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OPTIMAL FORAGING MODELS

In collaboration with David N. Bonter

Objectives

- Develop a spreadsheet model of foraging choices among two prey types, prey 1 and prey 2.
- Determine the conditions in which individuals should be specialists (consume either prey 1 or prey 2) or generalists (consume both prey types).

INTRODUCTION

What are you going to eat for lunch today? Your choices may be many or few, depending on how far you are from various restaurants, how much change you have in your pocket, or whether you packed a lunch from home. The decision of what to eat for most animals is not a matter of luxury, but of survival, and the decisions that organisms make in their selection of food can be strongly shaped by natural selection. Costs and benefits are ultimately calculated in terms of Darwinian fitness (survival and reproduction). In this exercise, we use energy gained from foraging as a surrogate measure of fitness.

Let's suppose that you are enjoying a snack consisting of peanuts (prey 1, still in their shell) and popcorn (prey 2, already popped). Let's further suppose that you are very, very hungry. Which food item will you choose to eat first? When will you stop eating the first food item and switch to the second? Ecologists think about the choices animals make in terms of economic **profitabilities**. Each food item has a benefit associated with it if consumed: energy (E). Each item also has a cost, which includes the time it takes to manipulate the food so that it can be consumed (called **handling time**, h). The "profitability" of a particular food item is E/h.

Should you eat the peanuts or popcorn? Peanuts have more energy per unit than the popcorn, but their handling time can be quite large, especially if the nuts are tightly closed. You, the predator, should eat the peanuts when:

$$E_{\text{peanuts}}/h_{\text{peanuts}} > E_{\text{popcorn}}/h_{\text{popcorn}} \qquad \text{Equation 1}$$

At the beginning of your snack, this is likely to be true. You simply find the peanuts that are cracked half-open, which have lower handling times and can be consumed fairly quickly. Spending time eating popcorn means that you'll be missing the opportunity to consume the more energetically profitable peanuts. But this may not continue to be the case. When should you start eating popcorn? When the gain from eating popcorn is greater than the gain from rejecting the popcorn and searching for the more profitable peanuts. That is, you should eat popcorn when

$$E_{\text{popcorn}} / h_{\text{popcorn}} > E_{\text{peanuts}} / h_{\text{peanuts}} \qquad \text{Equation 2}$$

Even if the search times were equal, you might switch to popcorn when you get to the last of the peanuts, where the nuts that are so tightly sealed that the handling time becomes enormous, sending the profitability of peanuts spiraling downward.

With this analogy in mind, in this exercise we will develop an optimal foraging model for two prey types. We will predict when a predator will specialize in the more profitable prey type, and when it will become a generalist and consume either prey type when encountered. Assuming that we can measure prey value, that handling times are fixed, that prey are recognized instantaneously, and that prey are encountered randomly, we can make a few predictions. First, the most valuable prey item will never be ignored. Second, the lower value prey will be ignored until

$$E_{\text{lower value}}/h_{\text{lower value}} > E_{\text{higher value}}/h_{\text{higher value}}$$

This simple ecological model suggests that foragers should make decisions that "optimize" their energy gain. Our model makes several assumptions in addition to those mentioned above: a single predator has only two choices of prey items; fitness is related to energy gain; and the predator can make "informed" decisions about whether to consume or bypass an encountered prey item.

Specialists and Generalists

In addition to handling time (h), prey **availability** (λ) may be added into the foraging cost portion of Equations 1 and 2. Prey availability ranges between 0 and 1, and the search time is defined as $1/\lambda$ (Figure 1). When the more profitable prey type is common ($\lambda \sim 1$), the search time is low and the predator wastes little energy locating the more profitable prey type. In such cases, it never pays to miss an opportunity to consume that prey type by spending time and energy pursuing or handling the less profitable prey. But as the more profitable prey item becomes less available ($\lambda < 1$), and search time increases nonlinearly. That is, even when E/h remains constant over time, decreasing availability (λ) leads the overall value of the prey to decline. Equation 3 shows how profitability (E/h) is modified to include both search and handling time costs:

$$\frac{E}{\frac{1}{\lambda} + h} \qquad \text{Equation 3}$$

which can also be written as

$$\frac{\lambda E}{1 + \lambda h}$$

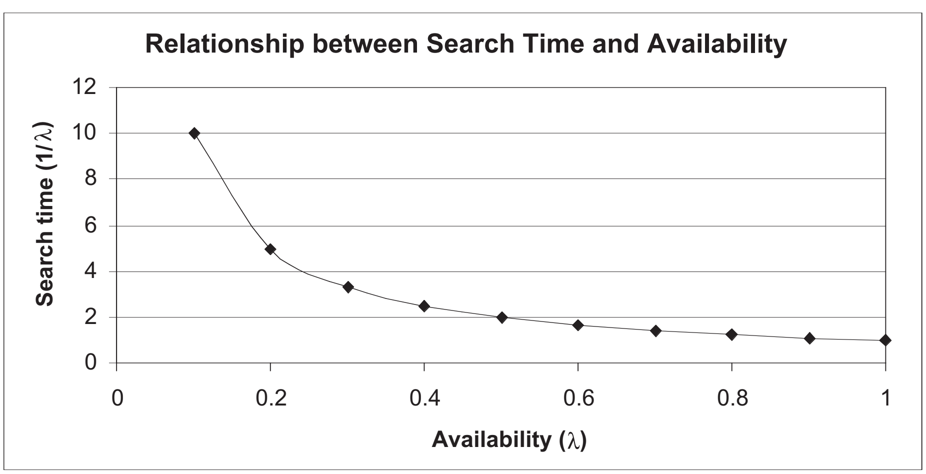

Figure 1 Search time is inversely related to prey availability. When availability is 0, search time is infinite.

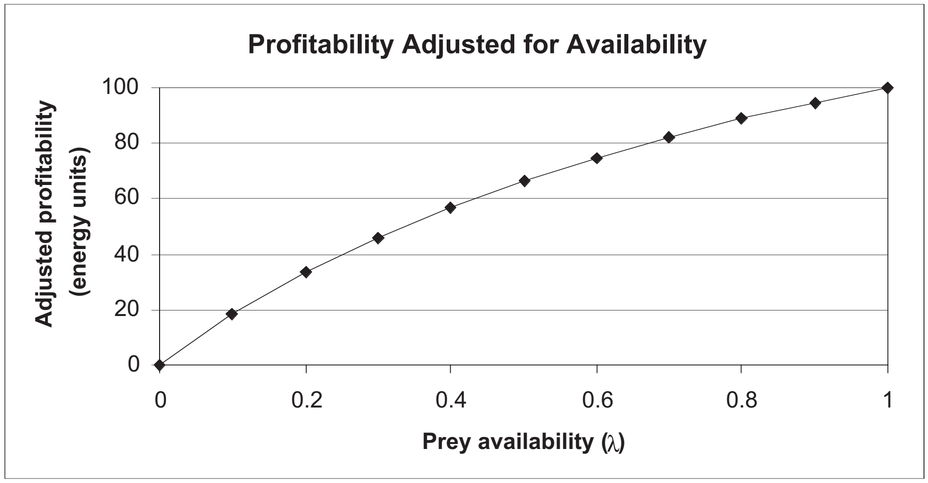

Figure 2 Profitability of a prey item after being adjusted for both handling time (h) and availability (λ) as shown by Equation 3. In this example, we set $E = 200$ and $h = 1$ to illustrate how adjusted profitability decreases sharply as prey availability decreases. This graph would differ if the values of E and h were changed.

if we multiply both the numerator and the denominator by λ. We can see that as availablity (λ) declines in Equation 3, the denominator increases, and profitability declines in a nonlinear manner (Figure 2). Even when $\lambda = 1$, profitability (E/h). is downwardly adusted to included energy involved with locating prey (i.e., search time).

As the more profitable prey type becomes rare, a point is reached where profitabilities of both prey types become roughly equivalent. Consuming the lesser quality prey will provide as much energetic benefit as spending time and searching for the remaining highly profitable items. In order to maximize energy gain per unit time, the predator will specialize on prey type 1 if

$$\frac{\lambda_1 E_1}{1+\lambda_1 h_1} > \frac{\lambda_1 E_1 + \lambda_2 E_2}{1+\lambda_1 h_1 + \lambda_2 h_2} \qquad \text{Equation 4}$$

That is, energetic gain from specializing on prey type 1 alone is greater than that from foraging on both prey types. As long as this inequality is true, the predator will ignore prey 2 and specialize on prey 1. At some point, the decreasing availability of prey 1 will force a change in foraging strategy, and our predator will become a generalist and consume either prey type it encounters. Figure 3 shows that the energetic value of foraging exclusively on prey 1 is higher than generalizing (consuming both prey types) until approximately the sixtieth encounter. At this point, the left side of Equation 4 is no longer greater than the right side. If the predator stays and continues to forage in the habitat patch, it will eventually deplete both prey types as the energy gained per unit time foraging steadily diminishes.

Optimal foraging models lead to a number of predictions (Begon et al. 1986):

- Predators with short handling times compared to search times are likely to be generalists. If the time lost handling less profitable prey items is small, the predator will consume the less profitable prey while continuing to search for preferred prey. Fish consuming aquatic insects may be an example. Once the prey item is located, time spent pursuing, subduing, and consuming the prey is negligible; the largest energetic costs are in finding the prey (search time), and any prey that are located are readily consumed.
- Predators with large handling times relative to search times should be specialists. A large carnivore (a lion, for example) may have negligible search times. Their potential prey (ungulates on an African savannah) are usually all around them. However, catching the prey—the handling time—is energetically expen-

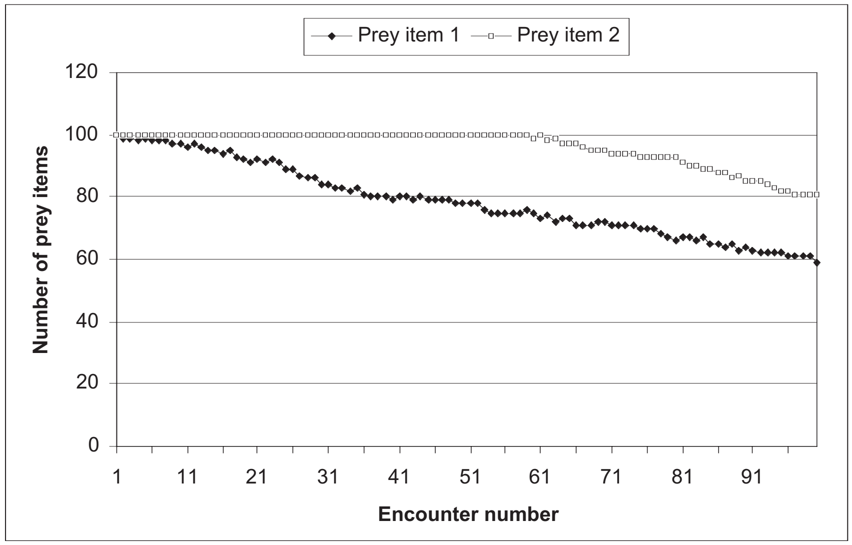

Figure 3 Here, a predator encounters prey types 1 and 2 and either consumes or bypasses them. The energetic value of foraging exclusively on prey 1 is higher than generalizing (consuming both prey types) until just shy of the sixtieth encounter. The overall reward of foraging diminishes as the more valuable prey type is depleted, and then as both prey types are depleted.

sive and often unsuccessful. Therefore, lions typically specialize in those prey items that are easier to handle (i.e., young, old, or sick individuals).

- Predators in unproductive environments are more likely to be generalists than predators in productive environments, as search times are likely to be high. On the other hand, when prey densities are high in a productive environment, the predator will benefit from specialization, as search times are negligible.
- Predators should specialize when profitable food types are common, and generalize when profitable items are rare.
- Predators should discriminate when the differences in profitabilities are great and be indiscriminate when the differences in profitabilities are negligible.

PROCEDURES

In this exercise, we'll see how these predictions are developed mathematically by modeling the conditions under which our energy-maximizing predator should be a specialist or a generalist. As always, save your work frequently to disk.

INSTRUCTIONS

ANNOTATION

A. Set up the model populations.

1. Open a new spreadsheet and set up column headings as shown in Figure 4.

	A	B	C	D	E
1	***Optimal Foraging***		**Handling**	**Initial**	**Current**
2	**Prey**	**Energy (*E*)**	**time (*h*)**	**profitability (*E*/*h*)**	**availability (λ)**
3	1	400	3		
4	2	50	1		
5		**Number prey 1 =>**	100	100	**<== Initial prey 1**
6		**Number prey 2 =>**	100	100	**<== Initial prey 2**
7		**Total prey =>**			

Figure 4

2. Enter **100** in cells C5–D6.

Let's assume that our predator is foraging in a patch that initially consists of 100 items of prey 1 and 100 items of prey 2. The initial numbers are given in cells D5–D6, and represent the number of each prey present before our forager enters a patch. The current number of prey items is given in cells C5 and C6. The values in cells C5–C6 will decrease as our forager consumes prey.

3. In cell C7, **SUM** the total prey in the patch.

Enter the formula **=SUM(C5:C6)** in cell C7.

4. Enter **400** in cell B3 and **50** in cell B4, and enter **3** in cell C3 and **1** in cell C4.

We need to establish the energy and handling times of each prey type. **In this model, prey 1 will always be more profitable than prey 2.** Let's assume that prey 1 has an energy of 400 calories/individual, and prey 2 has 50 calories/individual. Let's assume, like the peanuts and popcorn, that prey 1 has a slightly larger handling time (3 seconds vs. 1 second) than prey 2.

5. In cells D3 and D4, calculate initial profitability for each prey type.

Enter the formula **=B3/C3** in cell D3.
Enter the formula **=B4/C4** in cell D4.
Profitability is E/h for each prey type. (This profitability is not adjusted for availability.)

6. In cell E3 and E4, calculate the current availabilities (λ) of prey 1 and prey 2.

Enter the formula **=C5/($D$5+$D$6)** in cell E3.
Enter the formula **=C6/($D$5+$D$6)** in cell E4.
The availability λ (type the letter 'l' and change the font to Symbol) is the proportion of current prey type out of the total initial prey.

B. Determine a foraging strategy.

Now we are ready to determine which prey type should be eaten. Since prey 1 is more profitable than prey 2, the choices are whether to consume only prey 1 or to consume both prey 1 and prey 2.

1. Set up new column headings as shown in Figure 5.

	A	B	C
9	Which prey should be consumed?		
10	Prey 1	Either prey	Behavior
11			
12	Select prey	1	
13		.	

Figure 5

2. In cells A11 and B11, enter formulae based on Equation 4 to calculate the energy gain from specializing or generalizing.

Enter the formula **=(E3*B3)/(1+E3*C3)** in cell A11.
Enter the formula **=(E3*B3+E4*B4)/(1+E3*C3+E4*C4)** in cell B11.
Recall from Equation 4 that, in order to maximize energy per unit time, the predator specialize on prey type 1 if

$$\frac{\lambda_1 E_1}{1+\lambda_1 h_1} > \frac{\lambda_1 E_1 + \lambda_2 E_2}{1+\lambda_1 h_1 + \lambda_2 h_2}$$

If this inequality is true (the left side of the equation is indeed greater than the right side of the equation), only prey 1 should be consumed. Otherwise, both prey items should be consumed. This equation suggests that there can be a swift switch from being a specialist to being a generalist.

3. In cell C11, enter a formula to determine whether a predator should be a specialist on prey type 1, or a generalist.

In cell C11, enter the formula **=IF(A11>B11,"specialist","generalist")**.
This formula uses an **IF** function to return either the word "specialist" or the word "generalist." The C11 formula examines cell A11. If the value is greater than the value in cell B11, the inequality is true and the predator should specialize on prey type 1; otherwise it should be a generalist. (Given your initial conditions, a specialist strategy should be adopted.)

4. In cell B12 and B13, indicate which prey items will be selected given the foraging strategy employed.

In cell B12, enter the value **1** (because prey item 1 will *always* be taken, whether the predator is a specialist or not).
In cell B13, enter the formula **=IF(C11="generalist",2,".")**.
If only prey 1 is selected, we want the number 1 to appear in cell B12 and a missing value (a period) to appear in cell B13. If both prey are selected, we want the number 1 to appear in cell B12 and the number 2 to appear in cell B13. The **IF** statement in cell B13 returns the value 2 if the forager can consume both prey types, and returns a missing value if the forager is a specialist. Make sure your spreadsheet is working correctly by changing the energy associated with prey 1 (cell B3) from 400 to 200 calories per individual, and press F9 to see your results. Although prey 1 is still more profitable than prey 2, it is now economically most cost effective to consume both prey types, and this should be reflected in cells A11–B13. When you are finished, reset cell B3 to 400.

C. Simulate foraging decisions over time.

Now we'll set up a simulation to see what happens and what kinds of foraging decisions are made as the food in the patch is consumed. Assuming that our predator enters a patch with 100 items of prey 1 and 100 items of prey 2, it should consume prey 1 and bypass prey 2. The forager's first encounter is listed as Encounter X in cell A16.

	A	B	C	D	E	F
15	**Encounter**	**Prey**	**Selected?**	**Prey 1**	**Prey 2**	**Consumed**
16	x	2	no	100	100	0
17						
18						
19						
20	**Encounter**	**Prey**	**Selected?**	**Prey 1**	**Prey 2**	**Consumed**

Figure 6

1. Set up new column headings as shown in Figure 6.

Which prey our forager encounters is given in cell B16, and depends on prey availability, λ. The encounter number will change over time as our predator continues to forage. Cell C15 indicates whether the encountered prey was consumed or bypassed, and cells D16 and E16 indicate how many prey remain in the patch. If the encountered prey was pursued, the energy gained associated with the prey is given in cell F16.

2. In cell B16, enter an **IF** formula to specify whether the forager encounters prey 1 or prey 2.

Enter the formula **=IF(RAND()<C5/C7,$A$3,$A$4)** in cell B16.
This formula simply states that prey items are encountered according to their current proportions in the patch. If the random number (the **RAND()** portion of the formula) is less than the current proportion of prey 1, then the organism encounters prey 1, otherwise it encounters prey 2.

3. In cell C16, enter a formula to determine whether the prey encountered was consumed.

Enter the formula **=IF(OR(B16=$B$12,B16=$B$13),"yes","no")** in cell C16.
Now, although both prey 1 and prey 2 may be encountered, a prudent predator will bypass prey 2, since prey 1 is more profitable. Cell C16 returns the word "yes" if the prey encountered was consumed, and "no" if the prey was bypassed. It is an **IF** formula with an **OR** formula embedded in it. The **OR** portion of the formula—**OR(B16=$B$12,B16=$B$13)—**returns the value "true" if *any* of the arguments specified are true. Thus, if B16 = B12 *or* B16 = B13, the formula returns the value "true." Because the **OR** statement is embedded in an **IF** statement, the spreadsheet returns the word "yes" if either of the **OR** conditions is met, and "no" if neither condition is met.

4. In cells D16 and E16, adjust the number of each prey type remaining in the

Enter the formula **=IF(B16=1,$C$5-1,$C$5)** in cell D16.
Enter the formula **=IF(AND(B16=2,C16="yes"),$C$6-1,$C$6)** in cell E16.
The formulae in cells D16 and E16 reflect a decrease in number of prey 1 and prey 2,

patch (which depends on the decisions of the forager).

respectively, based on whether individuals of each type were consumed. The D16 formula is another **IF** formula: If cell B16 = 1, we know that prey item 1 was selected, so the total number of prey 1 is reduced by 1. The E16 formula is an **IF** formula with an **AND** formula embedded. In this case, cell B16 (the prey encountered) must equal 2 *and* cell C16 must equal "yes" in order for prey 2 to be depleted. Make sure these formulas are working correctly by pressing F9 several times. When prey item 1 is encountered, it should be selected and the total number of prey 1 should be reduced to 99 individuals. If prey 2 is encountered, it should be bypassed and the total number of prey 2 should remain at 100 individuals.

5. In cell F16, enter a formula to calculate the energy gained from a prey item, given that the prey item was selected and consumed.

Enter the formula **=IF(C16="no",0,IF(B16=1,B3,B4))** in cell F16.
This formula tells the spreadsheet to examine cell C16. If cell C16 has the word "no" in it, return a 0; otherwise, run through the second **IF** statement, **IF(B16=1,B3,B4**). If the prey encountered was prey 1, the energy consumed is given in cell B3. Otherwise, prey item 2 was selected and the energy consumed is given in cell B4.

6. Save your work.

D. Write a macro to simulate foraging over time.

Now we are ready to let our predator continue their foraging in the patch, encountering prey 1 and prey 2 according to their availabilities, which change as the predator forages. The best way to simulate our predator's behavior is to record a macro that repeats the steps in row 16 several times, keeping track of the total number of prey 1 and prey 2 left in the patch.

1. Set up a linear series from 1 to 100 in cells A21–A120.

Enter the number **1** in cell A21.
Enter the formula **=1+A21** in cell A22. Copy this formula down to cell A120.

2. Copy cells B16–F16, and paste the values into cells B21–F21.

You've already simulated the first encounter, so simply paste the values you obtained into the row associated with encounter 1 (when pasting, select Edit | Paste Special | Paste Values). Now you are ready for encounter 2.

3. Set the calculation key to manual.

From the menu, open Tools | Options | Calculation and select Manual.

4. Record a macro to simulate encounters 2–100.

Bring your spreadsheet macro program into record mode and assign a name and shortcut key. Your macro should repeat the steps in row 16 several times, keeping track of the total number of prey 1 and prey 2 left in the patch. Record the following steps in your macro:

- Press F9, to obtain a new random number that will generate which prey type is encountered by the predator.
- Highlight cells B16–F16 and select Edit |Copy.
- Highlight cell B20, then go to Edit | Find. Select Search by Columns (not by rows). Leave the Find What box empty and select Find Next, then Close. Cell B22 should be highlighted.
- Select Edit | Paste Special | Paste Values (not the formulas) and select OK.
- Select cell D16–E16, then select Edit | Copy.
- Highlight cell C5, then select Edit | Paste Special | Paste Values. Make sure to select the Transpose option.
- Stop recording.

Now when you press your shortcut key 99 times you should be able to see how the our predators' foraging decisions changed over the course of time.

5. (Optional) Edit your macro using the Visual Basic code.

You can edit Excel's Visual Basic Editor code to avoid pressing the shortcut key 99 times. Push <Alt>+<F8> and select `Edit`; the code should appear. After the first line, simply enter the code **`For counter = 1 to 100`** in the first line of your program. The word `Calculate` should now be the second line of code. At the end of your program, before the words `End Sub` appear, type in a new line of code that reads **`Next`**. Now when you press your shortcut key just once, the macro will repeat 100 times.

6. Save your work.

E. Create graphs.

1. Graph the prey items remaining as a function of encounter number.

Use the line graph option and label your axes fully. Your graph should resemble Figure 7.

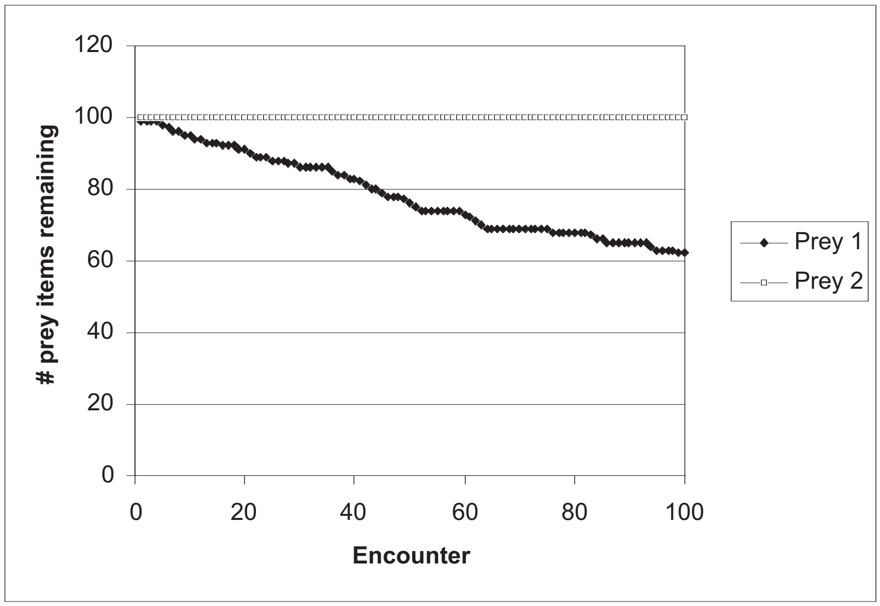

Figure 7

QUESTIONS

1. Interpret the results of your model. Did the forager specialize or generalize? Why?
2. Assuming your answer from Question 1 was "specialize," the forager must have bypassed several food items of the non-preferred prey. What is a major assumption of the model (not explicit in the model) regarding the metabolic costs of our forager while bypassing prey item 2?
3. Change the energy for prey 2 to 75 units (cell B4). Erase your macro results (cells B21–F120), and reset your initial prey abundances to 100 (cells C5–D6). Run your macro again. Interpret your results. Did the forager specialize or generalize? At what point did a change in behavior occur? Why?
4. Examine the availability λ as your simulation progressed. Why does the availability change as the simulation proceeds? How would availability (cells E3 and E4) change if one prey type were very rare, but highly profitable? Set the initial number of prey 1 to 10 individuals (cells C5–D5), and the initial number of prey 2 to 100 individuals (cells C6–D6). How are these differences reflected in availability? In the encounter probability (cell B16)? As prey is consumed, how do these values change?

5. Critically consider some assumptions of this model. Are energy content, handling time and prey availability the only factors that influence foraging decisions? Name other factors.
6. Which parameters drive the outcome of the model most: handling time, energy, or the initial prey availability? Run several trials that vary in 1 parameter (e.g., handling time) while keeping the other two parameters constant. Repeat for the other two parameters. Set up column headings so that you can track your results, and present your results graphically.

LITERATURE CITED

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