

	♀	♂
♀	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 local 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 nuptial 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  
influence.

The  $3 \times 3$  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  $p_N \neq p_D$  dependent on the details.

Note from Bishop & Cannings (1978) and Maynard Smith 1982 (e. 15), a stable mixed strategy

$$I \text{ requires: } E(I, I) = E(F, I) = E(N, I) = E(D, I)$$

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 nuptial gift, ' $b$ '.

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

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

Intuitively, we will end up with  $p_D = 0$  and  $p_F = p_N = \frac{1}{2}$ , 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,

$$\begin{aligned} p_F(0) + p_N(r+b) + p_D(r) &= \\ p_F(r-c) + p_N(0) + p_D(0) &= \\ p_F(r) + p_N(0) + p_D(0). \quad \text{So,} \end{aligned}$$

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

If 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

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

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

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

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

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| 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  $4 \times 4$  matrix,

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

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 reptual 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  $\delta$ .

We now need to work out the below

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

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

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

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

We can get rid of most terms

$$p_N(r+b) + p_D(r) = p_N(r+b) + p_D(r+\delta) =$$

$$p_F(r-c) + p_H(r-c) = p_F(r) + p_H(r-\delta)$$

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

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

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

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

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

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 capture equals fitness loss from cannibalism risk), now...

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

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

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

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

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

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

That's not terribly useful. Will try  
 $C$  (also  $\delta$ ) and an

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

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

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

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

Not much use yet

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

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

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

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

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

This has not helped much either,  
and we will be stuck. Let's  
try to isolate  $\rho_H$

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

Maybe we can make use of

$$1 = \rho_H + \rho_N + \rho_D$$

$$\rho_H = 1 - \rho_N - \rho_D,$$

so

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

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

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

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

Let's isolate  $p_N$ , actually

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

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

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

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

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

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

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

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

$$r+b - p_D b + p_D m = 2p_H r - p_H c + p_H b$$

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

$$p_H = \frac{r+b - p_D b + p_D m}{2r-c+b}$$

I really wanted that to be obviously  
 $\frac{1}{2}$ , in which case

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

$$2r-c+b = 2r+2b - 2p_D b + 2p_D m$$

$$2p_D b - 2p_D m = 2r - 2r + 2b - b + c$$

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

$$2\rho_D(b-m) = b+c$$

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

This would seem to imply that  $b$  must necessarily be greater than  $m$ , which doesn't make sense, but could be a consequence of forcing

$$\rho_t = \frac{1}{2} \text{ (or just bad maths).}$$

The benefit of a meal must exceed that of a meal 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:

$$p_D = 1 - p_H - p_H$$

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

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

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

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

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

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 making 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.
- pre egg hatching times number  
of eggs for males.
- Tuki et al J Evol Biol
  - If females hungry, then  
nuptial gift translates to  
offspring success.
- Maxwell et al nuptial gifts
- Studies do show that  
males with nuptial gifts  
less likely to be eaten
- No difference in cannibalism rate  
if dummy gift.

- For now, forget values of males and nuptial gifts.
- Female choice to eat or not, or mating or not.
- Is the sex ratio actually 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

♂ nuptial 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 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 worse than not eating given a dummy. A male pays a cost for the real nuptial, a lower one for the fake, and none for just showing up. Now we

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

	N	D	E	= male
F	$1, 1-C_2$	$1-h_1, 1-C_1$	$1, 1-C_3$	
H	$h_2, 1-C_2$	$1-h_2, 1-C_1$	$1-h_2, 1$	

Above we have female strategies of feeding (F) and hungry (H), i.e., not eating. We have male strategies of Neutral 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 nuptial 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 nuptial ( $c_2$ ), 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 R II.

Let's just remove D as an option.

Now we can use,

	N	E
F	$l, l - C_1$	$l - h_2, l - C_2$
H	$l - h_1, l - C_1$	$l - h_1, l$

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.

27 JUN

Based on Anders' work,

I will now simplify to two male strategies and two female strategies.

$M_1$ : Males that offer nuptial gifts

$M_2$ : Males that do not offer gifts.

$F_1$ : Females who accept males

$F_2$ : Females who eat males without gifts.

Assume that accepting a nuptial gift comes at some cost for males,  $C$ . Intuitively, it makes sense that males should offer a nuptial gift if the probability of encountering an  $F_2$  female is sufficiently high relative to  $C$ .

What makes less sense to me

is why a female would ever take a mixed strategy. It would seem that either the male sperm or food is worth more. So why would female strategy depend on male strategy at all?

The most straightforward exception that I can think of relates to female multiple mating. Maybe if a female has already mated, then the food increases fitness more than additional sperm? This would predict nuptial gifts to be rare in low density populations because mating rate would also decrease.

Interestingly, Toft and Albo (2016) did not find hunger of the mating female to predict whether or not she would eat the male, but nuptial gifts did make cannibalism less likely. It seems not unreasonable then that the cost to benefit ratio of eating

& male is based on whether a focal female has previously mated.

Tuni et al. (2013) do show a benefit of polyandry, but mating more than once must surely come with diminishing fitness returns that are at some point less than the benefit of a meal.

Then again, spider fitness really does seem to increase with multiple mating, and it is not at all clear to me that the benefit of a meal would outweigh the cost of a missed mating opportunity. But in all of these experiments, males offered a nuptial gift, so there is really no way to know the counterfactual. Tuni et al. (2013) also concluded that under low food conditions, it is likely that

there exists a trade-off between survival and reproduction. Hence, female that have already mated might be more inclined to eat males.

Also, they found that females got enough sperm to fertilise all eggs after one mating, so this idea of cannibalism being linked to mating rate might be quite plausible?