\delta_f} - 1 = 3.29.$$

The value 3.29 was used to parameterise γ for a set of simulations (Figure 3).

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Data availability: The simulation software was implemented in C and the full source code is available at https://github.com/bradduthie/Pisaura.

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