

Propagation of a green-beard altruism allele

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1 Introduction

A green-beard gene is defined as one that causes the organism carrying this gene to exhibit some externally recognizable phenotype and to behave differently to other organisms which also exhibit this phenotype[1]. In this study we will be concerned with the type of green-beards which cause the organism carrying that gene to behave altruistically to other organisms which exhibit the green-beard phenotype. This type of a gene is not commonly observed in evolutionary systems for various reasons outlined later. However, some instances of green-bearded genes have been shown to exist in nature, such as in the imported fire ant *Solenopsis invicta*[2].

I came across this topic in an example simulation which showed how an altruistic green-beard allele could spread accross a population of organisms and similarly how it could be destabilized by the addition of an imposter allele which exhibited the externally recognizable green-beard trait, without the altruistic behaviour for others with this trait. However, this example simulation left me wondering why do some species then exhibit ostensibly altruistic behaviour and how come green-beard alleles have been demonstrated to exist in nature, if they can be outcompeted via mimicry of the green-beard characteristic without exhibiting the altruistic behaviour. Maybe one possibility could be the intractability of mimicry of the external green-beard trait by an imposter to such a degree that it'd be indistinguishable from a true green-beard. So, I thought what would happen if the green beards had some chance of recognizing carriers of the imposter allele. Therefore, I decided to explore this question in my biology IA by creating my own simulation with the additional mechanic of the organisms which carry the green-beard allele having the possibility of recognising those that carry the imposter allele.

Hypothesis

If the imposter recognition rate rises above the survival rate of the warner, a trait for green beard altruism will tend toward becoming the most prominent allele and vice versa.

2 Method

The simulation consists of three types of objects: evolvers, food sources and predators. During one day in the simulation each evolver goes to a single randomly chosen food source in a randomly assigned order. At each food-source an event follows, the specifics of which are dependant on the other organisms at that food source, be they evolvers or a predator. This event leaves any given evolver either alive or dead. Each evolver which is alive at the end of a day in the simulation makes a copy of itself with the same allele.

Each food source has enough food to support 2 evolvers. Any evolvers that chose a food source which already has two evolvers feeding at it are unable to

survive the day. The order in which evolvers go to food sources is randomized. This mechanic was added such that the absolute number of all evolvers would stay around a given value and not continue to grow exponentially, which is analogous to real life where a population of organisms will continue to grow exponentially until the growth is limited by either nutrition or predation. The expectation of this mechanic is to randomly remove evolvers of all alleles present, proportional to the number of evolvers that are carrying a given allele at the time, therefore not affecting the focus of this study, which is the comparative propagation of different alleles in the population.

At the start of the study each food source is assigned to either contain or not to contain a predator, this process is randomised with an arbitrarily assignable probability. In this study the probability of a given food source containing a predator was set to 30% for each trial. The cases where evolvers feed at a food source without a predator are fairly trivial. This merely results in the death of any evolver that goes to that food source after the first two. In the case that the food source contains a predator and there is one evolver feeding at that food source, the evolver dies. However, in the case that two or more evolvers are feeding on a food source with a predator, the interaction between these evolvers and the predator depends on the alleles that the evolvers hold.

There are four different behaviour patterns which an evolver may exhibit: 'altruist', 'green-beard', 'imposter' and 'coward'. How a particular evolver will behave is solely determined by which allele of the altruism gene they carry. The allele that an evolver carries also determines whether they exhibit the externally visible phenotype of the green beard. The behaviour exhibited and the 'beardedness' of evolvers carrying each type of allele may be summarised as follows.

Altruist: Acts altruistically to other evolvers, regardless of whether they exhibit the recognizable feature of a green beard. The altruists themselves do not exhibit the externally visible green-beard trait.

Green-beard: Acts altruistically only to other evolvers that exhibit the green-beard trait, which it itself also exhibits.

Imposter: Does not act altruistically to other evolvers. exhibits a version of the green-beard trait.

Coward: Does not act altruistically to other evolvers and does not exhibit the green-beard trait.

During an interaction at a food source with a predator and two or more evolvers, the first evolver at a given food source will be oblivious to the existence of a predator and the second evolver to come to the food source will notice the predator and will act in one of two ways. Either it leaves quietly, causing the first evolver at the tree to die while it itself may escape unharmed or it will make noise, saving the oblivious evolver. However, this attracts the predator's focus in the process and the evolver which made the warning call will have some given probability of surviving which will be set to 50% for the instances in this

study. Table 1 features a compilation of the possible combinations of evolver’s alleles that can be found in evolvers which happen upon a food source with a predator. The value in each cell specifies the action of the second evolver to happen upon the food source.

first \ second	altruist	true beard	coward	imposter
altruist	warns	leaves	leaves	leaves
true beard	warns	warns	leaves	leaves
coward	warns	leaves	leaves	leaves
imposter	warns	warns*	leaves	leaves

Table 1: Behaviours in an interaction by allele

The starting conditions for these simulations will be a population where on average one fourth of the population will carry each allele. This is done by randomising the allele given to any one evolver with equal probability of any of the four options when creating each evolver. The number of evolvers and trees and probability for any given tree containing a predator in the beginning of a day are also inputted into the program. The values used in this study are given in table 2. The imposter recognition probability, gives the probability that in a given interaction, with an imposter as the first evolver on a food source with a predator and a green-beard as the second, the green beard will not warn the imposter, but will in stead leave and this is referred to as the ‘recognition’ that the imposter does not actually carry the green-beard allele.

The next step is to figure out the relationship between the propagation of the green beard allele and it’s imposter recognition probability, the focus of the study. In order to do this the simulation was ran multiple times with different imposter recognition rates, while keeping the other variables constant and analysing the subsequent data.

3 Safety, Environmental and Ethical considerations

There are no ethical nor environmental considerations with this study.

4 Results and Analysis

A sample simulation without the imposter recognition trait expectedly shows the altruism allele going extinct first, followed by the green beard allele with the imposter allele propagating more aggressively than the coward allele in the beginning as they are advantaged by both the green beards and altruists as seen in figure 1. This occurs until the green beards are extinct, as occurs around day 50 in the single sample simulation at which point cowards are indistinguishable

from imposters in the population, meaning that any variation in their proportions are random and ultimately cancel out as can be seen from the averaged values from 100 sample simulations.

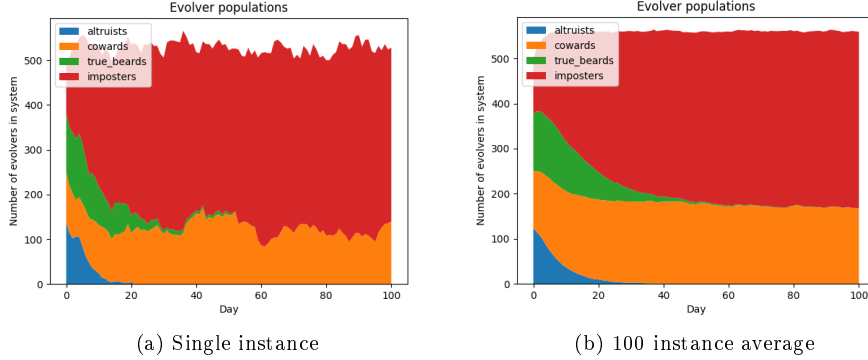


Figure 1: Results of running the simulation with values specified in table 2

Number of days	100
Beginning evolver count	200
Number of trees	180
Predator probability	0.3
Survival rate of warner	0.5
imposter recognition rate	0

Table 2: Values of variables for the simulation

The directions of propagation seen in the sample simulations in figure 1 can be reasoned based on the expected value of propagation from an interaction, calculated with the supposition that each allele is equally proportioned in the population. Which is the expected distribution in the starting conditions. These expectations are calculated by considering each possible interaction an evolver can have with another evolver at a tree with a predator and multiplying the probability that they survive by two times the probability of the interaction, reflecting the fact that if the evolver survives, it duplicates for the following day. The results of these calculations can be seen in figure 2.

It is of note that the expected value of propagation is above one for even the green beards, yet they still go extinct, this is because an interaction between evolvers on a tree is not the only possible fate for an evolver during a day and in a simulation with limited resources like the one in this study, the allele with the highest expectation of propagation will outcompete any alternate allele over time regardless of the absolute value of the expectations in a given interaction. The cowardice allele only survives because it becomes indistinguishable from

$$\begin{aligned}
P(x_i) &= \frac{1}{8} \\
E(\text{greenbeard}) &= \sum_{i=1}^8 x_i \cdot P(x_i) = 2 \cdot \frac{1}{8} + 2 \cdot \frac{1}{8} + 0 \cdot \frac{1}{8} + 0 \cdot \frac{1}{8} + 1 \cdot \frac{1}{8} + 1 \cdot \frac{1}{8} + 2 \cdot \frac{1}{8} + 2 \cdot \frac{1}{8} \\
&= \frac{10}{8} = 1.25 \\
E(\text{imposter}) &= 1.5 \\
E(\text{altruist}) &= 0.75 \\
E(\text{coward}) &= 1.25
\end{aligned}
\qquad
\begin{aligned}
E(\text{imposter}) &= 1 \\
E(\text{coward}) &= 1
\end{aligned}$$

(a) Propagation expectations given that each allele are expressed in 25% of the population

(b) When green-beards and altruists have gone extinct

Figure 2: Expectations expressed mathematically

the imposter allele in its relative expected interaction propagation before it has time to go extinct.

It may also be noted that the value of propagation in the interactions is higher for individual green-beards at the start of the simulation than for imposters at the end of the simulation. In fact, a population made up only of green beards or altruists would be more successful. However, as the base unit of selection is the gene rather than the group, the population will still tend toward being made up of only imposters and cowards.

In order to analyse the relationship between the imposter recognition rate the simulation was ran at different recognition rates, and for each the portion of the population which held the green-beard allele at the end of 200 days was taken. Figure 3 shows this data averaged out over 40 instances of the simulation at each recognition rate.

From the data a positive correlation can be seen. The R^2 value for linear regression on this data is 0.899, which is fairly strong. However, it can be seen that the relationship does not seem to be linear in nature. Rather the data would seem to be best modelled by a logistic function. Using non-linear least squares regression to fit a logistic function onto the data, yields the variables seen in figure 3c. The R^2 value for this regression model is 0.988, indicating a very strong fit.

A logistic function suggests an underlying classification problem, and this assumption proves to be highly justifiable in this case. The underlying mechanism for the emergence of a logistic function in this case is likely be that each individual simulation has tended to a population entirely made up of either green beards or of only imposters and cowards and the value of the logistic function at a given probability of recognition gives the probability that the green beards will end up as the only allele present in the population

Given that this interpretation of the logistic curve is correct, in order to prove or disprove the hypothesis we must find the point at which green beards tend to become the prominent allele in the population more than 50% of the

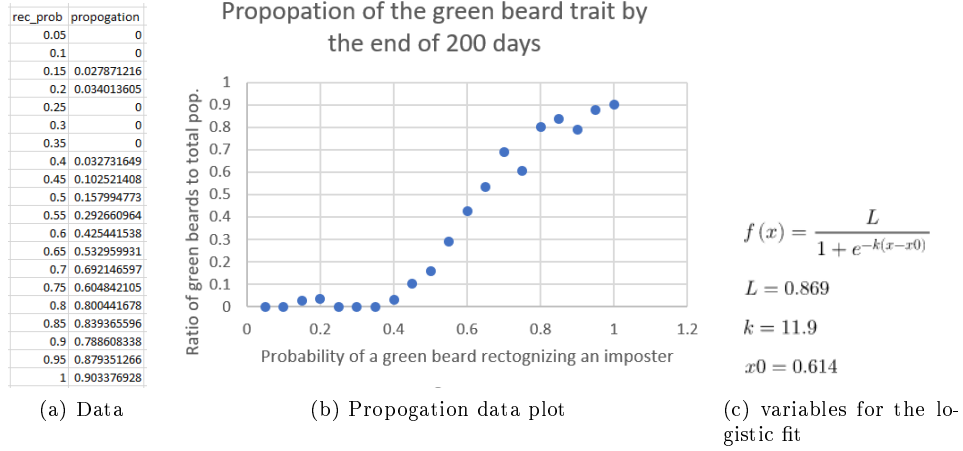


Figure 3: logistic function

time, which was hypothesized to be equal to the warner survival rate, 0.5. The value that the simulations suggest is at 0.614, the midpoint of the sigmoid curve. The p-value for this observation could be calculated. However, there is a simpler method of mathematical analysis that suggests that rather than the point being the same as the warner survival rate, 0.5, it would be $2/3 = 0.66$, a value that is also closer to the data from the simulations. Namely, by formulating functions for the expectations of propagation in an interaction in the starting conditions, in terms of the recognition rate, for the competing green beard and imposter alleles and calculating the point at which they intersect, as is shown in figure 4.

Since the function for the expectation of the greenbeard is increasing, it is larger for any probability of recognition above $2/3$ proving that in a population where one quarter of the evolvers hold each allele, the green beard will outcompete the imposter allele, given that it can recognise it more than $2/3$ of the time. Disproving the hypothesis that this value is equal to the warner survival rate, the exact relationship seems to be more complicated than that.

5 Improvements and further exploration

It is of note that the mathematical analysis in figure 4 does not prove that $2/3$ is the tipping point for the likeliest allele to dominate the population, as the analysis given does not give information about how the survival rates vary as the ratio of alleles begin to change in the population. Further mathematical analysis would be required to prove that statement. However, it can be intuited that the green-beard trait would benefit from it being more highly distributed in the population and would suffer from the inverse. Furthermore, since the data from the simulation more or less reflect this intuition, the conclusion may

$p = \text{probability of recognition}$

$$f(p) = E(\text{greenbeard})$$

$$g(p) = E(\text{imposter})$$

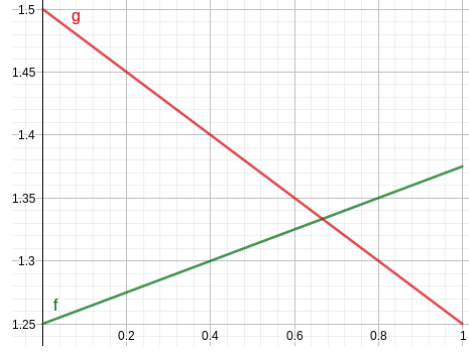
$$f(p) = \frac{9}{8} + \frac{1-p}{8} + \frac{2p}{8} = \frac{p}{8} + \frac{5}{4}$$

$$g(p) = \frac{10}{8} + \frac{2(1-p)}{8} = -\frac{p}{4} + \frac{3}{2}$$

$$g(p) = f(p) \Rightarrow \frac{p}{8} + \frac{5}{4} = -\frac{p}{4} + \frac{3}{2}$$

$$p = \frac{2}{3}$$

(a) Intersection point



(b) x-axis: probability of recognition; y-axis: expectation of propagation

Figure 4: Expectations of propagation expressed in terms of the probability of recognition, given that each allele is 25% of the population

be accepted.

There are also alternative interpretations of the logistic function than what was chosen in the conclusion of this study, such as that within 200 days the population has yet to arrive at its stable configuration of alleles. However, observing the data in Fig. 1 makes this explanation seem improbable as in those instances the stable state was arrived at within around fifty days. However, this does not prove this possible explanation false, to strengthen the conclusion of this study one could vary the length of the simulations and note how the logistic growth rate changes. Another possible interpretation is that a given instance would tend toward a distribution of alleles given by the logistic function in figure 3, this could be disproven by analysing what the instances of simulations at different imposter recognition rates look like rather than just analysing the aggregate. Another method would be to mathematically analyse how the expectations of propagation change with the distribution of the alleles at a given recognition rate and seeing whether there are some stable equilibria outside of one allele dominating the population.

Further exploration into the relationship of the logistic function and the warner survival rates should also be made as this study only considered the case where the warner survival rate is 0.5. This could be done via further mathematical analysis of the interactions between the evolvers or with further simulation while varying the warner survival rates and analysing the subsequent sigmoid curves' midpoints. The type of relationship these two variables have has some explanatory and predictive power to what is seen in nature. For instance, given a positively correlated relationship, we would expect more altruistic behaviour

to be seen in organisms that are in an environment with a low death rate in instances of conflict of interest between evolvers and vice versa.

The results of this study could have also been arrived to via only mathematical analysis of the given system of interactions via game theory which would bolster the results of this study. However, this fact does not trivialize the use of simulations for the analysis of these types of interactions. As simulations have certain key advantages to make up for the lack of rigour compared to purely mathematical analysis. One large advantage is that it makes incorporating the dynamic nature of evolution easier. The neglect of which can lead to error in purely mathematical analysis [3]. It may be noted that the simulation in this study also suffers from some neglect of the dynamics of evolution. Since the simulation ignores the chance of a random mutation once a dominant allele has established itself. Because of this, this simulation and subsequent analysis fails to prove that a given population of green beards or imposters is an evolutionarily stable state. If this were proven, it would affect the conclusion, since if a population of green beards at a given recognition rate isn't evolutionarily stable, sooner or later a mutation would cause the population to end up in an evolutionarily stable state and we could see something more like the hypothesis predicted where there is a critical value that causes either imposters or green beards to become and stay dominant. However, this may not be the case if a population of imposters is also not evolutionarily stable and this is likely since in a population of imposters, the coward allele is indistinguishable from the imposter allele, so the population could shift such that it is again viable for the green bearded allele to gain prevalence again, this may lead to an oscillating population between these two alleles. This would also likely produce a logistic curve in the results. However, it may have different constants, more exploration is needed.

The aforementioned ignorance of mutations is also reflected in the starting conditions, which would be extremely improbable to arise in nature. For instance, if the altruism allele is so aggressively outcompeted by the other alleles, it would not have ever actually gained 25% prevalence. A more realistic starting condition would be one where there is a dominant allele which is then challenged by a random mutation of, for example, a green-beard allele and then it is seen whether this allele will be able to disrupt the status quo.

Furthermore, the alleles present in this simulation are not comprehensive. There could also be an evolver that uses the warning call to its advantage to gain the fruit on a tree if there already is an evolver at a given food source and then if this became the dominant allele then an allele that would ignore the warning calls may develop, whether this is an evolutionarily stable state, is an open question, more research is required.

Further reasons as to why green beard alleles may be rarely seen in nature even if they could become dominant according to this study is that such "double effect" genes are rare. Since, if a green bearded gene were to exist it would have to code for some externally recognisable trait and for the behaviour of the organism and even if it would be more optimised for a population to be made up of green beards, evolution does not tend toward perfect optimisation, but

toward organisms that are good enough to survive and reproduce. For instance it is more likely for an imposter allele to arise, once there is a population of green-beards than for a green-bearded allele to have arisen in any population, since there could be a mutation in the evolvers which hold the coward allele, which only codes for the external trait utilized by the green beards for their recognition of each other.

Another issue for this study, and simulations in general, is the arbitrary nature of the values of the variables leaves the validity and predictive power of the simulation unverifiable by any actual observations of behaviour in nature. To rectify this issue the values for the survival rates could simply be chosen based on observations rather than arbitrarily. However, in order to do this some behaviour of a given organism would have to be chosen in which a duality of behaviour could be observed where one option is more altruistic than the other and then the survival and propagation rates of these organisms would need to be tracked. This ought to be possible for some relatively simple being, such as the fire ants in a previously cited study [2].

Some further differences with this study and observed evolutionary landscapes are the neglect of individual variety. However, random individual variety in, for instance, the imposter recognition rates by different individual green beards which result from factors outside of the allele itself would seem to be irrelevant as the spread of the allele would only be relational to the mean of the imposter recognition rate. So, in this model any variation, regardless of the deviation, can be simplified to each evolver having the mean recognition rate of the green beards. However, this claim would need to be proved by further analysis or simulation.

One final difference between the simulation and actual evolutionary landscapes is the fact that the evolvers in this study all reproduced asexually, while in the real world some organisms reproduce sexually.

References

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6 Appendix

A link to the github page with my program:

<https://github.com/MiikaVuorio/greenBeardSimulation>