| | ♀ | ♂ |
|---|---|---|
| ♀ | 0, 0 | 1, 1 |
| ♂ | 1, 1 | 0, 0 |

simple game, choose to play either female or male.

We can work out the mixed strategy from Maynard Smith (1982) p. 16

(Take the left as the focal strategy)

| | ♀ | ♂ |
|---|---|---|
| ♀ | a | b |
| ♂ | c | d |

$$p = \frac{(b-d)}{(b+c-a-d)}$$

$$p = \frac{1-0}{1+1-0-0} = \frac{1}{2}$$

I think that this recovers the 1:1 sex ratio assuming that individuals interact at random and produce an offspring when they encounter a member of the opposite sex. Note that it is trivial to generalise payoffs to any value 'W' and recover $p = \frac{1}{2}$

Let $F$ represent the female strategy,
$N$ represent a male with a nuptual gift
and $D$ represent a male without a gift.

Let $W(F)$, $W(N)$, and $W(D)$ be the fitness of each strategy.

Let $E(X, Y)$ be the payoff of an individual $X$ against a $Y$ opponent, as in Maynard Smith (1982).

Let $p_F$, $p_N$, and $p_D$ be the frequencies of $F$, $N$, and $D$, respectively, in the population.

I think we want to take the approach of assuming each $p$ is very low to see if it can invade.

The 3x3 payoff matrix will look something like the below

| | F | N | D |
|---|---|---|---|
| F | 0, 0 | | |
| N | | 0, 0 | 0, 0 |
| D | | 0, 0 | 0, 0 |

The empty boxes are the only areas with potentially nonzero fitness. F should thereby have positive fitness payoff when interacting with N or D (but not necessarily equal fitness), but N and D should only have positive fitness when interacting with F.

The intuition is that the stable $p_F = 0.5$, with $p_N$ & $p_D$ dependent on the details

Note from Bishop & Cannings (1978) and Maynard Smith 1982 (p. 15), a stable mixed strategy I requires: $E(I,I) = E(F,I) = E(N,I) = E(D,I)$

I think that we need to set the following equality,

$$p_F E(F,F) + p_N E(F,N) + p_D E(F,D) =$$
$$p_F E(N,F) + p_N E(N,N) + p_D E(N,D) =$$
$$p_F E(D,F) + p_N E(D,N) + p_D E(D,D).$$

For $W(F)$, perhaps we can assume the female gets some baseline reproductive output 'r', plus some added bonus 'b' if given a nuptual gift, 'b'.

For $W(N)$, assume that the reproductive output r comes at a cost 'c' (for the nuptual gift.

For $W(D)$, assume, for the moment, no cost.

Intuitively, we will end up with $p_N = 0$ and $p_F = p_D = \frac{1}{2}$, but let's work it out.

| | F | N | D |
|---|---|---|---|
| F | 0, 0 | r+b, r−c | r, r |
| N | r−c, r+b | 0, 0 | 0, 0 |
| D | r, r | 0, 0 | 0, 0 |

Therefore,

$p_F(0) + p_N(r+b) + p_D(r) =$

$p_F(r-c) + p_N(0) + p_D(0) =$

$p_F(r) + p_N(0) + p_D(0)$. So,

$$p_N(r+b) + p_D(r) = p_F(r-c) = p_F(r)$$

It is clear that $p_F(r-c) \neq p_F(r)$ unless $c=0$, so the neutral strategy cannot be stable under these conditions, and we are back to

$p_D(r) = p_F(r)$, so $p_D = p_F = \frac{1}{2}$.

It seems that we need something else for a nuptual strategy to be stable — perhaps either a condition dependent strategy, or maybe a second type of female.

Maybe a 'satiated' versus 'hungry' female, the latter of which will eat the D male but not the N male, removing some future fitness component, 'd'?

My intuition is that a mixed strategy could arise depending on the relative values of b, c, and d.

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1 JUN 2020

Working this out now, let's add the 'H' strategy to represent an especially hungry female (could have gone with F1 & F2 and M1 & M2 instead).

Here is the new 4x4 matrix,

| | F | H | N | D |
|---|---|---|---|---|
| F | 0, 0 | 0, 0 | r+b, r−c | r, r |
| H | 0, 0 | 0, 0 | r+b, r−c | r+m, r−δ |
| N | r−c, r+b | r−c, r+b | 0, 0 | 0, 0 |
| D | r, r | r−δ, r+m | 0, 0 | 0, 0 |

Note that all of the same 9 elements from the previous table involving interactions among F, N, and D are retain. The matrix just adds interactions with H.

- H does not have any fitness consequences from interactions with other females F or H.
- H interacts with nuptual providing males N in the same way that F does.
- H attempts to eat defecting D males, getting a meal benefit 'm', while these males suffer a fitness loss δ.

We now need to work out the below

$$p_F(0) + p_H(0) + p_N(r+b) + p_D(r) =$$
$$p_F(0) + p_H(0) + p_N(r+b) + p_D(r+m) =$$
$$p_F(r-c) + p_H(r-c) + p_N(0) + p_D(0) =$$
$$p_F(r) + p_H(r-\delta) + p_N(0) + p_D(0).$$

We can get rid of most terms

$$p_N(r+b) + p_D(r) = p_N(r+b) + p_D(r+m) =$$
$$p_F(r-C) + p_H(r-c) = p_F(r) + p_H(r-\delta)$$

I should have seen this coming. There is no cost, and only a benefit, of adopting H over F, so there cannot be a stable mixed strategy with both.

That's okay, we can come back to this later, if it seems beneficial to do so, perhaps by having some cost (e.g., risk), associated with the H strategy.

For now, we can just get rid of it,

| | H | N | D |
|---|---|---|---|
| H | 0, 0 | r+b, r−c | r+m, r−δ |
| N | r−c, r+b | 0, 0 | 0, 0 |
| D | r−δ, r+m | 0, 0 | 0, 0 |

I think that we can already simplify the above, but let's just calculate as before.

$p_H(0) + p_N(r+b) + p_D(r+m) =$

$p_H(r-c) + p_N(0) + p_D(0) =$

$p_H(r-\delta) + p_N(0) + p_D(0)$.

So we have,

$p_N(r+b) + p_D(r+m) = p_H(r-c) = p_H(r-\delta)$

For the above to hold, it is obvious that $c = \delta$ (fitness loss of nuptual equals fitness loss from cannibalism risk), now...

$$\rho_N(r+b)+\rho_D(r+m) = \rho_H(r-c)$$

$$\rho_N r + \rho_N b + \rho_D r + \rho_D m = \rho_H r - \rho_H c$$

$$\rho_N r + \rho_D r - \rho_H r = -\rho_H c - \rho_N b - \rho_D m$$

$$\rho_H r - \rho_N r - \rho_D r = \rho_H c + \rho_N b + \rho_D m$$

$$r(\rho_H - \rho_N - \rho_D) = \rho_H c + \rho_N b + \rho_D m$$

$$r = \frac{\rho_H c + \rho_N b + \rho_D m}{\rho_H - \rho_N - \rho_D}$$

That's not terribly useful. Will try $c$ (also $\sigma$) and $m$

$$\rho_N r + \rho_N b + \rho_D r + \rho_D m = \rho_H r - \rho_H c$$

$$\rho_H c = \rho_H r - \rho_N r - \rho_D r - \rho_D m - \rho_N b$$

$$\rho_H c = r(\rho_H - \rho_N - \rho_D) - \rho_D m - \rho_N b$$

$$c = \frac{r(\rho_H - \rho_N - \rho_D) - \rho_D m - \rho_N b}{\rho_H}$$

Not much use yet

$$p_N(r+b) + p_D(r+m) = p_H(r-c)$$

$$p_N r + p_N b + p_D r + p_D m = p_H r - p_H c$$

$$p_N b = p_H r - p_N r - p_D r - p_H c - p_D m$$

$$p_N b = r(p_H - p_N - p_D) - p_H c - p_D m$$

$$b = \frac{r(p_H - p_N - p_D) - p_H c - p_D m}{p_N}$$

This has not helped much either, and m will be similar. Lets try to isolate $p_H$

$$p_H = \frac{p_N(r+b) + p_D(r+m)}{r-c}.$$

Maybe we can make use of

$$1 = p_H + p_N + p_D,$$

$$p_H = 1 - p_N - p_D,$$

so

$$p_N(r+b) + p_D(r+m) = (1-p_N-p_D)(r-c)$$

$$\cancel{p_N r} + p_N b + \cancel{p_D r} + p_D M = r - c + \cancel{p_N r} - p_N c + \cancel{p_D r} - p_D c$$

$$p_N b + p_D M = r - c - p_N c - p_D c$$

$$c(1 + p_N + p_D) = r - p_N b - p_D M$$

Let's isolate $p_N$, actually

$$c + p_N c + p_D c = r - p_N b - p_D m$$

$$p_N c + p_N b = r - p_D m - p_D c - c$$

$$p_N = \frac{r - p_D m - p_D c - c}{(c+b)}.$$

This seems like a mess still. One more attempted trick. What if we instead set $p_N = 1 - p_H - p_D$

$$(r+b)(1-p_H-p_D) + p_D(r+m) = p_H(r-c)$$

$$(1-p_H-p_D)(r+b)+p_D(r+m) = p_H(r-c)$$

$$r-p_Hr-\cancel{p_Dr}+b-p_Hb-p_Db+\cancel{p_Dr}+p_Dm = p_Hr-p_Hc$$

$$r+b-p_Hr-p_Hb-p_Db+p_Dm = p_Hr-p_Hc$$

$$r+b-p_Db+p_Dm = 2p_Hr-p_Hc+p_Hb$$

$$p_H(2r-c+b) = r+b-p_Db+p_Dm$$

$$p_H = \frac{r+b-p_Db+p_Dm}{2r-c+b}$$

I really wanted that to be obviously $1/2$, in which case

$$2r-c+b = 2(r+b-p_Db+p_Dm)$$

$$2r-c+b = 2r+2b-2p_Db+2p_Dm$$

$$2p_Db-2p_Dm = 2r-2r+2b-b+c$$

$$2p_D(b-m) = b+c$$

$$2p_D(b-m) = b+c$$

$$p_D = \frac{b+c}{2(b-m)}$$

This would seem to imply that b must necessarily be greater than m, which doesn't make sense, but could be a consequence of forceing $p_t = \frac{1}{2}$ (or just bad maths).

The benefit of a nuptial must exceed that of a male meal can't be correct, so I will start over again.

I think m is actually completely extraneous, actually, so let's remove it.

| | H | N | D |
|---|---|---|---|
| H | $0, 0$ | $r+b, r-c$ | $r, r-\delta$ |
| N | $r-c, r+b$ | $0, 0$ | $0, \delta$ |
| D | $r-\delta, r$ | $0, 0$ | $0, 0$ |

Once more now,

$$p_H(0) + p_N(r+b) + p_D(r) =$$
$$p_H(r-c) + p_N(0) + p_D(0) =$$
$$p_H(r-\delta) + p_N(0) + p_D(0)$$

$$p_N(r+b) + p_D(r) = p_H(r-c) = p_H(r-\delta)$$

We again get $c = \delta$, so

$$p_N(r+b) + p_D(r) = p_H(r-c)$$

Again, note:

$$p_D = 1 - p_N - p_H$$

$$p_N(r+b) + (1-p_N-p_H)(r) = p_H(r-c)$$

$$\cancel{p_N r} + p_N b + r - \cancel{p_N r} - p_H r = p_H r - p_H c$$

$$p_N b + r - p_H r = p_H r - p_H c$$

$$p_N b = 2p_H r - p_H c - r$$

$$p_N = \frac{p_H(2r-c) - r}{b}$$

Something isn't right here.
Can't we just set $r=1$?

$$p_N = \frac{2p_H - p_H c - 1}{b} = \frac{p_H(2-c) - 1}{b}$$

Need to regroup and start again. I think $r$ can be standardised mating fitness of 1, leaving $b$ and $c$, which might not get much.

# Anders notes

- issue with defining fitness, sperm transfer obviously does not work for females.

- Is egg hatching times number of eggs for males.

- Tuni et al J Evol Biol
  - If females hungry, then nuptial gift translates to offspring success.

- Maxwell et al nuptial gifts

- Studies <u>do</u> show that males with nuptial gifts less likely to be eaten

- No difference in cannibalism risk if dummy gift.

- For now, forget values of meals and nuptual gifts.
- Female choice to eat or not, or mating or running.
- Is the sex ratio <u>actually</u> 1:1
- Females increase fitness by eating, but pay a cost if needs to eat male.
- Do females mate before eating their male mates.

♀ eat or don't

♂ nuptual or not.

9 JUN 2021

Trying this again now, but with a simpler set up. Females will eat or not, and males will provide a nuptial gift or not.

Where I appear to be stumbling a bit is the cost and benefit of the female eating. It is unclear under what circumstances a focal female could benefit by not eating. We might imagine that females benefit by eating the nuptial gift more than the male, but is it really realistic to assume that females might eat the male when it is more costly to do so? Perhaps eating benefits most given a nuptial gift, then male, but is <u>worse</u> than not eating given a dummy. A male pays a cost for the real nuptial, a lower on for the fake, and none for just showing up. Now we

Might have something. Let's first just do females vs. males.

male

Female

| | N | D | E |
|---|---|---|---|
| F | $1, 1-c_2$ | $1-h_1, 1-c_1$ | $1, 1-c_3$ |
| H | $1-h_2, 1-c_2$ | $1-h_2, 1-c_1$ | $1-h_2, 1$ |

Above we have female strategies of feeding (F) and Hungry (H), i.e., not eating. We have male strategies of Nuptual gift (N), Dummy (D), and Empty (E).

Avoiding the formal analysis, for the moment, we can assume that the cost of wasting energy eating a dummy ($h_1$) is higher for a female than just not eating ($h_2$), with the best fitness outcome being a real meal (1).

So F is best to play against N and E, but H is best to play against D (note, we could perhaps reasonably assume that eating the nuptual is less costly than eating the male.

For the male, we can perhaps assume that the cost of providing the dummy ($c_1$) is less than the cost of a real nuptual ($c_2$), and both are less than the cost of being eaten ($c_3$). In this case, best to play D against F, but play E against H.

This leads to a problem. It never makes sense for a male to play N, so we would expect the game to break down, with females perhaps just feeding on the males after all.

Let's just remove D as an option. Now we can use,

| | N | E |
|---|---|---|
| F | $1, 1-C_1$ | $1-h_2, 1-C_2$ |
| H | $1-h_1, 1-C_1$ | $1-h_1, 1$ |

Where $C_1 < C_2$ and $h_1 < h_2$. This kind of works. F is the best strategy against N, and H is best against E. For males, N is best against F, and E is best against H. You can even see how this is vulnerable to a male strategy D with a cost $< C_1$ and $C_2$, which could then cause a shift in female optimal strategy. Is $h_1 < h_2$ realistic? More costly to eat a male than just going hungry seems unlikely, except under some very limited scenarios.