DRURY UNIVERSITY
HONORS PROGRAM

Nutty Behavior: Optimal Foraging Behavior of *Sciurus carolinensis*

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Background

The activity and patterns of feeding animals often are studied under the argument of optimal foraging theory, which predicts that foraging animals will search for and capture the food source which maximizes their net energy intake per unit time spent foraging (Charnov 1976). Factors such as predation risk, distance to nearest safety, temperature variation, food preference, and nutritional needs can also play a role in this decision making process. If predators are a prevalent concern, the time spent capturing food is even less, and foraging animals will choose the most abundant food source, no matter its energy content (Brown and Morgan 1995).

Within optimal foraging theory, this study focuses on optimal diet selection, addressing what an animal chooses to feed on (Ebersole and Wilson 1980). There are two main predictions in optimal diet selection: 1) foragers will prefer the food source with higher energy/handling time ranking (Krebs and McCleery 1984) and 2) food item preference is independent of abundance of the food type and depends only on the food's higher rank (Charnov 1976; Estabrook and Dunham 1976). This study focuses on whether or not squirrels will expend more energy and time to obtain a food with higher energy content rather than lower energy content

Previous results suggest gray squirrels are able to determine optimal time spent foraging based on previous experience in the environment. Specifically, individuals spent very little time digging in containers known to house low energy sunflower seeds and spent most of their foraging time in containers known to house high energy walnut seeds (Colligan and Jansen, unpubl. data). However, when seed types were randomized daily, individuals spent equal times digging in the various containers holding different seed types (Colligan and Jansen, unpubl. data). Further, individuals acquired more seeds that were easier to reach than more difficult when food sources were randomized, even if the more difficult seeds were higher in energy content (Colligan and Jansen, unpubl. data). This study will determine if eastern gray squirrels prefer a difficult to obtain high energy content food or an easy to obtain lower energy content food, thus determining whether they follow predictions of optimal diet selection.

Hypotheses

Under equal conditions, squirrels will optimize their effort foraging for walnuts instead of sunflower seeds, following the first prediction of optimal diet selection. Thus, more nuts will be taken from and more dig sites will occur at walnut platforms than sunflower seed platforms during Phase 1.

Under unequal conditions, squirrels with expend more energy foraging for less walnuts as food preference is independent of food item abundance, following the second prediction of optimal diet selection. Thus, more nuts will be taken from and more dig sites will occur at walnut platforms than sunflower seed platforms during Phase 2.

Methodology

The experiment was divided into two phases. Phase 1 tested whether squirrels followed the first prediction of optimal diet selection: food item preference is shown for higher ranking food. Phase 2 tested whether squirrels followed the second prediction of optimal diet selection: food item preference is independent of food item abundance and is dependent on food item ranking, where higher food item ranking is preferred.

Walnuts and sunflower seeds were chosen as food options as they vary in fat, crude protein, and calories. Walnuts have higher caloric, fat, and crude protein values, so this food source is higher ranking to squirrels (Chung et al. 2013). Sunflower seeds have lower values of fat and crude protein, so this food source is lower ranking to squirrels (Chung et al. 2013).

The experiment took place at Drury's campus. Six wooden feeding platforms were placed in a yard. Platforms were placed under tree coverage to limit predation risk. Experimentation took place within squirrel habitat, allowing for close mirroring of the natural setting. Six platforms were placed 3 m away from two similar trees, three at each tree, eliminating variable predation between platforms. Platforms remained in the same location during the experiment. Platforms were filled with sand substrate and randomly assigned a treatment of walnuts or sunflower seeds, so that three platforms contained walnuts and three contained sunflower seeds (see details in Phase 1 and Phase 2). Half an hour before sunrise, platform lids were removed until 1 pm, allowing squirrels to forage. Dig sites (larger than 1 cm) were then counted along with the number of nuts left at each platform. According conditions were reset for the next day.

Methodology (Continued)

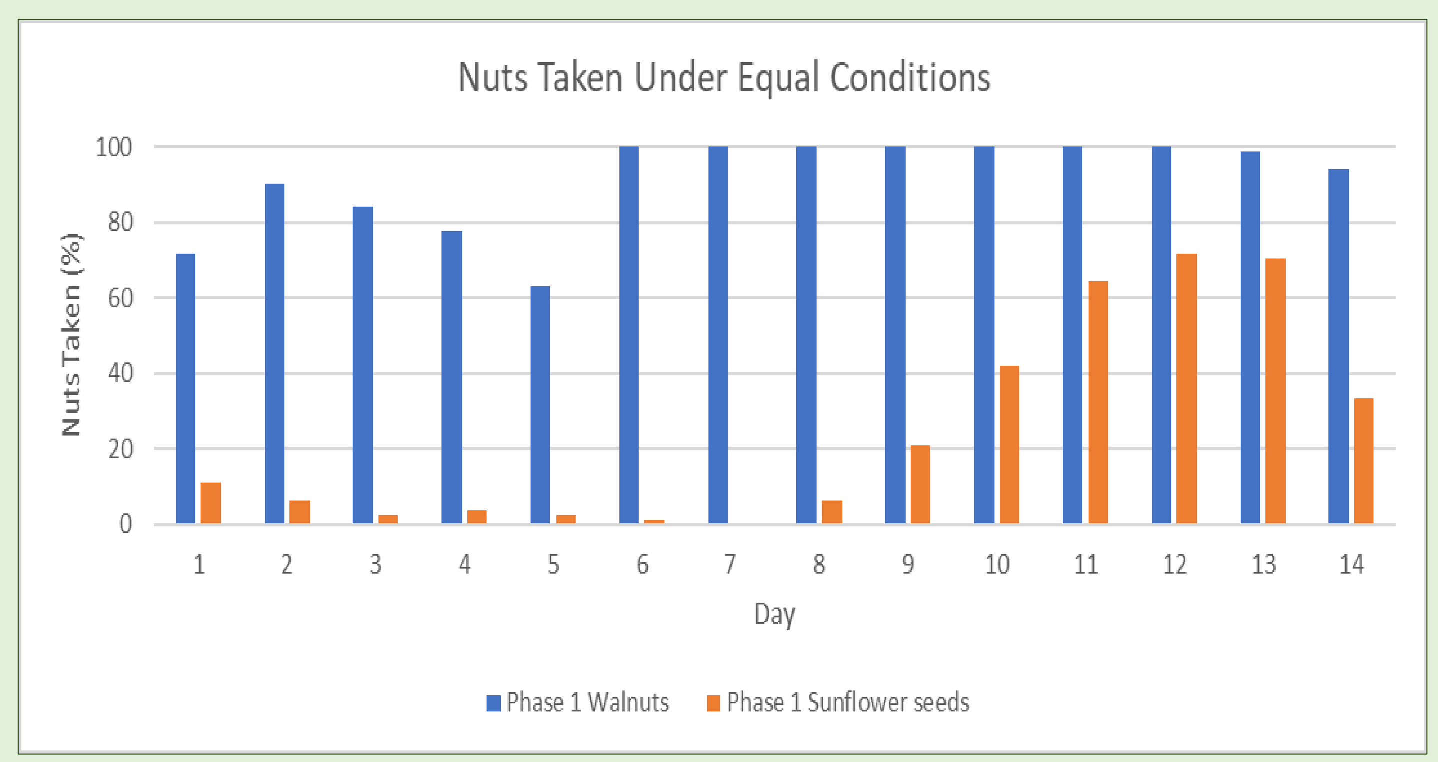
For both phases, data on number of food items taken from each treatment were analyzed using Mann-Whitney U tests as assumptions could not be met for Two-Sample T-tests. For both experiment phases, data on dig sites for each treatment were analyzed using Two-Sample T-tests. A significance level of 0.05 will be used for all tests, including a family-wise significance of 0.05 for both Mann-Whitney U tests and Two-Sample T-tests comparisons.

Phase 1: Equal Conditions
From the sand's surface within each platform, sunflower seeds or walnuts were placed in each platform (with layers occurring at 3 cm, 6 cm, and 9 cm depths, and 9 nuts occurring at each layer in a 3 x 3 formation). These conditions exhibit equal energetic expense, search time, and food availability. Platform conditions continued until squirrel foraging activity shifted, as determined by statistical significance, to walnut platform(s).

Phase 2: Unequal Conditions
Platforms containing walnuts as their food source had the 3 cm layer removed while the 6 cm and 9 cm layers still contained walnuts (again with 9 nuts at each layer in a 3 by 3 formation. Platforms containing sunflower seeds remained unchanged from Phase 1.

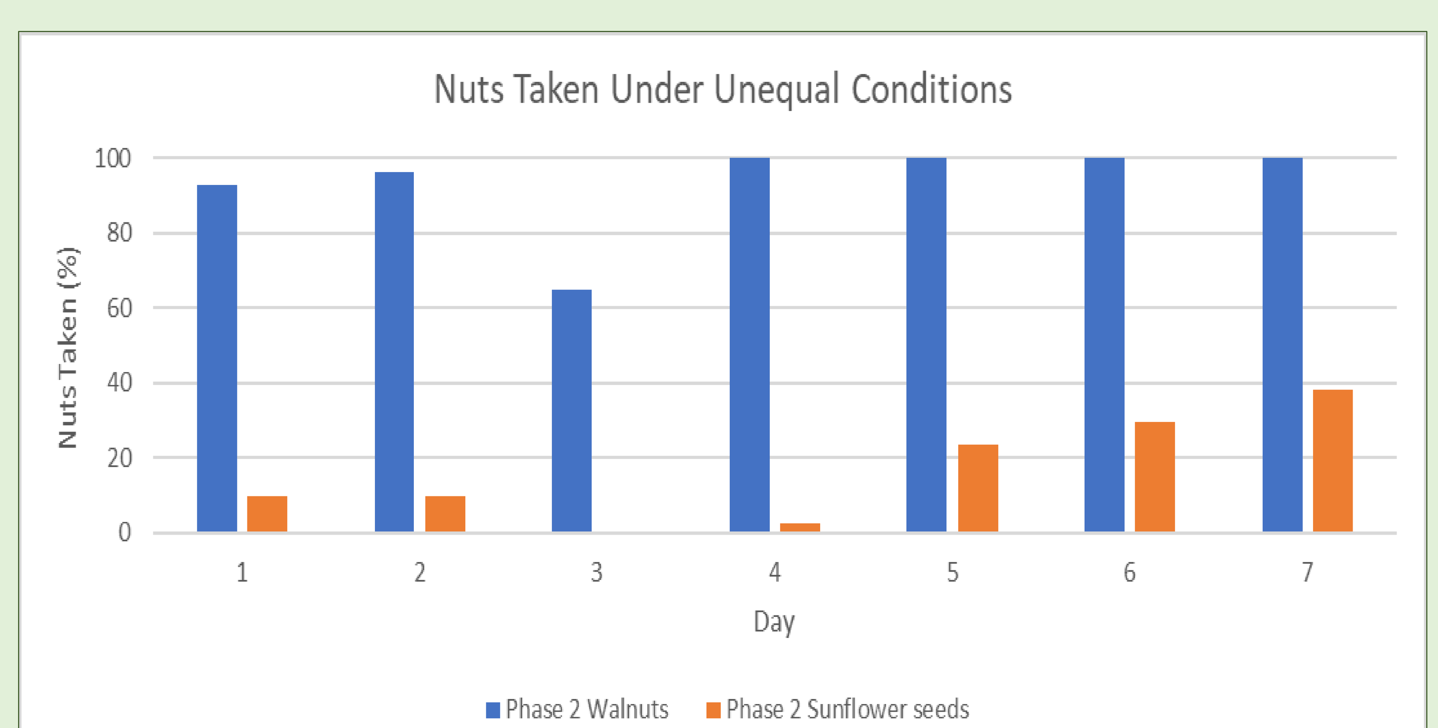
Results: Phase 1

Squirrels took 91.4 ± 13.1% (mean ± SD) walnuts and 24.0 ± 27.4% sunflower seeds per corresponding platform. Squirrels took was 24.7 ± 3.5 walnuts and 6.5 ± 7.4 sunflower seeds from each corresponding platform. Squirrels showed a significant preference for walnuts ($p < 0.001$). Squirrels made more dig sites, thus expending more energy, at walnut platforms with 16.0 ± 3.8 dig sites per platform compared to 9.0 ± 3.7 dig sites at sunflower seed platforms. Squirrels made significantly more dig sites at walnut platforms, thus expending more energy searching for and obtaining walnuts ($p < 0.001$).



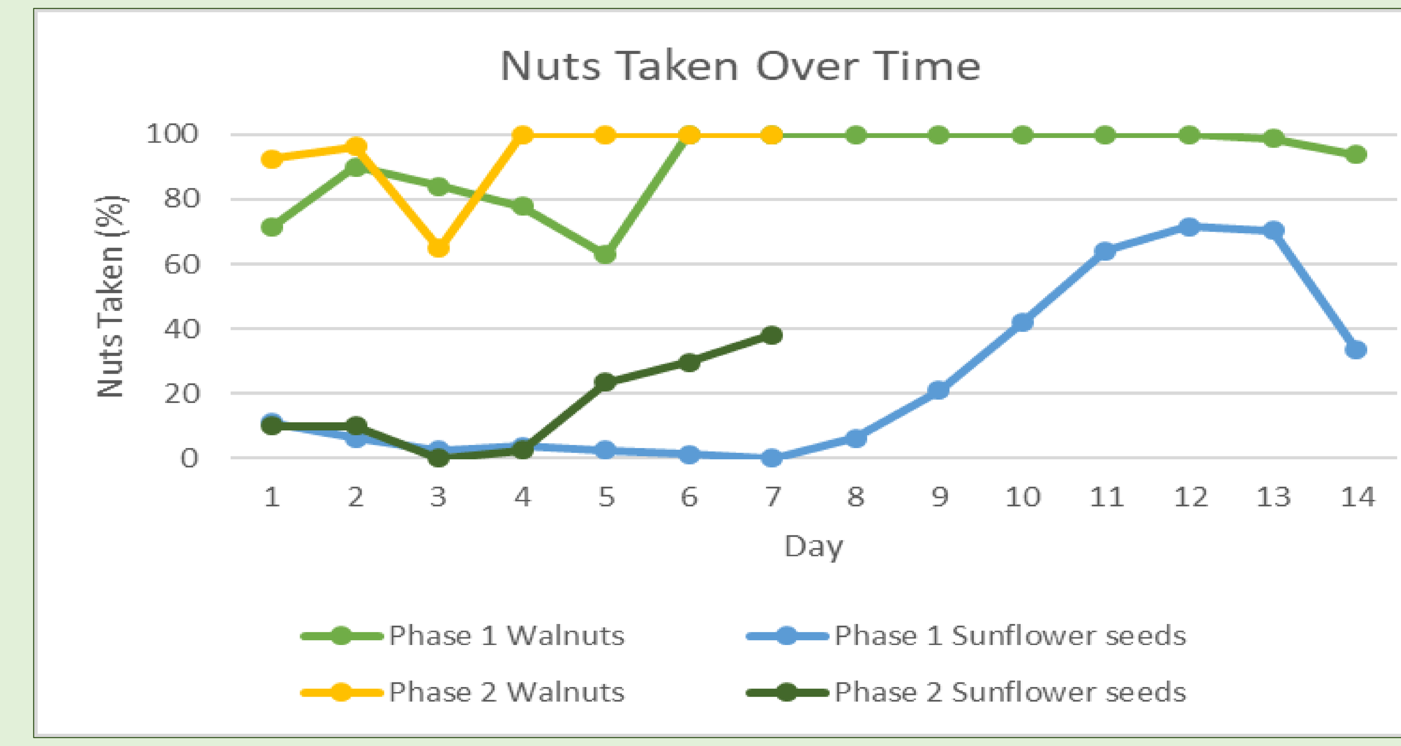
Results: Phase 2

Squirrels took 93.4 ± 13.7% of walnuts and 16.2 ± 16.5% of sunflower seeds per corresponding platform. Squirrels took 16.8 ± 2.5 walnuts and 4.4 ± 4.5 sunflower seeds from each corresponding platform. Squirrels significantly preferred walnuts ($p < 0.001$). Squirrels made more 20.4 ± 6.7 dig sites at walnut platforms compared to 9.5 ± 5.9 dig sites at sunflower seeds platforms. This difference was significant, showing squirrels expended more energy searching for and obtaining walnuts ($p < 0.001$).



Additional Results

Squirrels exhausted high-calorie food sources before consuming low-calorie food. This can be seen below by the lag time between taking the maximum amount of walnuts available and the increase in amount of sunflower seeds taken while still taking all walnuts available under both equal and unequal conditions.



Discussion

Squirrels followed both predictions of optimal diet selection. Squirrels optimized net energy gain by expending energy to obtain high ranking walnuts rather than low ranking sunflower seeds under equal contions. Squirrels tended to expend more foraging energy to obtain walnuts rather than sunflower seeds, as supported by the average dig site count. These findings supported the hypothesis and the first predication of optimal diet selection, that foragers will prefer higher ranking food items.Under unequal conditions, squirrels preferred walnuts despite their lower abundance. These results were expected based on optimal diet selection as food preference is independent of abundance of food item and depends only on food item ranking.

It was previously found that if food type in platforms was randomized each day, squirrels did not significantly prefer either food (Colligan and Jansen unpubl data) and that foraging animals tend to choose the most abundant food source, no matter its energy content, if predators are a prevalent concern (Brown and Morgan 1995). As squirrels still chose less abundant and harder to obtain walnuts (Phase 2), this could demonstrate that predation was not a prevalent concern when food sources are reliable (not randomized each day). As predators were present at the test site, it is likely that food source reliability decreased predation risk. When food is unreliable, foraging time and predation risk increases, causing squirrels to take any available food rather than the higher-ranking food, as seen by Brown and Morgan (1995) and Colligan and Jansen (unpubl. data).

Squirrels exhausted walnuts before consuming sunflower seeds under both equal and unequal conditions. When food options are reliable, squirrels can minimize foraging time and predation risk by knowing food item location in advance, allowing them to choose more rewarding food first before opting for lower reward food. This is demonstrated by the trend to increase sunflower seed consumption over time only after walnuts are fully exhausted.

References

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