Evolution of cooperative personalities in a cooperation game

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Introduction

Recently empirical research suggest that animals show different personalities within a population, which is defined as different individual behaviour that 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]](#footnote-1) This is also found in birds, chimpanzees, fish, amphibians[[2]](#footnote-2), spiders [[3]](#footnote-3)and insects[[4]](#footnote-4). From an adaptive perspective, an infinite plasticity of behaviour would be preferable, since an individual would have the right behaviour in any kind of situation. Than 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 have been subject to recent research, no models shed light on cooperation as a personality characteristic. As seen with aggressiveness, individuals of many different organisms show different behaviour on cooperativeness. While cooperation can be suggested as an inherited trait, some more properties could be the core of development of personalities, like responsiveness. The aim 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 of mutation? What is the consequence of cooperation in a population?

The way the cooperation was implemented in the models, was by taking a pay-off matrix of a snowdrift game.

*Snowdrift general benefits = 4, costs = 2*

*Table 1 and 2.*

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 tendency to cooperate is given, where the y-axis shows the fitness. When the whole population defects (tendency to cooperate is zero) the best strategy to play is to cooperate. See also the pay-off matrix. The equilibrium will move to the right, until the equilibrium is reached at about 0.67. 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 push the equilibrium to the left. An evolutionary stable strategy is predicted at around 2/3 (0.67) of the population.

For future research, more aspects of cooperation can be looked into from different games like the prisoner’s dilemma and stag hunt.

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[[5]](#footnote-5) 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 the basis for later developments, where the aim was mainly to see if the expected equilibrium from the pay-off matrix of the snowdrift game was found.

*Figure 1. 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. The extreme values are considered 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 fait to say no personalities emerged.

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

|  |  |  |
| --- | --- | --- |
| 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 who is responsive or not responsive will do 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 strategy of the last generation, where P0 is the intrinsic.

First,we show the data where the price is zero, so that responsiveness can definitely occur compared to the next case where the price is very high and no responsiveness can emerge.

*Price for responsiveness: 0.0*

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

The mean cooperativeness goes to the equilibrium at 2/3 cooperativeness in all three populations before the responsiveness can occur. Than responsiveness emerges very quick in all three cases, where in the low initial cooperativeness the responsives go to an equilibrium immediately. The high and medium 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 total 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 of a population with medium initial cooperativeness. For high and low initial cooperativeness, see extended data 3.*

The graph to the left shows the average cooperativeness which is almost the same as the cooperativeness of the unresponsives, while almost no responsives are present. This is seen in the graph the right. The price is to 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[[6]](#footnote-6) et al., 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 0.02. This leads to assume that the price can be no larger than 0.0012 if responsiveness is to emerge.

*Price for responsiveness: 0.001 …*

Responsiveness as a continuous trait

Instead of immediate change in strategy in a responsive individual, a slighter chance to do a certain strategy is introduced. This way the model would become more realistic, because sudden changes in strategy are not what we expect. From the personality’s perfective, a more static behaviour is expected, which is not totally fixed. Therefore, it is more logical to have a slight change in the responsiveness instead of a choice between responsive and unresponsive.

Unfortunately, the model showed no more than 10% responsiveness after 5 million generations. Within 300 generation about 1% responsiveness occurs, which indicates that the model does work properly. Only it showed no high level of responsiveness as model before. Therefore, we did not look into this further. (See extended data … for the graphs).

Introducing signalling

Conclusion and discussion

*Conclusion/discussion*

* *Further research possibilities 🡪 more cooperation games, metapopulations?*
* *Unresponsives always seem to choose defect over cooperation as soon as responsiveness emerges.*

Possible extensions model/extra analysis/further research

* Meta-populations
  + Randomly distribute the population into a community of size (between 20 and 100 or something). Than interactions only within community. Every generation, new randomly distributed meta-populations are defined. Unresponsive in population zero.
    - New meta-populations after every newly formed generation, because in our model no sexual reproduction is implemented.
  + Expectation: emerge of responsive individuals.
* Signalling implementation
* Is there a correlation between information tendency and the P0? *Ido Pen*

**Appendix**

Literature list

*Interesting not yet used literature:*

* Smaldino, P. E., Flamson, T. J. and McElreath, R. (2018) “The Evolution of Covert Signaling,” *Scientific Reports*, 8(1). doi: 10.1038/s41598-018-22926-1.

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 third 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 point represents the population with 95% cooperatives, grey with 67% and orange with 5%.*

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 as 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 with 200,000 generations. The last part is the most interesting, 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 mean cooperativeness of two of the three replicas. Blue is the average of the population, grey shows the average of the unresponsive individuals and orange 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 then the responsive individuals. This makes sense when responsive individuals randomly encounter unresponsive and responsive individuals and are there more liable for chance, while unresponsive tend to sick to the strategy they have.

*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 of 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. Different benefits and costs in snowdrift game

1. Sih, A., Bell A., Johnson J. C. (2004) “Behavioral syndromes: an ecological and evolutionary overview.” *Trends in Ecology and Evolution*. **19**, 372 – 378 [↑](#footnote-ref-1)
2. Gosling SD (2001) “From Mice to Men: What Can We Learn About Personality from Animal Research?” *Psychological bulletin*, 127(1), pp. 45–86. [↑](#footnote-ref-2)
3. Johnson J. C. & Sih A. 2005 precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for behavioural syndromes. *Behav. Ecol. Sociobiol.* **58**, 390 – 396 [↑](#footnote-ref-3)
4. 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. [↑](#footnote-ref-4)
5. 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-5)
6. 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. [↑](#footnote-ref-6)