Evolution of cooperative personalities in a cooperation game

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Introduction

Recently, empirical research suggests that animals show different personalities within a population, which is defined as different individual behaviour which is consistent over time (e.g. as a juvenile and as an adult) and context (e.g. in interaction with a predator and a potential mate). [1] This is found in for example birds, chimpanzees, fish, amphibians [2], spiders [3] and insects [4]. From an adaptive perspective, an infinite plasticity of behaviour would be preferable, since an individual would be able to exhibit optimal behaviour in any kind of situation. Then why is this not observed in the empirical data? Could some poorly understood evolutionary mechanism be at the core of this?

While aggressiveness and responsiveness [5] have been subject to recent research, no models shed light on cooperation as a personality characteristic. It has been suggested that consistent behavioural differences could be the result of social interactions. [6] As seen with aggressiveness, individuals of many different organisms show different behaviour regarding cooperativeness. While cooperation can be suggested as an inherited trait, some more properties could be the core of development of personalities, such as responsiveness. The aim of this study is to look at the influence of responsiveness on the development of cooperative behaviour. Do different cooperative personalities evolve to coexist in populations where responsiveness is subject to mutation? What is the consequence of cooperation in a population?

In order to simulate cooperation, a snowdrift game was used. In a snowdrift game, two individuals interact with one another to perform a certain task. When at least one individual decides to cooperate, both individuals gain the benefits of completing the task. However, cooperating does entail a cost. When both individuals cooperate, this cost is shared between them.

*Snowdrift general benefits = 4, costs = 2*

*Table 1 and 2. Pay-off matrices of snowdrift game.*

*Figure 1. Fitness graph of snowdrift game.* 🡪

The right shows the fitness graph of the snowdrift game. The benefits (4) and the costs (2) are the same as used in our model. On the x-axis the population’s mean tendency to cooperate is given, whereas the y-axis shows the expected fitness. When the whole population defects (tendency to cooperate is zero), the best strategy to play is to cooperate, because then the task will at least be performed. The mean tendency to cooperate will increase as a result of this. When the tendency to cooperate is 1 for the whole population, it would be better to defect. The chance is very high you’ll receive the benefits, without the costs. This would decrease the mean tendency to cooperate. An evolutionary stable strategy is predicted at around 2/3 (0.67) of the population.

Model set-up

*Payoff matrix*

**General: Snowdrift: Benefits = 4, costs = 2:**

C++ is used to implement the model. A population consists of 1000 individuals, who all have a certain intrinsic tendency to cooperate (P0) between 0 and 1. This trait determines whether the individual cooperates or defects during a given interaction. Each individual has 10 interactions within its lifetime with randomly chosen individuals from the population. The interactions are based on the snowdrift game, which means that when either individual cooperates, both receive the benefits, but only the one who cooperates receives the costs. When both cooperate, they share the costs. The payoff one receives from the interactions is taken to be the individual’s fitness. These fitness values are used as the weights for a weighted lottery[[1]](#footnote-1) in order to determine which individuals produce how many offspring for the next generation. During the reproduction, there is a chance (µ) of 0.01 that a mutation occurs. This mutation leads to a small change in the P0 value, taken from a Gaussian distribution with a standard deviation of 0.01.

Simple model without responsiveness

This model was used as the basis for later developments, but here the aim was mainly to see if the expected equilibrium from the pay-off matrix of the snowdrift game was found.

*Figure 2. The left shows the mean cooperativeness of three populations with different initial values. The right shows the standard deviation of the three populations.*

The first figure shows the three different populations to see if the equilibrium that is predicted is reached. The standard deviations show that the variation is relatively low, with some extreme outburst, which is due to stochasticity. With such a low standard deviation (more than 95% of the data is between 0.67±0.04), it is fair to say that no personalities emerged. The expected cooperativeness equilibrium is indeed found at approximately 0.67.

Introducing responsiveness

Responsiveness is introduced as another trait value (Pi) which is either 0 or 1. An individual with a Pi of 0 is unresponsive and one with a Pi of 1 is responsive. A responsive individual can observe which strategy its partner used in a previous interaction and respond to that by changing its own strategy. The responsive individual does have to pay a fitness price for this, however. Responsiveness is also affected by mutation; during the reproductive phase, there is a 0.01 chance of mutation (µ) which turns a responsive individual into an unresponsive individual and vice versa.

Responsiveness as a Boolean

*Price for responsiveness: 0.0*

*Figure 3. Three populations with different initial cooperativeness levels (high, medium and low). On the left, the mean cooperativeness is shown for the average of the population, unresponsive and responsive individuals. The right shows the fraction cooperatives in the population, while no responsiveness can occur during the first 100,000 generations.*

The mean cooperativeness goes to the equilibrium at 2/3 cooperativeness in all three populations before the responsiveness can occur. Then, responsiveness emerges very quickly in all three cases; in the one with low initial cooperativeness, the responsives go to an equilibrium immediately, but the ones with high and medium initial cooperativeness first reach a high fraction of responsives, before reaching the same equilibrium of around 55% responsives. At the moment the responsiveness emerges the unresponsive individuals reach an equilibrium where they always defect, while the responsives have a high cooperativeness. The high initial cooperativeness case shows an intermediate state, where unresponsives keep a high responsiveness for a bit longer before going to almost no cooperation. All the cases show a dip in the average of the population as responsiveness emerges.

Thus, responsiveness is able to emerge from a totally unresponsive population. Unresponsives always seem to choose defect over cooperation.

*Price for responsiveness: 5.0*

*Figure 4. The mean cooperativeness and the fraction responsives are shown for a population with medium initial cooperativeness. For high and low initial cooperativeness, see extended data 3.*

The graph on the left shows the average cooperativeness, which is almost the same as the cooperativeness of the unresponsives, because almost no responsives are present. This is seen in the graph on the right. The price is too high for responsiveness to maintain a substantial part of the population. Now, only due to stochasticity very low numbers of responsives are present in the population.

*Calculating the threshold price*

According to Wolf et al. [7], the fitness price an individual pays for obtaining information has to be sufficiently low in order for responsiveness to emerge in the population. The exact value can be calculated by the following formula.

The different α values are the values from the payoff matrix, see p. 2. This simplifies the formula to the following.

In the simulation with a price of 0.0, we found that the standard deviation was approximately 0.02. This leads to the assumption that the price can be no larger than 0.0012 if responsiveness is to emerge.

First, a price of 0.001 was tested to see if responsiveness could occur.

*Price for responsiveness: 0.001*

*Figure 4. responsiveness emerges when the price is 0.001.*

Responsiveness emerges very quickly, within 100 generations, so several other prices were simulated as well.

*Price for responsiveness: 0.5*

*Figure 5. population with low initial cooperativeness shows responsiveness by a price of 0.5.*

One of the three populations (different initial cooperativeness) which were tested at first, showed an emerge of responsiveness. Upon these findings, ten additional simulations were performed under the same circumstances. See extended data 5. Out of the ten simulations, eight showed an emergence of responsiveness. This seems to go directly against the previously shown equations of the maximum price for responsiveness.

Responsiveness as a continuous trait

Instead of individuals always being responsive or always being unresponsive, responsiveness was changed to be anything between 0 and 1. This way the model would become more realistic, because responsiveness is sort of like a spectrum: some individuals respond more than others, but don’t always respond. From the personality’s perspective, a more static behaviour is expected, but this can also be slightly plastic. Therefore, it is more logical to have a slight change in the responsiveness instead of a choice between responsive and unresponsive.

Results here

Conclusion and discussion

It seems that by introducing responsiveness to a population, a clear difference in strategy is sparked as two obvious personalities emerge. Responsive individuals tend to go for cooperation, while the unresponsive individuals end up defecting most of the time. This is probably due to a discrepancy in the pay-off matrix of the game dynamics of the snowdrift game. Between α12 (B – C) and α21 (B) for an unresponsive individual interacting with a responsive individual, α21 gives a higher fitness than α12, and therefore this is the strategy which will be more successful. As a result of this, unresponsive individuals in a highly responsive populations tend to defect after reaching equilibrium. See figure 3, high initial responsiveness. Due to the emergence of responsiveness, the average cooperativeness of the population dips and the number of unresponsive individuals becomes very low. Only until the unresponsive individuals change their strategy to defect more often, do they regain a substantial part of the population.

The equation stated by Wolf et al. was used to calculate the max price for responsiveness under certain variation in the population. It was found that even with a price as high as 0.5, responsiveness came about in the population, see extended data 6.

In this model, only the game dynamics of a snowdrift game were presented, while it would give a much clearer image of cooperation if other sorts of game were introduced as well. One direct suggestion would be to look at a snowdrift game with a more symmetric fitness matrix.

One could also imagine a population with several meta-populations, who all have a certain exchange of individuals. The interesting thing would be to see if big differences evolve next to each other and if they can trigger responsiveness for example in other non-responsive meta-populations.

**Appendix**

Literature list

1. Sih, A., Bell A., Johnson J. C. (2004) “Behavioral syndromes: an ecological and evolutionary overview.” *Trends in Ecology and Evolution*. **19**, 372 – 378

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Brodin, T. and Johansson, F. (2004) “Conflicting Selection Pressures on the Growth/predation-Risk Trade-Off in a Damselfly,” *Ecology*, **85**, pp. 2927–2932. doi: 10.1890/03-3120.

Wolf. M., van Doorn G.S., Weissing F.J., (2008) “Evolutionary emergence of responsive and unresponsive personalities”, *PNAS*, vol.105, no. 41, pp. 15825 – 15830.

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1. Wolf, M., Van Doorn, G. S. and Weissing, F. J. (2011) “On the Coevolution of Social Responsiveness and Behavioural Consistency,” *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 278(1704), pp. 440–448.

Extended data

1. Simple model 0.0 (no responsiveness)

Data of the first model, where strategy is a Boolean. As seen in the graph below, two thirds of the population will cooperate, as is expected.

*Above shows the development of the mean fraction of cooperatives in a population of three population with different initial conditions. The blue points represent the population with 95% cooperatives, grey the one with 67% and orange the one with 5%.*

1. Model 1.1, fitness chances used for implementation

|  |  |  |
| --- | --- | --- |
| Partner  Focal | Responsive | Unresponsive |
| Responsive | Cf = 1 – Pmean  Df = Pmean  Cp = 1 – Pmean  Dp = Pmean | Cf = 1 – P0(p)  Df = P0(p)  Cp = P0(p)  Dp = 1 – P0(p) |
| Unresponsive | Cf = P0(f)  Df = 1 – P0(f)  Cp = 1 – P0(f)  Dp = P0(f) | Cf = P0(f)  Df = 1 – P0(f)  Cp = P0(p)  Dp = 1 – P0(p) |

*Table 3. chances a focal individual and its partner receive a certain fitness based on the different strategies played in different scenario’s. The* f *means focal,* p *means partner,* D *is to defect and* C *is to cooperate.*

Above, four scenarios in model 1.1 are laid out an individual can be responsive and unresponsive and can interact with a responsive and unresponsive individual. It shows the chances an individual which is either responsive or not responsive will cooperate or defect when interacting with a responsive or not responsive individual. Cf = chance focal individuals cooperate, Df­ = chance focal individual defects, Cp and Dp­ are the same but than for the partner. Pmean is the average cooperativeness in the last generation, where P0 is an individual’s intrinsic cooperativeness.

1. Model 1.1, high price for responsiveness data

Below the data for the high price for responsiveness is shown for high and low initial conditions.

Both the graphs for high initial cooperativeness and the graphs for low initial cooperativeness show extremely low responsiveness and therefore a similar average to no responsiveness (first 100,000 generations).

1. Model 1.1 null (control on Model 1.1)

This is a control model to see if an equilibrium is found in the responsiveness. Therefore, no selection is made for the next generation based upon fitness. Instead of a weighted lottery, a uniform distribution is used for determining the next generation.

Three replica populations are run in a simulation over 200,000 generations. The last part is the most useful, due to the absence of initialisation effects (which come about when there is not much variation just yet), therefore only the last 500 generations are shown.

*Above shows the fraction of responsiveness in three replica populations, which oscillates around 0.5.*

As no selection is preformed on the populations, the population goes to random oscillations around 0.5 as is expected.

*Above shows the fraction of the populations which is responsive. The mean cooperativeness of two of the three replicas is also shown. Blue is the average of the population, grey shows the average of the unresponsive individuals and orange that of the responsive individuals.*

Two different outcomes of drift are shown in the graphs above, where drift pushes the two different population to different average cooperativeness. Interestingly, the unresponsive individuals always seem to have little variation, at least less than the responsive individuals. This makes sense when responsive individuals randomly encounter unresponsive and responsive individuals and are therefore more influenced by chance, while unresponsive stick to their intrinsic cooperativeness.

*Above shows the standard deviation of the unresponsive individuals of three populations.*

Although, more variation is perhaps expected in the three populations shown above, the small standard deviation is due to the small mutation rate (= 0.01). On top of that, these graphs show only the last 500 generation, more variation could be possible over the whole course.

The null model of model 1.1 shows that without selection on responsiveness an equilibrium of 0.5 is reached with high fluctuations. Generic drift takes over the main strategies for the populations. This shows the robustness of the model 1.1.

1. Responsiveness with a price of 0.5 extra data

Two of the 10 extra simulations run for responsiveness price of 0.5 with several different initial conditions. The simulations first run 100,000 generation to get to equilibrium as seen before. Then responsiveness is introduced by mutations. In 8 of the 10 simulations, responsiveness came up. The lower fraction of responsive individuals is in line with the higher price for responsiveness.

1. Responsiveness as continuous trait
2. Different benefits and costs in snowdrift game

*Fitness graph of snowdrift game with benefits = 5, costs = 4.*

To see if the dynamics of a snowdrift game change when benefits and costs are different, the equilibrium was changed to 1/3. This was done by calculating the new benefits and costs, 5 and 4 respectively.

*The left shows the mean cooperativeness for the average of the population, responsives and unresponsives. The right is the fraction of responsives in the population.*

It can be seen that the equilibrium is lower than expected, but that the dynamics qualitatively don’t change. Still the unresponsives defect resulting in the fact that the responsives cooperate more. Therefore, changing the benefits and costs doesn’t change the game dynamics qualitatively.

1. This weighted lottery only works with positive fitness values. To ensure that negative fitness doesn’t occur, every individual receives a baseline fitness of 11 times the price. Negative fitness doesn’t have a biological meaning, therefore this is implemented. [↑](#footnote-ref-1)