Sympatric Speciation in Framsticks
Virtual Life Research Project

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Contents

1 Abstract

Many examples of speciation are found in nature. In some cases this is caused by a physical barrier that forces a population to diverge into two different species *(allopatric speciation)*. However, speciation without physical isolation can also occur *(sympatric speciation)*. In this research project we try to model sympatric speciation in Framsticks [5]. We start out with a population of intermediate individuals varying in artificial trait X (atX) that is not geographically isolated and on whom disruptive selection is working. Unfortunately evolutionary branching into two different biospecies did not occur.

2 Introduction

2.1 Background

Species consist of interbreeding populations that evolve independently of other populations. Gene flow between different species is limited. For speciation to occur, it was always thought the following three steps were needed:

1. An initial step that isolates populations.
2. A second step that results in divergence in traits such as mating tactics or habitat use.
3. A final step that produces reproductive isolation.

The classic model that explains speciation in the natural world is that of allopatric speciation. In this model new species arise from geographically isolated populations.

An enduring debate in speciation research has been whether physical isolation is an absolute requirement for populations to diverge, or whether natural selection for divergence can overwhelm gene flow and trigger speciation. Sympatric speciation is the process by which new species arise from coexisting populations. There is growing evidence that sympatric speciation does occur in nature. Examples of sympatric speciation, primarily in insects and fish, are found in Lake Whitefish (populations of dwarf versus normal-sized individuals), in Three-spine sticklebacks (bottom-dwelling versus open-water dwelling individuals), in butterfly species (different habitats and warning coloration) and in a variety of other species that have different host plants.

Careful genetic modelling of sympatric speciation has suggested it is possible for populations to diverge even when they remain in physical contact. In these models populations can diverge even with low to moderate degrees of gene flow if there is strong disruptive selection. These models often start with a population of intermediate individuals, whose adaptation to the environment is suboptimal and on whom disruptive selection is working. Disruptive selection means there is an ecological disadvantage to intermediates, creating pressure for divergence into two populations of distinct phenotypes. For example, if a habitat contains two potential resources, i.e. large or small prey or hosts, then large or small predators will do better than intermediate sized predators that have a disadvantage on eating or catching prey, and thus will be selected against. Selection only favors both extremes however, if the population starts at an intermediate size (if the predators are initially all small, the slightly larger individuals will be less efficient at eating small prey, but still hardly any better at eating large prey). Thus the assumption is often made to start out with a population of intermediate individuals. It is often questioned, however, how the initial population comes to be in a state in which all individuals are intermediate and adaptation to the environment is suboptimal.

Sexual reproduction is also a disturbing factor. Even if assortative mating evolves and mating between different ecotypes occurs only with a low probability, it will still occur occasionally, and the recombination process that happens through sex might mix up genes for mating preference and ecotype. The production of offspring in this way will increase gene flow between the two developing species and oppose the process of speciation. This is why in theoretical models of sympatric speciation often another assumption is made: that there is a strong correlation between mate choice and the factor that is promoting the divergence (i.e. a single gene codes both for the trait and accidentally, as a consequence, create a mate preference), or that these genes are so close together on the chromosome they are always passed on together. This assumption is realistic for some situations, for example in the apple and hawthorn fly. The flies that parasitize apple fruits and the flies that parasitize hawthorn foods are distinct populations. Instead of being geographically isolated, or by chromosomal incompatibilities, these populations are isolated on different host species, because they each show a strong preference for their own fruit type and mating takes place on the fruit. In this way mate choice is strongly correlated with the factor that is promoting the divergence.

In general however, these assumptions are not plausible. Lately some theoretical models have been proposed which show that sympatric speciation can occur, but with more realistic assumptions. Especially Dieckmann and Doebeli's theoretical treatment [1] is interesting within this context. In their model they assume several separate genetic loci for ecological traits and mate preferences, and let disruptive selection implicitly arises from competition for a single resource. These are both more common and realistic biological situations and these models offer a good explanation for the occurrence of sympatric speciation in nature.

2.2 Objectives

In this project we try to show whether or not sympatric speciation can emerge in Framsticks. Following the Dieckmann & Doebeli model, individuals in the population differ in mate preference and in an ecological trait, important for acquiring resources. In our experiment, the ecological trait is called artificial trait X (atX) and mating preference is expressed by a mating character. Different from the Dieckmann & Doebeli model though, we start out with a population of intermediates and model disruptive selection explicitly.

2.3 Hypothesis

Speciation within Framsticks can emerge from one gene-pool and one population without a geological barrier. Starting with a population of intermediate individuals varying in artificial trait X (atX), that is not geographically isolated and on whom disruptive selection is working, evolutionary branching into two different biospecies can occur.

3 Research Design

3.1 Experimental Methods

3.1.1 Populations

We start with three populations. Two populations will represent two types of food, Food A (red) and Food B (green) visually distinguished by color. The third population initially consists of creatures that vary in atX, but can all be called intermediate (all can do better by diverging either in one direction or the other).

Interaction within the creature population (population 3) consists of collisions. When two creatures collide and their energy levels are sufficiently high, they will mate with a probability that depends on the value of the mating character and the difference in atX. The mating character ranges between -1 and 1. A mating character of 1 means that the mating probability between two individuals is high when there is a small difference in atX levels and is low when the atX difference is big. A mating character of -1 means that the mating probability is high for two individuals with high atX difference and vice versa. If two creatures collide, the two corresponding mating probabilities are computed and the lowest mating probability will be used.

Furthermore, a creature can collide with the two types of food. The value of atX determines the amount of energy obtained from the two different types of food. Creatures with low atX value obtain relatively more energy from Food B than creatures with an intermediate atX value will and will obtain more or less the same amount of energy as intermediates do from food A. And vice versa for creatures with a high atX value.

3.1.2 Individuals

Individuals are modified Foodfinders, genetically and morphologically identical to each other. The Foodfinder can be found in de walking.gen file that is included with the Framsticks program. Morphologically very simple, its design allows it to move around in a simple world, that is not a height field.

Our modified Foodfinder differs from the original Framsticks Foodfinder with respect to neurons. As shown in the picture, the lower part of the neural network is identical to that of the Foodfinder. This is the part that keeps the legs in motion. The upper part of the network is the steering mechanism, which causes chemotaxic behavior. From left to right there are two pairs of sensory neurons. One sensor of each pair is connected to the

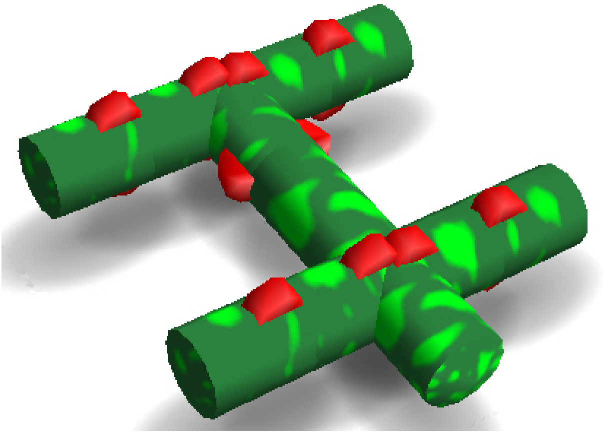

Figure 1: Phenotype of a Framstick individual

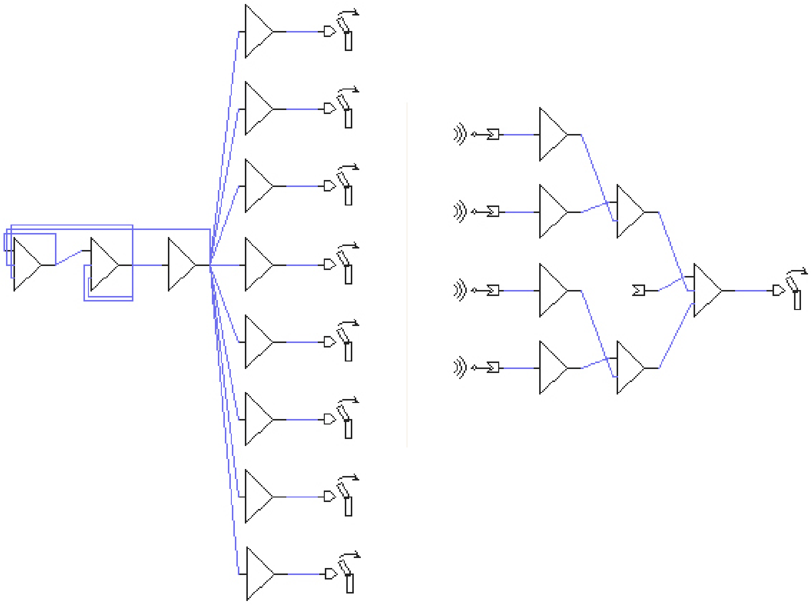

Figure 2: Neural network of a Framstick individual

front right leg and the other sensor of each pair is connected to the left leg. With this construction our modified Foodfinder functions like a Braitenberg vehicle that searches light. The upper pair of neurons (Sothers) smells other creatures; the lower pair (Sfood) smells both types of food. In the middle is an energy level neuron, which functions to sense the creatures current energy level. The output is a number that equals a percentage of the creatures starting energy. Further to the right, where the three branches connect, is the channel select symspec neuron. This is a neuron of our own design that has a changeable variable (d). In our experiment it's value is 2,200. When the input of the energy neuron exceeds this number (this is the case when the creatures current energy level equals 220 percent of its starting energy), it will base its output on the second input (finding mates). Effectively, after gaining enough energy from food, the creature will start to search for mates. The creatures cannot discriminate between different types of food, nor can they distinguish different mates (on the bases of atX-values).

All individuals have two characteristics in which they differ, namely mating character (whose value at initialization ranges between -1 and 1) and atX value (which at initialization ranges between -10 and 10, with an equal number initialized between -10 and 0 and between 0 and 10). These characteristics are not expressed in the genotype but are defined and stored in userfields, labels that will stick to an individual its whole life and whose content can be used when creating offspring or digesting food. The artificial trait X can be thought of as being the level of enzyme activity of a particular enzyme needed for digestion of a certain chemical more present in one type of food than another. Mating character can be thought of as reflecting mate preference. Both traits can be seen as artificial because they do not influence the morphology or neural network of an individual at all (the traits are not in the genotype nor in the phenotype).

Individuals all have the same neural network (architecture & weights) and the same morphology, except for their color. AtX codes for the hue of the creature in the simulation, so it is possible to visually track evolutionary branching. Intermediate creatures are purple, extreme atX-valued creatures are either blue or red. Color differentiation exerts no influence on the individual, it serves only the purpose of user friendliness.

Superficially, all individuals have the same interactions with the environment, as these interactions do not depend on the values of the traits. They actively search for sources of energy (other creatures and food), but they all search equally active, so on average they will all have the same amount of collisions. However, how well they do in their environment does depend on the value of the traits. That is, how much energy they can extract from food sources depends on their atX value and the chance of actually producing offspring when mating depends on their own mating character and atX and that of their mate.

3.1.3 World

The world is a flat surface of size 100 with no water or obstacles in it. The boundaries are 'teleport', which means that creatures that reach the outside boundaries of the world are teleported to the opposite side. Every part of the world is accessible for every individual creature. At the start of the experiment individuals and the two types of food are placed randomly into the world. During the experiment a stable number of food items is maintained in the world.

3.1.4 Parameters

The number of creatures in the initial population is set to 50. The starting energy of a (initial or newborn) creature is 10000 units; the idle metabolism is set to 0.5. This means that a creature loses 5 energy units per time step. Energy level required for mating is set to 22000. Two creatures have to wait 150 time steps before they can mate again. The number of food items (both Food A and Food B) is maintained at 60 throughout the whole experiment. A food item contains 50000 energy units. Creatures older than 300000 time steps are removed from the experiment. The population size is limited to 100 individuals.

3.1.5 Evolutionary Process

Individuals in the experiment will have a fixed morphology and neural network. The only aspects that evolve are atX and the mating character. The offspring will always have the same genotype, but different trait values (as expressed in the userfields). Evolution is endogenous, since the reproductive success of an individual is not determined by an explicit hard-coded fitness-function, but by interaction with the environment. All creatures in the initial population can do better by diverging either in one direction or the other. Creatures with lower or higher atX values receive more energy from food; consequently they are fitter because they will live longer and have more chance to produce offspring. Creatures with low mating character values will have a higher chance to mate with opposite atX-valued creatures. Thus they produce offspring with intermediate atX values that are less fit.

3.1.6 Implementation

Food collision: disruptive selection is explicitly modeled in the food collision procedure. If a creature collides with a Food A or Food B item, a function will be activated to calculate how much of the energy of the food item will be converted into energy for the creature. The function has the underlying form:

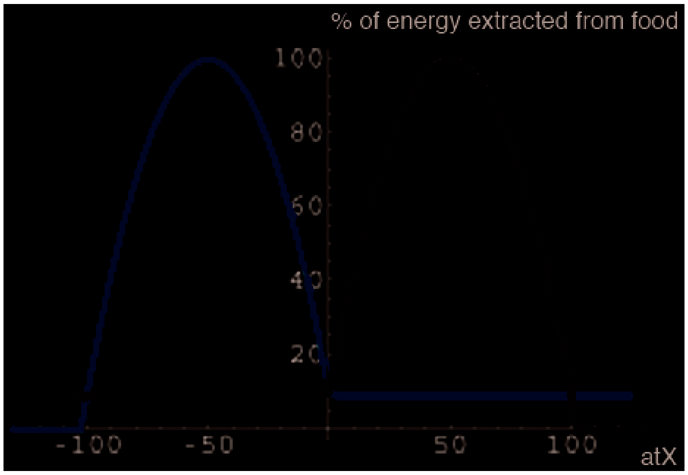

Figure 3: amount of energy extracted from food depending on atX

The graph is based on the principle that digestion has an optimal value at a certain point. For example, green food isnt digested well if the atX has a value below 0. But a creature with a positive atX will relatively extract a lot of energy from green food. This has also a maximum value and after reaching the maximum value the percentage energy extracting will be lowered to zero. The formulas to calculate the % of energy extracted from Food A are the following:

$$\begin{array}{lll} \forall atX \mid atX < 0: & \text{\% of energy from food} = & E^{atX} + 9 \\ \forall atX \mid 0 \leq atX \leq 103: & \text{\% of energy from food} = & (-0.036 \cdot atX^2) + (3.6 \cdot atX) + 10 \\ \forall atX \mid atX > 103: & \text{\% of energy from food} = & 0 \end{array}$$

For Food B the function is the same, only mirrored on the vertical axis. The result of this function is that a creature will extract more energy from a certain type of food if its atX is near 50 or -50 (depending on the type of food) and almost no energy from the other type of food.

Creature collision: When two creatures collide and they both have sufficient energy levels two mating chances are computed according to the following formula, one for each creature:
$Matingchance = (0.5 - absatXDiff \cdot \frac{matingCharacter}{2})$;
where $-1 < absatXDiff < 1$, with -1 corresponding with no difference in atX values between two creatures and 1 corresponding to maximal difference in atX values.

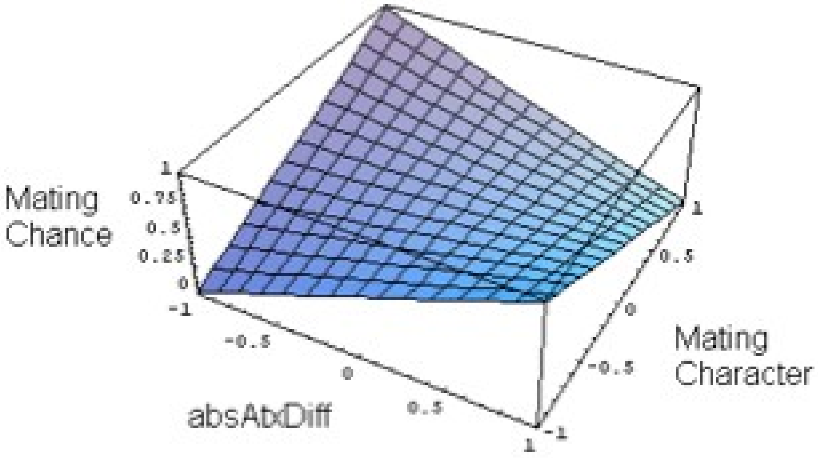

Figure 4: when mating character is 1, creatures have a high mating chance with creatures that have similar atX values (absatXDiff = -1) and their mating chance decreases as similarity decreases, going to 0 when similarity approaches minimal value (absatXDiff = 1). When mating character is 0, mating with a given individual is random: chance is 0.5. When mating character is -1, creatures have a low mating chance with creatures that have similar atX values and their mating chance increases as similarity decreases, going to 1 when similarity approaches minimal value.

Two creatures produce offspring with the probability of the lowest mating chance computed. When offspring is produced both the atX and the mating characters of the parents are averaged and then mutated. The mating character is mutated by adding a value according to a random Gaussian distribution (average: 0, standard deviation: 0.1). For the atX value two different types of mutation are used:

Mutation A : the atX is mutated by adding a value according to a random Gaussian distribution (average: 0, standard deviation: 0.5).

Mutation J : the atX is mutated by adding a value according to a random Gaussian distribution. The average is 0; the standard deviation is obtained through dividing the absolute difference of the two parent atX values by 2. If this number is smaller than 0.5, the standard deviation is set to 1.

3.2 Methods of Analysis

We use the biological definition of speciation. Two populations are different biospecies if they are reproductively isolated. This does not mean that it is impossible for them to mate. They are not genetically incompatible.

Under the biospecies concept, the criterion for identifying two species is reproductive isolation. This is when groups of creatures do not hybridize or fail to produce fertile offspring when they do hybridize. Although this concept of biospecies is sometimes problematic, we will use it to determine if or when two species have come into existence.

In our experiment this means that two members of different biospecies (that differ sufficiently in their atX value) have a very low mating possibility. Therefore every 1000 time-steps we measure the value of the atX and the mating character, and plot this data against time. If two groups of creatures differ sufficiently in atX values and are reproductively isolated (the mating character is close to 1) it will be justified to distinguish two different species.

4 Results

4.1 Experimental setup

With both mutation operators (mutation A and mutation J) ten experiments were done. Each experiment ran for 500.000 time steps. AtX and mating character values were measured and plotted against time.

4.2 Results

4.2.1 Mutation A

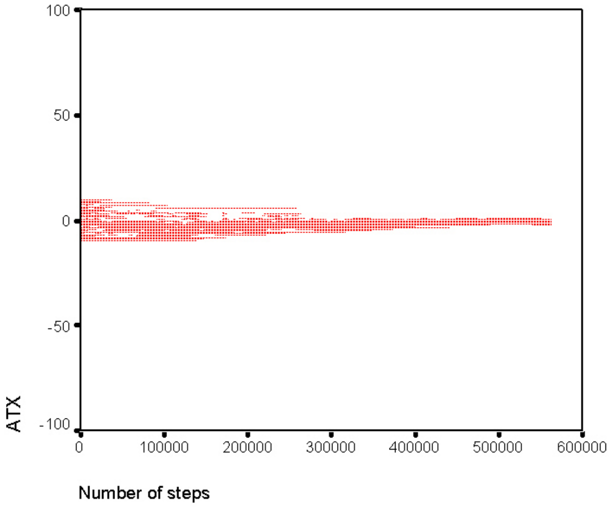

Figure 5: Variances in atX over time with mutation A

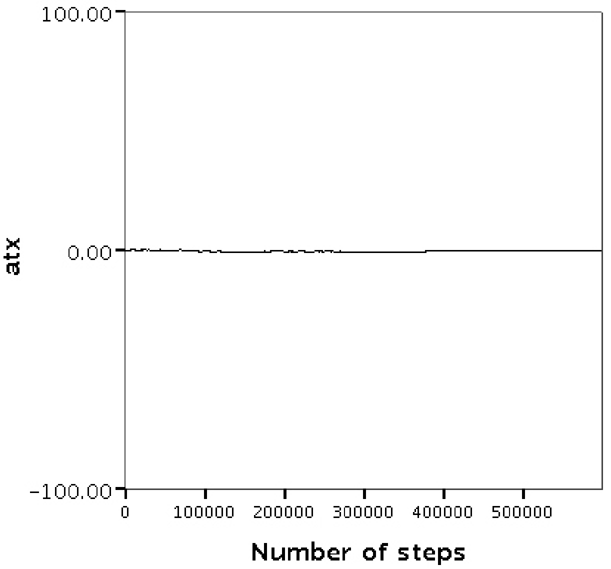

Figure 6: Mean atX over time with mutation A

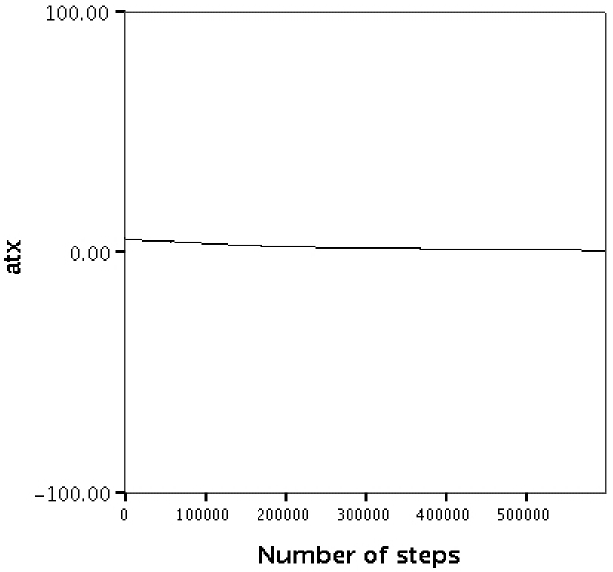

Figure 7: Standard deviation of atX over time with mutation A

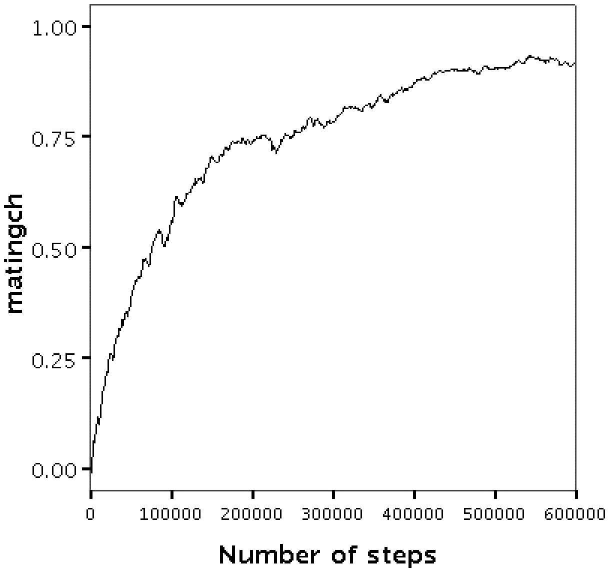

Figure 8: Mating character over time with mutation A

4.2.2 Mutation J

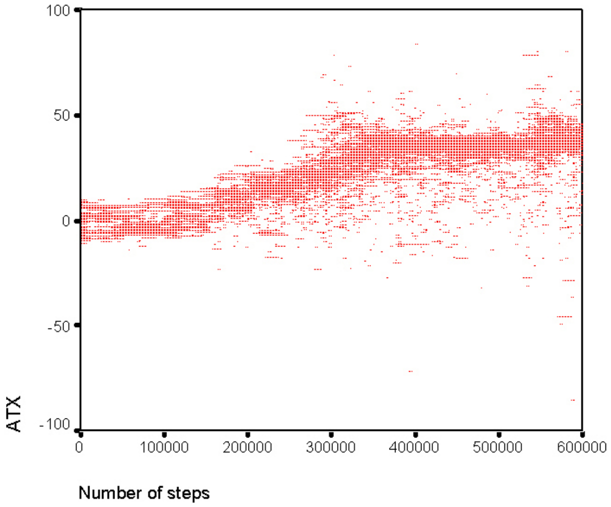

Figure 9: Variances in atX over time with mutation J (experiment 1)

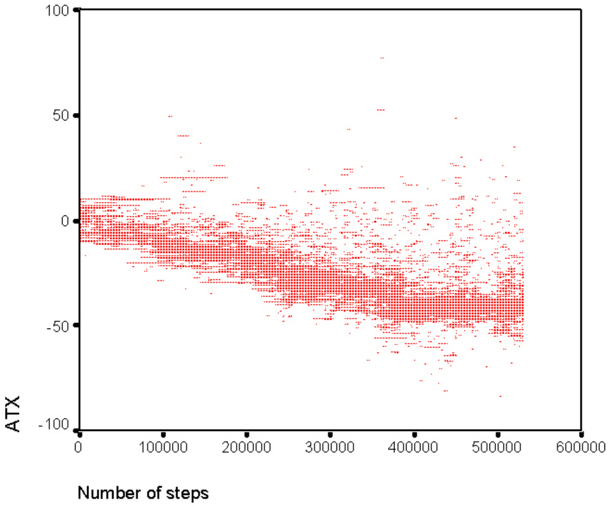

Figure 10: Variances in atX over time with mutation J (experiment 2)

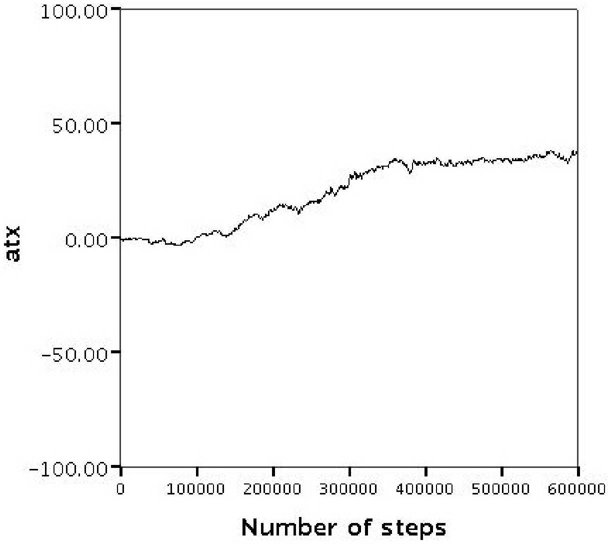

Figure 11: Mean atX over time with mutation J (experiment 1)

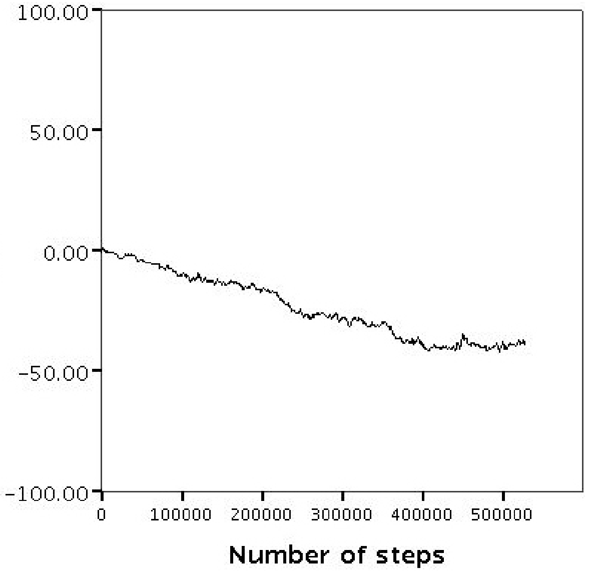

Figure 12: Mean atX over time with mutation J (experiment 2)

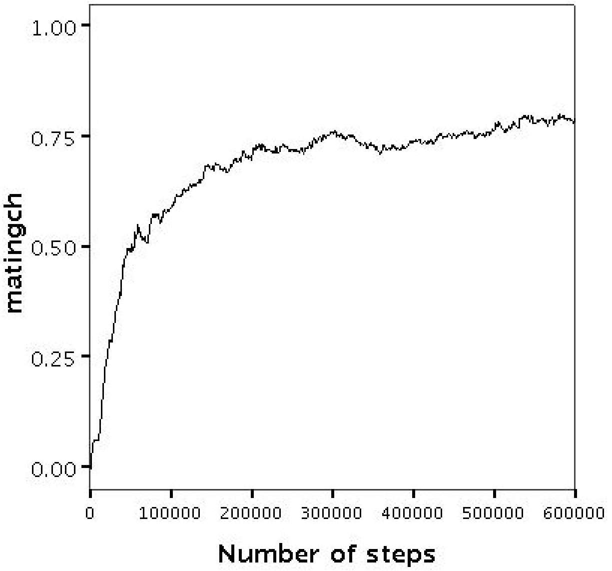

Figure 13: Mating character over time with mutation J

4.3 Analysis

Experiments with mutation type A: Figure 5 is a typical result obtained from experiments with mutation type A. In these experiments, the average atX value stays 0 throughout the experiment (figure 6), however variation diminishes with time as average standard deviation goes to zero at 500.000 timesteps (figure 7). The mating character always has an initial value between -1 and 1, and thus starts out with an average of 0. After 500.000 timesteps, mating character stabilizes at about 0.90 (figure 8).

Experiments with mutation type J: Figure 9 and figure 10 are typical results obtained from experiments with mutation type J. In these experiments, the atX value evolves typically either upwards from zero or downwards from zero. In all the experiments in which the atX evolves upwards, the atX goes from an average of zero to stabilize at an average of about 40 in 500.000 timesteps (figure 11). In all the experiments in which the atX evolves downwards, the atX goes from an average of zero to stabilize at an average of about -40 in 500.000 timesteps(figure 12). Either way, variation in atX values increases with time. The mating character starts out with an average of 0. After 500.000 timesteps, mating character stabilizes at about 0.77 (figure 13).

4.4 Conclusion and discussion

Sympatric speciation does not occur in experiments using either mutation A or J. When using mutation J the average atX value goes either up or down, but there is still too much variation to speak of speciation. Mating chances for creatures with intermediate atX values ($-10 < \text{atX} < 10$) and creatures with extreme atX values ($\text{atX} < -35$, $35 < \text{atX}$) are still relatively high. Although this does not qualify as speciation, we can speak of a development in the species of atX values towards 40 or -40.

A process like genetic drift might play a role here. Genetic drift is the cumulative effect of random events. Once one random event imbalances the number of high positive atX values compared to the number of low atX values, this has a bigger effect on the next random event and it drives evolution in either one direction or the other. Competition for food amplifies this effect by giving one direction a bigger advantage because they are greater in number and therefore find more food-items. The effects of genetic drift can be decreased by increasing population size and increasing differences in fitness between different atX values (increasing selection pressure), and by letting food that is not digested properly stay around in the world for other creatures that do digest it properly.

With mutation A no speciation occurs at all. Because all variation disappears from the population, selection has no the material to work on. This is because of the genetics in our model; it works as a sort of blending of characteristics (atX values of parents are averaged). No entities are passed on intact, so variation diminishes and disappears. In Darwin's time no good theories of heredity were around. Sexual recombination was thought to be a process of blending of characteristics, so for Darwin it was a big problem for his own theory how variation was maintained in a population. This is what happens in our experiments too. The experiments show pretty much the same results as earlier theoretical models of sympatric speciation predict. In our experiment, disruptive selection might not be harsh enough to overwhelm gene-flow. Mating of creatures with opposite atX values (even if mating character converges to 1 in time, chances for a creature with atX 5 to mate successfully with another creature with atX -5 are still pretty high) opposes the speciation process, reducing variation and taking atX values to zero.

The difference between the two mutation types is clearly important. Mutation A does not sustain variation and therefore evolution does not occur. Mutation J does sustain variation because although on average it middles the two parent atX values, it takes as standard deviation a fairly high and changeable value (compared to the standard value of 0.5 in the mutation A). Therefore evolution can still occur. The problem with mutation J is that it is very disruptive and variation increases over time.

5 Future Research

- The ability to efficiently search for food and mates can be further enhanced by improving the creatures' chemotaxis so they can distinguish between different food types and even 'smell' the atX value of their mates. This way the creatures can actively search for specific types of food and for mates that are most likely to produce fit offspring.

- Our model, as well as most classical models of sympatric speciation, starts out with a population of intermediate individuals whose adaptation to the environment is suboptimal and on whom disruptive selection is working. Future experiments could build on the work of Dieckmann and Doebeli's theoretical treatment [1]. In their model they let disruptive selection implicitly arise from competition for a single resource. This is a more common and realistic biological situation.

- Also, future research could make up of a different (more natural) system for genetics, in which different alleles play a role and units can be passed through to offspring intact and a different type of mutation can be used (not so disruptive).

- Effects of genetic drift might be weakened by increasing population size, increasing selection pressure (although disruptive selection is pretty strong in our experiment) or changing the competition for food.

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