Optimal Foraging Theory and Western Gray Squirrels (*Sciurus griseus griseus*)

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Abstract

Optimal foraging theory states that animals prefer high energy foods to low energy ones. We tested this theory and hypothesized that western gray squirrels (Sciurus griseus griseus) would prefer higher calorie cheddar cheese cubes over lower calorie white bread cuboids. We offered ninety-eight squirrels small piles of cheese and bread and observed which food item they chose to consume or cache. The squirrels took significantly more cheese than bread, thus reaffirming optimal foraging theory's predictions. However, many factors, including weather, the distracting proximity of peanuts, and the presence of rival crows may have construed our data, and further research should consider such variables.

Keywords: foraging, optimum foraging theory, squirrels, food choice
Optimal Foraging Theory and Western Gray Squirrels (*Sciurus griseus griseus*)

All animals need food and an intake of energy in order to survive. For some species, foraging can be extremely costly in terms of time lost while searching or handling a food item, energy expended to reach it, or the dangers encountered while foraging. In order for an animal's foraging strategy to be worthwhile, the benefits from the food must be great enough to compensate for the risks. Optimal foraging theory states that natural selection favors foraging behaviors that maximize an animal's net energy intake rate and therefore allow it better fitness. It asserts that animals rank food items by the ratio between energy gained by consuming it and energy lost searching for and handling it and predicts that they prefer higher energy foods (Pyke et al. 1977). Simply put, it maintains that, given a choice, an animal will choose foods that provide more energy and require less energy to obtain it than food with less energy and require a greater effort; energy is usually measured in calories.

Previous studies, such as Lewis's 1982 study on eastern gray squirrels (*Sciurus carolinensis*), have shown that some animals do exhibit a preference for more nutritional foods. Other studies, however, have indicated that additional factors affect animals' optimal foraging behavior beyond simple caloric value, including patch quality (Cowie 1977), food temperature (Kilpatrick 2003), and food abundance (Engen and Stenseth 1984).

We sought to reaffirm the basic idea of optimal foraging theory that a food's energy value. We conducted a much simpler experiment on western gray squirrels (*Sciurus griseus griseus*) by presenting them with lower calorie cuboids of bread and higher calorie cheese cubes and observing which food item they preferred. We hypothesized, as per optimal foraging theory, that squirrels would choose more cheese than bread.

**Methods**
Subjects

We passively observed a total of ninety-eight western gray squirrels that lived on the University of Washington campus. They were well-acclimated to human presence and were not deterred from approaching the food by our close proximity. Some squirrels could be differentiated by distinguishing features, such as shortened tails or larger body sizes; however, no formal methods were used to identify them. The squirrels were allowed to approach, retreat from, and return to the mat at will.

Materials

We used 1 cm cubes of Tilamook medium sharp cheddar cheese and 2 cm cuboids of Wonderbread white bread to attract the squirrels. We placed small piles of both food items on a 27.94 by 43.18 cm laminated, white paper mat that was divided into quadrants by fine, printed black lines. The mat did not seem to discourage the squirrels from approaching or touching the food.

Design

This was a simple between subjects observational study. The independent variables were bread and cheese, and the dependent variable was the squirrels' food preference, which was measured by the number of pieces that each squirrel took.

Procedure

Observations took place during three days in the northern half of Grieg Garden, one of the squirrels' habitats on campus that consisted of a small area of lawn surrounded by various trees and shrubs and ringed by a concrete pathway. Each observation session lasted for approximately ninety minutes each day in the mid to late morning.
Each observation day, we set the mat on the ground in different parts of Grieg Garden. On the first day, we put it in the northernmost inner flowerbeds at the foot of a tree, but then moved it to a small space between two shrubs in the flowerbeds along the west side of Grieg Garden. The next day, we laid it in the outer flowerbeds in front of the trees and bushes. The mat was placed on the northwestern half of the lawn on the third day. The mat was always placed within the squirrels' foraging range and in unobstructed, easily-accessible areas.

We piled equal amounts of cheese cubes on one half of the mat and bread cuboids on the other. Since both food items were situated close to each other and readily available, the foraging costs for both were equal. We waited for squirrels to approach the mat, and then recorded whether they took a piece of bread or cheese and, if more than one, how many pieces. We only noted squirrels that had taken a food item. A squirrel was considered to have taken a piece food if it picked up the bread or cheese with its mouth or paws and consumed at least half of it at or near the mat, carried it out of sight, or buried it.

**Results**

A total of 98 squirrels approached the mat and took a piece of cheese, a piece of bread, or both. As Figure 1 shows, a total of 126 pieces of cheese and 76 pieces of bread were taken; the squirrels took a total of 202 pieces of food. Figure 2 shows how many squirrels took more than one piece of bread, more than one piece of cheese, or both. Table 1 summarizes the mean number of cheese cubes and bread cuboids taken by each squirrel.

Squirrels did show a preference for cheese over bread. By conducting a $\chi^2$ test, we determined that each squirrel took significantly different amounts of bread and cheese than was expected, $\chi^2(1, N = 89) = 12.38, p = 0.0004$. Additionally, using a one-tailed t-test, we found that
they took a significantly greater number of cheese cubes (M = 1.41, SD = 2.36) than bread cuboids (M = 0.85, SD = 1.12), t(176) = 2.93, p < 0.0018.

Discussion

Optimal foraging theory states that animals forage in a way that will maximize their rate of energy intake and predicts that they prefer higher energy foods. We tested this theory by providing western gray squirrels with small piles of cheese and bread and observing which food item they took and how many pieces. Our results confirm our hypothesis. If squirrels did not forage as optimal foraging theory predicts, then, out of the total two hundred and two pieces of food taken, then we would expect them to choose equal amounts of bread and cheese. However, they took significantly greater amounts of cheese and significantly less amounts of bread than was expected. Additionally, they took a significantly greater number of cheese cubes than bread cuboids, which suggests a preference for cheese over bread, and therefore a preference for higher calorie foods.

Although our results support optimal foraging theory, several external factors could have interfered with our data. On the first day of observations, the outdoor temperature was approximately 4 degrees Celsius, and the weather was windy and lightly raining. Only a few squirrels approached the mat, and some that did showed no interest in the piles of food. The temperature of the food may have contributed to their indifference: studies have shown that American crows and eastern gray squirrels prefer warmer foods to colder ones (Kilpatrick 2003), and western gray squirrels may share this preference. Furthermore, we observed more squirrel activity on subsequent, warmer days.

It is more likely, however, that the squirrels that ran past our mat were lured away by peanuts. Another group that was conducting an experiment using peanuts had set up their
equipment on the other side of the flowerbed to the left of ours, and, although empirical studies have yet to confirm it, it seems that squirrels vastly prefer peanuts to white bread and cheddar cheese. This predilection for peanuts may explain the squirrels' disinterest in our proffered food; in their haste to get to the peanuts, several squirrels ran over our mat and the food without giving them as much as a curious sniff.

Our lack of adequate data on the first day may also be due to the simple possibility that the squirrels were not initially habituated to the presence of humans and piles of bread and cheese and were wary of approaching the mat. By the third day, they may have become more used to the presence of observers and the mat and were less hesitant to approach the food.

The presence of crows also affected the squirrels' foraging behaviors. American crows (Corvus brachyrhynchos) also reside on campus and compete with the squirrels for food. We noted them gathering in the nearby trees and heard them calling to each other at random intervals throughout the observation periods. Although we endeavored to chase off any birds that approached the mat, a few were able to take pieces of cheese. The crows' presence affected the squirrels' actions. Crows spotted the offered food earlier in the observation session, and their calls to summon their kin may have also alerted squirrels of the presence of food; shortly after the crows called, the number of squirrels that approached the mat increased. However, the sounds also may have deterred them. On the first day, the birds perched in the tree closest to the mat, and their proximity may have made some squirrels reluctant to approach the food. On the second and third days, many of the squirrels that were in the midst of approaching the mat when a crow cried turned and ran back in the direction from which they came. Those that were at the mat when they heard the crows immediately absconded with their chosen food item to
underneath the bushes. It is possible that squirrels might have been more willing to approach the mat had their competitors been absent.

Although the results of this study confirm the predictions of optimal foraging theory, they should be repeated and confirmed by further investigation. The simplistic nature of our study did not control for or consider many of the variables that could have affected squirrel choice, such as weather, the presence of more appealing foods, and the presence of competing species. Additionally, as other studies have suggested, caloric value is not the only factor that affects animals' food choices. Future studies should control for these factors and conduct the experiments in a laboratory setting in order to determine if energy is truly one of the main driving forces behind foraging strategies.
References


Figure 1. Number of Bread and Cheese Pieces Chosen. Squirrels chose a total of 126 pieces of cheese and 76 pieces of bread, a collective total of 202 pieces of food.
Figure 2. Number of Squirrels that Took Multiple Food Items. 7 squirrels took more than one piece of bread, 14 took more than one piece of cheese, and 11 took at least one of both.
Table 1

Mean and Standard Deviation for Number of Cheese Cubes and Bread Cuboids Taken by Each Squirrel

<table>
<thead>
<tr>
<th>Food Item</th>
<th>Mean</th>
<th>Standard Deviation</th>
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<tbody>
<tr>
<td>Bread</td>
<td>0.85</td>
<td>1.12</td>
</tr>
<tr>
<td>Cheese</td>
<td>1.42</td>
<td>2.36</td>
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