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 (fake or real) nuptial gifts. 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 gifts. We then describe the fitness consequences of female choice to accept or reject males based on their provision of a nuptial gift.

Male fitness

During time-out, males search for a nuptial gift for a time period of T_m. 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 true nuptial gift. 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,

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

Similarly, we assume that a male will only enter the mating pool with no gift if they are unsuccessful in obtaining a real or fake nuptial gift, so the probability that a male obtains no gift after T_m is modelled as,

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

We assume that $\alpha_1 > \alpha_2$ (i.e., it is more difficult to obtain a real nuptial gift than a fake one). For simplicity, we further assume that the fitness increments associated with a real, fake, and no nuptial gift are $V_G = 1 + \gamma$, $V_F = 1$, and $V_L = 1$, respectively. Male 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,

$$W_m = \frac{\Pr(G)V_G + \Pr(F)V_F + \Pr(L)V_N}{T_m + \frac{\sqrt{\beta}}{M}}.$$

We can simplify this with the fitness values,

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

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, α_2, 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, α_2, 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,

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

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 true nuptial gift (α_1; 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 solve for γ,

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

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.

Female fitness

During time-out, females process offspring over a duration of T_f. 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 assume that females cannot distinguish between true and fake nuptial gifts.

We model the probability that a female encounters a male with a nuptial gift (real or fake) after a duration of T_N in the mating pool as,

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

In the above, $\Pr(G)$ and $\Pr(F)$ are the probabilities that males within the mating pool have successfully obtained a true or fake nuptial gift, respectively (see below). 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., $\Pr(g) > \Pr(n)$).

For simplicity, we assume that offspring sired by a giftless male have a fitness of 1, so offspring sired by males providing gifts have a fitness of $1 + \gamma$. The inclusive fitness of a female whose offspring are sired by a giftless male is therefore $W_f(n) = \kappa(1/2)$, where κ is total number of offspring. For simply, we assume $\kappa = 1$, meaning that female fitness is $W_f(n) = 1/2$. The inclusive fitness of a female whose offspring are sired by a male with a gift is then,

$$W_f(g) = \frac{1}{2}\left(1 + \gamma\frac{\Pr(G)}{\Pr(G) + \Pr(F)}\right).$$

That is, the fitness increment γ multiplied by the probability that a male's gift is true.

We can now ask a relevant question for female fitness. Under what conditions should she reject a giftless male? Females will have a higher fitness when they reject a giftless male if $W_f(g)$ exceeds $W_f(n)$ after accounting for the opportunity cost associated with the additional search time spent in the mating pool T_N,

$$\Pr(g)\frac{W_f(g)}{T_F + T_N} > \frac{W_f(n)}{T_F}.$$

Verbally, this is the probability that a female finds a male with a gift that produces higher fitness offspring. Note that we do not need to subtract a term for the fitness loss that might happen if the female fails to find any male. This would be double counting. The right-hand side of the inequality is the expected fitness for the female if she sticks with the male without a nuptial gift. The left-hand side of the inequality is her expected fitness if she rejects that male and spends a time of T_N within the mating pool looking for a male with a nuptial gift.

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.


$\longrightarrow$

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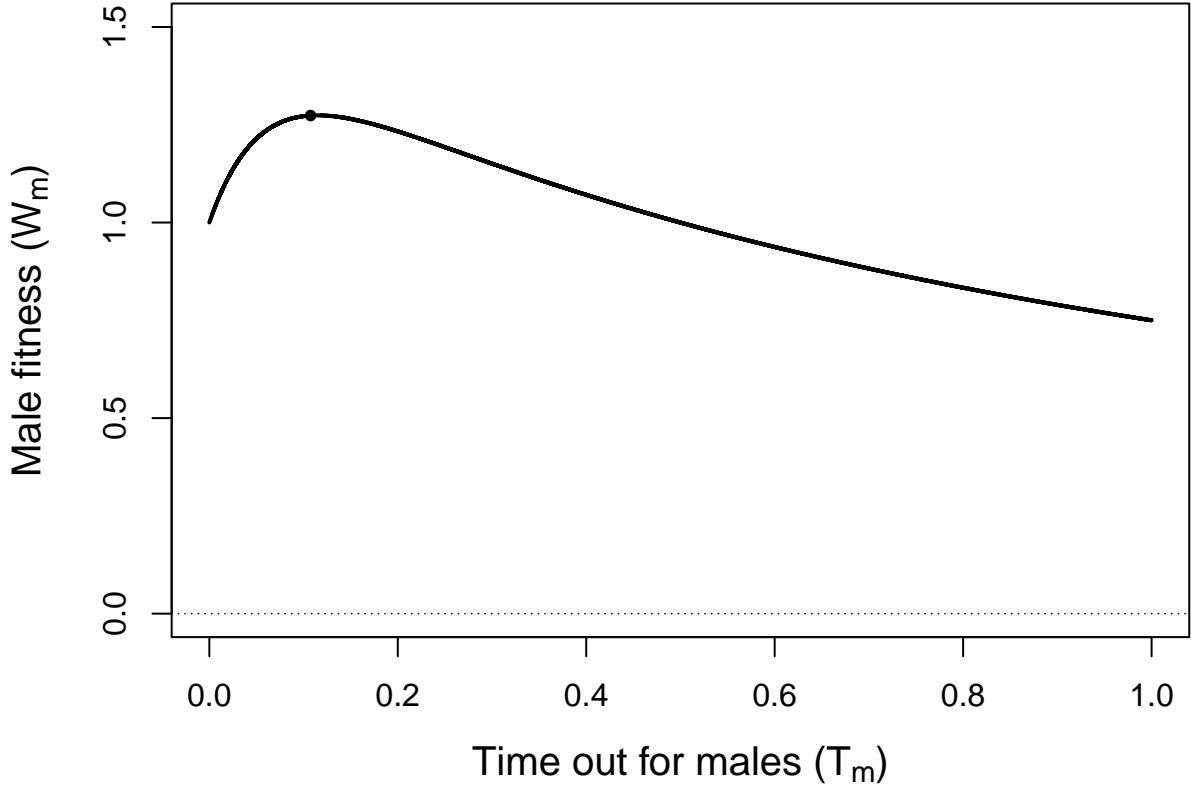
Second derivative of fitness

Second derivative of fitness with respect to search time,

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

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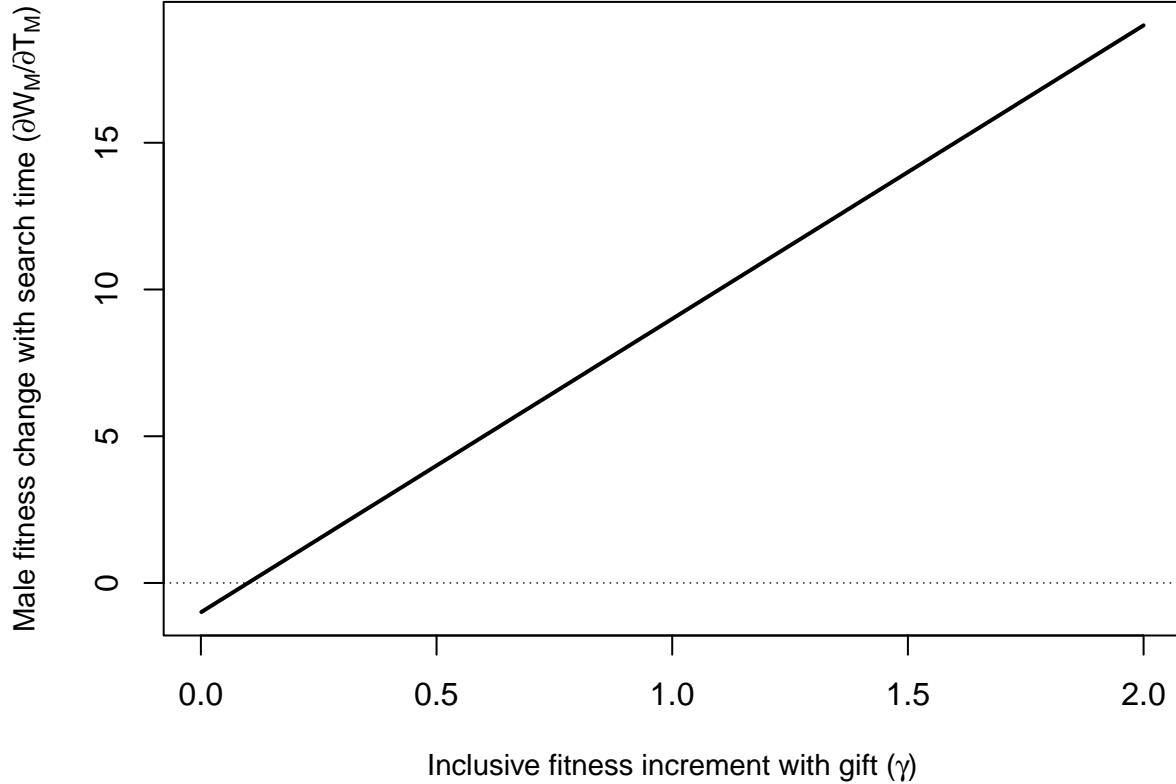
Again, this makes intuitive sense because unless $\gamma > 0$, fitness can not increase with increased search time. So for our hypothetical example, if $\gamma = 1/2$, then we have -1.1080102.

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.
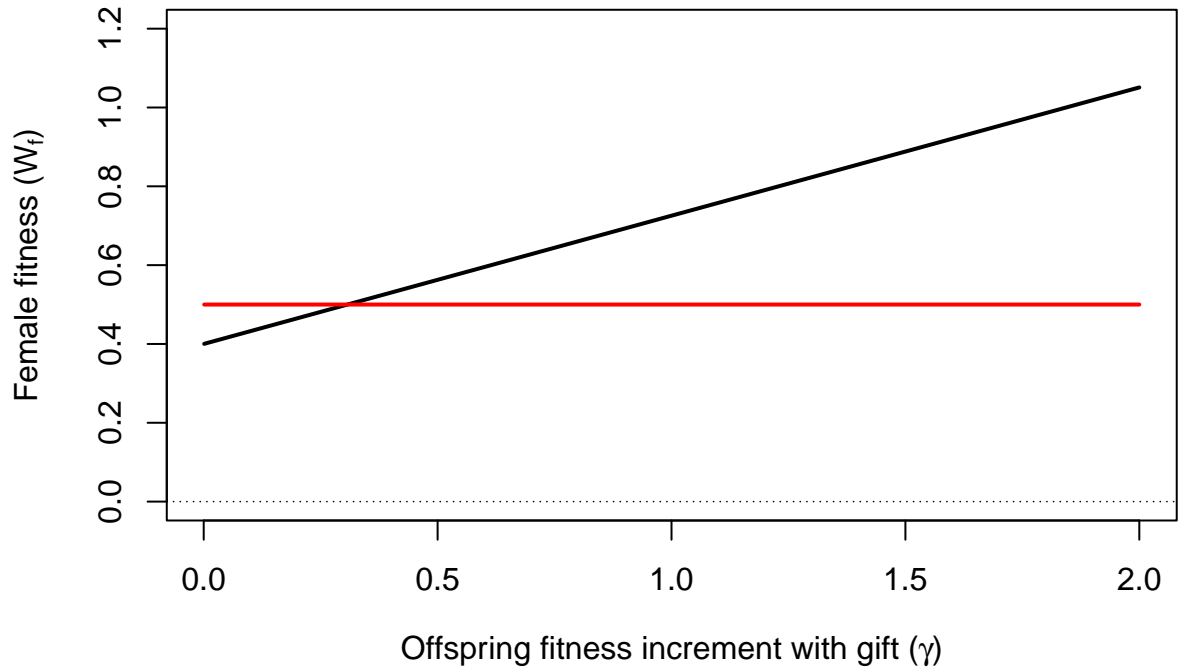
Here the intersection of the black and red lines identifies the inclusive fitness increment for offspring γ at which females do not benefit anymore from accepting a giftless male versus rejecting the giftless male in search of a new one. Where the black line is higher, females benefit by rejecting the 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.
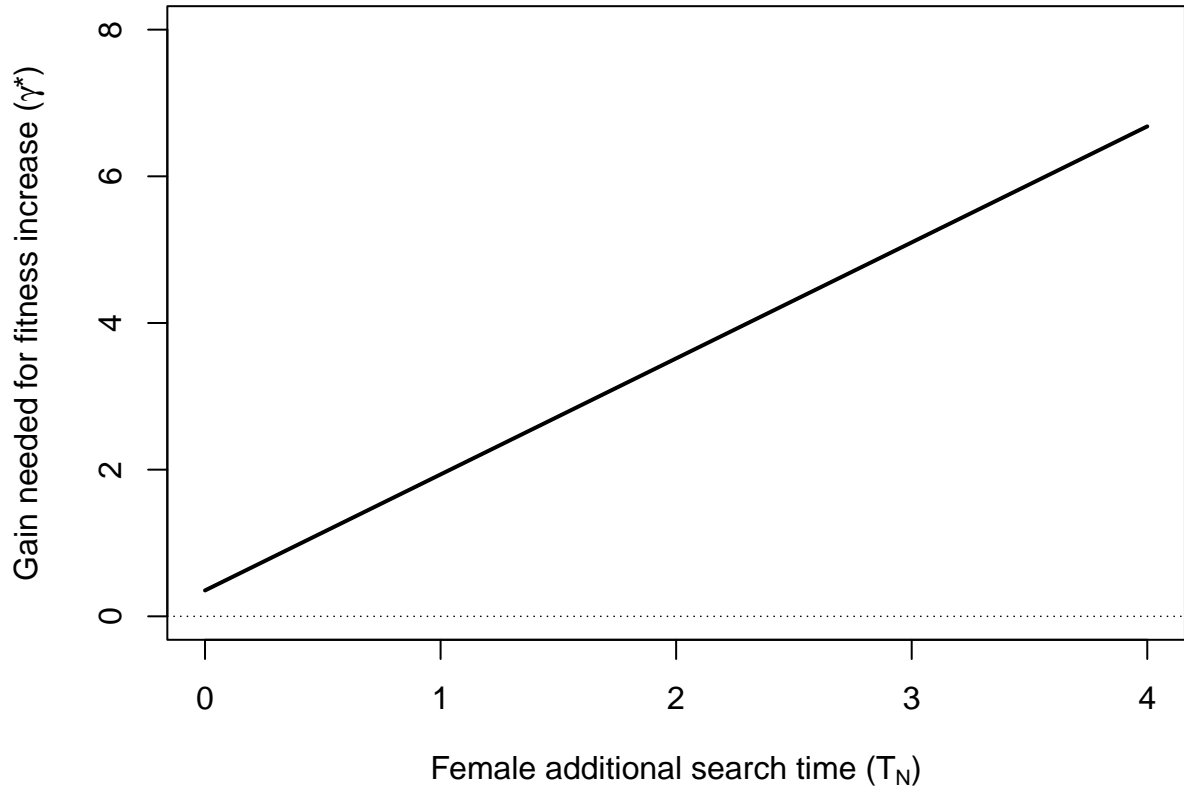
Upon rejecting a focal male, females will search for a new male for a duration of time T_N. The above plot illustrates how much of an fitness benefit provided to offspring (γ) is needed for the focal female to justify

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 $T_M = 1$.
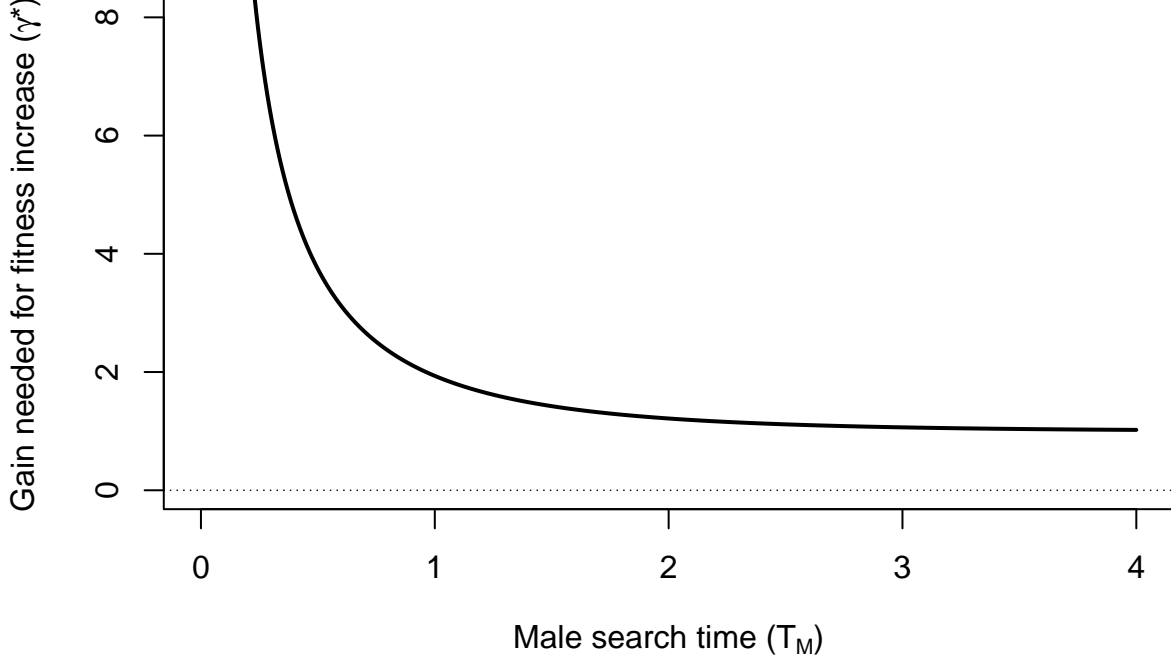
Operation sex ratio

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 pol waiting to encounter females ($\sqrt{\beta}/M$) divided by total time in and out,

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

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

$$P_{IF}(t) = \frac{M\sqrt{\beta}}{T_F + M\sqrt{\beta}}.$$

We therefore can define β as below,

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

The above can be simplified,

$$\beta = \frac{T_F\sqrt{\beta} + \beta M}{T_M \beta^2 \sqrt{M} + \beta M}.$$

Note that the equation is recursive, so we need to figure out a closed form solution if possible by figuring out the pattern. Note that this equation makes some intuitive sense. The value of β increases with higher female time out (T_F) and decreases with higher male time out (T_M). If $T_F = T_M = 0$, then we have $\beta = 0$; note that H. Kokko and Monaghan (2001) also multiplied the whole thing by a constant representing sex ratio upon reproductive maturity.

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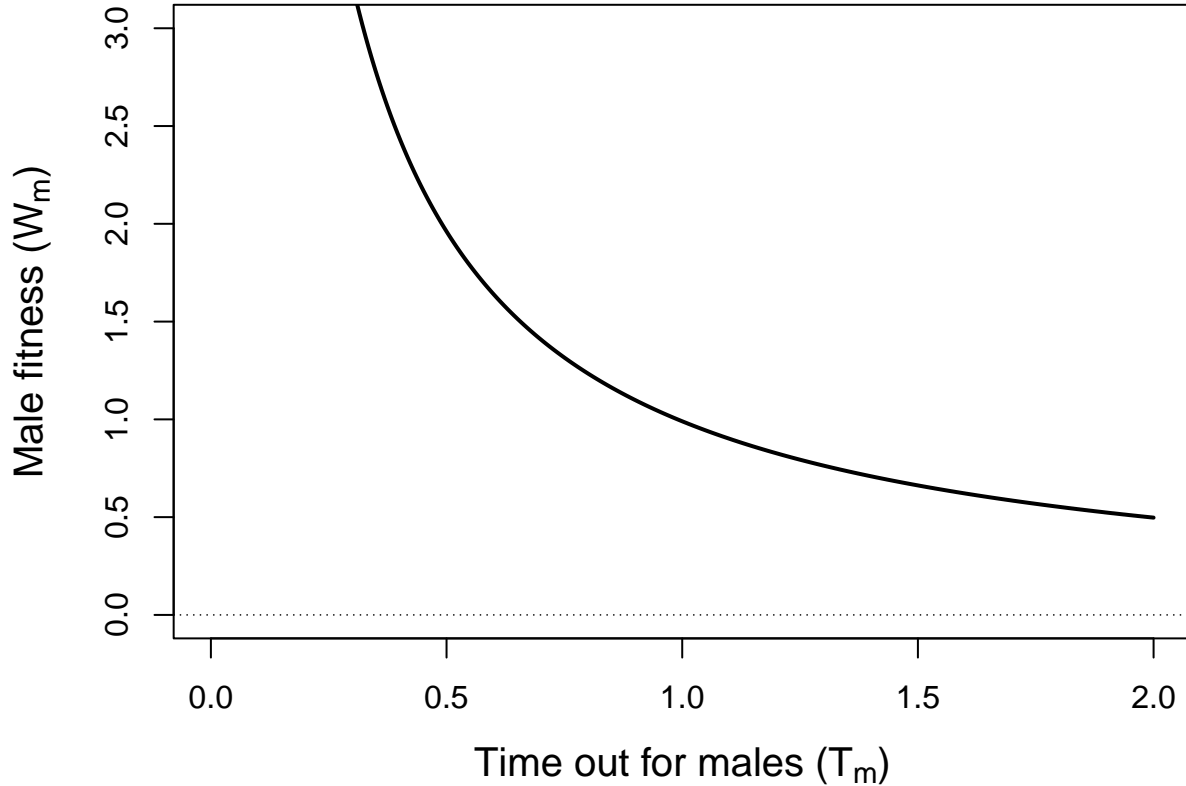
Note, however, that this is absolute fitness for a particular period of time out for males. What we are really interested in the change in male fitness given a change in time out. To do this, we can differentiate W_m with respect to T_m and simplify,

Testing

In the text, I am presenting the below,

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

This can be simplified,

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

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 $\alpha_2 \to \infty$),

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

Now,

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

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.