Co-evolution of song pattern and song preference on a cricket model

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Abstract

In understanding the behaviour of animals and humans, insects are a good starting point. The behaviour of insects is complex, but their brains are simple. It is often believed that understanding an insect brain is an important step in the process of understanding the human brain.

At the Institute of Perception, Action and Behaviour in Edinburgh, where I conducted my research, the auditory and motor system of a cricket has been modelled. The cricket behaviour that is simulated at the IPAB is phonotaxis, the behaviour by which a female cricket localizes a male cricket by its song.

Female crickets only respond to the song of their conspecific male. Hundreds of different species of crickets exist all around the world and each species has its own specific song. These different species and their songs have evolved over time.

In this research project I have tried to simulate this process of speciation. I implemented a genetic algorithm to co-evolve the male song patterns and the female song preference. I

combined my genetic algorithm with the existing model and conducted some evolutionary experiments.

Preface

In april 1999, months before I would start my study Computer Science and Artificial Intelligence, I saw an episode of VPROs Noorderlicht: Het Simpele Brein. This episode about Braitenberg, also contained some footage about a robot cricket build by Barbara Webb. Being very interested in this subject, this episode has stayed in my memory throughout my study. Now, 6 years later, I have done my graduation research with Barbara Webb on these same robot crickets.

Thanks to my supervisors Barbara Webb and Bart de Boer.

CHAPTER 1

Introduction

One of the ultimate goals within artificial intelligence is to be able to build a human or an animal which behaves exactly like a real human or animal. Insects are often simulated as their behaviour is complex and their brains are simple. Understanding an insect brain is an important step in the process of understanding the human brain.

At the Institute of Perception, Action and Behaviour of the University of Edinburgh an attempt has been made to simulate cricket behaviour. A vast amount of biological research has been done on crickets, their brains and their behaviour. Therefore it is possible to model a cricket much more realistically than other insects. The cricket behaviour that is simulated at the IPAB is phonotaxis, the behaviour by which a female cricket localizes a male cricket by its song.

All crickets have their own specific songs to attract their conspecific female. Females only

respond to males of their own species. This system has evolved over millions of years. In the beginning there was only one cricket species with one sound and now there are hundreds of different species each with their own song.

In this project I will try to simulate this process of co-evolution. In previous research projects, positive results have been found as to the realistic behaviour of the robot cricket. Therefore I wanted to take the simulation one step further and try to co-evolve the male song pattern with the female song preference.

This research project concerns the co-evolution of female mating choice and male song production. I will test some hypotheses on the co-evolution of crickets on a cricket model.

1.1 Research question

This research will concern the co-evolution of the male song pattern and the female song recognition. I will test if female preferences drove the development of certain patterns or if there where other influences that led to the current cricket songs. I will also test if female song preference could have led to speciation. This research will be based on previous research on the evolution of the cricket song [1] [3] [5] [10].

CHAPTER 2

Theoretical background

In this chapter I will give an overview of the underlying theory for this research. First I will explain something about co-evolution and speciation in general. Then I will go into the specifics of crickets. Finally I will give a short introduction of the model I have used. An extensive explanation of this model can be found in the next chapter.

2.1 Speciation

According to Darwin species evolve into new species over time. This process is called speciation. There are three different ways a new species can come into existence. These are anagenesis, cladogenesis and recombinational speciation. In the next paragraph these three

modes are futher explained.

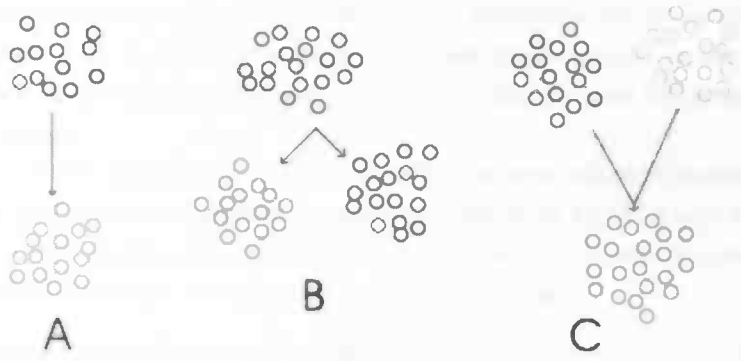

Figure 2.1: Different modes of speciation. A is anagenesis, B is cladogenesis and C is recombinational speciation.

When offspring completely replace their ancestors with different genes, it is called anagenesis (see figure 2.1, A). In this case the whole population changes in the same direction. After several generations this leads to such a significant change in genes that the ancestral population can be considered extinct. Another way is when the offspring of one type of species splits into two or more new species. This is called cladogenesis (see figure 2.1, B). A third way of speciation is when out of two different species a new kind of species evolves (see figure 2.1, C). This is called recombinational speciation and is very rare.

2.1.1 Isolating barriers

Isolating barriers are those biological features of organisms that impede the exchange of genes with members of other populations [2]. There are several types of isolating barriers. These isolating barriers can be divided into three groups:

- Premating isolating barriers

- Postmating isolating barriers
- Postzygotic isolating barriers

Premating isolating barriers are barriers that prevent gene flow by preventing intercourse altogether. Within premating isolating barriers there are two different types, behavioural isolation and ecological isolation. Behavioural isolation prevents different species from being attracted to each other. Ecological isolation prevents species from mating because of different ecological properties, for example different breeding periods.

Postmating isolating barriers are barriers whereby gene flow is prevented by the inability of two different species to mate properly. In this group there is mechanical isolation which means that the anatomical differences between the animals prevent the transfer of gametes to the females. The other type of isolation is gametic isolation in which gametes are transfered, but the eggs are not fertilized.

Postzygotic isolating barriers are barriers that cause an hybrid individual to either die young or to not be able to reproduce itself. The latter can be caused by ecological inviability or behavioural sterility. In the case of ecological inviability, the hybrid individual can not find a appropriate ecological identity. In the case of behavioural sterility the courtship behaviour of the hybrid individual is in between two species and not attractive to either species.

2.1.2 When can you speak of different species?

During the process of speciation there is always some hybrid state. As there is always some variation within a population, one can wonder when a new species comes into existence. This is a difficult question. In [2] a species is defined as 'a group of individuals fully fertile inter se', but prevented from breeding with other species by the above mentioned isolating barriers. The actual moment a new species comes into existence is quite arbitrary as it is determined by how strong the isolating barriers are.

2.2 Co-evolution through sexual selection

Co-evolution is the process through which two groups influence the evolution of each other. This can for example be prey-predator groups or female-male groups. In the latter case it is called co-evolution through sexual selection. In this case mate choice influences the evolution of both male and female.

Although often sexual selection is said not to influence speciation in a major way, there is evidence that this process does influence speciation. According to Todd and Miller [18] there is a correlation between the diversity of a taxa and its potential for sexual selection. Todd and Miller give three cases in which sexual selection can play a role:

- Create new peaks in the fitness landscape
- Find new peaks in the fitness landscape
- Evolve new species from existing species

In this research I will test the influence of sexual selection on a cricket model.

2.3 Crickets

Crickets are one of the first insects using auditory communication. Since the first noise of the cricket a wide range of cricket species has developed, all with their own specific sounds. Much research has been done on crickets and therefore a lot of data and information is available on crickets. This makes the cricket an interesting animal for research in biorobotics. Also, the nervous system of an insect is relatively simple thus very suitable for neural research. In the section I will give some general information on crickets and more specific information on the auditory communication between crickets and speciation in crickets.

Crickets use sound to communicate with each other. The male cricket produces sounds with its wings. The specific cricket chirp sound is made by opening and closing of the wings. If this is repeated several times, the cricket produces a song. Female crickets respond to some of

these songs by moving towards that song. This behaviour is called phonotaxis. Crickets have a wide range of sounds they use for communication [1]. In the following list a description is given with each song type.

Calling song This song is used in male-female interaction. Females respond to this song by moving towards it.

Courtship song This song is used for courtship.

Courtship interruption sound This songs is produced when for some reason the female breaks contact with the courting male.

Agressive sound This song is used in male-male interaction.

Post-copulatory song This song is used during the intercourse to prevend the female from leaving.

Recognition sound It is not entirely clear yet what this song does. It might be a way crickets notify others of their presence.

Not all species of crickets use all the different types of sound, there are even species that do not produce any songs at all. Most species of crickets do use the calling song, which is the most important, and most heard, song. Every species has its own specific calling song. The female only responds to the calling song of the conspecific male. These songs cannot be learned, they are genetic. The only way a song can change during the lifetime of a cricket is through mutilation or change in temperature. Temperature affects especially temporal features like pulse duration, pulse rate and interpulse interval. However, it seems that changes in temperature also effects the preference of the female as it has no effect on the communication between the sexes [9].

Songs are build up out of pulses. See figure 2.2 for the structure of a pulse. These pulses are the smallest audible sound units a cricket can produce. One pulse is called a syllable and together with the interpulse interval it is called the pulse period. Trills and chirps consist of

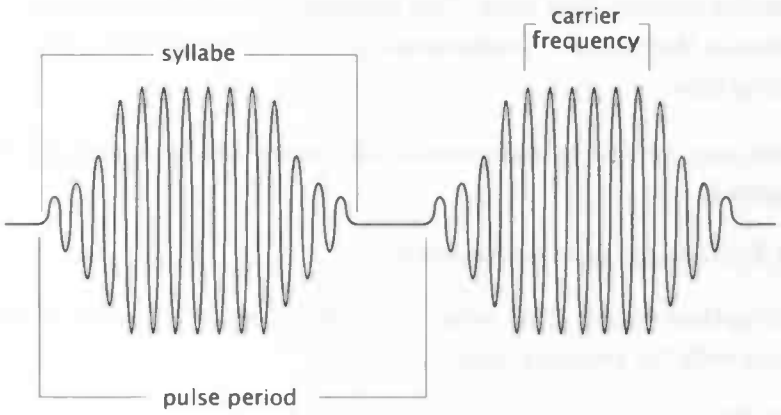

Figure 2.2: Two pulses

multiple pulses (see figure 2.3). Chirps are small series of pulses while trills are long series of pulses.

Several factors contribute to the specific song of a certain type of species. These factors include environment, other species in the same area, predators, etc. Crickets live in a wide range of places like forests, caves, deserts, etc. Different environments require different types of communications. Species that live in caves for example, don't use songs.

The calling song of a cricket is a premating barrier; it prevents females from other species to approach the male. However, it is also a way for parasites and predators to find their prey.

2.3.1 Auditory system

The cricket auditory system consists of four 'ears'. The four cricket ears can be viewed as an H shaped tube (see figure 2.4). Two ears are locate on the front legs nearby the tibia joint (see figure 2.5). The tibia joint is comparable to the human knee joint. These two ears are called spiracles, openings in the trachea without an eardrum. The other two ears are located on

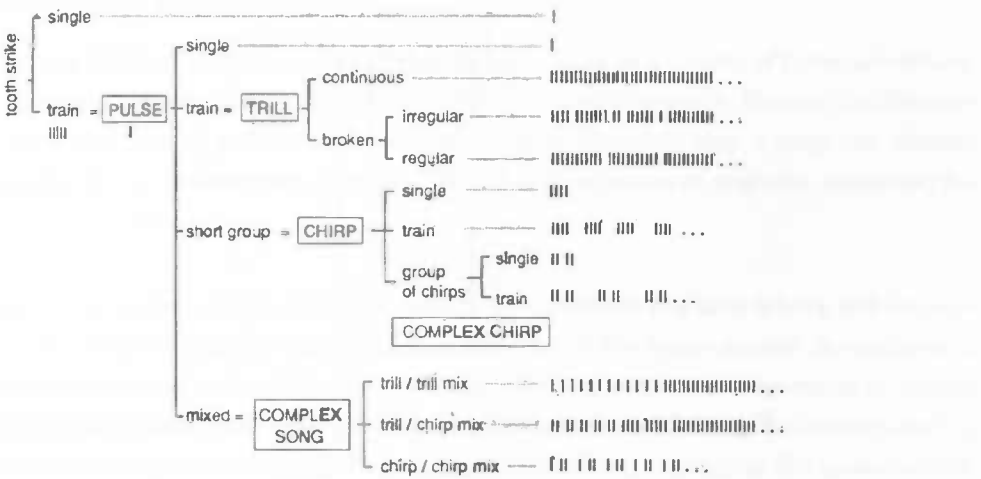

Figure 2.3: A scheme with the different song possibilities with trills and chirps [1]

both sides of the head of the cricket. These are called the tympana, openings with eardrums. The tympana receive sounds waves from both the spiracles as from the outside of the leg it is located on. With this system the cricket can localize where a sound comes from.

2.3.2 Auditory processing

The tympana mentioned in the previous section send their signals to neurons in the prothoracic ganglion. The prothoracic ganglion is located in the back of the cricket nearby its head. Schildberger [14] identified three groups of neurons involved in auditory processing in the cricket brain.

- Ascending neurons (AN1 and AN2) ascending from the prothoracic ganglion into the brain

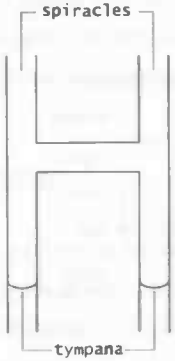

Figure 2.4: Schematical representation of the cricket ears

- Brain neurons with arborizations overlapping those of ascending cells (BN1)
- Brain neurons with arborizations that have no overlap with those of ascending cells (BN2)

AN1 neurons were found to be most sensitive to a carrier frequency between 4-5 kHz. This is the carrier frequency of the calling song. AN2 neurons were found to be most sensitive to a carrier frequency between 14-16 kHz, which is the carrier frequency of the courtship song. BN1 neurons had the same kind of sensitivity as the AN neurons, except that they only responded to higher intensities. The BN2 neurons were sensitive mainly to a frequency of 5 kHz, but also only to high intensities.

2.3.3 Song recognition

Temporal features are important in song recognition. These features include the structure of the chirp, pulse rhythm and chirp rhythm. The combination of these features is specific for the song of each species. In figure 2.6 the temporal response of AN, BN1 and BN2 can be seen.

2.3.4 Speciation in crickets

Crickets were among the first insects on this planet to use sound as a means of communication. The production of songs and preference for certain types of songs is genetic. During the lifetime of a cricket its song patterns or preferences will not change. The only way a song can change is because of mutilation or temperature change. Within a population of crickets, no examples of song varieties are known.

Song evolution It is believed that the first sounds produced by crickets where not on purpose. By closing the wings a sounds was produced. This led to the pulse sound. A continuous sequence of pulses is the most primitive type of song. These continuous sequences of pulses have evolved to more complex types of songs. There are several ways a song can change during evolution. A song can change by changing the frequency of the song, changing the pulse period, dropping pulses or adding pulses. When pulses are dropped with trills, chirps can evolve and the other way round.

Evolution of different songs depends on several factors for example surroundings and neighbouring species. When species in the same area use a similar song, there is a chance that females get confused and therefore choose the wrong species to mate with. This could result in no offspring at all, a hybrid species unable to reproduce or a hybrid species able to reproduce.

2.4 Robot Insects

In 1948 Grey Walter constructed the two first autonomous robots, Elmer and Elsie [19]. With these robots he showed that just a few brain cells could result in complex behaviour. In the decades following several insect robots with sensorimotor systems have been developed. Sensorimotor systems in insects are often very complicated and not many systems are well understood. In previous research the focus was often to develop an efficiently functioning robot instead of a good model of the real animal. In 1995 Barbara Webb [20] came up with the idea of a robot cricket. Much biological research has been done on crickets ([1], [9], [10], [11],

[13], [14], [16], [17]). Likewise, what we know about the functioning of the cricket brain, its neurons and phonotaxis is significant. Based on what was known, a cricket robot was built [21]. In the next chapter I will give a detailed explanation of this system.

2.5 Robots and simulations

Using robots or simulations to simulate behaviour of real animals has always been subject to debate. When using a simulation you make many simplifications of the reality. A physical robot already has realistic input for its sensors and therefore it could produce more realistic output. However, it is not possible to exactly rebuild an animal as a robot, at least not yet. Hence choosing to use a simulation or a robot both has its advantages and its disadvantages, but neither is perfect.

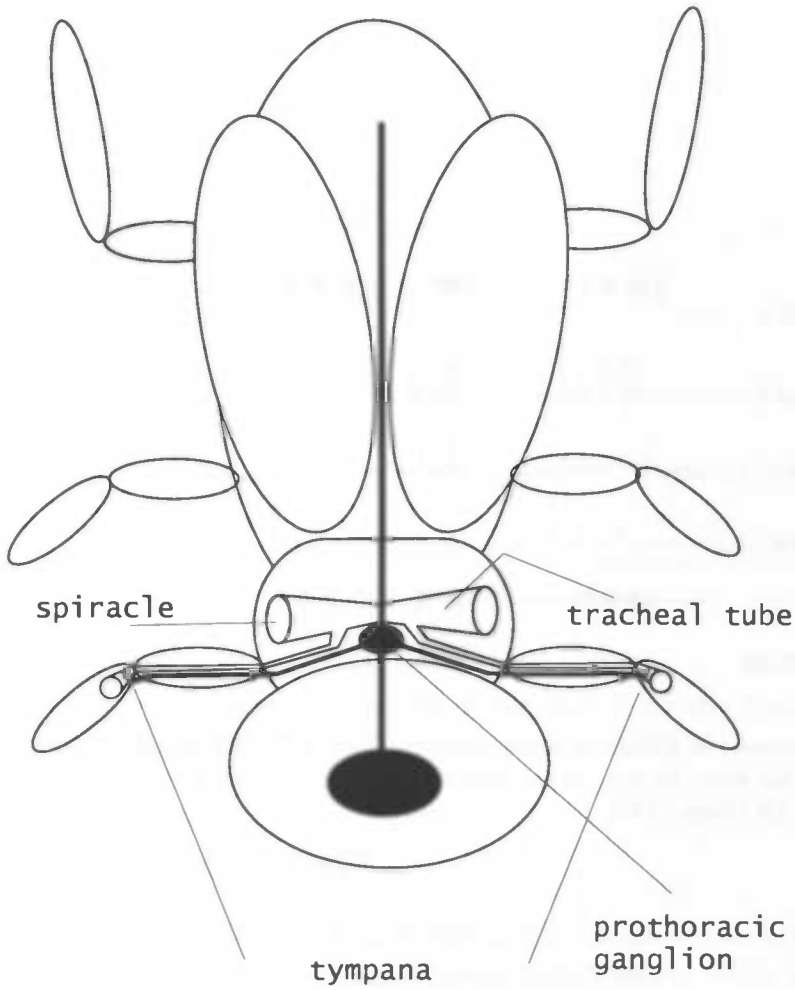

Figure 2.5: A cricket with its auditory system

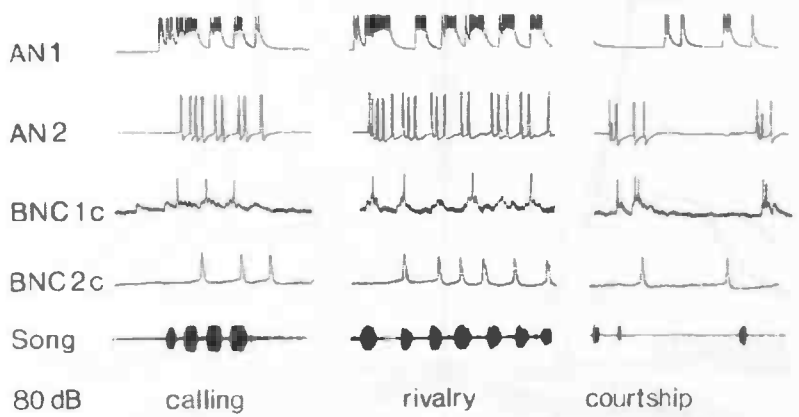

Figure 2.6: Responses of different brain neurons to a differing temporal structure. Syllable repetition intervals were 18 ms, 34 ms and 98 ms. The carrier frequency was 5 kHz and the intensity was 80 dB (from [14])

CHAPTER 3

Models

In this chapter I will give a detailed explanation of the current model. Furthermore I will explain my additions to this model.

3.1 Neural Robotic System

The Neural Robotic System or NRS is a system that models simple sensorimotor behaviours. It was developed by Reeve and Webb [12]. Previous to this model, Webb and Scutt [23] developed a simple cricket model. This model was based on a Braitenberg vehicle (see figure 3.1), there was a direct connection between the sensors and the motors in this model.

Later a more complex model was developed, the NRS. This model did not have a direct

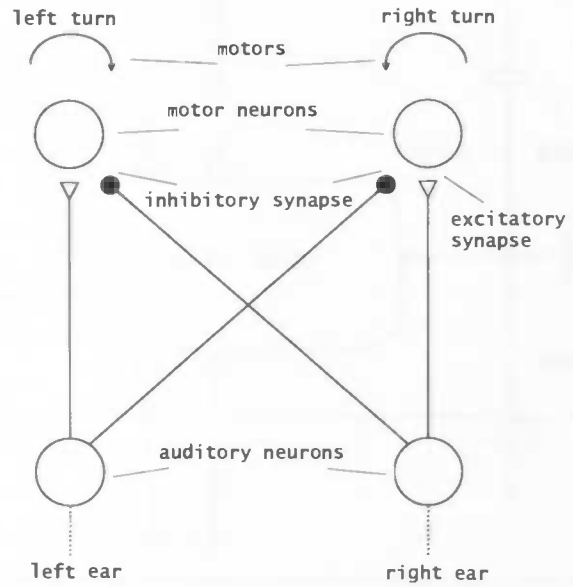

Figure 3.1: A schemat ic drawing of the oldest cricket model

connection between its sensors and its actuators. Instead it tried to model a real cricket brain in more detail. This model was more advanced and had a better mapping with a real cricket brain. In the following paragraphs a detailled description of this model will be given. I have used this model for my experiments.

3.1.1 Neurons

Brains of animals and humans consist of numerous neurons. All these neurons together produce complex behaviours. It is possible to divide neurons into three groups:

- neurons that receive information from the outside world, for example touch or taste. These neurons translate information to signals understandable for other neurons. These

are called sensory neurons.

- neurons that receive information from other neurons and send their information to other neurons. These are called interneurons.
- neurons that receive information from other neurons and send their information to muscles. These are called motor neurons.

All neurons have a cell body, an axon and dendrites. Information is received through the dendrites of a neuron. Neurons have multiple dendrites (see figure 3.2). In the cell body of a neuron the information from the dendrites is processed. As a result a decision is made to send a signal (fire) or do nothing. When a neuron fires, this is sent through the axon of the neuron. Every neuron only has one axon which does branch to connect to multiple dendrites. Axons are again connected to dendrites of other neurons through synapses.

Some of the input of neurons can be inhibitory. In figure 3.2 dendrites which are connected to the cell body with a circle are inhibitory and dendrites which are connected to the cell body with a triangle are excitatory. The different dendrites and synapses all influence the cell body, where all this input is weighted. If the weighted input is higher than the threshold of the neuron, a signal is sent through the axon to the next synapses and cells. For example, when the dendrites and synapses influence the neuron in such a way that the total of all the inputs results in a voltage difference of -30mV and the threshold of the neuron is -40mV then it will fire. However, when the threshold of the neuron is -20mV, nothing will happen.

3.1.2 Simulated neurons

In the model neurons are simulated. These neurons work in a way that is similar to real neurons (see figure 3.3). The simulated neurons have several parameters which are comparable to the properties of a real neuron. Signals in real neurons are electrical signals. Therefore neurons have electrical properties. In figure 3.4 the voltage change in a neuron when receiving signals can be seen. Exitatory input causes an excitatory postsynaptic potential (EPSP) and inhibitory input causes an inhibitory postsynaptic potential (IPSP). Two EPSPs close in time

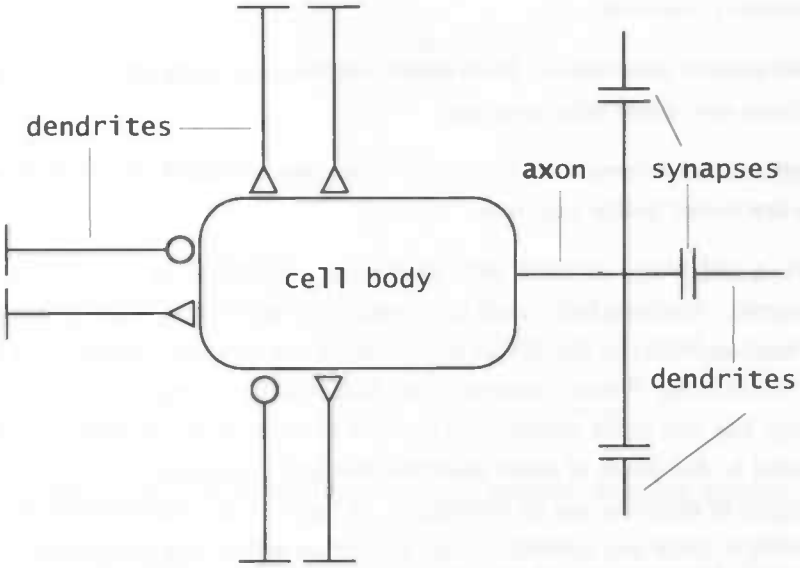

Figure 3.2: A schematically drawn neuron. Triangles are excitatory dendrites and circles are inhibitory dendrites

can cause the voltage difference to reach the threshold which causes an action potential. This is a list with several parameters of the neuron:

Resting potential for the membrane This is the voltage difference between the inside and the outside of a neuron when the neuron is at rest. Usually this is about -65mV.

Threshold for the membrane This is the voltage difference by which the neuron will fire.

Recovery potential This is the membrane potential when it is recovering from an action potential.

Action potential After a neuron fires, it will quickly depolarize to this voltage difference. This is the voltage reached when spiking.

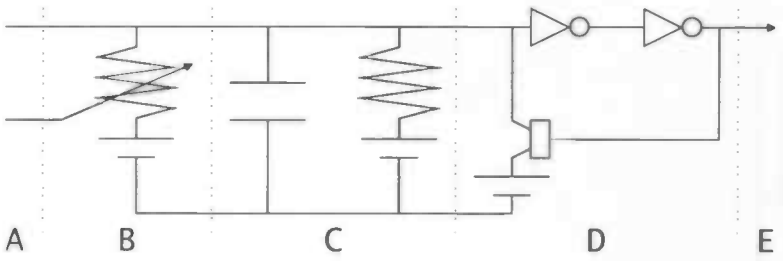

Figure 3.3: Electrical model of the neuron as used in the NRS. A is the pre-synaptic input, B is the synapse (explained in the next paragraph), C is the neuronal membrane, D is the spiking mechanism and E is the neural output.

Refractory period This is the time it takes for the neuron to get back into its orginal state after it spiked.

Base conductance of the cell membrane This is the permeability of the membrane when the neuron is at rest. The higher the base conductance the the sooner the membrane potential decays back to its resting potential.

Capacitance of the membrane This is the capacitance of the membrane. The higher the capacitance of a membrane the longer an EPSP will be.

In the used model all these parameters can be set for each neuron.

3.1.3 Simulated synapses

In the model, two types of synapses are used. The first one is the current injection synapse (see figure 3.5a). This can be seen as a variable current source. Every time the presynaptic neuron sends a signal, a packet of charge is sent to the postsynaptic neuron. The membrane potential increases or decreases immediately. A more natural synapse is the conductance-based synapse (see figure 3.5b). This can be seen as a variable resistor with a capacitor. These synapses

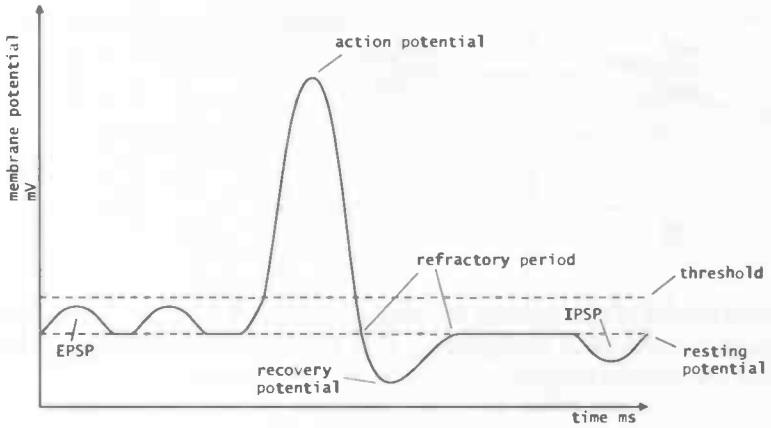

Figure 3.4: The membrane potential neuron receiving signals

pull the membrane potential of the postsynaptic neuron to the potential of the capacitor. The strength by which this happens is dependent on the resistor, which is variable.

Synapses also have several parameters (see figure 3.6). These parameters include:

the change in conductance or charge when a new spike arrives Every time a spike arrives at a synapse, this value is added conductance.

the depressive effects on this change in conductance The depressive effects also influences the conductance change. Each time a spike arrives the conductance is changed with the above mentioned change minus this depressive fraction.

the half-life for the decay of the conductance This half-life indicates how long it takes for the conductance to decay back to zero.

the half-life of the depressive effects This half-life determines how quickly the depressive effects decay back to zero.

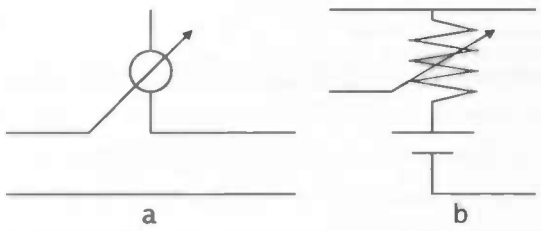

Figure 3.5: The electrical model of a current injection synapse (a) and a conductance-based synapse (b)

3.1.4 Neural circuit

In the previous chapter I explained the neural circuit in auditory system of a cricket brain. In the model there are four different neurons in the auditory circuit [12] (see figure 3.7):

- omega neurons (ON) which are mutually inhibitory and inhibit the AN neurons. Their function is to increase the difference in activation between the left and the right AN neurons.
- ascending neurons (AN) which are inhibited by the ON neurons and excite BN1 neurons. AN neurons function as low-pass filters to the BN1 neurons. The way this happens is by adding a depression factor to the synapse between the AN and BN1 neuron.
- brain neurons (BN1) which are connected to the AN neurons and excite the BN2 neurons. The synapses of these neurons also have a depression factor with a slow half-life. This way only the right syllable rate[1] will pass.
- brain neurons (BN2) which are not connected to the AN neurons. These neurons excite the motor circuit.

[1] syllable rate is the number of syllables per second.

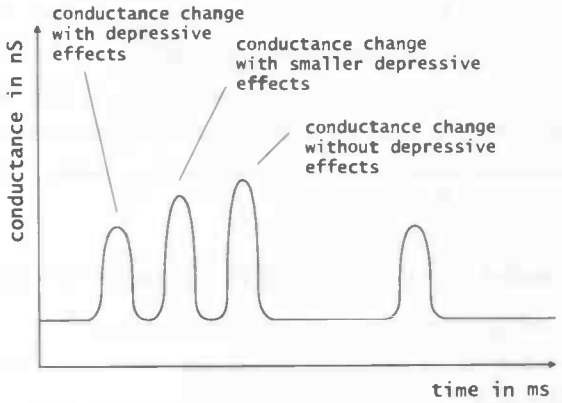

Figure 3.6: The conductance changes in the synapse

3.2 Simulated song

In the simulation, the songs of the male cricket are simplified. In figure 1.3 in the previous chapter a scheme with different song possiblities is given. In the simulation the song consists of a train of chirps. There only a few parameters that can be set. These are the length of the syllables and gaps between the syllables, the number of syllables per chirp and the gap between chirps (see figure 3.8).

3.3 Evolutionary additions to the model

For my experiments I added a genetic algorithm, so I could do evolutionary experiments with the model. I wrote a seperate program to evolve parameters. The program was not part of the model. In this section I will give a detailed description of the program I have written.

First I will give an explanation of how I represented the population. Then I will give an explanation on the evolutionary part of the program.

3.3.1 Individuals

Each individual has an array with gene values, its 'DNA'. These genes are the different parameters values I evolved. All the parameters are positive integer values. Five of these parameters were related to song recognition and three were related to song production. The song recognition parameters are located in the AN to BN1 synapse and the BN1 to BN2 synapse. The parameters that were evolved in the experiment are the conductance change when a new spike arrives, the half-life of the conductance and the half-life of the depressive effects (only for the AN to BN1 synapse). Besides these parameters, every individual also stores information about its parents and of course its gender.

Every female individual has an additional array in which it stores the fitness values. Every female-male pair receives a specific fitness value (I will explain this later in this chapter) and this is stored in the female individual.

3.3.2 First generation

Every generation consists of one third of males and two third of females. The parameters of each individual are initialized manually. The initialization values vary for each experiment.

3.3.3 Evolution

Every female is tested with pairs of males. The results of these test are fitness values which are stored for each male-female pair. Every female receives an overall fitness value, which is the highest fitness value it reached with a male. When a generation evolves, a selection of females is made for reproduction through roulette wheel selection. For each of these females a male is selected. This selection is also through roulette wheel selection. The new couple will produce two new individuals. A random value between 0.0 and 1.0 determines what fraction of each gene the new individual wil get from each parent.

$$n = r \cdot f + m \cdot (1.0 - r)$$

In this formula, n is the new gene value, r is the random value, f is the gene value of the father and m is the gene value of the mother. The result is rounded to an integer. For example: a certain gene has value 200 in the father and value 600 in the mother. The random value returns 0.6, which means that 60% of the genes will come from the mother and the remaining 40% from the father. This results in a value of $0.6 * 600 + 0.4 * 200 = 440$ for the new individual.

3.3.4 Mutation

There is always a chance on mutation in nature. In this program each gene has a certain chance to be mutated. This chance is the same for every gene, but differs per experiment. As all the genes can have a value varying from zero to infinity, I chose to change the value with a maximum percentage of 20%. This means that when a gene mutates, a random value between 0.0 and 0.2 will be chosen. This will be the percentage to be added or subtracted. The formula for this mutation is:

$$v = c \cdot (0.8 + 2 \cdot p)$$

In this formule v is the new value, c is the current value and p is the percentage. The result is rounded to an integer.

There is a downside to this method, it will evolve to zero in the end when the fitness function does not work properly. For example when percentage of 10% is subtracted from a value of 200 then the new value will be $200 - (0.1 * 200) = 180$. When adding that same percentage again the new value is $180 + (0.1 * 180) = 198$. So after many mutations, the values will decrease to zero (see figure 3.9).

3.3.5 Fitness function

A fitness function is used to decided which individuals will have the best chance of reproducing. Reproduction will only take place if a female can locate a male. Therefore a suitable fitness function would be to use the direct output of the motors. However, the NRS version that I used had an old motor model that was not suitable to be used as a fitness function.

Instead I used the output of the AN and BN2 neurons. This was based on the newest NRS model, NRS2, in which a new theory on the neural motor circuit has been implemented. In the new NRS the auditory neurons (AN and ON) have a direct influence on the motor output as well. However, the new theory is too complex to seize in a formula, because it is time dependent. Therefore I have used a simplified version of the new theory. The fitness is detemined by how often the activation of AN and BN2 overlaps. When AN and BN2 both have a membrane potential of -60mV or higher, then 1 is added to the fitness. Every two milliseconds AN and BN2 are checked. This means that the fitness function has a maximum value that is equal to the total time of the run in milliseconds divided by two. Each run lasted 20 seconds, so the maximum fitness value was 10000.

$$\sum_{t=0}^{T} f_{sim}(AN(t), BN1(t)) \tag{3.1}$$

$$f_{sim} = \begin{cases} 1 & (AN \wedge BN1) \geq -60mV, \\ 0 & else. \end{cases} \tag{3.2}$$

In this formula t is the number of time steps.

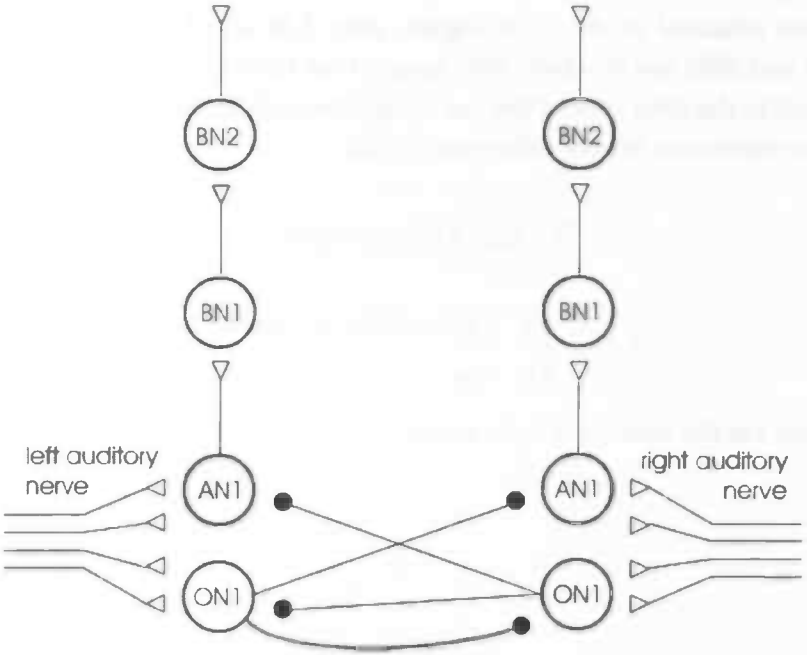

Figure 3.7: Structure of the used model. Black circles are inhibitory and the triangles are excitatory.

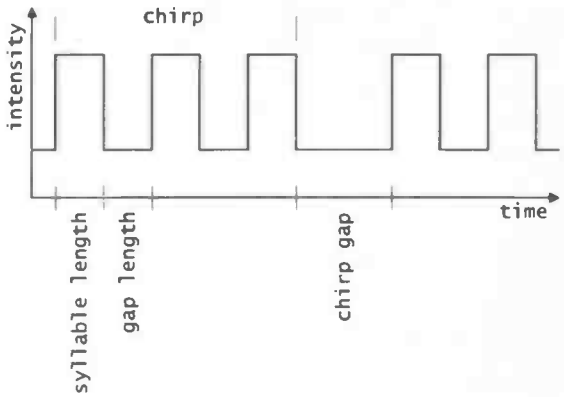

Figure 3.8: Simulated song structure

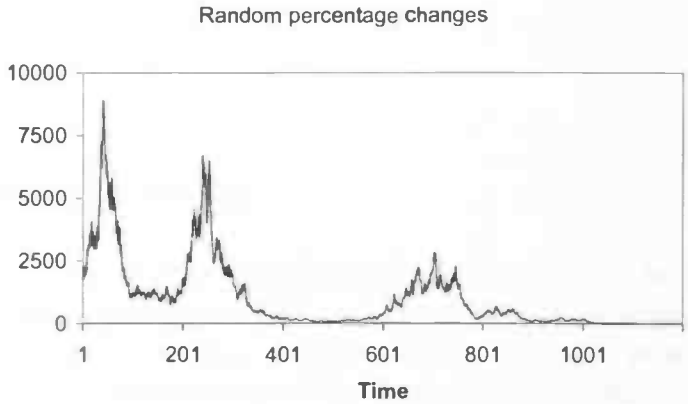

Figure 3.9: After many mutations the values will decrease to zero

CHAPTER 4

Results

4.1 Experimental setup

For the experments I have used the Neural Robot Simulator (NRS). I have written a genetic algoritm with the following structure. There are 30 individuals per generation, consisting of 10 male crickets and 20 female crickets. Each female cricket is tested with every male cricket. The fitness for each male/female pair is stored. Then the genetic algorithm decides for each female which male it will choose. This is done with random choice, however males with higher fitness have more chance of being chosen than males with a low fitness value, this is called roulette wheel sampling. The next step is crossing-over. For each gene, a percentage of the male and a percentage of the female is taken and, with a random chance, mutated. When a

gene will be mutated, a random percentage with a maximum of 20% of the gene value will be added or subtracted to the gene value. Every pair of crickets produces two offspring. This offspring will be added to the new generation. Every generation is completely new, the old generation is completely replaced.

4.2 Experiment A: Testing

A genetic algorithm (GA) is often used to reach a solution for a problem that could not easily have been solved in another way. It is hard to predict the exact results of a genetic algorithm and therefore it is also hard to exactly control the algorithm. Many things can go wrong when running a GA. Therefore I did some experiments to test my genetic algorithm. One of the things I have tested is if the evolutionary mechanism actually evolved to a specific direction. In the next sections an explanation of this experiment.

4.2.1 Setup

Instead of 10 male crickets and 20 female crickets, all of the 30 the individuals are female crickets, so there is no coevolution, just normal evolution. The male song is stable in this experiment. There is a mutation chance of 2% and a mutation range of 20%. The first 7 individuals (see table 4.1) in the first generation have varying parameters values. These values are based on the standard values I use for the remaining 23 individuals. The remaining 23 individuals are exactly alike. The parameters values of these individuals are described in the next paragraph.

Parameter values

The song parameters in this experiment are static. The song parameters values I used are 60ms syllable length and gap length, 8 syllables per chirp, 340ms gap between chirps.

AN Conductance change(in mV)	7.0	8.0	9.0	5.0	4.0	3.0	2.0
AN Half-life conductance (in ms)	5.5	4.0	3.5	2.5	8.0	5.0	7.0
AN Half-life depression (in ms)	8.5	7.5	9.5	3.5	5.0	6.0	6.8
BN1 Conductance change (in mV)	2.3	6.5	4.5	4.8	3.4	2.8	1.0
BN1 Half-life conductance (in ms)	40	50	33	20	25	22	19.5

Table 4.1: Parameters values of the first generation. Every column represents an individual.

The synapse parameters of the 23 identical individuals are for AN: a conductance change of 6.0mV, half-life of the conductance change of 5.0ms and half-life of the depressive changes of 7.0ms. For BN1 the parameter values are a conductance change of 3.7mV and half-life of the conductance change of 30ms. The remaining 7 individuals are listed in table 4.1.

The depressive change value is $0.3ms^{-1}$ for AN1 and $0ms^{-1}$ for BN1.

4.2.2 Results

In figure 4.1 the variation within the population is represented by taking the average standard deviation per generation of the 5 different parameters used for evolution.

At the start of the experiment the variation within the population is high, because the first 8 individuals all have different parameter values. After about 10 generation the variation has become stable. There is no significant increase in variation in any of the 30 generations.

The relative flow of the parameter values in the AN synapse is shown in figure 4.2. The half-life of the conductance change is only decreasing. Both the conductance change and the half-life of the depressive changes first increase untill generation 5 and 6, after that they both decrease. However, the conductance change stabilizes from generation 10 on.

The relative flow of the parameter values in the BN1 synapse is shown in figure 4.3. The average half-life of the conductance change first increases and then it starts fluctuating.

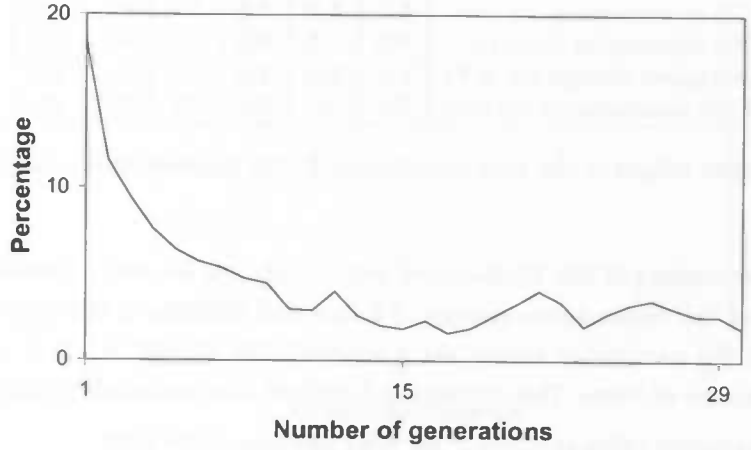

Figure 4.1: Percentage standard deviation for every generation.

4.2.3 Setup

The setup of this experiment is similar to the setup of the previous experiment. However, instead of testing each female on the male song parameters, in this experiment every female always receives the same fitness value. I expect this random drift to give a different percentage standard deviation.

4.2.4 Results

The results of this experiment can be seen in figure 4.4. The experiment was run five times. After about 8 generations the variation stabilizes. After that no obvious change in variation can be observed in each experiment.

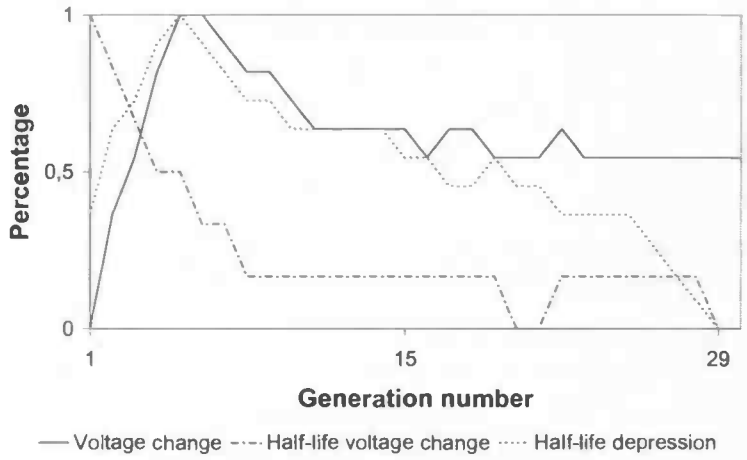

Figure 4.2: The flow of parameters of the AN to BN1 synapse. The voltage change increases over time, eventually stabilizing. The half-life of the voltage change decreases initially, but stabilizes after 8 generations. The half-life of the depression first increases, but starts decreasing after a few generations.

4.2.5 Conclusion

Even though is it not obvious that the values evolve in a specific direction, it is a fact that the parameters do not all evolve to zero (see figure 1.7). Also, in the previous experiments a clear difference can be seen between figure 4.1 and figure 4.4. Figure 4.1 shows much more change in variation after a certain stabilization occurs. Therefore, I conclude that the genetic algorithm is suitable to use for coevolution.

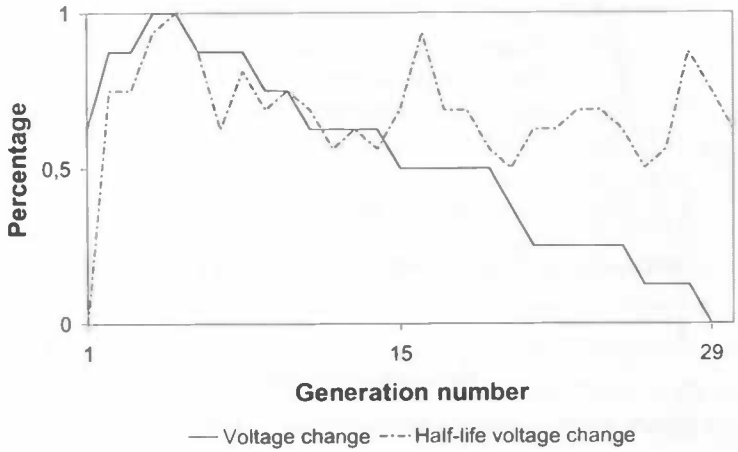

Figure 4.3: The flow of parameters of the BN1 to BN2 synapse. The voltage change decreases over time. The half-life of the voltage change increases in the first few generations and starts fluctuating after that.

4.3 Experiment 1: Speciation

According to Otte [11] the cricket population on Hawaii has evolved from only three species to its current variety. In this experiment I will try to evolve two different species, evolving from only one species.

4.3.1 Setup

The setup in this experiment is almost identical to the setup in the previous experiment. Again there are 30 individuals, 10 males and 20 females, and there is a mutation chance of 2% and a mutation range of 20%.

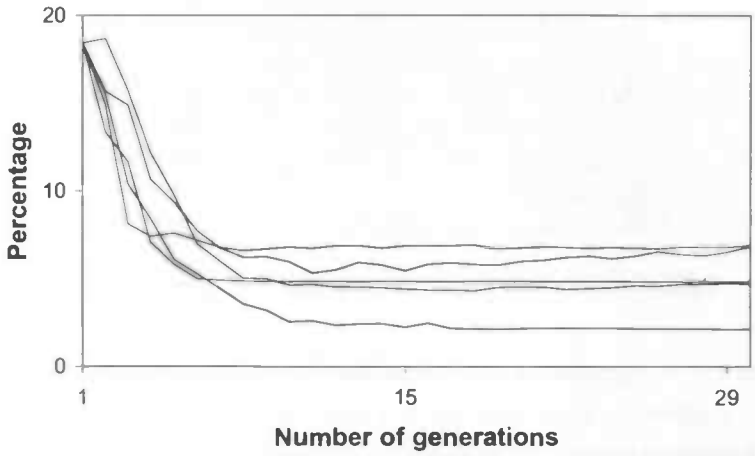

Figure 4.4: Five runs with pure random drift.

Parameter values

All of the 30 individuals have identical genes. See table 4.2 for the values of these parameters. These parameters values are based on the standard model values.

4.3.2 Results

In figure 4.5 the variation within the population is represented by taking the average standard deviation per generation of the 8 different parameters.

At the start of the experiment the variation within the population is 0, because the first 30 individuals are exactly alike. After a couple of generations a stable variation of about 4% is reached. There is no obvious point at which multiple species come into existence.

In figure 4.6 the different fitness values are represented. On the x-axis are the different males and on the y-axis the relative fitness from 0 to 1. Each line represents one female. In the

AN Conductance change(in mV)	6.0
AN Half-life conductance (in ms)	5.0
AN Half-life depression (in ms)	7.0
BN1 Conductance change (in mV)	3.7
BN1 Half-life conductance (in ms)	30
Syllable gap and length (in ms)	60
Number of syllables	8
Gap between chirps (in ms)	340

Table 4.2: Parameters values of the first generation

first generation there is no significant preference for any male. In generation 5 there is a clear preference for male number 4. Male number 2, 7 and 9 do not have high fitness values. From generation 15 to 25 there is a clear trend and similar preference for each female. However, the last generation is more similar to generation 10 again, where there is a trend, but not as clear as in the other generations. With two different species one would expect for part of the females to have a high preference for those males for which the other part of the females would have a low preference. There is no clear sign of such a trend.

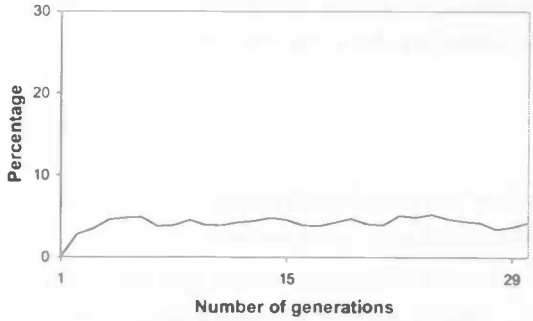

Figure 4.5: Percentage standard deviation for every generation

AN Conductance change(in mV)	6.0	6.6
AN Half-life conductance (in ms)	5.0	4.7
AN Half-life depression (in ms)	5.2	6.9
BN1 Conductance change (in mV)	2.8	3.2
BN1 Half-life conductance (in ms)	36.1	35.5
Syllable gap and length (in ms)	63	71
Number of syllables	6	15
Gap between chirps (in ms)	311	255

Table 4.3: Parameters values of the first generation

4.4 Experiment 2: Song Evolution

Crickets are very good at discriminating between their own species and other species of crickets. In this experiment two species of crickets with similar songs are put together. The songs are different enough that the majority of females choose the song of their own species.

4.4.1 Setup

Again, the size of the population is 30 individuals. Of these 30 individuals there are two groups of genes, half of the individuals belong to group 1 and half of the individuals belong to group 2. One would expect the songs of the different species to become less similar.

Parameter values

See table 4.3 for the parameter values. 50% of the individuals have the genes of the first column and 50% of the individuals have the genes of the second column. The genes of the first column are based on the standard model values. The genes of the second column are based on the outcome of experiment A.

4.4.2 Results

In figure 4.7 the variation within the population is represented by taking the average standard deviation per generation of the 8 different parameters.

The variation within the population starts around 12%. Soon, however, the variation decreases to a more or less stable state around 5%. The two different species the experiment soon mingle and disappear, instead of growing apart.

In figure 4.8 one would expect a different graph for the first generation. As mentioned in the previous section, when two different species exist in one generation, part of the females should have a high preference for those males for which the other part of the females would have a low preference. Instead all, of the females show a high preference for male 9 and 10. Both male 9 and male 10 are part of group 2. The preference of the females changes in generation 5. In generation 5 there is no clear common preference, except that male number 5 seems quite popular where male number 6 seems quite impopular. In generation 10 and 15 the female crickets tend to prefer the same males. However, from generation 20 on this changes again and the female preferences are not similar.

Syllable length = 58ms Number of syllables = 13 Gap between chirps = 430ms					
AN Conductance change(in mV)	5.4	5.8	20.0	8.8	9.8
AN Half-life conductance (in ms)	7.8	8.2	8.6	20.0	6.2
AN Half-life depression (in ms)	9.4	9.0	8.6	6.0	5.0
BN1 Conductance change (in mV)	2.7	2.9	3.1	4.4	4.9
BN1 Half-life conductance (in ms)	23.0	25.0	60.0	40.0	45.0

Table 4.4: Parameters values of females that prefer male number 4

4.5 Experiment 3: Random population

In this experiment I will take a random population to start with, to see where the population evolves to. This is not based on biological research.

4.5.1 Setup

The setup of this experiment again is similar to the previous experiments. I will start with a population of 30 individuals, 10 males and 20 females. The genes of all 30 individuals are different. They are random values based on the standard model values.

4.5.2 Results

The variation within the population starts high, because all the individuals in the population are different. Like in the previous experiment, after about 10 generations the variation decreases to a relatively stable 5%.

In generation 0 male number 4 and number 9 show a possible difference in species. See table 4.4 and 4.5 for the parameters of male 4 and 9 and the females that prefer these.

Generation 5 is not very clear, but male number 4, 5 and 6 are clearly impopular with most females. From generation 15 on the females develop a similar preference. Especially in generation 15 this is visible.

Syllable length = 98ms Number of syllables = 23 Gap between chirps = 46ms			
AN Conductance change(in mV)	8.0	8.2	8.4
AN Half-life conductance (in ms)	4.4	4.6	4.8
AN Half-life depression (in ms)	1.2	6.6	6.4
BN1 Conductance change (in mV)	4.0	4.1	4.2
BN1 Half-life conductance (in ms)	36.0	37.0	38.0

Table 4.5: Parameters values of females that prefer male number 9

4.6 Conclusions

The conclusion from these experiments is that female preference does not seem to make a difference in song evolution. However, there are only 30 generation and only 30 individuals. It turns out that after 30 generations and a population of 30 individuals no stable state could be reached.

It is interesting to see that in every experiment the standard deviation quickly moves to a percentage of about 5%. This means that the variation within a population stabilizes. This could mean two things. First, it could have something to do with the choice of mutation range and mutation chance. Second, it could mean that the range in which the parameters values make sense is quite small. Large differences in values, either low or high, do not stand a chance in this case.

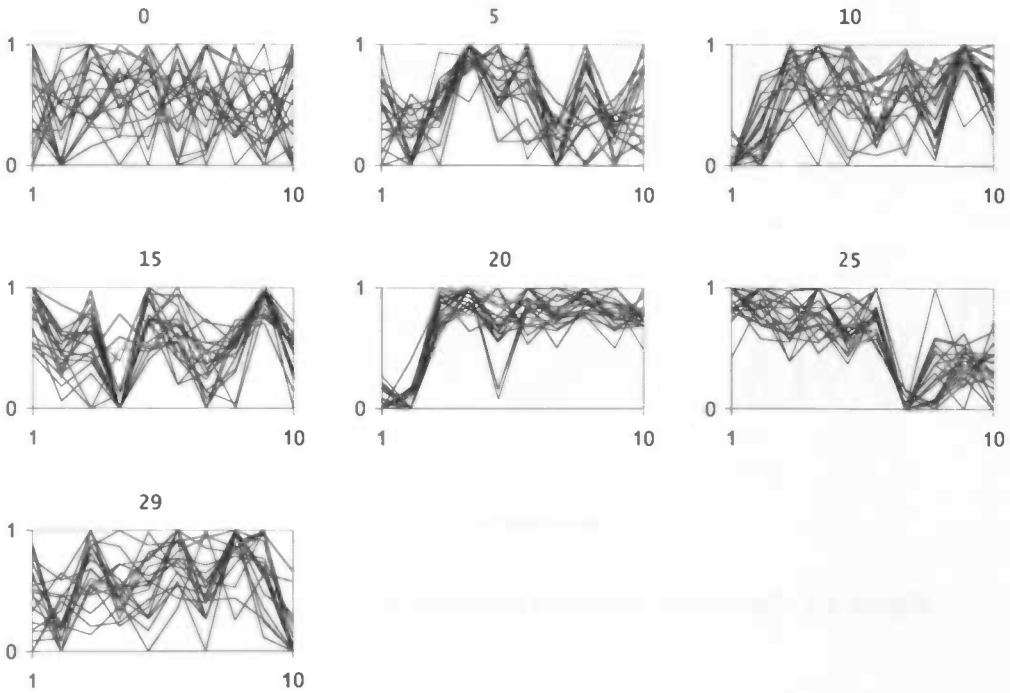

Figure 4.6: On the x-axis are the different male and on the y-axis the relative fitness from 0 to 1. Each line represents one female.

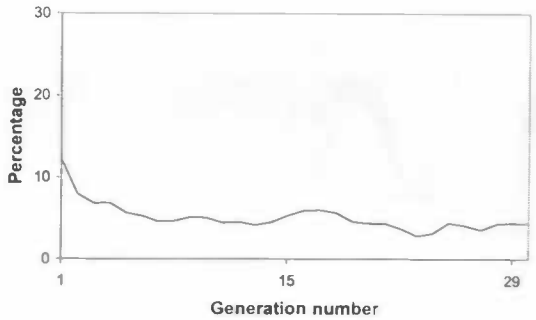

Figure 4.7: Percentage standard deviation for every generation

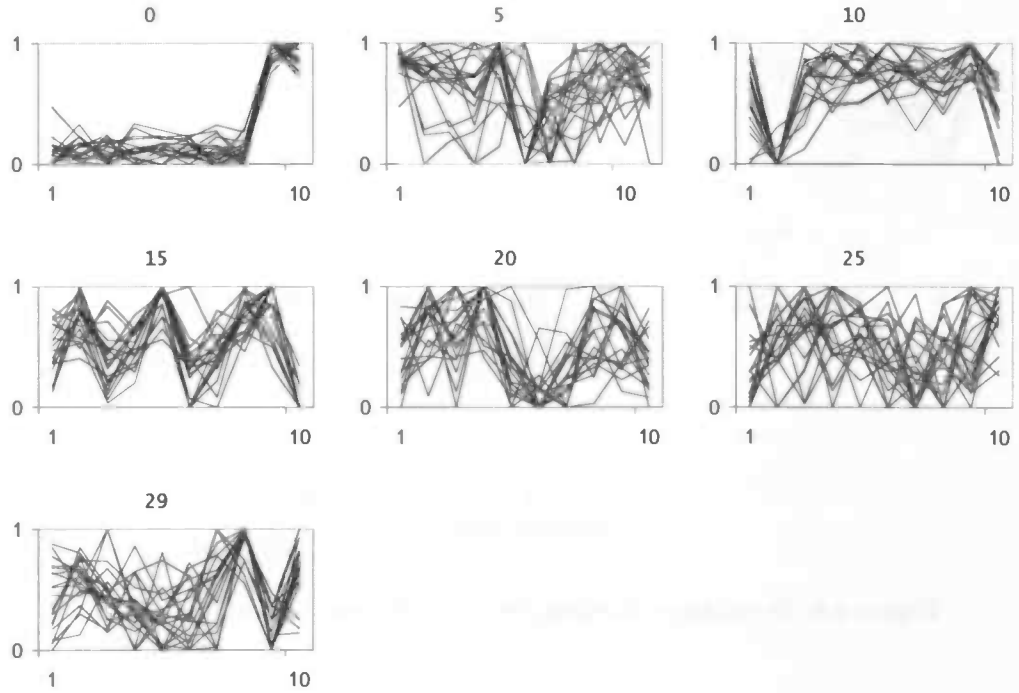

Figure 4.8: On the x-axis are the different male and on the y-axis the relative fitness from 0 to 1. Each line represents one female.

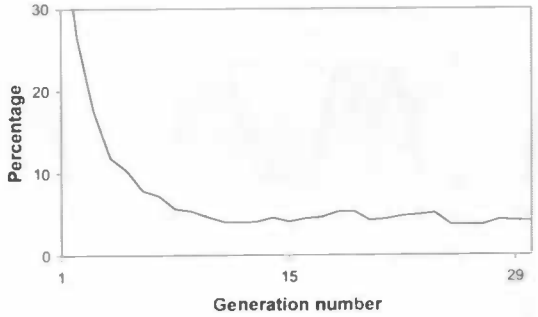

Figure 4.9: Percentage standard deviation for every generation

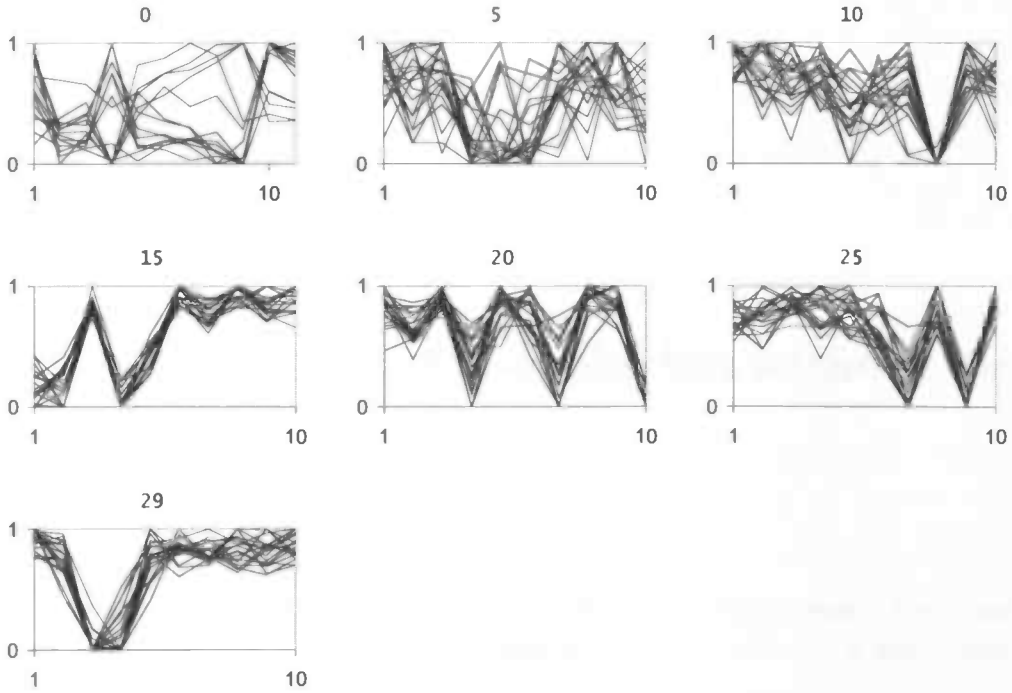

Figure 4.10: On the x-axis are the different male and on the y-axis the relative fitness from 0 to 1. Each line represents one female.

CHAPTER 5

Co-evolution without model

In this chapter I will conduct some simple co-evolutionary experiments. I will test if co-evolution is possible with a simple genetic algorithm. First I will give a description of the genetic algorithm I have used.

5.1 Genetic algorithm

The algorithm used in these experiments is similar to the one used in the previous experiments. The differences will be described in this section.

5.1.1 First generation

The total number of individuals in each generation is 300. The amount of females and males differs for each experiment. Each individual is represented as a value between 0.00 and 1.00, its phenotype. The first generation is initialized automatically. This initialization varies for each experiment.

5.1.2 Mutation

In these experiments the maximum mutation size is fixed and independent of the phenotype of the individual. This maximum mutation size is 0.05. The formula for the mutation is

$$v = c - 0.05 + 0.10r$$

In this formula v is the new value, c is the current value and r is a random value between 0 and 1. The new phenotype will be in the range of the old phenotype +/- 0.05.

5.1.3 Fitness

Initially the direct difference between two individuals was used as a fitness function:

$$f = |p1 - p2|$$

where f is the fitness, p1 is the phenotype of parent 1 and p2 is the phenotype of parent 2. The result of this fitness function was that when the phenotype changed by a small percentage, the change in fitness was so small that it did not influence the choice. Instead the whole species slowly moved from one phenotype to the other.

Instead, the species were defined in advance. A total of 100 species were defined. The bigger the difference in phenotype between two mating individuals, the lower their fitness.

$$f_{fit} = z = ||\lfloor a \cdot 100 \rfloor - \lfloor b \cdot 100 \rfloor|| \tag{5.1}$$

$$f_{fit} = \begin{cases} 1.0 & z = 0 \\ 0.9 & z = 1 \\ 0.8 & z = 2 \\ 0.5 & z = 3 \\ 0.2 & z = 4 \\ 0.0 & z = 5 \end{cases} \tag{5.2}$$

5.2 Experiments

In this section 5 experiments are described. This first experiment involves a normal evolution to test the genetic algorithm used. The remaining experiments will test co-evolution with a single species, with two species and with a random start population.

5.2.1 Experiment A: Normal evolution

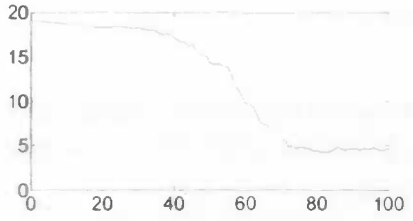

Figure 5.1: On the x-axis are the generations and one the y-axis the difference relative to the male phenotype of 0.80, which is represented as 80 in this figure. There is a clear movement to 80 visible and the difference stabilizes at about 5.

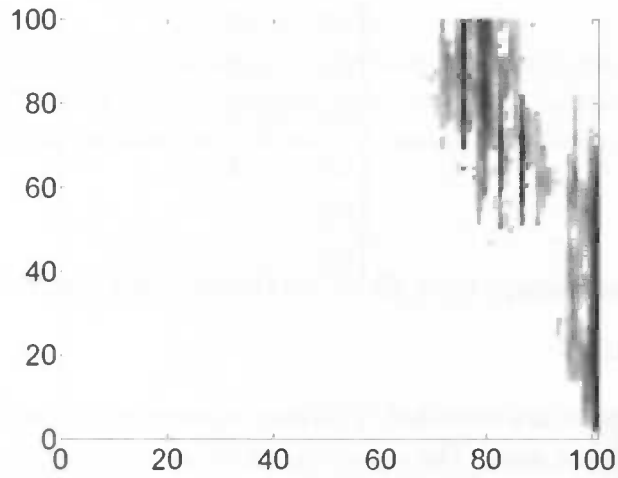

Figure 5.2: On x-axis are the different phenotypes and on the y-axis are the generations. Starting at a phenotype of 100 (1.00), the population soon evolves to a phenotype value of 80.

This experiment will test normal evolution. The male has a fixed phenotype. I expect the females to evolve in the direction of the male.

Setup

Instead of having a population with females and males, this population only has 300 females. All these females have the same phenotype of 1.0. The male phenotype is set to a value of 0.80. Mutation chance is 5% and the mutation range is 0.05.

Results

In figure 5.2 one can see how the population evolves over the generations. The darker the colour the more numerous the number of individuals. After about 55 generations the population evolves in the direction of the phenotype of the male. In figure 5.1 this is clearly visible.

After 100 generations the population has completely moved to the phenotype of the male and phenotypes looking very much like the phenotype of the male.

5.2.2 Experiment 1: Co-evolution with one species

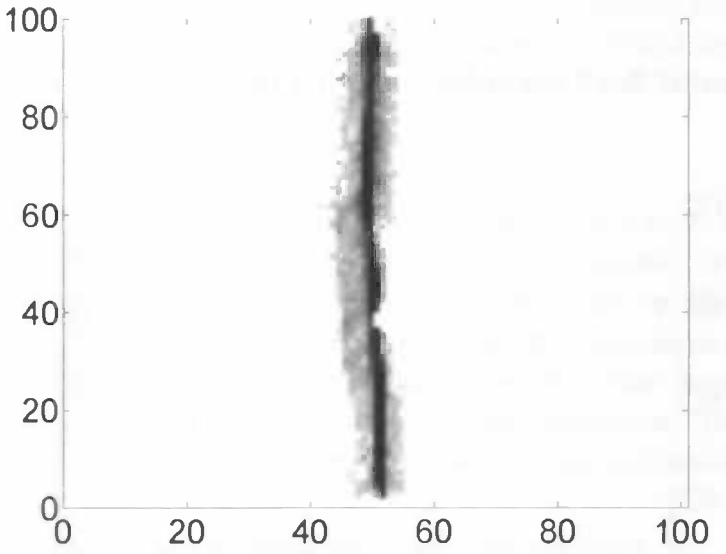

Figure 5.3: On x-axis are the different phenotypes and on the y-axis are the generations. The phenotype value is stable at 50 throughout the generations.

In this experiment I will test if speciation is possible when starting with one species.

Setup

In this experiment males and females co-evolve. The populations starts with one species. The phenotype of this species is 0.5. The mutation chance is 5% and the mutation range is 0.05.

Results

In figure 5.3 the results of this experiments can be seen. After only one generation the phenotype starts spreading, but only to phenotypes nearby. The reason for this is the mutation range of 0.05. These individuals mutate, but still stay attractive to a lesser extend. No speciation takes place.

5.2.3 Experiment 2a: Co-evolution with two opposite species

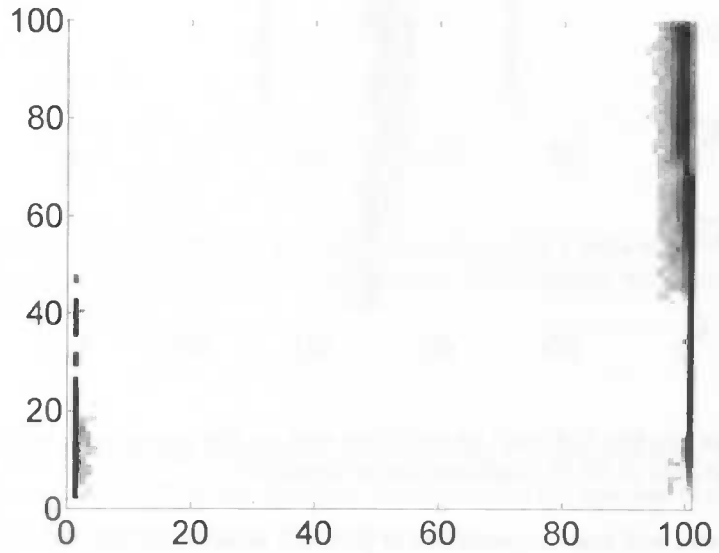

Figure 5.4: On x-axis are the different phenotypes and on the y-axis are the generations. The population starts with two different species, one with a phenotype of 0.00 (0) and one with a phenotype of 1.00 (100). After about 50 generations the species with the phenotype 0.00 completely disappear, while the species with the phenotype 1.00 grow.

In this experiment I will test if speciation is possible when starting with two species that have completely different phenotypes.

Setup

In this experiment males and females co-evolve. The population starts with two opposite species: 50 males and 100 females start with the phenotype 1.0 and the other 50 males and 100 females start with the phenotype 0.0. The mutation chance is 5% and the mutation range is 0.05.

Results

How the two species evolve over the different generations can be seen in figure 5.4. After 59 generations the 0.0 species completely disappears. The explanation for this is that the number of individuals in both species is always stable at 300. The reproducing females are chosen with roulette wheel sampling, which means that not their phenotype is important, but only the fitness. When one species is able to reproduce more often than the other species, the chances of survival of that species and extinction of the other species rise. This results is that one species often disappears. However, this seems to have nothing to do with co-evolution.

5.2.4 Experiment 2b: Co-evolution with two species

In this experiment I will test if speciation is possible when starting with two species. These two species have phenotype values that do not differ as much as in the previous experiment.

Setup

Like in the previous experiment, in this experiment males and females co-evolve. In this experiment the population starts with different species which are relatively similar: 50 males and 100 females start with the phenotype 0.3 and the other 50 males and 100 females start with the phenotype 0.7. The mutation chance is 5% and the mutation range is 0.05.

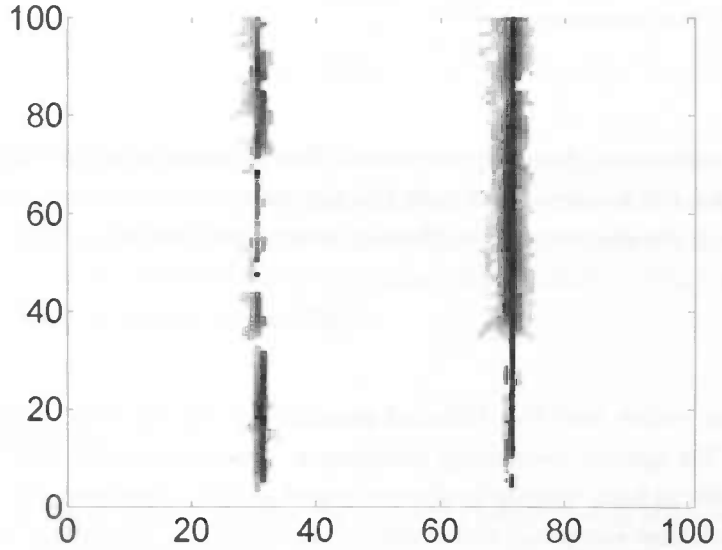

Figure 5.5: On x-axis are the different phenotypes and on the y-axis are the generations. The generations start and end with two different species. The species with phenotype 30 almost disappear a couple of times.

Results

In figure 5.5 one can see how the population evolves over the generations. The species do not change over the generations. Only the number of individuals per species varies per generation. In generation 56 the 0.3 species almost disappears even.

This result is to be expected. The maximum mutation range is 0.05, which means that an individual from species 0.3 can only go as far as species 0.35. This is not enough to get into the reach of the 0.7 species, because there is still a difference of 0.7 - 0.35 = 0.35. As mentioned in the fitness section earlier in the chapter, the maximum difference two mates can be apart to receive a fitness higher than 0 is 0.05. In this light, one would expect no other result than

with a single species co-evolving.

5.2.5 Experiment 3: Co-evolution with random start population

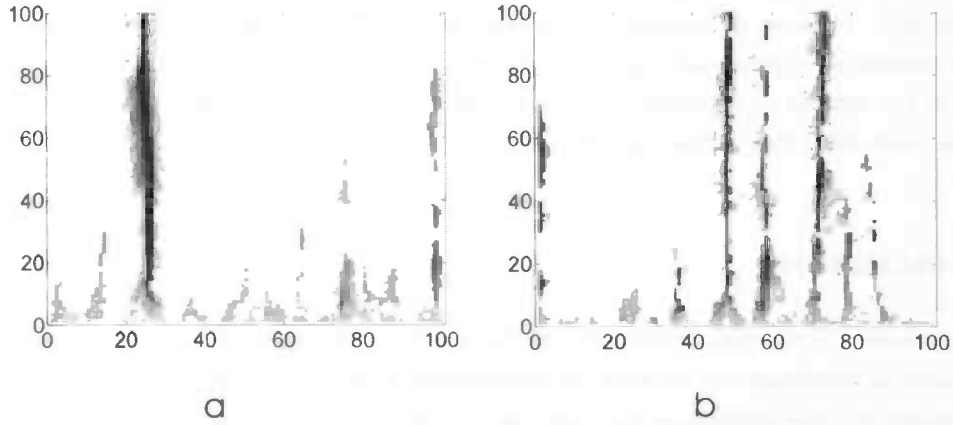

Figure 5.6: On x-axis are the different phenotypes and on the y-axis are the generations. The population starts with 300 random individuals. Speciation takes place in the first couple of generations, but most of the species disappear again after about 30 generations. In a) the species with phenotype 25 survive as only species in the end. In b) species are quite stable as in the end three species survive.

In this experiment I want to see what happens when the population starts out completely random. I expect speciation to take place.

Setup

In this experiment the population starts completely random. All 300 individuals receive a random phenotype value between 0.00 and 1.00. The mutation chance is 5% and the mutation

range is 0.05.

Results

The figures 5.6a and 5.6b the population flow over the different generation of three different runs can be seen. In every generation the experiment starts out with no obvious species, but after a few generations speciation appears. These species are stable in their phenotype, but again, like in the second experiment, vary in number of individuals. This causes some species to disappear soon after they came into existence.

5.3 Conclusion

Only in experiment 3 the was speciation. In the other experiments there was no speciation. There are several explanations for this. In experiment 1, no new species came into existence. If, with a mutation, one individual managed to 'escape' the existing population and together an individual of the opposite sex would change its preference to that individual, then they still would have a very small chance of survival. Reproducing couples are chosen on basis of their fitness, not on their phenotypes being exclusive. Therefor there is only a small chance that, when a large group of one species exists, a new species with only two individuals gets a chance to reproduce. Therefore it would need some other reason for success, for example a higher chance on survival.

In the case of experiment 2 there is another reason why species do not evolve. The mutation range is only 0.05. This means that when a species has a phenotype of value 0.70, the maximum it can change will be to 0.75 or 0.65. These values are not even near the 0.30 of the other species. As explained in the previous paragraph, these mutations do not evolve to a new species that could evolve to 0.30. The mutation range therefore limits the possibility of two species even coming in contact with each other. However, the higher the mutation range and mutation chance, the less stable a species.

Secondly there was also the case of the limited number of individuals in the total population. As mentioned before the choice for which individual would reproduce was solely based on fitness value. Therefore species could quickly disappear, but that did not have anything to do with sexual selection.

CHAPTER 6

Discussion

In this project I have tried to simulate the evolution of robot crickets. I wanted to look at the possibilities of evolving this robot cricket and see if I could simulate the evolution of real crickets. The conclusion that can be drawn from the experiments in this research project is that female song preference does not influence the male song pattern. Also speciation through sexual selection does not occur in these experiments.

6.1 Robot vs simulation

My original plan was to test my hypotheses on a robot. Soon after I started my project this turned out to be unfeasible. The main two problems were that it would take too much time

to evolve enough generations to actually get a valuable result. Secondly to automate the evolutionary process on the robot would be very time-consuming as well. Instead I used the simulation of the system. Using the simulation also meant using a simplified song wave. A real song wave could give a different result.

6.2 Size of population and generations

In these experiments a limited population size and generation size were used. In the next paragraphs a short explanation of the consequences.

6.2.1 Generations

The number of generations in this experiments was not sufficiently large enough to give a result on which a clear conclusion can be based. Initially I saved all the data produced by the simulation. Unfortunatly at least 3MB of data is produced in every run, which meant that I could only run 9 generations in total. As I originally wanted to evolve at least 100 generations, 9 generations was far from ideal. By summarizing the data after every run and removing the raw data, I managed to solve the space problem. However, the next bottleneck was time. Running many generations was very time-consuming, at least 1.5 hours per generation, and my time was limited. Therefore I only ran 30 generations in the experiments.

6.2.2 Population

As mentioned in the previous paragraph, running numerous generations is very time-consuming. Every run took about 30 seconds. In one run only one female was tested with two males and every generation each female was tested with all males, so the number of runs per generation was $\frac{females*males}{2}$. Increasing the number of individuals in a generation would increase the amount of time one generation would run.

6.2.3 Diversity

Not having a sufficient amount of individuals and not running sufficient generation will be at the expense of diversity and realistic linking with real crickets. Therefore it is doubtful if the results do have a realistic linking with real crickets and their evolution.

6.3 Parameters

I have evolved only a limited amount of parameters in the AN and BN1 synapses. These parameters are thought to have an influence on the evolution of sound recognition. Nevertheless the other parameters could also influence this evolution. It would be interesting to see the same experiment with different or more evolvable parameters.

However, these parameters do not have a direct link with genes in crickets. The neurons used in the simulation do not have a one-to-one mapping with neurons in the cricket brain. Hence evolving the parameters in the simuation could have a completely different effect than in real crickets.

6.4 Co-evolution without the model

There were several reasons why speciation did not happen. It would be interesting to co-evolve a population where the number of individuals are not limited to a specific number. In this experiment high fitness could be a reason for reproduction. This way, all individuals with a high fitness can reproduce, even in their species consists only of a few individuals.

Also a limited mutation range has a large influence on the evolution. It would be better if the mutation would make it possible for the individual to mutate to an opposite phenotype value. A possibility would be to use a log function. This way small mutation have a higher chance of happening than large mutations. However, as mentioned before, a higher mutation range makes a species less stable. Something has to chance as well to get a stable species. A

possibility is to lower the mutation chance. Another possibility would be to vary the mutation chance per generation or even per individual.

6.5 Future work

In the beginning of this thesis I have mentioned other parameters that could have influence the coevolution of song preference and song pattern, for example surroundings. It would be interesting to try and simulate the natural environment of the cricket and see if this results in different evolutionary patterns. For example, run the experiments on the robot model in a space with an echo similar to a cave.

In the future computers will be faster and the NRS model will be better. It would be interesting to do this same experiment with a large amount of individuals and generations and with a robot model. An improved model is being developed at the Institute of Action, Perception and Behaviour. This model has an improved motor system. It would be interesting to do these same experiments with the new NRS.

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