INQUIRY & INVESTIGATION

Optimal Foraging by Birds: Experiments for Secondary & Postsecondary Students

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ABSTRACT

Optimal foraging theory attempts to explain the foraging patterns observed in animals, including their choice of particular food items and foraging locations. We describe three experiments designed to test hypotheses about food choice and foraging habitat preference using bird feeders. These experiments can be used alone or in combination and can also provide a foundation for students to develop extensions incorporating the basic methodology. We see these experiments as most applicable in secondary and postsecondary education, but they could be adapted for a variety of educational environments and for students with a variety of backgrounds.

Key Words: *Optimal foraging; birds; feeder; optimal diet; predation risk.*

Most students are savvy practitioners of optimal foraging theory. Simply show them pictures of two neighborhoods, one with houses located very close together and another with houses spread far apart, and ask them where they would prefer to trick-or-treat and why. Students recognize that they can obtain more candy in less time when the houses are close together, and this type of calculation is the crux of optimal foraging theory. Animals will forage as efficiently as possible through, among other considerations, their choice of foods and foraging locations (Pyke et al., 1977).

Optimal food choice depends on the energy content of a potential food item and its handling time, or the cost associated with consuming the food item. Larger food items may provide a larger gross reward for an animal, but the high cost of consuming those items may make them less profitable than something smaller. Such was the case in a study of blue crabs (*Callinectes sapidus*), in which it was determined that the crabs preferred smaller mussels over larger mussels because of the relative ease of opening the smaller shells (Hughes & Seed, 1981). More recently, Sih & Christensen (2001) reviewed 134 articles on optimal diet choice and found that this behavior was more common among organisms that fed on stationary prey, such as seeds, as opposed to mobile prey items.

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Optimal choice of foraging location may be affected by either food density (as in our Halloween example above) or predation risk. When predation risk is a factor, small vertebrates such as rodents (Brown, 1988) and songbirds (Grubb & Greenwald, 1982; Schneider, 1984) generally prefer to feed in habitats that offer protective cover. However, not all covered sites are preferred equally. Suhonen (1993) determined that willow tits (*Poecile montanus*) and crested tits (*Lophophanes cristatus*) foraged in areas closer to the trunks of spruce trees during periods of increased predation risk by pygmy owls (*Glaucidium passerinum*). In addition, willow tits foraged at higher elevations within the canopy during these times of enhanced risk.

Here, we describe three field experiments designed to assess the foraging patterns of birds using feeders. One of the experiments addresses optimal food choice (Experiment 1), and the other two address optimal location (Experiments 2 and 3). Experiments designed to test elements of optimal foraging theory have been published in earlier volumes of *The American Biology Teacher* (Wellborn, 2000; Rop, 2001; Place & Abramson, 2006; Yahnke, 2006; Small & Newtoff, 2013), but our experiments are novel in the ways in which they incorporate food choice and foraging location. These experiments were developed in our sophomore-level ecology course at The College of New Jersey, but the conceptual simplicity at their core and minimal infrastructure would allow them to be adapted for use in a variety of other settings. The experiments are likely to be most useful at the secondary and postsecondary levels, but simplified versions could certainly be incorporated into curricula for elementary and middle school students. For example, the Core Curriculum Content Standards for New Jersey describe exposure to biological adaptations as early as grade 4 (http://www.state.nj.us/education/cccs/standards/5/5-3-E.htm). Behavioral adaptations tend to be overlooked in the discussion of adaptations, and these experiments emphasize those phenotypes and can help foster discussions about the evolution of behaviors. Further, the recently

Table 1. The laboratory schedule and student assessment methods we used for Experiment 1, followed by student development and execution of Experiment 3.

Schedule	Laboratory Content	Student Assessment
Week 1: Background information	1. Students discuss a paper about optimal foraging (we have used Hughes & Seed, 1981).	Student involvement in lab discussions can be included in the participation component of their course grade.
	2. Professor provides additional information about optimal foraging.	
	3. Class walks to bird-feeder site and practices the sampling procedure.	
	4. Students sign up for sample time(s).	
Week 2: Data collection, Experiment 1	1. There is no formal lab meeting.	Students are responsible for arriving on time for their selected sampling period and for participating in data collection.
	2. Students sample feeders and record consumption data (and make other observations such as bird identity), then submit their data to the professor.	
Week 3: Data analysis, Experiment 1	1. Professor provides complete data set and any necessary code for statistical programs.	Student involvement in lab discussions can be included in the participation component of their course grade.
	2. Students work within their lab groups to run statistical analyses and graph the data.	
	3. Students discuss the results as a class and then work within their lab groups to generate ideas for follow-up experiments.	
	4. Each lab group presents one of its ideas to the rest of the class.	
	5. Professor compiles a list of experiments proposed by students and sends survey to students for voting (Table 2).	
	6. Students select experiment.	
	7. Professor provides sign-up sheet for sampling.	
Week 4: Data collection, Experiment 3	1. Any necessary changes to feeder array for the new experiment can be made by students and/or professor.	
	2. Students form hypotheses for the new experiment and collect data.	
	3. We also ran an additional, unrelated experiment during the laboratory time this week.	
Week 5: Data analysis, Experiment 3	1. Students work within their lab groups to run statistical analyses and graph the data.	Each student writes a laboratory report in the form of a scientific manuscript.
	2. Students discuss the results as a class.	

developed *Next Generation Science Standards*, which have been adopted by several states and are being considered for adoption in many more, describe concepts related to optimal foraging theory as a disciplinary core idea to be covered in middle school (Standard MS-LS2.A, Interdependent Relationships in Ecosystems, http://www.nextgenscience.org/msls2-ecosystems-interactions-energy-dynamics).

We have successfully implemented the projects in multiple ways. In some cases, one experiment was used alone. In other cases, one of the experiments was used as the foundation of a multipart project. In this latter case, the students developed extensions by using their experience with the basic methodology. Three laboratory sections generated and discussed lists of potential experiments. The professors compiled five of the student-generated options into an online poll, and the students voted to determine which hypotheses and related approach they would collectively pursue. Specifically,

the students completed Experiment 1 (described below) and brainstormed/developed Experiment 3 (described below) as the extension (Table 1). The takeaway message is that the basic elements we describe are a practical and flexible framework within which students can explore optimal foraging theory and actively engage in scientific inquiry.

Basic Methods

In all three experiments, the experimental units are individual bird feeders. Any type of feeder could be used, but we have employed custom-made, pole-mounted feeders with a perch and a reserve of food held in place behind a clear plastic window (Figure 1). A piece of hardboard is mounted to the pole to prevent seed loss due to squirrel foraging. The piece of hardboard used as the squirrel guard is supported only by two small squares of plywood attached to the

Figure 1. One of the bird feeders used in the experiments. The feeders are made from PVC, have oak-dowel perches, and sit atop poles made from electrical conduit. The dark object below the feeder lid is a magnetic catch.

pole by a nut and bolt. As a consequence, the hardboard behaves much like a seesaw. Any weight applied to one side causes that side to dip and the opposite side to lift. This, in combination with the slick surface of the material, makes the hardboard quite effective in preventing squirrels from gaining access to the feeders. An array of feeders is established in the habitat(s) of interest, and each feeder is filled with a predetermined mass of food. For our feeders, we have found 200 g to be a good mass. The feeders should be installed well before the experiment is to be undertaken, to allow local birds to become familiar with the feeders; we have found that 2 weeks of lead time works well. Prior to the inception of the experiment, the feeders should be checked regularly and topped off with food to prevent any individual feeder from being exhausted. The number of feeders deployed will be determined, in part, by the space available and the amount of time available for students to check the feeders. We have used between 12 and 20 feeders in the past for 1- to 2-week experiments.

Once the experiment begins, the feeders are checked regularly by students to assess birds' foraging patterns. The checks involve weighing the mass of food remaining in each feeder using a portable balance and then replenishing the feeder to the predetermined mass of food. Subtracting the mass of food remaining in the feeder from the predetermined starting mass yields the mass of food taken by birds during the observation interval. The observation interval can be adjusted according to the availability of students to check the feeders and the hypothesis being tested. We have regularly used two daily checks of the feeders – early morning and late afternoon – to add the element of nighttime/early morning and daytime foraging patterns, respectively, to the design of the experiment.

Beyond the mass of food taken from the feeders, many other types of data can be collected, and this is an excellent opportunity to have students brainstorm potential variables of interest. Our students have augmented their measurements of food depletion in several ways. First, they have observed the feeders for a continuous hour during the day, with one student assigned to each feeder. While watching the

feeders, the students recorded the number of visits, the duration of visits, and the size classes of birds visiting the feeders (using a crude small–medium–large categorization based on a gauge affixed to the feeder beside the perch). Second, they have catalogued the different species of birds visiting the feeders and the number of individuals of each species. This can be accomplished by the students taking photographs of the birds using their cell phones and then identifying the birds by using a field guide or other resource, such as Project Feeder Watch (http://www.birds.cornell.edu/pfw/). Knowing the identity of the birds can aid in interpreting the data by considering the results of the experiment in the context of what is already known about the foraging habits of those species. Many students reported that they enjoyed observing the birds. These personal observations improved the quality of students' lab reports and formed the basis of some of their suggestions for extensions of the basic experiment.

The extent to which the data generated in the experiment are analyzed will be guided by the background of the students, the goals of the course in which the experiment is used, and the final design of the experiment in terms of factors and response variables. Our course is one in which development of quantitative skills is paramount, but we have nonetheless used only basic statistical procedures such as the t-test and analysis of variance (ANOVA).

Experiment 1: Optimal Food Choice

For this experiment, the hypothesis to be tested is that birds will adhere to the trend observed by Sih and Christensen (2001) and prefer foraging on sunflower kernels rather than sunflower seeds, because of the added handling time for the latter. We found that kernels and seeds do not differ in mass at the resolution provided by our balance. That is, the average number of kernels in 200 g of food and the average number of seeds in 200 g were not significantly different. Thus, the only variable in play is the added cost of removing the shell from the seeds. The feeders are all placed in the same habitat and arranged in pairs separated by ≥10 m, with the feeders in each pair separated by ~1 m. One feeder in each pair is filled with a set mass of sunflower seeds, and the other feeder is filled with the same mass of sunflower kernels. The feeders are regularly checked and refilled over a period of time, and the total volume of depletion is contrasted between food types.

During the spring of 2012, six pairs of feeders were checked twice daily for 5 days, once in the morning to measure overnight and early-morning foraging and once in the late afternoon to measure foraging during the day. Once the depletion data were log transformed to improve normality (Zar, 1999), they were analyzed using a two-way ANOVA, and there was no difference in depletion based on food type ($F_{1,20} = 1.19$, $P = 0.29$) or foraging time ($F_{1,20} = 2.15$, $P = 0.16$) (Figure 2). Further, there was no interaction between food type and foraging time ($F_{1,20} = 0.03$, $P = 0.86$). It is possible that the cost of shelling the sunflower seeds is negligible, but it is also possible that sunflower kernels represent a novel food item. Birds would not normally, in nature, encounter kernels without a shell and may not have exhibited a preference for them as a result. These points make excellent topics for discussion with students.

Experiment 2: Optimal Location & Time

This experiment focuses on the tradeoff between metabolic demands and predation avoidance. Most birds that use feeders are relatively
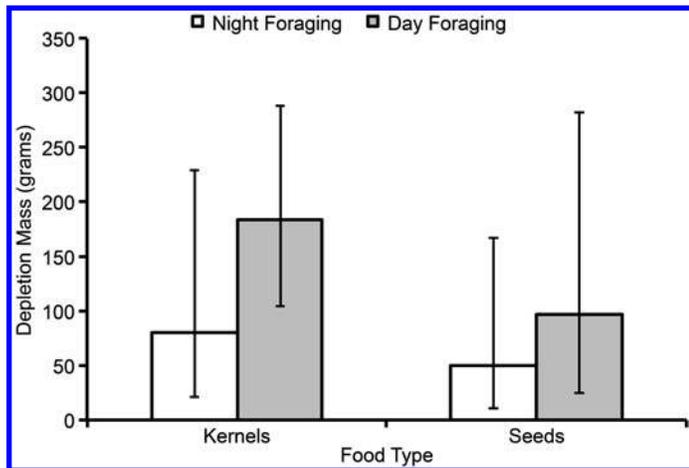
Figure 2. The mass of food (sunflower kernels and seeds) depleted over the observation period by birds foraging at night (or early in the morning) and during the day. Bars represent means ± 95% confidence intervals.
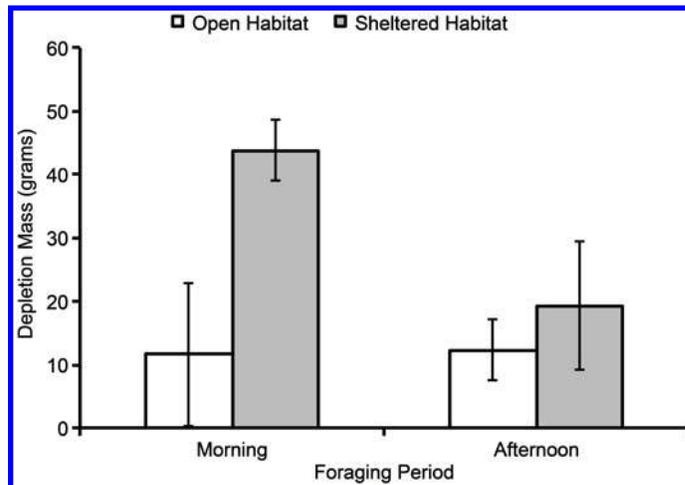

Figure 3. The mass of food (sunflower seeds) depleted over the observation period by birds foraging during the morning and afternoon in an open habitat (field) and sheltered habitat (woodlot). Bars represent means ± 95% confidence intervals.

small endotherms, so they use considerable energy maintaining body temperature to compensate for heat loss. This is especially important at night, when temperatures generally decrease, and birds without sufficient foraging success risk starvation (Lima, 1986; Cresswell, 1998; Olsson et al., 2000). However, a large meal can represent a substantial increase in short-term mass for such a small animal and cause reductions in agility that increase the risk of predation, so birds are expected to forage later in the day if resources are predictable and/or if predation risk varies with mass (Olsson et al., 2000; MacLeod et al., 2005). By contrast, if resources are unpredictable and/or located in a relatively safe environment, early-morning foraging is predicted to dominate because of the need to replenish food reserves expended during the previous night and the low cost of decreased maneuverability (Schneider, 1984; Olsson et al., 2000). Relatively safe environments for small birds are those that provide shelter, such as woodlots and brush piles (Grubb & Greenwald, 1982; Schneider, 1984).

To test the preferred location and time for foraging by birds, the experiment uses two habitat types (open and sheltered) and three observation times (0700, 1200, and 1700 hours). During the spring of 2013, the open habitat was a field, and the sheltered habitat was a beech–maple woodlot. The observation at 0700 hours was employed to reset the feeders for each day. The observations at 1200 and 1700 hours measured morning and afternoon foraging, respectively. We placed 10 feeders in the field and 10 feeders in the woodlot. The feeders were monitored for 4 days, and total depletion of food (sunflower kernels) was contrasted between habitats and foraging times using a two-way ANOVA. Foraging differed significantly between both habitats ($F_{1,36}$ = 11.21, P = 0.002) and foraging times ($F_{1,36}$ = 4.13, P = 0.05). More importantly, there was a significant interaction between habitat and time ($F_{1,36}$ = 4.61, P = 0.04). Subsequent t-tests revealed that depletion of food was (1) significantly greater in the woodlot than in the field in the morning (t_{18} = 3.15, P = 0.006) but not in the afternoon (t_{18} = 1.23, P = 0.23) and (2) significantly greater in the morning than in the afternoon in the woodlot (t_{18} = 2.47, P = 0.02) but not in the field (t_{18} = 0.11, P = 0.92). Thus, birds preferred to forage in the woodlot in the morning

over all other habitat × time combinations (Figure 3). This outcome supports our predictions and suggests that the birds perceived the food in the feeders as an unpredictable resource (i.e., a resource that is not consistently available at a given time and/or location; Olsson et al., 2000). An extension of the experiment would be to leave the feeders in place for an extended period, thereby causing a change in the perception of resource predictability, and repeat the observations.

Experiment 3: Optimal Location & Simulated Predators

This experiment was designed by students during the spring of 2012 after they completed Experiment 1. The students brainstormed possible extensions of the experiment, and they ranked those extensions to determine which experiment would be conducted (Table 2). The winning project was designed to measure the role of predation risk in decisions regarding foraging location by introducing models of a potential predator. The models were 40.5-cm-tall plastic owls with heads that bobbed and rotated with the breeze to appear more lifelike ("Garden Defense Owl," Easy Gardener Products, Waco, TX). The overall design was similar to that of Experiment 2, with feeders established in sheltered (woodlot) and open (field) habitats. Those conditions were altered by placing the owl models near half of the feeders in each habitat.

During the spring of 2012, there were two variables (habitat, predator) with two levels each (field, woodlot; owl, no owl). Each habitat × predator condition had three feeders, and the feeders were monitored for 6 days. Total depletion of food (sunflower kernels) was contrasted between habitat and predator conditions using a two-way ANOVA with log-transformed data. Foraging differed significantly between both habitat ($F_{1,8}$ = 8.89, P = 0.02) and predator conditions ($F_{1,8}$ = 8.65, P = 0.02), and there was no interaction between habitat and predator presence ($F_{1,8}$ = 0.99, P = 0.35). The birds foraged mostly in the sheltered habitat in the absence of a predator model, and least in the open habitat in the presence of the model, as the students predicted (Figure 4).

Table 2. Survey sent to students that allowed them to rank five proposed extensions of Experiment 1 that they brainstormed. The first extension was the winning choice, and its implementation is described under Experiment 3.

| Please rank the following experiments in order of your preference (1 = most preferred, 5 = least preferred).	
Project	Rank
Incorporate predation risk into the previous experiment by placing a model of a predator near some feeders, and test the prediction that birds will avoid feeders near the model.	
Incorporate predation risk into the previous experiment. The feeders are set up in groups of four: shells in the woods, kernels in the woods, shells in the open, kernels in the open. We can then simultaneously evaluate the effects of both food profitability and predation risk on foraging decisions.	
Examine the effect of seed type on subsequent behavior. Observe birds foraging to test the prediction that birds eating seeds in shells will be more likely to take a seed from the feeder, but then fly to cover to eat it. Birds eating kernels will be more likely to stay on the feeder, since handling time is reduced.	
Examine the effect of food quality on foraging decisions. Here, use two food types that are similar in handling time but that differ in nutritional value. In the previous experiment, foods differed in handling time but were equivalent in nutritional value.	
Examine the role of human disturbance on bird foraging. This experiment involves setting up feeders in identical habitats with one type of seed. Half of the feeders are refilled twice per day, and the other half are refilled every other day. The prediction is that birds will visit the less disturbed feeders at a higher rate.	
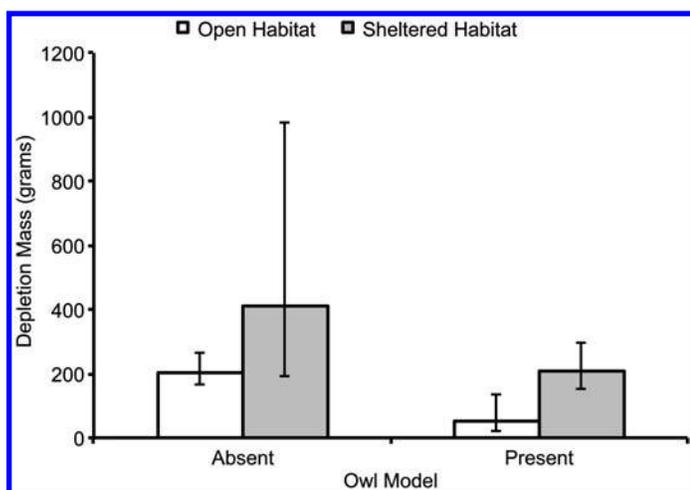
Figure 4. The mass of food (sunflower seeds) depleted over the observation period by birds foraging in an open habitat (field) and sheltered habitat (woodlot) in the absence or presence of a predatory owl model. Bars represent means ± 95% confidence intervals.

○ Conclusion

The three experiments described above exemplify how a little creativity combined with minimal infrastructure can allow for the testing of rather sophisticated ecological hypotheses. The extent to which the theoretical basis for the experiments is explored and the collected data are analyzed will depend on the audience for the experiments, but they can work well at a variety of levels and have been received positively by our students. For example, the following are a few responses from students to the question "Did this experiment [Experiment 3] help you to understand optimal foraging theory? Why or why not?"

"It did, with the previous seed vs. kernel experiment [Experiment 1] it narrowed down how animals make decisions to get the most out of feeding."

"This experiment helped because the decisions made by birds was [*sic*] dictated by resource availability, proximity of food, and predation risk."

We plan to continue the use of these experiments as both self-contained field projects and as springboards for expansion. Once students are familiar with the basic methods, there are many directions that additional work can take, and the students benefit from taking ownership of the projects they complete (e.g., comparing species-specific visitation rates or considering how patch arrangement and travel time affects foraging decisions). The following responses are from students asked "What did you think about the process of students suggesting ideas and voting for the second version of the optimal foraging experiment?"

"It was great to see that the professor [*sic*] were actually interested in what the students thought. Usually, the experiments are given to us with no suggestions from the students but the fact that we got a say in something made us feel more like growing scientists."

"Liked it a lot. Was really the first time students designed their own experiment, usually you just follow lab manuals."

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