

Evolution and Population Genetics

INTRODUCTION

In 1831 Charles Darwin began a five-year journey as ship's naturalist on the H.M.S. Beagle. During this time he visited South America, Australia, South Africa, and islands of the Pacific and South Atlantic. He later published his travels in *The Voyage of the Beagle* where he introduced many themes that later became crucial to the arguments presented in the more-familiar *The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life* (published in 1859 and more commonly known as "*The Origin of Species*"). Majors in the sciences and those interested in philosophy should read this monograph. You won't find it easy reading because the language is often archaic and the arguments are sometimes difficult to follow, but it represents one of the most important contributions made to Western culture.

Although Darwin is often referred to as "the father of evolution", he was not the first to introduce the idea of changing species. Maupertuis and Diderot in the mid 18th century, for example, wrote of evolution and the ideas of changing life are part of many religions. Darwin's contribution was to provide a mechanism through which evolution could function. Briefly, the Darwinian argument is as follows:

- **Variation exists within a species.** Although we may consider all houseflies as being more-or-less alike, on closer examination you find that they are nearly as recognizable as one person is from another.
- **Some of this variation has a genetic basis.** Evolution can act only on traits that are passed genetically from one generation to the next. Just as an animal or plant breeder has no interest in non-genetic traits, evolution can not work on differences caused by trauma, parasitism, and other environmental variation.
- **The reproductive potential of organisms is vast.** Darwin calculated that a single pair of elephants could have 19 million descendants within 750 years if each animal lived to be 100 and each pair had six calves. Calculations for other organisms produce similar increases in population size. Elephants are not the most common beasts, the oceans are not overflowing with fish and we aren't nose-deep in ragweed (although it sometimes seems that way). Therefore something must happen to all these extra offspring and, unless species other than man practice birth control, most of the young must die before they reproduce.
- **Because individuals differ from one another, some should be more capable than others in eluding predators, coping with environmental extremes, or in competing with members of their own or other species.** Those that are more capable should leave more offspring to the succeeding generation. Since some aspects of coping must be tied to genetic attributes, the favorable genes are passed on to the next generation. The genetic makeup of the population changes and evolution is said to occur. This varying **reproductive success** of individuals based on their different genetic constitutions is **natural selection**.

Often the concept of natural selection is simplified to "survival of the fittest". **Fitness** in evolutionary terms has an exact meaning related to the number of surviving offspring produced by an individual in comparison to less well-endowed individuals. Evolutionary fitness is therefore more than just the ability to run quickly or fight off competitors.

Evolution is not a historical process; it is occurring at this moment. Populations constantly adapt in response to changes in their environment and thereby accumulate changes in the genes that are available to the species through its **gene pool**. In today's lab you will explore some of the evidence for evolution and will examine a few of the mechanisms through which evolution acts.

The saga of the pepper moth (*Biston betularia*) and its response to industrial pollution in England is a well-known example of selection in natural populations. In brief, the pepper moth is found in two forms (or "MORPHS"): a mottled form and a dark-colored melanic morph. During the mid 1800s, the mottled form predominated the countryside near Manchester, England; making up better than 99 percent of the population. By 1898, however, the situation was reversed, with the melanic (dark) form comprising the greater percentage of the population.

Researchers noted that the spread of the melanic form paralleled an increase in industrial pollution and hypothesized that the melanic form was better camouflaged than the lighter morph when they rested on the soot-darkened tree trunks (Fig 1a). Apparently, the light forms were removed from the population by birds because they were so conspicuous on the trees. Additional support for this hypothesis came from non-industrial regions (or those areas upwind from polluters) where the mottled form greatly outnumbered the melanic moths. Here, situation was reversed and the mottled moths had the advantage in hiding from birds on the lichen-covered trunks (Fig 1b).

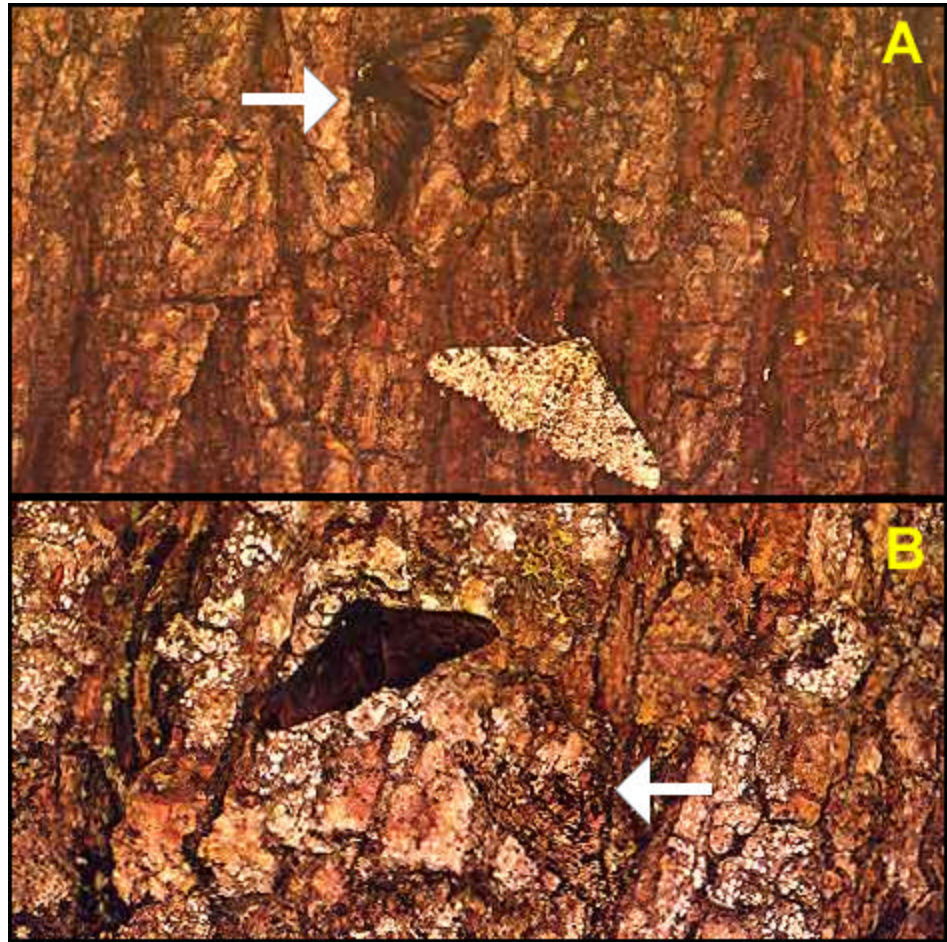


Figure 1. Melanic and mottled peppered moths on trees in polluted (A) and unpolluted environments (B)

The hypothesis was tested by releasing an equal number of melanic and mottled forms in an unpolluted area and then observing the feeding activities of birds from a blind. Apparently, birds had the same difficulty as the researchers in recognizing the mottled moths against the lichen background: they ate only 26 of the light forms while 164 of the poorly-camouflaged melanic moths were captured. In another series of experiments it was found that the melanic form had the advantage in polluted areas. Recent advances in controlling pollution have returned many areas of Great Britain to their previous state. With this, the pepper moth population is shifting again toward a predominance of the mottled form. It is also known that a single gene controls the expression of this trait and that the melanic gene is dominant over the light gene.

In this laboratory we will simulate the changes in a population of pepper moths. Before we can do so, however, we need to review both Mendelian and population genetics. Population genetics, in its' simplest form is only an extension of the familiar Mendelian genetics. As an example, let M represent the dominant melanic allele and m the recessive mottled form. Using this notation, moths with a homozygous mm genotype will have a mottled phenotype while those that are either homozygous for the melanic allele (MM) or heterozygous (Mm) will be dark in color. Assume that two heterozygous moths are mated (eg. $Mm \times Mm$). A punnett square for this mating is:

		Male Gametes	
		M	m
Female Gametes	M	MM	Mm
	m	Mm	mm

From such a cross you would expect that 25% of the offspring would be of the mottled form (*mm*) while the remainder would appear melanic (with genotypes of *Mm* or *MM*). This simple Mendelian cross can be easily expanded to a population problem. Assume that we have 100 moths (all heterozygous *Mm*). These moths carry 200 of the genes for the color trait, evenly divided between the *M* and *m* alleles. Let the frequency of the *M* allele be denoted as "*p*" and the frequency of the *m* allele as "*q*". In a population of 100 heterozygous moths, the frequency of each allele is 0.5 (*p*=0.5, *q*=0.5). In a general form, a population-based Punnett square would be:

		Male Gametes	
		p	q
Female Gametes	p	p^2	<i>pq</i>
	q	<i>pq</i>	q^2

In a more general format, the genotypic frequencies of the next generation are described by the Hardy-Weinberg formula: $p^2 + 2pq + q^2 = 1.0$. In our example, all you need do is substitute the frequencies of the *p* and *q* genes in the formula:

$$p^2 + 2pq + q^2 = 1.0$$

$$(.5)^2 + 2[(.5)(.5)] + (.5)^2 = 1.0$$

Finishing the calculations, and substituting the genotypes for *p* and *q* gives us:

$$.25MM + .50Mm + .25mm = 1.0$$

If we assume that the next generation will double in size to 200 moths, the expected number of each genotype is:

$$.25(200)MM + .50(200)Mm + .25(200)mm = 200$$

$$50MM + 100Mm + 50mm = 200$$

Note that when frequencies are used in the calculations, the equation must add up to 1.0 (or close if there is rounding error). For actual population numbers, the sum of the genotypes must add up to the total population size (assuming that there is no rounding). The phenotypic ratios for the next generation are 50 mottled moths to 150 melanic moths ($50MM + 100Mm = 150$).

EXERCISE 1

PURPOSE: To simulate selection in a population of pepper moths.

MATERIALS NEEDED:

- Pictures of pepper moth genotypes.
- Simulated habitats (low, medium, and high pollution).
- Scissors and tape.
- Calculators.

In this section of the laboratory you will simulate changes in a population of pepper moths due to selection in a polluted environment. Selection in the remaining two environments should be run at home. The general procedure is as follows:

Place 10 heterozygous moths in the environment. Gently shuffle the environment back and forth to redistribute the moths in the environment. Simulate birds feeding on the poorly-camouflaged moths. Make a count of the remaining moths for each genotype. Calculate the gene frequencies for the remaining population. Plug the gene frequencies into the Hardy-Weinberg formula to determine the expected gene frequencies for the next generation. Assume that the remaining population will double in size and use the results of the Hardy-Weinberg formula to calculate the expected numbers for each genotype. Round your calculations to the nearest whole number. Introduce new moths of each type to the arena. If your calculations indicate that the population should have five mottled moths and three remain in the environment, you should add only two (do not add five more). Shuffle the environment as before to redistribute your moths and then continue your calculations for four generations. See Table 1 for an example of the calculations.

DETAILED PROCEDURE:

- 1- Setting up the simulation. Cut out your pepper moths and the polluted habitat. Separate your pepper moths into three groups. Fold the habitat along the dotted lines and tape at the edge (Fig 2).
- 2- Work in groups of two for the first simulation. Complete the simulation of moths in the moderate and low pollution environments at home. Place 10 heterozygous (Mm) individuals (Fig 2) in the environment. Refer to the "Before Selection" example for Generation 0 in Table I during the following discussion and then run your experiment in the same fashion. For your own work, fill in the tables in the Results section.
- 3- Gently shuffle the habitat back and forth to randomly distribute the moths. If you shake the habitat too hard, they may pile up at one corner of the habitat or may stick together (pull them apart and try again).

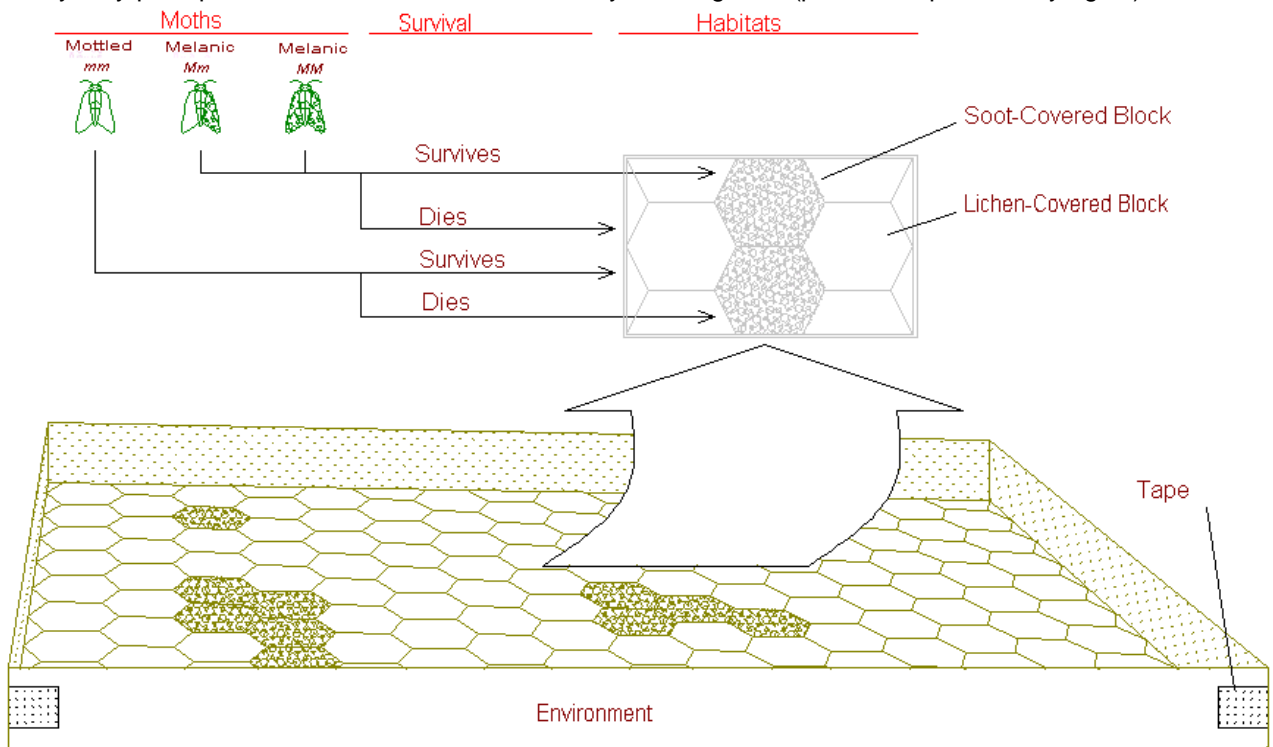


Figure 2. Procedure for setting up and running the simulation.

- 4- Select against moths that are poorly camouflaged. Remove all mottled moths (*mm*) from the dark (polluted) environment blocks and all melanic moths (*MM* and *Mm*) from the light (unpolluted) environment blocks. When a moth overlaps two or more blocks, use the position of the head to determine which block the moth is occupying. An example of the condition after selection is shown in table I. Note that three moths died in this simulation.
- 5- Determine the total number of M and m alleles by direct count (there are 7 of each in our example).
- 6- Continue with the Hardy-Weinberg calculations. First add up the total number of alleles (14 in the example) and determine the frequency of the M allele (*p*) by dividing the number of M alleles by the total number of alleles ($7/14=.5$ in the example). Do the same for the m allele and call this quantity "q" ($q=.5$).
- 7- Plug the values of *p* and *q* into the Hardy-Weinberg formula ($p^2+2pq+q^2=1.0$). This results in the expected frequencies of the *MM*, *Mn*, and *mm* genotypes in the next generation ($.25MM$, $.50Mm$, and $.25mm$ in our example).
- 8- Now that selection is finished, let the population double in size. Since there were 7 individuals left after selection, there should be 14 in the following generation.
- 9- Use the frequencies from the Hardy-Weinberg formula to determine the expected number of each genotype in the next generation if the total population size is 14. For the *MM* genotype, you would expect $.25(14)=3.5$ individuals (which rounds out to 4). Do the same for the *Mm* and *mm* genotypes.
- 10- The new quantities become the starting values for the next generation (generation 2 at the top of Table I). Add enough individuals of each genotype to the environment to bring each to the new generation size.
- 11- Continue with the simulation at step 3 in the procedure until 4 generations have been run. The example in Table I shows the results for the first generation.
- 12- Plot the frequency of each genotype (Y-axis) vs generation time (X-axis). Interpret the results of your graphs.
- 13- At home work through the simulations for the moderate and low pollution environments. Plot the frequencies and interpret your results.

Table 1. EXAMPLE CALCULATIONS FOR A POLLUTED ENVIRONMENT

Before Selection		#	Alleles		Always start with 10 Heterozygotes
Genotypes	Phenotypes	Moths	M	m	
MM	Melanic	0	0	0	
Mm	Melanic	10	10	10	
mm	Mottled	0	0	0	
After Selection		#	Alleles		Selection is simulated and 3 moths die. Since Mm moths have a copy of each allele, put a "7" in both blanks.
Genotypes	Phenotypes	Moths	M	m	
MM	Melanic	0	0	0	
Mm	Melanic	7	7	7	
mm	Mottled	0	0	0	
Hardy-Weinburg Calculations		f(M)=p	f(m)=q		7/14 = 0.5 (.5) ² + 2(.5 X .5) + (.5) ²
1) Frequency of M & m		0.5	0.5		
2) p ² + 2pq + q ² = 1.0		.25 + .50 + .25			
Expected Next Generation					
1) p ² (2 X Population Size)		.25(14)	3.5 MM		Double the remaining population for the next generation and multiply by the predicted frequencies
2) 2pq(2 X Population Size)		.50(14)	7.0 Mm		
3) q ² (2 X Population Size)		.25(14)	3.5 mm		
Before Selection		#	Alleles		Round the moth totals for the next generation.
Genotypes	Phenotypes	Moths	M	m	
MM	Melanic	4	8	0	
Mm	Melanic	7	7	7	
mm	Mottled	4	0	8	
After Selection		#	Alleles		Simulate selection by shaking the arena and getting the new allelic counts.
Genotypes	Phenotypes	Moths	M	m	
MM	Melanic	3	6	0	
Mm	Melanic	6	6	6	
mm	Mottled	1	0	2	
Hardy-Weinburg Calculations		f(M)=p	f(m)=q		There are 20 total alleles. 12/20=.6 (=p); 8/20=.4 (=q)
1) Frequency of M & m		0.60	0.40		
2) p ² + 2pq + q ² = 1.0		.36 + .48 + .16			(.6) ² + 2(.6 X .4) + (.4) ²
Expected Next Generation					
1) p ² (2 X Population Size)		.36(20)	7.2 MM		Compute the new expected frequencies for the third generation (now doubled to twenty).
2) 2pq(2 X Population Size)		.48(20)	9.6 Mm		
3) q ² (2 X Population Size)		.16(20)	3.2 mm		

Calculating Fitness Values.

Another series of calculations will allow you to quantify the effects of selection on the population. To perform these calculations you need the frequencies of each genotype both before and after selection. The values before selection can be actual counts or the expected values based on the Hardy-Weinberg formula. The values after selection are counts of those organisms left in the population after removal of the less well adapted individuals. As an example, consider the following population with two alleles (*M* and *m*).

	<i>MM</i>	<i>Mm</i>	<i>Mm</i>
Before Selection	100	150	50
After Selection	80	130	30

1. First calculate the survival rate (ω). This is the proportion of organisms of each genotype that survive after selection. Divide the number present after selection by the number that were present before selection for each genotype:

$$\omega_{MM}=80/100=0.80; \omega_{Mm}=130/150=0.87; \omega_{mm}=30/50=0.60.$$

2. Next compute the estimated fitness (λ). Fitness compares each genotype to that with the greatest survival rate (Mm). Divide each of the genotype's survival rate by the maximum survival rate:

$$\lambda = \omega_{MM} / \omega_{Mm} = .80 / .87 = 0.92$$

$$\lambda = \omega_{Mm} / \omega_{Mm} = .87 / .87 = 1.00$$

$$\lambda = \omega_{mm} / \omega_{Mm} = .60 / .87 = 0.69$$

These values show that the most fit genotype is *Mm*, followed by *MM*, with the lowest fitness held by the *mm* genotype.

REPORT

1. Enter the results for the peppered moth simulation in the following data sheets (Do one series for each of the environments).
2. Use bar graphs to plot the frequencies of the genotypes for the low, moderate, and high pollution environments. (Use the page with three graphs).
3. Plot the frequencies of the *p* and *q* alleles for each of the habitats on the page with two graphs. Make a line graph and use different colors or symbols to distinguish among the three habitats.
4. Show the results of your fitness calculations for the last generation (compared to the first).

Habitat	Number of Each Genotype						Survival Rate			Estimated Fitness		
	Before Selection			After Selection			<i>mm</i>	<i>Mm</i>	<i>MM</i>	<i>mm</i>	<i>Mm</i>	<i>MM</i>
	<i>mm</i>	<i>Mm</i>	<i>MM</i>	<i>mm</i>	<i>Mm</i>	<i>MM</i>						
Polluted												
Moderate												
Low												

5. Briefly interpret the results of your simulation.

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Data Sheet for Selection Simulation

Pollution Level (Check One)

High Pollution

Moderate Pollution

Low Pollution

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Data Sheet for Selection Simulation

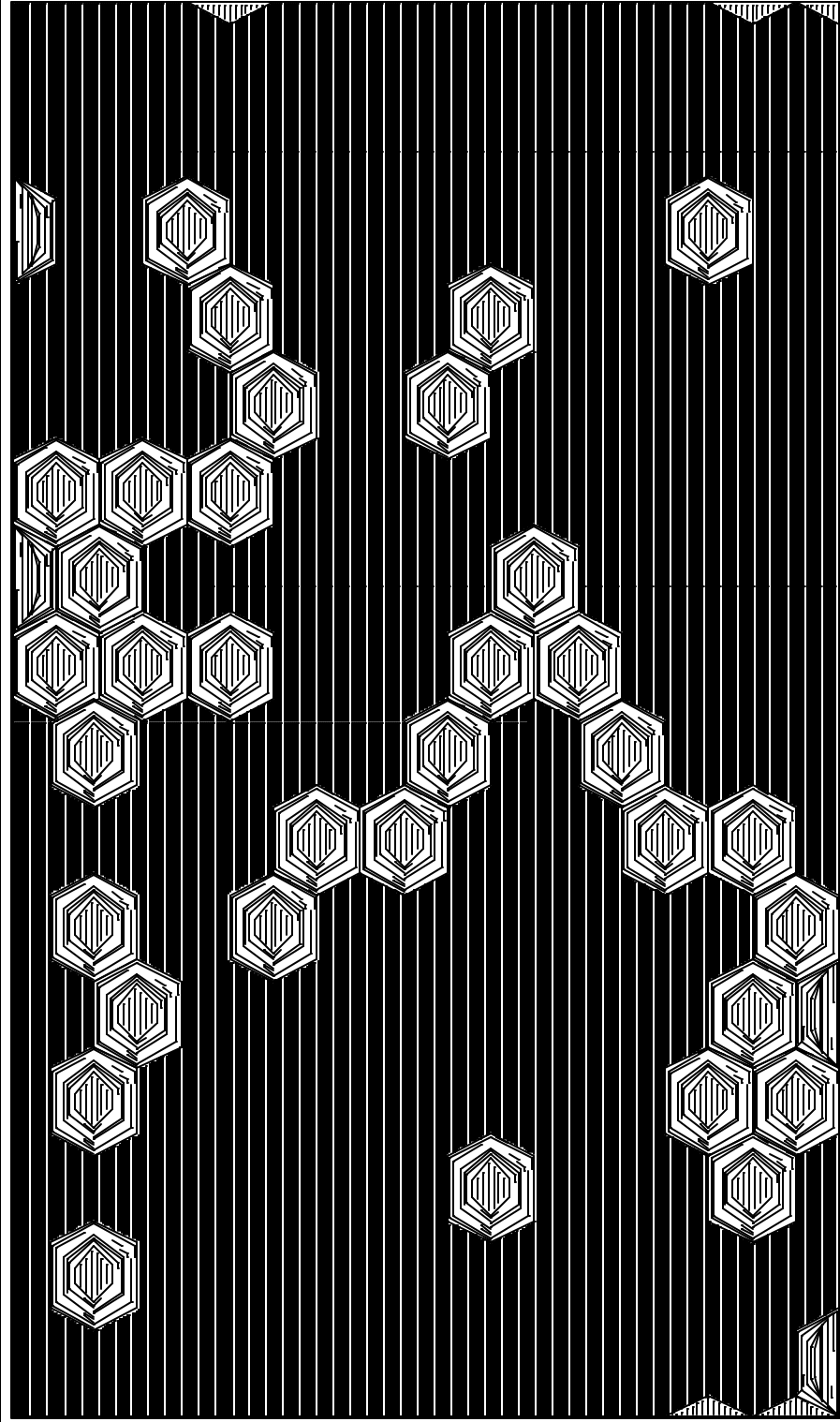
Pollution Level (Check One)

High Pollution

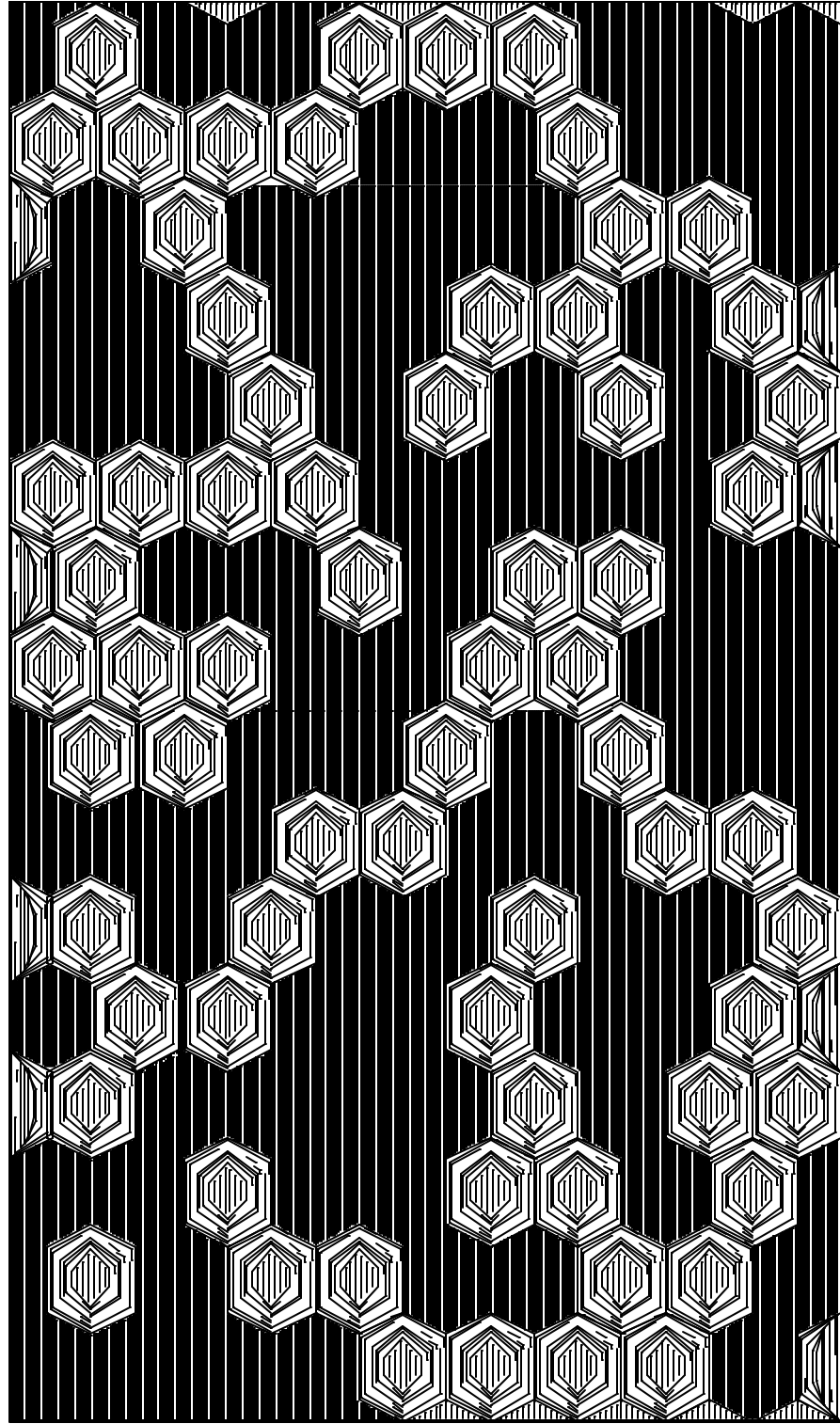
Moderate Pollution

Low Pollution

Polluted Environment



Moderately Polluted Environment



Low Pollution Environment

