Chapter 2

Coevolution of Altruism and Migrating Behavior\(^1\)

The evolution of altruism has been studied extensively within evolutionary biology. Its popularity originates partially in its relevance to human society. It raises important issues with respect to the way we live together and how we can maintain a cooperative society. The evolutionary origin of altruistic/cooperative or egoistic/aggressive behavior is also relevant for the affective processes, which have an important function in regulating such behavior. Altruism has also drawn interest because of its relevance to the discussion about the nature of the evolutionary process. It has been a central topic in the debate between proponents of group selection and proponents of individual selection (Hamilton, 1964; Maynard Smith, 1964; Wilson & Sober, 1994). In group selection evolution is seen as working for the good of the species. In the opposing theory, individual selection, evolution is seen as working for the good of the individual, or in Dawkins terms, for the good of the gene (Dawkins, 1976). For many purposes those views would not make much difference but they do with respect to altruism. Group selection would expect it to be widespread and individual selection would expect it to be very exceptional. Dawkins, who defends the individual selection perspective, says about the likelihood of altruism (in his gene centered terminology):

...as we shall see, there are special circumstances in which a gene can achieve its own selfish goals best by fostering a limited form of altruism at the level of individual animals. ‘Special’ and ‘limited’ are important words in the last sentence. Much as we might wish to believe otherwise, universal love and the welfare of the species as a whole are concepts that simply do not make evolutionary sense (Dawkins, 1976, p.2).

This is the view that has become more or less generally accepted, in which altruism is considered to be exceptional (for other views see Wilson & Sober, 1994). This paper is written from this individual/gene selection perspective, and the form of altruism discussed, should be considered one of those special cases, which depend on special circumstances.

---

\(^1\) This chapter is based on Brinkers and den Dulk (1999) and den Dulk and Brinkers (2000)
Much of the research on altruism is either theoretical or mathematical work. The current research investigates altruism through computer simulations. There is a large body of computer simulation work referred to as altruism research, but most of those studies have focused on Trivers’ (1971) concept of reciprocal altruism (Axelrod & Hamilton, 1981; Nowak & May, 1992). Reciprocal altruism is favored in evolution because the actor receives a reward in the long run, usually because others will act altruistic in return. Such behavior is, thus, in a sense not altruistic but self-serving in the long run. Therefore, both proponents of group selection and individual selection would grand reciprocal altruism possible, and it is thus less relevant to this discussion.

In this study the focus is on ‘true’ altruism, which we define as behavior which favors other individuals at the expense of the altruist itself. Reciprocal altruism is in this paper not considered altruism but self-serving behavior. And self-serving behavior is not defined as individual reproductive success, in which case parental care would not count as altruistic behavior. One of the special circumstances which allow altruism depends on a mechanism called kin selection (or inclusive fitness) in which altruism is selectively directed towards kin (Hamilton, 1964). A simple tool for understanding this mechanism is Hamilton’s rule (Hamilton, 1964), which states that altruism is favored when \( rb - c > 0 \), where \( c \) is the fitness cost to the altruist, \( b \) is the fitness benefit to the beneficiary and \( r \) is their genetic relatedness. An example is an inherited tendency of an organism to protect its children, while putting itself at risk. When a parent has this tendency it is likely his children will have this tendency too. Although the parent’s chances of survival will decrease when protecting its children, the chances of survival for the children (with that same tendency) will increase. When the product of benefit and relatedness is higher than the cost for the parent the tendency to protect children can spread. This kind of altruism towards kin seems quite limited, but it is not restricted to individuals who are recognized as close kin. In a population with little dispersal of individuals there is a high probability that randomly met others are relatives, and thus, altruism towards any other individual might evolve (Hamilton, 1964). In some cases the beneficiary might not be a relative, but such ‘misfiring of the rule’ (Dawkins, 1976) might be worth the cost if there is a high enough probability that the beneficiary is a relative.

The goal of this study is twofold. The first goal is to show that in a population with little dispersal the evolution of altruism is possible, even if it is not explicitly directed towards kin. This confirms earlier theoretical and simulation studies (Baalen & Rand, 1998; Hamilton, 1964; Todd, 1994; Wilson, Pollock, & Dugatkin, 1992). It remains a question, however, how common such situations of low dispersal are in natural environments (Wilson et al., 1992). Although this will probably not be very frequent, it might be underestimated, because, as van Baalen and Rand have mentioned, dispersal behavior is itself also subject to natural selection as any other trait (Baalen & Rand, 1998). Here our second goal comes in, which is to show that if the tendency to disperse is itself represented as a gene and controlled by an evolutionary process, a tendency not to disperse evolves among altruists. This suggests that the low dispersal condition, which is necessary for evolution of altruism, does not merely depend on coincidence, but is actively selected for. Populations with low dispersal might, thus, occur more often than could have been guessed without this prior knowledge.

We investigate the evolution of altruism in two different simulation setups. In both simulations dispersal is controlled by a probability of migration at birth. The first simulation is based on the classic prisoner’s dilemma paradigm (Axelrod & Hamilton, 1981). The second simulation uses free moving agents in an artificial life type of
setup. At a qualitative level the two different simulation setups produce the same results. The first part of both simulations shows that the evolution of altruism is possible with a limited dispersal of relatives, in concurrence with existing theories (Hamilton, 1964). The second part of both simulations demonstrates that a tendency not to migrate evolves among altruists if migration is itself selected for.

Simulation 1: The Evolution of altruism in a prisoner's dilemma

The purpose of this first simulation is to demonstrate that altruistic behavior can emerge in a world with limited migration of individuals. The simulation uses a two dimensional grid in which each cell is occupied by a player, who plays a prisoners dilemma game (Axelrod & Hamilton, 1981) with each of its neighbors. Within the prisoners dilemma two actors have to play a game in which both have the choice to either cooperate (C) or defect (D). If both choose to cooperate they both receive a certain reward $R$. If both choose to defect they both get a lower reward $P, R>P$. If, however, one decides to defect whereas the other decides to cooperate the defector gets the highest reward $T, T>R$, and the cooperator gets the lowest reward $S, P>S$. In sum, $T>R>P>S$. In a single trial prisoner's dilemma the best strategy is to always defect. In the iterated prisoner's dilemma, however, cooperation is an effective strategy because the players play repeatedly against the same opponent and have the opportunity to retaliate for the opponent's defections. Therefore, there is personal gain for the cooperator in the long run. In these simulations a single trial prisoner's dilemma is played between each pair of players. Nevertheless, cooperation can evolve because of the mechanism of kin selection. Kin selection can take effect, not because related individuals recognize each other, but because individuals are placed in a spatial representation of a 2 dimensional world, in which individuals remain next to each other during their lives. This causes games to be played primarily between related individuals.

The simulation world was a torus shaped grid of 100 by 100 cells, in which every cell was occupied by an agent. Each update cycle of the grid consisted of two parts. First, all agents played a one trial prisoner's dilemma with all of its eight direct neighbors. This resulted in a profit value, which was the summed return of these eight trials. Second, a new generation was created by replacing each agent with a copy of the neighboring agent with the highest profit value. Agents were thus born next to their parents, this way the migration was minimal. A successful agent could thus get eight children in the next generation. The agent itself was always replaced by a child of one of its neighbors, i.e. it could not get a child at its own position.

The agents performed one of two possible strategies, either always defect (all-D) or always cooperate (all-C). All-D agents were called egoists and all-C agents were called altruists. For the initial population, every cell was randomly set ($p = 0.5$) to altruist or egoist. This strategy was fixed for the duration of the simulation. Apart from this initial randomization the simulation was deterministic. When two cells had exactly the same profit value one had to be selected. Which parent was selected, however, made no difference because, as calculations showed, when two agents had the same profit value they also had the same strategy. This was because all 18 possible profit values were unique. These 18 values come from the 2 strategies (egoistic or altruistic) multiplied with the 9 possible neighbor configurations (the number of altruistic neighbors could ranging between 0 and 8, and the remainder would always be egoists).
The rewards for the prisoner's dilemma were: 10 points when you defect a cooperator, 9 points when both cooperate, 1 point when both defect, 0 points when you cooperate with a defector. This is a normal prisoner's dilemma pay-off in that it satisfies the $T>R>P>S$ relation. And also $2R > T + S$, which ensures groups of cooperators would do better on average than non-cooperators. For this simulation the difference between $R$ and $P$ had to be chosen such that in the practice of the simulation Hamilton's rule would be satisfied $(rb - c > 0)$. An example of how a small cluster of altruists could expand facing many egoists is described in Figure 1. With this pay-off scheme there was a relatively high reward in a $C-C$ game, compared to a $D-D$ game, but still less than a $D-C$ game, thus egoism will still be the best strategy in a one trial prisoner's dilemma.

![Figure 1](image)

Figure 1. In (a) four altruistic cells (All-C, shown in white) are facing a cluster of egoistic cells (All-D, shown in gray). Of the middle four cells we show the total profit values which would be gained after all games are played. The cells with profit 26 received their profit value from the two neighboring altruistic cells (2x10) and six neighboring egoistic cells (6x1). Whereas the altruist receives a total profit value of 27 from 3 neighboring altruists (3x9), it gains nothing from the egoists. In the next iteration all cells neighboring the altruist will be replaced by its children, as shown in (b).

To investigate the evolution of altruism a simulation was run with two conditions. In one condition—the no-migration condition—agents were born in a cell directly next to their parents. In the other condition—the migration condition—new agents were born on a random position on the map. By varying the location of birth (migration) we could investigate the influence of locality in the distribution of agents on altruism. Apart from the location of birth the two conditions were identical.

**Results:** In the no-migration condition ten simulations were run, all with a different initialization. All resulted in a stable amount of altruists, 96.5% averaged over all simulations. This demonstrated the main purpose of the simulation: altruism can be an evolutionarily stable strategy in viscous populations.

Most remaining egoists formed a static pair (like Figure 2 (a) and (b)), or a cycle of states (Figure 2 (c), (d) and (e)). These resemble the flasher and still-lifes in Conway's Game of Life (Poundstone, 1987). Interestingly, although not relevant for our purposes, there were also gliders that were very similar to the gliders in the Game of Life (Figure 2 (f)). Conway's glider was a configuration of cells in the game of life, which, because of the specific cell update rules, displaced themselves over the grid in a diagonal direction. Our 'glider' also displaced itself in a diagonal direction, only it was just a single configuration of cells and not a cycle of cells like Conway's glider.
Coevolution of altruism and migrating behavior

**Figure 2.** State (a) and (b) are static pairs of egoist (gray cells) which replace each other in consecutive iterations. States (c), (d) and (e) form a stable cycle; (b) to (c), (c) to (d) and (e) back to (c). State (f) is a 'glider' like configuration, which displaces one cell per iteration in the direction of the arrow.

In the migration condition the altruists all died in just a few iterations, demonstrating that the viscosity is a crucial factor and that with a high dispersal of relatives no altruism can evolve.

**Simulation 2: The evolution of migration in a prisoner's dilemma.**

In the first simulation there was low migration of the agents (new agents were placed besides their parent), whereas in the control simulation there was maximal migration (new agents could be placed anywhere on the map). In the following simulation, migration was not experimentally controlled but made an inherited property of the agents themselves, where a 'gene' controlled whether the agent was put next to the parent, or on a random position on the map. The migration 'gene' \( (p\text{-migrate}) \) could have values between 0 and 1, denoting the probability of migration, where 1 meant certain migrating. The initial population had random \( p\text{-migrate} \) values chosen from a uniform distribution between 0 and 1. The migration parameter of the parent determined the probability whether its child was put next to the parent or at a random cell. The random cell was always chosen from the population of cells which were occupied by migrating agents, so that they could not be placed on a cell which was already occupied by a non-migrating agent. At birth an agent inherited the migration parameter of the parent added with a random mutation between -0.01 and 0.01 chosen from a flat distribution. Resulting migration values outside the \([0,1]\) interval were clipped.

**Results:** Ten simulations with different initial seeds were run. All converged to a stable percentage of altruists. After 1000 iterations 79% of the agents were altruists whereas 21% were egoists (averaged over the last 100 iterations and all 10 replications). In Figure 3(a) we plotted the percentages over the first 200 iterations. Initially, the egoists rapidly increased in number, almost replacing all altruists. However, in each run a few clusters of altruists remained and these clusters expanded to fill the majority of the cells. The most interesting finding was that the migration probability for altruists approached 0.0 in all simulations. Averaged over all altruists of the last 100 iterations and 10 replications \( p\text{-migrate} \) was 0.017, whereas we should expect an average of 0.5 with undirected mutation. Thus, the evolutionary process itself had established the low migration, which is a precondition for the evolution of altruism. To formulate it another way: if altruism can benefit a sub-population which tends to stay together, then this tendency is itself subject to natural selection.

Besides altruists, there was a substantial percentage of egoists left in the population: 21% whereas in the first simulation only 3.5% were egoistic. Interestingly, the migration probability for all the egoists systematically approached 1.0 in all simulations. Averaged over all egoists of the last 100 iterations and 10 replications \( p\text{-migrate} \) was 0.96. The advantage of migration for the egoists is that it
offers a chance to get out of an environment of egoists into an environment of altruists. Although the probability of being born in an environment of altruists is low—because of the low $p$-migrate of the altruists—the benefit is very high once it happens, because an egoist surrounded by altruists will have eight children (see Figure 2 transition (c) to (d)). These eight children are again swapped somewhere else because of the high $p$-migrate of the egoists.

Figure 3(b) shows a density plot of all the individuals in the population over the first 160 iterations. All the high migration values belong to egoists and all low values to altruists. It is clear from this graph that two distinct groups of migration values emerged.

Figure 3. (a) Number of egoists and altruists (Y-axis) per iteration (X-axis). (b) Density plot of the p-migrate values (Y-axis) per iteration (X-axis). Per iteration a black dot was plotted for the p-migrate values of all individuals in the population. Initially all values between 0.0 and 1.0 were present, later two threads emerge, for high and low p-migrate values.

### Discussion on the prisoner's dilemma simulation

The main conclusion of the previous simulation is that the limited dispersal of relatives, which is necessary for the evolution of altruism, is itself controlled by natural selection.

In our simulation individuals stayed on exactly the same location after the start of their lives. This would not be a very realistic situation for freely moving animals in a natural setting. Strict immobility is not a necessity, however. Altruism could also evolve if relatives would migrate together in a group, for example in some kind of herding behavior. They do not need to be immobile with respect to their environment, but immobile with respect to the other individuals in their world.

The situation of total immobility might still be applicable to plants or trees. It would, for instance, be interesting to investigate 'aggression' between trees fighting for sunlight and resources in relation to the way they spread their seeds. This would thus predict that trees that are more aggressive to their neighbors tend to spread their seeds as far as possible, while those that are less aggressive will tend to spread them in their vicinity. If, however, a correlation between low aggression and vicinity spread of seeds is found, there is still the question whether, low aggression is caused by vicinity spread, or vicinity spread is caused by the mutual benefit of low aggression. On the basis of previous altruism research most theorists would probably consider the former explanation more readily. This research suggests the latter as a possible alternative.

A further conclusion, drawn from practical experience in designing the simulations, is that the evolution of altruism depends on the initial conditions. In
Coevolution of altruism and migrating behavior

Simulation setups with too few initial altruists (unreported), all altruists died out after just a few iterations. Once egoism had spread through the entire population it was resistant against invasion from altruists.

The river cross simulations

A general problem of simulation research is that arbitrary parameter settings can be crucial for the obtained results. The exact parameter settings have a rather obvious influence on the results, but there are many more choices made in the design of the simulation, or even in the structure of the computer program, that could be critical for the outcome. Even with great efforts to make the choices most carefully, there can still be no guarantee that the conclusions of the simulation can be generalized. Every simulation can in principle only tell us something about the behavior of that specific parameter set. In order to show that something is a general principle, no single simulation can suffice on its own, one has to demonstrate that the same principle occurs under a multitude of circumstances. To make a first step towards this more general claim we designed a second simulation, with a very different setup, in which we again let altruism evolve and again made migration subject to an evolutionary process. As Wiener put it 'Generality has to be found it can not simply be declared' (Webb, 1999).

In this simulation a population of agents had to survive and reproduce in a grid world consisting of islands. The islands were separated by narrow canals. In order to survive they had to gather food from the islands, but they could only reach these by crossing water while using another agent's body as a bridge. This other agent could form such a bridge by just stepping into the canal, as a consequence, however, this agent died of drowning. The tendency to step into water was taken as the measure of the altruistic behavior.

Simulation environment

The world consisted of 110 by 110 cells placed on a grid (torus). Each cell could either be a water cell or a land cell. Within this grid, 400 islands, each 10 by 10 cells, were placed. Canals of 1 cell in width separated the islands. Land cells could contain food or an agent, and water cells could contain a dead agent forming a bridge. A living agent could cross the canal by using this bridge.

Agent behavior: The agent's behavior was determined by four parameters: \( p_{water} \), \( p_{food} \), \( p_{land} \), \( p_{cross} \). In the first simulation all these parameters were subject to mutation. In the second and third simulation only \( p_{water} \) was subject to mutation, the others were fixed. The values for these parameters were based on the final values of the first simulation. Each of these parameters corresponded with one of four cells the agent could see in front of it: empty water, food on land, empty land, or a floating agent forming a bridge. The parameters represented the probability of stepping forward when in front of the corresponding type of cell. A random number, from the interval \([0,1]\) was drawn. When this number was below the corresponding \( p \) value the agent would step forward, otherwise it would randomly turn left or right on the spot. Apart from the cell in front of it the agent used no other information, and it had no internal state. Agents could not step on top of other living agents. When one was in front of it, it always turned randomly left or right on the spot. The agents were synchronously updated.

Food and Energy: After each cycle, hundred cells were randomly chosen anywhere on the map. On these cells a food patch was placed when it was an empty
land cell. When stepping on a food patch the energy of the food patch \((\text{EnergyFood})\) was added to the agent's energy and the food patch was removed. The agent always lost one unit of energy per iteration. When the agent used up all its energy it died of starvation.

**Water:** When stepping into water the agents immediately drowned. The agents remained 'floating' during a number of iterations as determined by the \(\text{BridgeTime}\) parameter. While floating, other agents could step on top of the agent using it as a bridge.

**Reproduction:** The agents could multiply through asexual reproduction. The agent gave birth when it had gathered enough energy \((\text{EnergyToGetChild})\). When a child was born the parent's energy was reduced by a certain amount of energy \((\text{EnergyCostChild})\) and this formed the starting energy of the child. The child inherited the parent's \(p\)-water value, but for each child a slight mutation was added. For each mutation, a random number was drawn from the interval \([-1,1]\) and this was multiplied by the \(\text{Mutation}\) parameter and was added to the \(p\)-water value. Resulting \(p\)-water values outside the \([0,1]\) interval were clipped. A newborn agent was placed on the cell directly behind its parent.

**Age:** When agents reached the maximum age \((\text{MaxAge})\), expressed in the number of iterations after birth, they died of old age.

**Initialization:** At the start of each simulation, a number of agents \((\text{InitNumAgents})\) and a number of food patches \((\text{InitNumFood})\) were placed at random locations, excluding water cells. For \(p\)-water initial \(p\) values were randomly chosen between zero and one. The initial agent's energy was randomly chosen from the interval \([0, \text{EnergyToGetChild}]\). Its initial age was randomly chosen from the interval \([0, \text{MaxAge}]\).

**Simulator:** The simulations were performed with a self-built simulator. To rule out any effect of bugs two simulators were independently developed by the two different programmers, without accessing each other's code, using two different languages.

\(p\)-migrate: Sometimes the agent's child was placed at a random location instead of next to the parent in order to distribute relatives over the map. The probability of migration was determined by the \(p\)-migrate parameter. As a consequence of this an altruist that would body-bridge would help unrelated others with this. The population was mixed up with the following procedure. When a parent \(A\) gave birth to a child \(X\), the child was not immediately placed on the map, but had to wait until a second parent \(B\) gave birth to a child \(Y\). Child \(X\) was then placed next to the parent \(B\), while child \(Y\) had to wait for a third parent \(C\) to give birth before it was placed on the map, etc. In practice the delay of placement was on average \(3/4\)th of a cycle. A full cycle is a single update (one step) of all agents in the world. Thus, once the parent had gathered enough food to give birth, the child was actually placed into the world before the next update of the parent. With this swap method the balance between food and newborns was not affected in any way. Also, it avoided placing newborns at random locations on the map, which would take away the need for island hopping because new agents could then be born onto an uninhabited island.

**Parameter settings were as follows:** \(\text{MaxAge} 250, \text{EnergyToGetChild} 120, \text{EnergyCostChild} 60, \text{EnergyFood} 9, \text{BridgeTime} 30, \text{Mutation} 0.004, \text{InitNumFood} 30/\text{Number Islands}, \text{InitNumAgents} 15\) per island.

The upcoming simulations follow the same pattern as those of the previous part; In Simulation 3, 4 and 5 we will first investigate the evolution altruism in
Coevolution of altruism and migrating behavior

various conditions of migration, analogous to Simulation 1. In Simulation 6 we will simulate the evolution of migration itself, analogous to Simulation 2.

Simulation 3: Evolution of altruism in river cross setup

Two simulations were run, both with the parameter settings as discussed above, but one with \( p\text{-migrate} \) at 0.0 for all individuals and the other with \( p\text{-migrate} \) at 1.0 for all individuals. Both simulations were run for 4 million iterations. All reported values are averaged over the last 100,000 iterations of the simulation.

Results: In the condition with \( p\text{-migrate} \) set to zero (children were born directly behind their parents) most average \( p \)-values changed rapidly right in the beginning of the simulation. In Figure 4(a) it is shown how the population averages changed over time for all four \( p \)-values.

Stepping forward when in front of food, determined by the \( p\text{-food} \) parameter, was obviously good because more food meant more energy, and thus a higher chance to survive and reproduce. The \( p\text{-food} \) parameter was the first to reach a value near 1.0. The probability to step onto a bridging agent, \( p\text{-cross} \), increases the chance a new island is reached once another agent had body-bridged. On average 21% of the islands were uninhabited, and these grew quickly full of food, reaching such an island would make it possible to give birth to a lot of children. The increase in \( p\text{-cross} \) was, however, quite slow, since the agent is not very often in a situation where it faces exactly towards a body-bridge, so there was not much selection on it.

The probability to step forward when in front of empty land, \( p\text{-land} \), seems to reach its stable value at 0.8. In general, forward movement seemed to be a good strategy, but not exclusively. This was because with a \( p\text{-land} \) parameter of 1.0, all agents would walk straight towards the edge right after birth, and would spend the rest of their life running along the edges of the islands, leaving all the food in the center untouched. An advantage of an overall high \( p\text{-land} \) is that it facilitates use of bridges. When all agents are running along the edge of the island they will all face water at the corners before they turn. This would, thus, be the place where altruist are most likely to body-bridge, the other agents will then bump into these bridges automatically if they keep walking along the edges. This can be an important advantage since the limited sight of the agents (only the cell in front of them) makes it hard to find a bridge.

The parameter of our main concern \( p\text{-water} \), which determines the probability to step into water, drops immediately to a value close to zero, right after the start of the simulation. There is obviously a high selection against high \( p\text{-water} \) values because body-bridging causes the agent to die immediately. The \( p\text{-water} \) parameter was only 0.0080. This seems quite low, but the percentage of agents that died of drowning, instead of old age or starvation, was still 20%. The percentage of drowning agents seems quite high considering the low \( p\text{-water} \), but this is because during the agent's life there is a chance to walk into water each time the agents stand in front of water. Although the percentage of drowning agents is high, it is not immediately clear whether the \( p\text{-water} \) value is caused by selection towards altruism or because of random fluctuations. Therefore, we will compare it to our control simulation.

In the control simulation \( p\text{-migrate} \) was set to 1.0, which undermines the effect of kin selection by distributing the relatives over the map so that when an altruist would body-bridge the other agents on that island, which would benefit from it, were
not likely to be relatives (and would not have a systematic higher \( p\)-water than the population average).

The general pattern of the control simulation was similar to that of the normal simulation, but \( p\)-water now reached a clearly lower stable value of 0.0046, indicating that at least part of the \( p\)-water value in the normal simulation is attributable to altruism (see Figure 4(b)).

![Figure 4. Average p values over 4 million iterations. Above the normal condition, below the migrate condition.](image)

**Simulation 4: Evolution of altruism in river cross setup: varying \( p\)-migrate**

In the next simulation we focussed more on the effect of the \( p\)-migrate parameter on the \( p\)-water values to investigate how crucial the exact distribution of relatives was for altruism. The other three \( p\)-values were now fixed at the values they converged on in an exploratory simulation of one million iterations: \( p\)-food at 1.0, \( p\)-land at 0.8, \( p\)-cross at 0.8. While in the previous simulation \( p\)-migrate was either 1.0 or 0.0, we now
ran 11 simulations over which we systematically varied the $p$-migrate from 0.0 to 1.0 in steps of 0.1. Thus, in this simulation each time an agent was born the $p$-migrate determined the probability the agent was swapped or placed next to the parent. To reduce the possibility of higher $p$-water values due to noise we lowered the Mutation parameter somewhat to 0.0016. All other parameters were identical to the previous simulation. In this simulation the conditions which had $p$-migrate set to 0.0 and 1.0 were essentially replications of the previous simulation with a lower Mutation value. All simulations were run for 500,000 iterations and were all replicated 10 times.

**Results:** Figure 5 displays the final $p$-water values averaged over the 10 replications for each condition. With the increase of $p$-migrate, $p$-water decreases rapidly, indicating that the amount of altruism is inversely proportional to the amount of kin mix up.

![Figure 5. The $p$-water values plotted against $p$-migrate.](image)

**Simulation 5: Evolution of altruism in river cross setup: extinction**

In the previous simulation the condition with $p$-migrate set to 1.0 resulted in a $p$-water value of 0.0028, which is lower than the 0.0046 of the simulation before that. This lower $p$-water value is probably a consequence of the lower Mutation parameter. Yet, the $p$-water value of 0.0028 still caused 9% agents to die of drowning. When the distribution of agents is truly random we should expect no altruism at all, and no agents to drown. We therefore suspect that the drowning rate is caused by the noise introduced by the mutation parameter. To reduce the average $p$-water value in the control simulation even further, we now lowered the mutation parameter to 0.0001. Two conditions were run; one with $p$-migrate set to 0.0 and one with $p$-migrate set to 1.0. Both conditions were replicated 10 times and were run for 2,500,000 iterations.

**Results:** In the no-migrate condition there was a rapid decrease in average $p$-water, which stabilized at 0.0071, the percentage of agents that die of drowning was 18%. We conclude from this that altruistic behavior is stable in this no-migrate condition. Figure 6 (a) shows a density plot sample of the $p$-water values over time.

In the migrate condition (Figure 6 (b)) $p$-water reached values as low as 0.0005 on iteration 80,000. Apparently all altruistic behavior in the migrate condition of the previous simulations was caused by the noise added by the mutation parameter. On iteration 120,000 the whole population even went extinct. Extinction happened in all 10 replications. This is probably because agents could not reach other islands any
more because there were not enough individuals that walked into water to form a bridge. This underlines that the intuition that altruism evolves because of its value for the whole population, is flawed. If altruism is not selectively directed towards kin it will not evolve, even at the cost of extinction.

Overall, the conclusion of the previous three simulations is analogous to the conclusion of Simulation 1: altruism can evolve, but only if it is preferentially directed towards kin.

**Simulation 6: The evolution of migration in river cross setup**

In the final simulation \( p\text{-migrate} \) was treated as a genetic trait, which was mutated in the same way as the \( p\text{-water} \) parameter. Initially, all agents were given a \( p\text{-migrate} \) of 0.0. The simulation was run for 10 million iterations. Because the initial population sometimes went extinct in the first iterations of the simulation, the initial population was made 4 times as big, and the world was increased accordingly to 220 by 220 cells (400 islands, and 15 * 400 initial agents).

![Figure 6](image)

**Figure 6.** The \( p\text{-water} \) values plotted for all agents for a number of iterations. In (a) the entire population goes extinct. In (b) a level of altruism is maintained throughout the simulation.

![Figure 7](image)

**Figure 7.** (a) Snapshot of the evolving \( p\text{-migrate} \) values. Eventually the top thread reaches values near 1.0. (b) \( p\text{-water} \) values (X-axis) against \( p\text{-migrate} \) (Y-axis)

**Results:** A sample of a density plot of the \( p\text{-migrate} \) values over time is shown in Figure 7 (a). It can be seen that two threads emerge. In Figure 7 (b) a density plot is shown of the \( p\text{-migrate} \) values against the \( p\text{-water} \) values. Two clearly separate blobs can be distinguished that differ in both \( p\text{-water} \) value and \( p\text{-migrate} \) value, where the group with low \( p\text{-migrate} \) has a high \( p\text{-water} \) (altruists, bottom right in Figure 7(b)) and the group with high \( p\text{-migrate} \) has a low \( p\text{-water} \) (egoists, top left in Figure 7(b)). At the end of the simulation the \( p\text{-migrate} \) of the egoistic group rose to a value close
to 1.0 and that of the altruistic group was close to 0.0. These two groups are thus very similar to the two groups that arose in the prisoner's dilemma of Simulation 2.

**Discussion**

In Simulation 1 and Simulation 3, 4 and 5 it was demonstrated that altruism can evolve in conditions of low migration. These finding are in line with the theory of inclusive fitness of Hamilton (1964) and earlier simulation work (Baalen & Rand, 1998).

Our main conclusion is that the tendency to migrate (or not) is itself subject to selection (Simulation 2 and 6), and tends towards low migration among altruists. Because of this finding the causal arrow in thinking about altruism may be reversed. For instance, when there is altruism within groups of closely related insects one could say the altruism evolved because of the genetic similarity within the group. On the other hand the habit to live in groups of relatives could itself evolve because of the benefits of altruistic company. Whereas one is usually inclined to question the evolution of altruism with the dispersal of relatives as a given premise, it is now shown how this dispersal itself is affected by the benefit of mutual altruism.

In both the river cross and prisoner’s dilemma simulations, the initial conditions were crucial for the evolution of altruism. The prisoner’s dilemma simulations had the \( p\text{-migrate} \) values initialized to 0.0. The river cross simulations had a somewhat higher initial \( p\text{-migrate} \), of around 0.05. This still allowed the evolution of altruism, but values that were random or above 0.1 did not. In such cases there was an immediate extinction of altruists, and with it the entire population. In the prisoner’s dilemma simulation a similar phenomenon was observed. There was no extinction of the entire population, however, merely replacement of all altruists by egoists. The dependence on such initial conditions comes from the fact that altruism capitalizes on mutual benefit. A single altruist is always worse off among egoists, and only by the clustering of altruists can they can maintain a stable population. Given the fact that \( p\text{-water} \) was randomly chosen at the start of the simulation in combination with a randomly chosen \( p\text{-migrate} \), the chance of having an almost uniform group of altruists that also has a low \( p\text{-migrate} \) was almost zero. Once altruism has disappeared, single mutations towards altruism are strongly selected against. It is hard to judge whether in natural situations those initial conditions are met. Of course, in a natural situation there is not such a discrete onset, and there are no clearly distinguishable initial conditions. Rather, evolution is a continuous process where different phyla evolve through all different kinds of situations. What we can conclude, however, is that if a situation allows the evolution of altruism, there will also be a selection pressure to preserve these conditions

It should also be stressed that the rather severe consequence of altruistic behavior in our simulation, death, is not a precondition for its evolution. Rather, it works only against it. Death was only chosen to be able to exclude reciprocal altruism as an alternative explanation. Forms of altruism that have less severe consequences may be more widespread than the forms with lethal consequences presented here. They are only problematic from a researchers perspective because it will be hard to rule out reciprocal altruism as an alternative explanation.

An interesting finding on its own right is that in both simulations a group of egoistic parasites emerged, which differed in both strategy and migration rate from the altruists. This outcome was, in fact, already considered by van Baalen and Rand (1998) in a mathematical analysis of altruism in viscous populations. They speculated:
Thus there may be a second type of outcome, coexistence of rapidly moving non-altruists ... and sedentary altruists..., This is an interesting result, because strategy sets of simple continuous shapes usually lead to monomorphic evolutionary stable strategies (Baalen & Rand, 1998, p.643). Our simulations were designed without this possible result in mind, nevertheless both simulation setups ended up with such a differentiation in the population.

The results of this study may seem similar to those of the hawk and dove game (Maynard Smith, 1964), in which individuals fight for resources with two possible strategies. The hawk strategy is to fight for victory without ever giving in, it either wins or loses with serious injuries. The dove strategy is to fight conventionally but give in when the opponent persists. With many hawks in the population it becomes better to employ a dove strategy, the costs of fighting will be too high. With many doves it becomes better to employ a hawk strategy, because there are many doves to take advantage of. This seems reminiscent of our simulation, where egoism becomes more productive with more altruists to take advantage of. There is an important difference, however. In the hawk and dove game the two different strategies can also be seen as two possible actions of a single strategy. The individual chooses the action with the highest expected reward, depending on the number of hawks or doves in the environment. In our simulation such a redefinition is not possible, because the individuals in our simulation do not maximize their personal gain. If they would, they should always defect, just like in a normal one trial prisoner’s dilemma. The two different strategies in our simulation should thus be interpreted as actual differences between individuals, which will be the topic of our next chapter.