ABSTRACT
Optimal foraging theory explains that organisms whose foraging is as energetically efficient as possible should be favored by natural selection. However, many individuals must exhibit trade-offs between foraging and other factors in their environment (i.e., predation risk, competitive interactions). We present a hands-on activity for undergraduates using just a deck of cards, bingo chips, and dice to introduce ecological concepts of foraging theory, predator–prey interactions, and energy trade-offs. Specifically, this activity will focus on optimal foraging theory and giving-up density. Students should gain an understanding of how organisms balance predation risk and competitive interactions with energetic demands. Further, this activity can be scaled for nonmajors and introductory courses to introduce general ecological concepts, or for upper-division courses to explore advanced topics in foraging theory.

Key Words: Giving-up density; predation; competition; optimal foraging theory.

Introduction
Foraging is an essential behavior that allows organisms to obtain sufficient energy to meet their daily energetic demands. However, individuals must make a variety of trade-offs throughout their life history in order to balance foraging with other behaviors (i.e., avoiding predators, caring for young) and maximize fitness. Evolutionary theories of optimal foraging explain that natural selection should favor individuals that forage as energetically efficiently as possible, with the assumption that energy supplies are limited (Emlen, 1966; MacArthur & Pianka, 1966). However, foraging patches can vary in type (i.e., species, size), quality, and density of food items. When given a choice between more than one type of prey, a predator should forage to optimize effort and profit by balancing search and handling time with caloric gain. Theoretically, the most profitable prey should offer the greatest energy reward per unit time. A classic example of optimal foraging theory occurs with shore crabs (Carcinus maenas), which prefer intermediate-sized mussels (Mytilus edulis) over smaller mussels (less energy efficient) and larger mussels (greater handling time) because of the greater energy gain per unit time (Jubb et al., 1983).

Prey must also make trade-offs between foraging efficiency and predation risk when selecting a foraging patch (Lima et al., 1985; Gilliam & Fraser, 1987). Ideally, prey should choose to forage in patches that are the most profitable until the risk of predation becomes too high. Eventually, a threshold is reached where the risk of predation outweighs the benefit of continued feeding and prey must move to another patch. Similarly, predators that optimize energy intake should aggregate in patches that are most profitable. When overcrowding of predators occurs, intraspecific competition for limited food resources should cause habitat shifts in which predators switch to a different foraging patch. This may lead to predators choosing less crowded patches (those with fewer competitors) and/or lower prey density. Ecologists can calculate the giving-up density, the point at which the density of food within a given patch is no longer profitable, causing the foraging animal to move to another patch (Brown, 1988).

Rationale & Pre-Laboratory
Class Discussion (30 minutes)
Organisms, including humans, make important foraging choices every day – such as choosing where to eat and selecting a food item that tastes good, has certain nutrients and enough calories, and fits within their cost of living. Modern-day grocery stores, butchers, and restaurants, however, eliminate most trade-offs that other animals must make when foraging, by reducing the energy spent searching and handling food items, in addition to...
eliminating predation pressure while foraging. Foraging theory is complex and depends on many variables, including seasonality, time of day, density of prey/food items, predator assemblage, and competitive interactions. Although animals tend to forage to maximize fitness, humans do not always fit these models. This activity was developed for undergraduate students to experience some of the important trade-offs made during foraging, which ultimately lead to optimal foraging among food patches. Throughout, they must balance energetic needs against the risk of predation, food density, and competitive interactions. Then, students are asked to analyze and interpret data they have collected. This activity gives students a hands-on experience that they can later apply to concepts in foraging theory, predator–prey interactions, and habitat selection and has been successful with both nonmajors biology and upper-division ecology courses. Although we have not completed this activity with high school students, it is possible that this activity could be handled at the high school level with some changes in the assessment and pre-laboratory activities.

Prior to the activity, discussion can be generated around the factors that influence the student's choices throughout the day. You could focus specifically on eating behaviors by asking them what influences their feeding patterns and choices. If time permits, you could extend the conversation to energy and time budgets in general. The goal is to get students to think about what kind of behavioral trade-offs they make during a day and, ultimately, discuss how these decisions may affect their overall fitness. More specifically, this conversation can be prompted by talking about the decisions or trade-offs they make when they are at the grocery store. Students usually answer with the price of the item, how healthy the food is, the taste, how it looks (freshness, damage, labels), and the expiration date, just to name a few. We have found that this discussion is generally very productive among food patches. Predators and prey should own by choosing one predator, two prey (herbivores or primary carnivores), and food for the prey. Prey should be selected so that one is more energetically expensive (e.g., defense mechanism, size, escape behaviors) than the other to establish trade-offs for optimal foraging.

**Game Board Setup**

Divide students into groups of eight, with three designated as predators (owls) and five as prey (skunks). Randomly distribute the jack, queen, and king cards to the owls, and cards 2 through 6 to the skunks (one card per student). To set up the game board, designate four areas on the table as separate foraging patches and distribute the appropriate number of chips to each patch (see Figure 1). Each red chip represents one mouse, and each green chip represents one vegetation bundle.

**Game Rules Overview**

Once a skunk has collected 12 vegetation bundles, they have some protection (enough energy to spray) against the owls (explained further below). This should encourage students to forage optimally.

**Turn Order**

- Skunks (cards 2–6) always play before owls (cards J–K).
- Players play in order of their card’s number (see below).
- Each player’s turn consists of moving to a new patch (optional) and then foraging for resources (required).
- Each player completes their entire turn before the next player begins.

### Materials (for a group of eight students)

- Deck of cards (2–6, jack, queen, and king)
- Two colors of bingo chips (at least 75 of each color; red and green used here)
- A rolling die
- Printable order-of-play cards and data sheets are available at [http://jenniferclark626.wordpress.com/teaching-resources/](http://jenniferclark626.wordpress.com/teaching-resources/)

### Food Web Introduction

At the beginning of the laboratory, introduce the food web that will be used for the activity. We use great horned owls as the top predator, white-footed mice and striped skunks as prey for the owls, and vegetation bundles as a food resource for both mice and skunks. Students will take on the role of owls and skunks. During this discussion, it should be made clear that the skunk is energetically more costly than the mouse as a prey item because of the skunk’s spraying defense and its lower density in foraging patches. Depending on time, you can use this suggested food web or have students develop their own by choosing one predator, two prey (herbivores or primary carnivores), and food for the prey. Prey should be selected so that one is more energetically expensive (e.g., defense mechanism, size, escape behaviors) than the other to establish trade-offs for optimal foraging.

**Laboratory Activity (30–45 minutes)**

During this activity, students will act as predators and prey foraging in patches of variable prey/food density. Predators and prey should forage optimally to acquire as much food as possible, while prey must also avoid predators. The goal is to survive until the end of the game with the most prey/food items. It is helpful to offer a small incentive to the winner(s) to promote thoughtful engagement during the activity.

**Figure 1.** The game should be set up on a table top with four patches. Circles represent bingo chips (G = green chips, R = red chips). Patch 1: two green, one red. Patch 2: three green, two red. Patch 3: five green, three red. Patch 4: eight green, four red.
Resource Chips
- Red chips are owl resources (mice), and green chips are skunk resources (vegetation).
- Skunks may not eat mice.
- All resource chips acquired throughout the game should be placed on top of the player's card.

Moving to New Patches
- At the beginning of each player's turn, they can choose to move to a new patch or stay in the current patch prior to foraging. Each player may only forage within a single patch on each turn.
- If the player moves, they must remove one resource chip from their card, place it back into the supply, and then move their card to the patch of their choice.
- Owls and skunks may want to consider moving if there are competitors in their patch that will forage on limited resources before them.
- Skunks may want to move if there are owls in their patch, making attack more likely.

Skunk Foraging
- Players (both skunks and owls) can forage only in the patch that they occupy.
- Each skunk must forage once, and only once, per round.
- A skunk removes one chip from their card (the energy cost of foraging), places the chip back into the supply, rolls the die, and takes that number of green chips from the occupied patch.
- The maximum number of resource chips acquired on each turn is limited to the total number of chips in the patch on the player's turn.
- If the resource chips are depleted from a player's patch before their turn, they must move to a new patch to forage; if they have no more chips after moving, they do not survive and are removed from the game.
- Skunks build up a defense after collecting 12 chips. If attacked successfully by owls, they lose half of their green chips but remain in the game until successfully attacked again.

Owl Foraging
- Owls have two options for foraging in each round — mice (required) and skunks (optional) and can do both if they have enough red chips. Owls must always forage for mice before skunks and cannot forage for mice after they have foraged for skunks.
- To forage for mice, the owl removes one chip from their card (the energy cost of foraging), places it back into the supply, rolls the die, and takes that number of red chips from the occupied patch.
- To forage for skunks, the owl must remove two red chips from their card, place them back into the supply, and roll the die. If the number rolled corresponds to the number of one of the skunks in the patch, that skunk is removed from the game (but see defense rule above), and the owl retains the skunk's card until the end of the game.
- The owl may choose to forage for skunks as many times as they wish, as long as they have two red chips available.

Replenish Resources
- First, roll the die for each patch individually and add that number of green chips from the supply to the patch.
- Then, add one red chip from the supply to each patch for every two green chips on that patch, rounding down.
- Note: Since it costs resource chips to forage, if any owl or skunk ends a turn with no chips left, they are immediately removed from the game.

Step-by-Step Specifics of Game Play

Setup Round
1. First, all skunks must choose a starting patch, starting with the 2 card.
2. Next, all owls must choose a starting patch, starting with the J card.
3. All skunks, in the same order, roll the die to take starting resources.
   - One chip taken for rolling an odd number; two chips taken for rolling an even number.
4. Then, owls perform step 3 to take starting resources.
5. Replenish resources.
6. All cards should now be placed on the playing area, with the remaining resource chip supply piles placed to the sides of the playing area (Figure 2).

Four Rounds of Play

Round 1 (start with the 6 card for skunks and K card for owls)
1. Each skunk moves to a new patch (optional, costs one chip) and forages (required, costs one chip).
2. Record the movement of each skunk (did they move or stay?) and the reason for that decision (Table 1).
3. Record the prey density (red chips plus number of skunk cards) in the patch occupied by each owl prior to foraging or moving (Table 2)
4. Owls move (optional, costs one chip) and forage for mice (required, costs one chip), then forage for skunks (optional, costs two chips). Remember: owls must feed on mice before skunks.
5. Record the movement of each owl (did they move or stay?) and the reason for that decision (Table 2).
6. Replenish resources.

Round 2 (start with the 2 card for skunks and J card for owls)
Round 3 (start with the 6 card for skunks and K card for owls)
Round 4 (start with the 2 card for skunks and J card for owls)
- Follow the same procedure from Round 1 for Rounds 2, 3, and 4.
- Do not replenish resources after Round 4.
**Figure 2.** A possible configuration of patches and players during gameplay, showing the setup of cards and chips in play in the four patches, how chips should be stacked on cards, and the supply piles. The J-card owl and 5-card skunk are in patch 3 (foreground). If this owl were to roll a 5 on its foraging turn, this skunk would be removed from the game and the owl would receive one red chip from the mouse supply (half of the three green chips on the skunk card, rounding down).

**Table 1.** Data sheet used for skunks (prey) that includes qualitative data collected during an actual classroom iteration. Answers generally include lack of food within a patch, an abundance of food, too many skunks, and/or too few mice, making attack likely. A column for vegetation density can also be used to calculate giving-up vs. stay-in-patch density (as shown in Tables 2 and 3 for owls).

<table>
<thead>
<tr>
<th>Round</th>
<th>Playing Card</th>
<th>Did You Stay in the Patch or Move?</th>
<th>Behavioral Decisions</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>6</td>
<td>stay</td>
<td>abundance of food (to build up defense)</td>
</tr>
<tr>
<td>1</td>
<td>5</td>
<td>stay</td>
<td>wanted to save resources</td>
</tr>
<tr>
<td>1</td>
<td>4</td>
<td>stay</td>
<td>abundance of food</td>
</tr>
<tr>
<td>1</td>
<td>3</td>
<td>stay</td>
<td>no predators in patch</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>move</td>
<td>no food resources available</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>move</td>
<td>predators present</td>
</tr>
<tr>
<td>2</td>
<td>3</td>
<td>stay</td>
<td>abundance of food resources and no predators</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
<td>stay</td>
<td>abundance of food</td>
</tr>
<tr>
<td>2</td>
<td>5</td>
<td>move</td>
<td>no food resources available</td>
</tr>
<tr>
<td>2</td>
<td>6</td>
<td>move</td>
<td>too many predators present</td>
</tr>
<tr>
<td>3</td>
<td>6</td>
<td>move</td>
<td>no food resources available</td>
</tr>
<tr>
<td>3</td>
<td>5</td>
<td>move</td>
<td>no food resources available</td>
</tr>
<tr>
<td>3</td>
<td>4</td>
<td>move</td>
<td>more food available in another patch</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td>stay</td>
<td>abundance of food resources</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>stay</td>
<td>enough food resources available</td>
</tr>
<tr>
<td>4</td>
<td>2</td>
<td>stay</td>
<td>enough food resources available</td>
</tr>
</tbody>
</table>
When there are no skunks left, only one owl remains, and/or at the end of Round 4.

Last remaining owl and skunk both win.

Tiebreaker – highest score wins:
- Owl: one point for each red chip on card, five points for each skunk card acquired.
- Skunk: One point for each green chip on card.

Post-Laboratory Discussion & Lecture (30–45 minutes)
Following the activity, have students share all numerical and behavioral data to combine into one dataset for analysis. Then, generate discussion on foraging theory using the behavioral data collected. Some questions we have used are

- What are the trade-offs that skunks (prey) and owls (predators) made while foraging?
- Which strategies were most effective?
- What ecological factors would make you change your strategy?
- How did the presence of conspecifics alter behavior of both predators and prey?

After discussion, introduce terms associated with foraging theory: optimal foraging theory, handling time, search time, search image, risk-sensitive foraging, and giving-up density. Introducing these concepts after the activity allows students to generate their own thoughts on foraging theory and on factors driving predator–prey interactions. Lecture notes are available at http://jenniferclark626.wordpress.com/teaching-resources/. For upper-division students, an article discussion can allow for exploration of advanced topics during the following class period. Some suggestions: Cowie, 1977 (great tits); Harper, 1982 (mallards); Jubb et al., 1983 (shore crabs); Lima & Valone, 1986 (gray squirrels).

Assessment
The following question set can be given as a take-home or an in-class assignment. This question set is intended for an upper-division ecology course and can be modified (i.e., removing standard-error calculation and/or statistical analysis) to fit the level of your students.
Students are given instructions on how to calculate standard error and run a t-test during the post-laboratory discussion and lecture.

1. (A) Make a graph displaying the average giving-up density versus the average stay-in-patch density for owl predators. Your graph must include standard error bars (see Table 3 for an example datasheet correlating with raw data collected [Table 2] and Figure 3 for an example graph generated from data collected). (B) Analyze your results using a Student’s t-test to determine whether giving-up density and stay-in-patch density are significantly different. (C) Interpret your graph and statistical analysis. As part of your interpretation, discuss exactly what the dataset means ecologically and discuss how the results are related to optimal foraging theory.

2. Find a peer-reviewed journal article that supports or contradicts behaviors and/or giving-up density results from the activity. Write a summary of the results from this study and discuss how it supports or contradicts the results from our laboratory activity. Provide the full citation.

3. Did the top skunk and owl (those that survived with the most food) forage optimally? Explain, using the optimal foraging theory.

**Acknowledgments**

We thank the students in Beginning Field Biology and General Ecology at Hiram College for allowing us to test this activity in the classroom. We give special thanks to Thomas Koehnle, Robert Krebs, and an anonymous reviewer for comments on the manuscript.

### Table 3. Data sheet used to calculate average giving-up density and stay-in-patch density from data collected during an actual classroom iteration (see Table 2).

<table>
<thead>
<tr>
<th>Giving-up Density (Prey Density When Owl Moves)</th>
<th>Stay-in-Patch Density (Prey Density When Owl Does Not Move)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>8</td>
<td>10</td>
</tr>
<tr>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td><strong>Average ± SE</strong> = 5.5 ± 1.89</td>
<td><strong>Average ± SE</strong> = 7.25 ± 0.96</td>
</tr>
</tbody>
</table>

**Figure 3.** Graph generated to answer assessment question 1 using data collected during an actual classroom iteration (see Tables 2 and 3). Bars represent average (mean ± SE) giving-up and stay-in-patch density for owls.

**References**


