

## Bees Foraging for Food

Foraging animals have a basic problem to solve, when their food supply is in patches (acorns under trees, flowers growing in patches, worms in apples, etc). Food is easy to collect food when they first begin searching a new area. As the animal continues feeding, food becomes more difficult to find and it has to search longer and longer for each additional morsel. This suggests that the curve relating the time spent foraging in the patch and the amount of food found (or energy gain) starts off with a steep slope but then gradually levels off. Food is easy to find in another patch, but 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. 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. An animal gains no energy while traveling.

Other situations are quite similar. Guppies are a small tropic fish found in freshwater streams in Trinidad. The males court females and the female chooses whether or not to mate with male. The longer a male courts a female, the greater his chance is of mating with her. The males are polygynous (they may mate with many females) but they must spend time searching for each female. How do they decide when to abandon the courtship and try another female?

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  $\mu g$ ) than for 15 second foraging (about 58  $\mu g$ ).

In this investigation, we want to determine the length of time that gives the largest total pollen accumulation in a fixed period of time.

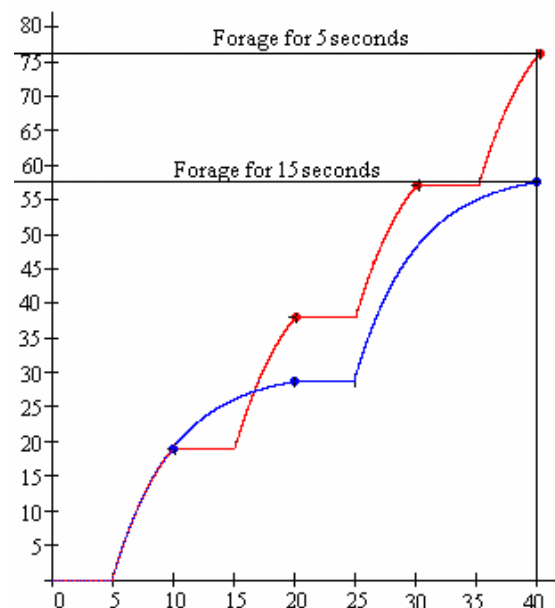
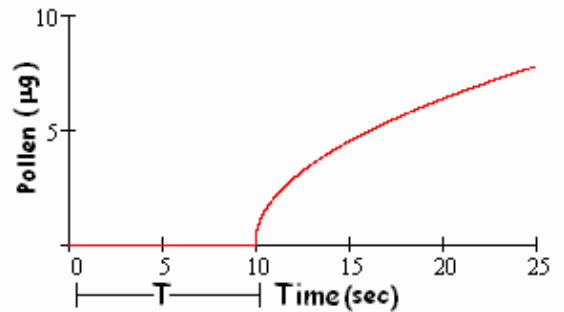
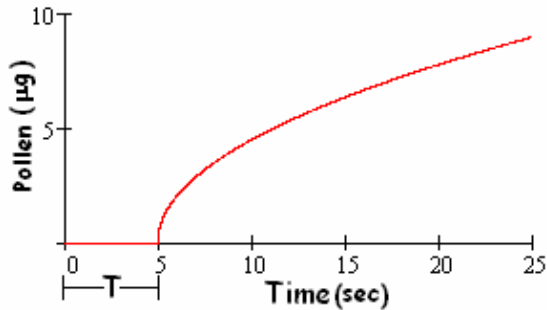


Figure 1: Comparing 5 and 15 second foraging times

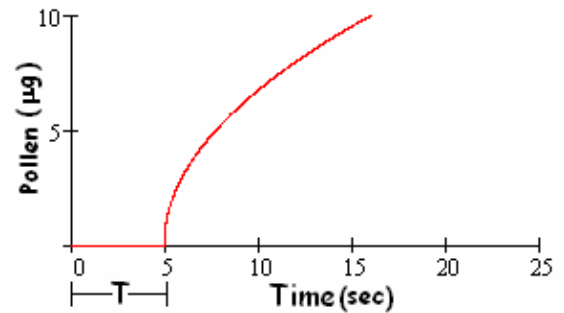
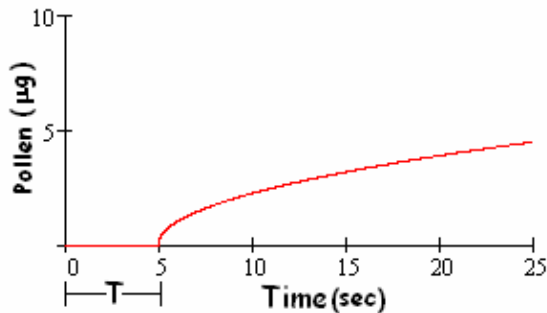
### The Effect of Travel Time and Rate of Collection

First, let's check our intuition. Upon what does the optimal foraging time depend? For each of the figures below, describe how the foraging time might depend on the time for travel between patches,  $T$ , and the shape of the function describing the energy gains over time.

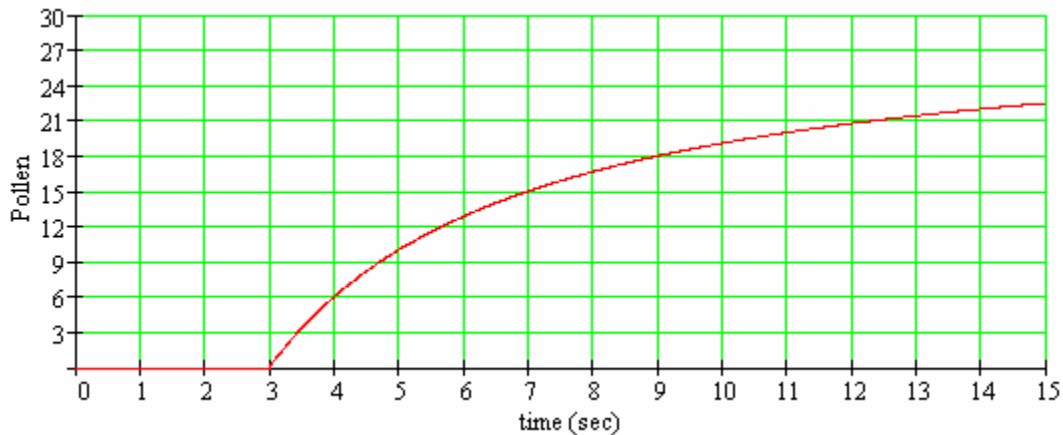
- 1) For the two Pollen curves shown below in which the travel times differ, would you expect the bee to spend longer or shorter periods of time on a flower if the travel time is longer?



- 2) For the two Pollen curves shown below in which the travel times are the same, for which Pollen curve would you expect the bee to spend the longer time foraging?



- 3) As a first approximation, consider the graph in Figure 4. Use the graph to compare foraging times of 1 and 12 seconds.



- a) If the bee forages for 1 second and then moves to another flower with the same collection curve, how much pollen will the bee have after 8 seconds?  
 b) If the bee forages for 4 seconds and then moves to another flower with the same collection curve, how much pollen will the bee have after 14 seconds?

- c) Based on these two examples, can you describe when it appears to be to the bee's advantage to leave a flower looking for easier gathering?
- d) For each of the following pollen collection curves, find the foraging time that satisfies the condition found in c).

$$\text{i) } C(t) = \begin{cases} 0 & \text{if } t < 3 \\ \sqrt{t-3} & \text{if } t \geq 3. \end{cases}$$

$$\text{ii) } C(t) = \begin{cases} 0 & \text{if } t < T \\ A\sqrt{t-T} & \text{if } t \geq T. \end{cases}$$

$$\text{iii) } C(t) = \begin{cases} 0 & \text{if } t < T \\ \sqrt[3]{t-T} & \text{if } t \geq T. \end{cases}$$

$$\text{iv) } C(t) = \begin{cases} 0 & \text{if } t < T \\ \frac{20(t-T)}{t-T+5} & \text{if } t \geq T. \end{cases}$$

Is your solution optimal?

- 4) Suppose the collection curve is  $C(t) = \begin{cases} 0 & \text{if } t < 3 \\ \sqrt{t-3} & \text{if } t \geq 3. \end{cases}$  Complete the table below to compare foraging times.

Time ( $t$ sec)	Foraging time ( $f$ sec)	Amount of Pollen in $t$ seconds
3	0	
4	1	
5	2	
6		
7		
8		
9		
10		
11		

- 5) Clearly, the bee can gather more pollen by staying on the flower, but what how efficient is the bee at gathering the pollen?

Time ( $t$ sec)	Foraging time ( $f$ sec)	Amount of Pollen	Rate of Pollen Collection
3	0		
4	1		
5	2		
6			
7			
8			
9			
10			
11			

If we want to accumulate the maximum amount of pollen in a fixed period of time, we can accomplish this by maximizing the rate at which we accumulate pollen, that is, maximize  $R(t) = \frac{C(t)}{t}$ . We must remember that our time  $t$  includes the traveling time  $T$  from patch to patch.

6) If  $R(t) = \frac{C(t)}{t}$ , find  $\frac{dR}{dt}$  in terms of  $R$  and  $C$ . Use this result to find the optimal foraging times for the four collection curves in 4 c), above. Upon what does the foraging time depend? Was your intuition correct in 1) and 2)?

7) The result you found in 6) is known as the Marginal Value Theorem and says that 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. Compare this theorem to the Mean Value Theorem. Will there always be a point at which the theorem is satisfied?

8) Use the Marginal Value Theorem to find the optimal foraging time for each of the collection function below. What does each of the parameters  $A$ ,  $T$ , or  $k$  represent in the function? Which parameter has the greatest effect on the foraging time?

a) 
$$C(t) = \begin{cases} 0 & \text{if } t < T \\ A\sqrt{t-T} & \text{if } t \geq T. \end{cases}$$

b) 
$$C(t) = \begin{cases} 0 & \text{if } t < T \\ \frac{A(t-T)}{t-T+k} & \text{if } t \geq T. \end{cases}$$

c) 
$$C(t) = \begin{cases} 0 & \text{if } t < T \\ A - Ae^{-k(t-T)} & \text{if } t \geq T. \end{cases}$$