

Chapter 5. Optimal Foraging².

Today's activities:

1. Discuss Dussault et al. 2005
2. Work through the marginal value exercise
3. Discuss our data analysis

What you should get out of today's class:

You should understand the concept of optimality, in particular how it relates to foraging, but also that it may relate to many other problems as well. You should understand the graphical illustration of the problem, including why the giving-up time occurs where it does. Also, you should see that some questions can be answered by setting up artificial systems that you can control.

Handouts:

1. Chapter 7. Energy and Water.
2. Stephenson, N. L. 1990. Climatic control of vegetation distribution: the role of the water balance. *American Naturalist* 135:649-670.

Introduction

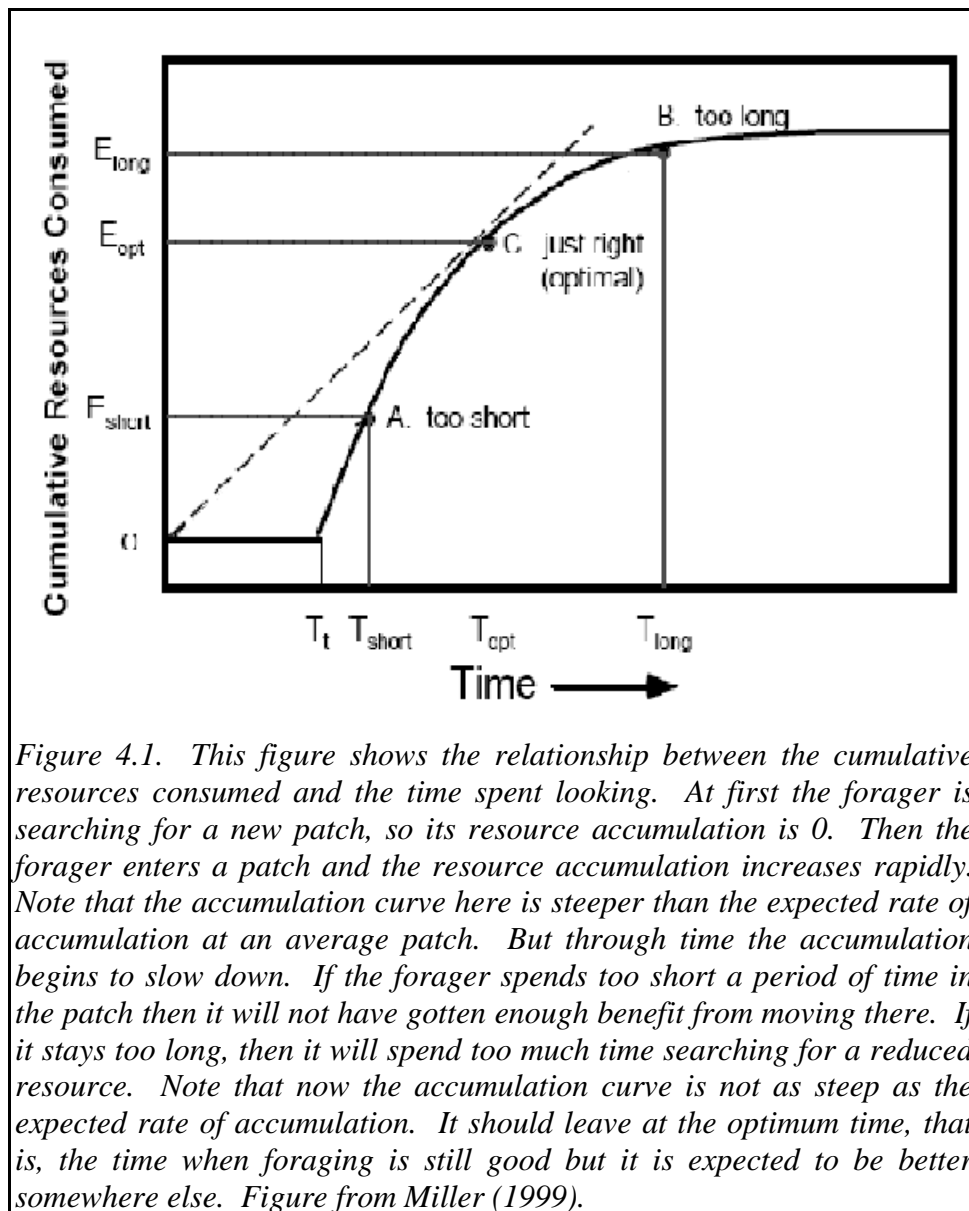
Animals foraging in the wild have to make many decisions about where to look for food and which food to select. Although we do not know what is going through the mind of a deer, we know there are several considerations in its food selection. Is the food nutritious? Does the food have defensive mechanisms making it difficult to eat (think cactus, poison ivy)? Is the food located near a mountain lion den? Are there 15 other deer eating that food already? Should the forager consume just one special type of food (i.e., be a specialist) or should it eat a wide variety of things (i.e., be a generalist)? These types of questions have led ecologists to develop several theories about what foraging animals *ought* to do in the wild. The theories are all based on the notion of **optimality**, wherein the choice made by a forager has greater rewards and fewer costs than the other possible choices.

There are three main theories under the optimal foraging umbrella: (a) diet-width or prey-switching (MacArthur and Pianka 1966), (b) the marginal value theorem or giving-up time (Charnov 1976), and (c) ideal-free distributions.

Diet-breadth theory is about which type of prey should be selected. It develops the notion that a prey type is optimal if the net energy yielded from capturing the prey, relative to the time it took to capture the prey, is maximized. If the predator chooses suboptimal prey, then it spends too much time and gets too little food or its effort. The marginal value theory is about how long a forager should stay foraging in a patch. As a forager spends more time in a patch, the resource becomes less dense, and it takes longer and longer to find more food. The marginal value theory explains how organisms should give up on certain patches and move to a new patch in order to optimize the amount of food obtained. And lastly, the ideal-free distribution is about how foragers should choose patches of resources depending on how many competitors are already using that resource.

2 The concept for this lab was derived from Miller (1999).

Today we will be focusing on the marginal value theorem (MVT, Charnov 1976). The MVT describes how animals forage in patches. A **patch** is a discrete unit of area that contains a resource such as food, potential mates, or perhaps nesting material. Patches usually differ in **quality**; some contain more resource than others. For example, a bee searching for nectar may go to a meadow (a patch) that has 10 flowers per square meter or to another meadow with 65 flowers per square meter. In addition, **patch density**, the number of patches per area, may vary through space. Through time, foragers choose to stay in a given patch or move to a new patch. The problem for a forager is that any given patch only has so much food in it (such as flowers with nectar, acorns, or mice). Because the forager effectively lowers the amount of food through time, the forager is forced to switch to another patch when the food seems too sparse to bother with. Of course, the forager does not know whether the next patch will have as much food as the one it currently is in. Also, it will take some time to travel to another patch, so the forager gives up good foraging time to switch patches. Hence, moving from patch to patch is a **cost**, and the forager must decide how to maximize the rate of food acquisition given this cost.



In the MVT, a forager should switch patches when the expected rate of food acquisition in a new patch (this is the rate that would be obtained in an average patch), minus the cost of moving to that new patch, exceed the rate of food acquisition in the current patch (Figure 4.1). The point where the forager should switch is called the **giving-up time** (GUT). Again, this suggests that the choice to switch patches is an optimality problem – switch only when you expect it to be better in the next patch. In Figure 4.1, time is on the x -axis and total energy gained is on the y -axis. Thus, the slope of a line on the graph has units "energy per time", E/t , which is the rate of energy gain. A smart forager will maximize that rate. You can see that the rate of resources consumed (E/t) is highest at point C on the graph. That is because the dashed line connecting the origin with point C has a steeper slope than the dashed lines going through points A or B. Visually you can see that switching at the marginal value (point C) maximizes E/t .

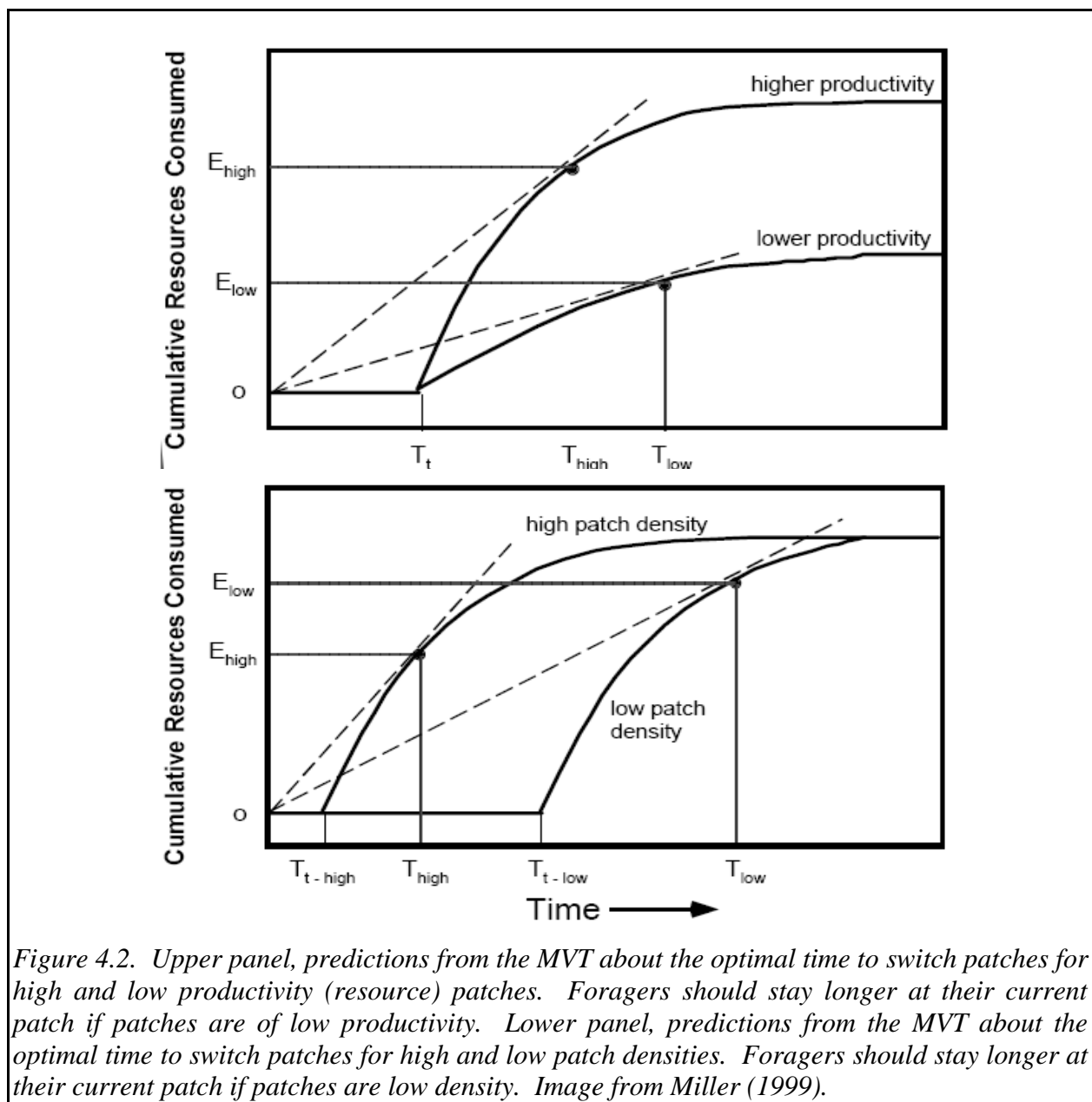


Figure 4.2. Upper panel, predictions from the MVT about the optimal time to switch patches for high and low productivity (resource) patches. Foragers should stay longer at their current patch if patches are of low productivity. Lower panel, predictions from the MVT about the optimal time to switch patches for high and low patch densities. Foragers should stay longer at their current patch if patches are low density. Image from Miller (1999).

From this basic construct a few predictions can be made. If it so happened that productivity was high (i.e., resource availability was high), a forager would be predicted to stay for a shorter period of time than if productivity was low, because the rate of accumulation would drop below the expected rate at an average patch more quickly (Figure 4.2 top). Or, if the distance between patches was relatively long (low patch density), the forager might be expected to stay longer, because the cost of moving has gone up and thus it takes longer to reach the giving-up time (Figure 4.2 bottom).

Of course, wild animals do not know about the MVT, and they do not have graphs and calculators to help them decide when to give up on a patch. But it appears that natural selection has led many organisms to develop a sense of resource acquisition rates that allow them to make a switch between patches at optimal times.

It could be argued that humans are foraging for various things all the time. We forage for food in our refrigerator, for the perfect pair of jeans, a great place to live, and for mates. We also forage for money that we can use to forage for other things. Today we will forage for beans in an effort to test some of the predictions of the MVT. We will forage for beans in buckets of rice, recording data on time and amount of resources consumed. We will do this for three different levels of patch productivity (i.e., density of beans) and observe our foraging decisions and calculate the GUTs of our system.

Hypotheses

1. High-resource buckets (lots of beans) will have marginal values that are reached sooner than in the low-resource buckets (not so many beans).
2. Students will forage optimally by switching between buckets near the GUT.

Materials

- buckets with rice and beans
- chopsticks or spoons
- prey cup for each bucket
- stopwatch
- data sheet
- graph paper
- pencil

Data Collection Methods

1. You will work in teams of three (a forager, a timer, and a recorder), switching until everyone has done each job once. The forager's job is to attempt to forage optimally. That is, the forager should try to recognize when the prey capture rate is going down and switch to the next bucket at the right time.
2. First, the forager should forage in the bucket marked "Average Density" to get a feel for the process.
3. Then start one of the runs. Travel (walk don't run) to one of the buckets in your bucket group and start foraging. Use only one hand, and your spoon or chopsticks only!, to search for beans. When you find a bean, raise up your hand and shout "found one!". This adds time to your prey capture that mimics handling time of real prey. It also gives your teammates a chance to record the time.

4. Place all found beans in the cup and leave that cup at that bucket so that the beans can be returned to the mix for the next round.
5. Move on to the next bucket, and do not revisit any buckets.
6. The recorder should make note of the start and end times, the time that a bucket is reached and then vacated, and the time at which each bean was found, using the data sheet.

Data Analysis Methods

1. Our goal in this analysis is to estimate the GUT for each run and compare them. So we need to draw out graphs for each run like the ones in Figures 4.1 and 4.2, but we will put all three buckets in sequence on one graph.
2. Write out a time scale that makes sense given your data, and then determine the number of beans accumulated at each time step and plot that number. Include the time it took to reach the bucket. There will be 0 accumulation until the forager reaches the bucket. Then you should see a rapid increase followed by a slowing down of the rate of capture until the person leaves for the next bucket. Continuing on that graph, reset to 0 captures and work through the next two buckets.
3. Draw a line from the starting point (either time = 0 or when leaving the previous bucket) to the accumulation curve so that the line just touches the curve (see Figure 4.2). This point of contact is the GUT. Do this for all the curves. You can estimate the GUT by drawing a line straight down to the x-axis and reading off the time. Do this by hand, estimating x's and y's from your graph. Calculate the GUT for each bucket and write your values in Table 4.1.

Table 4.1. GUTs for bean foraging.

<i>Low bean density</i>	<i>Medium bean density</i>	<i>High bean density</i>

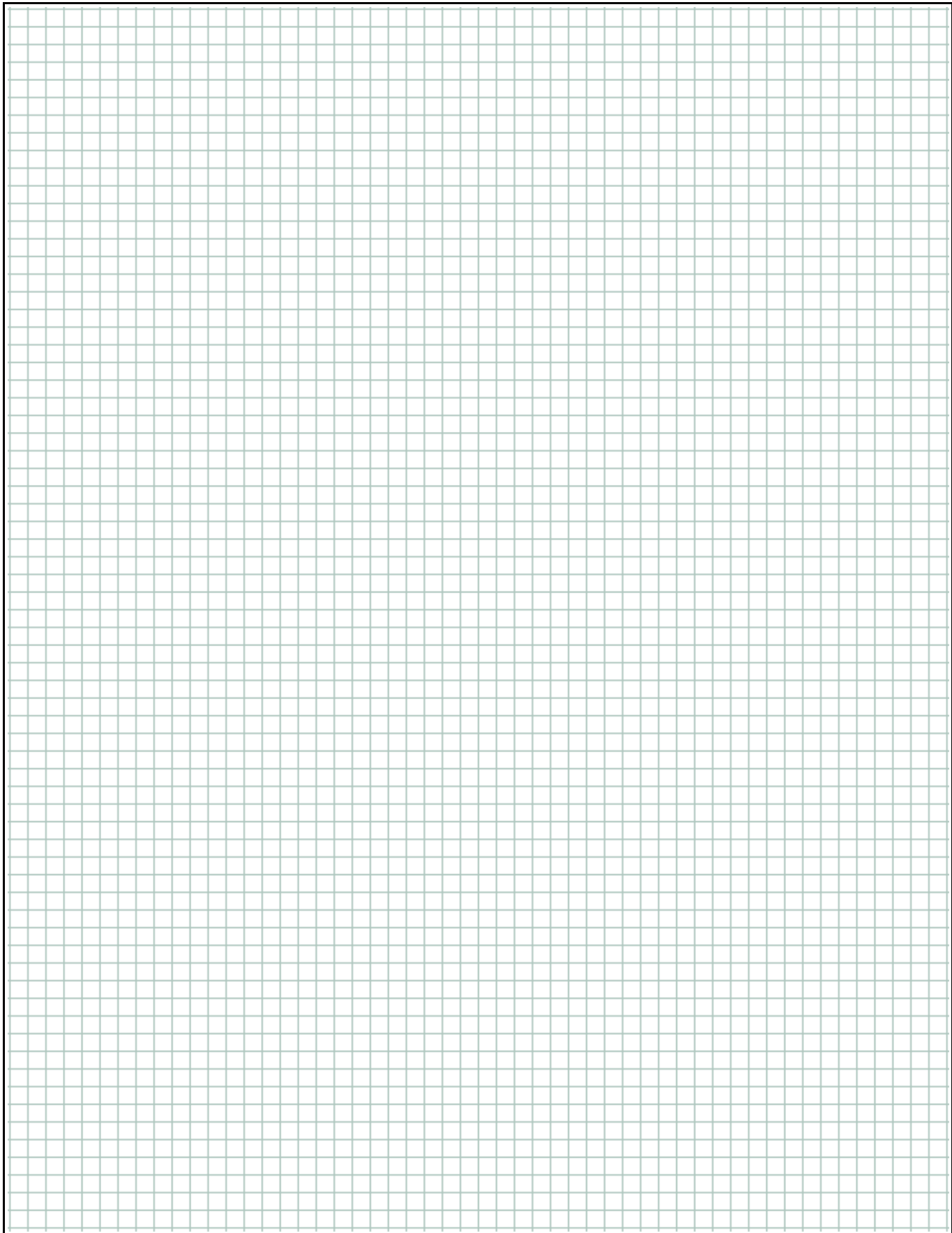
Questions

1. Were the GUTs higher for the higher productivity buckets (greater bean density) than the lower productivity buckets? Were you predicted to leave earlier? Did you?
2. Were the GUTs higher for the higher density buckets (greater bucket density) than the lower density buckets? Were you predicted to leave earlier? Did you?

3. What is the general relationship between a GUT and the steepness of the accumulation rate slope.

Literature Cited

- Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* 9:129-136.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603-609.
- Miller, T. E. 1999. Optimal foraging: Balancing costs and rewards in making foraging decisions. Pages 188-205, *in* Tested studies for laboratory teaching, Volume 20 (S. J. Karcher, Editor). Proceedings of the 20th Workshop/Conference of the Association for Biology Laboratory Education (ABLE), 399 pages.



Data sheet for bean foraging.

Bucket Id:		Bucket Id:		Bucket Id:	
Arrival Time		Arrival Time:		Arrival Time:	
Prey 1	21	Prey 1	21	Prey 1	21
2	22	2	22	2	22
3	23	3	23	3	23
4	24	4	24	4	24
5	25	5	25	5	25
6	26	6	26	6	26
7	27	7	27	7	27
8	28	8	28	8	28
9	29	9	29	9	29
10	30	10	30	10	30
11	31	11	31	11	31
12	32	12	32	12	32
13	33	13	33	13	33
14	34	14	34	14	34
15	35	15	35	15	35
16	36	16	36	16	36
17	37	17	37	17	37
18	38	18	38	18	38
19	39	19	39	19	39
20	40	20	40	20	40
Leave time:		Leave time:		Leave time:	

Homework # 5 – Questions about Stephenson 1990 (10 points).

Reading: Stephenson, N. L. 1990. Climatic control of vegetation distribution: the role of the water balance. *American Naturalist* 135:649-670.

Read the article and answer the following questions. Just write your answers out by hand on this piece of paper. You may have to read ahead through the next chapter.

1. Define AET and PET in your own words.
2. Study Figure 3. Does the climate in New Mexico jive with what is shown in the graph? How so?
3. Write out a simple, mathematical formula for water deficit and surplus, using the terminology given in this paper?
4. What is the significance of the temporal offset of water and energy availability for plants?