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What Pair Formation Can Do to the Battle of the Sexes: Towards More Realistic Game Dynamics

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In the various dynamic models of Dawkins' *Battle of the Sexes*, payoff matrices serve as the basic ingredients for the specification of a game-dynamic model. Here I model the sex war mechanistically, by expressing the costs of raising the offspring and performing a prolonged courtship via a time delay for the corresponding individuals, instead of via payoff matrices. During such a time delay an individual is not able to have new matings. Only after the delay has occurred, an individual (and its offspring) appears on the mating market again. From these assumptions I derive a pair-formation submodel, and a system of delay-differential equations describing the dynamics of the game. By a time-scale argument, I obtain an approximation of this system by means of a much simpler system of ordinary differential equations. Analysis of this simplified system shows that the model can give rise to two non-trivial asymptotically stable equilibrium points: an interior equilibrium where both female strategies and both male strategies are present, and a boundary equilibrium where only one of the female strategies and both male strategies are present. This behaviour is qualitatively different from that of models of the battle of the sexes formulated in the traditional framework of game-dynamic equations. In other words, the addition of a most elementary further assumption about individual life history fundamentally changes the model predictions. These results show that in analysing evolutionary games one should pay careful attention to the specific mechanisms involved in the conflict. In general, I advocate deriving simple models for evolutionary games, starting from more complex, mechanistic building blocks. The wide-spread method of modelling games at a high phenomenological level, through payoff matrices, can be misleading.

1. Introduction

One of the implicit assumptions in evolutionary game-theory models (Maynard Smith & Price, 1973; Maynard Smith, 1982), such as the *Battle of the Sexes*

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(Dawkins, 1976), is that the immediate fitness consequences of playing a certain strategy can be expressed in simple numbers: the *payoffs*. In other words, when a behavioural strategy (or life-history trait value) is played against another strategy, or a mixture of strategies, the expected fitness costs and benefits associated with that particular strategy in those particular circumstances can be calculated by summing up additive fitness contributions, yielding a fixed numerical value. The average overall fitness contribution to an individual playing a specific strategy in a population with a given strategy composition is then equal to the average of the payoffs of simple encounters.

In this paper, I will use Dawkins' sex war as a vehicle to argue that the assumption that the costs and benefits can be translated into simple additive payoff values is often questionable.

1.1. THE BATTLE OF THE SEXES

The term "Battle of the Sexes" was introduced into biology by Richard Dawkins in *The Selfish Gene* (1976). In biology, the phrase currently refers to a specific conflict described in his book: an evolutionary game between males and females about the costs of raising offspring. (Sociology and economics have their own versions of the game.) 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, cannot avoid making a larger investment in the offspring. Then the male is 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, and testing his fidelity by insisting on a long engagement period.

Dawkins used the following caricature of the possible types of behavioural strategies to help analyse this conflict. Males can be either *helpful* or *non-helpful*, and females can be *choosy* or *non-choosy*. (Actually, Dawkins and many authors after him used the terms "philanderous" and "faithful" for males, and "coy" and "fast" for females.) Choosy females insist that their partners perform a prolonged courtship before mating; non-choosy females do not. Helpful males help the female in raising the offspring, and they court if the (choosy) female insists; non-helpful males do not court, and leave immediately after conception. As a result, choosy females do not mate with non-helpful 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. He assumed that the beneficial value of a child is, say, a fitness units per parent, the total cost of raising the offspring is b, and the cost of wasting time by performing the prolonged courtship is c per parent, where the default values are $a = 15$, $b = 20$ and $c = 3$. Then the payoff in a helpful/choosy mating will be $a - (b/2) - c = 2$ for both parents, whereas in a helpful/non-choosy mating, the payoff will be $a - (b/2) = 5$, because they skip the courtship. From a non-helpful/non-choosy mating, the male will gain a fitness units, and the female will lose: $a - b = -5$. This game can be represented by the following pair of payoff matrices A and B, for males and females respectively:

$$\begin{aligned} A &:= \begin{pmatrix} a-b/2-c & a-b/2 \\ 0 & a \end{pmatrix} = \begin{pmatrix} 2 & 5 \\ 0 & 15 \end{pmatrix} \\ B &:= \begin{pmatrix} a-b/2-c & 0 \\ a-b/2 & a-b \end{pmatrix} = \begin{pmatrix} 2 & 0 \\ 5 & -5 \end{pmatrix}. \end{aligned} \tag{1}$$

This is an example of an *asymmetrical conflict* (Maynard Smith, 1982), and corresponds to the *bimatrix games* of classical game theory; there are two separate populations, males and females, with different strategy sets and payoff functions.

1.1.1. Static analysis

Writing x_1 for the frequency of helpful males in the population, x_2 $(= 1-x_1)$ for the frequency of non-helpful males, and y_1 and y_2 $(= 1-y_1)$, respectively for the frequencies of choosy and non-choosy females, I shall describe the state of the population by $(x, y) := (x_1, y_1)$, *i.e.* a point in the unit square $\Sigma^2 = \{(x, y) \in \mathbb{R}^2 \mid 0 \leq x, y \leq 1\}$. Then the expected payoff for a helpful male is $(a-b/2-c)\, y_1 + (a-b/2)\, y_2$ and for a non-helpful male $a\, y_2$. These payoffs are equal if, and only if, y is equal to $y^* := b/(2(a-c)) = 5/6$. The payoffs for the female strategies are equal if and only if $x = x^* := (a-b)/(a-b-c) = 5/8$. Consequently, (x^*, y^*) is a *totally mixed equilibrium point* of the game; all types of players are present and it does not pay for any player to deviate from the equilibrium strategy.

Dawkins claimed that this totally mixed equilibrium point 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 helpful and more choosy or less helpful 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. Therefore, the battle of the sexes is sometimes referred to as one of the most simple biological games without an ESS (Maynard Smith & Hofbauer, 1987).

1.1.2. Dynamic analysis

Another way to illustrate the instability of the mixed equilibrium is to formulate the model as 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 helpful males, the payoff for each male strategy stays the same. But in this situation it pays for the females to become less choosy, which in turn allows non-helpful males to be at an advantage. But if the frequency of non-helpful males is higher, choosy females fare better; with a lot of

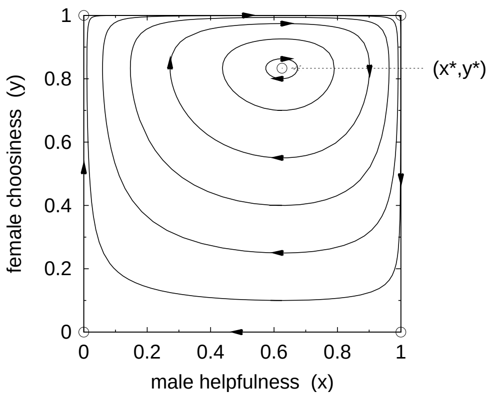

FIG. 1: Phase portrait of system (3), from Schuster & Sigmund (1981). Direction of flow is indicated with ▸ arrowheads and equilibrium points are marked with ⊙ symbols.

choosy females around, helpful 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 behaviour, 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 per capita rate of increase of each type of player, say $\dot{x}_i/x_i$ for the male type i, is equal to the difference between its expected payoff, $(A\mathbf{y})_i$, and the average payoff, *i.e.* the inner product $\mathbf{x}^{\mathrm{T}}A\mathbf{y}$, where $\mathbf{x}$ and $\mathbf{y}$ are the vectors of frequencies of male and female strategies, respectively. For an asymmetric conflict with two strategies for each type of player, this leads to the ordinary differential equation (ODE) system

$$\begin{aligned} \frac{dx_i}{dt} &= x_i\left((A\mathbf{y})_i - \mathbf{x}^{\mathrm{T}}A\mathbf{y}\right), \qquad & i \in \{1,2\} \\ \frac{dy_j}{dt} &= y_j\left((B\mathbf{x})_j - \mathbf{y}^{\mathrm{T}}B\mathbf{x}\right), \qquad & j \in \{1,2\} \end{aligned} \tag{2}$$

on the invariant space Σ^2. For the battle of the sexes Schuster & Sigmund (1981) analysed the equations

$$\begin{aligned} \frac{dx}{dt} &= x\,(1-x)\,(-10+12y) \\ \frac{dy}{dt} &= y\,(1-y)\,(5-8x)\,, \end{aligned} \tag{3}$$

derived by substituting Dawkins' matrices A and B from (1) into (2), where again x is the frequency of helpful males and y is the frequency of choosy females. The solutions of this ODE system are neutrally stable oscillations around the mixed equilibrium point (x^*, y^*), and this equilibrium point equals the time average of all these orbits (see Fig. 1). This behaviour 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 behaviour considerably. In continuous time the system can converge to an asymptotically stable equilibrium (Maynard Smith, 1982; Hofbauer & Sigmund, 1998). 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 destabilises 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, and this is of course hard to defend in the context of 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 behaviour from neutrally stable oscillations to an unstable equilibrium surrounded by a limit cycle (see also Maynard Smith, 1982, Appendix J).

So the different dynamic models for the battle of the sexes give rise to a variety of dynamics, always with an interior equilibrium, and often characterised by oscillatory behaviour.

2. A model with pair formation

The present modification of the sex-war game expresses the costs of raising offspring and performing a prolonged courtship by means of a time delay for the corresponding individuals, in a pair-formation submodel. During such a time delay courtship takes place and offspring is raised, and an individual is not able to have new matings. Only after the delay an individual appears on the mating market again, together with its offspring. A preliminary version of this pair-formation model can be found in Kumm *et al.* (1996).

First I will sketch, textually and graphically, the complete pair-formation model and the resulting dynamic system corresponding to the game. This translates directly into a delay-differential equation (DDE) system, given in Appendix A. (See also Nisbet 1996 for an overview of the use of DDE systems in biology.) This system is rather elaborate and complicated to analyse. Therefore I derive from the complete DDE system a much simpler ODE system. The derivation uses a time-scale argument and is given in Appendix B.

2.1. DESCRIPTION OF THE COMPLETE MECHANISTIC MODEL

Individuals can be free, paired or single parent. There are four types of free individuals: helpful and non-helpful males, and choosy and non-choosy females. Free individuals mix homogeneously, and the mating rate for a specific combination of male/female types is equal to the product of a mating rate constant α (with $\alpha > 0$) and the corresponding two densities, divided by the total density of free individuals. One justification for this choice is that it is the limiting case of a mechanistic model of the encounter process for large population densities, or for a large encounter rate constant; *cf.* Heesterbeek & Metz (1993). Other mechanisms than this homogeneous mixing case for modelling the mating rate are also possible, without changing the qualitative behaviour of the model.

Pairs are either courting (only in case of a helpful/choosy combination) or raising offspring. Because non-helpful males cannot mate with choosy females and do not help non-choosy females, there are three different types of pairs; courting helpful/choosy, raising helpful/choosy and (only raising) helping/non-choosy.

Suppose that performing courtship takes τ_c time units, and raising offspring takes τ_r time units ($0 < \tau_c$ and $0 < \tau_r$). The time needed for bringing up the offspring does not depend on the number of parents involved. I assume that when a 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 ($0 < \kappa_1 \leq \kappa_2$). 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. Male offspring inherits the strategy type of the father, and female offspring inherits the type of the mother: "like begets like". The offspring is mature and free immediately after weaning.

I assume a constant mortality rate μ for every individual, either free, paired or single parent. When one of the partners of a pair dies during the prolonged courtship, the former fiancé(e) returns to the free state, and no offspring is produced. When one of the partners dies during the raising of offspring, however, the widow(er) continues as single parent. He or she then produces an amount of offspring between κ_1 and κ_2: the longer the late partner was able to help, the closer the amount of offspring is to κ_2 (see Appendix A for details). When the second (single) parent also dies, no offspring is produced. Consequently, there are five types of single parents: widows and widowers from helpful/choosy and helpful/non-choosy matings, respectively, and non-choosy females impregnated by non-helpful males.

The different types of individuals, their states and the transitions between them are summarised in Fig. 2. Dashed curves indicate transitions of an individual when its partner dies (at time τ or τ'). At the column of dotted circles on the right, individuals and their offspring enter the free state. This column is equal to the column of solid circles on the left; it has been drawn twice for reasons of clarity. For the same reason the removal of dead individuals and the different offspring numbers κ_1 and κ_2 have not been indicated. The DDE system corresponding to this flow diagram is given in Appendix A: equations (A.10)–(A.12).

A typical phase portrait projected in (x, y)-space, obtained from numerical simulations of system (A.10)–(A.12), is shown in Fig. 3. I will explain this phase portrait in the next section.

2.2. DESCRIPTION OF THE SIMPLIFIED MODEL

Although the DDE model (A.10)–(A.12) is an infinite-dimensional dynamic system, its projection on the (x, y)-plane for the parameter values used in Fig. 3 behaves very much like a two-dimensional system. This observation indicates that the system can be simplified considerably. This can be done by assuming that the time-scale of pair formation and dissociation is short as compared to the life span of the individuals, *i.e.* by assuming that α is large, and that τ_c, τ_r, κ_1 and κ_2 are small. (See the mathematical formulation and the derivation in Appendix B.) Under this assumption the steady-state distribution of mated

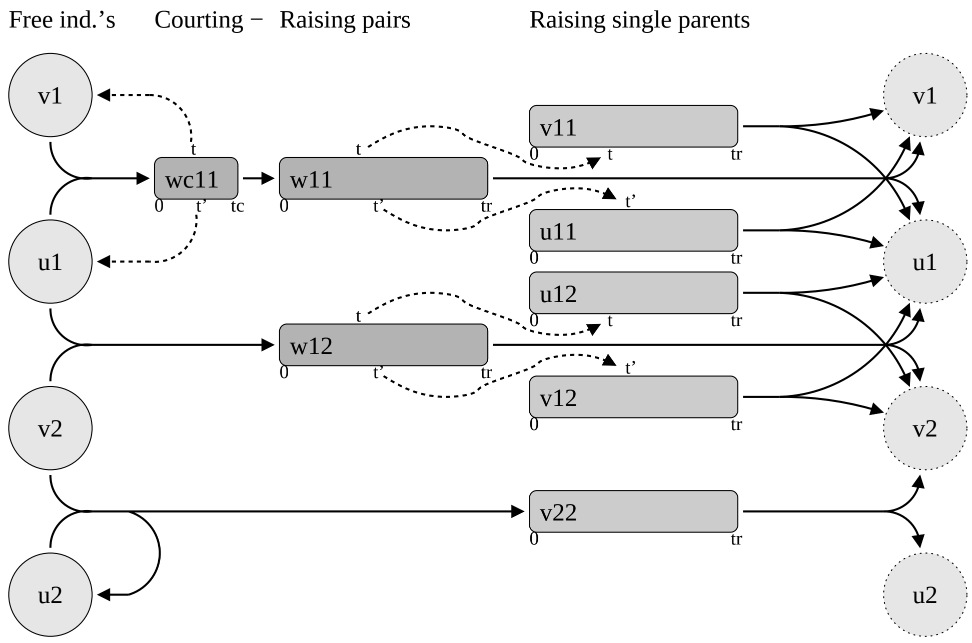

FIG. 2: Flow diagram depicting the different types of individuals and the transitions between them according to the complete pair-formation model. For explanation see the text.

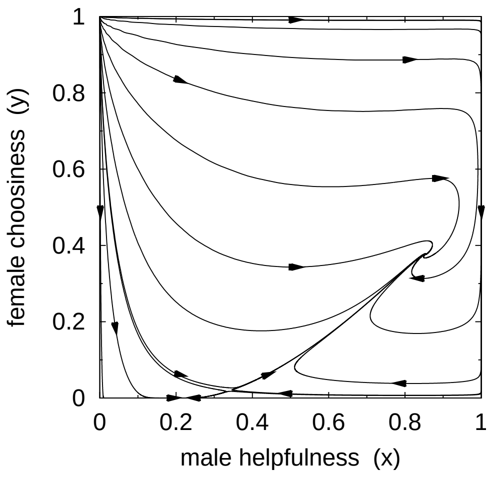

FIG. 3: Projection on the (x, y)-plane of some numerical simulations of the full DDE system (A.10)–(A.12), with $(\tau_c, \tau_r, \kappa_1, \kappa_2) = (1, 10, 0.55, 1)$, $\alpha = 1$, and $\mu = 0.02$. Direction of flow is indicated with ▸ arrowheads.

and free individuals of the different types can be calculated. After rescaling to frequencies the full system (A.10)–(A.12) boils down to the following two-dimensional ODE system:

$$\begin{aligned} \frac{dx}{dt} &= p_1\,(q_1+q_2) - \rho\, x \\ \frac{dy}{dt} &= p_1\, q_1 \qquad\quad - \rho\, y\,, \end{aligned} \tag{4}$$

where the variables x and y again are the frequencies of helpful males and choosy females, respectively, and

$$\rho \;:=\; p_1\,(q_1+q_2) + k\,(1-x)\,q_2\,, \tag{5}$$

where

$$k \;:=\; \kappa_1/\kappa_2 \tag{6}$$

is the ratio of the two reproductive outputs ($0 < k \leq 1$), which can be interpreted as a reproductive disadvantage multiplication factor for single parents.

The three variables p_1, q_1 and q_2 are the frequencies of free helpful males, free choosy females and free non-choosy females in the population, respectively. They have to satisfy three additional equations:

$$\begin{aligned} x &= p_1\left(1 + \frac{(t_c+t_r)\,q_1 + t_r\,q_2}{p_1 + (1-x) + q_1 + q_2}\right) \\ y &= q_1\left(1 + \frac{(t_c+t_r)\,p_1}{p_1 + (1-x) + q_1 + q_2}\right) \\ 1-y &= q_2\left(1 + \frac{t_r\,(p_1 + (1-x))}{p_1 + (1-x) + q_1 + q_2}\right)\,, \end{aligned} \tag{7}$$

where the new model parameters t_c and t_r are defined in terms of the limits of the old model parameters (see Appendix B):

$$t_c \;:=\; \alpha\,\tau_c \qquad \text{and} \qquad t_r \;:=\; \alpha\,\tau_r\,. \tag{8}$$

The parameters t_c and t_r can be interpreted as the time needed for courtship and for raising, respectively, corresponding to τ_c and τ_r, but measured on a different time-scale.

Notice that (4)–(8) is a two-dimensional ODE system, just as the Schuster–Sigmund model (3). The number of model parameters has been reduced from six to three: t_c, t_r and k. This system can be solved numerically by Runge–Kutta methods, with p_1, q_1 and q_2 being obtained at each time step by solving equations (7) with a Newton–Raphson root-finding algorithm (Press *et al.*, 1988).

3. Behaviour of the model

Comparison of Fig. 5C with Fig. 3 reveals that, for analogous parameter values, the behaviour of the simplified system (4)–(8) is very similar to that of the full system (A.10)–(A.12), as we already anticipated. These pictures also show that the models can give rise to two alternative stable states: in this case

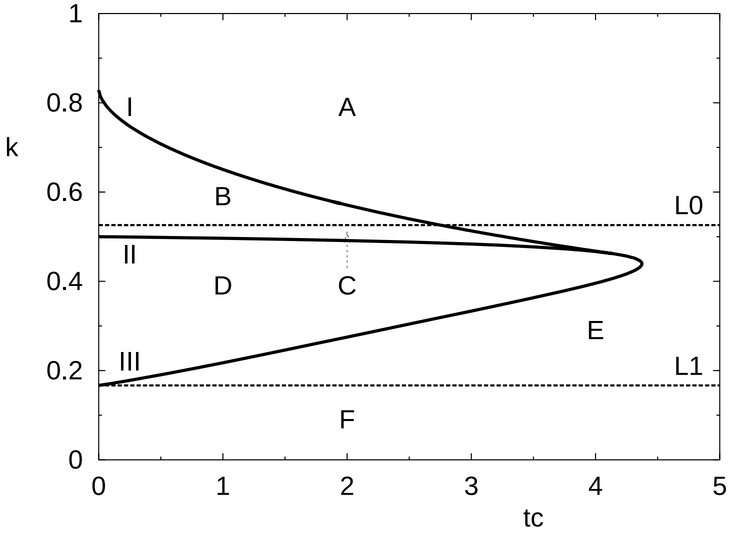

FIG. 4: Bifurcation diagram in (t_c, k)-space of the simplified ODE system (4)–(8), for $t_r = 10$. For explanation see the text.

there is an interior equilibrium point with polymorphism in both sexes, as well as a border equilibrium (at $y = 0$) with only non-choosy females but a polymorphic male population. It depends on initial conditions which equilibrium the systems will attain. This occurs for very reasonable situations, namely when courtship lasts one-fifth and one-tenth, respectively, of the raising period, and pairs raise approximately twice as many offspring as single parents.

First I will describe the full spectrum of the simplified model behaviour in a detailed manner, and then summarise these findings in more biological terms.

3.1. DETAILED DESCRIPTION OF THE MODEL BEHAVIOUR

There are always four trivial equilibria at the corners of Σ^2, where the variables x and y are equal to 0 or 1: if there are exclusively (non-)helpful males and exclusively (non-)choosy females, nothing changes. If there are only non-helpful males around (at $x = 0$), then the frequency of choosy females decreases ($dy/dt < 0$) because the latter cannot mate and reproduce. In a population of exclusively helpful males ($x = 1$), choosiness also decreases: non-choosy females reproduce faster because they skip the courtship. Only if the courtship period is zero, the whole ‘helpful border’ ($x = 1$) is a line of equilibria ($dy/dt = 0$). If all females are choosy ($y = 1$) helpfulness increases ($dx/dt > 0$) because non-helpful males cannot mate. (See the arrows on the corresponding borders in Fig. 5.) It is a straightforward exercise to show these properties analytically.

On the boundary where all females are non-choosy ($y = 0$) and in the polymorphic interior of Σ^2 the flow depends on the model parameters. A complete bifurcation analysis of the simplified system (4)–(8) is beyond the scope of this paper, but a two-parameter bifurcation diagram for t_c and k, with t_r fixed at 10, is shown in Fig. 4. The two horizontal dashed lines represent the limits of existence of the boundary equilibrium (at $y = 0$; without choosy females, so t_c is not of any importance here). At the upper line, L_0 (which can be calculated analytically: $k = (4 + t_r + \sqrt{4 + t_r^2})/(6 + 4t_r))$, the boundary equilibrium hits $x = 0$. At the lower line, L_1 (located at $k = 2/(2 + t_r))$, it hits $x = 1$. For larger t_r, the line L_0 shifts downward asymptotically to $1/2$, and L_1 to 0; both move up to 1 for smaller t_r.

The solid curves numbered I to III, indicating the existence limits of interior equilibria, were calculated using CONTENT, a program for numerical bifurcation analysis (Kuznetsov *et al.*, 1996). For other values of t_r the bifurcation curves can be at different positions, but topologically the diagram remains the same: From a biological viewpoint the important types of behaviour are all captured in Fig. 4.

Together, these lines and curves divide the diagram into six regions, A to F, with qualitatively different model behaviour (see the collection of phase portraits in Fig. 5).

Inside the wedge-shaped region $(B \cup C \cup D)$ a stable interior equilibrium exists, and between the horizontal lines L_0 and L_1 a stable boundary equilibrium exists, with both male strategies present. Consequently, in region $(B \cup C \cup D)$ it might pay off for females to be choosy, and in $(B \cup C \cup D \cup E)$ it might pay off for males to be helpful.

In region A, the trivial equilibrium located at the corner $(0, 0)$ is a global attractor for all orbits starting in the interior of Σ^2. At curve I, an asymptotically stable interior equilibrium (a focus) and a saddle point branch off from $(0, 0)$ if one changes parameters such that the system moves from region A into B. If the system moves from E into C these two interior equilibria branch off from the boundary equilibrium [in Fig. 5 located at $(0.2, 0)$]. Notice that region C qualitatively corresponds to Fig. 3. Moving from C into D, the interior saddle coalesces with the boundary equilibrium (at curve II). The boundary equilibrium then becomes a saddle point with its stable manifold on the boundary and its unstable manifold into the interior, and all orbits starting in the interior converge to the interior focus. At curve III (moving from D into E) the focus coalesces with the boundary equilibrium, which then becomes a global attractor. If k is decreased below L_0 (moving from E into F) the boundary equilibrium is absorbed by the trivial equilibrium at the corner $(1, 0)$.

In regions B and C the stable manifold of the interior saddle point, that is on both sides connected with the corner $(0, 1)$, divides the interior of Σ^2 into a basin of attraction of the interior focus, and a basin of attraction of the boundary equilibrium. The former is surrounded by the latter. The interior basin of attraction almost touches the boundary $x = 1$, where the boundary basin is extremely narrow.

When t_c is close to 0 (*i.e.* a very short courtship period), the proportion of helpful males in the interior focus is almost 1. Convergence is then very oscillatory (Fig. 5, panel D already hints in this direction): the frequency of non-helpful males repeatedly shrinks to small values and grows again while approaching the equilibrium. Without courtship ($t_c = 0$), the focus is absorbed by the boundary $x = 1$, which turns into a line of equilibria. This line attracts from the interior above some threshold value $\tilde{y}$; below this value it repels (see also Kumm *et al.*, 1996): Non-helpful males are able to invade if the proportion of choosy females is smaller than $\tilde{y}$, but after an initial increase they decrease in frequency again because the proportion of choosy females also increases. The system then settles on a boundary point with only helpful males, but with a higher proportion of choosy females than before; from there non-helpful males

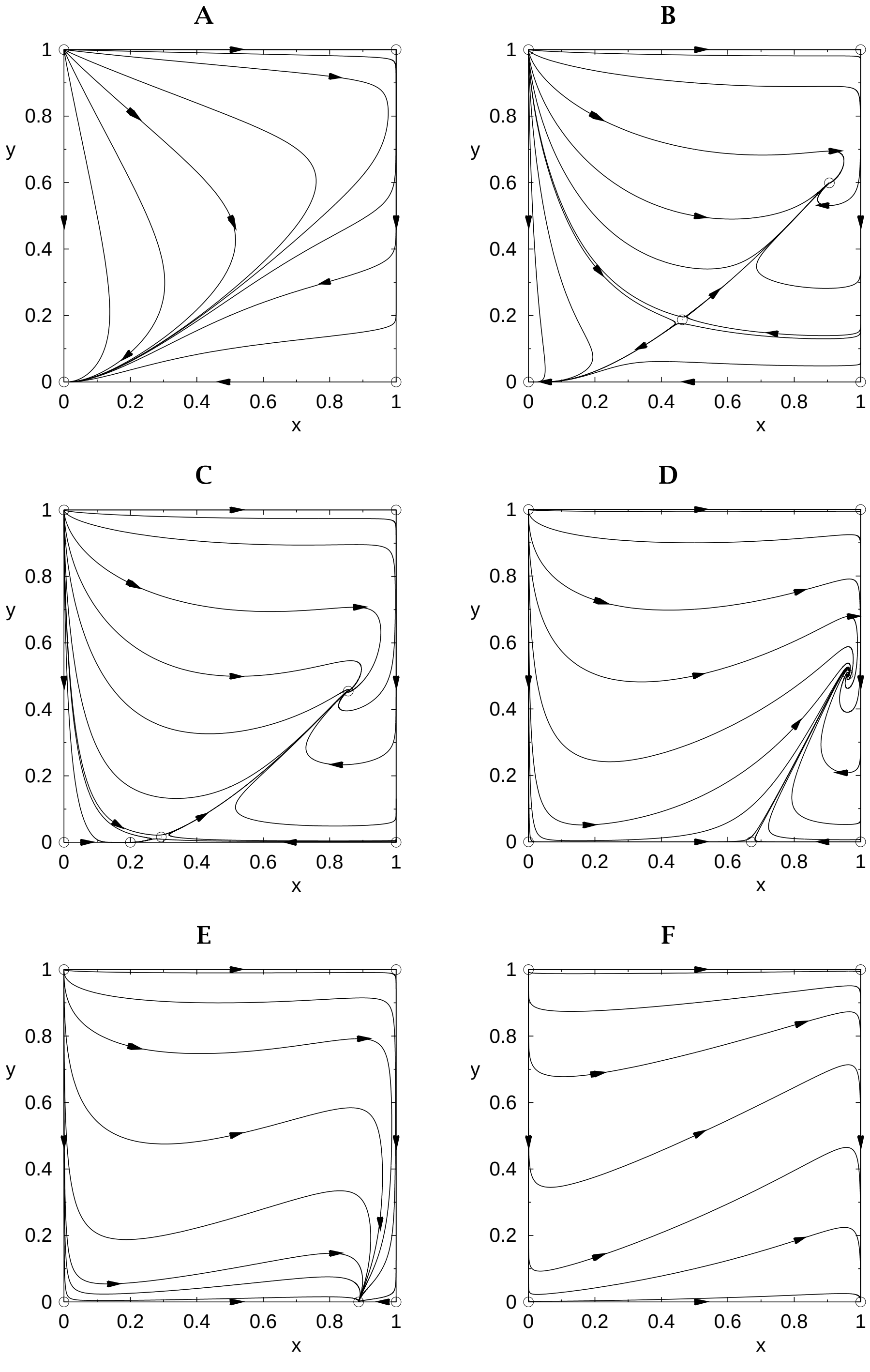

FIG. 5: Phase portraits of the simplified ODE system (4)–(8) in the regions marked A to F in Fig. 4. For all plots $t_r = 10$. Values of (t_c, k) in plot **A**: $(2, 0.8)$, **B**: $(1, 0.6)$, **C**: $(2, 0.5)$, **D**: $(1, 0.4)$, **E**: $(4, 0.3)$, and **F**: $(2, 0.1)$. Direction of flow is indicated with ▸ arrowheads and equilibrium points are marked with ⊙ symbols.

are not able to invade again.

Increasing the courtship period decreases the frequencies of helpful males and choosy females in the focus. If the system is in region B or C then the focus will move toward the corner $(0, 0)$ or to the boundary equilibrium, respectively, until the focus coalesces with the saddle point and the two disappear. Starting in region D, the focus is absorbed by the boundary equilibrium. For longer courtship periods the boundary equilibrium is the only non-trivial one, provided k is between L_0 and L_1.

The effect of a decrease in t_r is similar to an increase in t_c, except that the boundary equilibrium also moves to higher x values, whereas its location is independent of t_c. The system behaves roughly the same if the ratio $t_\mathrm{c}/t_\mathrm{r}$ and the product $k\,t_\mathrm{r}$ are kept constant.

3.2. BIOLOGICAL INTERPRETATION

The model behaviour described above has the following biological interpretation: If it hardly pays for the parents to raise the offspring together (k close to 1) then male helpfulness as well as female choosiness will not be able to survive. On the other hand, if the advantage of raising offspring as a pair is very high (k small), only helpful males survive, and then it also does not pay females to be choosy. For intermediate advantage of pairs, provided that the time needed for courtship is considerably smaller than the time needed for raising offspring, an attracting, totally mixed equilibrium exists. In this stable polymorphic state, choosy as well as non-choosy females coexist with helpful as well as non-helpful males. If the advantage of pairs is rather high (k has an intermediate value and is on the small side; region D in Fig. 4) then every perturbation from the state with only non-choosy females will cause the system to attain the total polymorphic state. These perturbations could originate from mutation or migration. If, on the other hand, the advantage is rather small (k intermediate and largish; region B) then, depending on the initial population state and on perturbations of the system, two things can happen. Either the population state moves toward the stable polymorphism, or toward the trivial state with only non-helpful males and non-choosy females. For even more intermediate advantage of pairs (region C) the alternative of the total polymorphism is a state where both types of males coexist with only non-choosy females. Summarising: The population converges to the total polymorphic state or to a state consisting exclusively of non-choosy females. Even in the latter case there can be a stable polymorphism in male strategies, depending on the exact parameter values.

4. Discussion

An intrinsic difference between the game-dynamic models (Schuster & Sigmund, 1981; Bomze *et al.*, 1983; Maynard Smith & Hofbauer, 1987) and the present model is seen in the behaviour which arises when there are only non-helpful males around (at $x = 0$). In this case, choosy females do not mate, so they cannot reproduce. Without reproduction, they disappear [at the mortality rate μ for the complete pair formation model (A.10)–(A.12), and at the scaled rate kq_2 for the simplified model (4)–(8)]. Non-choosy females have positive growth terms because of matings with non-helpful 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, in a fuller model which also considered changes in total population size, could cause the latter to decrease).

The local behaviour near the interior focus resembles the global behaviour of the game-dynamic model more closely: clockwise convergence and oscillations. Both can be explained by the argument that clarifies the lack of stability of the mixed equilibrium point in Dawkins' game: with more helpful males around, non-choosy females do better; with more non-choosy females, non-helpful males are at an advantage, and so on.

Another new phenomenon is the existence of the boundary equilibrium. In a population of only non-choosy females, helpful and non-helpful males can coexist in case of a suitable reproductive advantage for pairs. Remember that this reproductive advantage ($k < 1$) is not present in previous game-dynamic models of the battle of the sexes. Helpful males can invade a non-helpful population if they raise sufficiently more offspring by helping the females, and non-helpful males can invade a helpful population provided that this reproductive advantage for helpful males is not too large and the period needed for raising the offspring is sufficiently long. The raising period assists the helpful males to keep females out of the mating market and to unable females to mate with non-helpful males.

If there is an interior equilibrium for the mating-delay models, it is a stable focus, contrary to Maynard Smith's (1982) claim, that any time delay is destabilising. Without a gain in reproductive output for a helpful male (in other words, if $k = 1$), there is no interior equilibrium in the present model; apparently, this condition more than compensates for destabilisation due to time delays.

In the slightly different version of the pair-formation model presented in Kumm *et al.* (1996), the same time-scale argument as applied to the present model yields the same simplified ODE model (4)–(8). In that model paired individuals die together with their immature offspring of the same sex. The widowed partner, provided it stays alive, continues to raise its offspring of the opposite sex (possibly after courting a dead body). Several detailed ways of accounting for the mortality in pairs lead to even more complicated equations than in the present DDE model (A.10)–(A.12), but the global behaviour of the model remains unaltered.

Despite the added realism of the pair-formation submodel, the model of the battle of the sexes presented in this paper has serious flaws, like all models of this caricatural game have (see Schuster & Sigmund, 1981; Maynard Smith, 1982; Eshel & Akin, 1983). For the record I shall mention some of these flaws. The model 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; Maynard Smith & Hofbauer, 1987). Furthermore, the evolution of male and female strategies is not taken into consideration. For example, a male strategy that performs courtship but leaves after conception, thus cheating choosy females, would be a candidate for further analysis. In Dawkins' original battle of the sexes model, the male duration of courtship and participation in raising offspring are coupled artificially by assumption. The evolution of courtship duration might better be analysed as a problem of sexual selection, along the lines laid out by Fisher (1930) and Zahavi (1975). Also for the participation in rearing offspring, an analysis using continuous strategy sets might be preferable (*e.g.* Motro, 1994, and the references therein). A complete understanding of the parental investment conflict addressed by the battle of the sexes will surely have to take into account the coevolution of male and female strategies.

But this is not what I want to stress with this paper. Of course one can never get full realism. The present model formulation and the consequent results show that, in the analysis of evolutionary games, one should pay careful attention to the specific mechanisms involved in the conflict: Predictions from a whole class of models derived by the traditional approach of game-dynamic equations can fundamentally change by adding a most elementary further assumption about individual life history. The message of this paper is that it is fruitful to derive simple models for evolutionary games starting with more complex, mechanistic building blocks. From within the framework that results from those buildings blocks, one can try to derive more simple models, by various kinds of limiting procedures such as time-scale arguments. Clear assumptions then relate the simple models to the primary, more complex ones. As an added advantage one can interpret the resulting equations in real, mechanistic terms. By starting immediately with a simple framework at a high phenomenological level, like the traditional approach of game-dynamic equations, one can easily end up in a class of models from which it is impossible to generalise to the full spectrum of behaviour of the biological system that one wishes to study.

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APPENDIX A Formulation of the full mechanistic model

In this appendix I will derive a delay-differential equation (DDE) system describing the dynamics of the complete pair formation model that was sketched in the main text.

Define $u_i(t)$ and $v_j(t)$ to be the densities at time t of free males and females following strategies i and j, respectively. (For males, subscript 1 denotes helpful and 2 non-helpful; for females, 1 denotes choosy and 2 non-choosy.) The density of the total amount of unpaired males is $u(t)$, where

$u(t) := u_1(t) + u_2(t)$, and the density of all free females is $v(t)$, where $v(t) := v_1(t) + v_2(t)$.

Also define $w^{\mathrm{c}}_{11}(t)$ as the density of pairs of helpful males and choosy females that are courting at time t, and $w^{\mathrm{r}}_{ij}(t)$ [where $(i,j) \in \{(1,1),(1,2)\}$] as the densities of pairs of type-i males and type-j females that are raising offspring at time t.

Additionally, $u_{1j}(t)$ (where $j \in \{1,2\}$) denotes the density at time t of helpful males (widowers) that started raising offspring together with a type-j female, but continue on their own, because the female mate has died. In the same way, $v_{1j}(t)$ (where $j \in \{1,2\}$) denotes the density of type-j females (widows) raising offspring on their own, because the (helpful) male has died.

Finally, $v_{22}(t)$ denotes the density at time t of non-choosy females raising offspring on their own, because they mated with non-helpful males.

When one of the partners of a pair dies at, say, τ time units after they started raising offspring, the widow(er) produces $\kappa(\tau)$ offspring of each sex. Here $\kappa(\tau)$ is a linear interpolation between $\kappa(0) = \kappa_1$ and $\kappa(\tau_{\mathrm{r}}) = \kappa_2$:

$$\kappa(\tau) \;:=\; \kappa_1 + (\kappa_2 - \kappa_1)\,\frac{\tau}{\tau_{\mathrm{r}}} \qquad \text{for} \quad 0 < \tau < \tau_{\mathrm{r}}\,. \tag{A.1}$$

I 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-helpful/choosy mating and equal to $\alpha > 0$ for other combinations. For all but the non-helpful/choosy mating,

$$m_{ij}(t) \;:=\; \alpha\,\frac{u_i(t)\,v_j(t)}{u(t)+v(t)}\,, \qquad (i,j) \in \{(1,1),(1,2),(2,2)\}\,. \tag{A.2}$$

In the main text (see also Fig. 2) I specified the widowed individuals separately. I will denote them by the variables u_{11}, u_{12}, v_{11} and v_{12}, for widowers from helpful/choosy pairs, widowers from helpful/non-choosy pairs, widows from helpful/choosy pairs and widows from helpful/non-choosy pairs, respectively. In this appendix I will put raising individuals in one class per male/female strategy combination. The mortality and consequently lower reproductive output of the single parents can be accounted for by multiplying the inflow rates of the classes of raising individuals with the expected survival probabilities during the raising period, and the corresponding reproductive outputs, averaged over the time the partner passed away.

Let us call the density per unit time of parents that have just survived the raising period as a pair $w^{\mathrm{r}}_{1j}(t)^-$. In the same way, the density per unit time of individuals that have just survived the raising period as a widow(er) can be denoted as $x_{1j}(t)^-$, with $x \in \{u,v\}$. The outflows of the classes of pairs $w^{\mathrm{r}}_{1j}(t)^-$ are equal to the corresponding inflows τ_{r} time units ago, multiplied by the probability that both parents survived the raising period. The outflows of widow(er)s $x_{1j}(t)^-$ are equal to the corresponding inflow τ_{r} time units ago, multiplied by the probability that this parent survived and its partner died. Notice that for the inflow of helpful/choosy pairs we also have to account for (the mortality in) the courtship period, *i.e.* the inflow is then $m_{11}(t-(\tau_{\mathrm{c}}+\tau_{\mathrm{r}}))\,e^{-2\mu\tau_{\mathrm{c}}}$, as compared with $m_{12}(t-\tau_{\mathrm{r}})$ for the helpful/non-choosy combination. Summarising, we have

$$\begin{aligned} w^{\mathrm{r}}_{11}(t)^- &= m_{11}(t-\tau_{\mathrm{cr}})\, e^{-2\mu\tau_{\mathrm{c}}}\, e^{-2\mu\tau_{\mathrm{r}}} \\ w^{\mathrm{r}}_{12}(t)^- &= m_{12}(t-\tau_{\mathrm{r}})\, e^{-2\mu\tau_{\mathrm{r}}} \\ x_{11}(t)^- &= m_{11}(t-\tau_{\mathrm{cr}})\, e^{-2\mu\tau_{\mathrm{c}}}\, e^{-\mu\tau_{\mathrm{r}}}\, (1-e^{-\mu\tau_{\mathrm{r}}}) \\ x_{12}(t)^- &= m_{12}(t-\tau_{\mathrm{r}})\, e^{-\mu\tau_{\mathrm{r}}}\, (1-e^{-\mu\tau_{\mathrm{r}}})\ , \end{aligned} \tag{A.3}$$

with $x \in \{u, v\}$, and

$$\tau_{\mathrm{cr}} := \tau_{\mathrm{c}} + \tau_{\mathrm{r}}\ . \tag{A.4}$$

The production of offspring that have just been weaned by widowed parents can be calculated by multiplying the corresponding inflow with the expected reproductive output for a widow(er). To calculate the expected reproductive output we integrate, over the raising period ($0 < \tau < \tau_{\mathrm{r}}$), the product of the reproductive output if the partner died after τ time units ($\kappa(\tau)$) and the probability that the partner dies after τ time units ($\mu\, e^{-\mu\tau}\, d\tau$) and the probability that the widow(er) itself survives raising offspring ($e^{-\mu\tau_{\mathrm{r}}}$). This yields

$$\begin{aligned} &\int_0^{\tau_{\mathrm{r}}} \kappa(\tau)\, \mu\, e^{-\mu\tau}\, e^{-\mu\tau_{\mathrm{r}}}\, d\tau \\ &\qquad = e^{-\mu\tau_{\mathrm{r}}} \left(\kappa_1 - \kappa_2\, e^{-\mu\tau_{\mathrm{r}}} + \frac{\kappa_2 - \kappa_1}{\mu\,\tau_{\mathrm{r}}}\, (1-e^{-\mu\tau_{\mathrm{r}}}) \right) . \end{aligned} \tag{A.5}$$

Consequently, the production of offspring by widow(er)s from helpful/choosy and helpful/non-choosy matings, denoted as $\widetilde{\kappa x}_{11}$ and $\widetilde{\kappa x}_{12}$, respectively, is

$$\begin{aligned} \widetilde{\kappa x}_{11}(t) &:= m_{11}(t-\tau_{\mathrm{cr}})\, e^{-2\mu\tau_{\mathrm{c}}}\, e^{-\mu\tau_{\mathrm{r}}} \\ &\qquad \times \left(\kappa_1 - \kappa_2\, e^{-\mu\tau_{\mathrm{r}}} + \frac{\kappa_2 - \kappa_1}{\mu\,\tau_{\mathrm{r}}}\, (1-e^{-\mu\tau_{\mathrm{r}}}) \right) \\ \widetilde{\kappa x}_{12}(t) &:= m_{12}(t-\tau_{\mathrm{r}})\, e^{-\mu\tau_{\mathrm{r}}} \\ &\qquad \times \left(\kappa_1 - \kappa_2\, e^{-\mu\tau_{\mathrm{r}}} + \frac{\kappa_2 - \kappa_1}{\mu\,\tau_{\mathrm{r}}}\, (1-e^{-\mu\tau_{\mathrm{r}}}) \right) , \end{aligned} \tag{A.6}$$

with $x \in \{u, v\}$.

With the help of (A.3) and (A.6) we can calculate that the inflow at time t in the class of free helpful males from the classes of helpful/choosy matings, counting surviving pairs as well as widowers, and all their offspring, is equal to:

$$\begin{aligned} &w^{\mathrm{r}}_{11}(t)^- + u_{11}(t)^- + \kappa_2\, w^{\mathrm{r}}_{11}(t)^- + \widetilde{\kappa u}_{11}(t) + \widetilde{\kappa v}_{11}(t) \\ &\qquad = m_{11}(t-\tau_{\mathrm{cr}})\, e^{-2\mu\tau_{\mathrm{c}}}\, e^{-\mu\tau_{\mathrm{r}}} \\ &\qquad\qquad \times \Big(e^{-\mu\tau_{\mathrm{r}}} + (1-e^{-\mu\tau_{\mathrm{r}}}) + \kappa_2\, e^{-\mu\tau_{\mathrm{r}}} \\ &\qquad\qquad\qquad + 2\,\kappa_1 - 2\,\kappa_2\, e^{-\mu\tau_{\mathrm{r}}} + 2\, \frac{\kappa_2 - \kappa_1}{\mu\,\tau_{\mathrm{r}}}\, (1-e^{-\mu\tau_{\mathrm{r}}}) \Big) \\ &\qquad = m_{11}(t-\tau_{\mathrm{cr}})\, e^{-2\mu\tau_{\mathrm{c}}}\, e^{-\mu\tau_{\mathrm{r}}}\, (1+K)\ , \end{aligned} \tag{A.7}$$

where

$$K := 2\kappa_1 - \kappa_2\, e^{-\mu\tau_{\mathrm{r}}} + 2\, \frac{\kappa_2 - \kappa_1}{\mu\,\tau_{\mathrm{r}}}\, (1-e^{-\mu\tau_{\mathrm{r}}})\ . \tag{A.8}$$

is the reproductive output of a surviving parent from either a helpful/choosy- or a helpful/non-choosy mating, averaged over the survivorship of the partner. The same amount from the classes of helpful/choosy matings as in (A.7) flows into the class of free choosy females. And by the same argument we can calculate that from the classes of helpful/non-choosy matings an amount $m_{12}(t-\tau_r)\, e^{-\mu\tau_r}\,(1+K)$ flows into the classes of free helpful males as well as free non-choosy females.

From non-helpful/non-choosy matings, an amount $m_{22}(t-\tau_r)\, e^{-\mu\tau_r}\,(1+\kappa_1)$ flows into the class of free non-choosy females, and $m_{22}(t-\tau_r)\, e^{-\mu\tau_r}\,\kappa_1$ into the class of non-helpful males.

The only remaining cross-term is from courting helpful/choosy pairs, that disappear due to mortality of the male or the female partner, at a rate 2μ. Half of this mortality term [*i.e.* the surviving fiancé(e)s] flows back into the free helpful male- and the free choosy female class.

After τ_r time units, $u_{11}(t) = v_{11}(t)$ and $u_{12}(t) = v_{12}(t)$. So after τ_r time units we can define for males as well as for females the densities of mated individuals

$$\begin{aligned} w_{11}(t) &:= w^{r}_{11}(t) + u_{11}(t) = w^{r}_{11}(t) + v_{11}(t) \\ w_{12}(t) &:= w^{r}_{12}(t) + u_{12}(t) = w^{r}_{12}(t) + v_{12}(t)\,. \end{aligned} \tag{A.9}$$

Now we are ready to combine all ingredients described above, and obtain a DDE system for the dynamics of the densities of free individuals $u_1(t)$, $u_2(t)$, $v_1(t)$ and $v_2(t)$, of the courting individuals $w^{c}_{11}(t)$, and of the raising individuals $w_{11}(t)$, $w_{12}(t)$ and $v_{22}(t)$.

$$\begin{aligned}
\frac{du_1(t)}{dt} &= -\,m_{11}(t) + m_{11}(t-\tau_{cr})\, e^{-\mu(2\tau_c+\tau_r)}\,(1+K) + \mu\, w^{c}_{11}(t) \\
&\quad -\,m_{12}(t) + m_{12}(t-\tau_r)\, e^{-\mu\tau_r}\,(1+K) - \mu\, u_1(t) \\
\frac{du_2(t)}{dt} &= m_{22}(t-\tau_r)\, e^{-\mu\tau_r}\,\kappa_1 - \mu\, u_2(t) \\
\frac{dv_1(t)}{dt} &= -\,m_{11}(t) + m_{11}(t-\tau_{cr})\, e^{-\mu(2\tau_c+\tau_r)}\,(1+K) + \mu\, w^{c}_{11}(t) \\
&\quad - \mu\, v_1(t) \\
\frac{dv_2(t)}{dt} &= -\,m_{12}(t) + m_{12}(t-\tau_r)\, e^{-\mu\tau_r}\,(1+K) \\
&\quad -\,m_{22}(t) + m_{22}(t-\tau_r)\, e^{-\mu\tau_r}\,(1+\kappa_1) - \mu\, v_2(t) \\
\frac{dw^{c}_{11}(t)}{dt} &= m_{11}(t) - m_{11}(t-\tau_c)\, e^{-2\mu\tau_c} - 2\mu\, w^{c}_{11}(t) \\
\frac{dw_{11}(t)}{dt} &= m_{11}(t-\tau_c)\, e^{-2\mu\tau_c} - m_{11}(t-\tau_{cr})\, e^{-\mu(2\tau_c+\tau_r)} - \mu\, w_{11}(t) \\
\frac{dw_{12}(t)}{dt} &= m_{12}(t) - m_{12}(t-\tau_r)\, e^{-\mu\tau_r} - \mu\, w_{12}(t) \\
\frac{dv_{22}(t)}{dt} &= m_{22}(t) - m_{22}(t-\tau_r)\, e^{-\mu\tau_r} - \mu\, v_{22}(t)\,,
\end{aligned} \tag{A.10}$$

with

$$m_{ij}(t) = \alpha\, \frac{u_i(t)\, v_j(t)}{u(t) + v(t)} \tag{A.11}$$

and

$$K = 2\kappa_1 - \kappa_2\, e^{-\mu\tau_\mathrm{r}} + 2\,\frac{\kappa_2 - \kappa_1}{\mu\,\tau_\mathrm{r}}\,\left(1 - e^{-\mu\tau_\mathrm{r}}\right)\,. \tag{A.12}$$

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

$$\begin{aligned} x(t) &= \frac{u_1(t) + w^\mathrm{c}_{11}(t) + w_{11}(t) + w_{12}(t)}{M(t)} \\ y(t) &= \frac{v_1(t) + w^\mathrm{c}_{11}(t) + w_{11}(t)}{F(t)}\,, \end{aligned} \tag{A.13}$$

where

$$\begin{aligned} M(t) &:= u_1(t) + u_2(t) + w^\mathrm{c}_{11}(t) + w_{11}(t) + w_{12}(t) \\ F(t) &:= v_1(t) + v_2(t) + w^\mathrm{c}_{11}(t) + w_{11}(t) + w_{12}(t) + v_{22}(t) \end{aligned} \tag{A.14}$$

are the total densities of males and females, respectively.

From (A.10) it is clear that

$$\begin{aligned} \frac{d}{dt}M(t) &= \frac{d}{dt}\left[\, u_1(t) + u_2(t) + w^\mathrm{c}_{11}(t) + w_{11}(t) + w_{12}(t)\,\right] \\ &= K\, m_{11}(t-\tau_\mathrm{cr})\, e^{-\mu(2\tau_\mathrm{c}+\tau_\mathrm{r})} + K\, m_{12}(t-\tau_\mathrm{r})\, e^{-\mu\tau_\mathrm{r}} \\ &\quad + \kappa_1\, m_{22}(t-\tau_\mathrm{r})\, e^{-\mu\tau_\mathrm{r}} - \mu\, M(t) \end{aligned} \tag{A.15}$$

and

$$\begin{aligned} \frac{d}{dt}F(t) &= \frac{d}{dt}\left[\, v_1(t) + v_2(t) + w^\mathrm{c}_{11}(t) + w_{11}(t) + w_{12}(t) + v_{22}(t)\,\right] \\ &= K\, m_{11}(t-\tau_\mathrm{cr})\, e^{-\mu(2\tau_\mathrm{c}+\tau_\mathrm{r})} + K\, m_{12}(t-\tau_\mathrm{r})\, e^{-\mu\tau_\mathrm{r}} \\ &\quad + \kappa_1\, m_{22}(t-\tau_\mathrm{r})\, e^{-\mu\tau_\mathrm{r}} - \mu\, F(t)\,. \end{aligned} \tag{A.16}$$

Then it immediately follows that

$$\frac{d}{dt}\left[\, M(t) - F(t)\,\right] = -\mu\,\left(M(t) - F(t)\right)\,, \tag{A.17}$$

from which we can conclude that

$$M(t) - F(t) = \left(M(0) - F(0)\right) e^{-\mu t}\,, \tag{A.18}$$

so the manifold of equal male and female densities is invariant and attracting. Thus, if the total densities of males and females are initially equal, they will remain equal.

Notice that equations (A.10) are generally only valid τ_cr time units after time zero, unless we choose the initial conditions such that for all $t \in (-\tau_\mathrm{cr}, 0)$ we have $u_{11}(t) = v_{11}(t)$ and $u_{12}(t) = v_{12}(t)$. But this is exactly what was done in the numerical simulations shown in Fig. 3.

It is important to realise that the densities acting as state variables in the full DDE system (A.10)–(A.12) cannot simply be scaled to frequencies. In ODE systems such a scaling of variables is equivalent to a change in time-scale; the orbit in state space is preserved and only the information about the total population size is lost. For the DDE system considered here, the densities are contained in the delay terms (see equations (A.10)), while a change in time-scale also affects the time delay.

Finally, notice that there is no density dependence in the model; in the long run the values of the parameters produce an exponentially growing or an exponentially decaying population.

We can integrate system (A.10)–(A.12) numerically using the SOLVER program by Gurney & Tobia (1995). The three mating rates $m_{ij}(t)$ are stored as history variables (see also Nisbet, 1996) 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 assuming that the total number of males is equal to the total number of females, and using 'quasi-steady-state' conditions, with the help of equations (7) and a Newton–Raphson root-finding algorithm (Press *et al.*, 1988).

APPENDIX B Derivation of the simplified model

In this appendix I will derive the ODE system (4)–(8) that is presented in the main text.

First define the densities of male and female types 1 and 2, respectively, as follows:

$$\begin{aligned} U_1(t) &:= u_1(t) + w^{\mathrm{c}}_{11}(t) + w_{11}(t) + w_{12}(t) \\ U_2(t) &:= u_2(t) \\ V_1(t) &:= v_1(t) + w^{\mathrm{c}}_{11}(t) + w_{11}(t) \\ V_2(t) &:= v_2(t) + w_{12}(t) + v_{22}(t)\,. \end{aligned} \tag{B.1}$$

(So $U_1 + U_2 = M$ and $V_1 + V_2 = F$.) To get the time derivatives of (B.1) we substitute from (A.10), and after cancelling most of the terms we get

$$\begin{aligned} \frac{dU_1(t)}{dt} &= K\,m_{11}(t-\tau_{\mathrm{cr}})\,e^{-\mu(2\tau_{\mathrm{c}}+\tau_{\mathrm{r}})} + K\,m_{12}(t-\tau_{\mathrm{r}})\,e^{-\mu\tau_{\mathrm{r}}} - \mu\,U_1(t) \\ \frac{dU_2(t)}{dt} &= \kappa_1\,m_{22}(t-\tau_{\mathrm{r}})\,e^{-\mu\tau_{\mathrm{r}}} - \mu\,U_2(t) \\ \frac{dV_1(t)}{dt} &= K\,m_{11}(t-\tau_{\mathrm{cr}})\,e^{-\mu(2\tau_{\mathrm{cr}}+\tau_{\mathrm{r}})} - \mu\,V_1(t) \\ \frac{dV_2(t)}{dt} &= K\,m_{12}(t-\tau_{\mathrm{r}})\,e^{-\mu\tau_{\mathrm{r}}} + \kappa_1\,m_{22}(t-\tau_{\mathrm{r}})\,e^{-\mu\tau_{\mathrm{r}}} - \mu\,V_2(t)\,, \end{aligned} \tag{B.2}$$

with $m_{ij}(t)$ and K as defined by (A.2) and (A.8), respectively.

The mathematical translation of the assumption that pair formation and dissociation is on a shorter time-scale than the life span of individuals, is to take the limits

$$\alpha \to \infty\,, \quad \tau_\star \downarrow 0 \quad \text{and} \quad \kappa_i \downarrow 0 \tag{B.3}$$

(for $\star \in \{\mathrm{c}, \mathrm{r}\}$ and $i \in \{1, 2\}$) in such a way that $\alpha\,\tau_\star$ and $\alpha\,\kappa_i$ have finite limits. Having applied these limits we define the new parameters

$$t_\star := \alpha\,\tau_\star \qquad \text{and} \qquad k_i := \alpha\,\kappa_i\,. \tag{B.4}$$

(*cf.* Heesterbeek & Metz 1993.)

Additionally, applying these limits we find $m_{11}(t-\tau_{\mathrm{cr}}) \to m_{11}(t)$, $m_{12}(t-\tau_{\mathrm{r}}) \to m_{12}(t)$, $m_{22}(t-\tau_{\mathrm{r}}) \to m_{22}(t)$, $e^{-\mu(2\tau_{\mathrm{c}}+\tau_{\mathrm{r}})} \to 1$, $e^{-\mu\tau_{\mathrm{r}}} \to 1$, and, using

Taylor series expansion, $K \to \kappa_2$. So on the long time-scale we have

$$\begin{aligned} \frac{dU_1(t)}{dt} &= \kappa_2\, m_{11}(t) + \kappa_2\, m_{12}(t) - \mu\, U_1(t) \\ \frac{dU_2(t)}{dt} &= \kappa_1\, m_{22}(t) \qquad\qquad\quad - \mu\, U_2(t) \\ \frac{dV_1(t)}{dt} &= \kappa_2\, m_{11}(t) \qquad\qquad\quad - \mu\, V_1(t) \\ \frac{dV_2(t)}{dt} &= \kappa_2\, m_{12}(t) + \kappa_1\, m_{22}(t) - \mu\, V_2(t)\ . \end{aligned} \tag{B.5}$$

Taking the limits $\alpha \to \infty$ and $\tau_\star \downarrow 0$ as in (B.3)–(B.4), we also have $w^{\mathrm{c}}_{11}(t) \to \tau_{\mathrm{c}}\, m_{11}(t)$, $w_{11}(t) \to \tau_{\mathrm{r}}\, m_{11}(t)$, $w_{12}(t) \to \tau_{\mathrm{r}}\, m_{12}(t)$, $v_{22}(t) \to \tau_{\mathrm{r}}\, m_{22}(t)$, and

$$\tau_\star\, m_{ij}(t) \ \to\ t_\star\, \frac{u_i(t)\, v_j(t)}{u(t) + v(t)} \tag{B.6}$$

[where $(\star, i, j) \in \{(\mathrm{c}, 1, 1), (\mathrm{r}, 1, 1), (\mathrm{r}, 1, 2), (\mathrm{r}, 2, 2)\}$]. Consequently, using (B.1),

$$\begin{aligned} U_1 &= u_1 \left(1 + t_{\mathrm{cr}}\, \frac{v_1}{u + v} + t_{\mathrm{r}}\, \frac{v_2}{u + v}\right) \\ U_2 &= u_2 \\ V_1 &= v_1 \left(1 + t_{\mathrm{cr}}\, \frac{u_1}{u + v}\right) \\ V_2 &= v_2 \left(1 + t_{\mathrm{r}}\, \frac{u_1}{u + v} + t_{\mathrm{r}}\, \frac{u_2}{u + v}\right)\ , \end{aligned} \tag{B.7}$$

where we write

$$t_{\mathrm{cr}} \ := \ t_{\mathrm{c}} + t_{\mathrm{r}}\ . \tag{B.8}$$

We assume that

$$M \ = \ F \ =:\ N \tag{B.9}$$

[see equation (A.18) for justification] and define the frequencies

$$\begin{aligned} P_1 &:= \frac{U_1}{N}\ , & P_2 &:= \frac{U_2}{N}\ , & Q_1 &:= \frac{V_1}{N}\ , & Q_2 &:= \frac{V_2}{N}\ , \\ p_1 &:= \frac{u_1}{N}\ , & p_2 &:= \frac{u_2}{N}\ , & q_1 &:= \frac{v_1}{N}\ , & q_2 &:= \frac{v_2}{N}\ . \end{aligned} \tag{B.10}$$

From (B.5) it follows easily that

$$\begin{aligned} \frac{dP_1(t)}{dt} &= \frac{k_2\, p_1 q_1 + k_2\, p_1 q_2}{p_1 + p_2 + q_1 + q_2} - \nu\, P_1 \\ \frac{dP_2(t)}{dt} &= \frac{k_1\, p_2 q_2}{p_1 + p_2 + q_1 + q_2} - \nu\, P_2 \\ \frac{dQ_1(t)}{dt} &= \frac{k_2\, p_1 q_1}{p_1 + p_2 + q_1 + q_2} - \nu\, Q_1 \\ \frac{dQ_2(t)}{dt} &= \frac{k_2\, p_1 q_2 + k_1\, p_2 q_2}{p_1 + p_2 + q_1 + q_2} - \nu\, Q_2\ , \end{aligned} \tag{B.11}$$

where

$$\nu \ := \ \frac{k_2\, p_1 q_1 + k_2\, p_1 q_2 + k_1\, p_2 q_2}{p_1 + p_2 + q_1 + q_2}\ . \tag{B.12}$$

Division of the right-hand sides of system (B.11)–(B.12) by $k_2/(p_1+p_2+q_1+q_2)$ introduces only a change in velocity, simplifies the system, and reduces the number of parameters by one: k_1 and k_2 can be combined in one parameter,

$$k \quad := \quad k_1/k_2 \,. \tag{B.13}$$

By assumption, $0 < k \leq 1$. On the manifold satisfying $P_1+P_2 = 1 \wedge Q_1+Q_2 = 1$ [which is invariant and attracting: see equation (A.18)] the new system can be written as the two-dimensional ODE system (4)–(8) with variables

$$\begin{aligned} x &:= P_1 \\ y &:= Q_1 \,. \end{aligned} \tag{B.14}$$

On this manifold, the p_i and q_i have to satisfy

$$\begin{aligned} x &= p_1 \left(1 + \frac{t_{\mathrm{cr}}\, q_1 + t_{\mathrm{r}}\, q_2}{p_1 + p_2 + q_1 + q_2}\right) \\ 1 - x &= p_2 \\ y &= q_1 \left(1 + \frac{t_{\mathrm{cr}}\, p_1}{p_1 + p_2 + q_1 + q_2}\right) \\ 1 - y &= q_2 \left(1 + \frac{t_{\mathrm{r}}\, p_1 + t_{\mathrm{r}}\, p_2}{p_1 + p_2 + q_1 + q_2}\right) \,. \end{aligned} \tag{B.15}$$

By substituting $1 - x$ for p_2 (remember that type-2 males are always free) in (B.15), we arrive at the equations (7).