

# Electronic Supplementary Material

## On the coevolution of social responsiveness and behavioural consistency

Max Wolf, G. Sander van Doorn & Franz J. Weissing

Proc. R. Soc. B 278, 440-448; 2011

### 1. Basic set-up of the model

Consider the model as described in the main text. Individuals within an evolving population are engaged in a large number of rounds of pairwise interactions. In each round, individuals in the population are randomly matched in pairs. Within any interaction between a focal individual and its opponent, each of the two individuals can adopt one out of two actions. Payoffs are obtained according to the payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} \text{action 1} & \text{action 2} \end{array} \\ \begin{array}{c} \text{action 1} \\ \text{action 2} \end{array} & \begin{array}{cc} a_{11} & a_{12} \\ a_{21} & a_{22} \end{array} \end{array} \quad (1)$$

such that  $a_{ij}$  represents the payoff to a focal individual that played action  $i$  against an opponent that played  $j$ . Throughout, we assume that

$$a_{21} > a_{11} \quad \text{and} \quad a_{12} > a_{22}. \quad (2)$$

to ensure that a mixed-strategy ESS exists for the single-shot game.

Individuals can either adopt a responsive or an unresponsive strategy. The strategy of unresponsive individuals is given by a single number  $p$ ,  $0 \leq p \leq 1$  that determines the probability with which an individual chooses action 1 in each of its interactions. Responsive individuals take into account the last interaction of their partner and choose their behaviour according to a simple eavesdropping strategy: “choose action 1 if opponent chose action 2 in its last interaction, otherwise choose action 1”. Responsiveness is costly and reduces the payoff of responsive individuals per interaction by  $c$ .

## 2. Payoffs

At each point in time, our population can be characterized by the tuple  $(f, \theta(p))$ , where  $f$  gives the frequency of responsive individuals in the population and  $\theta(p)$  gives the frequency distribution of unresponsive strategies in that population. For any distribution  $\theta(p)$ , we denote its expected value by  $E(p)$  and its variance by  $Var(p)$ .

The expected payoff of an unresponsive individual with strategy  $p$  in a resident environment  $(\hat{f}, \hat{\theta}(\hat{p}))$  is given by

$$W_u(p, \hat{f}, \hat{\theta}) = \hat{f} \cdot w_{u, \hat{r}} + (1 - \hat{f}) \cdot w_{u, \hat{u}} \quad (3)$$

per interaction, where  $w_{u, \hat{i}}$  are the expected payoffs to an unresponsive individual dependent on whether it interacts with a responsive or an unresponsive individual. These payoffs are given by:

$$\begin{aligned} w_{u, \hat{u}} &= p \cdot \int_0^1 (\hat{p} \cdot a_{11} + (1 - \hat{p}) \cdot a_{12}) \hat{\theta}(\hat{p}) d\hat{p} + (1 - p) \cdot \int_0^1 (\hat{p} \cdot a_{21} + (1 - \hat{p}) \cdot a_{22}) \hat{\theta}(\hat{p}) d\hat{p} \\ &= p \cdot (E(\hat{p}) \cdot a_{11} + (1 - E(\hat{p})) \cdot a_{12}) + (1 - p) \cdot (E(\hat{p}) \cdot a_{21} + (1 - E(\hat{p})) \cdot a_{22}) \\ w_{u, \hat{r}} &= p \cdot (p \cdot a_{12} + (1 - p) \cdot a_{22}) + (1 - p) \cdot (p \cdot a_{11} + (1 - p) \cdot a_{21}). \end{aligned} \quad (4)$$

The expected payoff of a responsive individual in the resident environment  $(\hat{f}, \hat{\theta}(\hat{p}))$  is given by:

$$W_r(\hat{f}, \hat{\theta}) = \hat{f} \cdot w_{r, \hat{r}} + (1 - \hat{f}) \cdot w_{r, \hat{u}} - c \quad (5)$$

per interaction, where  $w_{r, \hat{i}}$  are the expected payoffs to an responsive individual dependent on whether it interacts with a responsive or an unresponsive individual. These payoffs are given by:

$$\begin{aligned} w_{r, \hat{u}} &= \int_0^1 (\hat{p} \cdot (\hat{p} \cdot a_{21} + (1 - \hat{p}) \cdot a_{22}) + (1 - \hat{p}) \cdot (\hat{p} \cdot a_{11} + (1 - \hat{p}) \cdot a_{12})) \cdot \hat{\theta}(\hat{p}) d\hat{p} \\ &= a_{21} \cdot (Var(\hat{p}) + E(\hat{p})^2) + (a_{22} + a_{11}) \cdot (E(\hat{p}) \cdot (1 - E(\hat{p}))) - Var(\hat{p}) + \\ &\quad a_{12} \cdot (1 - E(\hat{p})) \cdot (2 - E(\hat{p})) + Var(\hat{p}) \\ w_{r, \hat{r}} &= \Phi_r \cdot (\Phi_r \cdot a_{22} + (1 - \Phi_r) \cdot a_{21}) + (1 - \Phi_r) \cdot (\Phi_r \cdot a_{12} + (1 - \Phi_r) \cdot a_{11}) \end{aligned} \quad (6)$$

where  $\Phi_r$  is the proportion of responsive individuals that chose action 1 in their last round, which changes according to the difference equation:

$$\Phi_r^t = \hat{f} \cdot (1 - \Phi_r^{t-1}) + (1 - \hat{f}) \cdot (1 - E(\hat{p})). \quad (7)$$

The unique stable equilibrium solution of this recurrence relation is given by:

$$\Phi_r = \frac{\hat{f} + (1 - \hat{f}) \cdot (1 - E(\hat{p}))}{1 + \hat{f}}. \quad (8)$$

### 3. Evolutionary Equilibrium

#### Responsive individuals invade a population of unresponsive individuals

Consider a population of unresponsive individuals, that is  $\hat{f} = 0$ . We assume that this population is at its evolutionary equilibrium. At that point, the frequency distribution of  $p$  is constrained by the fact that both actions achieve equal payoff.

The expected payoff to action 1 is given by

$$E(\hat{p}) \cdot a_{11} + (1 - E(\hat{p})) \cdot a_{12}, \quad (9)$$

the expected payoff to action 2 by

$$E(\hat{p}) \cdot a_{21} + (1 - E(\hat{p})) \cdot a_{22}. \quad (10)$$

At evolutionary equilibrium, the frequency distribution of  $p$  thus satisfies

$$E(\hat{p}) = (a_{12} - a_{22}) \cdot \delta^{-1} \quad (11)$$

where  $\delta = (a_{12} - a_{22}) + (a_{21} - a_{11})$ .

Consider the invasion prospects of a rare responsive mutant in such a population. With equations (3) and (5), the payoff difference  $\Delta_{r,\hat{u}}$  between this mutant and the unresponsive resident is given by

$$\Delta_{r,\hat{u}} = w_{r,\hat{u}} - w_{\hat{u},\hat{u}} - c \quad (12)$$

per interaction, which, with equations (4) and (6), simplifies to

$$\delta \cdot \text{Var}(\hat{p}) - c. \quad (13)$$

Responsive individuals can thus invade a population of unresponsive individuals whenever the variation present in this population is large enough, that is

$$\text{Var}(\hat{p}) > \frac{c}{\delta}. \quad (14)$$

### Responsive individuals do not go to fixation

Consider the invasion prospects of a rare unresponsive mutant with strategy  $p$  in a population of responsive individuals, that is  $\hat{f} = 1$ . With equations (3) and (5), the payoff difference between this mutant and the responsive resident is then given by:

$$\Delta_{ur,\hat{f}}(p) = w_{ur,\hat{f}} - w_{\hat{f},\hat{f}} + c \quad (15)$$

per interaction, which, with equations (4), (6) and (8) reduces to

$$\Delta_{ur,\hat{f}}(p) = \delta \cdot \left( p^2 - p + \frac{1}{4} \right) + \left( \frac{1}{2} - p \right) \cdot (a_{21} - a_{12}) + c. \quad (16)$$

From this follows directly that an unresponsive mutant with  $p = \frac{1}{2}$  obtains a higher payoff than the resident since

$$\Delta_{ur,\hat{f}}\left(\frac{1}{2}\right) = c > 0, \quad (17)$$

which shows that a population of responsive individuals is not evolutionarily stable. In fact, whenever  $a_{12} > a_{21}$ , all unresponsive mutants with  $p > \frac{1}{2}$  obtain a higher payoff than the resident since  $\Delta_{ur,\hat{f}}(p)$  is a strictly convex function in  $p$ , that is

$$\frac{d^2 \Delta_{ur,\hat{f}}}{dp^2} = 2 \cdot \delta > 0 \quad (18)$$

and

$$\left. \frac{d\Delta_{ur,\hat{f}}}{dp} \right|_{p=\frac{1}{2}} = a_{12} - a_{21}. \quad (19)$$

Similarly, whenever  $a_{12} < a_{21}$ , all unresponsive mutants with  $p < \frac{1}{2}$  obtain a higher payoff than the resident.

### Coexistence of unresponsive and responsive strategies

From the last two sections follows directly that, at any evolutionary equilibrium, both responsive and unresponsive strategies coexist, that is

$$0 < f^* < 1. \quad (20)$$

### Unresponsive individuals adopt pure strategies

At an evolutionary equilibrium, unresponsive individuals will always adopt one of the pure strategies, that is  $p = 0$  or  $p = 1$ . To see this, consider that an internal evolutionary equilibrium,  $0 < p < 1$ , is characterized by a vanishing selection gradient,  $dW_u/dp = 0$  (no directional selection), and a negative second derivative  $d^2W_u/dp^2 < 0$  ( $p$  is a local ESS) at that equilibrium. From this follow directly that an internal  $p$  can never be a local ESS since

$$\frac{d^2W_u}{dp^2} = 2 \cdot \hat{f} \cdot \delta > 0. \quad (21)$$

### Dimorphisms are evolutionarily unstable

It follows from the above analysis that there are three candidate evolutionary equilibria left: two dimorphic equilibria at which responsive individuals coexist with one unresponsive type ( $p = 0$  or  $p = 1$ ) and a trimorphic equilibrium at which responsive individuals coexist with two unresponsive types ( $p = 0$  and  $p = 1$ ).

Let  $f_1$  and  $f_2$  denote the frequency of individuals that always choose action 1 ( $p = 1$ ) and 2 ( $p = 0$ ), respectively, and  $f_r = 1 - f_1 - f_2$  the frequency of responsive individuals in the population. Dependent on  $(f_r, f_1, f_2)$  the payoffs to these three behavioural types per interaction are given by

$$\begin{aligned} W_1 &= f_1 \cdot a_{11} + f_2 \cdot a_{12} + f_r \cdot a_{12} \\ W_2 &= f_1 \cdot a_{21} + f_2 \cdot a_{22} + f_r \cdot a_{21} \\ W_r &= f_1 \cdot a_{21} + f_2 \cdot a_{12} + f_r \cdot w_{r,r} \end{aligned} \quad (22)$$

where

$$w_{r,r} = \Phi_r^2 \cdot a_{22} + \Phi_r \cdot (1 - \Phi_r) \cdot (a_{12} + a_{21}) + (1 - \Phi_r)^2 \cdot a_{11} \quad (23)$$

gives the expected payoff of an responsive individuals when encountering another responsive individual, and  $\Phi_r$  the proportion of responsive individuals that chose action 1 in their last round, which is, with equation (8), given by

$$\Phi_r = \frac{f_r + f_2}{1 + f_r}. \quad (24)$$

We now show that, whenever

$$a_{12} > a_{21} \quad (25)$$

neither of the two dimorphic equilibria is evolutionarily stable. The proof for  $a_{12} < a_{21}$  runs analogously.

Consider first a dimorphic candidate equilibrium with  $f_1 = 0$ . At that candidate, individuals that adopt the pure strategy 2 obtain the payoff

$$W_2 = f_2 \cdot a_{22} + f_r \cdot a_{21}. \quad (26)$$

Compare this with the payoff to an unresponsive mutant that always adopts action 1 which is given by

$$W_1 = f_2 \cdot a_{12} + f_r \cdot a_{12} = a_{12} \quad (27)$$

which, since  $a_{12}$  is the maximal payoff that can be obtained, is always higher than that of the unresponsive resident individual. A dimorphic candidate with  $f_1 = 0$  is thus never evolutionarily stable.

Consider next a dimorphic candidate equilibrium with  $f_2 = 0$ . At that candidate, individuals that adopt the pure strategy 1 obtain the payoff

$$W_1 = f_1 \cdot a_{11} + f_r \cdot a_{12} \quad (28)$$

Compare this with the payoff to an unresponsive mutant that always adopts action 2 which is given by

$$W_2 = f_1 \cdot a_{21} + f_r \cdot a_{21} = a_{21}. \quad (29)$$

The payoff difference between the unresponsive mutant and the unresponsive resident is thus given by

$$W_2 - W_1 = a_{21} - a_{11} + f_r \cdot (a_{11} - a_{12}). \quad (30)$$

The unresponsive mutant can invade if and only if this payoff difference is positive, that is, whenever

$$f_r < \frac{a_{21} - a_{11}}{a_{12} - a_{11}} \quad (31)$$

at that candidate. The unresponsive mutant can thus invade if and only if the frequency of responsive types at the candidate is not too large. We now show that condition (31) is in fact always true at our candidate.

To simplify matters, we make use of the fact that we can always rescale our payoff matrix (1) by multiplying all elements with the same number and/or adding the same number to all elements without changing the equilibrium properties (1) of our game. In particular we first subtract  $a_{11}$  from all elements and then divide all elements by  $(a_{12} - a_{11})$ . Our new payoff matrix is thus given by

$$\begin{array}{cc}
 & \text{action 1} & \text{action 2} \\
 \text{action 1} & 0 & 1 \\
 \text{action 2} & \tilde{a}_{21} & \tilde{a}_{22}
 \end{array} \tag{32}$$

where

$$\tilde{a}_{21} = \frac{a_{21} - a_{11}}{a_{12} - a_{11}} \tag{33}$$

and

$$\tilde{a}_{22} = \frac{a_{22} - a_{11}}{a_{12} - a_{11}} \tag{34}$$

with, in view of our assumptions (2) and (25),

$$0 < \tilde{a}_{21} < 1 \tag{35}$$

and

$$\tilde{a}_{22} < 1. \tag{36}$$

At the candidate, the payoff differences between the responsive resident and the unresponsive resident type is given by

$$\Delta_{r,u} = (W_r - W_1) \Big|_{f_2=0} \tag{37}$$

which is strictly decreasing in the frequency  $f_r$  of responsive individuals in the populations since

$$\frac{\delta \Delta_{r,u}}{\delta f_r} = A \cdot (f_r^3 + 3 \cdot f_r^2) + B \cdot f_r - 1 - \tilde{a}_{21} < 0 \tag{38}$$

where

$$\begin{aligned}
 A &= \tilde{a}_{22} - \tilde{a}_{21} - 1 < 0 \\
 B &= -\tilde{a}_{21} - 1 < 0.
 \end{aligned} \tag{39}$$

Notice that the responsive mutant can invade if and only if

$$f_r < \tilde{a}_{21} \quad (40)$$

At that threshold the payoff difference between the responsive resident and the unresponsive resident type is given by

$$\Delta_{r,u} \Big|_{f_r=\tilde{a}_{21}} = \tilde{a}_{21}^3 \cdot (\tilde{a}_{22} - 1) - \tilde{a}_{21}^4 \quad (41)$$

which, in view of (35) and (36) is always negative. Since the payoff difference is strictly decreasing in the frequency  $f_r$  of responsive individuals in the populations and all resident types have to achieve equal payoff at an equilibrium, the equilibrium frequency of responsive types at the candidate equilibrium must always satisfy (41). From this follows that the unresponsive mutant that always adopts action 2 obtains a higher payoff than the unresponsive resident (see equation (30)). The candidate is thus never an evolutionary equilibrium.

## 4. References

1. Hofbauer J & Sigmund K (1998) *Evolutionary Games and Population Dynamics*. (Cambridge Univ. Press, Cambridge, UK).