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A “Battle of the Sexes” with Pair Formation

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I extend Dawkins’ *Battle of the Sexes* by introducing a population with mating structure. Previous models of the battle of the sexes specify a dynamic system on the basis of the payoff matrices of the evolutionary population-game. Here I model the sex war by expressing the costs of raising offspring and performing a prolonged courtship in terms of a time delay during which individuals cannot mate anew. Only after the delay has occurred, an individual (and its offspring) appears on the mating market again. This gives rise to a pair-formation submodel, and a system of delay-differential equations describing the dynamics of the game. The dynamics of this model are qualitatively different from those of the ‘homogeneous’ models of the battle of the sexes. Evolutionary predictions of a game-theoretical model, in which the costs and benefits of a strategy are summarized by a single entry in a payoff matrix, may be quite different from a model that explicitly considers the mechanisms controlling mating in a structured population.

Introduction and historical background

The term “Battle of the Sexes” was introduced by Richard Dawkins in *The Selfish Gene* (1976). Currently, the phrase refers to a specific conflict described in his book: an evolutionary game between males and females about the costs of raising offspring. The conflict is rooted in Trivers’ (1972) theory of parental investment and sexual selection, and has the following rationale.

In many species, raising offspring requires a considerable investment by the parents. One parent may find it tempting to reduce its investment, at the expense of the other. Often one of the sexes, typically the female, makes a larger investment in the offspring. The male is then not as committed to the children as the female and is tempted to desert shortly after the mating, leaving the female with the task of raising the offspring. A female could prevent this by choosing a faithful partner, perhaps testing his fidelity by insisting on a long engagement period.

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Dawkins used the following caricature of the possible types of behavioral strategies to help analyze this conflict. Males can be either (1) *helping* or (2) *non-helping*, and females can be (1) *choosy* or (2) *non-choosy*. (Actually, Dawkins and many others used the terms “philanderous” or “faithful” for males, and “coy” or “fast” for females.) Choosy females insist that their partner performs a prolonged courtship before mating; non-choosy females do not. Helping males help the female in raising the offspring, and they court if the (choosy) female insists; non-helping males do not court, and leave immediately after conception. As a result, choosy females do not mate with non-helping males.

Dawkins constructed a game-theory model of this scenario (*sensu* Maynard Smith & Price 1973), assigning fixed numerical values to the various costs and benefits. These can be represented by different payoff matrices for males and females. An *asymmetrical conflict* (Maynard Smith 1982) corresponds to the *bimatrix games* of classical game theory; there are two separate populations, males and females, with different strategy sets and payoff functions.

Dawkins’ analysis leads to a totally mixed equilibrium of the game, at which all types of players are present and it does not pay any player to deviate from the equilibrium strategy. He claimed that this is an *evolutionarily stable strategy* (ESS). Schuster & Sigmund (1981) refuted this on the grounds that it lacks certain stability properties. The male and female payoffs for a “rare mutant” strategy in a resident population at the Dawkins equilibrium are independent of the frequencies of the mutants. Hence, any mutant strategy is an alternative best reply to the mixed equilibrium, which therefore satisfies the first (Nash equilibrium) condition of the definition of an ESS (see Maynard Smith 1982). But if the mutant males and females are either more faithful and more choosy or less faithful and less choosy, then the mutants fare better against themselves than do the residents against the mutants. Hence, the mixed equilibrium point does not satisfy the second condition for an ESS. Selten (1980) has shown that for asymmetrical games in general, only pure strategies can be ESS’s. The battle of the sexes is sometimes referred to as one of the most simple biological games without an ESS (Maynard Smith & Hofbauer 1987).

Dynamic models

Another way to illustrate the instability of the mixed equilibrium is from the point of view of a dynamic system. Because the payoffs for the male strategies depend only on the state of the female population, and the payoffs of the female strategies depend only on the male population, there is no penalty for a one-sided deviation from the equilibrium frequencies. If a fluctuation increases the proportion of helping males, the payoff for each male strategy stays the same. But in this situation, it pays the females to become less choosy; then, non-helping males are at an advantage. But if the frequency of non-helping males is high, choosy females fare better; with a lot of choosy females around, helping males increase, and we are back at the beginning. However, there is no guarantee of a return to equilibrium, and there is a tendency to oscillatory behavior, for which the static game-theory approach is not sufficient.

Taylor & Jonker (1978) introduced a class of ordinary differential equations, known as *game-dynamic equations*, to model the dynamics of games. They assumed that the rate of increase of each type of player is equal to the difference between its expected payoff and the average payoff. For the battle of

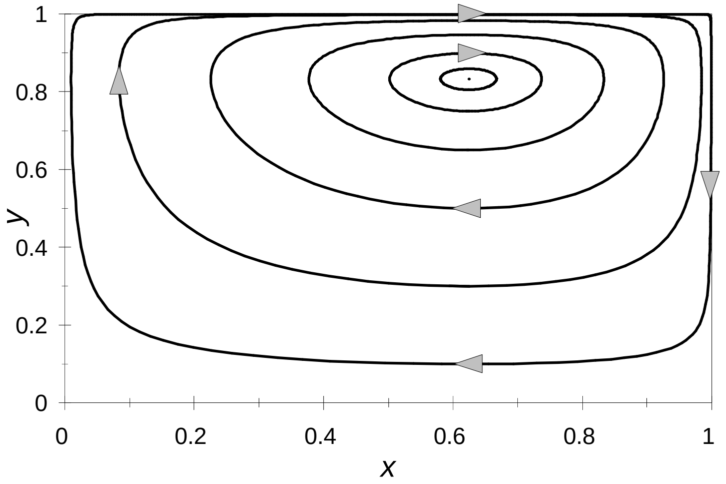

FIGURE 1: Phase portrait of the system from Schuster & Sigmund (1981). The fraction of helping males, x, is plotted on the abscissa, and the fraction of choosy females, y, on the ordinate.

the sexes, using Dawkins' (1976) payoff matrices, Schuster & Sigmund (1981) derived corresponding dynamic equations. The solutions of these are neutrally stable oscillations around the Nash equilibrium, which is the time average of all these orbits (see Fig. 1). This behavior is similar to that of models of predator–prey dynamics of Lotka–Volterra type.

Especially for games without an ESS, small modifications of the underlying dynamics can change the qualitative behavior considerably. With somewhat different equations in continuous time, the system converges to an asymptotically stable equilibrium (Maynard Smith 1982; Hofbauer & Sigmund 1988). With discrete-time game dynamics, however, the equilibrium is always unstable (Eshel & Akin 1983), in agreement with Maynard Smith's (1982) remark that any time delay destabilizes the equilibrium solution.

Note also that in the game-dynamic equations, just as in the static game-theory approach of Dawkins, "like begets like": male offspring inherit the strategy of the father, and female offspring inherit the strategy of the mother. All these models assume asexual reproduction, an awkward assumption for a biological war between the sexes. Incorporating diploid sexual inheritance in the Schuster–Sigmund model (Bomze *et al.* 1983) still gives rise to periodic oscillations. Converting the game dynamics for the diploid model from continuous time (Bomze *et al.* 1983) to discrete time (Maynard Smith & Hofbauer 1987) changes the qualitative behavior from neutrally stable oscillations to an unstable equilibrium surrounded by a limit cycle (see also Maynard Smith 1982, appendix J).

A model with pair formation

One of the (often implicit) assumptions in game-theory models is that all consequences of the behavioral strategies can be expressed in the payoffs. The fitness gain for an individual playing a certain strategy is then equal to the expected payoff for playing that strategy in the population. In many cases this assumption is questionable. Our modification of the sex-war game expresses the costs of raising offspring and performing courtship by means of a time delay for the corresponding individuals in a pair-formation model. We stay close to the model of Schuster & Sigmund (1981), the first and simplest dynamic version of the game.

Formulation of the model

Suppose that raising offspring takes τ_{r} time units, and performing courtship plus raising offspring takes τ_{cr} time units ($0 < \tau_{\mathrm{r}} \le \tau_{\mathrm{cr}}$). The time needed for raising offspring does not depend on whether the male helps the female. We assume that when the female does the raising by herself, she produces κ_1 male offspring and also κ_1 female offspring, whereas when the male helps her, κ_2 offspring of each sex are produced ($0 < \kappa_1 \le \kappa_2$). The difference between κ_1 and κ_2 is not in the original game (Dawkins 1976) and its descendants, but it is a natural extension.

Define $u_i(t)$ and $v_j(t)$ to be the densities at time t of unmated males and females following strategies i and j, respectively. The density of all unmated males is $u(t)$, where $u(t) := u_1(t) + u_2(t)$, and the density of all free females is $v(t)$, where $v(t) := v_1(t) + v_2(t)$. Furthermore, $w_{ij}(t,\tau)\,d\tau$ is either the density of type-i males mated with type-j females during a time interval of length $d\tau$ around τ time units before time t, or the density of (the same) type-j females mated with (the same) type-i males. Notice that, for $(i,j) = (1,1)$, $0 < \tau < \tau_{\mathrm{cr}}$, and for $(i,j) \in \{(1,2),(2,2)\}$, $0 < \tau < \tau_{\mathrm{r}}$. Additionally, $w_{22}(t,\tau)$ denotes only the density of type-2 females mated with type-2 males because these males are always free.

We assume that mating between a type-i male and a type-j female occurs at a rate $m_{ij} = \alpha_{ij}\, u_i v_j/(u+v)$. Here, α_{ij} is a mating rate constant, equal to zero for a non-helping/choosy mating and positive for all other combinations. For all but the non-helping/choosy mating,

$$m_{ij}(t) \;:=\; \alpha\,\frac{u_i(t)\,v_j(t)}{u(t)+v(t)}\,, \qquad ij \in \{11,12,22\}\,. \tag{1}$$

It is only after raising the offspring that the individuals are free to mate again, along with the offspring.

For example, at time t, free males of type 1 disappear at a rate $m_{11}(t)$ by mating with females of type 1; free males reappear at a rate $w_{11}(t,\tau_{\mathrm{cr}})$ following matings of this type that occurred at time $t - \tau_{\mathrm{cr}}$. Assuming that “like begets like” and that individuals are mature immediately after raising, we can account for the male type-1 offspring by multiplying $w_{11}(t,\tau_{\mathrm{cr}})$ by $(1+\kappa_2)$.

Assuming a constant mortality rate μ, the following partial differential equations describe the densities of mated individuals:

$$\begin{aligned}
\frac{\partial w_{11}(t,\tau)}{\partial t} &= -\frac{\partial w_{11}(t,\tau)}{\partial \tau} - \mu\, w_{11}(t,\tau)\,, && 0 < \tau < \tau_{\mathrm{cr}}\\
\frac{\partial w_{12}(t,\tau)}{\partial t} &= -\frac{\partial w_{12}(t,\tau)}{\partial \tau} - \mu\, w_{12}(t,\tau)\,, && 0 < \tau < \tau_{\mathrm{r}}\\
\frac{\partial w_{22}(t,\tau)}{\partial t} &= -\frac{\partial w_{22}(t,\tau)}{\partial \tau} - \mu\, w_{22}(t,\tau)\,, && 0 < \tau < \tau_{\mathrm{r}}\,,
\end{aligned} \tag{2}$$

with the side conditions that

$$w_{ij}(t,0) \;=\; m_{ij}(t)\,, \qquad ij \in \{11,12,22\}\,. \tag{3}$$

Considering all possible combinations of matings, together with reproduction and mortality, the following system of ordinary differential equations describes the densities of free individuals:

$$\begin{aligned}
\frac{du_1(t)}{dt} &= -\,m_{11}(t) + (1+\kappa_2)\,w_{11}(t,\tau_{\mathrm{cr}}) \\
&\quad -\,m_{12}(t) + (1+\kappa_2)\,w_{12}(t,\tau_{\mathrm{r}}) \;-\mu\,u_1(t) \\
\frac{du_2(t)}{dt} &= \kappa_1\,w_{22}(t,\tau_{\mathrm{r}}) \qquad\qquad -\mu\,u_2(t) \\
\frac{dv_1(t)}{dt} &= -\,m_{11}(t) + (1+\kappa_2)\,w_{11}(t,\tau_{\mathrm{cr}}) - \mu\,v_1(t) \\
\frac{dv_2(t)}{dt} &= -\,m_{12}(t) + (1+\kappa_2)\,w_{12}(t,\tau_{\mathrm{r}}) \\
&\quad -\,m_{22}(t) + (1+\kappa_1)\,w_{22}(t,\tau_{\mathrm{r}}) \;-\mu\,v_2(t)\,.
\end{aligned} \tag{4}$$

The fractions of helping males and choosy females in the population at time t, $x(t)$ and $y(t)$ respectively, are

$$x(t) \;=\; \frac{u_1(t) + W_{11}(t) + W_{12}(t)}{M(t)} \qquad \text{and} \qquad y(t) \;=\; \frac{v_1(t) + W_{11}(t)}{F(t)}\,, \tag{5}$$

where the densities of mated individuals, either males or females (except W_{22}, which represents only females) at time t, are

$$W_{ij}(t) \;:=\; \int_0^{\tau_\star} w_{ij}(t,\tau)\,d\tau\,, \qquad ij \in \{11,12,22\} \tag{6}$$

— here and below, $\tau_\star = \tau_{\mathrm{cr}}$ if $(ij) = (11)$ and $\tau_\star = \tau_{\mathrm{r}}$ if $(ij) \in \{(12),(22)\}$ — and the total densities of males and females, respectively, are

$$\begin{aligned}
M(t) &:= u_1(t) + u_2(t) + W_{11}(t) + W_{12}(t) \\
F(t) &:= v_1(t) + v_2(t) + W_{11}(t) + W_{12}(t) + W_{22}(t)\,.
\end{aligned} \tag{7}$$

The appendix shows how the manifold on which male and female densities are equal is invariant and attracting. Thus, if the total densities of males and females are initially equal, they will remain equal. Finally, notice that there is no density dependence in the model; in the long run the values of the parameters (notably α and μ) produce an exponentially growing or an exponentially decaying population.

An equivalent model with delay-differential equations

We can easily convert the system of equations (2)–(4) into an equivalent system of delay-differential equations. Defining

$$\begin{aligned}
u_{1\mathrm{w}}(t) &:= W_{11}(t) + W_{12}(t) \\
v_{1\mathrm{w}}(t) &:= W_{11}(t) \\
v_{2\mathrm{w}}(t) &:= W_{12}(t) + W_{22}(t)\,,
\end{aligned} \tag{8}$$

for mated individuals of type-1 males and for type-1 and type-2 females, respectively, and adding these three variables to equations (4), we obtain

$$\begin{aligned}
\frac{du_1(t)}{dt} &= -m_{11}(t) + (1+\kappa_2)\,n_{11}(t,\tau_{\mathrm{cr}}) \\
&\quad\; -m_{12}(t) + (1+\kappa_2)\,n_{12}(t,\tau_{\mathrm{r}}) \qquad\qquad -\mu\,u_1(t) \\
\frac{du_2(t)}{dt} &= \kappa_1\,n_{22}(t,\tau_{\mathrm{r}}) \qquad\qquad\qquad\qquad\qquad\quad\; -\mu\,u_2(t) \\
\frac{dv_1(t)}{dt} &= -m_{11}(t) + (1+\kappa_2)\,n_{11}(t,\tau_{\mathrm{cr}}) \qquad\qquad -\mu\,v_1(t) \\
\frac{dv_2(t)}{dt} &= -m_{12}(t) + (1+\kappa_2)\,n_{12}(t,\tau_{\mathrm{r}}) \\
&\quad\; -m_{22}(t) + (1+\kappa_1)\,n_{22}(t,\tau_{\mathrm{r}}) \qquad\qquad -\mu\,v_2(t) \\
\frac{du_{1\mathrm{w}}(t)}{dt} &= m_{11}(t) - n_{11}(t,\tau_{\mathrm{cr}}) + m_{12}(t) - n_{12}(t,\tau_{\mathrm{r}}) - \mu\,u_{1\mathrm{w}}(t) \\
\frac{dv_{1\mathrm{w}}(t)}{dt} &= m_{11}(t) - n_{11}(t,\tau_{\mathrm{cr}}) \qquad\qquad\qquad\qquad -\mu\,v_{1\mathrm{w}}(t) \\
\frac{dv_{2\mathrm{w}}(t)}{dt} &= m_{12}(t) - n_{12}(t,\tau_{\mathrm{r}}) + m_{22}(t) - n_{22}(t,\tau_{\mathrm{r}}) \;\; -\mu\,v_{2\mathrm{w}}(t)\,,
\end{aligned} \tag{9}$$

where

$$n_{ij}(t,\tau_\star) \;:=\; m_{ij}(t-\tau_\star)\,e^{-\mu\tau_\star} \tag{10}$$

is the mating rate between type-i males and type-j females at time $t-\tau_\star$, multiplied by the survival probability over the time interval $(t-\tau_\star, t)$.

We can integrate this system of seven delay-differential equations numerically using the Solver program (Blythe *et al.* 1990[a]). The three mating rates $m_{ij}(t)$ are stored as *history variables* (Blythe *et al.* 1990[b]) in the Solver equations. Initial conditions of the system are set by entering (x_0, y_0) and the total population size. The distribution over free and mated individuals at and before $t = 0$ is calculated by assuming that 99 percent of the individuals are mated. Total numbers of males and females are equal. Unless stated otherwise, $\alpha = 1$ and $\mu = 0.1$.

Notice that the time-delayed system (9) cannot keep track of the types of the partners of the mated individuals. From the definitions (8) there is sufficient information to calculate x and y using equations (5). With respect to x and y the systems (2)–(4) and (9) are equivalent, as long as the initial conditions are equivalent.

Results

In this section we discuss the qualitative behavior of the model in (x, y)-space, as we are interested mainly in the dynamics of the frequencies of the male and female behavioral strategies.

At the corners of $\Sigma^2 := \{(x,y) \mid 0 \le x, y \le 1\}$ are always four trivial equilibria, where the variables x or y are equal to 0 or 1. It is laborious but straightforward to show analytically that on the boundary of Σ^2 the following holds. If $x = 0$, then $\dot{y} < 0$. For $x = 1$, $\dot{y} < 0$ if $\tau_{\mathrm{cr}} > \tau_{\mathrm{r}}$, and $\dot{y} = 0$ if $\tau_{\mathrm{cr}} = \tau_{\mathrm{r}}$. If $y = 1$, then $\dot{x} > 0$. On the border $y = 0$ and in the interior, the situation is more complicated. From here on we discuss the qualitative behavior of x and y as it appears from numerical simulations of the model with delay-differential equations (9).

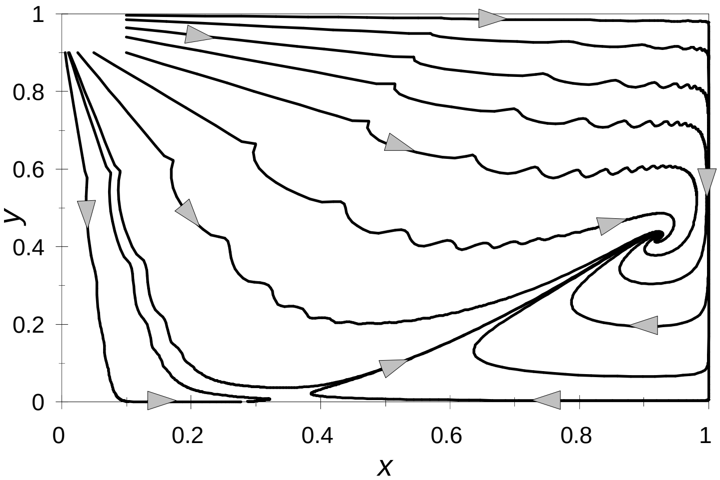

FIGURE 2: Phase portrait of system (9), with $(\tau_r, \tau_{cr}) = (10, 10.5)$ and $(\kappa_1, \kappa_2) = (1, 2)$. Again, x is the fraction of helping males, and y is the fraction of choosy females in the population. For explanation, see the text.

The simulations show that the system can have at least two non-trivial equilibria. We employ, as typical, the parameter values $(\tau_r, \tau_{cr}) = (10, 10.5)$ and $(\kappa_1, \kappa_2) = (1, 2)$. Figure 2 shows that on the border $y = 0$ is an asymptotically stable equilibrium at $(x, y) \approx (0.28, 0)$, connected through the 'unstable manifold' of an interior 'saddle point' at $(0.34, 0.01)$ with a (totally mixed) stable interior equilibrium at $(0.92, 0.42)$. All trajectories in this figure started in the upper left corner. The irregular shape of the orbits is due to imperfect initialization of the system.

Note that the dynamic systems (2)–(4) and (9) have infinite dimensions. Here, the dynamics of x and y are a two-dimensional projection of these systems, which strictly speaking rules out discussion of saddle points, stable and unstable manifolds, separatrices, etc. Nevertheless, it is convenient to continue to do so. But the fact that the behavior in (x, y)-space is reminiscent of a two-dimensional system suggests that this system can be simplified considerably.

The stable manifold of the saddle separates the basins of attraction of the interior and the boundary equilibrium. The basin of attraction of the interior equilibrium lies inside the interior of Σ^2 and is surrounded by that of the boundary equilibrium, except that they both touch the corner $(x, y) = (0, 1)$. The interior basin of attraction almost touches the boundary $x = 1$, where the boundary basin is extremely narrow. The system can make large excursions through (x, y)-space before settling down. An example is the uppermost curve in Fig. 2, which starts at $(0.1, 0.997)$ and converges to the interior equilibrium. Trajectories starting with y even closer to 1 follow approximately the same route, but on the boundary side of the stable manifold of the saddle, finally converging to the boundary equilibrium.

The effect of varying the courtship period $(\tau_{cr} - \tau_r)$ is shown in Fig. 3. Again, all trajectories start in the upper left corner, except for some curves in panel A, where the courtship period is zero. For a very short courtship period, the proportion of helping males in the interior equilibrium is almost 1 (see panel B). Convergence to the interior equilibrium is, in this case, oscillatory: curves re-

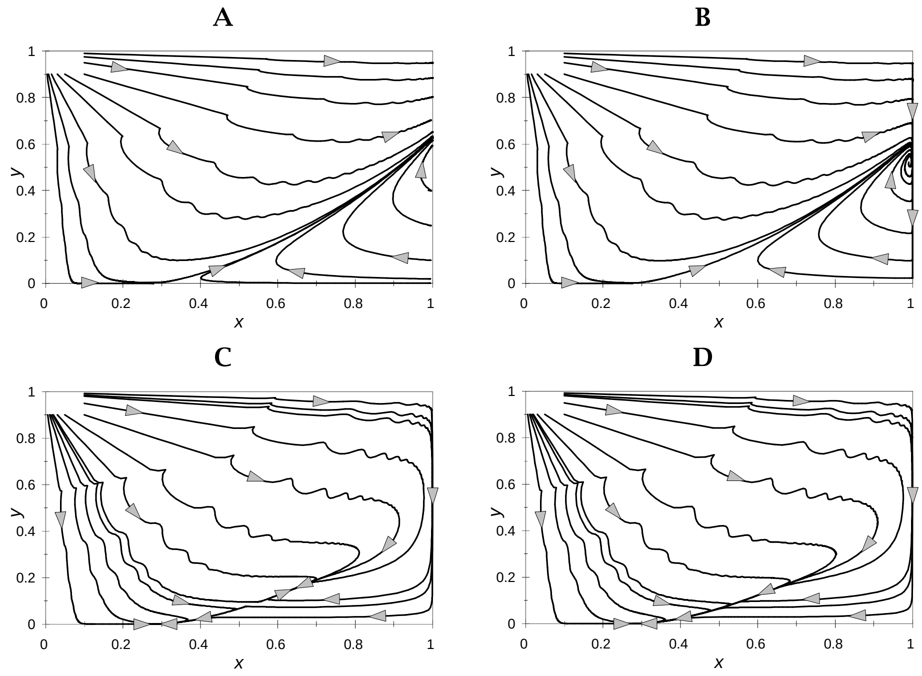

FIGURE 3: Phase portraits of system (9), with varying courtship durations and $\tau_r = 10$, and $(\kappa_1, \kappa_2) = (1, 2)$. The courtship duration is (**A**) zero: $\tau_{cr} = 10$; (**B**) very short: $\tau_{cr} = 10.05$; (**C**) long: $\tau_{cr} = 11.2$; (**D**) slightly longer: $\tau_{cr} = 11.25$. Again, x is the fraction of helping males, and y is the fraction of choosy females in the population.

peatedly pass extremely close to the boundary $x = 1$ while approaching the equilibrium. When $\tau_r = \tau_{cr}$ (no courtship: panel A), the interior equilibrium is absorbed by the boundary $x = 1$, which turns into a line of equilibria. Above $y \approx 0.52$, the boundary is attracting in the x-direction; below this value it is repelling. Non-helping males are able to invade if the proportion of choosy females is smaller than 0.52, but after an initial increase they decrease in frequency again because of the number of choosy females increases. The system settles on a boundary point with only helping males, but with a higher proportion of choosy females than before; from there non-helping males are not able to invade again.

Increasing the courtship period (panels B and C) decreases the frequencies of helping males and choosy females in the interior equilibrium, and the basin of attraction for the interior equilibrium shrinks until the equilibrium hits the saddle point and the two disappear near $\tau_{cr} \approx 11.22$. For higher τ_{cr} values, the boundary equilibrium is the only non-trivial one, and all trajectories from the interior of Σ^2 converge to it (panel D).

The effect of a decrease in τ_r is similar to an increase in τ_{cr}, except that the boundary equilibrium moves to higher x values, whereas its location is independent of τ_{cr}. At $\tau_r = \tau_{cr} = 10.5$, the boundary equilibrium is located about where $x \approx 0.26$. At $\tau_r \approx 9.42$ the interior equilibrium and the saddle annihilate each other and only the boundary equilibrium remains. With a decrease in τ_r, the boundary equilibrium moves to the right until it coincides with $(1, 0)$ at $\tau_r \approx 2.8$.

Varying κ_1 yields approximately the same scenario as varying τ_r, except that the location of the boundary equilibrium now spans the whole range of $0 \le x \le 1$. When $\kappa_1 \approx 1.08$ and higher, the boundary equilibrium is located at $(0, 0)$; when $\kappa_1 \approx 0.47$ and lower, at $(1, 0)$; and for κ_1 between these values, a non-trivial boundary equilibrium exists. Additionally, decreasing κ_1 lets the y value of the interior equilibrium drop (!), whereas its x value remains almost constant. Here, the disappearance of the interior equilibrium and the saddle point takes place at higher values of x. The interior equilibrium emerges again through a 'saddle–node bifurcation' where $\kappa_1 \approx 1.19$. When $\kappa_1 \approx 0.55$, the interior equilibrium and the saddle seem to annihilate each other at the boundary equilibrium, which remains. Varying κ_2 amounts to the same thing as varying κ_1; it is the difference between the two that counts.

Choosy females can persist (and an interior equilibrium point exists) if the advantage of both parents' raising the offspring together is neither too small nor too large and the length of the courtship period is not too large relative to the time needed for raising the offspring. The window of $\tau_\star$ values for a totally mixed equilibrium point to exist is wider for intermediate differences between κ_1 and κ_2, and *vice versa*. Outside this cone of values for τ_r, τ_{cr}, κ_1 and κ_2 the population consists of exclusively non-choosy females. Even then, there can be a stable polymorphism in male strategies, depending on the exact parameter values.

Discussion

An important difference between the game-dynamic model and the present models is seen in the behavior which arises when there are only non-helping males around (at $x = 0$). In this case, choosy females do not mate, and they cannot reproduce. Without reproduction, their density must decrease at the mortality rate μ. Non-choosy females have positive growth terms because of matings with non-helping males. Consequently, the proportion of choosy females decreases. In the game-dynamic model, however, the joint representation of reproduction and parental investment in one payoff value gives the choosy females a zero growth rate and the non-choosy females a negative growth rate. This causes the proportion of choosy females to increase (and, if modeled, the total population size to decrease).

Another interesting difference is the existence of the boundary equilibrium (at $y = 0$). In a population of only non-choosy females, helping and non-helping males can coexist because of the difference in their reproductive outputs. This is not true in the game-dynamic models. Helping males can invade a non-helping population if they raise sufficiently more offspring by helping the females, and non-helping males can invade a helping population provided that the reproductive advantage for helping males is not too large and the period needed for raising the offspring is sufficiently long. This observation shows that the raising period assists the helping males to keep females out of the mating market and unable to mate with non-helping males.

The local behavior near the interior equilibrium point resembles the global behavior of the game-dynamic model more closely: clockwise convergence and oscillations. Both can be explained by the argument given in the section “Dynamic Models”, clarifying the lack of stability of the mixed-equilibrium point: with more helping males around, non-choosy females do better; with more non-choosy females, non-helping males are at an advantage, and so on.

If there is an interior equilibrium for the mating-delay models, it is a stable one, weakening Maynard Smith’s (1982) claim, that any time delay is destabilizing. Without a gain in reproductive output for a helping male ($\kappa_1 < \kappa_2$), there is no interior equilibrium; apparently, this condition more than compensates for destabilization due to time delays.

There are difficulties in formulating a more mechanistic model of the game, while keeping the model close to the Schuster–Sigmund model. This form maintains a necessary equality between the rates of mating of males and females. However, the Schuster–Sigmund model involves only quadratic terms of the form $u_i v_j$. The form used here is convenient, but does not have a clear biological derivation; such a derivation would be a useful addition to dynamic models.

The densities acting as state variables in system (2)–(4) cannot simply be scaled to frequencies. In the work of Taylor & Jonker (1978), Schuster & Sigmund (1981), and Hofbauer & Sigmund (1988), such a scaling of the variables is equivalent to a change in time scale, and only the information about the total population size is lost. For our system with delays, the densities are necessary in the delay terms, while a change in time scale also affects the time delay.

In the model presented here, paired individuals die individually, together with their would-be offspring (see eqs. 2, 4). The widowed partner, provided it stays alive, continues to raise its offspring (possibly courting a dead body). More detailed ways of accounting for the mortality in pairs lead to more complicated equations, but the global behavior of the model remains unaltered.

A striking drawback of this model (and those of Schuster & Sigmund 1981; Maynard Smith 1982; and Eshel & Akin 1983) is that it discusses the dynamics of the battle of the sexes without taking sexual inheritance into account, thus implying that the organisms are haploid. An improvement would be to treat a diploid organism, for example, with two autosomal loci, one locus of which is expressed only in males and the other expressed only in females (as in Bomze *et al.* 1983 and Maynard Smith & Hofbauer 1987).

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Literature Cited

Blythe, S.P., W.S.C. Gurney, P. Maas & R.M. Nisbet. 1990^a. *Introduction & Installation Guide for* SOLVER *(Rev. 4)*. Applied Physics Industrial Consultants, University of Strathclyde, Glasgow, Scotland. 6

Blythe, S.P., W.S.C. Gurney, P. Maas & R.M. Nisbet. 1990^b. *Programming & Model Building Guide for* SOLVER *(Rev. 4)*. Applied Physics Industrial Consultants, University of Strathclyde, Glasgow, Scotland. 6

Bomze, I.M., P. Schuster & K. Sigmund. 1983. The role of Mendelian genetics in strategic models on animal behaviour. *J. theor. Biol.* 101, 19–38. 3, 11

Dawkins, R. 1976. *The Selfish Gene*. Oxford University Press, Oxford, U.K. 1, 3, 4

Eshel, I. & E. Akin. 1983. Coevolutionary instability of mixed Nash solutions. *J. Math. Biol.* 18, 123–133. 3, 10

Hofbauer, J. & K. Sigmund. 1988. *The Theory of Evolution and Dynamical Systems: Mathematical Aspects of Selection*, vol. 7 of *London Mathematical Society Student Texts*. Cambridge University Press, Cambridge, U.K. 3, 10

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge, U.K. 2, 3, 10

Maynard Smith, J. & J. Hofbauer. 1987. The "Battle of the Sexes": A genetic model with limit cycle behavior. *Theor. Popul. Biol.* 32, 1–14. 2, 3, 11

Maynard Smith, J. & G.R. Price. 1973. The logic of animal conflict. *Nature* 246, 15–18. 2

Schuster, P. & K. Sigmund. 1981. Coyness, philandering and stable strategies. *Anim. Behav.* 29, 186–192. 2, 3, 4, 10

Selten, R. 1980. A note on evolutionarily stable strategies in asymmetric animal conflicts. *J. theor. Biol.* 84, 93–101. 2

Taylor, P.D. & L.B. Jonker. 1978. Evolutionarily stable strategies and game dynamics. *Math. Biosci.* 40, 145–156. 2, 10

Trivers, R. 1972. Parental investment and sexual selection. pp. 136–179 *in* B. Campbell, ed., *Sexual Selection and the Descent of Man*. Aldine, Chicago, U.S.A. 1

Appendix

Male and female densities stay equal

The manifold on which male and female densities are equal is attracting, that is,

$$\lim_{t\to\infty} [M(t) - F(t)] \;=\; 0\,.$$

Using the definitions in (4) and (7), we have

$$\begin{aligned}\frac{d}{dt}[M(t) - F(t)] \;&=\; \frac{d}{dt}[u_1(t) + u_2(t) + W_{11}(t) + W_{12}(t)]\\ &\quad - \frac{d}{dt}[v_1(t) + v_2(t) + W_{11}(t) + W_{12}(t) + W_{22}(t)]\\ &=\; -\mu\,[u_1(t) + u_2(t)] + \mu\,[v_1(t) + v_2(t)]\\ &\quad + m_{22}(t) - w_{22}(t,\tau_{\mathrm{r}}) - \frac{d}{dt}W_{22}(t)\,.\end{aligned}$$

Because

$$\frac{d}{dt}W_{ij}(t) \;=\; -w_{ij}(t,\tau_\star) + m_{ij}(t) - \mu\,W_{ij}(t)\,,$$

this is equal to

$$-\mu\,[u_1(t) + u_2(t)] + \mu\,[v_1(t) + v_2(t)] + \mu\,W_{22}(t)\,.$$

Adding and subtracting $-\mu\,[W_{11}(t) + W_{12}(t)]$ leads to

$$\frac{d}{dt}[M(t) - F(t)] \;=\; -\mu\,[M(t) - F(t)]\,,$$

and, therefore,

$$M(t) - F(t) \;=\; [M(0) - F(0)]\,e^{-\mu t}\,.$$

This proves that the manifold of equal male and female densities is invariant and, furthermore, that after disturbance the system returns to this manifold. □