Optimal Foraging Theory

USING BIRD PREDATION ON GOLDENROD GALLS

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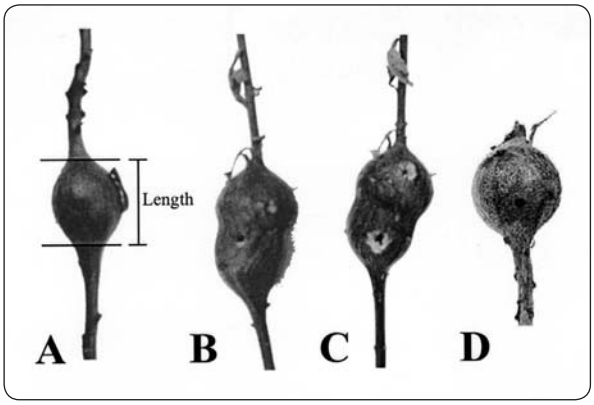
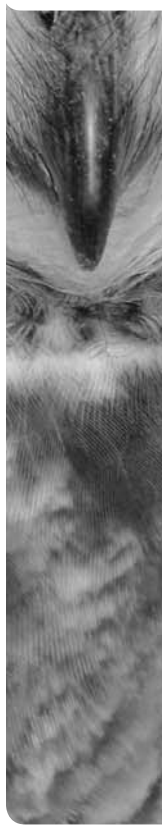
Are you the type of person who would drive 10 miles to the nearest Burger King instead of eating at the McDonald's down the block? How many freeway food billboards will you pass up looking for that perfect submarine sandwich before you give up and settle for anything? Too tired to cook and would rather grab a pizza? Although I don't personally condone fast food culture, the gastronomic choices we make are a good place to start when discussing optimal foraging theory with our students because we, like animals, live in variable environments and are often forced to make decisions about where to forage, how long to forage, what types of food are available, etc. Optimal foraging theory attempts to explain these behaviors in terms of costs and benefits (Molles, 1999; Ricklefs, 2001). A bird flying through a meadow is likely to encounter a variety of different food types. Each potential food item has an intrinsic value based on its nutrient and energy content, how much time is required to extract the food (handling time), and how long it takes to locate the food (search time). Optimal foraging predicts that, given equal handling time, the prey item with a large energy gain will be chosen over the prey item with a small energy gain. Also, animals are more likely to select prey with a large energy gain when availability is high because it decreases search time. When search time increases, animals are less selective (Abrahamson & Weis, 1997; Anderson, 1984; Krebs et al., 1977). A number of optimal foraging experiments have been illustrated in *The American Biology Teacher* (Rop, 2001; Wellborn, 2000). Here I present a simple field experiment investigating the goldenrod gall fly and its winter predators, mainly birds. The experiment is designed to get students to work together in groups, solve problems together in the field, understand the design of ecological experiments and hypothesis testing, and learn basic statistical calculations.

The goldenrod gall fly (*Eurosta solidaginis*) is common and widely distributed in North America. A female gall fly typically lays a single egg in the terminal bud of a newly emerging goldenrod stem in spring, and may lay a hundred eggs over the course of her two week adult lifespan (Weis & Abrahamson, 1998). After the egg hatches, the larva will burrow its way through the bud, down the stem, and induce the plant to produce a tumor-like structure called a gall. The gall of *Eurosta* has a characteristic spherical shape (Figure 1). It is distinguishable from the gall of another gall-forming insect, the elliptical gall moth (*Gnorimoshema gallaesolidaginis*), which forms a long, narrow gall (Weber et al., 2002). The larva will graze on the inner tissue of the gall and remain in the central chamber of the gall for 50 weeks, emerging as an adult fly the following spring to begin the cycle all over again (Weis & Abrahamson, 1998). Gall flies are particular regarding which species of goldenrod they parasitize. Across the northern states from New England through the Great Plains, the common gall-forming species most likely to be encountered in meadows or along roadsides include Canadian goldenrod (*Solidago canadensis*) and late goldenrod (*S. gigantea*), whereas the common gall-forming species in the Mid-Atlantic States is tall goldenrod (*S. altissima*) (personal observation, Weis & Abrahamson, 1998).

While inside the gall, the larva may be parasitized by the parasitoid wasp *Eurytoma gigantea* or preyed upon by birds or small mammals. Birds such as downy woodpeckers and black-capped chickadees open galls and extract larvae during winter when other food is scarce (Abrahamson & Weis, 1997; Schlichter, 1978), and squirrels may also use gall fly larvae as a food source in winter (Shealer et al., 1999). In general, wasps parasitize smaller galls because the ovipositor of the wasp can reach the central cavity of the gall (Weis et al., 1985). Evidence suggests that in some areas, predatory birds like the downy woodpecker show a marked preference for larger galls,

Figure 1.
Gall formation on Canadian goldenrod (*Solidago canadensis*). Goldenrod galls showing disturbance by downy woodpecker (B) black-capped chickadee (C) and gall fly emergence (D).





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possibly because a smaller gall is likely to contain larva of the parasitic wasp (Weis & Abrahamson, 1998). The larva of the parasitic wasp is about one tenth the size of *Eurosta* larva, and therefore a less rewarding meal energetically. Also, Shealer et al. (1999) found that larva of *Eurosta* is significantly smaller in smaller galls than larger galls. A classic study by Tscharntke (1992) looked at a similar system in Germany and found that the blue tit, a predator of the gall fly *Giraudiella inclusa*, responded both to gall abundance between habitats and gall clusters within habitats. This observation is consistent with optimal foraging theory as there is a potentially higher energetic benefit of being in a high quality habitat patch versus a lower quality patch. Also, search time for the next food item will decrease in patches where resources are clustered and where there is a higher density of resources.

Table 1.
Sample data table that students use to record gall measurements.

Undisturbed gall		Disturbed gall (chickadees)		Disturbed gall (woodpeckers)	
Length (mm)	Width (mm)	Length (mm)	Width (mm)	Length (mm)	Width (mm)

Plot number_____ Total number of galls_____

Experiment 1: Prey Choice

Objective

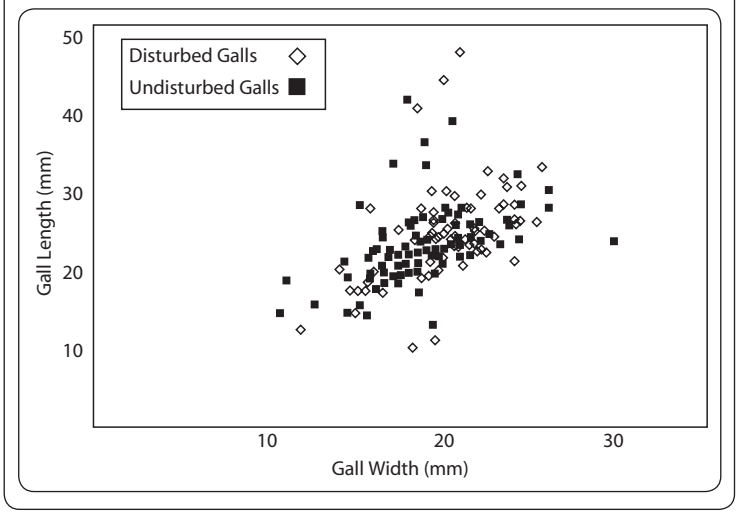
Test the hypothesis that birds choose larger galls (null hypothesis: birds do not choose galls based on size). Optimal foraging theory would predict that foraging birds would select larger galls than are randomly available in the environment.

Materials & Methods

I suggest having students read Weis and Abrahamson (1998) during the week this lab will be conducted to understand the interactions involved. It will also aid students in thoughtfully interpreting the results.

Each group of students will need a dial caliper, pencil, and datasheet (Table 1). When you arrive at the study site, demonstrate to the students how to measure the length and width of a gall using the caliper. Length is more challenging to measure than width, and the important point to emphasize is consistency. I have students measure at the point where the gall begins to widen dramatically, rather than where the stem begins to widen (see Figure 1A). Also show them examples of undisturbed galls and disturbed galls (Figure 1). Black-capped chickadees make messy, large irregular holes whereas downy woodpeckers locate the emergence tunnel of the gall-making larva (Abrahamson & Weis, 1997). One source of confusion may be distinguishing fly emergence from avian disturbance. My rule-of-thumb is that if the hole has a clean border (i.e., it appears to have been made with a fine drill bit), it is likely emergence (Figure1D). Also, it may be difficult to differentiate black-capped chickadee and downy woodpecker disturbance, so I have also pooled these and simply compared disturbed versus undisturbed galls. Have the groups spread out at the study site. Each group is responsible for taking measurements on all galls found within a 1.0m^2 plot. Plot size can be varied depending on the density of goldenrods at your study site.

Figure 2.
Scatter plot of gall length versus width from data collected in the field. Students can draw this by hand or generate it using software packages like Excel.



Results

The level of statistical analysis I require in class depends on the course I am teaching. For my non-majors biology course, I show them how to calculate mean, variance, and standard deviation using Excel, and how to generate a scatter plot of disturbed versus undisturbed galls to visualize the data (Figure 2). For biology majors and ecology students I show them how to run an independent-samples *t*-test (using gall width as the test variable and testing chickadees and woodpeckers separately) using statistical software available to them (in our case SPSS).

Experiment 2: Patch Choice

Objective

Test the hypothesis that birds forage more in patches with higher gall densities (null hypothesis: birds do not

choose patches based on gall densities). Optimal foraging theory would predict that a greater proportion of galls would be disturbed in goldenrod patches with high gall densities than patches with low gall densities.

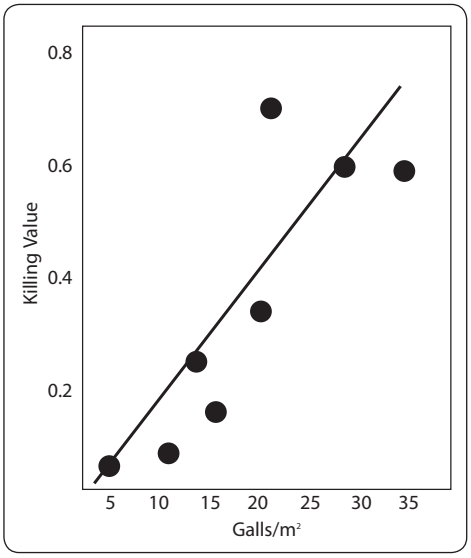
Materials & Methods

This experiment does not require that you measure individual galls, but can easily be combined with Experiment One because you already have the data required. Each group of students counts the total number of galls in a 1.0m^2 plot. If a different size plot is used, record data as number of galls/m^2 (Table 2). Next count the number of disturbed galls. The killing value (Tscharntke, 1992) is the number disturbed divided by the number of galls/m^2.

Table 2.
Sample data table that students use to record class data for Experiment 2.

Plot Number	Number of Galls/m^2	Number Disturbed	Killing Value

Figure 3.
Scatter plot of killing value and galls/m^2 with "best fit" line from the regression equation $Y = a + bX$, where Y is the dependent variable (killing value), X the independent variable (galls/m^2), b is the slope of the line and a is the Y-intercept.



Results

Again the level of statistical analysis will depend on the level of the course. For my non-majors biology course I have the students generate a scatter plot of killing value (dependent variable) and number of galls/m^2 (independent variable). For biology majors I require running and interpreting a regression analysis (Figure 3).

Additional Questions for Discussion

1. How do you score double galls (see Figure 1C)? Defend your choice.
2. Is there a spatial pattern to the different types of disturbance you observed based on distance to water, proximity to trees or shrubs, or other landscape elements that you can think of? Why might this be?

3. Describe a situation where you would predict birds would not select larger galls.
4. The next time you go grocery shopping, think about how your choices fit optimal foraging theory. Make a list of the costs and benefits of where you choose to shop or eat, and the types of food you choose to buy.

Summary

The field where we conduct this experiment is adjacent to our campus near a large student-housing complex and is usually pretty desolate when we are there in April. After this lab the students have commented that they don't look at this field as just a field anymore, but as a complex biological community right outside their windows. Therefore, in addition to allowing students to work in groups, solve problems in the field, and use the scientific method, this lab also gives students a new way to view the world around them.

References

Abrahamson, W. G. & Weis, A. E. (1997). *Evolutionary Ecology Across Three Trophic Levels: Goldenrods, Gallmakers, and Natural Enemies.* Princeton, NJ: Princeton University Press.

Anderson, O. (1984). Optimal foraging by largemouth bass in structured environments. *Ecology, 65,* 850-861.

Krebs, J. R., Erichsen, J. T., Webber, M. I. & Carnov, E. L. (1977). Optimal prey-selection by the great tit (*Parus major*). *Animal Behavior, 25,* 30-38.

Molles, M. C. (1999). *Ecology: Concepts and Applications.* Dubuque, IA: WCB/McGraw-Hill.

Ricklefs, R. E. (2001). *The Economy of Nature, Fifth Edition.* New York: W.H. Freeman.

Rop, C. J. (2001). Foraging behavior in guppies: Do size and color make a difference. *The American Biology Teacher, 63*(3), 194-197.

Schlichter, L. (1978). Winter predation in black-capped chickadees and downy woodpeckers on inhabitants of goldenrod ball gall. *Canadian Field Naturalist, 92,* 71-74.

Shealer, D. A., Snyder, J. P., Dreisbach, V. C., Sunderland, D. F. & Noval, J. A. (1999). Foraging patterns of eastern gray squirrels (*Sciurus carolinensis*) on goldenrod gall insects, a potentially important winter food resource. *American Midland Naturalist, 142,* 102-109.

Tscharntke, T. (1992). Cascade effects among four trophic levels: Bird predation on galls affects density-dependent parasitism. *Ecology, 73,* 1689-1698.

Weber, P. G., Cox, D. D., Stamm, A. J., Swift, J. N., Weber, S. P., Esslinger, C., Peron, S.A., Pens, D.R. & Taylor, L.A. (2002). *Winter Science Curriculum Project: What's Inside Goldenrod Galls?* Retrieved April 7, 2004, from http://www.oswego.edu/wscp/.

Weis, A. E. & Abrahamson, W. G. (1998). Just lookin' for a home. *Natural History, 107*(7), 60-63.

Weis, A. E., Abrahamson, W. G. & McCrea, K. D. (1985). Host gall size and oviposition success by the parasitoid *Eurytoma gigantea*. *Ecological Entomology, 10,* 341-348.

Wellborn, G. A. (2000). Testing concepts of animal foraging behavior: An experiment using seed trays. *The American Biology Teacher, 62*(1), 46-49.