POW #6 **Due Tuesday, December 11**

Foraging For Food or "Do Bees Know Calculus?"

Foraging animals have an important problem to solve when their food supply is found in clusters or patches (acorns under trees, flowers growing in patches, worms in apples, etc). The problem is that, while food is easy to collect food when they first begin searching a new area, as the animal continues feeding, food becomes more and more difficult to find. Consequently, the foraging animal must search longer and longer for each additional morsel. At some point, the animal must decide to leave this patch and seek another, where food will be easier to find. However, it takes time to find and travel to the next patch, and the animal gains no food while it is traveling.

The choice about how long to stop for a feeding is one of the basic decisions for an organism that is searching for resources among widely scattered patches. Foraging animals have a classic max-min problem to solve. What is the optimal "giving up time" (when an organism should leave a patch that it is exploiting). When should the animal say enough is enough and move on to find the next patch? One crucial parameter that governs this decision is the travel time between patches.

For our example, we will consider a bee foraging for pollen on flowers that are dispersed across a yard. It gathers pollen rapidly when it first arrives at a new plant, but then finds it more difficult to pick up additional pollen. At some point, the bee must decide when to leave for "greener pastures". Figure 1 illustrates the consequences of this choice.

Suppose it takes 5 seconds to travel between flowers and the pollen collection function is

$$C(t)=\begin{cases}0 \text{ if } t<5\\ 30-30e^{-0.2(t-5)} \text{ if } t\geq 5.\end{cases}$$

Figure 1 illustrates the difference in total pollen accumulation in a 40 second period if the bee forages for 5 seconds before moving on and foraging for 15 seconds before moving on.

Notice the total amount accumulated in a 40 second period is greater for 5 second foraging (about 76 μg) than for 15 second foraging (about 58 μg).

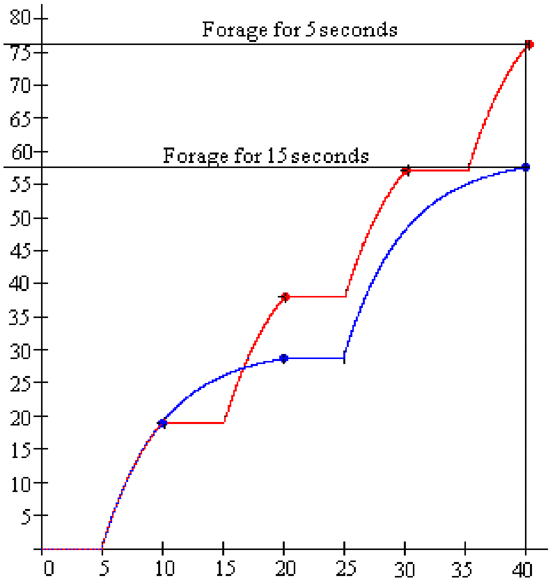
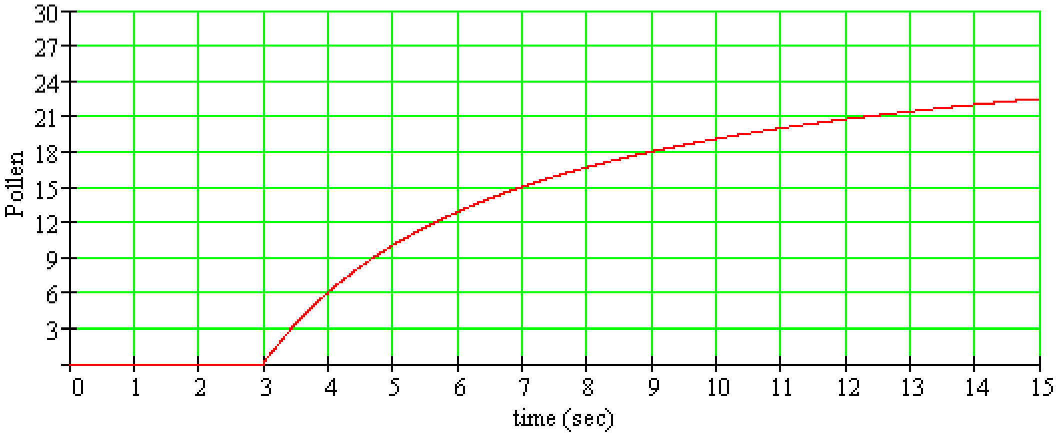
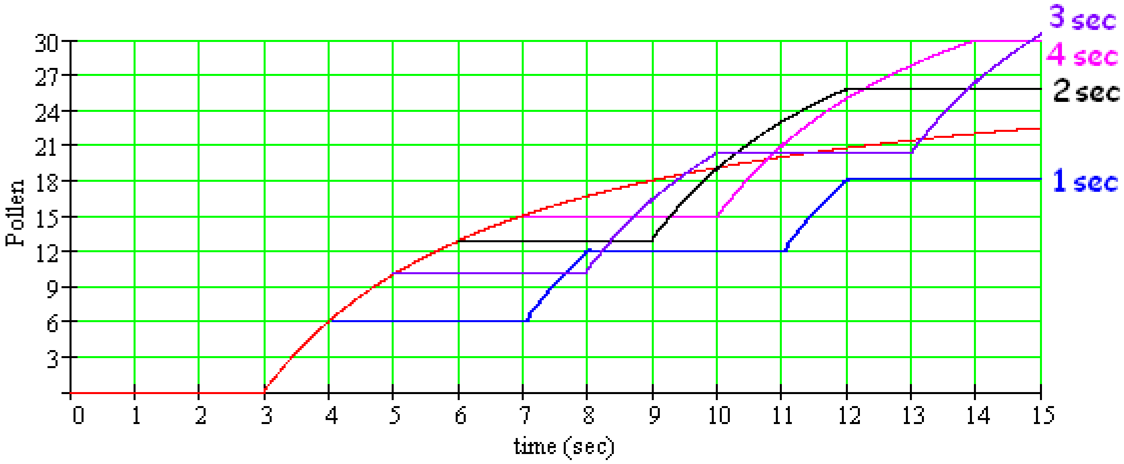


Figure 1: Comparing 5 and 15 second foraging times

1) For the collection curve defined by the graph below, approximate the best foraging time. (1 pt)



The best way to begin is to just begin. Select some times and see what happens. Some will be better than others. Try to figure out why.



Look at the results from foraging for 1, 2, 3, and 4 seconds. In 15 seconds, foraging for three seconds seems to be the best, yielding a little more than 30 units of pollen (or 2 units per second). Perhaps there is a value between 3 and 4 seconds that is even better.

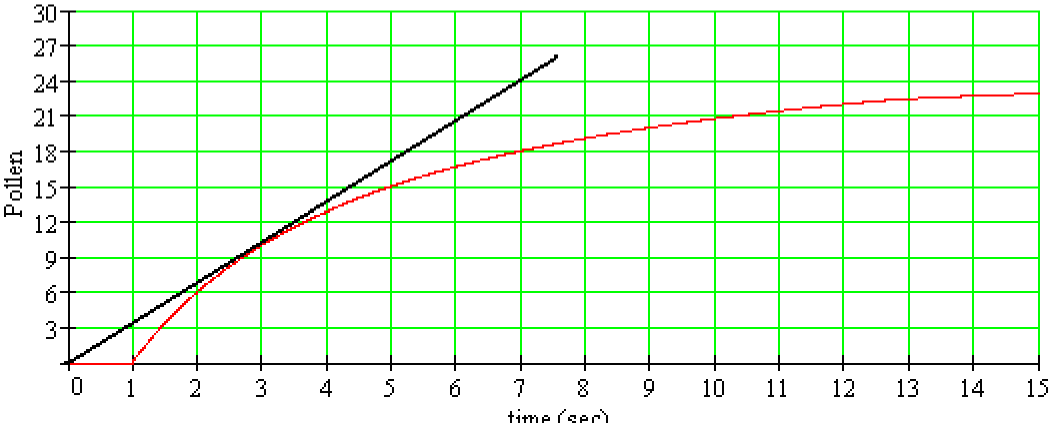
You want to maximize the amount gathered over time. By playing around with some specific curves like this one you may see that the goal is to find the point on the curve where the instantaneous rate of gathering pollen begins to fall behind the average rate (as long as you are gathering faster at this moment than you have on average, keep gathering. If your average rate of change is larger than your instantaneous rate, you are falling behind, so go to another flower.

Students recognize this point in a number of ways. It is the point on the curve where:

b) the slope of the secant line is the same as the slope of the tangent line
b) the tangent line has 0 for its *y*-intercept
c) the amount gathered per unit time is at a maximum
d) the line through the origin just touching the curve has the steepest slope.

All of these lead to the same solution and hopefully, the students would have seen one of them.

2) If the travel time were reduced to 1 second, what happens to the location of the optimal foraging time? Does it increase or decrease? Was your intuition correct? (1 pt)



In this case, we see that about *t* = 3 or 2 seconds of foraging is the best time. It generates about 10 units every 3 seconds. As expected, the foraging time is reduced when the travel time is reduced.

3) If the height of the curve is doubled, what happens to the location of the optimal foraging time? Does it increase or decrease. Was our intuition correct? (1 pt)

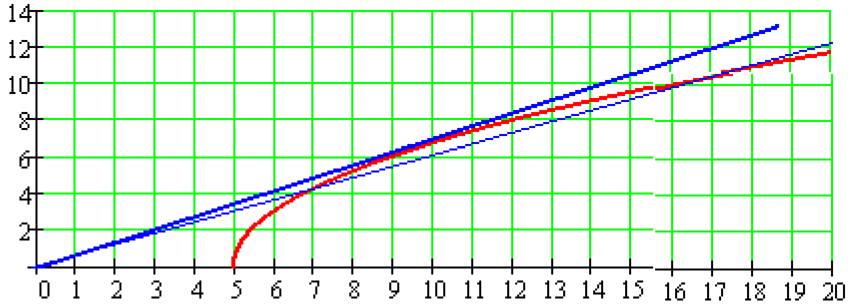
Increasing the height is equivalent to changing the vertical scale. This should not affect the foraging time but will change the amount gathered.

4) Consider the collection function $C(t) = \begin{cases} 0 \text{ if } t < T \\ A\sqrt{t-T} \text{ if } t \geq T \end{cases}$. What is the best foraging time in terms of *A* and *T*? Do the parameters *A* and *T* have the effect you expected? (1 pt)

Based on 3) we should not expect to see *A* in the solution, but *T* should be important.

Students can approach this problem from several directions as noted before If they are looking for the point at which the net gain per unit time is maximized, then they must maximize the function $Y = \frac{A\sqrt{t-T}}{t}$. So, $Y = \frac{A\sqrt{t-T}}{t}$ and $\frac{dY}{dt} = \frac{\frac{tA}{2\sqrt{t-T}} - A\sqrt{t-T}}{t^2} = 0$. This means $\frac{tA - A\left(2\sqrt{t-T}\right)^2}{2\sqrt{t-T}} = 0$. This simplifies to $tA = A2(t-T)$ and $t = 2T$. Notice that the solution is independent of *A*, as expected, and depends entirely on *T*. The larger the traveling time, the longer the foraging time. The best total time is $t = 2T$, so the foraging time is $2T - T = T$. For this function, forage for as long as it takes to travel from plant to plant. Is it clear that vertical stretches do not affect the solution?

If the students notice that the location where the tangent line has the same slope as the secant line (where the instantaneous rate of change is equal to the average rate of change.
) is the best point, then their work will be different.

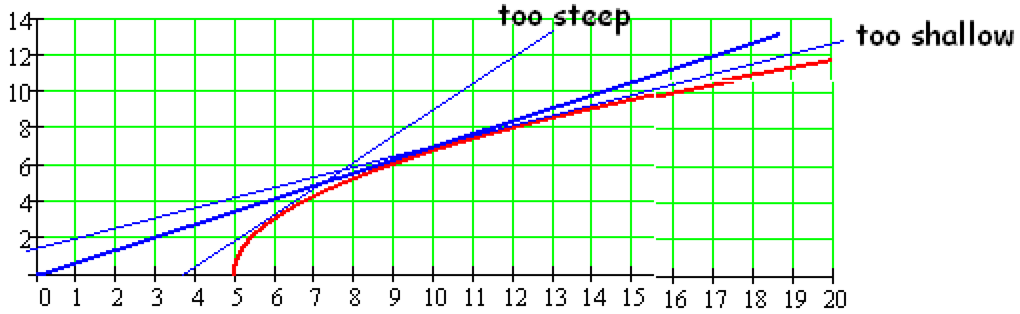


The average rate of change is the slope the secant line through the origin, so this slope is $\frac{C(t)}{t}$.

In this case, we should find *t* so that $C'(t) = \frac{C(t)}{t}$. If $C(t) = A\sqrt{t-T}$, then $C'(t) = \frac{A}{2\sqrt{t-T}}$,

so we need to solve the equation $\frac{A}{2\sqrt{t-T}} = \frac{A\sqrt{t-T}}{t}$. Solving we find, $tA = A2(t-T)$ and $t = 2T$ is the solution, as before.

If the students seek the location at which the intercept of the tangent line is zero the work is again different, but, of course, leads to the same solution.



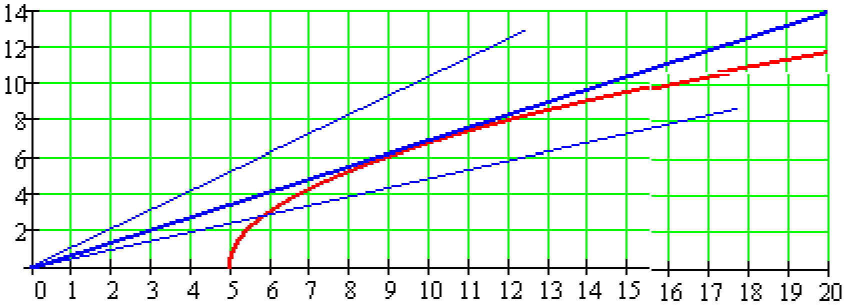
Find the location at which the intercept of the tangent line is zero.

The equation of the tangent line at $t = a$ is $y = C(a) + C'(a)(t-a)$ or

$y = C'(a)t + C(a) - C'(a)a$. We want $C(a) - C'(a)a = 0$ so $C(a) = C'(a)a$.

$$If\ \ C(a) = C'(a)a\text{, } then\ \ A\sqrt{a-T} = a\left(\frac{A}{2\sqrt{a-T}}\right)\ \ or\ \ a = 2T.$$

If the student are looking for the line through the origin intersecting the graph that has the steepest slope.



The slope of a line through the origin is $m = \frac{C(t)}{t}$. This is equivalent to the first solution, and the algebra is the same, but the inspiration came from a different perspective.

The result you found is known to biologists as the **Marginal Value Theorem**. The optimal foraging time is found when the *instantaneous rate of accumulation is equal to the average rate of accumulation.* This point on the graph is sometimes called the "knee" of the graph. If you Google *Marginal Value Theorem* you will find various biological references. I used Frederick R. Adler, *Modeling Dynamics of Life*, Brooks/Cole Publishing, 2005.

5) For an arbitrary collection function $C(t)$, describe the location *t* at which the forager should leave its present situation in search of greener pastures? (1 pt)

If we consider the general case, $\frac{dY}{dt} = \frac{t \cdot C'(t) - C(t)}{t^2} = 0$. So, $t \cdot C'(t) = C(t)$ or the value of *t* for which $C'(t) = \frac{C(t)}{t}$. We can also read this equation as describing the point at which the slope of the tangent line is the same as the slope of the secant line (that's our second approach). The third approach was to find the point on the graph at which the tangent passed through the origin. The equation of the tangent line at $t = a$ is $y = C(a) + C'(a)(t-a)$ or

$y = C'(a)t + C(a) - C'(a)a$. We want $C(a) - C'(a)a = 0$ so $C(a) = C'(a)a$ or find *a* so that $C'(a) = \frac{C(a)}{a}$.

No matter how you look at it, the value of t for which $C'(t) = \frac{C(t)}{t}$ is the "knee" of the graph and maximizes the amount collected per unit time.