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). Males must spend time out of the mating pool to replenish sperm and 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.

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.

Male fitness

During time-out, males search for a nuptial gift for a time period of T_m. The probability that a male obtains a true nuptial gift (G) during this time is modelled as,

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

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,

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

In the above, α_1 and α_2 are parameters modulating the probability of successful search, where we assume $\alpha_1 < \alpha_2$ (i.e., it is more difficult to obtain a real nuptial gift than a fake one). 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,

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

Initial conditions

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, $\sqrt{\beta}/M$, γ, m_{im}, and m_{om}. For simplicity, and following Kokko, Jennions, and Brooks (2006), we assume $m_{im} = m_{om} = 1$ and $M = 100$. This leaves α_1, α_2, β, and γ. We assume that the sex ratio at maturation is unity (i.e., equal number of males and females upon maturation). Under this condition, Kokko and Monaghan (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. 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,

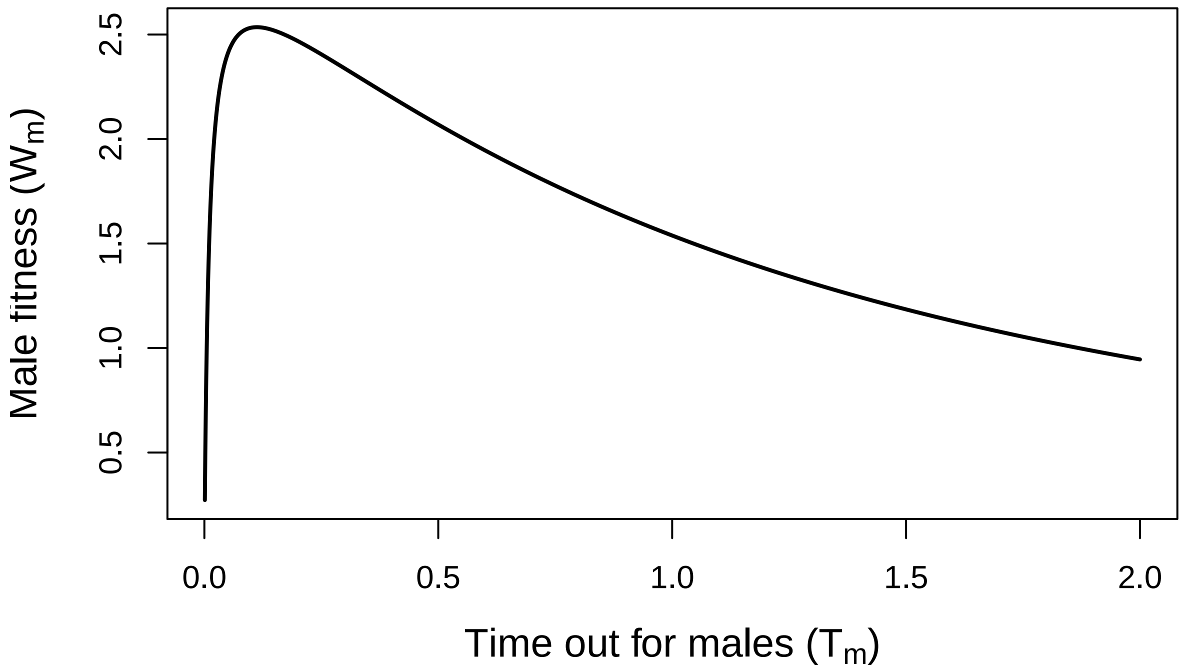
$$\beta = \frac{T_F\sqrt{\beta} + \beta M}{T_M \beta^2 \sqrt{M} + \beta M}.$$

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 Kokko and Monaghan (2001) also multiplied the whole thing by a constant representing sex ratio upon reproductive maturity.

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.

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. What we are really interested in the change in male fitness given a change in time out. If we differentiate W_m with respect to T_m and simplify, we have this monstrosity,

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

For our purposes,

$$\frac{\partial W_m}{\partial T_m} = \frac{\gamma \left(\frac{T_M + \frac{101}{100}}{e^{T_M}} - 1 \right) - 1}{\left(T_M + 1 \right)^2}.$$

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.

And -0.2825703

References

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.

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