

Exercise 11: Behavioral Ecology

Are You Smarter Than a Beaver?

Learning Goals

1. Define behavioral ecology and fitness in your own words.
2. Know components of natural selection and explain how natural selection can theoretically shape behavior.
3. Use a mathematical model to predict behavior based on optimizing profitability.
4. Derive and interpret a graph associated with experimental data.
5. Compare and contrast experimental results from this lab with field research on behavioral ecology.

Evolution Connections

Evolution of Behavior

Many traits evolve, and behavior is no exception. Because behaviors are phenotypic traits influenced by genetics, they are subject to natural selection, which can result in the evolution of a population. But how can territoriality be adaptive? An adaptive trait is a trait that increases the ability for the individual to pass on its genes. To explore behavioral adaptation, this takes some examination in both a proximate (current) and ultimate (historical) context. Niko Tinbergen, a 20th century animal behaviorist, is well known for his four questions to investigate behavior further. Territoriality in Cichlid fish is explored in the table using these four questions.

Proximate “How does the animal perform the behavior?”	Development: How does territoriality change over the lifetime of the fish?	Mechanism: How does physiology of the fish change as a result of an intruder?
Ultimate “Why does the animal perform the behavior?”	Evolution: Are other closely related species or recent ancestors territorial?	Adaptive Value: How does being territorial affect reproduction (passing on genes)?

Table 1: Adaptation of Tinbergen's Four Questions.

The ability for an organism to analyze the costs and benefits of a behavior is also an adaptive trait. Territoriality can have many benefits, including retaining breeding area, shelter from predators, and mates; however, it also comes with costs. If a fish fights over a territory, it may suffer from being injured and still lose its territory, or it may be killed. Costs will likely be minimized, as they are detrimental to survival, while benefits will be maximized if they increase chances reproduction.

This lab allows you to analyze which traits a fish use to assess the costs or benefits with each interaction, while also illustrating how behaviors can evolve if the fish is then able go on to reproduce.

By Chelsea Cook

1 Tinbergen, N. 1950. The heirarchical organizaion of nervous mechanisms underlying instinctive behavior. Symposium of the Society for Experimental Biology, 4: 305-12.

Introduction

Today, we will explore the question: Does evolution through natural selection apply to behavior?

Behavioral ecology is the study of how the environment shapes behavior and utilizes an evolutionary approach. At its most basic level, animal behavior is defined as a complex set of responses to various stimuli. Behavioral ecologists often ask, "Is a set of given behaviors genetically determined and/or passed down to offspring (i.e. determined by evolution through natural selection), or is the set of behaviors environmentally determined and not necessarily passed from parents to offspring (i.e. not determined by evolution through natural selection)?" Of course these questions are too complex to be answered in a simple 2 - 3 hour lab class, but we can use these questions as a general overlay to guide an investigation in the behavioral ecology of both people and beavers.

Evolution through natural selection should favor characteristics of individuals that successfully produce and rear the most offspring. A mathematical example can support this contention very well. Suppose that for a given species, individual "A" has 10 offspring that survive to reproduce and individual "B" only has 3 offspring that survive to reproduce. It follows that relatively more of the genes in individual "A" will be present in the population during the next generation. If this principle applies to animal behavior, then behaviors that maximize successful reproduction or **fitness** should be the behaviors exhibited most often in a population. In short, behavior is ultimately driven by successful reproduction (offspring that survive to reproduce successfully). Since the environment is extremely complex and variable, a single behavior will not always give an individual the best fitness in all situations. Therefore, just like variability in phenotypic traits (how people and organisms look), there is variability in behaviors for a given situation.

How do you Research an Evolutionary Hypothesis?

In order for a hypothesis to be considered in the realm of scientific hypotheses, it must be testable. Because macroevolution has been occurring over the course of millions of years, a typical controlled experiment that is set up today and is run over a given amount of time isn't possible. So how do biologists test evolutionary hypotheses? To test evolutionary hypotheses, we can use fossil evidence like we did in the Human Evolution lab. However, for behavioral ecology, there is no fossil record. All that we have for evidence is current behaviors of animals.

One way to test if behaviors are driven by evolution through natural selection is through mathematical modeling. Mathematical models are based on hypotheses and are used to predict the outcome that we should see from an experiment. For example, our research question today deals with whether or not certain aspects of animal behavior are determined by evolution through natural selection (i.e. genetically driven). If behaviors are based on evolution through natural selection, we should see consistencies in behaviors between different organisms (including people) in similar conditions. Thus, a mathematical model predicting animal behaviors under certain conditions can be derived and then the predictions can be tested for a variety of different animals.

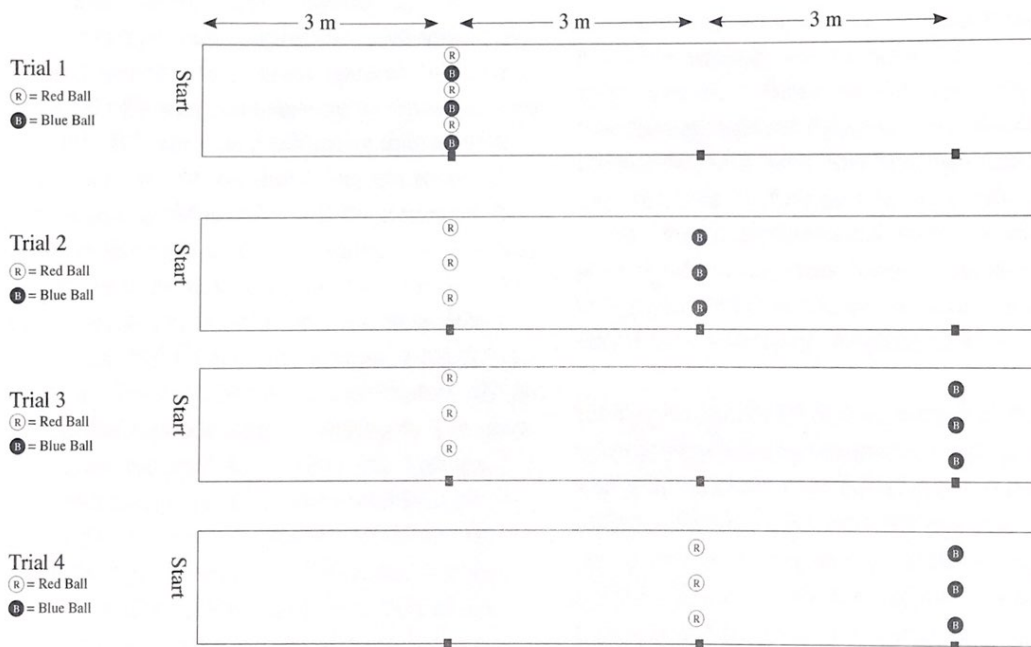
In this lab, you will play a game that simulates common conditions beavers are exposed to and you will compare your behaviors to those of beavers. Since we do not want the outcome of the game altered, we are not going to expose you to the mathematical model until after you have played the game and gathered data.

Procedure 1

1. The lab activities are potentially hazardous. Before starting the lab, please read over the procedures and sign the liability waiver if you agree to participate.
2. Divide into groups of 4. Extra students can join to have a group of 5.
3. In the game, 3 members of the group will need to run and 1 member will be a timekeeper. For best results, the 3 runners should continue to be the runners during the entire lab.
4. Go to an open field where there are at least 10 meters of flat grass without any holes or depressions. Good locations are west of the library, Farrand Field, and south of Duane Physics.
5. Set up the game field by spreading out the rope into a rectangular shape and pushing the corners into the grass. Make sure the grass within the rope is level with no holes to twist an ankle in. The rope has marks at 3, 6, and 9 m from the start. Start by placing 3 balls at the 3 m mark.
6. The three members of the group who are running should warm up carefully by slowly jogging for two minutes then gently stretching.
7. Get baseline data. The three runners will be a part of a relay. The first runner will start behind the starting line, run out to the 3 m mark, pick up a ball, then run back. As soon as runner 1 crosses the start line runner 2 will do the same, followed by runner three. The timer should have one time for the entire relay from start to finish. Record that time in Table 11.1. Repeat with balls at 6 m and 9 m from the start line.

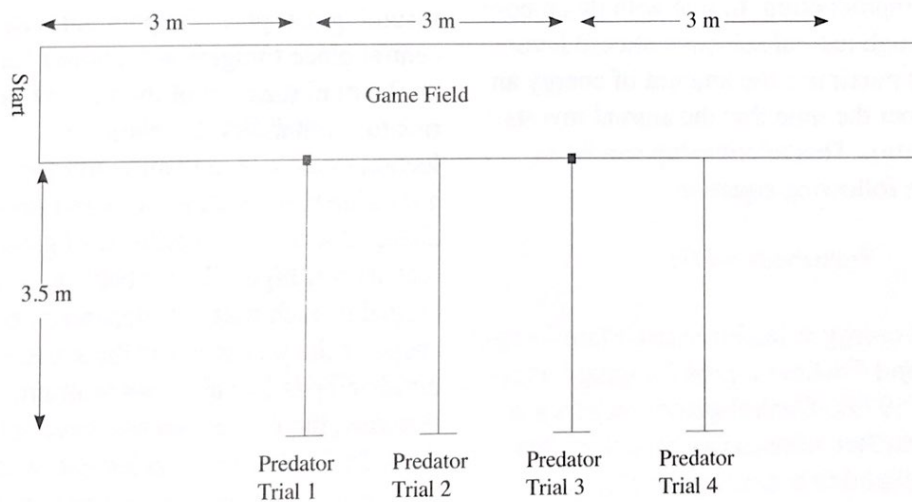
Game 1: Without Predation

1. The game involves 4 trials. It will be a relay in the same field used for the baseline data with the same 3 runners and timer measuring the total time of the relay.
2. There will be 3 blue balls (worth 8 points each) and 3 red balls (worth 5 points each) placed at various distances from the starting line as indicated in the figure below.
3. Each runner will run from the starting line and either take one blue or one red ball (not two) then return. Upon crossing the line, the next two runners in the relay will do the same in turn. Note: You cannot step outside the sidelines indicated by the ropes.
4. The timer will time from the start until the last member of the relay crosses the line and enter the data in Table 11.3. (Note: while filling out Table 11.3, be sure you know which group # you are. After you finish your data gathering, you will combine data with other groups to get a class data set.)
5. The goal of the game is to get the most number of points per relay time. (Note: it is not as simple as always taking the blue balls.)
6. Prior to each trial, take a few minutes to figure out your strategy for maximizing the points earned for the time invested.



Game 2 -- With Predation

1. Game 2 is exactly like game 1 with the exception that there will be a predator.
2. Each group will have a volunteer be the predator for a different group (e.g. group 1 will supply a predator for group 2 and group 2 will supply a predator for group 1, etc.).
3. Use the meter stick to make a predator line 3.5 m from the game field as shown in the diagram below.
4. The predator line will be placed the following distance from the start line in each trial as follows -- Trial 1 = 3 m, Trial 2 = 4.5 m, Trial 3 = 6 m, Trial 4 = 7.5 m.
5. The predator must stay behind the predator line until a runner touches a ball. Once a ball is touched the predator may try to tag the runner. If the runner is tagged, the runner gets no points for the ball, but the time will continue. As soon as a runner is tagged and crosses the end line, the next runner can leave. The predator must return to behind the predator line before attempting to tag the next runner. If a runner is tagged, tally the ball in the column for # of balls chosen even though you do not get points for it.
6. Note: The runner cannot step outside the game field. Neither the runner nor the predator can dive to evade or tag. The predator needs to be careful so that the runner is not injured.
7. Run the same 4 trials as in game 1: Trial 1 = red and blue at 3 m, Trial 2 = red at 3 m and blue at 6 m, Trial 3 = red at 3 m and blue at 9 m, Trial 4 = red at 6 m and blue at 9 m.
8. Record your data in Table 11.4 .



Background Information

Evolution through natural selection requires variation in some trait or behavior, heritability of that trait or behavior (i.e. genetic basis), and variable reproductive success associated with that trait or behavior. In today's lab, the model used will be based on foraging theory by central-place foragers. A central-place forager is an animal that moves out from a central place to select or capture food and then brings the food back to the central place to be ingested. Burrowing mammals like Prairie Dogs are good examples because they move out from a burrow and back to the same burrow while feeding. Beavers are also a good example because they move out from their pond to select trees then carry the trees back to the pond for food. Theoretically, animals are limited in their abilities to acquire energy through food (people are currently an exception because of our ability to grow and harvest; however, over evolutionary time, people's behaviors were likely derived when energy from food was limited.) Once basic demands of an animal are met, to maximize fitness, an animal should put remaining resources into reproduction. Thus, an animal that meets the basic necessities more efficiently will have more time and/or energy to allocate to reproduction. In line with this theory, evolution through natural selection should favor behaviors that maximize the amount of energy an animal gains per the time that the animal invests (i.e. profitability). This relationship can be expressed by the following equation:

$$\text{Profitability} = E/T;$$

where E = net energy gained from a certain foraging behavior and T = time for the foraging behavior (Schoener 1979). Central-place foragers are great to test whether animals use behaviors that maximize profitability because profitability of foraging items changes at greater distances from the central-place. Profitability for a central-place

forager can be estimated with the following equation:

$$\text{Profitability} = (E_{\text{total}} - E_{\text{travel}} - E_{\text{handle}}) / (T_{\text{travel}} + T_{\text{handle}});$$

where E_{total} = total energy gained, E_{travel} = energy lost due to moving to the food item and back and E_{handle} = energy lost due to *handling* the food item, T_{travel} = the travel time to the item and back, and T_{handle} = the time it takes to handle the food item. Since travel energy and time increases as the food items are farther away from the central place, overall net E/T changes for that food item as distance from the central place increases.

To see if you are smarter than a beaver in your selection of red versus blue balls, you must first calculate profitability. In this case profitability will be points/time instead of E/T . See the info box on "Theoretical Profitability" for information concerning the calculation.

When we add a predator, however, if a forager is killed and eaten by the predator, that forager can no longer reproduce at all. The relationship changes. Evolution through natural selection would not favor an animal that does not account for predation risk when selecting food items. Thus, a new model was produced assuming that potential prey animals that are central place foragers will choose food based on the minimization of the ratio of predation risk to profitability. In relation to our game, selection of a close red ball worth less points and a far blue ball worth more points should have changed when the likelihood of getting tagged (eaten) was high. The probability of getting tagged in each trial was dependent on the speed of the predator and the speed of the runner. For Trial 3 in all cases to minimize predation risk, the runners should have selected red balls. In Trials 2 and 4 selection of red or blue balls was dependent on the speed of the runner and the speed of the predator. In Trial 1 predation risk was the same for red and blue balls so the runners should have selected the balls with the higher profitability.

Exercise 11: Behavioral Ecology

Procedure 2

Background. The question for this lab is: Are you as smart as a beaver? To answer this question you will need information on how beavers respond under the same conditions as in your games. The two games were patterned after a study on beavers by Basey and Jenkins (1995).

1. Get onto the computer and access the article in the site for this class.
2. Read the *Introduction*, the first three paragraphs under *The models*, *Size distance experiments* in the Methods section, and look at Figure 4.
3. In the lab report, use the graph paper to make a figure similar to that of Figure 4 in Basey and Jenkins (1995).
4. Complete the lab report.

Theoretical Profitability

1. In games 1 and 2, you played a game similar to a situation that might confront a beaver. If you are smarter than a beaver, you should have used a strategy to maximize the net rate of points per time (i.e. profitability). To see if you are smarter than a beaver, calculate the profitability for red and blue balls in each trial. The best strategy is one that maximizes the theoretical points per time.
2. To calculate the theoretical profitability, simply take the points for a given ball (red = 5 and blue = 8), then figure out the distance of the ball from the starting line. Look at Table 11.1 to figure out the theoretical time for that distance, then simply do points/time.

For example, to calculate out the profitability for red and blue balls in trial 2 do the following. A red ball was worth 5 points so three red balls were worth 15 points. If you took only red balls, the profitability is 15 points divided by the relay time at 3 m in Table 11.1. For blue balls only, the total points for 3 balls is 24, so take 24 and divide by the relay time at 6 m in Table 11.1. To be smarter than a beaver, you theoretically should have selected the color of ball associated with the higher profitability.

If you used a different strategy such as a fast runner going 6 m to get a blue ball and a slow runner going 3 m to get a red ball, then you could estimate those theoretical times and use points/time for the theoretical profitability of that strategy.

3. Use Table 11.2 to calculate the theoretical profitability for red and blue balls in each trial. Then indicate the strategy (red or blue balls) that maximizes profitability in that trial under conditions of no predator.

Name: _____
 Instructor: _____
 Date: _____

On my honor, as a University of Colorado at Boulder student, I have neither given nor received unauthorized assistance on this assignment.
 Signature _____

Lab Report

Table 11.1. Baseline data on the time it takes to complete the relay at each distance.

Relay Distance (m)	Relay Time (s)
3	
6	
9	

Table 11.2. Theoretical profitability for each trial. See directions on how to fill out this table in the Theoretical Profitability info box. The theoretical prediction should be selection of the color of ball that maximizes theoretical profitability in that trial. In Trial 1 red and blue balls were both at 3 m. In Trial 2 red balls were again at 3 m while blue balls were at 6 m. For red balls the theoretical profitability will be the same in Trial 1 and Trial 2, while that for the blue balls will change.

Trial	Theoretical Points/Time Red	Theoretical Points/Time Blue	Theoretical prediction for selection (red or blue balls)
1			
2			
3			
4			

Table 11.3. Student selection of red and blue balls in each trial when there is no predation (Game 1).

Trial	Group	# of Red	# of Blue	Proportion Red*	Time (s)	Points/ Time
1	1					
	2					
	3					
	4					
	Mean					
2	1					
	2					
	3					
	4					
	Mean					
3	1					
	2					
	3					
	4					
	Mean					
4	1					
	2					
	3					
	4					
	Mean					

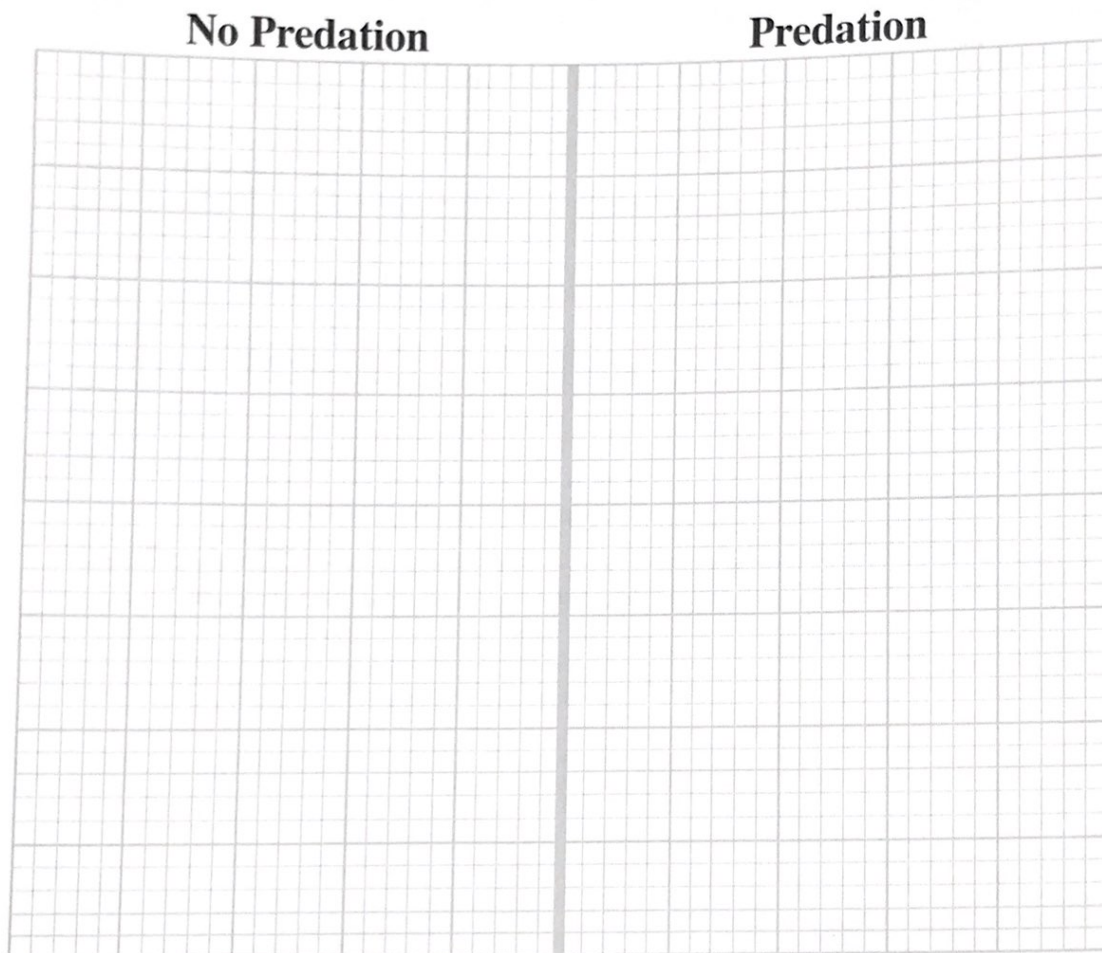
* To calculate the proportion of red use the following equation: # of red taken/3.

Table 11.4. Student selection of red and blue balls in each trial when there is predation (Game 2). In this scenario, students are expected to choose a strategy that minimizes the risk of predation/profitability.

Trial	Group	# of Red	# of Blue	Proportion Red*	Time (s)	Points/Time
1	1					
	2					
	3					
	4					
	Mean					
2	1					
	2					
	3					
	4					
	Mean					
3	1					
	2					
	3					
	4					
	Mean					
4	1					
	2					
	3					
	4					
	Mean					

* To calculate the proportion of red use the following equation: # of red taken/3.

On the graph paper below, make a graph that represents the proportion of red balls selected in relation to model predictions based on evolution through natural selection. Be sure to include each trial for the first set of experiments without predation and the second set of experiments with predation. A single y-axis will work for both graphs. (Hint: Examine Figure 4 in Basey and Jenkins (1995)). Don't forget axis titles, any necessary legends, and a figure caption below the figure. (2 pts.)



1. Write a brief interpretation of what the graph shows. (2 pts.)

2. Succinctly explain what profitability is and why evolution through natural selection should favor animals that behave in ways that maximize profitability. (3 pts.)

3. Are you smarter than a beaver? Compare and contrast the results of this study with those of the study of Basey and Jenkins (1995). (3 pts.)