

Environmental and Nutritional Trade-Offs in Squirrel Foraging Strategies

Thalia Leon Rodriguez

Department of Biology
Lake Forest College
Lake Forest, Illinois 60045

Introduction

Optimal foraging theory suggests that animals have evolved to maximize their net rate of energy intake by balancing foraging efficiency with environmental constraints. Specifically, animals are predicted to leave a depleting patch when an alternative patch offers either more or faster food. However, natural conditions are rarely ideal, and factors such as uncertainty about the value of alternative patches, travel time, and potential risks associated with switching patches can influence decision-making, potentially delaying optimal departures (Chandel, 1983). This theory highlights the central question of how animals choose the most effective strategy for nutrient acquisition while accounting for environmental variability.

Despite criticisms of being tautological (Pierce, 1987), optimal foraging theory has been extensively validated through experimental research. Various studies have demonstrated that species adjust their foraging strategies in response to diverse factors. For instance, pigeons may alter their foraging patterns depending on the time of day (Chandel, 1983), and gerbils are influenced by moonlight levels that affect predator visibility (St. Juliana, 2017). Pollinators, such as bees, modify flower choices in the presence of predators like crab spiders (Huey, 2017), while ants make decisions based on nutrient availability ratios (Adams, 2002). These findings underscore the complexity and adaptability of foraging behaviors across species, influenced by competition, stress, predator detection, and other ecological pressures.

In this study, we focus on squirrels as model organisms to investigate how environmental stressors shape foraging decisions. The experiments were conducted in the backyard of a residence in Northbrook, Illinois, which is home to Eastern Gray Squirrels (*Sciurus carolinensis*). While squirrels have a varied diet, nuts represent a staple food source, with notable differences in nutritional value and accessibility depending on nut type and condition (Lewis, 1982). Previous research suggests that squirrels prioritize nutrient-rich food sources, but the specific ranking of their preferences remains unclear.

Based on prior information, we hypothesize that squirrels will prefer foraging in covered trays placed under trees, regardless of nut type, because these locations likely reduce perceived predation risk. Additionally, we predict that squirrels will favor nuts with shells in covered areas over nuts with no shells in uncovered areas, prioritizing the safety of a covered environment over the ease of access provided by nuts with no shells, which they would not need to invest time or energy in removing. Our rationale is that unshelled nuts require less effort and energy to consume, allowing for quicker nutrient intake. However, when exposed to potential threats in uncovered areas, the perceived risk may outweigh the benefits of faster consumption, driving a preference for safer, covered environments. Therefore, we anticipate that the safety of a covered environment will outweigh the accessibility of food when unshelled nuts are available. The goal of this research is to better understand how environmental stressors influence foraging behavior in squirrels. Specifically, we aim to determine whether they prioritize reduced visibility of predators in covered foraging areas or the effort required to consume food, such as shelled versus unshelled nuts. By addressing these factors, this study aims to provide insights into the ecological pressures shaping squirrels' foraging strategies in their natural environment.

Methods

Our study consisted of two experiments designed to assess squirrel foraging preferences under varying environmental conditions. Both

*This author wrote this paper for Biology 220: Ecology and Evolution taught by Dr. Josh Hedge.

experiments employed a within-subjects design, as each squirrel was exposed to all conditions. This approach allowed us to assess general preferences rather than tracking the behavior of specific individuals. Our analysis focused on overall choice patterns using giving-up density (GUD) as the primary metric. GUD, a commonly used measure in foraging ecology, assesses animals' perceived predation risk by quantifying the proportion of food left behind after foraging (McMahon, 2018). This method assumes that animals have fixed food preferences, allowing higher GUD values to be interpreted as higher perceived risk. For clarity, specific terms were operationalized in this study. For example, "eat at tray" (EAT) refers to the squirrel's tray choice for foraging. No trials were conducted under rainy conditions or at night, given the squirrel's diurnal foraging preference.

The first experiment tested our hypothesis about squirrels' foraging location preferences, based on whether the foraging trays were in covered or uncovered areas. In the first experiment, we prepared two large trays by filling each approximately one-third full of sand, ensuring consistent sand levels across trays. The tray has dimensions of 23.5 cm (length) x 12 cm (width) x 2.5 cm (height) and was supplied with 45 grams of peanuts in shells. An acclimatization trial of approximately 2.5 hours was conducted to familiarize the squirrels with the tray's placement, which were approximately 15 meters apart to minimize overlap in their foraging areas. A total of 32 trials were conducted, each lasting approximately 15 minutes. During these trials, we allowed the squirrels to forage freely, ensuring that trials ended before all food was consumed to retain sufficient GUD data. These data were used to infer patterns in location preference under consistent nut conditions.

Results

To investigate whether squirrels prioritize environmental protection or nutritional reward when foraging, we conducted a second experiment using the identical trays from Experiment 1. Each tray measured 23.5 cm (length) x 12 cm (width) x 2.5 cm (height) and was filled approximately one-third full with sand. The food type and placement were modified to create a contrast between energy investment and environmental safety. One tray, located under a tree in a covered area, contained 23 grams of peanuts with shells.

These peanuts not only provided a greater nutritional reward due to the inclusion of the shell but also offered the squirrels an opportunity to file their teeth, which continuously grow, as is typical of rodents. The second tray, placed in an uncovered area closer to the house, contained 29 grams of peanut kernels, offering easily accessible food with less energy required for consumption. This design allowed us to compare the influence of safety (provided by the covered area) with the reduced energy investment required when harvesting from uncovered areas. After each trial, the GUD was measured for the different conditions.

We conducted 19 trials over four days, with trials occurring between late morning and afternoon. Each trial lasted approximately 15 minutes, and environmental conditions, including temperature and weather, were kept relatively constant. The data collected from both experiments were analyzed using Jamovi. Two paired-sample tests were conducted: the first evaluated whether there was a statistically significant relationship between the location of the trays (covered vs. uncovered) and the squirrels' giving-up densities (GUDs), while the second assessed their preference for peanuts with shells versus without shells.

Results:

Two paired-sample t-tests were conducted to analyze the relationship between squirrels' giving-up densities (GUDs) and the positioning of food trays under different conditions in Experiments 1 and 2.

Experiment 1:

In the first experiment, the analysis revealed a statistically significant difference in GUDs between the uncovered and covered areas. On average, 6.38 g of peanuts were left in the uncovered area compared to 24.6 g in

the covered area. The paired-sample t-test showed a significant effect, $t(31) = -7.40, p < .001$, indicating that squirrels foraged more intensively in the covered area (see Fig. 1).

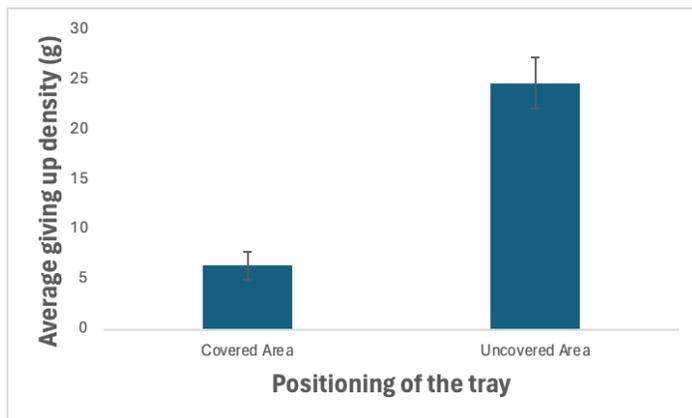


Figure 1. Mean giving-up density (GUD) as a function of tray location (covered vs. uncovered) in Experiment 1.

Experiment 2:

In the second experiment, a paired-sample t-test was conducted to compare GUDs for two conditions: peanuts with shells located close to the tree (covered area) versus peanuts without shells in the uncovered area. Results revealed a statistically significant difference, $t(18) = -2.12, p = .048$. Squirrels exhibited a preference for the covered area, leaving an average GUD of 6.52 g for the peanuts with shells in the covered area compared to 12.6 g for the peanuts without shells in the uncovered area (see Fig. 2).

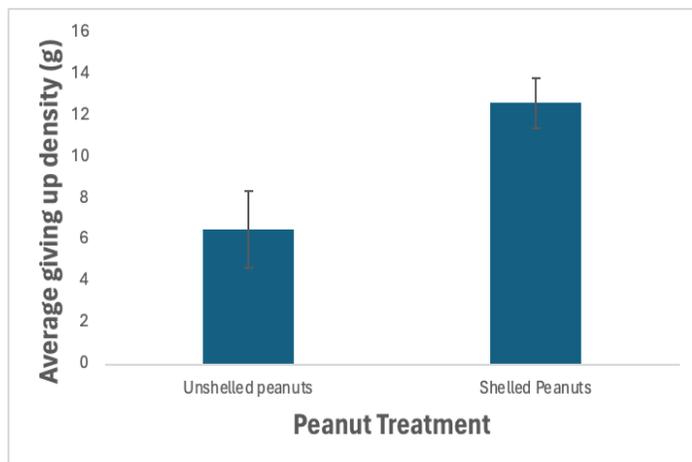


Figure 2. Mean giving-up density (GUD) as a function of peanut type and whether the peanuts were unshelled in a covered environment or shelled in an uncovered environment in Experiment 2.

Discussion

The results of both experiments supported the hypotheses, with squirrels demonstrating a clear preference for covered food. This outcome aligns with the predictions of the first experiment, in which squirrels consistently selected covered food at a higher rate. One possible explanation for this behavior is the type of tree under which the covered tray was located. The sugar maple (*Acer saccharum*), a species that can reach heights of 27–37 meters (90–120 feet), may have been perceived as offering significant protection from aerial predators, such as eagles, hawks, falcons, and owls, which use high vantage points to spot prey (MIT Press, 2002). Future studies could explore how tree height or alternative vegetation, such

as dense bushes, might influence perceived safety and foraging duration.

Another variable to consider is the presence of backyard dogs (*Canis lupus*), which are known predators of squirrels (Tobajas, Ramos-López, Piqué, & Sanchez-Rojas, 2023). While the squirrels in this study appeared accustomed to the dogs, as they typically ran away when they saw them, they also used the tree to protect themselves. The dogs' absence during the trials and the greater distance of the covered tray from the house may have influenced squirrel behavior. This highlights the need to account for predator presence and environmental context in similar studies.

The trial durations were shorter than anticipated, averaging approximately 15 minutes, whereas previous studies have shown squirrels foraging for more extended periods. This deviation may be attributed to the seasonal timing of the experiments, conducted during the transition from fall to winter. During this period, squirrels intensify their foraging and caching activities to prepare for winter scarcity, engaging in scatter hoarding by burying nuts and seeds in multiple locations.

This behavior is driven by hormonal and metabolic changes, as well as the need to secure high-calorie foods for colder months when mobility is reduced (van der Merwe et al., 2005; Michigan State University, n.d.). When assessing the Giving-Up Density (GUD), it is also essential to consider the potential impact of other species. For example, blue jays (*Cyanocitta cristata*), which inhabit the study area and also consume nuts, may have influenced the results. Although their impact is unlikely to have been substantial, their presence underscores the need to control for interspecies interactions in future research to ensure accurate data interpretation.

Lastly, this summer's rare double emergence of the *Magicicada septendecim* and *Magicicada tredecim* cicadas likely altered squirrel foraging behavior. This unique event, which occurs only once every 221 years, created an unusual abundance of cicadas, providing a significant food resource (Clay, Shelton, & Winkle, 2009). The temporary surplus during their reproductive period may have reduced squirrels' reliance on experimental food trays and influenced their caching and feeding patterns later in the season. This highlights the importance of considering unique environmental events when analyzing animal behavior.

This study is significant because it demonstrates that squirrels prioritize perceived threats in their foraging, often valuing safety over greater nutritional rewards. The focus on urban squirrels is particularly relevant, as these animals navigate environments with diverse challenges, including human activity that can indirectly hinder their foraging. Although dogs were the perceived predator in this study, urban squirrels are exposed to a range of disturbances, highlighting the complexity of their risk assessments.

Squirrels play a vital ecological role by dispersing seeds and pollinating plants—services essential for ecosystem stability. Disruptions to their foraging activities could have cascading effects, potentially altering plant regeneration and broader ecological interactions (Lurz, Garson, & Rushton, 1995). Moreover, a deeper understanding of squirrels' foraging habits not only informs conservation efforts for these rodents but also enhances our knowledge of animal behavior and decision-making under environmental stress, contributing to the broader field of wildlife ecology and management.

Note: Eukaryon is published by students at Lake Forest College, who are solely responsible for its content. This views expressed in Eukaryon do not necessarily reflect those of the College. Articles published within Eukaryon should not be cited in bibliographies. Material contained herein should be treated as personal communication and should be cited as such only within the consent of the author.

References:

- Chandel, Henna, et al. "Should I Stay or Should I Go? Pigeons' (Columba Livia) Performance of a Foraging Task Has Implications for Optimal Foraging Theory and Serial Pattern Learning." *Journal of Comparative Psychology*

- (1983), vol. 135, no. 2, 2021, pp. 266–72. <https://doi.org/10.1037/com0000263>.
2. Charnov, E. L. (1976). Optimal foraging: The marginal value theorem. *Theoretical Population Biology*, 9(2), 129–136. [https://doi.org/10.1016/0040-5809\(76\)90040-X](https://doi.org/10.1016/0040-5809(76)90040-X)
 3. St. Juliana, J.R.et al. 2017. Stress as an adaptation I: Stress hormones are correlated with optimal foraging behaviour of gerbils under the risk of predation. *Evolutionary Ecology Research* 18:571- 585
 4. Huey, R. B., & Nieh, J. C. (2017). Foraging at a safe distance: crab spider effects on pollinators. *Ecological Entomology*; Royal Entomology Society, The ;Retrieved from <https://labs.biology.ucsd.edu/nieh/papers/HueyNieh2017.pdf>
 5. Pierce, G. J., & Ollason, J. G. (1987). Eight reasons why optimal foraging theory is a complete waste of time. *Oikos*, 49(1), 111–117. <https://doi.org/10.2307/3565560>
 6. Lewis, Allen R. "Selection of Nuts by Gray Squirrels and Optimal Foraging Theory." *The American Midland Naturalist*, vol. 107, no. 2, 1982, pp. 250–57, <https://doi.org/10.2307/2425376>.
 7. Kay, Adam. "Applying Optimal Foraging Theory to Assess Nutrient Availability Ratios for Ants." *Ecology (Durham)*, vol. 83, no. 7, 2002, pp. 1935–44, [https://doi.org/10.1890/0012-9658\(2002\)083\[1935:AOFTTA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1935:AOFTTA]2.0.CO;2).
 8. Animal Control Specialists. (n.d.). Squirrels of Illinois: Species, habits, and tips for identification. Retrieved from <https://www.dacontrol.com/illinois-squirrels>
 9. McMahon, Jordan D., et al. "Covariance between Predation Risk and Nutritional Preferences Confounds Interpretations of Giving-up Density Experiments." *Ecology*, vol. 99, no. 7, 2018, pp. 1517–22. <https://doi.org/10.1002/ecy.2365>.
 10. Michigan State University. (n.d.). *How squirrels survive winter: Seasonal changes in behavior and physiology*. Retrieved November 26, 2024, from <https://www.canr.msu.edu>
 11. *The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition*. (2002). United Kingdom: MIT Press.
 12. Van der Merwe, M., Brown, J. S., & Manjerovic, M. B. (2005). Seasonal and habitat differences in food cacheability and foraging costs: A comparison of fox and grey squirrels. *Evolutionary Ecology*, 19(5), 707–720. Retrieved from www.evolutionary-ecology.com
 13. Lurz, P.W.W., Garson, P.J., & Rushton, S.P. (1995). The ecology of squirrels in spruce-dominated plantations: Implications for forest management. *Forest Ecology and Management*, 79(1-2), 79–90. [https://doi.org/10.1016/0378-1127\(95\)03617-2](https://doi.org/10.1016/0378-1127(95)03617-2)
 14. World Deer. (n.d.). *Seasonal behavior changes in squirrels*. Retrieved November 26, 2024, from <https://worlddeer.org>
 15. Field Museum. (2024). Cicadas in Illinois 2024. Retrieved from <https://www.fieldmuseum.org>
 16. Clay, K., Shelton, A. L., & Winkle, C. (2009). Differential susceptibility of tree species to oviposition by periodical cicada. *Ecological Entomology*, 34(3), 277–286. <https://doi.org/10.1111/j.1365-2311.2008.01076.x>
 17. Tobajas, J., Ramos-López, B., Piqué, J., & Sanchez-Rojas, G. (2023). Predation risk in tree squirrels: Implications of the presence of free-ranging dogs. *Journal of Zoology*, 320(1), 12–20. <https://doi.org/10.1111/jzo.13047>