04/06/21 AC

Some points from the literature:

Check fine print on sexual cannibalism in P. mirabilis - are males eaten before or after sex?:

I checked, and sexual cannibalism does indeed occur BEFORE mating (i.e. it is pre-copulatory).

https://academic.oup.com/beheco/article/19/3/546/185057
https://royalsocietypublishing.org/doi/10.1098/rsbl.2005.0392

This means that risking sexual cannibalism ought to be expensive (in terms of fitness).

Check whether or not there is evidence for deviations from a 1:1 sex ration in P. mirabilis:

I found no conclusive evidence for P. mirabilis not having a 1:1 sex ratio, only a study that could suggest that changes in the operational sex ratio of the species occurs over the mating season.

https://pure.au.dk/portal/files/119094395/COMPLETE_THESIS.pdf

Therefore, I think it should to be safe to assume that we're dealing with a 1:1 sex ratio.

Define pay-off matrix with single unit (number of offspring):

We will (initially) consider 4 strategies; Male who give nuptial gifts (*M1*) and male who don't (*M2*). Female who accept all males (*F1*) and females who cannibalize all male who don't offer nuptial gifts (*F2*).

In both sexes, we can define fitness as the expected number of offspring. For males, the expected number of offspring is calculated as the proportion of eggs hatched after mating a virgin female once (see page 18-20 in manuscript draft for details) multiplied by the mean number of eggs produced per female, $\overline{g}$. The value of a meal is m (whether cannibalized male or nuptial gift). If we further assume that all individuals mate only once, we get the following pay-off matrix, A.

$$A = \begin{array}{cc} & \begin{array}{cccc} M1 & M2 & F1 & F2 \end{array} \\ \begin{array}{c} M1 \\ M2 \\ F1 \\ F2 \end{array} & \begin{bmatrix} (0,0) & (0,0) & (0.58\cdot\overline{g} - m, 0.58\cdot\overline{g} + m) & (0.58\cdot\overline{g} - m, 0.58\cdot\overline{g} + m) \\ (0,0) & (0,0) & (0.47\cdot\overline{g} + m, 0.47\cdot\overline{g}) & (0, m) \\ (0.58\cdot\overline{g} + m, 0.58\cdot\overline{g} - m) & (0.47\cdot\overline{g}, 0.47\cdot\overline{g} + m) & (0,0) & (0,0) \\ (0.58\cdot\overline{g} + m, 0.58\cdot\overline{g} - m) & (m, 0) & (0,0) & (0,0) \end{bmatrix} \end{array}$$

For clarity, lets break down a few match-ups. For example in M1 vs F1, the male fertilizes 58% of the females $\overline{g}$, getting $0.58\cdot\overline{g}$ offspring minus whatever values m has (in term of numbers of offspring). The female gets the same number of offspring (since individuals, currently, mate only once) plus she gains the value of the nuptial gift m.

What about M2 vs F2? The male offers no nuptial gift, giving him a shorter copulation duration, allowing him to fertilize fewer eggs; data suggest only 47% compared to 58% (the details on how I arrive at these numbers are in the manuscript draft) .Thus, he gets $0.47\cdot\overline{g}$ offspring and keeps the benefit of m. The female gets only $0.47\cdot\overline{g}$.

In M2 vs F2, the female eats the male gaining m and the male has no offspring (obviously, if individuals only mate once, the female would have no offspring either, but lets ignore this for now - a possible way could be Maynard Smith's trick saying that we're not dealing with total fitness, but just some extra, possible fitness gain; we could assume that everyone has already reproduced once prior to the game).

Let's see what happens when we throw in some more numbers; given [2] a good candidate for the mean number of eggs can be calculated as an approximate weighted average of the relevant row in table 1 of [2]:

$$\overline{g} = \frac{1}{(19 + 17 + 25 + 8 + 7 + 12)}\cdot(47.4\cdot 19 + 49\cdot 17 + 46.8\cdot 25 + 23\cdot 8 + 21\cdot 7 + 24.3\cdot 12) \approx 40$$

so we have

$$A = \begin{array}{cc} & \begin{array}{cccc} M1 & M2 & F1 & F2 \end{array} \\ \begin{array}{c} M1 \\ M2 \\ F1 \\ F2 \end{array} & \begin{bmatrix} (0,0) & (0,0) & (23.20 - m, 23.20 + m) & (23.20 - m, 23.20 + m) \\ (0,0) & (0,0) & (18.80 + m, 18.80) & (0, m) \\ (23.20 + m, 23.20 - m) & (18.80, 18.80 + m) & (0,0) & (0,0) \\ (23.20 + m, 23.20 - m) & (m, 0) & (0,0) & (0,0) \end{bmatrix} \end{array}$$

These numbers use a sound fitness proxy (numbers of offspring), while incorporating the best data available on the male sperm competition. If you like, we could try checking for any equilibria in A and see what the predicted sex ratio becomes. My intuition is that it will yield predictions on how valuable food needs to be in order for M2 to be favoured (that is, predictions on how valuable a nuptial gift needs to be before it is no longer worth offering up one to females).

After this, I could try to relax some of the assumptions made above; this could include:
i) allowing for more strategies.
ii) allowing for different values of g in different female strategies (i.e. female increase their egg production if they have more food [2]).
iii). allowing for individuals to mate more than once, possibly by applying ideas from [3].

I might have time to look a bit further into i-iii early next week but if not, let's take it from here when we meet Thursday.

References:

[1] Tuni, C. Albo, M. J. Bilde, T. (2013). Polyandrous females acquire indirect benefits in a nuptial feeding species. Journal of Evolutionary Biology, 26, 6, 1307-1316.

[2] Toft, S. Albo, M, J. (2016). The shield effect: nuptial gifts protect males against pre-copulatory sexual cannibalism. Biology Letters, 12, 5.

[3] Ball, M.A. Parker, G.A. (2003). Sperm competition games: sperm selection by females. Journal of Theoretical Biology. 224, 27-42.

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