

Green-beard altruism

a numerical model on the evolution of
altruism in the red imported fire ant,
Solenopsis invicta

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Abstract - We conducted research on altruistic behaviour in the imported red fire ant, *Solenopsis invicta*. First, we explore theoretical altruism and its expected effects. Afterwards, we show that the red fire ants appear to contradict the traditional ideas of evolution, after which we provide evidence for our theory of why that happens. The homozygous genotype for altruism is lethal, and therefore all altruists are heterozygous. This means that altruistic colonies inadvertently get non-altruistic offspring, but non-altruistic colonies can only get non-altruistic offspring. We could conclude that red fire ants survive because they work together, against the more self-centered non-altruists. The size of the altruistic colonies gives them an advantage against the non-altruists, that make more, but smaller-sized colonies.

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Introduction

ANTS WERE HARDLY OUR FIRST CHOICE. I never blamed anybody for their disinterest when we were discussing our research. I did not blame them when we joked about Hamilton's rule and a bus full of school children; I will not blame you for looking cynical at this work. Research about... about ants!? Truth be told: I am not sure whether I would have continued this line of research if we had found the ants sooner. It all started with altruism.

The concept of altruism is interesting, as it appears to contradict well-established theories on evolution. An organism that is genetically different from another, and therefore can produce more offspring, will eventually become dominant in the population, out-competing the others. Why has this not happened in billions of years of evolution? A non-altruistic individual in a sea of altruists would have no trouble becoming dominant, would it not?

That is where the ants came in. They are one of the few examples of species that show a particular kind of altruism, *green-beard altruism*. They are living proof that altruism can survive natural selection. Evidently, being altruistic is not necessarily a disadvantage to them. How does that work? We knew that it would not be feasible to conduct experiments on actual ants, but we could use our knowledge about computers to our advantage.

Thus, the question arose:

Question 1 Under what circumstances does a green-beard altruism allele continue to exist in a numerical model based on the red imported fire ant, *Solenopsis invicta*?

To answer this, we first had to develop a model to work on, a model that would provide the necessary tools to explore theoretical altruism in an environment built by us. We opted to use Jupyter notebooks, in a *Google Colab* environment. This would allow us to write python code in an online environment. Firstly, we would explore the naive approach to altruism: acting selfless. We had to prove that our assumptions were valid. Does an altruist in fact have an evolutionary disadvantage? It seems trivial, but that is hardly evidence.

Subquestion 1.1 Which parameters does a model require in order to accommodate an altruism allele?

After we had a thorough understanding of our basic model, we needed to dig in further. Altruism did not survive in this naive approach, and we found plenty of reasons why. Therefore, we had to change our approach around to reflect a real-life species, the red imported fire ant. They came up while we were reading established literature, and we chose to include them, because they show *green-beard* altruism and because there had been previous research conducted on them.

Subquestion 1.2 How can we adapt our basic model to the red imported fire ant's altruistic behaviour?

After that, we were closer to answering the main question, but we needed to relate our controlled, theoretical environment to real life. There has been an abundance of research conducted on the red

imported fire ants, so we would only have to conduct a literary study on them and compare it to our model results.

Subquestion 1.3 *How does a green-beard allele persist in a colony of red imported fire ants, Solenopsis invicta?*

Hypothesis

The fact that the altruistic allele still exists in the imported red fire ant, indicates that it has some form of advantage over other alleles, that counteracts or even overpowers the expected disadvantage inherited by its altruistic behaviour. It appears that the altruistic allele has a behavioural effect on the phenotype, besides merely the altruistic behaviour. Which it is exactly, remains unclear. We suspect that the altruistic ants, known for their unique co-operation, achieve an edge because they live in bigger colonies, whereby protecting most ants and being able to accomplish impressive feats, such as attacking a wasps nest or building a raft made entirely of ants.

All code is available via <https://github.com/MikeKuijper/ModelsOnAltruism>.

Chapter 1

On the origin of altruism

Altruism, the Oxford Concise English Dictionary defines it as either "selfless concern for the well-being of others", or as "behaviour of an animal that benefits another at its own expense" depending on context [9]. In this work, the behaviour of any organism or entity that is in favour of other organisms at the cost of its own good, and thereby places itself in a disadvantaged position, is referred to as *altruistic behaviour*, and an individual showing it as *altruistic*.

Further in this work, an extra requirement is added to qualify for this term, as an individual will be considered altruistic if it has the genetic properties that will be defined as the requirement for altruistic behaviour. An organism might be considered altruistic if it is heterozygous and the altruism allele is dominant. Any individual that does not show altruistic behaviour will be referred to as *selfish*¹.

1.1 Altruism

There are many examples of altruism in nature. However, sacrificing yourself for someone else decreases your own probability of survival. How is it possible that it still exists in nature? To explain this, we first need to see how different species came into existence.

1.2 Evolution

1.2.1 Theories on the differentiation of species

Throughout history, people have tried to explain how different phenomena can be explained. One of these questions is how the Earth is populated with so many different species. Many of the first reasons on how this is possible are rooted in creationism. Creationism is a umbrella term for all theories that assume all the different life forms were created by divine power, be it a god, multiple gods or some other phenomenon. An example of this is Genesis, which says that one god created everything around us, including plants and animals in just six days. He seems to have forgotten the prokaryotes and fungi, but we can assume they were also created in those six days [8]. A similar origin story comes from the Zulu in Southern Africa. In their origin story, a man named Unkulunkulu creates all different humans and animals from reeds [12]. Many cultures from around the world have these kinds of stories, but they are not a primary source, since they explain events that create the first humans. This is why many biologists started to look for other reasons as to how different species came to be during the 19th century.

¹There is no judgement attached to the word *selfish* here. *Self-prioritising* might be a more accurate label, but for clarity and stylistic reasons, we will use *selfish* instead.

1.2.2 Catastrophism

One of the first of these new theories was Catastrophism. This theory was first put together by Georges Cuvier, a palaeontologist. While researching different rock layers, he discovered that every layer had radically different fossils inside them. It was already known that these layers formed on top of each other with the oldest layers at the bottom and the later slices at the top. From these two statements, he concluded that almost all life in certain areas was periodically getting completely wiped out due to a natural disaster, after which the biome is repopulated by organisms from the surrounding terrain [11]. This explains the layered structure of fossils in the Earth and does not yet contradict the Bible, which still dictated a lot of scientific research. And although Cuvier never mentions Noah's ark and the flood or even the Bible in general, his work was later used to discredit more radical theories. Today, however, Catastrophism itself is out of grace. Although there is proof for a catastrophic event that changed the composition of ecosystems, such as the meteorite that ended the reign of the dinosaur [10], it lacks any explanation on how different species developed and instead explains how they go extinct. The theory is not completely disregarded but has very little use because of its incompleteness.

1.2.3 Lamarckism

A second theory to consider when modelling altruism is Lamarckism. Jean Lamarck, a biologist who lived from 1744 to 1829, wrote his evolution theory in 1809. In his book, he describes how he thinks organisms develop. He writes that organisms develop their most utilised features at the cost of others. They would then pass these characteristics on to their offspring [13]. As an illustration, he explained how giraffes who use their necks to pluck high hanging leaves gain elongated necks or how the children of strong smiths will also have more muscle mass. It was later discovered this, safe for a few exceptions [15], does not really hold up. There is, however, a place where his theory is important: some bacteria can actively alter their genes if their environment puts a lot of pressure on them. Crispr-Cas systems are also a place where Lamarckian Evolution can be seen in action. The bacteria from which this system stems alter their DNA by adding copies of the DNA of their enemies. In this way, they can easily identify future viruses, and this database of virus-DNA is inherited by their offspring. This theory can sometimes be very important for research on prokaryotes, but for eukaryotes, it is irrelevant [14]. Another important part of Lamarck's ideas was the belief that species always evolve to become more complex. This assumption seems logical and would make sense if a higher being pushed species to a certain goal, but nature has many different occasions where organs devolved and life became less complex than before. See numerous different cave animals who get rid of their eyes as they are useless in the eternal darkness of their caves [3].

1.2.4 Darwinism

In 1859, however, our modern understanding of evolution was born. Charles Darwin published his theory of evolution in his work, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* [2]. The core of his work consists of two observations. First, individuals of the same species vary in their appearance and traits. Second, species have more offspring than the environment can sustain. This means a lot of individuals will die early. The ones with the best traits have the highest chance to survive and pass those traits to their offspring. These offspring are likely to have similar traits, which makes their survival likely once again. The last puzzle piece is the random change in the traits of the descendants. These changes occur due to a few different effects. All of these effects revolve around the way genetic information is stored.

1.2.5 DNA and mutations

DNA is the molecule that stores this genetic data. It consists of a double helix of nucleotides, phosphorus and sugar molecules bound together into a polymer, and molecules that connect these strings. The connecting molecules can be read by enzymes and translated to instructions for the cell. These DNA strings are not indestructible, however, and can dynamically change. The first way this happens is via mutations. DNA gets damaged constantly by processes such as ionizing radiation and some chemicals.

This damage is usually repaired but sometimes lingers in the cell. Some of the different types of damage are substitution when an array of nucleotides is replaced by another array, deletion when a part of the DNA is completely removed, insertion, which means extra base pairs are added. All of these forms can also occur as a point mutation. This is a mutation of a single gene. This seems like an irrelevant change considering a human has about three billion base pairs, but some sicknesses such as sickle cell anaemia are directly caused by a single point mutation. These mutations can sometimes lead to a new phenotype, how a creature looks or functions. In this way a population can change, but only very slowly: the human genome changes at a rate of about 175 mutations per generation [6], a large part of which have little effect because they are non-coding DNA and thus do not influence the organism. This slowness can kill a population if it is not capable of quickly adapting to its surroundings. That is why many organisms have complementary systems to this mutation system. Bacteria, for instance, can collect DNA from their surroundings and implement it into their own DNA, or they can exchange it with other bacteria. For eukaryotes, this is a bigger problem. They cannot just pick up DNA from the ground because they are too large and complex for this. This is why they have a dedicated sexual reproduction system. Two individuals can mate, which combines halves of the chromosomes of the father and half of the chromosomes of the mother into a completely new set. These chromosomes also often exchange a bit of DNA via a process called crossing over. Crossing-over literally cuts both helices of a chromosome up and pastes the cut-off parts onto the other chromosome. This leads to more variety among different chromosomes. It is important to note that mutations and variation do not necessarily improve the chances of the species, but solely that of the individual. This, in turn, leads to improved chances for the species. In that sense, an individual's survival chance is only relevant insofar as it prevents an individual from reproducing, as is explained above. Furthermore, it is advisable to shift the point of reference to the allele, instead of the individual. A carrier for an autosomal gene, has a certain chance, supposedly near 50%, of passing on the allele to the next generation for every time it reproduces.

1.3 Simulation of Altruism

In order to simulate any evolutionary process, one must first determine what kind of evolution to choose. Since Creationism has very little proof and Lamarckism and Creationism are highly situational, solely focusing on Darwinian evolution will be perfectly fine for determining how well Altruism works in nature. Secondly, we need variation within the population. This can be achieved in many ways, but the simplest is to divide a population into two categories: one altruistic and one selfish. We will then need a way of simulating evolutionary pressure. A simple way to do this is to make the modelled creatures have an intense craving for tea. If they run out of tea meter, they will die. Alternatively, this can be named food or a similar term. Food units are then randomly handed out. This food meter simulates the general success of an individual using randomness. This food can then be shared by altruists if they have a lot of it and can be given to creatures that are almost dying. As more creatures die, however, their evolution pressure gets lower. Usually, they would reproduce in order to keep their population large and simultaneously maintain the evolution pressure, but this step can be omitted if you purely want to look at the chances of a single trait. The only difference is that you need to make the pressure sufficiently high at the beginning and compare the altruistic to selfish creature ratio at the start to somewhere near the end of the simulation. This also means that any systems for reproduction and random variation in DNA can be omitted for now.

Chapter 2

Modelling evolutionary phenomena

Evolutionary research highly relies on computer models. It is hardly feasible - or productive, for that matter - to conduct evolutionary research on living organisms over the course of a human lifetime. Even before factoring in the sizeable error bars, it requires an organism that shows both the desired behaviour and has a lifespan that allows for enough generational transitions during the research period; not to mention additional requirements, such as either sexual reproduction, as opposed to asexual reproduction, which requires a vastly different environment and may take significantly longer.

Additionally, computer models allow for less speculative research, as they are capable of providing experimental evidence in a controlled environment. The flip side of this, however, is that a wrongly constructed model can confirm a false hypothesis - or negate a true one. In that sense, models are an extension of the researcher both in bias and quality. It is therefore highly important that models are thought out carefully and, perhaps more importantly so, that the exact model is included for reproducibility and scientific review.

2.1 The basic model

All code is available via <https://github.com/MikeKuijper/ModelsOnAltruism>.

2.1.1 Model definition

The basic model assumes N organisms that are binarily either altruistic or selfish. All organisms have a *saturation* value, that describes their food reserves. A saturation of 1 means the organism does not need food and an organism with a saturation of 0 dies of starvation. Once an organism dies, it does not contribute to the rest of the model, but N stays constant. Every iteration¹, every (still) living organism's saturation is reduced by C . Portions of food are distributed randomly among organisms², whereby their saturations increase by F . The amount of food portions is dependent on the size of the starting population, N , and a proportion factor, p , where $p \in [0, 1]$. However, the saturation is capped at 1. This means that every organism has a chance of p to receive food³.

Altruists may decide to give their food to another organism. They do so if their saturation is above A . Note that altruists are unrecognisable in phenotype in this basic model. Therefore, altruists are at a disadvantage, as they help both selfish and altruistic organisms, which means they have a higher

¹One might consider an *iteration* a set duration, such as a day or a week. However, that would introduce interpretation on the type of organism and was therefore decided against.

²Note that the model allows for double portions of food per iteration. This was intentional, as it represents real-world situations better.

³This statement is not entirely accurate, as organisms can receive multiple portions of food. This reduces the probability for any given organism of receiving at least one portion of food to $1 - \text{binomcdf}(pN, \frac{1}{N}, 0)$. This results in an approximate 10% decrease in probability for $N = 1000$ and $p = 0.2$, for example.

chance of helping an organism that does not receive the favour, and because they reduce their own chance of survival.

2.1.2 Model pseudocode

Algorithm 1: Iteration in the basic model. It describes the computational steps that the model takes for every iteration in pseudocode. The first loop reduces all living organism's saturation by C , whereas the second 'feeds' a random organism pN times, taking altruism into account.

```

for organism in population.organisms do
    if organism.isAlive then
        | organism.saturation -= C
    end
    if organism.saturation  $\leq 0$  then
        | organism.isAlive  $\leftarrow$  false
    end
end

n  $\leftarrow pN$ 
while n  $> 0$  do
    while true do
        | organism = SampleRandom(population)
        | if organism.isAlive then
            | | if not (organism.isAltruistic and organism.saturation  $\geq A$ ) then
            | | | organism.saturation += F
            | | | continue
            | | end
            | end
        | end
    n -= 1
end

```

2.1.3 Mathematical implications

The chance of survival, $p_s \in [0, 1]$, and the chance of death, $p_d \in [0, 1]$, relate to each other as:

$$p_s = 1 - p_d \quad (2.1)$$

As such, the chances of survival for any given organism for the next n iterations, with saturation S , is given by:

$$p_s(S) = 1 - \Pr(S + XF - nC \leq 0) \quad (2.2)$$

where X is a stochastic variable that equals the amount of times the organism receives food, and $i \in \mathbb{N}$. This leads to the following binomial distribution.⁴

$$p_s(S) = \Pr\left(X > \left\lceil \frac{nC - S}{F} \right\rceil\right) = 1 - \Pr\left(X \leq \left\lceil \frac{nC - S}{F} \right\rceil - 1\right) \quad (2.3)$$

$$p_s(S) = 1 - \text{binomcdf}(n, p, k - 1) \quad (2.4)$$

$$k = \left\lceil \frac{nC - S}{F} \right\rceil \quad (2.5)$$

where $k \in \mathbb{N}^0$ represents the minimal amount of times the organism has to receive food in the next n iterations in order to stay alive. As such, it the fraction rounded up to the nearest integer.

$$p_s(S) = 1 - \binom{n}{k-1} p^{k-1} (1-p)^{n-k-1} \quad (2.6)$$

⁴Unless denoted as \mathbb{N}^0 , \mathbb{N} does not include 0 in this work.

Then, the binomial coefficient can also be evaluated to give:

$$p_s(S) = 1 - \left(\frac{n!}{(k-1)!(n-k-1)!} \right) p^{k-1} (1-p)^{n-k-1} \quad (2.7)$$

It becomes most apparent in 2.4, that decreasing k improves the chances of survival for the organism.



Note: The survival probability function, $p_s(S)$, as established in equation 2.4, takes only the situation at n into account. The organism is considered to be alive if it ends with a high enough saturation, while it ignores the situation in between. This means that the saturation may have dropped below 0, which would lead to the death of the organism. Therefore, the exact value of the function is not perfectly accurate. It is, however, an approximation of the problem.

Furthermore, the function assumes a constant p . Although pN organisms receive food, dead organisms are ignored, for obvious reasons. This is also not accurate. Because of that, the function is the best fit at the beginning of the model, before organisms have had the time to die. Also, the difference between our proposed function and the real function is constant over all values of S , which means that the relations between values of S are contained.

We do not consider these inaccuracies problematic, as the aim of the function was not to find the absolute probability. The relations between the different probabilities at two different values of S are significantly more valuable, and we see no reason to doubt those.

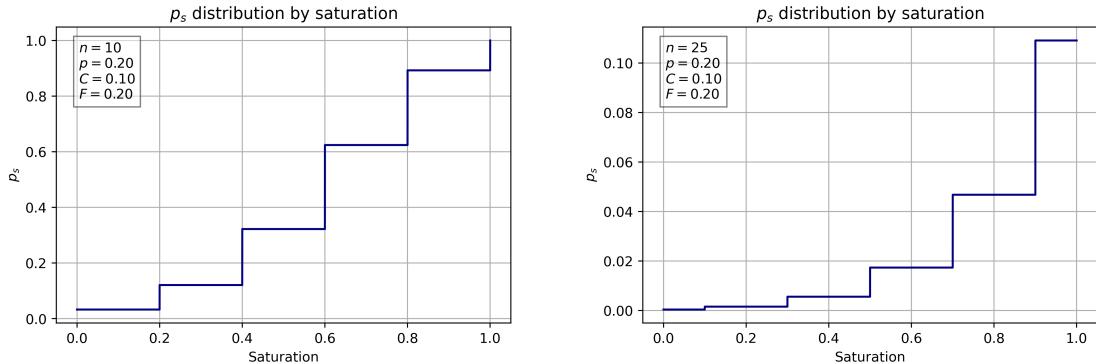


Figure 2.1: Two graphs of $p_s(S)$, equation 2.4. Both portray the probability that any given organism survives the next n iterations, given that $p = 0.2$, $C = 0.1$, and $F = 0.2$. They show a significant negative influence on p_s when an organism behaves altruistically, as its saturation will stay between A and $1 - C$, when it could be as high as 1. Further, it shows that a higher S yields a higher chance of survival. One would be forgiven for finding it trivial, but it is evidence of a disadvantage of altruistic behaviour. Note the difference in vertical scaling between the two plots.

2.2 Observations

As illustrated in figure 2.1 and 2.2, the basic model shows an evolutionary disadvantage for altruistic individuals among both non-altruistic and altruistic individuals, although the model lacks consistent evolutionary pressure. Therefore, the effect is not as acute as expected.

To measure evolutionary pressure, we propose the *hunger-to-food ratio*, hereafter denoted as η . It is defined as the ratio between the total amount of unwasted nutrition that the system can consume and the total nutrition available. In other words, it represents the food scarcity in a system.

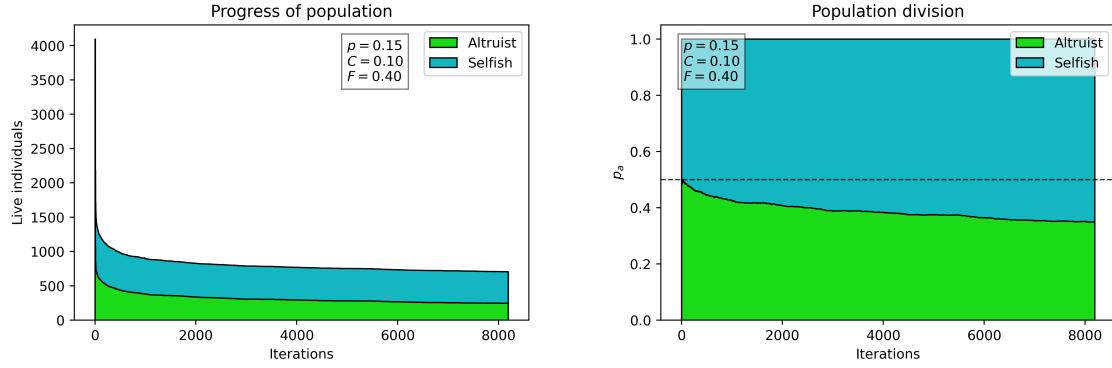


Figure 2.2: Two graphs showing the progression of the basic model’s two groups, the altruists and the selfish. The left graph shows absolute numbers for the population, whereas the right shows the proportion of altruists in relation to the total population. The most substantial decrease in p_a can be observed in the first few iterations of the simulation. To address the elephant in the room: approximately 80% of the organisms starve at that point, as there is simply not enough food for the entire population. At that point, food is quite scarce and the situation is most disadvantageous for the altruists, as can be seen in the right plot.

In the basic model, this leads to the following.

$$\eta = \frac{\sum_{n=0}^{N_l} 1 - S_n}{pNF} \quad (2.8)$$

Further, the Δp_a presents itself as a relevant measure for evaluating the effect of altruistic behaviour, relative to selfish behaviour. By definition, it is the difference in altruist proportion between two consecutive iterations. One might interpret it as a measure for how well a certain genetic property, in this case, altruism, performs.

We see a negative correlation between η and Δp_a , as high values for η represent times of high food scarcity, and therefore high need and value of the food. The altruist loses more food value, if it gives it away in times of hunger, and consequently reduces its chances of survival more, which can be observed in figure 2.3. In other words, one would not expect much harm in giving away food if there’s plenty more. Similarly, people are unlikely to share their food in a famine, as they will likely need it themselves.

The model starts with many organisms and only limited food. As individuals start to starve, the hunger decreases, whereas the food supply stays constant. Thus, the η decreases. The η appears to approach 0.5 in our models, because fewer individuals die at low values, which leads to a decrease in consumers, and therefore food scarcity. Why it is 0.5 specifically, remains unclear. It means there is twice as much food available as there is demand for it, which makes the Δp_a insignificantly small. We suspect that the value of 0.5 is arbitrary.

2.3 Shortcomings and applications

Besides evidently being a simplification of the problem, the basic model lacks realism in the sense of uncertainty; when observing behavioural phenomena, it quickly becomes extremely important to take probability into account, which the basic model does not. An individual’s behaviour is only predictable to a certain degree, and the basic model does not reflect that. The model could be improved with the addition of a probability function for deciding whether an altruistic organism behaves altruistically.

Further, it completely ignores reproduction. The organisms do not pass on any genes and mutations are non-existent. These two processes are arguably at the centre of evolution, but the model lacks them.

Additionally, the model assumes individuals are binarily either altruistic or not, which does not seem to be the case in reality. It would be more representative if there were some variable to define how altruistic an individual is. An easy implementation of this would be to give every individual a separate A , and to use some form of randomness to decide whether an individual acts altruistically or not. A possible method would be to pick a random number between 0 and 1, and decide on altruistic behaviour based on whether it is above the organism's A or not. An additional modifier could be added to the random number, based on the effect of the decision, or the other organism's altruism threshold.

Finally, all individuals are exactly the same, apart from whether they are altruistic or not. There is no measure for their strength or endurance, for example. The simple fix here would be to make C a variable that is unique for every individual. This could serve as a fitness variable, that could come in useful with the addition of reproduction.

Considering this, the basic model is not suited for answering the relevant questions, and another model is required.



Note: As figure 2.3 shows, the implementation of the moving average significantly influences the correlation. Although we consider the result plausible, one must be careful when interpreting smoothed data, as the process may very well introduce new, unjustified interpretations of the data. Presenting such a conclusion without this nuance would indicate a confirmation bias [5].

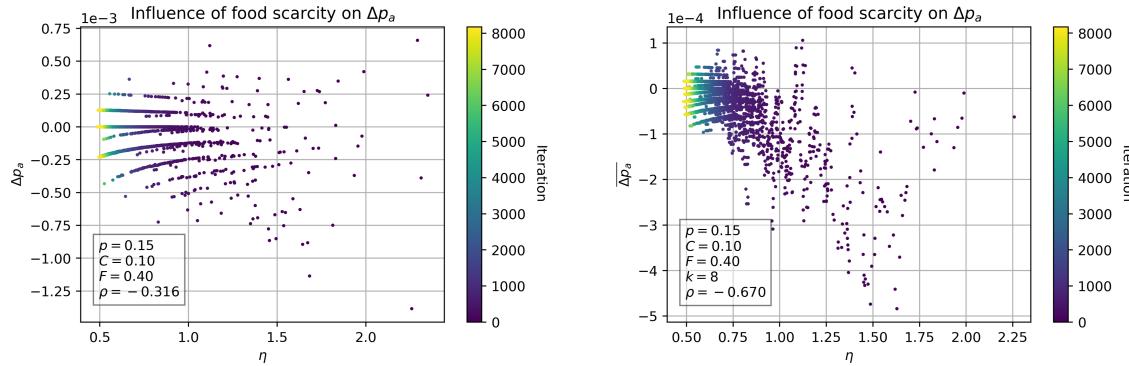


Figure 2.3: The relationship between the hunger to food ratio, η , and its influence on the population division between altruists and non-altruists. The colour of the dot shows its corresponding iteration. A negative Δp_a means altruists have a disadvantage, compared to non-altruists. The right plot is based on the same data but shows the moving average. The data was also smoothed, because data points were results of a partly random process, and are therefore considered noisy. Our calculations for correlation⁵ show $\rho = -0.316$ for the raw data. It illustrates that altruism's prevalence reduces most with higher values for η .

Interestingly, the points appear to form field lines of sorts. A tendency towards 0 might be expected, as it is the result of an iteration where no individuals die, but we have yet to find a satisfactory explanation for the other curves.

⁵ ρ is the correlation coefficient. It is a value between -1 and 1 that describes the change of a variable, as another increases. A high correlation, of 1 , shows a straight ascending line, whereas a very low correlation, of 0 for example, shows a cloud of points placed seemingly at random. The same is true for negative values, but the value decreases is descending.

⁶In other words: the probability that any randomly selected individual from the population is altruistic.

2.4 Table of symbols

Symbol	Description	Remark
S_n	Saturation, the food reserves an individual has	$S_n \in [0, 1]$
C	Reduction of saturation per iteration, an organism's food need	$C \in [0, 1]$
A	Altruism threshold for S_n	$A \in [0, 1]$
p	Proportion of individuals receiving food	$p \in [0, 1]$
N	Amount of individuals at the start of the simulation	$N \in \mathbb{N}^0$
I	Total number of iterations per simulation	$I \in \mathbb{N}$
n	Individual iterator of N	$n \in \mathbb{N}^0 \wedge 0 \leq n < N$
i	Iterator of I , iteration number	$i \in \mathbb{N}^0 \wedge 0 \leq i < I$
N_l	Amount of living individuals	$N_l \in \mathbb{N}^0 \wedge 0 \leq N_l \leq N$
p_s	Probability of survival	$p_s \in [0, 1]$
p_a	Proportion of altruistic individuals in the population ⁶	$p_a \in [0, 1]$
Δp_a	Difference in the population's proportion of altruists	$\Delta p_a = \frac{\Delta p_a(i)}{\Delta i} \approx \frac{dp_a(i)}{di}$
η	Hunger-to-food ratio, a measure for evolutionary pressure	$\eta = \frac{\sum_{i=0}^{N_l} 1 - S_i}{pNF}$

Chapter 3

Green-beard altruism in the wild

3.1 The paradox of altruistic behaviour

3.1.1 Hamilton's rule

Importantly, individuals that show altruistic behaviour are at an evolutionary disadvantage as compared to the other, selfish organisms. The population as a whole might benefit if you sacrifice your own life to save multiple others, but since you will no longer be able to reproduce, your DNA will not survive. As we have established in chapter 2, the DNA that gives itself the greatest survival chance over other DNA in the population will usually become the only DNA variation. There are, however, some exceptions. An example would be Hamilton's Rule. This rule states that

$$BR - C > 0 \quad (3.1)$$

where B is the number of people saved by your altruistic deed, R how closely related they are and C how much your sacrifice costs.

For example, if you can save one sibling while having a 70% chance to die, the equation gives:

$$1 \cdot 0.5 - 0.7 = -0.2 \quad (3.2)$$

Because you only save one person that has on average 50% of your DNA in common, this sacrifice is not worth it. If you can save three siblings, however, the equation becomes:

$$3 \cdot 0.5 - 0.7 = 0.8 \quad (3.3)$$

As a result, it becomes worthwhile to try to rescue them. This mean altruism can be very good as long as you help your own family, and there are a lot of animals, such as ants, wolves and humans that exhibit this kind of behaviour. One might even consider multi-cellular life as cells that work together and can sacrifice themselves to make sure their DNA survives.

3.1.2 The Hawk-Dove game

Sacrificing your own DNA to save the DNA of familiars with similar genes might seem like cheating, and we fully agree that it is. There is, however a second way that altruism can pay off. To look at it, however, we must first examine a classic problem from game theory. The hawk-dove game goes as follows. Two players have to share a resource. They can try to get it aggressively or passively. If they are both passive, the resource is divided equally among them. If only one plays aggressive, he gets a bigger share and his opponent nothing. If both play aggressive, they lose so much energy fighting that they lose more resources than they win. This means that if the other person plays passive, you must play aggressively to win the most. If the other person plays aggressive, you must take your loss and play

dove. These two states, where one is the hawk and the other the dove, are called a stable equilibrium. most people will not want to do either of these things, however. If the other plays hawk they will do the same to show they are willing to sacrifice their own share to teach the other person a lesson, and if the other player chooses dove they will want to share equally and also pick dove. This is because they know the other player will remember them and do not want him to turn against them. Altruism can thus also exist in a population that can remember the behaviour of individuals. If you can be judged for your actions later, you are more likely to help others in the hopes that they will help you, and if they do not you will know not to help them later.

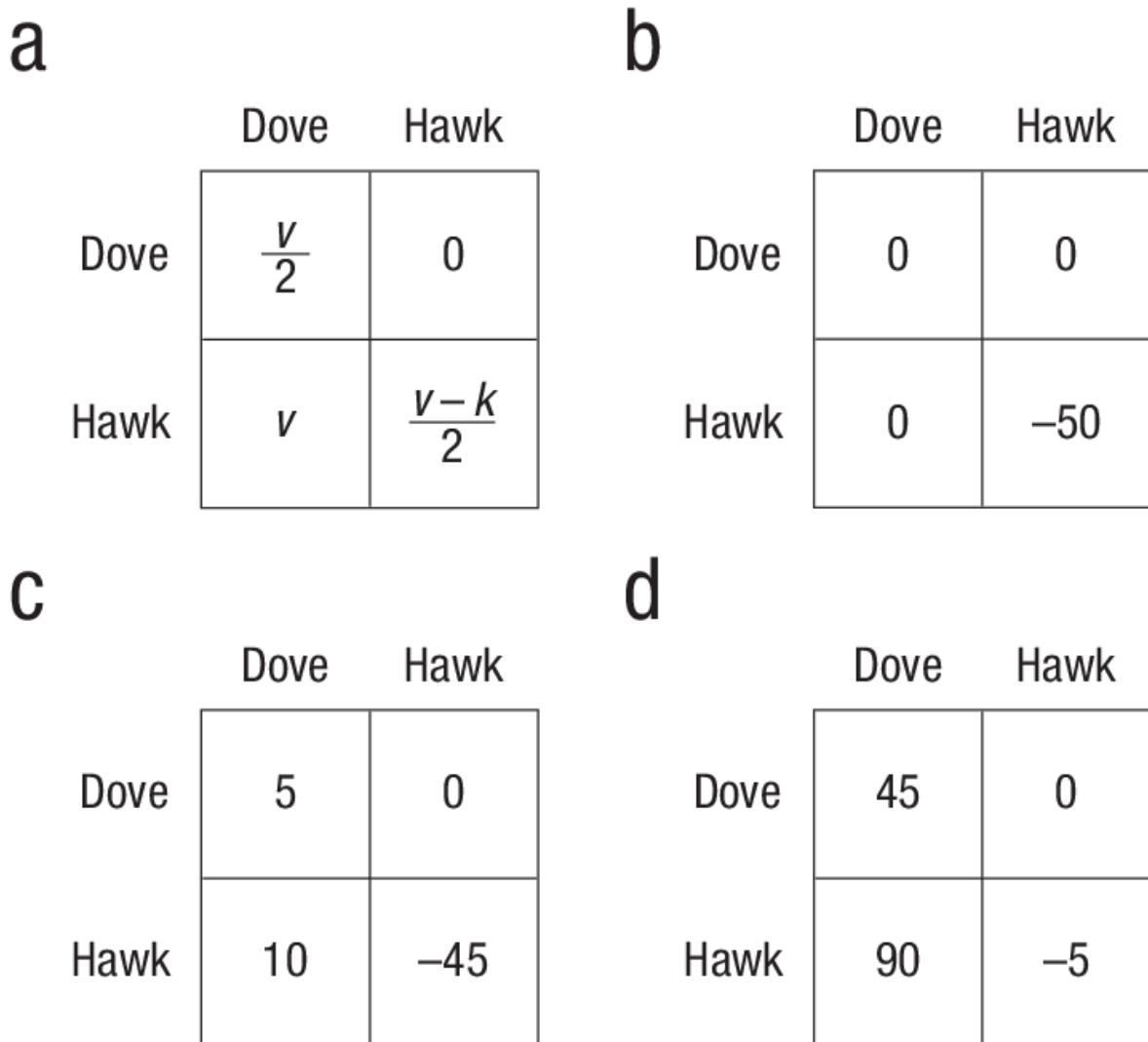


Figure 3.1: Pay-off scheme for the Hawk-Dove game. [17]

3.1.3 Green-beard altruism

Imagine how the world would look if, instead of having to learn to trust people, you could just see if they will be altruistic or not? As it turns out, we do not have to imagine. There are multiple species right now that are capable of sensing whether others are altruistic or not. This green-beard allele is recognisable in for instance brewers yeast [16] and red imported fire ants [1]. Green-beard altruism works as follows: a gene for altruistic behaviour and a gene that results in a very visible phenotype are located right next to another on a chromosome. If you can recognise the phenotypical change, you can deduct who is altruistic and who is not. This means you as an altruist can be altruistic to fellow

altruists only. In this way, helping each other can be an effective survival strategy. Why is it then, that we rarely see it in nature? Crossing-over heavily undermines the effect of altruism. If a crossing-over occurs right in between the green-beard gene and the altruism gene, so-called impostors can get all the advantages from sharing with the green beards, without giving anything in return. This is likely a reason why Green-beard altruism is so rarely seen in nature. It also explains why it is mostly seen in single-celled organisms: they have a smaller chance for crossing-over to occur.

3.2 The red imported fire ant

The best-known organism with a green-beard allele might be the red imported fire ant, *Solenopsis invicta*. It originates from central South America but has spread to other regions, such as North America and Australia. At 1.5mm to just over half a cm it is not particularly impressive, but it is very aggressive and is often considered a plague insect because it has very few natural predators in many regions, can out-compete local species and is capable of damaging houses, outdoor appliances and local plant life. The queens start out as normal eggs, but during their larval state, they get more food, leading to their development to queens. This process happens in every season but is most prevalent in spring. After the queens went through their larval and pupal stages, they turn into an adult and fly out of the nest. During this time they mate with a male ant and dig a hole into the soil [7]. They can, however, also find another colony: if this happens their green-beard allele comes into play: The altruistic queens will be accepted into the colony, but the selfish queens will be killed. This is caused by their genotypes: the Altruists are heterozygous (Bb) at the Gp-9 locus, while the selfish ants are homozygous dominant (BB) at the locus. Being homozygous recessive (bb) is lethal: the queens with this genotype die in the larval stadium. It is worth noting that workers with this genotype do survive and are often responsible for killing selfish queens [1]. This means that an altruistic population can not exist without accidentally producing more selfish ants. This seems like a very likely place for crossing-over to occur: an ant that can get inside the cooperative hive without having to contribute to the hive itself would have an enormous advantage. Because the selfish and the altruistic ants are frequently in contact it would also be a very useful adaptation to their environment.

3.3 Simulating the red imported fire ant

The previous model is of course not very well adapted to the red imported fire ant. This is why a new model is required. This model must be capable of the following things: first of all, it must be able to simulate the gathering of supplies. the queens of the nests must be able to produce workers who can collect food. As they get older, they can produce more workers per time unit. The workers do not need to physically touch food, but can just randomly get assigned food. This means that larger colonies that have a lot of workers can gather more food and small nests will gather less. Every ant of course needs food, which is subtracted from the nest's total. The ants again need to be able to die if they have too little food, but this time the workers of a hive die first and the queens later. To fully simulate the green-beard allele in the ant species, they must also be able to give birth to offspring. This means that every queen in every hive must be able to reproduce and the offspring must be reorganised into the colonies. For the reproduction, two existing queens can be bred, which is not really biologically accurate, but can be seen as the offspring of two different queens mating. The offspring get their DNA from the parents. they get one Gp-9 allele from each parent. The random reorganisation into colonies can be handled by putting every queen in the nest of one of the parents. This makes it really simple to convert the food reserves of the hive into offspring and quickly simulates how queens can encounter existing nests. In the real world, not every queen encounters a hive, but this does not really matter as we are looking at the interactions of the hives where the ants do meet. When a selfish queen enters an altruistic hive, she will either get killed, costing the colony a very small amount of food for the effort they put in it, or have an impostor green beard and survive, stealing a larger chunk of the hive's food supply. An altruistic queen in an altruistic colony will of course simply integrate into the colony. Altruistic hives that become very large may split into two smaller ones.

Chapter 4

Modelling green-beard alleles

The basic model that was discussed in chapter 2 only covers altruism that is exclusively behavioural: individuals acted altruistically, but could not anticipate the behaviour of other individuals, as altruism was not discernible from individual to individual. In reality, there are examples of species, such as the *Solenopsis invicta* that exhibit different behaviour based on an altruism allele, that other individuals of the species can recognise. As discussed in chapter 3, this altruism allele yields a discernible feature, besides their behaviour. This feature, often referred to as a *green-beard*, is the focus of this chapter.

4.1 The green-beard model

All code is available via <https://github.com/MikeKuijper/ModelsOnAltruism>.

4.1.1 Model definition

The green-beard model attempts to model the red fire ant's altruism by expanding upon the basic model, as discussed in chapter 2. Primarily, the model moves away from the individual-focused approach, and places the colony at the centre of attention. Individual ants are still modelled, but, as the altruists are characterised by forming colonies where non-altruists are quickly killed by the colony, colonies are the focus.

It differentiates worker and queen ants. Queen ants are responsible for reproduction, and worker ants for acquiring food. For simplicity, and to reduce modelling time, the reproduction is only modelled for queens. Every season, which consists of a set number of iterations, all queens procreate to make new queens. The number of times a queen can reproduce is dependent on her colony's saturation: she can reproduce once for every C_r of saturation but does not use everything. p_r is the amount of saturation reserved for means other than reproduction. If an altruistic queen is born in an altruistic colony, and the colony's saturation surpasses T_s , the colony splits into two. Workers are added each iteration; the amount is based on the number of queens in a colony. A worker ant has an age, which determines its efficacy while acquiring food: the older it is, the more food it can take to the colony, up to a maximum, P_{max} .

Each queen has an intermediary stealth gene, p_s . It describes the probability of it escaping a colony in case the workers reject the queen. This happens when a selfish queen is born in an altruistic colony. The gene is present in both selfish and altruistic ants. It starts at s_0 and mutates by a random factor with a maximum magnitude of M_m . If a queen is rejected and fails to escape, the colony's saturation is reduced by C_k , the cost for killing the queen. A new colony starts with $\#w_0$ workers.

Each iteration, a total amount of F_{total} saturation points is distributed over the population. This yields:

$$f(n) = \varepsilon(n) \sum_{j=0}^{N_n} \min(w_j + 1, P_{max}) \quad (4.1)$$

where $\varepsilon(n)$ is a random value based on seed n . It can be described as follows:

$$f_{total} = \sum_{n=0}^N f(n) = \sum_{n=0}^N \left(\varepsilon(n) \sum_{j=0}^{N_n} \min(w_j + 1, P_{max}) \right) \quad (4.2)$$

There w_j represents the age of worker j in colony n and N_n the number of workers in colony n . One might consider the following.

$$F(n) = F_{total} \frac{f(n)}{f_{total}} = F_{total} \frac{\sum_{j=0}^{N_n} \min(w_j + 1, P_{max})}{\sum_{n=0}^N \left(\varepsilon(n) \sum_{k=0}^{N_n} \min(w_k + 1, P_{max}) \right)} \quad (4.3)$$

There, $F(n)$ describes the food a colony receives, $f(n)$ is the food score of colony n , and $\min()$ is the minimum function, which returns the smallest of its inputs¹.

Further, the green-beard model keeps track of seasons. The basic model showed that these simulations have a tendency to quickly converge on an equilibrium², and are therefore undesirable when high evolutionary pressure is desired. Therefore, the green-beard model periodically allows colonies to procreate, as is true in the real world as well. Each ‘season’ lasts N_s iterations. Thus, this method periodically increases the food scarcity, and therefore the evolutionary pressure.

The green-beard model uses two alleles to distinguish between altruistic and selfish behaviour. In previous literature[1], b is used to denote the **dominant** allele for altruistic behaviour, and B for the **recessive** allele for selfish behaviour. A genotype of bb is lethal in an early stage after conception and is therefore not present in the population. Thus, this model holds two different phenotypes in the population: altruistic and selfish.

\times	B	b
B	BB (selfish)	bB (altruist)
b	Bb (altruist)	bb (lethal)

Table 4.1: The Punnett square [4] for the green-beard altruism allele, b , and its counterpart, B , as described above, including phenotype. Note that, although the selfish allele is recessive, this does not mean its occurrence will naturally decrease. On the contrary: the selfish gene is always carried by two altruistic parents, and the selfish phenotype has a 1 in 3 probability of occurring, whereas selfish ants can only produce selfish offspring.

4.1.2 Model pseudocode

The green-beard model works through three main subroutines. At the centre is the `iteration()` function, which defines the model’s behaviour for every iteration. This function performs the model’s primary tasks: managing colonies’ saturations and calling the secondary functions, the `reproduction()` and `mate()` functions.

For food production, the model uses a weighted division, as described in equation 4.3. This is counteracted by a daily saturation reduction, dependent on the number of worker ants. A queen needs significantly more nutrients than a worker ant and can be weighted accordingly with M_q . The queen does not contribute to the food supply.

¹One might consider using the logarithm of the age, or something similar, but we opted against it due to time constraints.

²See figure 2.2 and 2.3

Algorithm 2: Iteration function. Calls the `reproduce()` function.

```

totalFoodMultiplier = 0
for colony in population do
    | colony.saturation -= C * (2* colony.queens.size() + colony.workers.size())
    | if colony.saturation  $\leq 0$  then
        | | colony.isAlive  $\leftarrow$  false
    | end
    foodMultiplier  $\leftarrow$  0
    for worker in colony do
        | | add min(i - worker's dateOfBirth, maxEfficiency)+1 to foodCoefficient
    | end
    totalFoodMultiplier += foodMultiplier
    colony.foodMultiplier  $\leftarrow$  foodMultiplier
end
for colony in population do
    | | colony.saturation +=  $\frac{\text{colony.foodMultiplier}}{\text{totalFoodMultiplier}}$  * totalFood
end
if i % seasonLength = 0 and i  $\neq 0$  then
    | | reproduce()
end

```

If the iteration number is exactly divisible by the season length, N_s , or, in other words, if N_s iterations have passed, the `reproduce()` function is called. It is responsible for pairing the population's queens and determining the number of times a queen is allowed to reproduce.

Algorithm 3: Reproduction in the green-beard model. Is called every season.

```

for colony in population do
    for queen in colony do
        for other queen in  $\frac{\text{queen's saturation}}{\text{childCost}}$  random other queens do
            offspring = mate(queen, other queen)
            if offspring survives then
                if offspring is not altruistic and colony is altruistic then
                    if random(0, 1) > offspring's stealth then
                        newColony  $\leftarrow$  Colony
                        newColony.queens  $\leftarrow$  offspring
                        population.append(newColony)
                    end
                    else
                        | | colony.saturation -= killCost
                    end
                end
                else
                    | | colony.append(offspring)
                end
            end
        end
    end
end

```

The `mate()` function determines the genotype of the offspring.

Algorithm 4: Mating function. Returns the child of two parents.

```

output  $\leftarrow$  new Ant
if firstParent.isSelfish and secondParent.isSelfish then
| isAltruistic  $\leftarrow$  false
end
else if not firstParent.isSelfish and not secondParent.isSelfish then
| isAltruistic  $\leftarrow$  random(0, 1)  $\leq \frac{1}{3}$ 
| isLethal  $\leftarrow$  random(0, 1)  $\leq \frac{1}{4}$ 
end
else
| isAltruistic  $\leftarrow$  random(0, 1)  $\leq \frac{1}{2}$ 
end

if not isLethal then
| output.isAltruistic  $\leftarrow$  isAltruistic
| output.stealth  $\leftarrow$  mean(firstParent.stealth, secondParent.stealth) + random(-1, 1) *
  mutationMagnitude
| output.dateOfBirth  $\leftarrow$  i
| return output
end

```

4.2 Observations

We have run various simulations with the model. Most obvious was the fact that the model environment is quite unstable. Small differences in even a few variables bring about sizeable effects on the population. Particularly, the split threshold, T_s , and the proportion of reserves, p_r , influence the result of the model considerably.

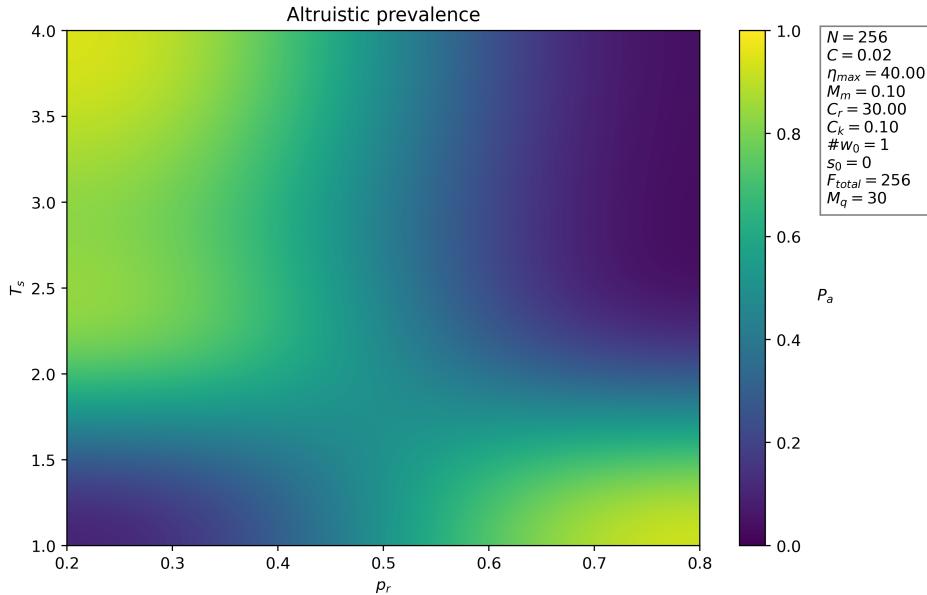


Figure 4.1: An approximation of the altruistic prevalence in the green-beard model, interpolated based on 16 data points. It suggests an optimum near $(0.2, 4)$, as well as a diagonal symmetry. $p_r \in \{0.2, 0.4, 0.6, 0.8\} \wedge T_s \in \{1, 2, 3, 4\}$

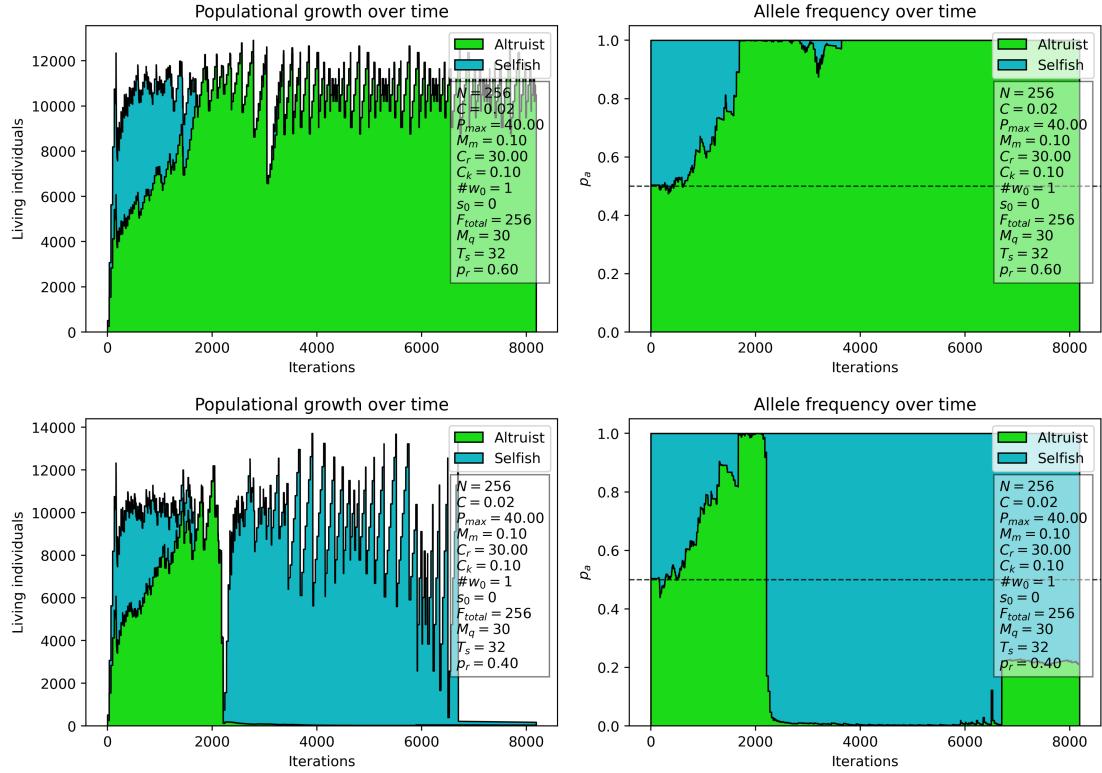


Figure 4.2: Two runs, demonstrating the effect of the p_r value. Its value determines which portion of their saturation the colonies keep as reserves. The bottom run shows a very typical progression of a win for the selfish. At first, the altruists seem to win, but the selfish seem to outperform the altruists after around 2200 iterations. We have not found an explanation for that, but the general shape is common among simulations. It also clearly shows a periodic variation as a result of the implementation of seasons.

4.3 Shortcomings and applications

This model is significantly more thorough than the basic model. The setup is based on actual living ants, but it simplifies in a few areas. To start, reproduction is only modelled among the queens. This is not accurate. Further, the model does not take living space into account.

Firstly, it offers very little feedback about what is happening under the hood. This could be improved. Although the simulation is executed with a lot of individuals, more can make it even more reliable and less susceptible to random effects and luck which can kill off one of the groups by using even more simulated ants. It also suffers from some flaws inherent to modelling, mainly by not necessarily being accurate to its real-life counterpart. This could technically be solved by looking at a real ant population, but this is extremely hard, expensive and time-consuming. One very interesting thing we found during the modelling of red fire ants, is that the selfish colonies seem to get the upper hand if all hives hoard a lot of food instead of quickly using it to produce offspring. We suspect this might be because their flaw of being more susceptible to variations in food production is mitigated somewhat by this.

4.4 Table of symbols

This table expands on table 2.4

Symbol	Description	Remark
P_{max}	Maximum efficiency for older worker ants	$P_{max} \in \mathbb{N}$
M_m	Magnitude of stealth mutations	$M_m \in [0, 1]$
C_r	Cost of reproduction	$C_r \in [0, \rightarrow]$
C_k	Cost of killing a selfish queen	$C_k \in [0, \rightarrow]$
$\#w_0$	Number of starting workers per colony	$\#w \in \mathbb{N}$
s_i	Stealth property, of individual i	$s_i \in [0, 1]$
s_0	Starting stealth	$s_0 \in [0, 1]$
F_{total}	Total nutrition	$F_{total} \in \mathbb{N}$
M_q	Weight of queen from a nutritional standpoint	$M_q \in \mathbb{R}$
p_r	Proportion of food reserved for use other than reproduction	$p_r \in [0, 1]$
$\varepsilon(n)$	Random factor with seed n	$\varepsilon(n) \in [0.5, 2]$
N_s	Season length	$N_s \in \mathbb{N}$

Chapter 5

In conclusion

Which parameters does a model require in order to accommodate an altruism allele?

We stated that a simple evolutionary model for testing altruism alleles requires the following things: an evolution theory and a population that partially consists of altruistic and partially of selfish organisms. These organisms need a resource for which they can compete and if they fail they should die. The altruist should be able to help the selfish and the other altruists, but the selfish will hoard all the resources. These resources can be randomly handed out. These resources must be so scarce, that a lot of individuals will die. This model proves that giving away resources is not a good survival strategy.

How can we adapt our basic model to the red imported fire ant's altruistic behaviour?

We can adapt our basic model of evolution to red imported fire ants by adding reproduction, giving queens workers that can collect food and making the colonies able to die if there is too little food. The model must also be able to let the queens create offspring, give them a genotype and assign the offspring to different colonies. It must then let those colonies be able to react to the new queens according to their genetics.

How does a green-beard allele persist in a colony of red imported fire ants, *Solenopsis invicta*?

Altruistic red imported fire ants form large colonies, whereas the selfish live in more, but smaller colonies. This means that the evolutionary advantage comes not from the individual behaviour that was described in chapter 2, but from their cooperation. The selfish are difficult to outperform, as they naturally get born in altruistic colonies, but altruists can only be born in an altruistic colony. That evolutionary disadvantage is not exclusive to altruism and can be overcome.

Under what circumstances does a green-beard altruism allele continue to exist in a numerical model based on the red imported fire ant, *Solenopsis invicta*?

A green-beard allele continues to exist if its circumstances allow for more than just a simple disadvantage. That is, it needs to be able to show complex behaviour. The *Solenopsis invicta* succeeds in that regard, as it is able to turn its initial disadvantage into an evolutionary advantage by working together with other altruists. The red imported fire ant is famous for its brilliant cooperation, and uses this advantage to compete with the non-altruistic fire ants. The fact is genetic circumstances are not ideal, but the altruists work around that by brutally murdering non-altruistic queens.

If chromosomal crossing-over were to mimic the green-beard effect, this would cause a massive advantage. Therefore, we conclude that this has not happened. Or rather, it is not happening to the current gene. It is quite likely that such a mutation has occurred, but, as all offspring from those ants have the gene, the advantage has become insignificant. Therefore, we believe that our hypothesis was correct.

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Appendices

Appendix: Logbook

Mike

Date	Activity	Time spent
August	TEX Template	10:00
September 19	Background research	1:15
September 22	Background research	1:10
September 23	Background research	1:00
October 10	Call with Van Dam	1:15
October 12	Sources and background research	1:00
October 13	Sources and background research	2:30
October 16	Chapter 1 start	0:45
October 17	Chapter 1 and begin basic model	5:15
October 18	Chapter 1, 2 and continue with basic model	3:50
October 19	Library visit	2:10
October 20	Continue with chapter 2 and 'Mathematical implications'	3:30
October 22	Statistics and p_s over S	4:30
October 23	p_s over S and algorithm listing	4:00
October 25	p_s over S and criticism	1:00
November 9-11	Call with Van Dam and writing	4:00
November 14	Definition η and Δp_a and relation	2:00
November 15	Call with Van Dam and η and Δp_a plot	5:00
November 21	Finished chapter 1 and started chapter 4	4:00
November 22	Call with Van Dam and continue chapter 4	2:00
November 23	Green beard model	2:00
November 24	Planned chapters and layout	1:00
November 25	Finished chapter 1 and continued chapter 4. Model designed	4:00
November 26	Chapter 4: Model and writing; further revisions throughout	10:00
December 4	Implemented feedback	3:00
December 5	Worked on chapter 4: model and revisions	5:00
December 6	Worked on chapter 4: model and revisions	3:00
December 8	Chapter 4: model	1:00
December 8	Chapter 4: model	5:00
December 11	Chapter 4: model	2:00
December 12	Chapter 4, revisions throughout, front page	14:00
December 19	Final revisions	5:00

Stijn

Date	Activity	Time spent
September 19	Call with Van Dam	1:15
September 22	Background research and choosing topic	2:10
September 23	Background research	1:30
October 10	Call with Van Dam and research	1:45
October 11	Sources and background research	1:45
October 13	Sources and background research	2:00
October 17	Chapter 1 start	5:15
October 18	Chapter 1 and more background research	3:40
October 19	Library visit	2:10
October 23	Background research	1:45
October 25	Discussion about the math used	0:30
October 26	Evaluating the basic model	2:45
November 8	Call with Van Dam	2:35
November 10	Writing chapter 1	1:45
November 11	Writing	1:30
November 14	Reading sources and writing	3:15
November 15	Call with van Dam, checking work	3:45
November 16	Writing chapter 3 and reading sources	1:20
November 17	Writing Chapter 1	2:30
November 21	Going through red ant model specifications	1:15
November 22	Writing chapter 1	2:25
November 24	Background research	3:30
November 25	Writing chapter 3	4:15
November 26	Red ant model discussing and writing chapter 1	7:00
December 5	Implementing feedback	5:00
December 6	Split part of chapter 1 into chapter 3	3:30
December 8	Writing on chapter 3	4:15
December 10	Writing on chapter 1 and 3	3:20
December 11	Introduction and chapter 5	2:40
December 12	Finishing chapter 1 and 3, revisions on chapter 0 and 5	12:30
December 19	Copied over logbook	0:30

