

# A general model for the evolution of nuptial

## 2 gift-giving

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## Abstract

14 Nuptial gift-giving occurs in several taxonomic groups including insects, snails,  
birds, squid, arachnids and humans. Although this trait has evolved many times  
16 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  
18 derive analytical results describing the requirements necessary for selection to  
favour nuptial gift-giving. Specifically, selection will favour nuptial gift-giving if  
20 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  
22 choosiness in the opposite sex if the value of a nuptial gift exceeds the inverse of  
the time taken to produce offspring multiplied by the rate at which mates with  
24 nuptial gifts are encountered. Importantly, selection can differ between the sexes,

potentially causing sexual conflict. We test these results using an individual-based  
26 model applied to a system of nuptial gift-giving spiders, *Pisaura mirabilis*, by  
estimating parameter values using experimental data from several studies. Our  
28 results provide a general framework for understanding when the evolution of  
nuptial gift-giving can occur and provide novel insight into the evolution of  
30 worthless nuptial gifts, occurring in multiple taxonomic groups with implications  
for understanding parental investment.

## 32 Introduction

Nuptial gift-giving occurs when the choosy sex (usually the female) receives gifts  
34 from the opposite sex (usually the male) during courtship. It is a widespread  
phenomenon, occurring within several diverse taxonomic groups such as insects,  
36 snails, birds, squid, arachnids and humans (Lewis and South 2012; Albo et al.  
2013b; Lewis et al. 2014). Despite the ubiquity of this behaviour, little effort has  
38 been made to conceptualise the evolution of nuptial gift-giving within a general  
modelling framework (Lewis et al. 2014; Iwasa and Yamaguchi 2022). Recent  
40 models describing the evolution of nuptial gift-giving have focused on co-  
evolution between male nuptial gift-giving and female propensity to remate, and  
42 evolutionarily stable nuptial gift sizes (Kamimura et al. 2021; Iwasa and  
Yamaguchi 2022), but a general framework describing the conditions **under which**  
44 nuptial gift-giving **can be** initially favoured by selection is needed to understand  
when gift-giving should evolve.

46 Nuptial gift-giving may allow males to increase fitness by acquiring additional  
mates, indirect benefits (by increasing the fitness of offspring), prolonged  
48 copulations, and success in sperm competition (Albo et al. 2013a; Ghislandi et al.  
2014; Lewis et al. 2014). However, this potential fitness increase comes at the  
50 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  
52 nuptial gifts, but expressing a preference for males with gifts might result in a  
mating opportunity cost if available males without gifts are rejected. With respect  
54 to nuptial gift-giving, the evolutionary interests of both sexes may not always  
fully overlap. This can cause sexual conflict, which is a difference in the  
56 evolutionary interest between sexes that occurs when interaction between sexes  
result in situation where both sexes cannot achieve an optimal outcome  
58 simultaneously (Parker 2006). That is, under some conditions, it might for  
example be optimal for males but not females to mate if females do not benefit  
60 from mating with males without nuptial gifts.

62 Much work has sought to explain how gift-giving tactics are maintained, with ex-  
planations including condition-dependent strategies, gift-giving as a way to de-  
64 crease female aggression during copulation, or gifts as sensory traps (Lubin and  
Bilde 2007; Toft and Albo 2016; Ghislandi et al. 2018; Albo et al. 2019). An ex-  
66 ample of such a system is the nuptial gift-giving nursery-web spider *Pisaura*  
*mirabilis* where males may court females with or without nuptial gifts (Bristowe  
68 and Locket 1926). Here, males may provide females with costly nuptial gifts in  
the form of captured arthropod prey, and females may exhibit preference for  
70 males with a nuptial gift by rejecting males without a nuptial gift (Albo et al.  
2013a).

72 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 indi-  
74 vidual-based model (Clutton-Brock and Parker 1992). Specifically, we derive  
conditions under which selection will favour male search for nuptial gifts and fe-  
76 male rejection of gift-less males. We show that selection for searching and choosi-  
ness depends on whether a threshold fitness value of the nuptial gift is exceeded.  
78 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  
80 evolution of nuptial gift-giving. Importantly, we show that the threshold value dif-  
fers for males and females. We test predictions of our analytical model by formu-  
82 lating an individual-based model, which further supports the main theoretical re-  
sults of our analytical model. Further, we apply our model to an example system  
84 with nuptial gifts, the nursery web spider *Pisaura mirabilis*, where we use experi-  
mental data to estimate a key model parameter. Our results provide a general  
86 framework for understanding why nuptial gift-giving evolves in some systems and  
not in others, how the evolution of nuptial gift-giving can give rise to sexual con-  
88 flict, and it provides insight into the evolution of worthless and deceitful nuptial  
gifts, which occur in several different taxonomic groups (LeBas and Hockham  
90 2005; Ghislandi et al. 2014).

## Methods

### 92 Model

Here we first present more detail for the derivation of fitness threshold values  $\gamma_m$   
94 and  $\gamma_f$ . We then present full details for IBM simulations (see Supporting  
Information S1). Code for simulations is available on GitHub (see “Simulations”).  
96 Datasets used for the plots are also available (see “Data availability”).

### Derivation of fitness thresholds

98 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  
100 mating pool (time-out; Figure 1).

After mating, females must spend some time processing offspring ( $T_f$ ). Male time  
 102 to replenish sperm is assumed to be negligible, but males can spend time out of  
 the mating pool to search for a nuptial gift. We define the random variable  $T_m$  as  
 104 the time until a gift is found by a searching male. When males return from time-  
 out, they encounter females with some probability that is a function of the en-  
 106 counter rate between opposite sex conspecifics ( $R$ ) and the sex ratio ( $\beta$ ; males/fe-  
 males). Mortality occurs for females and males in ( $\mu_{i,f}$ ,  $\mu_{i,m}$ ) and out ( $\mu_{o,f}$ ,  $\mu_{o,m}$ ) of  
 108 the mating pool. Following Kokko and Ots (2006), we assume  $\mu_{i,f} = \mu_{o,f} = 1$  and  
 $\mu_{i,m} = \mu_{o,m} = 1$ . While this choice is arbitrary, we conducted a sensitivity analysis  
 110 which shows that the mortality parameters have no influence on the propensity for  
 male search and female choice to evolve (Supporting Information S1). First, we  
 112 describe the fitness consequences of male search time for a nuptial gift. We then  
 describe the fitness consequences of female choice to accept or reject males based  
 114 on their provision of a nuptial gift.

### Male fitness

116 During time-out, males have the opportunity to search for a nuptial gift.  
 Males can adopt one of two strategies; either search or do not search for a nuptial  
 118 gift. Males with the former strategy continue to search until they find a nuptial  
 gift, while males that do not search will immediately re-enter the mating pool. In  
 120 this case, time searching for a nuptial gift will come at the cost of mating opportu-  
 nities but might increase offspring fitness offspring. We therefore need to model  
 122 the expected time  $E[T_m]$  spent outside the mating pool for males that search for  
 nuptial gifts, which is simply  $\alpha$ . Note that we can integrate search time  $t$  over the  
 124 rate at which nuptial gifts are encountered ( $\exp(-1/\alpha)$ ) to show  $E[T_m] = \alpha$ ,

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

126 , The rate at which a focal male that searches for a nuptial gift ( $M_G$ ) increases his  
 fitness is therefore the fitness of his offspring ( $1+\gamma$ ) divided by expected time  
 128 spent searching for a nuptial gift ( $\alpha$ ) plus time spent in the mating pool,  $(\beta+1)/R$   
 (recall that females produce  $\lambda$  offspring),

$$130 \quad W_{M_G} = \lambda \frac{1+\gamma}{\alpha + \left(\frac{\beta+1}{R}\right)}.$$

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

$$W_{M_L} = \lambda \frac{1}{\left(\frac{\beta+1}{R}\right)} = \lambda \frac{R}{\beta+1}.$$

134 We can then determine the conditions for which  $W_{M_G} > W_{M_L}$ , isolating  $\gamma$  to find  
 how large of a fitness benefit must be provided by the nuptial gift to make the  
 136 search cost worthwhile, which simplifies to ineq. 2. When this inequality holds,  
 males are favoured to search until they find a nuptial gift, which would result in  
 138 an average search time of  $\alpha$ . When the male trait is continuous (i.e., males search  
 for time period  $T_m$ ), it can be shown that the same threshold can be reached by  
 140 evaluating the partial derivative of the male fitness function (Supporting  
 Information S2). Hence, the thresholds are consistent under different assumptions  
 142 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  
 144 and female encounter rate.

### **Female fitness**

146 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

148 pool, they encounter males at a rate of  $R\beta/(\beta+1)$ . If a female encounters a male  
 with a nuptial gift, we assume that she will mate with him. But if a female  
 150 encounters a male with no nuptial gift, then she might accept or reject the male. If  
 she rejects the male, she will remain in the mating pool. The rate at which a  
 152 female encounters a male with a nuptial gift is,

$$R_{F_G} = R \left( \frac{\beta}{\beta+1} \right) \left( 1 - e^{\frac{-1}{\alpha} T_m} \right).$$

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

$$R_{F_L} = R \left( \frac{\beta}{\beta+1} \right) \left( e^{\frac{-1}{\alpha} T_m} \right).$$

156 We can recover the rate at which a female encounters any male,

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

158 .

If  $R_{F_G}$  is sufficiently high and  $R_{F_L}$  is sufficiently low, then finding a male with a  
 160 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  
 162  $1/R_{F_G}$ , while the expected time spent in the mating pool before a focal female  
 encounters any male will be  $1/(R_{F_G} + R_{F_L})$ . Finally, the rates at which a female  
 164 encounters males with and without a gift,  $R_{F_G}$  and  $R_{F_L}$ , are different from the  
 probabilities that a male encounter has or does not have a gift. The rate of  
 166 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  
 168 gift is simply,

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

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

$$P(L) = e^{\frac{-1}{\alpha} T_m}.$$

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

$$174 \quad W_{f,G} = \lambda \frac{1+\gamma}{T_f} + \frac{1}{M_{f,G}}. \quad (6)$$

176 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  $R_{F_G}$  is inverted because it represents the expected time to encountering a male with a gift. We can expand Eq. 6,

$$180 \quad W_{f,G} = \lambda \frac{1+\gamma}{T_f + \frac{1}{R \left( \frac{\beta}{\beta+1} \right) \left( 1 - e^{\frac{-1}{\alpha} T_m} \right)}}.$$

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

$$W_{F_{G,L}} = \lambda \frac{(1+\gamma) \left( 1 - e^{\frac{-1}{\alpha} T_m} \right) + e^{\frac{-1}{\alpha} T_m}}{T_f + R \left( \frac{\beta}{\beta+1} \right)}.$$

184 We then evaluate the conditions under which  $W_{F_G} > W_{F_{G,L}}$ . We isolate  $\gamma$  to determine how much offspring fitness must increase to make choosiness

186 beneficial ( $\gamma_f$ ),



$$\gamma_f > \frac{1 + \frac{1}{\beta}}{DT_f \left( e^{\frac{1}{\alpha} T_m} - 1 \right)}.$$

188 The above reduces to Eq. 7 below,

$$\gamma_f > \frac{1}{T_f} R \left( \frac{\beta}{\beta + 1} \right) \left( 1 - e^{-\frac{1}{\alpha} T_m} \right). \quad (7)$$

190

Note that the expression  $R \left( \frac{\beta}{\beta + 1} \right) \left( 1 - e^{-\frac{1}{\alpha} T_m} \right)$  defines the rate at which a female

192 in the mating pool encounters males with nuptial gifts. Hence, female choosiness  
is determined by time spent out of the mating pool to process offspring ( $T_f$ ) and  
194 the rate at which a female in the mating pool encounters males with nuptial gifts.

### Operational sex ratio

196 We assume that the sex ratio is equal upon maturation. Given this, Kokko and  
Monaghan (2001) show that the operational sex ratio depends on the probability  
198 of finding an individual in ‘time in’,

$$\beta = \frac{\int_{t=0}^{\infty} P_{\mathfrak{M}}(t) dt}{\int_{t=0}^{\infty} P_{IF}(t) dt}. \quad (8)$$

200 In Eq. 8,  $P_{\mathfrak{M}}(t)$  and  $P_{IF}(t)$  are the probabilities of finding a male and female in  
‘time in’, respectively. There is no closed form solution to the operational sex ra-  
202 tio, so we used recursion to calculate  $\beta$  values for a given  $T_f$ ,  $T_m$ , and  $R$  (see Sup-  
porting Information S3),

## 204 **Individual-based model**

We formulate an individual-based simulation model to test whether the  
206 predictions made by the analytical time-in time-out model are qualitatively the  
same under a similar simulation model. We use the individual-based model to test  
208 whether the prediction hold in finite populations. The IBM was written in C.

210 We use available experimental data on the effect of nuptial gifts on female  
offspring production to estimate the key parameter  $\gamma$  (fitness increment from  
212 nuptial gift) and conducted a series of simulations where  $\gamma$  was parameterised  
using this estimated value. Details of the estimation of  $\gamma$  are described in the  
214 supporting information (see Supporting Information S4). Separate evolution of  
male search and female choice (i.e., without co-evolution) is simulated in  
216 Supporting Information S6.

### *Initialisation*

218 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  
220 probability of 0.5, else male. Each individual  $i$  is initialised with a starting value  
of female offspring processing time ( $T_f^i$ ), rejection probability of gift-less males (  
222  $\rho^i$ ), and male search time ( $T_m^i$ ). For all simulations, initialised values are set to  
 $T_f^i=2$ ,  $\rho^i=0$ , and  $T_m^i=0$ . All individuals are initialised outside of the mating pool  
224 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  
226 searching for nuptial gifts.

### *Time-in*

228 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  
230 it after searching for nuptial gifts (see ‘Time-out’ below). Up to  $\Psi = N\psi$   
interactions between individuals can occur in a single time step, where  $N$  is  
232 population size and  $\psi$  is a scaling parameter. In each time step,  $\Psi$  pairs of

individuals are selected at random to interact. For each interaction, two different  
 234 individuals are randomly selected from the population with equal probability. If  
 the selected individuals are of different sexes, and both are in the mating pool,  
 236 then a mating encounter occurs. If the male does not have a nuptial gift, then the  
 female will reject him with a probability of  $\rho^i$ ; if rejection occurs, then both  
 238 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  
 240 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  
 242 might re-enter the mating pool immediately within the same time step given  
 sufficiently low search time; see Time-out below).

#### 244 *Time-out*

During time-out, offspring production and time outside of the mating pool are  
 246 realised for each female by sampling from a Poisson distribution. A focal female  $i$   
 will produce  $Poisson(\lambda)$  offspring if no nuptial gift was provided or  $Poisson(\lambda + \gamma)$   
 248 if a gift was provided. Females remain outside of the mating pool to process  
 offspring for  $Poisson(T_f^i)$  time steps. Offspring are added to the population  
 250 immediately, with  $\rho^i$  and  $T_m^i$  values that are the average of each parent plus some  
 normally distributed error  $\epsilon_R$  and  $\epsilon_{T_m}$ . For example,

$$252 \quad T_m^{offspring} \sim \frac{T_m^{mother} + T_m^{father}}{2} + N(0, \epsilon_{T_m}).$$

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

A focal male  $i$  outside the mating pool will enter it if he has searched for a fixed  
 260 number of  $T_m^i$  time steps, which is also sampled randomly from a Poisson  
 distribution,  $Poisson(T_m^i)$ . If  $T_m^i = 0$ , then the male immediately returns to the  
 262 mating pool (in the same time step). If  $T_m^i > 0$ , then the male must wait outside the

mating pool for  $Poisson(T_m^i)$  time steps, but will enter the mating pool with a  
264 nuptial gift with a probability,

$$P(G^i) = 1 - e^{-\frac{1}{\alpha} T_m^i}.$$

266 Males must always spend  $T_m^i$  time steps outside of the mating pool regardless of  
whether or not they are successful in obtaining a nuptial gift.

### 268 *Mortality*

At the end of each time step, mortality occurs first with a fixed probability for all  
270 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  
272 with a fixed probability of  $\mu$  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  
274 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  
276 newly added offspring becoming adults.

### *Simulations*

278 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,  $N$   
280 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  
282 of  $\alpha = \{0.1, 0.2, \dots, 1.9, 2.0\}$  and  $\gamma = \{0, 0.1, \dots, 1.9, 2.0\}$  parameter values for 3200  
replicates. Summary statistics for mean trait values, population size, sex ratios,  
284 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  
286 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  
288 and individual movement through the landscape. A neutral evolving trait was also  
modelled to ensure that the code functioned as intended, and processes were  
290 compartmentalised into individual functions to facilitate code testing. All code is  
publicly available on GitHub

292 ([https://github.com/bradduthie/nuptial\\_gift\\_evolution](https://github.com/bradduthie/nuptial_gift_evolution)).

A set of simulations with a value of  $\gamma$  calculated from empirical data was also  
294 conducted (100 replicates). Here,  $\gamma$  was parameterised using data on egg  
production as a function of eating nuptial gifts (see below). Additional simulation

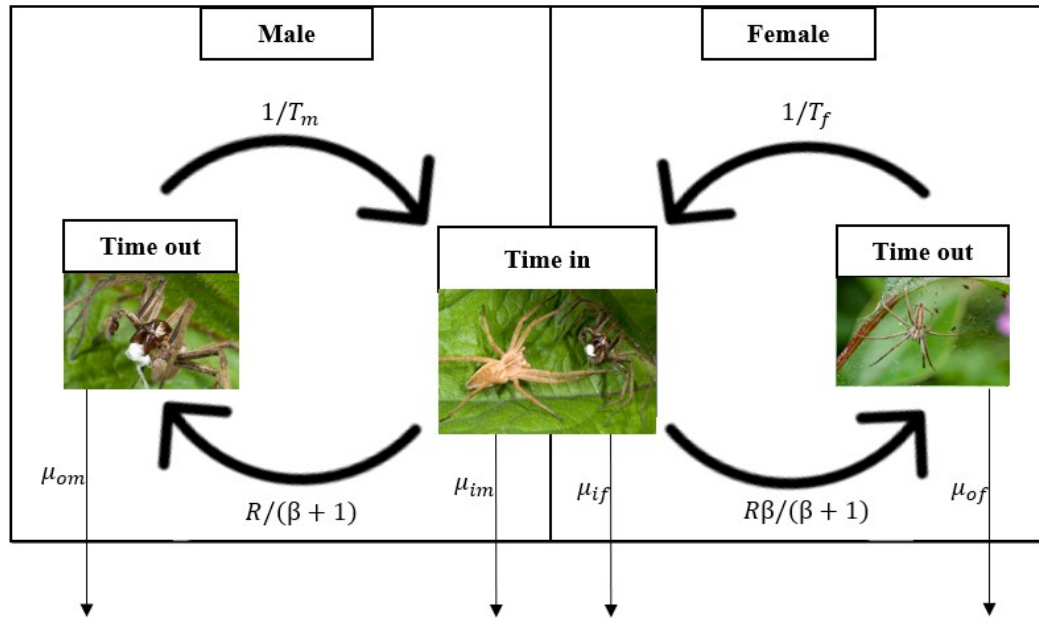
296 sets with lower and upper bounds of the estimated  $\gamma$  were subsequently run. In the  
simulation sets with experimentally derived parameter values, all other parameters  
298 were identical to previous simulation batches.

We can produce an estimate of the fitness increment obtained by females when  
300 receiving a gift ( $\hat{y}$ ) by using data on female *P. mirabilis* egg production and  
hatching success under different feeding regimes from (Tuni *et al.*, 2013). Tuni *et*  
302 *al.* (2013) found differences in egg production and hatching success in female *P.*  
*mirabilis* under different feeding regimes. Assuming these differences in feeding  
304 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).  
306

## Results

### 308 Analytical model

We use a time-in and time-out model (Clutton-Brock and Parker 1992; Kokko and  
310 Monaghan 2001; Kokko and Ots 2006) in which choosy (female) and non-choosy  
(male) individuals spend some period of time within the mating pool searching for  
312 a mate (time-in) followed by a period outside the mating pool (time-out). During  
time-out, females spend some time ( $T_f$ ) gestating or rearing (hereafter  
314 ‘processing’) offspring. We define the number of offspring produced by a female  
per reproductive cycle as  $\lambda$ . Since females enter time-out after mating, this  
316 assumption is equivalent to assuming a system with sequential polyandry. For  
simplicity, we assume male time to replenish sperm is negligible, but males can  
318 spend some time ( $T_m$ ) out of the mating pool searching for nuptial gifts.



**Figure 1.** Conceptual figure inspired by Kokko and Ots (2006) illustrating how the modelling framework maps onto an example of a system with nuptial gifts are used, here *Pisaura mirabilis* as an example. 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 gift ( $T_m$ ), and leave the mating pool (i.e., enter time-out) at a rate which is dependent on the sex ratio and encounter rate ( $R$ ). The choosy sex (females) enters the mating pool at a rate depending on the time spent processing offspring ( $T_f$ ), and leave the mating pool (i.e., enter time-out) at a rate which is dependent on the sex ratio and the encounter rate). Males and females undergo sex-specific mortality  $\mu$  during time-in ( $\mu_{im}$ ,  $\mu_{if}$ ) and time-out ( $\mu_{om}$ ,  $\mu_{of}$ ). Images left to right: (1) *P. mirabilis*, male; (2) *P. mirabilis*, male presenting a nuptial gift (white) to a female; (3) *P. mirabilis* female protecting offspring. Photos: Alamy.

## 336 **Criteria for male search and female choosiness**

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

$$338 \quad G = 1 - e^{\frac{-1}{\alpha} T_m} \cdot (1)$$

In Eq. 1,  $\alpha$  defines the expected search time before encountering a nuptial gift.

340 Thus, the probability of finding a nuptial gift is higher the more time  $T_m$  is spent searching. During time-in, a focal individual will encounter conspecifics of the

342 opposite sex at a rate of  $R/2$  if the ratio of males to females in the mating pool  $\beta$  is equal. More generally, males will be encountered at a rate of  $R\beta/(\beta+1)$ , and fe-

344 males will be encountered at a rate of  $R/(\beta+1)$ . An example of how the structure of the time-in time-out model applies to a system with nuptial gift-giving is given

346 in Figure 1. We assume that mating with a nuptial gift increases the fitness of each offspring by an increment of  $\gamma$ . We proceed to find the thresholds  $\gamma_m$  and  $\gamma_f$  above

348 which males and females are favoured by selection to search for mates with nuptial gifts and exhibit choosiness for nuptial gifts, respectively. We show (see

350 Methods) that the initial threshold value of  $\gamma$  ( $\gamma_m$ ) necessary for males to increase their fitness by investing time searching for a nuptial gift (time that could other-

352 wise be spent searching for a mate) is,

$$\gamma_m > \alpha \frac{R}{\beta+1} \cdot (2)$$

354 Inequality 2 means that if nuptial gifts are not abundant and thus require a long time to find (i.e., high  $\alpha$ ) or if males encounter many females per unit time, (i.e.,

356 high  $R/(1+\beta)$ ), then the nuptial gift must result in a high fitness increment for selection to favour gift-searching. In general, when ineq. 2 is satisfied, we predict

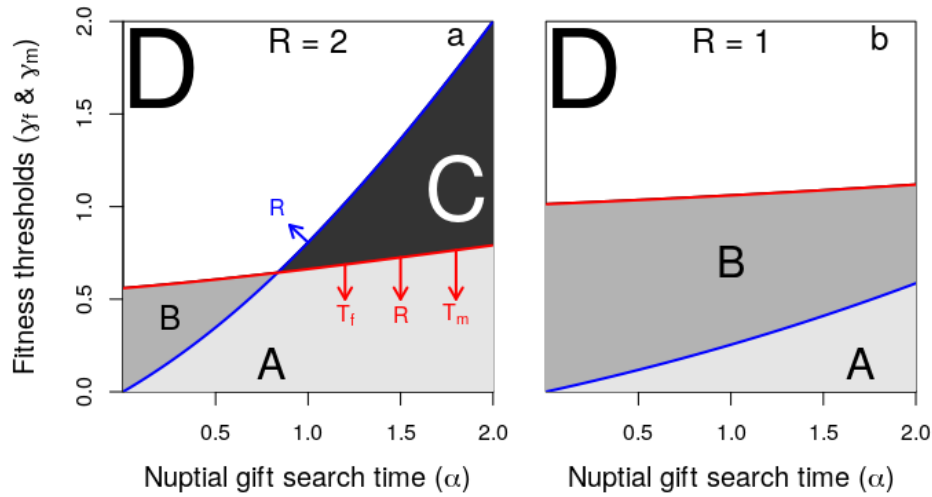
358 selection to favour the evolution of nuptial gift-giving.

We can similarly predict the conditions for which there is selection for female  
 360 choosiness. If  $\gamma$  is sufficiently high, then females increase their fitness by rejecting  
 males without gifts and mating only with males that provide nuptial gifts. To illus-  
 362 trate, we assume that all males in a population search for a duration of  $T_m$ , in  
 which case the threshold fitness increment for females ( $\gamma_f$ ) is,

$$364 \quad \gamma_f > \frac{1}{T_f R \left( \frac{\beta}{\beta+1} \right) \left( 1 - e^{-\frac{T_m}{\alpha}} \right)} \cdot (3)$$

366 Inequality 3 shows that as offspring processing time ( $T_f$ ), mate encounter rate ( $R\beta/(\beta+1)$ ), or the probability of a male finding a nuptial gift ( $1 - \exp(-T_m/\alpha)$ )  
 368 decreases, the threshold value of fitness above which selection will favour  
 choosiness ( $\gamma_f$ ) increases. This can be understood intuitively by realising that  
 370 rejecting a prospective male represents an opportunity cost for the female. This  
 opportunity cost becomes small if many males with gifts are encountered, hence  
 372 the appearance of the rate at which males with gifts are encountered in the  
 denominator. Figure 2 shows how  $\gamma_m$  and  $\gamma_f$  change with increasing  $\alpha$ . For  $\gamma_f$ , we  
 374 assume that males search for the expected time required to obtain a nuptial gift ( $T_m = \alpha$ ). Note that  $\beta$  does not have a closed form solution given  $R$ ,  $T_f$ , and  $T_m$ , so  
 376  $\beta$  was calculated using recursion (see Methods).





378 Fitness thresholds above which males increase their fitness by searching for nup-  
 380 tial gifts (blue lines; Eq. 2) and females increase their fitness by rejecting males  
 382 that do not offer gifts (red lines; Eq. 3). Parameter space includes areas in which  
 384 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 in panel a indicate the  
 effect of increasing interaction rate ( $R$ ), female time-out ( $T_f$ ), and male search  
 time ( $T_m$ ). As an example, trajectories for  $T_f=2$ , and  $T_m=\alpha$  are shown for values  
 386 of  $R=2$  (panel a) and  $R=1$  (panel b). Females are assumed to be the choosy sex,  
 which is maintained as long as  $\alpha < T_f$ .

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

### Evolution of male search and female choosiness

398 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.

400 The IBM was written to satisfy the assumptions of our analytical time-in and time-out model as much as practical (see Methods). Using the IBM, we modelled

402 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

404 potentially interact and mate. After mating, males and females may leave the mating pool to search for nuptial gifts and to produce offspring, respectively

406 (time-out). Mortality occurs with a fixed probability in each time step, then a ceiling regulation is applied to limit population growth (see Methods).

408 The rates at which females are encountered by males  $R_{f,m}$  and males with nuptial gifts  $R_{mG,f}$  are encountered by females are both calculated directly from the IBM,

410 thereby modelling how these rates might be estimated from empirical data, so the male threshold for increasing fitness by searching is,

$$412 \quad y_{m,IBM} > \alpha R_{f,m}. \quad (4)$$

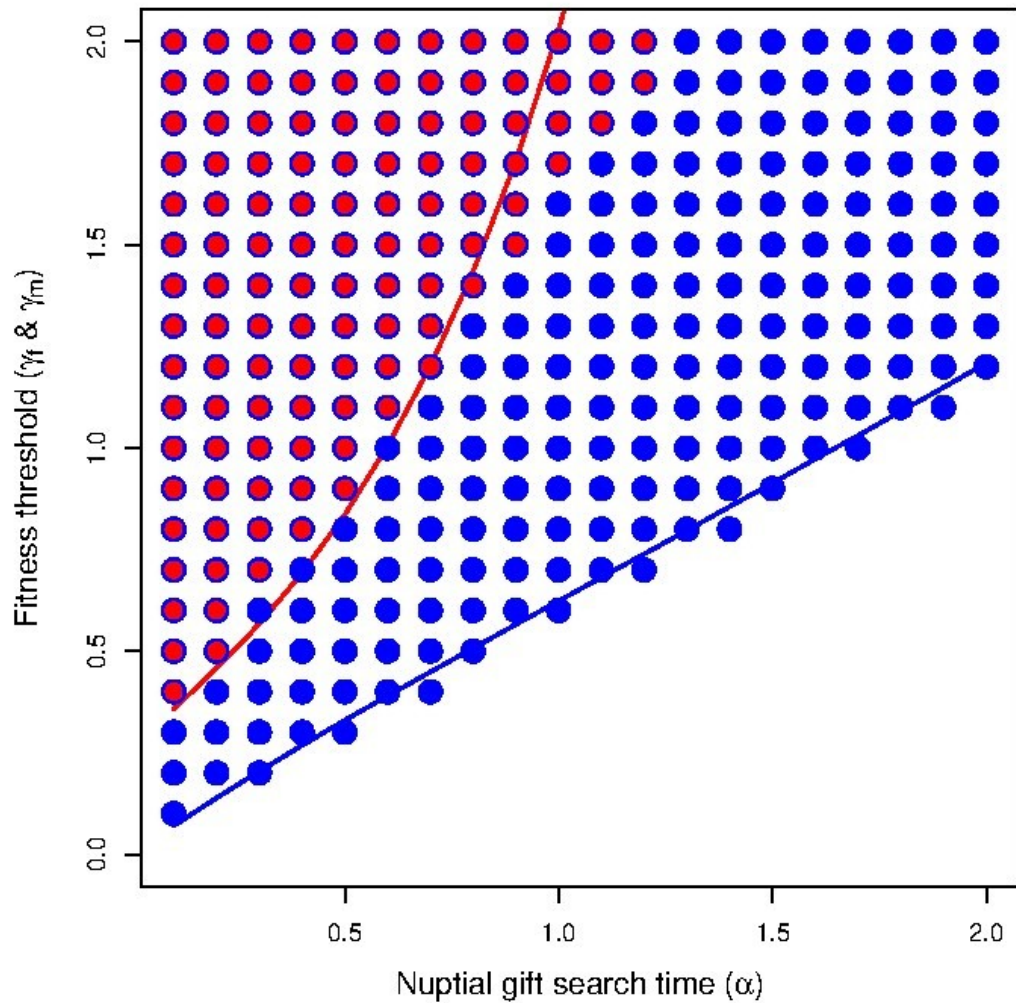
414 Similarly, female threshold for increasing fitness by choosiness is,

$$y_{f,IBM} > \frac{1}{T_f R_{mG,f}}. \quad (5)$$

416 Consequently, the IBM and the analytical model differ slightly (e.g., time is discrete in the IBM but continuous the analytical model, and in the IBM a fitness increment is applied to the focal female in the form of birthrate increase rather than

418

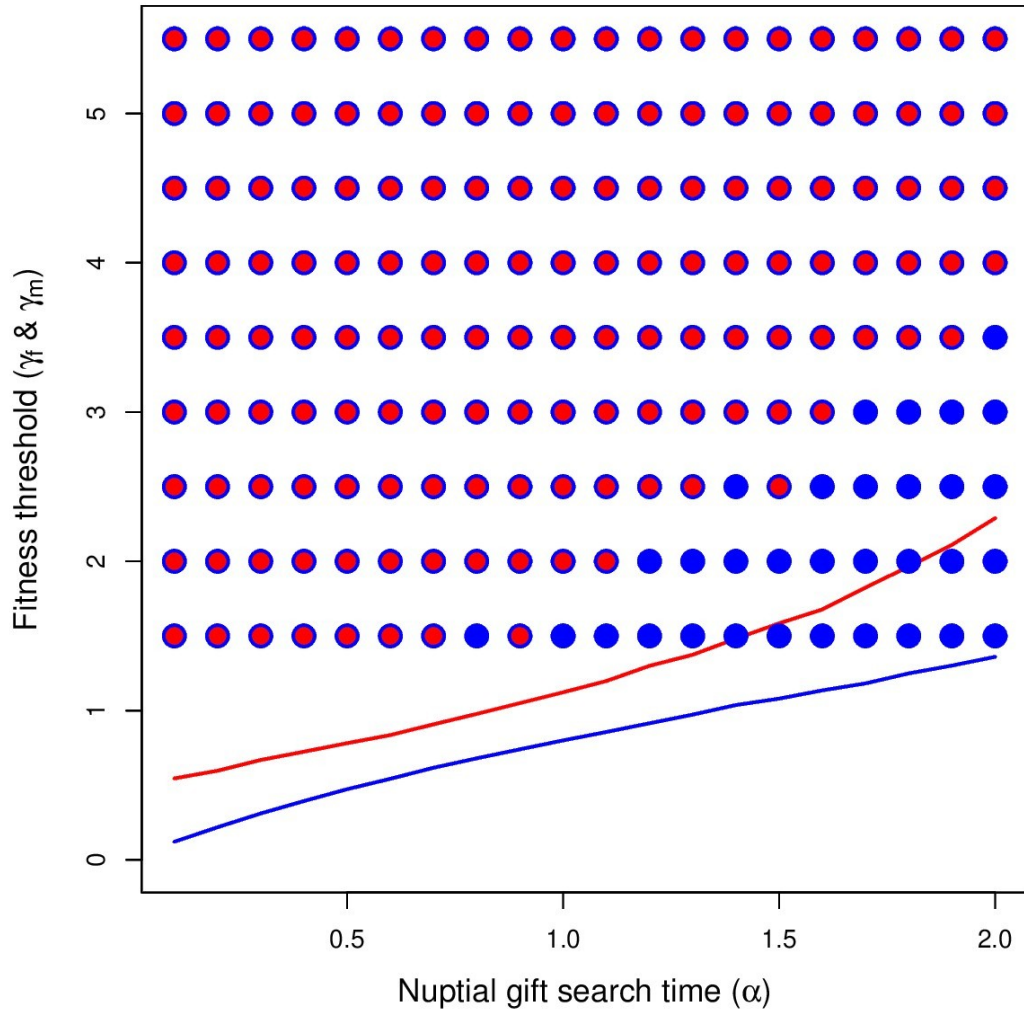
offspring; see Methods for details). But the predicted thresholds are theoretically  
 420 equivalent and yield predictions that are qualitatively the same (Figure 3).



422 **Figure 3.** The coevolution of male searching and female choosiness as a function  
 of nuptial gift search time ( $\alpha$ ). Points show where the lower 95% confidence  
 424 interval of female choosiness (red) and male search (blue) exceeds zero,  
 indicating evolution of choosiness or nuptial gift search. Each point includes data  
 426 from 3200 replicate simulations with identical starting conditions. Red and blue  
 lines show thresholds above which the mathematical model predicts that females  
 428 should be choosy and males should search, respectively (in agreement with Figure  
 2). Minor deviations between the analytical model and the simulation results are  
 430 expected due to the finite population size and the substantial stochasticity inherent

to the simulation model (for details, see Methods). The parameters  $M=1$ ,  $T_f=2$   
432 and  $\gamma$  and  $\alpha$  values in the range  $[0.0, 2.0]$  and  $[0.2, 2.0]$ , respectively, were used.

434 Male thresholds  $\gamma_{m,IBM}$  given by ineq. 4 accurately predict the evolution of search-  
ing in the IBM across  $\alpha$  values, and the female threshold  $\gamma_{f,IBM}$  (ineq. 5) accu-  
436 rately predicts the evolution of female choice (Figure 3). In other words, IBM  
simulations demonstrate that nuptial gift search in males, and choosiness in fe-  
438 males, will evolve from an ancestral state of no searching and no choosiness in  
similar parameter space (Figure 3) as predicted by the analytical model (Figure  
440 2b). We further ran the IBM values of  $\gamma$ , estimated using data from the *P.*  
*mirabilis* system wherein choosiness among females, and nuptial gift search  
442 among males, occur (Figure 4). We found that our IBM predicts both the evolu-  
tion of choosiness and nuptial gift searching observed in the *P. mirabilis* system.



444

**Figure 4.** The joint evolution of male search and female choosiness using a  
 446 nuptial gift fitness increment that was estimated from experimental data for the  
 species *P. mirabilis* (Tuni et al. 2013) (mean  $\gamma = 3.29 \pm \text{SE}$  via propagation of error  
 448 for estimates of nuptial feeding a non-nuptial feeding groups: [1.47; 8.32]).  
 Points show where the 95% confidence interval exceeds 0 for female choosiness  
 450 (red) and male search (blue). Each point includes data from 100 replicate  
 simulations with identical starting conditions. The blue line shows the threshold  
 452 above which females should be choosy and the red line shows the threshold above  
 which males should search. As predicted by the analytical model, both male  
 454 search and female choosiness evolved for a range of  $\gamma$  values around the empirical  
 estimates. This occurs because these values result in a  $\gamma$  above the fitness

456 threshold necessary for selection to favour male search of nuptial gifts (red line)  
and female choosiness (redline). The parameters  $M=1$ ,  $T_f=2$  and  $\gamma$  and  $\alpha$  values  
458 in the  $[0.2, 2.0]$ , respectively, were used. The parameter  $\gamma$  was estimated as  
relative increase in offspring production such that  $\gamma$  is the factor by which fitness  
460 increases (relative to the baseline fitness) given a nuptial gift (See Supporting  
Information S4).

462

## Discussion

464 Nuptial gift-giving has arisen several times independently throughout the animal  
kingdom (Lewis and South 2012), so understanding how selection favours nuptial  
466 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  
468 favour the evolution 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  
470 encounter rate between males and females and the cost or time necessary to find  
or produce a nuptial gift (see ineq 2). This result makes intuitive sense because if  
472 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  
474 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  
476 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  
478 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  
480 search is favoured by selection.

## Threshold fitness values

482 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 thresh-  
484 old value at which males are favoured to search for nuptial gifts, potentially lead-  
ing to sexual conflict (Arnqvist and Rowe 2005; Oliveira et al. 2008). Here, we  
486 are defining sexual conflict as occurring when interactions between sexes result in  
situation where both sexes cannot achieve an optimal outcome simultaneously  
488 (Parker, 2006). As an example, sizable areas of parameter space exists wherein  
the female optimum would be to exhibit preference for (and receive) nuptial gifts,  
490 while the male optimum is to not search for (and give) nuptial gifts (see Figure 2a,  
Zone C). **As a result, the evolutionary interests of both sexes do not always over-**  
492 **lap with respect to mating strategy.** In many systems, ecological variables such as  
search time required to find a nuptial gift will likely depend on prey abundance,  
494 which can vary substantially with time in some species with nuptial gift-giving  
(Ghislandi et al., 2018). Since several ecological variables are likely to affect the  
496 value of these thresholds, our results can be seen as providing a formalised de-  
scription of why nuptial gift-giving only occurs in some but not all systems.

498 At first, the analytical model seems to suggests that nuptial gifts must cause a very  
high fitness increase (approximately 25%) before male search and female  
500 choosiness is favoured by selection (Figure 2). Similarly the IBM model seems to  
suggest that a fitness benefit of approximately 50% is required (see Figure 3).  
502 However, it is important to recognise that these thresholds depend on multiple  
parameters. For example, if female processing time ( $T_f$ ) is high, the female  
504 threshold for choosiness with respect to  $\gamma$  drops such that male search and female  
choosiness are favoured at lower  $\gamma$  (see Supporting Information S1). If  $T_f$  is  
506 sufficiently high, then an initially rare gift-giving trait might be favoured by  
selection even if the fitness benefit of a nuptial gift is low. The effect that nuptial  
508 gifts have on fitness might vary across species, or even populations. Effects on

female fecundity have been estimated in crickets, fireflies, butterflies, and spiders,  
510 but these estimates vary considerably between species suggesting a large positive  
effect to no effect at all (Bergström & Wiklund, 2002; Rooney & Lewis, 2002;  
512 Maxwell & Prokop, 2018; Gao et al., 2019).

514 We modelled the evolution of nuptial gift-giving using both a mathematical model  
and an individual-based model. Our mathematical model makes simple  
516 assumptions about the relationship between nuptial gift search time ( $\alpha$ ),  
conspecific encounter rate ( $R$ ), female processing time ( $T_f$ ), and the fitness  
518 increment of a nuptial gift for offspring fitness ( $\gamma$ ). It then derives the threshold  $\gamma$   
values above which males increase their fitness by searching ( $T_m > 0$ ) for a nuptial  
520 gift ( $\gamma_m$ ) and females increase their fitness by choosing to reject males without  
gifts ( $\gamma_f$ ). In contrast, our IBM models individuals over discrete time steps, and  
522 key processes of nuptial gift acquisition, conspecific encounters, and female  
processing are stochastic and varying among individuals. The mathematical model  
524 and IBM make qualitatively identical predictions (compare Figure 2b versus  
Figure 3), but differences between the two models inevitably lead to quantitative  
526 differences for  $\gamma_m$  and  $\gamma_f$  thresholds. For example,  $\gamma_f$  increased more rapidly with  
increasing  $\alpha$  in the IBM compared to the analytical model. Some differences are  
528 expected to occur due to stochastic effects inherent to IBMs (e.g., Wilson *et al.*,  
2003). Other differences are more likely caused by more subtle assumptions  
530 between, and limitations of, the two models. In general, the IBM did not do a  
good job of controlling for conspecific interaction rate, making it difficult to  
532 directly compare  $R$  between models. The IBM also allowed for coevolution  
between male search and female choosiness (Figure 3), which was not allowed in  
534 the analytical model (Figure 2). It was not our goal to exactly recover the  
quantitative predictions of the analytical model in our IBM. Future development  
536 of the IBM could further bridge the gap between models while also developing  
new theory on how aspects of the system such as explicit space, individual life  
538 history, or genetics affect the evolution of nuptial gift-giving behaviour.



## Nuptial gift-giving theory

540 When modelling nuptial gift evolution, the challenge is to construct a modelling  
framework that captures the frequency-dependent selection between male nuptial  
542 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  
544 of nuptial gift giving using evolutionary game theory (Maynard Smith 1982; Vin-  
cent and Brown 2005). Two such studies formulated a quantitative genetics model  
546 to study evolutionarily stable nuptial gift sizes in populations where the female  
propensity to remate was evolving (Kamimura et al. 2021; Iwasa and Yamaguchi  
548 2022). The results obtained in these studies complement our results by giving  
equilibrium solutions to the evolutionary stable nuptial gift size, whereas we de-  
550 termine the general conditions under which nuptial gift-giving will evolve as  
given by the inequalities we derive.

552 A previous study considered the evolution of female choosiness as a function of  
mating and mortality rates and found that choosiness may generally be a costly  
554 trait which is not always expected to evolve (Kokko & Mappes 2013). Our results  
suggest that this is also the case when co-evolution with the relevant male trait is  
556 taken into account. Numerous studies have modelled mate choice as a function of  
a single variable or effect (for a review, see Edward 2015), such as direct benefits,  
558 indirect benefits or so-called chase-away sexual selection (Holland & Rice 1998;  
Kokko et al. 2003). Our results describe the evolution of mating choice from a dif-  
560 ferent perspective by taking ecological variables and coevolution into account at  
the same time.

562 Other modelling frameworks have made general predictions about sexually se-  
lected traits, and these predictions are not mutually exclusive to those made by our

564 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  
566 signals to females that their genes confer high fitness precisely because they can  
afford this cost (Kirkpatrick 1996; Byers and Waits 2006; but see Fromhage and  
568 Henshaw 2022). In other words, costly sexually selected traits are favoured be-  
cause they are indicators of overall genetic quality (Martinossi-Alilibert et al.  
570 2019). Because of this, nuptial gift-giving could be a case of condition-depen-  
dence where engaging in nuptial gift-giving is only favourable for male in good  
572 condition (e.g., males capable of successful search (Maynard Smith 1982; En-  
gqvist and Taborsky 2015; Ghislandi et al. 2018)). In general, our model demon-  
574 strates how nuptial gift-giving initially evolves before other mechanisms, such as  
good gene effects, become relevant.

576 A nuptial gift can also constitute a dishonest signal of good body condition since  
worthless, deceptive nuptial gifts have evolved in several systems (LeBas and  
578 Hockham 2005; Ghislandi et al. 2014). This is also the case in *P. mirabilis* where  
males will wrap plant parts or an empty exoskeleton in silk, as opposed to an  
580 arthropod prey, and use this as a nuptial gift (Albo et al. 2011; Ghislandi et al.  
2014). In such systems, worthless nuptial gifts have been shown to reduce the  
582 likelihood that a male is rejected by a female compared to the case where no nup-  
tial gift is given. However, males offering worthless nuptial gifts may be at a  
584 slight disadvantage in sperm competition since worthless gifts result in a shorter  
copulation duration and hence less sperm transfer (Albo et al. 2013a; Ghislandi et  
586 al. 2014). 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 nup-  
588 tial gift.

Given our modelling framework, worthless nuptial gifts may be expected to  
590 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 such that selection will not  
592 favour male search. This scenario would correspond to zone C of Figure 2 where  
the value of the nuptial gift exceeds the female fitness threshold for choosiness to  
594 be favoured, but due to high search time, selection will not favour male search for  
true nuptial gifts. Our model also predicts the possibility of the opposite scenario,  
596 in which males provide nuptial gifts, but females do not exhibit preference for  
nuptial gifts (zone B of Figure 2a). Fascinatingly, an example of such system has  
598 been documented by a recent study of the genus *Trechaleoides*, which contains  
two species with true nuptial gift-giving, but a lack of preference for nuptial gifts  
600 among females (Martínez Villar et al. 2023).

The main drivers of male nuptial gift-giving are thought to be indirect fitness ben-  
602 efits and increased success in sperm competition, since providing a nuptial gift  
can result in longer copulation duration which is correlated with increased sperm  
604 transfer along with female cryptic choice promoting males who provide nuptial  
gifts (Albo et al. 2011, 2013a). However, nuptial gifts might also function to  
606 modulate female aggression and prevent sexual cannibalism. In some systems,  
such as *P. mirabilis*, males have been shown to reduce the risk of being canni-  
608 balised by the female after mating when offering a nuptial gift, such that the nup-  
tial gift may result in a “shield effect”, protecting the male (Toft and Albo 2016).

## 610 **Empirical estimates**

The simulations parameterised with an experimentally estimated value of  $\gamma$   
612 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

614 with the estimated fitness value of nuptial gifts should exhibit both search for nup-  
tial gifts and preference for males with nuptial gifts, and this is what is observed  
616 in natural populations. Parameterising  $\gamma$  with data from experimental studies may  
only yield a rough approximation of the true  $\gamma$ . This is because the estimated  
618 value of  $\gamma$  is based on data from current populations (rather than ancestral popula-  
tions, which are being simulated), and because the literature is inconclusive as to  
620 how much (if any) effect nuptial gifts have on female fitness (Maxwell and  
Prokov 2018). The effect of nuptial gifts on female fecundity has been estimated  
622 in a variety of system such as crickets, fireflies, butterflies and spiders, but these  
estimates vary considerably between species suggesting a large positive effect to  
624 no effect at all (Bergström and Wiklund 2002; Rooney and Lewis 2002; Maxwell  
and Prokov 2018; Gao et al. 2019).

626 Our model assumes something akin to sequential polyandry. That is, a system  
wherein female mating and reproduction with multiple males occurs in sequence,  
628 rather than multiple matings occurring before reproduction. In some systems with  
nuptial gift-giving, female have been documented to mate multiple times before  
630 reproduction occurs, including the genus of bark lice *Neotroglia* (Kamimura et al.  
2021) and even our example system of *P. mirabilis* where females will sometimes  
632 engage in multiple mating before reproducing, especially if starved because multi-  
ple mating may result in more nuptial gifts (Toft and Albo 2015; Matzke et al.  
634 2022)(Toft and Albo 2015; Matzke et al. 2022). It is unclear what effect (if any)  
assuming non-sequential polyandry would have on the threshold we derive. Under  
636 non-sequential polyandry, a viable strategy for females might be to accept any  
male (with or without gift) for fertilisation assurance, then exhibit a preference for  
638 nuptial gifts. This might make choosiness less costly since it would entail less of  
an opportunity cost to be choosy, and this could potentially make female prefer-

640   ence for nuptial gifts more likely to evolve. Our model also assumes that males  
search in time-out, rather than contribute to parental care, which is likely to be ac-  
642   curate for most systems but not all. Expanding the model to explore these possi-  
bilities would be a worthwhile goal for future research.

## 644   **Conclusion**

Overall, we found that a simple relationship between nuptial gift search time and  
646   mate encounter rate yields a threshold that determines whether selection will  
favour males that search for nuptial gifts. Similarly, we found that the threshold  
648   determining whether females will be favoured to reject males without nuptial gifts  
is also dependent on these variables, along with offspring processing time. To-  
650   gether, these thresholds describe the conditions under which nuptial gift-giving is  
expected to evolve. The applications of these thresholds are numerous. They can  
652   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 popu-  
654   lations can evolve to use worthless or token nuptial gifts.

656   **Author contributions:** APC and ABD conceived the study. ABD constructed the  
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658   ABD and ABD wrote the IBM model. TB and GB provided substantial comments  
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666 source code is available at <https://github.com/bradduthie/Pisaura>. Dataset used for  
the plots are also publicly available: [link to Dryad will be made available should  
668 the paper be accepted for publication].

670 **Competing interests:** The authors declare no competing interests.

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## Supporting Information

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**S1:**

**S1: Sensitivity analysis of parameters in IBM**

We investigated the sensitivity of our results to individual mortality during time-  
in ( $\mu_i$ ) and time-out ( $\mu_{out}$ ), female processing time ( $T_f$ ), potential for interactions  
between conspecifics ( $\psi$ ), and initialised male search time ( $T_m$ ). Across all of  
these simulations, there were challenges with statistical power. Evidence for the  
evolution of male search (blue points in figures) and female choosiness (red points  
in figures) was determined by the lower 95% bootstrapped confidence interval of  
 $T_m$  and  $T_f$  values being greater than zero, respectively. This required a lot of  
replicate simulations in the main text (Figure 3), especially for values just above  
predicted thresholds and for female choosiness. Computation time was a limiting  
factor, even using a compiled language (C) and with access to a computing  
cluster. Absence of points above threshold values are not necessarily evidence that  
evolution of male search or female choosiness is not predicted to evolve in these  
regions of parameter space, but it does indicate that evolution of these traits is not  
necessarily assured given the stochasticity inherent to the IBM. Additional  
simulations can be conducted using the C code in the 'src' folder of the GitHub  
repository ([https://github.com/bradduthie/nuptial\\_gift\\_evolution](https://github.com/bradduthie/nuptial_gift_evolution)). Below, we  
explain the parameter values used in the sensitivity analysis in more detail.

*Mortality*

We conducted a sensitivity analysis of the effect of the mortality parameters  $\mu_i$   
and  $\mu_{out}$  (the probability of mortality in time-in and time-out, respectively, which  
we assumed to be equal for all individuals) on the evolution of male search and  
female choice using the IBM (See S1). The results revealed no correlation  
between the value of the mortality parameters and the evolution of male search or  
female choice (Fig. S1.1).

*Female processing time*

We also conducted a sensitivity analysis of female processing time  $T_f$ . To do this,  
we ran simulations at default values, but with  $T_f=0.4$  (Figure S3.2) and  $T_f=10.0$   
(Figures S3.3).

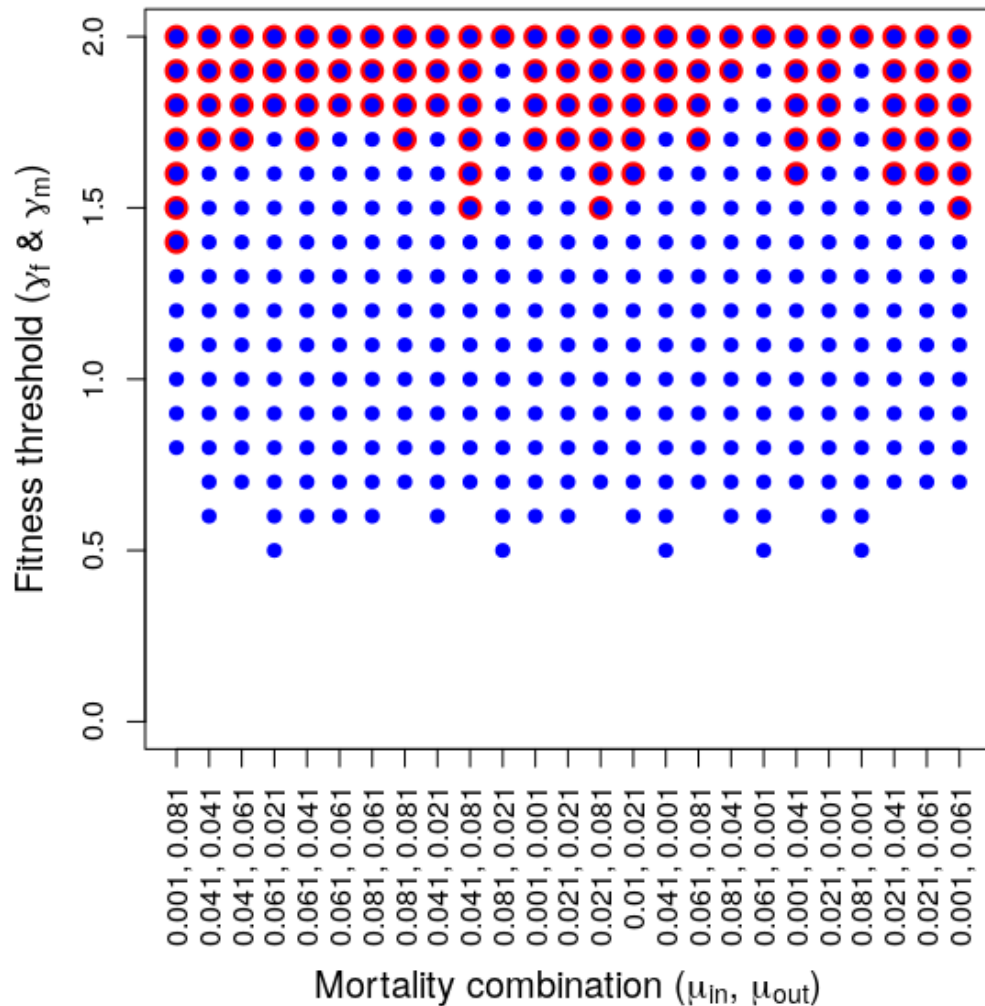
*Interactions between conspecifics*

We conducted a sensitivity analysis on the encounter rate between conspecifics ( $R$ )  
by varying the value of  $\psi$  (see S1). Under default simulations,  $\psi=3$ . We also ran

788 simulations in which  $\psi = 1$  (Figure S3.4),  $\psi = 2$  (Figure S3.5),  $\psi = 4$  (Figure S3.6),  
and  $\psi = 6$  (Figure S3.7), with all other parameters being set to default values.

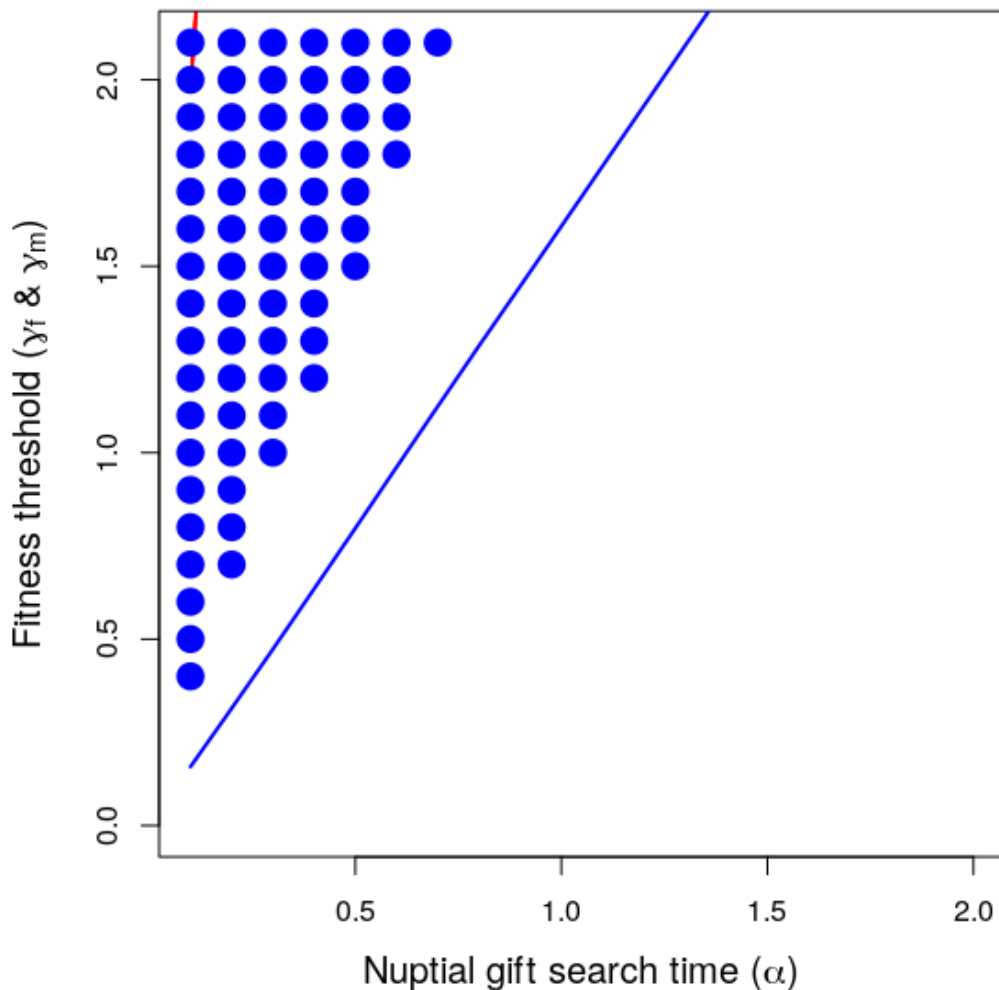
#### 790 *Initialised male search time*

Lastly, we conducted a sensitivity analysis on initialised male search time ( $T_m$ ).  
792 To do this, we ran simulations at default values, but initialised all males at  
 $T_m = 0.5$  (Figure S3.8) or  $T_m = 2.5$  (S3.9). Note that under these initialisation  
794 conditions, it no longer makes sense to test whether or not  $T_m$  evolves to positive  
values, so we do not show predicted male search thresholds and focus only on  
796 female choosiness. Interestingly, while predictions given initialised  $T_m = 0.5$  are  
quite close for female choosiness thresholds, female choosiness does not appear to  
798 evolve given  $T_m = 2.5$ . This might be due to low selection pressure to reject males  
without gifts due to their low frequency. In other words, while females would  
800 benefit from a strategy of rejecting gift-less males, a lack of realised encounters  
with gift-less males preclude the evolution of sustained selection for choosiness.



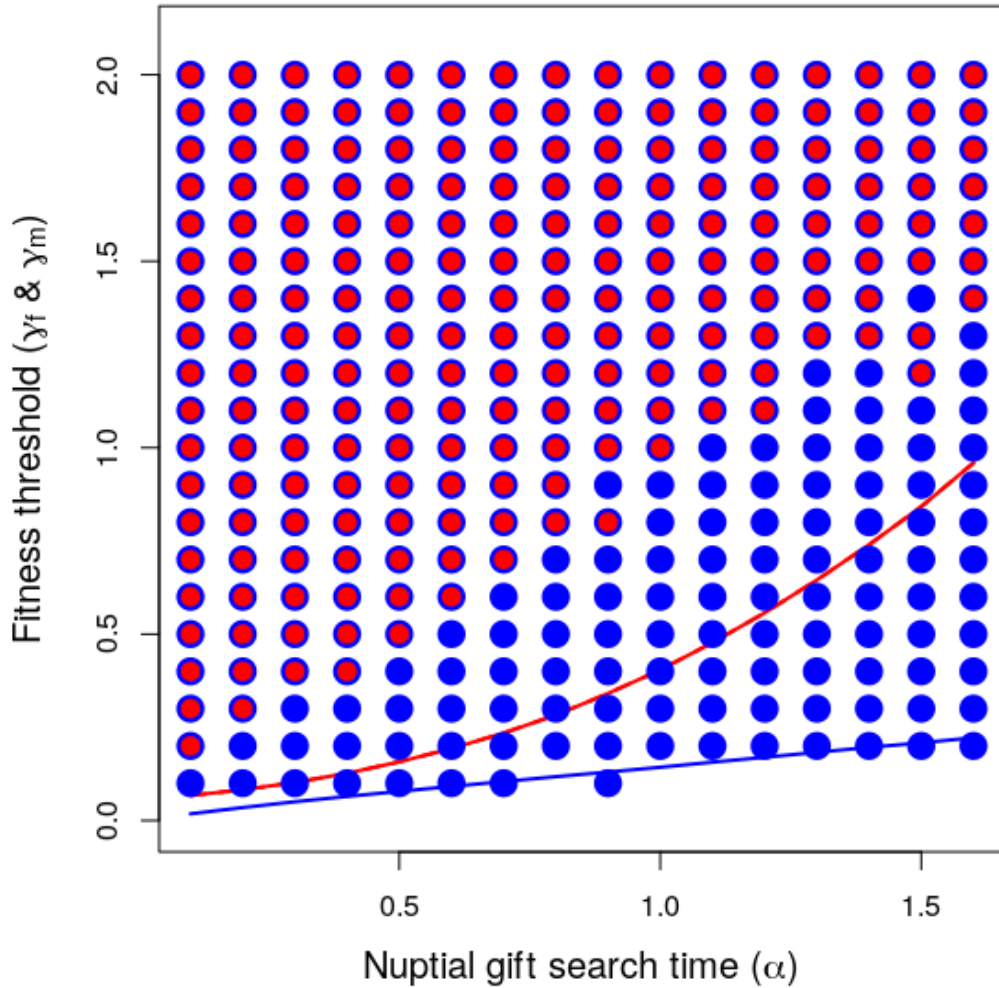
802

804 Figure S1.1: Evolution of both male search (blue) and female choice (red) under  
different combinations of the mortality rates  $\mu_{in}$  and  $\mu_{out}$  (mortality in time-in and  
806 out, respectively). The y-axis is the threshold fitness that leads to evolution of  
male search (blue) or female choice (red). The results show noise, but no  
808 correlation between the value of the mortality parameters and the propensity for  
male search and/or female choice to evolve. For each of the  $25 \times 20$  combinations  
810 of  $\mu_{in}$  and  $\mu_{out}$ , 1600 replicate simulations were run.



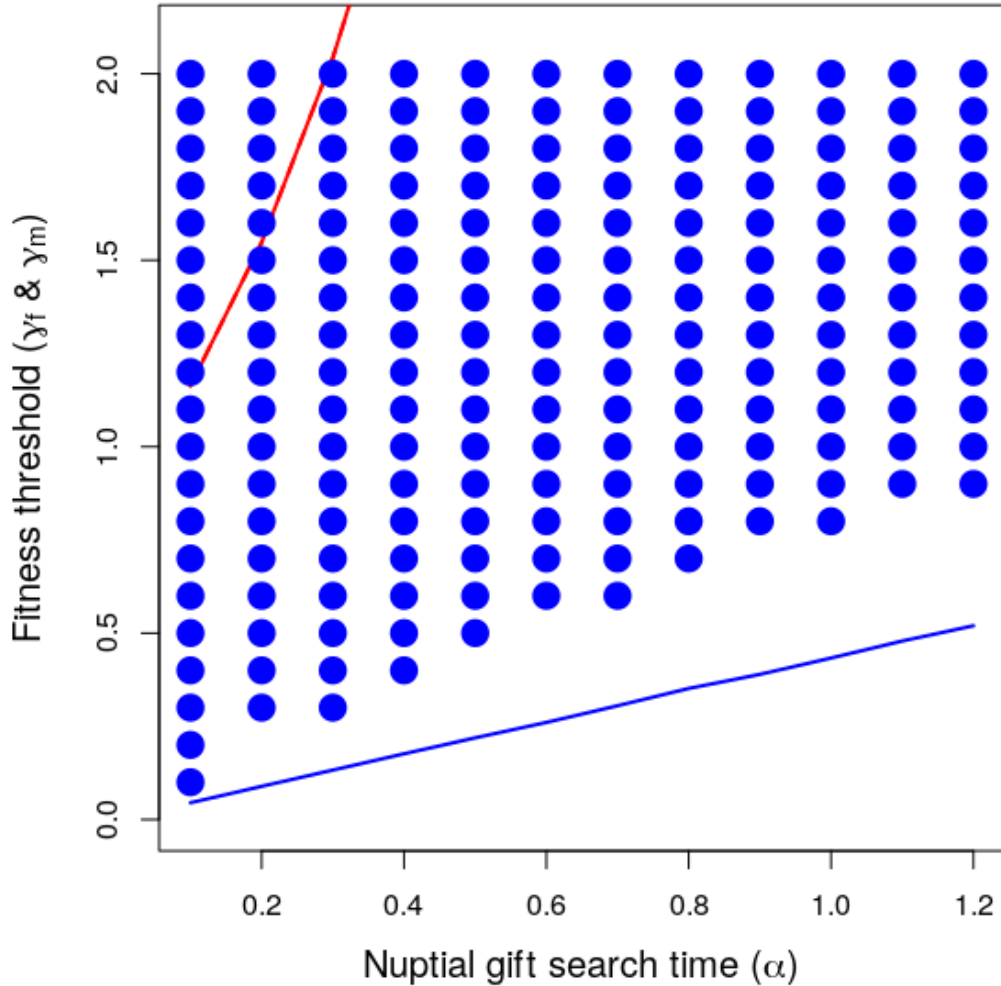
812 Figure S1.2 ( $T_f=0.4$ ): The coevolution of male search and female choosiness as a  
function of nuptial gift search time ( $\alpha$ ). Points show where the lower 95%  
814 confidence interval of female choosiness (red) and male search (blue) exceeds  
zero, indicating evolution of choosiness or nuptial gift search. Each point includes  
816 data from 720 replicate simulations with identical starting conditions. Red and  
818 blue lines show thresholds above which the mathematical model predicts that

females should be choosy and males should search, respectively. Up to 3000  
820 interactions occur between individuals in each time step ( $\psi=3$ ), potentially  
resulting in a mating interaction. The number of individuals in the population  
822 remained at or near carrying capacity of  $K=1000$ . Expected female processing  
time was set to  $T_f=0.4$  time steps, and  $\gamma$  and  $\alpha$  values in the range  $[0.5, 1.5]$  and  
824  $[0.1, 2.1]$ , respectively, were used.



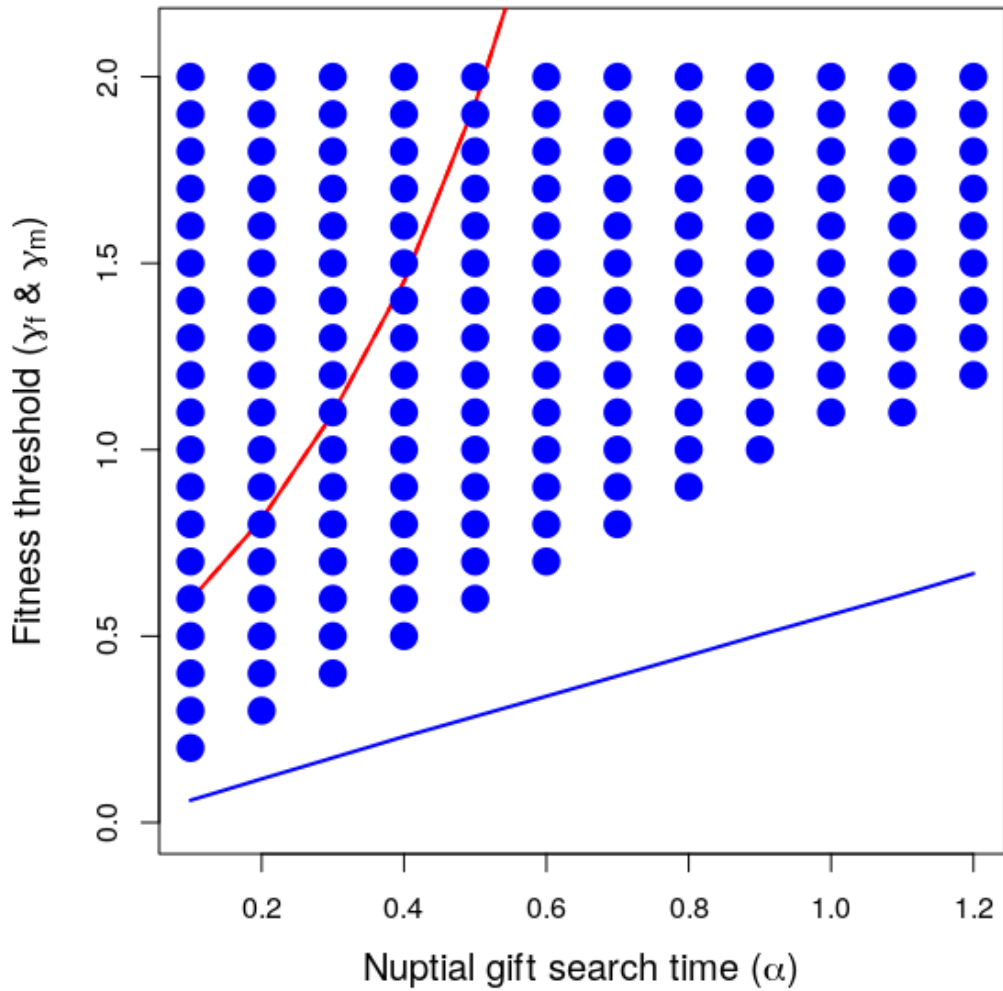
826  
Figure S1.3 ( $T_f=10.0$ ): The coevolution of male search and female choosiness as  
828 a function of nuptial gift search time ( $\alpha$ ). Points show where the lower 95%  
confidence interval of female choosiness (red) and male search (blue) exceeds  
830 zero, indicating evolution of choosiness or nuptial gift search. Each point includes  
data from 720 replicate simulations with identical starting conditions. Red and  
832 blue lines show thresholds above which the mathematical model predicts that  
females should be choosy and males should search, respectively. Up to 3000  
834 interactions occur between individuals in each time step ( $\psi=3$ ), potentially

resulting in a mating interaction. The number of individuals in the population  
 836 remained at or near carrying capacity of  $K=1000$ . Expected female processing  
 time was set to  $T_f=10.0$  time steps, and  $\gamma$  and  $\alpha$  values in the range  $[0.5, 1.5]$  and  
 838  $[0.1, 2.1]$ , respectively, were used.



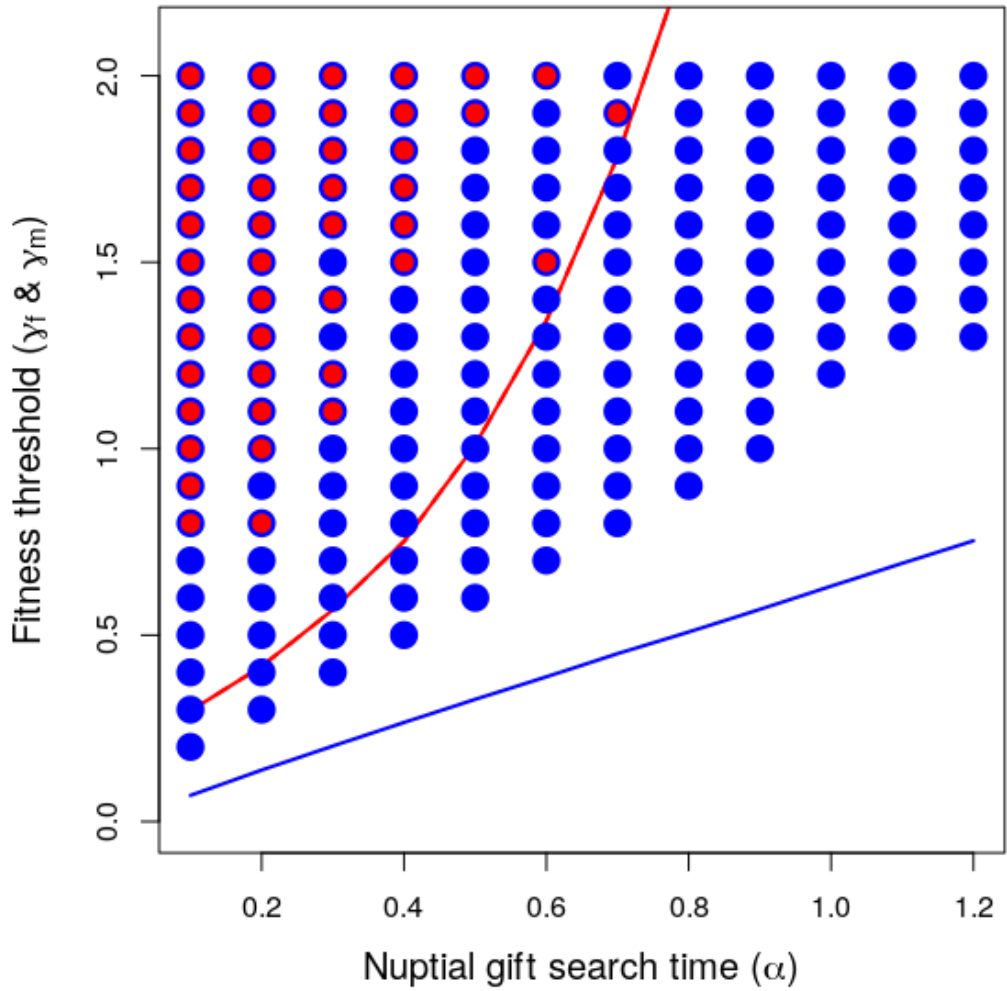
840  
 Figure S1.4 ( $\psi=1$ ): The coevolution of male search and female choosiness as a  
 842 function of nuptial gift search time ( $\alpha$ ). Points show where the lower 95%  
 confidence interval of where male search (blue) exceeds zero, indicating evolution  
 844 of choosiness or nuptial gift search. Each point includes data from 720 replicate  
 simulations with identical starting conditions. Red and blue lines show thresholds  
 846 above which the mathematical model predicts that females should be choosy and  
 males should search, respectively. Up to 1000 interactions occur between  
 848 individuals in each time step ( $\psi=1$ ), potentially resulting in a mating interaction.  
 The number of individuals in the population remained at or near carrying capacity

850 of  $K=1000$ . Expected female processing time was set to  $T_f=2$  time steps, and  $\gamma$  and  $\alpha$  values in the range  $[0.0, 1.4]$  and  $[0.1, 1.2]$ , respectively, were used.



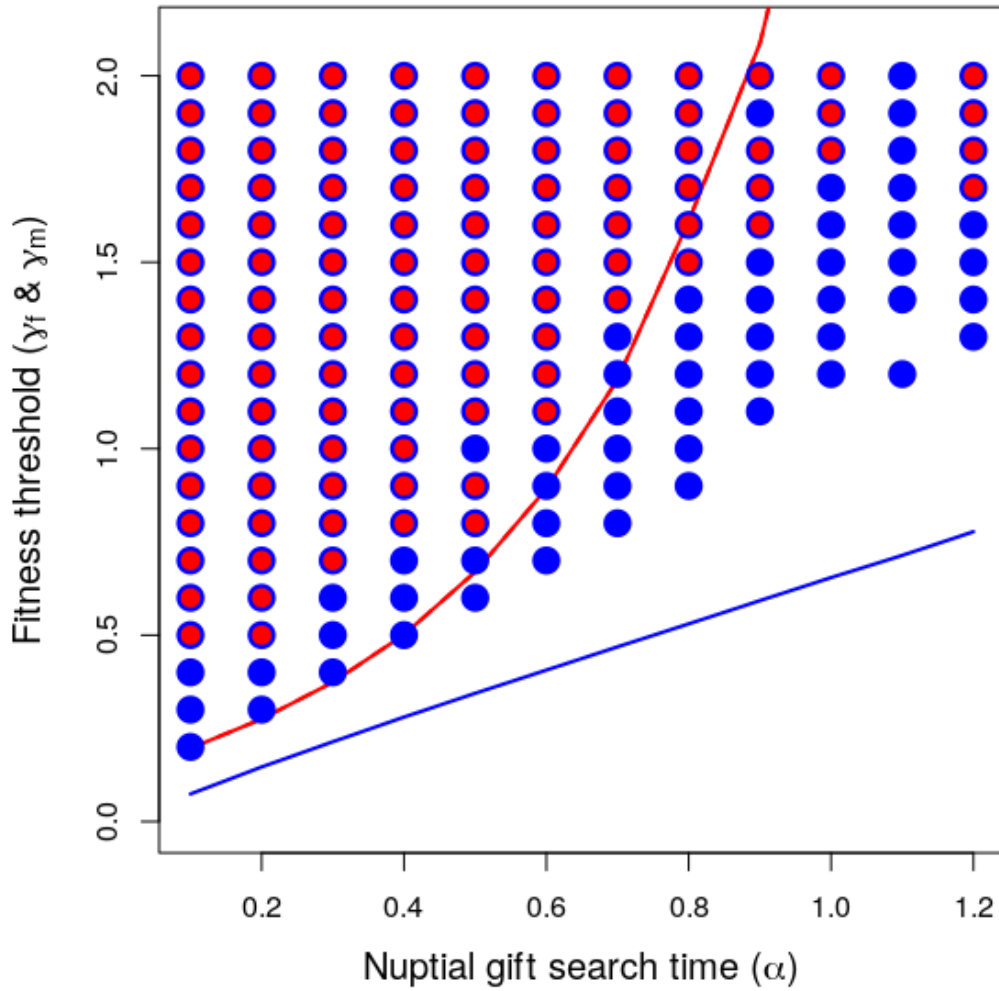
852

854 Figure S1.5 ( $\psi=2$ ): The coevolution of male search and female choosiness as a  
 856 function of nuptial gift search time ( $\alpha$ ). Points show where the lower 95%  
 858 confidence interval of where male search (blue) exceeds zero, indicating evolution  
 860 of choosiness or nuptial gift search. Each point includes data from 720 replicate  
 862 simulations with identical starting conditions. Red and blue lines show thresholds  
 864 above which the mathematical model predicts that females should be choosy and  
 males should search, respectively. Up to 2000 interactions occur between  
 individuals in each time step ( $\psi=2$ ), potentially resulting in a mating interaction.  
 The number of individuals in the population remained at or near carrying capacity  
 of  $K=1000$ . Expected female processing time was set to  $T_f=2$  time steps, and  $\gamma$   
 and  $\alpha$  values in the range  $[0.0, 1.4]$  and  $[0.1, 1.2]$ , respectively, were used.



866

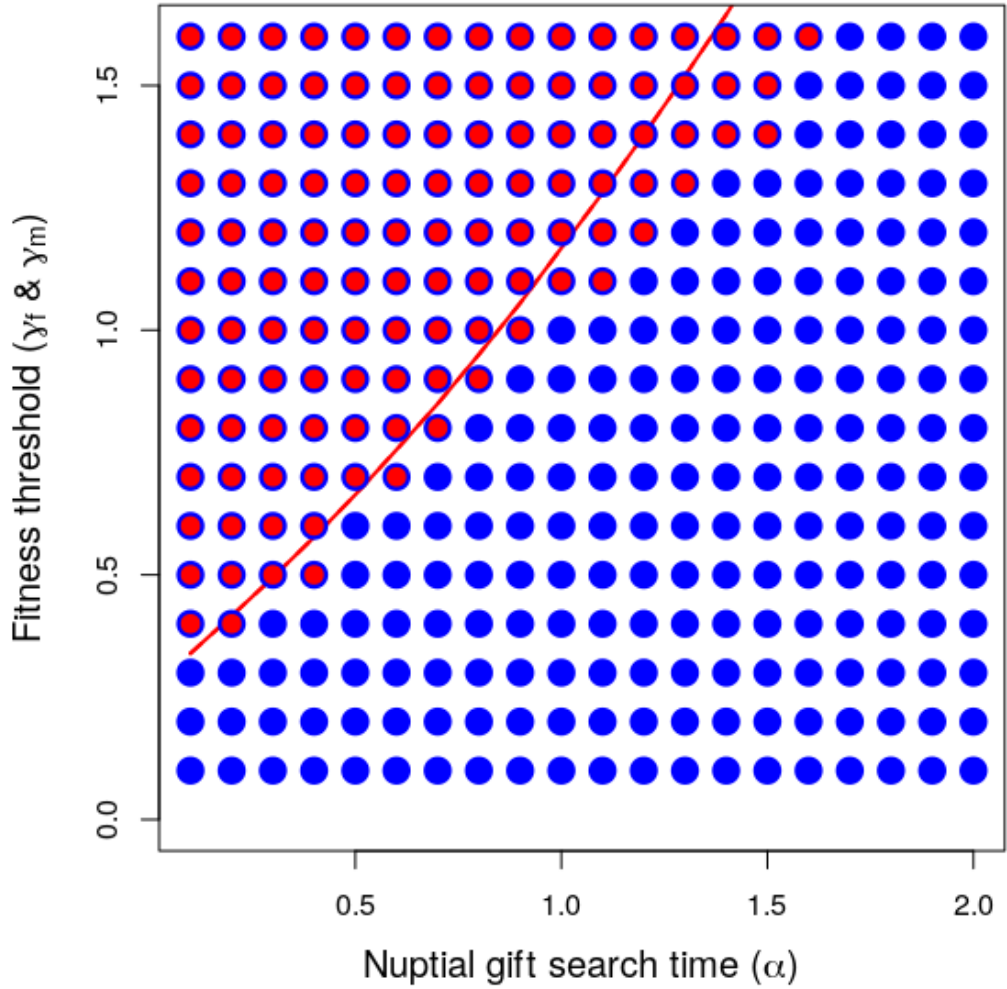
Figure S1.6 ( $\psi=4$ ): The coevolution of male search and female choosiness as a  
 868 function of nuptial gift search time ( $\alpha$ ). Points show where the lower 95%  
 confidence interval of where male search (blue) exceeds zero, indicating evolution  
 870 of choosiness or nuptial gift search. Each point includes data from 720 replicate  
 simulations with identical starting conditions. Red and blue lines show thresholds  
 872 above which the mathematical model predicts that females should be choosy and  
 males should search, respectively. Up to 4000 interactions occur between  
 874 individuals in each time step, potentially resulting in a mating interaction ( $\psi=4$ ).  
 The number of individuals in the population remained at or near carrying capacity  
 876 of  $K=1000$ . Expected female processing time was set to  $T_f=2$  time steps, and  $\gamma$   
 and  $\alpha$  values in the range  $[0.0, 1.4]$  and  $[0.1, 1.2]$ , respectively, were used.



878

880 Figure S1.7 ( $\psi=6$ ): The coevolution of male search and female choosiness as a  
 882 function of nuptial gift search time ( $\alpha$ ). Points show where the lower 95%  
 884 confidence interval of where male search (blue) exceeds zero, indicating evolution  
 886 of choosiness or nuptial gift search. Each point includes data from 720 replicate  
 simulations with identical starting conditions. Red and blue lines show thresholds  
 above which the mathematical model predicts that females should be choosy and  
 males should search, respectively. Up to 6000 interactions occur between  
 individuals in each time step, potentially resulting in a mating interaction ( $\psi=6$ ).  
 888 The number of individuals in the population remained at or near carrying capacity  
 of  $K=1000$ . Expected female processing time was set to  $T_f=2$  time steps, and  $\gamma$   
 890 and  $\alpha$  values in the range  $[0.0, 1.4]$  and  $[0.1, 1.2]$ , respectively, were used.

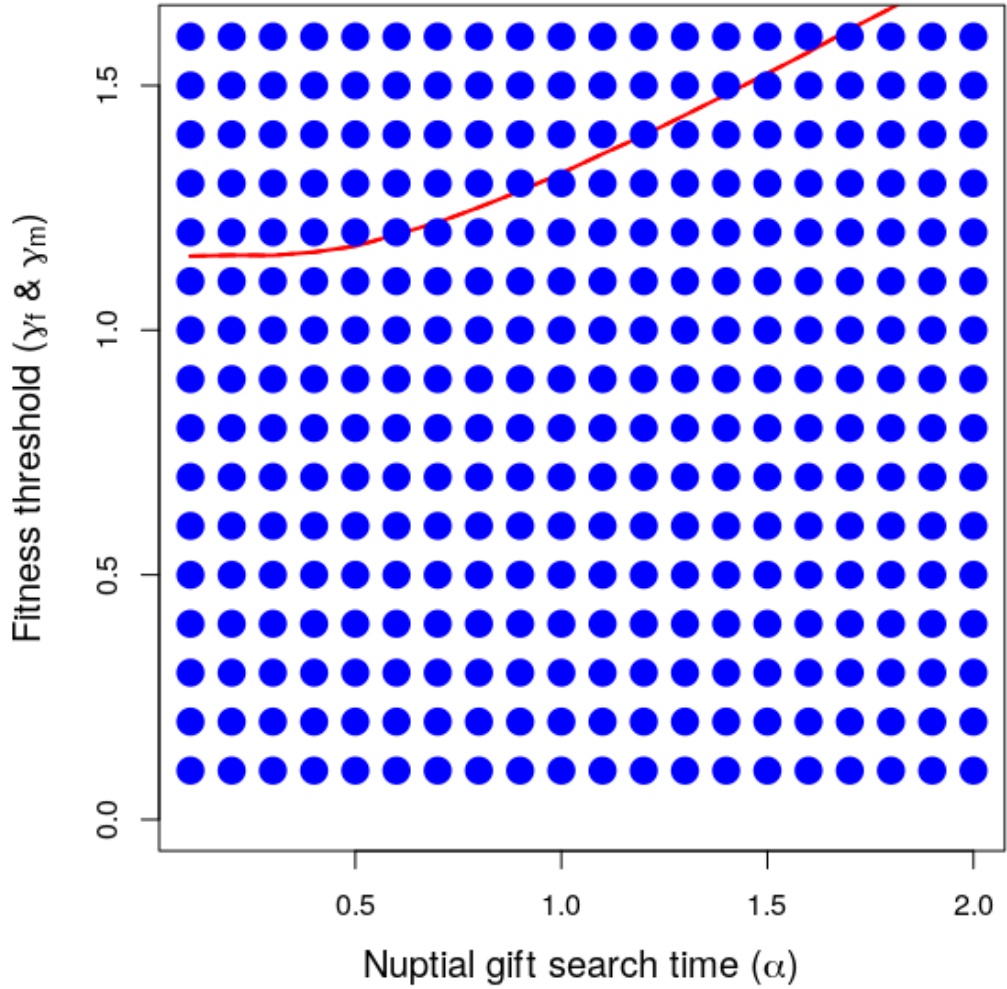




892

Figure S1.8 ( $T_m=0.5$ ): The coevolution of male search and female choosiness as a  
 894 function of nuptial gift search time ( $\alpha$ ). Points show where the lower 95%  
 confidence interval of where male search (blue) exceeds zero, indicating evolution  
 896 of choosiness or nuptial gift search. Each point includes data from 1600 replicate  
 simulations with identical starting conditions. The red line shows the threshold  
 898 above which the mathematical model predicts that females should be choosy  
 (male thresholds for search are not shown because simulations were initialised  
 900 with males already searching for nuptial gifts). Up to 3000 interactions occur  
 between individuals in each time step, potentially resulting in a mating interaction  
 902 ( $\psi=3$ ). The number of individuals in the population remained at or near carrying  
 capacity of  $K=1000$ . Expected female processing time was set to  $T_f=2$  time  
 904 steps, and  $\gamma$  and  $\alpha$  values in the range  $[0.0, 1.4]$  and  $[0.1, 1.2]$ , respectively, were  
 used.

906



908 Figure S1.9 ( $T_m=2.5$ ): The coevolution of male search and female choosiness as a  
 910 function of nuptial gift search time ( $\alpha$ ). Points show where the lower 95%  
 912 confidence interval of where male search (blue) exceeds zero, indicating evolution  
 914 of choosiness or nuptial gift search. Each point includes data from 1600 replicate  
 916 simulations with identical starting conditions. The red line shows the threshold  
 918 above which the mathematical model predicts that females should be choosy  
 (male thresholds for search are not shown because simulations were initialised  
 with males already searching for nuptial gifts). Up to 3000 interactions occur  
 between individuals in each time step, potentially resulting in a mating interaction  
 ( $\psi=3$ ). The number of individuals in the population remained at or near carrying  
 capacity of  $K=1000$ . Expected female processing time was set to  $T_f=2$  time  
 steps, and  $\gamma$  and  $\alpha$  values in the range  $[0.0, 1.4]$  and  $[0.1, 1.2]$ , respectively, were  
 920 used.

## S2: Alternative derivation of male fitness threshold

922 In the main text, we assumed that males made the decision to search or not search  
for a nuptial gift. The expected length of time for which searching males are  
924 expected to remain outside of the mating pool is  $E[T_m] = \alpha$  (see Methods).  
Alternatively, we can assume that males search for a period of  $T_m$  and spend this  
926 full duration of  $T_m$  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  
928 in Eq. 1,

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

930 In Eq. 1,  $\alpha$  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  
932 they are unsuccessful in obtaining a gift, so the probability that a male obtains no  
gift after  $T_m$  is,

$$934 \quad P(L) = e^{-\frac{1}{\alpha} T_m}.$$

We assume that the fitness increments to offspring associated with receiving a  
936 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  
938 from their nuptial gift search divided by  $T_m$  plus the time spent in the mating pool  
waiting to encounter a mate,

$$940 \quad W_m = \lambda \frac{P(G)(1 + \gamma) + P(L)}{T_m + \left(\frac{\beta + 1}{R}\right)}.$$

Our objective now is to determine the conditions under which a focal male  
942 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  
944 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  
946 based solely on  $\alpha$ ,  $\beta$ ,  $R$ , and  $\gamma$ .

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

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

950 Because  $T_m=0$ , the above simplifies,

$$\frac{\partial W_m}{\partial T_m} = \lambda \frac{\frac{R\gamma(\beta+1)}{\alpha} - R^2}{(1+\beta)^2}.$$

952 We can re-arrange the above,

$$\frac{\partial W_m}{\partial T_m} = \lambda \frac{R\gamma}{\alpha(\beta+1)} - \lambda \frac{R^2}{(1+\beta)^2}.$$

954 Note that if  $R=0$  or  $\lambda=0$ , then, trivially, no change in fitness occurs (since  
 956 females and males cannot mate or do not produce offspring). Fitness is increased  
 by searching for nuptial gifts when  $\gamma$  is high, scaled by the expect search time  
 needed to find a nuptial gift. A second term on the right-hand side is subtracted,  
 958 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  
 960 increases by searching for a nuptial gift are found by setting  $\partial W_m / \partial T_m = 0$  and  
 solving for  $\gamma$  to get Eq. 2 in the main text.

### 962 **S3: Operational sex ratio**

We assume that the ratio of males to females is the same upon individual  
 964 maturation. Consequently, the operational sex ratio  $\beta$  will be a function of  $R$ ,  $T_f$ ,  
 and  $T_m$  because these parameters determine the density of females and males in  
 966 the mating pool versus outside of the mating pool. We start with the definition of  
 $\beta$  as being the probability of finding an individual in time-in (Kokko &  
 968 Monaghan, 2001),

$$\beta = \frac{\int_{t=0}^{\infty} P_{\text{f}}(t) dt}{\int_{t=0}^{\infty} P_{\text{m}}(t) dt}$$

970 We can substitute the equations for  $P_{\text{f}}(t)$  and  $P_{\text{m}}(t)$ , which define the probabilities  
 of males and females being within the mating pool at time  $t$ , respectively.

972 We can therefore calculate  $\beta$  as below,

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

974 This can be simplified,

$$\beta = \frac{(\beta(R+T_f)+T_f)(\beta+1)}{\beta(R^2T_m+R)+\beta^2R}.$$

976 There is no closed form solution for  $\beta$ , but a recursive algorithm can be used to calculate  $\beta$  to an arbitrary degree of precision.

```

978 recursive_b <- function(B, D, Tf, Tm, crit = 0.0001, maxit = 9999){
  conv <- 1;
980 iter <- 0;
  while(conv > crit & iter < maxit){
982   Fe <- D * (B / (1 + B));
   Me <- (1 + B) / D;
984   Bn <- (Me / (Tm + Me)) / (Fe / (Tf + Fe));
   iter <- iter + 1;
986   conv <- abs(Bn - B);
   B <- Bn;
988 }
  return(list(B = B, conv = conv, iter = iter));
990 }

```

We used the above function to calculate values of  $\beta$  for the analytical model.

#### 992 **S4: Estimation of key model parameters using experimental data**

Estimates showing the mean number of offspring produced by female *Pisaura*  
994 *mirabilis* that ate nuptial gifts and females who did not. Means were calculated  
with raw data from Tuni *et al.* (2013) and results are shown  $\pm$  SE (Table 1). Under  
996 these assumptions, the relative gain in fitness from receiving nuptial gifts for a  
female is,

998  $\hat{\delta}_f = \frac{25.74}{6.00} = 4.29$

Since the baseline fitness is 1, the increase in fitness resulting from a nuptial gift  
 1000 then becomes,

$\hat{\gamma} = \hat{\delta}_f - 1 = 3.29.$

1002 The value 3.29 was used to parameterise  $\gamma$  for a set of simulations (Figure 4 in the  
 main text).

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

1004 Table 1: Estimates showing mean number of offspring produced by female *P.*  
*mirabilis* that ate nuptial gifts and females who did not. Means were calculated  
 1006 with raw data from Tuni *et al.* (2013) and results are shown ± SE.

## 1008 **S6: Separate evolution of male search and female choice**

We used the individual-based simulation model (see Supporting Information S1)  
 1010 to unpack the effect of coevolution on the evolution of male search and female  
 choice. Here we replicated the simulations shown in the main text under the  
 1012 condition where only one trait at a time was allowed to evolve and studied how  
 this affected the trait evolution.

1014 First, we submitted a set of simulations wherein male search did not evolve, but  
 was fixed at different values (see Fig. S6.1). Next, we ran the same set of  
 1016 simulations wherein male search evolved, but female choice was not possible. The  
 results thus show how each trait evolves in the absence of any coevolution (Fig.  
 1018 S6.1).

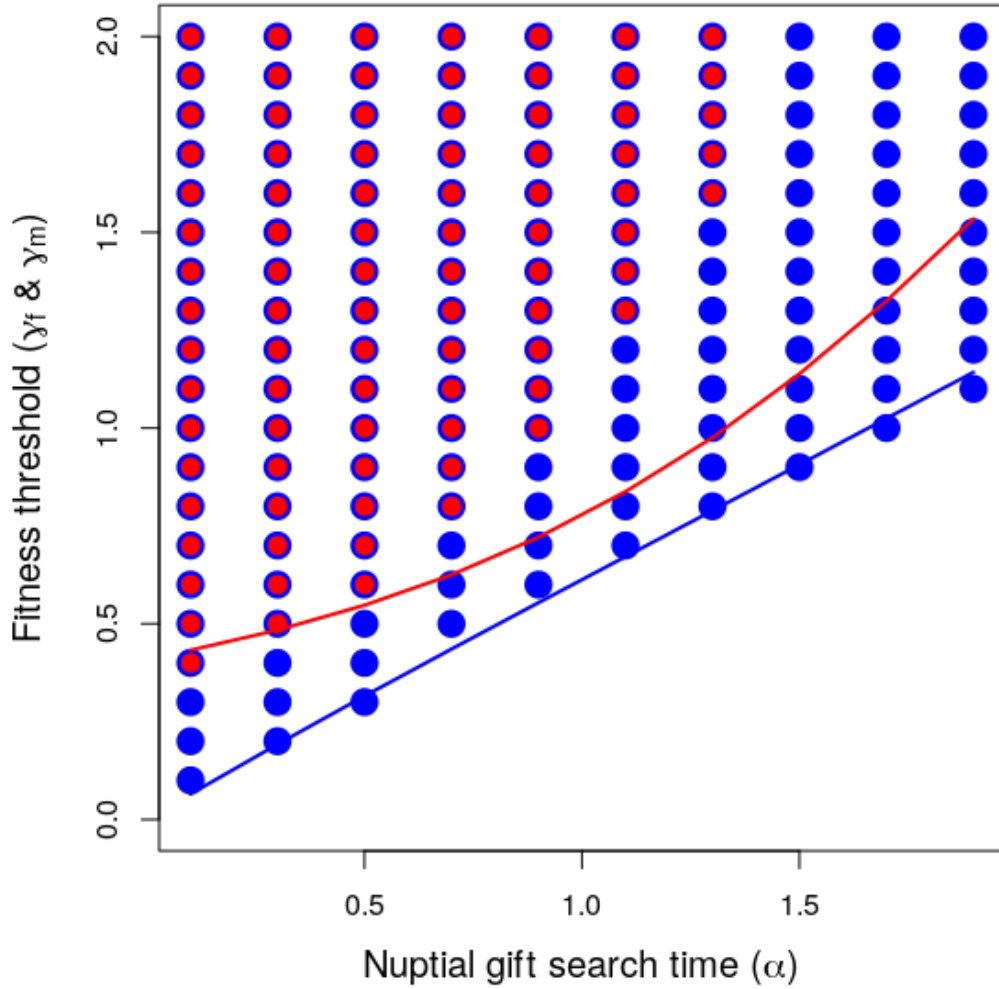


Figure S6.1: The separate evolution of male search and female choosiness as a function of nuptial gift search time. Points show where the lower 95% confidence interval of male search (blue) and female choosiness (red) exceeds zero, indicating evolution of nuptial gift search or choosiness. Each point includes data from  $2 \times 1600$  replicate simulations with identical starting conditions. In the first batch, male search was constant and initialized at  $T_m = \alpha$ , and female choice was evolving. In the second batch, male search was evolving, and there was no option for female choice. The parameters  $T_f = 2$ , and  $\gamma$  and  $\alpha$  values were set within the range  $[0.1, 2.0]$  and  $[0.3, 1.7]$ , respectively.