

Learning and Behavior

Studies of animal foraging have a long tradition in ecology, including a well-developed body of theory. Much of this theory has been translated into elegant mathematical models, which produce precise predictions about how efficient or effective foragers should behave. While tests of this theory have provided insights about animal behavior and have helped ecology mature as a science, the theory has faced much criticism. Most criticism has focused on assumptions used to develop the theory and whether those assumptions are plausible. A deeper issue concerns the complexity of foraging decisions predicted by the theory relative to the cognitive abilities of real foragers making those decisions. How relevant are theory and resultant predictions if they require foragers to make decisions beyond their cognitive abilities?

This dilemma can be resolved if one considers that foragers could apply simple rules to learn efficient foraging strategies that converge on the same behaviors predicted by complex theoretical calculations. Similar approaches by computational biologists have begun to reveal mechanisms underlying complex behaviors of social organisms (Couzin et al. 2005; Couzin 2007). In this project, you will evaluate this idea with simulated “foraging” in a simplified environment. Members of the class will act as central-place “foragers” that decide whether or not to pursue food items that appear periodically at random distances from the central perch. Foragers in the first set of trials will be naïve, making foraging decisions without knowledge about efficiency calculations or rules. In the second set of trials, the same foragers will repeat the process using a decision rule to generate optimal foraging behavior.

Theoretical Background

The following is excerpted from Roughgarden (1995), concerning optimal behavior of a central-place forager or a sit-and-wait predator. Roughgarden (1995) used the example of arboreal *Anolis* lizards, which pursue insect prey from elevated perches and then return to those perches to await appearance of more prey. The theory applies equally well to birds that hunt from a perch including flycatchers and many raptors, many cats, and other ambush predators.

Suppose a forager enjoys an unobstructed view of the environment in front of it, and that food items appear at random distances (r) away from the forager’s perch at frequency a . If the forager moves with “sprint speed” v , then the time required to pursue a food item and return to the perch is $2r/v$. The average time required to pursue food items appearing up to distances r_c away from the perch is the product of distance-specific pursuit times multiplied by probabilities that prey appear at each distance, integrated over distances 0 to r_c

$$\int_0^{r_c} \frac{a\pi r}{\int_0^{r_c} a\pi r dr} \frac{2r}{v} dr \quad (1)$$

The average time spent per food item, T/I , is determined by adding average waiting time per item to average pursuit time,

$$T/I = \frac{1}{\int_0^{r_c} a\pi r dr} + \int_0^{r_c} \frac{a\pi r}{\int_0^{r_c} a\pi r dr} \frac{2r}{v} dr \quad (2)$$

The optimal foraging distance is the value of r_c that minimizes the above expression for T/I . To obtain this value, or the maximum distance a forager should pursue food items, evaluate the integrals in the expression above and minimize T/I with respect to r_c .

$$r_c = \sqrt[3]{\frac{3v}{\pi a}} \quad (3)$$

For the “foraging” arena used in this project, foragers observe a strip 10.0m long and 1.0m wide, within which items appear at a rate of one per five seconds. Consequently, $a = 1/5.00\text{sec}/10.0\text{m}^2 = 0.02/\text{sec}/\text{m}^2$. Pursuit speeds, v , for each forager are listed below in Table 1. For example, Ben’s pursuit speed is 3.09 m/sec. Inserting these values in eq.(3) yields Ben’s optimal foraging radius, $r_c = 5.28$ meters.

Learning to Forage Optimally

WWU students are renowned for their intelligence and ability to think quickly, but perhaps calculating cubed roots in the field without electronic aids would be an unreasonably high expectation. We might expect even less from foragers of more modest cognitive ability. Instead, consider the following simple foraging strategy.

- 1 When food item (1) appears, pursue regardless of distance from perch.
- 2 When item (2) appears, pursue if (2) is equal to or closer than (1); otherwise ignore (2).
- 3 When item (3) appears, pursue if (3) is equal to or closer than the average of (1) and (2); otherwise ignore (3).
- 4 When item (4) appears, pursue if (4) is closer than the average of all preceding it; otherwise ignore.
- 5 Repeat rule (4) for all subsequent items.

Using this strategy, foragers may pursue food items beyond r_c early on, but after experience with a small number of items, they should pursue all items within r_c and ignore all items beyond r_c . This strategy could be modified to allow foragers to adapt to an environment in which food distribution or abundance changes over time by calculating the “average” distance within a time window corresponding to the temporal scale of change. Hence, flycatchers could be more selective during peak insect emergence in late spring/early summer, and pursue insects at greater distances when food abundance declines as summer progresses.

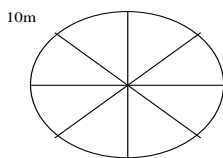
Field Methods:

Equipment:

- 30m tapes (8)
- Flags, 100-200, multiple colors:
 - orange = current food item; yellow = pursued items; white = ignored items
- Stopwatch

Field Procedure:

- 1 Establish foraging circle w/ 10 meter radius: set up spokes of "wheel" using 30m tapes.



- 2 Measure pursuit speed of each forager: time to walk/run 10m).

- 3 Select one student as forager. Instructor or TA act as timer. Rest of students are food "providers."
- 4 Food providers move to points around perimeter.
Each has: table of random digits and many flags of various colors
- 5 Forager & timer move to center:
timer has stopwatch
forager has bundle of flags of contrasting color (e.g., yellow)
- 6 Each food provider places flag at first random number
- 7 Food provider and timer rotate around center of circle; timer says "go" every 5 seconds.
- 8 At each "go," forager decides to pursue or ignore flag in that direction.
 - if ignore, rotate toward next flag & wait for next "go"
 - if pursue, travel to flag (at same speed as measured in step 2), and plant yellow flag next to it, then return to center
- 9 Food provider of above flag selects next random digit, and places flag there.
- 10 Continue until forager has pursued or ignored a total of 50 flags.
- 11 Repeat so that all students get to act as forager.
- 12 Repeat steps 3-11 using the optimal learning strategy outlined above.

Data Analysis:

- 1 Pursuit speeds and foraging radius for each forager are listed in Table 1.
- 2 Calculate critical radius for each forager using eq.(3), with $a = 0.02/\text{sec}/\text{m}^2$
(food items appeared in each 10m^2 radius at a rate of $1/5\text{sec}$)
- 3 For each forager, compare observed foraging radius, learned foraging radius, and r_c values calculated in step 2. You should summarize your comparisons by plotting foraging radius vs. pursuit speed. Plot r_c (ordinate axis) as a function of pursuit speed (v) as a line. Then plot observed foraging radius as points on the same figure. Finally, add learned foraging radii to the plot as points using a different symbol.

Questions and Interpretation

- 1 Compare observed foraging radius vs. r_c among foragers. Can you detect any pattern in the values, such as tendency for observed values to exceed or fall below theoretically optimal values (r_c)?
- 2 Compare observed foraging radius vs. learned radius among foragers.
- 3 Compare learned foraging radius vs. r_c among foragers. If the simple rule converges to r_c , then points for the learned radii should fall on or near the line plotted as described above. Do the data provide evidence for this?
- 4 Do the data suggest that learned behavior using a simple rule can produce results equivalent to a complex calculation (eq.3)?

References

- Couzin ID, Krause J, Franks NR, Levin SA. 2005. Effective leadership and decision-making in animal groups on the move. *Nature* 433:513-516.
- Couzin ID. 2007. Collective minds. *Nature* 445:715.
- Roughgarden J. 1995. *Anolis Lizards of the Caribbean: Ecology, Evolution, and Plate Tectonics*. Oxford Univ. Press, Oxford, UK.
- Stephens DW, Krebs JR. 1985. *Foraging Theory*. Princeton Univ. Press. Princeton, NJ.

Table 1. Pursuit speeds, foraging radius observed without learning, foraging radius observed with learning, and critical foraging radius calculated from optimal foraging theory.

Forager	Pursuit speed (m/sec)	Foraging radius, observed(m)	Foraging radius, learned(m)	r_c
Rachel F	2.61	7	4	
Jayme	2.30	6	4	
Stephen	2.42	7	4	
Ellie	3.45	6	5	
Rylie	2.92	7	5	
Elcena	3.24	6	3	
Lindsey	2.69	7	5	
Hannah	2.18	5	7	
Catherine	2.79	7	5	
Rachel O	2.72	7	6	
Reno	2.71	9	4	
Houston	2.86	4	5	
Logan	3.32	8	7	
Matt	3.29	8	3	
Miranda	3.40	8	6	
Kyle	3.88	8	6	
Caleb	4.20	9	6	
Ben	3.09	7	8	
Blake	3.66	9		
Audrey	3.45	9	7	