Hi Brad,

Below are my notes and ideas on how to proceed - I hope you enjoy :-)

The aim:

We are interested in understanding the occurence of alternative reproductive tactics in the P. mirabilis system by taking a game theoretical approach to modelling the selection pressures imposed by males on females and vice versa. This will be done either in addition to the existing manuscript or as a seperate paper.

A possible modelling approach:

A classical, symmetric pay-off matrix is inappropriate, since players never encounter their own strategy or, for that matter, any strategy played by their own sex. To use the Hawk-Dove game as an analogy, we are dealing with a case where, say, Dove players never face off against their own strategy (since we model pairwise contests between males and females), yet Dove players indirectly compete with other Dove players. To circumvent this problem, a possible solution could be to construct an asymetric pay-matrix of 2D-vectors (basically a kind of tensor) to represent this asymetry. In the following, I attempt to breifly sketch a formal description of this idea and I then apply it to the P.mirabilis system. I then briefly throw into the mix some of the numbers we have from the manuscript, i.e. from existing datasets.

Assume a population of P. mirabilis and let i, j be the total number of different strategies available to males and females, respectively. The evolutionary game being played amongst males and females (via pay-off values determined by the opposite sex) might now be described by the matrix A

$$\begin{array}{cc} & \underline{\text{Female}} \\ \underline{\text{Male}} & \begin{bmatrix} \begin{bmatrix} M_{1,1} & F_{1,1} \end{bmatrix} & \begin{bmatrix} M_{1,2} & F_{1,2} \end{bmatrix} & \ldots & \begin{bmatrix} M_{1,j} & F_{1,j} \end{bmatrix} \\ \begin{bmatrix} M_{2,1} & F_{1,1} \end{bmatrix} & \begin{bmatrix} M_{2,2} & F_{2,2} \end{bmatrix} & \ldots & \begin{bmatrix} M_{2,j} & F_{2,j} \end{bmatrix} \\ \vdots & \vdots & \vdots & \vdots \\ \begin{bmatrix} M_{i,1} & F_{i,1} \end{bmatrix} & \begin{bmatrix} M_{i,2} & F_{i,2} \end{bmatrix} & \ldots & \begin{bmatrix} M_{i,j} & F_{i,j} \end{bmatrix} \end{bmatrix} = A \end{array}$$

Such that if a male using the ith strategy plays a female using the jth strategy, they receive pay-offs of $M_{i,j}$ and $F_{i,j}$, respectively. Obviously, as a necessary ingredient for frequency dependence (which is really the essence of game theory in many ways), the probability of obtaining certain pay-offs should depend on the frequency of players using certain strategies. To account for this frequency dependent aspect, let's scale all entries of A by some scalar $a_{i,j}$ with the property

$$0 \leq a_{i,j} \leq 1, \forall\, i, j \in \mathbb{N}$$

such that we get a version of A, denoted A_{scaled}, where all entries are scaled by their probability of occuring. Put less formally (and less pretentiously :D), we are simply multiply all pay-offs by their probability of them being obtained by some player. For example, if the probability of male using the ith strategy encountering a female using the jth strategy is $50\ \%$, then $a_{ij} = \frac{1}{2}$. We can now define A_{scaled} as

$$\begin{array}{cc}
 & \textbf{Female} \\
\textbf{Male} & \begin{bmatrix}
a_{11} \cdot \begin{bmatrix} M_{1,1} & F_{1,1} \end{bmatrix} & a_{1,2} \cdot \begin{bmatrix} M_{1,2} & F_{1,2} \end{bmatrix} & \dots & a_{1,j} \cdot \begin{bmatrix} M_{1,j} & F_{1,j} \end{bmatrix} \\
a_{2,1} \cdot \begin{bmatrix} M_{2,1} & F_{1,1} \end{bmatrix} & a_{2,2} \cdot \begin{bmatrix} M_{2,2} & F_{2,2} \end{bmatrix} & \dots & a_{2,j} \cdot \begin{bmatrix} M_{2,j} & F_{2,j} \end{bmatrix} \\
\vdots & \vdots & \vdots & \vdots \\
a_{i,1} \cdot \begin{bmatrix} M_{i,1} & F_{i,1} \end{bmatrix} & a_{i,2} \cdot \begin{bmatrix} M_{i,2} & F_{i,2} \end{bmatrix} & \dots & a_{i,j} \cdot \begin{bmatrix} M_{i,j} & F_{i,j} \end{bmatrix}
\end{bmatrix} = A_{scaled}
\end{array}$$

and the neat thing is now that we can get fitness functions straight out of A_{scaled} by summing over parts of specific rows and columns. For example, the total expected fitness of a male using the ith strategy, hereby denoted $W(i)$, is

$$W(i) = \sum_{k=1}^{j} a_{i,k} \cdot M_{i,k}$$

and analgously, the total expected fitness of a females using the jth strategy can be obtained of summing over the second entry of the relevant column of A_{scaled} (rather than row)

$$W(j) = \sum_{k=1}^{i} a_{k,j} \cdot F_{k,j}$$

Frequency dependence should occur because W is also a function of a, and values of a will depend on the proportion of players using different strategies. If we assume that fitness is proportional to reproductive success, the values of W and a would feedback on each other in evolutionary time and create an evolutionary game. For example, we could assume that the frequency of , say, the ith male strategy increases in frequency in the next generation if $W(i) > \overline{W}$, that is, if it confers a higher fitness than the mean fitness of males.

Notice, that if the ith male strategy is being played more often $a_{i,j}$ would increase (for all values of j). That way, the frequency of different strategies will influence how often their pay-off are realized. Formal definition of how W and a interact shouldn't be hard to get a handle of, but I will stop here for now.

Back to reality:

Let's get back to reality - or at least closer to it :-). What happens when we apply this to the P. mirabilis system using the data that we already have in the manuscript? First step is the construction of a pay-off matrix. We might assume that males have the three tactics of the manuscript. no gift, worthless gift and genuine gift (GG, WG, NG). Let's say females have three options as well: accept all males (AA), reject males unless they have a gift (RM) or canibalize all males expect when they use the gg tactic (CM):

$$
\begin{array}{c|cccc|}
 & & & \textbf{\textit{Female}} & \\
 & & AA & RM & CM \\
 & GG & \begin{bmatrix} M_{1,1} & F_{1,1} \end{bmatrix} & \begin{bmatrix} M_{1,2} & F_{1,2} \end{bmatrix} & \begin{bmatrix} M_{1,3} & F_{1,3} \end{bmatrix} \\
Male & WG & \begin{bmatrix} M_{1,2} & F_{1,2} \end{bmatrix} & \begin{bmatrix} M_{2,2} & F_{2,2} \end{bmatrix} & \begin{bmatrix} M_{2,3} & F_{2,3} \end{bmatrix} \\
 & NG & \begin{bmatrix} M_{1,3} & F_{1,3} \end{bmatrix} & \begin{bmatrix} M_{3,2} & F_{3,2} \end{bmatrix} & \begin{bmatrix} M_{3,3} & F_{3,3} \end{bmatrix}
\end{array} = A
$$

If, for the sake of example, all tactic were used equally often, we would get $a_{i,j} = \left(\frac{1}{3}\right)^2 \; \forall\, i,j \in \mathbb{N}$

$$
\begin{array}{c|cccc|}
 & & & \textbf{\textit{Female}} & \\
 & & AA & RM & CM \\
 & GG & \frac{1}{9}\cdot\begin{bmatrix} M_{1,1} & F_{1,1} \end{bmatrix} & \frac{1}{9}\cdot\begin{bmatrix} M_{1,2} & F_{1,2} \end{bmatrix} & \frac{1}{9}\cdot\begin{bmatrix} M_{1,3} & F_{1,3} \end{bmatrix} \\
\textbf{\textit{Male}} & WG & \frac{1}{9}\cdot\begin{bmatrix} M_{1,2} & F_{1,2} \end{bmatrix} & \frac{1}{9}\cdot\begin{bmatrix} M_{2,2} & F_{2,2} \end{bmatrix} & \frac{1}{9}\cdot\begin{bmatrix} M_{2,3} & F_{2,3} \end{bmatrix} \\
 & NG & \frac{1}{9}\cdot\begin{bmatrix} M_{1,3} & F_{1,3} \end{bmatrix} & \frac{1}{9}\cdot\begin{bmatrix} M_{3,2} & F_{3,2} \end{bmatrix} & \frac{1}{9}\cdot\begin{bmatrix} M_{3,3} & F_{3,3} \end{bmatrix}
\end{array} = A_{scaled}
$$

And if, like the manuscript we use male reproductive succes as a proxy for male fitness (see Table 3 of manuscript), we can fill in some entries of the pay-off matrix. For example,

$$
\begin{array}{c|cccc|}
 & & & \textbf{\textit{Female}} & \\
 & & AA & RM & CM \\
 & GG & \frac{1}{9}\cdot\begin{bmatrix} (0.58 - N) & (\mathrm{N}+\mathrm{C}) \end{bmatrix} & \frac{1}{9}\cdot\begin{bmatrix} (0.58 - N) & (N+C) \end{bmatrix} & \frac{1}{9}\cdot\begin{bmatrix} (0.58 - N) & (N+C) \end{bmatrix} \\
\textbf{\textit{Male}} & WG & \frac{1}{9}\cdot\begin{bmatrix} 0.52 & C \end{bmatrix} & \frac{1}{9}\cdot\begin{bmatrix} 0.52 & \mathrm{C} \end{bmatrix} & \frac{1}{9}\cdot\begin{bmatrix} \text{-X} & \mathrm{N}-\mathrm{C} \end{bmatrix} \\
 & NG & \frac{1}{9}\cdot\begin{bmatrix} 0.47 & \mathrm{C} \end{bmatrix} & \frac{1}{9}\cdot\begin{bmatrix} 0 & -C \end{bmatrix} & \frac{1}{9}\cdot\begin{bmatrix} \text{-X} & \mathrm{N}-\mathrm{C} \end{bmatrix}
\end{array}
$$

$$= A_{scaled}$$

where N could represent the nutritional value of a meal (nuptial gift or canibalized male), C could represent the cost or benefit which the female earns by corpulating an securing sperm to fertilize eggs, and X could represent the male oppotunity cost of being canibalized. Such definitions would allow us to determine the fitness of, for example, the NG tactic:

$$W(NG) = \sum_{k=1}^{3} a_{3,k} \cdot M_{3,k} = \frac{1}{9} \cdot 0.47 + \frac{1}{9} \cdot 0 - \frac{1}{9} \cdot X = \frac{1}{9} \cdot (0.47 - X)$$

and comparing $W(NG)$ to $W(WG)$ and $W(GG)$ would allow us to see what tactic selection would favour and thus which males tactic would increase in frequency. This would change the scaling coefficients ($a_{i,j}$) and change the selection pressure acting on females, which in turn would feedback on the selection pressures acting on males, and so on until some equilibrium is reached.

As far as I can see, this approach should also be alright despite the fact that the no gift, worthless gift and genuine gift strategies and not actually distinct strategies, but components (tactics) of some mixed strategies (the same is very likely true of all females strategies). Thus, in the context of this model, statements like "selection favours the GG tactic, so it will increase in frequency" should not be taken to mean that an increasing number of males, who only use GG, will appear. Rather, it should be understood as "selection favours the GG tactic, so any genetic variation which will influnce males to, as part of their mixed strategy, adopt the GG tatic more often, will increase in frequency". In fact, the matrix notation given above works even if we assume that all male (or all females for that matter) use a mixed strategy composed of the same tactics. All we need to postulate for the evolutionary game is variation in the frequency with which these tactics are used.