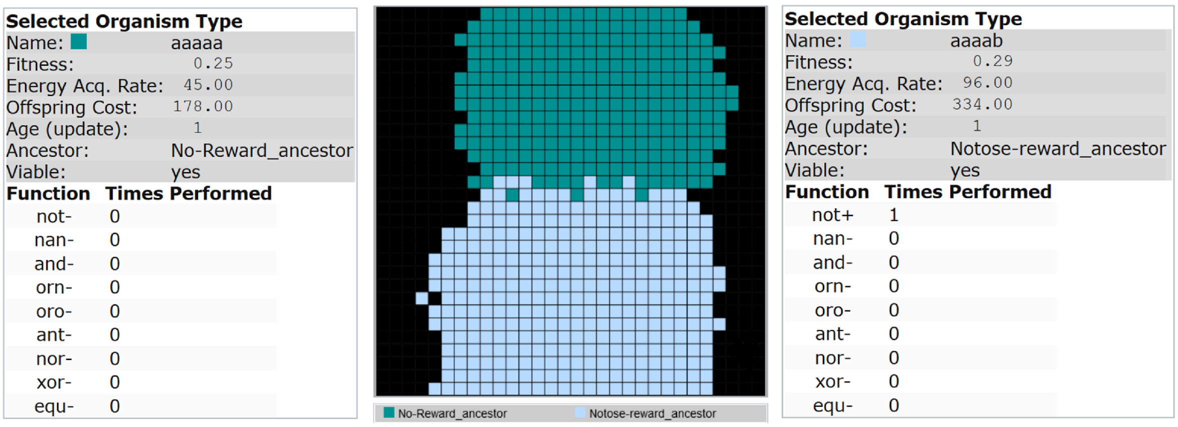
Exercise 3 – Exploring Fitness and Population Change under Selection



Avidians descended from ancestors with different adaptations are competing in a selective environment. Can we predict how natural selection will influence the evolution of this population?

Student Learning Goals

- Students will be able to explain the process of adaptation by natural selection, leading to genetic frequency change in a population over many generations.
- Students will be able to explain the concept of fitness as used in biology, and that fitness is dependent on the environment.
- Students will be able to explain that natural selection is non-random.

Questions to Consider While Doing Exercise #3

- What does “fitness” mean, in an evolutionary context? Why is this a useful term for biologists studying evolutionary patterns and processes?
- Does the fitness of an organism ever change? Explain.
- What do biologists mean by, “adaptive evolution”? How do we know when adaptive evolution has occurred?
- Why is natural selection considered to be a “non-random” process?
- Can we observe evolution occurring?

The type of variation in a population acted upon by natural selection is phenotypic or trait variation, which changes gradually over successive generations. Differences in traits may be beneficial, allowing some individuals in a population to reproduce more than others; these individuals have greater fitness relative to organisms lacking such advantageous traits. These advantageous traits, or adaptations, are favored within the selective environment and will become more frequent in the population over generations of change. This is guaranteed to occur because individuals possessing the adaptations contribute more offspring on average than do individuals in the population lacking the advantageous traits. An individual’s fitness is therefore dependent upon the interaction between its phenotype and the selective environment, and is relative to other individuals in the population.

In Exercise #3, we will observe the process of natural selection in action: beneficial mutations will randomly occur for some individuals, these mutant organisms will have a greater relative fitness due to their adaptation to the environment and will tend to increase in frequency in the population over successive generations.

Measuring Fitness

In biology, the concept of fitness has crucial importance for how evolution by natural selection occurs, but the term fitness is often difficult to define and even more difficult to measure. For our purposes we will simply state that fitness is the number of offspring an individual contributes to later generations, or lifetime reproductive success. Fitness is incredibly difficult to measure for most organisms, so instead biologists typically use one or more related measures, called fitness components or proxies. For some study systems, biologists might use foraging success, mating success, survival, or other types of fitness proxies. When choosing which to use, a biologist needs to weigh the ease of collecting data with how strongly correlated the measure is to the true evolutionary fitness of the organisms under study.

In Avida-ED we call our fitness proxy “Fitness”, but it is more precisely a measure of reproductive rate. This is a good measure of an organism’s fitness because the quicker an organism can reproduce the more offspring it can contribute to the population over time. When an Avidian is able to perform a function corresponding to a resource in its environment it is rewarded with an increased energy acquisition rate. In Avida-ED, fitness is calculated as the ratio of energy acquisition rate divided by offspring cost, in terms of energy necessary to complete the reproduction process. The energy aspects of the ratio cancel out, so fitness is the rate of reproduction. An Avidian rewarded for performing a function will have an increased fitness, producing offspring quicker. Importantly, Avidians can also have higher fitness by reducing offspring cost, so populations in Avida-ED are always under selection to reduce offspring cost no matter the presence of resources in the environment. Note that performing a function tends to increase offspring cost, because to do so generally requires more instructions needing to be executed before reproduction is completed.

Fitness can be further thought of as having two related measurement types, called absolute fitness and relative fitness. Absolute fitness is that which we have discussed; in Avida-ED a displayed “Fitness” value for an organism is precisely the absolute reproductive rate – the number of offspring an organism can reproduce in an amount of time. Relative fitness is the ratio of two absolute fitness values, the fitness of the focal organism relative to a reference fitness. The denominator of the ratio, the reference fitness, is often the average fitness of all organisms in the population. In Avida-ED you can calculate the relative fitness of an Avidian by dividing its “Fitness” from the “Selected Organism Type” panel by “Average Fitness” from the “Population Statistics” panel.

Frequency Change in a Population

Evolution can be defined as change in genetic frequencies over successive generations. Genetic variation in a population can be described in terms of the relative frequencies of the different genotypes present in the population. When a mutation occurs, a new genetic

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variant is introduced into the population (a new genotype). When the mutation appears in only a single individual, it occurs at the minimum possible (non-zero) frequency in the population. If the new genetic variant increases in frequency and becomes present in all individuals over successive generations, we say that the mutation has "gone to fixation", which is the maximum possible frequency in the population (frequency = 1.00). Evolution is what occurs between these frequency extremes. Unlike most biological systems, the simple genetic machinery in Avida-ED allows us to simplify genetic transmission concepts; an Avidian's entire genomic sequence is its genotype, and it is this genotype that can change frequency in an evolving Avidian population. Thus we can discuss the fitness of an organism as equivalent to the fitness of its genotype, with all identical Avidians having the same fitness.

To understand how natural selection operates, it is useful to use the concept of relative fitness. Populations tend to have a great deal of genotypic variation (ultimately due to mutation), and thus phenotypic variation, and thus the individuals present have a range of absolute fitness values. A specific genotype will change in frequency at a rate directly proportional to the genotype's relative fitness value. The greater the value's magnitude, the faster the population will change due to selection. A relative fitness greater than one indicates that the genotype will increase in frequency, and a value less than one indicates that the genotype will decrease in frequency due to selection. The frequency of a phenotype can be similarly described as increasing or decreasing in a population. The concept of relative fitness can be applied to phenotypes as well, and is calculated as the average fitness of all distinct genotypes that confer the phenotype.

In this exercise, we explore relationships between variation, selection, and fitness by competing organisms against each other that are adapted to different environments. Organisms that are used as ancestors in these competitions are adapted to different selective environments in Ancestor Treatments 1 & 2. In Ancestor Treatment 1, we evolve an Avidian population with no resources present (all resources are absent), while in Ancestor Treatment 2, only the resource notose is present. Selected organisms will then serve as the ancestors In Competition Treatments 1 & 2, in which the ancestors compete within each of these two selective environments. By selecting and freezing organisms from each of these two environments, and competing them against each other in both of these environments, we can test whether there is a "home-field advantage" in these "battles"!

Competitions such as these allow us to explore the concepts of genotypic or phenotypic frequencies changing in a population over time. By synthesizing data recorded near the beginning and at the conclusion of each competition experiment, we can explore whether or not a population will evolve to have a greater proportion of individuals better adapted to that environment – i.e., that natural selection is non-random.

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Freezing individuals evolved in different selective environments

Ancestor Treatment 1 – Evolving a high fitness organism when no resources are present.

1. In the Population viewer, flip to Setup.
2. Drag "@ancestor" from the Freezer to the Ancestral Organism(s) box.
3. Set the following parameters:
   Dish Size 30x30; 2% Per Site Mutation Rate; Place Offspring Near their parent; **Uncheck all resources**; Repeatability Mode Experimental; Pause **At update 1,000**.
4. Return to Map view and select Run.
5. Once 1,000 updates have completed, use the Fitness Scale coloration and the "Selected Organism Type" panel to identify an individual with a relatively high fitness. It *does not matter* if this Avidian can perform any functions.
6. Once selected, freeze the individual by choosing the "Save Selected Organism" option from the Freezer menu. Name the organism **"No-Resource_ancestor"**.
7. Switch to the Organism viewer to confirm your frozen organism's phenotype.
8. Drag the organism from the Freezer to the genetic code box. Select Run, then End.
9. A genetic code symbol labeled "Offspring Genome" should appear within the offspring's genome, and the Details window should indicate that it can perform whichever phenotypes you observed it being able to perform when you chose it. If your frozen organism unable to reproduce, return to the Population viewer and repeat steps 5-9. (Note: right-clicking a Freezer item allows you to rename or delete an organism.)

Ancestor Treatment 2 – Evolving a high fitness organism when *only* notose is present.

Repeat Ancestor Treatment 1 with the same parameters, ***except*** add notose to the environment by **marking notose with a check**. Leave all other resources absent (unchecked). At step 5, you must identify an Avidian with a relatively high fitness that **can perform NOT**. If you do not have an organism that can perform NOT after 1,000 updates then continue the run until an individual that can perform NOT occurs in the population. Then confirm its phenotype and ability to reproduce following steps 7-9, making sure that your organism successfully performs NOT. The selected frozen organism should be named **"Notose_ancestor"**.

Respond to the following before proceeding to the Competition Treatments:

- ☐ Considering the design of experiments in science, explain the importance of replicating the procedures conducted in one experimental treatment as much as possible for other experimental treatments.

- ☐ Why is it important that the ancestral populations in Ancestor Treatment 1 & 2 ran for a long time (1,000 updates)? What would the implications be if these treatments ran for only 500 updates (assume a NOT performing individual still occurred)?

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- When competing the evolved ancestors in each of their ancestral environments, do you predict the same ancestor will "win" (that is, contribute a greater frequency of descendants to the population) in both environments? *Why or why not?*

Recording your data. Complete the tables below for Competition Treatments 1 & 2.

Table 1. Fitness attributes of organisms chosen for use as ancestors in competitions in two different selective environments.

	"**No-Resource_ancestor**" (may or may not perform function)			"**Notose_ancestor**" (performs NOT)		
Selective Environment	Fitness (absolute)	Energy Acq. Rate	Offspring Cost	Fitness (absolute)	Energy Acq. Rate	Offspring Cost
All resources absent						
Notose present						

Table 2. Frequency of individuals performing NOT after 300 updates of competition in two different selective environments.

Selective Environment	Number performing NOT	Number of viable organisms	Percent of viable organisms performing NOT
All resources absent			
Notose present			

Competing individuals in their ancestral selective environments

Competition Treatment 1 – Competing ancestors when all resources absent.

1. In the Control menu choose "Start New Experiment".
2. In the Population viewer, flip to Setup.
3. Drag **both** "No-Resource_ancestor" and "Notose_ancestor" from the Freezer to the Ancestral Organism(s) box.
4. Set the following parameters:
   Dish Size 30x30; **0.2%** Per Site Mutation Rate; Place Offspring Near their parent; **Uncheck all resources**; Repeatability Mode Experimental; Pause **At update 300**.
5. Return to Map view. *NOTE: Do not press Run until step #9 (on next page).*
6. Below the Map, set Mode to "Ancestor Organism." In the "Population Statistics" panel select the "NOT" button. Change the graph's Y-axis to "Number of Organisms."
7. In the Control menu choose "Do one update".
8. Record in **Table 1** the (absolute) fitness, energy acquisition rate, and offspring cost for each ancestor by selecting each and using the "Selected Organism Type" panel.

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Respond to the following before proceeding to step 9:

- In this environment with all resources absent, use the concept of adaptation to describe and compare the starting fitness values of each ancestor.
- Use the concept of fitness to predict which ancestor will contribute a greater proportion of descendants to the population after 300 updates.

9. After responding to the two questions on adaptation and fitness (above), press Run.
10. Observe the <u>number of descendants</u> of each ancestor over time (colored differently on the Map, as per step #6). Also observe the <u>number of individuals performing NOT</u> over time (outlined on the Map and graphed in green, as per step #6).
11. After 300 updates, consult the "Population Statistics" panel and record in **<u>Table 2</u>** the number of Avidians performing NOT and the number of viable organisms. Use these to calculate the percent of viable Avidians performing NOT and record this in Table 2. Note: We are focusing on only the viable organisms because only these have the ability to perform NOT and be rewarded for this by reproducing quicker.

After completing Competition Treatment 1:

- Compare the relative frequencies of the descendants of the ancestors by observing the two colors on the Map. Does this match your prediction? Explain.

Competition Treatment 2 – Competing ancestors when notose present.

Repeat steps 1-11 of Competition Treatment 1 using the same parameters and procedures, except add notose to the environment by **<u>marking notose with a check</u>**.

Respond to the following before proceeding to step 9:

- In this environment with notose present, use the concept of adaptation to describe and compare the starting fitness values of each ancestor.
- Use the concept of fitness to predict which ancestor will contribute a greater proportion of descendants to the population after 300 updates.

After completing Competition Treatment 2:

- Compare the relative frequencies of the descendants of the ancestors by observing the two colors on the Map. Does this match your prediction? Explain.

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- How does this differ from what you observed in Competition Treatment 1?

Recording your data. Experiments in biology often involve investigating processes or phenomena with lots of variation, we will therefore be examining the data generated by all students in the course.

Enter your *final column of Table 2 data*, the percentage of viable Avidians performing NOT in each experimental treatment, in the document linked here:

Exercise 3 - Data Collection

Follow the "Example" in column B. Find the first column on the right that does not contain data; enter your name in row 4, and your final column of Table 2 data in the following rows. The instructors will periodically collect these data, anonymize it, and add it to the course data set.

Exercise 3 - Data Analysis

Discussion Questions and Wrap-up. After examining the course data, work with your lab team to respond to the following questions.

- How does this *experimental setup* test the influence of selection on leading to the increased frequency of certain phenotypes?

- On average, how does the final frequency of individuals performing NOT compare in the different environments?

- Describe a mechanism that could explain this result.

- Explain adaptation in the context of the *all resources absent* environment.

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- Explain adaptation in the context of the *notose present* environment.

- **Thought experiment –** Even after many thousands of updates of evolution in a selective environment for NOT performance, why might this phenotype never quite reach 100% frequency in the population? Describe your hypothesized mechanism. Hint: observe the number of individuals performing NOT over time (outlined on the Map and graphed in green) near the end of Competition Treatment 2, and allow the experiment to run longer if you wish.

- We used Avida-ED and this experimental protocol to model what occurs when biological populations experience natural selection. What are some limitations or constraints to our modeling in this exercise?

Reflection and Metacognition

Think-Pair-Share: Work with your lab team to answer the following questions.

- What did you learn from this exercise?

- What are you still wondering about?

- What would you change in this exercise?