

A time-in time-out model

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Model

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

After mating, we assume that females must spend some time processing offspring (T_f). Male time to replenish sperm is 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 in (μ_{if}) and out (μ_{of}) of the mating pool, and for males in (μ_{im}) and out (μ_{om}) of the mating pool. First, we 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 on their provision of a nuptial gift.

Male fitness

During time-out, males search for a nuptial gift for a time 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 true nuptial gift (G) during this time is modelled as,

$$\Pr(G) = 1 - e^{-\frac{1}{\alpha_1} T_m}.$$

In the above, α_1 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 gift, so the probability that a male obtains no gift after T_m is modelled as,

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

For simplicity, we assume that the fitness increments to offspring associated with nuptial gift versus no nuptial gift are $V_G = 1 + \gamma$ and $V_L = 1$, 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,

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

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 ($T_m = 0$).

Initial conditions for nuptial gift-giving

We assume that the ancestral condition is one in which no nuptial gifts are sought by males (i.e., $T_M = 0$) and females therefore exhibit no choice in males with or 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_1 , β , M , γ , m_{im} , and m_{om} . For simplicity, and following Hanna Kokko, Jennions, and Brooks (2006), we assume $m_{im} = m_{om} = 1$. This leaves M , α_1 , β , and γ .

Ignoring the recursion for now and just letting $\beta = 1$ (equal sex ratio in time-in stage), we can move on to seeing how fitness changes with a change in T_M .

The first question that we want to ask is under what conditions does male inclusive fitness increase with nuptial gift search time? We can determine this by differentiating W_m with respect to T_m ,

$$\frac{\partial W_m}{\partial T_m} = \frac{\gamma \left(\frac{\left(\frac{T_M + \frac{\sqrt{\beta}}{M}}{\alpha_1} + 1 \right)}{e^{\frac{1}{\alpha_1} T_M}} - 1 \right) - 1}{\left(T_M + \frac{\sqrt{\beta}}{M} \right)^2}.$$

If we assume an initial condition in which $T_M = 0$ (i.e., a population in which males do not search for nuptial gifts at all) and evaluate accordingly, then the above simplifies,

$$\frac{\partial W_m}{\partial T_m} = \frac{\gamma M}{\alpha_1 \sqrt{\beta}} - \frac{M^2}{\beta}.$$

The above equation makes intuitive sense. First note, trivially, that if the interaction rate is $M = 0$, then no change in fitness occurs (since females and males cannot mate). The change in fitness caused by searching for nuptial gifts is increased when γ is high, scaled by the search time needed to find a nuptial gift (recall that $Pr(G)$ decreases with increasing α_1). From this first term, a second term is subtracted that reflects a loss in fitness proportional to the encounter rate of potential mates in the mating pool. We can identify the conditions under which male inclusive fitness increases by searching for a nuptial gift by setting $\partial W_m / \partial T_m = 0$ and solving for γ ,

$$\gamma_m > \alpha_1 \frac{M}{\sqrt{\beta}}.$$

Verbally, the inclusive fitness benefit to offspring provided by the nuptial gift must exceed the search time needed to find a nuptial gift (α_1) times the male mate encounter rate ($M/\sqrt{\beta}$). Hence, we should expect nuptial gift giving to evolve when the fitness benefit of the nuptial gift to offspring is high relative to the time needed to find a nuptial gift and the encounter rate of females and males in the mating pool.

An alternative for male gift giving

Up until now, we have assumed that males invest a fixed amount of time T_m in the time-out phase searching for nuptial gifts. While this simplifying assumption is unlikely to be problematic for determining the initial evolution of nuptial gift searching behaviour ($\partial W_m / \partial T_m$), it might not reflect the strategy of males in real systems. For example, instead of spending a fixed amount of time in time-out phase, males might instead to select one of two strategies; either search or do not search for a nuptial gift. Males with the former strategy might simply continue to search until a nuptial gift is found, while males that do not search will simply

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_1 . Note that we can integrate search time t over the rate at which nuptial gifts are encountered ($\exp(-1/\alpha_1)$) to show $E[T_m] = \alpha_1$,

$$\int_0^\infty e^{-\frac{1}{\alpha_1}t} dt = \alpha_1.$$

The rate at which a focal male that searches for a nuptial gift increases his fitness is therefore fitness of offspring $(1 + \gamma)$ divided by expected time spent searching for a nuptial gift (α_1) plus time spent in the mating pool ($\sqrt{\beta}/M$),

$$W_{m,G} = \frac{1 + \gamma}{\alpha_1 + \left(\frac{\sqrt{\beta}}{M}\right)}.$$

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,

$$\gamma_m > \alpha_1 \frac{M}{\sqrt{\beta}}.$$

Recall that this is the exact same inequality that we obtained when assuming the initial condition $T_M = 0$ and evaluating $\partial W_m / \partial T_m$. If $M = 1$ and $\beta = 1$, then we get the elegant $\gamma > \alpha_1$. That is, the inclusive fitness increase must be greater than the time spent searching for a nuptial gift. As the interaction rate M increases, the fitness benefit must be even higher to compensate for the opportunity cost of being able to enter the mating pool early by not searching for a nuptial gift.

Female fitness

During time-out, females process offspring over a duration of T_f (we assume that $T_f > \alpha_1$, else females are no longer the choosy sex). When females re-enter the mating pool, they will then encounter males at a rate of $M\sqrt{\beta}$. We assume that female offspring receive a fitness increment of $\gamma \geq 0$ from males that provide a true nuptial gift. Female fitness therefore never decreases by mating with a male with a nuptial gift versus a male without one. Therefore, 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. We model the probability that a female encounters a male with a nuptial gift after a duration of T_N in the mating pool as,

$$\Pr(g) = 1 - e^{-T_N (M\sqrt{\beta}) \Pr(G)}.$$

We can similarly model the probability that a female encounters a giftless male after T_N as,

$$\Pr(n) = 1 - e^{-T_N (M\sqrt{\beta}) \Pr(L)}.$$

Note that $\Pr(g)$ and $\Pr(n)$ need not sum to unity, and if $\Pr(L)$ is sufficiently low, then finding a male with a gift will be easier than finding a male without one (i.e., $\Pr(g) > \Pr(n)$). Also note that the expected time spent in the mating pool before a focal female encounters a male with a gift will be $1/(\Pr(G) \times M\sqrt{\beta})$, while the expected time spent in the mating pool before a focal female encounters any male will be $1/(M\sqrt{\beta})$ (since $\Pr(G) + \Pr(L) = 1$). We can use this to determine the rate at which a female increases her fitness when she is choosy and mates only with males that have gifts versus when she is not choosy and mates with the first male she encounters. The rate at which a female increases her fitness by being choosy and mating only when she encounters a male with a gift is as follows,

$$W_f(g) = \frac{1 + \gamma}{T_F + \left(\frac{1}{\Pr(G) \times M\sqrt{\beta}} \right)}.$$

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 as follows,

$$W_f(n) = \frac{(1 + \gamma) \Pr(G) + \Pr(L)}{T_F + \left(\frac{1}{M\sqrt{\beta}} \right)}.$$

We can now ask a relevant question for female fitness. Under what conditions should she be choosy and only accept males with nuptial gifts? To answer this question, we can evaluate the conditions under which $W_f(g) > W_f(n)$,

$$\gamma_f > \frac{e^{\frac{1}{\alpha_1} T_M}}{T_F M \sqrt{\beta} \left(e^{\frac{1}{\alpha_1} T_M} - 1 \right)}.$$

Under the above conditions in which the fitness increase caused by the nuptial gift is sufficiently high, females will increase their own fitness by rejecting males that do not have a nuptial gift.

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, H. Kokko and Monaghan (2001) show that the operational sex ratio depends on the probability of finding an individual in ‘time in,’

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

In the above, $P_{IM}(t)$ and $P_{IF}(t)$ are the probabilities of finding a male and female in ‘time in,’ respectively. H. Kokko and Monaghan (2001) find these probabilities in terms of the cost of mating. For our purpose, we can find the probability of find 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 can 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,

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

The above 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,

$$\beta = \frac{1}{2} \left((M(T_F - T_M))^2 \pm \left((M(T_F - T_M))^4 + 4(M(T_F - T_M))^2 \right)^{\frac{1}{2}} \right) + 1.$$

We can use this solution 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 $\beta = 1$).

Male nuptial search and female choosiness

We can now investigate the values of γ_m and γ_f across parameter space. First, we look across values of α_1 given fixed values of $M = 1$, and $T_F = 2$. Note that expected male search time for a nuptial gift will be $T_M = \alpha_1$, meaning that $\exp(T_m/\alpha_1) = e$.

In Figure 1, γ_m and γ_f values are indicated by the sloping and horizontal lines, respectively, which divide the plot into four distinct zones (A-D). In zone A, γ is too low relative to α_1 for males to benefit from searching for nuptial gifts, and too low for females to benefit by being choosy. In zone B, γ is sufficiently high relative to α_1 for males to benefit from searching, but females do not benefit from being choosy. In zone C, males do not benefit from searching for nuptial gifts, but females would benefit from being choosy. Lastly, in zone D, we expect males to benefit from searching for nuptial gifts and for females to benefit by choosing only males that offer nuptial gifts. Note that it is tempting to suggest that zone C is where we might expect male searching for fake nuptial gifts to evolve, but in this zone, no males actually benefit from procuring a nuptial gift. Hence, nuptial gifts should be only fake in zone C, eroding the benefit of female choosiness. Consequently, we could conclude that fake nuptial gift giving should evolve and persist only in zone D, with subsequent effects on β (due to more males being in time out) that might affect γ_f .

If we increase M to a value of $M = 2$, then the slope at which γ_m increases with increasing α_1 increases, and the value of γ_f decreases. The increased rate of interaction between females and males effectively decreases the area of parameter space in which males benefit from searching for nuptial gifts but females do not benefit from choosiness, and it increases the area of parameter space in which males benefit from searching and females benefit from being choosy. As M increases further, zone B becomes smaller and zone C becomes larger, as the increased mating rate simultaneously increases the opportunity cost of males that search for nuptial gift and decreases the cost of female choosiness. Increasing T_F , however, does not affect the slope of γ_m with α_1 , but it does lower γ_f , thereby increasing the size of zone D.

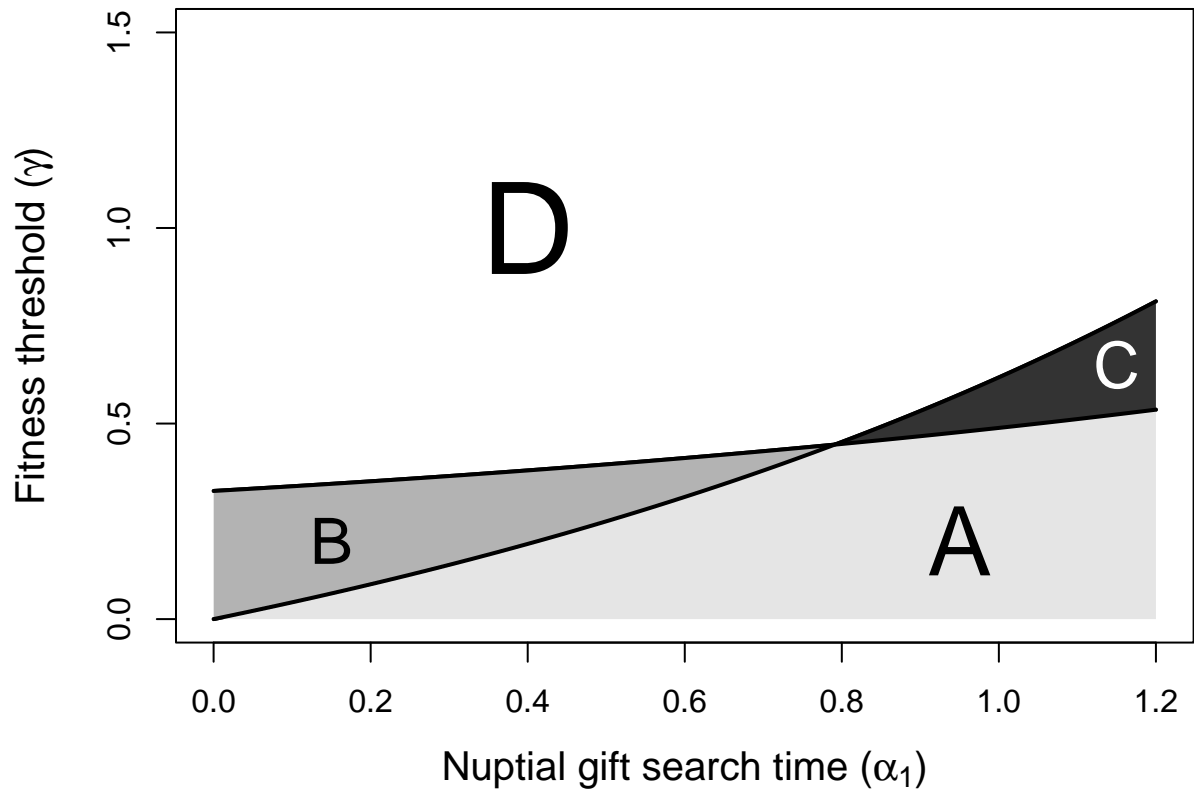


Figure 1: Parameter space in which males do not search for nuptial gifts and females are not choosy (A), males search but females are not choosy (B), females would be choosy but males do not search (C), and males search and females are choosy (D).

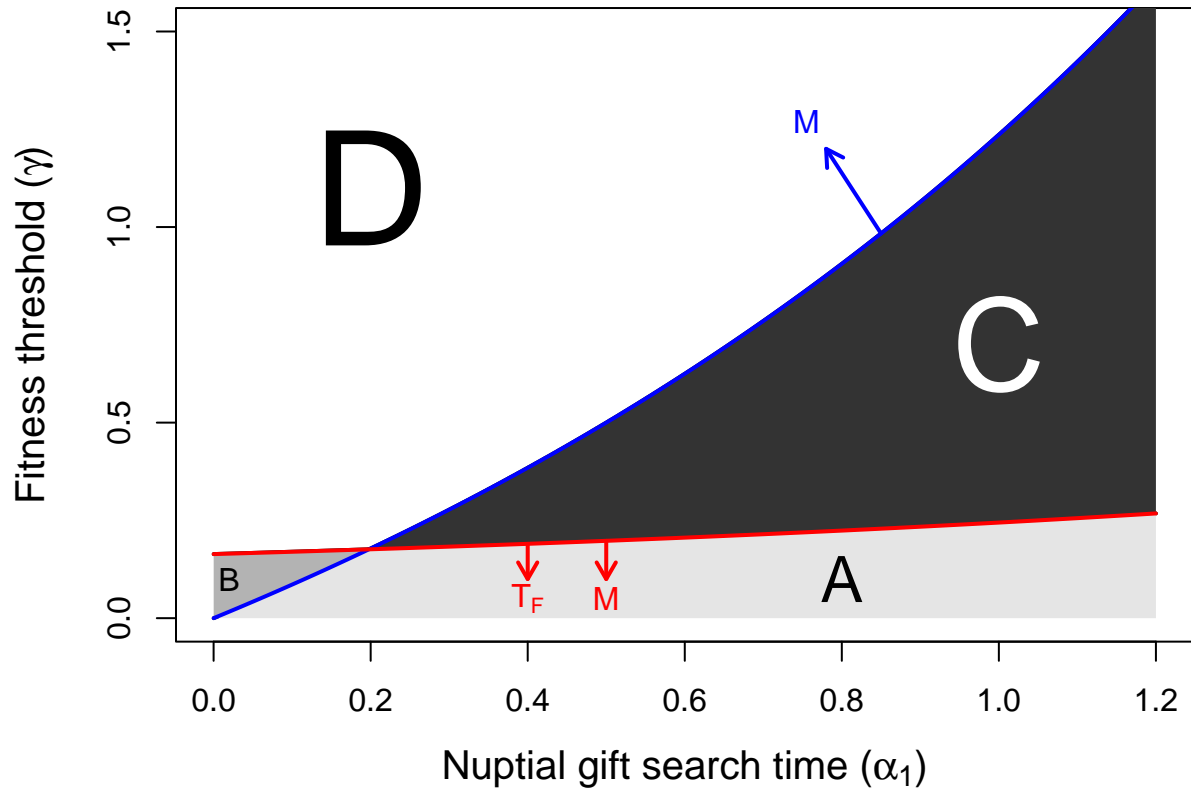
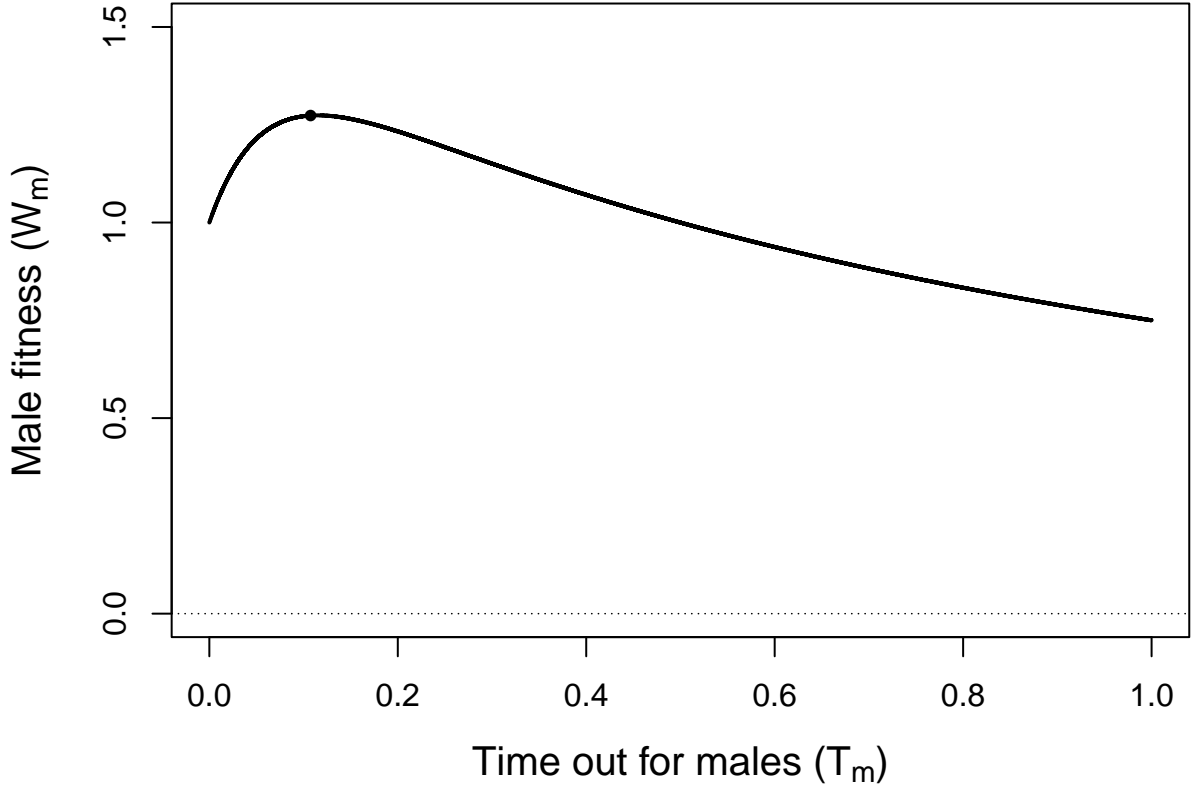


Figure 2: Areas of parameter space in which males do not search for nuptial gifts and females are not choosy (A), males search but females are not choosy (B), females would be choosy but males do not search (C), and males search and females are choosy (D). Arrows indicate the effect of increasing interaction rate (M) and female time-out (T_F)

Evolution of nuptial gift giving

To model the evolution of nuptial gift giving from an ancestral state in which no nuptial gifts are provided, we first evaluate male fitness for an initial set of conditions. We assume that males first evolve optimal search time for nuptial gifts, then that females will evolve to accept or reject males without gifts. Evolved female choosiness can subsequently alter male fitness. We thereby simulate the evolution of male nuptial gift search and female choice. We do this first assuming that males do not search for fake nuptial gifts (setting $\alpha_2 = \infty$ so $\Pr(F) = 0$), determining the dynamics of T_m when only real nuptial gifts are provided before introducing fake nuptial gifts as an option for males.

For male fitness, given that the condition $\gamma > \alpha_1(M/\sqrt{\beta})$ is fulfilled, fitness will peak at some positive value of T_m . For illustration, we first select values $M = 1$, $\beta = 1$, $\alpha_1 = 1/16$, and $\gamma = 1/2$. Under these conditions, we can find the value of W_m across T_m to determine its optimal value, T_m^* . Using a squeeze algorithm, we find $T_m^* = 0.1074219$, as indicated by the point in Figure 1.



Given $T_m^* = 0.1074219$, we can now calculate $\Pr(G) = 0.8207099$ and $\Pr(L) = 0.1792901$. We can then feed these values into the equation for female fitness to determine if females should or should not be choosy.

Introducing fake nuptial gifts

I think that for simplicity, we need to wait to do this.

Similarly, we define α_2 to be the amount of time expected to pass before a male encounters a fake nuptial gift. We assume that a male will always prefer a true nuptial gift to a fake nuptial gift (F) or no nuptial gift (N), so a fake nuptial gift is only obtained when a true one is not. Hence, the probability that a male obtains a fake nuptial gift during a time period of T_m is modelled as,

$$\Pr(F) = \left(1 - e^{-\frac{1}{\alpha_2} T_m}\right) e^{-\frac{1}{\alpha_1} T_m}.$$

$$\Pr(L) = e^{-T_m \left(\frac{1}{\alpha_1} + \frac{1}{\alpha_2}\right)}.$$

Notes and old text

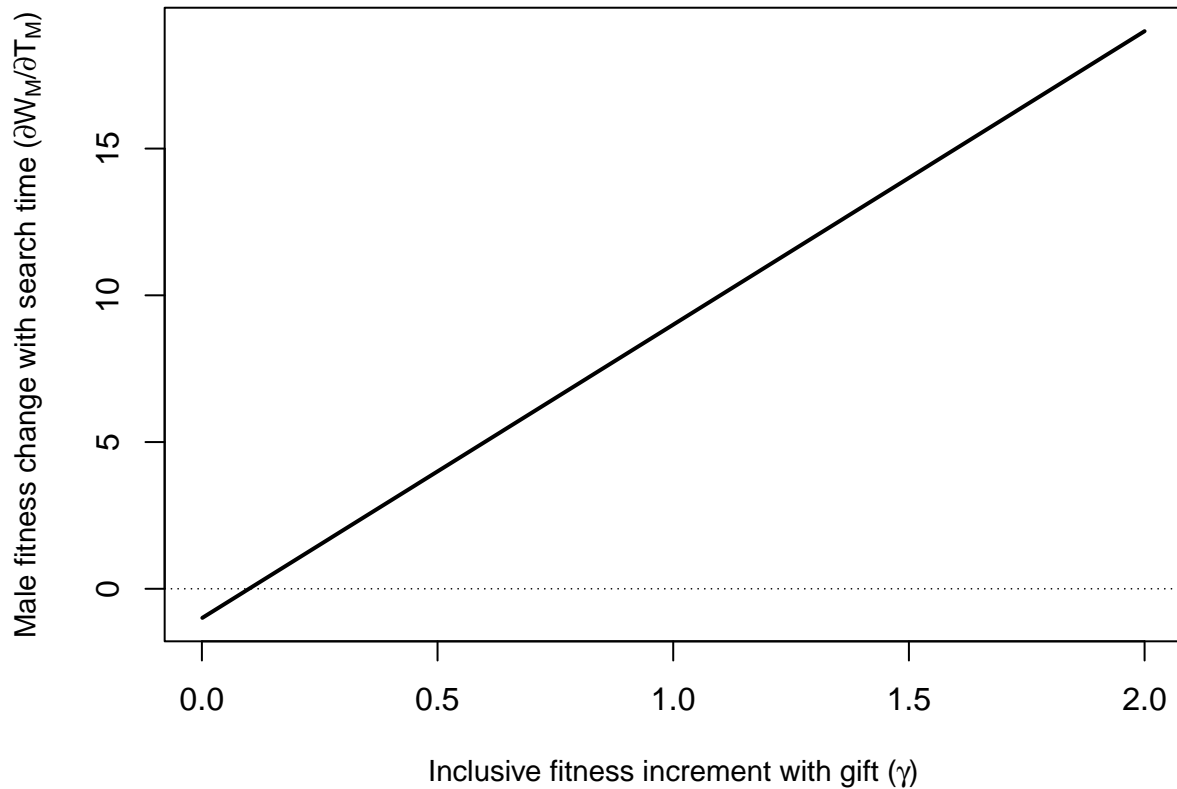
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I am just leaving this in here for now. Second derivative of fitness with respect to search time,

$$\frac{\partial^2 W_m}{\partial T_m^2} = \frac{\frac{2 \left(1 + \gamma \left(1 - \frac{1 + \frac{\sqrt{\beta}}{M} + T_m}{e^{\frac{1}{\alpha_1} T_m}} \right) \right)}{\left(T_m + \frac{\sqrt{\beta}}{M} \right)^2} - \frac{\gamma}{\alpha_1^2 e^{\frac{1}{\alpha_1} T_m}}}{T_m + \frac{\sqrt{\beta}}{M}}.$$

Old stuff

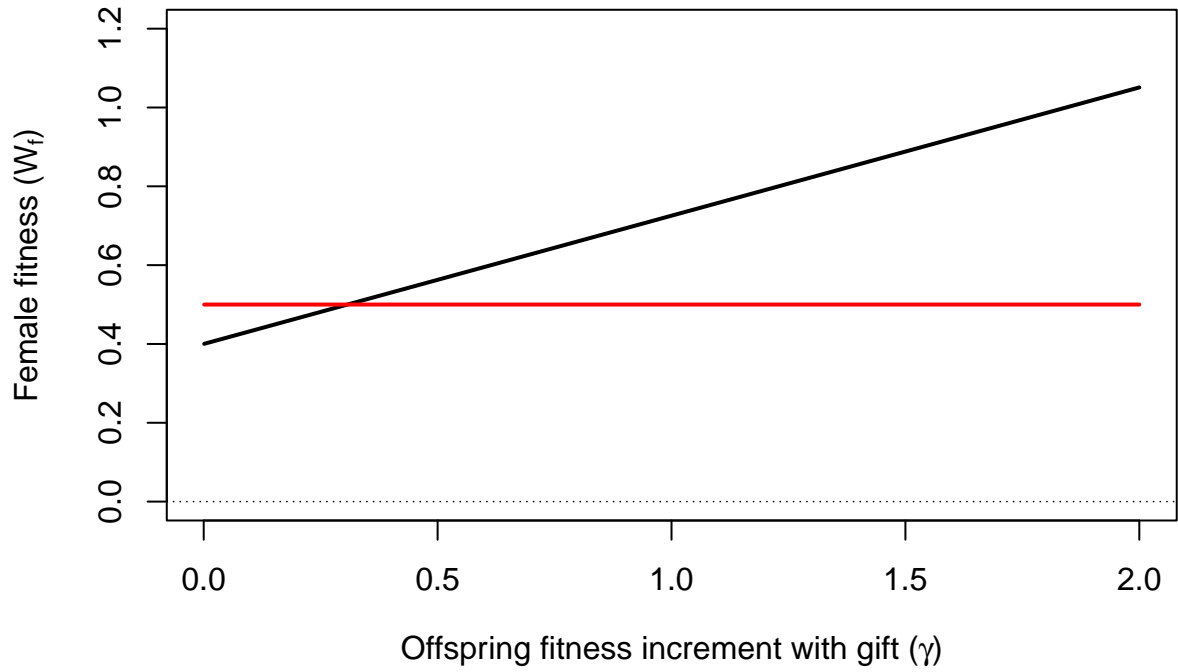
The plot below shows $\partial W_m / \partial T_m$ across a range of inclusive fitness increments to offspring associated with a nuptial gift (γ). Given a sufficiently high value of γ , males will increase their fitness by increasing their search time, evaluated at $T_M = 0$.



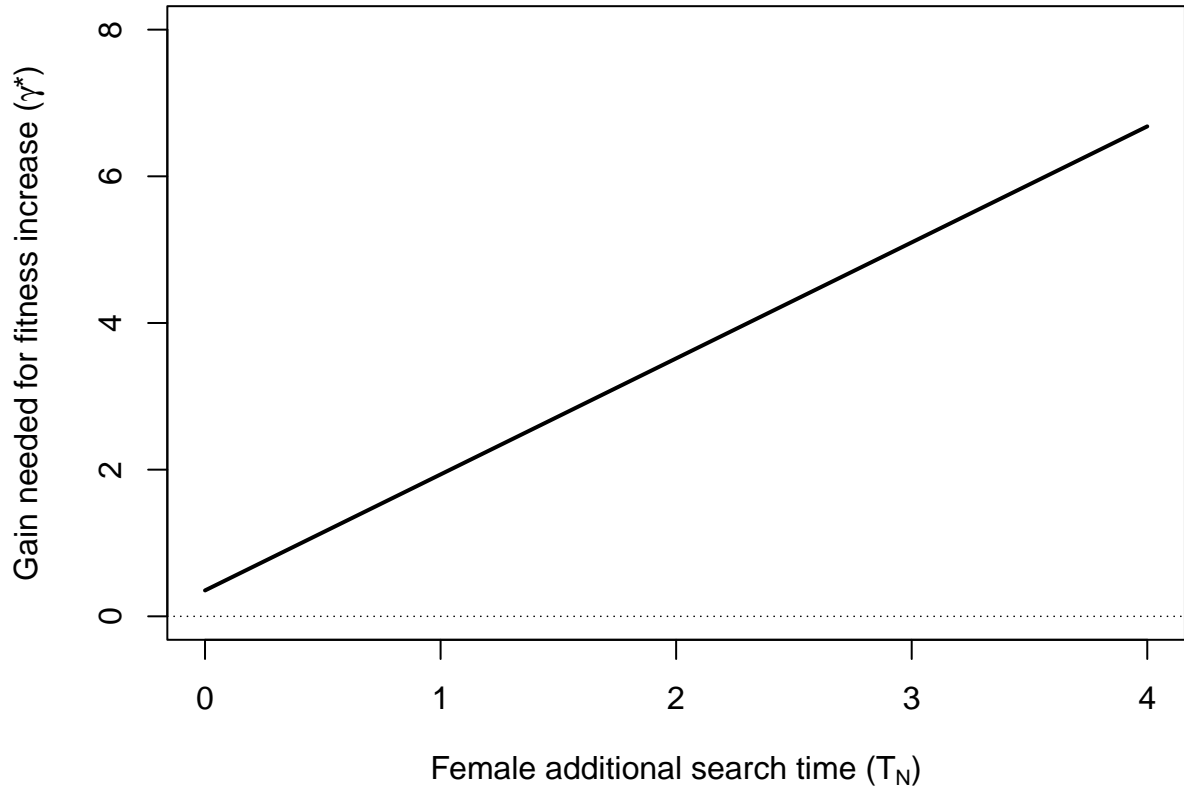
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Again, this makes intuitive sense because unless $\gamma > 0$, fitness can not increase with increased search time. So for our hypothetical example, if $\gamma = 1/2$, then we have -1.1080102.

For females, we can plot $W_f(n)/T_F$ and $Pr(g)(W_f(g)/(T_F + T_N))$ as a function of γ .



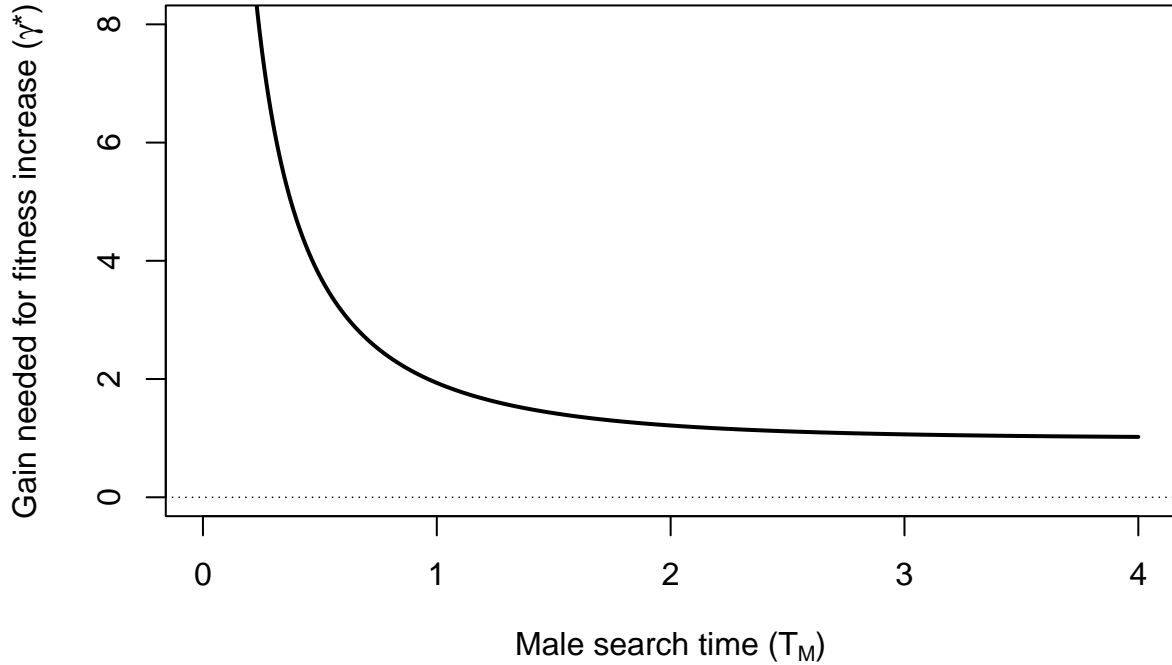
Here the intersection of the black and red lines identifies the inclusive fitness increment for offspring γ at which females do not benefit anymore from accepting a giftless male versus rejecting the giftless male in search of a new one. Where the black line is higher, females benefit by rejecting the giftless male in favour of searching for a new male. Where the red line is higher, females benefit by mating with the giftless male and entering the time out stage.



Upon rejecting a focal male, females will search for a new male for a duration of time T_N . The above plot illustrates how much of an fitness benefit provided to offspring (γ) is needed for the focal female to justify

the new search duration (γ^*) given $T_F = 1$ and $T_M = 1$. Note that upon rejecting a focal male, there is a nonzero probability that the focal female will fail to find a new male entirely after T_N , so there is no reason to expect the line above to pass through the origin. The value of γ^* when $T_N = 0$ is $\gamma^* = 0.3529867$. As a focal female invests more time, a larger fitness increment to her offspring is needed for rejecting the focal male to be beneficial.

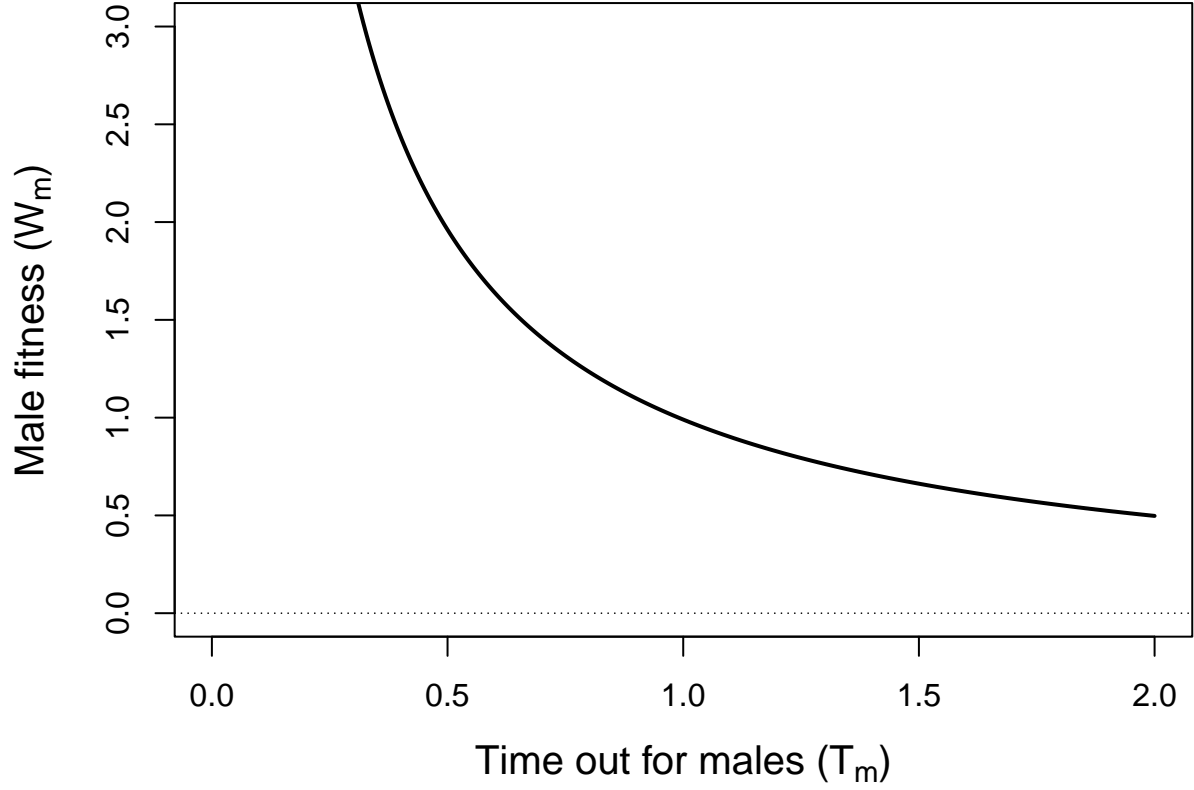
Below, we show how male search time affects γ^* when $T_N = 1$ and $T_M = 1$.



Old calculations

We select some values $\alpha_1 = 1$ and $\alpha_2 = 2$. From here, we can initially assume $\gamma = 0$ and plot how W_m changes as a function of T_M .

If we set $T_F = 1$, then simulate a range of $T_M = \{0.001, 0.002, 1.999, 2.000\}$, we can calculate W_M .



Note, however, that this is absolute fitness for a particular period of time out for males. What we are really interested in the change in male fitness given a change in time out. To do this, we can differentiate W_m with respect to T_m and simplify,

Testing

In the text, I am presenting the below,

$$\frac{\partial W_m}{\partial T_m} = \frac{\gamma \left(\left(\frac{\left(T_M + \frac{\sqrt{\beta}}{M} \right)}{\alpha_1} + 1 \right) - 1 \right)}{\left(T_M + \frac{\sqrt{\beta}}{M} \right)^2}.$$

This can be simplified,

$$\frac{\partial W_m}{\partial T_m} = \frac{\gamma \left(M^2 + \frac{M^2 T_m + M \sqrt{\beta}}{\alpha_1} \right) - M^2 (1 + \gamma)}{(T_m M + \sqrt{\beta})^2}.$$

But I do not really like this simplification. To me, it is easier to understand a bit of the biology with the first equation.

Stop searching when found

This is all wrong because of a mistake with $\Pr(G)$. I don't think that this is worth it unless absolutely necessary.

This was the original fitness equation,

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

But here is the fitness equation if males stop searching once they have found something, and I am getting rid of the fake nuptial gift now just to keep things tractable (assume $\alpha_2 \rightarrow \infty$),

$$W_m = \frac{\Pr(G)(1 + \gamma)}{\alpha_1 + \frac{\sqrt{\beta}}{M}} + \frac{\Pr(L)}{T_m + \frac{\sqrt{\beta}}{M}}.$$

Now,

$$\frac{\partial W_m}{\partial T_m} = \frac{\frac{\gamma+1}{\alpha_1^2 + \frac{\alpha_1 \sqrt{\beta}}{M}} - \frac{\frac{T + \frac{\sqrt{\beta}}{M}}{a} + 1}{\left(T_m + \frac{\sqrt{\beta}}{M}\right)^2}}{e^{\frac{1}{\alpha_1} T_m}}.$$

From here, we end up with,

$$\gamma > \frac{(M\alpha_1)^2}{\beta} - \frac{2M\alpha_1}{\sqrt{\beta}}.$$

References

- Kokko, H., and P. Monaghan. 2001. "Predicting the direction of sexual selection." *Ecology Letters* 4 (2): 159–65. <https://doi.org/10.1046/j.1461-0248.2001.00212.x>.
- Kokko, Hanna, Michael D Jennions, and Robert Brooks. 2006. "Unifying and Testing Models of Sexual Selection." *Annual Review of Ecology, Evolution, and Systematics* 37 (1): 43–66. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110259>.