BIOLOGY 1240: BIOLOGY LABORATORY
SPRING SEMESTER

OPTIMAL FORAGING I: THE THEORY

Optimal Foraging I: Theory

Introduction

Acquiring energy is a fundamental process for living systems. This process is, however, complicated for organisms that can choose among several prey items.

We will ask these questions:

1. What problems must a predator solve in order to consume its prey?
2. When presented with several types of prey, what is the best choice for a fish to make?
3. Can real fish make the correct choice?

Our study system will be guppies foraging on small invertebrates in small aquaria.

Optimal Foraging Background

Natural selection is one of the mechanisms by which evolution occurs. The logic of the argument is as follows: if a phenotype (e.g., body size) of an organism is inherited and confers higher fitness than the phenotype of a competitor, then the more fit individual will contribute genes to the next generation in a higher proportion than the less fit individual. After a sufficiently long time, we predict that the population will be composed primarily of individuals with the more fit phenotype.

Testing Natural Selection

The above statement is a verbal hypothesis. In order to test it, we must make a clear prediction which can be compared to observation. The prediction can be either qualitiative or quantitative, but the latter is especially powerful. To make a quantitative prediction, we need an equation that computes the predicted number to test for. In the case of body size, we would need an equation that predicts the size of organism that can contribute the most offspring to the next generation.

Natural Selection for Foraging Behavior

The theory of evolution by natural selection applies to any phenotype: morphological or behavioral. If natural selection is an important force, then we expect that many components of an organism's phenotype will be affected. This includes behavior such as the decisions a predator makes while foraging.

Here is the logic for our hypothesis about the evolution of foraging behavior.

- The number of offspring that an organism contributes to the next generation is related to the amount of energy that the organism has available for the production of eggs, caring for the young, and so on.
- The amount of energy an organism has for reproduction is related to the energy obtained through foraging.
- Foraging behavior is a hereditable trait.

- More efficient foragers will consume more prey and have more energy for reproduction. Inefficient foragers will produce relatively fewer offspring.
- *Therefore, natural selection, if it is important for these traits, will cause populations to be dominated by organisms that are efficient foragers.*

Efficient Foraging

The last point above is our main scientific hypothesis. We now need to describe what we mean by efficient foraging. We know from our previous exposure to the Holling disc equation that most predators (e.g., blind-folded humans) require some time to consume and digest each prey item attacked. We saw that handling time causes the rate of prey consumed to level off at high prey densities. When the handling time is significant and prey density is high, more prey in the environment will not permit the predator to consume at a higher rate.

We hypothesized that energy acquired through foraging translates into energy available for reproduction. More energy for reproduction means more offspring will be produced. Since organisms must spend time and energy in many activities (e.g., avoiding predators, foraging, mating, caring for young, etc.) a reasonable working hypothesis is that the **rate** of energy acquisition (net energy gained ÷ time spent foraging) is a reasonable index of the ability of the organism to contribute to the next generation. The faster an organism gathers energy, the more time and energy will be available for other important activities.

With this idea, we now need an equation that makes a quantitative prediction. Before we do this, however, we'll see if you are as smart as a fish and can find the foraging behavior which will maximize your energy acquisition rate.

Mini-quiz:

1. *What is the biological definition of fitness? How is it measured?*
2. *What is an adaptation? Give an example.*
3. *What is an optimal solution? Is it the same as maximizing a quantity? Why or why not?*
4. *Is a male peacock's tail adaptive? Why? Are there circumstances when it might not be adaptive?*
5. *Why are many flowers brightly colored? Is this an adaptation? Why?*
6. *Is human behavior adaptive? How? For example,*
   - *"binge drinking" among college students (not here of course!).*
   - *"altruism": e.g., saving the life of a stranger*
7. *Why is equating energy acquisition rate with reproductive potential only an approximation?*

Humans as Predators: Are People as Smart as Guppies?

In this exercise we will gain an intuitive grasp for some of the problems foragers have by becoming a forager ourselves. Alas, we will not be eating hamburgers or peanuts, rather we will be searching for and "consuming" sandpaper discs attached to a board. True, these aren't very nutritious, but they are easy to manipulate.

The Question

We have two inter-related questions:

1. **Which of two foraging strategies provides the most energy to the predator?** I.e., which is the optimal strategy?
2. **Is the same strategy optimal at all prey densities?**

The two foraging strategies are:

1. **Strategy A:** Consume both prey as they are encountered.
2. **Strategy B:** Consume only the most profitable prey.

Experimental Design

We will have two **treatments**: foraging strategy and prey density. We will examine two types of each of the two treatments. This design will give us four different experiments as follows:

1. Strategy A at high prey density (60 prey of two different profitabilities: "60:60")
2. Strategy A at low prey density (10 prey of two different profitabilities: "10:10")
3. Strategy B at high prey density (60:60)
4. Strategy B at low prey density (10:10)

Each bench will **replicate** each of the experiments twice. So in total we will do 8 predator-prey simulations. To reduce the number of boards and discs, we will share boards among benches. When you have done all the replicates with the board initially at your bench (either 10:10 or 60:60) swap with a bench that has a board with the other density.

Materials

1. a large styrofoam board
2. sandpaper discs (1 inch diameter) thumb-tacked to the board. Some have a number on them.
   (a) The discs with "1" represent prey with the highest **profitability** (i.e., energy content ÷ handling time).
   (b) The blank discs represent prey with the lowest profitability.
3. 1 timer (stop watch or count-down timer)
4. 2 event counters
5. a data sheet to record your results

Student Assignments

Each group of students assigned by the teacher will work as a team with the following assignments for each students.

1. One student will be the designated predator for all of the experiments.
2. A second student will call out to the predator “one!” when the predator captures a disc labeled “1” and will click the event counter to keep a running total of the “1” discs captured by the predator.
3. A third student will call out to the predator “blank!” when the predator captures a blank disc and will click the event counter to keep a running total of the blank discs captured by the predator.
4. The fourth student will use the timer to time the 60-second foraging bout. In addition, for the low prey density experiments (10:10), this student will move each disc captured to a new random location after the predator leaves the prey and continues searching. This action is not required at the high density treatments.

Protocol

The predator will **NOT** remove the discs from the board. Leave the discs on the board and follow the rules given below.

1. Examine the board at your bench and make sure that the discs are evenly distributed. Make sure that equal numbers of the “1” and blank discs are randomly spaced on each of the quarters of the board. Count the discs.
2. Blind-fold the predator and rotate the board so that he or she will not remember the placement of the prey on the board.
3. **Predator Behavior:**
    (a) tap on the board vertically with your finger. Sliding the finger around once on the board is very serious cheating. If no prey is found at the tip of the finger, the predator lifts his finger and tries again.
    (b) **Hold** your finger on the disc until informed of its identity (“blank” or ”one”) by one of the students with an event counter. This should happen immediately after you stop at the disc.
    (c) if you encountered a 1-disc, immediately continue searching. This represents a handling time of 0.5 seconds. Do NOT remove the disc from the board.
    (d) if you encountered a blank disc, count out a handling time of 5 seconds by reciting “one-one-thousand, two-one-thousand, three-one-thousand, etc.” This represents a handling time of 5 seconds. Try to be consistent and accurate. Do NOT remove the disc from the board.
    (e) Repeat the above until informed by the fourth student that 60 seconds have elapsed.
4. **Student Counter of 1-discs**

   (a) If experiment is Strategy A or B: When the predator stops on a 1-disc, say "one" immediately and click the counter

5. **Student Counter blank discs**
   (a) If experiment is Strategy A: When the predator stops on a blank disc, say "blank" immediately and click the counter
   (b) If experiment is Strategy B: When the predator stops on a blank disc, say "blank" and DO NOT click the counter (the predator is ignoring blanks).

6. **Timer**
   (a) At the beginning of each bout, remind the predator on the rules for the current bout. I.e.,
      - If bout is Strategy A: "if you hit a 1-disc, continue to search immediately, if a blank disc, count 5 seconds."
      - If bout is Strategy B: "if you hit either a 1-disc or a blank disc, continue to search immediately (ignore blanks and very short handling time for 1-disc)."

   (b) Start the timer and tell predator to begin.
   (c) If the experiment is the low density (10:10), after the predator encounters a prey, move it to a new location. This is to prevent the predator from memorizing the prey locations. This is NOT necessary at high density (60:60).
   (d) When 60 seconds has elapsed on the timer, stop the bout.

Data to Record

After each 1-minute foraging bout, record the following data on your data sheet (distributed during lab):

1. the number of blank discs captured
2. the number of "1" discs captured
3. the total energy gained during the foraging bout (i.e., num_1-disce_1+num_blank disce_2, where the energy contents are listed on the data sheet)

After the two replicates for a treatment are completed, record the average in the last column.

Foraging Parameters to Use

For the homework, use the following values for your calculations. Note especially v, which we will need later.

"1" disc	e_1	14 Kcal
	T_{h1}	0.5 sec
"blank" disc	e_2	18 Kcal
	T_{h2}	2 sec
	v	28.0

Conclusions

Before returning to the whole lab discussion, your group should write down answers to these questions:

1. If you could choose to eat just one type of food, which of the two would it be?
2. Was the best the strategy the same regardless of prey density? If not, why did density change things?

Data Sheet for Sandpaper Disc Experiments

Density ("1":blank)	Strategy	# Prey Taken ("1")	# Prey Taken (blank)	Energy of 1 "1"	Energy of 1 blank	T_h "1"	T_h blank	Total Energy	Mean Energy
60:60	Both			14	18	0.5	2		
60:60	Both			14	18	0.5	2		
60:60	Ones		—	14	—	0.5	—		
60:60	Ones		—	14	—	0.5	—		
10:10	Both			14	18	0.5	2		
10:10	Both			14	18	0.5	2		
10:10	Ones		—	14	—	0.5	—		
10:10	Ones		—	14	—	0.5	—		

Summary of Class Data by Bench

Density	Strategy	1	2	3	4	5	6	Mean (Energy/minute)
10:10	Both							
	Ones							
60:60	Both							
	Ones							

Optimally Foraging Fish

After foraging on sandpaper discs, you now have a better appreciation for the problems a fish faces. Primarily, these are: what should I eat? and how often should I eat it? Now we want to see if we can predict what a fish will do so that we may test if fish are foraging optimally in accordance with our hypothesis that natural selection acts on foraging behavior.

Maximize: Energy Per Time

The equations we will produce are based on a situation very much like the game we just played with the discs. We consider a predator that is capable of moving significantly faster than its prey. The predator completely consumes a single prey item before resuming foraging. There is a measurable search and handling time associated with each prey item consumed. The prey are randomly placed in space (not in patches). The 2 types of prey differ by their energy content and the time required for the predator to handle them after capture. We wish to determine the best method by which the predator should consume them in order to maximize the predator's fitness.

Profitability of a food type*: The energy content of a food item divided by the time to handle the food item.*

As we discussed above, we will assume that a predator's fitness will be related to the rate of energy acquisition or: energy/time $f = E/T$, where E is the **net** energy gained from a single prey item and T is the total time required to consume 1 prey item. We now need an equation for f in terms of the behavior of the predator. To solve this problem, we will calculate energy/time in two steps. First, we will calculate the denominator in terms of (t). Second, we will calculate the numerator. When E is divided by T we will have energy/time. Finally, we will use the equation to predict the optimal foraging strategy for the predator.

Analogy: *You are buying a car and must choose between two types. You want to buy the fastest of the two and ask the dealers for the results of their speed test. One dealer says his car can go 1 mile (distance only). The second dealer says his car took 2 minutes (time only). Neither value answers your question. You need to know the ratio of the distance traveled and time taken.*

Time Spent Foraging = Search + Handling

When foraging, a predator spends time either searching for prey or consuming and handling the captured prey. In symbols, for a single prey type

$$\text{time/item} = T = T_s + T_h \tag{1}$$

where T_h is the handling time which can be measured directly or calculated by the functional response (remember the Holling disc equation lab). T_s, as the search time, is more difficult. We know from previous work with the Holling disc equation for the Type II functional response that as the density of prey increases, the total search time decreases. We can measure T_s directly if we wished, but it is time consuming to do so. Instead, we will simplify by assuming that search time is proportional to the inverse of the prey density. Mathematically, this verbal assumption is equivalent to:

$$T_s = v(1/n) \tag{2}$$

where n is prey density and v is the constant of proportionality. This makes sense: as the density increases so does the chance that a predator will be near a prey item, and this will shorten the distance to travel for a capture. From your board and disc exercise, you have the data needed to check this assumption, if you wish. We have verified that this approximation is valid for the fish you will be using.

Three Strategies for Time

There are three strategies for a predator with 2 possible prey types: (1) eat only type 1, (2) eat only type 2, (3) eat both type 1 and 2 according to their proportion in the environment. Which is best?

Since there are only 3 possibilities, a simple approach is to calculate the rate of energy return (E/T) for all 3 and then compare to determine which one gives the largest rate of energy return. First, we do the time per prey item (T). Later, we'll do the energy gained (E).

Strategy 1: (*eat only type 1*)

$$\text{time/item} = T_1 = v/n_1 + T_{h1} \tag{3}$$

Strategy 2: (*eat only type 2*)

$$\text{time/item} = T_2 = v/n_2 + T_{h2} \tag{4}$$

Strategy 3: (*eat types 1 and 2*)

$$\text{time/item} = T_{12} = \underbrace{\frac{v}{n_1 + n_2}}_{\text{search time}} + \underbrace{\left[T_{h1}\frac{n_1}{n_1 + n_2} + T_{h2}\frac{n_2}{n_1 + n_2}\right]}_{\text{handling time}} \tag{5}$$

Equations 3 and 4 are search times plus handling times for prey type 1 and 2, respectively.
In Equation 5, the term on the right in brackets gives the average handling time per prey when the predator encounters both prey randomly. To calculate this, we weight the handling time for prey 1 by the fraction of the total number of prey that is prey 1 (i.e., $n_1/(n_1 + n_2)$). We weight the handling time of prey 2 in a similar way.
In Equation 5, the other term on the right is the search time when both prey are present ($n_1 + n_2$). Remember: $T_s = v/n$ and in this case $n = n_1 + n_2$.
This concludes the equation for the denominator (T) in the equation for energy/time: E/T. Now we will do the numerator E in the equation for energy per time: E/T.

Energy Per Item = Gain - Loss

Next, we do the net energy gained for each prey item consumed. Here we use a simple energy budget approach; it's just like humans: net energy at the end of the day is equal to the number of tofu shakes consumed for breakfast minus energy expended in walking to class minus energy used taking notes minus energy used finding sandpaper discs in biology lab, and so on.

The energy balance is the same for fish predators: net energy is energy input obtained from the prey consumed minus the energy output expended while foraging. For a single prey type, this is:

$$\begin{aligned} \underbrace{E}_{\text{net energy}} &= \underbrace{e}_{\text{prey energy}} - \underbrace{e_s T_s}_{\text{search energy}} - \underbrace{e_h T_h}_{\text{handling energy}} \\ &= e - e_s v/n - e_h T_h \end{aligned}$$

where E is the net energy gained, e is the total energy per prey item, e_s is the energy cost of searching for one time unit, n is the density of prey (remember: $T_s = v/n$), e_h is the energy cost of 1 time unit of prey handling, and T_h is the handling time for 1 prey item.

This is too complicated, so let's make the simplifying assumption that the energy costs of searching and handling are negligible (i.e., $e_s = 0$ and $e_h = 0$). In other words, the predator expends no **energy** while searching or while eating its prey. This not only makes the equation simpler, but it is justifiable for the fish we will be using. Fish are not like cheetahs that use a lot of energy in long stalks, long fast pursuits, and energetically costly kills. Fish float around, make one quick strike and then inhale the prey more or less in one bite.

Three Strategies for Energy

The energy costs of the three strategies are
Strategy 1: (*eat only type 1*)

$$E_1 = e_1 \tag{6}$$

Strategy 2: (*eat only type 2*)

$$E_2 = e_2 \tag{7}$$

Strategy 3: (*eat types 1 and 2*)

$$E_{12} = e_1 \frac{n_1}{n_1 + n_2} + e_2 \frac{n_2}{n_1 + n_2} \tag{8}$$

The fraction $n_1/(n_1 + n_2)$ weights the energy from a single prey 1 item according to how common that food type is in the environment. Same for prey 2 and how common it is.

Simplify

This is hard to read, so let's make it clearer by letting N be the total prey available for both types:

$$N = n_1 + n_2 \tag{9}$$

Now Strategy 3 is:

$$E_{12} = \underbrace{e_1 \frac{n_1}{N} + e_2 \frac{n_2}{N}}_{\text{2 prey energy}} \tag{10}$$

Energy/Time = Energy/item ÷ Time/item

Now we put the net energy per item equation together with the time per item equation by dividing the former by the latter for each strategy. When considering only one prey type, the ratio of energy to time is fundamental concept.
Using the concept of profitability, we can calculate value of three different strategies: (1) eat only food type 1, (2) eat only food type 2, and (3) eat both type 1 and type 2.
Strategy 1:

$$\frac{E_1}{T_1} = \frac{\text{EQN 6}}{\text{EQN 3}} = \frac{e_1}{\frac{v}{n_1} + T_{h1}} = \frac{e_1 n_1}{v + T_{h1} n_1} \tag{11}$$

Strategy 2:

$$\frac{E_2}{T_2} = \frac{\text{EQN 7}}{\text{EQN 4}} = \frac{e_2}{\frac{v}{n_2} + T_{h2}} = \frac{e_2 n_2}{v + T_{h2} n_2} \tag{12}$$

Strategy 3:

$$\frac{E_{12}}{T_{12}} = \frac{\text{EQN 8}}{\text{EQN 5}} = \frac{e_1 \frac{n_1}{N} + e_2 \frac{n_2}{N}}{\frac{v}{N} + \left[T_{h1} \frac{n_1}{N} + T_{h2} \frac{n_2}{N}\right]} \tag{13}$$

After multiplying top and bottom by N, this simplifies to

$$\frac{E_{12}}{T_{12}} = \frac{e_1 n_1 + e_2 n_2}{v + T_{h1} n_1 + T_{h2} n_2} \tag{14}$$

The final equations are:

$$\frac{E_1}{T_1} = \frac{e_1 n_1}{v + T_{h1} n_1} \tag{15}$$

$$\frac{E_2}{T_2} = \frac{e_2 n_2}{v + T_{h2} n_2} \tag{16}$$

$$\frac{E_{12}}{T_{12}} = \frac{e_1 n_1 + e_2 n_2}{v + T_{h1} n_1 + T_{h2} n_2} \tag{17}$$

Graphing the Equations

The above equations tell us the average **energy intake rate (E/T)** that a predator will experience if it forages by one of the three strategies. But, we still haven't answered the question: What is the optimal strategy?

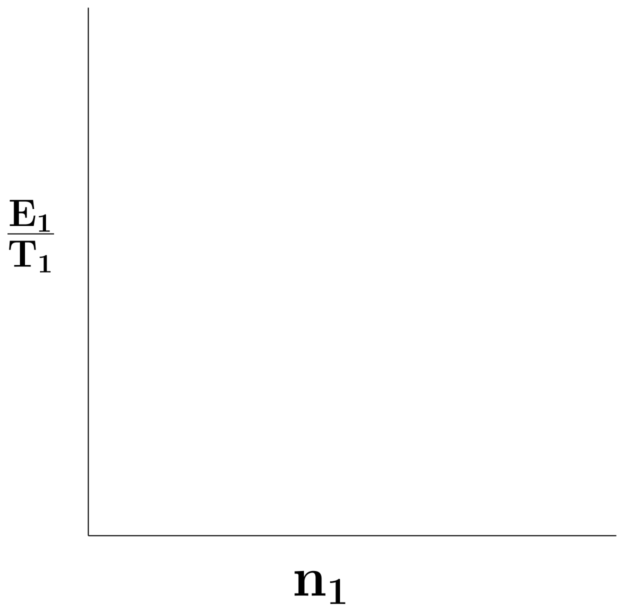
The optimal strategy is the one that gives the largest E/T, but the rate depends on handling time, search time, and prey density. How does the optimum change with these quantities? Which of these quantities should we examine?

We could examine either v or T_h. We know that the answer will change with these values. But, they aren't the most *interesting* ones to study, because they are more or less constant properties of the organisms. We really can't manipulate these because they are presumably evolved characteristics that are part of the phenotype of the predator. The densities of the prey, however, are much more variable in nature, not part of the phenotype of the predator, and are a quantity we can easily manipulate in the laboratory. So, this is a good candidate for our *independent variable.*

To make a testable prediction, we plot E/T for each strategy against the density of the most profitable prey. On the next page, work in your group to answer the questions and graph the equations.

Class Exercise: Graph Strategy 1 and Strategy 3. Assume n_1 is the independent variable and $n_2 = n_1$.

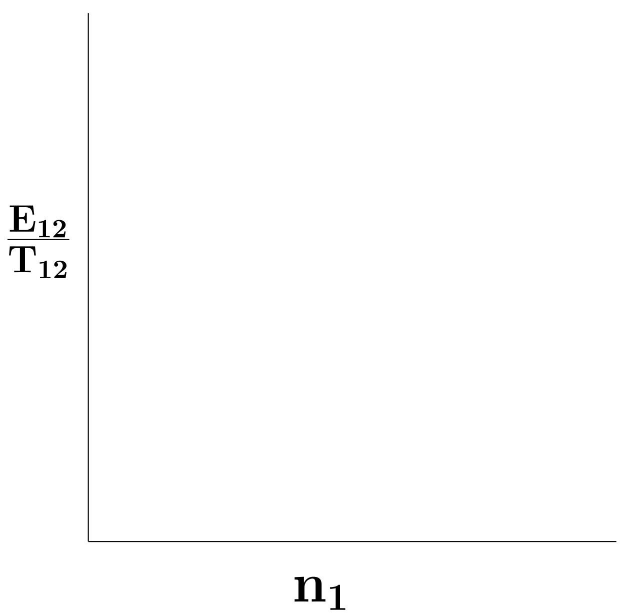
Strategy 1



$\frac{E_1}{T_1} = \frac{e_1 n_1}{v + T_{h1} n_1}$

- What is the value of the equation when n_1 is 0.0?
- What is the equation approximately when n_1 is not 0.0, but is very small ($n_1 \ll v$)?
- What is the value of the equation when n_1 is very, very large?

Strategy 3



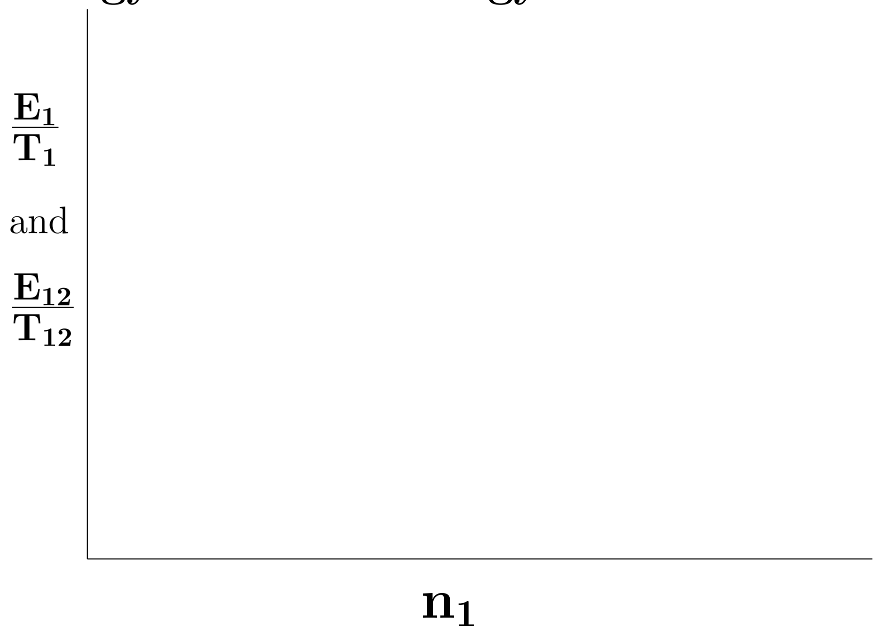
$$\frac{E_{12}}{T_{12}} = \frac{e_1 n_1 + e_2 n_2}{v + T_{h1} n_1 + T_{h2} n_2}$$

- What is the value of the equation when n_1 is 0.0?
- What is the equation approximately when n_1 is not 0.0, but is very small ($n_1 \ll v$)?
- What is the value of the equation when n_1 is very, very large?

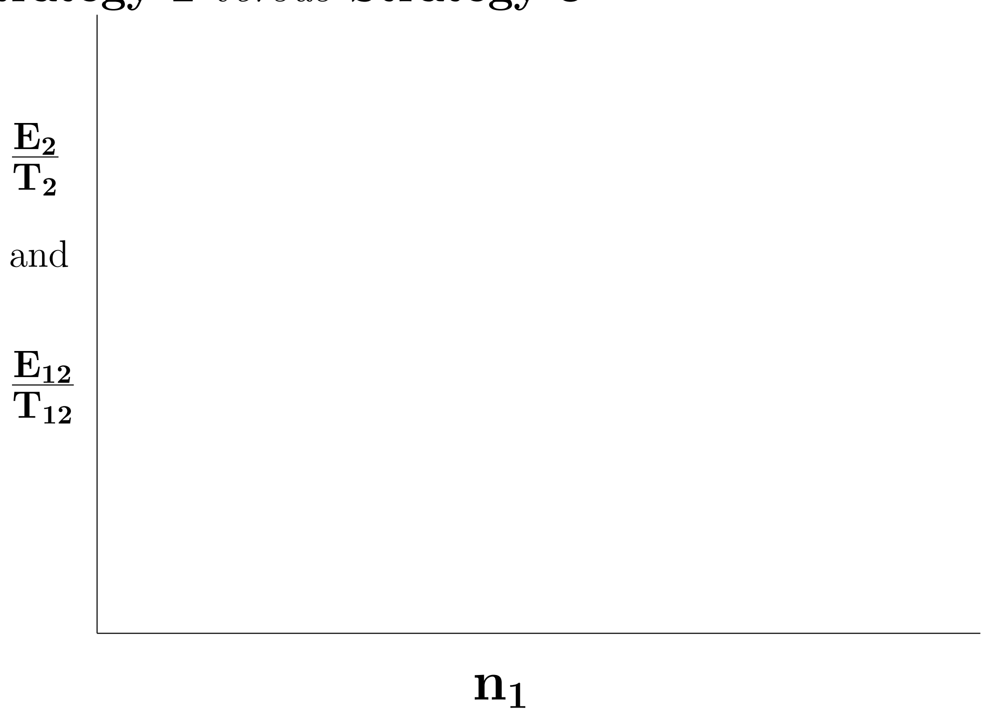
Could the two curves cross?

The Strategies Compared:

Strategy 1 *versus* **Strategy 3**



Strategy 2 *versus* **Strategy 3**



In the Juicy Hamburger versus Bag of Peanuts scenario, what was Strategy 2?

Measuring the Handling Time of Guppies

Energy and Search Time

Our predictions are based on the hypothesis that fish are optimal foragers. We will now test this hypothesis by comparing the theoretical expectation with the actual behavior of fish. The equations, however, require information we currently do not have. We need to know the energy content of prey (e), the handling time (T_h), and the search time (T_s). The energy content of living organisms is difficult to measure, and we will not attempt to do that here. The quantities are, however, of great interest to ecologists, and we will use published values. Search time, as stated above, is related to v/density, where v is a constant of proportionality. This parameter varies with predator and prey type. We will provide you with estimates for each of the possible prey that you might be using in the experiments. Handling time, however, is a quantity we can measure and we will do that next.

Handling Time

In this experiment, we will estimate the predator's average handling times per prey item. The fish predator we will use is the common guppy, *Poecilia reticulata* (Poeciliidae).

The prey will either by the Great Salt Lake brine shrimp: *Artemia salina* (Artemiidae), or *Daphnia*.

Your instructor will point out the location in the lab of the two organisms. The fish to use will be in an aquarium labeled **HUNGRY FISH**. Don't confuse this aquarium with the one labeled **FED FISH**.

You are about to perform a behavioral experiment with these organisms. As a result, if you mishandle your study organisms, they will not perform well. You must handle them gently and avoid sudden movements when you are taking data. The fish startle easily.

Also remember that we must use these same organisms in subsequent labs, so please do not injure them. When you have made the necessary observations, carefully return them to the aquarium labeled **FED FISH**.

PLEASE DO NOT return them to the container from which you collected them.

Materials

At each group bench, you will find

1. Stop watches
2. Disposable plastic pipettes and small beakers for collecting, transferring and holding the prey.
3. A cotton-meshed net for capturing and transporting the fish
4. A small aquarium to serve as a foraging arena for measuring individual fish handling time.

At the side bench of the lab, you will find

1. Two containers of *Artemia* or *Daphnia* sorted into 2 size classes.
2. One or more aquaria of fish about 30–35mm in length that have been starved for 2 days (**HUNGRY FISH**).
3. An aquarium initially empty labeled **FED FISH** into which you will put the fish you have used in a trial

Protocol

The procedure is as follows.

1. From the containers on the side of the lab, use a pipette to gently remove about 6 individuals of the prey from each container and put them in separate, labeled beakers with a small volume of water.

2. From one of the aquaria holding the unused fish, gently net and remove a guppy and transfer it to a small beaker of water to carry it to your bench. Gently pour the water and fish into the large section of test aquarium at your bench. Let the guppy acclimate to the arena for 5–10 minutes. The fish should be calmly swimming.

   If your guppy does not calm down in 10 minutes, get a new one, and place the stressed one in the used fish container.

3. When the guppy is calm, one student will carefully pipette 1 (and only 1) prey item into the arena.

4. With the stop watches, two other students will measure the *handling time* of the guppy after the prey item is pipetted into the arena. Handling time is the time from the attack of the prey (first contact) to the time the prey is swallowed. If the attack is unsuccessful, continue timing the foraging bout to include the second chase and recapture time.

   Normally, the handling time will be very short for the small prey size (¡ 1 second) and longer for larger prey. Your group should pick the students to be timers who have good reaction time and hand-eye coordination.

   Use the average of the two times.

   Practice with the stop watches before the first trial until you have mastered its use.

5. With the same guppy, repeat this procedure 4–5 times with the same size of prey.

   If the guppy stops feeding, put the satiated or stressed-out guppy in the aquarium labeled FED FISH, and get a new guppy.

6. Repeat the above steps with the other size of prey.

Record your measurements of handling time (T_h) in the data sheet supplied on the day of the lab; you will need these numbers for the next experiment.

Data Sheets for Fish Handling Time Experiment

Our prey species was (circle one): *Daphnia* *Artemia*

Prey Characteristics

Species	Caloric Content (Kcal/gm)	Size (mm)	Dry wt (μgm)	Calories per item (e)	v	Predicted Crossover Density
Daphnia	5.5	1.0	108		32	
		2.0	371			
Artemia	6.73	6–8	76		3.26	
		>10	488			

Group T_h: Handling Time in seconds

REPLICATE	Small Prey	Large Prey
1		
2		
3		
Mean T_h (seconds)		
Energy Content (from above table)		
e/T_h		

Class T_h: Handling Time in seconds

BENCH	Small Prey	Large Prey
1		
2		
3		
4		
5		
6		
Mean T_h (seconds)		
Energy Content (from above table)		
e/T_h		